FINE-SCALE DISTRIBUTION, HABITAT USE, AND MOVEMENTS OF SPERM WHALES

by

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This one is for you Jocasta

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ABSTRACT

Sperm whales (*Physeter macrocephalus)* are nomadic species typically studied across broad (>100km) spatial scales. In this study, I model fine-scale (or submesocale) habitat preferences, determine how organization into distinctive units of associating female and juveniles influences habitat use, and describe how movements change across the 24-hour cycle. This study concerns a well-studied population of sperm whales off Dominica in the Eastern Caribbean. Statistical models suggest that overall habitat use is rather homogenous, and social behaviour is best predicted by the presence of mature males. Variation among social units in the amount of time spent, and space occupied, within the study area indicates habitat preferences at the level of the social unit. Finally, movements are influenced by the diurnal cycle, as whales tend to move from inshore to offshore at dusk. This study betters our understanding of sperm whale habitat decisions over fine-scales, and has implication for conservation and management strategies.

LIST OF ABBREVIATIONS USED

ANOVA	Analysis of Variance
Asp	Aspect
AUC	Area Under the Curve
AVISO	Archiving, Validation, and Interpretation of Satellite Oceanographic data
Bal	Research vessel Balaena
Chan	Proximity to Channels
cm	Centimetres
dd	Decimal Degrees
df	Degrees of freedom
Dep	Depth
Dist	Distance to Dominica's shoreline
EKE	Eddy Kinetic Energy
FF	Dedicated outboard motorboat
GAM	Generalized Additive Model
GEE	Generalized Estimating Equation
GLM	Generalized Linear Model
GPS	Global Positioning System
hr	Hour
IFREMER	Institut Français de Researche pour l'Exploitation de la Mer
IPGP	Institute de Physique du Globe de Paris
k	Circular parameter of concentration
km	Kilometres
Lat	Latitude
Long	Longitude
m	Metres
m_1	Circular mean angle
m_2	Circular axial mean
MANOVA	Multivariate Analysis of variance
ME	Mideast habitat cell
MH	Dedicated outboard motorboat
MW	Midwest habitat cell
Mon	Month
N	North
NE	Northeast habitat cell
NW	Northwest habitat cell
ROC	Receiver Operating Characteristic
P	P-Value
ρ	Mean resultant length of a vector of circular data
ρ	Spermans's rho

s	Seconds
SD	Standard Deviation
SE	Southeast habitat cell
SF	Dedicated outboard motorboat
Slo	Slope
SSH	Sea Surface Height
SW	Southwest habitat cell
u	Zonal (Eastward) Geostrophic Current Velocity
v	Meridional (Northward) Geostrophic Current Velocity
V	Cramér's Phi
Wav	Wave or swell height
WW	Whale Watch
χ^2	Chi-Squared test statistic
Yr	Year

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CHAPTER 1   Introduction

The problem of scale is a central theme in ecology (Levin 1992). Animals must make decisions about what habitat to use across a wide range of scales (Hutto 1985). Understanding how decisions vary with scale is perhaps most challenging in wide-ranging nomads. Nomads exploit environments where the timing and location of high-resource areas is variable and dynamic (Dean 2004; Jonzén et al. 2011). Their movement patterns are outwardly unpredictable, presenting many challenges to management and conservation efforts. In this thesis, I examine fine-scale distribution patterns in a wide-ranging nomadic predator, the sperm whale.

1.1   The Sperm Whale

Sperm whales (*Physeter macrocephalus*) are often considered animals of extremes. They are one of the world's deepest and longest diving mammals, with a global distribution. They are significant marine predators which consume mesopelagic and bathypelagic squid (Clarke 1980) each year in quantities that roughly match the net weight of the combined catch from all human fisheries (Kanwisher & Ridway 1983). By consuming prey at depth and defecating at the surface, sperm whales release iron into the photic zone and promote primary productivity in the open ocean (Lavery et al. 2010). Associated with both top down and bottom up interactions, sperm whales play major roles in ecosystem functioning in the oceans.

Sperm whales are also extreme in their differences between the sexes, for both their life history and sexual dimorphism. Females and juveniles are generally found in tropical to subtropical waters (Whitehead 2003). They live their lives in long-term stable associations called social units (Christal et al. 1998). Social units are organized into acoustic clans recognised by their distinct vocal dialect and behavioural variants (Rendell and Whitehead 2003; Whitehead and Rendell 2004), which appear to be culturally inherited (Rendell & Whitehead 2001). Males, which are nearly twice the size of females at maturity, leave their natal groups at about age 10, and slowly move into higher latitudes (Whitehead 2003). From their late twenties onwards they periodically return to the tropics and rove between social units, usually spending only a few hours with a given unit (Coakes and Whitehead 2004; Whitehead 2003).

Sperm whales are a highly mobile species that range across spatial scales of hundreds to thousands of nautical miles (Jaquet and Whitehead 1996; Mizroch and Rice 2013; Whitehead et al. 2008). Their ranging behaviour is generally described as nomadic (Whitehead 2003), as the

movements of social units are wide and outwardly unpredictable across time and space. This strategy enables them to exploit areas with high cephalopod densities, which vary in timing and location of occurrence. Since sperm whales are wide-ranging, studies on habitat and behaviour are typically conducted at broad-scales (>100km), creating gaps in our knowledge sperm whale behavioural patterns at finer spatial scales (<100km).

In this thesis, I describe fine-scale (or submesocale) patterns of distribution and movement in sperm whales, and examine the relationship between habitat use and social group behaviour and identity. Specifically, I begin by modeling overall habitat preferences, and the occurrence of social behaviour in CHAPTER 2. In CHAPTER 3, I address the question of whether habitat use patterns differ among the individual social units that make up the population. Finally, in CHAPTER 4 I examine whether use of habitat changes across the 24-hour cycle, by describing changes in horizontal movement with time of day. This study is significant for its ability to examine distributional and behavioural patterns at a finer spatial scale than previous work on sperm whales.

1.2   The Study Area

This study concerns a population of sperm whales in the Eastern Caribbean off the Commonwealth of Dominica, where behaviour can be examined at fine resolution. Dominica is situated in the Lesser Antilles arc which lies between the Atlantic Ocean and Caribbean Sea. The major oceanographic influences on the island originate from winds and currents of the Atlantic. Winds are predominantly the North Atlantic trade winds which blow east to west at a magnitude of 3-5 on the Beaufort scale (3.5 to 10.5 m/s) throughout most of the year (Gallegos 1996). Water in the Atlantic, originating from the Guiana Current, North Equatorial Current (Gallegos 1996), and sometimes rings shed from the North Brazil Current (Fratantoni et al. 1995), flow through passages between islands in the Lesser Antilles, feeding into the Caribbean Current. This study was conducted on the leeward (western) coast of Dominica, in an area covering approximately 2,000 km^2, where downstream turbulence is thought to promote increased primary productivity and chlorophyll levels (Cram and Hanson 1974; Hargrave et al. 1970).

Since 2005, the Dominica Sperm Whale Project has identified over 250 individuals in the study area, belonging to at least 17 social units, using photo-identification (S. Gero, Personal Communication). The sperm whales of the Eastern Caribbean are apparently separate from

populations in neighbouring regions of the North Atlantic Ocean (Gero et al. 2007); however, individuals identified in the study area have been sighted off other islands in the Lesser Antilles arc, including Guadeloupe, Martinique, Saint Lucia, Grenada (Gero et al. 2007), and Saint Vincent (Gero, personal communication). Yet whales have demonstrated fidelity to the waters near Dominica by returning across periods exceeding a decade (Gero et al. 2007), for a maximum of 27 years (S. Gero, personal communication). The waters off Dominica thus appear to have long-term importance for some sperm whales in the Caribbean.

Individual reidentification rates, calculated as the percentage of individuals identified on more than one year, were reported at 29% for the Eastern Caribbean (Gero et al. 2007) and 42% within the study area (Gero 2012). These rates are relatively high compared to 12% for females and juveniles in the Galapagos Islands (Whitehead 1993) and 18% for females in the Azores (Matthews et al. 2001). Given the wide-ranging behaviour of sperm whales, high resighting rates in the study area are noteworthy when one considers that research off Dominica is conducted in a space over an order of magnitude smaller than studies in the Galapagos and Azores. Dominica appears to be unusual for high sperm whale residency and resighting rates within a small area. In this thesis, I also will examine one overarching question: why do sperm whales have fidelity to waters off Dominica?

CHAPTER 2   Fine-scale sperm whale habitat preferences: overall and with behavioural state

2.1   Introduction

Habitat selection is a hierarchical process by which individuals determine what habitat to use at different environmental scales (Hutto 1985). High spatial and temporal variability in available resources favours the development of nomadism (Sinclair 1983). Nomadic animals are characterized by their unpredictable movements in both space and time, which are thought to optimize their ability to exploit stochastic resources (Dean 2004; Jonzén et al. 2011). Habitat studies on nomadic species often focus on understanding how distribution relates to food availability, since nomads must track food resources (Jonzén et al. 2011). However, food resources are one of multiple extrinsic factors in the environment that can drive habitat selection (Cañadas and Hammond 2008). Distribution and habitat use can be influenced by factors that are intrinsic to individuals, such as reproductive status, feeding strategy, social associations, or behavioural state (Cañadas and Hammond 2008). Since animals experience and respond to influences across a range of scales (Levin 1992), consideration must also be given to how these interactions vary with spatial and temporal scale.

Sperm whales (*Physeter macrocephalus)* are nomadic predators with a global distribution. They are a wide-ranging species that exploit areas spanning hundreds or thousands of kilometres (Jaquet and Whitehead 1996), feeding mainly on mesopelagic and bathypelagic squid (Clarke 1980). Males and females have distinct life history strategies. Females and juveniles live in multileveled societies (Rendell et al. 2012). At its base, individuals live in long-term stable associations called social units (Christal et al. 1998), generally found in tropical to subtropical waters (Whitehead 2003). These social groups are thought to have evolved to either increase protection of calves, or improve foraging efficiency through communal foraging (Best 1979; Whitehead 1996a). Males, in contrast, leave their natal groups at about age of ten, and slowly move into higher latitudes (Whitehead 2003). From their late twenties onwards, they periodically return to the tropics and rove between social units, usually spending only a few hours with a given unit (Coakes and Whitehead 2004; Whitehead 2003).

In general, sperm whale density is predicted to be higher in areas with high cephalopod density, where foraging efficiency is greater (Selzer and Payne 1988)*.* Since cephalopod abundance

cannot be measured directly (Clarke 1996a), oceanographic features, which may increase productivity or concentrate prey, are used as proxies for prey abundance and availability (Redfern et al. 2006). Several studies have found correlations between sperm whale distribution and spatial or oceanic features, including proximity to oceanic islands, continental shelf breaks, cyclonic eddies, and warm-core rings spinning off the Gulf Stream (Davis et al. 2002; Gregr and Trites 2001; Griffin 1999; Jaquet and Whitehead 1996). However, most studies examine distribution at broad (>100km) spatial scales (Jaquet 1996). Multiscale studies suggest that factors influencing habitat use at fine (<100km) spatial scales differ from those at broad scales. Jaquet and Whitehead (1996) found sperm whale distribution to be related to topography, temperature, and productivity at a scale of 148 to 1185 kilometres, but found no correlation between sperm whale density and environmental features or productivity at finer scales. This raises the question of whether factors other than prey availability drive habitat choices at fine-scales.

Sperm whale social units spend three quarters of their time foraging, and a quarter of their time socializing at or near the surface, in slow moving close-clustered groups (Watwood et al. 2006; Whitehead and Weilgart 1991). Social behaviour ranges from active periods, of whales physically interacting and producing social vocalizations or "codas" (Watkins and Schevill 1977), to behaviour stereotypical of resting where whales hang vertically in the water column (Miller et al. 2008). As communal behaviour may be more efficient among animals with well-reinforced bonds, this intrinsic behavioural state is likely important in reinforcing relationships between these cooperative animals (Whitehead and Weilgart 1991). Social behaviour is also considered to be tied to the fitness of female sperm whales (Whitehead and Weilgart 1991), since time and energy spent socializing may be a tradeoff for energy acquisition during foraging (Dunbar and Dunbar 1988). Some cetaceans use different habitats when engaged in socializing and foraging activities (Cañadas and Hammond 2008; Lusseau and Higham 2004), and understanding how social behaviour influences distribution in sperm whales can provide insight into what drives their fine-scale habitat selection.

The objective of this study is to describe fine-scale (or submesoscale) habitat preferences among sperm whales, and to examine how these may vary when foraging and socializing. I produce a statistical model of sperm whale habitat preferences using spatial, oceanographic, and temporal covariates to identify areas with higher likelihoods of being occupied by whales. I then model

the occurrence of sperm whale social behaviour. A good understanding of the influences affecting distribution across a range of temporal and spatial scales, and between behavioural states, is required for the effective management and conservation of this nomadic species (Dufault et al. 1999). A well-studied population of sperm whales in the Caribbean, off the leeward coast of Dominica, provides the opportunity for a fine-scale examination of distribution and behaviour in an oceanic nomad.

2.2   Methods

2.2.1   Field Methods

Fieldwork was conducted off the leeward (western) coast of the Commonwealth of Dominica. Each year from 2005-2011, we surveyed an area covering approximately 2000 km^2 between the months of January to May. We searched for whales systematically along tracks largely parallel to the island, using visual and passive acoustic (using hydrophones) detection (Whitehead and Gordon 1986; Whitehead 2003). Once detected, we tracked whales using visual and acoustic cues. During daylight hours, we approached individuals spotted at the surface to within 100 metres and photographed their flukes for individual identification (Arnbom 1987). We recorded group composition (numbers of adults or juveniles, mature males, calves) and general behaviour (foraging or socializing) hourly. Vessel tracks were recorded at 10 minute to 10 second intervals with a GPS.

In 2005, 2008, and 2010, we studied sperm whales aboard a dedicated 12m auxiliary sailing vessel equipped with a duel element (Benthos AQ-4) towed hydrophone array on a hundred metre tow cable. From this platform we tracked whales acoustically 24 hours a day. In 2007, 2008, 2009, and 2011 fieldwork was conducted during daylight hours from a 5m to 11m outboard motorboat, and occasionally a larger motorized catamaran whale watching vessel outfit with Cetacean Research CR1 or CR2 hydrophones (see Table 2.1 for a breakdown of effort). Although fieldwork took place in 2006, no position data were collected so the year was excluded from analyses.

Table 2. 1 Summary of research effort described by a) days at sea and b) research platform. Data was collected from a dedicated 12m auxiliary sailing vessel (BAL), 5m (SF) and 11m (FF or MH) outboard motorboats, or motorized catamaran whale watch (WW).

	2005	2007	2008	2009	2010	2011	Total
January	**14** BAL	**3** SF,WW		**14** SF,WW	**10** BAL		*41*
February	**25** BAL	**27** SF,WW	**19** SF,WW	**22** SF,WW	**25** BAL		*118*
March	**12** BAL		**26** SF,WW, BAL	**26** SF,WW	**22** BAL	**26** FF,MH	*112*
April	**9** BAL		**25** BAL		**13** BAL	**9** FF,MH	*56*
May			**7** BAL				*7*
Total	*60*	*30*	*77*	*62*	*70*	*35*	*334*

2.2.2   Sperm Whale Distribution

2.2.2.1   Presence/Absence Data

I modeled the habitat preferences of sperm whales off Dominica using binomial-based Generalized Additive Models with Generalized Estimating Equation extensions following the methodology of Pirrotta et al. (2011). The unit of analysis of this study was points corresponding to GPS fixes at 20 minute (or greater) intervals. I characterized each point as a presence/absence if they occurred during/outside of sperm whale encounters, respectively. Encounters began when sperm whales were first detected using passive acoustic monitoring or visual observations. Encounters ended when leaving whales (i.e. for end of day or rough weather) or when audio or visual contact with whales was lost for two hours.

Since survey effort was not uniform across the study area, I restricted the analysis to a core region defined by effort intensity. This minimized potential biases originating from lower survey effort along the edges of the study area, where whales could be followed but were rarely searched for. I divided the study area into 5 by 5 kilometre cells, and calculated the number of presence/absence points within each cell. Cells containing over fifty locations were included in models.

2.2.2.2   Environmental Predictors

For each presence/absence location, I calculated environmental variables that may influence the probability that sperm whales are present in a location at a given time. These variables included spatial and oceanographic covariates (Table 2.2). Fixed spatial variables, which tend not to change on shorter time scales, include depth, bottom slope (angle of incline), aspect (the direction a slope faces), distance to shore, and proximity to channels (the channels between Dominica and neighbouring islands to the north and south), whereas oceanographic variables, such as current speed and sea surface height, may vary over periods ranging from hours to seasons.

Depth, slope, aspect, and distance values corresponding to presence/absence points were managed and extracted using the ArcGIS 10 (ERSI) Spatial Analyst Toolbox. Depths were obtained from a high resolution bathymetric model provided by the Institute de Physique du Globe de Paris (IPGP) and Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER). Collected during the 1998 Aguadomar campaign, and modelled to a resolution of 100 by 100 metres, this was the highest resolution information available for the region (Figure 2.1). Depth was converted into slope and aspect using Surface Tools. Distance to shore was measured using the Euclidean Distance Tool to create a raster layer with 5 by 5 metre resolution. Input shoreline information was obtained from the Government of the Commonwealth of Dominica, Land and Surveys Division. I defined the proximity to the nearest channel between Dominica and adjacent islands based on relative latitude. Points were considered to be in the channels when latitude was north of N15.64° or south of N15.21° (respectively), which represent the northern and southern tips of the island (Figure 2.1). By this measure the highest value possible was 0.215° (the latitudinal center of the island), values of 0° indicate a latitude equal to either the northern or southern extremes of the island, and negative values indicated points inside the channels.

Oceanographic variables were obtained from Ssalto/Duacs satellite altimetry data. Global mean sea level anomaly data, available as delayed time, referenced, and merged products (at 1/3°x1/3°resolution) were downloaded from AVISO (Archiving, Validation, and Interpretation of Satellite Oceanographic data) using the Marine Geospatial Ecology Toolbox in ArcGIS 10. Because products were not available at daily resolution for the entire study period, products gathered at seven-day intervals were used for analysis. Sea surface height anomalies (SSH),

zonal (eastward) and meridional (northward) geostrophic current velocities (u and v respectively), and eddy kinetic energy (EKE- an indicator of mesoscale variability in turbulence and flow) data obtained were measured relative to a seven year mean. From Jan 2005 to Dec 2010, the absolute mean difference between daily and weekly altimetry data within six cells covering our study area was 17.8cm^2/s^2 (SD=30 cm^2/s^2) for EKE, and 0.568 cm (SD=0.629cm) for SSH, representing less than two percent of their total range of variation.

