AN EVALUATION OF HOME RANGE MODELS FOR MARINE FISH TRACKING AND FINE SCALE HABITAT USE AND MOVEMENT PATTERNS OF AGE 1 GREENLAND COD (*GADUS MACROCEPHALUS OGAC*)

by

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Thesis Abstract

My thesis examines fine-scale habitat use and movement patterns of age 1 Greenland cod (*Gadus macrocephalus ogac*) tracked using acoustic telemetry. Recent advances in tracking technologies such as GPS and acoustic telemetry have led to increasingly large and detailed datasets that present new opportunities for researchers to address fine-scale ecological questions regarding animal movement and spatial distribution. There is a growing demand for home range models that will not only work with massive quantities of autocorrelated data, but that can also exploit the added detail inherent in these high-resolution datasets. Most published home range studies use radio-telemetry or satellite data from terrestrial mammals or avian species, and most studies that evaluate the relative performance of home range models use simulated data. In Chapter 2, I used actual field-collected data from age-1 Greenland cod tracked with acoustic telemetry to evaluate the accuracy and precision of six home range models: minimum convex polygons, kernel densities with plug-in bandwidth selection and the reference bandwidth, adaptive local convex hulls, Brownian bridges, and dynamic Brownian bridges. I then applied the most appropriate model to two years (2010-2012) of tracking data collected from 82 tagged Greenland cod tracked in Newman Sound, Newfoundland, Canada, to determine diel and seasonal differences in habitat use and movement patterns (Chapter 3). Little is known of juvenile cod ecology, so resolving these relationships will provide valuable insight into activity patterns, habitat use, and predator-prey dynamics, while filling a knowledge gap regarding the use of space by age 1 Greenland cod in a coastal nursery habitat. By doing so, my thesis demonstrates an appropriate technique for modelling the spatial use of fish from acoustic telemetry data that can be applied to high-resolution, high-frequency tracking datasets collected from mobile organisms in any environment.

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BB	Brownian bridge movement model
dBB	Dynamic Brownian bridge movement model
HPE	Relative horizontal positioning error (unitless)
HPEm	Actual horizontal positioning error (m)
KDplug	Kernel density using plug-in bandwidth selection
KDref	Kernel density using the reference bandwidth
LCH	Alpha-local convex hulls
MCP	Minimum convex polygons
UD	Utilization distribution
σ^2_{M}	Brownian motion variance

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Chapter 1: Introduction and Overview

An animal's habitat is the sum of resources and conditions necessary for growth, survival, and reproduction (Krausman 1999). "Good habitat" provides resources such as food, shelter, nesting sites, and migration corridors, and thus increases the chances of survival of individuals of a species as well as the species’ long-term persistence (Krausman 1999). Environmental components that collectively constitute good habitat change as individuals grow and mature throughout life.

As animals move through their environment, they make behavioral decisions about their use of space that affect individual fitness (Forrester et al. 2015). Individuals assess surroundings, moving into habitats providing the best balance of quality, and both conspecific and heterospecific density (Stamps 2001). These movement decisions are a product of intrinsic and extrinsic factors, and they ultimately affect population dynamics and species distribution (Nathan et al. 2008). Studying animal movement reveals much about the ecology of a species and the behaviour of individuals. By tracking an animal through space and time, we can observe how an animal interacts with its environment and what constitutes its habitat. Understanding why animals move requires evaluating which resources an animal uses at specific times and places, and what threats it encounters while doing so (Cagnacci et al. 2010).

An organism’s habitat is often related to its role within the community, or its ‘ecological niche’. Grinnell (1917) associated the ecological niche of a species with its spatial distribution, redefining the niche as the range of environmental factors required for a species to carry out its life history. The occurrence of a species would be expected to follow the distribution of its niche, with species density positively correlated with the intensity of niche conditions (James et al. 1984). Hutchinson (1957) expanded upon the Grinellian niche concept to define the ‘fundamental niche’ as an *n*-dimensional resource space that includes all abiotic and biotic factors that allow a species to persist, as well as all species other than the species of interest. In reality however, interspecific competition prevents a species from utilizing the full fundamental niche and instead utilization of a subset of the fundamental niche, the ‘realized niche’, is observed (from James et al. 1984). Under both the Grinellian and Hutchinsonian models, determining the niche of a species begins with mapping the area of occurrence, or ‘home range’.

Many researchers define home range as the area of an animal's habitat in which it moves and carries out its normal activities (e.g., foraging, mating, caring for young and avoiding predators) (Burt 1943). The idea that animals restrict their movements to a specific home range has been in place for over a century (Darwin 1859), and numerous methods exist to delineate a home range (reviewed in Laver & Kelly 2008). Many studies utilize a two-dimensional probability distribution to model the intensity of use over an area (Van Winkle 1975). These utilization distributions (UDs) can be contoured to represent those areas used more than others, and to exclude outliers. Often, researchers use the 95% contour to represent an animal's 'home range' and the 50% contour to define the 'core area of use', which represents the habitat used most (Laver & Kelly 2008).

Methods of calculating "home range" have been available for decades. The "minimum convex polygon" or MCP represents the oldest and simplest method of calculating home range (Mohr 1947). MCPs are basic perimeters that encompass all positions but with no internal angles greater than 180 degrees. Although easily implemented and widely used (Laver & Kelly 2008) in animal ecology, MCPs do not facilitate calculation of utilization distributions. Therefore, they do not model the intensity of use within an area of an animal's habitat. Local convex hull methods build upon the concept of MCPs by creating smaller localized MCPs ('hulls') around each position (Getz & Wilmers 2004). The resulting hulls are then ranked by size, uniting the smallest *X*% of hulls to represent the *X*% contour of the UD. This method performs well in geographic regions that contain inaccessible habitats or barriers to movement (Getz et al. 2007), such as mountain ridges, fences, or for aquatic organisms, land.

Kernel density estimators (Worton 1989), perhaps the most widely used home range method (Laver & Kelly 2008), determine UDs by smoothing the contribution of each observed data point over a local area called a kernel (Worton 1989). The width of the kernel, or bandwidth, determines the amount of smoothing and can significantly impact results (Worton 1995). The bandwidth can be chosen manually, but most studies utilize automated methods. These methods can be sensitive to the volume (Seaman et al. 1999) and distribution of data (Walter et al. 2011). However, when used correctly, they accurately represent how individuals partition spatial use within an area. Kernel density estimates are based on the spatial density of positional data alone; the model does not consider sequence of positions or the time between them. In fact, kernel methods assume positions represent independent random samples (Worton 1989).

Path-based estimators – such as Brownian bridges (Horne et al. 2007) and dynamic Brownian bridges (Kranstauber et al. 2012) – improve on the spatial density estimators described above. Path-based approaches incorporate the time between sequential positions into models of movement paths. The inclusion of movement trajectory into a home range model allows for better representation of movement corridors and migration routes (Horne et al. 2007). These models perform well with the large volumes of autocorrelated data typically produced by most tracking techniques (Kranstauber et al. 2012).

Studies often seek to match habitat use to specific drivers, and home ranges can easily be linked to environmental data such as bathymetry or habitat maps in order to resolve ecological relationships such as habitat use and animal experience. In a tracking experiment that involved eastern gray squirrels (*Sciurus carolinensis*) in urban areas, Tounzen et al. (2013) used Google Earth™ maps to document selection of upland and riparian forests by squirrels, and avoidance of open grassy or developed areas. Cory's shearwaters (*Calonectris borealis*) fitted with GPS loggers revealed age-dependent habitat use that reflected foraging patterns (Haug et al. 2014). Younger birds exhibited more exploratory behaviour and relied on less productive pelagic feeding areas within their habitat; in contrast, older, more experienced birds showed high site-fidelity towards productive shallow feeding grounds.

Many size-structured populations of fish species exhibit ontogenetic shifts in habitat as changes in body size often lead to changes in energy requirements, risk of predation, and foraging strategy (Werner and Gilliam 1984). While most marine demersal fish exhibit such a shift when settling out of the planktonic phase to the seabed, ontogenetic shifts in habitat use can also occur between juvenile and adult lifestages. For example, schoolmaster snapper (*Lutjanus apodus*) shift from shallow mangrove forests as juveniles to outer reef habitat as adults (Huijbers et al. 2015). By providing cover and abundant food, mangroves often act as nursery areas for young reef fish prior to their migration to adult reef habitats (Mumby et al. 2003). Nursery areas typically produce a disproportionately higher number of recruits relative to other juvenile habitats (Beck et al. 2001). In coastal Newfoundland, shallow complex habitats provide juvenile cod a refuge from predation (Laurel et al. 2003b) and enhanced foraging opportunities (Joseph et al. 2012).

Greenland cod (*Gadus macrocephalus ogac*) are demersal marine teleost fishes with a circumpolar distribution that stretches from Alaska to Greenland, and South to New England (Scott & Scott 1988). They are a subspecies of Pacific cod, *G. macrocephalus* (Coulson et al. 2006), and they overlap in range with their congener, Atlantic cod (*G. morhua*). Most adult Greenland cod remain coastal, mature at age 3-4 years old, and spawn demersal eggs annually in late March - April (Mikhail & Welch 1989). In contrast, Atlantic cod mature between 3 and 8 years old, move offshore as adults, and spawn pelagic eggs annually between March and June (Fleming 1960). In Newfoundland, juvenile Greenland and Atlantic cod settle into shallow bays along the coast where they occupy the same complex habitats in the nearshore such as cobble-pebble seabeds (Gregory & Anderson 1997) and eelgrass (Tupper & Boutilier 1995, Laurel et al. 2003a). As juveniles grow, they move to progressively deeper waters with coarser seabeds (Gregory & Anderson 1997) until recruiting into adult populations at age 3-4 (Mikhail & Welch 1989; Fleming 1960). Although there has been some effort to investigate habitat associations of juvenile Atlantic cod, fewer studies describe the habitats of juvenile Greenland cod (e.g., Laurel 2003a, Knickle & Rose 2014b). However, evidence suggests that juveniles of these two species use similar habitat, allowing inferences on patterns of habitat use in the lesser-studied species (Laurel 2003a, Knickle & Rose 2014b).

Generally, previous studies on either species concentrated on age 0 (Linehan et al. 2001; Laurel et al. 2003ab, 2004), and older age 2-4 juveniles (Clark & Green 1990; Cote et al. 2002, 2003, and 2004; Knickle & Rose 2014b), leaving a knowledge gap for age 1. At age 0, high densities of juveniles of both species associate with shallow, complex habitats such as cobble (Gotceitas et al. 1995; Gregory & Anderson 1997; Cote et al. 2001) and eelgrass beds (Laurel et al. 2003a, 2004), and are readily sampled using methods such as beach seines (Laurel et al. 2004, Linehan et al. 2001). Age 2 and older cod generally occur deeper than the range of a beach seine (Gregory & Anderson 1997), but they are large enough to support traditional tagging experiments involving mark-recapture (e.g., Solmundsson et al. 2015; reviewed in Cadigan & Brattey 1999) and acoustic telemetry (Clark & Green 1990; Cote et al. 2002, 2003, 2004). Older juvenile Atlantic cod (2-4 years old) generally select coarse substrates such as cobble and boulder, and avoid finer substrates (Gregory & Anderson 1997). Individuals often associate with macroalgae (e.g., kelp; Keats et al. 1987, Gotceitas et al. 1997, Cote et al. 2001 and 2003), but not always (Gregory & Anderson 1997). The only study of habitat associations in Greenland cod reported that age 2-4 juveniles also selected areas with cobble, boulder, and macrophyte cover (Knickle & Rose 2014b). The scarcity of data on fishes younger than 2 years creates a significant knowledge gap, however, new advances in tracking technology that support tagging of small fishes open up new opportunities to assess habitat use in younger juvenile fishes.

Acoustic telemetry uses sound to transmit signals, and provides a means of tracking tagged fishes in the marine environment, where radio and GPS tracking are not feasible (reviewed in Huepel et al. 2006). Since many of the components used in modern tracking systems are also used in mass-consumer electronics, they benefit from industry-driven improvements to processor efficiency, battery life, and miniaturization (Kays et al. 2015). These developments have allowed researchers to implant transmitters into smaller juvenile fishes, and to collect tracking data with increasing resolution and volume (e.g., Shapiera et al. 2014; Hussey et al. 2015). Indeed, some home range techniques in use today do not work with the massive quantities of dependent data that characterize recent tracking methods such as GPS (e.g., Hemson et al. 2005) and acoustic telemetry (see Chapter 2). Furthermore, autocorrelation of high frequency tracking data violates assumptions of independence inherent in models such as kernel density (Worton 1989) and local convex hulls (Getz et al. 2007). Researchers can subset data to achieve independence (e.g., Kenward 1992), but doing so removes valuable information that can reduce the relevancy or accuracy of home range estimates (De Solla et al. 1999). Therefore, there is a demand for a home range model that can exploit the additional information contained within large, high-frequency tracking datasets (Urbano et al. 2010).

In general, most authors agree that no one home range model is superior to all others in all scenarios, and that the project goals should dictate the choice of home range model (Laver & Kelly 2008). The choice is important, as the sensitivity of many home range models to the distribution of underlying data leads to uneven performance across applications, potentially leading to inaccurate home range estimates and misleading results (Gitzen et al. 2006). Many studies that compare home range models use simulated data (e.g., Getz & Wilmers 2004; Borger et al. 2006) or data from terrestrial (reviewed in Harris et al. 1990) or avian species (e.g., Farmer et al. 2010, Walter et al. 2011). In Chapter 2 of my thesis, I assess the performance of six home range models applied to a subset of high-frequency, field-collected positional data from age 1 Greenland cod tracked using acoustic telemetry. These datasets are highly autocorrelated and contain frequent missed transmissions and periods of absence that are known to cause problems for some home range models, but are typical of tracking datasets collected from marine environments. Although this study is the first comprehensive comparison of home range models that uses acoustic telemetry data specifically, the techniques presented can be used with any recent tracking method that produces large quantities of high-frequency, high-resolution positional data.

In Chapter 3, I apply the most suitable model to the full two years of data (2010-2012) collected from all 82 tagged Greenland cod tracked in Newman Sound, Newfoundland, Canada, to determine diel and seasonal differences in habitat use and movement patterns. Although it has long been known that age 0 Greenland cod associate with eelgrass, it has until now been unclear whether age 1 cod continue to associate with such shallow coastal habitat, actively relocate to other habitat, or simply broaden their home range to include other habitats nearby (e.g., move into the deeper macroalgae and cobble habitats inhabited by age 2 and older juveniles). Resolving this relationship would provide insight into predator-prey dynamics, connectivity, and habitat use in juvenile cod, while demonstrating how an appropriate model can leverage the extra information contained in modern high-frequency, high-resolution tracking datasets to address detailed ecological questions.

Finally, in Chapter 4 I discuss the implications of my thesis findings for juvenile cod and animal movement ecology. While little is known about the spatial habits of juvenile Atlantic cod, even less is known about Greenland cod. Not only will my results fill a knowledge gap for this relatively understudied species, but similarities between the two species at this stage allow us to make inferences on the habits of exploited Atlantic cod. The development of effective conservation strategies requires knowledge of habitat use and activity patterns, and initiatives to increase future cod stocks must consider juvenile habitat, including an understanding of where juveniles occur, their association with their environment, and when these patterns change. Researchers can investigate these issues by modelling home ranges from high-resolution tracking data, but the choice of model should be made carefully. With recent advances in GPS and acoustic telemetry technology, the need for a comprehensive assessment of home range models applied to modern tracking data has never been greater. Only by using an appropriate model can researchers begin to investigate ecological relationships accurately and with confidence.

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Co-Authorship Statement

The research described in this thesis was conceived and designed by Dustin Schornagel in collaboration with Dr. Bob Gregory, Dr. Corey Morris, Dr. Paul Snelgrove, Dr. Dave Cote, and Curtis Pennell. Dustin Schornagel, Dr. Bob Gregory, Dr. Corey Morris, Curtis Pennell, and Dr. Dave Cote collected the data. Dustin Schornagel analyzed the data with assistance from Dr. Bob Gregory, Dr. Dave Cote, Dr. Paul Snelgrove, and Curtis Pennell. All manuscripts were written and prepared by Dustin Schornagel, with edits and guidance from Dr. Bob Gregory, Dr. Paul Snelgrove, and Dr. Corey Morris. Manuscripts of Chapters 2 and 3 will be submitted to peer-reviewed journals for publishing after submission to the School of Graduate Studies.

Chapter 2: An evaluation of home range use models for a marine fish using telemetry data

Abstract

For over a century, researchers have recognized that mobile animals restrict their movements to a home range. However, the debate on how to delineate home range from location data continues. The choice of home range model can dramatically affect results, and no single home range model performs best in all applications. Most studies that compare home range methods use simulated data that result in home ranges that may simply reflect the distribution used to generate the data. I used actual field-collected data from age-1 Greenland cod tracked with acoustic telemetry to evaluate six home range models: minimum convex polygons (MCP), kernel densities with plug-in bandwidth selection and the reference bandwidth (KDplug and KDref), adaptive local convex hulls (LCH), Brownian bridges (BB), and dynamic Brownian bridges (dBB). I found MCP, KDref, and KDplug produced the largest, most generalized home range estimates, whereas smaller, more complex LCH, BB, and dBB estimates better represented expected habitat use based on interpretation of behavior from the literature. I calculated differences between observed and available habitat proportions to assess methodological assumptions inferring habitat selection. LCH, BB, and dBB yielded similar patterns of habitat selection whereas MCP, KDref, and KDplug produced more variable patterns. Acoustic telemetry produces large quantities of autocorrelated data, often including frequent instances of missed transmissions and periods of absence by marked individuals. All of these data traits cause well-known issues with well-established home range models (such as MCP, KDref, KDplug and LCH), in contrast with the dBB approach presented here. Because dBB provided the best balance

of accuracy and precision and the best description of movement corridors, it offers the preferred approach for studies of habitat selection in fish tracked with acoustic telemetry.

Introduction

The idea that animals restrict their movements to an area called a “home range” dates as far back as Darwin (Kie et al. 2010), who noted that 'most animals and plants keep to their proper homes, and do not needlessly wander about' (Darwin 1859). Burt (1943) later formally defined home range as the area through which an animal travels during its normal activities of food gathering, mating, and reproducing, excluding exploratory trips. More recently, the use of two-dimensional probability density functions called utilization distributions (UDs) has lead to the adoption of a more statistical definition of home range. UDs model the intensity of use across an area, and can be contoured to represent areas with varying degrees of use (Van Winkle 1975). Most studies use the 95% contour to represent the home range (equivalent to where an animal occurs 95% of the time), whereas the 50% contour represents the core area of use (Laver & Kelly 2008).

Ecologically, a home range can provide much information on animal growth, survival, and reproduction (Powell & Mitchell 2012). By delineating a home range and relating it to the environment, researchers can calculate habitat associations (Cote et al. 2003), identify inaccessible areas and barriers to movement (Gulsby et al. 2011), resolve migration routes (Farmer et al. 2010), and ultimately, infer *why* an animal uses its home range (Kie et al. 2010). For threatened species, home ranges can help in identifying critical habitats to include in conservation efforts such as reserves or marine protected areas, or as a means to monitor their effectiveness (Kramer & Chapman 1999). When a temporal component is added home ranges can be used to monitor shifts in distribution over time, allowing researchers to predict future range expansions of invasive species (e.g., Brownscombe et al. 2012), or explore interactions between species or sup-populations (e.g., Zimmerman et al. 2013). Logistics, costs, and animal behaviours often make continuous observation of animal movements impossible, and most studies instead represent occurrence from multiple samples of locations. Tracking methods such as radio telemetry, acoustic telemetry, and satellite tracking provide periodic animal locations, and a home range interpolates the use of space between them (Kernohan et al. 2001). How best to delineate home range has generated considerable debate, but most authors agree that no single home range approach is best in all applications (Huck et al. 2008, Laver & Kelly 2008, Kie et al. 2010, Lichti & Swihart 2011, Walter et al. 2011).

Recent technological advances allow collection of tracking data with increasing resolution and volume (Getz & Wilmers 2004). Many home range techniques in current use were developed when radio-tracking was standard (Kie et al. 2010), and they fail to converge on an estimate when applied to the massive quantities of high-resolution data that characterize recent tracking methods (Hemson et al. 2005). Strong autocorrelation in high frequency tracking data violate assumptions of independence inherent in kernel density (Worton 1989) and local convex hull models (Getz et al. 2007). The marine environment presents particularly difficult challenges to tracking. Although radio telemetry is frequently used in freshwater environments (reviewed in Thorstad et al. 2013), radio and GPS transmission signals do not transmit through saltwater, and limited visibility (e.g., phytoplankton) generally precludes direct observation. GPS tracking can be used in the marine environment, but is limited to larger 'pop-up' archival tags (e.g., Stokesbury et al. 2007). Alternatively, acoustic telemetry employs sound signals to track fish in the marine environment, and produces high resolution data in quantities comparable to satellite tracking.

Acoustic telemetry uses electronic transmitters that emit acoustic pulses at a programmed time interval. Each transmitter produces unique, coded signals that receivers, or hydrophones, detect and log to uniquely identified tags. Analyses from hydrophones positioned as a clustered array with overlapping ranges can use hyperbolic positioning to estimate a two-dimensional position with less than 1 m horizontal positioning error when three or more hydrophones receive a single transmission. Transmitters can be programmed with variable transmission frequencies to balance trade-offs between data resolution and battery life; indeed, some studies can track individuals for years. The limited range of hydrophones adds a requirement for line-of-sight to transmitters. Sound pollution, habitat complexity, cryptic behaviours (e.g., burrowing), simultaneous transmissions, and equipment fouling (e.g., settlement of algae & molluscs) can all increase rates of missed transmissions for acoustic telemetry (Cooke et al. 2013). Gaps in movement paths can complicate path-based home range estimators that describe the use of space between successive locations. As the time between locations increases, uncertainty in the use of space between them also increases, leading to over-inflated home ranges and the inclusion of unused areas into home range estimates (Horne et al. 2007).

Although most studies that evaluate the relative performance of home range models use simulated locations or UDs, few apply real field data to compare models (Borger et al. 2006). Simulations may not capture all behaviours encountered in field-collected data, and home ranges estimated from simulated data may only reflect the distribution used to generate them (Borger et al. 2006). Estimators that perform well on simulated data may not accurately represent the space use of real animals (Huck et al. 2008). Most published home range studies use radio-telemetry

(Laver & Kelly 2008) or satellite data (Tomkiewicz et al. 2010) that track terrestrial mammals (reviewed in Harris et al. 1990) or avian species (e.g., Farmer et al. 2010, Walter et al. 2011) with few missed transmissions. In this study, I compare six home range models in their application to marine fish tracking data collected with acoustic telemetry: minimum convex polygons (MCP), kernel densities with the reference bandwidth (KDref), kernel densities with 'solve-the-equation' plug-in bandwidth selection (KDplug), adaptive local convex hulls (LCH; Getz et al. 2007), Brownian bridges (BB; Horne et al. 2007), and dynamic Brownian bridges (dBB; Kranstauber et al. 2012). Specifically, I compare home range models using actual acoustic telemetry data on the movements of age-1 Greenland cod (*Gadus macrocephalus ogac*). I assess differences in area and complexity, and determine which model best represents expected habitat use by juvenile cod. Although I do not test habitat selection statistically, I also assess differences in the conclusions reached with each model. These high-frequency datasets represent the large quantities of autocorrelated data that recent tracking techniques typically produce, as well as the frequent missed transmissions and periods of absence that characterize most acoustic telemetry data collected from the marine environment.

Methods

Data Source

I estimated home ranges for two age-1 Greenland cod (*Gadus macrocephalus ogac*) that I tracked using acoustic telemetry as part of a larger study of activity and habitat selection (see Chapter 3). These specific fish spanned the range of observed movement behaviours, and were used to illustrate potential differences among approaches. Greenland cod are demersal marine gadid fish that inhabit shallow coastal marine waters as juveniles (up to 3 years old). Fish A

(15.5 cm standard length) and fish B (16 cm standard length) were captured by beach seine from Heffern's Cove (48.5639° N, 53.8907° W) in October 2010; age was determined from known age-length relationships (Gregory et al. 1997). Heffern's Cove is a small (0.2 km^2) bay located on the south shore of Newman Sound, in Bonavista Bay, NL (Fig. 2.1). Although relatively shallow in depth (mean of 6.5 m), a ledge at the mouth quickly drops to over 30 m. Habitat patch configuration was digitized manually from a combination of aerial photographs (30 cm resolution; Parks Canada), and ground-truthing using submersible video cameras (JVC HD Everio™ camcorder in a watertight housing, or a SeaView™ SeaMaster) at 278 target locations. I classified habitat type as the substrate or macrophyte comprising the largest proportion of the video frame once the camera landed on the bottom; Heffern's Cove was 54% kelp (*Laminaria* spp., *Saccharina latissima*), 13% mud/sand/gravel (grain size $\leq$ 2.5 cm), 12% cobble (grain size 25 – 100 cm), 9% eelgrass (*Zostera marina*), 8% boulder/bedrock (grain size > 1m), and 4% rockweed (*Fucus* spp., *Ascophyllum nodosum*). I estimated the error of the habitat map at < 5 m (Chapter 3).

I inserted Vemco™ V7-4L coded acoustic transmitters (Vemco V7-4L; 22.5 mm long, 7 mm diameter, 1.8 g in air, 136 dB re 1 uPa at 1 m, random transmission interval of 240 ± 70 s, tag life 415 days) into the belly of the fish through a surgical incision (approximately 1 cm long) off center of the ventral midline. Two sutures closed the incision, and individuals were allowed to recover overnight in a 1 m^3 net pen before release at the study site October 8, 2010. Within the study site, I deployed a network of 12 omni-directional acoustic telemetry receivers (approximate range of 500 m), or hydrophones, configured to provide overlapping ranges (Fig. 2. 2). Because receivers require a line-of-sight to the transmitter, and juvenile cod typically occur within a meter of the bottom (Gregory & Anderson 1997), hydrophones were moored 1 m off the seabed. I also deployed stationary reference transmitters (i.e., synctags) with regular transmission intervals in each cove. These synctags provide a means to correct drift in the hydrophone's internal clock, producing more accurate position estimates.

Data Analysis

Home range estimators

I created 100% MCP, 95% KDref, and 95% *a*-LCH home ranges using the 'adehabitatHR' package (Calenge 2006) in R statistical programming software (R core team 2013). KDref home ranges were constructed with a bivariate normal kernel and a grid size of 200 (~ 5 m cells). I followed a rule of thumb for selecting values of *a* for *a*-LCH, and used the maximum distance between two positions for each fish (fish A = 459 m, fish B = 493 m; Getz et al. 2007). I used the statistical program Geospatial Modelling Environment (ver. 0.7.2, Beyer 2011) to create 95% KDplug home ranges using a bivariate normal kernel and a UD cell size of 5 m. I used the R package 'BBMM' (Nielson et al. 2013) to create BB home ranges for each fish using a maximum interval equivalent to 15 missed transmissions (77.5 min). This parameter prevents a Brownian bridge from connecting sequential positions extending more than 77.5 minutes, ensuring that home ranges represent the space used by fish only while within the study site. The R package 'move' (Kranstauber & Smolla 2013), which I used to construct dBB home ranges, lacks a maximum interval setting. Instead, I created subsets of the data based on a time lag threshold of 77.5 min and established separate dBB UDs for each subset. I then standardized each subset UD by time and averaged it into the final UD. Because the minimum sample size for a dBB model equals the length of the sliding window, I chose a relatively small window length of 9 positions in order to maximize the number of dBB subsets. Choosing the minimum margin length of 3 positions ensured that the maximum positions contribute to estimates of path variance.

Accuracy Assessment

I visualized the home range estimates and calculated the total area (m^2), area over land (m^2), and the number of polygons (‘fragments’) in each home range using ArcGIS 10.2 (ESRI 2014). Using my habitat map, I calculated the proportions of each habitat type within each home range, and compared observed and expected habitat areas to assess the accuracy of each model in representing true habitat use. For real tracking data (as opposed to simulated), true habitat use is unknown but can be estimated by multiplying the proportion of positions in each habitat type by the total home range size (expected area). I then subtracted the expected from the observed area for each habitat type, with values close to zero indicating an accurate representation habitat use. To assess methodological differences in conclusions regarding habitat selection, I compared the proportions of each habitat used to the proportions available. I considered the entire study site as available habitat, and subtracted the proportions available from the proportions used such that positive differences indicate habitat selection and negative differences indicate avoidance.

Results

I tracked fish A for 546 positions over 6 days before it left the study area, and fish B for 2,259 positions over 15 days before suspected tag expulsion or death. Generally, both fish were active throughout the study area and beyond during the day, and inactive over shallow habitats at night.

The area, shape, and configuration of the home range estimates differed greatly among methods (Fig. 2.3). Home range areas varied from 25,332 m^2 to 128,021 m^2, and were the largest for MCP, KDref, and KDplug relative to LCH, BB, and dBB (Table 2.1). Generally, MCP, KDref, and KDplug produced similar estimates that differed from those produced by LCHs, BBs, and dBBs, although for fish B KDplug more closely resembled LCH, BB, and dBB models. In terms of obviously erroneous outcomes, KDref home ranges encompassed the most land, followed by MCP. KDplug home ranges encompassed a higher proportion of land for fish A than fish B. Brownian bridge and dBB home ranges included relatively little land, whereas LCH home ranges did not overlap land at all. MCP and KDref home ranges consisted of a single polygon for both fish, whereas KDplug and LCH created single-polygon home ranges for fish A only. Brownian bridge and dBB produced more fragmented home ranges, although less so for dBB and fish A.

Observed and expected habitat use also differed with home range method (Fig. 2.4). MCP, KDref, and KDplug home ranges differed most, whereas LCH, BB, and dBB values were generally close to zero. Eelgrass and kelp use differed most relative to other habitats with all models underestimating eelgrass use and all but BB overestimating kelp use.

Habitat selection conclusions depended on the home range method (Fig. 2.5). Differences between the proportions of habitats used and their availability were more extreme for LCH, BB, and dBB relative to the other models. All models indicated selection of eelgrass, and all but MCP showed avoidance of kelp. All the models indicated similar selection of mud/sand/gravel, and avoidance of rockweed, boulder/bedrock, and cobble. MCP, KDref, and KDplug indicated selection of land.

