Niche partitioning in sympatric Greenland cod (*Gadus ogac*) and Atlantic cod (*Gadus morhua*) in coastal Newfoundland

By

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Dedication

This dissertation is dedicated to my parents

Thesis Abstract

Niche partitioning, the process by which evolutionary pressures divert competing species into different patterns of resource use, is often used to explain the coexistence of closely related species. In this thesis, I test the theory that niche partitioning facilitates the coexistence of two sympatric gadid species (Atlantic cod and Greenland cod) in a coastal region of Newfoundland using a multi-method approach.

Dietary and isotopic analyses were used to examine the degree of trophic niche overlap between species. Results revealed a general partitioning of food resources; *G. morhua* consumed more pelagic prey and showed a more pelagic (more negative) δ^{13}C signature while *G. ogac* consumed more benthic prey and had a more benthic (more positive) δ^{13}C signature. It was concluded that interspecific competition for prey resources and dietary overlap is low and that trophic niche partitioning is likely a key mechanism enabling coexistence.

Acoustic-radio telemetry was used to examine the spatial and temporal movement patterns of juveniles during summer. *G. morhua* were wider ranging, moved at faster rates and were active throughout the diel cycle compared to *G. ogac* of the same size suggesting spatial and temporal niche partitioning occurs between species during the summer season.

Fine-scale habitat use and vertical distributions were investigated using radio-acoustic positioning and habitat mapping. Both species preferred coarse substrates with moderate or dense vegetation, areas of low bathymetric relief and shallow (<10 m) water. *G. ogac* remained closer to the seafloor while *G. morhua* was generally distributed more pelagically and showed greater variation in vertical positioning. Results indicated high overlap in microhabitat use but differential use of vertical habitat which may reduce competitive interference between species.

Size-at-age and maturity data were used to compare growth rates and maturity patterns between species. Age and size at maturity were lower for *G. ogac* than for *G. morhua* despite similar growth rates. Length-weight relationships suggested slightly positive and negative allometric growth, for *G. ogac* and *G. morhua* respectively. It was concluded that differences in maturity patterns may promote coexistence by decreasing resource competition between species.

In summary, the findings from this thesis suggest that niche partitioning occurs along several niche dimensions which facilitate coexistence between ecologically similar Atlantic and Greenland cod in coastal waters of Newfoundland.

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Chapter 1. Introduction and Overview

This body of work tests theoretical assumptions about the coexistence of closely-related species. Studies of species coexistence and competitive interactions are essential to improving our understanding of the ecological principles governing ecosystem functioning (Holt 2001). Furthermore, comparative studies of sister-species are particularly useful for examining potential mechanisms underlying the diversification of a genus (Brooks and McLennan 1991; Holt 2001).

In Newfoundland and Labrador, Atlantic cod is a highly valued commercial species whose populations have undergone dramatic declines in the latter part of last century (Rose 2007). A better understanding of its ecology and the potential effects of interspecific competition are important for developing stock rebuilding strategies and for the management of all remaining stocks. Furthermore, this thesis comprises novel and previously unreported information on Greenland cod and its ecological role in coastal waters of Newfoundland.

This Chapter provides a short introduction to the theory of niche partitioning, a review of the ecology of Atlantic and Greenland cod and a synopsis of the work presented in this thesis.

1.1 Ecological Niche Partitioning

In community ecology, the term ecological niche describes an organism's position within an ecosystem with respect to its abiotic and biotic environments. This fundamental concept comprises the environmental conditions and resources necessary for an organism's survival as well as its functional role in its ecosystem (*sensu* Hutchinson 1957). Niche overlap is simply the common use of a resource, or resources by two or more species (Colwell and Futuyma 1971). According to basic principles of niche theory, complete niche overlap is not evolutionarily possible because competitive interactions for resources will inevitably result in the local extinction of one species (Volterra 1926; Lotka 1932; Gause 1934; Hutchinson 1957; MacArthur and Levins 1967). Niche partitioning (also referred to as niche segregation, niche separation, or niche differentiation), the process by which evolutionary pressures divert competing species into different patterns of resource use, has been widely used to explain the coexistence of similar species (e.g., Schoener 1974; Giller 1984; Ross 1986). Coexistence may arise from the segregation of *specific resources* (classical resource partitioning) or from differences in *when* (temporal resource partitioning) and *where* (spatial resource partitioning) resources are utilized (Pianka 1969; Schoener 1974; Ross 1986). In reality however, competing species often segregate along multiple niche dimensions (e.g., Pianka 1969; Schoener 1974; Ross 1986; Nagelkerken et al. 2006). Indeed, it has been suggested that the understanding of factors responsible for patterns in resource use and the role of resource partitioning in shaping ecological communities have been hampered by a focus on single factors (Hilborn and Stearns 1982).

Studies of coexistence and niche partitioning are widespread in the scientific literature. Theoretical, field and experimental studies across a wide variety of environments and taxa, including plants (see Silvertown 2004), microbes (e.g., Nyree and

Scanlon 1999; Sampayo et al. 2007; Hunt et al. 2008), invertebrates (e.g., Vance 1972; Albrecht and Gotelli 2001; Richardson and Hanks 2009), fish (see Ross 1986), amphibians and reptiles (see Toft 1985), birds (MacArthur 1958; Reynolds and Meslow 1984; Randler et al. 2010), and mammals (e.g., Arlettaz 1999; Stewart et al. 2002; Friedlaender et el. 2009), have demonstrated resource partitioning as the primary mechanism enabling coexistence. In his review of field studies on resource partitioning in fish assemblages, Ross (1986) found fish groups from a number of diverse habitats showed high separation of coexisting species along at least one resource dimension. In most habitats, including temperate marine systems, trophic separation was most important, followed by habitat separation and temporal separation. Many studies indicated that biotic interactions, such as competition and predation were important in producing the observed patterns, however, other factors such as differing tolerances to physical variables, environmental change and spatio-temporal resource availability were identified as potential sources of niche separation.

1.2 Biology and Ecology of Atlantic cod and Greenland cod

The family Gadidae includes some of the most economically valuable fish species in the world (e.g., Atlantic cod, pollock, whiting, saithe, haddock, hake). Gadids are mainly found in the circumpolar and temperate waters of the northern hemisphere where they inhabit coastal areas, continental shelves and slopes to depths of 1300 m (Scott and Scott 1988). The genus *Gadus* includes three species: Atlantic cod (*G. morhua*) in the North

Atlantic, and Alaska pollock [*G.* (= *Theragra*) *chalcogrammus*] and Pacific cod (*G. macrocephalus*) in the North Pacific. Greenland cod (*Gadus ogac*) was previously classified as a separate species but is now considered a genomically distinguishable subspecies of *G. macrocephalus* (Carr et al. 1999; Coulson et al. 2006). In coastal Newfoundland, *G. ogac* and *G. morhua* have overlapping geographic distributions and diets (Scott and Scott 1988; Rose 2007) (Figure 1.1). The two species are physically very similar, particularly as juveniles and appear to have similar life histories and habitat requirements (Figure 1.2). As competitive interactions are known to be stronger between morphologically similar and phylogenetically closely-related sympatric species (Schoener 1974), it has been suggested that competition for resources likely occurs (Cohen et al. 1990). However, very few studies on their potential competitive interactions exist.

1.2.1 Atlantic cod

The Atlantic cod (*Gadus morhua*) is found throughout the Northwest and Northeast Atlantic (Rose 2007). Cod are primarily demersal but can be found at mid-water and near the surface. They inhabit a range of marine habitats from shallow coastal waters to the edge of the continental shelf (Scott and Scott 1988). Distinct inshore and offshore stocks exist, however the delineation of sub-populations is not always clear and geographic distributions invariably overlap, particularly as cod undergo seasonal migrations (Brander 2005). Maximum size and age varies among stock location, however may reach 100 cm in length and live as long as 19 years (Rose 2007). Adult female cod are highly fecund,

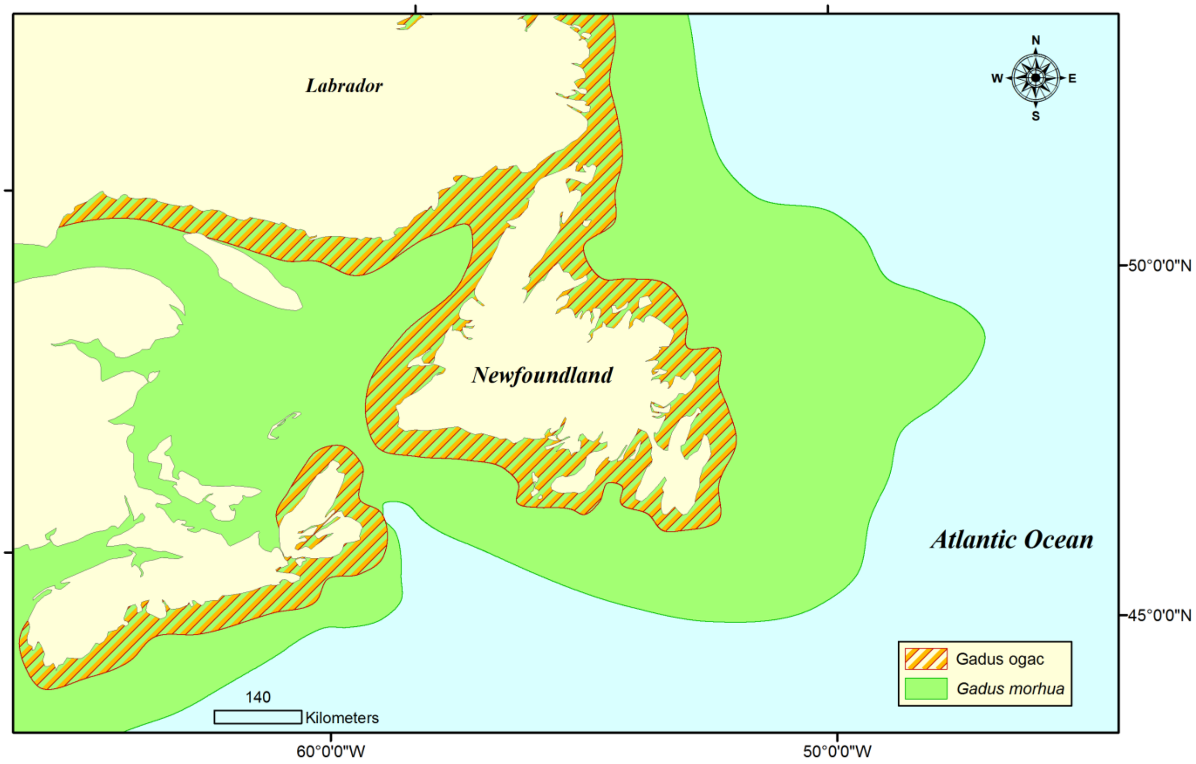

Figure 1.1 Distributions of Atlantic cod (*Gadus morhua*) and Greenland cod (*Gadus ogac*) in Atlantic Canadian waters (*adapted from Rose 2007*).

Figure 1.2 Juvenile Atlantic cod (*Gadus morhua*) (top) and Greenland cod (*Gadus ogac*) (bottom) collected from Smith Sound, Trinity Bay, Newfoundland in July 2010.

often releasing more than a million eggs over the spawning period. The tiny eggs (~1.5 mm in diameter) are semi-buoyant and ascend to the near-surface where they are dispersed by natural forces. As they grow, eggs and newly hatched larvae are often advected to coastal nurseries where pelagic larvae eventually settle to the seafloor where they grow and develop for the next couple of years. Young cod initially feed on zooplankton but shift to larger prey items and a more piscivorous diet as they grow. Juveniles begin to join adult seasonal migrations at three-four years of age and most reach sexual maturity at five-six years of age. Historically, cod was the most important fish species in the Northwest Atlantic, supporting a fishery for centuries. Newfoundland's 'northern cod' stock (NAFO subdivisions 2J and 3KL) was the most abundant - reaching a historical maximum of 3.5 million tonnes (Rose 2007). After a dramatic decline during the 1980's and early 1990's, a moratorium on commercial fishing was placed on most stocks. Although the northern cod stock abundance (and that of most stocks in Newfoundland) has increased in recent years, showing an expansion of age structure, and improved catch rates (DFO 2013), the stock remains at low levels and the directed fishery for northern cod remains minimal.

1.2.2 Greenland cod

The Greenland cod (often referred to as rock cod in Newfoundland) has very similar physical characteristics as the Atlantic cod but doesn't appear to grow as large reaching a maximum size of about 77 cm and 7.6 kg (Nielsen 1992). It is found from Alaska to West Greenland and further south to the Gulf of St. Lawrence in the Canadian Atlantic (Figure

1.1). It is predominantly coastal, is rarely found in deep water or offshore and does not undergo extensive migrations. It is an omnivorous predator feeding on crustaceans, annelids, molluscs, and fishes such as capelin and Arctic cod. *G. ogac* is thought to reach maturity at 2-4 years of age. Females spawn dermersal eggs that adhere to the substrate or vegetation. It is fished locally at small scales throughout its range and has been commercially exploited in West Greenland since the 1970's, although stock numbers were greatly reduced in the 1980s (Cohen et al 1990).

1.3 Thesis Overview

In this thesis, I evaluate the ecological differences between co-occurring Atlantic cod and Greenland cod in a coastal area of Newfoundland in order to test theoretical assumptions about their coexistence. In the first part of the thesis, I examine stomach contents and stable isotope signatures (δ^{13}C and δ^{15}N) of 47 Atlantic and 42 Greenland cod. It is proposed that the level of trophic overlap may reflect the degree of competitive interactions between species. Previous comparisons of dietary habits and trophic overlap have yielded conflicting results (Chaput 1981; Nielsen and Anderson 2001) but have not examined long-term diet through stable isotopic analysis. I test the null hypotheses of no difference between prey species, feeding styles (benthic or pelagic) and trophic position within the ecosystem. Observed differences in short- and long-term dietary habits in the context of inter-specific competition and species coexistence are discussed.

In Chapter 3, I examine and compare home range estimates, residency rates, rates of movements and temporal activity patterns for 10 Atlantic cod and 10 Greenland cod during the summer season using spatial analyses of radio-acoustic telemetry data. Working null hypotheses were that no differences would be measured in: 1) home range, 2) rates of movement, and 3) temporal activity patterns. Observed differences and similarities in movement patterns are discussed in relation to environmental conditions, morphology, foraging and predator avoidance.