Table 2. 2 Spatial and oceanographic covariates

Term	Unit	Spatial Resolution	Description
Dep	m	100 x 100m	Depth from bathymetric model obtained from IPGP/ IFREMER.
Slo	°	100 x 100m	Slope extracted from above bathymetry model
Asp	°	100 x 100m	Aspect extracted from above bathymetry model
Dist	m	5 x 5m	Distance to the Dominica shoreline
Chan	dd	-	Proximity to channels as defined by the relative position between N15.64° and N15.21°. The latitudinal center of the island occurs at 0.215°, and negative values are within channels
SSH	cm	1/3°x1/3°	Sea Surface Height at seven-day intervals
u	cm/s	1/3°x1/3°	Zonal (eastward) geostrophic current velocity at seven-day intervals
v	cm/s	1/3°x1/3°	Meridional (northward) geostrophic current velocity at seven-day intervals
EKE	cm^2/s^2	1/3°x1/3°	Eddy Kinetic Energy at seven-day intervals
Lat	dd	-	Latitude
Long	dd	-	Longitude
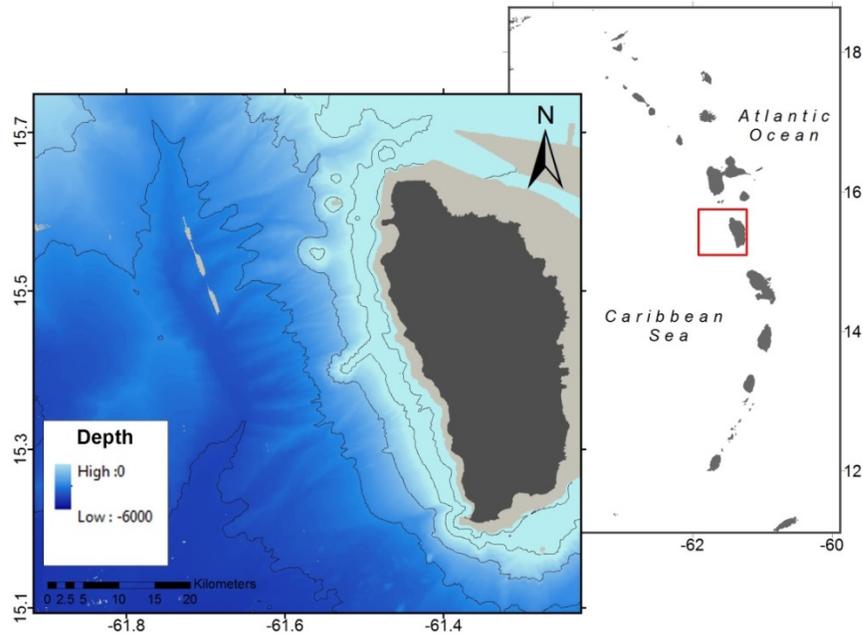
Figure 2. 1 Model of bathymetry (m) off Dominica with thousand metre contours and latitudes used as references for channels, N15.2°1 and N15.64°.   Areas with missing values are shown in grey.

2.2.2.3   Other Predictors

To account for sperm whale presence differing within and between seasons, I included year (*Yr*) and month (*Mon*) as factors in the models. Since only 7 of 334 days at sea occurred during in May, I excluded the month May from all analyses to eliminate potential biases arising from low sampling effort. In addition to temporal predictors, the latitude and longitude of each presence/absence data point were included as model covariates. While Pirrotta et al. (2011) did not subject latitude and longitude to model selection, regardless of their significance, I subjected these terms to model selection. Including latitude and longitude in the models makes each presence/absence point unique so that no offset term is required to account for survey effort, but their forced inclusion potentially obscure relationships with correlated covariates that may function as better explanatory predictors of sperm whale abundance.

Several factors which may influence distribution and behaviour were not considered in this study. I was unable to assess the effect of predation (although there was no evidence of predation), calving behaviour (which is very rare), or human disturbances (potentially important). I also did not examine the influence of primary production, assessed using chlorophyll concentration, on sperm whale distribution in this study. Though chlorophyll levels

potentially influence distribution across time, one of the limitations of using satellite imagery is obscuration caused by clouds. Due to regular cloud formation over Dominica, a major portion of the chlorophyll a values were not available during the study period. Sperm whales do not directly consume phytoplankton and a lag time of several months is required for increases in chlorophyll levels to translate to prey abundance. Vinogradov (1981) estimated a 4 month lag between maximum chlorophyll concentration and peak cephalopod densities; however this lag may vary regionally depending on nekton assemblage and trophic structure.

2.2.2.4   GAM-GEE Models

I generated models of the presence/absence of sperm whales using a binomial-based generalized additive model (GAM) framework based on logit link functions. GAMs are non-parametric alternatives to binomial generalized linear models.   GAMs required independence between samples, a condition frequently violated by transect and follow data in which data points are correlated over both space and time. Spatial autocorrelation leads to underestimation of uncertainty associated with model estimates, increasing the probability of obtaining Type 1 errors which make non-significant relationships appear significant in final models (Redfern et al. 2006). To account for spatial autocorrelation between data points, Generalized Estimation Equations extensions were added to the GAM framework. GEEs do not assume distributions, and are used to fit the parameters of a model when an unknown autocorrelation is present. They function by grouping data into blocks. Points within a block may be correlated, but points between blocks cannot be. Thus the analysis is run under the assumption that data points between blocks are independent (Liang and Zhang 1986). GAM-GEE models are flexible tools that have previously been applied to modelling habitat preference in sperm whales (Pirotta et al. 2011), and other cetaceans (Panigada et al. 2008).

To use GEEs, the structure of within block correlation, known as the working correlation matrix, must be defined *a priori* using one of six different models: Independent, Exchangeable, Autoregressive, M-dependent, Unstructured or Fixed (Horton and Lipsitz 1999). A major advantage of GEEs is that they are robust to misspecification of the working correlation matrix (Pan 2001), and can produce consistent coefficient estimates when the underlying structure of the dependence between the residuals is uncertain (Liang and Zhang 1986). I used an independence working correlation matrix. In cases where the underlying correlation pattern is unknown the simplest pattern, the independence working model, should be assumed (Pan

2001), particularly in habitat selection models (Fieberg et al. 2010). While the independence working correlation model generates coefficients identical to a standard GAM, it produces reliable standard errors and p-values from which unbiased model selection can occur (Panigada et al. 2008).

I generated GAM-GEE models of whale presence following a two-step selection process described by Pirotta et al. (2011). Blocks were defined as periods of consecutive presences (an encounter) or absences.   This allowed for multiple observations of the same individuals during an encounter to occur within a block. In the event that the timing between consecutive data points exceeded two hours (i.e. when off effort, or from the GPS being offline), a new block was begun. Increasing this period to five hours had no effect on the best model selected. Sperm whale presence/absence was then modeled in R 2.15.1. The "yags" package was used to fit a binomial based GEE-GLM (Carey 2004). The "splines" package then allowed for cubic splines to be built within the GEE-GLM framework, creating a GEE-GAM (R Core Team 2012). Because the splines package does not allow one to select varying degrees of smoothness, each predictive variable was tested for its fit to the model as both a linear predictor, and B-spline with one knot positioned at the average value. The most appropriate form was included in a full model. Manual backwards stepwise regression was then used to determine the best subset of variables predicting the presence/absence of sperm whales through a sequence of reduced models. Since GEEs are considered quasi-likelihood methods, model selection was based on quasi-likelihood under the independence model criterion (QIC_u) (Pan 2001). QIC_u is analogous to Akaike's Information Criterion (AIC), but based on quasi-likelihood rather than maximum likelihood principles (Pan 2001). At this point the reduced model was fit using the "geepack" package (Halekoh et al. 2006; Yan 2002). The geeglm function enables testing of covariate significance in the model via Repeated Wald's Test. Only significant variables ($\alpha \leq 0.05$) were retained in final models.

2.2.2.5   Model Assessment

I assessed the accuracy of predictive models using confusion matrices. A confusion matrix compares observed values to model predictions (Fielding and Bell 1997). When the model predicts all absences as absences, and all presences as presences, it is completely accurate. Since GAMs generate predictions as probabilities (e.g. probability of whale presence), the creation of a confusion matrix requires the conversion of probabilities into presences and

absences. An appropriate threshold value must be chosen, above and below which whales are predicted to be present or absent. I used a Receiver Operating Characteristic (ROC curve) to select the cut-off threshold. An ROC curve is a plot of sensitivity over the false positive fraction for a range of threshold values (Pearce and Ferrier 2000). The best cut-off probability occurs where the distance between the diagonal and ROC curve is maximized (Pearce and Ferrier 2000). The "PresenceAbsence" and "ROCR" packages in R were used to produce confusion matrices (Freeman and Moisen 2008; Sing et al. 2005). In addition to confusion matrices, I used the area under the curve (AUC) to indicate model performance. The closer the AUC approaches 1, the better the model (Boyce et al. 2002).

2.2.2.6 Model Predictions

Model predictions were visualized using partial residual plots to view the contribution of individual model covariates, and predictive maps to show their combined effect in predicting whale presence across the study site. Partial residual plots show the estimated relationship between responses on the link scale and each predictor (where the $odds\ ratio = e^{logit\ link}$). To create a predictive map, I generated a grid of points at the same resolution as the bathymetric layer (i.e. a point created in the center of every 100 by 100 metre cell), and extracted the values of each environmental predictors corresponding to each grid centroid. I then predicted the probability of finding whales at each point in R. When year and month were kept in the model, predictive maps were drawn for the best represented year and month, February 2008.

2.2.3 Distribution of Socializing Sperm Whales

2.2.3.1 Analysis

To determine the probability of finding whales exhibiting social behaviour off Dominica, I modelled the probability of socializing given that whales were present. The unit of analysis was thus points corresponding to GPS fixes, gathered at 20 minute intervals, during sperm whale encounters. Because behavioural state could not be determined outside daylight hours, only data collected between 6:00 and 18:00 were analyzed. In this analysis, "presence" referred to the socializing behavioural state, and "absence" to the foraging behavioural state, and periods where behaviour was uncertain. Models predicting the presence of socializing whales were generated using the binomial based GAM-GEE framework, and model covariates and the steps for model selection and visualization methods were consistent with those described above for

general distribution. However, I did not restrict the dataset based on effort intensity as I did in describing habitat preferences. Since presences and absences correspond to the distributional and behavioural choices of whales, and not biases imposed by searching effort, no correction was required. All positions collected between latitude N15.10° and N15.75° were included in the models.

Three additional covariates were considered as potential predictors of behaviour. Time of day *(Tim)*, treated as a factor with four levels (three hour intervals), was included to account for behavioural predispositions across a day. Maximum wave or swell height (*Wav*), recorded at hourly intervals by observers on the research vessel, was used to identify if model predictions are influenced by sea surface roughness, which may be associated with deteriorating ability for visual detections. Finally, the presence of mature males (*Male)* was included as a potential predictor (see below).

2.2.3.2　　　　Behaviour State

The behavioural state of sperm whales was classified as "socializing "or "foraging" using criteria outlined by Whitehead (2003, see also Whitehead, Weilgart 1991). Typical socializing behaviour is observed when whales remain near the surface in larger clusters, move slower and less consistently, and rarely fluke up (Whitehead 2003). Under this definition socializing ranges from active periods of whales physically interacting to stereotypical resting behaviour. High similarity between resting and socializing prevent their discrimination. In contrast, typical foraging behaviour is identified by whales moving in a steady direction, forming single or small clusters at the surface, fluking up at the beginning of deep dives, and producing "usual" echolocation clicks on deep foraging dives (Whitehead 2003). Behavioural state was summarized across hour long periods. Hours when no whales were seen, or behaviour was uncertain, were counted as absences, making the analysis conservative. Since foraging and socializing behaviour are not mutually exclusive (behaviour may be divided amongst group members, or whales may transition from one state to another during an hour), the reverse predictions for socializing are not identical to foraging.

2.2.3.3　　　　Males as Predictors of Behaviour

Because social behaviour was often observed while groups of females and juveniles were accompanied by mature males, the presence of males was included as a factor in the model. Mature sperm whales are highly sexually dimorphic and can be distinguished from females

based on size. While females reach physical maturity at about 10.7m, males reach physical maturity at about 15.7m (Rice 1989). Thus distinctively large sperm whales (>12.5m) were assumed to be mature males (Whitehead et al. 1992a; Whitehead et al. 1992b). The presences of males was considered at two levels, if visually observed or photoidentified within an hour period, or if observed or photoidentified within an encounter. This allowed us to differentiate between immediate and prolonged effects that males may have on behaviour. QIC_u scores were used to determine if male presence best fit to the model at an hourly, or encounter level.

2.3 Results

2.3.1 Habitat Preferences

Six years of GPS tracks divided into 20 minute intervals, and corrected for effort, yielded a database containing 11,793 points. Fifty-eight percent of GPS fixes occurred during encounters with whales (Figure 2.2). Sperm whales were encountered on 242 occasions, and over 2419 hours were spent in the presence of whales. In this dataset, encounters lasted an average of ten hours and twelve minutes.

Depth, aspect, distance to shore, channel, latitude, longitude, and eastward geostrophic current (u), were best fit to the model as B splines, while slope, northward geostrophic currents (v), log(EKE),and SSH had improved fit as linear terms. A full model containing all terms could not be produced due to collinearity between latitude and channel. Removing latitude from the full model generated a better model fit than removing channel, so I dropped latitude from this analysis. Backwards stepwise regression selected a model containing month, year, depth, longitude, proximity to channels, and slope as predictive terms (Table 2.3). All terms were significant and were retained in the final model (Table 2.4). A confusion matrix suggests the model correctly predicts presence in 66.4%, and absence in 71.1% of cases. This result was based on a cut-off threshold of 0.607 determined by an ROC curve with an AUC of 0.759. A similar model was generated when I restricted the extent of the analysis to areas containing >80 locations/cell, suggesting that >50 locations/cell is an adequate control for lower search effort along the outer margins of the study area. When restricted to >30 locations/cell, the best selected model was similar but its parameter estimates possessed wider confidence intervals and it contained distance to shore as the final term rather than slope. Whale presence was predicted to increase when distance exceeded twenty-five kilometres from shore, in regions where we tended to be led by tracked whales rather than to search.

The relationship between model covariates and the probability of sperm whale presence can be seen in partial residual plots (Figure 2.3). Sperm whale presence varies annually, appearing to decline slightly between January and April. Inshore waters within the 1000 metre contour line are least preferred. Predictive mapping provides a spatial display of model predictions (Figure 2.4), and suggests that whales prefer deep (>3000m) waters, areas closer to channels, and inshore waters off the southern end of the island (~2000m deep).
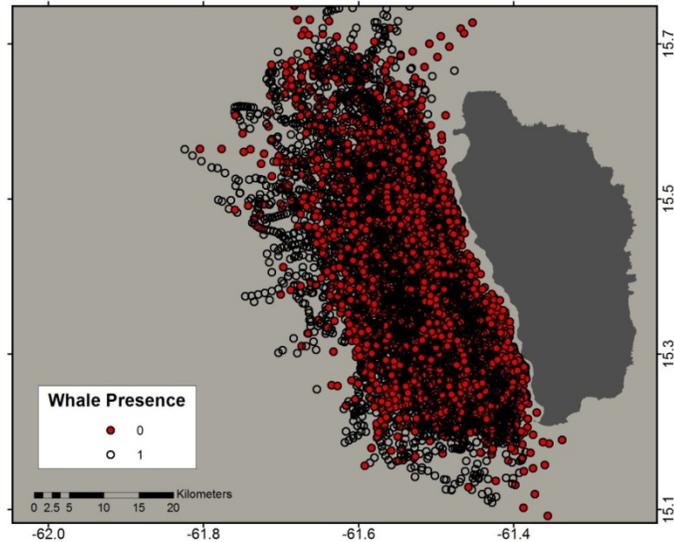
Figure 2. 2 Distribution of sperm whale presence/absence datapoints across the study area.

Table 2. 3 Backwards stepwise regression of a GAM-GEE model predicting sperm whale presence off the Lee coast of Dominica. Bolded terms in the best predictive model are significant.

Terms	QIC_u	ΔQIC_u
Mon+Yr+Dep+Long+Chan+Slo+Dis+Asp+v+EKE+u+SSH	14,524.2	270.5
Mon+Yr+Dep+Long+Chan+Slo+Dis+Asp+v+EKE+u	14,469.4	215.7
Mon+Yr+Dep+Long+Chan+Slo+Dis+Asp+v+EKE	14,354.3	100.6
Mon+Yr+Dep+Long+Chan+Slo+Dis+Asp+v	14,296.3	42.6
Mon+Yr+Dep+Long+Chan+Slo+Dis+Asp	14,264.0	10.3
Mon+Yr+Dep+Long+Chan+Slo+Dis	14,255.8	2.1
Mon+Yr+Dep+Long+Chan+Slo	14,253.7	-

Table 2. 4 Wald's statistic for terms in GAM-GEE model predicting sperm whale presence off the Lee coast of Dominica.

Term	χ^2	df	P
Month	16.5	3	8.88e-04
Year	30.3	5	1.31e-05
Depth	50.5	4	2.83e-12
Longitude	16.4	4	2.51e-03
Channel	28.0	4	1.24e-05
Slope	5.68	1	0.0172
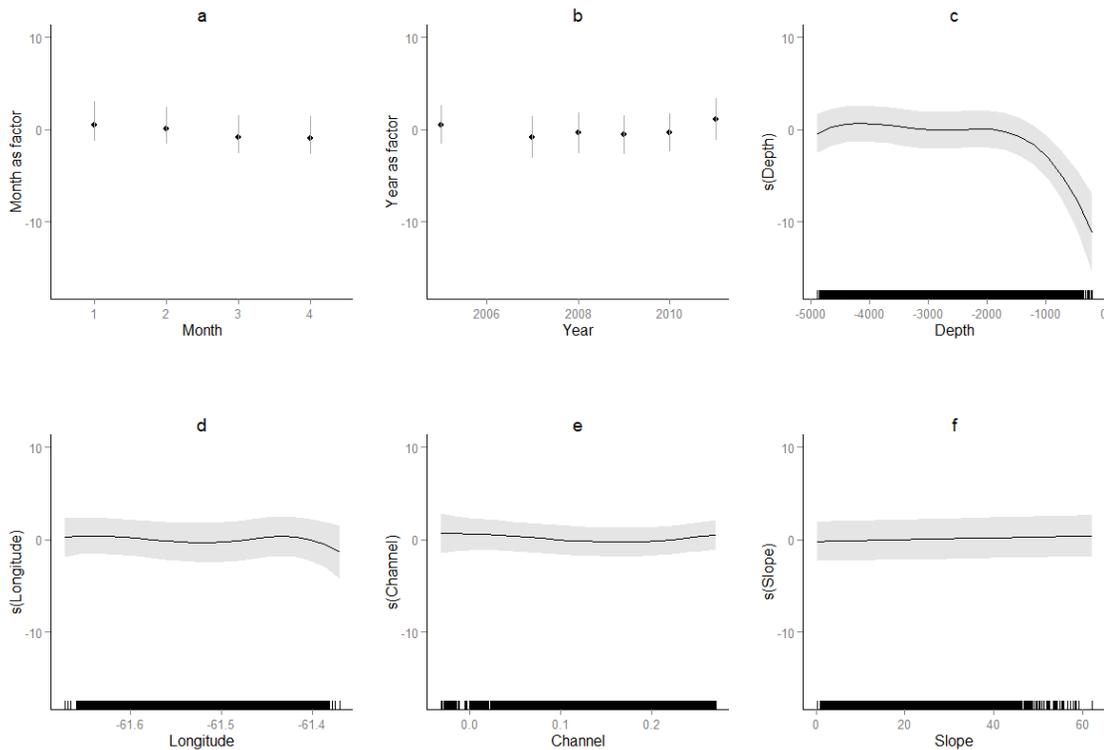
Figure 2. 3 Partial residual plot showing whale presence modeled as a smooth function of (a) month, (b) year, (c) depth (m), (d) longitude (°E), (e) proximity to channels, and (f) slope (°), with 95% confidence intervals based on GEEs. Rug plots of actual data values are shown for continuous predictors.
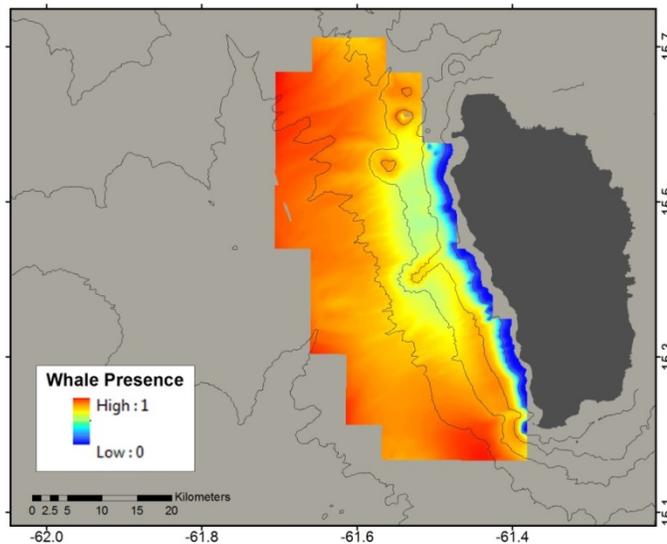
Figure 2. 4 Prediction map of sperm whale presence drawn for February 2008 from a GAM-GEE model of year, month, depth, distance to the shoreline, and longitude.

