AN ABSTRACT OF THE THESIS OF

Theresa Kirchner for the degree of Master of Science in Wildlife Science presented on August 15, 2016.

Title: Spatial Association of Humpback Whales (*Megaptera novaeangliae*) and their Prey in the Southern Gulf of Maine, USA.

Abstract approved: ____

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Efficient foraging strategies result in a predator spatially overlapping with its prey, foraging in the most profitable patches, and minimizing the time transiting between patches. Previous studies investigating baleen whale foraging strategies have generally focused on investigating spatial overlap with prey patches, patch profitability or movement within feeding grounds. The present study investigated the fine-scale strategies of movement between individual prey schools and larger prey patches in humpback whales (*Megaptera novaeangliae*) bubble-feeding on sand lance (*Ammodytes* spp.) in and around the Stellwagen Bank National Marine Sanctuary, USA. The goal was to investigate the presence of hierarchically nested spatial structures in both sand lance patches and whale bubble-feeding behavior, and to compare the scales and geometry of these patches between predator and prey behavior on each hierarchical scale. Furthermore, the profitability of sand lance schools in feeding areas was investigated.

Using animal-borne tag technology to record underwater movement of whales in combination with surface observations of whale behavior, the locations of bubble-feeding events were identified. Concurrent hydroacoustic measurements of the prey distribution in the water column were used to identify the locations and energetic parameters of sand lance schools around tagged whales. First Passage Time analysis was used to determine the spatial scale of individual bubble-feeding events. Based on spatial proximity, feeding events and prey schools were grouped into larger feeding bouts and prey patches to investigate the presence of hierarchically nested scales.

Up to three hierarchy levels were found in bubble-feeding behavior of nine whales tagged on six days between 2008 and 2012, and up to five hierarchy levels in the sand lance prey field around the tagged whales. There was a significant positive correlation between the lengths of whale bubble-feeding bouts and the lengths of sand lance patches over three common hierarchy levels. On each hierarchy level, the lengths of whale bubble-feeding bouts were significantly smaller than those of sand lance patches. Mean inter-feeding bout distances were significantly positively correlated with mean inter-prey patch distances over two hierarchy levels. Mean distances between feeding events were similar to the mean distances between prey schools. On larger hierarchy levels, mean inter-bout distances were greater than mean distances among prey patches. Mean school height and density tended to be greater in schools recorded inside than outside of feeding bout areas.

The prey field structures found here were likely a result of the specific habitat requirements of sand lance. The results of this study suggest that the tagged whales were able to adapt their foraging movement to the structure of the prey field. By feeding on neighboring schools, whales could minimize the time spent between prey schools. On larger spatial scales, whales did not feed on neighboring prey patches. This could be a result of decreased abilities to find the nearest patch, or because, rather than restricting their foraging movement to neighboring patches, the whales were targeting specific patches. The foraging movement observed in this study led to spatial overlap of the tagged whales with sand lance schools that were characterized by properties rendering them more energetically profitable for bubble-feeding whales.

While hierarchically structured foraging movement has been found in other marine predators, this is the first study that demonstrates this kind of foraging mechanism for baleen whales.

Spatial Association of Humpback Whales (*Megaptera novaeangliae*) and their Prey in the Southern Gulf of Maine, USA

by

Theresa Kirchner

A THESIS

submitted to

Oregon State University

in partial fulfillment of

the requirements for the

degree of

Master of Science

Presented August 15, 2016

Commencement June 2017

Master of Science thesis of Theresa Kirchner presented on August 15, 2016

APPROVED:

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Theresa Kirchner, Author

ACKNOWLEDGEMENTS

I would like to thank my advisor Ari Friedlaender for his support of my studies, for his trust and patience during the work on my project, for letting me go into the field as much as possible, and for the photography lessons in Antarctica.

Thank you to my committee members Elliott Hazen, Leigh Torres, Robert Kennedy and Anthony Klotz who invested their time and energy to support the work on my project.

Thank you to the Hatfield Marine Science Center for the William and Francis Mc Neil Fellowship Award, the Department of Fisheries and Wildlife for the Thomas G. Scott Achievement Award and the Munson Wildlife Graduate Travel Scholarship, and the College of Earth, Ocean and Atmospheric Sciences for the Ecology of Marine Nekton Award, for financial support.

I would like to thank the fantastic team of the Stellwagen Bank tagging project, especially David Wiley, Mike Thompson and the Volgenau Foundation, for facilitating such a fantastic and inspiring project.

Thank you to my fellow BTBEL lab mates and the wonderful group of people that is the Marine Mammal Institute for their support.

Thank you to the staff of the OSU Valley and Guin Library, especially Hannah Rempel, as well as the Roots IT Support Group and the HMSC Computer and Network Support Group, for support and assistance during my studies, and Jerry Mohr for her helpful workshop on thesis formatting.

I would like thank everyone who ever has enabled, or ever will enable, me to work in the field, for their trust, the ability to learn from and with them, and for unforgettable experiences working in magnificent environments studying and being around the coolest animals.

Thank you to everyone who ever made me laugh during the last two years for lifting my spirits.

Most of all, I would like to thank my friends and family for their love and support.

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CHAPTER 1: GENERAL INTRODUCTION

Optimal Foraging Theory and spatial predator-prey associations

In order to understand the behavior of an animal, it is critical to understand its foraging behavior (Bartumeus and Catalan, 2009). An important concept in the area of foraging ecology is Optimal Foraging Theory (OFT) (MacArthur and Pianka, 1966; Pyke et al., 1977). OFT is a body of theory that describes behavioral strategies leading to the maximization of the net rate of energy intake by a predator, and ultimately its fitness, when foraging on patchily distributed prey (Charnov, 1976; Prasad and Borges, 2006; Pyke et al., 1977; Schoener, 1971). Important factors that determine the optimality of a foraging strategy include prey type as well as foraging space, period and group size (Schoener, 1971). In the natural environment where resources are unevenly distributed (Levin, 1992; MacArthur and Pianka, 1966; Wiens, 1976) and form patches with higher resource abundance within an environment with comparatively lower resource abundances (Bartumeus and Catalan, 2009), the optimal choice and use of a foraging space is determined not only by the type of contained foraging patches, but also by an animal's movement within and among patches (Pyke, 1978; Pyke et al., 1977; Schoener, 1971). Choice and use of a foraging space can lead to the maximization of the net rate of energy intake if they enable the predator to (1) overlap spatially with its prey (Fauchald, 2009; Fretwell and Lucas, 1969) (2) forage in areas with the highest prey densities (Bell, 1991), and (3) minimize the time spent between prey patches (Austin et al., 2004; Pyke, 1978).

Optimal Foraging in marine predator species

While other constraints including genetic, social and ecological factors might prevent the expression of optimal foraging performance of predators (Bartumeus and Catalan, 2009; Thums et al., 2011; Womble et al., 2014), several studies have found that the behavior of some marine predators in their natural environment is in accordance with that would be expected based on OFT. For example, the distribution of Atlantic cod (*Gadus morhua*) (Rose and Leggett, 1990), Hawaiian spinner dolphins (*Stenella longirostris longirostris*) (Benoit-Bird and Au, 2003), black-legged kittiwakes (*Rissa tridactyla*), thick-billed murres (*Uria lomvia*) and northern fur seals (*Callorhinus ursinus*) (Benoit-Bird et al., 2013b) was found to be closely linked to the spatial distribution of their prey. The foraging effort of black-legged kittiwakes, thick-billed murres, northern fur seals, humpback (*Megaptera* *novaeangliae*), blue (*Balaenoptera musculus*), Blainville's and Cuvier's beaked whales (*Mesoplodon densirostris* and *Ziphius cavirostris*) was concentrated in areas where aggregations of their prey were more dense (Benoit-Bird et al., 2013b; Croll et al., 2005; Hazen et al., 2011, 2009). Hazen et al. (2015) showed that blue whale foraging movement in the vertical dimension also depended on prey density, as the depths were increased feeding rates were observed corresponded to the depths of high prey densities. Hawaiian spinner dolphins and northern fur seals were observed to forage more frequently in prey patches characterized by close spatial proximity to other patches (Benoit-Bird et al., 2013a; Benoit-Bird and Au, 2003), illustrating the importance of the spatial configuration of prey patches on predator foraging success.

Hierarchically nested resource structures in the pelagic marine environment

The pelagic marine environment is characterized by the structurally complex, heterogeneous distribution of resources (McManus and Woodson, 2012; Sims et al., 2006; Steele, 1978; Wolanski and Hamner, 1988). For example, individual krill (*Euphausia* spp.) aggregate together to form a swarm (Brierley and Cox, 2015; Marr, 1962; Miller et al., 1993), inside which local krill densities can be highly variable (Barange et al., 1993; Godlewska and Klusek, 1987). Multiple krill swarms are thought to aggregate together into larger patches (Levin, 1992; Weber et al., 1986), which in turn can be further aggregated, forming individual krill populations (Fauchald, 1999; Murphy et al., 1988). Similarly, individual fish aggregate together, forming a school (Pavlov and Kasumyan, 2000). Often, independent schools with high fish densities are concentrated in areas of high biological productivity (Fauchald et al., 2000; McManus and Woodson, 2012; Wolanski and Hamner, 1988), thereby forming larger aggregations (Benoit-Bird et al., 2013c; Kotliar and Wiens, 1990). Capelin (*Mallotus villosus*) in the Barents Sea aggregate on scales as small as several meters representing the diameter of individual schools (Gjøsæter, 1998), and on scales as large as 300 km corresponding to the spawning migration (Fauchald et al., 2000), as well as on intermediate scales of ca. 0.1 km, 3km and 50 km, likely corresponding to the scales of predation response and oceanographic features (Fauchald et al., 2000; Radakov and Mills, 1974). Similar aggregation structures have also been found for juvenile walleye pollock (*Theragra chalcogramma*) with aggregations occurring at less than 0.001 km, 0.4 km and over 10 km horizontal extent (Benoit-Bird et al., 2013a; Benoit-Bird et al., 2013c). On each aggregation scale, the distances among the patches were comparable to the horizontal extent of the patches (Benoit-Bird et al., 2013a). These examples show that fish aggregations can form hierarchically nested spatial structures, in which each level of the hierarchy occurs on a distinct spatial scale (Benoit-Bird et al., 2013c; Fauchald et al., 2000; Murphy et al., 1988; Russell et al., 1992; Wu and Loucks, 1995).

Hierarchically nested foraging behavior of marine predators

Hierarchically structured predator foraging behavior has been reported for a variety of marine predator taxa. Wandering albatross (*Diomedea exulans*) in the Indian Ocean showed zig-zag movements at fine scales of 0.1 km for optimal wind use, movements within feeding areas at scales of 0.1-10 km, and movements corresponding to travel between feeding areas and the use of larger weather systems at larger scales (Fritz et al., 2003). Pinaud and Weimerskirch (2005) showed that yellow-nosed albatross (*Thalassarche carteri*) in the Indian Ocean focused their foraging effort at scales of ca. 130 km corresponding to productive meso-scale oceanographic features inside the larger area of a turbulent and productive ocean current. The foraging behavior of Antarctic petrels (*Thalassoica antarctica*) showed characteristic scales at tens of kilometers corresponding to search behavior within larger foraging areas at scales greater than 100 km (Fauchald and Tveraa, 2006). Fauchald et al. (2000) found that the foraging behavior of murres (*Uria* spp.) in the Barents Sea showed spatial structures at scales of ca. 3 km, 50 km and 300 km. Benoit-Bird et al. (2013a) found that in the Bering Sea, northern fur seals (*Callorhinus ursinus*) foraged in patches of less than 0.001 km extent that were grouped together on scales of ca. 0.4 km, that were in turn clustered at scales of 30-50 km. The spacing between foraging areas was similar in size to the horizontal extent of the foraging areas, on each level of the nested hierarchy (Benoit-Bird et al., 2013a). These examples illustrate that there is often not just a single spatial scale that characterizes predator foraging behavior (Levin, 1992).

Spatial correlation and configuration of marine predator foraging and prey aggregation behavior

The foraging success of a predator depends on its ability to adapt a foraging strategy that successfully exploits the encountered prey field (Stephens and Charnov, 1982). Where prey aggregations are spatially nested, predators need to be able to respond to multiple scales of the prey aggregation (Benoit-Bird et al., 2013a; Fauchald et al., 2000; Russell et al., 1992). By tracking large-scale low-density aggregation as well as the nested small-scale high-density patches, a predator can maintain spatial overlap with high prey densities (Benoit-Bird et al., 2013a; Fauchald et al., 2000; Russell et al., 1992). Fauchald et al. (2000) found that the spatial scales of murre foraging behavior corresponded to the spatial scales of capelin aggregations on all scales of the prey aggregation hierarchy. They concluded that murres were able to track capelin movement, and were attracted to patches with high capelin densities (Fauchald et al., 2000; Sih, 1984). Spatial overlap between the similarly sized foraging areas and prey aggregations was observed on all but the smallest spatial scale, likely due to the ephemerality of such small capelin aggregations or their predator avoidance behavior (Fauchald et al., 2000; Sih, 1984). Benoit-Bird et al. (2013a) found similar correlations of the sizes of northern fur seal foraging areas in the Bering Sea to the sizes of their prey aggregations, on all observed spatial scales of the prey aggregations. Similarities were also found in the spatial configuration of foraging areas and prey aggregations, as the distances between foraging aggregations were similar to the distances between prey aggregations, on multiple scales of the nested hierarchy (Benoit-Bird et al., 2013a). The authors concluded that fur seals movement was not random but instead the result of the development of successful behavioral strategies to exploit patchily distributed fish (Benoit-Bird et al., 2013a). The development of such successful foraging strategies can be explained by an increase of the fitness of efficiently foraging animals (Gende and Sigler, 2006; Pyke et al., 1977).

Movement patterns of marine predators foraging on heterogeneously distributed prey

Different marine predator taxa have been shown to use similar movement patterns when feeding on patchily distributed prey. Area-restricted search (ARS) (Kareiva and Odell, 1987) is a deterministic movement pattern (Sims et al., 2014) where a prey encounter elicits intensive search behavior through an increase in movement tortuosity and decrease in movement speed (Benhamou, 1992). When prey is aggregated in patches, this behavior increases the likelihood of successive prey encounters by increasing time inside the encountered patch (Benhamou, 1992). A lack of prey encounters leads to extensive search behavior through a decrease of tortuosity and increase in movement speed, causing greater spatial displacement, leading to a departure from the area where no prey is encountered, and increasing the chance of additional prey encounters in a different area (Benhamou, 1992). ARS has been suggested for a range of taxa and trophic levels from copepods (*Acartia clausi*) (Leising and Franks, 2002) to manta rays (*Manta alfredi*) (Papastamatiou et al., 2012), short-tailed albatross (*Phoebastria albatrus*) (Suryan et al., 2006), bottlenose dolphins (*Tursiops truncatus*) (Bailey and Thompson, 2006) and Southern elephant seals (Thums et al., 2011). Spatially nested ARS behavior has been observed in some predators foraging on spatially nested prey patches such as Antarctic petrels (Fauchald and Tveraa, 2006) and yellow-nosed albatross (Pinaud and Weimerskirch, 2005).

Area-avoided search (AAS) is a movement strategy where, following an initial prey encounter, the chance of successive prey encounters is greater further away from the initial encounter, either due to predator avoidance behavior of the prey (Amano and Katayama, 2009; Brown et al., 1999; Charnov et al., 1976) or dispersed prey distributions (Amano and Katayama, 2009; Klaassen et al., 2006). AAS behavior has been observed in several species including European plaice (*Pleuronectes platessa*) (Amano and Katayama, 2009; Gibson, 1980) and three-spined sticklebacks (*Gasterosteus aculeatus*) (Amano and Katayama, 2009; Thomas, 1974).

Probabilistic searches in the form of random walks are advantageous for predators with limited information on resource locations foraging on random, patchily distributed resources. Lévy walks are a scale-invariant form of random walk, where displacement lengths of a predator stem from a heavy-tailed power law distribution (Sims et al., 2014), resulting in a large number of short movements randomly interspersed by a few large-scale displacements (Humphries and Sims, 2014; Klafter et al., 1993). This search pattern is repeated over multiple spatial scales (Humphries and Sims, 2014; Klafter et al., 1993) and increases encounter probabilities with sparsely distributed prey (Humphries and Sims, 2014; Viswanathan et al., 2002). Lévy walk movement has been observed in movement data from a variety of taxa from jellyfish (*Rhizostoma octopus*) (Reynolds, 2014) to great white sharks (*Carcharodon charcarias*) (Sims et al., 2012).

Feeding activity has also been observed in the absence of dedicated search effort. Grey-headed albatross (*Thalassarche chryostoma*) were observed to feed during apparent transit movement between their colonies on South Georgia and predictable foraging areas in the productive Antarctic Polar Front (Catry et al., 2004). Southern elephant seals (*Mirounga leonina*) in the Southern Ocean appeared to opportunistically feed on randomly encountered, abundant prey during uninterrupted travel to their regularly frequented foraging sites, where they employed ARS to feed on predictably abundant prey (Thums et al., 2011). Similarly, (Benoit-Bird et al., 2013a) suggested that northern fur seals base their general foraging movement patterns on the predictable locations of prey aggregations, and feed opportunistically on more randomly distributed prey encountered during the execution of these movement patterns.

Studying individual scales of marine predator-prey interactions

Where a predator-prey relationship is characterized by multiple spatial scales, it is important to identifying the individual scales of this relationship separately to prevent the masking of interactions on one scale by interactions on another scale (Benoit-Bird et al., 2013a; Rose and Leggett, 1990). Therefore, studies of predator-prey interactions need to be designed in a way that is suitable to resolve interactions over the variety of spatial and temporal scales that might exist (Benoit-Bird et al., 2013; Rose and Leggett, 1990). Marine predator foraging behavior on fine spatial scales that would not be observed using only surface observations can be recorded using animal-borne tags with accelerometer, magnetometer and pressure sensors (Benoit-Bird et al., 2013a; Friedlaender et al., 2016; Goldbogen et al., 2015; Hazen et al., 2011; Johnson and Tyack, 2003; Thums et al., 2011; Wiley et al., 2011). A variety of studies have used scientific echosounders to map the prey distribution in the water column around foraging marine predators (Benoit-Bird et al., 2013a; Cox et al., 2009; Croll et al., 2005; Hazen et al., 2011, 2009). Behavioral observations of marine predator foraging behavior from animal-borne tag data in combination with concurrent measurements of the prey distribution around the predator using scientific echosounders allows for the investigation of trophic interactions over multiple spatial scales (Benoit-Bird et al., 2013a; Croll et al., 2005; Friedlaender et al., 2009; Hazen et al., 2009; Sveegaard et al., 2012).

Sand lance as important, patchily distributed prey

For many marine piscivore predators in the northern hemisphere, sand lance (*Ammodytes* spp.) are an essential forage fish (Robards et al., 1999; Springer and Speckman, 1997). Sand lance are small schooling fish that feed on zooplankton in the water column during the day and burying into shallow benthic substrates at ca. 30-70 m water depths at night for predator avoidance (Payne et al., 1986; Reay, 1970; Robards et al., 1999; Scott, 1968; Winslade, 1974; Wright et al., 2000). To bury into the substrate, sand lance require specific sediment grain sizes and frequent substrate oxygenation (Behrens et al., 2007; Holland et al., 2005; Meyer et al., 1979; Reay, 1970; Wright et al., 2000). Suitable substrate areas are limited and heterogeneously distributed (Robards et al., 1999; Scott, 1968), and consequently, sand lance likely return to these areas repeatedly (Behrens et al., 2007; Haynes and Robinson, 2011; Robards et al., 1999). Due to their limited swimming abilities, they appear to remain close to both suitable benthic habitat and productive feeding areas in the water column at all times (Freeman et al., 2004; Haynes and Robinson, 2011; Reay, 1970; van der Kooij et al., 2008), resulting in a patchy distribution of sand lance within their distributional range (Robards et al., 1999; Scott, 1968). Increased sand lance abundance in an area appears to lead to an increase in sand lance patchiness through an increase in the number of schools, rather than an increase in school sizes (Brierley and Cox, 2015; Haynes and Robinson, 2011; van der Kooij et al., 2008; Wright et al., 2000). Predation does not appear to influence the patchiness of sand lance distribution, as schools have been shown to rarely break apart under predation (Pitcher and Wyche, 1983).

Optimal Foraging in humpback whales

Large baleen whales with body masses of around 30 tons (Meijler et al., 1992), humpback whales (*Megaptera novaeangliae*) undertake seasonal migrations of up to several thousand kilometers in length between breeding grounds in tropical, less productive waters and their feeding grounds in colder, productive areas (Dawbin, 1966; Kennedy et al., 2013). Consequently, they need to satisfy their high energetic demands of an entire year during the limited time they spent on their feeding grounds. Bulk filter-feeding (Potvin et al., 2012) is an energetically efficient foraging strategy that enables humpback whales to prey on small, schooling or swarming prey organisms; mainly krill and small schooling fish (Fleming and Jackson, 2011; Kennedy et al., 2013). Humpback whales feeding on fish schools in the upper 20 m of the water column are often observed to produce air bubbles around the schools to contain the fish prior to engulfing them, a behavior termed ‘bubble-feeding’ (Sharpe and Dill, 1997; Smith, 1961; Wiley et al., 2011).

The use of minimally invasive animal-borne archival tags has greatly facilitated the study of the foraging ecology of humpback whales and other baleen whales in their natural habitat (Friedlaender et al., 2011; Goldbogen et al., 2015a, 2013; Hussey et al., 2015; Potvin et al., 2012). Studies analyzing tag data were able to clearly demonstrate that humpback whales exhibit plasticity in their foraging behavior that facilitates the maximization of their energy intake (Friedlaender et al., 2016; Wiley et al., 2011). Friedlaender et al. (2016) showed that, when patches with high and low krill densities were found at similar depths, humpback whales in Antarctica fed on higher-density patches. However, when less-dense krill patches were located at shallower depths compared to deeper and more-dense patches, the whales fed on the more easily accessible less-dense patches (Friedlaender et al., 2016).

When herring stocks in the southern Gulf of Maine collapsed due to overfishing, sand lance abundances increased significantly, rendering them a major forage fish in this area (Meyer et al., 1979; Payne et al., 1986; Sherman et al., 1981). Within a few years, humpback whales foraging in this area were observed to innovate two foraging tactics, lobtail feeding and bottom (side-roll) feeding, suitable to exploit this prey species (Allen et al., 2013; Friedlaender et al., 2009; Hain et al., 1995; Ware et al., 2014; Weinrich et al., 1992; Wiley et al., 2011). During lobtail feeding, the striking of the water surface prior to the production of feeding bubbles and subsequent engulfment of the prey potentially serves to compact the sand lance school (Allen et al., 2013; Weinrich et al., 1992). Bottom feeding takes advantage of daily occurring sand lance aggregations at the surface of or within the sea floor substrate (Hain et al., 1995; Ware et al., 2014). Friedlaender et al. (2009) observed diurnal transitions between bubble-feeding and bottom feeding corresponding to the diurnal vertical migration of sand lance between the water column and the sea floor (Reay, 1970).

Wiley et al. (2011) described two different bubble-feeding tactics in humpback whales feeding on sand lance in the southern Gulf of Maine. Each tactic was hypothesized to have a different effect on targeted fish schools, resulting in either school containment or compaction (Wiley et al., 2011). Therefore, the two tactics could be the result of inter-individual variation in foraging tactics, or of the adaptation of different foraging tactics depending on prey patch characteristics (Wiley et al., 2011). Hazen et al. (2009) found that humpback whale bubble-feeding in the southern Gulf of Maine was significantly associated with sand lance schools with a pronounced vertical extent, possibly due to the facilitation of the vertically oriented bubble-feeding tactic. They also found that bubble-feeding whales fed more frequently around schools with higher fish densities (Hazen et al., 2009).

Motivation of the current study

Sand lance are an important prey for humpback whales in the southern Gulf of Maine (Hain et al., 1995; Payne et al., 1990; Wiley et al., 2011). In this area, inter-annual variations in sand lance abundance and length frequency distribution have been observed (Kaufman and Brown, 2008; Payne et al., 1990; Sherman et al., 1981; Stellwagen Bank National Marine Sanctuary Final Management Plan and Environmental Assessment, 2010). Within the southern Gulf of Maine, the abundance of humpback whales on Stellwagen Bank has been linked to the abundance of sand lance (Payne et al., 1990, 1986; Stellwagen Bank National Marine Sanctuary Final Management Plan and Environmental Assessment, 2010). However, a similar correlation between humpback whale abundance and sand lance abundance has not been found for the area of Georges Bank southeast of Stellwagen Bank in the southern Gulf of Maine, suggesting that additional factors such as the aggregation of sand lance near the steep edges of Stellwagen Bank could facilitate humpback whale foraging in this area (Payne et al., 1986).

The goal of the current study was to quantify the sizes and inter-patch distances of sand lance aggregations and humpback whale bubble-feeding behavior on and around Stellwagen Bank over multiple spatial scales. By comparing predator foraging behavior to prey aggregation behavior, potential movement strategies of humpback whales feeding on sand lance can be identified, and inferences can be drawn regarding their efficiency.

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CHAPTER 2: SPATIAL ASSOCIATION OF HUMPBACK WHALES AND THEIR PREY IN THE SOUTHERN GULF OF MAINE, USA

Abstract

By minimizing the time spent between profitable prey patches, predators can increase their foraging efficiency. Baleen whales have been shown to forage in profitable prey patches, but their strategies for finding these patches are poorly understood. The present study investigated the fine-scale movement of bubble-feeding humpback whales (*Megaptera novaeangliae*) within and between sand lance (*Ammodytes* spp.) patches in the southern Gulf of Maine, USA. Hydroacoustic measurements of sand lance schools around tagged whales revealed spatially nested prey field structures, likely caused by the high sand lance habitat specificity. Animal-borne tags and surface observations of the bubble-feeding behavior of nine whales tagged on six days between 2008 and 2012 revealed spatially nested bubble-feeding behavior with structures strongly correlated with those of the sand lance, suggesting that whales adapted their foraging behavior to the encountered prey field. Sequential feeding events appeared to target neighboring prey schools; a movement strategy that limited whale movement to the interior of larger prey patches. On higher hierarchy levels, distances between bubble-feeding bouts were greater than distances between prey patches, indicating a decreased ability of whales to minimize time spent between prey patches with increasing spatial distance, or active prey patch selection. Schools inside feeding bout areas had properties rendering them more energetically profitable; either greater mean height or density, compared to schools outside these areas. The current study presents evidence for the adaptation of the movement of a marine predator to the structure of its prey field. This is the first time this kind of foraging mechanism has been demonstrated for baleen whales.