In Chapter 4, I investigate microhabitat partitioning using substrate and bathymetric slope selection patterns and vertical distributions derived from a combination of habitat maps and radio-acoustic positioning. I test the hypotheses that both species would select for similar habitat types and show a preference for coarse substrates and areas with macroalgae while avoiding open areas and fine substrates. I also test the hypothesis that *G. ogac* would be more benthically distributed as compared to more pelagic distributions of *G. morhua*. Environmental and behavioural factors contributing to observed similarities in substrate selection as well as differences in vertical distribution are discussed.

In Chapter 5, I use size-at-age data from otolith readings and maturity estimates from examination of gonad condition to compare growth and maturity rates between species. The hypotheses that Atlantic cod grow larger and reach maturity at a later age are tested. Similar growth rates and different maturity rates observed are discussed with respect to environmental factors and variations in life history strategies.

In the final part of the thesis, I provide a summary of the results and conclusions from each chapter and discuss functional explanations for the behaviours observed, study limitations and directions for future research.

1.4 Co-authorship Statement

I am the major intellectual contributor and principal author of all chapters presented in this thesis. I was responsible for the design and implementation of the field research, as well as data analysis and manuscript preparation. Dr. George Rose is second author on all papers, and provided conceptual suggestions and aid during all stages of the thesis, including editorial comments on previous drafts.

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Chapter 2. Dietary niche partitioning in sympatric gadid species in coastal Newfoundland: evidence from stomachs and C-N isotopes

Abstract

The feeding habits of two co-occurring gadid species Atlantic cod (*Gadus morhua*) and Greenland cod (*Gadus ogac*), in coastal waters of Newfoundland, were examined using stable isotopes (δ^{13}C and δ^{15}N) and stomach content analysis. The results indicated little dietary niche overlap and interspecific competition for food resources despite similar trophic levels. Both species consumed a variety of invertebrates and fish but showed a preference for different prey items. Polychaetes, fish and small crustaceans dominated *G. ogac* stomach contents while small crustaceans, in particular hyperiid amphipods and fish, dominated those of *G. morhua*. In general, *G. morhua* consumed more pelagic prey and had a significantly more pelagic (more negative) δ^{13}C signature while *G. ogac* consumed primarily benthic prey and had a more benthic (more positive) δ^{13}C signature. δ^{15}N levels were similar in these species suggesting similar trophic positions, with levels increasing with fish length in both species. Dietary overlap was not significant in both stomach and stable isotope analyses. We conclude that interspecific competition for food is low between *G. ogac* and *G. morhua* and is unlikely to be a factor in the slow rebuilding of Atlantic cod in this region.

2.1 Introduction

Despite the coexistence of similar species across many taxa, the basic principles of niche theory suggest that complete niche overlap is not evolutionarily possible (Gause 1943; Hutchinson 1957; Hardin 1960). Niche partitioning (Levins 1968; MacArthur 1972) (also termed *niche differentiation* or *niche segregation*), the process by which competing species evolve different forms of resource use is a fundamental process in community ecology and has been widely used to explain the coexistence of similar species (Schoener 1974; Giller 1984; Ross 1986). Coexistence may arise from the segregation of *specific resources* (classical resource partitioning) or from differences in *when* (temporal resource partitioning) and *where* (spatial resource partitioning) resources are utilized (Pianka 1969; Schoener 1974; Ross 1986). In fish assemblages, partitioning of food resources is often the principal mechanism of niche segregation (Gascon and Leggett 1977; Gerking 1994).

In coastal Newfoundland, the closely related gadids Greenland cod (*Gadus ogac*) and Atlantic cod (*Gadus morhua)* are opportunistic predators with overlapping geographic distributions (Scott and Scott 1988). Juveniles of both species are common nearshore inhabitants and found intermixed in most bays (Rose 2007) and there is a long-standing view that competition is likely between the two species (Cohen et al. 1990). Since the early 1990s, *G. morhua* stocks around Newfoundland have been in a depleted state (for much longer further north off Labrador) (Rose 2007). There are little data to assess changes in *G. ogac* stocks, but *a priori* inference would suggest less or no change, as unlike *G. morhua, G. ogac* is a cold water species (McAllister 1977) and would not have been negatively influenced by the cold conditions of the early 1990s. In addition, *G. ogac* were never commercially harvested. Local knowledge of fishermen along the Newfoundland coast tends to support this inference (pers. comms.). Feeding competition between these species in inshore waters, where most juvenile *G. morhua* (Lear et al. 1980; Dalley and Anderson 1997; Methven and Schneider 1998) and all *G. ogac* reside (Scott and Scott 1988; Mikhail and Welch 1989), could help explain the slow rebuilding of depleted *G. morhua* stocks over the past decades, but few data existed to test this hypothesis.

Despite its historic commercial importance, the feeding ecology of older *G. morhua* juveniles (ages-2-4) in coastal areas of Newfoundland is poorly known. Clark and Green (1990) examined their diel activity patterns in Conception Bay using sonic telemetry and inferred that the higher activity rates observed were related to feeding, but provided no information on prey selection. Studies on age 1-2 juveniles in Conception Bay yielded differing results: Keats et al. (1987) found small (< 12.5 cm) juveniles fed on pelagic prey and larger (16 – 23.5 cm) juveniles fed on benthic organisms whereas Keats and Steel (1992) reported that all juveniles (< 23.5 cm) consumed mainly pelagic crustaceans.

Previous studies of diet overlap between *G. morhua* and *G. ogac* further north have yielded conflicting results. Feeding patterns from two inshore locations in southern Labrador suggested that the two species had dissimilar diets (Chaput 1981). In contrast, substantial overlap in diets was reported from West Greenland by Nielsen and Andersen (2001). In coastal Newfoundland, no comparisons of diet overlap have been made.

Studies of dietary resource partitioning in co-occurring or closely related fish have typically used stomach content analysis to examine dietary overlap (e.g., Grossman 1986; Garrisson 2002; Corrêa 2009). This method offers several benefits: stomachs samples are relatively easy to collect and prey items can be identified often to species and life stage. However, stomach analyses provide only a "snapshot" of dietary habits, often with many empty stomachs, and may also show bias toward prey items with lower digestion rates (Hyslop 1980). In contrast, stable isotope (δ^{13}C and δ^{15}N) signatures reflect biologically integrated nutrients in the diet over a long time period - up to several months for muscle tissue (Peterson and Fry 1987; Lorrain et al. 2002). Hence, isotope analysis identifies the longer term feeding habits of an individual, no matter their last meal. Used in conjunction, these methods provide a more complete representation of an organism's dietary habits.

In this study, our objective was to compare the feeding habits of *G. morhua* and *G. ogac* in coastal Newfoundland and quantify dietary overlap using both stomach content and stable isotope analyses. The degree of overlap in dietary resources was expected to reflect the amount of interspecific feeding competition between these co-occurring species. Working null hypotheses were that *G. morhua* and *G. ogac* would not differ in: 1) diet, 2) pelagic and benthic oriented feeding, and 3) trophic position within the coastal ecosystem.

2.2 Methods

2.2.1 Collection of Samples

Forty-seven mostly juvenile *Gadus morhua* and 42 *Gadus ogac* of comparable sizes (17-63 cm) were caught by hook and line over several (2-7) days in July of 2009 and 2010 from a small research vessel (*RV Gecho II*) within an area of approximately 2.5 ha near Petley Beach in Smith Sound, Trinity Bay, Newfoundland (Figures 2.1 and 2.2). Forty-one fish (20 *G. ogac* and 21 *G. morhua*) were collected in 2009 and 48 fish (22 *G. ogac* and 26 *G. morhua*) were collected in 2010. Water depths at the site varied from <1 m to >40 m; most fish were caught within 1-2 meters of the bottom. All fish were put on ice onboard the vessel and later sampled for total length, weight, sex, and reproductive stage. Stomachs were removed, weighed and frozen for later analysis and a small sample (1-2 cm^2) of dorsal muscle tissue posterior to the head was removed and frozen for stable isotope analysis.

2.2.2 Stomach Contents Analysis

Stomachs contents were sorted and identified to species or nearest taxonomic level, with weights recorded to the nearest 0.01 g. Cumulative prey curves were used to judge if n was sufficient to effectively describe diet compositions (Hoffman 1979; Cailliet et al. 1986; Cortés 1997). The order in which stomachs were analyzed was randomized 10 times and the mean number of new prey items found consecutively in the stomachs plotted against the number of stomachs that contained prey. Linear regressions were then performed on the last four points of the curve to assess if an asymptote had been reached

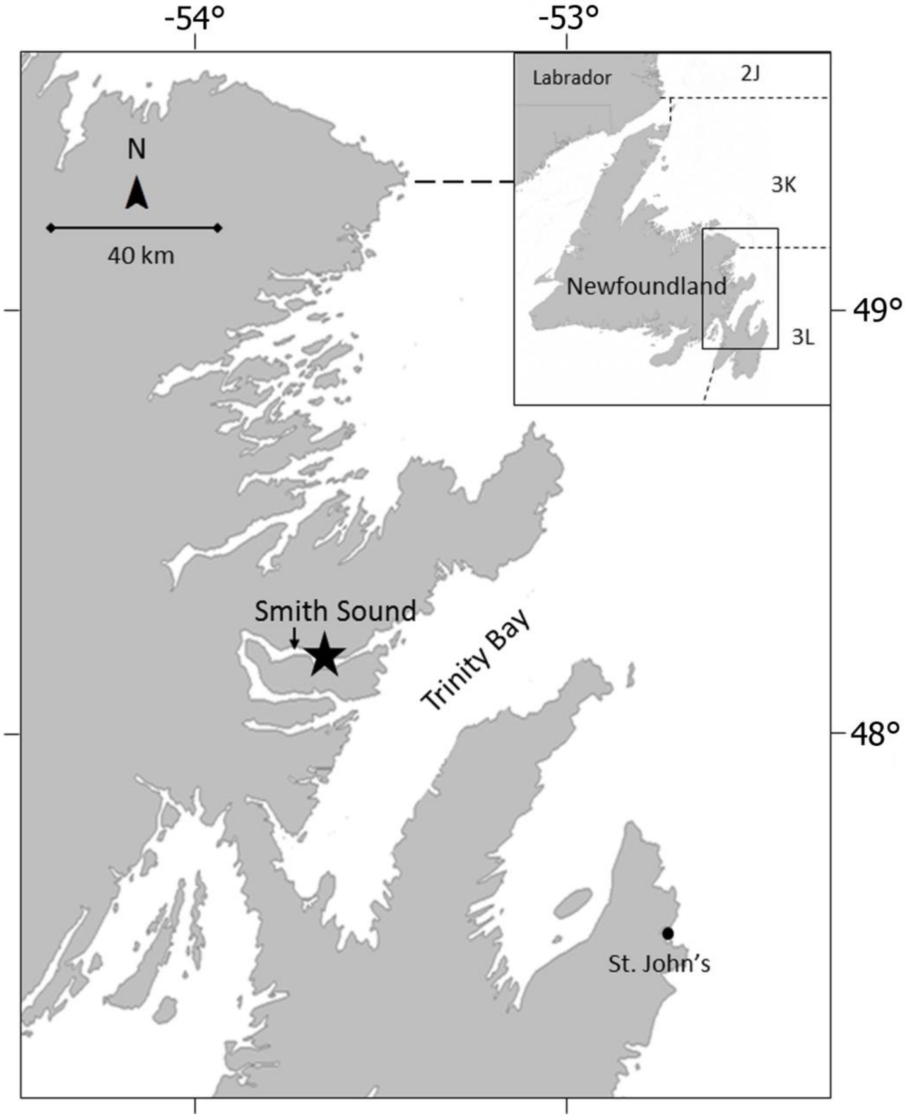

Figure 2.1. Map of the Eastern portion Newfoundland showing location of sampling area (black star) within Smith Sound. Inset shows position of enlarged map relative to the Island of Newfoundland and NAFO Divisions 2J, 3K and 3L.

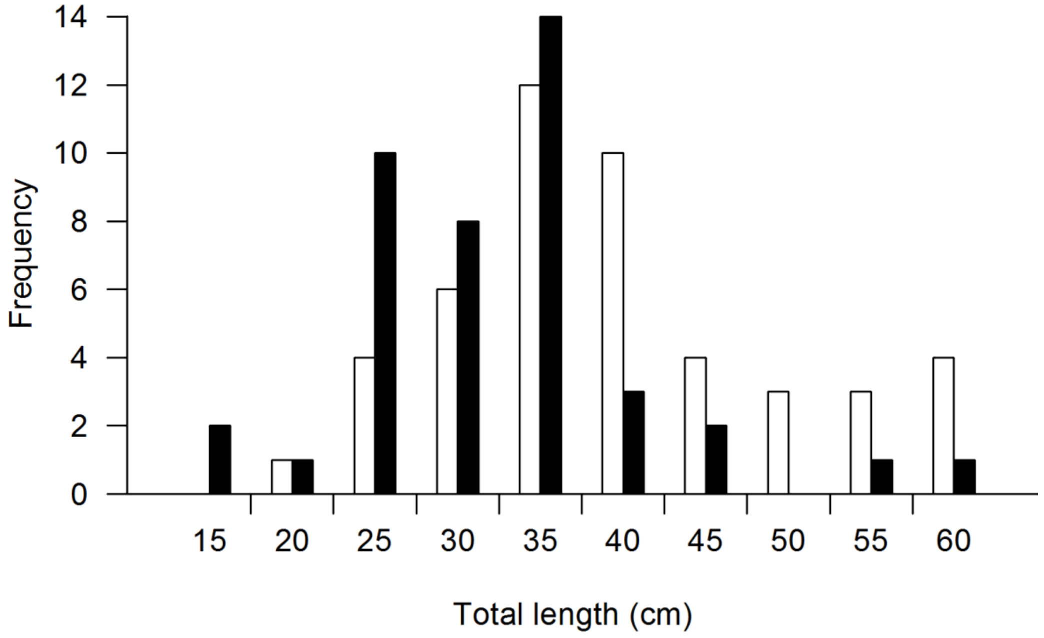

Figure 2.2. Size frequency distribution of sampled fish. Black bars = *G. ogac*; open bars = *G. morhua*.