2.3.2   Habitat Selection and Behaviour

Sperm whales were observed socializing during eleven percent of the 5011 datapoints collected during daylight hours (Figure 2.5). Mature males were seen on 28 of 240 encounters, and were observed primarily with/near social units. Twenty different mature males were photoidentified across the study, and up to two individuals were seen at a time. When males were present, socializing occurred fifty nine percent of the time, making up twenty two percent of all observed periods of socializing.

Depth, slope, distance to shore, longitude, log(EKE), eastward geostrophic current (u), and SSH were best fit to the model of social behaviour as B splines, while aspect, channel, latitude, northward geostrophic currents (v), and wave height had improved fit as linear terms. The presence of males had an improved fit to the model when males were present across hour-long segments rather than encounters. Backwards stepwise regression selected a model containing male, wave, time category, year, EKE, u, latitude, and distance to Shore, and v as predictive terms (Table 2.4). Male, time, year and EKE are significant terms and were retained in the final model (Table 2.5). A confusion matrix shows model accuracy is greater for presences (77.8%) than presences (64.8%) as predicted by an ROC curve with a 0.0931 cut-off threshold, and AUC of 0.786. Partial residual plots suggest that socializations occur more frequently when mature males are present, and between the hours of 12:00-15:00. Partial residual plots show social

behaviour varies among years, and notably less social behaviour was seen in 2005 (Figure 2.6). Social behaviour also decreases with increasing EKE. Because no fixed spatial environmental variables were included in this model, no predictive map was generated.
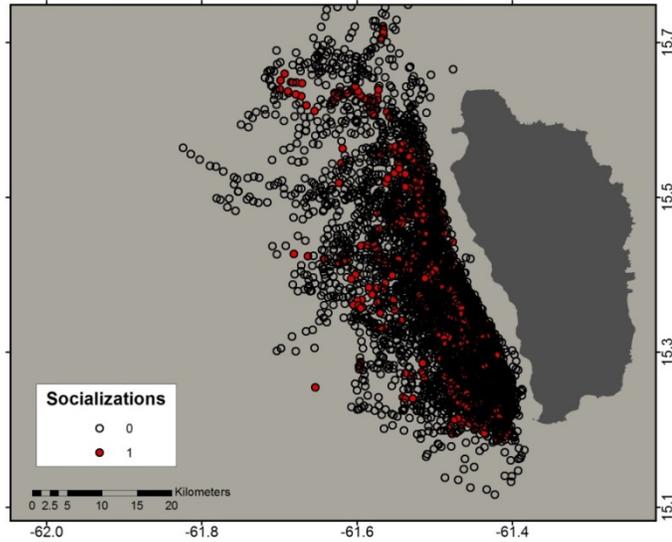
Figure 2. 5 Distribution of socializing/ non-socializing datapoints during daytime encounters (between 6:00-18:00).

Table 2. 5 Backwards stepwise regression of a GAM-GEE model predicting sperm whales socializing off the Lee coast of Dominica. Bolded terms in the best predictive model are significant.

Terms	QIC_u	ΔQIC_u
Male+Wav+Tim+Yr+EKE+u+Lat+Dis+v+Asp+Slo+Chan+Mon+Lon+Dep+SSH	2890.2	104.1
Male+Wav+Tim+Yr+EKE+u+Lat+Dis+v+Asp+Slo+Chan+Mon+Lon+Dep	2853.7	67.6
Male+Wav+Tim+Yr+EKE+u+Lat+Dis+v+Asp+Slo+Chan+Mon+Lon	2832.5	46.4
Male+Wav+Tim+Yr+EKE+u+Lat+Dis+v+Asp+Slo+Chan+Mon	2820.4	34.3
Male+Wav+Tim+Yr+EKE+u+Lat+Dis+v+Asp+Slo+Chan	2809.1	23.0
Male+Wav+Tim+Yr+EKE+u+Lat+Dis+v+Asp+Slo	2797.1	11.0
Male+Wav+Tim+Yr+EKE+u+Lat+Dis+v+Asp	2789.6	3.5
Male+Wav+**Tim**+**Yr**+**EKE**+u+Lat+Dis+v	2786.1	-

Table 2. 6 Wald's statistic for terms in a GAM-GEE model predicting sperm whale socializations off the Lee coast of Dominica.

Term	χ^2	df	P
Male	84.8	1	*2.20e-16*
Wave	3.84	1	0.0502
Time	10.6	3	*0.0141*
Year	18.3	5	*2.57e-03*
EKE	14.2	4	*6.65e-03*
u	9.44	4	0.510
Lat	1.23	4	0.267
Dis	7.47	4	0.113
v	0.37	1	0.542
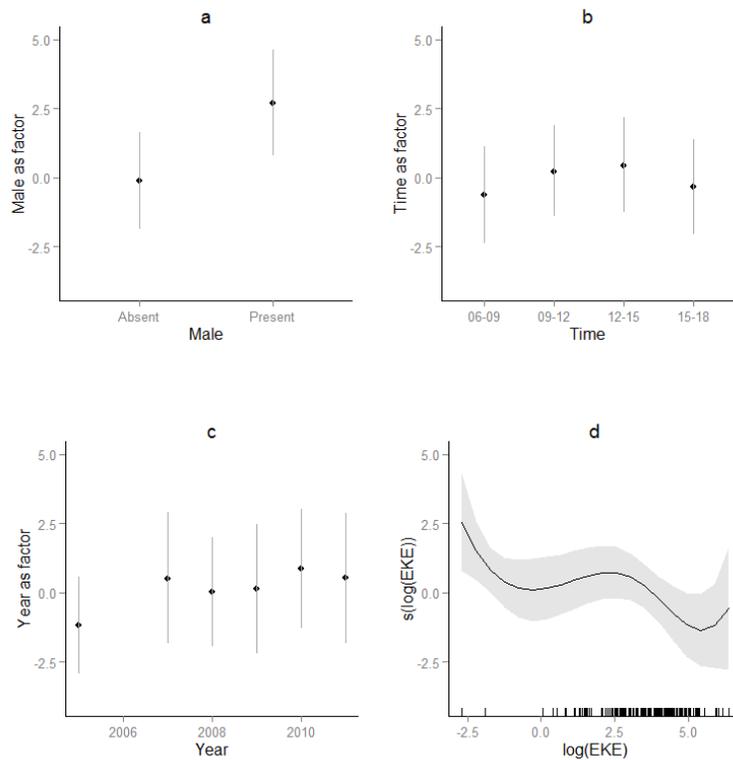
Figure 2. 6 Partial residual plot showing the occurrence of social behaviour modelled as a smooth function of (a) male presence, (b) time of day, (c) year, and(d) EKE, with 95% confidence intervals based on GEEs. Rug plots of actual data values are shown for continuous predictors.

2.4   Discussion

2.4.1   Habitat Preferences

Fine-scale habitat preferences of sperm whales off Dominica are best predicted by a combination of temporal and spatial variables. The retention of month and year within the predictive habitat model indicates that whale occurrence is weakly influenced by monthly and inter-annual variation. However, there is the caveat that these predictions are not representative of distribution across seasons. Local whale-watch operators believe that sperm whales are less abundant during summer months, but as most researchers avoid working during the hurricane season there is very little quantitative data available distribution patterns across the entire year (Gordon et al. 1998). Spatially, whale presence is associated with depth, longitude, proximity to channels, and distance to shore. Independently, these covariates explain variation occurring largely in the east-west, or north-south direction. In combination, they predict a slight preference for areas offshore and near channels. They also suggest a distinct aversion to waters shallower than 1,000m, which is consistent with preferences for deeper waters generally assumed for groups of females (Whitehead 2003), though females may use shallow waters in some areas (Jaquet and Gendron 2002; Pirotta et al. 2011).

Altogether, the overall variation in whale presence explained by model covariates is minimal. Moreover the best predictive model possesses only moderate discriminatory power, which suggests that habitat preferences are rather homogeneous. Gordon et al. (1998) also found little quantitative evidence for favoured areas off Dominica. This indicates that while seasonal and spatial predictors may have a small influence over when and where whales are seen, only slight habitat preferences are evident at the population level off Dominica.

In the marine environment, patchiness is often caused by dynamic oceanographic features such as fronts, eddies, and upwellings (Olson and Backus 1985). Although there is evidence that eddies form in the study area, from water of the North Atlantic flowing into the Caribbean Sea through passages between islands of the Lesser Antilles (Richardson 2005), oceanographic variables were not among the best predictors of sperm whale presence. This may be due to generalizations made for oceanographic variables as the scale of satellite data suppresses considerable ecological detail (Levin 1992). I was unable to examine associations between sperm whales and submesoscale (<10km) oceanographic current features, which may be more informative (Hyrenbach et al. 2006).

2.4.2   Habitat Selection and Behaviour

Social behaviour was best predicted by the presence of mature males, time of day, year and EKE. How each of these predictors dictates when sperm whales socialize is best understood by considering benefits and trade-offs associated with socializing. The primary disadvantage of socializing is that it takes time away from foraging, which potentially reduces energetic intake. Socializing likely has a key role in maintaining the all-important bonds between individuals upon which the sperm whales depend (Whitehead and Weilgart 1991), given that movement, defense against predators, babysitting, and suckling are all performed communally or cooperatively (Best 1979; Gero et al. 2009; Whitehead 1996a). Socializing may also give opportunities for social learning (CoussiKorbel and Fragaszy 1995), and thus the development and maintenance of sperm whale culture (Rendell and Whitehead 2001; Rendell and Whitehead 2003). In this study social behaviour also includes resting, which is undoubtedly vital.

Another benefit of social behaviour may be interacting with potential mates. Since mature males rove between social units instead of defending territories or females (Coakes and Whitehead 2004), infrequent encounters between males and social units are important social occurrences that possibly lead to reproduction. The model suggests that social behaviour is 15.9 times more likely to occur in the presence of mature males. This corresponds with Gordon et al.'s (1998) observations of intense interactions between social units and males in the Caribbean. However, it should be noted that socializing was defined quite broadly, and the observed interactions between males and females were equally variable, ranging from active physical interaction to apparent resting behaviour. Although we were unable to determine whether mating occurred, and the nature of the interactions between units and males vary, it appears that interactions which potentially lead to reproduction are significant drivers of social behaviour.

Social behaviour may also be influenced by changes occurring across the diurnal cycles. The model suggests that whales are 2.9 times more likely to socialize at 15:00-18:00 than 6:00-9:00. Similar changes in behaviour corresponding with time of day have been described in the Pacific, where social behaviour peaks in the late afternoon, dropping rapidly before sunset (Whitehead and Weilgart 1991). Generally whales are foraging when they are not socializing, and it is feasible that changes in behavioural state with time of day may correspond with changes in prey availability. As many cephalopod species perform diel vertical migration, the assortment of prey

species and sizes available to predators may vary across the 24-hour cycle (Watanabe et al. 2006). However, there is some dispute as to whether sperm whale feeding patterns are influenced by diurnal cycles (Papastavrou et al. 1989; Whitehead and Weilgart 1991; Whitehead 2003), and more studies after dark are required.

The presence of year in the final model suggests that annual effects influence the occurrence of social behaviour. Annual effects are potentially driven by inter-annual variation in environmental conditions and food availability. Differences in the social units observed or the number of males seen each year could also contribute to annual variation. It is worth noting that in 2005, the year where less social behaviour was indicated, one particular social unit (Unit F) was followed the majority of time (40 of 55 days with whales). Residency for this length of time in the study area is unparalleled. While this study suggests there is some annual variation in social behaviour, whales in the Galapagos did not differ in the number of hour spent socializing between months of study (Whitehead 2003; Whitehead 1999). This discrepancy may reflect social, cultural, or environmental differences between oceans (see Whitehead et al. 2012). Annual variations in the frequency of social behaviour may be influenced by complex interactions between social and environmental factors.

Finally, the model predicts that social behaviour generally decreases with increasing eddy kinetic energy. EKE is an indicator of mesoscale variability which is used to identify the presence of eddies, current meanders, and fronts (Pascual et al. 2006). EKE potentially represents a proxy for sperm whale prey abundance with changing levels of turbulence. It is well established that changes in the quality or quantity of feeding patches can affect animal activity budgets (Pyke et al. 1977), and changes in prey availability corresponding to oceanographic variability could mediate the trade-off between spending time and energy socializing versus foraging. However, since social units are capable of swimming towards or away from mesoscale oceanographic features, a correlation between behavioural state and EKE at the scale of this study does not necessarily indicate that activity budgets over longer time periods are influenced by oceanographic variability. Many social animals conserve social interactions, even when conditions deteriorate. Lactating baboons (*Theropithecus gelada*) that require additional feeding time to supplement their energy budgets will initially reallocate time from resting to feeding, preserving social behaviour (Dunbar and Dunbar 1988). Conservation of social behaviour was described in sperm whales in the Galapagos where females did not change the

amount of time spent socializing during periods with decreased feeding success (Whitehead 2003).

Understanding the relationship between behaviour and distribution is vital to management and conservation efforts. Cetaceans are exposed to a number of anthropogenic disturbances that may influence behaviour, including ocean noise (Weilgart 2007), and wildlife viewing (Frid and Dill 2002). The effect of human disturbance on individuals potentially varies with their behavioural state. In dolphins, the presence of tour-boats and swimmers can disrupt socializing and resting behaviour (e.g. Danil et al. 2005; Lusseau 2003). Thus discerning what influences behavioural state is an important element in understanding how populations are both distributed and impacted by disturbances.

2.5   Conclusion

The unpredictable movements of nomadic animals enable them to exploit spatially-temporally variable resources. Decisions about what habitat to use are influenced by intrinsic and extrinsic factors, on a range of spatial, temporal scales. Understanding how these decisions shape distribution patterns is essential knowledge required for the creation of conservation and management strategies. Off Dominica, this study emphasizes that small-scale distribution at the population-level is not much influenced by spatial or temporal effects. Sperm whales appear to be predisposed to socialize when they can interact with potential mates, and the propensity for social behaviour varies with time of day, eddy activity, and among years. Future work should examine habitat preferences across seasons, and at broader scales, to gain a better understanding of the processes driving the distribution of these wide-ranging nomadic animals.

CHAPTER 3   Variation in habitat use, foraging success, and exposure to disturbances among sperm whale social units

3.1   Introduction

Conservation and management efforts generally focus on populations. However populations are composed of individuals, which exhibit a range of behaviours. Individuals generally occupy habitat that contain the resources they require to survive and reproduce (Krausman 1999). Their habitat requirements can vary with age, sex, or reproductive status. Furthermore variation in experience, learning ability, personality, decision making, and social relationships can influence individual habitat preferences (Agostinelli and Lund 2011; Cañadas and Hammond 2008; DeAngelis and Mooij 2005; Krausman 1999; Réale et al. 2010). Accounting for variation among individuals is a major challenge in habitat studies.

Many animals benefit from sociality, the act of living in groups (Alexander 1974). Group size and composition have a large bearing on many aspects of behaviour (Silk 2007). When individuals form groups that are stable over time, it may be relevant to examine variation in habitat use among social groups. Social groups do not necessarily form at random, but are generally the product of relationships developed from repeated interactions between individuals (Hinde 1976). One of the potential benefits of sociality is that it allows individuals to gain from the sum of knowledge and experience contained by other group members. Thus individual characteristics can lead to variation in behaviour and fitness among social groups. This has been demonstrated in elephants where social groups with older matriarchs, which are better able to discriminate familiar and unfamiliar associates, have significantly higher reproductive success (McComb et al. 2001).

Group membership can also have a large influence on behaviour in animals that learn socially. Individuals that associate regularly are more likely to possess shared behaviours, since close interactions between group members can encourage social learning, conformism of behaviour and separation into culturally distinctive groups (CoussiKorbel and Fragaszy 1995; Whitehead et al. 2004). Variation in ecology, interactions with the environment, and responses to disturbances among social groups is potentially reinforced by social learning and cultural inheritance within social groups (Cantor and Whitehead 2013). In recent years there is growing recognition that socially and culturally sub-divided populations may require special

consideration in wildlife management (Whitehead et al. 2004). This is especially true when examining habitat use in animals with complex social systems, such as cetaceans (Connor et al. 1998).

Cetaceans are increasingly exposed to anthropogenic disturbances including chemical pollutants (Martineau et al. 1994), ship strikes (Laist et al. 2001), changes in prey availability due to overfishing (Bearzi et al. 2006), ocean noise (Weilgart 2007), and wildlife viewing (Frid and Dill 2002). Disturbance stimuli created by humans can cause animals to deviate from their behavioural patterns (Frid and Dill 2002). Even seemingly benign activities can elicit immediate behavioural responses. In cetaceans, individuals may respond with changes in vocalization, respiration, and movement patterns (Frid and Dill 2002; Richter et al. 2006). These small responses can sometimes translate to large effects (Bejder et al. 2006). Human disturbance can divert time and energy from feeding, parental care, and mating displays to fleeing, increased vigilance and habitat shifts (Bejder et al. 2006; Frid and Dill 2002). Demonstrated effects include lost foraging opportunities due to increased travel time in orcas (*Orcinus orca*; Williams et al. 2006), and shifts in habitat use from areas with high to low vessel traffic in bottlenose dolphins (*Tursiops sp.*; Bejder et al. 2006). Long-term responses to disturbances are generally difficult to measure in natural populations (Bejder et al. 2006a; Bejder et al. 2006b), and few studies have examined how human disturbance affect social groups rather than populations (e.g. Lusseau et al. 2009).

In this study, I describe variability in distribution among social groups in a wide-ranging predator, the sperm whale (*Physeter macrocephalus*). Sperm whales live in complex multileveled societies (Rendell et al. 2012). Females and juveniles live in long-term stable social units (Christal et al. 1998; Whitehead et al. 1991). Units are organized into acoustic clans by their distinct vocal dialect and behavioural variants (Rendell and Whitehead 2003; Whitehead and Rendell 2004), which appear to be culturally inherited (Rendell et al. 2012; Rendell and Whitehead 2001). Differences in distribution, movement patterns, and foraging and reproductive success are attributed to vocal clan membership (Marcoux et al. 2007a; Marcoux et al. 2007b; Whitehead and Rendell 2004). In this study I describe differences in habitat use patterns among sperm whale social units, the base level of a sperm whale society, and examine the effect of unit membership on feeding success and exposure to potential anthropogenic activity.   This study concerns a well-studied population of sperm whales in the Caribbean off the

leeward coast of the Commonwealth of Dominica, where an unparalleled dataset has been amassed based on eight years of study, and social units have previously been delineated (Gero 2012).

3.2 Methods

3.2.1 Study Population
The population of sperm whales inhabiting the eastern Caribbean Sea live in stable social units containing an average of seven individuals (Gero 2012). Social units seen off Dominica are thought to range throughout the Lesser Antilles (Gero et al. 2007; Gero 2012). Units in the Caribbean have relatively high residency times and resighting rates off the island of Dominica, and some units are known to have been using these waters since at least 1984 (Gero 2012). A total of 419 individuals have been photographically identified in the Eastern Caribbean since 1984 (Gero 2012).