Introduction

For predators feeding on patchily distributed prey, Optimal Foraging Theory (OFT) suggests the evolution of behavioral strategies (Charnov, 1976; MacArthur and Pianka, 1966; Prasad and Borges, 2006; Pyke et al., 1977; Schoener, 1971) that lead to a concentration of foraging effort in areas with the highest prey densities (Bell, 1991; Schoener, 1971), and a minimization of the time spent between prey patches (Austin et al., 2004; Pyke, 1978). In the marine environment where spatial resource distribution is often complex and heterogeneous (McManus and Woodson, 2012; Sims et al., 2006; Steele, 1978; Wolanski and Hamner, 1988), several movement strategies have been shown in different marine predator taxa than enable efficient foraging. When prey is aggregated in patches, area-restricted search (ARS) (Kareiva and Odell, 1987) increases the likelihood of successive prey encounters by increasing time inside the encountered patch (Benhamou, 1992). ARS is a deterministic movement pattern (Sims et al., 2014) where an initial encounter of prey or of cues indicating the presence of prey elicit intensive search behavior through an increase in movement tortuosity and decrease in movement speed (Benhamou, 1992; Weimerskirch et al., 2007). A lack of prey encounters leads to extensive search behavior through a decrease of tortuosity and increase in movement speed, causing greater spatial displacement, leading to a departure from the area where no prey is encountered, and increasing the chance of additional prey encounters in a different area (Benhamou, 1992). ARS has been indicated for a range of taxa and trophic levels (Bailey and Thompson, 2006; Leising and Franks, 2002; Papastamatiou et al., 2012; Suryan et al., 2006; Thums et al., 2011). Probabilistic searches in the form of random walks are advantageous for predators with limited information on resource locations that forage on random, patchily distributed resources. Lévy walks, a scale-invariant form of random walk (Sims et al., 2014), result in a large number of short movements randomly interspersed by a few large-scale displacements (Humphries and Sims, 2014; Klafter et al., 1993), increase encounter probabilities with sparsely distributed prey (Humphries and Sims, 2014; Viswanathan et al., 2002) and have been observed in movement data from a variety of marine predator taxa (Reynolds, 2014; Sims et al., 2012).

Based on OFT, marine predators should be able to adjust their foraging movement to the structure of the encountered prey field, thereby increasing their foraging success (Stephens and Charnov, 1982). Wandering albatross (*Diomedea exulans*) were shown to use different cues for the initiation of ARS on small and large spatial scales, likely adapting to differences in the prey distribution (Weimerskirch et al., 2007). Where prey is distributed in a spatially nested hierarchy, predators can achieve spatial overlap with small, high-density prey patches nested located within larger, low-density prey patches, by tracking the prey distribution over multiple nested scales (Benoit-Bird et al., 2013a; Fauchald et al., 2000; Russell et al., 1992).

Where predator-prey interactions occur over multiple nested spatial levels, studying the interaction each level separately prevents interactions on one level from masking interactions on another level (Benoit-Bird et al., 2013a; Fauchald et al., 2000; Rose and Leggett, 1990). Animal-borne tags recording detailed underwater movement of marine predators with motion and orientation sensors (e.g. accelerometer, magnetometer and pressure sensors) can reveal fine scales of foraging behavior that would not be observed using only surface observations (Benoit-Bird et al., 2013a; Friedlaender et al., 2016; Goldbogen et al., 2015; Hazen et al., 2011; Johnson and Tyack, 2003; Thums et al., 2011; Wiley et al., 2011). Scientific echosounders have been used to map the prey distribution in the water column around foraging marine predators in a variety of studies (Benoit-Bird et al., 2013a; Cox et al., 2009; Croll et al., 2005; Hazen et al., 2011, 2009). Studies recording predator foraging movement and prey distribution in the same area, at the same time can reveal important insights into marine predator-prey relationships over multiple spatial scales (Benoit-Bird et al., 2013a; Croll et al., 2005; Friedlaender et al., 2009; Hazen et al., 2009; Sveegaard et al., 2012).

Important forage fish with an extremely patchy distribution, sand lance (*Ammodytes* spp.) are prey for a variety of marine piscivore predator taxa in the northern hemisphere (Robards et al., 1999; Springer and Speckman, 1997). Feeding on zooplankton in the water column during the day and burying into shallow benthic substrates at ca. 30-70 m water depths at night for predator avoidance, there is a strong diurnal component to the behavior and distribution of these small schooling fish (Payne et al., 1986; Reay, 1970; Robards et al., 1999; Scott, 1968; Winslade, 1974; Wright et al., 2000). Substrate conducive to their burying is characterized by specific sediment grain sizes and frequent substrate oxygenation (Behrens et al., 2007; Holland et al., 2005; Meyer et al., 1979; Reay, 1970; Wright et al., 2000). Because sediment areas fulfilling these requirements are limited and heterogeneous (Robards et al., 1999; Scott, 1968), sand lance likely return to suitable areas repeatedly (Behrens et al., 2007; Robards et al., 1999). As poor swimmers, they likely remain in proximity to both preferred burying habitat and productive feeding areas in the water column at all times (Freeman et al., 2004; Haynes and Robinson, 2011; Reay, 1970; van der Kooij et al., 2008), resulting in a patchy distribution of sand lance schools throughout their distributional range (Robards et al., 1999; Scott, 1968).

Extremely large predators undertaking extensive seasonal migrations, humpback whales (*Megaptera novaeangliae*) need to satisfy their energetic demands of an entire year during the limited time spent on their feeding grounds by feeding on small, patchily distributed prey organisms (Dawbin, 1966; Fleming and Jackson, 2011; Kennedy et al., 2013; Meijler et al., 1992; Potvin et al., 2012). High energetic demands and limited time spent on their feeding grounds suggests that humpback whales adapt foraging strategies suitable to maximize their energetic intake. Studies using minimally invasive animal-borne archival tags were able to clearly demonstrate that humpback whales forage in energetically profitable prey patches and exhibit plasticity in their foraging dive behavior that facilitates the maximization of their energy intake (Friedlaender et al., 2016, 2009; Hazen et al., 2009; Wiley et al., 2011). However, how the whales locate profitable patches, and whether their movement strategies enable the minimization of time spent between them, is unclear.

The goal of the current study was to investigate the movement efficiency of a marine predator within and between prey patches over multiple spatial scales. Specifically, this study analyzed the bubble-feeding movement patterns of humpback whales in the southern Gulf of Maine relative to the distribution of patches of sand lance, their main prey in the area (Payne et al., 1990; Wiley et al., 2011). Bubble-feeding is a conspicuous surface-feeding behavior during which humpback whales produce air bubbles around fish schools in the upper 20 m of the water column prior to engulfing them (Sharpe and Dill, 1997; Smith, 1961; Wiley et al., 2011). While the distribution and abundance of humpback whales in the southern Gulf of Maine has been linked to the distribution and abundance of sand lance (Payne et al., 1990; Stellwagen Bank National Marine Sanctuary Final Management Plan and Environmental Assessment, 2010), Payne et al. (1986) suggested that sand lance abundance alone could not explain the observed local whale distributions, suggesting that additional factors such as the characteristics of sand lance aggregations influence the foraging ecology of the whales in this area. To investigate the influence of sand lance aggregations on humpback whale foraging movement and efficiency, the current study investigated how the movement of bubble-feeding humpback whales relates to the spatial structure of their sand lance prey field over multiple spatial scales, by testing the hypotheses that (1) humpback whale bubble-feeding in the southern Gulf of Maine occurs at multiple discrete spatial scales, (2) sand lance in the southern Gulf of Maine aggregate at multiple discrete spatial scales, (3) the spatial scales of humpback whale bubble-feeding behavior are linearly related to the spatial scales of sand lance aggregations. To investigate whether this relationship results in whales foraging in profitable patches, the hypothesis was tested that (4) sand lance schools inside whale foraging areas differ from schools outside of foraging areas in fish density and vertical extent.

Methods

DATA COLLECTION

Whale behavior data collection

The data analyzed here stems from a long-term research project investigating the foraging behavior of humpback whales in and around the Stellwagen Bank National Marine Sanctuary (SBNMS) in the southern Gulf of Maine, USA (Friedlaender et al., 2009; Hazen et al., 2009; Parks et al., 2014; Ware et al., 2014; Wiley et al., 2011).

Stellwagen Bank is an underwater plateau within Massachusetts Bay. Bottom depths on the Bank range from 18 to 77 m, and reach up to 370 m in the surrounding basins (Meyer et al., 1979; Stellwagen Bank National Marine Sanctuary Final Management Plan and Environmental Assessment, 2010). Upwelling promoted by this dynamic topography causes enhanced biological productivity within the SBNMS, rendering it an important feeding ground for a variety of animals from commercially important fish such as cod to apex predators from sea birds to marine mammals (Stellwagen Bank National Marine Sanctuary Final Management Plan and Environmental Assessmen*t*, 2010). Internal waves created by the interaction of tidal currents with the Bank redistribute plankton in the water column (Haury et al., 1979) and may influence the distribution of pelagic predators (Hazen et al., 2009; Pineda et al., 2015). Stellwagen Bank was created by glacial deposits and comprises mainly sandy sediments, rendering it an important habitat for sand lance (Meyer et al., 1979).

Between 2004 and 2015, in the months of June and July, DTAGs (Digital Acoustic Recording Tags) (Johnson and Tyack, 2003) were deployed on foraging humpback whales, to record their three-dimensional subsurface movements. DTAGs are minimally invasive archival tags attached to an animal with suction cups and equipped with accelerometer, magnetometer and pressure sensors to record movement, heading and depth of the animal 50 times per second (Johnson and Tyack, 2003; Wiley et al., 2011). Tags were deployed from a small rigid-hull inflatable boat (RHIB) using a 7 m carbon-fiber pole (Friedlaender et al., 2009; Wiley et al., 2011). Tag release was programmed prior to the deployment, and usually occurred no later than 24 hours after deployment. To facilitate tag recovery and subsequent downloading of the data, tags were equipped with VHF transmitters. Focal follows were conducted during the daytime from a RHIB following the tagged whale, to record detailed observations of the whale's surface behavior (Friedlaender et al., 2009; Hazen et al., 2009; Wiley et al., 2011). Laser-rangefinder measurements of the range and bearing of the whale relative to the focal follow boat were taken at least once per surfacing (Hazen et al., 2009). Together with the GPS positions of the boat, which were logged automatically every 10 seconds, the GPS position of the whale could then be calculated using triangulation.

Prey data collection

The distribution of prey in the water column around the tagged whales was measured using calibrated, scientific SIMRAD EK60 echosounders operating at 38 and 120 kHz with a ping rate of up to 10 pings/sec (Hazen et al., 2009). Two prey-mapping vessels were used, each moving at ca. 2-5 knots. The R/V AUK (15 m long catamaran) centered its prey-mapping effort on the approximate location of the tagged whale, moving several hundred meters away from the whale and then returning to the position of the whale, before moving into a different direction and returning to the whale, thereby sampling the area and moving in a four-leaf clover pattern around the tagged whale (Hazen et al., 2011, 2009). The towfish-mounted echosounders were retrieved during fast transit of the ship, which interrupted the prey mapping during these times. The R/V Nancy Foster (57 m long NOAA survey vessel) recorded the prey distribution on a larger scale using continuously recording hull-mounted echosounders, moving up to several thousand meters away from the tagged animal.

DATA ANALYSIS

The focal follow data was used to select tag deployments with a large number of bubble-feeding events for further analysis. Spatially nested hierarchy levels are numbered based on an increase in the spatial scale; e.g. level 1 is the lowest hierarchy level with the smallest spatial scales of whale and sand lance behavior and encompasses individual whale feeding events and sand lance schools, level 2 has the second-smallest spatial scales and includes L2 feeding bouts (groups of feeding events) and L2 sand lance patches (groups of sand lance schools), etc. When referring to whale feeding bouts across multiple spatial scales, the term 'bout' is used, which can include single feeding events as well.

The general term for sand lance aggregations across multiple spatial scales is ’patch’, which can include sand lane schools as well. The term ‘geometry’ is used to refer to the spatial arrangement of bouts and patches, and refers to both patch lengths and distances among them.

Whale behavior data analysis

To determine the locations of bubble-feeding events, the three-dimensional track of each whale was reconstructed, using the movement and orientation data recorded by the tag. Assuming a constant swimming speed of 1 m per second (Wiley et al., 2011), the position of the whale was dead-reckoned five times per second, starting at the GPS location of the tag deployment. The resolution of the resulting track was down-sampled to one location per second, and its spatial accuracy improved through geo-referencing with the R package BayesianAnimalTracker (Liu et al., 2015) using the GPS positions of the whale recorded at the surface.

Based on the behavioral descriptions of surface behaviors of the whales from the focal follows, the times of bubble-feeding events were determined. Here, the term ‘feeding event’ refers to all bubble-feeding events, independent of the different types described in Wiley et al. (2011). To identify feeding events that were missed during the behavioral observations, the dead-reckoned track was visualized using TrackPlot software (Ware et al., 2006). For time periods without behavioral observations, bubble-feeding events were identified based on characteristic loops in the track and intense body rolls of the whale (Wiley et al., 2011), and their times noted. The geo-referenced track of the whale was then used to determine the location of the whale during the time of every feeding event.

In order to group feeding events into feeding bouts, the distances between sequential feeding events were calculated and their frequency distribution was plotted as a histogram. The first break in the data in the form of a clear minimum in the frequency distribution was visually identified by expert knowledge, and all feeding events located closer to the sequential feeding event than this distance, were grouped into feeding bouts called L2 bouts (Benoit-Bird et al., 2013a). The number of feeding events within each bout as well as the number of associated whales during each bout was determined. The mean distance between sequential feeding events within each bout was calculated.

The length of each bout was calculated as the greatest of all pairwise distances between feeding events within each bout. The distance between sequential bouts was calculated as the shortest of all pairwise distances between feeding events from the two bouts.

The grouping of L2 feeding bouts into larger bouts called L3 bouts, and the measurement of the lengths and arrangement of these larger bouts, was conducted similar to the method described above: L2 bouts were grouped into L3 bouts based on the first break in the frequency distribution of distances among sequential feeding bouts. The length of these larger bouts was calculated as greatest of the pairwise distance between all feeding events belonging to bouts contained within the larger bouts. The distance between sequential larger bouts was calculated as the shortest of all pairwise distances between feeding events from the bouts contained within the larger bouts.

This grouping of feeding events and bouts into larger groups was repeated until no clear break could be identified in the frequency distribution of distances between sequential groups. The greatest pairwise distances among all feeding events was calculated to determine the spatial extent of the recorded foraging behavior.

To calculate the smallest foraging scale of each whale, the geo-referenced track of the whale was divided into segments representing the different L2 feeding bouts. Each bout segment started with the last dive before the first feeding event in the bout. Each segment ended with the first dive following the last feeding event inside the bout. First-Passage Time analysis (FPT) (Fauchald and Tveraa, 2003) was then run on each track segment. FPT creates a circle with a specified minimum radius around each location in the track of an animal, and calculates the time the animal spent within the area represented by the circle centered on each track location, called ‘first-passage time’. Then, the circle radius is increased based on a specified increment, and first-passage time calculated for all circles with the new radius. The circle radius is increased until it reaches a specified maximum. The circle radius at which the variance of the logarithm of the first-passage time is greatest is interpreted as the scale of the foraging behavior of the animal (Bailey and Thompson, 2006; Fauchald and Tveraa, 2003; Pinaud, 2007), and is called rFPT in the current analysis. Here, FPT was implemented using the adehabitatLT package in R (Calenge, 2006), with circle radii ranging from 0 m to the total length of the track segment within the bout, and increasing in two meter increments.

Prey data analysis

Data from the R/V AUK mapping the fine-scale prey distribution within approximately 500 meters around the tagged whales was visualized using the software Echoview (version 5). All data above 3.5 m depth and within 2 m of the sea floor, as well as regions with bad data, were excluded from further analysis. A school detection algorithm (Coetzee, 2000) was run to detect schools comparable to a visual analysis of the data (maximum vertical linking distance of 10 m and a maximum horizontal linking distance of 20 m based on previous analyses). The detected schools were visually scrutinized, and schools missed by the algorithm were added manually. The detected schools were classified as either sand lance, herring or unknown species schools, or as individual targets representing larger fish or whales based on their frequency-dependent scattering. Because sand lance do not have a swimbladder, sand lance schools could be identified based on higher acoustic backscattering coefficients (s_V) on the 120 kHz echogram compared to the 38 kHz echogram (Yasuma et al., 2009), as well as their shape and location in the water column. For each sand lance school, data from the 120 kHz echogram was exported for further analysis including mean volume backscattering strength, mean height, mean depth, mean length and three-dimensional volume of the school as well as the geographic coordinates of the school center and the time the school was recorded. Because actual school geometry is unknown, the length of each school determined by the acoustic data does not necessarily reflect the longest horizontal extent of the school, but simply the horizontal extent captured by the echosounder beam. However, because all schools were orientated randomly relative to the path of the prey-mapping ship, the mean of the school lengths measured by the echosounder data is likely an accurate representation of a mean horizontal bisection of the schools.

For the following calculations, a mean sand lance length of 14.4 cm was assumed, based on length measurements of *A. dubius* caught on Stellwagen Bank between 2006 and 2008 provided in Kaufman and Brown (2008). Based on a preliminary analysis, the most suitable equation for calculating the target strengths of individual sand lance of this size at 120 kHz was published by Yasuma et al. (2009) for adult Japanese sand lance *A. personatus*:

$$TS = 20.7 \times log_{10}(length) - 92.1 \; [dB, length\ in\ cm]$$

Using this target strength, the backscattering cross-section σ_{bs} was calculated using the formula from Simmonds and MacLennan (2005) and Maclennan (2002):

$$\sigma_{bs} = 10^{(\frac{TS}{10})} \; [m^2]$$

The mean volume backscattering strength of each sand lance school was used to calculate the volume backscattering coefficient s_v of that school based on Simmonds and MacLennan (2005):

$$s_v = 10^{(\frac{Sv\_mean}{10})} \; [m^{-1}]$$

The sand lance density per cubic meter of the respective school was then calculated using the formula by Maclennan (2002) and Boswell et al. (2010):

$$\rho_v = \frac{s_v}{\sigma_{bs}} \; [m^{-3}]$$

By multiplying sand lance density per cubic meter with the three-dimensional school volume, the total number of sand lance in each school was calculated.

The weight of an individual sand lance was calculated using the weight-length relationship for *A. dubius* in the Northwest Atlantic from Scott (1972):

$$W = 0.002 \times L^{2.994} \; [g, L \; in \; cm]$$

Multiplying the weight of an individual sand lance by the number of sand lance per school, the biomass of every sand lance school could be calculated. During the remainder of the analysis, the energetic differences between groups of sand lance schools will be discussed, rather than actual energetic values. Therefore, measures of uncertainty associated with the calculations described above are not included here.

The sand lance schools that contained at least ten fish were included in the subsequent analysis. Because prey-mapping occurred in a single, linear dimension along the track of the prey-mapping ship, the distances between prey schools and patches calculated here are the distances between sequentially recorded schools and patches, i.e. between schools and patches in chronological order.

The distances between schools along the track of the prey-mapping ship were calculated, and their frequency distribution displayed as histogram (Figure 1). The distance at which the first clear minimum in the frequency distribution occurred was identified, and all sequentially recorded schools separated by distances shorter than this distance were grouped into patches called L2 patches (Benoit-Bird et al., 2013a). The length of each L2 patch was calculated as greatest pairwise distance between all schools inside the patch. The distances between sequentially recorded L2 patches was calculated as smallest pairwise distance between schools from the two patches.

Similar to the grouping of schools into L2 patches, L2 patches were grouped into larger L3 patches, based on a clear break identified in the frequency distribution of distances among L2 patches. The length of each L3 patch was calculated as greatest pairwise distance between schools belonging to the L2 patches inside each L3 patch. The distance between each L3 patch was calculated as smallest pairwise distance between schools belonging to the L2 patches inside sequentially recorded L3 patches.

The identification of these patches as well as the measurement of the length and distances among patches was repeated until no clear break could be identified in the frequency distribution of patch distances. The greatest pairwise distances among all schools was calculated to determine the spatial extent of the prey field mapped during the day.

Comparison of spatial scales of sand lance aggregations and bubble feeding behavior

To investigate the correlation between the mean scale of whale foraging and the mean scale of prey aggregation at the same nested hierarchical level, the mean size of feeding events and bouts of every whale at every hierarchy level were plotted as a function of the mean size of prey schools and patches recorded that day on the respective hierarchy level. The data from all deployments were combined to calculate Spearman Rank Correlation of the mean scale of whale foraging with the mean scale of prey aggregation. Similarly, the mean distances between feeding events and bouts of every whale were plotted as a function of the mean distances between prey patches on the respective hierarchy level. The data from all deployments was combined to calculate Spearman Rank Correlation of the mean distances between feeding events and bouts with the mean distances between prey schools/patches over all common hierarchy levels.

To analyze the differences between the lengths of feeding bouts and sand lance patches and the distances between them, all data on the sizes and distances of all bouts and patches (not just the means which were used in the correlation analysis) were used to create boxplots summarizing the scales of whale feeding bouts and prey aggregations on every hierarchy level. Two sample one-sided Wilcoxon Rank Sum tests were used to investigate, whether on each hierarchy level, feeding activity was limited to areas where sand lance patches were aggregated. For these tests, the null hypothesis was that there was no difference between the lengths of prey patches and feeding bouts, and the alternative hypothesis that the lengths of feeding bouts were smaller than the lengths of prey patches. To examine whether, on each hierarchy level, whales moving between prey patches minimized time between the patches, two sample one-sided Wilcoxon Rank Sum tests investigated the null hypothesis that there was no difference between the distances between sequentially recorded prey aggregations and the distances between sequential whale foraging areas, and the alternative hypothesis that the distances between whale foraging areas were greater than the distances between prey aggregations.

For all statistical hypothesis tests, p-values smaller than 0.01 were considered to provide strong evidence, p-values greater than 0.01 but smaller than 0.05 were considered to provide moderate evidence, p-values greater than 0.05 but smaller than 0.1 were considered to provide suggestive evidence and p-values greater than 0.1 were considered to provide no evidence to support the alternative hypothesis.

Comparison of sand lance schools inside and outside of feeding bout areas

In ArcGIS, the locations of all foraging events of the foraging whale were plotted onto a bathymetric chart of the study region. Around each feeding event, a circle was drawn using the buffer command with a radius approximately representing the radius in which sand lance schools could be available to the whale. This radius was determined by calculating the mean of the mean distances between sequential feeding events inside the bouts, to approximate the distance swum by the whale from one feeding event to the next. Half of the mean length of all sand lance schools recorded that day were added, to represent the distance from the edge of an averaged-size sand lance school to its center. The circles around feeding events from the same bout were merged to create areas referred to as 'feeding bout areas'. For each feeding bout recorded that day, sand lance schools recorded during the time the whale was foraging inside the bout were identified, and grouped based on whether their center was located inside or outside of the area marked by the merged circles outlining the foraging bout area. Schools located inside of the bout areas were grouped together, and schools outside of the bout areas were grouped together. Mean height and density of schools recorded inside and outside of the feeding bout areas of each whale were visualized as boxplots, and two sample one-sided Wilcoxon Rank Sum tests were used to compare mean school height and density between the two groups (Mann and Whitney, 1947; Zar, 1999). These comparisons were made for all tagged animals for which each group contained at least six schools. For each test, the null hypothesis was that there was no difference in mean height or mean density between schools inside and outside of feeding bout areas. The alternative hypothesis was that schools inside feeding bout areas had a greater mean height or higher mean density than schools outside of feeding bout areas.

Results

WHALE BEHAVIOR DATA ANALYSIS

Data on the bubble-feeding behavior of nine whales tagged on six days in 2008, 2009 and 2012 was included in the analysis (Table 1). At least two hierarchy levels were found in the feeding behavior all whales (Figure 2). For eight out of the nine whales, three hierarchy levels were found (Table 2). The frequency distributions of distances between sequential feeding events and bouts used to form L2 and L3 bouts can be found in the Appendix. Bout length increased with increasing hierarchy level from a mean rFPT value of 6.6 m to a mean L3 bout length of 629.5 m on the third level. Inter-bout distance increased with increasing hierarchy level from a mean distance between feeding events of 142.4 m to a mean distance between L3 bouts of 1610.4 m.

PREY DATA ANALYSIS

Sand lance schools were recorded on all six days during which prey mapping was conducted around the tagged whales (Table 3). At least three hierarchy levels were found in the prey data on each day (Figure 3). On three of the six days, four hierarchy levels were found, and on the day with the greatest spatial prey mapping extent, five levels were found (Table 4). The frequency distributions of distances between sequentially recorded sand lance schools and patches used to form L2-L5 patches can be found in the Appendix. Patch length increased with increasing hierarchy level from a mean school length of 47.1 m to a mean length of 3906.9 m of L5 patches. Inter-patch distance increased from a mean inter-school distance of 140.5 m to a mean distance between L4 patches of 1185.5 m, and decreased to 560. 8 m between the two L5 patches identified.

COMPARISON OF SPATIAL SCALES OF SAND LANCE AGGREGATIONS AND WHALE BUBBLE-FEEDING BEHAVIOR

The relationship between the mean size of the feeding bouts of every whale at each hierarchy level against the mean size of prey patches recorded that day on the respective hierarchy level is shown in Figure 4. Spearman Rank Correlation revealed a significant positive association between the mean lengths of feeding bouts and the mean lengths of prey patches on the three common hierarchy levels ($r_S = 0.81$, $p < 0.001$).

The relationship between the mean distance between the feeding bouts of each whale and the mean distance between prey patches recorded that day on the respective hierarchy level is shown in Figure 5. The mean distance between prey patches increased between hierarchy level 2 and 3 on all days except one (July 2, 2008). Consequently, the correlation of mean distances between feeding bouts with the mean distances between prey patches could only be calculated for the first two hierarchy levels. Spearman Rank Correlation revealed a significant positive association between the mean distances among feeding bouts and the mean distances among prey patches on the first two hierarchy levels ($r_S = 0.72$, $p < 0.001$).

The lengths of and distances among feeding bouts and prey patches were compared on each common level of the nested hierarchy using all data (not just the means used in the correlation analysis). On all three common hierarchy levels, mean prey patch length was greater than the mean length of feeding bouts (Figure 6). The differences in patch lengths were statistically significant for all three levels according to one-sided Wilcoxon Rank Sum tests with the null hypothesis that that there was no difference in mean patch and bout length, and the alternative hypothesis that mean bout length was shorter than mean patch length (Level 1: $W = 9568$, $p < 0.001$, level 2: $W = 3229$, $p < 0.001$, level 3: $W = 141$, $p < 0.01$) For all three common levels of the nested hierarchy, the mean distance between sand lance patches was at least slightly smaller than the mean distance between whale feeding areas on all three hierarchy levels, and this difference increased with increasing hierarchy level (Figure 7). These differences in distances were statistically significant for only the third hierarchy level according to one-sided Wilcoxon Rank Sum tests with the null hypothesis that there was no difference in mean distance among bouts and patches, and the alternative hypothesis that the mean distance among bouts was greater than distances among patches (Level 1: $W = 166010$, $p = 0.978$, level 2: $W = 3992$, $p = 0.798$, level 3: $W = 184$, $p < 0.01$).