Discussion

No single home range method may be considered superior to all others in all applications, and the overall goal of a project should guide selection of a home range method (Laver & Kelly

2008). My study evaluated the suitability of new and older but frequently used home range methods to acoustic telemetry data by applying multiple models to real datasets from tagged juvenile cod. As in many aquatic telemetry studies, high-frequency datasets are autocorrelated, adjacent to a shoreline barrier, and contain missed transmissions and frequent periods of disappearance. These traits complicate models of space use. My results demonstrate that method of home range determination can seriously affect estimates of home range area, shape, configuration, and ultimately, conclusions of habitat selection. LCH, BB, and dBB models most accurately represented true habitat use (based on actual proportions of time spent in each habitat type), whereas MCP, KDref, and KDplug produced larger, more generalized estimates. By incorporating a time element, path-based models (BB and dBB) better represent movement corridors and reveal more detail in intensity of spatial use, making them ideal for fine-scale studies of habitat selection. Statistical improvements to the dBB model make it more robust to irregular sampling and changes in behaviour than the BB model (Kranstauber et al. 2012), and it therefore represents the recommended model for home ranges of juvenile cod.

The MCP method represents the oldest, and most established technique for delineating home range (Mohr 1947; Laver & Kelly 2008). MCP boundaries connect the most peripheral locations so that the home range contains all locations, and no internal angles greater than 180 degrees. They are essentially "minimum bounding boxes" with no inflected sides, and offer no information on the intensity of use within. Thus, an animal could spend 99% of its time within a smaller subset of the MCP but the model would infer home range as the broader area. Because MCPs delineate the perimeter, they are highly dependent on sample size, and the inclusion of outliers can encompass areas in the home range that the animals never used (Worton 1987). Despite its shortcomings, its simplicity and intuitive nature have led to widespread use of the

MCP approach in the literature, often as a means of comparing home ranges across studies (Harris et al. 1990).

Kernel density estimation (Silverman 1986) was first used as a home range estimator by Worton (1989), and it has since become the most widely used method of constructing UDs (Laver & Kelly 2008). To produce a kernel density estimate, a moving window, or kernel is moved across a spatial grid to estimate the probability of occurrence for each cell based on the density of positions that fall under the kernel centered over it. The shape of the kernel (e.g., Gaussian or Epanechnikov function) can vary, but has little effect on the final UD (Silverman 1986). The radius of the kernel (or bandwidth) has the greatest effect on the resulting UD (Worton 1995). The bandwidth of a kernel can either remain constant across a distribution ('fixed kernel'), or vary according to some rule ('adaptive kernel'), but fixed kernels generally outperform adaptive kernels (Seaman & Powell 1996). Although the bandwidth can be set at a specified value, most researchers estimate bandwidth by various automated techniques. Many researchers default to a 'reference' bandwidth, defined as the optimum bandwidth assuming an underlying standard multivariate true distribution of the data (Silverman 1986). Therefore, kernel density estimation with the reference bandwidth (KDref) best describes normal distributions around a single center of activity (Worton 1989). With multi-modal or patchy distributions, KDref tends to oversmooth the home range, increasing bias and including unused areas (Kie et al. 2010).

Several researchers recommend kernel bandwidth selection using least-squares cross-validation (Worton 1995, Seaman & Powell 1996, Borger et al. 2006), an approach used frequently in home range studies (Laver & Kelly 2008). This method estimates the bandwidth by minimizing the integrated square error between the estimated and true distributions (Worton

1989, Gitzen et al. 2006). Sensitivity to repeat locations and failure to converge on a bandwidth for large datasets produced by recent tracking methods limit its utility (Hemson et al. 2005). The plug-in method (Wand & Jones 1994) offers an alternative bandwidth selector that performs better on large datasets. This method first estimates a formula for the asymptotically optimum bandwidth, then "plugs in" kernel estimates of the unknown functions using a normal distribution as a starting estimate (Wand & Jones 1995). Relative to KDref, kernel density estimation with direct plug-in bandwidth selection (KDplug) offers a more reasonable trade-off between bias and variance, particularly for fragmented or multi-modal distributions (Walter et al. 2011). In a study that compared the performance of kernel bandwidth selectors against several simulated datasets, only KDref outperformed KDplug when a single peak dominated the distribution, and least-squares cross-validation performed best when multiple tight clusters dominated the distribution (Gitzen et al. 2006).

Kernel density estimates reduce variance through smoothing, which can include totally unused areas (Kie et al. 2010). The local convex hull model was developed specifically to minimize the inclusion of unused areas in home range estimates (Getz & Wilmers 2004). This model creates localized MCPs, or 'hulls', for each location and its closest neighbors. The union of all local hulls produces the full UD; the union of the smallest local hulls to encompass the required percentage of the positions represents the UD contours (e.g., the 95% contour envelops 95% of the positions; Getz & Wilmers 2004). In the original local convex hull model, the researcher chooses a fixed number of nearest neighbors to include in hull construction *a priori* (Getz & Wilmers 2004). In the adaptive local convex hull model (LCH), an adaptive sphere of influence determines the number of nearest neighbors such that the sum of the distances between nearby points and the root point is less than or equal to a user-specified distance, *a* (Getz et al.

2007). This leads to smaller local hulls in areas of high point density, and UD contours that represent true use more accurately (Getz et al. 2007). The longest distance between two points in the dataset offers a rule of thumb for choosing a value for *a*, noting that LCH is robust to changes in the parameter *a* (Getz et al. 2007). Local convex hull models excel at identifying hard boundaries such as the effects of tall tree canopies on butterfly movement (Bennett et al. 2013) and the effectiveness of fences as barriers to deer movement (Gulsby et al. 2011).

The Brownian bridge movement model (BB) is a "path-based" estimator of space use that uses the actual sequence of positions to model movement trajectories (Horne et al. 2007). The model uses a conditional random walk approach (conditioned on the start and end locations) to calculate a probability density function between pairs of sequential positions based on the time and distance between them, and the Brownian motion variance, σ^2_M. Brownian motion variance relates to the animal's mobility, and is estimated via maximum likelihood techniques (Horne et al. 2007). High σ^2_M indicates high displacement and deviation from a straight-line path; low σ^2_M indicates low displacement and movement in a straight path (Fischer et al. 2013). The model assumes normally distributed location error and requires autocorrelated data (Horne et al. 2007). Brownian bridges connect areas of intense use, and identify movement corridors better than density-based home range methods. Brownian bridge models are often used to study connectivity in mobile animals (e.g., Pages et al. 2013), and have resolved migration routes of birds (Farmer et al. 2010; Fischer et al. 2013) and deer (Sawyer et al. 2009).

Whereas BB calculates a single estimate of σ^2_M and applies it to the entire path, the dynamic Brownian bridge movement model (dBB) improves upon BB by allowing σ^2_M to vary along a path (Kranstauber et al. 2012). The width of Brownian bridges expand or contract according to $\sigma^2_{M,}$ accounting for changes in behaviour and irregular sampling. A "sliding window” estimates σ_M^2 in segments identified using behavioural change point analysis (Gurarie et al. 2009). Multiple σ_M^2 estimates produced for each transmission interval are averaged into the final estimate of σ_M^2 for the segment (Byrne et al. 2014). Therefore, single path, long-distance migratory movements would yield a higher value for σ_M^2 than short, sinuous movements that keep an animal in a particular area. The ability to partition σ_M^2 makes this method robust to irregularly sampled tracks, as well as changes in behaviour (Kranstauber et al. 2012). These attributes are particularly important for long-term tracking projects that likely encounter changes in behaviour over time. In a study that compared BB and dBB models using real and simulated data, dBB produced the most accurate and realistic home ranges (Kranstauber et al. 2012).

My study applied MCP, KDref, KDplug, LCH, BB, and dBB models to real tracking data from marine fish, and found LCH, BB, and dBB models represented expected habitat use most accurately. As a probability function, a UD is subject to both type I and type II errors, where type I errors describe false positives or the inclusion of completely unused areas (Zar 1984, Getz & Wilmers 2004). By minimizing the inclusion of areas that fall outside of the true UD, home range methods such as LCH, BB, and dBB decrease type I errors at the expense of increasing type II errors (Lichti & Swihart 2011). In contrast, the more general, or 'smoothed' estimates of MCP, KDref, and KDplug include large regions where no observations occurred (i.e., no usage), and therefore add greater risk of type I error. Smoothing generalizes estimates by using information from nearby sample locations to reduce the effects of single positions (Simonoff 1998). Less smoothing results in more irregular and fragmented home range boundaries, revealing more structure in how space is used within an area (Worton 1989, Seaman et al. 1999).

MCP and KDref produced the largest, most general, and least accurate home range estimates. MCP home ranges are area perimeters with no convex sides, and do not represent

UDs. As such, MCPs often produce the largest home ranges that encompass inaccessible areas (Ryan et al. 2006, Huck et al. 2008, Scull et al. 2012), and they fit poorly to non-convex distributions (Getz & Wilmers 2004). Comparative studies that include KDref produce over-smoothed home ranges (Kie et al. 2010, Walter et al. 2011) that exceed estimates using KDplug (Walter et al. 2011), LCH (Lichti & Swihart 2011), and BB (Fischer et al. 2013). In my study, KDplug estimates were more accurate than KDref, but performance varied between fish. Kernel density estimation is sensitive to the distribution of data as well as the bandwidth used, and can either overestimate or underestimate habitat use (Getz & Wilmers 2004). In my study, I tracked fish A over twice as long as fish B, resulting in four times as many positions - dissimilarities that could potentially contribute to these performance differences. Therefore, kernel density estimates may be inconsistent when behaviour or sample size varies within and between individuals.

In contrast to the over-generalized home ranges produced by MCP, KDref, and KDplug models, LCH, BB, and dBB yielded smaller, more fragmented, but the most accurate representations of expected habitat use. In other studies, LCH methods produced smaller home range estimates than KDref (Huck et al. 2008), KDplug (Lichti & Swihart 2011), and MCP (Scull et al. 2012). I also found LCH home ranges were more accurate than KDref or KDplug home ranges. While this result confirms previous reports (Huck et al. 2008, Getz & Wilmers 2004), it contrasts those of Lichti & Swihart (2011) who found that KDref and KDplug outperformed nearest neighbors-LCH in terms of overlap with known UDs. Despite potential inaccuracies, LCH home range models consistently outperform other models at minimizing the area that falls outside the true UD (Getz et al. 2007, Huck et al. 2008, Lichti & Swihart 2011), and the relative accuracy of LCH models increases in the presence of these barriers (Getz et al. 2007).

While many comparative home range studies utilize LCH, few examine BB or dBB models (Huck et al. 2008, Walter et al. 2011, Kranstauber et al. 2012). Huck et al. (2008) report BB estimates so inflated that they used the 40% contour in order to compare with 95% contours of KDref estimates, and Walter et al. (2011) found BB areas were slightly less than KDref, but more than KDplug. Kranstauber et al. (2012) found that compared to BB, dBB represented simulated UDs more accurately from randomly sampled positions, and better represented changes in behaviour (such as resting) and movement corridors. Although I found comparable accuracy for BB and dBB models, my results support those of Kranstauber et al. (2012) in that dBB better represented movement corridors. However, my results contradict those of Walter et al. (2011) and Huck et al. (2008) in that I found the BB model (along with the dBB model) most accurately represented expected habitat use. In both of those cases, the authors did not account for large gaps in tracks or variable time lags, likely leading to skewed home range estimates.

Home range accuracy is important, but comparisons of home ranges across individuals or studies must also consider precision. The performance of kernel density estimates depends in part on the distribution of the data, whereas LCH performs consistently across cases (Huck et al. 2008, Getz et al. 2007). My results confirm this generalization in that they showed differences in accuracy of KDplug (and to some extent KDref) estimates among fish, however, LCH fit better with larger sample size. Larger sample size and more clustered data also produced a tighter fit for BB home ranges, whereas dBB performed more consistently. The dBB method uses a dynamic estimate of path variance; therefore, the width of the bridges can fluctuate according to path variance (Kranstauber et al. 2012). In contrast, BB uses a single estimate of path variance that applies to the entire path (Horne et al. 2007). Therefore, the tightness of a BB home range fit to the data remains consistent throughout the home range and depends on the variance estimate, whereas dBB partitions the variance based on path segments. This partitioning allows path variance to fluctuate along a path so the dBB model performs more consistently across sample units. This attribute makes dBB more suitable than BB when comparing individuals with different behaviours and movement patterns.

Recent improvements in tracking technology - such as longer battery life, increased data storage capacity, and higher accuracy have resulted in increasingly autocorrelated and larger datasets (Kie et al. 2010). Kernel density and LCH methods assume data independence that, if violated, can increase bias, underestimate variance, and ultimately produce inaccurate home range estimates (Swihart & Slade 1985, Seaman & Powell 1996). However, recent work places greater importance on obtaining a representative sample of locations (that may be autocorrelated) than on subsampling to achieve independence of locations (Borger et al. 2006, Fieberg 2007). Indeed, shorter time intervals increase accuracy and precision of kernel density estimates, despite increasing autocorrelation (De Solla et al. 1999). Furthermore, autocorrelated data includes useful behavioural information, and its removal could affect the biological relevance of results (De Solla et al. 1999, Blundell et al. 2001). Path-based estimators such as BB and dBB eliminate concern with autocorrelation by incorporating a time element directly into the model (Horne et al. 2007, Kranstauber et al. 2012).

The high volumes of data produced by recent tracking methods such as acoustic telemetry cause problems for some home range models. Some kernel density bandwidth selection methods may fail to converge on a bandwidth for large datasets or clustered distributions (see Walter et al. 2011). I attempted to use least-squares cross-validation as a bandwidth selector on samples of 546 and 2,259 positions, but both efforts failed. Other home range studies report failure of bandwidth selection by least-squares cross-validation with sample sizes over 1,000 positions (Fischer et al. 2013), and plug-in bandwidth selection failure on samples of 1,000-10,000 positions (Walter et al. 2011). Despite the suggestion that the accuracy of kernel density estimates increases with increasing sample size (Seaman et al. 1999), studies that examined the effects of sample size tested with only 100-1,000 positions (Seaman et al. 1999, Lichti & Swihart 2011). Although my KDref and KDplug estimates were more accurate for the larger sample size, there may be an upper limit that causes failure with >10,000 positions. Future work to test the accuracy of kernel density models should test sample sizes of 10,000-100,000 positions by randomly sampling simulated UDs and comparing home range estimates to the known UD.

Although unaffected by sample size directly, the accuracy of LCH models depends on position density. LCH home range estimates converge on the true UD when positions are clustered, aiding the resolution of obstacles and impassable barriers such as fences or shorelines (Getz & Wilmers 2004). In contrast, kernel density home ranges will always extend beyond the data by a distance equal to the bandwidth (Getz et al. 2007), and BB home ranges will extend beyond the data by a distance related to the mobility of the animal (Horne et al. 2007). This limitation leads to inaccuracies that will overestimate some areas and underestimate others. Because the dBB model allows mobility to vary along a path, the width of dBB home ranges will also vary relative to changes in behaviour. For example, when an animal rests, the probability of finding the animal at that specific location increases and the area narrows. The fluctuating bridges allow the accuracy of the model to remain constant along the path, providing a more accurate representation of habitat use than density-base methods when the goal is to examine animal behaviour.

The differences I observed between models in inferring habitat use punctuates the importance of selecting a home range model with the goal of the project in mind. MCP, KDref, and KDplug home ranges differed least in comparing used and expected habitat proportions. Relative to LCH, BB, and dBB, these models over-smoothed home ranges and predicted home ranges that covered much of the study area so that observed habitat use approximated availability (the entire study area). Though inappropriate for resolving the fine-scale differences in habitat selection in my study, these models nonetheless offer utility in other applications. Generalized home ranges (such as those produced by MCP and KDref models) may be more appropriate for ensuring exploratory movements are captured, and those with less smoothing (such as KDplug) could be appropriate for less mobile species in patchy habitat (Walter et al. 2011). Some authors suggest the use of MCP when the goal is to infer absolute area covered by an animal in order to identify a range that contains sufficient resources for its survival (Huck et al. 2008; Lichti & Swihart 2011). However, MCP home ranges do not extend beyond the observed positions. Therefore, a kernel density method that overestimates the boundary by a distance equal to the bandwidth may reduce type II errors, offering greater confidence that the estimated area encompasses the necessary resources. MCP is not recommended because of its sensitivity to sample size, and the inability to produce a UD. Many studies have continued to use MCP for comparisons with older studies (Harris et al. 1990), however, doing so proliferates the misleading idea that it produces a good estimator of spatial use (Laver & Kelly 2008). I recommend against use of MCP for estimating use of space by animals because of its sensitivity to sample size and inability to produce a UD.

In my study, only LCH home range estimates never included land. This model minimizes the inclusion of inaccessible areas, and thus reduces the chances of type I errors. In a study that tracked vultures, BB and KDref home ranges both included ocean areas that an LCH model would likely have excluded (Fischer et al. 2013). LCH home ranges of gorillas tracked in a reserve revealed barriers within the habitat such as mountain ridges and fences (Scull et al. 2012). Therefore, for species restricted by barriers (such as shore-frequenting fish species) LCH may provide the best option for depicting spatial use while minimizing type I error. Although BB and dBB models included land the amount was relatively small and these models, unlike LCH, offer the advantage of better describing movement corridors. The density-based LCH home ranges often smoothed over areas identified in BB and dBB home ranges as separate movement paths. This loss of information could potentially lead to false conclusions when examining habitat selection on a fine-scale.

Conclusions

Relative to other models, dBB provides the best balance of accuracy and precision, while simultaneously providing the most information on structuring of space use within a home range. This model best describes movement corridors, and is robust to missed fixes and changes in behaviour. Juvenile cod display diel (Cote et al. 2001) and seasonal (Shapiera et al. 2014) shifts in movement along edges or barriers (Gorman et al. 2009), and they also use cover-providing habitats that can block acoustic transmissions (Clark & Green 1990). The dynamic variance in the dBB model allows modeling of changes in behaviour, and adds robustness to missed transmissions or irregular sampling. It remained accurate with large, autocorrelated data sets, and produced less extreme results than the traditional BB model. For these reasons, I recommend the use of the dBB model for examining habitat selection in species such as age-1 Greenland cod, which move regularly among habitats but nonetheless exhibit habitat preferences.

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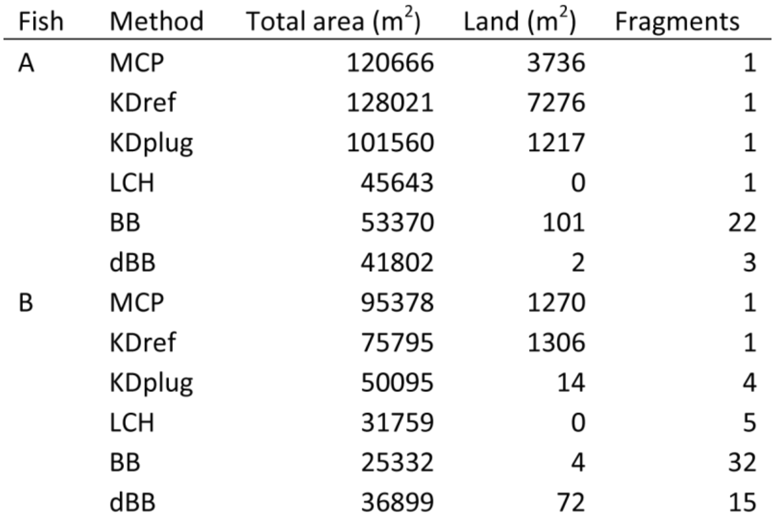
Figures and Tables

Table 2.1. Total home range sizes (m^2), area over land (m^2), and number of home range polygons (‘fragments’) for two age 1 Greenland cod using six different home range estimators (MCP: 100% minimum convex hull, KDref: 95% kernel density with reference bandwidth, KDplug: 95% kernel density with plug-in bandwidth estimation, LCH: 95% alpha-local convex hulls, BB: 95% Brownian bridges, dBB: 95% dynamic Brownian bridges).



Fish	Method	Total area (m^2)	Land (m^2)	Fragments
A	MCP	120666	3736	1
	KDref	128021	7276	1
	KDplug	101560	1217	1
	LCH	45643	0	1
	BB	53370	101	22
	dBB	41802	2	3
B	MCP	95378	1270	1
	KDref	75795	1306	1
	KDplug	50095	14	4
	LCH	31759	0	5
	BB	25332	4	32
	dBB	36899	72	15

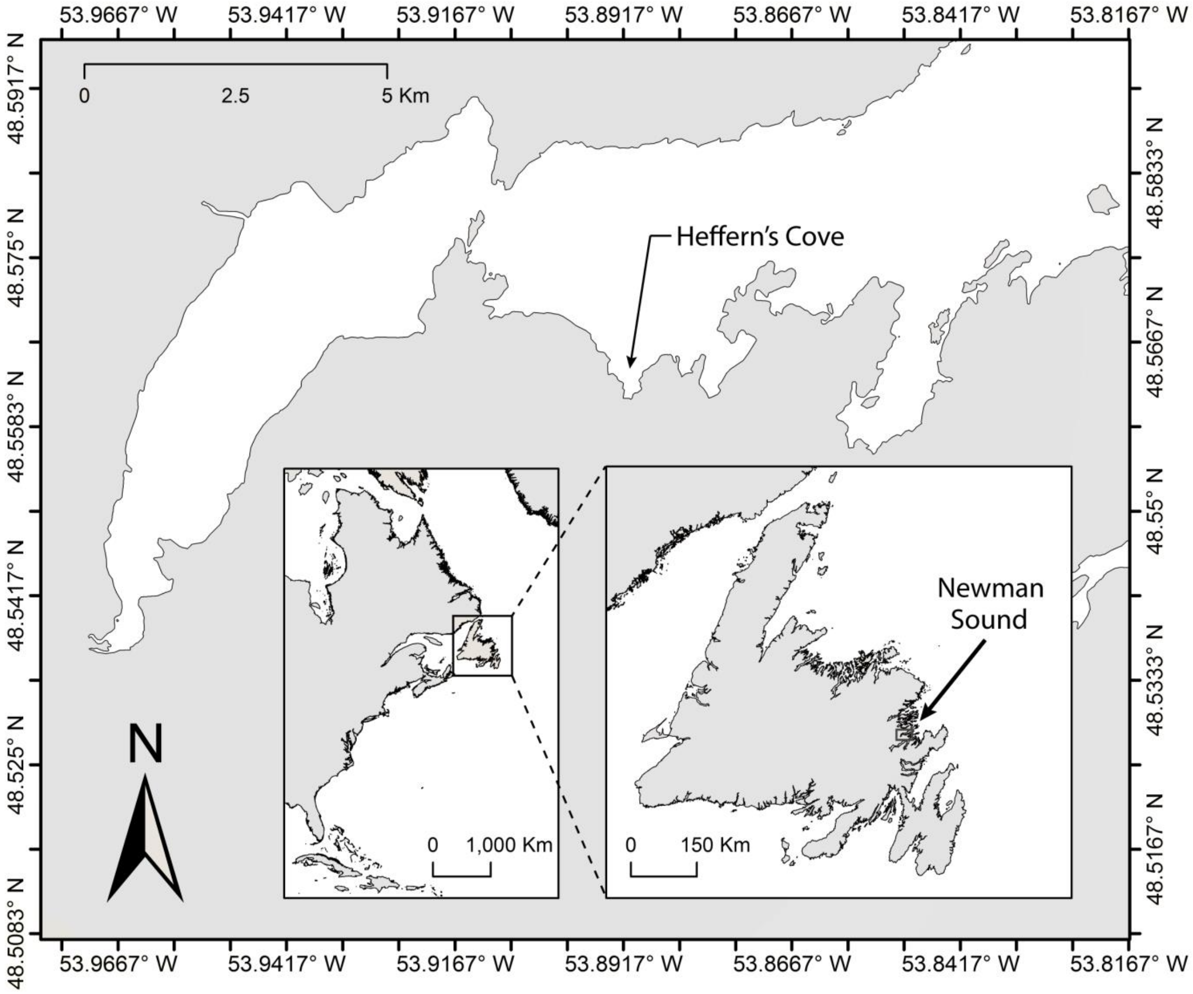


Fig. 2.1. Heffern's Cove study site location in Newman Sound, on the east coast of Newfoundland, Canada.

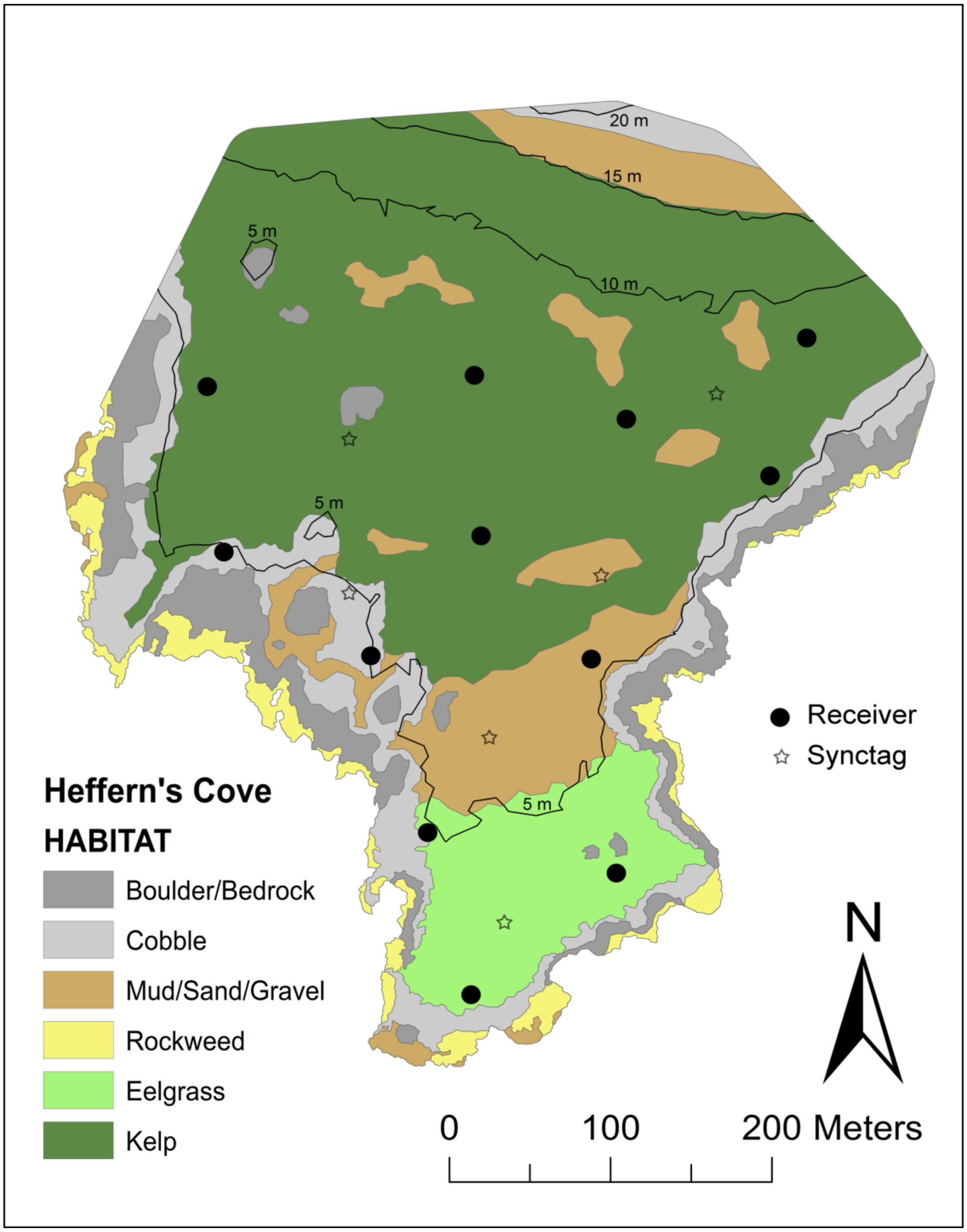


Fig. 2.2. Habitat map of Heffern's Cove with 5-m isobaths (black lines), receivers, and synctags. Habitat was classified from aerial photographs and *in situ* video samples with an estimated error of 5 m. Inert habitat types were classified to grain size: Boulder/bedrock (> 1 m), cobble (25 cm – 1 m), and mud/sand/gravel (≤ 2.5 cm). Macrophyte habitat types were kelp (*Saccharina latissima* and *Laminaria* spp.), eelgrass (*Zostera marina*), and rockweed (*Fucus* spp., *Ascophyllum nodosum*).