3.3.2 Field Methods
We surveyed an area covering approximately 2000 km^2 off the western coast of Dominica annually during 2005-2012, for one to four months each year between the months of January and June (Table 3.1). Groups of sperm whales were detected and tracked using visual and passive acoustic methods following protocols established from previous boat-based research (Whitehead and Gordon 1986; Whitehead 2003). During daylight hours, we approached individuals spotted at the surface from behind to within 100 meters, and photographed their flukes (tails) for individual identification (Arnbom 1987). Calves, which rarely show their tails, were identified from photographs of the dorsal fin (Gero et al. 2009). The GPS position corresponding to each photo-identification was obtained from vessel tracks, recorded at 10 minute to 10 second intervals, for all years except 2006. To control for the influence of vessel size on study results, I excluded data collected onboard the larger whale-watches from some analyses, including those on anthropogenic effects.

Table 3. 1 Summary of research effort described by a) days at sea and b) research platform. Data was collected from a dedicated 12m auxiliary sailing vessel (BAL), 5m (SF) and 11m (FF or MH) outboard motorboats, or 18m motorized catamaran whale watch (WW).

	2005	2007	2008	2009	2010	2011	2012	Total
January	14	3		14	10			41
	BAL	SF,WW		SF,WW	BAL			
February	25	27	19	22	25			118
	BAL	SF,WW	SF,WW	SF,WW	BAL			
March	12		26	26	22	26		112
	BAL		SF,WW, BAL	SF,WW	BAL	FF,MH		
April	9		25		13	9		56
	BAL		BAL		BAL	FF,MH		
May			7				23	30
			BAL				BAL	
June							6	6
							BAL	
Total	*60*	*30*	*77*	*62*	*70*	*35*	*29*	*363*
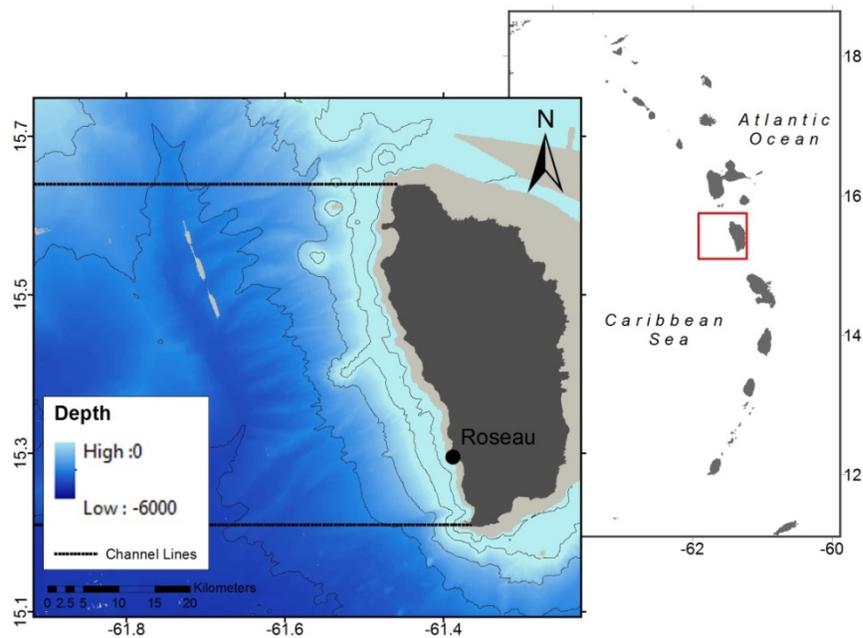
Figure 3. 1 Map of study area showing location of Roseau, lines marking channels at N15.64° and N15.21°, and thousand meter bathymetric contour lines.   Areas with missing bathymetry are shown in light grey.

3.3.3   The Social Unit

Social units were defined based on long-term associations between individuals (Gero 2012). Individuals were identified from high quality photographs (Q3-Q5; Arnbom 1987), and were considered associating if identified within two hours of each other (Christal et al. 1998). Sets of individuals observed associating over two or more years were defined as social units (Gero 2012). Unit membership is transitive, in that if A and B are unit members and B and C are unit members, then A and C are members of the same unit. Under this definition, unit membership has a more stringent minimum duration of association than social units described by Christal et al. (1998) in the Pacific, who considered associations separated by 30 days rather than years. I focused on social units in which two or more individuals were seen for a minimum of ten days, spread across two or more years of study between 2005 and 2007-2012. These social units were considered "prevalent", and differences in habitat use were examined between prevalent units.

3.3.4   Habitat Use

3.3.4.1   Analysis of Habitat Use among Social Units

To investigate whether habitat use differs between social units, I tested the null hypothesis that the proportion of time whales occurred in different habitat regions off Dominica was independent of social unit. I designated habitat regions within an area covering approximately 0.3 by 0.6 decimal degrees, arranged parallel to the island. This space was divided into 2x2 and 2x3 habitat grids which separate inshore and offshore areas, and the northern and southern ends of the island (Figure 3.2). Whether the amount of time spent in each habitat cell was independent of social grouping was tested within the four and six cells using chi-squared tests, and the strength of association between variables was calculated using Cramér's Phi (V) (Cramér 1946). I quantified the presence of units in each habitat cell at three different time scales, by counting the number of years, days, and hours observed in each cell. Additionally, I tested for differences in the number of standardized hours (hours divided by days observed) that socials units were observed in each cell. A second set of tests was performed to determine whether prevalent social units differed in habitat use from units seen less frequently off Dominica, by comparing habitat use of prevalent social units to all other photoidentified whales. Though are limitations with examining habitat use using chi-squared test since dependency issues arise due to the spatial proximity between habitat cells and correlation between serial

observations made across hours, this approach helps to identify where spatial variation between social units is likely.
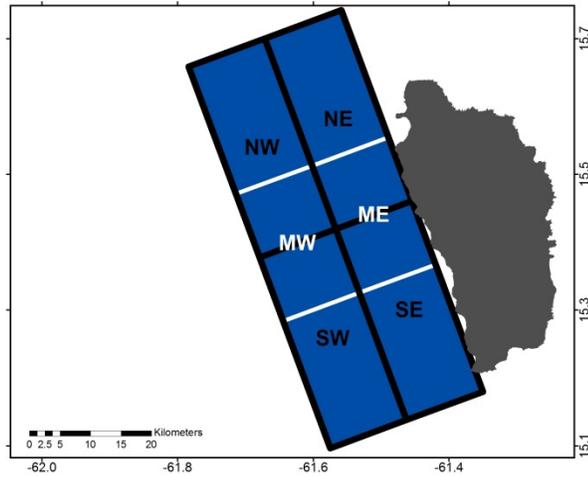
Figure 3. 2 Division of study area (blue) into 2x2 (black outline) and 2x3 habitat regions (y axis divisions shown in white) for the examination of the relationship between habitat and social unit membership.

3.3.4.2   Associations between Social Units and Habitat Overlap

To determine if habitat use was correlated between social units known to associate I examined the relationship between unit association and their degree of habitat overlap. An index of association between social units was calculated as the number of days one or more individuals from two separate social units were seen in clusters together, over the total number of days either social unit was seen (i.e. "simple ratio" association index, Cairns and Schwager 1987). Clusters are composed of all individuals occurring within approximately 3 adult-body lengths of their nearest neighbour, with coordinated behaviour (see Whitehead 2003). I plotted the association index against habitat overlap to visualize the relationship between overlapping habitat and the strength of association between each pair of social units. Habitat overlap was estimated using Pianka's index of niche overlap:

$$O_{jk} = \frac{\sum^{n} p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 \; \sum p_{ik}^2}}$$

Where O_{jk} = Overlap in habitat between social unit j and k, p_{ij} = Proportion of time (hours) spent by social unit j in habitat region i, p_{ik} = Proportion of time (hours) spent by social unit k in habitat region i, and n = Total number of habitat regions (Pianka 1974).

3.3.4.3   Discriminating Between Social Units

Using multivariate analysis of variance (MANOVA) and discriminant function analysis, I tested for significant differences between the habitats used by social units at a predetermined time of day, and identified the set of environmental variables which best define habitat in multivariate space (Table 3.2). The unit of analysis was the average location of photo-identified individuals from each of the prevalent social units, on dates they were identified between 12:00 and 13:00 local time (hereafter referred to as mid-day). I estimated unit location by averaging the positions of unit members seen at mid-day, using only the first position each unit member was photo-identified at within the hour.

Environmental predictors that represent potential proxies of forage abundance were selected to represent sperm whale habitat. Depth, slope, and proximity to channels are predictors of preferred habitat off Dominica (Chapter 2). Depth and slope were derived from a high resolution bathymetric model, created from data collected during the 1998 Aguadomar campaign, and provided by the Institute de Physique du Globe de Paris (IPGP) and the Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER). I also considered distance to shore, and whale's proximity to channels between Dominica and adjacent islands to the north or south. Whales were considered to be in the channels when their latitude was north of N15.64° or south of N15.21° (respectively), which represent the northern and southern tips of the island. By this measure the highest value possible was 0.215° (the latitudinal center of the island), values of 0° indicate a latitude equal to either the northern or southern extremes of the island, and negative values indicated points inside the channels (Figure 3.1). Finally I considered two oceanographic variables, eddy kinetic energy (EKE) and sea surface height anomalies (SSH), obtained from Ssalto/Duacs satellite altimetry data. Global mean sea level anomaly data were extracted using ArcGIS 10 Spatial Analyst Tools (ERSI) as a delayed time, merged, and referenced product.

I tested for differences between social units, years, and units+ years using MANOVAs. I also nested year within social unit to examine whether differences between units varied by year. To ensure adequate sampling, only units with seven or more samples were analyzed. I then

identified the best subset of variables predicting social units using linear discriminant function analyses with leave-one-out cross validation from both directions. All statistics were run in R 2.15.1 (R Core Team 2012). To eliminate biases potentially arising from vessel size and search behaviour, I excluded locations taken from whale watching vessels from the analysis.

Table 3. 2 Predictive terms for MANOVAs and linear discriminant function analysis of social units.

Term	Unit	Spatial Resolution	Description
Depth	m	100 x 100m	Depth from bathymetric model obtained from IPGP/ IFREMER.
Slope	°	100 x 100m	Slope extracted from above bathymetry model
Distance	m	5 x 5m	Distance to Dominica's shoreline (log transformed)
Channel	dd	-	Proximity to channels as defined by the relative position between N15.64° and N15.21°. The latitudinal center of the island occurs at 0.215°, and negative values are within channels
SSH	cm	1/3°x1/3°	Sea Surface Height, obtained at seven day intervals
EKE	cm^2/s^2	1/3°x1/3°	Eddy Kinetic Energy, obtained at seven day intervals (log transformed)

3.3.5   Feeding Success

In the absence of an effective method for directly observing sperm whales consuming their cephalopod prey, defecation rate has become established as a proxy for foraging success (Whitehead et al. 1989; Whitehead 1996b). The majority of observed defecations occur at the onset of dives when individuals lift their tails or "fluke-up" (Whitehead 1996b). Defecation rate is measured as the proportion of sperm whale fluke-ups where defecations (easily observable brown patches in the water) are observed. Observations from the surface are thought to represent overall defecation rate because physiological constraints make it unlikely that sperm whales defecate often during deep foraging dives (Whitehead 1996b). I tested for variation in defecation rate between social units, as well as between years using chi-squared statistics. Defecation rates were calculated only for fluke-ups when observers were able to confirm if defecation had or had not occurred. Yearly defecation rates were calculated from all observed dives, whereas the defecation rates of prevalent social units were calculated only from fluke ups accompanied with high quality photographs (Q3-Q5: Arnbom 1987) of unit members. Particular social units were not seen each year, and I was unable to examine how defecation rate may vary with social unit and year using a two way contingency table. Therefore to determine if

defecation rate differed between social units while accounting for yearly variation, I also generated binomial-based generalized linear models of the presence/absence of defecations at each fluke-up, using social unit, year, and these terms in combination as predictive variables. The best model was selected using the Akaike information criterion (AIC).

3.3.6 Anthropogenic Effects

I used the distance from Roseau, the capital of Dominica, as an indicator of potential exposure to anthropogenic activity. Roseau is the primary point of departure for whale-watching and swim-with-the-whale tours directed at sperm whales. This metric assumes that whales located closer to Roseau are encountered more frequently and followed for greater lengths of time than whales located farther away from Roseau. Additionally, the main port facility, through which all goods are landed in this island nation, is located in Roseau. Since marine traffic into and out of Roseau is higher than surrounding waters, I assumed these waters were noisier.

I tested for differences in distance from Roseau between eleven prevalent social units observed at mid-day using a one way analysis of variance. Roseau, for the purpose of this study, was situated at latitude 15.295° North and 61.388° West. Distance from the capital was calculated in kilometres from Universal Transverse Mercator coordinates. Differences in distance between research platforms, and years were tested for using Kruskal-Wallis Tests. I also used linear regression to investigate possible trends in the mean distance from Roseau across the study period.

An important element of this study is the use of vessel-based research. The presence of a research vessel can increase the exposure and disturbance of animals to vessels, and could influence both distribution and behaviour of the targeted animals. However, in the absence of alternative means of data collection, vessel based studies are currently a requirement for most studies relying on visual observations of cetaceans at sea. Several studies suggest that research vessels tend to be less invasive and elicit fewer behavioural responses than other vessel types (Bejder et al. 2006; Lusseau 2003; Nowacek et al. 2006). Research vessels are generally smaller, with quieter engines compared to larger vessels which require larger, louder, engines to operate (Bejder et al. 2006).

3.4 Results

In total 16,058 photographs were taken across 288 days with whales. From 2005-2012, 266 individuals from over 17 distinct social units were identified during the study (Gero 2012). Eleven social units were considered as prevalent as they were seen off Dominica on ten or more days, across two or more years of the study. Prevalent social units were seen for an average of 5 years (SD=1), 28 days (SD=21), and 128 hours (SD=122). At least one photo-identified member from nine of the prevalent social units was identified in the study area between 1984 and 1996, suggesting that prevalent social units' use of habitat off Dominica exceeds the eight years of study (Gero 2012).

We typically saw only a single social unit during an encounter; however, two or more social units were occasionally identified within a day and sometimes together. Unit F was seen the most frequently. We encountered this unit every year, and twice as often as any other unit.

3.4.1 Habitat Use

3.4.1.1 Analysis of Habitat Use among Social Units

The proportion of time whales spent in different habitat regions was not significantly influenced by social unit identity when examined across years (Cells=4: χ^2= 14.0, df=30, P=0.994, V=0.196; Cells=6: χ^2= 37.7, df=50, P=0.901, V=0.216), or hours standardized across days (Cells=4: χ^2=12.6, df=30, P=0.998, V=0.188; Cells=6: χ^2=24.8, df =50, P=0.999, V=0.183). However, social units show a moderate difference in the amount of time spent within habitat cells at hourly scales (Cells=4: χ^2=237.7, df=30, P=2.2e-16 V=0.234; Cells=6: χ^2=320.7, df=50, P=2.2e-16, V=0.209) (Figure 3.3-3.4a). At daily scales, units are moderately different in their allocation of time in the six cell habitat design (χ^2=81.9, df=50, P=0.00300, V=0.187), but not the four cell design (χ^2=42.8, df=30, P=0.0599, V=0.190) (Figure 3.4b). Though statistical significance was only found for tests examined at hourly or daily time scales, effect sizes indicate there is a weak but substantive relationship between unit identity and time spent in habitat regions across all time scales. Furthermore, the strength of the effect is similar at each scale (Cramér's V of 0.18-0.22).

Social units varied in how time was allocated to different habitat cell. Some units spent relatively more time offshore (western cells) or in northern cells, while others used the area more uniformly or spent proportionately more time inshore (Figure 3.3-3.4).   The strongest

differences were found in the southeastern cell, where almost half of the social units spent proportionately less time than expected (Table 3.3).

When prevalent social units were compared to all other whales, no difference in time spent in habitat cells was evident across years (Cells=4: χ^2=0.321, df=3, P=0.956, V=0.080; Cells=6: χ^2=0.307, df=5 P=0.995, V=0.069), days (Cells=4: χ^2=1.119, df=3, P=0.773, V=0.052; Cells=6: χ^2=4.12, df=5 P=0.532, V=0.092), standardized hours (Cells=4: χ^2=0.216, df=3, P=0.975, V=0.095; Cells=6: χ^2=0.434, df=5 P=0.994, V=0.118), or hours in the four cell design (χ^2=6.28, df=3, P=0.0987, V=0.063). Small effect sizes (V<0.1) likewise indicate that there is no effect of unit prevalence on habitat used, with the possible exception of standardized hours across six cells. Prevalent units and other whales are moderately different in the proportion of hours spent within the six cell habitat cells (χ^2=18.0, df=5 P=0.00290, V=0.107). Other whales spent relatively more time in the SW cell and less in the ME and NE cells (Figure 3.5).
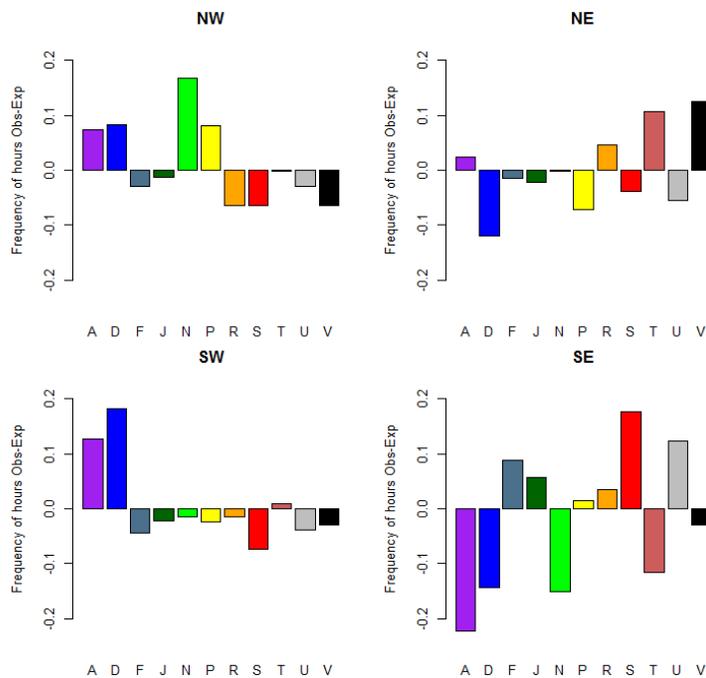
Figure 3. 3 The percentage of hours each unit was observed minus expected within four habitat regions. Colours represent prevalent social units seen on a minimum of ten days across two years.