COMPARISON OF SAND LANCE SCHOOLS INSIDE AND OUTSIDE OF FEEDING BOUT AREAS

For six out of the nine tagged animals, mean height and density of sand lance schools inside and outside of feeding bout areas could be compared (Table 5, Figure 8). In four out of the six animals, mean height was greater in schools recorded inside than outside of feeding bout areas, and two of these differences were found to be statistically significant (Figure 9). In four out of six comparisons, mean density was greater in schools inside than outside of feeding bout areas, and one of these differences was found to be statistically significant (Figure 10). For each animal, at least one parameter – either mean height or mean density – was greater in schools recorded inside than outside of feeding bout areas.

Discussion

In the marine environment, resource distribution often occurs over multiple, spatially nested scales. Previous studies have found that the adaption of a similar spatially nested structure in the movement of predators foraging on heterogeneously distributed resources can lead to an increase in their foraging efficiency (Benoit-Bird et al., 2013a; Fauchald et al., 2000; Russell et al., 1992). Using tag technology to record underwater movement in combination with surface observations of whale behavior and concurrent hydroacoustic measurement of prey distribution around tagged whales, the present study found evidence for spatially nested behavior of humpback whales bubble-feeding in in spatially nested prey patches, and a strong positive correlation between the geometry of humpback whale feeding bouts and their prey patches over multiple scales. Prey schools inside feeding areas were characterized by properties that rendered them energetically more profitable for whale foraging than schools within close spatial proximity where feeding did not occur. Spatially nested foraging behavior in baleen whales has been suggested but not demonstrated for North Atlantic right whales (Kenney et al., 2001). The present study is the first to demonstrate spatially nested foraging in a baleen whale species, and to show significant correlations with the geometry of the spatially nested prey field.

CAVEATS OF SAMPLING METHODS

Potentially confounding the spatial predator-prey relationship observed here is that the fact that the prey mapping did not always occur in the exact location at the exact time of bubble feeding activity. While focused on the location of the feeding whales, the prey mapping always lagged behind the actual feeding locations, due to the unpredictable movement of the whale. However, by quantifying the overall effect of the prey field geometry on the overall geometry of feeding areas during each deployment, the need for strictly synoptic measurement of predator and prey behavior was overcome. Another potentially confounding factor is the spatial accuracy of the locations of bubble feeding events, which was dependent on the spatial accuracy of the triangulated whale positions, and estimated to be around 80 m (Thompson, pers. comm.). By geo-referencing each whale's pseudotrack, the tag-based whale locations were forced to approximate as many triangulated positions as possible (Liu et al., 2015). In this way, the effect of inaccurate, outlying triangulated positions was reduced, and the most likely location for each whale at every second within a 95% credible interval was calculated (Liu et al., 2015). Another potentially confounding factor of the predator-prey relationship studied here is the assumption that the prey field remained static during the prey mapping period each day. The apparent decrease of inter-patch distances with increasing spatial scale recorded for some days could be explained by the displacement of sand lance by currents or the swimming activity of the fish relative to the prey mapping activity. This effect could result in an overestimation in the number or sizes of patches or an underestimation of inter-patch distances, and is likely minimal for patches recorded over short spatial and temporal scales and increases with increasing scales. While the present study is based on a small sample size, the results are based on multiple, independent prey mapping periods conducted on six days in three different years, and prey mapping period would likely be effected differently by the spatial displacement of sand lance schools. Therefore, it is unlikely that these caveats influence the observed correlation between whale feeding and prey patch geometry.

ENERGETIC PROFITABILITY OF SCHOOLS INSIDE AND OUTSIDE OF FEEDING BOUT AREAS

While synoptic predator-prey measurements were not pivotal for the current analysis, for at least six out of the nine tag deployments, the prey mapping did overlap in both space and time with the feeding activity of the tagged whales. This confirms that the sand lance patches recorded during the prey mapping represented the prey field of the feeding whales. Analyzing the prey field of these six whales showed that prey schools inside compared those outside feeding bout areas were always characterized by either greater mean height or higher mean density; properties rendering them more energetically profitable for bubble-feeding whales. However, it is unclear whether these properties were the result of prey manipulation or evidence for active choice of more profitable patches by the whales. Components of whale foraging behaviors have been assumed to corral or compact prey schools and could be responsible for the increased heights and densities of schools inside feeding bout areas (Hain et al., 1982; Wiley et al., 2011). Undisturbed sand lance schools observed by Meyer et al. (1979) in the southern Gulf of Maine were estimated to be ten times longer than tall, suggesting that the increased vertical extent of schools recorded in whale foraging areas might have been the result of prey manipulation by the whales. However, analyzing humpback whale foraging behavior around SBNMS in 2006, Hazen et al. (2009) found bubble-feeding to occur more commonly near vertically pronounced, dense sand lance schools. Schools that already have a pronounced vertical orientation may be easier to manipulate during bubble-feeding, and may therefore be actively sought out by foraging whales (Hazen et al., 2009). It is possible that different whales have different patch preferences where, depending on their feeding technique, schools with either a pronounced vertical extent or an increased fish density could be sought out (Wiley et al., 2011).

SAND LANCE PATCH GEOMETRY

The observed geometry of sand lance patches over multiple spatial scales likely was the result of a combination of spatial proximity to both suitable benthic and pelagic habitat. Due to their high benthic habitat specificity targeting particular substrate compositions in certain hydrological conditions within a specific depth range (Behrens et al., 2007; Holland et al., 2005; Meyer et al., 1979; Reay, 1970; Wright et al., 2000), benthic habitat suitable for sand lance burying is likely very heterogeneously distributed (Robards et al., 1999; Scott, 1968). Due to their relatively poor swimming abilities, they likely do not move far from suitable burying habitat when foraging in the water column; and consequently, their occurrence is assumed to be limited to areas where productive areas in the water column and suitable burying habitat are within close spatial proximity to each other (Freeman et al., 2004; Haynes and Robinson, 2011; Reay, 1970; van der Kooij et al., 2008).

On five of the six days of this study, prey mapping was conducted immediately on or around Stellwagen Bank; and consequently, the scales of sand lance aggregations associated with the Bank were likely the main drivers of the sand lance patch scales quantified here. Hazen et al. (2009) found that sand lance biomass in SBNMS was highest near the steep western slope of the Bank. In this area, upwelling promotes increased biological productivity, and the interaction of tidally driven currents with the slope creates internal waves that can aggregate zooplankton and, consequently, sand lance (Haury et al., 1979; Hazen et al., 2009; Pineda et al., 2015). The scale of sand lance aggregation along the western side of the 39 km long Bank (Meyer et al., 1979) exceeds even the greatest spatial extent of prey mapping conducted for this study (9100.8 m). Therefore, the aggregation of sand lance caused by hydrodynamic effects of the steep western slope of the Bank was likely not fully captured here. However, on the day where the spatial extent of the prey mapping was greatest, the largest scale of sand lance aggregations was found, with a mean length of 3906.9 m for two L5 patches. This largest scale could represent the aggregation of sand lance over part of the western slope of Stellwagen Bank. It is likely that with greater spatial extent of the prey mapping effort, additional scales of sand lance aggregations could be found. Smaller scales of sand lance aggregations were found nested within the largest spatial scale. While the largest spatial scale likely represents the overall aggregation of sand lance over the western slope compared to the remaining shallow areas of Stellwagen Bank, the nested smaller scales could represent successively smaller areas with increased slope or upwelling, leading to a denser aggregation of sand lance schools in these smaller areas. The smallest scale of sand lance aggregations was the average length of sand lance schools, 47 m. The small standard deviation of 7 m indicates a consistency in sand lance schools length over the three years analyzed, suggesting that this scale is dictated by the behavior sand lance in the study area (Brierley and Cox, 2015).

CORRELATION IN PREDATOR-PREY PATCH GEOMETRY

The current study found that whale feeding bouts were always shorter than sand lance patches on all common hierarchy levels. Fauchald and Tveraa (2006) suggested that the scales of foraging movement of individual Antarctic petrels (*Thalassoica antarctica*) were likely smaller than the sizes of their prey patches, as they might not explore the entire patch area. This suggests that the predators are able to remain within the edges of their prey patches (Bell, 1991), as an excursion beyond the patch edges would render the scales of the predator’s foraging movement greater than the patches themselves. In the present study, the notion that the tagged whales feeding alone or in small groups were able to remain inside patches is supported by the fact that feeding bouts were always shorter than prey patches. Fauchald et al. (2000) showed that aggregations of murres in the Barents Sea were of the same size as aggregations of their capelin prey over multiple, spatially nested scales. This further supports the idea that the size of predator foraging areas relative to prey patch areas depends on the ability to explore the patches. Likewise, (Benoit-Bird et al., 2013a) found that the foraging behavior of tagged northern fur seals showed spatially nested scales corresponding to the nested scales of their pollock prey patches. In contrast to a feeding event of a northern fur seal, which targets an individual fish (Hocking et al., 2014), each humpback whale bubble-feeding event targets a part of a fish school (Potvin et al., 2012). When a whale is feeding inside a patch, this feeding activity may elicit predator avoidance behavior of the sand lance (Pitcher and Wyche, 1983), rendering the patch unprofitable for sustained bubble-feeding activity (Sih, 1984). This would cause the whale to abandon the patch before completely moving through it, and result in shorter feeding bout lengths compared to prey patch lengths. In this way, differences in the foraging strategies of humpback whales and northern fur seals could explain the differences in the correlation between predator and prey patch geometry in these systems.

On the lowest hierarchy level L1 with the smallest spatial scale, the distribution of distance between sequential feeding events was similar to the distribution of distances between sequentially recorded sand lance schools, with average distances of 142.4 m and 140.5 m, respectively. This could suggest that sequential feeding events targeted neighboring schools. This, in turn, would suggest that on the lowest hierarchy level, the whales did not move randomly, but were aware of the locations of neighboring schools. Moving between neighboring prey schools would cause the whales to remain inside a prey patch on the second level of the spatial hierarchy. On the larger L2 scale, the distances between bouts were greater than the distances between prey patches, and this spatial discrepancy was statistically significant on the third L3 hierarchy level. This suggests that whales that terminated a feeding bout did not concentrate the foraging effort of the next bout in the nearest patch. This could be because an increased level of satiation following the termination of a feeding bout resulted in the whale moving past nearest patch (Beukema, 1968), or because the feeding activity of other whales in the nearest patch forced the whale to move on to another patch. Another explanation could be that the ability of the whales to locate the nearest patch decreased with increasing distance to the patch. However, the whales may have also been actively targeting patches with certain characteristics instead of simply moving to the nearest patch. (Benoit-Bird et al., 2013a) found that the distances among the foraging patches of fur seals matched the distances among their prey patches over all hierarchy levels found in the study, and that on each hierarchy level, the fur seals preferentially foraged in patches located in close proximity to each other. This could indicate that the fur seals had an increased awareness of their prey field compared to the whales studied here that allowed them to minimize the time between patches. However, this could also suggest that inter-patch distance was not the only factor driving the inter-patch movement of the foraging whales. Instead, their movement may have been driven by the locations of patches that were more conducive to their bubble-feeding strategy, i.e. by the locations of patches containing schools with either increased vertical extent or increased fish density (Hazen et al., 2009). This is supported by the findings presented here that schools inside whale feeding bout areas differed from those outside whale feeding bout areas.

Conclusion

The results presented here suggest that bubble-feeding humpback whales minimize time and energy spent between prey patches, and looking for new patches, by feeding on neighboring prey schools, thereby remaining within the edges of a prey patch. Based on the current findings that the whales appear to adapt their bubble-feeding movements to the geometry of prey schools at the lowest hierarchy level, it appears that the spatially nested foraging movements described here are a consequence of the adaptation of foraging movement to the encountered prey field, and not an inherent search strategy (Miramontes et al., 2012). A successful bubble-feeding event in a profitable prey patch could lead to an increase in localized foraging effort, leading to a feeding bout. A reduction in bubble-feeding success through resource depression – either an exploitation of the sand lance in the patch, or sand lance predator avoidance behavior (Bell, 1991; Pitcher and Wyche, 1983) – could lead to the whale swimming slightly longer distances than the mean distances between schools inside the initial patch, and arriving in a new patch. In this way, the movement of the whales could be described as area-restricted search. However, the triggers that lead to the initial encounter with a sand lance school remain unclear. Due to their high habitat specificity, sand lance exhibit site fidelity to their preferred burial habitat (Haynes and Robinson, 2011). Whales encountering sand lance schools might be able to learn in what areas they can expect to find sand lance patches, and visit these areas habitually. Stevick et al. (2006) suggested the use of spatial memory as foraging strategy in Western North Atlantic humpback whales. They observed strong inter-annual site fidelity of individually identified humpback whales to small areas several thousand meters in length, likely corresponding to productive prey patches (Stevick et al., 2006). Such site fidelity could explain the frequent observations of large numbers of humpback whales on the northern and southern part of the western edge of Stellwagen Bank; areas characterized by benthic habitat suitable for sand lance burial (Hazen et al., 2009; Stellwagen Bank National Marine Sanctuary Final Management Plan and Environmental Assessment, 2010).

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Figures

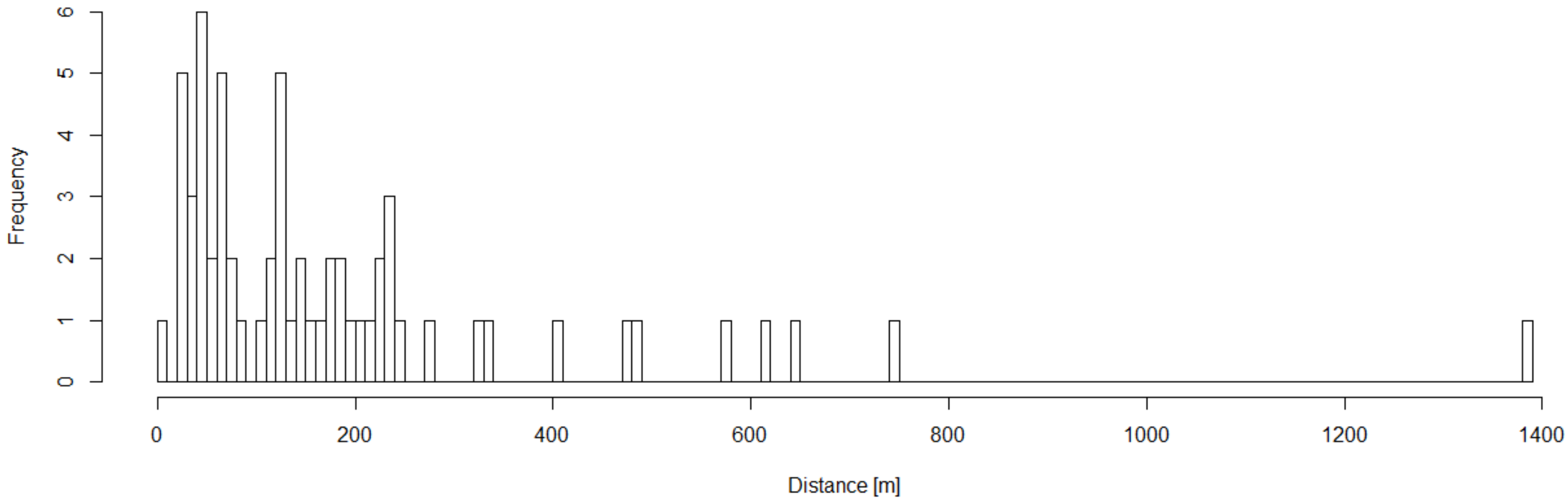

Figure 1: Frequency distribution of distances between sequentially recorded sand lance schools on July 22, 2009. The first break, based on which schools were grouped into L2 patches, was identified at 90 m.

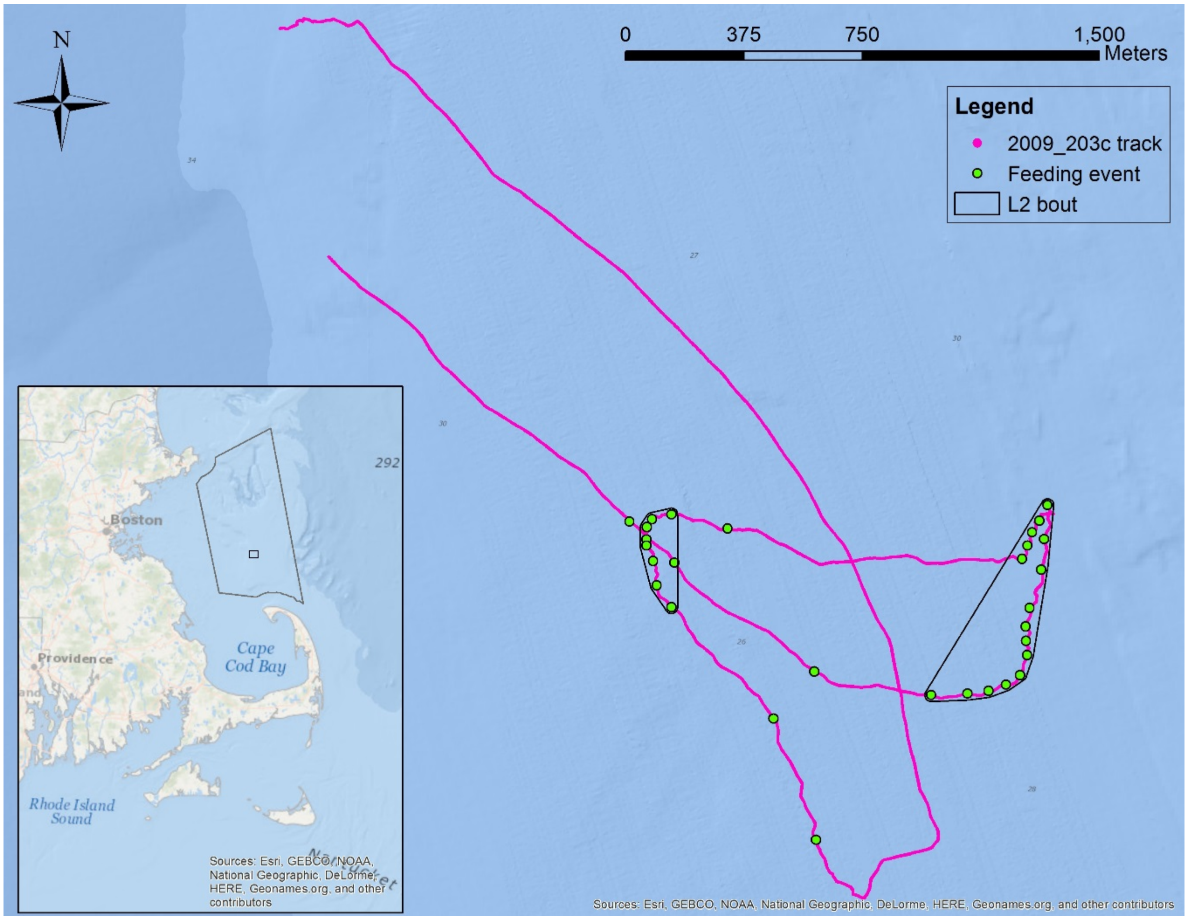

Figure 2: Grouping of feeding events into L2 bouts for whale Mn09_203c tagged on July 22, 2009. The small inset shows the location of the track in the boundaries of SBNMS.

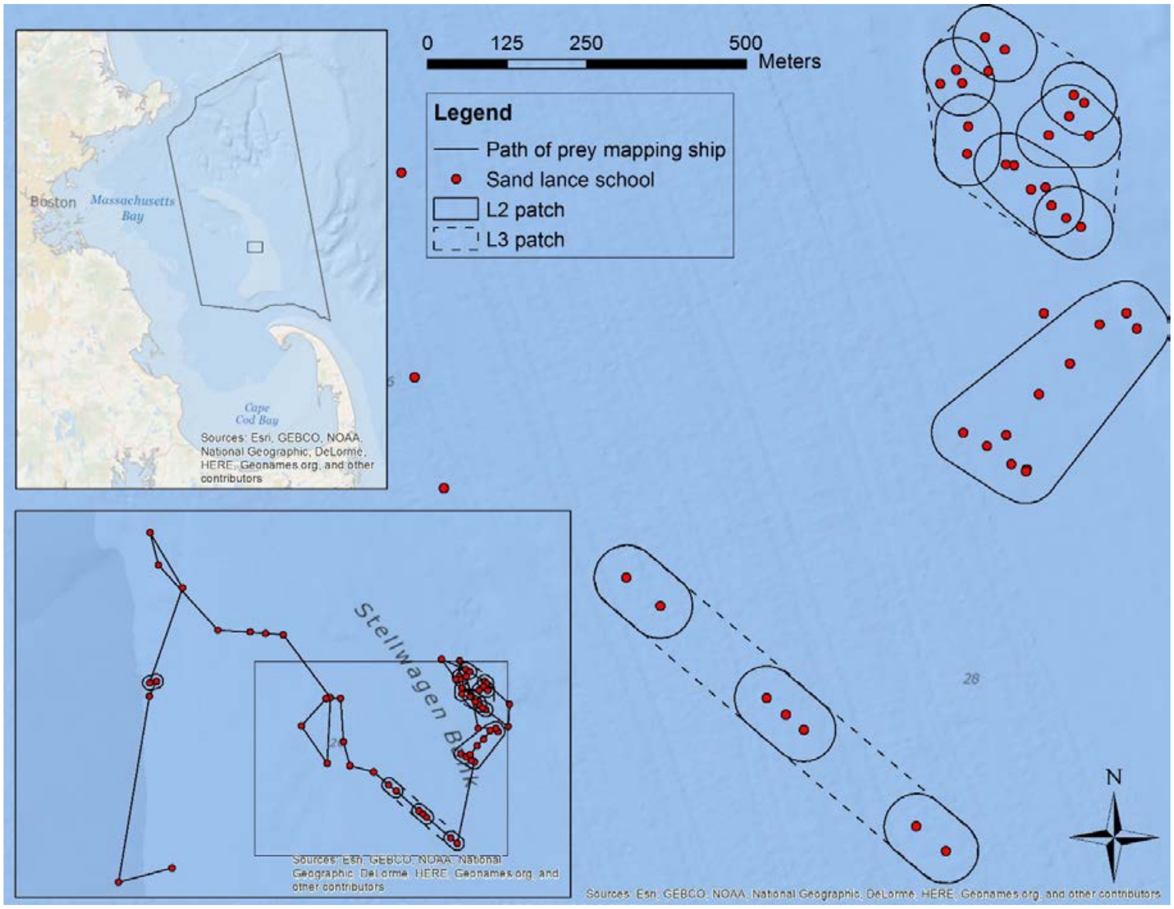

Figure 3: Spatially nested sand lance patches recorded on July 22, 2009 around tagged whale Mn09_203c. The top inset shows the location of the prey mapping effort within SBNMS that day. The bottom inset shows the path of the prey mapping ship, the recorded sand lance schools and the locations of L2 and L3 patches. The main map is focused on the main concentration of patches in the eastern part of the prey mapping effort. For clarity, the path of the prey mapping ship is not shown on the main map.

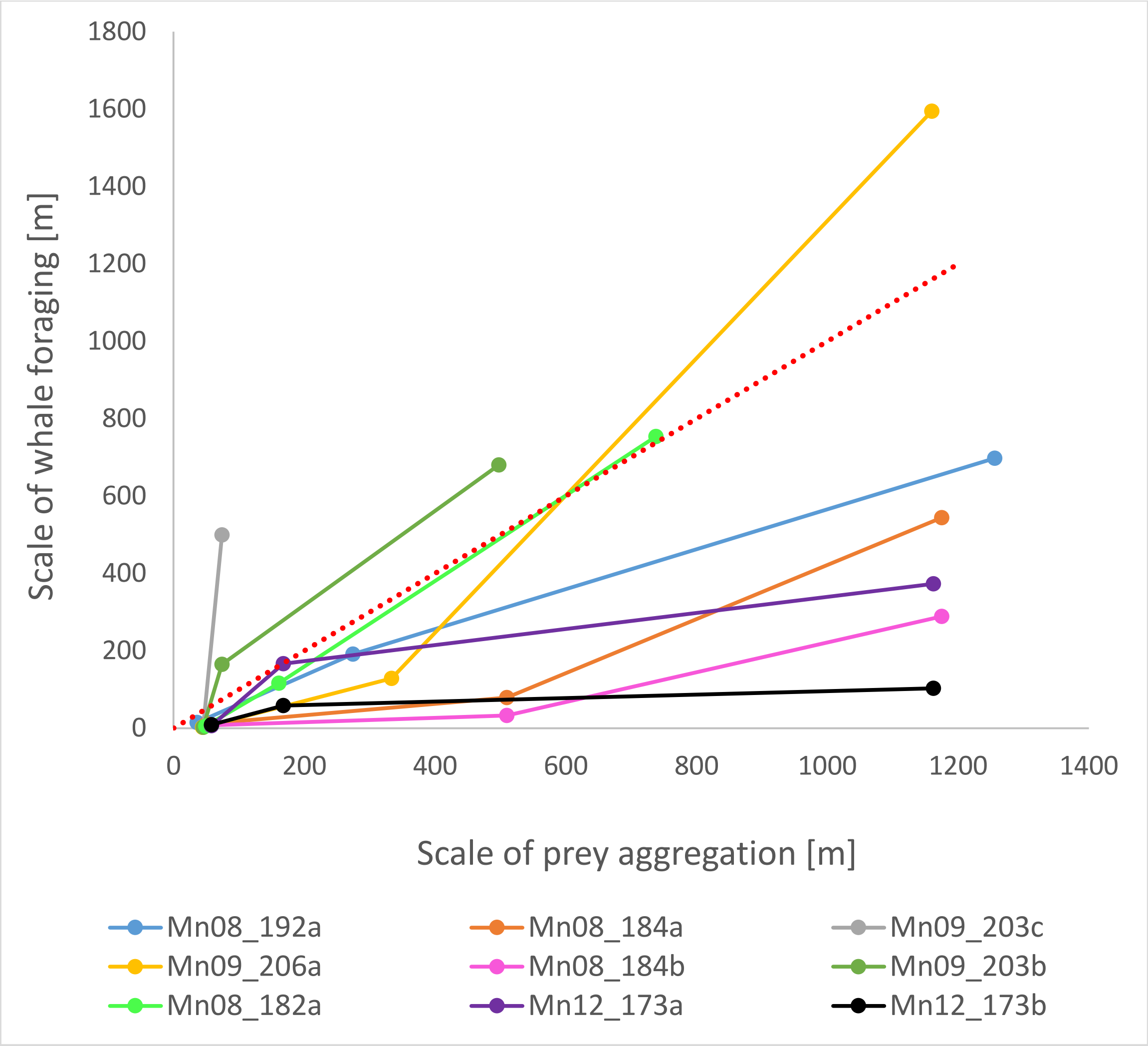

Figure 4: Mean length of feeding events/bouts on each hierarchy level as a function of the mean length of prey patches on the respective hierarchy level. The dotted red line indicates a 1:1 ratio between the lengths of whale foraging areas and the lengths of prey aggregations.