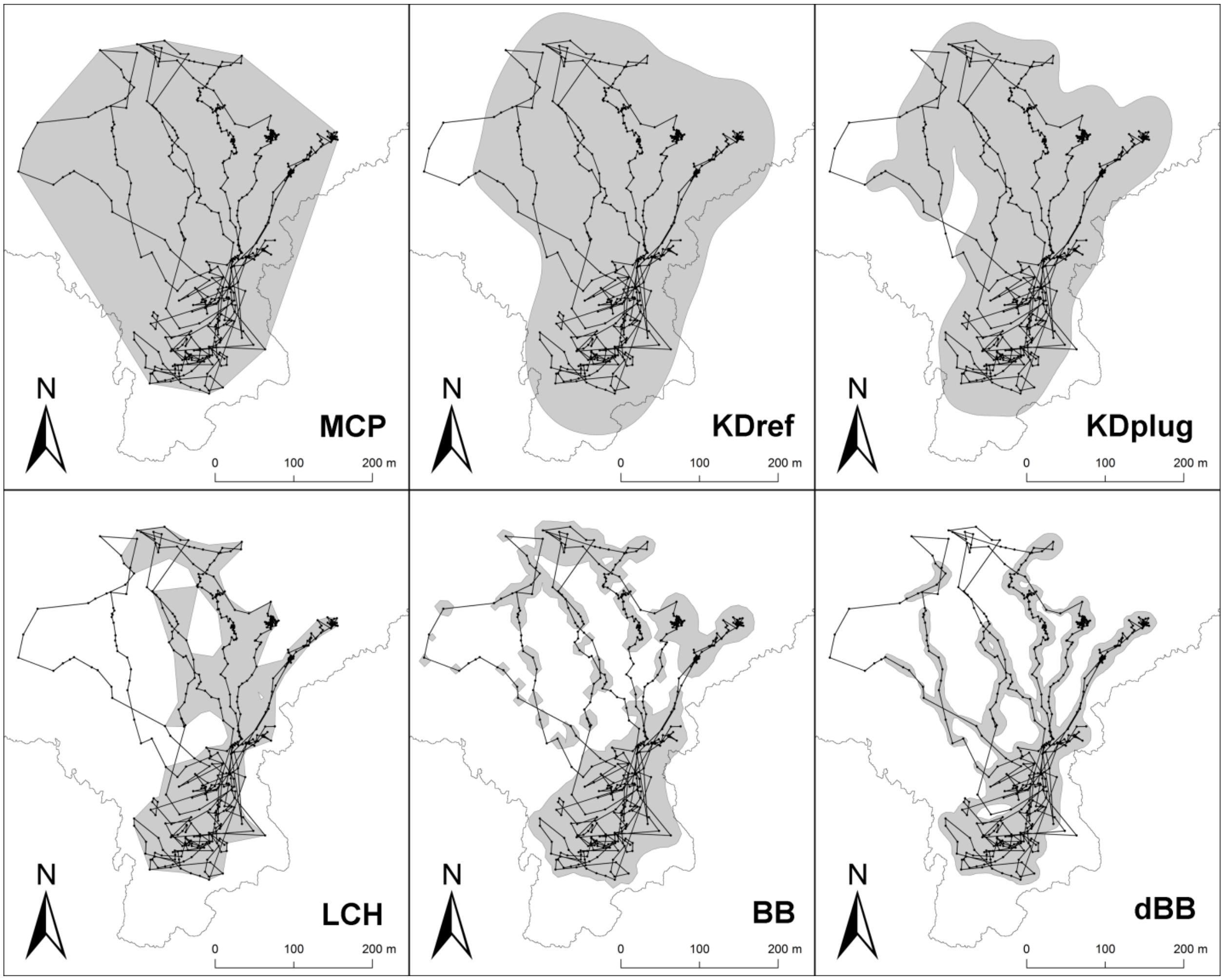


Fig. 2.3A. Home range estimates of an age-1 Greenland cod tracked for 546 positions over 6 days with acoustic telemetry in Heffern's Cove. Estimates were created using 100% minimum convex polygon (MCP), 95% kernel utilization distribution with reference bandwidth (KDref), 95% kernel utilization distribution with plug-in bandwidth selection (KDplug), 95% alpha local convex hulls (LCH), 95% Brownian bridge (BB), and 95% dynamic Brownian bridge (dBB) models.

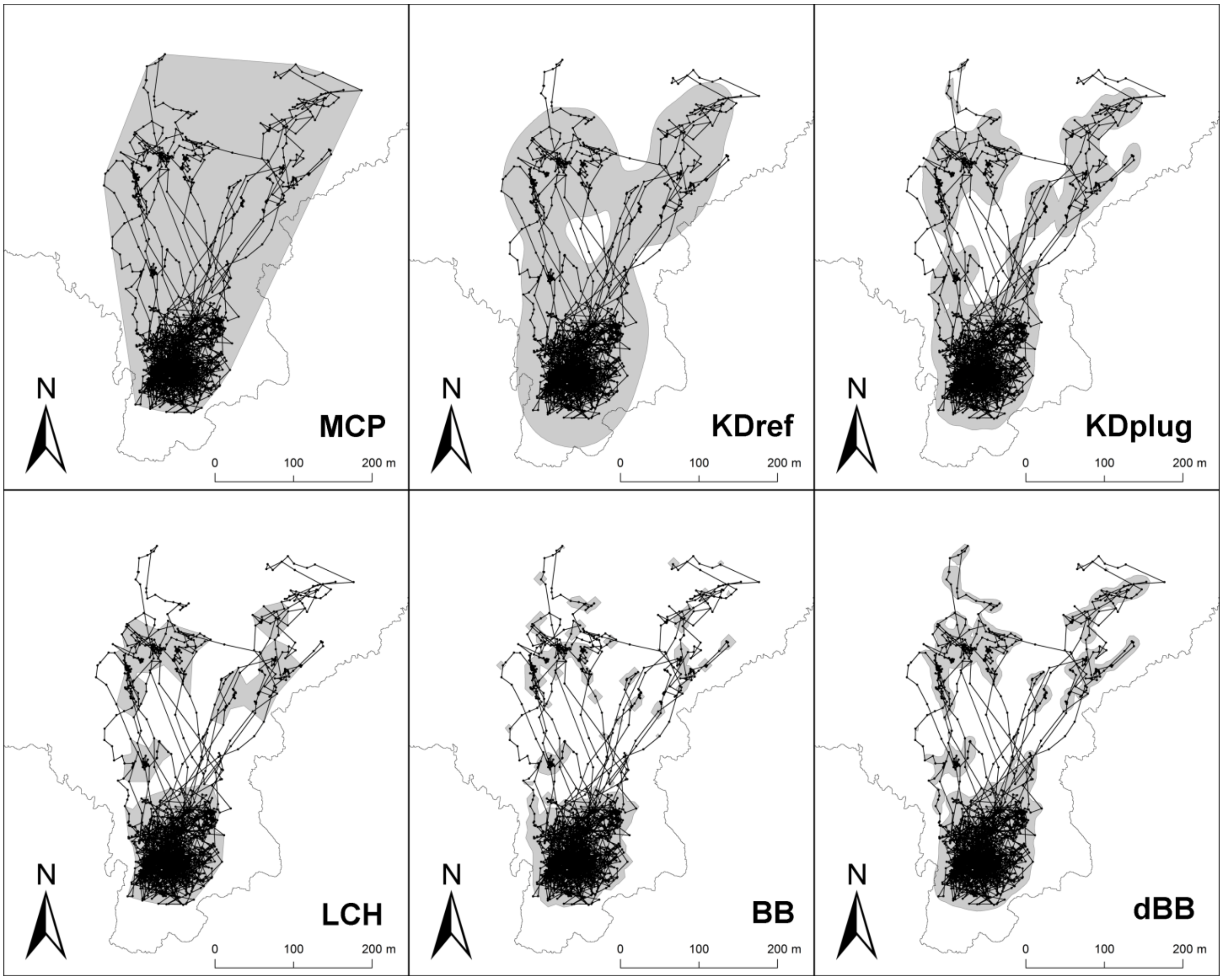


Fig. 2.3B. Home range estimates of an age-1 Greenland cod tracked for 2,259 positions over 15 days with acoustic telemetry in Heffern's Cove. Estimates were created using 100% minimum convex polygon (MCP), 95% kernel utilization distribution with reference bandwidth (KDref), 95% kernel utilization distribution with plug-in bandwidth selection (KDplug), 95% alpha local convex hulls (LCH), 95% Brownian bridge (BB), and 95% dynamic Brownian bridge (dBB) models.

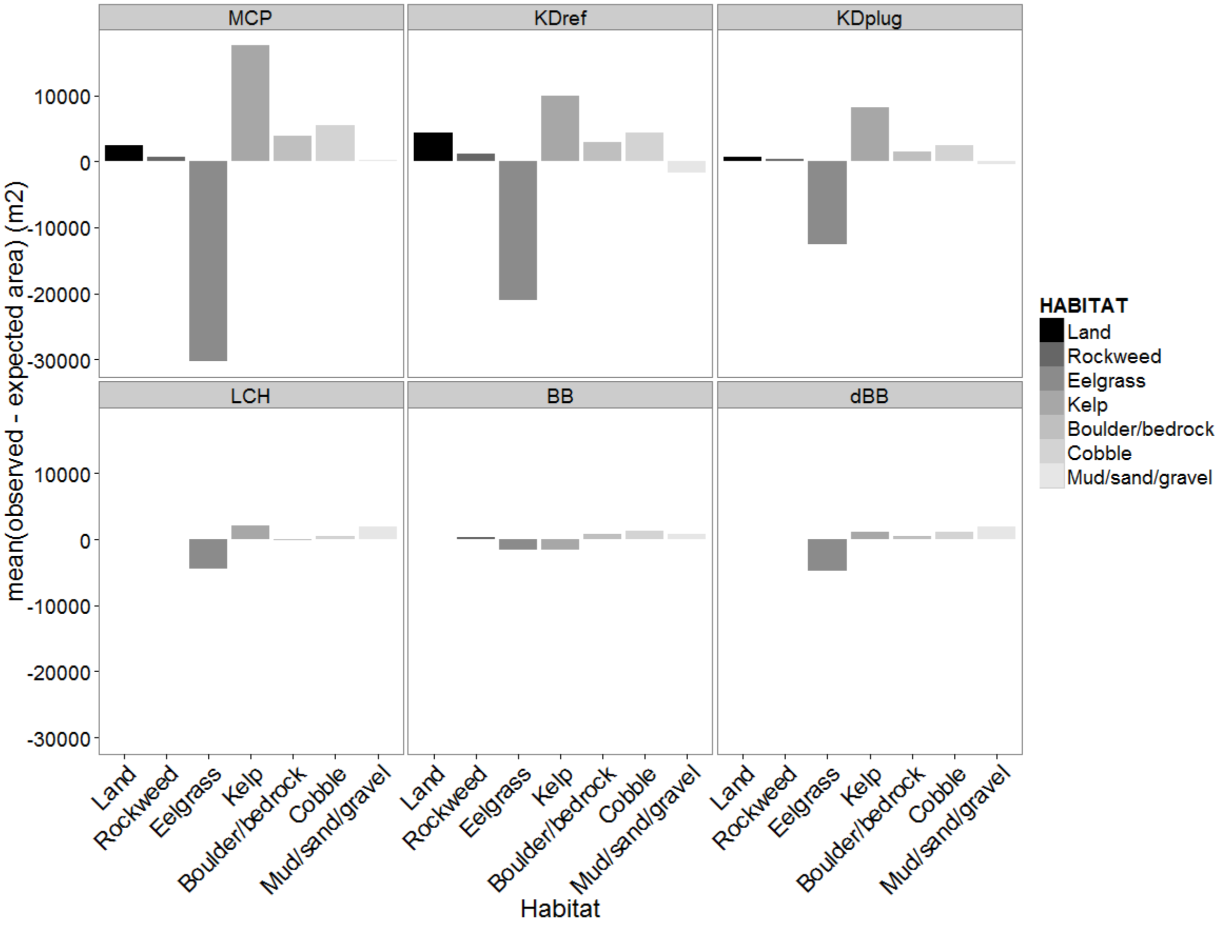


Fig. 2.4. Mean difference between observed and expected habitat coverage (m^2) for two age 1 Greenland cod using six home range estimators (MCP: 100% minimum convex hull, KDref: 95% kernel density with reference bandwidth, KDplug: 95% kernel density with plug-in bandwidth estimation, LCH: 95% alpha-local convex hulls, BB: 95% Brownian bridges, dBB: 95% dynamic Brownian bridges). Values close to zero indicate an accurate representation of habitat use.

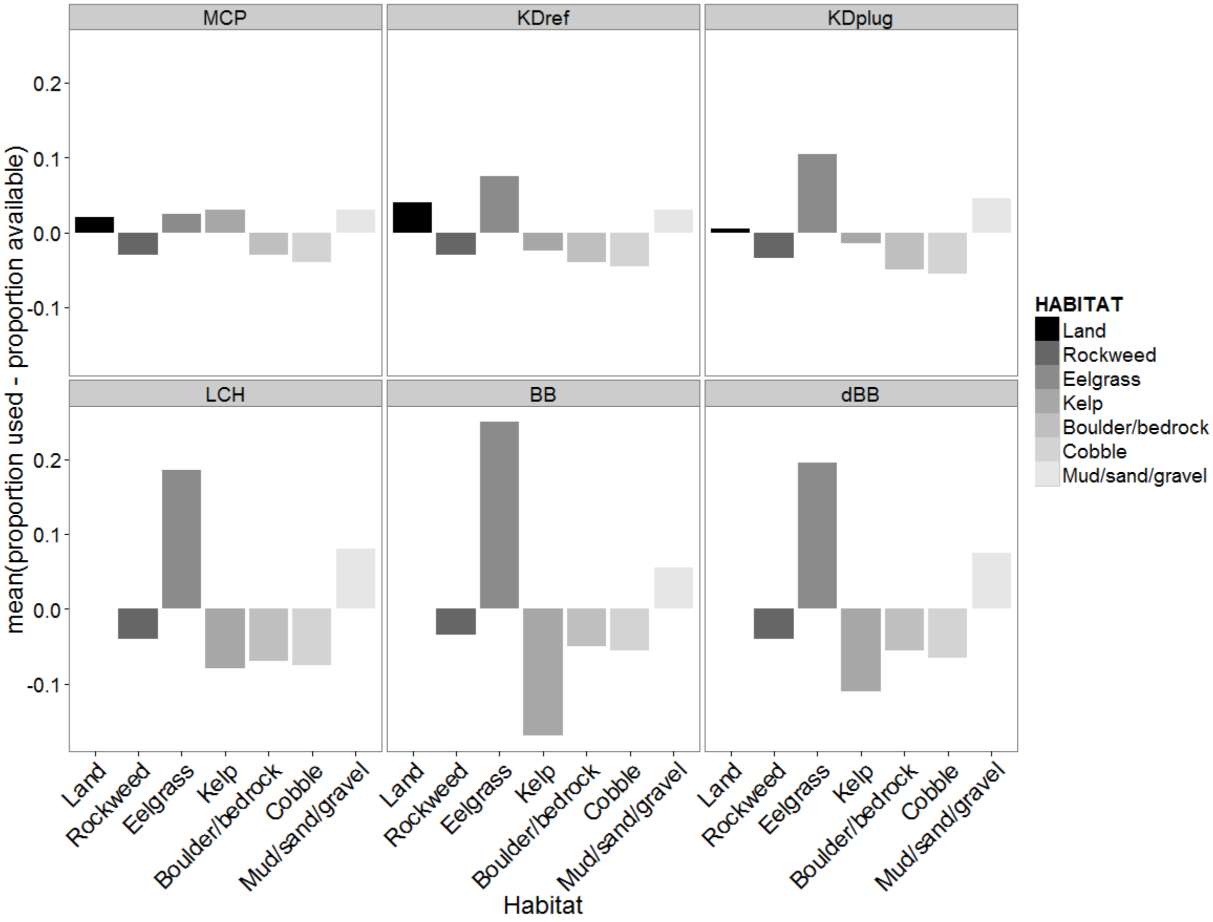


Fig. 2.5. Difference between proportions of habitat types within the home range and proportions available for two age 1 Greenland cod using 6 home range estimators (MCP: 100% minimum convex hull, KDref: 95% kernel density with reference bandwidth, KDplug: 95% kernel density with plug-in bandwidth estimation, LCH: 95% alpha-local convex hulls, BB: 95% Brownian bridges, dBB: 95% dynamic Brownian bridges). Positive values indicate selection while negative values indicate avoidance.

Chapter 3: Diel and seasonal patterns in movement and habitat use by age 1 Greenland cod (*Gadus macrocephalus ogac*) in Newman Sound as revealed by acoustic telemetry

Abstract

Nursery habitats enhance recruitment of juvenile fish by supporting higher densities of juveniles, faster growth rates, increased survival, and greater movement to adult habitats. Although it is well-established that shallow eelgrass beds serve as nurseries for age 0 juvenile cod, and that older juveniles (age 2-3) associate with complex features in deeper habitats, little is known about the habitat requirements of the age 1 class. I used acoustic telemetry to study the movement patterns and habitat use of age 1 Greenland cod (*Gadus macrocephalus ogac*) in Newman Sound, NL. Over autumn and winter of two consecutive years (2010-11, 2011-12), I tracked 75 individuals to create utilization distributions from positional data using a dynamic Brownian Bridge movement model. In parallel, I developed a seabed habitat map in two coves using aerial photography, video, and heads-up digitization. From these two data sources, I compared the proportions of habitats used by individual fish within the core area of use and full home range to the proportions available in the study area. The highest movement rates occurred during the crepuscular periods, when fish generally moved into the shallows at dusk and into deeper water at dawn. Eelgrass and macroalgae dominated age-1 juvenile habitat use in time spent, with a seasonal shift from eelgrass use in autumn to kelp use in winter. Because my analysis considers not only location, but also movement trajectory and time spent in each habitat, it provides comprehensive and conclusive evidence of habitat dependence in age 1 Greenland cod. The use of these complex habitats and the timing of movement suggests these habitats

provide not only an important refuge for juvenile cod, but also increased connectivity to adult habitats. Since the spatial distribution of juvenile fish is largely determined by predation pressure, resolving these movements and habitat associations will provide insight into predator-prey dynamics, and will increase our understanding of the nursery function of juvenile fish habitat.

Introduction

Habitat offers more than just a physical location, and instead represents the sum of resources and conditions necessary for an organism to grow, survive, and move within the general location in which it lives (Krausman 1999). By providing resources such as food, shelter, nesting sites, and migration corridors, habitat can increase an organism's chances of survival, as well as the probability a species will persist (Krausman 1999). As animals move through their environment, they make behavioural decisions about use of space that ultimately affect individual fitness (Sih 1980). Therefore, knowledge of movement patterns and habitat use can help in understanding behaviours that affect growth and survival.

Spatial and temporal movement patterns and habitat use provide insight into how an animal interacts with its environment, conspecifics, predators, and prey. Understanding why an animal moves requires understanding the resources an animal uses at specific times and places (Cagnacci et al. 2010). Tracking experiments involving GPS-collared black-tailed deer (*Odocoileus hemionus columbianus*) revealed that utilizing differences in elevation increased chances of survival by using habitats that provided separation from puma (*Puma concolor*) predators. Furthermore, deer that remained within established home ranges were 60% more likely to survive than those that left their home range (Forrester et al. 2015). Cory's shearwaters (*Calonectris borealis*) outfitted with GPS loggers displayed age-dependent habitat use that reflected foraging patterns. Younger birds were more exploratory and relied on less productive pelagic feeding grounds, whereas older, more experienced birds showed high site fidelity towards productive shallow feeding grounds. Only as the birds aged and gained experience did habitat use shift (Haug et al. 2015).

Although many of the same behavioural questions in the marine environment parallel those on land, tracking in the marine environment adds a unique, and particularly difficult set of logistical challenges. The omnipresence of opaque (phytoplankton, suspended material) water precludes constant, direct visual observation in most situations, and saltwater effectively eliminates most transmission signals, such as radio or GPS. Despite these issues, advances in technology such as acoustic telemetry (detailed in Chapter 2) can generate high-resolution tracking data over extended periods of time, sometimes even multiple years (e.g., Ng et al. 2007). Such data sets support the application of quantitative landscape ecology habitat utilization techniques developed for terrestrial applications to the marine environment. For example, Hitt et al. (2011) used telemetry to track the movements of fish species on a reef, and reported interspecific variability in diel movement patterns and habitat use caused by species-specific differences in predation pressure, competition, and dietary requirements. In another example, although juvenile blacktip sharks (*Carcharhinus limbatus*) were known to occupy shallow nearshore environments that exclude their larger predators, the behavioural link to food abundance or predator-avoidance remained unresolved. The application of acoustic telemetry to study movements of juvenile sharks relative to prey abundance demonstrated predator avoidance as the main driver for use of shallow habitats (Heupel & Hueter 2002).

Animal behaviours often reflect a trade-off between the benefits of engaging in activities such as moving or foraging, and the risk of predation (Lima & Dill 1990). For juvenile fish in nursery habitats, the balance between finding food and escaping predators may favour use of predator refuges, leading to behaviours largely driven by predator avoidance (Linehan et al. 2001). Nursery habitats denote areas used by juvenile stages of fishes that produce elevated recruitment compared to other such areas by supporting higher densities of juveniles, faster growth rates, increased survival, and greater movement to adult habitats (Beck et al. 2001). In Newfoundland, eelgrass provides cover and enhanced feeding opportunities to juvenile cod, but there is a current lack of evidence showing increased movement to adult habitats (Joseph et al. 2012).

Activity levels, measured as rate of movement, can indicate predation risk and resource availability. Juvenile grunts (Haemulidae) were most active when local abundance of predatory lizardfish (*Synodus intermedius*) was lowest (Helfman 1986). On a coral reef, predatory rockcod (*Cephalopholis cyanostigma*) and their juvenile lemon damselfish prey (*Pomacentrus moluccensis*) exhibited inverse diel activity patterns. Whereas rockcod were most active in crepuscular periods with peak attacks at dusk, lemon damselfish were less active in crepuscular periods and reduced their distance to cover at dusk (Bosiger et al. 2014). Age 2-3 juvenile Atlantic cod (*Gadus morhua*) moved most during crepuscular periods and least at night, possibly resulting from changing foraging strategies under dynamic light conditions (Cote et al. 2002). Clark & Green (1990) also reported seasonal changes in diel patterns in activity for age-3 Atlantic cod, and attributed the pattern to seasonal abundance of predators.

Game Theory (Hugie & Dill 1994) predicts that when predators can freely select habitat based on their own individual fitness, habitat selection by juvenile fish will depend mostly on predator avoidance rather than forage quality. For most demersal fish species, body size increases with depth (reviewed in Macpherson & Duarte 1991). Given that predation rates on juvenile fishes increase with depth, the pattern of increased body size with depth may reflect particularly strong anti-predator behaviour and habitat usage in younger individuals (Linehan et al. 2001). By providing a refuge from predation, shallow nearshore areas can function as nurseries for juvenile fish. For juvenile fish, nursery habitats often occur in shallow coastal zones such as mangrove swamps and seagrass meadows (Nagelkerken et al. 2001).

Greenland cod (*Gadus macrocephalus ogac*) are demersal marine teleost fish with a circumpolar distribution stretching from Alaska east to Greenland, and south to New England (Scott & Scott 1988). Though a subspecies of Pacific cod (*G. macrocephalus;* Coulson et al. 2006), Greenland cod in the Atlantic Ocean overlap much of their range with Atlantic cod (*G. morhua*). Adult Greenland cod remain coastal in deeper waters, mature at age 3, and spawn annually in late March - April (Mikhail & Welch 1989). In Newfoundland, juveniles settle into shallow bays along the coast where they occupy complex habitats near shore such as cobble (Gregory & Anderson 1997) and eelgrass (Tupper & Boutilier 1995) that act as nurseries by providing predator refuges (Laurel et al. 2003b) and a greater abundance of prey (Joseph et al. 2013). As age 0 year old juveniles, Greenland cod occupy the same habitats as Atlantic cod (Laurel et al. 2003b). The main predators on juvenile cod are older conspecifics and other fish (Linehan et al. 2001), birds, and mammals (Cote et al. 2008). Juvenile *G. macrocephalus ogac* and *G. morhua* both feed opportunistically, and they shift their diet from pelagic to benthic prey species at 60-100 mm standard length (Lomond et al. 1998). As juvenile cod grow, they occupy progressively deeper waters until they recruit to adult populations at age 3-4 (Mikhail & Welch 1989).

While reports of habitat use in juvenile Atlantic cod are numerous, few describe the habits of juvenile Greenland cod (Laurel 2003b, Knickle & Rose 2014ab). Furthermore, previous studies on either species concentrated on age-0 individuals (Linehan et al. 2001, Laurel et al. 2003ab, Gorman et al. 2009, Warren et al. 2010), and older age 2-4 juveniles (Clark & Green 1990; Cote et al. 2002, 2003, and 2004; Knickle & Rose 2014ab), leaving a knowledge gap for age-1 individuals (but see Cote et al. 2013). At age 0, high densities of juveniles of both species associate with shallow, complex habitats such as cobble (Gregory & Anderson 1997) and eelgrass beds (Laurel et al. 2003b, 2004; Cote et al. 2013), and are readily sampled using methods such as beach seines (Linehan et al. 2001, Laurel et al. 2003b). Although these habitats may provide enhanced foraging opportunities to young cod (Thistle et al. 2010), they are largely thought to serve as a refuge from predation (Linehan et al. 2001, Laurel et al. 2003a). Blades of eelgrass (Gotceitas et al. 1997, Laurel et al 2003a, Laurel & Brown 2005) and the interstitial spaces between cobble (Gotceitas & Brown 1993) provide cover for juveniles, and can reduce predation risk by impeding the swimming of a predator or reducing prey visibility (Gorman et al 2009, Ryan et al 2012). Tethering experiments on age-0 Atlantic cod support this theory, demonstrating lower predation rates in eelgrass patches than in open areas (Linehan et al. 2001, Laurel et al. 2003a, Gorman et al. 2009).

Temporal shifts in behaviour can suggest changes in predation pressure or foraging quality (Lima & Dill 1990) and other researchers report diel and seasonal variations in habitat use by juvenile cod. For example, Cote et al. (2001) found age-0 Atlantic cod lived deeper and used more kelp during the day, with higher abundance of age1 individuals in the nearshore at night. These authors hypothesized that juveniles delayed occupying these habitats until light levels declined near dusk, impairing visual predators. Age-3 Atlantic cod shifted seasonally, occupying deeper habitats during the summer and shallow habitats in the autumn and winter (Clark & Green 1990). Because adult cod (the main predator on juvenile cod) migrate to deeper waters at the onset of winter (Keats et al. 1990, Cote et al. 2001), the seasonal use of shallow habitats by age-3 cod may suggest another anti-predator mechanism. Shallow habitats may offer increased foraging quality but the benefits may outweigh the risk only when predator abundance decreases in winter.

I used acoustic telemetry to track the movements of age-1 *G. macrocephalus ogac* in nearshore nursery habitats of Newman Sound, NL over the fall and winter in two consecutive years 2010-11 and 2011-12. Building from benthic habitat maps I created for two coves, I applied a dynamic Brownian bridge model to movement data for individual fish, and analyzed habitat proportions within the 50% (core area of use) and 99% (full range) contours of the utilization distributions. To investigate diel and seasonal shifts in habitat use and movement rate, I used multivariate statistics and linear mixed effects models. The distributions of age 0 (Laurel et al. 2003b) and age 2 and older cod (Cote et al. 2003) are known to be habitat-dependent, so *a priori* I expected disproportionate use of habitat in age-1 Greenland cod. As these patterns are thought to be mainly driven by predator-avoidance (Linehan et al. 2001, Laurel et al. 2003a), I also expected diel and seasonal distributional shifts in response to changing predation risk. In addition, I expected dependence of movement rates on diel period, with lowest rates at night, the period of the diel cycle when cod visual abilities are lowest (Anthony 1981).

Methods

Study Area

Newman Sound, a sheltered fjord located in Bonavista Bay on the north east coast of Newfoundland, Canada (Fig. 3.1), measures approximately 22 km long by 2 km wide, with an area of 44 km^2. The rocky coastline of Terra Nova National Park surrounds the sound, with little nearby development. Seven kilometers from the head of the sound a shallow sill (18 m) divides the fjord into an inner (maximum depth 55 m) and outer sound (maximum depth > 300 m towards open ocean). I chose two sites within Newman Sound known from previous studies (e.g., Warren et al. 2010) to support abundant juvenile cod - Heffern's Cove and Buckley's Cove (Fig. 3.1). Heffern's Cove, located on the south shore of the outer sound, extends 600 m in width by 500 m in length, with a surface area of 0.2 km^2. It is a shallow basin (average depth 6.5 m) that slopes gradually from the shoreline at its head to approximately 10 m depth at its mouth, where depth drops below 25 m. Basaltic bedrock largely flanks a gravel beach at the head of the cove. Buckley's Cove on the north side of the inner sound measures roughly 750 m wide by 700 m long, with a surface area of 0.3 km^2. A soft, sedimentary shore to the west and rocky cliffs to the east enclose a large, sandy beach at the head. The largely flat-bottomed shelf of Buckley's Cove (average depth 6 m) slopes gradually to a maximum depth of 10 m and then drops away to a basin over 50 m deep, bringing the overall average depth in Buckley's Cove to 14.5 m. The average tidal range in Newman Sound is low (0 - 1.5 m).

Using a single-beam echo-sounder, I collected detailed bathymetry data in each cove and standardized it to depth using chart data (lowest tide level under average meteorological conditions) corrected for tidal height at the time of the measurement. I then interpolated a bathymetric surface grid (5-m cells) by modeling the data as triangulated irregular networks (ArcGIS 10.1). This method creates Delaunay triangles using the point samples as nodes. The planar surface created by each triangle represents an interpolation surface based on the linear interpolation between nodes.

I moored a temperature logger (Mini-T-II, Vemco, accuracy ± 0.01 °C from -5 °C to 35 °C) 0.5 m off the seabed in each of the two study sites that provided bi-hourly readings. The

Heffern's Cove logger failed August 12, 2011 and remained offline until November 23, 2011. I calculated missing temperatures for Heffern's Cove during this time period from the average of probes at Buckley's Cove and two other inner sound stations. Heffern's Cove is situated in the outer sound, which is often cooler than the inner sound. Therefore, I corrected the interpolated values for Heffern's Cove using a calculated annual offset between the Heffern's Cove and three inner sound loggers (0.56 °C). In Heffern's Cove, annual water temperatures ranged from -0.88 to 16.2 °C in 2011, and -1.4 to 18.5 °C in 2012. Annual water temperatures in Buckley's Cove ranged from -1.67 to 15.55 °C in 2011, and -1.27 to 18.7 °C in 2012. In both coves, annual temperature lows occurred in February with annual temperature highs in August.

Habitat Mapping

I created habitat maps for each study site using a combination of aerial photography, 'heads-up' digitization, and field sampling (Fig. 3.2). Parks Canada provided geo-referenced aerial photographs (30 cm resolution) of Terra Nova National Park, including Heffern's and Buckley's Coves. By adjusting the contrast, brightness, and color balance of the images using Adobe Photoshop CS5, I brought as much detail as possible to underwater features. Using 'heads-up' digitization in ArcGIS 10.1 I delineated patch boundaries manually, and used video point samples collected in the field to identify habitat types within patches.