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Table 3. 3 Root mean square of the percentage of hours or days sperm whales were observed minus expected within (a) four and (b) six habitat regions. Regular text shows differences among prevalent social units and italicized text shows differences between prevalent social units and other whales.

a)

Cell	Hours
SE	12.3
SW	7.4
NE	7.1
NW	75

b)

Cell	Hours	Days	*Hours*
SE	10.7	8.5	*0.5*
SW	2.6	3.8	*2.8*
ME	9.4	6.3	*1.4*
MW	8.9	8.0	*0.2*
NE	4.4	2.7	*1.5*
NW	5.6	6.2	*0.4*

a)   b)
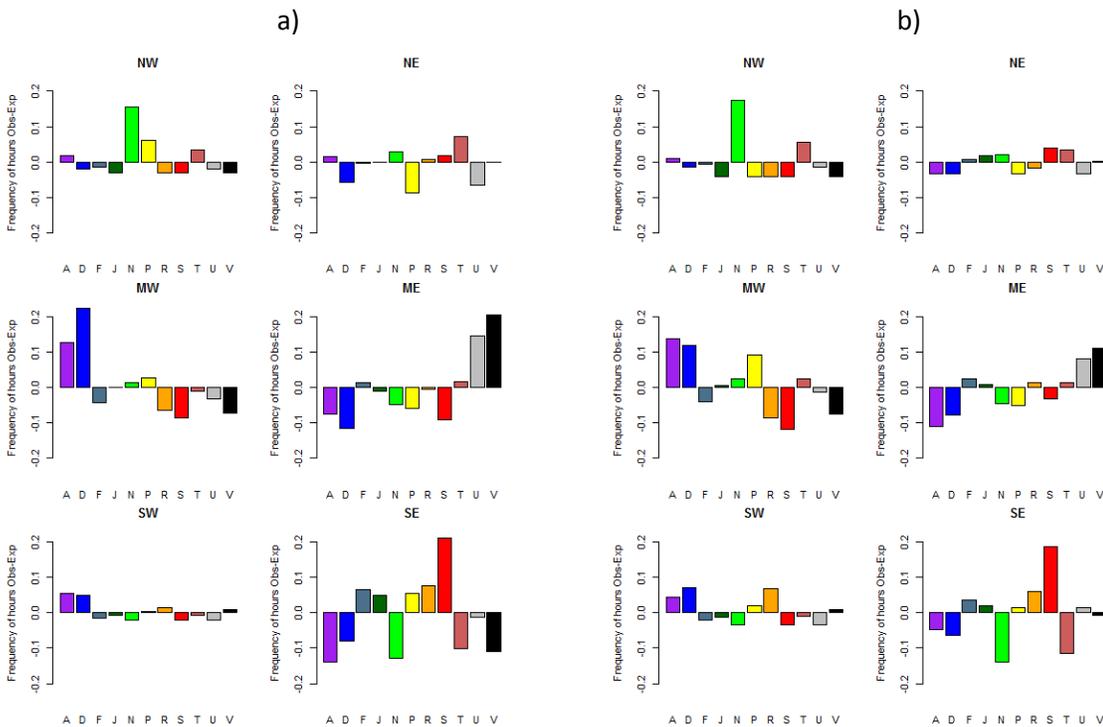
Figure 3. 4 The percentage of (a) hours and (b) days each unit was observed minus expected within six habitat regions. Colours represent prevalent social units seen on a minimum of ten days across two years.
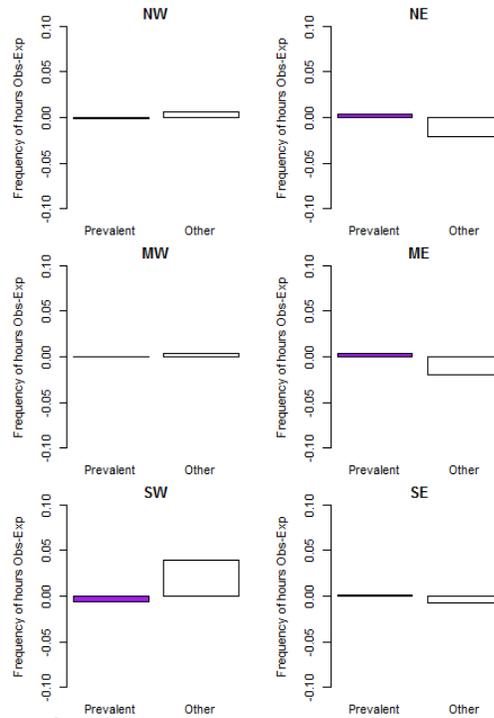
Figure 3. 5 The percentage of hours that prevalent social units and all other whales were observed minus expected within six habitat regions.

3.4.1.2   Associations between Social Units and Habitat Overlap

The highest rates of association were observed between four social unit pairs (Table 3.4). Three of these (F-U, A-D, and T-V) were described by Gero (2012). Individuals from units F-U were observed clustered together in multiple years, and the units T-V were seen socializing in 2010. Individuals from units A-D were only occasionally seen within the same cluster; however, these two units were frequently seen on the same day (Gero 2012). Had I defined association as number of days both units were seen, their association index would be much higher (0.36). I found high association index in a fourth unit pair (R-S). R-S possess a high association index largely due to a single female 'TBB' (#5759) from Unit S, who was seen exclusively with Unit R for a period in 2008 (Gero 2012). When the amount of time allocated to habitat regions is considered, these four social unit pairs appear to have similar patterns in the proportion of time they spent in habitat cells (Figure 3.3-3.4).

Overall, social unit pairs exhibit high degrees of habitat overlap (Figure 3.6). The median overlap of unit pairs was 0.95 to 0.91 for the four and six habitat regions (respectively). The four social unit pairs with strong associations had high or higher than average measures of habitat overlap.

Table 3. 4 Index of association between prevalent social unit pairs.

	A	D	F	J	N	P	R	S	T	U
D	0.03									
F	0.01	0.02								
J	0.00	0.01	0.01							
N	0.00	0.00	0.00	0.00						
P	0.00	0.00	0.00	0.00	0.00					
R	0.00	0.00	0.00	0.00	0.00	0.00				
S	0.00	0.00	0.00	0.00	0.00	0.00	0.08			
T	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		
U	0.00	0.02	0.13	0.00	0.00	0.00	0.00	0.00	0.00	
V	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00
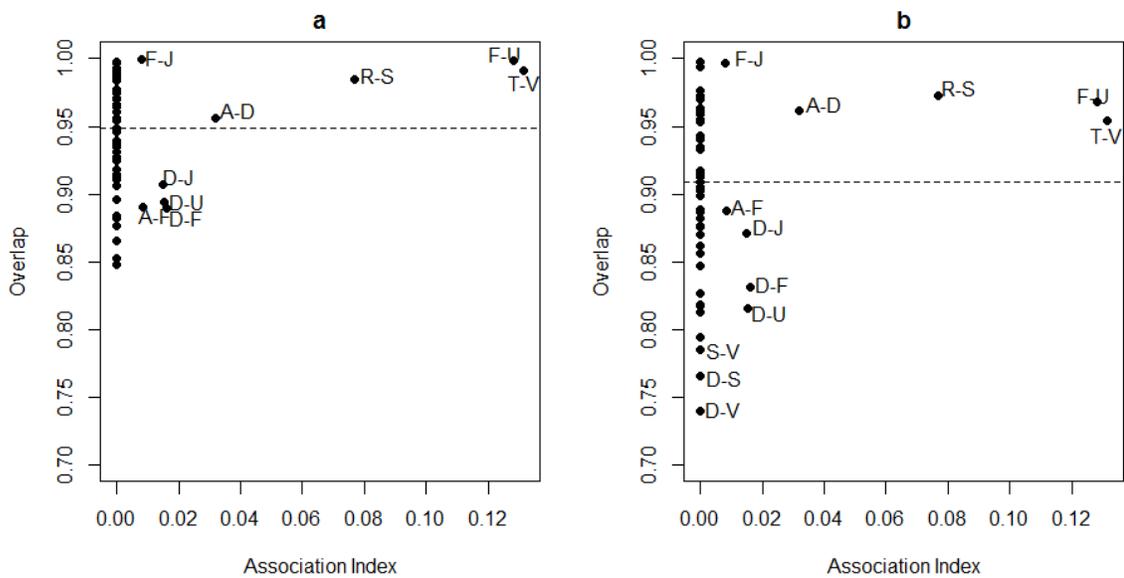
Figure 3. 6 Relationship between the association index and the habitat overlap (O_{jk}) for each social unit pair. Habitat overlap was measured from the proportion of hours spent in (a) four and (b) six habitat regions. Median overlap values are marked with dashed lines.

3.4.1.3　　　Discriminating Between Social Units

Nine prevalent social units were seen at mid-day on seven or more occasions. These units were observed 130 times across 117 days, for an average of 14 days each. On twelve days, two or more social units were observed within the same hour. Two social unit pairs overlapped four

times (D-J and T-V) and a third pair overlapped three times (F-U). In one instance three units were seen within the same hour, units A+D+J.

Multivariate predictors differ significantly between social units (Wilks=0.470, df=8, F=1.99, P=1.21e-04), years (Wilks=0.222, df=5, F=7.27, P=2.20e-16), social units+years (Unit: Wilks=0.532, df=8, F=1.57, P=0.0104; Year: Wilks=0.195, df=5, F=7.51, P=2.00-16), and years nested in social units (Unit: Wilks=0.247, df=8, F=3.23, P=5.22e-11; Unit/Year: Wilks=0.0836 df=21, F=2,27 P=7.93e-12). While variance is homogeneous between social units (Levene's test: F=1.67, df=8, P=0.112) and years (Levene's test: F=2.13, df=5,P=0.0660), both units and years lack multivariate normality (Table 3.5).

A full discriminant function model accurately predicts social unit in 30.8% of cases (Figure 3.7a). Stepwise selection of predictor variables, from both directions, identified depth as the best predictor of social grouping. Depth accurately predicts social unit in 36.9% of cases, and has an eigenvalue of 1.97 (Figure 3.8). Year is better discriminated than social unit with 59.2% accuracy. Year is best predicted by SSH (eigenvalue=7.37) with 62.3% accuracy (Figure3. 7b & 3.9).

Table 3. 5 Shapiro-Wilk test for multivariate normality in spatial, temporal, and oceanographic predictors of position at mid-day among (a) social unit and (b) years.

a)

Unit	Wilks	P
A	0.704	*9.22E-04*
D	0.487	*1.43E-05*
F	0.557	*7.90E-10*
J	0.457	*4.84E-10*
N	0.443	*1.37E-06*
R	0.483	*6.51E-06*
T	0.776	*1.33E-03*
U	0.453	*4.14E-06*
V	0.429	*1.43E-06*

b)

Year	Wilks	P
2005	0.599	*3.67E-08*
2008	0.670	*2.50E-05*
2009	0.577	*2.97E-05*
2010	0.802	*1.42E-09*
2011	0.530	*8.15E-06*
2012	0.453	*4.14E-06*
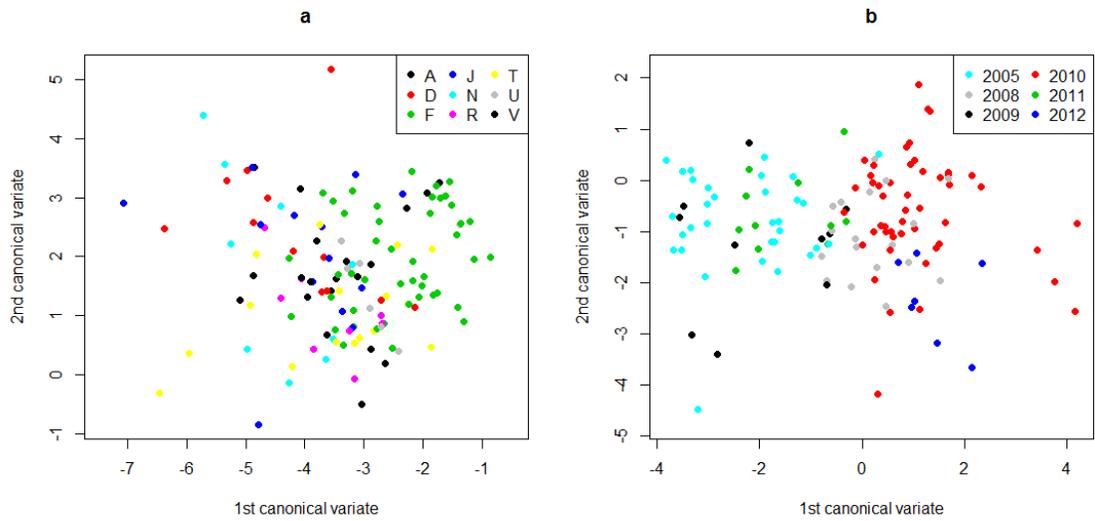
Figure 3. 7 Full discriminant function models for (a) social units and (b) years from all multivariate predictors of nine social units on days they were seen at mid-day. Predictions are accurate in 30.8%, and 59.2% of cases, respectively.
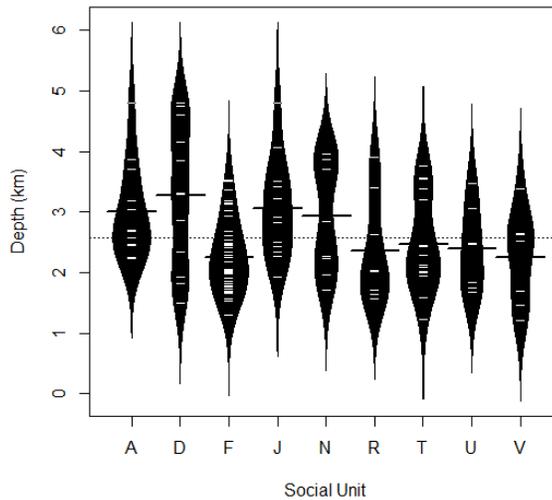
Figure 3. 8 Beanplot showing variation in depth between social units observed at mid-day. Beans are mirrored density traces (Kampstra 2008). Individual datapoints are shown as small lines, and overall and group means are marked by dashed and black line(s) respectively.
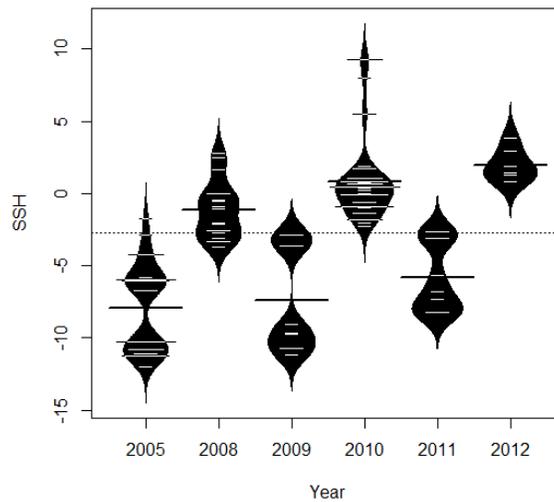
Figure 3. 9 Beanplot showing variation in SSH anomaly (cm) between years. Individual datapoints are shown as small lines, and overall and group means are marked by dashed and black line(s) respectively.

3.4.2 Feeding Success

Across the study, we confirmed the presence or absence of defecations in 1456 of the total 4611 observed fluke-ups. Defecations were observed in 30% of confirmed fluke-ups. Defecation rates differ between both social units (χ^2=47.6, df=11, P=1.70e-06), and years (χ^2=25.3, df=7, P=6.74e-04). An average of 182 defecations (SD=144, min=26) were observed per year, and 120 samples (SD=104, min=33) per social unit. Defecation rate was greatest for Unit V, a larger than average social unit seen only in 2010 and 2011, as well as two of the smallest social units (J and U), which did not contain young calves for much of the study. Unit N and other whales (Z) had the lowest feeding success rates. Across years, 2011 and 2012 had much higher and lower (respectively) feeding success than expected rates (Figure 3.10).

Defecation rate is best predicted by a GLM model containing social unit and year as predictive covariates (Table 3.6). Units N, V and other whales (Z), along with the years 2011 and 2012 are significant coefficients within the model (Unit N: SE=0.277 , Z=-2.49, P=0.0128; Unit V: SE=0.367, Z=2.05, P=0.0402; Other whales (Z): SE=0.300 , Z=-3.03, P=0.0214; 2011: SE=0.247 , Z=2.82, P=0.0479; 2012: SE=0.370 , Z=-2.23, P=0.02560). Partial residual plots show that the estimated relationship between responses on the logit link scale and each predictor (where the $odds\ ratio = e^{logit\ link}$) correspond with the relationships predicted from the chi-squared

analyses (Figure 3.11). Defecations were accurately predicted in 62.7% of cases, and the absence of defecation was accurately predicted 60.9% of the time. Accuracy was determined from a confusion matrix using a cut-off threshold of 0.317 selected from a receiver operator characteristic curve with an area under the curve of 0.660.
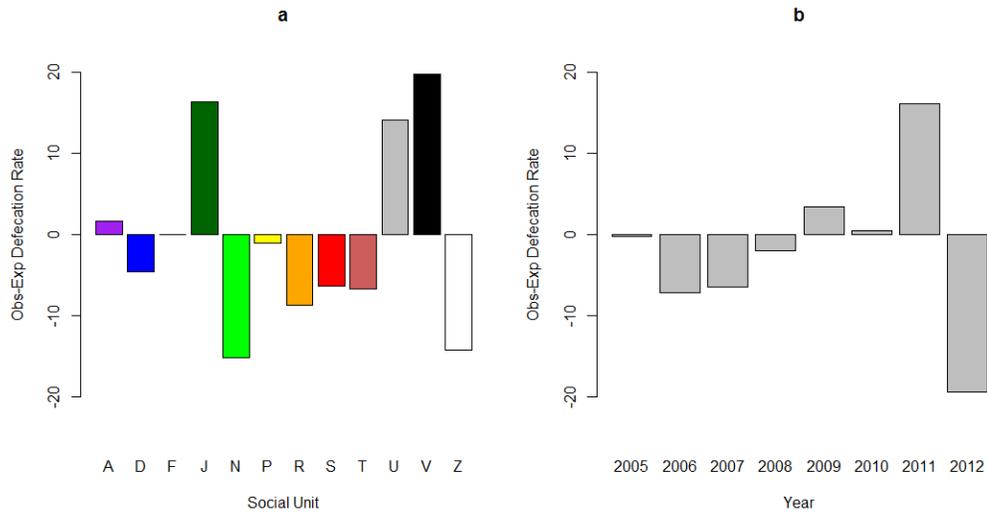
Figure 3. 10 Defecation rate observed minus expected across (a) social units, and (b) years. Defecation rates are measured as the percentage of observed fluke-ups containing defecations. The social unit labelled Z contains all individuals from non-prevalent units and is not a defined social unit.
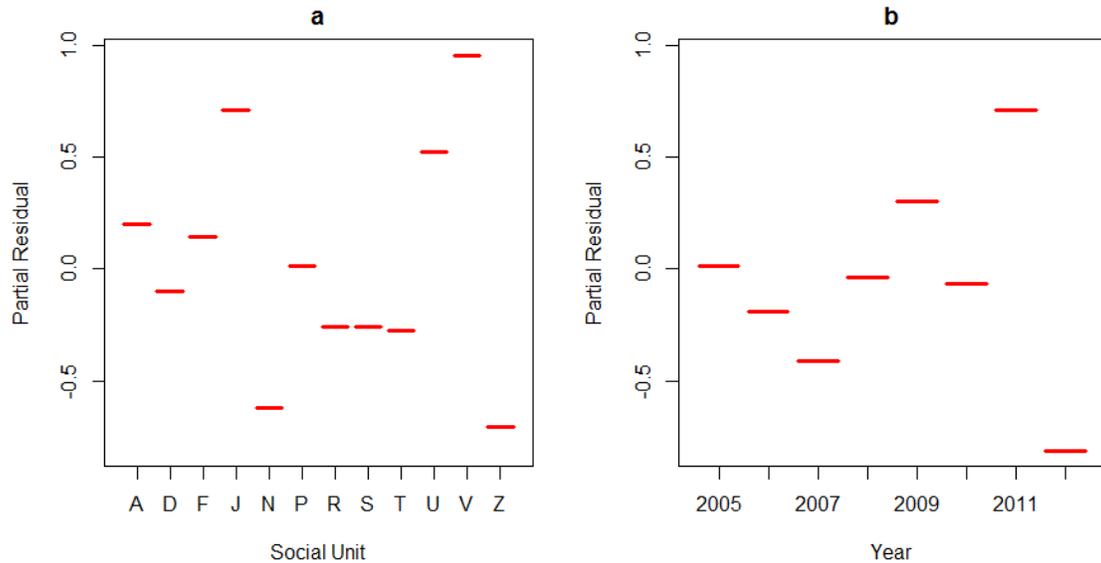
Figure 3. 11 Partial residual plot of a GLM model predicting the presence of defecations from (a) social unit and (b) year. The social unit labelled Z contains all individuals from non-prevalent units and is not a defined social unit.