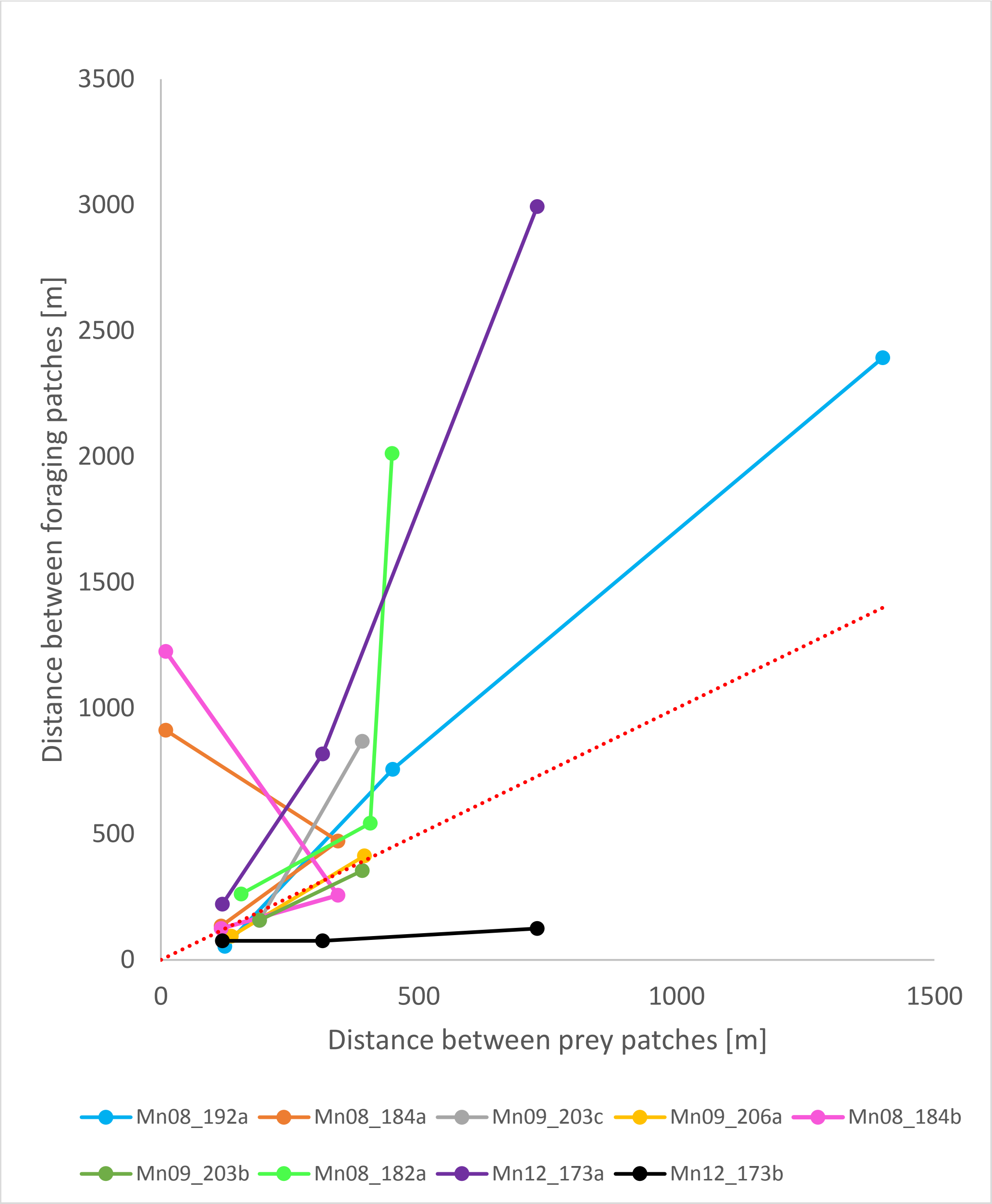

Figure 5: Mean distance between feeding events and bouts as a function of the mean distance between prey patches on each hierarchy level. The dotted red line indicates a 1:1 ratio between the mean distances between whale foraging areas and the mean distances between prey patches.

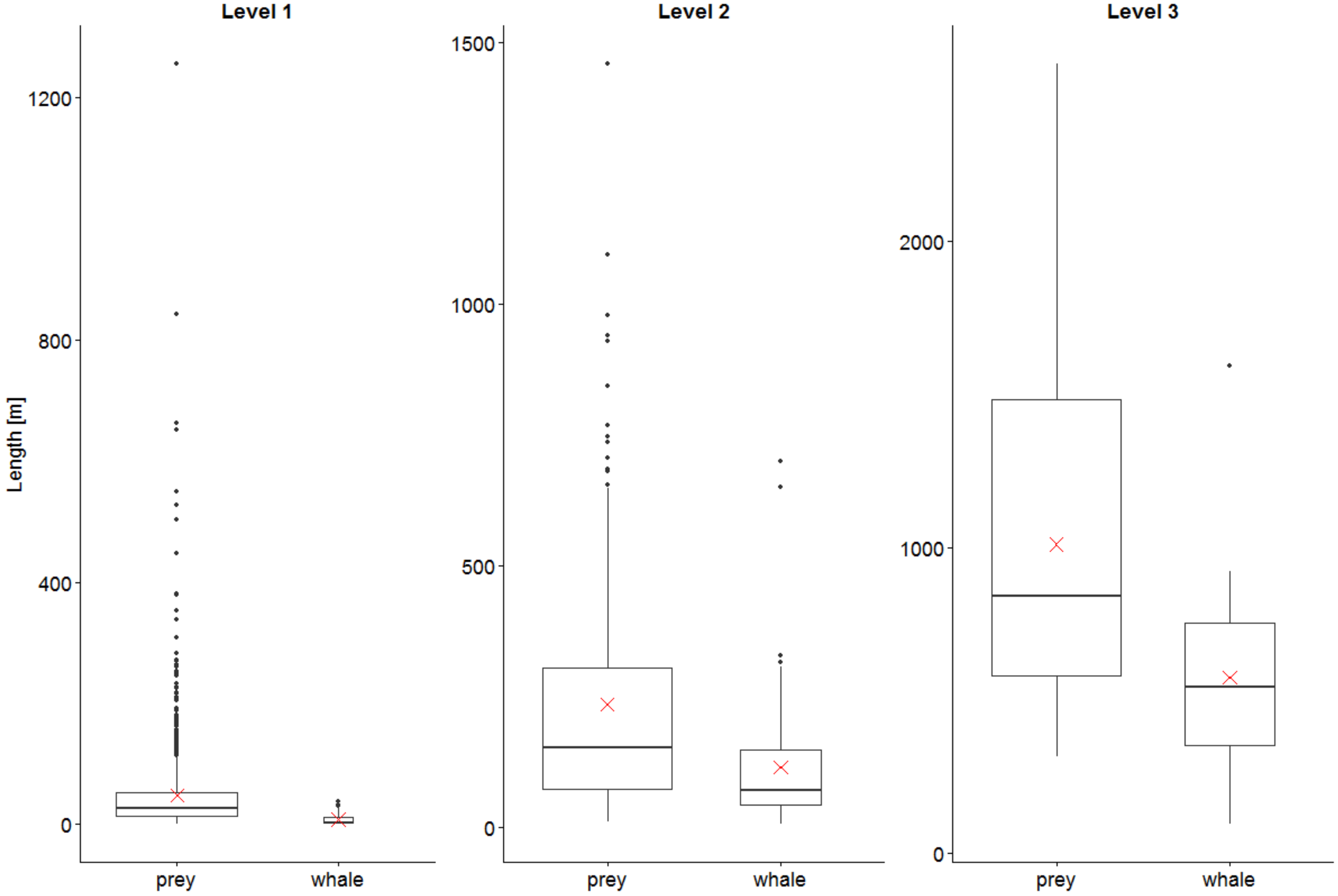

Figure 6: Boxplots comparing the lengths of sand lance schools/patches to the lengths of whale feeding events/bouts for all 3 common levels of the nested hierarchy - level 1 compares sand lance schools (n=1040) to the rFPT determined for all bouts (n=63), level 2 compares L2 sand lance patches (n=163) to L2 bouts (n=63), and level 3 compares L3 sand lance patches (n=34) to L3 bouts (n=16). The width of each box is scaled relative to the sample size for each comparison. Red crosses indicate the location of the mean.

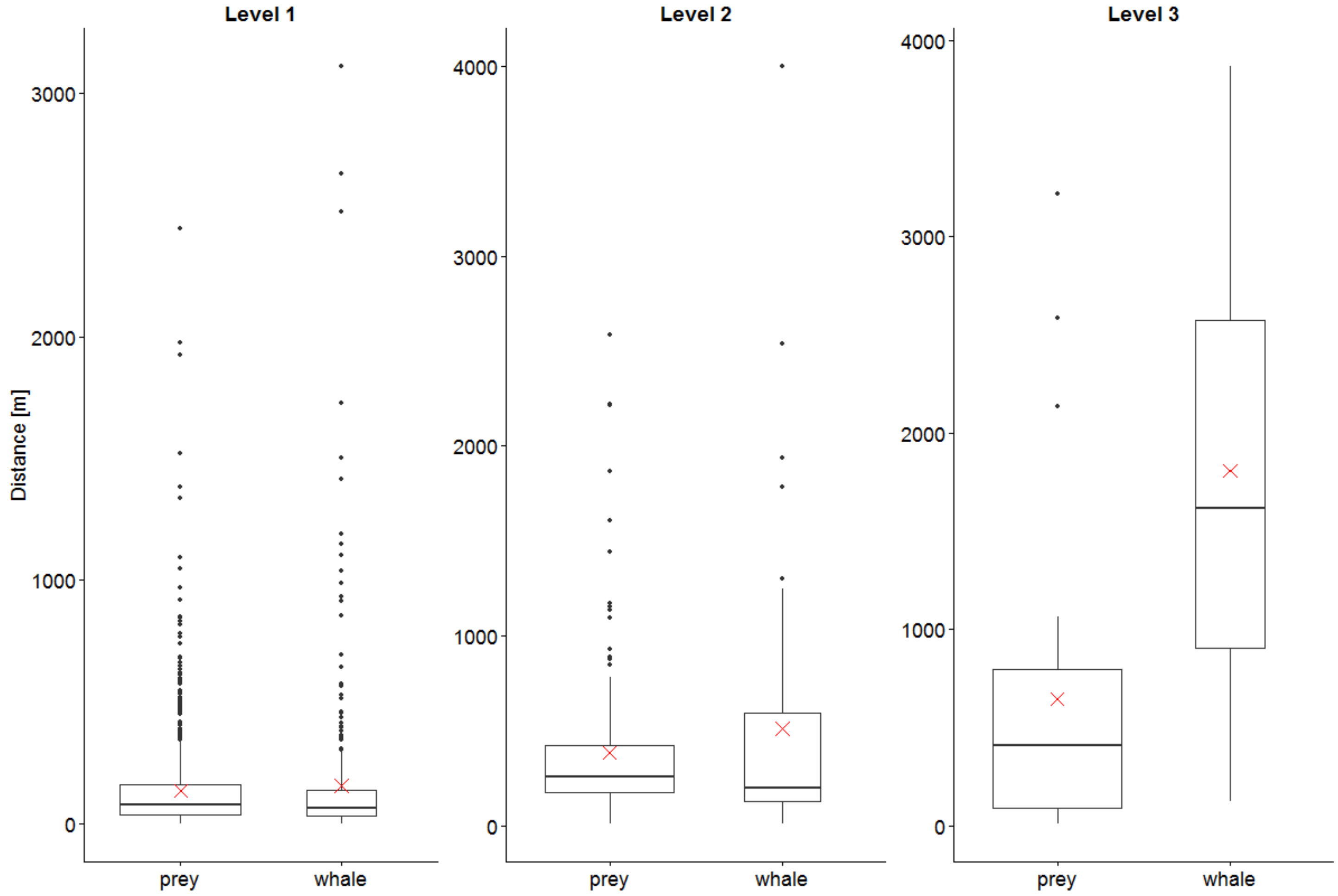

Figure 7: Boxplots comparing the distances between sequentially recorded sand lance schools/patches and the distances between sequential feeding events and bouts for all 3 common levels of the nested hierarchy – level 1 compares the distances between schools (n=1034) and feeding events (n=346), level 2 the distances between L2 patches (n=157) and L2 bouts (n=55), and level 3 the distances between L3 patches (n=28) and L3 bouts (n=8). The width of each box is scaled relative to the sample size for each comparison. Red crosses indicate the location of the mean.

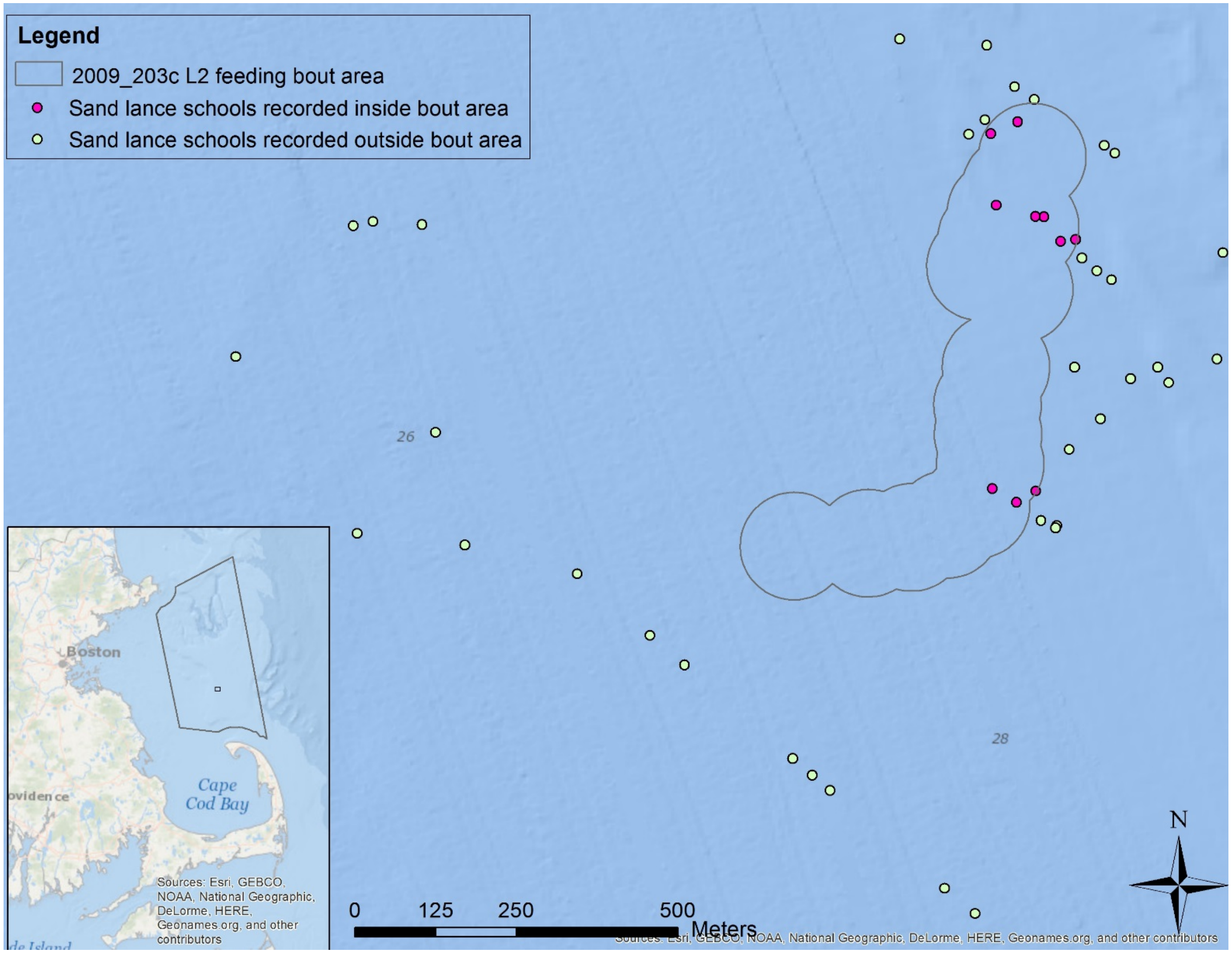

Figure 8: Locations of sand lance schools recorded inside and outside of one of the two feeding bout areas of whale Mn09_203c on July 22, 2009.

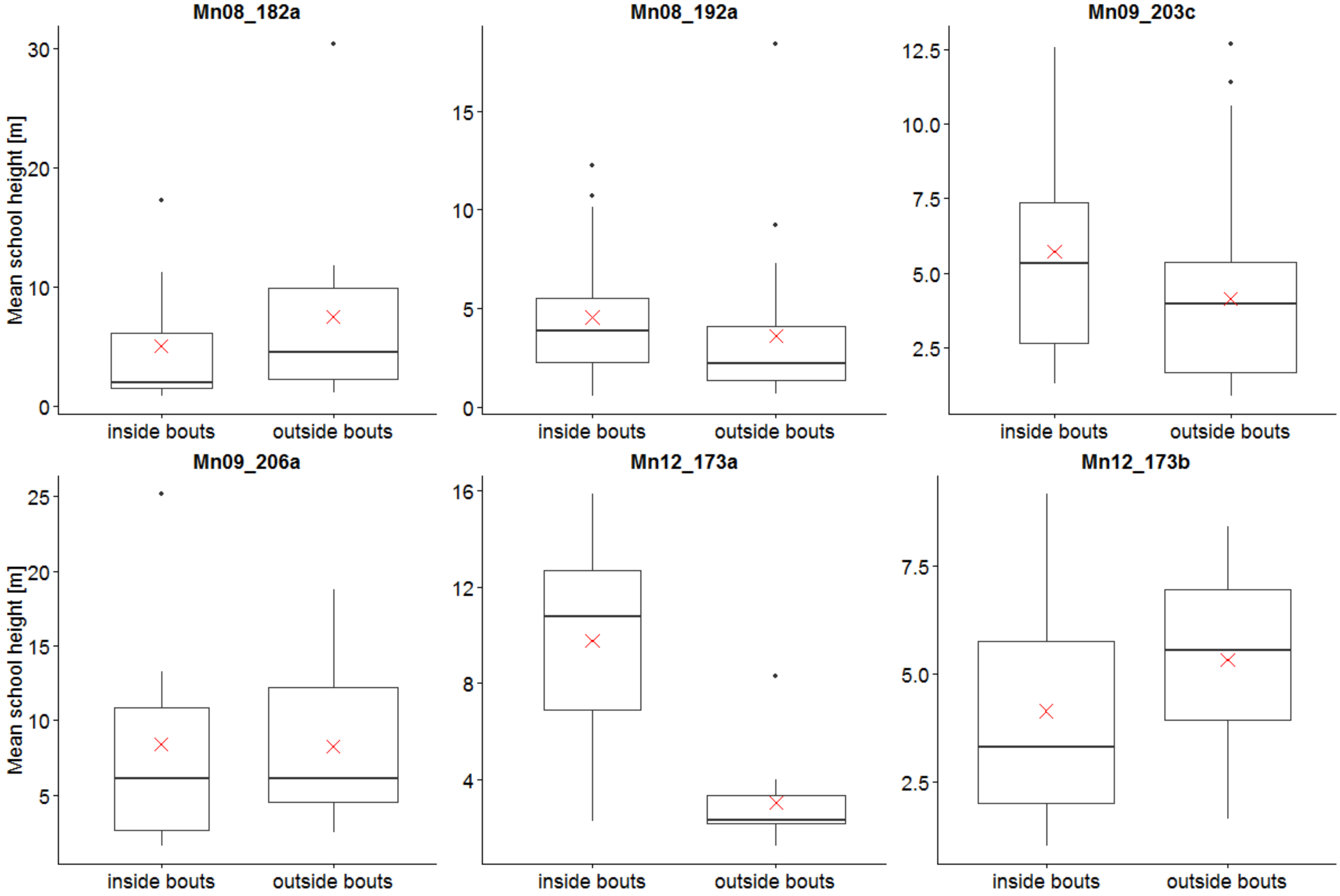

Figure 9: Boxplots visualizing the mean height of schools recorded inside and outside the feeding bout areas of each of the six tagged animals included in the analysis. Red crosses indicate the location of the mean.

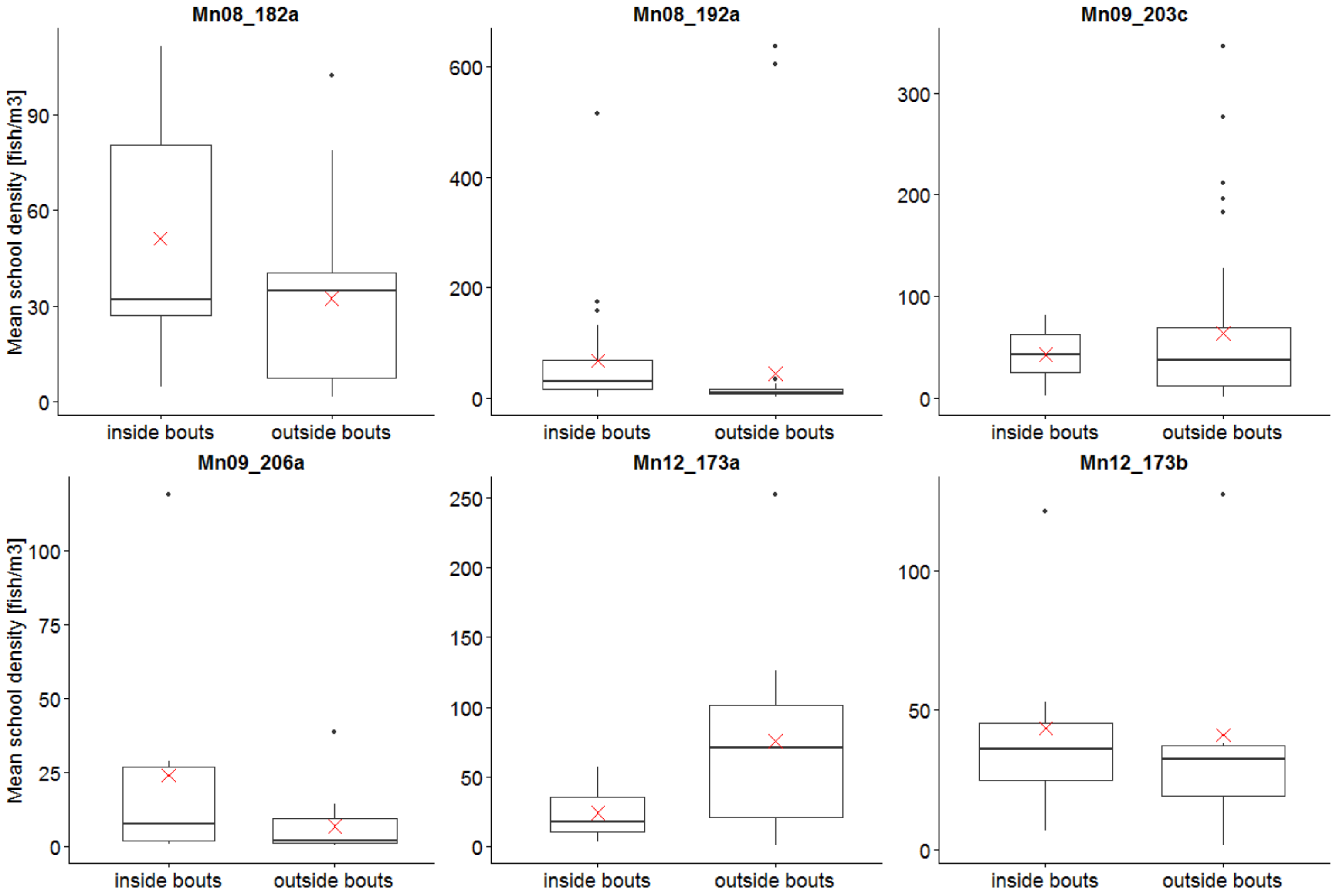

Figure 10: Boxplots visualizing the mean density of schools recorded inside and outside the feeding bout areas of each of the six tagged animals included in the analysis. Red crosses indicate the location of the mean.

Tables

Table 1: Overview over the nine DTAG deployments included in the analysis.

Deployment	**Date**	**Time of first feeding event (time zone: EDT)**	**Duration of recorded foraging behavior (h:mm:ss)**	**Spatial extent of foraging (m)**	**No. feeding events**	**Distance between feeding events (m)**
08_182a	6/30/08	10:31:42	8:11:58	3373.3	44	262.2 (532.9)
08_184a	7/2/08	13:57:47	4:48:06	3434.4	59	134.3 (222.5)
08_184b	7/2/08	15:49:19	2:54:53	2724.2	42	125.3 (176.8)
08_192a	7/10/08	13:05:25	4:26:45	4681.1	98	54.3 (378.6)
09_203b	7/22/09	15:04:33	2:17:41	1469.1	29	157.2 (221.6)
09_203c	7/22/09	15:06:09	2:16:06	1328.2	30	156.5 (206.8)
09_206a	7/25/09	12:51:59	1:49:50	1814.7	31	94.3 (78.3)
12_173a	6/21/12	10:11:40	3:30:26	3820.3	33	221.7 (432.3)
12_173b	6/21/12	15:35:46	0:52:04	392.0	18	75.6 (58.5)
Average			**3:27:32**	**2559.7**	**42.7**	**142.4**
SD			**2:02:47**	**1392.1**	**23.8**	**67.0**

Table 2: Spatially nested hierarchies of the foraging behavior of all tagged whales. The average values for each measurement were calculated for each animal wherever the sample size was at least two; the standard deviation is included in parentheses. Where a range of rFPT values was calculated, this range is also given.

Deployment	Date	No. hierarchy levels	No. L2 bouts	No. feeding events/L2 bout	Bout duration (min)	Length L2 bout (m)	Distance between L2 bouts (m)	rFPT (m)	No. L3 bouts	Length L3 bouts (m)	Distance between L3 bouts (m)
08_182a	**6/30/08**	3	8	4.4 (4.4)	8.9 (9.7)	116.1 (88.5)	543.3 (496.3)	5.3 (6.0) 2-16	2	754.1 (8.5)	2012.6
08_184a	**7/2/08**	3	12	4 (1.9)	6.7 (3.4)	78.9 (41.5)	471.7 (501.5)	11.2 (10.5) 2-38	2	544.0 (83.8)	912
08_184b	**7/2/08**	3	11	2.6 (0.7)	5.3 (2.2)	32.5 (23.7)	256.5 (284.8)	7.6 (8.8) 2-30	2	288.8 (116.4)	1225.2
08_192a	**7/10/08**	3	12	8.5 (10.9)	12.7 (19.1)	191.5 (229.6)	757.1 (1170.2)	14.8 (12.1) 2-38	4	697.9 (228.3)	2393.3 (1491.7)
09_203b	**7/22/09**	3	5	4.8 (2.8)	11.0 (8.2)	164.7 (129.4)	355.3 (469.6)	2.0 (0.0)	1	680.5	NA
09_203c	**7/22/09**	2	2	12 (5.7)	45.8 (39.2)	499.9 (291.1)	868.4 (0)	2.0 (0.0)	0	NA	NA
09_206a	**7/25/09**	3	5	4.2 (2.5)	7.0 (4.0)	128.3 (91.6)	413.0 (205.7)	2.0 (0.0)	1	1595	NA
12_173a	**6/21/12**	3	6	4.2 (2.6)	17.2 (9.7)	166.3 (120.3)	818.6 (1002.5)	6.3 (9.7) 2-26	2	373.3 (118.7)	2994
12_173b	**6/21/12**	3	4	3.3 (1.0)	7.4 (2.6)	58.6 (21.3)	76.3 (89.9)	8.5 (5.7) 2-16	2	102.7 (12.2)	125.3
Average		**3**	**7.2**	**5.3**	**13.6**	**159.6**	**506.7**	**6.6**	**1.8**	**629.5**	**1610.4**
SD		**0**	**3.7**	**3.0**	**12.6**	**138.1**	**267.6**	**4.4**	**1.1**	**450.6**	**1051.7**

Table 3: Overview over the prey field recorded around the tagged whales.