By lowering a submersible video camera to within 1 m of the seabed, I collected a total of 540 video point samples (278 in Heffern's Cove, 262 in Buckley's Cove), marking each location on a hand-held GPS (Garmin 60cs). Video sampling utilized two cameras : a SeaView™ SeaMaster with a black and white display, and a color JVC™ HD Everio camcorder in a custom housing. The housing consisted of a piece of PVC pipe with transparent end caps, placed on a 1-

m length of angle steel with a 10 lb dive weight as a base. When this housing sat on the bottom it positioned the video camera 1 m off the seabed looking downward at an approximately 45 degree angle. For each sample, I lowered a camera so that the frame sat on the bottom for 5 seconds before retrieval. Through video analysis, I classified habitat type based on the substrate or macrophyte comprising the largest proportion of the sample frame: rockweed (*Fucus* spp., *Ascophyllum nodosum*), eelgrass (*Zostera marina*), kelp (*Agarum cribrosum, Laminaria* spp., *Saccharina latissima*), bedrock/boulder (grain size > 1 m diameter), rock (grain size 25 cm - 1 m), cobble (grain size 2.5 - 25 cm), and mud/sand/gravel (grain size < 2.5 cm). A mixed habitat type, mud/sand/gravel with patchy kelp, occurred only in Buckley's Cove, and featured an expanse of mud/sand/gravel with isolated clumps (~ 1 - 5 m diameter) of kelp dispersed throughout (~ 2 - 15 m separation). Rock never dominated substrate type.

A large, continuous patch of kelp dominated the habitat in Heffern's Cove, comprising 106,079 m^2 and 54% of the study area (Table 3.1; Fig. 3.2A). Coverage of other habitat types ranged from 7,035 - 26,182 m^2, forming alternating bands parallel to the shore. Rockweed occupied intertidal and shallow sub-tidal areas along the shore in the shallowest zones. Cobble dominated the shoreline at the shallow head of the cove, whereas exposed bedrock/boulder dominated the steeper slopes, with a band of broken cobble along the base. Dense eelgrass covered the shallow head to a depth of approximately 7 m, where a patch of mud/sand/gravel transitioned into dense kelp coverage. Clear patches of mud/sand/gravel and a few bedrock/boulder outcrops interspersed with the otherwise continuous large patch of kelp.

A large patch of mixed habitat type (mud/sand/gravel with patchy kelp) dominated Buckley's Cove, covering 123,751 m^2 and over 29% of the study site (Table 3.1; Fig. 3.2B). The other habitat types covered between 1,992 and 107,071 m^2, with alternating bands parallel to shore similar to those in Heffern's Cove but with relatively little bedrock/boulder cover. Kelp coverage became continuous towards the center of the cove, broken by the steep slopes of the deep basin. Broken cobble covered the steeper slopes, alternating with accumulated mud/sand/gravel on flatter areas. Eelgrass dominated the more gradual slopes of the inner cove, with rockweed patches in intertidal and shallow sub-tidal cobble zones.

Acoustic Telemetry

Fisheries and Oceans Canada deployed a network of 11 acoustic telemetry receivers (Vemco™ VR2W, 69kHz receiving frequency) in Heffern's Cove in 2010 (Fig. 3.2A). The omni-directional, data-logging receivers had an approximate range of 500 m (confirmed with field range tests), and were positioned to provide overlapping coverage. This arrangement facilitated the calculation of a two-dimensional position estimate for single tag transmissions picked up by three or more receivers. In 2011, I added an array of 12 receivers (Vemco™ VR2W, 69kHz receiving frequency) to Buckley's Cove and positioned them to provide similar overlapping ranges (Fig. 3.2B). To improve 'line-of-sight' with tagged cod, I moored the receivers 1 m above the seabed. I also deployed stationary reference transmitters emitting at regular intervals ("synctags") in each cove (Fig. 3.2). These synctags provide a means of correcting drift in the internal clocks of hydrophones, increasing accuracy of position estimates. Every 6-7 months, I retrieved the receivers to download data, change batteries, and remove bio-fouling, before re-deploying them at the same locations.

Over the two years of my study, I caught a total of eighty-four age 1 Greenland cod using a beach seine, and surgically implanted each fish with a coded acoustic transmitter tag (Vemco™ V7-4L; 22.5 mm long, 7 mm diameter, 1.8 g in air, 136 dB re 1 uPa at 1 m output, random transmission interval of 240 ± 70 s, tag life 415 days). In October, 2010, I tagged 21 fish from each of Heffern's and Buckley's Coves, and released all in Heffern's Cove (mean standard length = 16.3 ± 0.9 cm). In November, 2011, I captured 28 fish in Buckley's Cove, and 14 in Heffern's Cove (overall mean standard length 17.2 ± 1.3 cm). I released half in Heffern's Cove (n = 21) and half in Buckley's Cove (n = 21). The reciprocal transplant design was a requirement of a companion study (Shapiera et al. 2014), simultaneously investigating homing behaviour in juvenile cod. I believe that the transplant design had no effect on my study results, as the findings of the companion study (Shapiera et al. 2014) did not indicate homing behaviour at age 1-2. While I tracked most tags from 1 hour after release onward, insufficient receiver coverage initially delayed tracking of 2011 Buckley's Cove releases until 14 days after release. At this time, I added another hydrophone and re-positioned another to provide full coverage of the study site. A trained DFO technician surgically implanted a unique transmitter 'tag' into the belly of each fish through an abdominal incision just off-center of the mid-ventral line, halfway between the pelvic girdle and the anus, before closing the ~2 cm incision with 2 sutures. I circulated fresh seawater over the gills throughout the 30 second procedure, and only used sterilized materials during surgery. Juvenile cod's high sensitivity to common anesthetics such as clove oil precluded their use, and protocol for surgeries was approved through DFO (NAFC-2010-03). Fish recovered in a 1.0 m^3 net pen overnight (October 2010) or for one hour prior to release (November 2011).

Data Analysis

Vemco Ltd. processed the raw detection data at the end of each study year to generate position estimates. For each tag transmission picked up by three or more receivers, Vemco used the time-difference-of-arrival of the signal at each receiver to estimate a two-dimensional position (Smith 2013, hyperbolic positioning). Along with estimates of latitude and longitude, processed data includes tag IDs, time-stamps, and measures of horizontal positioning error (HPE). Specifically,

> "HPE is a unitless error measurement that describes the sensitivity of the positioning system to the variables that affect horizontal accuracy (e.g., array geometry, water temperature, salinity, etc.)" (Dean et al. 2014).

Only synctag transmissions measure actual positioning error (HPEm), because only they remain stationary at known locations. Following Smith (2013) and Coates et al. (2013), I plotted the relationship between HPE and HPEm for all synctag positions to visualize the effects (i.e., data loss) of various HPE thresholds (Fig. 3.3). I calculated and examined the median, mean, 90th, and 95th percentiles of HPEm for single-unit HPE bins and chose a threshold that balanced information loss with increased confidence in individual positions (Coates et al. 2013). Below a threshold of 6 HPE, synctag positions were 0.3 m median distance from the known location (HPEm), with a 90th percentile of 1.0 m (mean = 0.5 m). Because tag position calculations duplicate those for synctags, I expect the same accuracy for tag positions filtered to ≤ 6 HPE (84.7% retained).

I defined seasons based on changing water temperatures, and by comparing swim speed and habitat use across seasons and diel periods I examined temporal shifts in behaviour. Winter spanned the period when the water column was < 4 °C (November 15 to May 15; 6 months), and I divided the remaining 6 months into 2-month "seasons" characterizing spring by steadily rising water temperatures (May 15 - July 15), summer by highest temperatures (July 15 - September 15), and autumn by sharply declining water temperatures (September 15 - November 15). Nautical twilight (the time of day when the center of the sun is geometrically 12 degrees below the horizon) and sunset times for Gander, NL (Thorsen 2013) defined diel periods. I differentiated dawn (range 1-2 hours), day (range 8-16 hours), dusk (range 1-2 hours), and night (range 4.5-13 hours) periods.

Habitat Use

In order to examine space usage by age-1 Greenland cod, I created utilization distributions (UDs) for each individual. A UD two-dimensional probability density function represents the relative probability of finding an individual in a location over time (van Winkle 1975). I estimated UDs by applying a dynamic Brownian Bridge movement model (dBBMM) to processed positions using the R package *move* (Kranstauber and Smolla 2014). In contrast to commonly used kernel density methods that treat positions as a random and independent sample of locations, the dBBMM estimates UDs from autocorrelated movement paths, resulting in better representation of movement corridors and resting sites (Kranstauber et al. 2012). The model estimates the use of space along a path from the time and distance between successive positions, location error, and Brownian motion variance, which quantifies path irregularity assuming a conditional random walk. Whereas the traditional Brownian Bridge movement model of Horne et al. (2007) applies a single estimate of Brownian motion variance to the entire path, the dBBMM identifies behavioural change points along a path and estimates Brownian motion variance for each partition separately with the "leave-one-out" method (Kranstauber et al. 2012). In a sequence of three positions, the "leave-one-out" method connects the first and third positions with a Brownian Bridge, while treating the second as an independent sample. This method then calculates Brownian motion variance by maximizing the likelihood of observing the second position assuming Brownian motion and normally distributed location errors (Palm et al. 2015). A "sliding window" that encompasses *w* positions along the path identifies behavioural change points and calculates Brownian motion variance for the entire path within each window. Then, the window is iteratively split into two sections at each position prior to calculating Brownian motion variance for each section. Selection of the model with the lowest Bayesian information criterion follows comparison of models with two Brownian motion variance estimates to the model with a single Brownian motion variance. If a single Brownian motion variance estimate proves superior then that variance is applied to the entire path, otherwise variance is partitioned accordingly (Byrne et al. 2014). Because the "leave-one-out" method requires a minimum of three positions, Brownian motion variance cannot be estimated within a margin of at least three positions at either end of the window. Longer margins increase the power to detect behavioural change points at the risk of missing breakpoints in the margin (Palm et al. 2015). Longer windows increase reliability of Brownian motion variance estimates at the risk of missing short-term changes in behaviour (Kranstauber et al. 2012). If an interval appears in multiple windows and assigned multiple Brownian motion variance estimates, I used the average. I applied the dBBMM using a window length of 9 positions (equivalent to 36 minutes) and a margin of 3 positions (equivalent to 12 minutes).

Noting the limited detection range of the VPS array, and that fish were free to leave the study area, I calculated UDs in multiple parts, or "bursts" in order to ensure that UDs only represented spatial use by fish while within the array (Dean et al. 2014). I defined a burst as a sequence of positions within a period of no more than 77.5 minutes (maximum of 15 missed transmissions). In order to create UDs for every burst I averaged time-step UDs created with the *moveud* package (Collier 2013) in R and then weighted burst UDs by time and averaged them to produce a final UD for each individual and period combination. I then converted UDs to cumulative probability density functions, and used the areas represented by the 50% and 99%

contours as the core area of use and home range, respectively. By overlaying the core areas and home ranges onto the habitat maps I was then able to calculate proportions of each habitat type within each UD contour.

To test differences in habitat use across seasons and diel periods, I analyzed the proportional area of each habitat type within the 50% core areas of use and 95% home ranges of each individual using multivariate statistics. Few cod were detected during the spring and summer, presumably moving to deeper, cooler water beyond the range of detection. Therefore, I limited the analysis of habitat use to the fall and winter seasons in Heffern's Cove, and winter only in Buckley's Cove, which only became operational at the beginning of winter in year two of the study. I examined the proportions of rockweed, eelgrass, kelp, boulder/bedrock, cobble, and mud/sand/gravel habitat used by each individual, adding the additional habitat of mud/sand/gravel with patchy kelp for the analysis of Buckley's Cove data. Beginning with calculations of resemblance matrices based on Euclidean distance I analyzed habitat use within the core area and home range separately. I then tested for seasonal and diel differences in the full suite of habitat proportions using type III Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson 2001). Heffern's Cove required a two-way crossed design with season (fall and winter) and diel period (dawn, day, dusk, and night) as fixed factors, whereas Buckley's Cove required a one-way design with diel period (dawn, day, dusk, night) as a fixed factor. In order to test for differences between the levels of the fixed factors season (Heffern's Cove only) and diel period I used pair-wise PERMANOVA contrasts. Similarity percentage analysis (SIMPER) determined which habitat types contributed most to dissimilarity and similarity in habitat use between seasons (Heffern's Cove only) and diel periods. To summarize mean differences in habitat use across seasons and diel periods in Heffern's Cove, I constructed a multi-dimensional scaling (MDS) plot based on Euclidean distance from the centroids of combined season-diel period factors. All PERMANOVA tests used 999 permutations of residuals under a reduced model. All multivariate tests (PERMANOVA, pair-wise contrasts, SIMPER, and MDS) were carried out using PRIMER (v.6.1.11) software, including the PERMANOVA+ (v.1.0.1) add-on.

Movement Pattern

I used movement rate as a measure of activity, calculated from the straight-line velocity between two successive positions. These rates represent conservative underestimates, given that fish rarely swim in a straight line. To control for growth effects, I converted movement rates from m s^{-1} to body lengths per second (L s^{-1}) using length measurements gathered in the field. In support of a long-term monitoring program in Newman Sound (DFO), I helped sample the nearshore fish community, including juvenile cod, by beach seining 12 sites throughout Newman Sound (including Heffern's and Buckley's Coves) once in May, and bi-weekly from July to November in each year between 2010 and 2012. I used body length measurements (standard length) of the age-1 cohort of Greenland cod to establish linear growth rates for each calendar year based on linear regression (2010: 0.23 mm day^{-1}, 2011: 0.28 mm day^{-1}, 2012: 0.31 mm day^{-1}). Growth rates were applied to estimate the length of each fish on each date when I sampled it in order to facilitate conversion of movement rates from m s^{-1} to L s^{-1}.

Positioning error and the length of time between locations both affect the accuracy of movement rate estimates. Positioning error can affect the perceived distance (and ultimately the speed estimate) between positions and should be minimized. The time between positions also affects the speed calculation, yielding lower speed estimates when the interval is long. Too short an interval can also cause perceived movement where none occurs (Cote et al. 2002). Therefore, relative comparisons of movement rate should only include estimates calculated from similar time intervals. For analyses involving movement rate, I removed all estimates from time intervals longer than the maximum possible transmission interval of 310 seconds. This strategy limited movement rate estimates to those calculated from intervals ranging 170-310 s and none were calculated over a missed transmission detection.

To avoid issues with autocorrelation and pseudoreplication, I averaged movement rates for each individual. Therefore, the sample size for a test involving movement rate equaled the number of individuals tested rather than the number of movement rate estimates. Because the number of individuals present in each cove declined over time, I limited analysis of movement rate to the autumn (48 individuals) and winter (30 individuals) in Heffern's Cove, and winter only in Buckley's Cove (14 individuals). I used linear mixed effects modeling in the R package, *nlme* (Pinheiro et al. 2013) to test the fixed effects of season (2 levels: fall and winter), diel period (4 levels: dawn, day, dusk, and night), habitat (5 levels: boulder/bedrock, cobble, mud/sand/gravel, eelgrass, and kelp; rockweed was omitted because too few fish used it), and study site (2 levels: Buckley's Cove and Heffern's Cove) on the mean movement rates of individual age1 Greenland cod. To compensate for differences in the number of movement rate estimates per tag, I included tag in the model as a random factor. In order to test for differences in movement rates between open (mud/sand/gravel and cobble) and complex (boulder/bedrock, eelgrass, and kelp) I used a planned orthogonal contrast. I then developed a second model to test the fixed effects of study site and diel period on movement rates of individuals in winter of year two in both study sites, with tag as a random factor.

I used the restricted maximum likelihood method for my linear mixed effects models, following the model selection procedure of Zuur et al. (2009). I plotted the residuals against fits for each model, and assessed assumptions of normality, heterogeneity, and independence visually, and square-root transformed data when appropriate to meet these assumptions. In the case of heterogeneity, I added terms that allow variance to differ between levels or combinations of fixed effects to the model iteratively until variance in the residuals became homogeneous. If multiple variance structures corrected heterogeneity, I selected the best model according to Bayesian information criterion.

To test movement paths for diel patterns in directionality, I examined the distributions of heading angles using circular statistics in Oriana™ statistical software (v. 4.02; Kovach Computing Services). I analyzed Heffern's Cove (fall and winter) and Buckley's Cove (winter only) data separately, calculating heading as the angle of the path trajectory from true north (0° or 360°). To ensure the headings used described the trajectory of movement accurately rather than the direction of longer-term displacement, I filtered out angles for time intervals longer than 310 s (maximum transmission interval). For movement distances of less than 3 m, I calculated most heading angles as regular multiples of 45° and interpreted them as artefacts of the VPS and therefore removed them. I constructed circular histograms for diel subsets (dawn, day, dusk, and night) to visualize the angular distributions, and tested them for uniformity via non-parametric Rao's spacing tests (Rao 1969, 1976; but see also Batschelet 1981). Non-multi-modal, non-uniform distributions indicate movement in a single direction, so I calculated the mean angle and standard error with 95% confidence intervals.

Results

Acoustic Tracking

Spanning both years and study sites, I generated 646,853 raw position estimates from 84 individual tags (Table 3.A1 in appendix) from the two VPS arrays. I examined tracks individually; if a tag became stationary at a single location with no movement, I inferred fish death or tag expulsion, and deleted positions thereafter from that tag. After removing these positions, along with any position with HPE greater than 6 units, 275,102 position estimates from 75 individuals remained. In Heffern's Cove I tracked 41 of 42 individuals for periods of up to 414 days and a total of 171,294 positions (mean = 4,178 ± 1,485 positions standard error) in Year 1, and 20 of 21 individuals for periods up to 371 days and a total of 95,830 positions (mean = 4,792 ± 2,340 positions S.E.) in Year 2. Because the Buckley's Cove array was added in Year 2, and was offline for the first 14 days of observations, I tracked only 14 of 21 individuals for periods of up to 353 days and a total of 7,978 positions (mean = 570 ± 264 positions S.E.) at that site. Because fish could swim freely beyond the range of the hydrophone arrays, the number of fish detected in the study coves naturally declined over time, with few reappearing after winter (Fig. 3.A1-3, appendix).

Activity Patterns

A. Movement Rate

I) Heffern's Cove

Significant interactions precluded analysis of movement rate as a single model with season, diel period, and habitat type as variables. Therefore, I divided Heffern's Cove data into autumn and winter movements and assessed the effects of diel period and habitat type in each season separately. I transformed the response variable, the mean movement rate (Ls^{-1}) for each individual for every diel period-habitat combination, to the square-root to satisfy assumptions of homogeneous residuals. Main effects of diel period and habitat were significant in both Fall (Table 3.2; diel: $F_{3,449} = 31.87$, p-value < 0.0001; habitat: $F_{4,449} = 16.70$, p-value < 0.0001) and

Winter (diel: $F_{3,353} = 33.96$, p-value < 0.0001; habitat: $F_{4,353} = 5.07$, p-value = 0.0006). The random effect of tag was also significant in both seasons (Fall: $F_{1,449} = 459.37$, p-value < 0.0001; Winter: $F_{1,353} = 609.00$, p-value < 0.0001).

Tukey's pair-wise comparisons revealed significant differences in movement rates among diel periods in both seasons (Table 3.3). In autumn, I observed the highest movement rates at dawn (mean = 0.4929 Ls^{-1}) and dusk (mean = 0.4392 Ls^{-1}), when movement rates averaged 25.5% higher than day (mean = 0.3577 Ls^{-1}) and 62.7% higher than night (mean = 0.2641 Ls^{-1}; Fig. 3.5). In winter, I also observed the highest movement rates at dawn (mean = 0.4755 Ls^{-1}) and dusk (mean = 0.3995 Ls^{-1}), although dusk movement rates were not significantly different from day (mean = 0.3856 Ls^{-1} ; p-value = 0.3807). On average, crepuscular movement rates were 13.5% higher than day, and 89% higher than night (mean = 0.2312 Ls^{-1}). Planned orthogonal contrasts revealed movement rates were significantly higher over open habitats (mud/sand/gravel and cobble) than over complex habitats (boulder/bedrock, eelgrass, and kelp) in both autumn (Fig. 3.6; mean difference = 0.1171 ± 0.0354 Ls^{-1}, Z = 3.309, p-value = 0.0009) and winter (mean difference = 0.1329 ± 0.0372 Ls^{-1}, Z = 3.572, p-value = 0.0004).

II) Buckley's Cove Comparison

I compared movement rates in winter of Year 2 across coves in addition to the three variables in Year 1 (diel period, season, and habitat type variables) using a linear mixed effects model with square-root transformed movement rates as the response variable, and cove and diel period as main (fixed) effects. I included tag as a random effect, and a variance structure that allowed variance to differ among diel periods. A significant effect of diel period ($F_{3,66} = 5.47264$, p-value = 0.0020) contrasted the non-significant main effect of cove ($F_{1,66} = 0.1760$, p-value =

0.6762), and the cove-diel period interaction ($F_{3,66} = 2.6035$, p-value = 0.0592). The random effect of tag was significant ($F_{1,66} = 307.5021$, p-value < 0.0001). Tukey's pair-wise contrasts revealed significantly higher dusk movement rates than at night (p-value < 0.0001); other contrasts were not significant (Fig. 3.7, Table 3.4).

B. Movement Direction

The circular distribution of heading angles depended on diel period and cove (Fig. 3.8). In Heffern's Cove (fall and winter), Rao's spacing tests showed all diel distributions (dawn, day, dusk, and night) differed significantly from a uniform distribution (Table 3.5; p-values < 0.01). I calculated mean angles for dawn (359.2 ± 2.3°) and dusk (173.7 ± 3.1°) subsets, but not day and night because of the presence of multiple modes. For winter movements in Buckley's Cove, day and night distributions were not significantly different from uniform (p-value > 0.05 and p-value > 0.10, respectively). The dawn heading angles produced a uni-modal distribution with a mean of 190 ± 8°, however, the bimodal dusk distribution precluded calculation of a mean.

Habitat Use

Heffern's Cove Autumn and Winter

My analysis of the 50% core area of use, using two-way PERMANOVA revealed significant differences in average habitat proportions between seasons (Table 3.6; Pseudo-F = 42.3, P(perm) = 0.001) and diel periods (Pseudo-F = 2.1, P(perm) = 0.04)(Fig. 3.9A). I found significant differences between day and night periods (pair-wise PERMANOVA, t = 2.2, P(perm) = 0.008), but no significant differences between other diel periods. SIMPER analysis showed that eelgrass use contributed most to dissimilarity across all diel periods (38-47%), followed by kelp (31-40%)(Table 3.7). Other habitat types contributed little to dissimilarity (< 10%) across all diel periods, with the exception of boulder/bedrock which increased to 17% at night. Contributions to the overall dissimilarity also varied by season. In autumn, eelgrass use contributed most (47%) followed by kelp (27%), reversing order to kelp (41%) and eelgrass (33%) in winter. The contribution of bedrock/boulder use increased from fall to winter, with decreasing contributions of the remaining habitat types.

My analysis of the 99% home range, showed that average habitat proportions varied significantly among seasons (Two-way PERMANOVA, Pseudo-*F* = 34.6, *P*(perm) = 0.001) and diel periods (two-way PERMANOVA, Pseudo-*F* = 4.0, *P*(perm) = 0.003; Table 3.6). Pair-wise PERMANOVA on diel periods (Fig. 3.9B) showed significant differences in habitat use between day-dawn (*t* = 2.4, *P*(perm) = 0.005), day-dusk (*t* = 2.6, *P*(perm) = 0.003), and day-night (*t* = 3.0, *P*(perm) = 0.001). Habitat contributions to overall dissimilarity differed among diel periods (Table 3.7B). Kelp (40-51%) and eelgrass (27-39%) use contributed most to diel period differences, with eelgrass use exceeding kelp only at night. Rockweed contributed only 5% to dissimilarity in the day and 14% at night, while boulder/bedrock, cobble, and mud/sand/gravel fluctuated only slightly among diel periods. Seasonal contributions of habitat types also varied. In autumn, eelgrass contributed most to variance in habitat use (39%), followed by kelp (34%). In winter this pattern reversed; kelp was highest (47%), followed by eelgrass (27%). Boulder/bedrock, cobble, and mud/sand/gravel use again fluctuated slightly among seasons.

NMDS plots visualized differences in the suite of habitat proportions within the core (50%) area of use and full range (99%) (Fig. 3.10). Seasonal groups separate more clearly than diel periods for core area use. In both seasons, day and night diel periods clearly differed most in habitat use, with dawn and dusk as intermediates. Diel periods separated most in the autumn. For the full range (99%) area, seasonal groups separated more distinctly than diel periods, although autumn daytime use was closer to winter groups than to the other autumn diel periods. Day and night also differed most in habitat use, with dawn and dusk as intermediates.

Buckley's Cove Winter

For winter data in Buckley's Cove, I found no significant effect of diel period on habitat use in the core (50%) area of use or the full range (99%) (Table 3.8; p-values > 0.50).

Discussion

Habitat Use

In my study movement rate and habitat use by age-1 Greenland cod in Newman Sound varied by season and diel period. Eelgrass dominated habitat use in autumn, in contrast to kelp in the winter, whereas shallow habitats (rockweed, boulder/bedrock, and cobble) were used more at night than during the day. Activity levels varied throughout the 24-hour period, with highest movement rates in crepuscular periods. Fish moved relatively little at night, often remaining stationary at frequently used locations. Fish also tended to move into the shallows (~1-5 m depth) at dusk and towards deeper (> 7 m depth) habitats away from the shore at dawn. Seasonal and diel patterns in movement and habitat use often reflect a response to changing resource availability or predation risk (Lima & Dill 1990), and resolving such movements may provide insight into drivers of behaviour.

In Heffern's Cove, habitat use differed strongly between autumn and winter seasons for both the core area of use and full range. Whereas eelgrass use dominated in autumn, tagged fish shifted to kelp-dominated habitat use in winter. While little is known of habitat use by age-1 cod, younger age-0s associate closely with shallow eelgrass beds (Tupper & Boutilier 1995, Gotceitas et al. 1997), and older age-2-3 juveniles occur in deeper, cover-providing habitats such as kelp and boulder (Gregory & Anderson 1997, Cote et al. 2004). The seasonal shift from eelgrass to kelp-dominated habitat use for age-1s in my study indicated an ontogenetic transition between habitat use strategies within the juvenile life stage and between age-0s and age-2s.

In Atlantic Canada, juvenile cod associate closely with eelgrass beds in their first year of life (Tupper & Boutilier 1995, Gotceitas et al. 1997). While these habitats may provide enhanced foraging conditions (Thistle et al. 2010), predator avoidance likely drives use of eelgrass by age-0s (Laurel et al. 2003ab, Gorman et al. 2009, Thistle et al. 2010, Ryan et al. 2012). In lab studies, age-0 Atlantic cod moved from sand and gravel patches to artificial eelgrass following introduction of a predator (age-3+ conspecific) (Gotceitas et al. 1997). Furthermore, field studies showed lower predation rates on age-0 cod in eelgrass than in unvegetated sites (Laurel et al. 2003b, Gorman et al. 2009), and increased predation rates with depth (Linehan et al. 2001). The seasonal movement from shallow eelgrass beds to deeper kelp habitats observed in my study indicates that either the benefits of occupying these high-risk habitats has increased (e.g., increased food abundance), or the risk of predation has decreased (e.g., decreased predator abundance).

Juvenile Greenland and Atlantic cod contain anti-freeze proteins in their blood that allows over-wintering in shallow habitats (Morin et al. 1991, Goddard et al. 1992). Lower concentrations of these proteins force adult and older juvenile cod to migrate to deeper, warmer water at the onset of winter (Morin et al. 1991, Cote et al. 2004). The timing of the migration in Newman Sound corresponds to the decline of nearshore temperature below 4°C and subsequent breakdown of the thermocline (Cote et al. 2004), which I used to define the boundary between fall and winter seasons in my study. Therefore, cod may shift from eelgrass to kelp-dominated habitats between seasons in response to reduced cannibalism risk as older juveniles emigrate seasonally from deeper inshore habitats such as kelp. Based on related telemetry data, Shapiera et al. (2014) showed increased movement distances in winter, and suggested reduced predation pressure at this time of year. Growth might also contribute to seasonal reduction in predation risk. In Newman Sound, age-1 Greenland cod range ~10-22 cm SL, while age-2s range 22-33 cm SL. Larger body size may represent a size refuge as individuals outgrow the gape limitation of piscivorous fishes and lower the risk of occupying deeper waters. Alternatively, increased visibility associated with larger body size may increase risk of predation by avian or terrestrial predators in shallow water. For example, river otters (*Lontra canadensis*) selectively target juvenile cod greater than 10 cm long (Cote et al. 2008).

Diel patterns of habitat use were apparent in Heffern's Cove. For core and full home range areas, juvenile cod used higher proportions of boulder/bedrock, cobble, and rockweed at night than in the day, in contrast to higher proportions of kelp in the day than at night. These three habitat types comprise the shallowest habitats in Heffern’s Cove. In my study, age-1s moved out of the shallows at dawn, and back into the shallows at dusk, often returning to well-defined night resting sites. Previous studies report such resting behaviour in age-3 Atlantic cod, and suggest that individuals entered crevasses and cracks in the bedrock, or interstitial spaces between cobbles, possibly as a refuge from predation (Clark & Green 1990). My results support this hypothesis, in that fish often “disappeared” at dusk only to reappear at the same location at dawn before becoming active again, perhaps occupying resting sites where the receiver array could not detect them. Other studies report increased use of kelp by juvenile cod during the day. In daytime seine surveys, age-1 Atlantic cod associated closely with macroalgal habitats such as kelp (Gotceitas et al. 1997) and a diel transect-based study reported significantly higher density of age-1 Atlantic cod during the day than dusk or night (Cote et al. 2001). Other authors, however, found no daytime associations with macroalgae (Keats et al. 1987, Gregory & Anderson 1997); seasonal effects could explain these discrepancies (Cote et al. 2001). I found no significant season-diel interactions in my study, but proportion of a habitat used nonetheless varied by season in a couple of cases.