(*sensu* Bizzarro et al. 2007). If the slope did not differ significantly from 0 (i.e., p >0.05), the curve was considered to have reached an asymptote with n adequate to describe diet.

The relative quantity of stomach contents and relative importance of individual prey types were assessed using the following indices: 1) relative frequency of occurrence (FO%) = number of stomachs with prey item, i, as a percentage of the total number of stomachs, 2) relative gravimetric abundance (W%) = total weight of prey item i, as a percentage of the weight of total stomach contents summed for all fish, 3) mean total fullness index (TFI) = $\frac{1}{n}\sum_{f=1}^{n}(\text{weight of stomach contents of fish} f/(\text{length of fish} f)^3) \times 10^4$, and 4) mean partial fullness index (PFI) = $\frac{1}{n}\sum_{f=1}^{n}(\text{weight of prey item}, i, \text{in fish} f/(\text{length of fish} f)^3) \times 10^4$, where n is the number of stomachs examined, weight is in 0.1 g and fish length is in cm. Niche breadths for each species were estimated using Levins' standardized index (Levins 1968; Hurlbert 1978; Krebs 1989): $B = 1/(n\sum p_{xi^2})$, where p_{xi} is the proportion of species x using prey item i, and n is the number of prey items available. Prey items available included all prey species identified in the study and availability was assumed to be the same for both species and size classes. B ranges from $1/n$ (use of a single resource) to 1 (equal usage of resources). Dietary niche overlap between species was assessed with Schoener's (1970) overlap index: $C = 1 - 0{\cdot}5\,(\sum|p_{ix} - p_{iy}|)$, where p_{ix} and p_{iy} are the proportions by weight of prey item i in the diets of species x and species y, respectively. Index values range from 0 to 1, with 0 representing no overlap and 1 representing complete overlap and values ≥0.6 generally considered biologically significant (Wallace 1981).

Food items were also classified into pelagic, suprabenthic and benthic categories based on studies of the prey taxa and previous cod diet studies (e.g., Scott and Scott 1988; Parrish et al. 2009). To compare the relative importance of prey categories, the gravimetric abundance (W%) for each prey category was calculated for all individuals and tested statistically for differences between species using a Kruskal-Wallis test.

A one-way analysis of similarity (ANOSIM) (Clarke 1993) of gravimetric abundance (W%) and frequency of occurrence (FO%) of prey items for each individual was used to assess dietary differences between species. The proportion by mass of each prey item in the stomach contents of each individual was used to calculate gravimetric abundance (W%) while the presence or absence of each prey item was used to determine frequency of occurrence (FO%). Prior to analysis, data were square-root transformed and used to construct a Bray-Curtis similarity matrix. Similarity percentages (SIMPER) analysis was used to identify which prey categories contributed most to dissimilarities between species (Clarke 1993). Both ANOSIM and SIMPER were performed using PRIMER 6 software (Clarke and Gorley 2006).

2.2.3 Stable Isotope Analysis

Dorsal muscle tissue samples were thawed, dried to constant weight (48 h at ~80° C in a drying oven), crushed to a fine powder using a mortar and pestle and sent to the CREAIT Network Stable Isotope Lab Facility at Memorial University of Newfoundland. Stable carbon and nitrogen isotope ratios and elemental determinations for each sample were determined by analysis of CO^2 and N^2, respectively, produced by combustion using a

Carlo Erba NA1500 Series II Elemental Analyser followed by gas chromatograph separation and online analysis by continuous-flow mass spectrometer. Stable carbon and nitrogen ratios were expressed in delta (δ) notation, defined as the parts per thousand (‰) differences from a standard material: $\delta X = \left[\left(R_{sample}/R_{standard}\right) - 1\right] \times 10^3$, where δ = the measure of heavy to light isotope in the sample, X = ^{13}C or ^{15}N and R = the corresponding ratio (^{13}C/^{12}C or ^{15}N/^{14}N). International Standard references are Vienna Pee Dee Belemnite (VPDB) for carbon, and atmospheric N_2 for nitrogen.

To estimate trophic niche breadth and structure, quantitative metrics based on the position of individuals in trophic niche space developed by Layman et al. (2007) and described by Jackson et al. (2011) were applied at the population level using individuals as measurement units. Metrics were calculated using the Stable Isotope Analysis in R (SIAR) package (Parnell et al. 2008) for R statistical computing package (R Development Core Team 2007) and are briefly defined as follows: 1) δ^{15}N Range (NR): a measure of degree of trophic diversity calculated as the distance between the most enriched and most depleted δ^{15}N values for a given species or group; 2) δ^{13}C Range (CR): distance between the highest and lowest δ^{13}C which indicates the variability of food sources consumed; 3) Standard Ellipse Area (SEA): a measure of the total trophic niche breadth for a given species or group; 4) Mean distance to centroid (CD): average Euclidean distance of each individual to the mean δ^{13}C and δ^{15}N value which provides a measure of the average degree of trophic diversity within a species or group; 5) Mean nearest neighbour distance (MNND): mean of the Euclidean distances to each species' nearest neighbour in bi-plot space which provides a measure of the overall density of species packing (i.e., a group comprised of many individuals with similar trophic ecologies would show a smaller MNND than a group in which individuals are more varied in terms of their trophic niche); 6) Standard deviation of nearest neighbour distance (SDNND): a measure of the evenness of species packing in bi-plot space with lower SDNND values suggesting a more even distribution of trophic niches.

Stable isotope ratios (δ^{13}C and δ^{15}N) and metric data (CD, MNND, and SDNND) were tested for normal (Gaussian) distribution using probability plots and frequency distributions and non-normal data were transformed using the Johnson transformation tool in Minitab 16. Between species differences in metrics and effect of body size on δ^{13}C and δ^{15}N values were evaluated using *t*-tests and regression analysis, respectively. Trophic niche overlap was estimated as the percent of overlapping SEA between species.

2.3 Results

Stomachs of *G. morhua* and *G. ogac* contained a substantial variety of prey items (Table 2.1). Cumulative prey curve regressions on the last four measures for both species had slopes that did not differ from 0 (regression, t = 3.66, p = 0.07 for *G. morhua* and t = 2.54, p = 0.13 for *G. ogac*) (Figure 2.3).

2.3.1 Stomach Contents

Indices of relative importance (FO%, W%, and PFI) for all prey items (Table 2.1) indicated that for *G. ogac,* polychaetes and mysids/euphausiids were the dominant prey

Table 2.1 Importance of all prey items based on frequency of occurrence (FO%), relative weight (W%), and mean partial fullness (PFI) for G. ogac and G. morhua. Prey types: B = benthic; SB = suprabenthic; P = pelagic. Bold values indicate maximums for each index.

		Gadus ogac (n=42; size range=17-60 cm)			*Gadus morhua* (n=47; size range=21-63 cm)		
Prey Item	Prey type	FO (%)	W (%)	Mean PFI	FO (%)	W (%)	Mean PFI
Invertebrates							
Ophiuroidea	B	0.0	0.0	0.000	2.1	0.3	0.005
Polychaeta	B	28.6	**36.5**	**0.797**	8.3	0.3	0.011
other annelids	B	0.0	0.0	0.000	4.2	19.1	0.136
All annelids	B	28.6	36.5	0.797	12.5	19.4	0.148
Bivalvia	B	2.4	0.0	0.000	0.0	0.0	0.000
Hyperiidae	P	2.4	0.1	0.002	62.5	**38.7**	**0.406**
other amphipods	P	4.8	0.9	0.021	6.3	0.0	0.000
All amphipods	P	7.1	1.0	0.023	68.8	38.7	0.406
Idotea balthica (Isopoda)	B	2.4	0.1	0.001	0.0	0.0	0.000
Mysidae	SB	2.4	2.9	0.071	8.3	0.1	0.002
Euphausidae	SB	11.9	8.6	0.165	37.5	5.4	0.114
Mysidae and/or Euphausiidae	SB	35.7	1.8	0.026	20.8	2.5	0.066
All mysids/euphausiids	SB	**50.0**	13.3	0.262	**66.7**	8.0	0.182
Pandalus montagui	B	0.0	0.0	0.000	2.1	0.1	0.002

Table 2.1 (continued)

Eualus fabricii	B	2.4	0.4	0.010	0.0	0.0	0.000
Spirontocaris sp	B	0.0	0.0	0.000	2.1	0.1	0.001
Sabinea sarsi	B	2.4	4.8	0.034	0.0	0.0	0.000
Hyas coarctatus	B	0.0	0.0	0.000	2.1	0.2	0.010
Hyas sp	B	0.0	0.0	0.000	0.0	0.0	0.000
Pagurus sp	B	0.0	0.0	0.000	6.3	0.4	0.016
All decapods	B	4.8	5.2	0.043	12.5	0.8	0.029
Fish							
Clupea harengus	P	0.0	0.0	0.000	2.1	0.0	0.000
Mallotus villosus	P	0.0	0.0	0.000	2.1	0.2	0.002
Gadus morhua	B	4.8	20.0	0.107	4.2	16.5	0.104
Gadus ogac	B	0.0	0.0	0.000	2.1	7.2	0.040
Gadus sp	B	0.0	0.0	0.000	2.1	2.1	0.012
Myoxocephalus sp	B	4.8	5.8	0.075	0.0	0.0	0.000
Myoxocephalus scorpius	B	2.4	0.1	0.001	0.0	0.0	0.000
Ulvaria subbifurcata	B	4.8	2.3	0.024	2.1	0.5	0.012
Stichaeus punctatus	B	2.4	0.1	0.001	2.1	1.2	0.033
Lumpenus maculatus	B	2.4	0.7	0.002	0.0	0.0	0.000
Unidentified fish	-	9.5	3.4	0.022	12.5	5.1	0.045
All fish	-	31.0	32.3	0.232	29.2	32.8	0.248
Other							
Stone	-	7.1	1.4	0.013	2.1	0.0	0.000
Unidentified organic material	-	2.4	9.1	0.064	2.1	0.0	0.001
Plant material/seaweed	-	9.5	1.0	0.010	4.2	0.0	0.000
N (%) of empty stomachs			10 (23.8%)			2 (0.04%)	

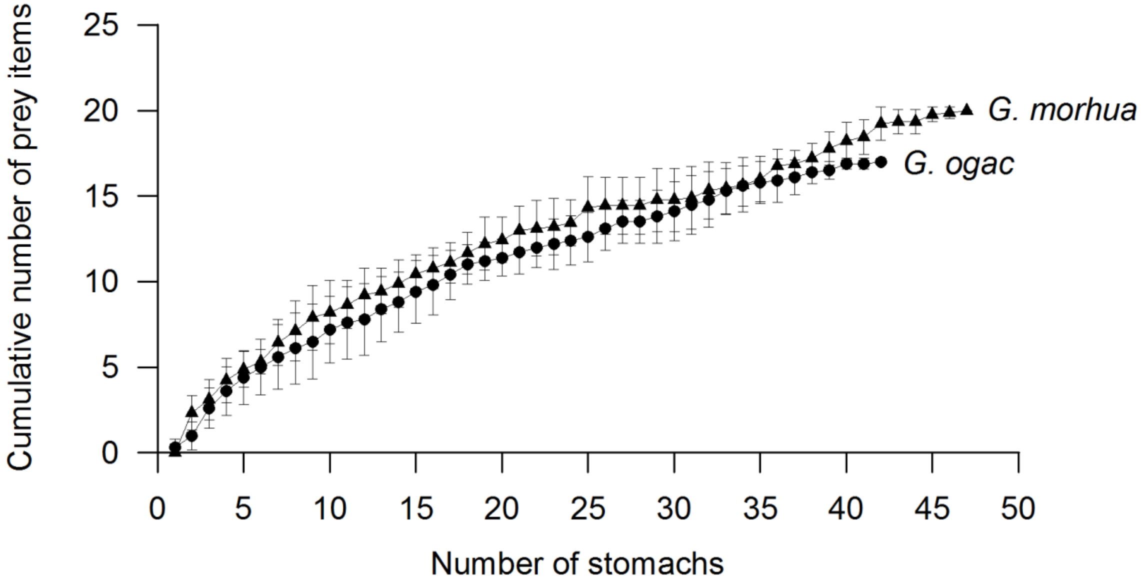

Figure 2.3 Cumulative prey curves for *G. ogac* (●) and *G. morhua* (▲). Symbols show the mean cumulative number of prey items per stomach sampled and error bars indicate SD.

items, occurring in 28.6% and 50% of stomachs and making up 36.5% and 13.3% of the total diet by weight. Polychaetes and mysids/euphausiids also had the highest PFI values at 0.797 and 0.262, respectively. Unidentified bony fish was the next most important prey item by frequency of occurrence (9.5%) while *G. morhua* had the next highest relative weight (20%) and PFI value (0.107).

In the stomachs of *G. morhua*, mysids/euphausiids and hyperiids had the highest frequency of occurrence (FO%) (mysids/euphausiids = 66.7%; hyperiids = 62.5%) and PFI values (mysids/euphausiids = 0.182; hyperiids = 0.406) while hyperiids and polychaetes had the highest relative weights at 38.7% and 19.4%, respectively. Annelids (12.5%) and polychaetes (12.5%) had the next highest frequency of occurrence while *G. morhua* had the next highest relative weight (16.5%) and PFI (0.104) values.

G. morhua had significantly higher proportions by weight of pelagic prey items in their diet than *G. ogac* (Kruskal-Wallis, $H = 28.8$, $p < 0.01$) (Figure 2.4). This was attributed almost entirely to the high relative weight of hyperiids in the stomachs of *G. morhua* (Table 2.1). In comparison, *G. ogac* had a higher relative abundance of benthic prey items (Kruskal-Wallis, $H = 5.25$, $p = 0.02$) (Figure 2.4). No significant difference between species was found for the suprabenthic prey category (Kruskal Wallis, $H = 1.27$, $p = 0.26$) (Figure 2.4).