Date	**Time first school recorded (EDT)**	**Duration prey mapping (h:mm:ss)**	**Spatial extent prey mapping (m)**	**No. of schools recorded**	**Length school (m)**	**Distance between schools (m)**
6/30/08	10:02:46	7:09:42	4448.8	191	49.3 (71.2)	155.3 (203.1)
7/2/08	11:59:11	3:53:44	4847.2	123	50.4 (54.7)	116.9 (135.6)
7/10/08	13:33:32	4:11:17	4925.9	146	35.8 (36.6)	123.7 (209.3)
7/22/09	13:47:28	2:40:15	3207.9	63	45.2 (47.9)	191.4 (225.7)
7/25/09	10:23:34	6:52:40	9100.8	284	44.1 (60.4)	136.5 (196.3)
6/21/12	11:19:44	5:23:22	4646.7	233	58.0 (124.4)	119.3 (209.7)
Average		**5:01:50**	**5196.2**	**173.3**	**47.1**	**140.5**
SD		**1:46:09**	**2012.7**	**79.5**	**7.4**	**28.7**

Table 4: Spatially nested hierarchies of the sand lance prey field recorded around the tagged whales. The average values for each measurement were calculated for each day wherever the sample size was at least two; the standard deviation is included in parentheses.

Date	**No. hierarchy levels**	**No. L2 patches**	**No. schools per L2 patch**	**Length L2 patch (m)**	**Distance between L2 patches (m)**	**No. L3 patches**	**Length L3 patches (m)**	**Distance between L3 patches (m)**	**No. L4 patches**	**Length L4 patches (m)**	**Distance between L4 patches (m)**	**No. L5 patches**	**Length L5 patches (m)**	**Distance between L5 patches (m)**
6/30/08	4	38	4.3 (3.2)	161.1 (154.6)	405.6 (389.6)	10	737.6 (350.4)	448.2 (369.7)	1	2527.3	0	0		
7/2/08	3	9	13 (14.3)	509.6 (450.3)	343 (458.9)	2	1175.0 (400.0)	9.3	0			0		
7/10/08	4	19	7.5 (7.7)	274.4 (191.2)	449.6 (503.7)	4	1255.7 (417.2)	1399.9 (1575.9)	2	2596.4 (1199.2)	862.6	0		
7/22/09	3	12	3.1 (2.6)	73.9 (80.3)	390.3 (510.2)	2	497.4 (231.1)	854	0			0		
7/25/09	5	43	6.3 (5.3)	333.3 (279.7)	394.6 (413.4)	11	1159.6 (657.5)	607.8 (774.5)	4	1764.5 (807.8)	1754.2 (1366.1)	2	3906.9 (2216.9)	560.8
6/21/12	4	42	5.2 (4.9)	167.9 (157.1)	313.6 (308.1)	5	1162.2 (743.2)	729.7 (985.0)	2	2503.5 (1010.7)	2125	0		
Average	**4**	**27.2**	**6.7**	**253.4**	**382.8**	**5.7**	**997.9**	**674.8**	**1.5**	**2347.9**	**1185.5**	**0.3**		
SD	**1**	**15.6**	**3.9**	**155.3**	**48.1**	**3.9**	**306.3**	**460.4**	**1.5**	**390.9**	**951.4**	**0.8**		

Table 5: Sample size, test-statistic (W) and p-value of the Wilcoxon Rank Sum test on the differences in mean height and mean density between schools inside and outside of feeding bout areas. P-values smaller than 0.01 are indicated by an asterisk, p-values greater than 0.01 but smaller than 0.05 are indicated by a circle. Mean height and density of the schools inside and outside of feeding bout areas are given for further reference. Where the mean height or mean density was greater in schools inside than outside of feeding bout areas, the value is marked with a plus sign.

Whale	Number of schools		Test of differences in mean school height		Test of differences in mean school density		Mean height (m)		Mean density (fish/m3)	
	Inside	Outside	W	p	W	p	Inside	Outside	Inside	Outside
Mn08_182a	8	13	40	0.813	63	0.228	5.1	7.5	51.3^+	32.4
Mn08_192a	25	37	595	< 0.05°	730	< 0.001*	4.6^+	3.6	67.4^+	44.8
Mn09_203c	10	37	229	0.131	194	0.414	5.7^+	4.1	43	63.9
Mn09_206a	8	15	50	0.747	76	0.162	8.4^+	8.2	24.1^+	6.9
Mn12_173a	6	12	63	< 0.01*	17	0.967	9.8^+	3.1	24.2	75.6
Mn12_173b	7	6	14	0.853	23	0.418	4.1	5.3	43.5^+	41.1

CHAPTER 3: GENERAL CONCLUSION

Studies of the movement strategies that lead to spatial overlap of baleen whales with their prey usually focus on spatial scales much greater than those of the actual feeding events and prey schools themselves and, in a top-down approach, infer the efficiency of the whales in finding individual schools based on their movement on a disproportionately large scale (Curtice et al., 2015; Dalla Rosa et al., 2008; Skern-Mauritzen et al., 2011). In contrast, the present study focused on whale foraging movement over multiple scales, and, in a bottom-up approach, based the analysis on the movement between single feeding events and prey schools. The spatially nested structure of the prey field investigated here likely resulted from the habitat specificity of the prey. By adapting their foraging movement to the encountered structure of the prey field, whales were able to achieve spatial overlap with energetically profitable prey schools. The correlations between the geometry of whale foraging movement and the geometry of the surrounding prey field shown here suggest that whales employ a different foraging strategy on a smaller spatial scale compared to a larger spatial scale. Between single feeding events, the whales moved between neighboring schools. According to OFT, this can be considered an efficient foraging strategy because it leads to a minimization of time spent between prey patches (Austin et al., 2004; Pyke et al., 1977). When moving between larger groups of schools, the whales did not target neighboring patches. This could be the result of an increased awareness of the prey field over shorter spatial scales, or of active prey patch selection. Whales might use direct cues of the sand lance schools to move between neighboring schools within a patch, such as tactile cues (Berta et al., 2015; Dehnhardt et al., 1998; Kenney et al., 2001). On a larger spatial scale where the perception of direct cues of the schools is unlikely, the whales might rely on their memory to re-visit patches where they successfully foraged previously (Fagan et al., 2013; Stevick, 1999), or localize promising prey patches based on cues of other foraging animals (Fauchald, 2009; Gong et al., 2014; Grünbaum and Veit, 2003; Leighton et al., 2007; Parks et al., 2014, 2010; Silverman et al., 2004; Skern-Mauritzen et al., 2011; Stimpert et al., 2011; Thompson et al., 1986).

Studying the prey field structure on George’s Bank could reveal whether differences in the structure of the prey field cause whale foraging to be concentrated on and around Stellwagen Bank (Payne et al., 1986).

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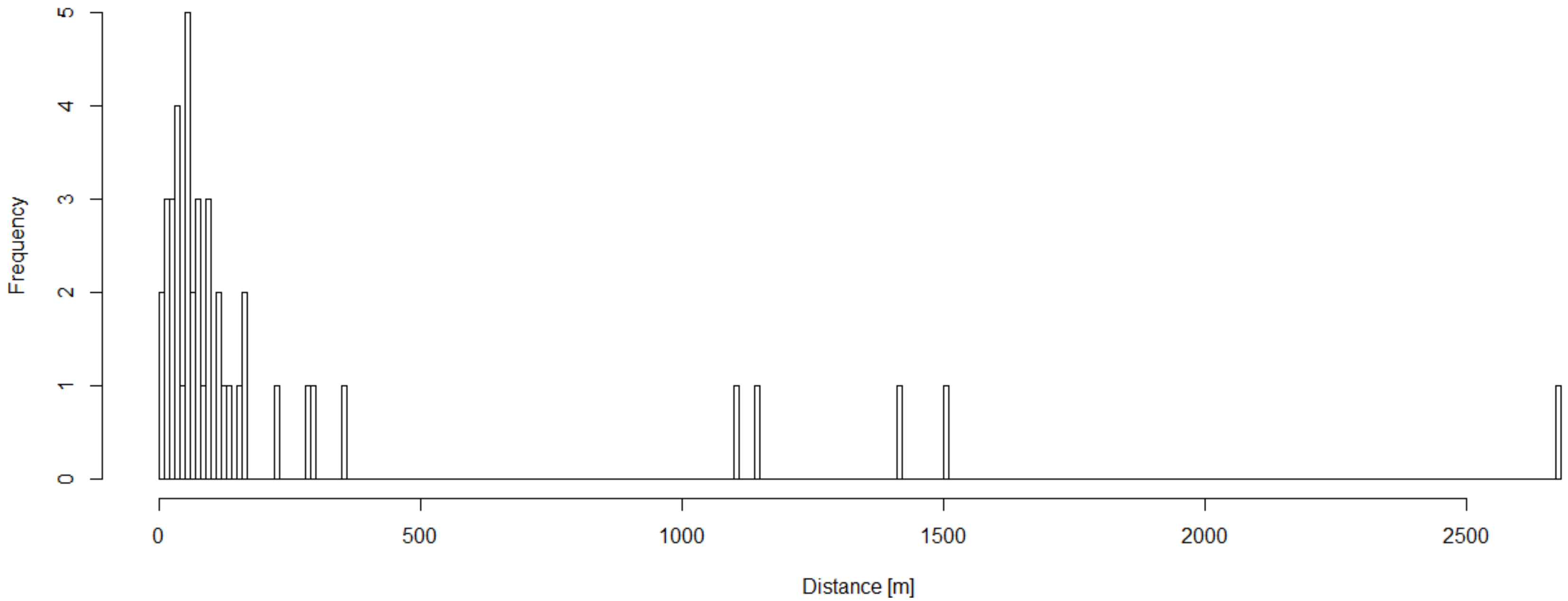
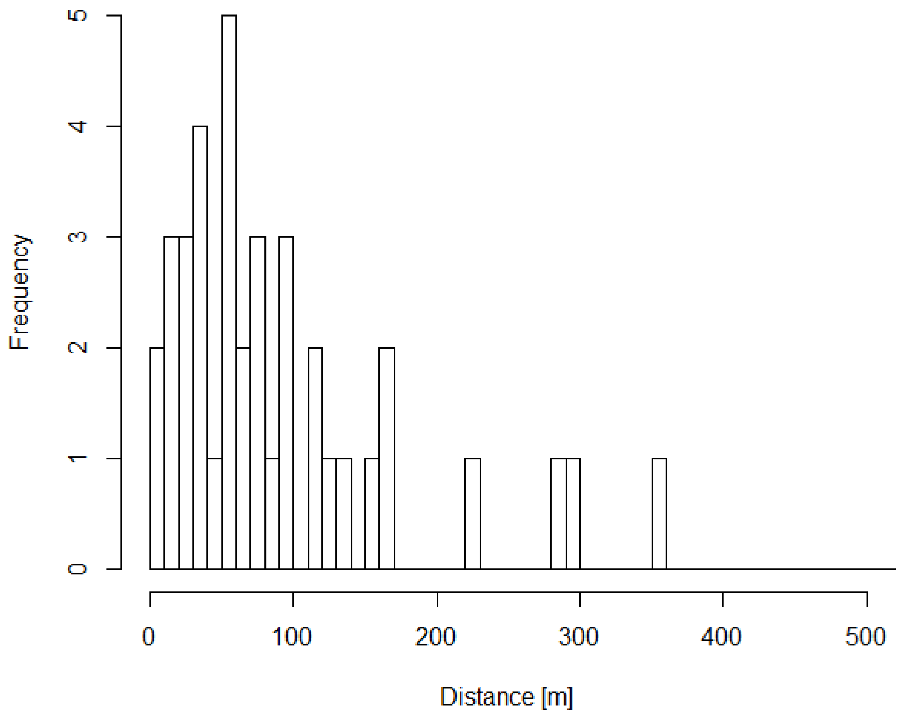
APPENDICES

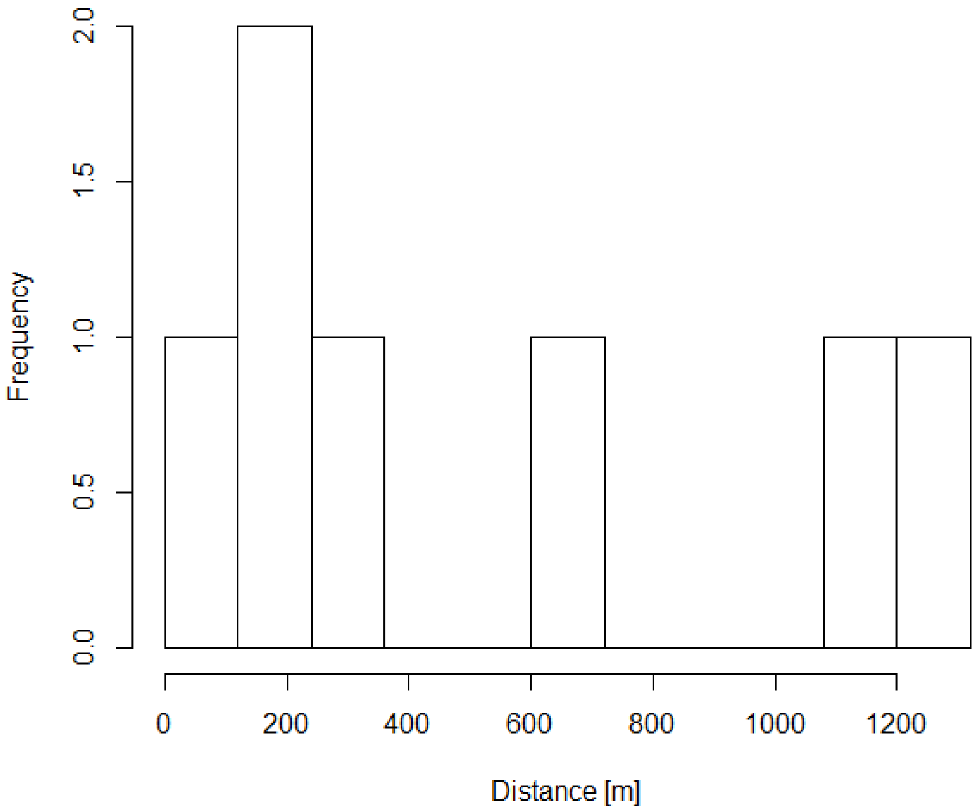
Frequency distributions of distances between feeding events and L2 bouts



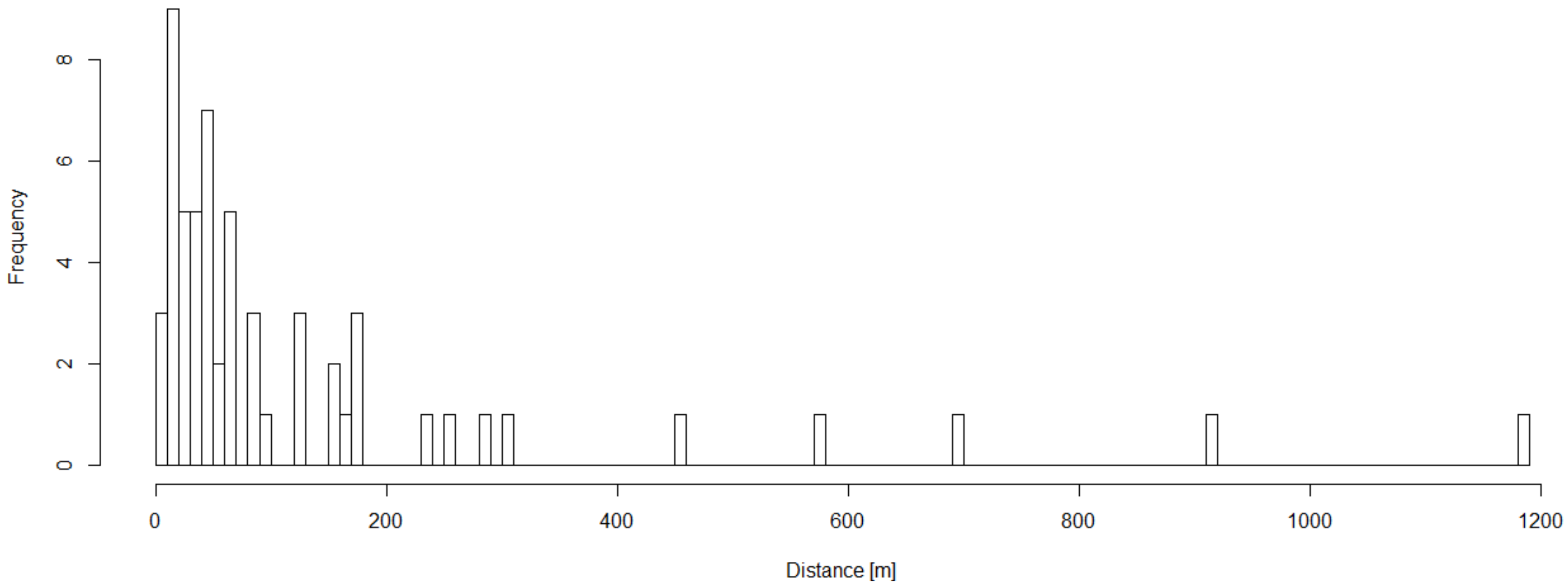
Appendix 1: Frequency histogram of distances between sequential feeding events for whale Mn08_182a. A detailed view is given in Appendix 2.



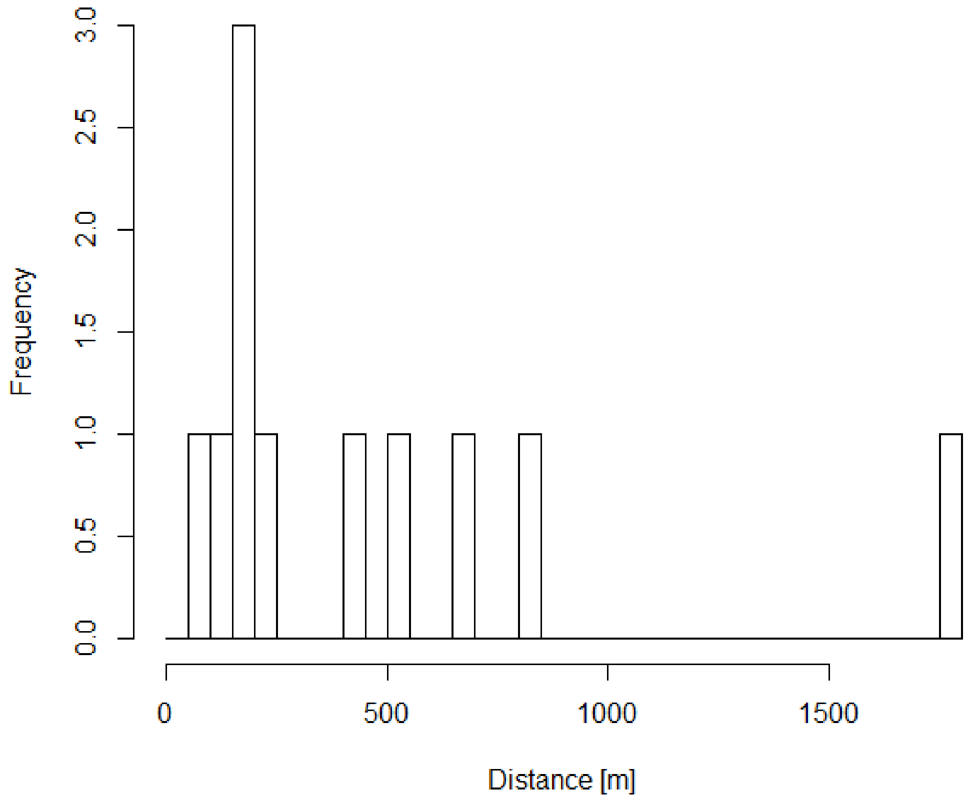
Appendix 2: Frequency histogram of distances between sequential feeding events for whale Mn08_182a between 0-500 m. The first break, based on which feeding events were grouped into L2 bouts, was identified at 100 m.



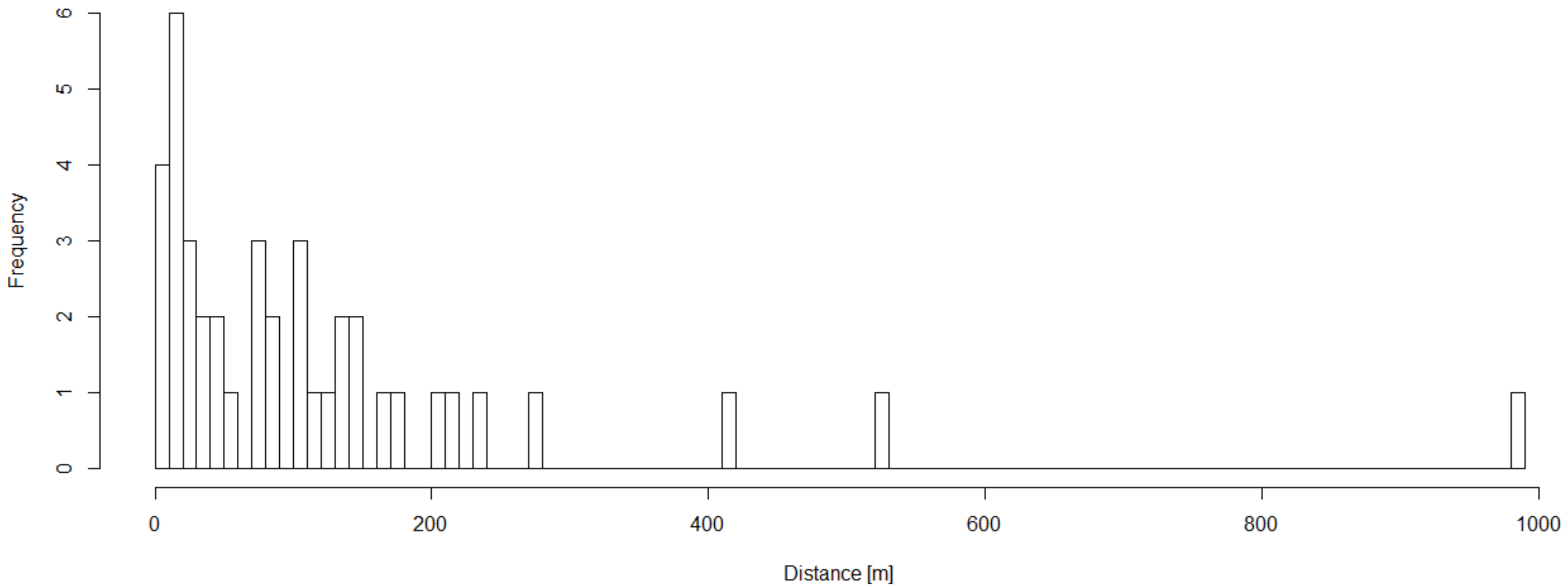
Appendix 3: Frequency histogram of distances between sequential L2 feeding bouts for whale Mn08_192a. First break, based on which L2 bouts were grouped into L3 bouts, was identified at 360 m.



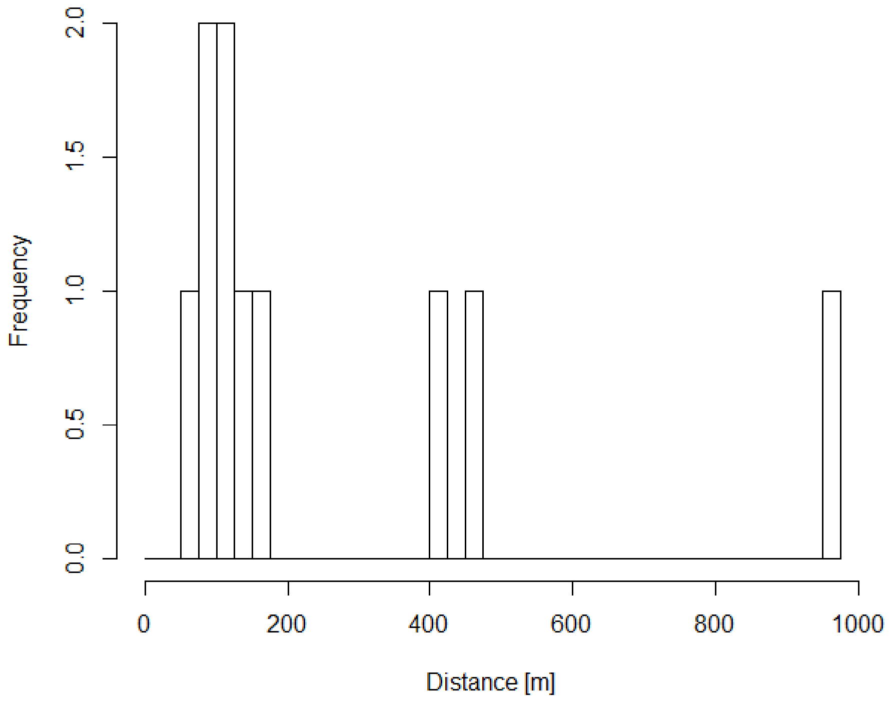
Appendix 4: Frequency histogram of distances between sequential feeding events for whale Mn08_184a. The first break, based on which feeding events were grouped into L2 bouts, was identified at 70 m.