Prior to shifting from eelgrass-dominated habitat use in the fall to kelp-dominated use in the winter, age 1 Greenland cod used kelp habitat far more during the day than at night in both the core and full range areas. Multivariate dissimilarity plots showed that for the full range, autumn daytime habitat resembled the winter periods more closely than the other autumn diel periods. Together, these results suggest that age-1 juvenile cod could make exploratory trips in the autumn during the day to search out patches of resources for future exploitation. In their review of lab and field studies that investigate fish learning and navigation, Odling-Smee & Braithwaite (2003) argue that many fish species can learn spatial information and use it to orientate through their environment. By relying on landmarks, external cues, and internal clocks, fish can identify locations associated with resources or risk, and adjust their behaviour accordingly. That many fish in my study returned to the same night resting sites on a regular basis suggests the capacity for spatial learning and memory in age-1 Greenland cod. By learning potentially dangerous but resource-rich locations, individuals can monitor them during forays and exploit them when predation risk decreases enough that the benefits outweigh the costs. In a telemetry study of schoolmaster snapper, *Lutjanus apodus,* fish undertook brief exploratory trips to the reef prior to shifting abruptly from mangrove nurseries to adult reef habitat. Only fish that grew to a critical size shifted permanently, although whether reduced predation risk, the need for larger prey, or maturation motivated the move remained unresolved (Huijbers et al. 2015).

For winter data from Buckley's Cove, I found no significant diel effect on habitat use for either core or full range areas. The habitat in Buckley's Cove consisted mostly of a mixed habitat type of mud/sand/gravel with patchy kelp that Heffern's Cove lacks. The majority of use in Buckley's Cove concentrated in this habitat of small kelp clumps separated by gaps of 2-15 m, regardless of diel period. Juveniles in Heffern's Cove during winter favoured kelp with a more continuous configuration in all diel periods. The total number of positions observed in Buckley's Cove during winter comprised only 10% of the number of positions in Heffern's Cove over the same period, and although many potential explanations are possible (e.g., differences in food availability, temperature, and depth, or associations on scales not studied), kelp patchiness may contribute to the difference. A study investigating the effects of eelgrass patch complexity on the distribution of age-0 cod found highest densities in sites with intermediate patchiness (Thistle et al. 2010). In lab experiments, age-0 Atlantic cod reduced the frequency of gap-crossing by 75% for gaps between patches of 7.5 m relative to 3.5 m (Ryan et al. 2012).The small size of kelp clumps relative to the distance across gaps could potentially pose too much risk to juvenile fish to risk venturing into the open habitat between patches; therefore, individuals may favour the more continuous kelp habitats in Heffern's Cove over those in Buckley's Cove.

Many fish species shift habitat use during ontogeny. For example, newly-settled blue-striped grunts (*Haemulon sciurus*) predominantly use seagrass beds before shifting to mangroves at ~4-6 cm (Mumby et al. 2004). The mangroves offer refuge from predators, and function as intermediate nursery habitats prior to migration to the adult reef habitat. By definition, nursery habitats produce elevated numbers of recruits per unit area relative to other locations through four mechanisms: 1. higher densities of juveniles, 2. faster growth rates, 3. increased survival, and 4. greater movement to adult habitats (Beck et al. 2001). In their review of the nursery function of eelgrass for juvenile cod, Joseph et al. (2013) provided evidence that eelgrass beds in Newfoundland meet the first three of those factors, but point to a current lack of evidence of movement to adult habitat. In my study, the ontogenetic shift from eelgrass to kelp habitats represents a transition from known age-0 nurseries (Joseph et al. 2013) to older juvenile habitats (e.g., Keats et al. 1987, Gotceitas et al. 1997). Therefore, when adjacent to kelp eelgrass may provide enhanced connectivity to adult cod habitat through intermediate kelp habitats.

Activity

Juvenile Greenland cod in Newman Sound displayed diel patterns in movement rate during my study. Tracking interval length affects the accuracy of swim speed estimates for juvenile cod (Cote et al. 2002), and although the length of my tracking interval precluded an accurate estimate of true swimming speed it nonetheless provides a relative measure of activity. In my study, juvenile movement rates were generally highest in crepuscular periods and lowest at night. These results echo those of Cote et al. (2002), who reported activity in age 2-3+ Atlantic cod in the autumn during all diel periods, but heightened activity in diurnal and crepuscular periods. In contrast with my observations, Knickle & Rose (2014a) reported activity in age 2-4 Greenland cod during all diel periods in summer months, but greatest activity at night. Another study reported highest levels of activity in age-3 Atlantic cod during crepuscular periods, but a shift from nocturnal activity in the spring and summer seasons to diurnal activity in autumn (Clark & Green 1990). Collectively, these results suggest that diel activity levels in juvenile cod depend on season, with a shift from diurnal activity in the fall and winter to nocturnal activity in the spring and summer. I could not test for this in my study as only three fish appeared in all seasons; however, in all seasons fish were generally most active at dawn and dusk while day and night activity varied between individuals.

Diel activity patterns may largely reflect a response to changing foraging patterns in juvenile cod (Cote et al. 2002). It has been suggested that the relatively low nocturnal activity observed in both age-2-3 (Cote et al. 2002) and adult cod (Lokkeborg & Ferno 1999) could be caused by increased reliance on chemosensory cues during prey location, which could lead to longer search times (Lokkeborg & Ferno 1999). Furthermore, Knickle & Rose (2014a) observed different diel activity patterns in juvenile Greenland cod and Atlantic cod, and speculated that differences in foraging strategies might explain the inconsistency, assuming similar predation risk for both species. In our study, however, age-1 Greenland cod displayed similar diel patterns to those reported for juvenile Atlantic cod (Knickle & Rose 2014a), with peak activity in crepuscular periods and more activity diurnally than at night. Fine-scale tracking revealed that fish often became stationary at a single location through the night period, when foraging is unlikely to occur. The use of complex, cover-providing habitats during these periods of inactivity is consistent with a strategy of predator-avoidance (Lima & Dill 1990). Many fishes exhibit diel activity patterns driven by predator-avoidance and food. Sockeye salmon (*Oncorhynchus nerka*) move from lakes to streams during periods when bears are least active (Bentley et al. 2014). In a freshwater lake, the opposing diel activity patterns of juvenile ruffe (*Gymncocephalus cernuus*) and perch (*Perca fluviatilis*) are driven by differences in foraging strategy: ruffe are nocturnal benthivores while perch are diurnal, pelagic planktivores (Okun et al. 2005).

When activity rates were highest, fish moved directionally. In both coves, individuals moved at dusk into the shallows towards frequently-used night resting sites, in contrast to dawn movement out of the shallows. Movement direction in day and night were uniform (Buckley's Cove), or approximately uniform (Heffern's Cove); large data volume likely contributed to significant difference from uniform distribution (48,466 data points in day, 23,395 at night). In the northeast Atlantic, Reubens et al. (2014) reported diel activity in adult Atlantic cod with elevated levels during crepuscular periods. By analyzing stomach contents, these authors determined that heightened periods of activity corresponded to foraging behaviour. If older cod in Newman Sound feed mainly during crepuscular periods, other times may elevate the risk of predation to age-1 Greenland cod, providing motivation to move quickly to cover-providing habitats or established night resting sites. Increased predation levels in fish often occur during crepuscular periods. For example, predation rates on juvenile Pacific salmon (*Oncorhynchus* spp.) in a low-turbidity stream were highest at dusk (Gregory & Levings 1998), a period associated with high levels of activity in salmonids (Clark & Levy 1988).

In Heffern's Cove, habitat complexity affected movement rate of age 1 *G. macrocephalus ogac*, with higher rates over open habitats (mud/sand/gravel and cobble) than those that provide some form of cover (boulder/bedrock, eelgrass, and kelp). Complex habitats can affect movement rates of juvenile cod. Age 2-3 Atlantic cod swam faster over open habitats relative to complex bottoms, perhaps because of predator-avoidance or changes in foraging strategy (Cote et al. 2002). Evading a predator in open habitat requires out-swimming the predator, leading to higher rates of movement. Conversely, taking refuge in complex habitats would also decrease movement rates. In lab experiments that examined gap-crossing behaviour in age-1 Atlantic cod, Ryan et al. (2012) found age-1s swam faster and crossed less frequently over larger gaps, and that smaller fish crossed faster in the presence of a predator. These results suggest higher predation risk over open habitats, and that minimizing the time within them would maximize chances of survival. Although juvenile Greenland cod eat mostly benthic prey, they feed opportunistically on a wide variety of prey (Knickle & Rose 2014b). Complex habitats may facilitate ambush predation, or increase search times for benthic prey, both of which may decrease movement rates (Cote et al. 2002). Although a combination of predation risk and foraging strategy likely drive differences in movement rates with habitat complexity, the abundant prey provided by nearshore nursery means predation risk is likely the largest influence (Walters & Juanes 1993).

My study demonstrated that movement patterns and habitat use by age 1 Greenland cod vary over diel periods and seasons in Newman Sound. While some combination of predation risk, resource availability, and ontogeny likely drive these shifts in behaviour, my results suggest juvenile cod occupy nearshore habitats mainly as a refuge from predation. Eelgrass and kelp both provide important habitats for age-1 Greenland cod, and likely serve as nurseries by promoting increasing survival. Reduced predation pressure could drive the seasonal or ontogenetic shift from eelgrass-dominated habitat use in the fall to kelp-dominated use in the winter, though freezing risk in shallow eelgrass may also play a role. Juvenile Greenland cod coexist with juvenile Atlantic cod in coastal Newfoundland, where they occupy the same habitats through early life. Therefore, these results can inform management and conservation strategies directed towards Atlantic cod as well as Greenland cod. Given that juvenile survival directly affects future adult population sizes, marine protected areas established with the goal of increasing cod populations should consider coastal nursery areas as part of marine protected area planning. When assessing the quality of these areas, the abundance, patchiness, and configuration of available habitat types should be considered together along with the seasonal and diel distributions of juvenile cod.

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Figures and Tables

Table 3.1. Area table for habitat maps of Heffern's Cove and Buckley's Cove in Newman Sound, NL. Habitat maps were created from aerial photos, video, and heads-up digitization. Estimated error is ± 5 m. Habitat types were classified to dominant macrophyte cover or sediment grain size: rockweed (*Fucus* spp., *Ascophyllum nodosum*), eelgrass (*Zostera marina*), kelp (*Laminaria* spp., *Saccharina latissima*), bedrock/boulder (grain size > 1 m diameter), rock (grain size 25 cm - 1 m), cobble (grain size 2.5 - 25 cm), and mud/sand/gravel (grain size < 2.5 cm). A mixed habitat type, mud/sand/gravel with patchy kelp, was observed in Buckley's Cove only and was characterized by an expanse of mud/sand/gravel with isolated clumps of kelp dispersed throughout.

	Heffern's Cove		Buckley's Cove	
Habitat	Area (m^2)	Proportion	Area (m^2)	Proportion
Boulder/bedrock	16,538	0.08	1,992	0.00
Cobble	23,663	0.12	107,071	0.25
Mud/sand/gravel	26,182	0.13	91,115	0.21
Rockweed	7,035	0.04	15,159	0.04
Eelgrass	17,123	0.09	59,748	0.14
Kelp	106,079	0.54	25,584	0.06
Mud/sand/gravel with patchy kelp	NA	NA	123,751	0.29
Total	196,620	1	424,420	1

Table 3.2. Linear mixed effects models applied to seasonal subsets of Heffern's Cove movement rates, with model terms, degrees of freedom (numerator, denominator), F values, and p-values (α = 0.05). The response variable, mean movement rate of each individual for every habitat-diel period combination, was untransformed in the fall model and square-root transformed in the winter model. Tag was included as a random variable in both models. Residual variance was free to vary between habitat types and diel periods in both models. Models were validated, assumptions of normality, homogeneity, and independence were checked, and the best models were selected according to BIC.

Season	Term	df	F	P
Fall	(Intercept)	1, 449	459.3682	<.0001
	Diel	3, 449	31.8667	<.0001
	Habitat	4, 449	16.702	<.0001
	Diel*Habitat	12, 449	1.7594	0.0525
Winter	(Intercept)	1, 353	608.9958	<.0001
	Diel	3, 353	33.9596	<.0001
	Habitat	4, 353	5.0707	0.0006
	Diel*Habitat	12, 353	1.6764	0.0702

Table 3.3. Tukey's pair-wise comparisons for the significant effect of diel period on the square-root transformed mean movement rates of individual age 1 Greenland cod in fall and winter in Heffern's Cove. Separate models were created for each season, and mean differences with standard error (S.E.), Z values, and p-values (α = 0.05) are given for each pair-wise combination of diel period.

Season	Test	Estimate	SE	Z	P
Fall	Dawn-Day	-0.09786	0.01667	-5.869	<.0001
	Dawn-Dusk	-0.01337	0.02275	-0.588	0.934519
	Dawn-Night	-0.17219	0.02139	-8.05	<.0001
	Day-Dusk	0.0845	0.02097	4.03	0.000332
	Day-Night	-0.07432	0.01951	-3.809	0.000781
	Dusk-Night	-0.15882	0.02473	-6.423	<.0001
Winter	Dawn-Day	-0.07816	0.02102	-3.719	0.00111
	Dawn-Dusk	-0.03523	0.02203	-1.599	0.37873
	Dawn-Night	-0.20231	0.02137	-9.467	<.0001
	Day-Dusk	0.04293	0.02206	1.946	0.20881
	Day-Night	-0.12415	0.0215	-5.774	<.0001

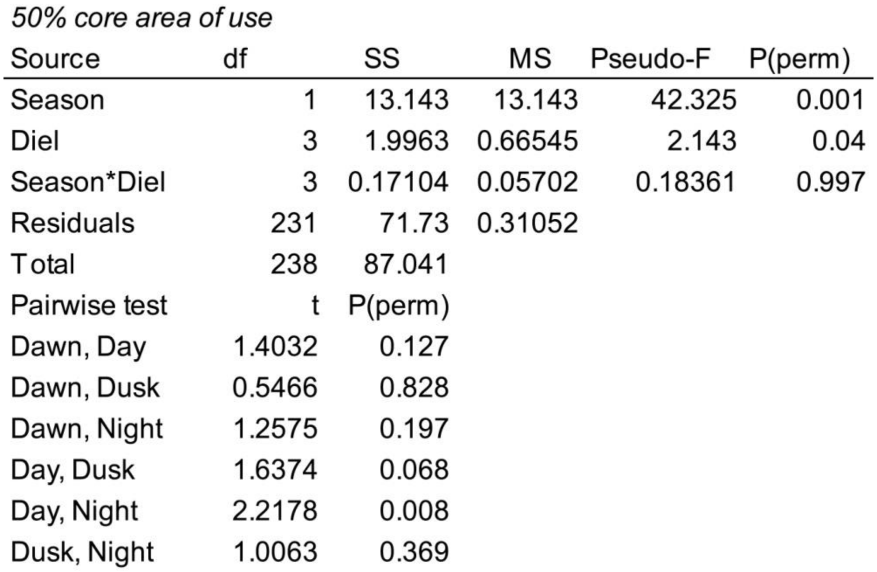
Table 3.4. Tukey's pair-wise comparisons for the significant effect of diel period on the square-root transformed mean movement rate of individual age 1 Greenland cod in winter of year 2 in of both study sites. Separate models were created for each season, and mean differences with standard error (S.E.), Z values, and p-values (α = 0.05) are given for each pair-wise combination of diel period.

Test	Estimate	SE	Z	P
Dawn-Day	0.0412	0.04658	0.885	0.811
Dawn-Dusk	0.117	0.05189	2.255	0.1074
Dawn-Night	-0.0552	0.04414	-1.251	0.591
Day-Dusk	0.0758	0.04686	1.618	0.3654
Day-Night	-0.0964	0.03792	-2.543	0.0523
Dusk-Night	-0.1722	0.04432	-3.886	<0.001

Table 3.5. Summary of heading angle analysis, including tests against a random (uniform) distribution and calculations of mean angles when distributions are non-random and uni-modal for Heffern's Cove (fall and winter of both study years) and Buckley's Cove (winter of year two).

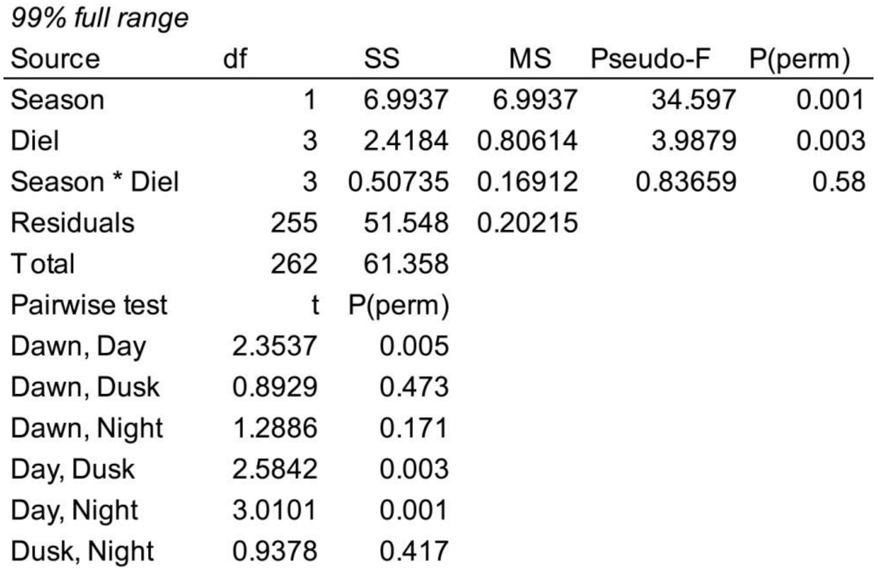
Data	Subgroup	Night	Day	Dusk	Dawn
Heffern's Cove	Number of observations	23395	48466	3454	4511
Fall and winter	Mean angle (μ) ± standard error	multi-modal	multi-modal	173.65 ± 3.1°	359.18 ± 2.3°
	95% Confidence interval for μ	NA	NA	167.51° - 179.8°	354.65° - 3.71°
	Rao's spacing test (U)	225.58	198.63	160.52	157.92
	Rao's spacing test (p)	p < 0.01	p < 0.01	p < 0.01	p < 0.01
Buckley's Cove	Number of observations	295	1314	98	88
Winter	Mean angle (μ) ± standard error	multi-modal	multi-modal	189.9 ± 7.8°	58.3 ± 11.4°
	95% Confidence interval for μ	NA	NA	174.7° - 205.2°	36° - 80.6°
	Rao's spacing test (U)	134.36	136.56	165.65	154.03
	Rao's spacing test (p)	p > 0.10	p > 0.05	p < 0.01	p < 0.01

Table 3.6. Heffern's Cove permutational analysis of variance (PERMANOVA) results from testing the effects of diel period (dawn, day, dusk, and night) and season (fall and winter, both years) on untransformed habitat proportions based on Euclidean distance similarity matrices. Habitat proportions are the proportions of each habitat type (rockweed, eelgrass, kelp, boulder/bedrock, cobble, and mud/sand/gravel) within the 50% (core area of use) and 99% (full range) contours of utilization distributions constructed with the dynamic Brownian Bridge movement model.



50% core area of use

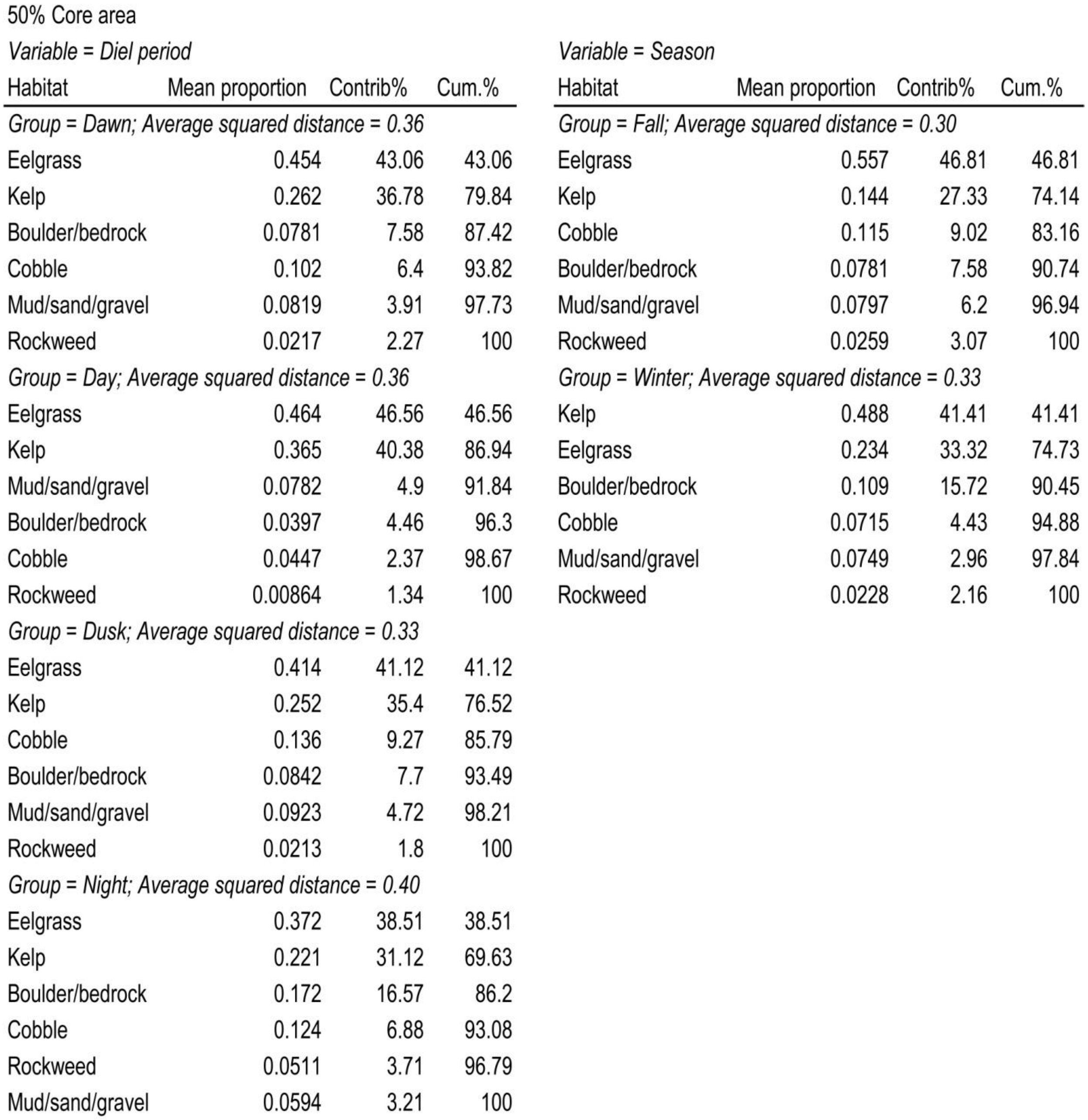
Source	df	SS	MS	Pseudo-F	P(perm)
Season	1	13.143	13.143	42.325	0.001
Diel	3	1.9963	0.66545	2.143	0.04
Season*Diel	3	0.17104	0.05702	0.18361	0.997
Residuals	231	71.73	0.31052		
Total	238	87.041			
Pairwise test	t	P(perm)			
Dawn, Day	1.4032	0.127			
Dawn, Dusk	0.5466	0.828			
Dawn, Night	1.2575	0.197			
Day, Dusk	1.6374	0.068			
Day, Night	2.2178	0.008			
Dusk, Night	1.0063	0.369			



99% full range

Source	df	SS	MS	Pseudo-F	P(perm)
Season	1	6.9937	6.9937	34.597	0.001
Diel	3	2.4184	0.80614	3.9879	0.003
Season * Diel	3	0.50735	0.16912	0.83659	0.58
Residuals	255	51.548	0.20215		
Total	262	61.358			
Pairwise test	t	P(perm)			
Dawn, Day	2.3537	0.005			
Dawn, Dusk	0.8929	0.473			
Dawn, Night	1.2886	0.171			
Day, Dusk	2.5842	0.003			
Day, Night	3.0101	0.001			
Dusk, Night	0.9378	0.417			

Table 3.7A. Results of similarity percentage (SIMPER) analyses showing the contributions (Contrib%) of each habitat type to the overall dissimilarity (Euclidean distance) in habitat proportions within the core area of use (50% UD contour) by diel period (dawn, day, dusk, and night) and season (fall and winter, both years) in Heffern's Cove. Mean proportions (Mean prop) and cumulative contributions (Cum.%) of each habitat, as well as the average squared distance for each group are also given.



50% Core area

Variable = Diel period

Habitat	Mean proportion	Contrib%	Cum.%
Group = Dawn; Average squared distance = 0.36			
Eelgrass	0.454	43.06	43.06
Kelp	0.262	36.78	79.84
Boulder/bedrock	0.0781	7.58	87.42
Cobble	0.102	6.4	93.82
Mud/sand/gravel	0.0819	3.91	97.73
Rockweed	0.0217	2.27	100
Group = Day; Average squared distance = 0.36			
Eelgrass	0.464	46.56	46.56
Kelp	0.365	40.38	86.94
Mud/sand/gravel	0.0782	4.9	91.84
Boulder/bedrock	0.0397	4.46	96.3
Cobble	0.0447	2.37	98.67
Rockweed	0.00864	1.34	100
Group = Dusk; Average squared distance = 0.33			
Eelgrass	0.414	41.12	41.12
Kelp	0.252	35.4	76.52
Cobble	0.136	9.27	85.79
Boulder/bedrock	0.0842	7.7	93.49
Mud/sand/gravel	0.0923	4.72	98.21
Rockweed	0.0213	1.8	100
Group = Night; Average squared distance = 0.40			
Eelgrass	0.372	38.51	38.51
Kelp	0.221	31.12	69.63
Boulder/bedrock	0.172	16.57	86.2
Cobble	0.124	6.88	93.08
Rockweed	0.0511	3.71	96.79
Mud/sand/gravel	0.0594	3.21	100

Variable = Season

Habitat	Mean proportion	Contrib%	Cum.%
Group = Fall; Average squared distance = 0.30			
Eelgrass	0.557	46.81	46.81
Kelp	0.144	27.33	74.14
Cobble	0.115	9.02	83.16
Boulder/bedrock	0.0781	7.58	90.74
Mud/sand/gravel	0.0797	6.2	96.94
Rockweed	0.0259	3.07	100
Group = Winter; Average squared distance = 0.33			
Kelp	0.488	41.41	41.41
Eelgrass	0.234	33.32	74.73
Boulder/bedrock	0.109	15.72	90.45
Cobble	0.0715	4.43	94.88
Mud/sand/gravel	0.0749	2.96	97.84
Rockweed	0.0228	2.16	100

Table 3.7B. Results of similarity percentage (SIMPER) analyses showing the contributions (Contrib%) of each habitat type to the overall dissimilarity (Euclidean distance) in habitat proportions within the full range (99% UD contour) by diel period (dawn, day, dusk, and night) and season (fall and winter, both years) in Heffern's Cove. Mean proportions (Mean prop) and cumulative contributions (Cum.%) of each habitat, as well as the average squared distance for each group are also given.

99% Full range

Variable = Diel period

Habitat	Mean proportion	Contrib%	Cum.%
Group = Dawn; Average squared distance = 0.36			
Kelp	0.253	40.13	40.13
Eelgrass	0.396	39.62	79.75
Mud/sand/gravel	0.144	5.97	85.72
Rockweed	0.0441	5.51	91.23
Cobble	0.0964	4.78	96.01
Boulder/bedrock	0.0662	4	100
Group = Day; Average squared distance = 0.36			
Kelp	0.389	50.86	50.86
Eelgrass	0.287	27.05	77.91
Rockweed	0.0392	9.53	87.44
Mud/sand/gravel	0.155	5.68	93.12
Boulder/bedrock	0.0521	4.84	97.96
Cobble	0.078	2.04	100
Group = Dusk; Average squared distance = 0.33			
Kelp	0.222	36.15	36.15
Eelgrass	0.357	34.47	70.62
Rockweed	0.0795	13.96	84.58
Mud/sand/gravel	0.167	8.41	92.99
Boulder/bedrock	0.0705	3.65	96.64
Cobble	0.105	3.35	100
Group = Night; Average squared distance = 0.40			
Eelgrass	0.349	37.26	37.26
Kelp	0.201	35.44	72.7
Rockweed	0.0766	8.13	80.83
Boulder/bedrock	0.114	7.25	88.08
Cobble	0.143	7.01	95.09
Mud/sand/gravel	0.117	4.91	100

Variable = Season

Habitat	Mean proportion	Contrib%	Cum.%
Group Fall; Average squared distance = 0.30			
Eelgrass	0.425	38.7	38.7
Kelp	0.172	34	72.7
Rockweed	0.0586	8.77	81.47
Mud/sand/gravel	0.147	7.94	89.41
Cobble	0.121	5.57	94.98
Boulder/bedrock	0.0779	5.02	100
Group Winter; Average squared distance = 0.33			
Kelp	0.421	46.55	46.55
Eelgrass	0.228	26.85	73.4
Rockweed	0.0578	11.54	84.94
Boulder/bedrock	0.0691	6.23	91.17
Mud/sand/gravel	0.145	5.22	96.39
Cobble	0.0798	3.6	100

Table 3.8. Buckley's Cove permutational analysis of variance (PERMANOVA) results from testing the effects of diel period (dawn, day, dusk, and night) on untransformed habitat proportions based on Euclidean distance similarity matrices. Habitat proportions are the proportions of each habitat type (rockweed, eelgrass, kelp, boulder/bedrock, cobble, and mud/sand/gravel, mud/sand/gravel with patchy kelp) within the 50% (core area of use) and 99% (full range) contours of utilization distributions constructed with the dynamic Brownian Bridge movement model.