Total fullness (TFI) values were somewhat higher for *G. ogac* than for *G. morhua* but did not differ significantly between species (Kruskal Wallis, $H = 0.13$, $p = 0.72$) (Table 2.2). *G. ogac* had a significantly higher niche breadth index than *G. morhua*

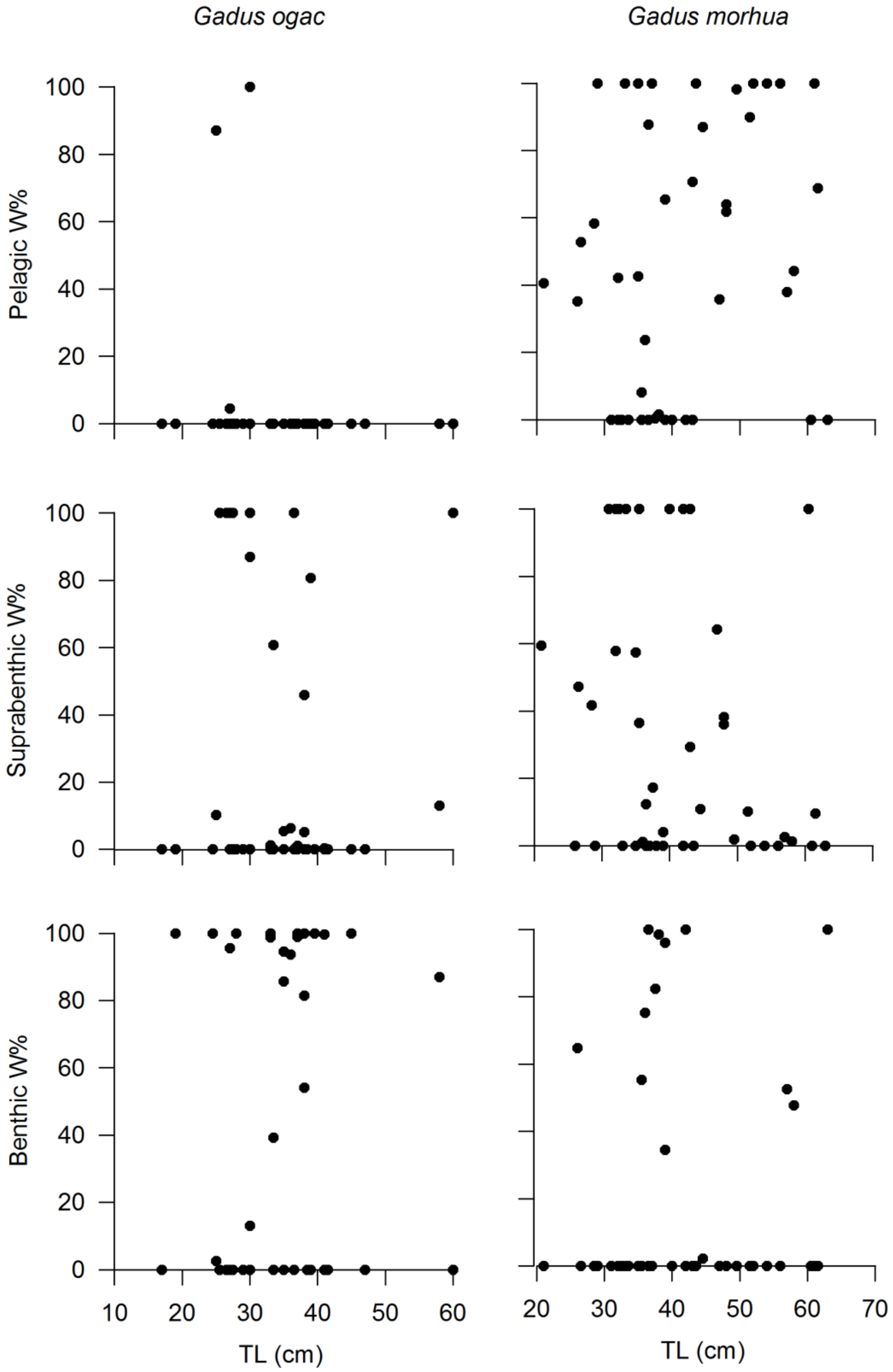

Figure 2.4 Plots of relative gravimetric abundance (W%) of pelagic, suprabenthic and benthic prey categories by fish length (cm) for *G. ogac* and *G. morhua.*

Table 2.2 Mean total fullness index (TFI), dietary niche breadth (*B*) (Levins 1968) and dietary overlap (Schoener 1970) for *G. ogac* and *G. morhua*.

Species	n	Mean TFI (± SE)	Dietary Breadth (*B*)	Niche Overlap (*C*)
G. ogac	42	1.45 ± 0.34	0.14	0.28
G. morhua	47	1.02 ± 0.31	0.06	

(Kruskal Wallis, H = 11.25, $p < 0.01$) and low (C = 0.28) overlap in diet was found between species (Table 2.2).

ANOSIMs showed significant differences in diet composition between *G. ogac* and *G. morhua* by both gravimetric abundance (W%) (R = 0.243 $p < 0.01$) and frequency of occurrence (FO%) (R = 0.227, $p < 0.01$) (Table 2.3). Results from SIMPER analyses revealed high average dissimilarity between species (W%: 93.3% dissimilarity; FO%: 90.3%) with hyperiids euphausiids, mysids/eupausiids and polychaetes contributing most to the dissimilarity for both dietary indices (Table 2.3).

2.3.2 Stable Isotopes

Carbon isotope (δ13C) levels in tissues of *G. ogac* were significantly more positive, or enriched in 13C, as compared to those of *G. morhua*, which were relatively depleted in 13C (t-test, t = 4.82, $p < 0.01$) (Table 2.4, Figure 2.5). In contrast, no significant difference in mean δ^{15}N values was found between species (t-test, t = 1.59, p = 0.12) (Table 2.4). A significant positive relationship between body size (TL) and isotopic δ13C values was evident in both species (regression, t = 3.52, $p < 0.01$ and t = 2.13, p = 0.04 for *G. morhua* and *G. ogac*, respectively) (Figure 2.6). No significant relationship between body size and isotopic δ^{15}N values was observed for either species.

Neither mean distance to centroid (CD) or mean nearest neighbour distance (MNND) differed between species (CD: t-test, t = -1.16, p = 0.25; MNND: t = -1.30, p = 0.20). SDNND was lower for *G. ogac* than for *G. morhua* (Table 2.4). The percentages of

Table 2.3 Percent contribution to average dissimilarity by prey item and dietary index for *G. ogac* and *G. morhua*.

Relative frequency of occurrence (FO%)		**Relative gravimetric abundance (W%)**	
Prey Item	**% contribution**	**Prey Item**	**% contribution**
Hyperiids	24.9	Hyperiids	27.2
Euphausiids	16.8	Euphausiids	16.5
Mysids/Euphausiids	16.0	Mysids/Euphausiids	14.7
Polychaetes	9.9	Polychaetes	12.0
Unidentified fish	5.9	Unidentified fish	4.9
Mysids	3.5	Gadus morhua	3.3
other amphipods	3.3	Other amphipods	2.4
Gadus morhua	2.4	*Ulvaria subifurcata*	2.3
Ulvaria subifurcata	2.3	*Myoxocephalus sp*	2.1
Pagurus sp	1.8	*Pagurus sp*	2.0
Myoxocephalus sp	1.8	Mysids	1.8
Stichaeus punctatus	1.3	*Myoxocephalus scorpius*	1.2
other annelids	1.3		

Table 2.4 Summary of isotopic metrics by species. NR = δ^{15}N range; CR = δ^{13}C; SEA = standard ellipse area; CD = distance to centroid; MNND = mean nearest neighbour distance; SDNND = standard deviation of nearest neighbour distances.

Species	n	Mean δ^{15}N ±SE (‰)	Mean δ^{13}C ±SE (‰)	NR	CR	SEA (units^2)	SEA overlap (units^2 (%))	CD	NND	SDNND
G. ogac	42	14.71 ± 0.08	-17.91 ± 0.15	2.06	4.15	1.50	0.65 (43.3)	0.96	0.22	0.16
G. morhua	47	14.50 ± 0.11	-18.99 ± 0.17	2.47	4.50	2.63	0.65 (24.7)	1.11	0.29	0.31

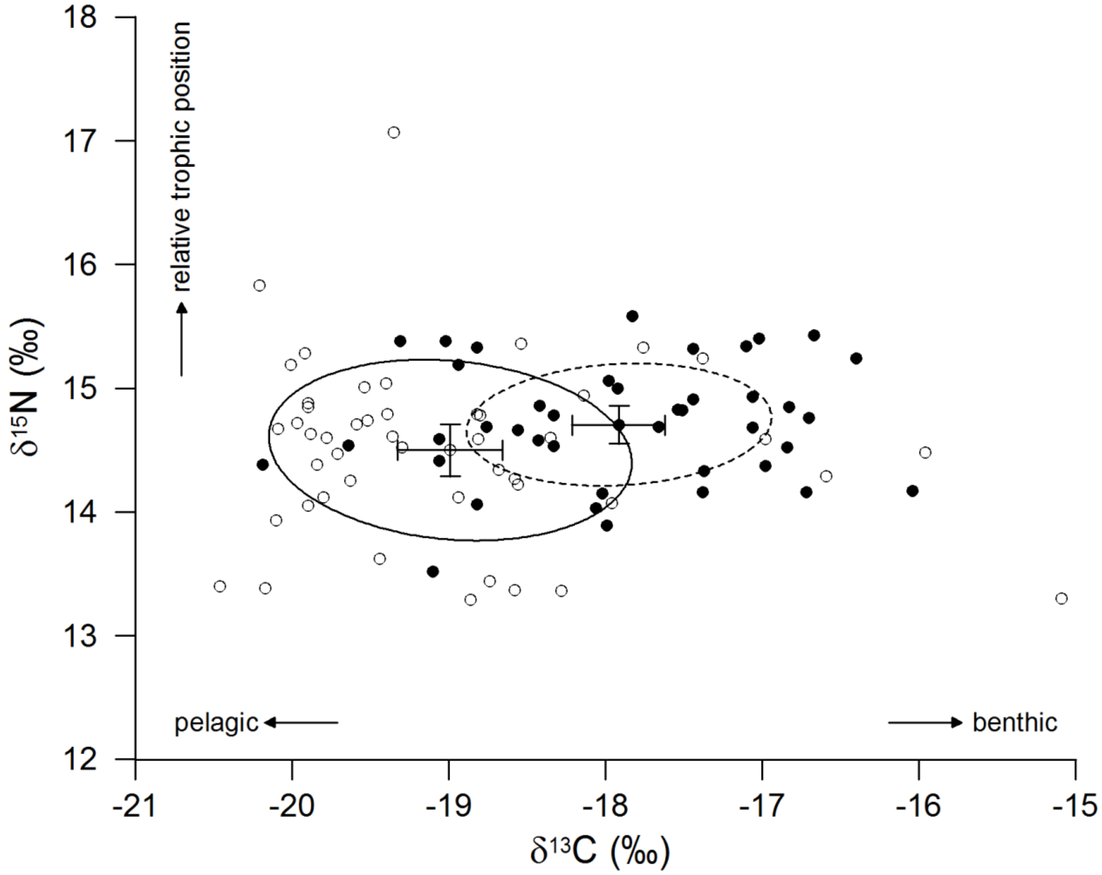

Figure 2.5 δ^{15}N - δ^{13}C bi-plots and group means (± 2 SE) of sampled *G. ogac* (●) and *G. morhua* (○). Enclosed areas represent the standard ellipse trophic niche area (SEA) occupied by each group (dashed line = *G. ogac*; solid line = *G. morhua*).

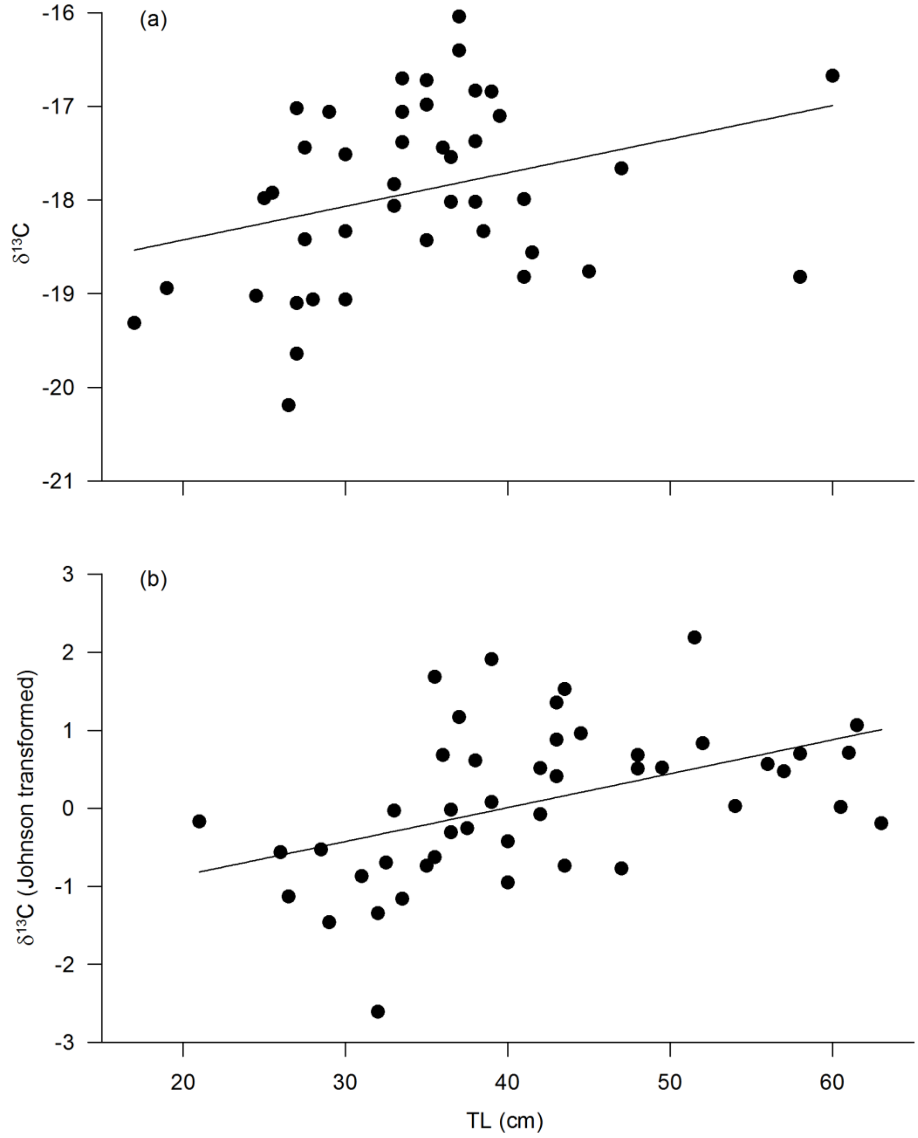

Figure 2.6 Plots of δ^{13}C versus TL and regression slopes for (a) *G. ogac* and (b) *G. morhua*. Both regressions were significant at $p < 0.05$.