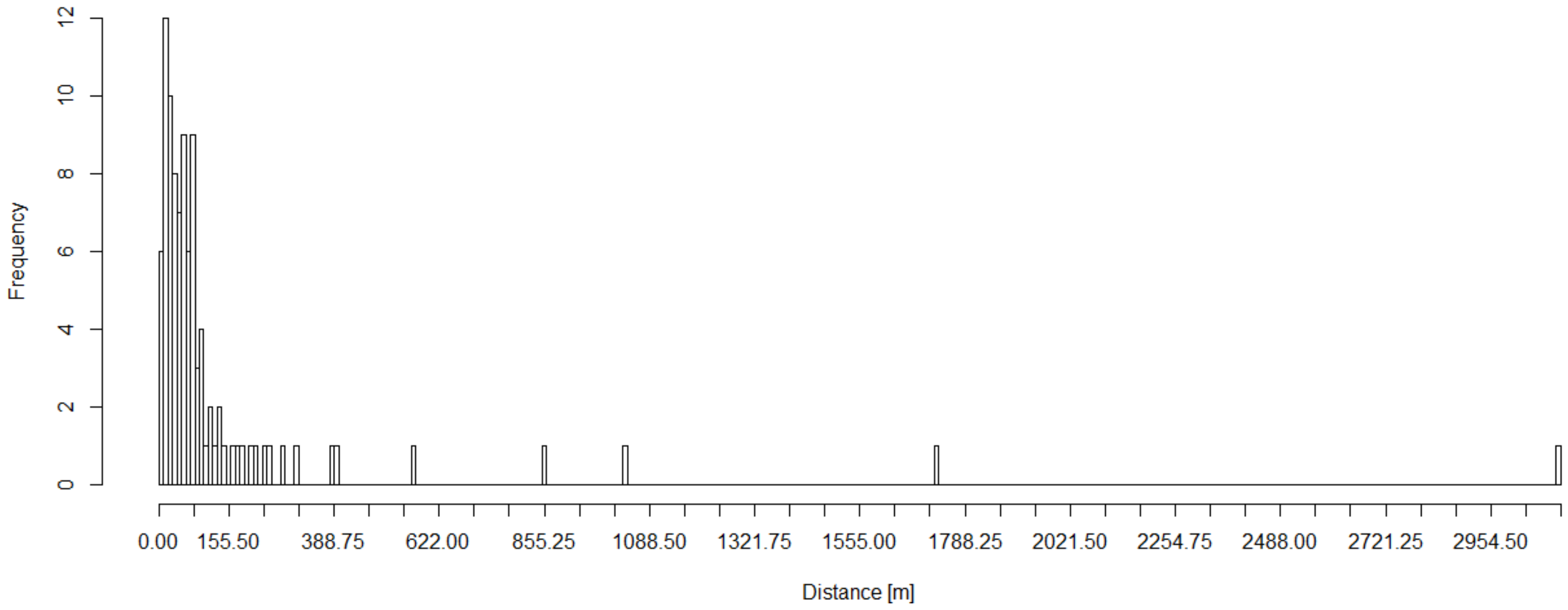
Appendix 5: Frequency distribution of distances between sequential L2 feeding bouts for whale Mn08_184a. The first break, based on which L2 bouts were grouped into L3 bouts, was identified at 250 m.



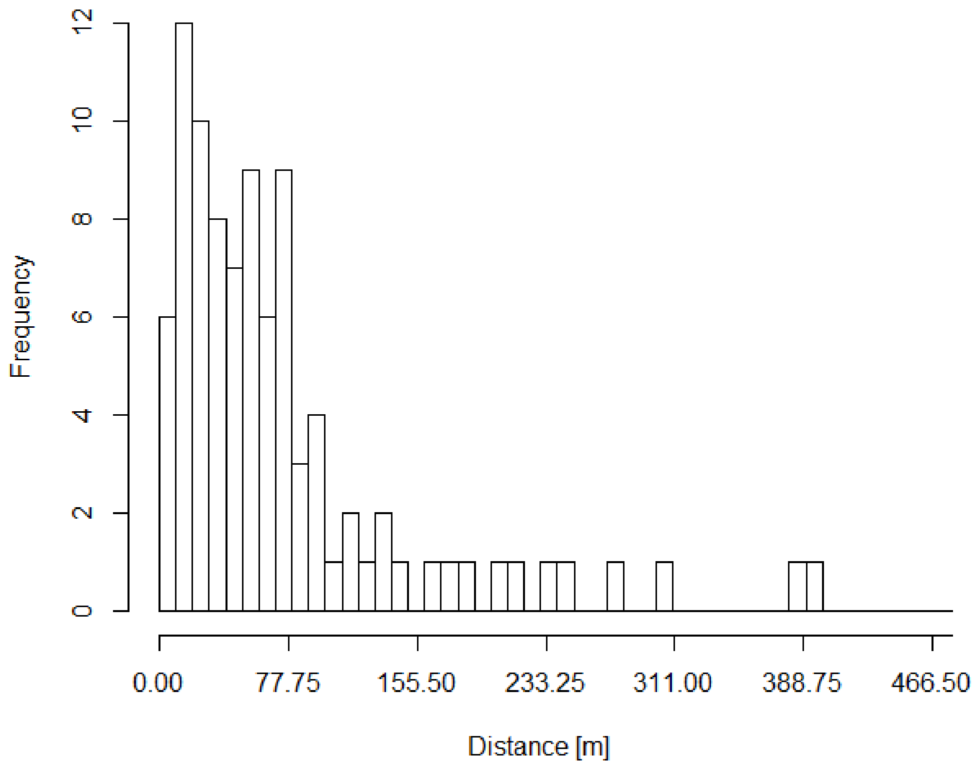
Appendix 6: Frequency distribution of distances between sequential feeding events for whale Mn08_184b. The first break, based on which feeding events were grouped into L2 bouts, was identified at 60 m.



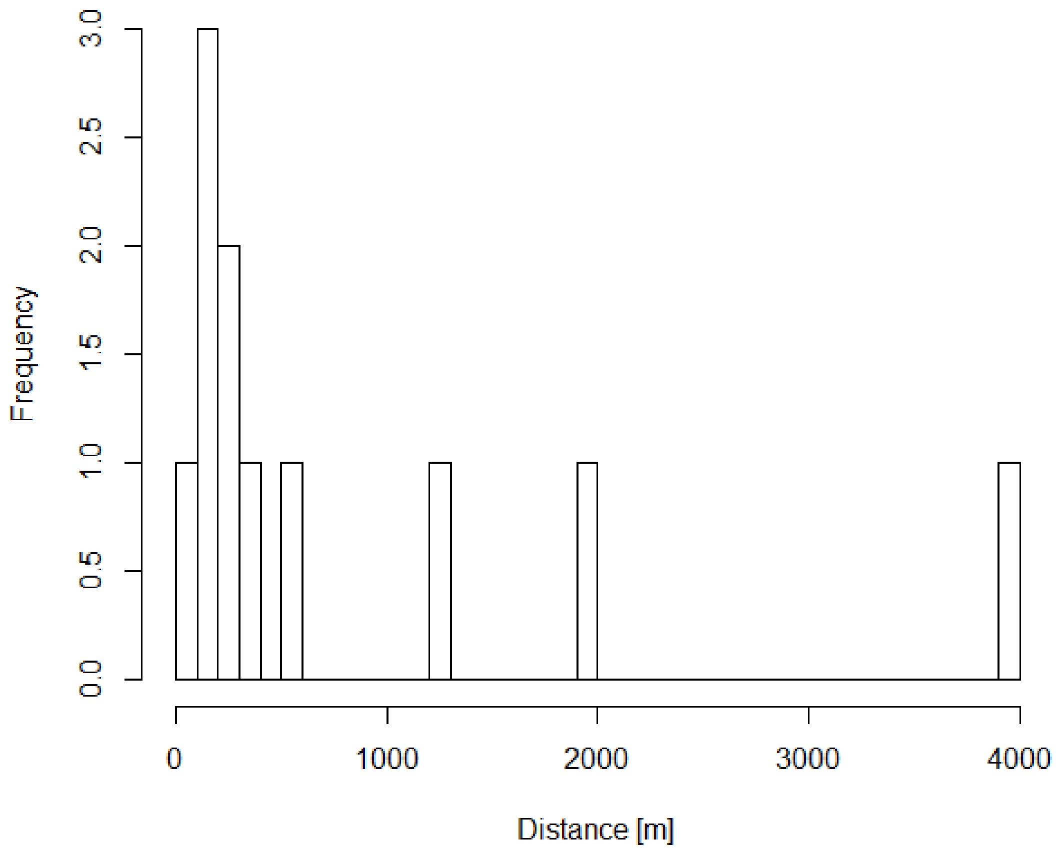
Appendix 7: Frequency distribution of distances between sequential L2 bouts for whale Mn08_184b. The first break, based on which L2 bouts were grouped into L3 bouts, was identified at 175 m.



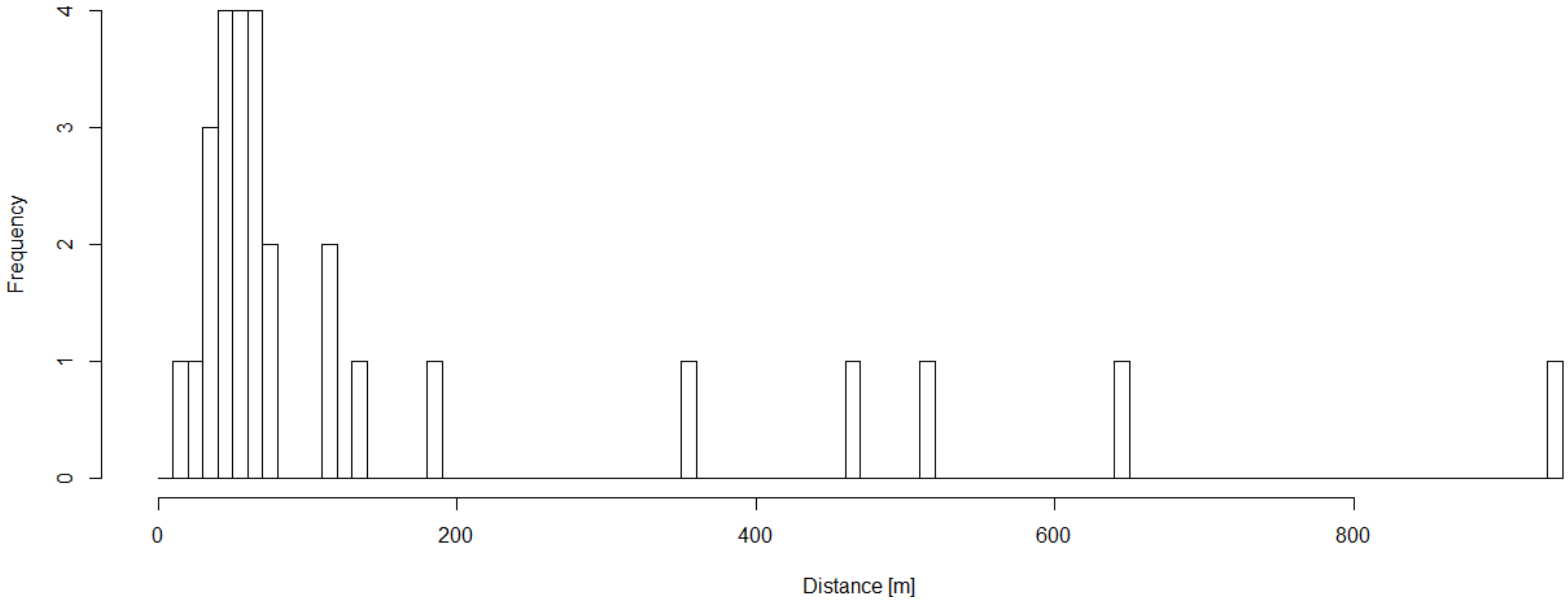
Appendix 8: Frequency distribution of distances between sequential feeding events for whale Mn08_192a. A detailed view is given in Appendix 9.



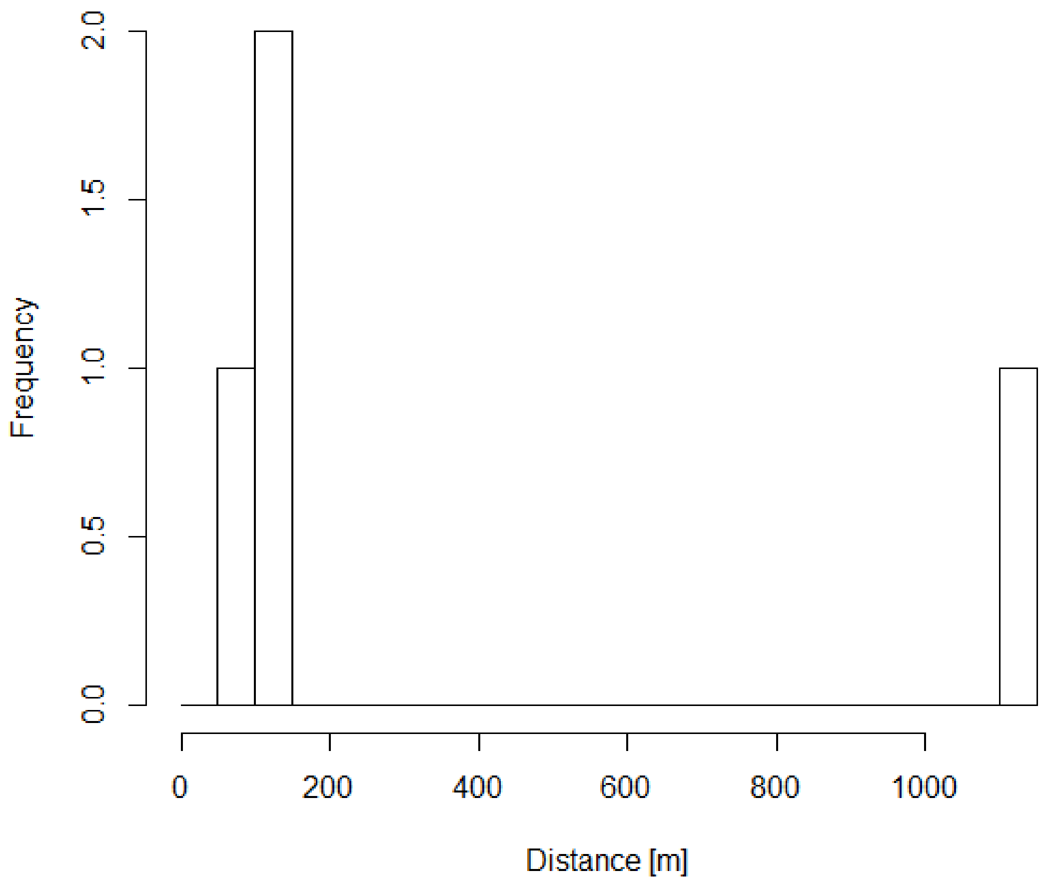
Appendix 9: Frequency distribution of distances between sequential feeding events for whale Mn08_192a between 0-470 m. The first break, based on which feeding events were grouped into L2 bouts, was identified at 150 m.



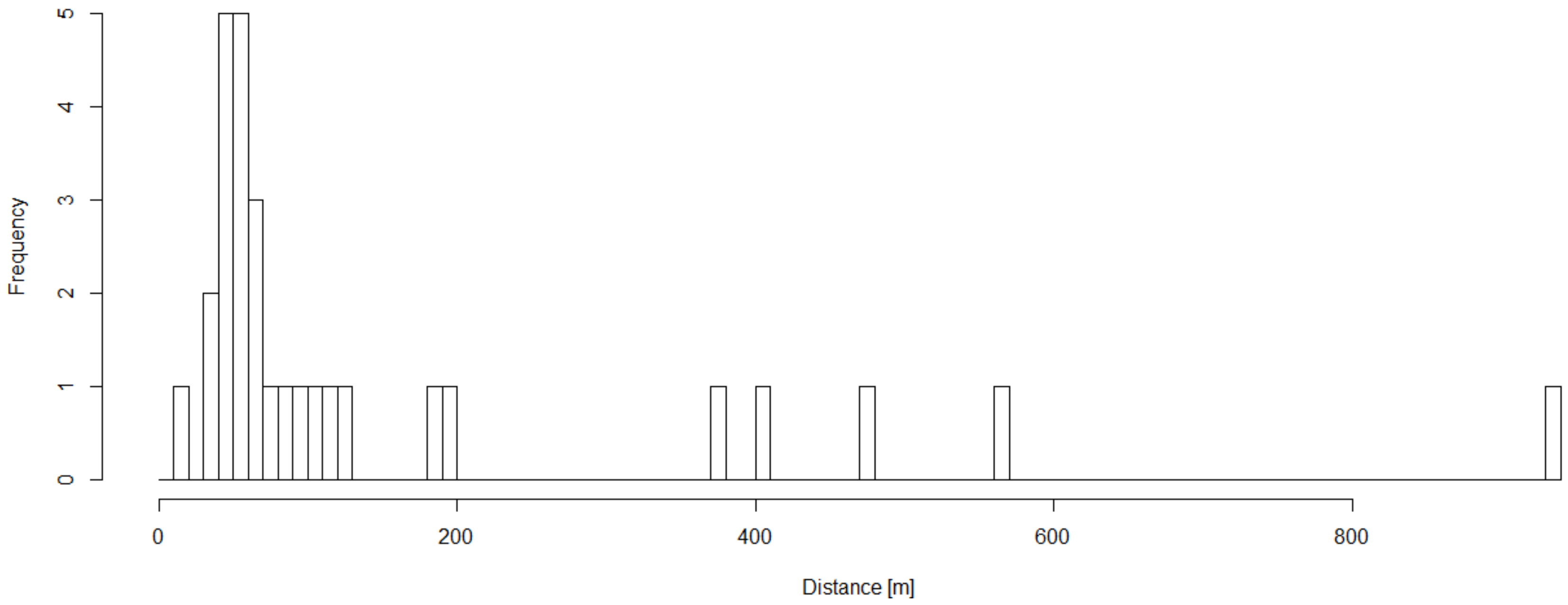
Appendix 10: Frequency distribution of distances between sequential L2 bouts for whale Mn08_192a. The first break, based on which L2 bouts were grouped into L3 bouts, was identified at 400 m.



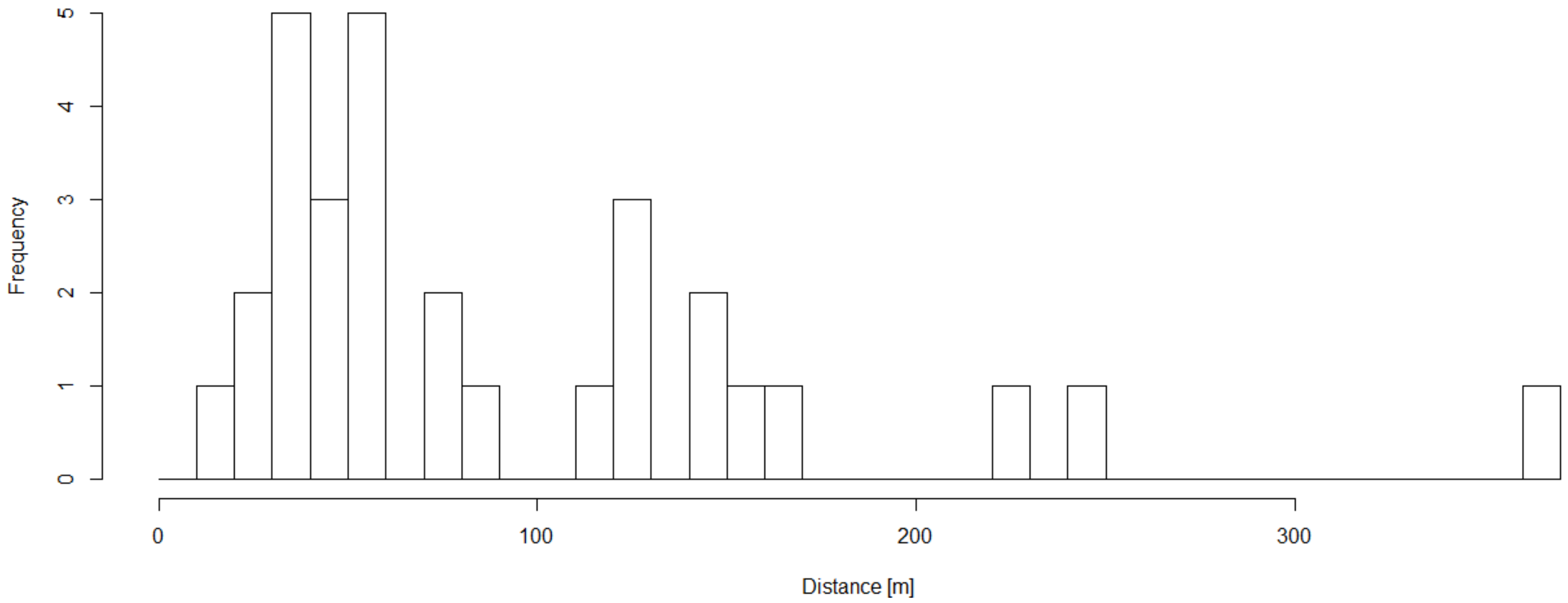
Appendix 11: Frequency distribution of distances between sequential feeding events for whale Mn09_203b. The first break, based on which feeding events were grouped into L2 bouts, was identified at 80 m.



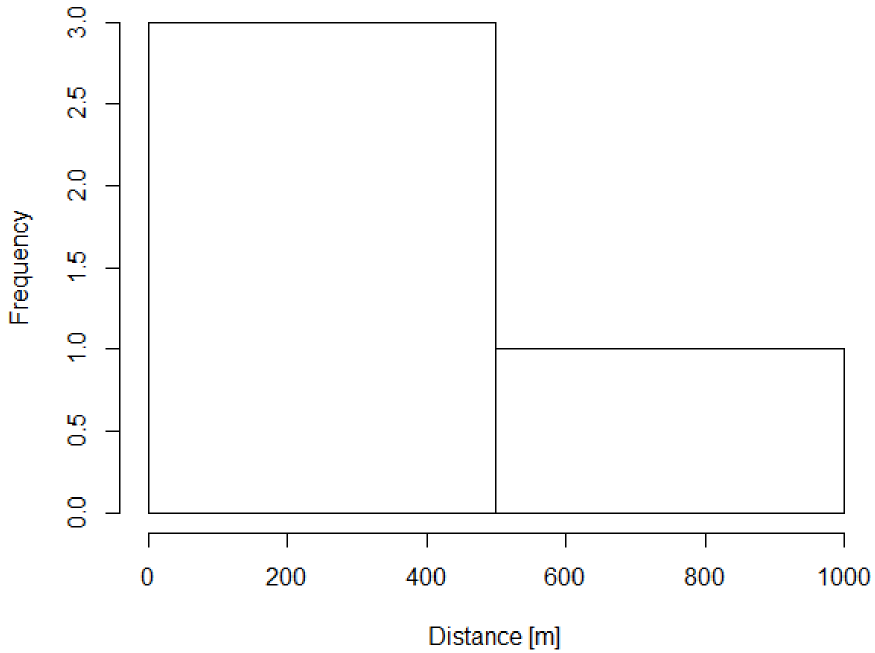
Appendix 12: Frequency distribution of distances between sequential L2 bouts for whale Mn09_203b. The first break, based on which L2 bouts were grouped into L3 bouts, was identified at 150 m.



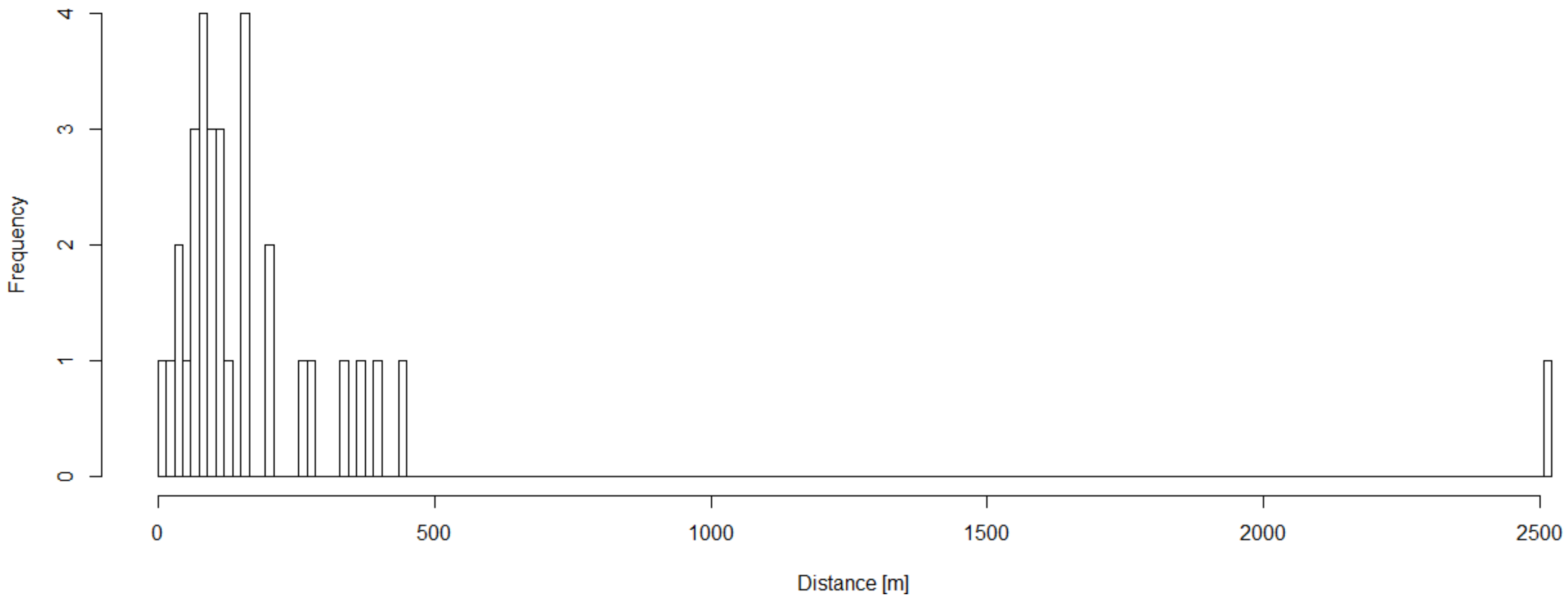
Appendix 13: Frequency distribution of distances between sequential feeding events for whale Mn09_203c. The first break, based on which feeding events were grouped into L2 bouts, was identified at 130 m.



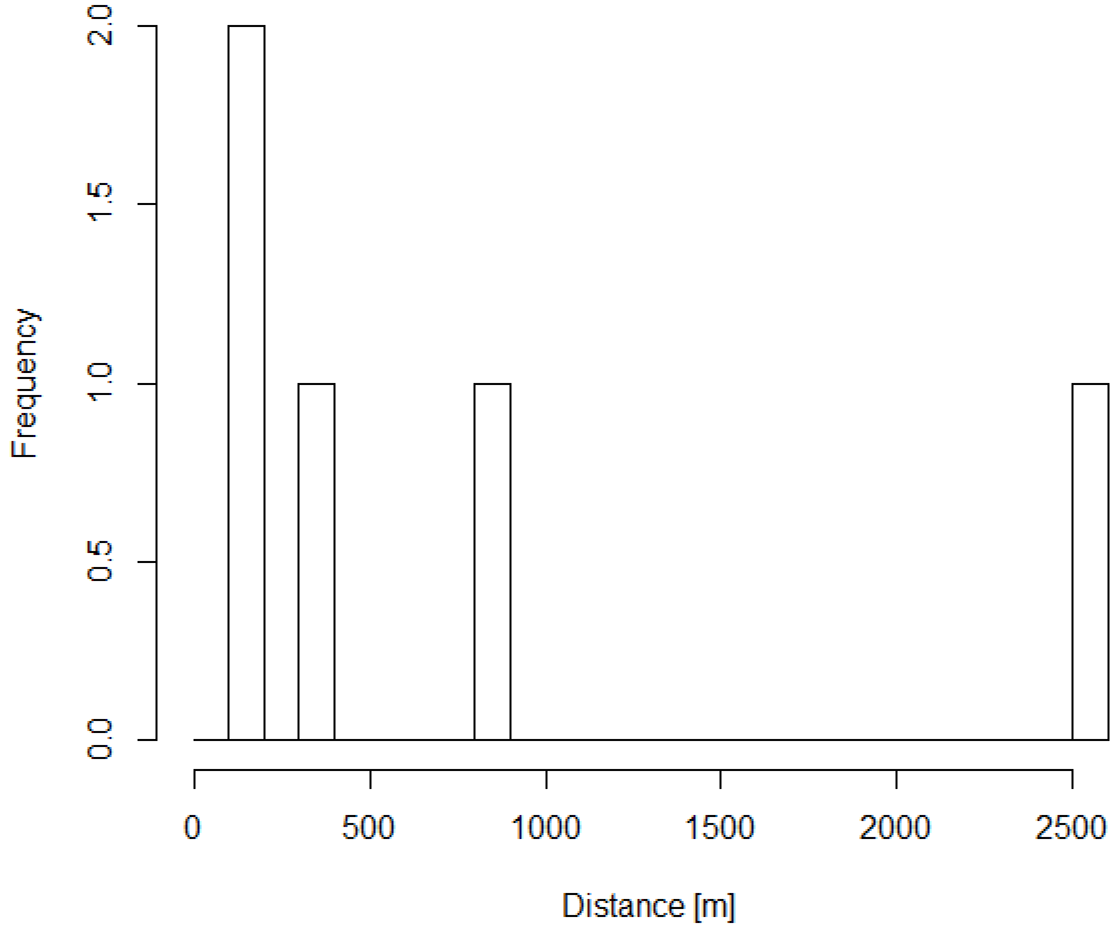
Appendix 14: Frequency distribution of distances between sequential feeding events for whale Mn09_206a. The first break, based on which feeding events were grouped into L2 bouts, was identified at 60 m.