50% Core area of use

Source	df	SS	MS	Pseudo-F	P(perm)
Diel period	3	0.7693	0.25643	0.63326	0.712
Residuals	37	14.983	0.40494		
Total	40	15.752			

99% full range

Source	df	SS	MS	Pseudo-F	P(perm)
Diel period	3	0.4276	0.14252	0.76058	0.593
Residuals	37	6.9331	0.18738		
Total	40	7.3607			

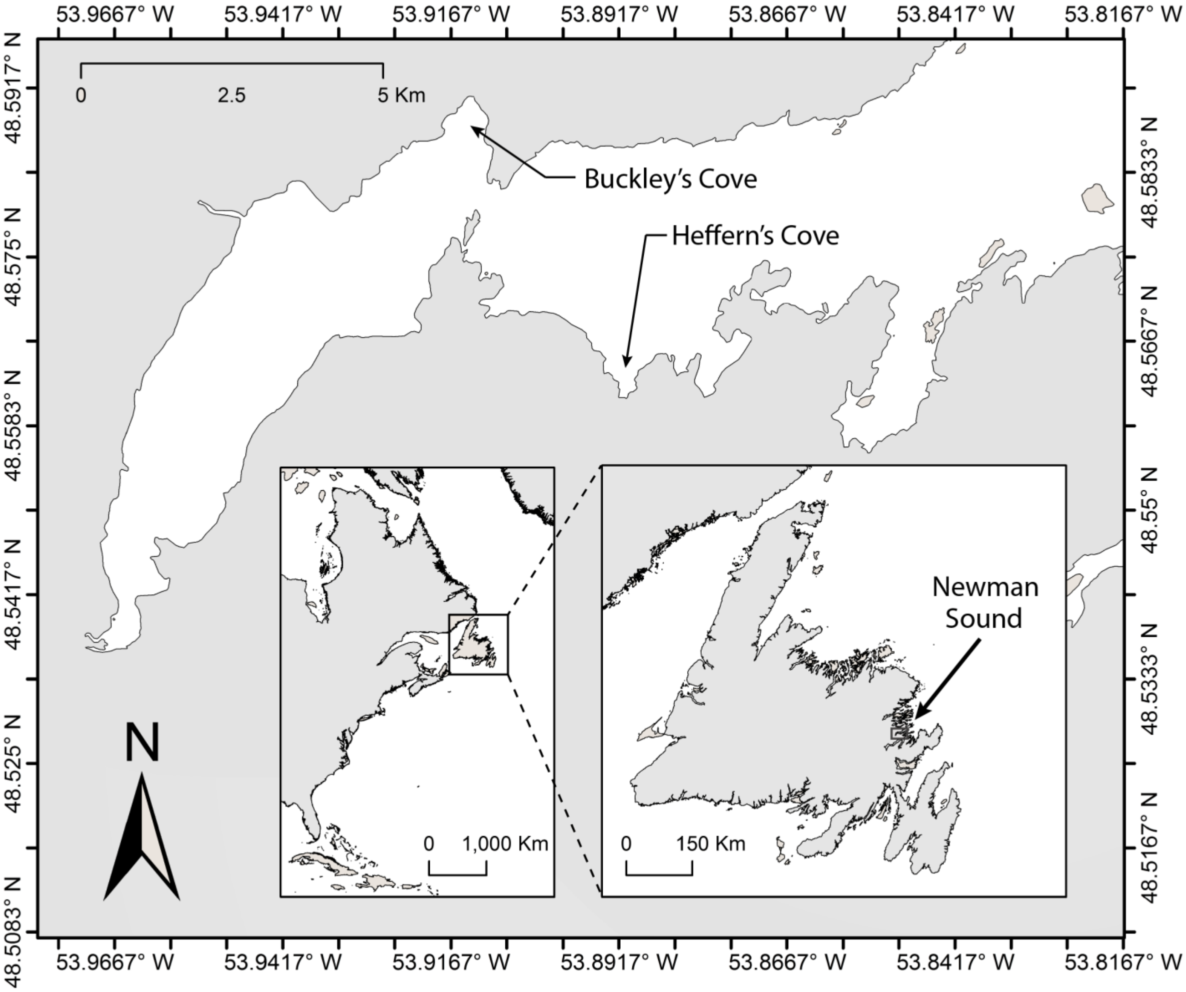


Fig. 3.1. Map of study sites within Newman Sound, located in Bonavista Bay on the east coast of Newfoundland, Canada (black box, inset).

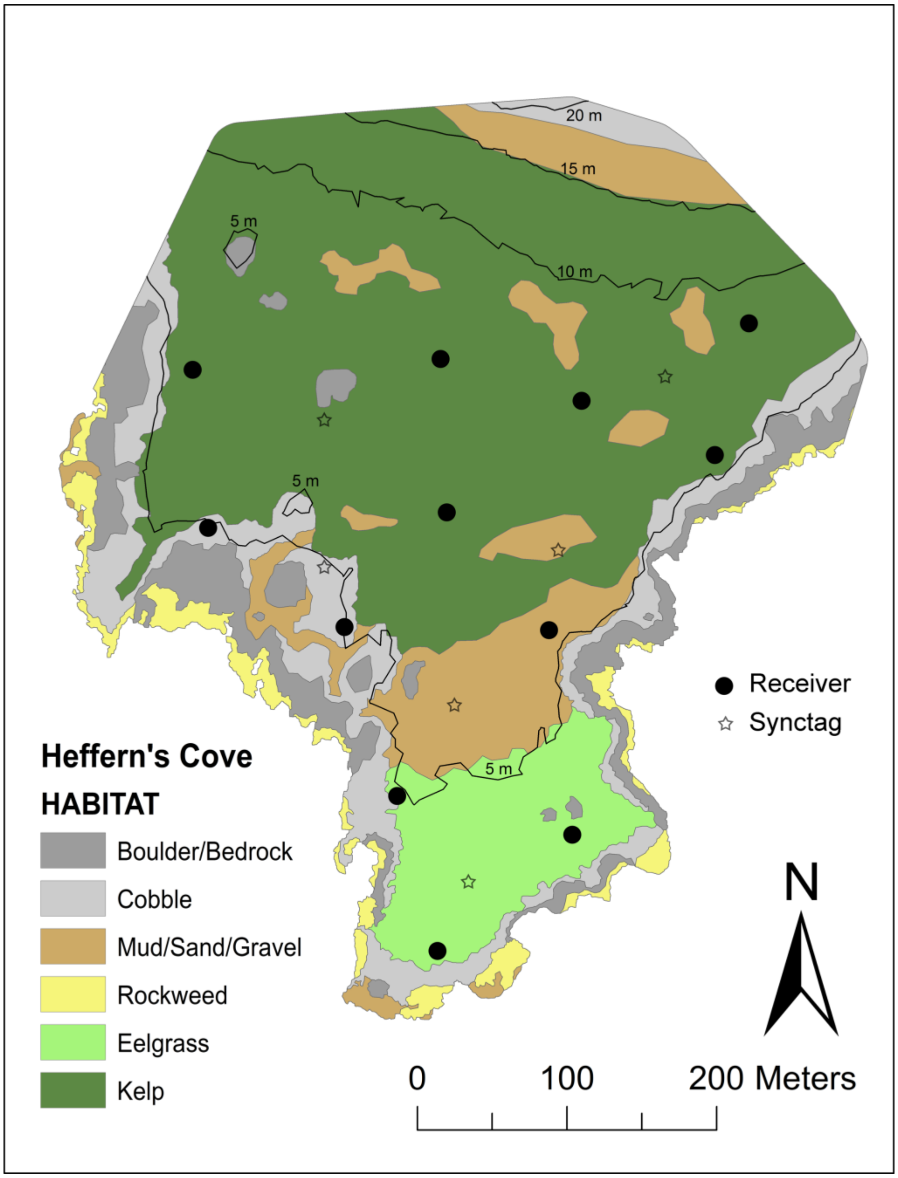


Fig. 3.2A. Habitat map of Heffern's Cove study site with 5-m isobaths (black lines), receivers, and synctags. Habitat was classified from aerial photographs and *in situ* video samples with an estimated error of 5 m. Inert habitat types were classified by grain size: Boulder/bedrock (> 1 m), cobble (25 cm – 1 m), and mud/sand/gravel (≤ 2.5 cm). Macrophyte habitat types were kelp (*Saccharina latissima* and *Laminaria* spp.), eelgrass (*Zostera marina*), and rockweed (*Fucus* spp., *Ascophyllum nodosum*).

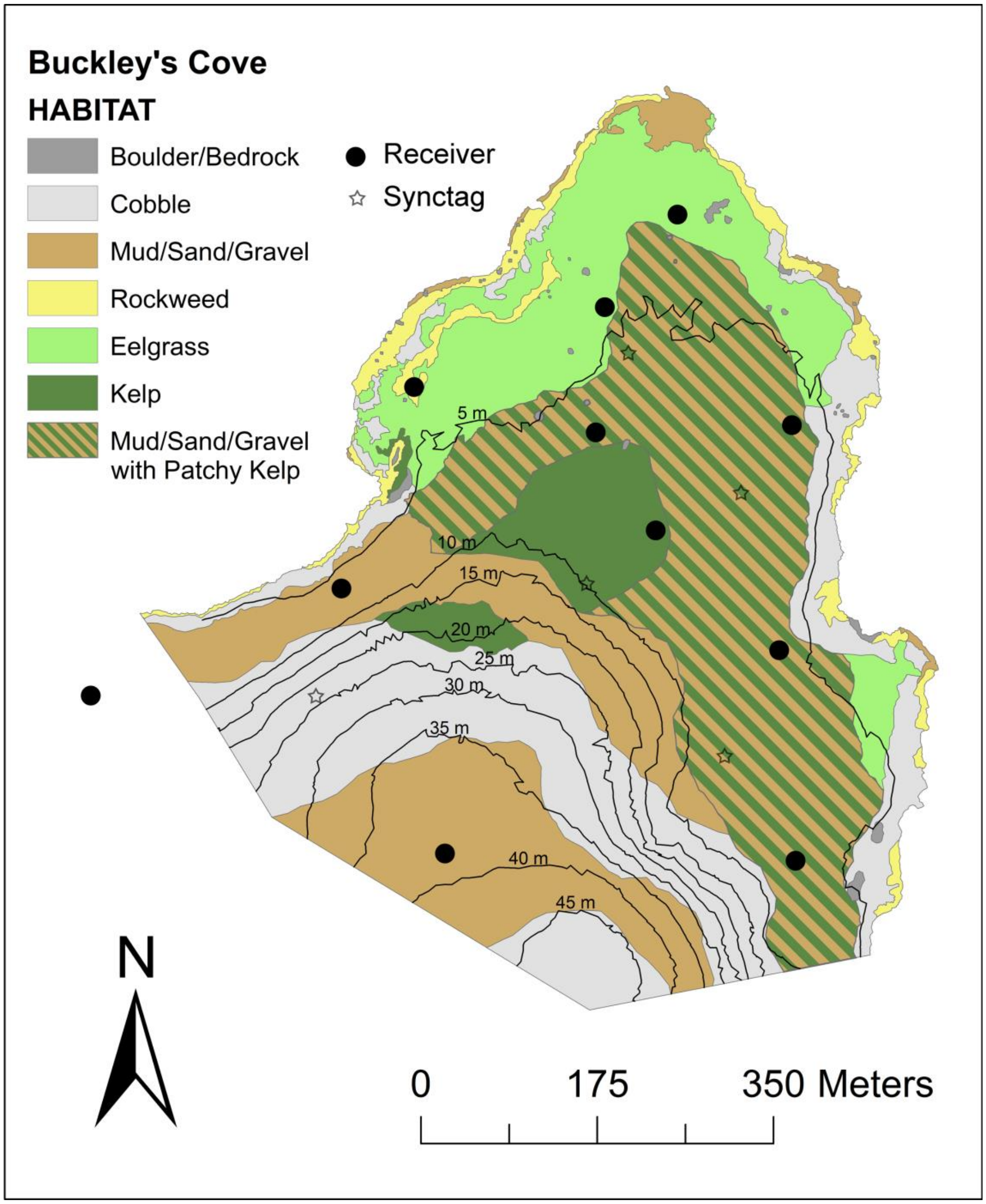


Fig. 3.2B. Habitat map of Buckley's Cove study site with 5-m isobaths (black lines), receivers, and synctags. Habitat was classified from aerial photographs and *in situ* video samples with an estimated error of 5 m. Inert habitat types were classified by grain size: Boulder/bedrock (> 1 m), cobble (25 cm – 1 m), and mud/sand/gravel (≤ 2.5 cm). Macrophyte habitat types were kelp (*Saccharina latissima* and *Laminaria* spp.), eelgrass (*Zostera marina*), and rockweed (*Fucus* spp., *Ascophyllum nodosum*). An expanse of sediment bottom interspersed with isolated patches of kelp characterizes intermediate type, mud/sand/gravel with patchy kelp.

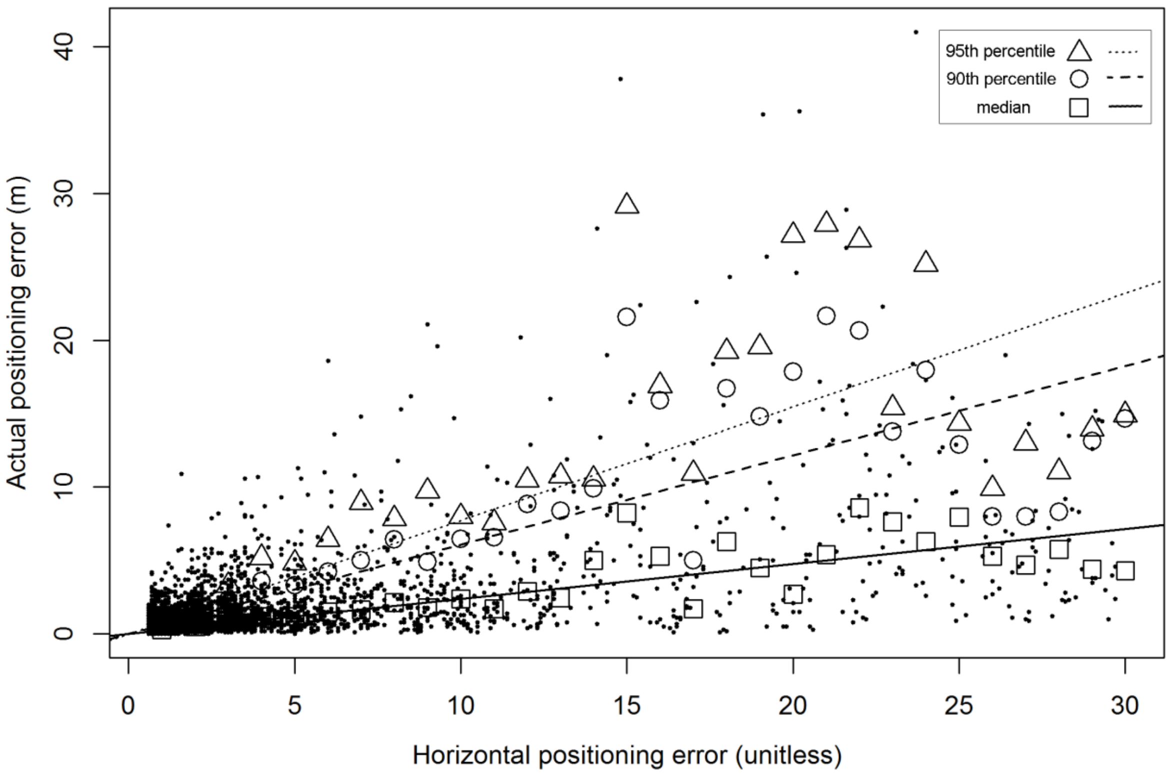


Fig. 3.3. Real positioning error (m; HPEm) as a function of Horizontal positioning error (unitless; HPE). Median, 90th percentile, and 95th percentile HPEm values were calculated from 1 HPE bins for 18,431 positions from 6 synctags over 1 month (October - November, 2010) in Heffern's Cove. Below a threshold of 6 HPE, positions had a median of 0.3 m, 90th percentile of 1.0 m, and a 95th percentile of 1.6 m.

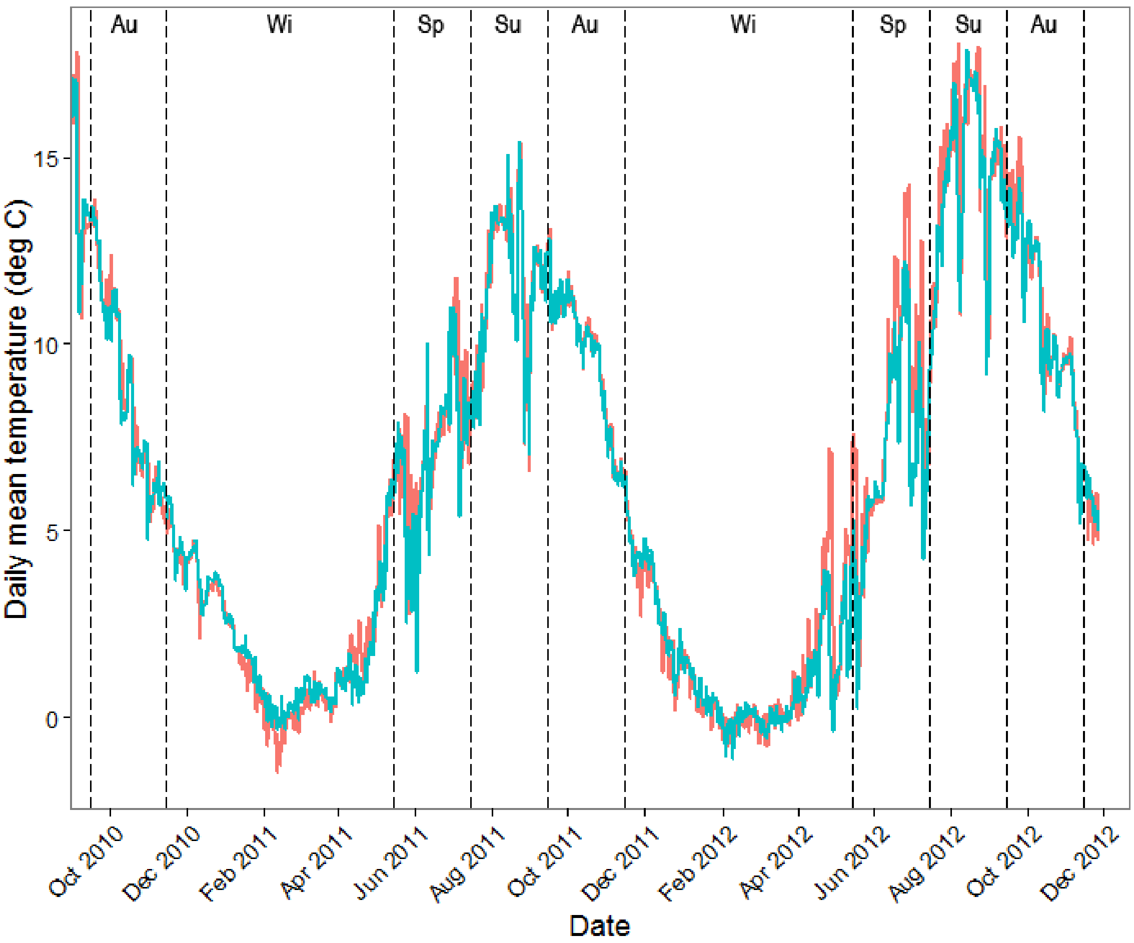


Fig. 3.4. Weekly mean temperature in Heffern's Cove (blue) and Buckley's Cove (red), with autumn (Au), winter (Wi), spring (Sp), and summer (Su).

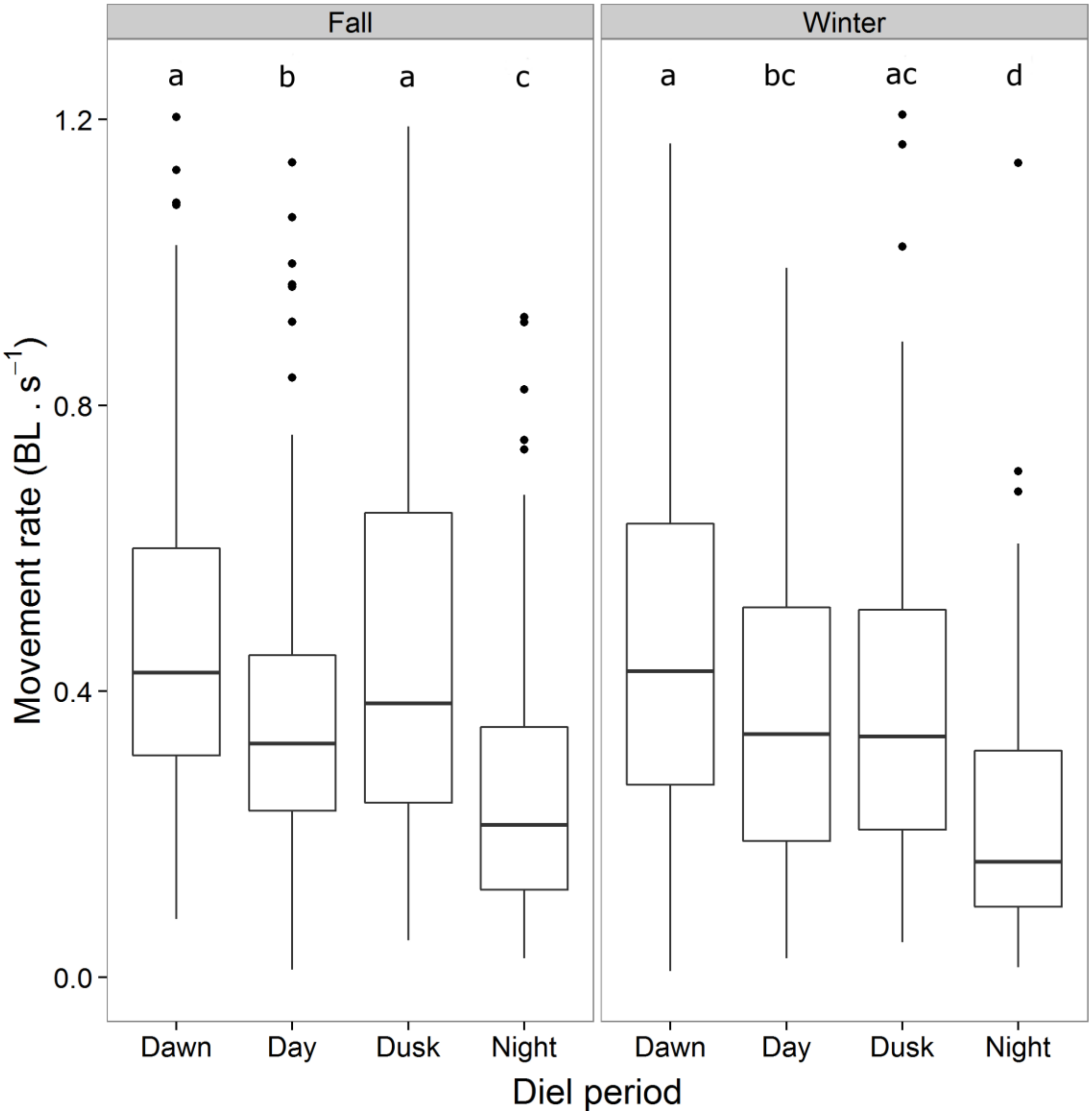


Fig 3.5. Boxplots of mean movement rate (body lengths per second) by diel period for seasonal subsets of Heffern's Cove data. Letters shared among time periods designate pairs that are not significantly different (α = 0.05). Boxes display the median (horizontal line), 25th percentile (lower box hinge), and 75th percentile (upper box hinge). Whiskers extend from the box to the most extreme data point which is no more than 1.5 times the length of the box.

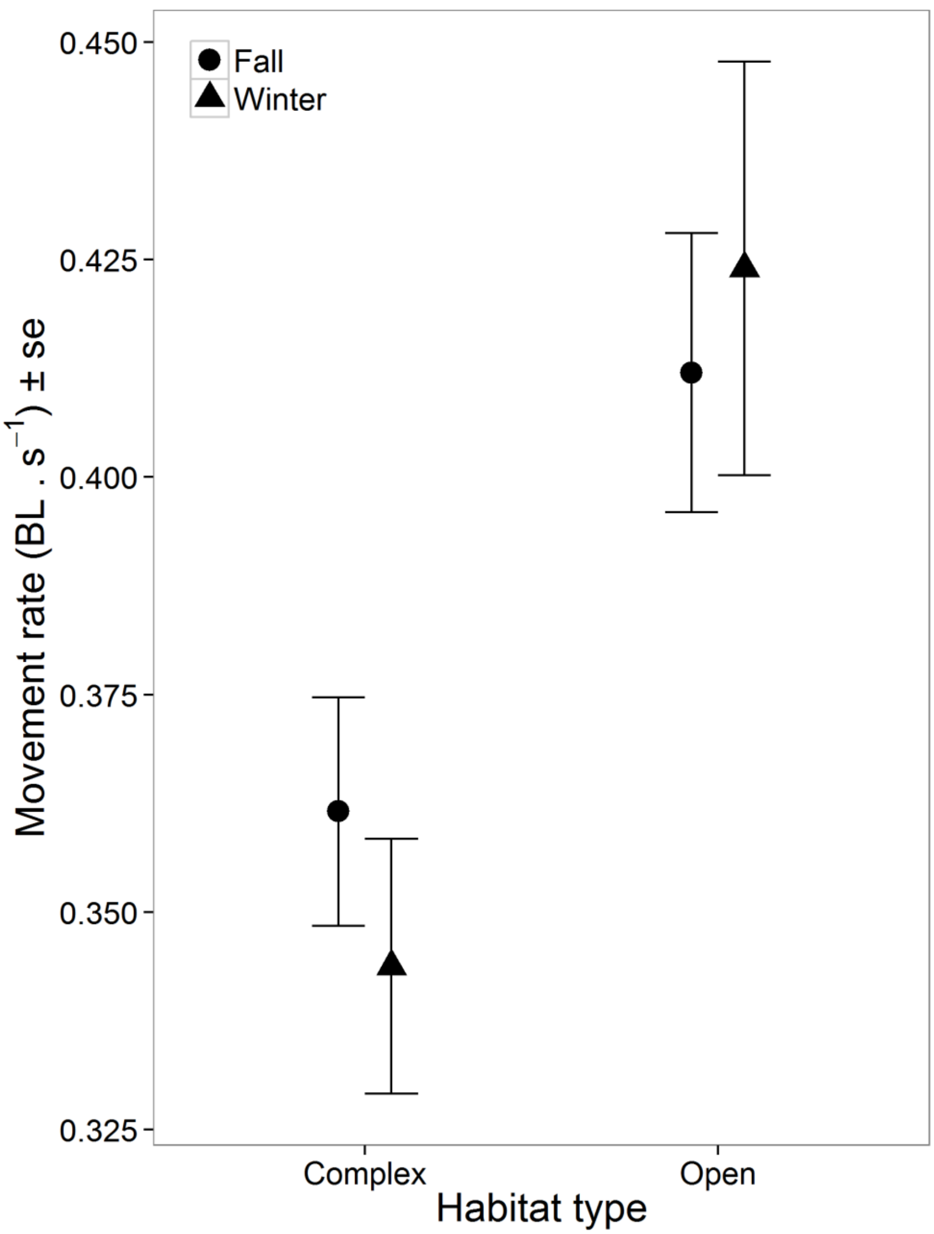


Fig. 3.6. Mean movement rates (± standard error) in open (mud/sand/gravel and cobble) and complex (boulder/bedrock, eelgrass, and kelp) habitats for individuals in the fall and winter seasons in Heffern's Cove. Movement rates in open habitats were 33% higher than complex habitats in the fall, and 39% higher in the winter (p-values < 0.001).

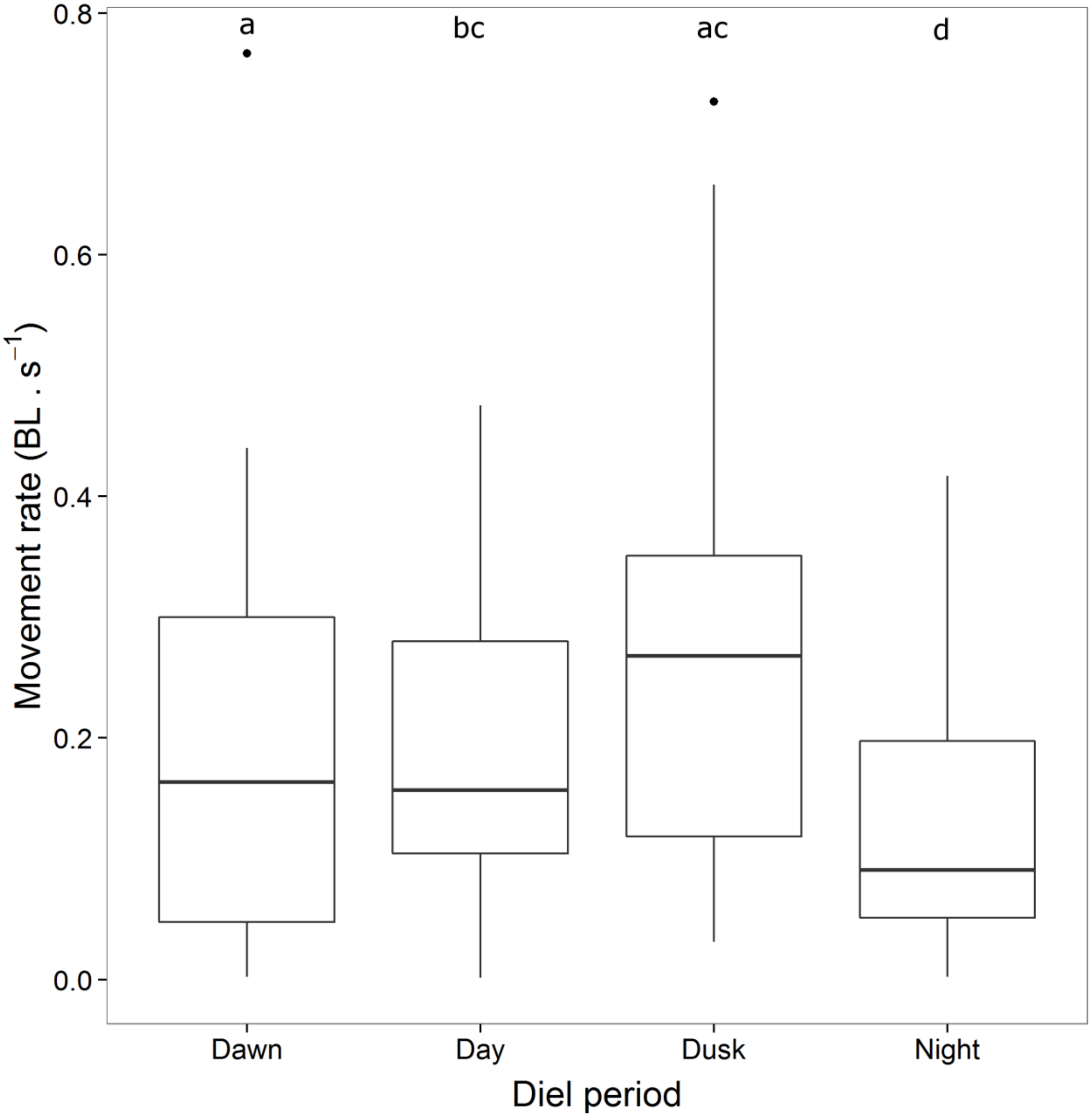


Fig. 3.7. Boxplots of mean movement rate by diel period for the winter season of year two in both study sites. Boxes display the median (horizontal line), 25th percentile (lower box hinge), and 75th percentile (upper box hinge). Whiskers extend from the box to the most extreme data point which is no more than 1.5 times the length of the box. Letters shared among time periods designate pairs that are not significantly different (α = 0.05).