Table 3. 6 Comparison of binomial-based GLM models predicting the presence/absence of defecations.

Terms	AIC	ΔAIC
Year	1755.0	30.6
Unit	1738.6	14.2
Unit*Year	1731.3	6.9
Unit %in% Year	1728.0	3.6
Unit + Year	1724.4	-

3.4.3 Anthropogenic Effects

Prevalent social units were observed at mid-day on 127 days at a median distance of 13.7 km from Roseau. There was no significant effect of social unit (ANOVA: df=10, SS=7.43, MS=0.743, F=1.41, P=0.182) or research vessel (Kruskal-Wallis: χ^2=4.67, df=3, p=0.197) on the logged distance whales were observed from Roseau. Year has an effect on the logged distance whales are seen from Roseau (ANOVA: df=5, SS=20.5, MS=4.10, F=10.0, P=3.6e-08) (Figure 3.14).

Furthermore, year and distance to Roseau on the log-scale are positively correlated (ρ =0.336, S=3.04e05, P=4.98e-05).
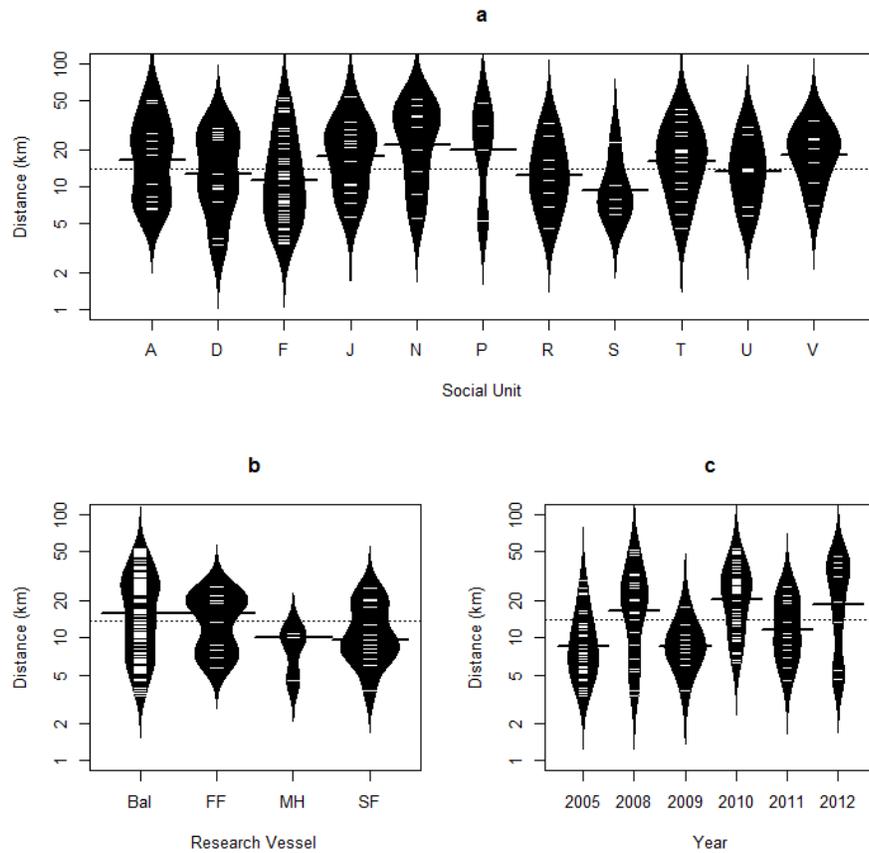
Figure 3. 12 Beanplots showing log scale distance from Roseau observed at mid-day for (a) eleven prevalent social units, (b) research platforms and (c) years. Individual datapoints are shown as small lines, and overall and group means (social units and years) or medians (research platforms) are marked by dashed and black line(s) respectively.

3.5   Discussion

3.5.1   Habitat Use

Prevalent social units identified in the study area show a degree of spatial and temporal variability in their patterns of habitat use. Temporally, social units differ in the overall amount of time seen in the study area. Most notably, unit F is seen more frequently than any other unit. Spatially, social units do not allocate their time evenly across habitat regions. There is currently little evidence to indicate that these habitat use patterns are shaped by conspecific interactions since avoidance behaviour and agonistic interactions among social units have not been described (see Whitehead 2003). This suggests that some areas are preferred over others, and these preferences differ with social unit membership. The amount of time spent within habitat regions by prevalent social units also differs significantly from all other whales. This indicates

that habitat use patterns are not homogeneous among social units observed off Dominica, and conservation efforts may need to consider variation attributed to social unit identity.

Relationships between members of a social unit may promote the sharing of behaviour through conformism and social learning, potentially reinforcing differences in habitat use among social units. Additionally, relationships between individuals from separate social units potentially lead to habitat similarities between units. I found high habitat overlap in four social unit pairs observed exhibiting behavioural coordination or synchrony, where individuals from separate units swam in the same direction at the same speed within metres of each other. This synchrony is not always observed between social units in close spatial and temporal proximity and is indicative of associations or relationships between units (Whitehead 2003). While using similar habitat might encourage such associations because social units overlap in time in space, similarity in habitat is also a potential outcome of social learning or conformity between associating unit pairs (Cantor and Whitehead 2013). Since the genetic relationships between social units are currently unresolved, we are not yet able to examine how similarities or differences in habitat use patterns correlate with kinship. I do not expect patterns of habitat use to have a genetic component; however, kinship may be important in determining which social units form associations, as past and present behavioural proximity between kin could lead to social learning and shared behaviours.

Sperm whales are estimated to spend three quarters of their time searching for and consuming prey (Watwood et al. 2006; Whitehead and Weilgart 1991). Nearly a third of the variation among prevalent social units corresponded to depth. Years were discriminated by sea level anomalies, an indicator of cyclonic and anticyclonic eddy activity (Davis et al. 2002; Hyrenbach et al. 2006). Oceanic cyclones, which possess high concentrations of zooplankton and micronekton, are associated with foraging preferences of deep diving mammals such as sperm whales (Davis et al. 2002), and the southern elephant seal (Bailleul et al. 2010). Variation among units and years may, in part, be associated with prey availability or foraging strategy.

3.5.2 Feeding Success

Thirty percent of fluke-ups were accompanied with defecations, which is three times higher than the overall average reported in the Galapagos (Whitehead 1996b), but consistent with previous findings in the study area (Gero et al. 2009). Given that defecations are thought to correspond with feeding within the previous 24 hours (Whitehead et al. 1989), and whales may

have arrived from neighbour islands during that time, defecation rate is not a direct indication of foraging success in the habitat where these whales were observed. Defecation rate is also liable to be influenced by unmeasured factors such as correlation between serial fluke-ups, weather conditions, group size, differential effort between years, or differing research platforms which may provide different opportunities for seeing defecations. Nonetheless, variability in defecation rates suggests that there is variation in observed feeding success between both social units and years.

Consistent variation in defecation rates among social units implies that habitat choices at a group level may influence foraging success. Given the scale of analysis, and duration individuals spend within the study area at a given time (an order of hours or days), differences in defecation rates do not necessarily indicate fitness differences among social units; however, if particular social units are consistently better at anticipating and exploiting the space and timing of prey patches then unit membership will influence individual fitness. Collectively, all individuals not belonging to prevalent social units have low defecation rates in the study area. This could be interpreted as a relationship between a unit's experience with an area and foraging success, or this trend may reflect animals extending their foraging efforts to regions they infrequently occupy when forage availability deteriorates regionally. A better understanding of how prey availability in the study area compares to adjacent waters at a given time would further our understanding of how habitat decisions are made by social units, and how these decisions may influence fitness.

3.5.3 Anthropogenic Effects

Sperm whales encounter a number of influences throughout their range which may affect their behaviour and distribution patterns. I examined the effect of anthropogenic disturbance on distribution using proximity to Roseau, the island capital, as a proxy for the strength of disturbance activity. There was no significant difference between social units in the distance from the capital; however, to maintain independent samples I only considered their location at mid-day. Though I anticipate vessel activity to be high mid-day, and whales are generally closer to shore at noon (CHAPTER 4), mid-day may give too small a sample size to detect biologically significant differences. Certainly, heterogeneous distribution patterns between prevalent social units suggest that exposure to anthropogenic disturbances is unevenly felt throughout the

population. Prevalent social units vary in both the overall amount of time observed off Dominica and allocation of time to habitat regions.

The study suggests that habitat used by prevalent social units may be shifting away from Roseau over time. Animals which do not tolerate disturbances will often vacate areas at the onset of anthropogenic activity (Bejder et al. 2009). A shift of sensitive animals away from areas with higher disturbance is thought to in part explain the movement of bottlenose dolphins (*Tursiops sp.*) in Shark Bay Australia from whale-watching areas to areas where whale-watching was restricted (Bejder et al. 2006). This effect occurred with a low-level of tourism, where whale-watching activity increased from none, to one, to two operators, while a research vessel remained constant. Long-term site avoidance is thought to occur when the costs of tolerating an ongoing disturbance exceed the benefits of using habitat (Bejder et al. 2006). Furthermore, the current distribution patterns of social units off Dominica may already be shaped by human influences. It is likely that a habitat shift occurred prior to this study, and that non-prevalent social units are seen less frequently off the island because they are less tolerant of anthropogenic activity than prevalent units (Gero 2012).

Given that both the whale watching industry and commercial shipping were present well before this study commenced, this study lacks the adequate controls required to distinguish anthropogenic effects from other environmental influences, including conspecific interactions, predation, and prey availability, which may influence distribution (see Bejder et al. 2006). Yet agonistic behaviour has not been observed or described in this species (Whitehead 2003), and there is little evidence for predation events in the Atlantic (Whitehead et al. 2012). Distribution may be influenced by prey availability and other environmental changes, but I do not anticipate these influences to be correlated with distance from Roseau. Two examples of on-going anthropogenic influences include whale-watching, active since 1988, which generates the third highest income of all whale-watching nations in the greater Caribbean (Hoyt and Hvenegaard 2002), and an increasing number of cruise ships arriving in ports since the 1980s (Wood 2000). As these influences are concentrated near Roseau, the island's capital, it is highly probable that variability in habitat use patterns seen off Dominica is shaped by long-term exposure to human activity rather than other environmental influences.

3.6   Conclusion

This study suggests that sympatric social units have heterogeneous patterns of habitat use and vary in feeding success. Differential habitat use leads to different levels of exposure to human influences between social units. Furthermore, this study raises concern that social units are shifting their habitat away from Roseau, an area with relatively high levels of anthropogenic activity.

The local conservation and management of a wide-ranging, multinational, marine species such as the sperm whale introduces many challenges that may not apply to terrestrial animals with territoriality or predictable migration routes. I recommend that managers of social species adopt adaptive management plans that incorporate diversity between social groups. For instance, it may be wise to regulate the amount of time each social unit is exposed to disruptive activities such as whale watching, rather than allow these activities to proceed without consideration for which social unit is being affected. Future investigation should examine the factors influencing long-term habitat use patterns, and quantify the influence of environment variability, prey abundance, human disturbances on distribution.

CHAPTER 4   Diurnal movement patterns in an oceanic nomad

4.1   Introduction

Marine mammals require two major resources, air and food. While mates, refuges, or haul-out sites are important for some individuals at certain times, air and food are fundamental requirements for survival and are anticipated to have a large bearing over their vertical (diving) and horizontal (ranging) movements (Hooker and Baird 2001). The dive patterns of animals that forage at depth should optimize food acquisition under oxygen limitation (Kramer 1988). As air is freely available at the surface, horizontal movements should generally reflect how individuals range between patches of food resources (Hooker and Baird 2001). Thus both diving and ranging behaviour of marine mammals relate to foraging behaviour. Considering that foraging success can be optimized by maximizing encounter rates with prey, both diving and ranging should reflect prey distribution (Hooker and Baird 2001).

Horizontal movements can be measured across scales ranging from seconds to seasons, and a major challenge of ranging studies is incorporating the spatial and temporal resolution at which behaviour is measured (Hooker and Baird 2001). The ranging behaviour of a number of ocean predators can be described as nomadic. Nomads respond to variation in the timing and location of available resources with movements that are generally unpredictable in time and space (Dean 2004; Jonzén et al. 2011). However, nomadism does not imply animals have no regularity in their movement patterns. As nomadic animals experience and respond to influences across a range of scales (Levin 1992), patterns of activity may emerge at different spatial and temporal scales. For instance, the irruptive movements of some northern finches (e.g. *Carduelis flammea*), which are related to food availability, are considered to be nomadic, yet their movement patterns can be seasonally predictable as they move southwards in early winter and later return to northern areas to breed (Dingle 1996; Hochachka et al. 1999). In some pinnipeds, nomadic ranging behaviour is restricted to the non-breeding season (Sinclair 1983). The term nomadism thus presents a caveat in that it must be applied with reference to scale, as animals whose movements are defined as unpredictable may exhibit some regularity across other scales.

Sperm whales (*Physeter macrocephalus)* are wide-ranging nomadic predators. Each year sperm whales consume mesopelagic and bathypelagic squid in quantities that roughly match the net weight of the combined catch from all human fisheries (Kanwisher and Ridgway 1983).

Generally sperm whales are found in areas with high cephalopod abundance, where foraging efficiency is greater (Selzer and Payne 1988)*.* They are estimated to spend nearly three quarters of their time foraging, and their movements over short time intervals, from hours to days, are thought to be based on the need for food (Whitehead 2003). Little is known about the ecology of deep sea squid (Clarke 1996a), and much of what information is available was discerned from the stomach contents of their predators (Clarke 1996b). An examination of sperm whale ranging behaviour may therefore provide information on sperm whale foraging ecology and insight into the ecology of their relatively inaccessible prey.

Here, I examine whether sperm whale direction of travel is random or patterned across fine-spatial scales and the daily cycle. Previous studies on diurnal changes in sperm whale foraging activity and diving patterns are inconclusive; however, none have examined direction of travel. This study was designed to detect and test for changes in movement patterns, based on anecdotal observations suggesting that sperm whale off Dominica are predictable in their movements from inshore to offshore according to the diurnal cycle.

4.2   Methods

4.2.1   Field Research

We surveyed an area covering approximately 2000 km^2 off the leeward (western) coast of the Commonwealth of Dominica annually from 2005 to 2012, for one to four months per year (Gero 2012). We detected and tracked groups of female and juvenile sperm whales using visual and passive acoustic methods (Whitehead and Gordon 1986; Whitehead 2003). In 2005, 2008, 2010, and 2012 we followed whales acoustically 24 hours a day from onboard a 12m auxiliary sailing vessel equipped with a duel element (Benthos AQ-4) towed hydrophone array on a hundred metre tow cable. In other years, research was conducted during daylight hours (6:00 to 18:00) from a 5m or 11m outboard motorboat (2008, 2009, and 2011), or 18m motorized catamaran whale watching vessel (2007, 2008, and 2009) outfit with Cetacean Research CR1 or CR2 hydrophones.

4.2.2   Analysis

I estimated the travel direction of groups of sperm whales from the movements of our research vessel while following sperm whales. While there are limitations with assuming that vessel movements represent sperm whale movements, alternative methods utilizing individual

observations, i.e. net movement between photoidentifications, would not have enabled a comparison of movements across the entire diurnal cycle as photographs cannot be taken at night. We estimate that the research vessel was usually within 2km of the group of whales being tracked, representing 15% of the width of a habitat cell. A small number of cases where sperm whales reversed their travel direction, or we switched from one group of whales to another are not expected to impact the overall trends described.

I described trends in the direction sperms whale were traveling, or heading within four habitat cells arranged parallel to the island (Figure 4.1), and within six categories of time. This was carried out using a two-step process of characterizing then testing the distribution of headings in each category using two separate datasets. Since headings are measured as angles, circular statistics were used to describe probability distributions.
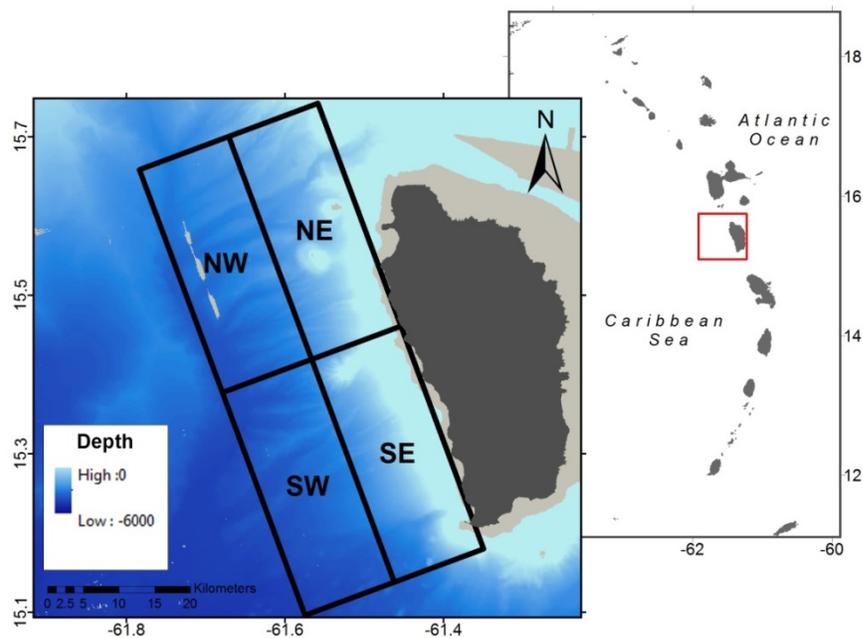
Figure 4. 1 The location of four habitat cells, covering an area of 0.3 by 0.6 decimal degrees, off the leeward coast of Dominica.

4.2.2.1   Data Partitioning

A conservative approach was used first to identify and then to verify patterns within the data. Dates on which research took place were partitioned into two datasets at random (training and testing data- see Fielding and Bell 1997), which were used to develop and test predictions. The

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training dataset was used to characterize the frequency distribution of sperm whale headings. The testing dataset was then used to test each hypothesized circular distribution.

I created the training dataset by dividing the GPS track into two hour segments. Since the training data suggested movements were influenced by time of day when examined within six time categories (i.e. 4-hr intervals), the testing dataset was created by separating vessel tracks into segments between 00:00-4:00, 04:00-8:00, 8:00-12:00, 12:00-18:00, 18:00-20:00, and 20:00-24:00 lasting a minimum of three hours. I calculated the angle of travel from Universal Transverse Mercator coordinates using the "adehabitatLT" package in R2.15.1 (Calenge 2006; R Core Team 2012). Each segment was attributed to a spatial or temporal category based on the time and position of its midpoint.

4.2.2.2   Characterizing the Direction of Travel

Using the training dataset, I characterized the circular distribution of headings travelled within each habitat cell and time category as being even, unimodal, or bimodal. Movements with circular uniformity were considered to be even, and those with circular normality (the von Mises distribution) to be unimodal. Uniformity and circular normality were evaluated using Watson's test for uniformity and Watson's test for the von Mises distribution, respectively, from the "circular" package in R (Agostinelli and Lund 2011; R Core Team 2012). Circular normal distributions are readily summarized by m_1, the mean angle (Batschelet 1981). Additionally, I used the parameter of concentration k to show how much distributions were concentrated around the mean direction, with higher values indicating more concentration (Batschelet 1981). As k approaches zero, circular distributions degenerate into uniform distributions, which cannot be summarized using a mean angle (Batschelet 1981). I also reported the mean resultant length of a vector of circular data, ρ, which is measured by treating each observation as a unit vector.