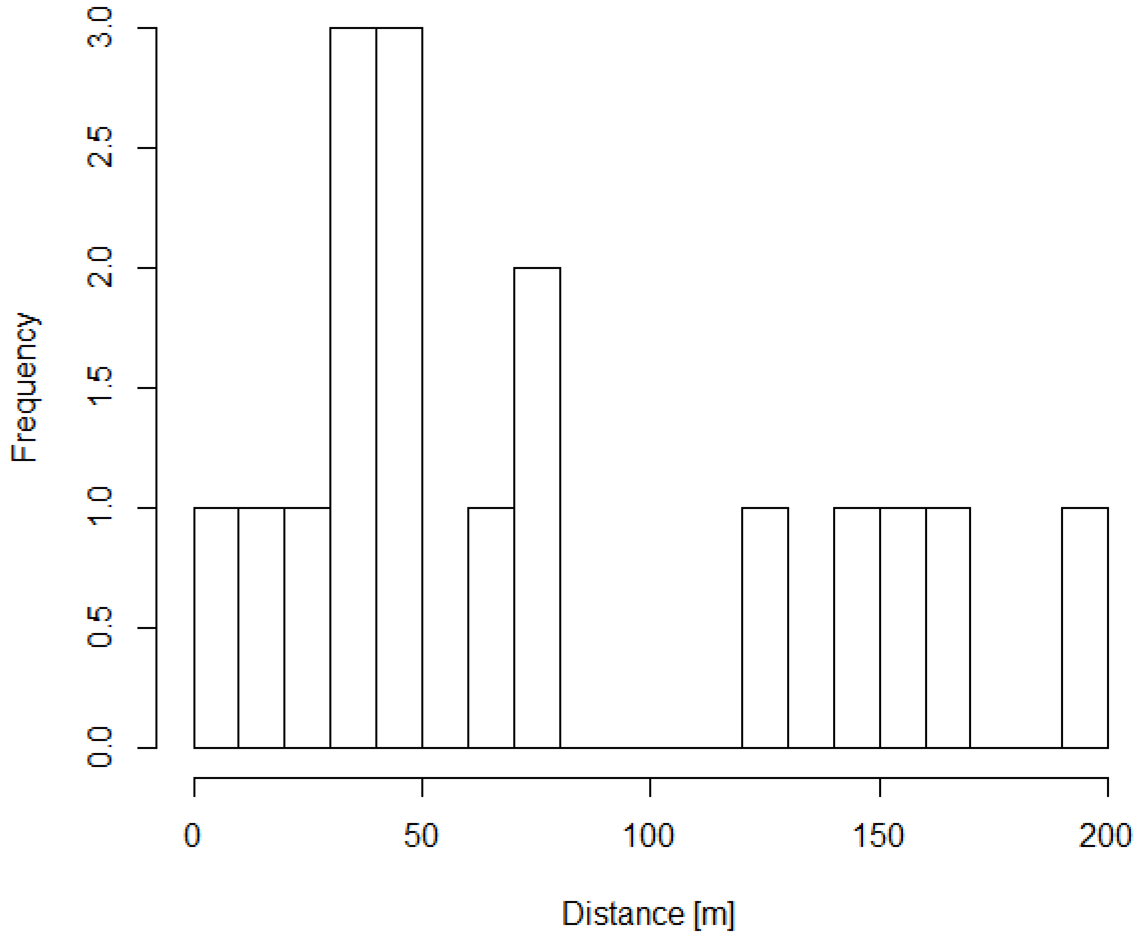
Appendix 15: Frequency distribution of distances between sequential L2 bouts for whale Mn09_206a. L2 bouts within 1000 m of each other were grouped into L3 bouts.



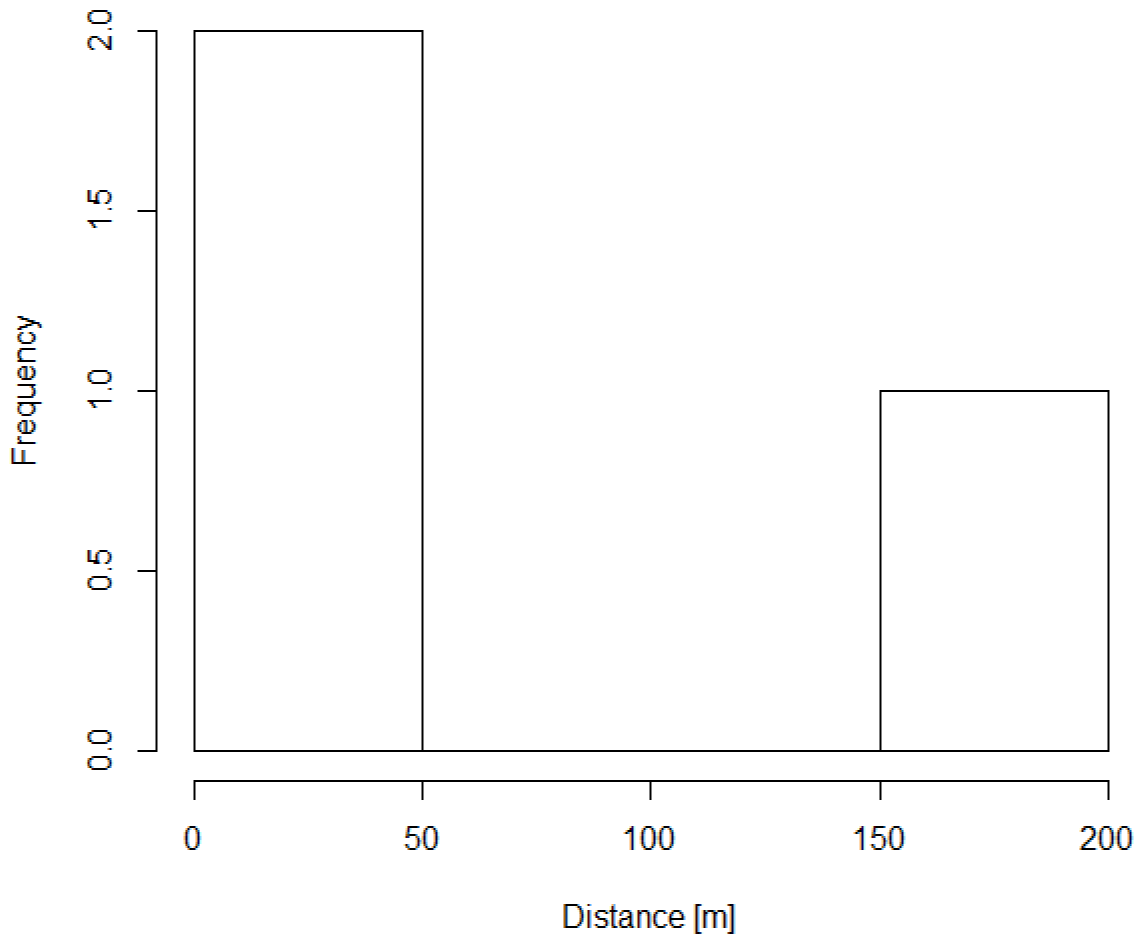
Appendix 16: Frequency distribution of distances between sequential feeding events for whale Mn12_173a. The first break, based on which feeding events were grouped into L2 bouts, was identified at 135 m.



Appendix 17: Frequency distribution of distances between sequential L2 bouts for whale Mn12_173a. The first break, based on which L2 bouts were grouped into L3 bouts, was identified at 200 m.

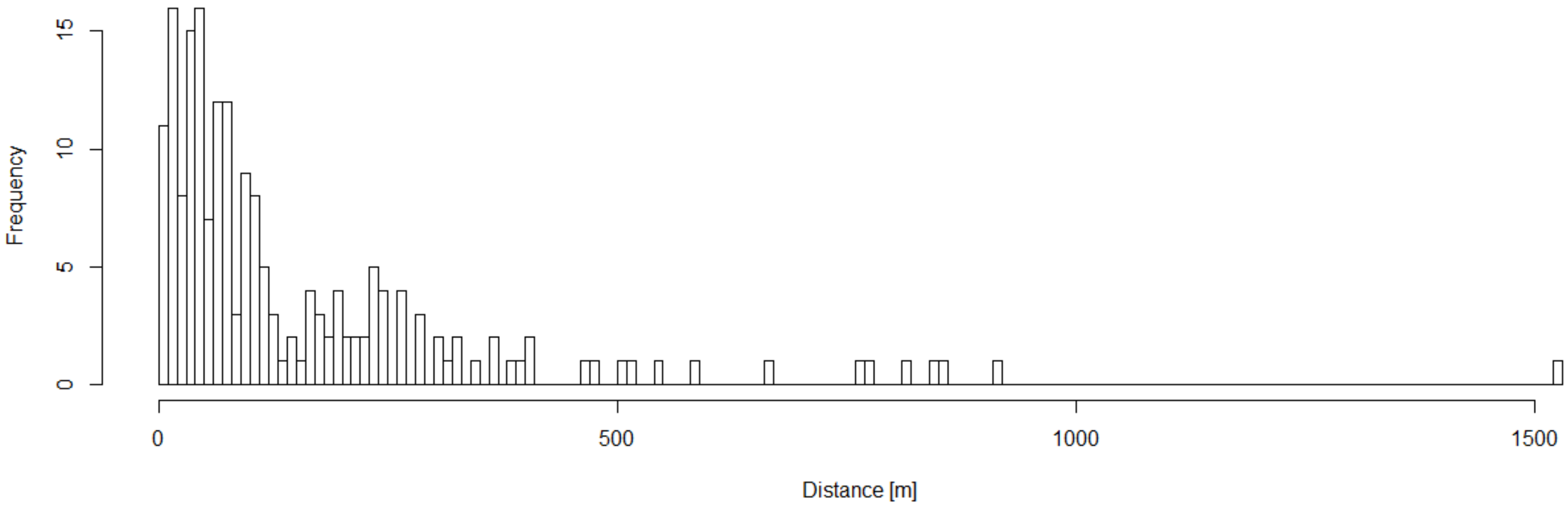


Appendix 18: Frequency distribution of distances between sequential feeding events for whale Mn12_173b. The first break, based on which feeding events were grouped into L2 bouts, was identified at 50 m.

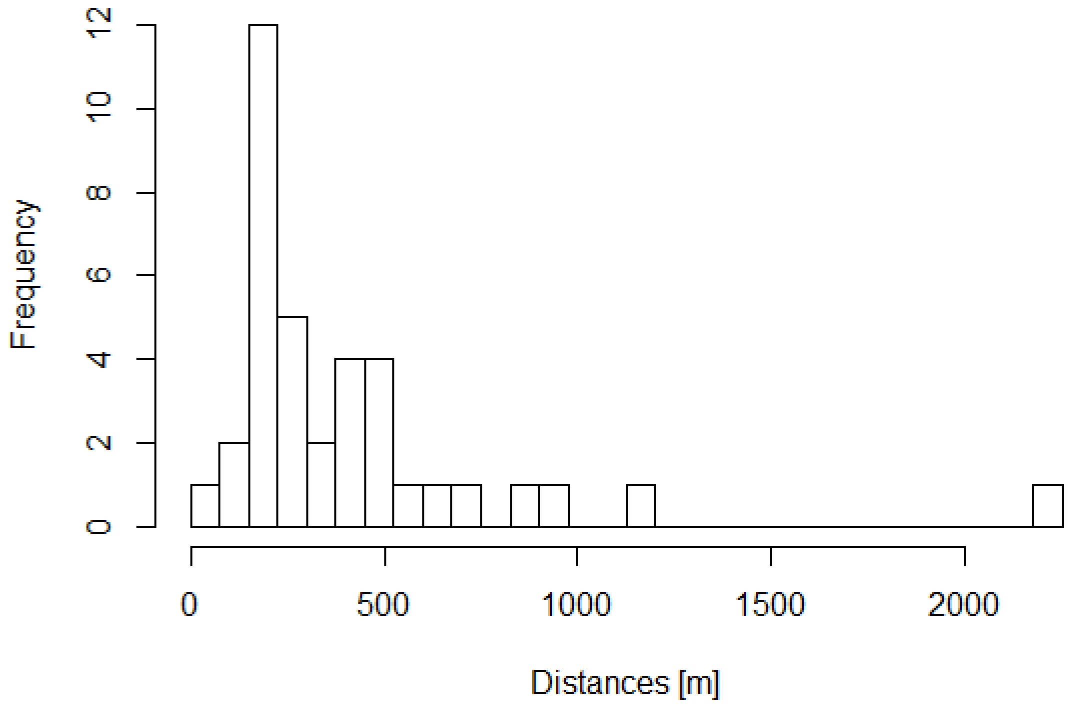


Appendix 19: Frequency distribution of distances between sequential L2 bouts for whale Mn12_173b. The first break, based on which L2 bouts were grouped into L3 bouts, was identified at 50 m.

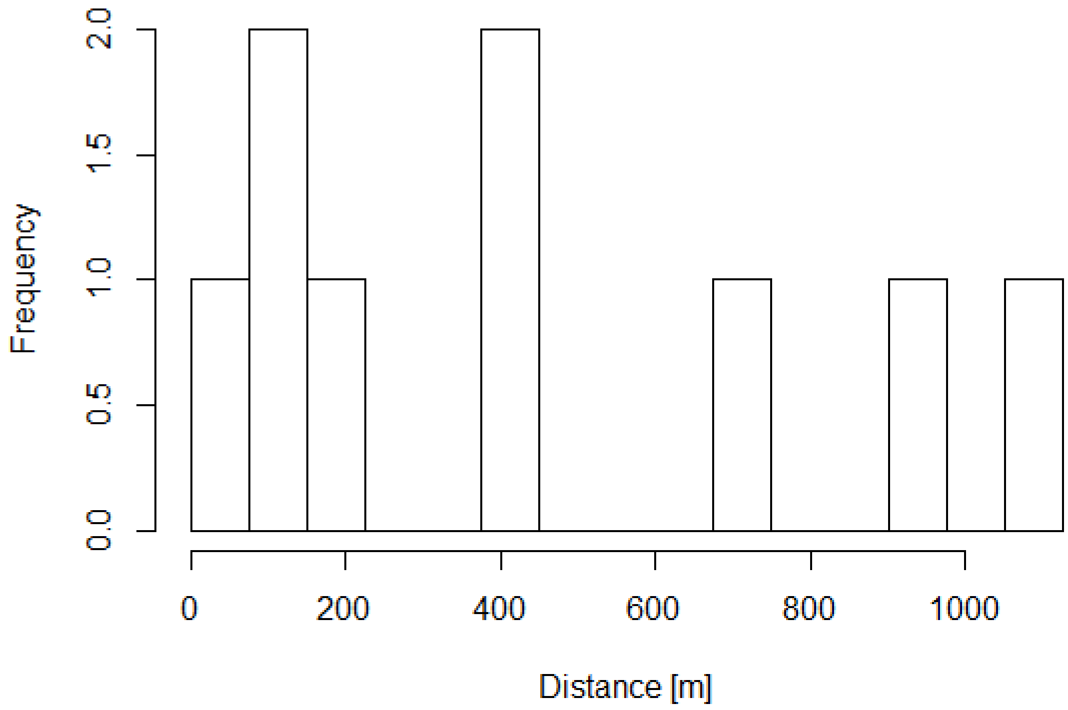
Frequency distributions of distances between sand lance schools and L2-L4 patches



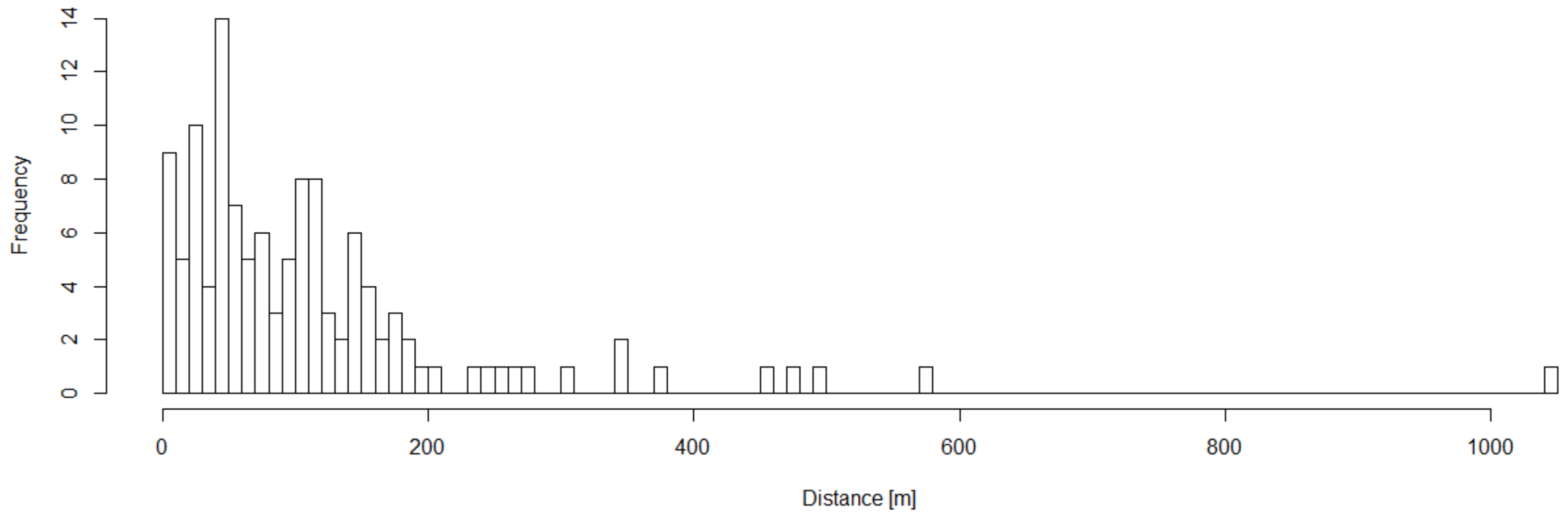
Appendix 20: Frequency distribution of distances between sequentially recorded sand lance schools on June 30, 2008. The first break, based on which schools were grouped into L2 patches, was identified at 140 m.



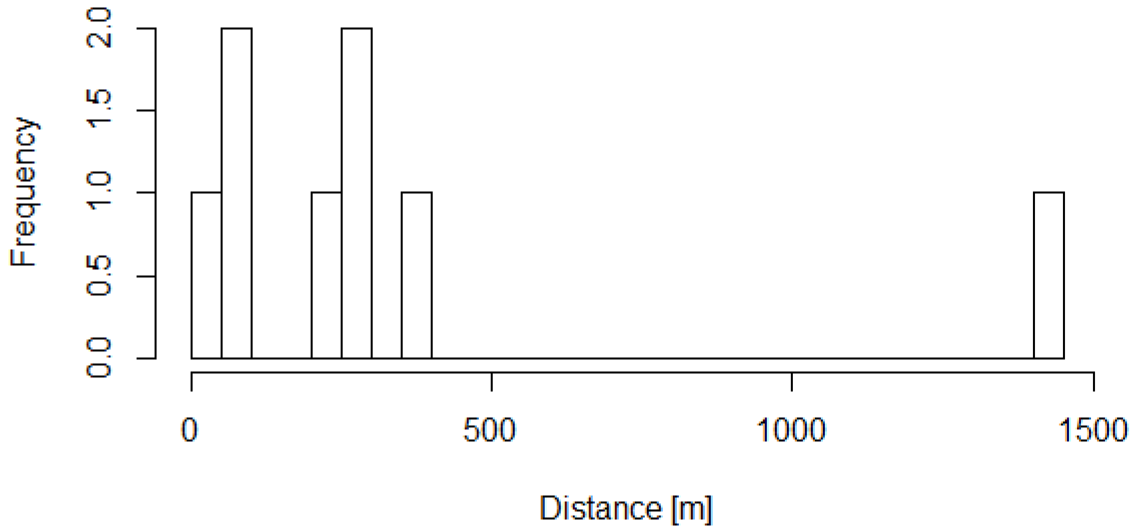
Appendix 21: Frequency distribution of distances between sequentially recorded L2 sand lance patches on June 30, 2008. The first break, based on which L2 patches were grouped into L3 patches, was identified at 375 m.



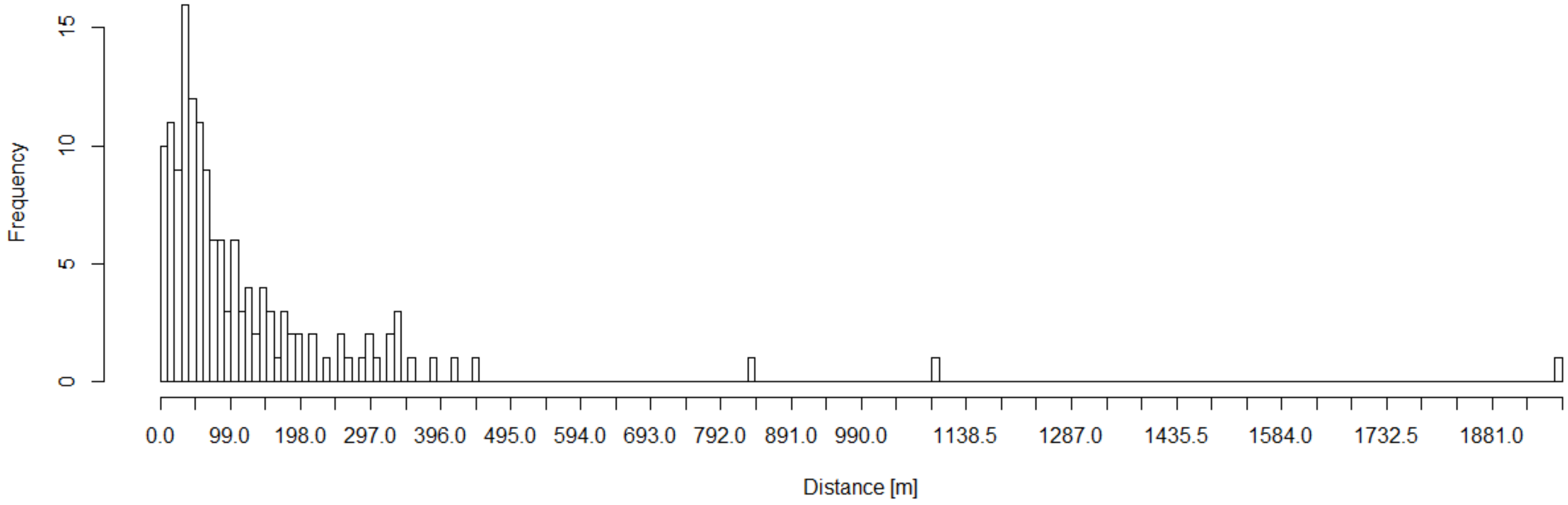
Appendix 22: Frequency distribution of distances between sequentially recorded L3 sand lance patches on June 30, 2008. The first break, based on which L3 patches were grouped into L4 patches, was identified at 225 m.



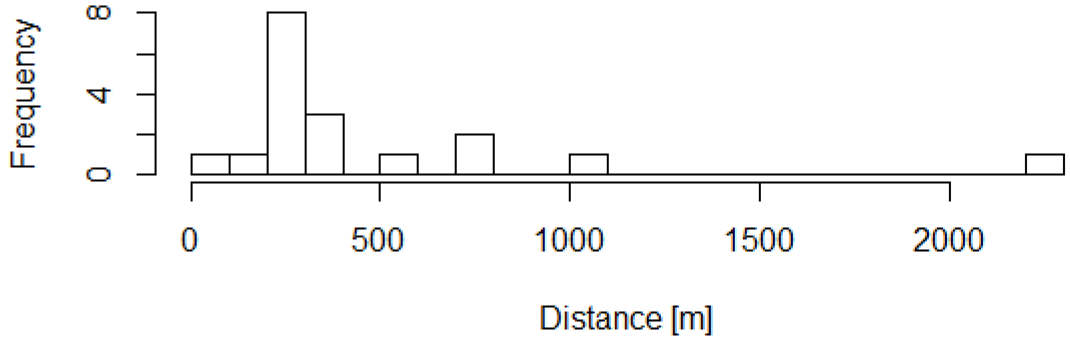
Appendix 23: Frequency distribution of distances between sequentially recorded sand lance schools on July 2, 2008. The first break, based on which schools were grouped into L2 patches, was identified at 210 m.



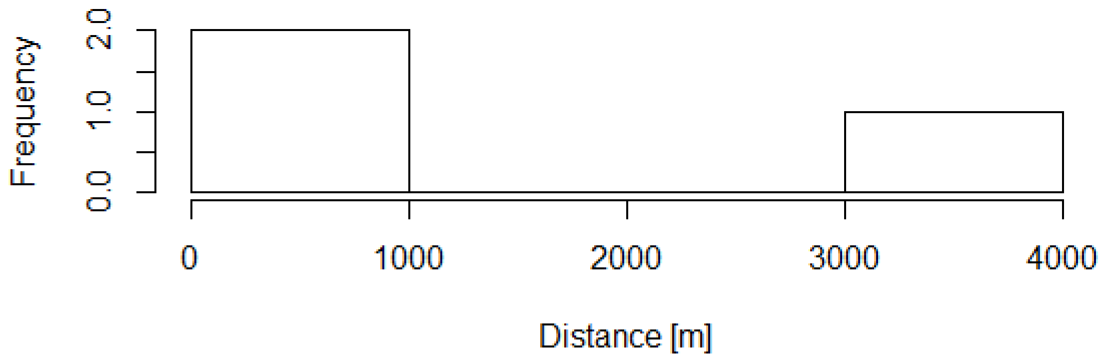
Appendix 24: Frequency distribution of distances between sequentially recorded L2 sand lance patches on July 2, 2008. The first break, based on which L2 patches were grouped into L3 patches, was identified at 100 m.