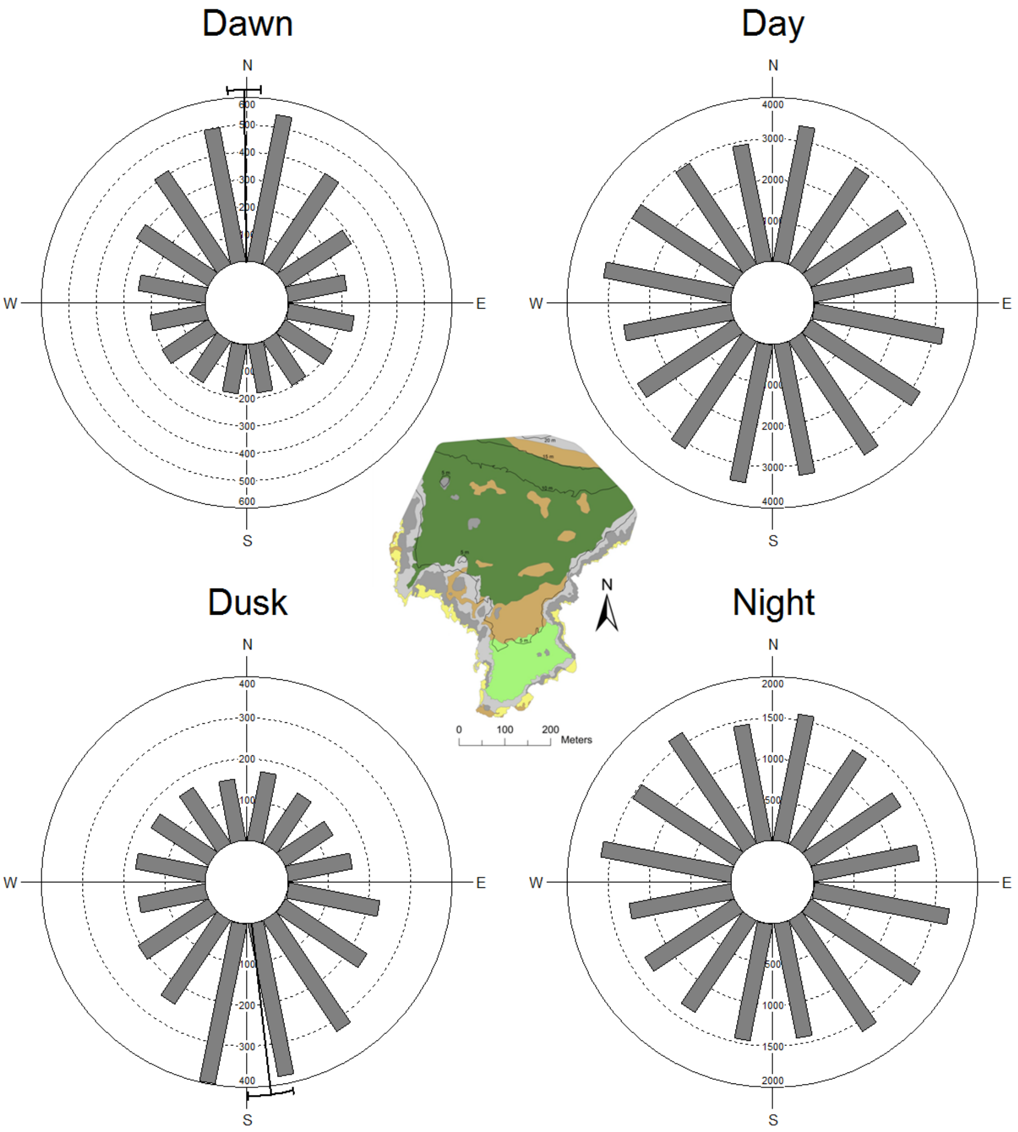


Fig. 3.8A. Circular histograms of heading angles for autumn and winter movements in Heffern's Cove with 22.5° bins. Mean angles and 95% confidence intervals are indicated by a black line and arc when appropriate. Headings were measured as the angle (degrees) of the movement trajectory from true north (0° or 360°). Movements under 3 m were excluded. Mean angles were calculated for dawn (359.2 ± 2.3°) and dusk (173.7 ± 3.1°), but the presence of multiple modes prevented the calculation for day and night periods. All distributions were significantly different from a random distribution (Rao's spacing test, all p-values < 0.01).

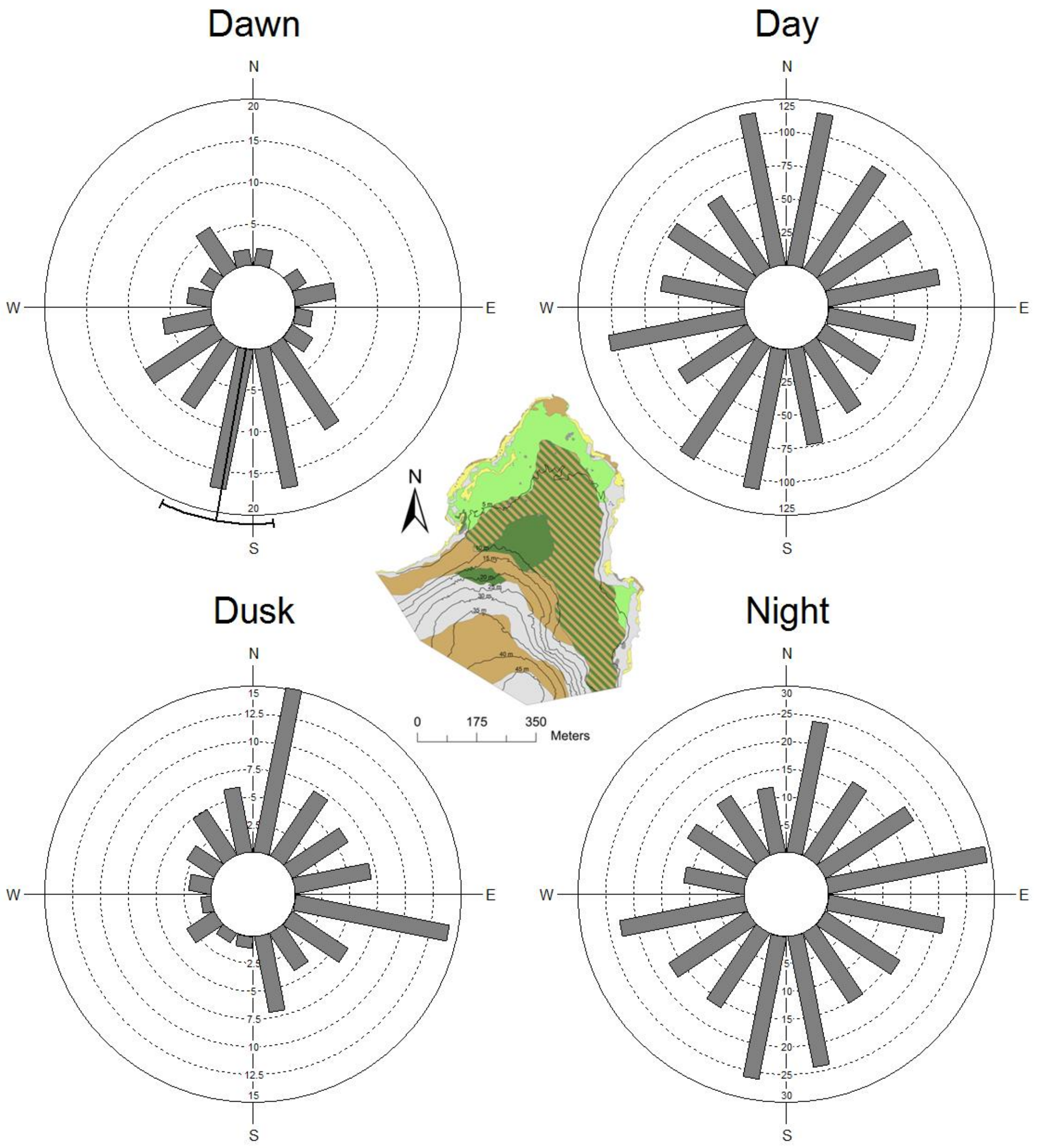


Fig. 3.8B. Circular histograms of heading angles for winter movements in Buckley's Cove with 22.5° bins. Mean angles and 95% confidence intervals are indicated by a black line and arc when appropriate. Headings were measured as the angle (degrees) of the movement trajectory from true north (0° or 360°). Movements under 3 m were excluded. Day and night distributions were not significantly different from a uniform distribution (Rao's spacing test; p-value > 0.05 and p-value > 0.10, respectively). The bi-modal distribution for dusk prevented the calculation of a mean angle, while at dawn the average was 189.9 ± 7.8°.

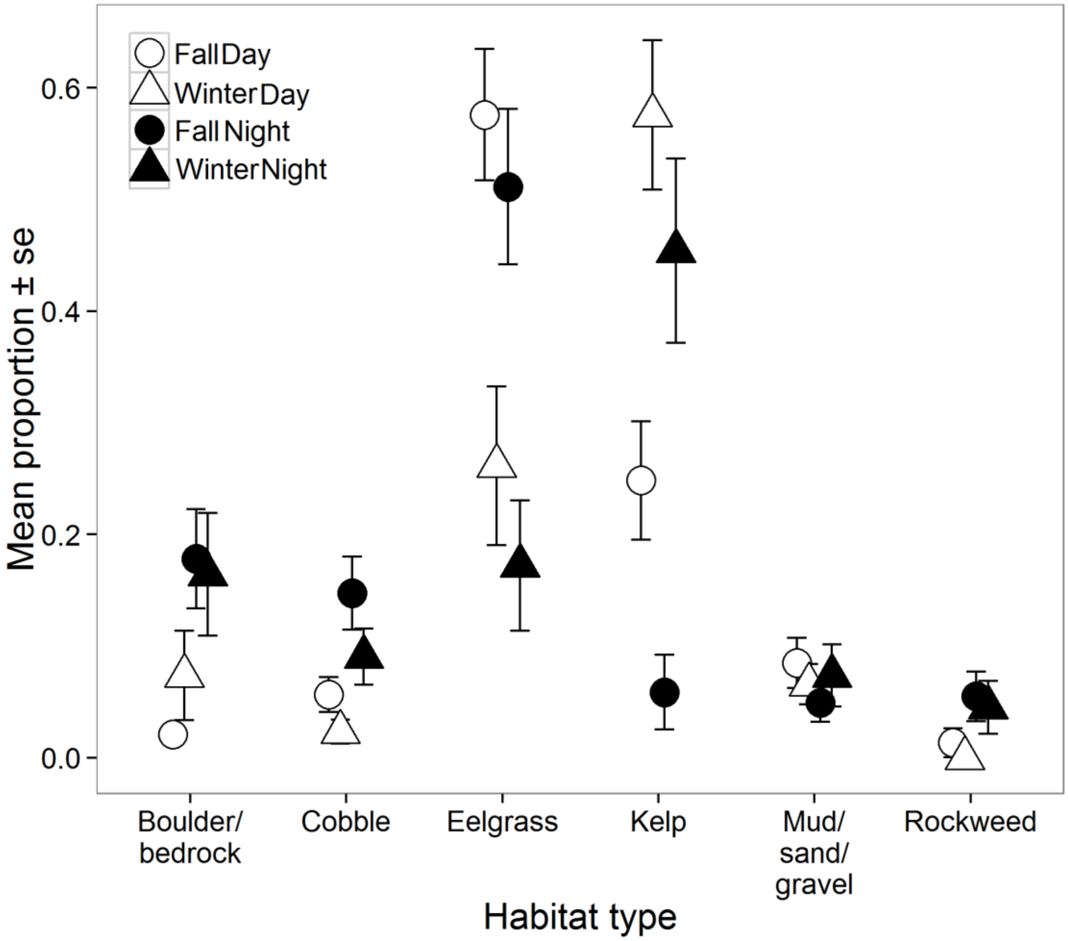


Fig. 3.9A. Mean proportions (± standard error) of each habitat type within the 50% Brownian Bridge UD contour (core area of use), by diel period and season in autumn (fall) and winter of years 1 and 2 in Heffern's Cove. Proportions used during dawn and dusk were in most cases intermediate to the proportions used during day and night periods, so they were removed from the plot for clarity (see Table 3.7B).

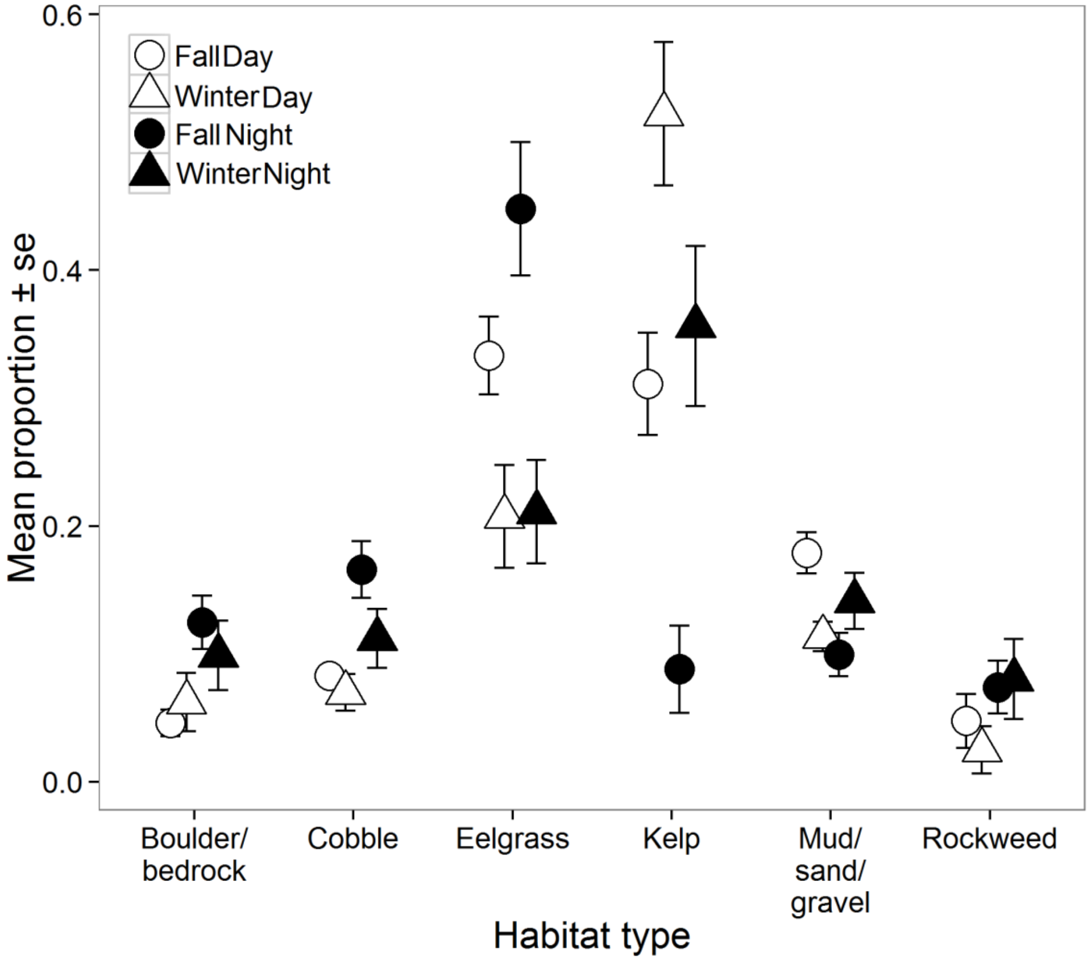


Fig. 3.9B. Mean proportions (± standard error) of each habitat type within the 99% Brownian Bridge UD contour (full range), by diel period and season in autumn (fall) and winter of years 1 and 2 in Heffern's Cove. Proportions used during dawn and dusk were in most cases intermediate to the proportions used during day and night periods, so they were removed from the plot for clarity (see Table 3.7B).

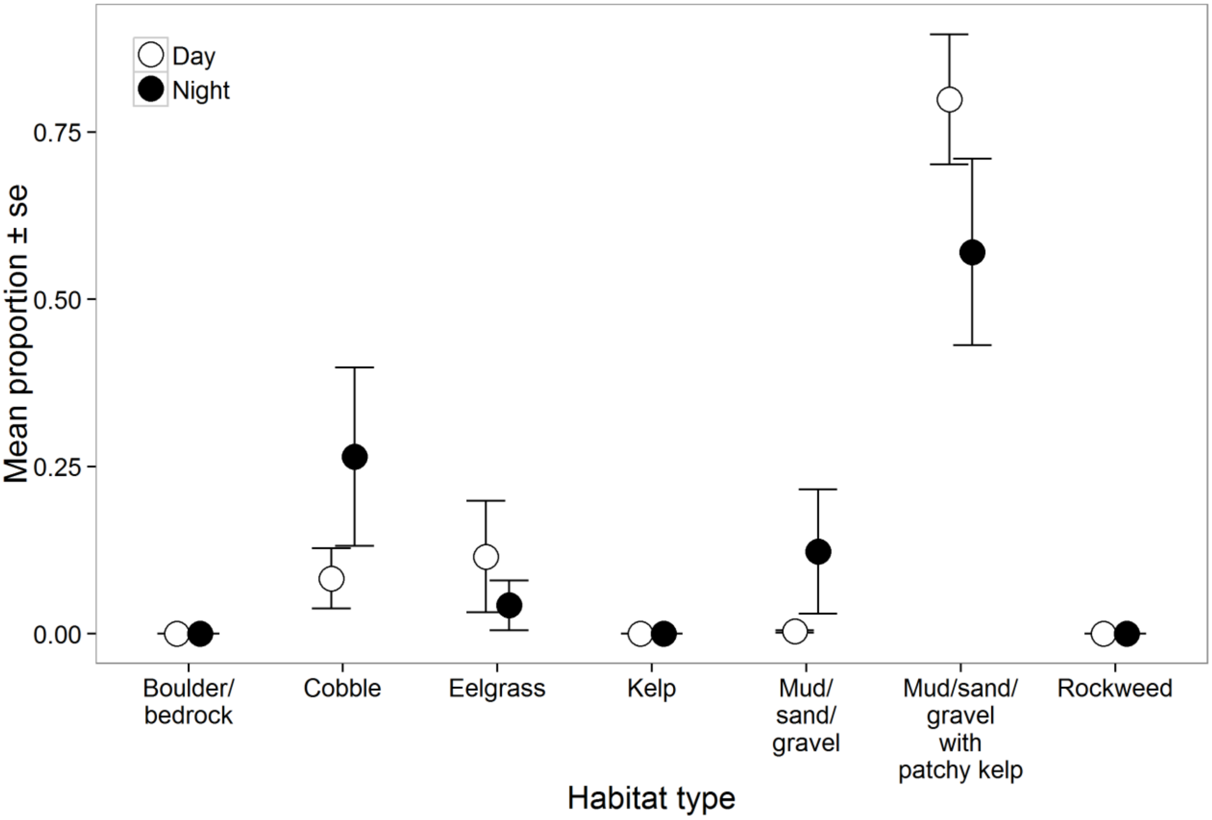


Fig. 3.9C. Mean proportions (± standard error) of each habitat type within the 50% Brownian Bridge UD contour (core area of use) by diel period in winter of Year 2 in Buckley's Cove. Proportions used during dawn and dusk were in most cases intermediate to the proportions used during day and night periods, so they were removed from the plot for clarity.

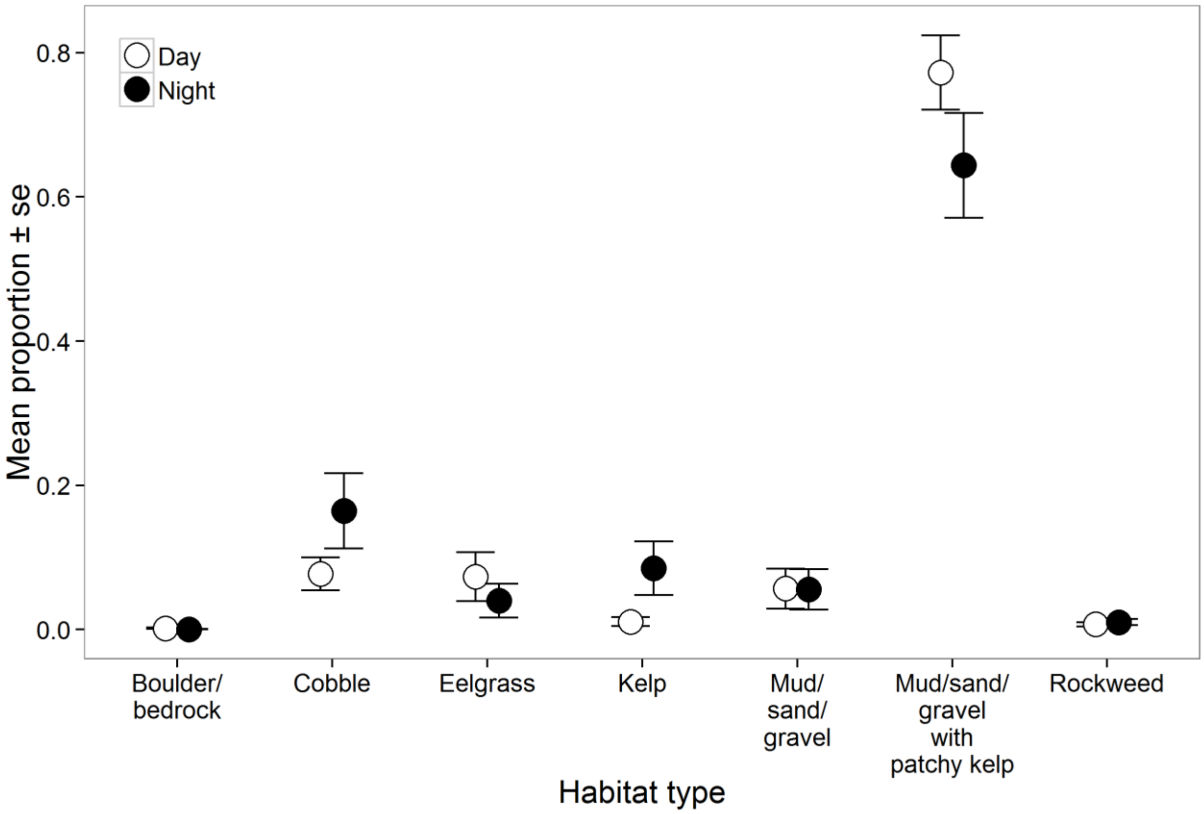


Fig. 3.9D. Mean proportions (± standard error) of each habitat type within the 99% Brownian Bridge UD contour (core area of use) by diel period Buckley's Cove. Proportions used during dawn and dusk were in most cases intermediate to the proportions used during day and night periods, so they were removed from the plot for clarity.

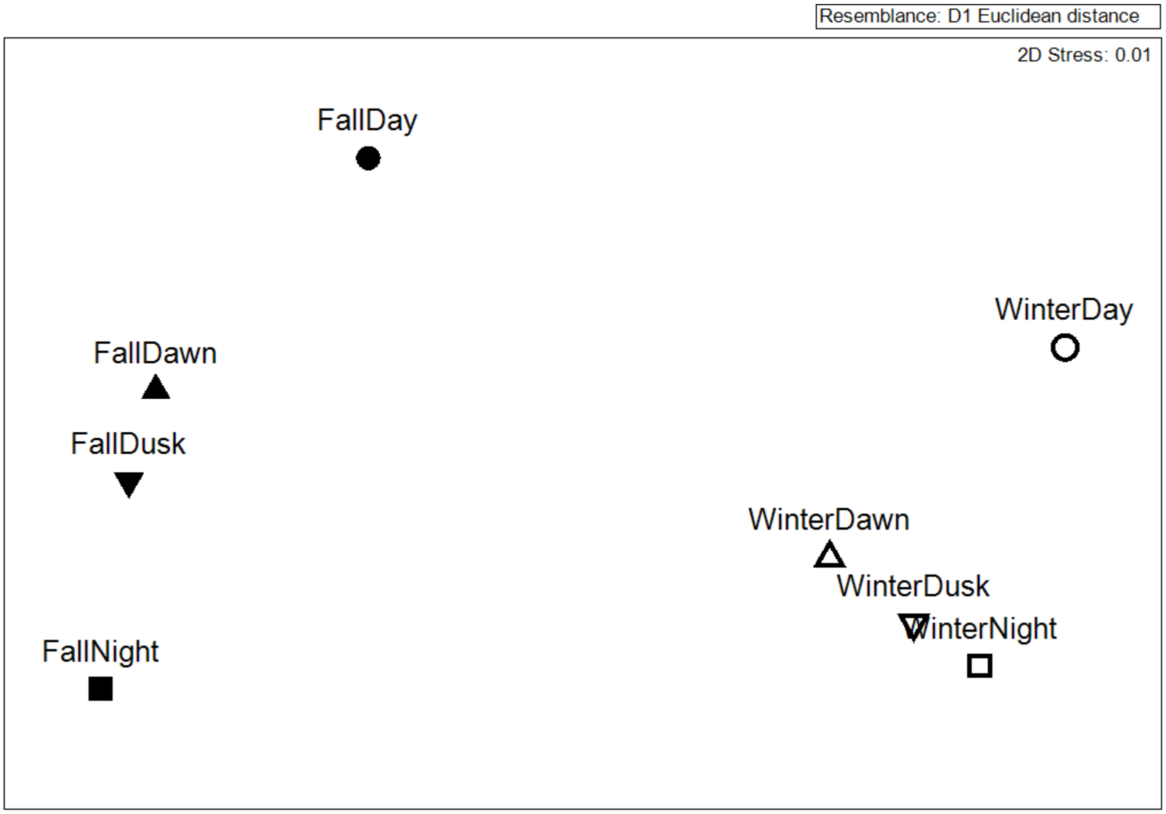


Fig. 3.10A. Core area of use (50% UD contour) non-metric multi-dimensional scaling (nMDS) plot (Euclidean distance) of the centroids of combined season-diel period groupings of multivariate habitat proportions in autumn (fall; closed symbols) and winter (open symbols) of years 1 and 2 in Heffern's Cove. Shapes represent diel periods (dawn = triangle, day = circle, dusk = inverted triangle, night = square).

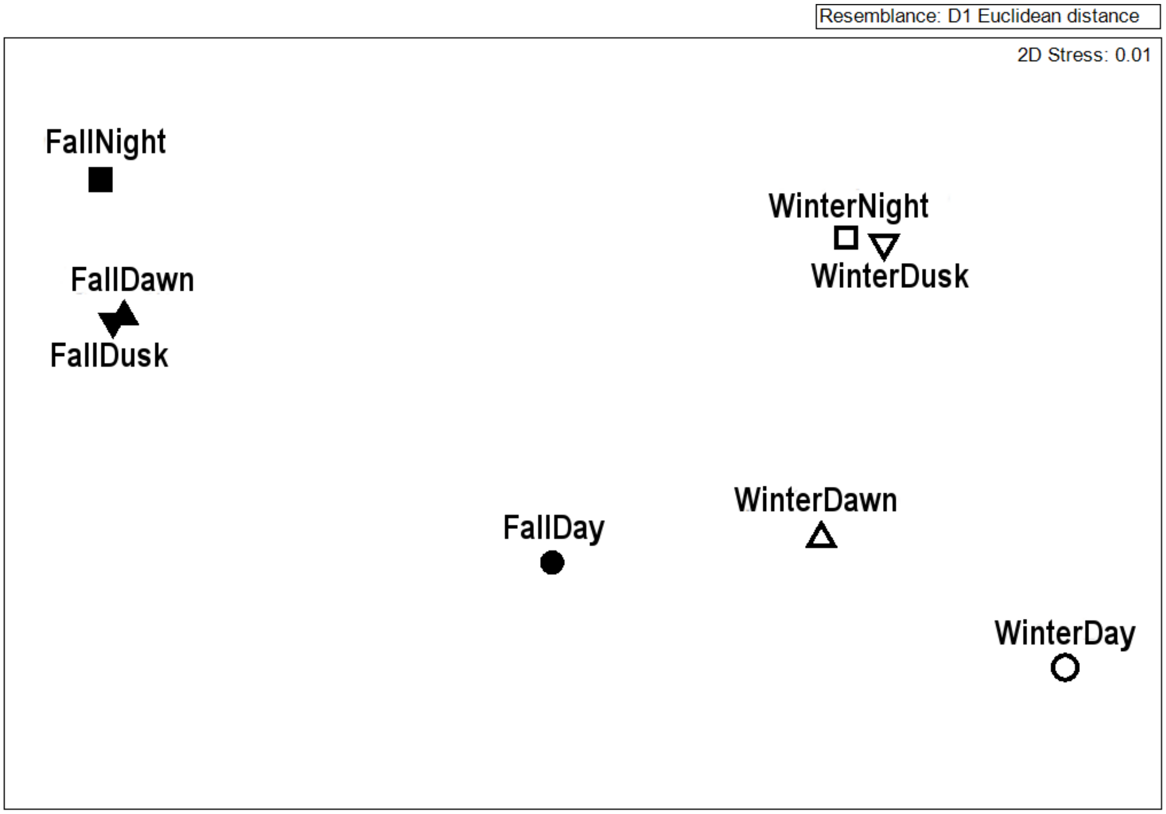


Fig. 3.10B. Full range (99% UD contour) non-metric multi-dimensional scaling (nMDS) plot (Euclidean distance) of the centroids of combined season-diel period groupings of multivariate habitat proportions in autumn (fall; closed symbols) and winter (open symbols) of years 1 and 2 in Heffern's Cove. Shapes represent diel periods (dawn = triangle, day = circle, dusk = inverted triangle, night = square).