The bimodal distribution is another circular distribution that often arises when animals travel in two preferred directions (Batschelet 1981). This is true of animals that may travel along features of the environment. Bimodal data can pose challenges because data summaries, including mean values, are not intuitive. Instead observed movements with a bimodal distribution can be treated as axial data, i.e. either direction along the axis is considered rather than a single direction. Axial movements are calculated by doubling the observed headings, and reducing the result to modulo 360 (Figure 4.2). The resulting distribution has values of 0° representing

movement in the north or south direction, while values of 180° represent movements made in the east or west direction. Generally, the transformation of bimodal datasets into their axial distribution generates a unimodal distribution (Taylor and Auburn 1978), which can be summarized by m_2 the axial mean. The direction of the axial mean m_2 can be transformed into the mean axes directions d_1 and d_2 by:

$$d_1 = \frac{m_2}{2} \quad \text{and} \quad d_2 = \frac{m_2}{2} + 180$$

To determine whether the movements of sperm whales were bimodal, I first tested the distribution of headings for circular uniformity and normality. If neither probability distribution was supported, I then tested their axial movements for circular uniformity and normality. Axial movements with circular normality were characterized as bimodal, and those with circular uniformity were characterized as even.
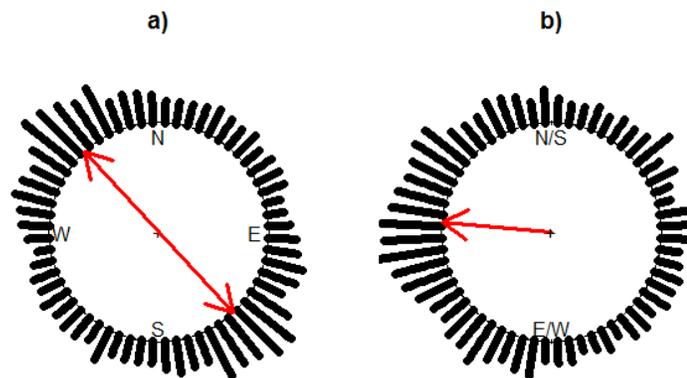
Figure 4. 2 Example transformation of (a) observed movements with a bimodal distribution into (b) axial movements with a unimodal distribution by doubling the angles. The axial mean m₂ is marked with a single arrow, and the corresponding mean axis directions d₁ and d₂ are marked with double arrows.

4.2.2.3   Testing the Direction of Travel

I used the testing dataset to confirm the shape of circular distributions suggested by the training dataset. Hereafter, I refer to sperm whale headings within the testing dataset as "displacements". Chi-squared tests were used to test for differences in the number of displacements occurring within two or four angular categories, which were defined based on the

shape and parameters of each probability distribution characterized by training data (see Figure 4.3). For each probability distribution, I tested the null hypothesis that the distribution of displacements across angular categories was even against the alternative hypothesis that displacements were unevenly distributed. When circular distributions were characterized as even by the training dataset, I compared the number of displacements falling within four angular categories delineated by the cardinal directions. Null chi-squared test results indicate that movements are even within the testing dataset, and therefore show agreement between the training and testing datasets. In the case of distributions characterized as unimodal, I tested for independence in the number of displacements recorded within two angular categories, delineated by the axis perpendicular to the mean angle of the training data. Finally, for distributions characterized as bimodal I tested for independence in the number of displacements inside four angular categories, offset 45 degrees from the mean axis of the training data. For distributions characterized as unimodal and bimodal, the rejection of the null hypothesis in tests of significance indicates that displacements are not evenly allocated to angular categories inside the testing dataset. I then calculated the odds ratio (OR_{mode}) of displacements occurring within angular categories containing the circular mean/mean axis (direction of the mode) or not. I considered an $OR_{mode}>2$, i.e. whales in the testing data are over twice as likely to head in the direction of the mode of training data, as an indication that the training and testing datasets were in agreement.

4.2.2.4   Distance from Shore

To determine whether whales were farther away from, or closer to, shore at night, I also tested for differences in the distance from shore at six times of day (0:00, 4:00, 08:00, 12:00, 16:00, and 20:00) during sperm whale encounters. I assumed independence between consecutive positions since the average speed of the research vessel when following whales was 2.6km/hr, suggesting that whales could travel the median distance from shore (9.23km) within a four-hour period. Distance was acquired from a 5x5m resolution raster layer created using the Euclidean distance tool in ArcGIS 10 (ERSI), with shoreline information obtained from the Government of the Commonwealth of Dominica, Land and Surveys Division.
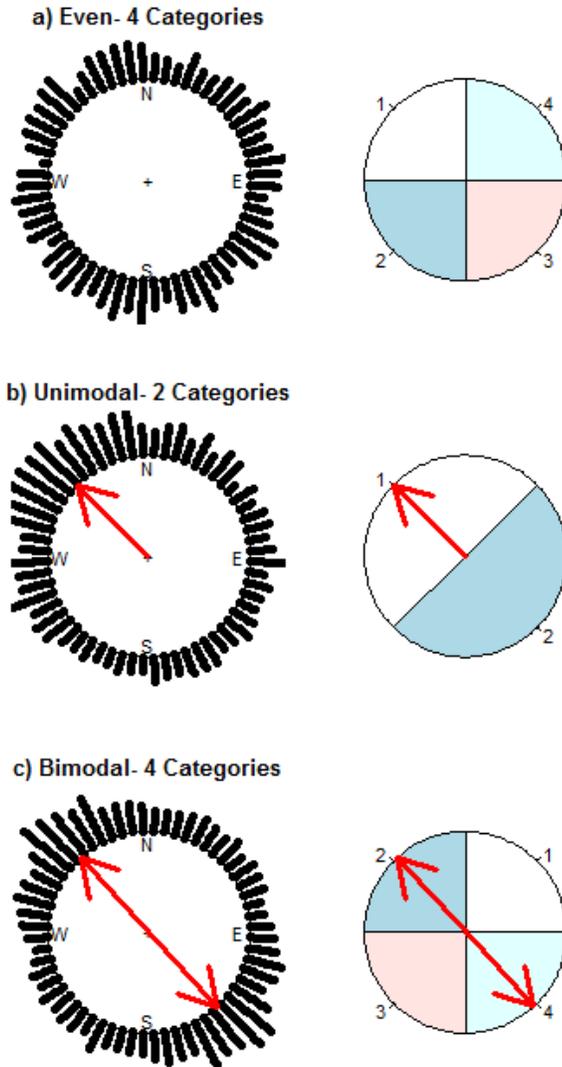
Figure 4. 3 Example showing the origins and establishment of angular categories (right column) used to test the testing data for presence of circular distributions suggested by the training data (left column). I established (a) four angular categories delineated by the cardinal directions for distributions characterized as even by training data, (b) two angular categories divided by the axis perpendicular to the circular mean of training data for unimodal distributions, and finally (c) four angular categories offset by 45° from axial mean of training data for bimodal distributions.

4.3　Results

Data were collected on 227 days of research across 198 encounters with sperm whales. The

training dataset was created from 110 randomly selected dates divided into 456 two-hour

movement tracks. The testing dataset contained 306 displacements, collected on 117 days of

research.

4.3.1   Spatial Patterns of Travel Direction

Using the training data set, the distribution of sperm whale headings was characterized as bimodal along the coastline within the SE cell, and even within NW and SW cells (Table 4.1 & 4.2).   Circular normal headings in the NE cell indicate unimodal movements towards the northwest; however, circular normality and high ρ and K scores for axial movements indicate that training data could be bimodally distributed parallel to the shoreline (Table 4. 1 & 4.2). I therefore tested the NE cells for a both unimodal and bimodal probability distributions.

Chi-squared tests of independence using the testing data indicate that displacements were evenly distributed across angular categories in the NW and SW cells, and unevenly distributed across angular categories within the NW cell (Table 4.3). In the NW cell whales are over twice as likely to head parallel to the shoreline, than inshore/offshore, in the testing data. In the NE cell the testing data corresponded with a bimodal distribution, with 2.7 times more displacements occurring parallel to the shoreline, than inshore/offshore. Together, the training and testing datasets suggest that whales in eastern, inshore, cells tended to move parallel to the coastline while whales in western, offshore, cells have more uniform movements (Figure 4.4).

Table 4. 1 Results of Watson's test for the Von Mises distribution and Watson's test for uniformity for observed and axially transformed movements across habitat regions using training data.

	Observed Movements				Axial Movements			
	Normality		*Uniformity*		*Normality*		*Uniformity*	
Cell	Test	P	Test	P	Test	P	Test	P
NW	0.113	*<0.01*	0.600	*<0.01*	0.147	*<0.01*	0.180	>0.05
NE	0.057	>0.05	0.283	*<0.025*	0.014	>0.10	0.249	*<0.025*
SW	0.035	>0.10	0.076	>0.10	-	-	-	-
SE	0.026	*<0.01*	0.411	*<0.01*	0.0369	>0.10	1.01	*<0.01*

Table 4. 2 Shape of circular distributions characterized within four habitat cells using training data. Distributions were characterized as even or unimodal if observed movements possessed circular uniformity or normality (respectively). Distributions were characterized as bimodal when axially transformed movements possessed circular normality.   The mean resultant length of a vector of circular data ρ, and parameter of concentration *k,* are shown for movements and axial movements. For distributions characterized as unimodal or bimodal, the corresponding circular mean (m_l), mean axis (d_l and d_2), and standard deviation around the mean/mean axis (SD) are included.

Cell	Observed Movements					Axial Movements				
	Distribution	m_1	SD	P	*K*	Distribution	d_1, d_2	SD	P	*K*
NW	-	-	-	0.380	0.822	Even	-	-	0.114	0.229
NE	Unimodal	333	1.9	0.180	0.367	Bimodal	167, 347	1.8	0.202	0.413
SW	Even	-	-	0.190	0.388	-	-	-	-	-
SE	-	-	-	0.119	0.240	Bimodal	155, 335	1.6	0.299	0.627

Table 4. 3 Results of chi-squared tests on the testing dataset for circular distributions characterized using training data within four habitat cells. For modal distributions, the odds ratio of whales in the testing dataset heading along the training mode, to not heading along the mode in the testing data is given (OR_{mode}). Distributions that are confirmed by both training and testing data are marked with an *.

Time	Distribution	χ^2	df	P	OR_{mode}
NW	Even*	6.4	3	0.0952	-
NE	Unimodal	0.9	1	0.345	0.77
NE	Bimodal*	12.4	3	0.00608	2.67
SW	Even*	3.7	3	0.300	-
SE	Bimodal*	28.0	3	3.56e-06	2.20
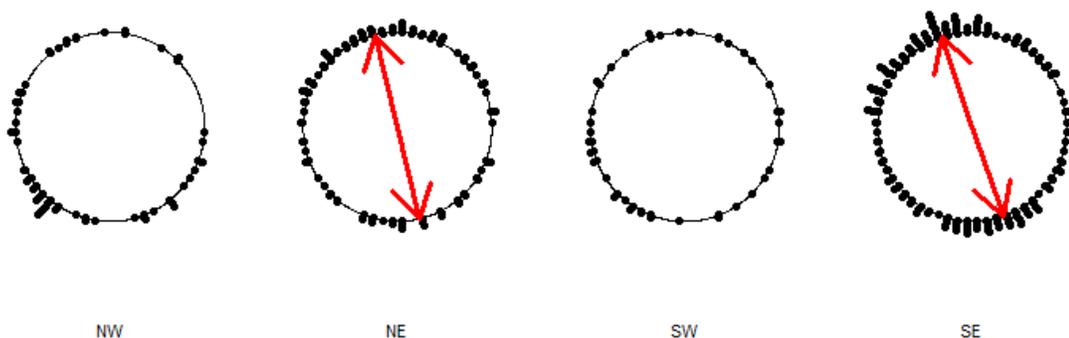
Figure 4. 4 Distribution of sperm whale movements among habitat cells within the training dataset. The mean axes of distributions confirmed as bimodal are marked with double arrows.

4.3.2   Diurnal Patterns of Travel Direction

Using the training dataset, I characterized sperm whale movements as bimodally distributed parallel to the shore between 4:00-16:00, unimodally distributed towards the west between 16:00-20:00, and evenly distributed between 20:00-4:00 (Table 4.4 & 4.5, Figure 4.5). The testing data agrees with the training data for all time categories except 00:00-04:00. Chi-squared tests on the testing data show displacements are unevenly allocated to angular categories between 04:00 and 20:00. Between 04:00 and 16:00 whales are over twice as likely to head parallel to the shoreline, than inshore/offshore in the testing data.   Around dusk (16:00 to 20:00), whales in the testing data are three times more likely to head offshore than inshore (Table 4.6, Figure 4.6). Displacements are evenly allocated to angular categories between 20:00-24:00, indicating that whales head in no preferred direction. Between 00:00 and 04:00, headings were characterized as even using training data, but chi-squared tests suggest displacements were unevenly allocated to angular categories.

I also attempted this analysis using four six-hour time categories rather than six four-hour categories; however, patterns were less clear when movements were averaged across six hours. Using the observational dataset, whales appeared to move any direction but inshore between 12:00 and 18:00, and whales were predicted to head offshore between 18:00 and 24:00, though chi-square tests on the experimental data set suggested movements were evenly distributed among angular categories. The different results obtained when using four and six time categories emphasizes the apparent effect of dusk (at approximately 18:00) on travel direction.

Table 4. 4 Results of Watson's test for the Von Mises distribution and Watson's test for uniformity for observed and axial transformed movements during six time categories using training data.

	Observed Movements				Axial Movements			
	Normality		*Uniformity*		*Normality*		*Uniformity*	
Time	Test	P	Test	P	Test	P	Test	P
00-04	0.020	>0.10	0.018	>0.10	-	-	-	-
04-08	0.140	*<0.01*	0.224	*<0.025*	0.460	>0.10	0.470	*<0.01*
08-12	0.105	*<0.01*	0.299	*<0.01*	0.036	>0.10	0.428	*<0.01*
12-16	0.108	*<0.01*	0.276	*<0.01*	0.037	>0.10	0.329	*<0.01*
16-20	0.020	>0.10	1.05	*<0.01*	-	-	-	-
20-24	0.070	*<0.05*	0.128	>0.10	-	-	-	-

Table 4. 5 Shape of circular distributions characterized within six time categories using training data. Distributions were characterized as even or unimodal if observed movements possessed circular uniformity or normality (respectively). Distributions were characterized as bimodal when axially transformed movements possessed circular normality.   The mean resultant length of a vector of circular data ρ, and parameter of concentration *k,* are shown for movements and axial movements. For distributions characterized as unimodal or bimodal, the corresponding circular mean (m_1), mean axis (d_1 and d_2), and standard deviation around the mean/mean axis (SD) are included.

Time	Observed Movements					Axial Movements				
	Distribution	m_1	SD	P	*K*	Distribution	d_1, d_2	SD	ρ	*K*
00-04	Even	-	-	0.011	0.023	-	-	-	-	-
04-08	-	-	-	0.175	0.356	Bimodal	165,345	1.4	0.359	0.770
08-12	-	-	-	0.184	0.376	Bimodal	166,346	1.6	0.267	0.555
12-16	-	-	-	0.183	0.373	Bimodal	160,340	1.7	0.234	0.482
16-20	Unimodal	260	1.1	0.531	1.254	-	-	-	-	-
20-24	Even	-	-	0.145	0.294	-	-	-	-	-

Table 4. 6 Results of chi-squared tests on the testing dataset testing for the presence of circular distributions characterized using training data within six time categories. For modal distributions, the odds ratio of whales in the testing dataset heading along the training mode, to not heading along the mode in the testing data is given (OR$_{mode}$). Distributions that are confirmed by both training and testing data are marked with an *.

| Time	Distribution	χ^2	df	P	OR$_{mode}$
00-04	Even	8.7	3	0.0337	-
04-08	Bimodal*	8.9	3	0.0305	2.14
08-12	Bimodal*	13.0	3	0.00464	2.13
12-16	Bimodal*	20.7	3	1.20e-04	2.56
16-20	Unimodal*	9.0	1	0.00270	3.00
20-24	Even*	2.3	3	0.518	-
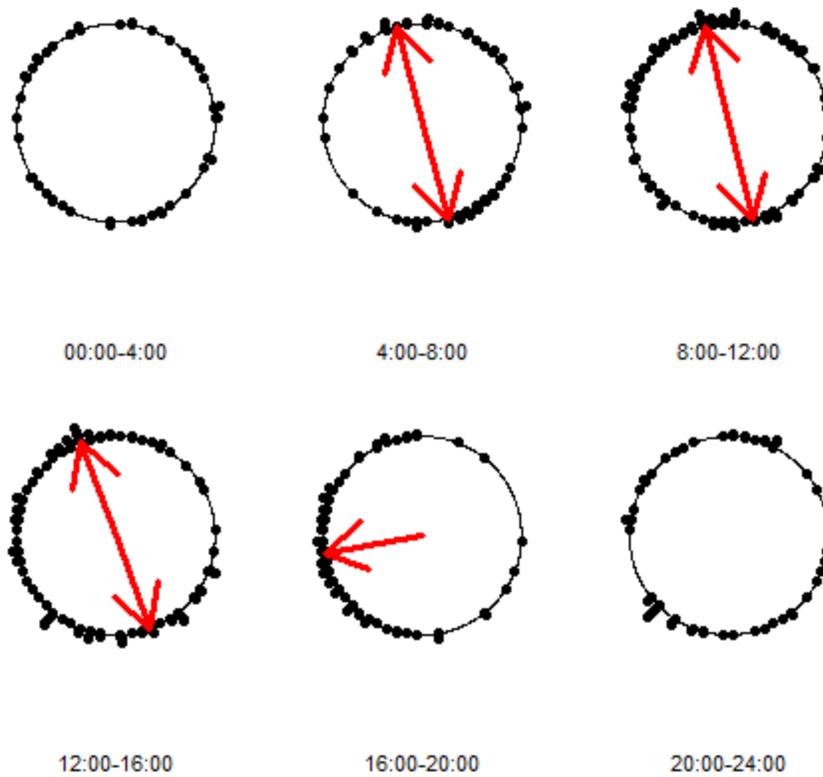
Figure 4. 5 Distribution of sperm whale movements across time of day within the training dataset. The mean axes of distributions confirmed as bimodal are marked with double arrows, and the circular mean of unimodal distributions are marked with single arrows.
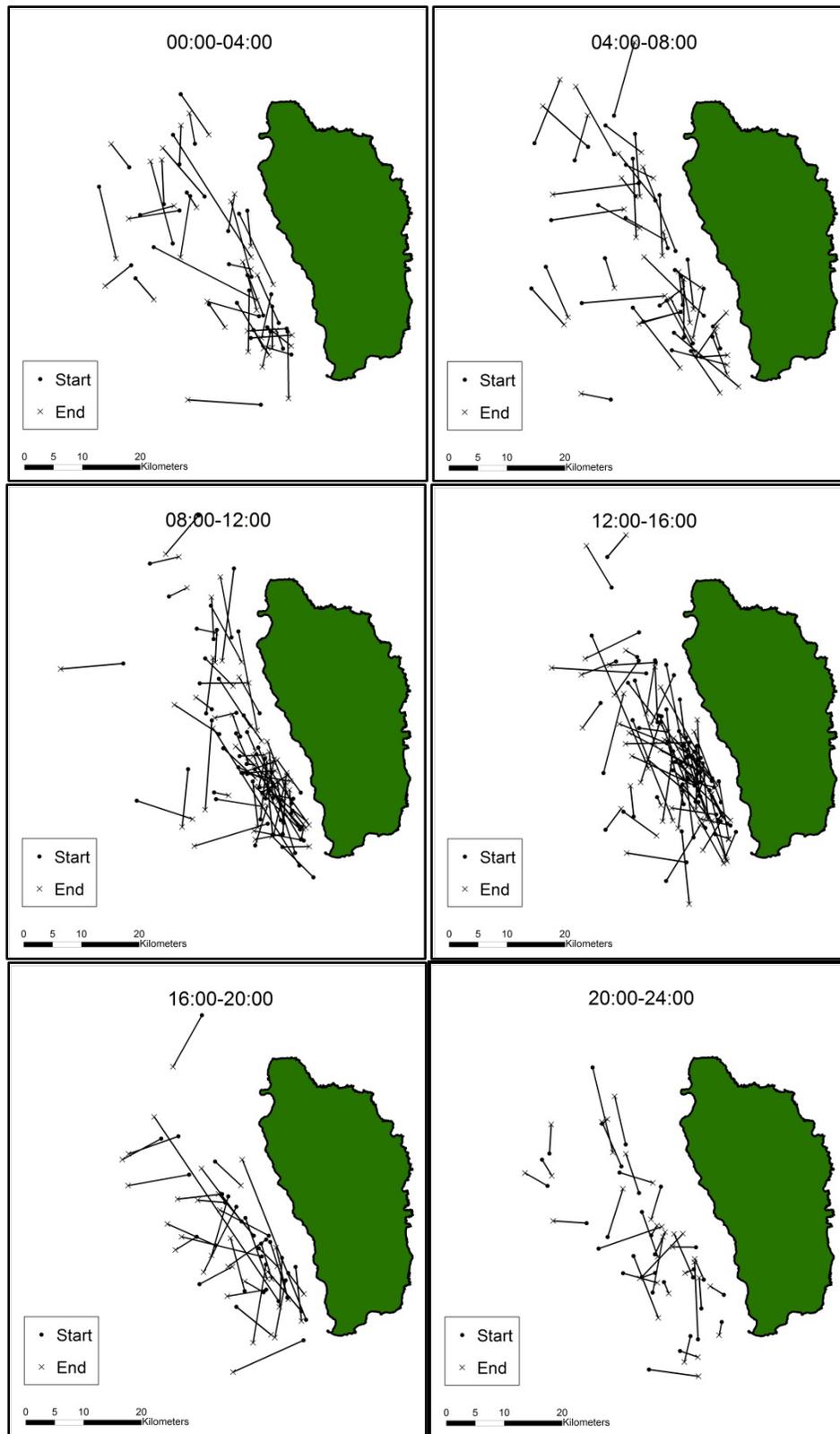
Figure 4. 6 Sperm whale movements across time of day within the testing dataset.