SEA overlap between *G. ogac* and *G. morhua* were moderate at 43.3% and 24.7%, respectively (Table 2.4; Figure 2.5).

2.4 Discussion

Results from both stable isotope and stomach analyses provide support for dietary niche partitioning between *G. ogac* and *G. morhua* and suggest only minor competition for food resources between species during the summer. This conclusion is based on rejection of the working null hypotheses on diet similarity and benthic-pelagic prey similarity. Stomach analyses indicated differing prey and a higher proportion of benthic items for *G. ogac* and pelagic items for *G. morhua*. In support of these conclusions, isotopic signatures for *G. ogac* were significantly more enriched in 13C, indicating more benthic feeding, whereas signatures for *G. morhua* were relatively depleted in 13C, indicative of more pelagic feeding (Davenport and Bax 2002; Hobson et al. 2002; Sherwood and Rose 2005).

Consistent with the present study, Chaput (1981) concluded that diets of *G. morhua* and *G. ogac* were dissimilar based on low correlation coefficients for major prey items identified from stomachs from specimens caught in shallow (<25 m) water at two nearshore sites in Labrador (NAFO Div 2J). The authors attributed these differences to the high frequency of occurrence and contribution to total fullness of pelagic invertebrates for *G. morhua* and shrimp, fish and polychaetes for *G. ogac*. In contrast, Nielsen and Andersen (2001) found no difference in the diet of *G. morhua* and *G. ogac* in

West Greenland and concluded the two species compete for food where their ranges overlap.

The differing results between the present and Labrador study and the Greenland study may relate to timing and differing prey fields. The present results indicate that larger *G. ogac* feed primarily on fish (capelin, *Mallotus villosus*, when available), crustaceans and polychaetes, which is consistent with previous reports (Jensen 1948; Chaput 1981; Mikhail and Welch 1989; Morin et al. 1991; Nielsen and Andersen 2001). The main prey items for *G. morhua* found in the present study were in accordance with results from numerous feeding studies from Newfoundland waters (e.g., Templeman 1965; Lilly et al. 1984; Paz et al. 1991; Sherwood et al. 2007; Krumsick and Rose 2012) with the exception that capelin was found in only a single stomach. Capelin are only available seasonally in coastal Newfoundland, and have had depressed stock levels since 1990 (DFO 2010). In the present study, very few capelin were observed during daily echosounding of the study area, and none spawned on the beach prior to or during the course of the study. When capelin are available, they are likely to be preyed on heavily by both species, and this predation is likely to temporarily influence the degree of diet overlap. Nonetheless, competition may still be limited, as a consequence of the typical high density of spawning capelin. Similar increases in resource sharing at times of very high prey abundance has been demonstrated across several taxa (reviewed by Schoener 1982) including among co-occurring gadid species in south-western Norway (Høines and Bergstad 1999). Furthermore, in West Greenland, in contrast to Newfoundland, capelin have a quasi-continuous distribution along the coast and undergo more limited spawning migrations (Friis-Rødel and Kanneworff 2002). West Greenland *G. morhua* and *G. ogac* both had capelin as their dominant prey (Nielsen and Andersen 2001) but it remains unclear if feeding competition exists there.

Large *G. ogac* did show evidence of feeding on juvenile *G. morhua*, as did larger *G. morhua* to a lesser extent. Although the present study did not attempt to evaluate predation as a potential impact on either species, large *G. ogac* were relatively rare in our study area, hence despite their predatory habits they may be too few to impact the overall abundance of *G. morhua*.

The present stable isotope results were consistent with the wider ranging records for *G. morhua* from northeast Newfoundland (NAFO Division 3KL) (Sherwood and Rose 2005; Sherwood et al. 2007) and represent the first records of stable isotope signatures (δ^{15}N and δ^{13}C) for *G. ogac* in Newfoundland waters. For both gadids, isotope values shifted from pelagic (more negative δ^{13}C values) to more benthic (more positive δ^{13}C values) with increasing body size. This shift is consistent with diet transitions from invertebrates to fish as gape size increases and young gadids are able to exploit the higher energy content of piscivorous prey (e.g., Høines and Bergstad 1999; Nielsen and Andersen 2001; Link and Garrison 2002; Sherwood et al. 2007).

Although no significant differences were found, mean total fullness indices for *G. ogac* were higher than for *G. morhua*, a pattern previously reported by Chaput (1981), who suggested that in the absence of capelin, *G. ogac* are more efficient predators (in terms of prey weight consumed per predator body weight). It is possible that slight differences in relative stomach fullness between species may be due to differences in preferred prey availability or from differential habitat utilization. It may also be that *G. ogac* has a more generalist (less discriminate) feeding approach than *G. morhua*. This theory is supported by dietary breadth indices that were more than twice as high for *G. ogac* as for *G. morhua* of the same size. However, it should be noted that in the absence of prey availability data indices of niche breadth must be interpreted with caution (Hurlbert 1978; Feinsinger et al. 1981; López et al. 2009).

Differences in diet between *G. morhua* and *G. ogac* could also reflect differences in pelagic habitat use that lead to differences in prey availability (e.g., Baker and Ross 1981; Shpigel and Fishelson 1989; Helland et al. 2008). Specifically, *G. morhua* could occupy a broader vertical distribution that encompasses both benthic and pelagic environments while *G. ogac* maintain a closer association with the bottom (Scott and Scott 1989). This hypothesis will be tested in a further study. In addition, the more slender body and lighter colouration of *G. morhua*, is suggestive of more pelagic behaviour, whereas the stouter form and darker colouration of *G. ogac* is consistent with more demersal habits.

In contrast to the competition hypotheses, the trophic position null hypothesis was not rejected, as ^{15}N signatures were similar between species (Minagawa and Wada 1984; Post 2002). These results suggest that despite differing diets, *G. morhua* and *G. ogac* occupy similar trophic positions within the coastal Newfoundland ecosystem. However, it should be noted that in the absence of measured isotope values for specific prey items some degree of caution must be used in the interpretation of the results.

In conclusion, *G. morhua* and *G. ogac*, that co-occupy much of the coastal zone of Newfoundland and Labrador and other areas of the north Atlantic, appear to have similar trophic positions but limited diet competition. Our evidence provides little support for the notion that feeding competition could be limiting *G. morhua* recovery in these waters.

2.5 Acknowledgements

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Chapter 3. Examination of fine scale spatial-temporal overlap and segregation between two closely related congeners (*Gadus morhua* and *Gadus ogac*) in coastal Newfoundland

Abstract

The spatial and temporal movement patterns of sympatric juvenile Atlantic cod (*Gadus morhua*) and Greenland cod (*Gadus ogac*) were studied using high resolution radio-acoustic positioning in a coastal area of Newfoundland during the summers of 2009 and 2010. Twenty fish (10 *G. ogac* and 10 *G. morhua*) were equipped with acoustic transmitters and monitored for periods up to 23 days. Most fish showed high site fidelity with mean residence times of 12.4 (*G. morhua*) and 14.4 days (*G. ogac*). A few individuals showed a transient use of the study area, ranging distances up to ~4 km. Mean daily home ranges (95% kernel utilization distributions (KUDs)) and core activity areas were significantly larger for *G. morhua* (3.8 and 0.5 ha) than for *G. ogac* (2.7 and 0.3 ha). Home ranges were not related to body size for *G. morhua* but showed a weak positive relationship for *G. ogac*. *G. morhua* occupied larger areas during the day while *G. ogac* occupied slightly larger areas at night. Mean rates of movement for *G. ogac* and *G. morhua* ranged from 0.83 to 1.24 $bl \cdot s^{-1}$ and 0.76 to 1.76 $bl \cdot s^{-1}$, respectively, and were highest during crepuscular periods. Overall, *G. morhua* were wider ranging, moved at faster rates and were active throughout the diel cycle compared to *G. ogac* of the same size. We suggest that differential use of space and activity periods play an important role in the successful coexistence of these two species.

3.1 Introduction

Niche partitioning explains the coexistence of similar species in fish communities, most often through different diets (Ross 1986). Partitioning may also occur in the 3-dimensional water column (Baker and Ross 1981; Goldschmidt et al. 1990) and in different temporal or spatial usage of habitat (Jepsen et al. 1997; Sala and Ballesteros 1997; Weston et al. 2010). Testing hypotheses about spatial and temporal habitat partitioning has historically been logistically difficult, but advances in biotelemetry enable quasi-continuous monitoring of free-swimming individuals in 2 or 3-dimensions over time (Sauer et al. 1997; Cote et al. 1998; O'Dor et al. 1998; Klimley et al. 2001). Resultant data can be used to measure spatial utilization and temporal activity at high resolution (± 1-2 m, O'Dor et al. 1998). Most applications of this technology have studied movements of single species, but there is also potential for novel studies of interactions among co-occurring species. Such studies are useful for examining potential mechanisms underlying the diversification of a genus and the coexistence of congeneric species (Brooks and McLennan 1991).

In coastal Newfoundland, Greenland cod *Gadus ogac* (Richardson 1836) and Atlantic cod *Gadus morhua* (L. 1758) have overlapping geographic distributions (Scott and Scott 1988; Cohen et al. 1990), with juveniles intermixed in most bays (Rose 2007). Studies of dietary overlap are few and contradictory (e.g., Chaput 1981; Nielsen and Andersen 2001), but recent work in coastal Newfoundland has shown that these species exhibit dietary niche partitioning (Knickle and Rose 2013). How diet partitioning occurs, however, is not known. Both species are thought to be opportunistic feeders (Scott and

Scott 1988, Cohen et al. 1990), however it is feasible that opportunism could result in different diets if habitat usage differs at small spatial or temporal scales.

Life history characteristics of older juvenile (> 2 yrs) and adult Greenland cod in Canadian waters are known from a limited number of studies (Chaput 1981; Mikhail and Welch 1989; Morin et al. 1991; 1992), but fine-scale movement patterns have not been reported. Older juvenile (age-2-4) Atlantic cod are better studied; Clark and Green (1990) revealed distinct seasonal patterns for age-3 juveniles which were wide-ranging and nocturnally active in summer and relatively stationary and diurnally active in the fall. However, data on fine-scale movements were only available for fish tagged in the fall when most were tracked for only a few days. Cote et al. (2004) reported that cod showed strong site fidelity and generally occupied small (~2 ha) home ranges in the fall in a neighbouring bay but tracking effort was manual and limited to twice a week during daylight hours. Cote et al. (2002) monitored the swimming speeds of age 2-3 juveniles using a fixed hydrophone array but did not quantify space use.

In this study, we quantified and compared movement patterns (residency, home range and rate of movement) of juvenile co-occurring *G. morhua* and *G. ogac* using an acoustic positioning system (VRAP, VEMCO Division, AMIRIX Systems Inc., NS, CAN) in a coastal region of Newfoundland. The objective of the study was to determine the extent of spatial and temporal overlap or segregation to help explain the co-existence of these ecologically similar species. Working hypotheses were that no differences would be measured in: 1) home range, 2) rates of movement, and 3) temporal activity patterns.

To the best of our knowledge, the present study is the first to simultaneously quantify the distributions and movements of these co-occurring species using telemetry.

3.2 Materials and Methods

3.2.1 Study Area

The study was conducted in a small cove located in Smith Sound on the western side of Trinity Bay, Newfoundland, Canada (Figure 3.1), a typical fjord well known for acoustic telemetry experiments (Wroblewski et al. 1994; 1995; Winger et al. 2002). Water depth at the site ranged from <1 to ~50 m and tidal heights ranged from 0.2 to 1.3 m. Substrate types within the study area varied, ranging from sand and fine gravel to bedrock. Vegetation was dominated by kelp (*Laminaria sp.*) and coverage ranged from dense to sparse. The hydrophone buoy array encompassed an area of about 5.7 ha while the positional range (i.e., the area over which individuals could reliably be detected by all three hydrophone buoys) covered an area of approximately 25 ha (Figure 3.1).