Appendix 3.A. - Supplementary Material

Table 3.A1. Tracking summary for 42 age 1 Greenland cod tracked in year 1 in Heffern's Cove. Sites of capture (origin) and release (release), standard length at release (SL), tracking period start, end, and length (TP), number of positions, fate (died/expulsion, left area, or battery expired), unique days detected (DD), and residency index (RI = DD/TP) are given for each individual.

Tag ID	SL	Origin	Release	Track start	Positions	Track end	Fate	DD	TP	RI
29912	14	HC	HC	08/10/2010 11:57:00	606	22/10/2010 10:33:40	left	13	15	0.87
29913	16	HC	HC	08/10/2010 11:57:00	709	20/10/2010 20:57:18	died	13	13	1
29914	15	HC	HC	08/10/2010 11:57:00	289	12/10/2010 11:00:17	died	5	5	1
29915	16	HC	HC	08/10/2010 11:57:00	7362	13/02/2011 10:20:45	left	128	129	0.99
29916	16	HC	HC	08/10/2010 11:57:00	2079	06/11/2010 13:39:01	left	30	30	1
29917	15.5	HC	HC	08/10/2010 11:57:00	1390	08/11/2010 00:16:23	left	20	32	0.62
29918	16.5	HC	HC	08/10/2010 11:57:00	51038	25/11/2011 14:01:27	battery	412	414	1
29919	15.5	HC	HC	08/10/2010 11:57:00	839	17/10/2010 13:34:57	died	10	10	1
29920	15	HC	HC	08/10/2010 11:57:00	78	10/10/2010 23:07:49	died	3	3	1
29921	16.5	HC	HC	08/10/2010 11:57:00	24207	20/10/2011 11:55:26	left	242	378	0.64
29922	17	HC	HC	08/10/2010 11:57:00	848	29/10/2010 22:30:44	left	22	22	1
29923	17	HC	HC	08/10/2010 11:57:00	2958	09/12/2010 15:37:12	left	61	63	0.97
29924	16	HC	HC	08/10/2010 11:57:00	1266	01/04/2011 12:05:27	left	38	176	0.22
29925	15	HC	HC	08/10/2010 11:57:00	1319	30/08/2011 14:19:55	left	43	327	0.13
29926	16.5	HC	HC	08/10/2010 11:57:00	1542	22/01/2011 20:03:42	left	82	107	0.77
29927	15.5	HC	HC	08/10/2010 11:57:00	585	17/10/2010 20:41:52	left	9	10	0.9
29928	16	HC	HC	08/10/2010 11:57:00	4	08/10/2010 13:37:21	died	1	1	1
29929	16.5	HC	HC	08/10/2010 11:57:00	2087	04/11/2010 10:11:03	left	28	28	1
29930	15.5	HC	HC	08/10/2010 11:57:00	546	13/10/2010 22:42:28	left	6	6	1
29931	16.5	HC	HC	08/10/2010 11:57:00	3264	26/01/2011 12:53:35	left	92	111	0.83
29932	16	HC	HC	08/10/2010 11:57:00	2259	22/10/2010 13:00:38	died	15	15	1
29933	18	BC	HC	08/10/2010 11:57:00	421	15/12/2010 19:40:39	left	5	69	0.07
29934	17	BC	HC	08/10/2010 11:57:00	28563	02/05/2011 23:35:05	left	194	207	0.94
29935	17	BC	HC	08/10/2010 11:57:00	964	26/10/2010 19:36:08	left	19	19	1
29936	17.5	BC	HC	08/10/2010 11:57:00	2775	17/11/2010 23:22:41	left	41	41	1
29937	16	BC	HC	08/10/2010 11:57:00	12111	01/05/2011 14:20:37	left	121	206	0.59
29938	17	BC	HC	08/10/2010 11:57:00	80	13/10/2010 18:45:45	left	6	6	1
29939	17	BC	HC	08/10/2010 11:57:00	6266	22/12/2010 17:44:40	left	71	76	0.93
29940	17.5	BC	HC	08/10/2010 11:57:00	4085	13/12/2010 10:48:35	left	67	67	1
29941	16	BC	HC	08/10/2010 11:57:00	1443	13/11/2010 08:54:22	left	16	37	0.43
29942	16	BC	HC	08/10/2010 11:57:00	575	14/10/2010 21:06:05	left	6	7	0.86
29943	16.5	BC	HC	08/10/2010 11:57:00	133	12/10/2010 19:16:06	left	4	5	0.8
29944	16.5	BC	HC	08/10/2010 11:57:00	459	13/10/2010 22:04:15	left	6	6	1
29945	16	BC	HC	08/10/2010 11:57:00	1137	04/11/2010 13:28:52	left	25	28	0.89
29946	17	BC	HC	08/10/2010 11:57:00	63	08/10/2010 20:59:32	left	1	1	1
29947	17.5	BC	HC	08/10/2010 11:57:00	2028	21/10/2010 13:00:15	died	14	14	1
29948	19	BC	HC	08/10/2010 11:57:00	3037	24/12/2010 18:29:25	left	75	78	0.96
29949	17	BC	HC	08/10/2010 11:57:00	334	16/10/2010 12:38:33	left	8	9	0.89
29950	16	BC	HC	08/10/2010 11:57:00	573	19/12/2010 18:48:42	left	20	73	0.27
29951	15	BC	HC	08/10/2010 11:57:00	287	12/10/2010 12:42:51	left	5	5	1
29952	15.5	BC	HC	08/10/2010 11:57:00	NA	NA	never	NA	NA	NA
29953	16.5	BC	HC	08/10/2010 11:57:00	685	26/11/2010 23:09:02	left	12	50	0.24

Table 3.A2. Tracking summary for 42 age 1 Greenland cod tracked in year 2 in Heffern's and Buckley's Coves. Sites of capture (origin) and release (release), standard length at release (SL), tracking period start, end, and length (TP), number of positions, fate (died/expulsion, left area, or battery expired), unique days detected (DD), and residency index (RI = DD/TP) are given for each individual.

Tag ID	SL	Origin	Release	Track start	Positions	Track end	Fate	DD	TP	RI
3962	15.5	BC	HC	23/11/2011 19:00:00	2512	08/01/2012 11:35:11	left	46	47	0.98
3963	17	BC	BC	23/11/2011 18:50:00	NA	NA	never	NA	NA	NA
3964	18	BC	HC	23/11/2011 19:00:00	14367	13/11/2012 11:47:46	left	279	357	0.78
3965	17	BC	HC	23/11/2011 19:00:00	22	28/11/2011 02:47:22	left	4	6	0.67
3966	19.5	BC	HC	23/11/2011 19:00:00	1540	07/12/2011 10:26:46	died	15	15	1
3967	NA	BC	BC	23/11/2011 18:50:00	141	18/12/2011 01:01:43	left	11	26	0.42
3968	16	BC	HC	23/11/2011 19:00:00	2	24/11/2011 01:36:24	left	2	2	1
3969	18	BC	HC	23/11/2011 19:00:00	854	13/06/2012 02:43:23	left	13	204	0.06
3970	16	BC	BC	23/11/2011 18:50:00	29	18/12/2011 12:06:27	left	4	26	0.15
3971	18	BC	BC	23/11/2011 18:50:00	2	23/11/2011 19:03:49	left	1	1	1
3972	16.5	BC	BC	23/11/2011 18:50:00	929	02/01/2012 14:04:58	left	36	41	0.88
3973	18	BC	BC	23/11/2011 18:50:00	409	25/01/2012 20:22:45	left	40	64	0.62
3974	17	BC	HC	23/11/2011 19:00:00	4684	17/05/2012 19:30:15	left	140	177	0.79
3975	17	BC	BC	23/11/2011 18:50:00	108	21/01/2012 05:53:31	left	25	60	0.42
4934	15	BC	BC	23/11/2011 20:02:00	1324	09/11/2012 14:25:35	left	105	353	0.3
4935	16	BC	HC	09/11/2011 19:07:00	477	15/11/2011 21:54:06	left	7	7	1
4936	15.5	BC	BC	23/11/2011 20:02:00	291	06/03/2012 11:32:50	left	45	105	0.43
4937	17	BC	HC	09/11/2011 19:07:00	6540	04/05/2012 21:32:15	left	95	178	0.53
4938	17.5	BC	BC	23/11/2011 20:02:00	23	03/12/2011 15:15:49	died	3	11	0.27
4939	18.5	BC	HC	09/11/2011 19:07:00	9	11/11/2011 15:15:48	left	2	3	0.67
4940	20	BC	BC	23/11/2011 20:02:00	452	23/07/2012 05:17:46	left	42	244	0.17
4941	17	BC	HC	09/11/2011 19:07:00	16124	14/05/2012 15:18:11	left	175	188	0.93
4942	16	BC	BC	23/11/2011 20:02:00	442	18/12/2011 16:06:12	left	22	26	0.85
4943	17.5	BC	HC	09/11/2011 19:07:00	283	08/10/2012 13:27:00	left	6	335	0.02
4944	17	BC	BC	23/11/2011 20:02:00	61	21/01/2012 16:03:34	left	13	60	0.22
4945	16.5	BC	HC	09/11/2011 19:07:00	9	09/11/2011 21:00:04	left	1	1	1
4946	16.5	BC	BC	23/11/2011 20:02:00	NA	NA	never	NA	NA	NA
4947	17	BC	HC	09/11/2011 19:07:00	2541	13/05/2012 11:50:32	left	86	187	0.46
4948	17	HC	BC	23/11/2011 20:02:00	NA	NA	never	NA	NA	NA
4949	15	HC	BC	23/11/2011 20:02:00	NA	NA	never	NA	NA	NA
4950	17.5	HC	HC	09/11/2011 20:12:00	484	22/11/2011 18:46:47	left	14	14	1
4951	17	HC	HC	09/11/2011 20:12:00	NA	NA	never	NA	NA	NA
4952	15	HC	BC	23/11/2011 20:02:00	40	17/12/2011 06:57:18	left	6	25	0.24
4953	19.5	HC	HC	09/11/2011 20:12:00	4	09/11/2011 21:09:50	left	1	1	1
4954	19	HC	BC	23/11/2011 20:02:00	NA	NA	never	NA	NA	NA
4955	18	HC	HC	09/11/2011 20:12:00	585	23/08/2012 09:46:21	left	16	289	0.06
4956	20	HC	HC	09/11/2011 20:12:00	44624	13/11/2012 12:40:08	left	296	371	0.8
4957	18	HC	BC	23/11/2011 20:02:00	3727	02/05/2012 21:26:43	left	36	162	0.22
4958	16.5	HC	BC	23/11/2011 20:02:00	NA	NA	never	NA	NA	NA
4959	18	HC	HC	09/11/2011 20:12:00	164	13/01/2012 10:11:24	left	10	66	0.15
4960	17.5	HC	BC	23/11/2011 20:02:00	NA	NA	never	NA	NA	NA
4961	17	HC	HC	09/11/2011 20:12:00	5	12/11/2011 05:55:29	left	2	4	0.5

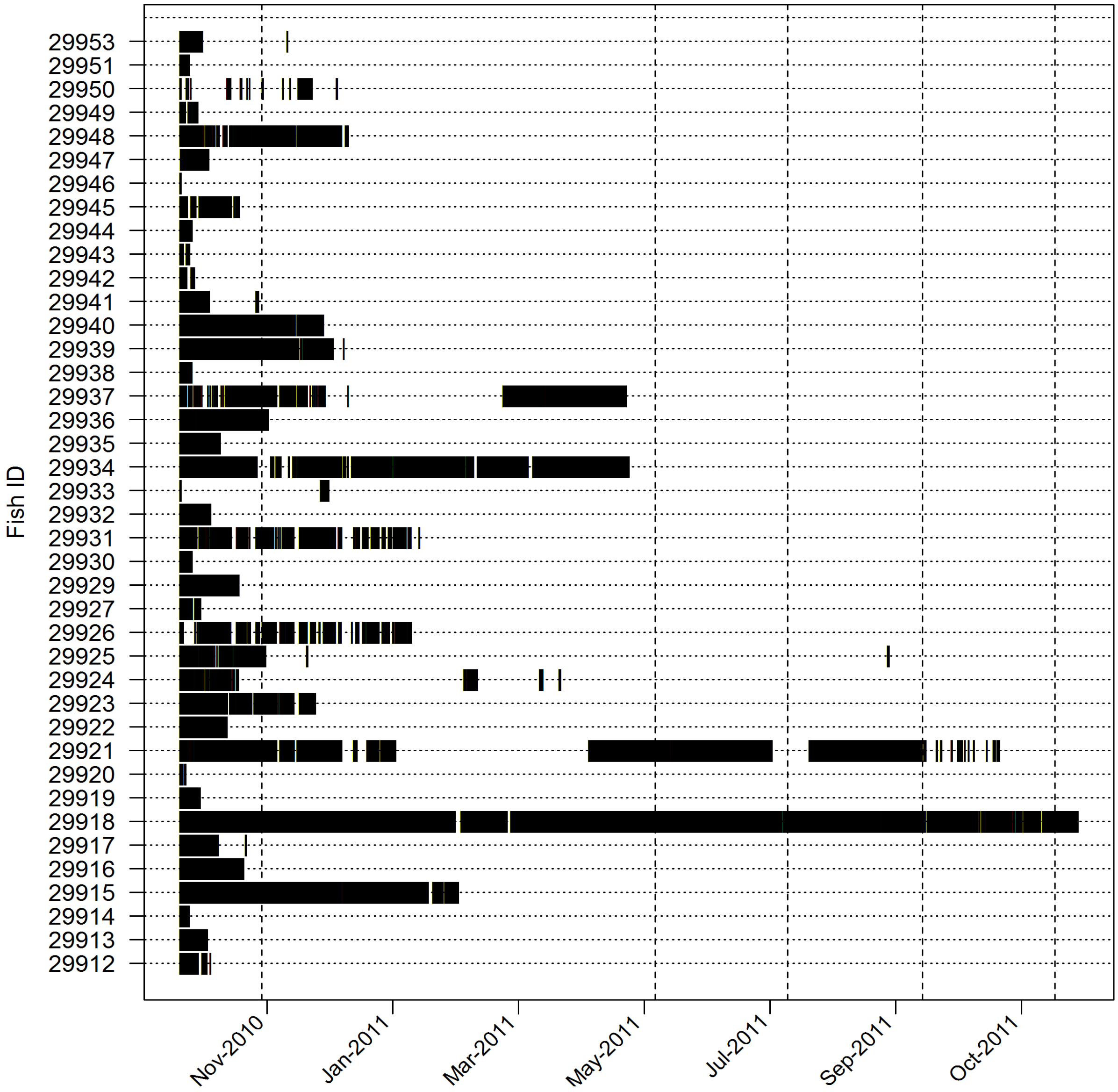


Fig. 3.A1. Positions over time for all individuals tracked in Year 1 (2010-2011) in Heffern's Cove. Positions with horizontal positioning error (HPE) greater than 6 units were removed.

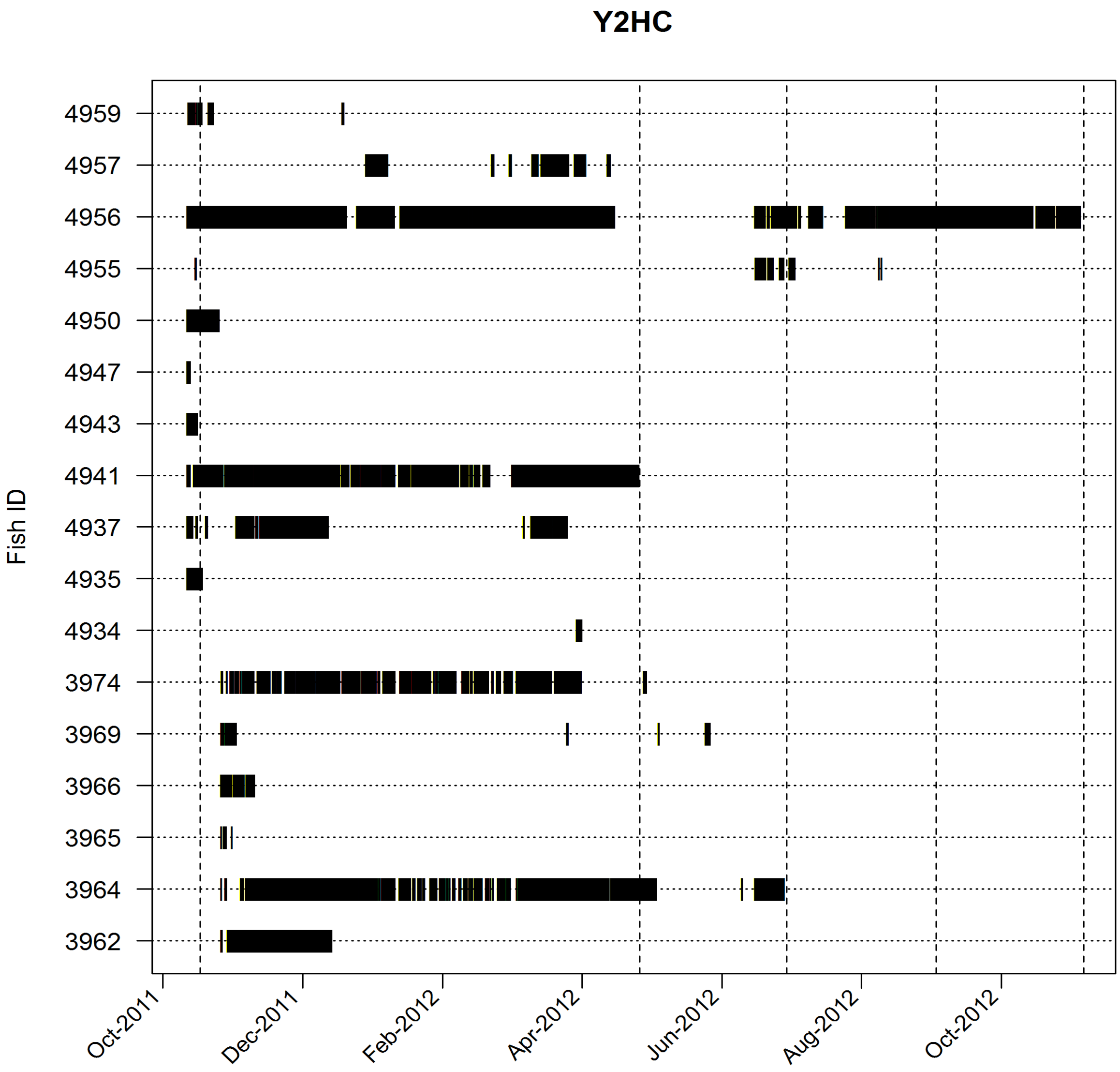


Fig. 3.A2. Positions over time for all individuals tracked in Year 2 (2011-2012) in Heffern's Cove. Positions with horizontal positioning error (HPE) greater than 6 units were removed.

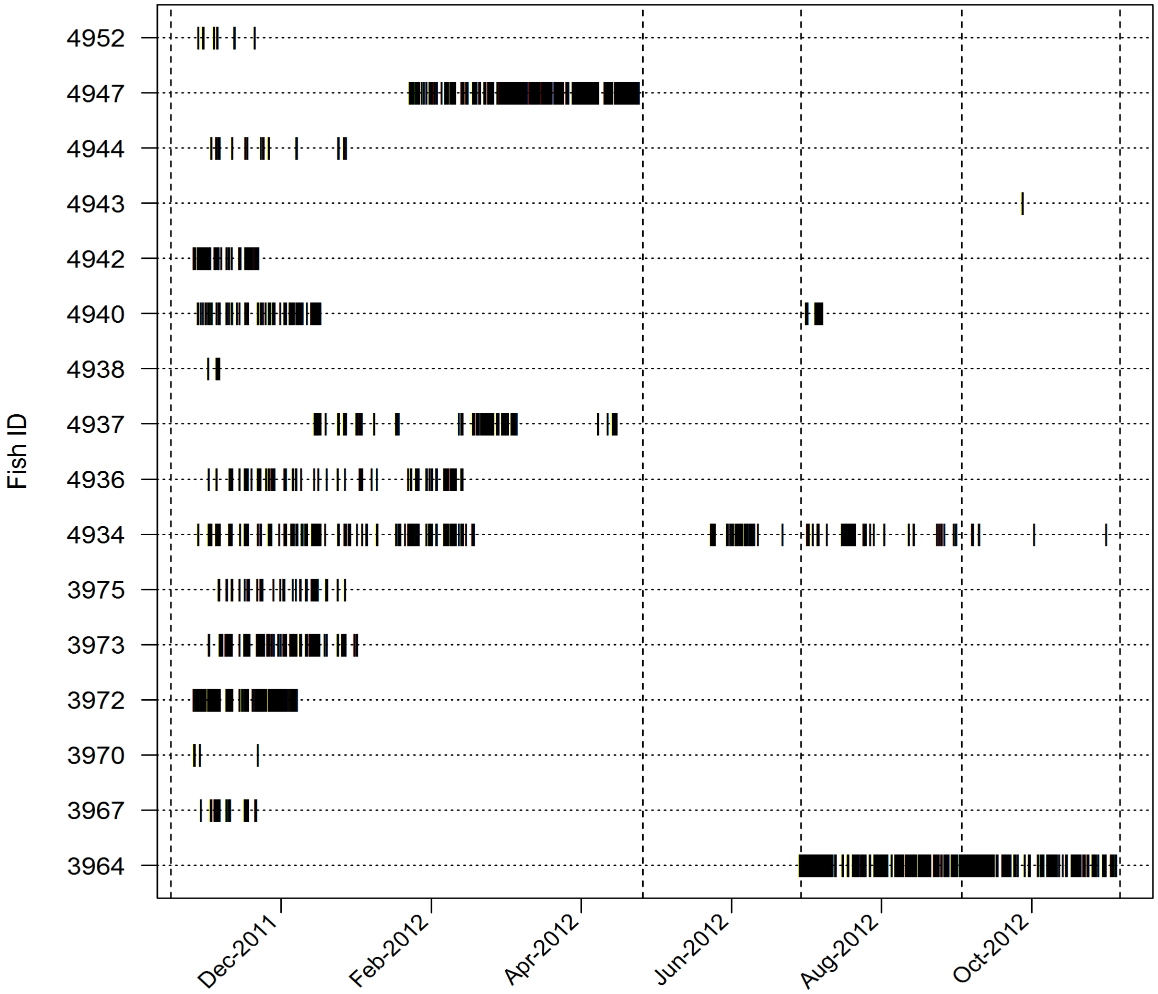


Fig. 3.A3. Positions over time for all individuals tracked in Year 2 (2011-2012) in Buckley's Cove. Positions with horizontal positioning error (HPE) greater than 6 units were removed.

Chapter 4: Summary

In my thesis research, I attempted to identify a suitable method for modelling home ranges of mobile organisms from large quantities of highly autocorrelated positional data characteristic of recent tracking methods, and to apply that model to acoustic telemetry data for examination of habitat use and movement patterns of age 1 Greenland cod in Newman Sound, Newfoundland, Canada. I used field-collected positional data to assess the accuracy, precision, and risks of type I and II statistical errors associated with minimum convex polygon (Mohr 1947), kernel density (Worton 1989), adaptive local convex hull (Getz et al. 2007), Brownian bridge (Horne et al. 2007), and dynamic Brownian bridge (dBB; Kranstauber et al. 2012) home range models. I found dBB home ranges provided the best balance of accuracy and precision with a low risk of both type I and II error. Using this model I determined age 1 Greenland cod shifted their use of habitat from eelgrass in the autumn to kelp in the winter. Activity levels were highest during crepuscular periods when individuals moved into the shallows at dusk and out of the shallows at dawn, and lowest at night when fish often became stationary or disappeared in frequently used resting sites. My results demonstrate an effective tool for accurately describing home ranges of fish tracked with acoustic telemetry, and fill a knowledge gap regarding the use of space by age 1 Greenland cod in a coastal nursery habitat. The approach I used is applicable to any autocorrelated tracking dataset, and addresses the current need for a home range model that can utilize the additional information inherent within high frequency datasets produced by recent GPS, radio telemetry, and acoustic telemetry techniques.

Model choice can significantly alter determination of home range results (Huck et al. 2008, Laver & Kelly 2008, Kie et al. 2010, Lichti & Swihart 2011, Walter et al. 2011). Most home range studies involve mammalian or avian species readily tracked by radio telemetry or

GPS tracking, which have relatively lower rates of missed transmissions (Laver & Kelly 2008). Furthermore, studies that compare home range methods generally use simulated data (Borger et al. 2006). Testing the performance of specific home range models on real field data is important, because some models are sensitive to the distribution of positions (Gitzen et al. 2006), and some models may not accurately simulate complex behaviours observed in the field (Borger et al. 2006). For example, fish in my study often "disappeared" over complex habitats at dusk only to "reappear" at the same position at dawn. They were also free to swim beyond the detection range of the hydrophone array. Further, my datasets demonstrated frequent irregular periods of absence. Datasets produced from acoustic telemetry positioning systems contain large quantities of autocorrelated data that are typical of most recent tracking techniques, but are unique in that they are also interspersed with frequent missed transmissions and periods of absence. The dBB model uses these autocorrelated positions to model paths, thereby eliminating the need to subsample until independence is achieved. This approach retains behavioural information captured by high frequency tracking that would otherwise be lost through subsampling (Horne et al. 2007). The dBB model also identifies changes in behaviour along a path (such as between resting and migration) and partitions the variance accordingly, making it more effective at accounting for changes in behaviour and more robust to missed transmissions and gaps in movement paths relative to the other models (Kranstauber et al. 2012).

A home range model inappropriate for the research question at hand will produce uninformative or, possibly misleading results (Powell & Mitchell 2012). For my own data, home range results varied widely by model type. When linked to habitat data, MCP and kernel density models indicated selection of terrestrial locations by juvenile fish, whereas the other models correctly showed no use of such "erroneous habitat". These type I errors could potentially decrease the ability of the model to detect an effect, or lead to inaccurate results. For example, had I chosen the MCP model for my analysis in Chapter 3, many individual home ranges would have included most of the study area. Since there would be little difference between the observed habitat proportions and what is available in the study site, the chances of detecting an effect would be low. Or worse, the inflated home ranges could include habitats that were never used (such as land), potentially leading to false conclusions (e.g., fish use terrestrial habitat) and type I errors. Differences between home range models can be attributed to each model's unique set of data requirements, assumptions, and biases, prompting some researchers to implement multiple models in single studies (e.g., Knickle & Rose 2014a; Pfeiffer & Meyburg 2015). While the use of multiple models could potentially be informative, I argue that it unnecessarily increases effort and computation time, and may produce contradictory results. Instead researchers should choose a single, defendable model *a priori* that best describes the aspects of spatial use of greatest interest to the researcher.

The ability to track animals over an extended periods of time facilitates the examination of temporal shifts in behaviour. Seasonal and diel patterns in movement and habitat use are often responses to changing resource availability or predation risk (Lima & Dill 1990). Although juvenile cod habitats such as eelgrass may offer increased food supply (Joseph et al. 2013), multiple studies show that predation risk, which increases with depth (Linehan et al. 2001), primarily drives the spatial distribution of juvenile cod (Laurel et al. 2003ab, Gorman et al. 2009, Thistle et al. 2010, Ryan et al. 2012). Given that juvenile cod move into progressively deeper waters with age (Gregory & Anderson 1997), the move must impart some benefit on individuals, such as enhanced feeding opportunities. An energetic or survival advantage worth occupying risky, but higher quality habitats, must exist. Either the fitness benefits offered by deeper habitats increase or the risk of predation must in some way decrease. Exploration of such phenomena was beyond the scope of my thesis research, but offer compelling questions nevertheless.

The shift from eelgrass-dominated habitat use in the fall to kelp-dominated use in the winter I observed likely represented a response to the decreased risk of predation brought on by the seasonal migration of older conspecifics to deeper water. However, it is unclear whether this habitat shift is seasonal or ontogenetic in nature, given that both occur concurrently. Individuals returning to eelgrass the following spring when older conspecifics return to the nearshore would suggest a seasonal response to the fluctuating risk associated with deeper kelp habitats. In contrast, juveniles remaining in kelp habitats in the spring, when older conspecifics return to the nearshore, would suggest an ontogenetic shift associated with individual size (or length) between juvenile habitats. Future research could address this question by tracking age 2 cod in the spring and summer to determine habitat associations.

In Newfoundland, Greenland cod and Atlantic cod use similar habitats at age 1 (Laurel et al. 2003a), allowing inferences to be drawn on the habitat use and movement patterns of both species. Although no fishery for Greenland cod has ever existed in Newfoundland, Atlantic cod were historically over-fished until the fishery collapsed in the 1990s (reviewed in Hutchings 1996). My findings are important because future adult population sizes depend directly on the survival of juveniles. Conservation measures with the goal of protecting future cod stocks should consider the home range extent and habitat requirements of juveniles, as well as seasonal and diel shifts in these patterns. In contrast to the current spreading of eelgrass in my coastal study area (Warren et al. 2010; Cote et al. 2013), global decline (reviewed in Duarte 2002) raises concerns regarding impacts on associated species. It is reasonable to expect that cod population recovery will require protection of juvenile habitat and the techniques outlined in this thesis offer a new approach to assessing that need.

As tracking technology continues to improve, transmitters are becoming smaller, batteries more efficient, and datasets increasingly large and detailed (reviewed in Kays et al. 2015). While the ability to follow individuals over long periods of time presents new opportunities to investigate long-term patterns of behaviour, they also present a new set of challenges. Autocorrelation, repeat locations, and the sheer quantity of data can cause statistical and computational problems for many well-established home range models (Horne et al. 2007, Urbano et al. 2010). My thesis demonstrates the ability of the dynamic Brownian bridge movement model to handle large quantities of high-frequency, high-resolution tracking data, while accurately representing fine-scale details such as movement corridors and changes in behaviour. These characteristics make the dBB model ideal not only for applications involving acoustic telemetry, but also any project that uses modern tracking techniques to follow mobile species over extended periods of time.

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