4.3.3 Distance from Shore

Sperm whales were observed at a mean of 9.23km from shore at a median bottom depth of 3130m. Distance from shore differs between six times of day (ANOVA; W=0.997, SS=25.0, F= 20.0, P=2.00e-16), and whales were seen closer to shore at noon than any other time of day (Figure 4.7). Post hoc comparisons show that distance to shore at noon differs from distance at all other times of day except 08:00 (Table 4.7). Differences were also present when tests were restricted to data collected from the primary research vessel, which may range farther from shore than other research platforms.

Table 4. 7 Pairwise comparison of distance from shore at six times of day using pairwise T-tests with Bonferroni adjustment.

	00:00	04:00	8:00	12:00	16:00
04:00	1.0	-	-	-	-
08:00	<0.001	<0.01	-	-	-
12:00	<0.001	<0.001	1.0	-	-
16:00	<0.001	>0.05	1.0	<0.05	-
20:00	1.0	>0.50	<0.001	<0.001	<0.001
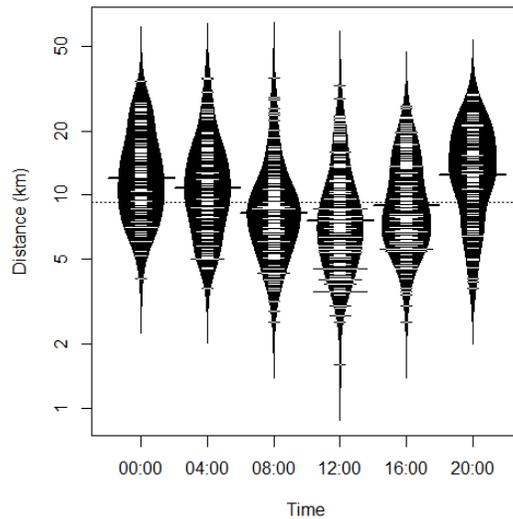
Figure 4. 7 Beanplots showing distance to shore at six times of day. Beans are mirrored density traces (Kampstra 2008). Individual datapoints are shown as small lines, and overall and hourly medians are marked by dashed and black line(s) respectively.

4.4 Discussion

This study described clear fine-scale diurnal movement patterns in an oceanic nomad, the sperm whale. Generally, sperm whales travelled parallel to the west coast of Dominica during the daytime, and headed offshore around dusk. In early mornings, they were equally likely to head in any direction. This pattern was consistent between random subsets of data, and was also

evident when examining distance from shore because whales are closer to shore at noon and farthest at midnight. This is also consistent with reports of two individual whales tagged with acoustic transponder tags off Dominica in 1991 moving offshore with nightfall (Watkins et al. 1993). Underlying this diurnal pattern there is a tendency for inshore animals to travel north and south along the coastline and offshore animals to have more uniform movements. Since whales in the Atlantic spend an average of 72% of their time foraging (Watwood et al. 2006), a consistent trend of whales moving from inshore to deeper offshore waters at dusk suggests these nomads have a diurnal pattern of foraging activity, and poses the question of why do sperm whales tend to head offshore at night?

Diurnal movement patterns have been described in several odontocete species, and are thought to correspond with the vertical movements of their prey with changing time of day (Baird et al. 2001; Baird et al. 2002; Baird et al. 2008; Benoit-Bird and Au 2003b; Benoit-Bird et al. 2004). Many zooplankton undergo diel vertical migration where they rise in the water column at night, and evade predators at depth during daytimes (Hays 2003). Predators at increasing trophic levels may adapt their behaviour to exploit these moving resources, creating a community of vertically migrating organisms often referred to as the deep-scattering layer for its ability to be detected with echo-sounders (Hays 2003). In cetaceans, diving patterns often correspond to the movement of the deep scattering layer. Both pantropical spotted dolphins (*Stenella attenuata*) near Hawaii and short-finned pilot whales (*Globicephala* spp.) near Italy dive the deepest after sunset when the deep scattering layer starts to ascend (Baird et al. 2001; Baird et al. 2002). Dusky dolphins (*Lagenorhyncus obscurus)* off New Zealand dive shallower, and in larger groups, at night when prey is more accessible at the surface (Benoit-Bird et al. 2004). They also perform daily movements from inshore, where there may be fewer predators, to offshore at night (Würsig et al. 1997). Finally spinner dolphins (*S. longirostris*) near Hawaii follow both the vertical and horizontal migration of prey in the mesopelagic boundary layer at night (Benoit-Bird and Au 2003a).

There is some dispute in the literature as to whether feeding patterns of sperm whales are influenced by time of day (Clarke 1980; Whitehead 2003). Sperm whales have a stereotypical foraging behaviour where they dive for an average of 45 minutes at 400-1200m depth (Watwood et al. 2006).   Dive depth generally does not vary across the diurnal cycle (Davis et al. 2007; Papastavrou et al. 1989; Watkins et al. 2002). There is also little evidence to suggest that

feeding rate varies with time of day. When examining stomach contents of harvested whales, Clarke (1980) found no evidence of a correlation between feeding rates and time of day, though his observations are limited since whales were not caught at night. Yet there are some hints that foraging effort may differ between daytime and nighttime. Sperm whales in Japan dove deeper during the day than at night off the Ogasawara Islands, though no diel rhythm was observed off the Kumano Coast (Aoki et al. 2007). Sperm whale behaviour can be divided into to two modes, foraging and socializing. Social behaviour has been reported to peak in the mid to late afternoon, though it remains unclear if sperm whales have a preferred mode at night (Chapter 2, Whitehead & Weilgart 1991). Uncertainty over whether diurnal patterns exist in sperm whales is likely a reflection of the difficulty in obtaining fine scale observations on both whales and their prey, and a lack of investigation across the 24-hour cycle. Furthermore, diurnal patterns are potentially tied to local geographic features or prey community composition.

Sperm whales off Dominica have clear patterns of horizontal movement corresponding to time of day. It remains unclear what drives these patterns. Does foraging effort vary across the circadian cycle, does forage availability vary across space with time of day, or do both scenarios occur? If prey movements are not influenced by the 24-hour cycle, then diurnal horizontal movement patterns could reflect changes in sperm whale foraging effort. While sperm whales may switch behavioural modes from foraging to socializing, often during mid to late afternoons (Chapter 2, Whitehead and Weilgart 1991), habitat modeling gives no indication that spatial variables are important in predicting the occurrence of social behaviour during daytimes (Chapter 2). At night we predominantly followed foraging sperm whales, as socializing whales are difficult to follow acoustically. The observation that whales tend to move offshore at dusk, rather than inshore in the morning, suggests that movements from inshore to offshore are influenced by changes occurring at dusk. I therefore predict that horizontal movement patterns are reflections of prey behaviour rather than changes in sperm whale behavioural state.

I propose that sperm whale patterns of horizontal movement across the 24-hour cycle could be explained by their cephalopod prey undergoing a diel horizontal migration or whales switching to deeper-water, vertically migrating, prey at night (see Baird et al. 2008). Both scenarios rely on the assumption that the act of heading offshore at dusk is aimed at intercepting the ascent of the deep scattering layer. During the daytime, sperm whales tend to feed closer to shore where shallower bathymetry perhaps concentrates the vertical distribution of cephalopods. At dusk

they may head offshore to forage on deep-water cephalopods as they ascend with the deep scattering layer. Alternatively, sperm whales could follow patches of non-vertically migrating squid, which may likewise head offshore at night to forage in the ascending scattering layer.

As predatory searching behaviour is generally built on previous experiences with prey, the presence of either diel vertical or horizontal migration in the sperm whale's cephalopod prey could influence their diurnal patterns of activity. Diel vertical migration, which is characteristic of many cephalopod species (Roper and Young 1975), could lead to changes in the assortment of prey species and sizes available to predators with time of day (Hays 2003), or improve feeding efficiency by concentrating the vertical distribution of prey at night (Aoki et al. 2007). Diel vertical migration may also facilitate feeding even when cephalopods migrate above the depth at which sperm whales are thought to forage (see Davis et al. 2007). Horizontal movement patterns are poorly described in pelagic cephalopods. Sasaki (1914) described diel horizontal migrations towards the shore at night by the squid *Watasenia scintillans* in Japanese waters. Diurnal horizontal movements are also reported off the Hawaiian Islands, where squid in the boundary community move from offshore during daytimes to inshore at night (Benoit-Bird et al. 2001). Horizontal movements could also result from squid migrating vertically between current layers flowing in opposite directions (see Hays 2003).

An analysis of squid beaks collected within fecal samples in the study area found 80% of sixty-five samples to belong to the genus *Histioteuthis* and 10% belonging to *Discoteuthis* (Wong 2012).   Two species of the genus *Histioteuthis* which likely occur in the study area, *H. arcturi* (see Wong 2012) and *H. corona corona*, apparently undergo diel vertical migrations approaching surface waters as juveniles (Voss et al. 1998); however, *H. arcturi* adults and subadults were caught during nighttime trawls at depths between 600m and 2700m, and *H. corona corona* at depths below 400m (Voss et al. 1998). As estimated mantle lengths of squid beaks collected in defecations (10.1 ± 0.85cm, by Wong 2012) fall within the size range of immatures to adults (Voss et al. 1998), it is difficult to relate sperm whale behaviour to the vertical distribution of their cephalopod prey. Little is known of movements of *Discoteuthis.* Additionally, fecal analyses have several limitations since smaller squid are more likely to be eaten whole and be represented within fecal samples, smaller beaks sink slower than larger beaks and are therefore more likely to be collected by observers with dip nets, and it is impossible to distinguish prey consumed from the prey of prey consumed using only beaks (Clarke et al. 1988; Clarke and

Paliza 2001). It is therefore inconclusive as to whether sperm whales consume *Histioteuthis* directly, *Histioteuthis* predators, or if they may switch between consuming *Histioteuthis* and other species with time of day. Thus the relationship between fine-scale horizontal ranging behaviour of sperm whales in the study area and the diving or ranging behaviour of their cephalopod prey remains uncertain.

4.5   Conclusion

Horizontal movements from inshore to offshore at dusk indicate that foraging behaviour of nomadic sperm whales varies with time of day, though we remain uncertain what mechanism drives these patterns. Special consideration is required for the study and conservation of populations whose behavioural patterns are influenced by time of day. Habitat use studies based on data collected during a portion of the day may be ineffective in describing habitat use across the 24-hour cycle (Beyer and Haufler 1994). Inshore-offshore displacement with time of day could influence shore-based population estimates (Perryman et al. 1999). If animals are more susceptible to vessel impacts when they remain at or near the surface, changes in behavioural state or vessel activity corresponding to the 24-hour cycle can make individuals more susceptible to disturbance at certain times of day (see Danil et al. 2005). Furthermore, if animals are more or less easily detected during certain behavioural states, the ability to detect them using audio or visual cues will vary with time of day when behaviour is influenced by diurnal cycle (Baird et al. 2008). Thus consideration for changing behavioural patterns across the 24-hour cycle is important for both conservation and management of any species.

CHAPTER 5   Conclusion

In this thesis I explored the question: why do sperm whales have high fidelity to waters near the island of Dominica? I suspect the answer lies in prey availability off the island and/or habitat preferences at the level of the social unit.

Sperm whales are generally thought to occur in areas with high cephalopod abundance, where foraging success tends to be greater (Selzer and Payne 1988). However multi-scale studies have failed to find effective predictors of distribution at fine-scales (Jaquet and Whitehead 1996). In this fine-scale analysis, I have shown that at a population level there no areas whales clearly prefer to occupy, or socialize in. By extension, since whales are foraging when they are not socializing, there are no clear areas preferred for foraging. Thus despite the bathymetric and oceanographic variability in the study area, sperm whale occurrence is not correlated with features that may act as proxies for prey abundance at the scale of the analysis. Yet, sperm whales have clear diurnal patterns of movement from inshore to offshore at night, which are most likely correlated with changes in prey availability across the 24-hour cycle. Furthermore, relatively high defecation rates in the study area compared to other places in the world suggest that Dominica, or its vicinity, is likely an important foraging area.

The lack of an effective predictor of whale presence at fine-scales may reflect the hierarchical distribution of resource patches in marine systems (Russell et al. 1992). At broad-scales sperm whales may search for oceanographic features that concentrate prey. At finer spatial scales, individuals may use different cues to search for patches of prey, which are aggregated within broad-scale patches (Russell et al. 1992). Generally the structure of prey patches changes more rapidly at fine than broad spatial scales (Fauchald et al. 2000). It is feasible that sperm whale movements are more closely associated with the aggregation behaviour of prey at fine-scales than overall prey abundance. The diet of sperm whales in the study area may be dominated by medium-sized, weakly muscled cephalopods from the genus *Histioteuthis* (Wong 2012).   A sperm whale eating a *Histioteuthid* has been likened to a human eating a walnut (Clarke et al. 1993), and sperm whales would need to consume hundreds per day to meet their energetic requirements (Clarke 1980; Whitehead 2003). Prey aggregation behaviour would therefore be an important proponent of feeding success. Since predator behaviour can also affect prey

distribution (e.g. Benoit-Bird 2009), the dynamics between predator abundance and prey availability are potentially highly complex.

Another important influence on sperm whale distribution patterns is their complex social and cultural organization. Individuals that associate regularly are more likely to possess shared behaviours, since close interactions between group members can encourage social learning, conformism in behaviour and separation into culturally distinctive groups (CoussiKorbel and Fragaszy 1995; Whitehead et al. 2004). Thus variation in ecology, interactions with the environment, and responses to disturbances among social groups are potentially reinforced by social learning and cultural inheritance within social groups (Cantor and Whitehead 2013). This study demonstrates that social units vary in both the amount of time spent in the study area and space occupied, indicating that social organization is a key source of variability in distribution within sperm whale populations. Feeding success can be increased by social learning (Hughes et al. 1992), and the slight differences in habitat use between social units may indicate differences in foraging strategies learned within the different social units.

5.1   Conservation

In the 18th and 19th century, open-boat whaling was a major influence on Atlantic sperm whale populations (Whitehead et al. 2012). Today whaling no longer poses a significant threat to sperm whales, yet whales are still vulnerable to a number of anthropogenic threats. Cetacean populations can be influenced by chemical pollutants (Martineau et al. 1994), ship strikes (Laist et al. 2001), changes in prey availability due to overfishing (Bearzi et al. 2006), ocean noise (Weilgart 2007), and wildlife viewing (Frid and Dill 2002). While these disturbances do not necessarily have immediate, dramatic effects, their cumulative effect over time can significantly impact populations.

This study and others preceding it (see Jaquet 1996; Jaquet and Whitehead 1996) suggest sperm whale distribution is not tightly coupled to fine-scale oceanographic or environmental processes. This finding has major implications for conservation efforts. If wide-ranging sperm whales lack "hotspots" in which to feed, socialize or generally occupy, then they are truly generalists in terms of their habitat requirements. Conservation efforts must therefore encompass their broad-scale use of the pelagic environment, which differ in many ways from terrestrial systems (Hyrenbach et al. 2000). The conservation of highly-mobile, unpredictable species living in dynamic marine environments is a major challenge (Hyrenbach et al. 2000).

Sperm whales wander freely between international waters and the Exclusive Economic Zones of multiple nations, making conservation at regional or larger scales necessary. However, Dominica is currently in the position of being able to link their efforts with the AGOA marine mammal sanctuary, established in 2010, which covers neighbouring waters under French jurisdiction in the West Indies. The addition of Dominica to the AGOA project would connect waters north and south of the island, creating a continuous zone spanning approximately 250 km along the Lesser Antilles Arc between Guadeloupe and Martinique.

This leads to the question of whether local, fine-scale, management efforts are effective tools for conserving nomadic species. The answer likely depends on the species, habitat, scale, and type of activities regulated. In the study area, the propensity for social units to return year after year has enabled studies on sperm whales at the level of the individual (e.g. Antunes et al. 2011; Gero et al. 2009; Schulz et al. 2011). But this propensity also suggests that individuals are routinely exposed to anthropogenic disturbances over the long-term. Whale watching and "swim-with" activities in the study area are occurring at the time of day when whales are closest to shore, and perhaps more likely to socialize. A positive correlation between distance from the island capital, where disturbances are expected to be concentrated, and year raises the question of whether sperm whales in the study area are shifting their habitat away from areas associated with disturbances over time. While correlation is not causation, human disturbance has caused bottlenose dolphins (*Tursiops sp.*) to shift habitat use from areas with high to low vessel traffic (Bejder et al. 2006). Indeed the situation in Dominica may already be a shifted baseline, where sensitive animals already avoid the area (Gero 2012). The issue of long-term disturbance and shifting habitat use should concern managers. Adaptive local management plans, which regulate the amount of time social units are exposed to invasive activities such as whale watching or swim-with programs, may be effective tools for mitigating human disturbances.

5.2   Final Note

Sperm whales are best described as *surfacers*, since they spend the majority of their lives underwater in deep water environments which we have a limited ability to survey and describe. The key to understanding how sperm whales interact with their environment will ultimately be resolving the dynamics between this predator and their elusive cephalopod prey. Suction-cup tags provide high resolution data on the movements of animals below the surface of the water (e.g. Watwood et al. 2006). The precision and volume of these data will improve as the tags are developed and increasingly used. However, there is still much insight is to be gained from studies conducted from the surface where a larger number of animals can generally be documented. As our knowledge on sperm whales and their cephalopod prey increases, so will our understanding of their distributional patterns at local, regional, and global scales.

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