3.2.2 Data Collection

Tagging

Juvenile (~30-45 cm TL) Atlantic cod and Greenland cod were caught by angling using single, barbless hooks and selected for tagging to provide a comparable size range between species. Fish were caught near the bottom (< 2 m) within the study area. Prior to

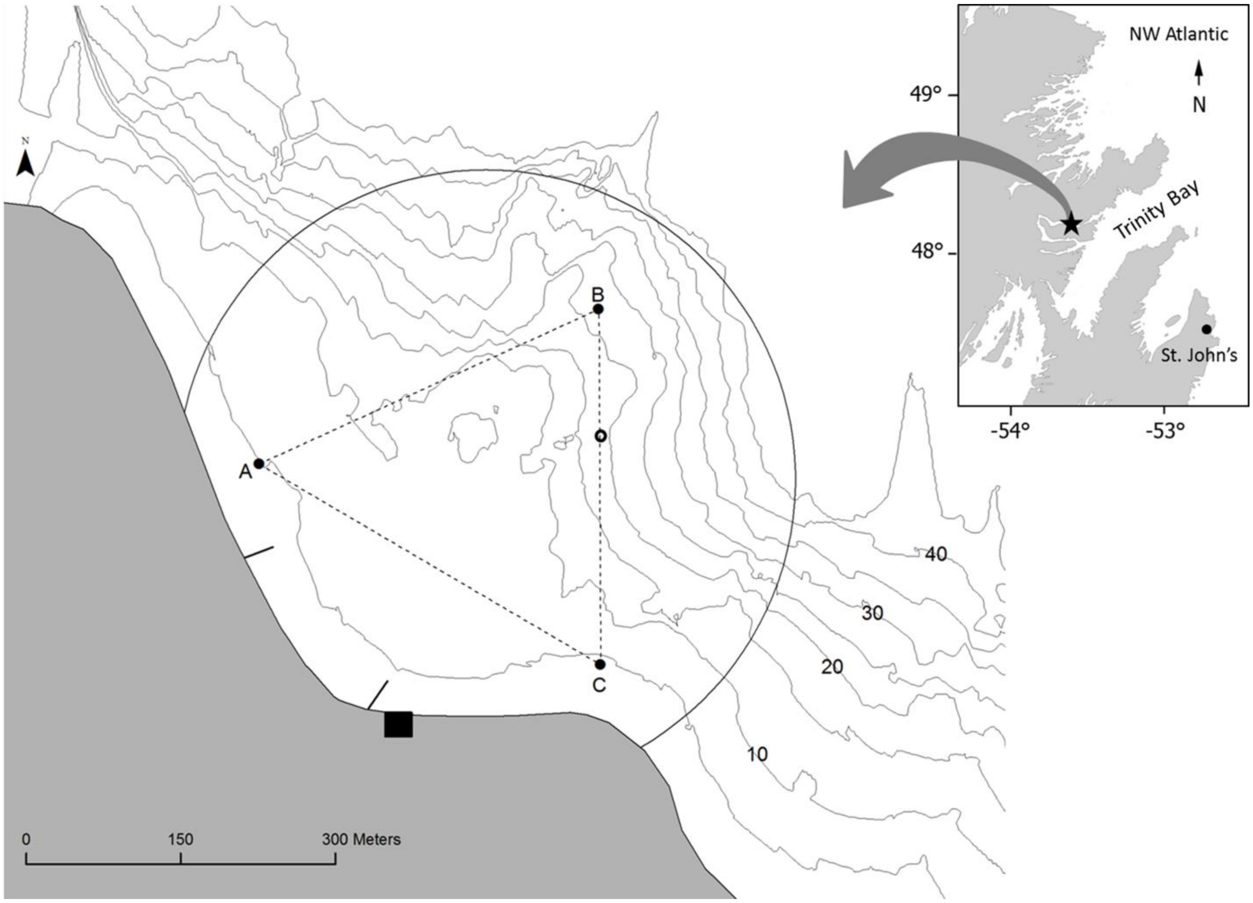

Figure 3.1 Map of study area. Inset shows study site relative to the eastern portion of Newfoundland. Enlarged area shows position of hydrophone array (● - radio-acoustic buoys A-C), base station (■), position of temperature loggers (○), wharves (—), positional range (circular black line - 300 m radius from array centre) and depth contours.

tagging, fish were placed in an anaesthetic solution of MS-222 and sea water (~0.1 g per L) until equilibrium was lost. Individuals were then measured and a continuous acoustic transmitter (Model V9P-1H, 9 x 40 mm, 5.2 g in air; VEMCO Division, AMIRIX Systems Inc., NS, CAN) was implanted in the body cavity through a small (1 cm) incision made in the belly anterior to the vent and parallel to but offset from the mid-ventral line. Transmitters emitted acoustic pulses every 15-35 s at 150 dB re 1 μPa sound pressure level (SPL) @ 1 m on one of three frequencies (65, 73 and 81 kHz) and were programmed to last ~22 days. A single suture (Monosof 3-0 with a C-14, 24 mm needle) was used to close the wound and fish were placed in fresh sea water to recover. Once recovered, fish were released into the study area.

Tracking

Tagged fish were tracked continuously using a radio-acoustic positioning system (VRAP, VEMCO Division, AMIRIX Systems Inc., NS, CAN) consisting of three fixed hydrophone buoys equipped with radio antennas arranged in a triangle over the study area (Figure 3.1). Buoy hydrophones received acoustic pulses from transmitters and relayed the information via radio signal to a land-based station where the data was viewed and stored on computer disc. The exact position of each transmitter was triangulated autonomously by the system based on the time delay in pulses arriving at each buoy. Scan time for each tag frequency was set at 60 s and buoys were programmed to calibrate their positions every 60 min. The accuracy of the positioning system was tested by mooring a stationary transmitter at a known location within the study area.

Mean (± SE) positional accuracy was 2.48 m ± 0.25 m inside the buoy array and 6.53 ± 0.17 m outside the array and was similar to other studies (Sauer et al. 1997; O'Dor et al. 1998; Klimley et al. 2001; Barnett et al. 2010). To determine the acoustic range of the system, a single transmitter was lowered to a depth of ~10 m from a research vessel at increasing 50 m intervals from the centre of the array on several bearings. Range tests showed successful detections beyond 450 m, however, a conservative 300 m effective detection range was used since positional accuracy decreases with distance from the array (e.g., O'Dor et al. 1998; Klimley et al. 2001; Espeland et al. 2007). A manual tracking receiver (VR100, VEMCO Division, AMIRIX Systems Inc., NS, CAN) equipped with an omnidirectional hydrophone was used to detect the presence/absence of fish that moved out of range of the positioning system and presence/absence within the array when sea state conditions inhibited VRAP system performance, or at times when transmitter signal to one or more hydrophones was blocked by bathymetric features (such as when a fish entered a rocky crevice). In the latter two cases, it was inferred that a fish was present within the study area if it was detected manually from within the study area despite not being detected by the VRAP system. Manual tracking was performed on a daily basis from two wharves located within the study area (Figure 3.1) and at irregular intervals (once every 1-5 days) from a 9 m research vessel (*Gecho II*) from various positions outside the array. The effective range of the VR100 was tested by mooring a stationary transmitter within the array and attempting to detect it from the vessel at increasing distances. Tests showed an effective detection radius of about 250 m.

Acoustics (echosounding)

To investigate the potential effect of predator distribution on juvenile cod movements, the distribution and abundance of cod in the study area were monitored acoustically from the *Gecho II* using a calibrated (Foote et al. 1987) Biosonics DT-X digital system (Biosonics Inc., Seattle, WA, USA) with 120 kHz single beam (6º) and 200 kHz split-beam (6.5º) transducers. Acoustic signal species classification and fish size were verified by catches using hook and line.

Environmental data

Surface (~1 m), mid-water (~10 m) and bottom (~20 m) water temperatures were recorded at 5 minute intervals at a fixed location within the study area (Figure 3.1) using Minilog (VEMCO Division, AMIRIX Systems Inc., NS, CAN) data loggers. Wind speed and direction were recorded continuously from a RainWise Inc. (Bar Harbor, ME, USA) MK-III weather station located at the base station. Predicted local tide data and sunrise and sunset times were obtained from the Canadian Hydrographic Service (*www.waterlevels.gc.ca*) and Environment Canada (*www.weatheroffic.gc.ca*).

3.2.3 Data Analysis

Tracking data obtained within the first 24 hours after tagging and release were omitted from analyses to remove any potential effect of surgical implantation on fish behaviour (see Cote et al. 1999). Beyond this initial period there was no indication of lethargic behaviour that differed from the remainder of the study period. No mortality of tagged fish occurred during the study period (evident from non-mobile tags).

Residency/Site fidelity

Hourly presence/absence data for the study period for each tagged fish was plotted to examine residence times. In the present study, the terms *residency* and *side fidelity* are used synonymously and refer to presence over time. Continuous residence times were measured as the number of continuous days with a minimum of one detection (either with the VRAP system or manually) within the study area. Residency was also examined using the total number of days an individual was detected within the study area. Residency (both continuous residence times and total number of days present) was compared between species using nonparametric Kruskal-Wallis ANOVAs and relationships with fish size (TL) were tested with Spearman rank correlations.

Spatial Distribution/Home Range

Positional fixes were plotted on a georeferenced map of the study area and invalid fixes (i.e., detections on land, detections from unrecognized transmitter IDs, etc.) were removed. To examine use of space, positional fixes were used to generate 95% and 50% (core areas) kernel utilization distributions (KUDs) and 95% minimum convex polygons (MCPs) for each fish using the MCP analysis and kernel density estimation (KDE) functions of the Home Range Tools (HRT) (Rodgers et al. 2007) extension for ArcMap (ESRI, Redlands, CA). We defined home range as the area within an animal's utilization distribution in which it has a 95% probability of being located and the core activity space as the area in which it has a 50% probability of being located (Van Winkle 1975; Worton 1987). MCPs are generated by connecting the outermost points in a group and are used to demonstrate an individual's range over a given time period. Although they have been criticized (e.g., Worton 1987), MCPs have been widely used to describe home ranges and are thus useful when comparing results to previous studies (Harris et al. 1990). Furthermore, their use allowed for comparison with estimates generated with kernel methods. KUDs offer a probabilistic measure of space use and are generated by applying a probability density function (a kernel) over each position, superimposing a grid over the points and calculating a probability density estimate at each grid intersection. The overlapping volumes of the kernels are then summed and a utilization distribution calculated over the entire grid. Contour lines (i.e., isopleths) can be applied to utilization distributions and areas within each isopleth calculated. We used an adaptive kernel method with a standard bivariate normal kernel density function for all KUD estimates. The smoothing factor (i.e., bandwidth) for each KDE analysis was determined from a proportion of the reference bandwidth using the "ad hoc" method by Berger and Gese (2007) as described by Rodgers and Kie (2010). We used n = 30 as the minimum number of detections required to estimate KUDs as suggested by Seaman et al. (1999). In cases where KUDs overlapped with land, they were cropped using the Clip tool in the ArcToolbox of ArcMap (ESRI, Redlands, CA) and the area recalculated. Serial autocorrelation (temporal correlation) of telemetry data has traditionally been considered a problem in tracking studies because it violates basic assumptions of statistical inference and can result in biased estimates of home range sizes (Swihart and Slade 1985a; Harris et al. 1990; Hansteen et al. 1997). However, reducing the number of positions to achieve independence of observations (a widely used method of overcoming autocorrelation) often reduces the significance of the estimate and can obscure other biologically relevant behaviour (DeSolla et al. 1999; Fieberg 2007; Boyce et al. 2010). In the present study, randomly removing positional data to achieve acceptable Schoener (1981) and Swihart and Slade (1985b) index values would have resulted in a loss of > 90% of data points. Therefore, no attempt to account for autocorrelation of tracking data was made. KUDs and MCPs were estimated for each tracked fish over three time periods: daily (24 hours), 3-days, and total study period. No difference in KUD and MCP estimates between years was observed (Kruskal-Wallis, $p > 0.05$) so data were pooled for the two years. Differences in home ranges between species were tested using nonparametric Kruskal-Wallis ANOVAs. Spearman rank correlations were performed to determine whether home range size (total period KUDs and MCPs) was related to the number of consecutive or total number of days an individual was present. The relationship between fish size and home range was examined using Spearman rank correlations.

Rates of movement

Rates of movement (ROMs) and mean distance traveled per day were derived from successive positional fixes and calculated for each fish using the Calculate Interfix Times and Distances function of the HRT (Rodgers et al. 2007) in ArcGIS (ESRI, Redlands, CA). Only positional data with successive position intervals <180 s were used to calculated ROMs. ROMs were adjusted for bias associated with increasing position-fixing interval using the relationship between estimated rate of movement and position-fixing interval from Løkkeborg et al. (2002) which reduced the interval over which ROMs were estimated to 17 s. A swimming endurance filter for cod (see Winger et al. 2000) was then applied and erroneous rates removed. Relative ROMs (body length·s^{-1}) were derived by dividing filtered absolute ROMs (cm·s^{-1}) by body length (cm). Statistical testing of ROMs within and between species and among diel periods were conducted using nonparametric Kruskal-Wallis ANOVAs. ROMs in relation to tidal cycle were also examined within and between species using Kruskal-Wallis ANOVAs while Spearman rank correlations were used to evaluate whether ROMs were related to fish size (TL). In each case, experimental units were individual fish. Spearman rank correlations were used to examine relationships between distance traveled and fish size for each species and Kruskal-Wallis ANOVAs were used to detect differences between species.

3.3 Results

Twenty fish (5 *G. morhua* and 5 *G. ogac* in each year) were implanted with acoustic transmitters and tracked continuously for periods up to 23 days resulting in a total of 18 803 detections with the VRAP system from 24 June-17 July, 2009 and 7-28 July, 2010 (Table 3.1, Figure 3.2). All fish survived implantation and were detected with the VRAP system except for fish 21 (*G. ogac*, 49.0 cm) which left the study area immediately after release and was detected manually 13 days later, approximately 4 km from the release point (Figure 3.3). Mean (± SE) fish length (38.8 ± 1.7 cm for *G. morhua* and 36.9 ± 1.9

Table 3.1 Summary data for all fish monitored in Smith Sound.