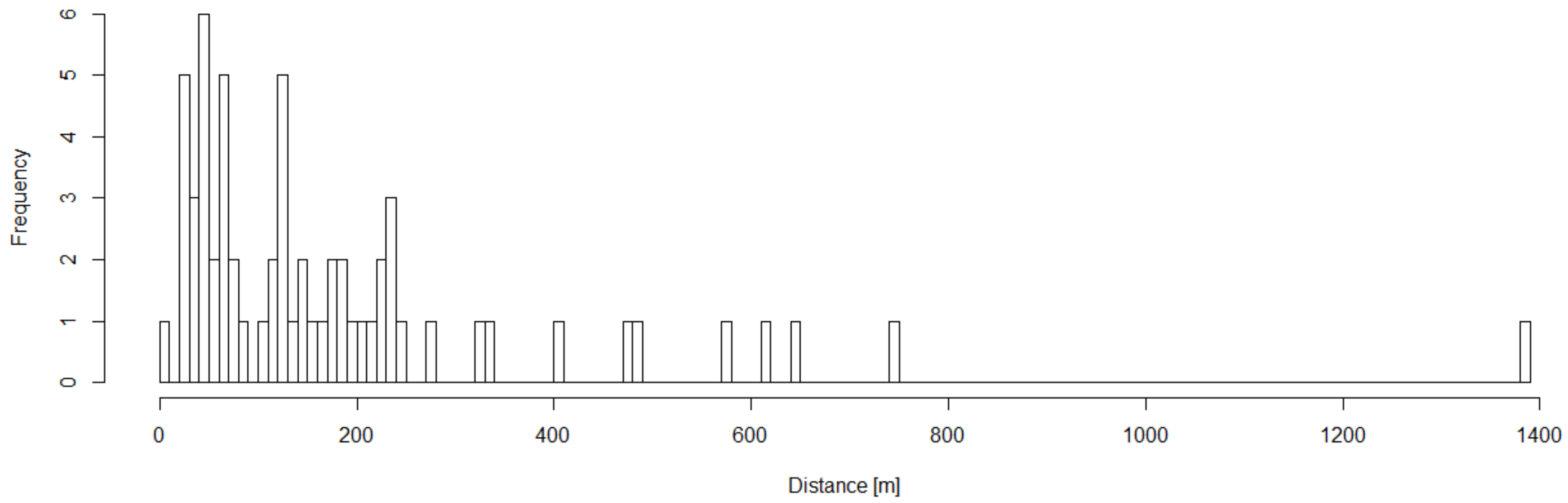
Appendix 25: Frequency distribution of distances between sequentially recorded sand lance schools on July 2, 2008. The first break, based on which schools were grouped into L2 patches, was identified at 200 m.



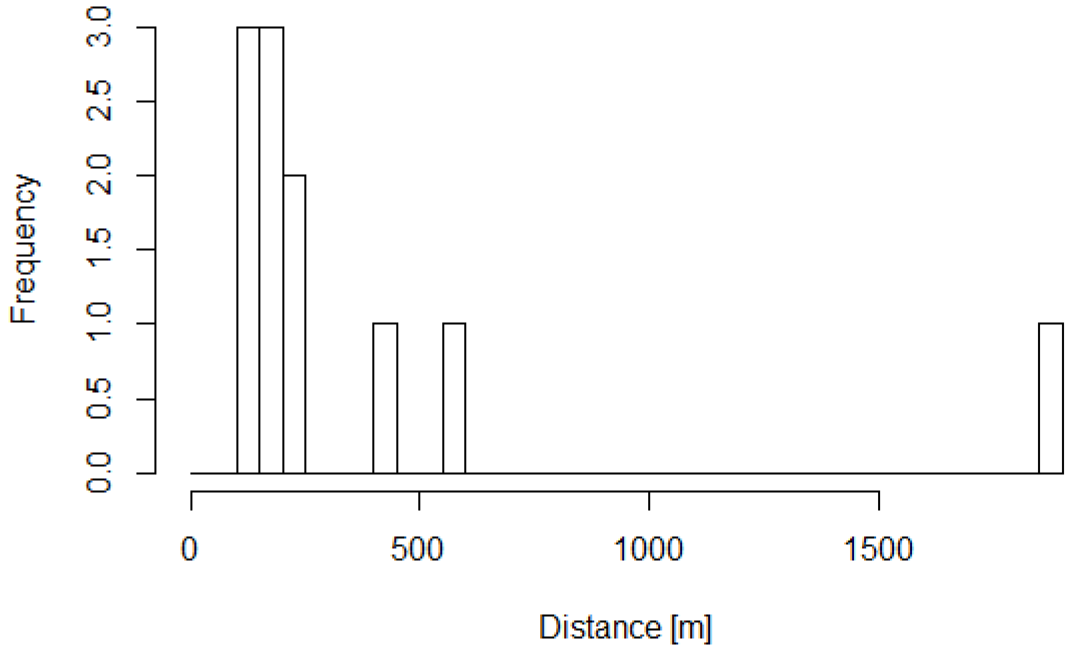
Appendix 26: Frequency distribution of distances between sequentially recorded L2 sand lance patches on July 2, 2008. The first break, based on which L2 patches were grouped into L3 patches, was identified at 400 m.



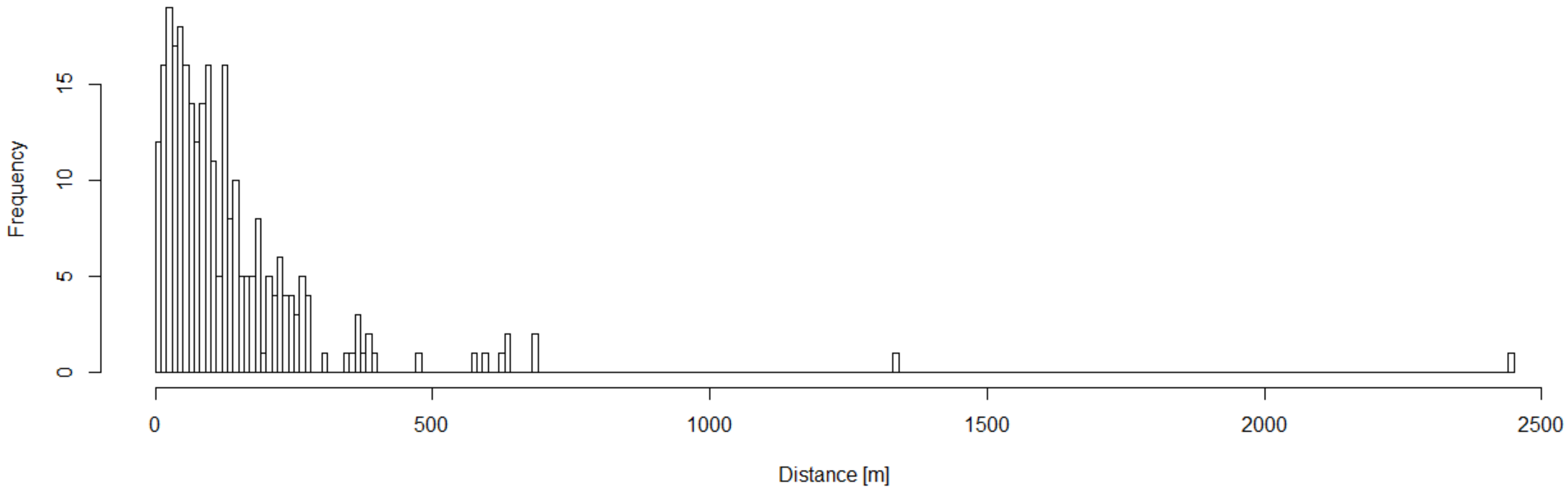
Appendix 27: Frequency distribution of distances between sequentially recorded L3 sand lance patches on July 2, 2008. The first break, based on which L3 patches were grouped into L4 patches, was identified at 1000 m.



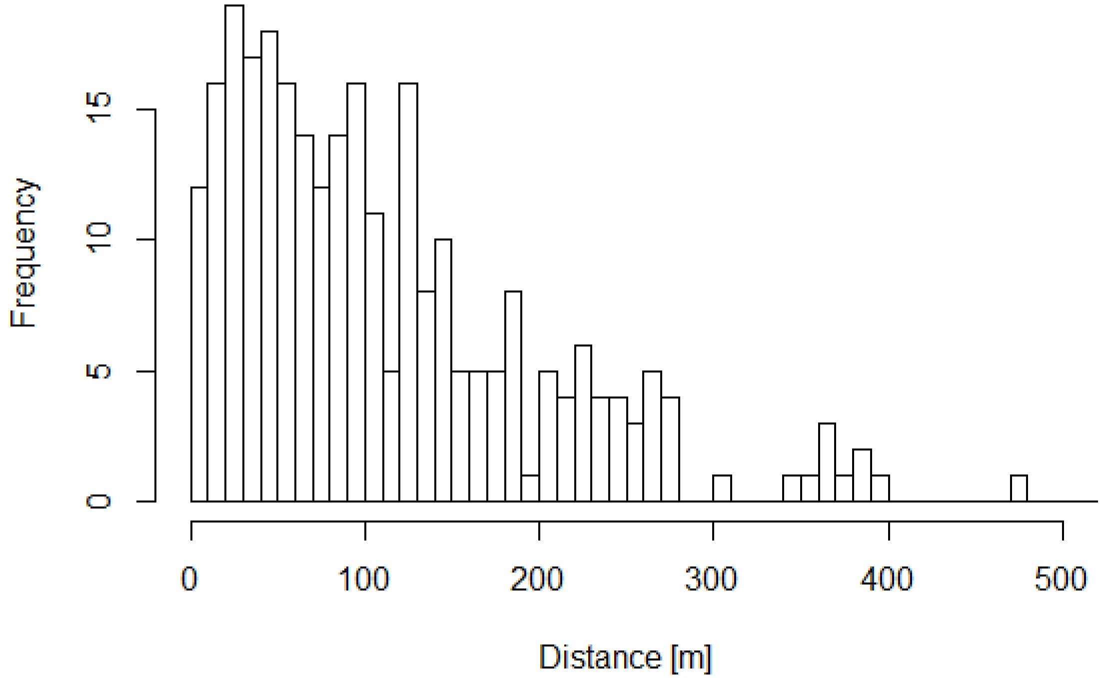
Appendix 28: Frequency distribution of distances between sequentially recorded sand lance schools on July 22, 2009. The first break, based on which schools were grouped into L2 patches, was identified at 90 m.



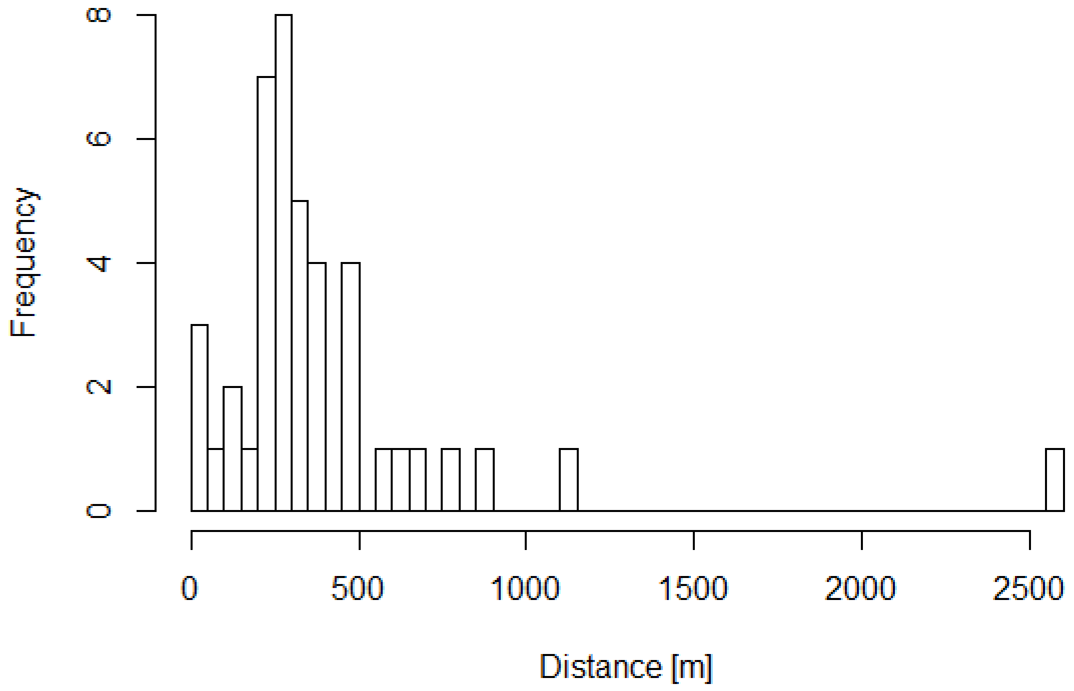
Appendix 29: Frequency distribution of distances between sequentially recorded L2 sand lance patches on July 22, 2009. The first break, based on which L2 patches were grouped into L3 patches, was identified at 250 m.



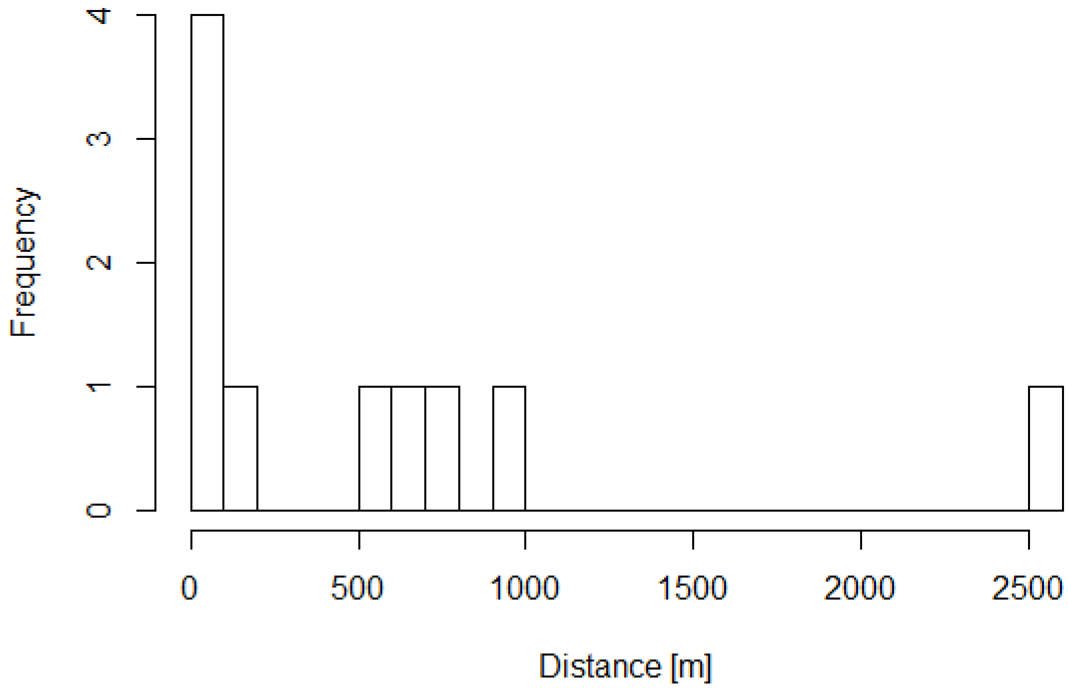
Appendix 30: Frequency distribution of distances between sequentially recorded sand lance schools on July 25, 2009. Appendix 31 shows the range of distances between 0-500 m.



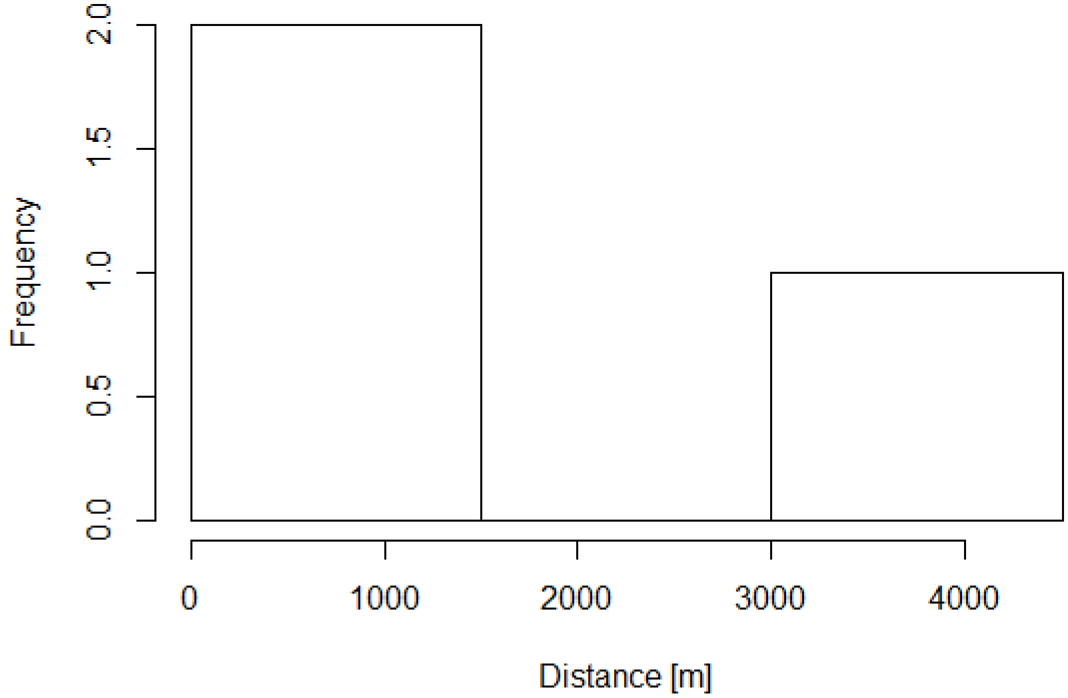
Appendix 31: Frequency distribution of distances between sequentially recorded sand lance schools on July 25, 2009, between 0-500 m. The first break, based on which schools were grouped into L2 patches, was identified at 200 m.



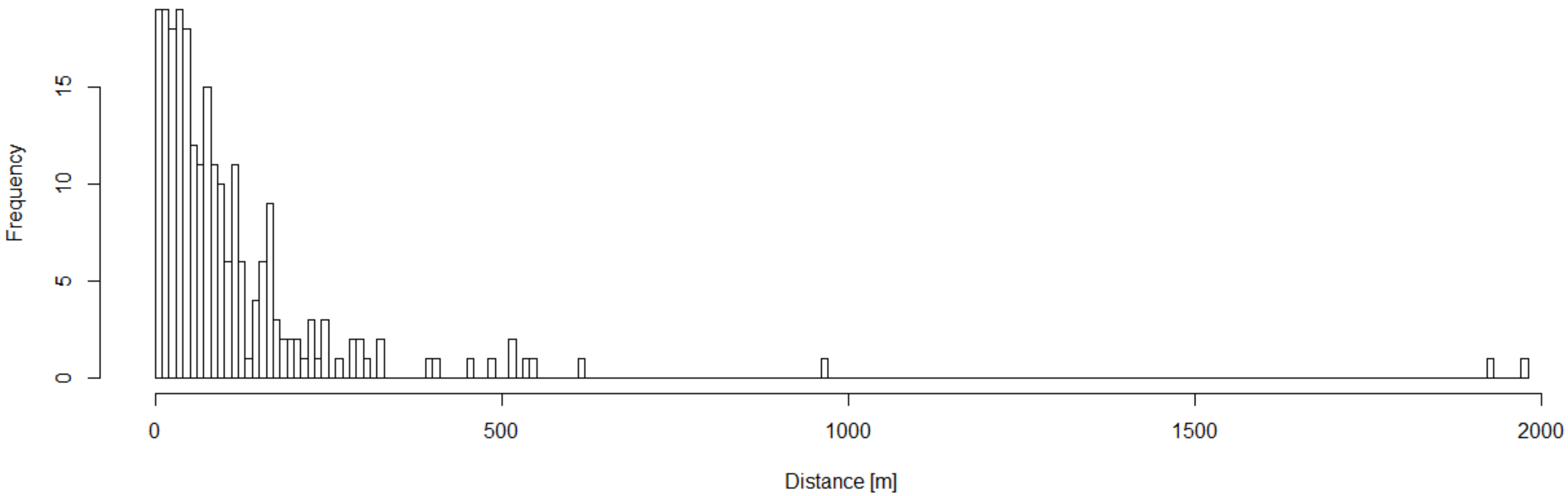
Appendix 32: Frequency distribution of distances between sequentially recorded L2 sand lance patches on July 25, 2009. The first break, based on which L2 patches were grouped into L3 patches, was identified at 400 m.



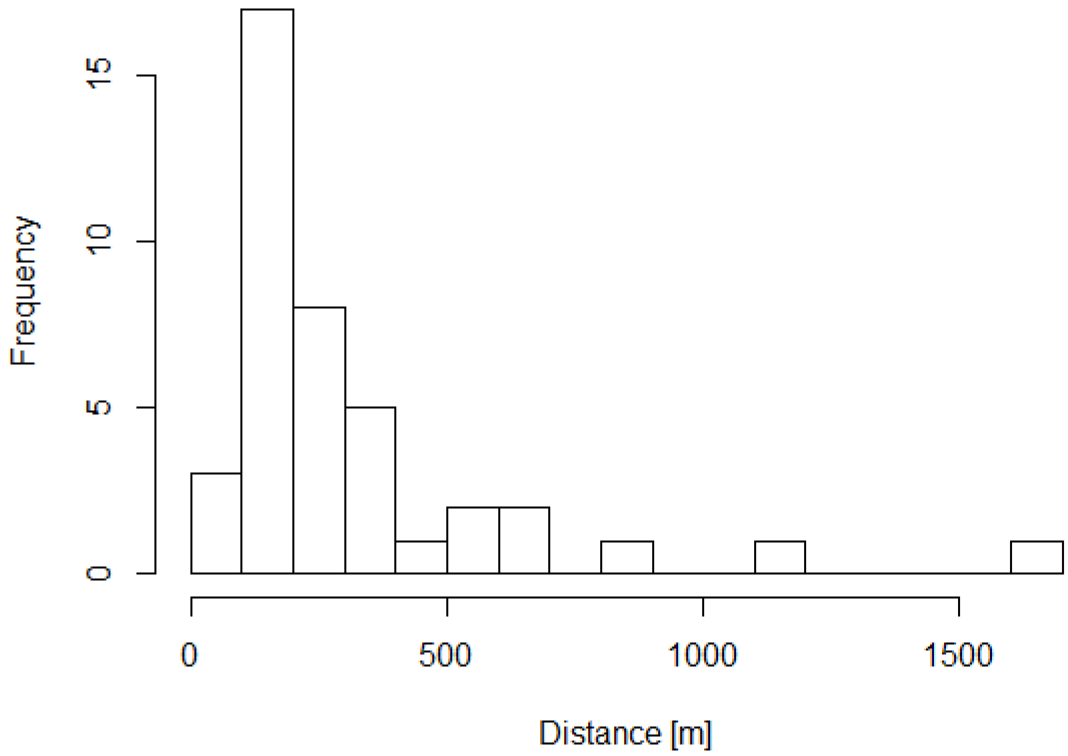
Appendix 33: Frequency distribution of distances between sequentially recorded L3 sand lance patches on July 25, 2009. The first break, based on which L3 patches were grouped into L4 patches, was identified at 200 m.



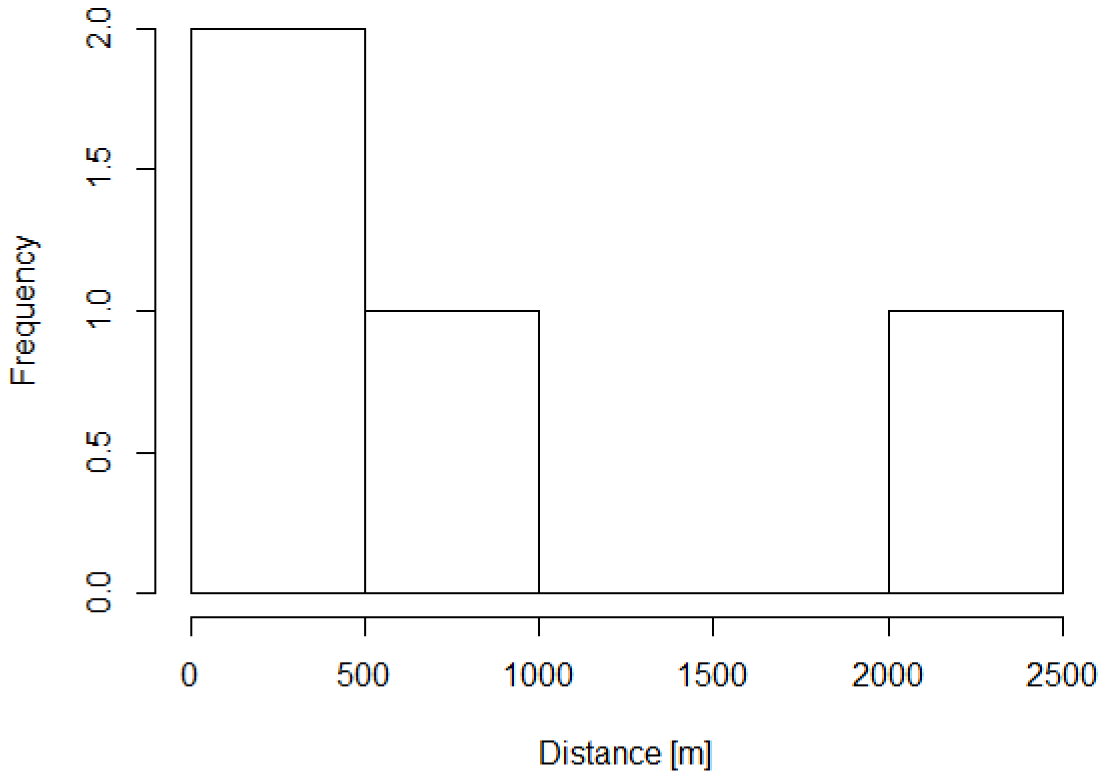
Appendix 34: Frequency distribution of distances between sequentially recorded L4 sand lance patches on July 25, 2009. The first break, based on which L4 patches were grouped into L5 patches, was identified at 1500 m.



Appendix 35: Frequency distribution of distances between sequentially recorded sand lance schools on June 21, 2012. The first break, based on which schools were grouped into L2 patches, was identified at 140 m.



Appendix 36: Frequency distribution of distances between sequentially recorded L2 sand lance patches on June 21, 2012. The first break, based on which L2 patches were grouped into L3 patches, was identified at 500 m.



Appendix 37: Frequency distribution of distances between sequentially recorded L3 sand lance patches on June 21, 2012. The first break, based on which L3 patches were grouped into L4 patches, was identified at 1000 m.