Fish no.	Species	TL (cm)	Date tagged	Total days detected	Consecutive days detected	No. VRAP detections	Mean distance traveled per day (m)
1	*G. ogac*	34	06/24/09	22	22	635	507
2	*G. ogac*	41	06/24/09	22	11	847	1180
3	*G. ogac*	29.5	06/24/09	21	16	744	800
4	*G. morhua*	42.5	06/24/09	22	22	1742	2689
5	*G. ogac*	35.5	06/24/09	22	22	1702	1174
6	*G. ogac*	44	06/24/09	14	6	296	885
7	*G. morhua*	41	06/24/09	10	10	582	1837
8	*G. morhua*	38.5	06/26/09	15	7	136	675
9	*G. morhua*	35.5	06/26/09	21	21	1589	1875
10	*G. morhua*	33.5	06/26/09	21	21	1707	1328
20	*G. ogac*	35	07/07/10	13	13	1159	1249
21	*G. ogac*	49	07/07/10	0	0	0	-
22	*G. ogac*	37	07/07/10	22	22	2932	2180
23	*G. ogac*	32	07/07/10	19	9	1399	1340
24	*G. ogac*	31.5	07/07/10	20	21	876	625
25	*G. morhua*	45	07/07/10	22	22	1053	926
26	*G. morhua*	47	07/09/10	1	1	8	480
27	*G. morhua*	38.5	07/09/10	6	3	56	799
28	*G. morhua*	29	07/09/10	14	8	731	1223
29	*G. morhua*	37	07/09/10	8	8	609	2051

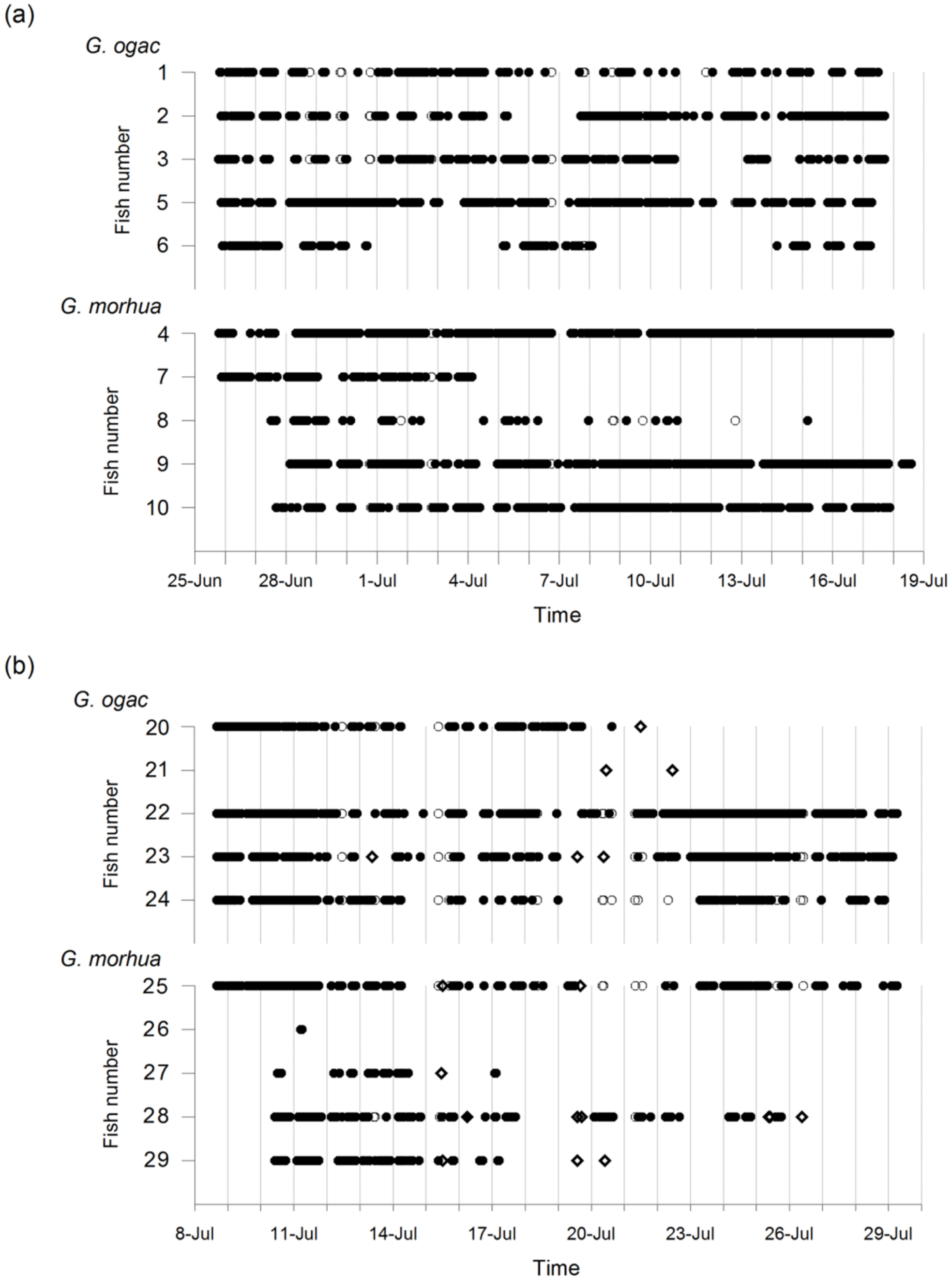

Figure 3.2 Hourly presence of *G. ogac* and *G. morhua* in Smith Sound in (a) 2009 and (b) 2010. ● - VRAP detection; ○ - VR100 detection inside study area; ◊ - VR100 detection outside study area.

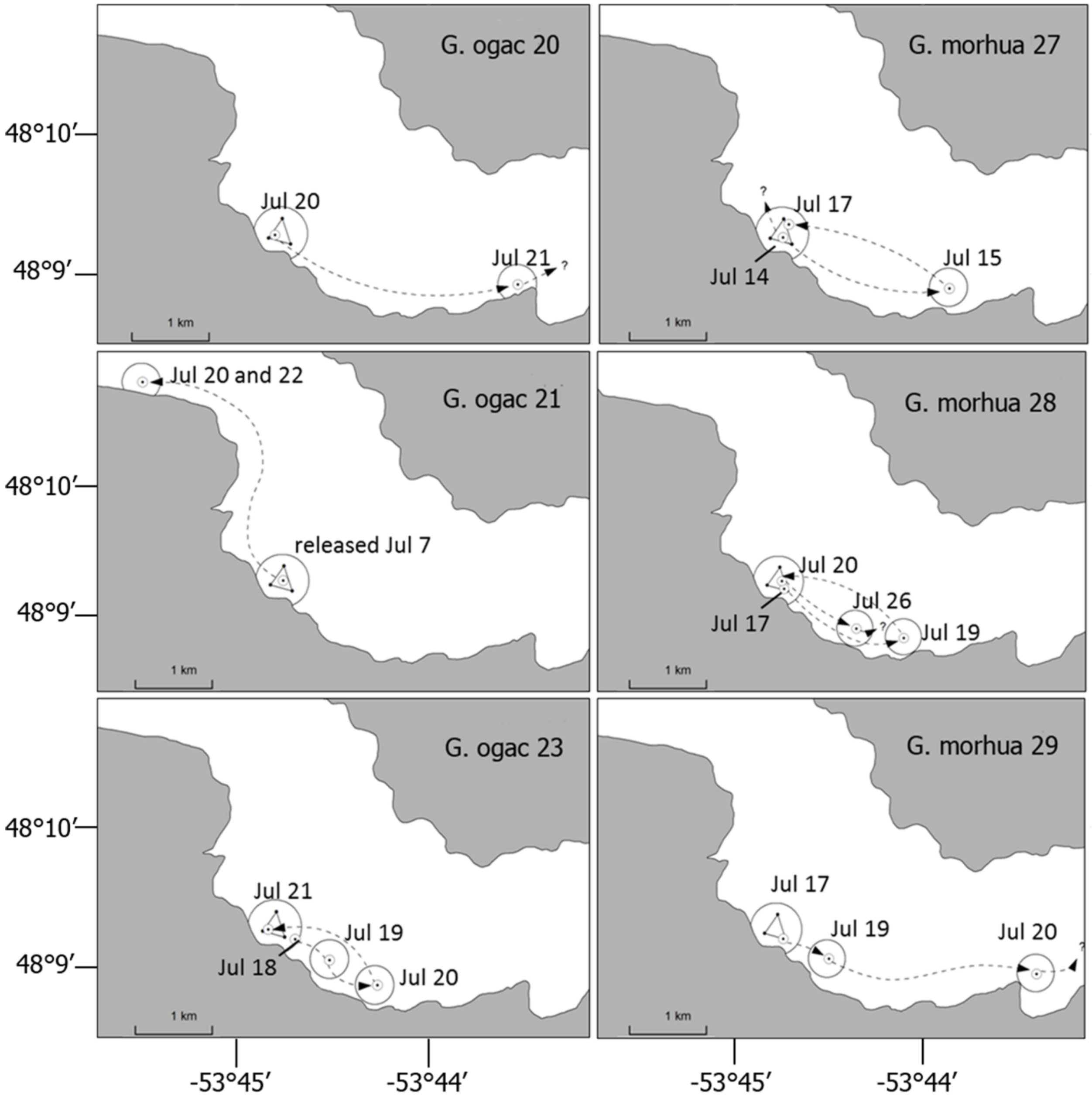

Figure 3.3 Manual detections and movements outside the hydrophone array (triangle) for six fish in 2010. In each panel, · indicates a VR100 detection and the dashed lines and arrows show travel distance and direction.

cm for *G. ogac*) did not differ between years (ANOVAs, p > 0.05), so data for both years were pooled by species.

3.3.1 Residency/Site fidelity

Both species showed individual variation in residence times (continuous days detected) as well as total number of days detected which ranged from 0-23 (Table 3.1; Figure 3.2). Four *G. morhua* (#s 4, 9, 10, 25) and 4 *G. ogac* (#s 1, 5, 22, 24) were detected within the study area for the duration of the study periods (Figure 3.2). Three *G. ogac* (#s 2, 3, 23) and 1 *G. morhua* (#28) stayed mainly within the study area and performed occasional, short (1-2 days) excursions out of the range of the VRAP system (Figures 3.2 and 3.3). *G. ogac* #6 showed a regular movement pattern in and out of the study area, remaining within the range of the VRAP system for 4-6 days then moving to an unknown location for 4-5 days (Figure 3.2). *G. morhua* #8 was detected within the array on a regular basis and on two occasions within < 1 km of the array but appeared not to remain in one location for any length of time (Figure 3.2). One *G. ogac* and 1 *G. morhua* (#s 20, 29) remained within the study area for several days following release, then travelled down the Sound and were not detected again (Figures 3.2 and 3.3). Similarly, *G. morhua* #27 stayed within the study area for several days, moved outside and was detected ~2 km from the array on 15 July, then re-entered the study area on 17 July and was not detected thereafter (Figures 3.3 and 3.4). *G. morhua* #7 was regularly detected within the study area for 10 days after its release but not beyond 4 July while *G. morhua* #26 was only detected 8 times, all on the day after its release. *G. ogac* #21 was never detected with the

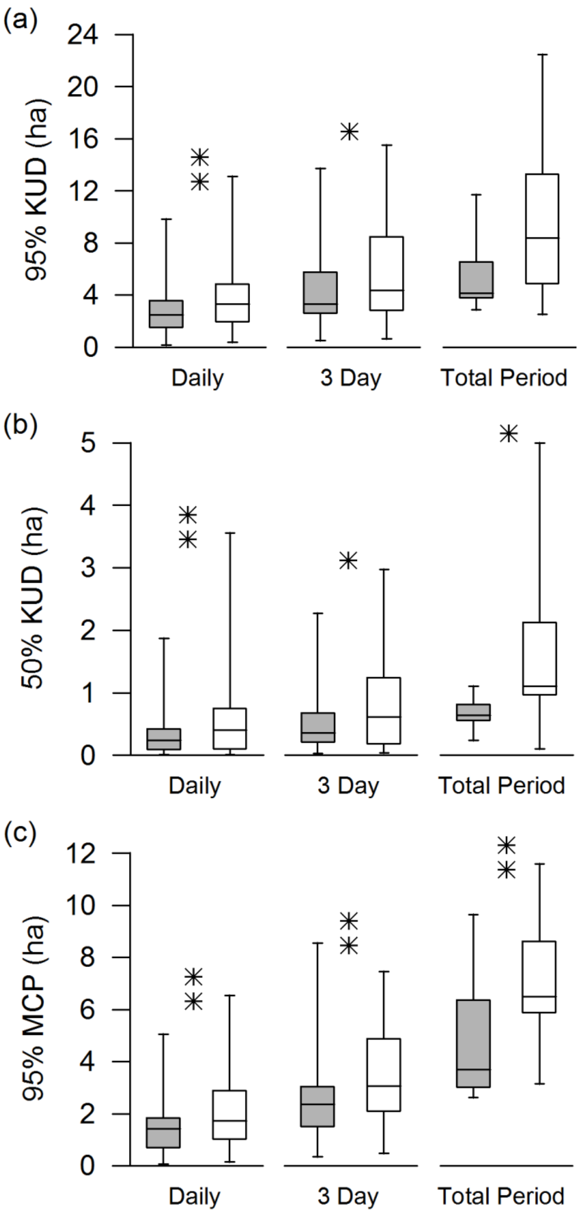

Figure 3.4 Box-Whisker plots of daily, 3 day and total period (a) 95% KUD and (c) 95% MCP home ranges and (b) 50% KUD core activity areas for *G. ogac* (shaded boxes) and *G. morhua* (open boxes). The box is defined by the lower and upper quartiles, also shown are the median and the caps delimiting extreme values. Asterisks indicate significant differences between species at $p < 0.05$ (**) and $p < 0.10$ (*) (Kruskal-Wallis ANOVAs).

VRAP system but was manually detected outside the study area on two separate occasions > 4 km from the study site (Figures 3.2 and 3.3). Neither residence times nor total number of days tracked differed significantly between species (Kruskal-Wallis ANOVAs, $p > 0.05$) and neither were related to fish size for either species (Spearman rank correlation, $p > 0.05$).

3.3.2 Utilization Distributions/Home Range

Mean daily, mean 3-day and total period home range estimates (95% KUD and MCP) and core activity areas (50% KUD) for each individual are shown in Table 3.2. For three fish (#s 21, 26 and 27), the number of daily detections was too small (< 30) to estimate home range size. For all other individuals, daily MCP home range estimates were lower than those estimated by kernel methods, as were 3-day estimates (Table 3.2, Figure 3.4).

G. morhua occupied significantly larger home ranges and core activity areas than *G. ogac* for each time period except for total period 95% KUDs which did not differ between species (Figure 3.4). Total period KUDs were not related to residence time for either species (Spearman rank correlations, $p > 0.05$). In addition, home range and core activity area estimates were not related to the total number of days monitored for either species (Spearman rank correlations, $p > 0.05$). Total period home ranges showed an increase with increasing fish length for *G. ogac* (particularly for fish >36 cm) however relationships were not significant (Spearman rank correlations, $p > 0.05$). In comparison, total period home ranges showed no relation to fish size (TL) for *G. morhua* (Spearman rank correlation, $p > 0.05$) while daily and 3-day home ranges were not related to fish

Table 3.2 Mean (±SE) daily and total period home range estimates (ha) (95% KUD and 95% MCP) and core activity areas (50% KUD) for all fish monitored in Smith Sound.

		Daily			**3 Day**			**Total Period**		
Fish no.	**Species**	**95% KUD**	**50% KUD**	**95% MCP**	**95% KUD**	**50% KUD**	**95% MCP**	**95% KUD**	**50% KUD**	**95% MCP**
1	*G. ogac*	1.42 ± 0.30	0.12 ± 0.03	0.80 ± 0.15	2.79 ± 0.69	0.34 ± 0.16	1.49 ± 0.39	3.80	0.64	3.02
2	*G. ogac*	3.54 ± 0.26	0.41 ± 0.06	1.79 ± 0.20	5.32 ± 0.62	0.76 ± 0.22	3.17 ± 0.39	6.40	0.67	6.38
3	*G. ogac*	3.87 ± 0.81	0.33 ± 0.10	1.63 ± 0.35	4.15 ± 1.11	0.33 ± 0.09	2.58 ± 0.87	6.55	0.56	4.89
5	*G. ogac*	2.96 ± 0.23	0.47 ± 0.04	2.01 ± 0.17	4.11 ± 0.68	0.60 ± 0.05	3.32 ± 0.40	3.54	0.45	3.18
6	*G. ogac*	1.57 ± 0.24	0.22 ± 0.06	0.86 ± 0.14	2.34 ± 0.41	0.27 ± 0.07	1.54 ± 0.28	11.71	1.10	9.65
4	*G. morhua*	5.12 ± 0.71	0.33 ± 0.03	2.51 ± 0.53	8.39 ± 1.01	0.60 ± 0.19	3.70 ± 0.98	4.87	0.97	6.49
7	*G. morhua*	5.34 ± 1.23	0.76 ± 0.22	2.69 ± 0.80	8.41 ± 2.54	1.55 ± 0.51	4.50 ± 1.23	10.15	1.58	8.63
8	*G. morhua*	6.16 ± 0.80	0.74 ± 0.01	2.84 ± 0.06	11.73 ± 3.22	1.03 ± 0.02	4.63 ± 0.25	22.46	5.00	8.10
9	*G. morhua*	4.79 ± 0.58	0.84 ± 0.19	2.51 ± 0.33	5.87 ± 0.68	0.86 ± 0.19	4.24 ± 0.57	6.61	1.07	6.29
10	*G. morhua*	2.01 ± 0.26	0.19 ± 0.10	1.00 ± 0.14	2.04 ± 0.34	0.11 ± 0.02	1.47 ± 0.28	2.53	0.10	3.16
20	*G. ogac*	2.90 ± 1.06	0.23 ± 0.09	1.50 ± 0.34	3.76 ± 1.11	0.39 ± 0.16	2.62 ± 0.52	2.87	0.24	2.62
21	*G. ogac*	-	-	-	-	-	-	-	-	-
22	*G. ogac*	3.03 ± 0.53	0.45 ± 0.11	1.79 ± 0.30	5.30 ± 1.47	0.84 ± 0.26	3.83 ± 0.88	4.90	0.76	5.45
23	*G. ogac*	2.79 ± 0.24	0.32 ± 0.06	1.69 ± 0.23	5.02 ± 1.25	0.78 ± 0.21	2.90 ± 0.65	4.16	0.82	3.69
24	*G. ogac*	1.79 ± 0.44	0.17 ± 0.06	0.87 ± 0.21	2.93 ± 0.57	0.35 ± 0.11	1.59 ± 0.31	3.93	0.55	2.89
25	*G. morhua*	1.58 ± 0.34	0.15 ± 0.05	0.94 ± 0.22	3.36 ± 1.26	0.33 ± 0.13	2.22 ± 0.39	3.60	0.26	5.52
26	*G. morhua*	-	-	-	-	-	-	-	-	-
27	*G. morhua*	-	-	-	12.27 ± 0.00	2.51 ± 0.00	4.87 ± 0.00	11.10	2.13	5.89
28	*G. morhua*	6.98 ± 0.94	0.82 ± 0.16	3.38 ± 0.44	7.98 ± 1.83	1.21 ± 0.32	4.60 ± 1.05	13.27	1.20	11.59
29	*G. morhua*	6.11 ± 2.15	1.11 ± 0.43	3.32 ± 0.86	8.32 ± 2.37	1.57 ± 0.64	5.11 ± 1.46	8.39	1.10	7.93

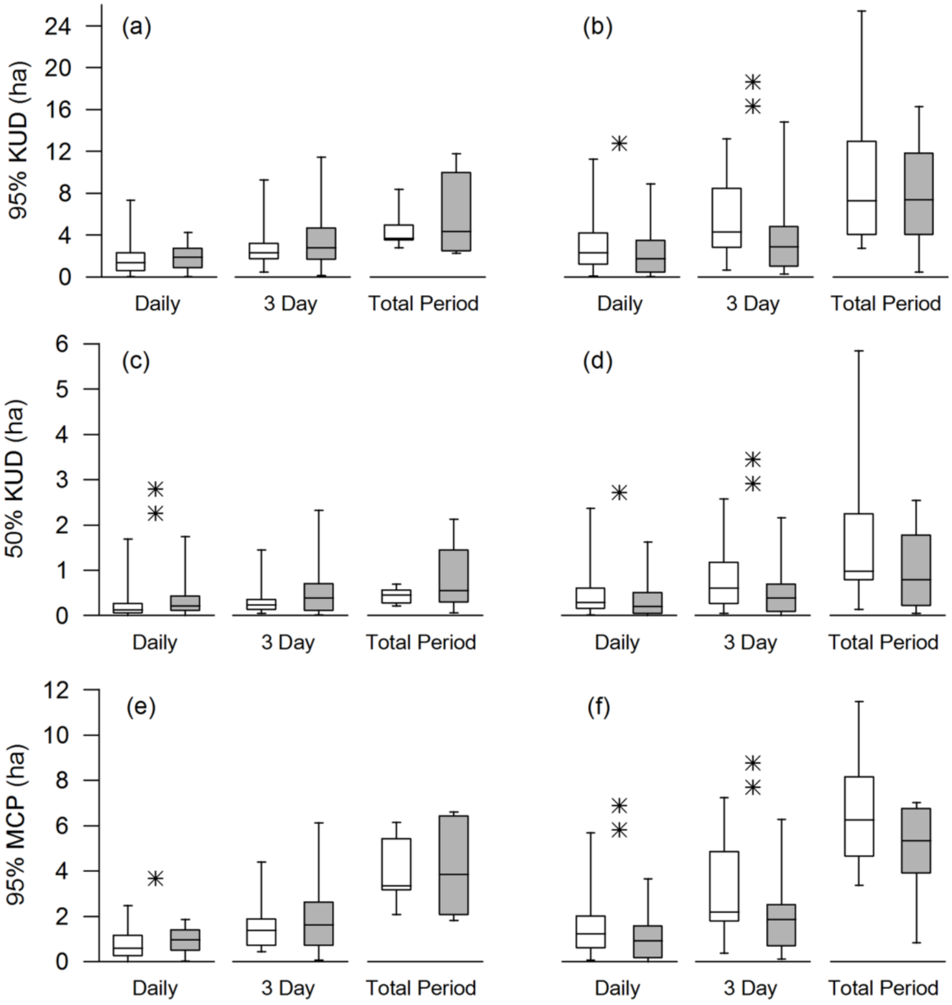

Figure 3.5 Box-Whisker plots of day (open boxes) and night (shaded boxes) home ranges and core activity areas for *G. ogac* (a), (c), and (e) and *G. morhua* (b), (d) and (f).). The box is defined by the lower and upper quartiles, also shown are the median and caps size for either species (Spearman rank correlations, $p > 0.05$). Nighttime KUDs and MCPs were consistently larger than daytime estimates for *G. ogac*, however only night and day delimiting extreme values. Asterisks indicate significant differences between night and day estimates ($p < 0.05$ ** and $p < 0.10$ *; Kruskal-Wallis ANOVAs).

size for either species (Spearman rank correlations, p > 0.05). Nighttime KUDs and MCPs were consistently larger than daytime estimates for *G. ogac*, however only night and day differences in daily core areas (50% KUDs) were significant (Kruskal-Wallis ANOVA, H = 5.18, df = 1, p = 0.023) (Figure 3.5). In contrast, *G. morhua* had larger daytime home ranges and core areas over both daily and 3-day monitoring periods with daily 95% and 50% KUDs significantly different at p = 0.10 (Kruskal-Wallis ANOVAs, 95%KUD: H = 3.58, df = 1, p = 0.058; 50%KUD: H = 3.47, df = 1, p = 0.062) and daily MCPs and all 3-day measures significant at p = 0.05 (Kruskal-Wallis ANOVAs, daily 95%MCP: H = 6.70, df = 1, p = 0.010; 3-day 95%KUD: H = 4.20, df = 1, p = 0.040; 3-day 50%KUD: H = 4.58, df = 1, p = 0.032; 3-day 95%MCP: H = 4.25, df = 1, p = 0.039) (Figure 3.5) . Comparison of daytime and nighttime home ranges and core activity areas between species revealed significantly larger daytime estimates for *G. morhua* for all measures and time periods except for total period 95%KUDs which were just short of significant (Table 3.3, Figure 3.5). Nighttime home ranges and core areas were generally larger for *G. morhua* than *G. ogac* however these differences were not statistically significant (Table 3.3, Figure 3.5).

3.3.3 Rates of Movement

A total of 4829 estimates of instantaneous rates of movement (1733 for *G. morhua* and 3096 for *G. ogac*) from 17 fish were derived from tracking data (Table 3.4). Few estimates were obtained for two individuals (#s 8 and 27) and these data were excluded from further analyses. The ranges of rates of movement were near identical, 0 to 5.08

Table 3.3 Kruskal-Wallis ANOVA results for between species differences in daytime and nighttime home ranges (ha). Significant (< 0.05) p levels in bold.

Period	Factor	*G. ogac* Median	*G. morhua* Median	H	df	p
Daytime	Daily (24-hr)					
	95kud	1.36	2.30	12.82	1	**<0.001**
	50kud	0.12	0.29	17.56	1	**<0.001**
	95mcp	0.60	1.24	15.61	1	**<0.001**
	3-Day					
	95kud	2.33	4.28	12.54	1	**<0.001**
	50kud	0.23	0.60	13.91	1	**<0.001**
	95mcp	1.39	2.20	14.44	1	**<0.001**
	Total Period					
	95kud	3.70	7.27	3.28	1	0.070
	50kud	0.45	0.98	7.25	1	**0.007**
	95mcp	3.35	6.26	7.74	1	**0.005**
Nightime	Daily (24-hr)					
	95kud	1.87	1.75	0.10	1	0.748
	50kud	0.21	0.20	0.01	1	0.903
	95mcp	0.97	0.93	0.18	1	0.667
	3-Day					
	95kud	2.77	2.85	0.00	1	0.975
	50kud	0.38	0.39	0.13	1	0.716
	95mcp	1.63	1.87	0.05	1	0.829
	Total Period					
	95kud	4.36	7.38	1.33	1	0.248
	50kud	0.56	0.80	0.93	1	0.336
	95mcp	3.85	5.35	1.56	1	0.211

Table 3.4 Rate of movement (ROM) data for all tagged fish. (*- excluded from analyses).

					ROM (bl·s^{-1})			ROM (cm·s^{-1})		
Year	**Species**	**Fish No.**	**TL**	**n**	**Mean**	**SE**	**Median**	**Mean**	**SE**	**Median**
2009	*G. ogac*	1	34	125	0.906	0.099	0.382	0.308	0.034	0.130
	G. ogac	2	41	136	1.243	0.085	0.869	0.509	0.035	0.357
	G. ogac	3	29.5	133	1.029	0.106	0.427	0.304	0.031	0.126
	G. morhua	4	42.5	248	1.643	0.061	1.676	0.698	0.026	0.713
	G. ogac	5	35.5	379	1.017	0.055	0.525	0.361	0.020	0.187
	G. ogac	6	44	40	1.030	0.134	0.911	0.453	0.059	0.401
	G. morhua	7	41	186	1.155	0.074	0.854	0.508	0.032	0.376
	G. morhua	8*	38.5	6	3.895	0.059	3.910	1.500	0.023	1.505
	G. morhua	9	35.5	271	1.599	0.067	1.438	0.568	0.024	0.510
	G. morhua	10	33.5	345	1.050	0.058	0.601	0.352	0.019	0.201
2010	*G. ogac*	20	35	660	0.833	0.035	0.505	0.291	0.012	0.177
	G. ogac	21*	49	-	-	-	-	-	-	-
	G. ogac	22	37	1169	1.127	0.031	0.782	0.417	0.011	0.289
	G. ogac	23	32	454	1.036	0.050	0.621	0.332	0.016	0.199
	G. ogac	24*	31.5	-	-	-	-	-	-	-
	G. morhua	25	45	341	0.762	0.041	0.501	0.343	0.019	0.225
	G. morhua	26*	47	-	-	-	-	-	-	-
	G. morhua	27*	38.5	2	2.590	0.044	2.590	0.997	0.017	0.997
	G. morhua	28	29	169	1.661	0.109	1.257	0.482	0.032	0.365

$bl \cdot s^{-1}$ (0 to 1.57 $m \cdot s^{-1}$) for *G. morhua* and 0 to 5.07 $bl \cdot s^{-1}$ (0 to 1.53 $m \cdot s^{-1}$) for *G. ogac* but medians differed significantly between species with *G. ogac* on average moving at slower speeds (Kruskal-Wallis ANOVAs, ROM: H = 4.34, df = 1, p = 0.037; relative ROM: H = 3.87, df = 1, p = 0.038). ROMs and relative ROMs did not vary within species or between years (Kruskal-Wallis ANOVAs, $p > 0.05$) (Table 3.4). Neither mean ROMs nor mean relative ROMs were significantly correlated with body size for *G. morhua* (Spearman rank correlations, $p > 0.05$). For *G. ogac*, a significant positive correlation between TL and mean ROM was observed (Spearman rank correlation, $r_s(8) = 0.81$, p = 0.015) however, mean relative ROMs were not related to body size. For *G. morhua*, ROMs and relative ROMs did not vary among diel periods (Kruskal-Wallis ANOVAs, ROM: H = 2.96, df = 2, p = 0.228; relative ROM: H = 2.55, df = 2, p = 0.280). For *G. ogac* relative ROMs differed among diel periods, with fish moving faster during crespuscular and nighttime periods (H = 7.28, df = 2, p = 0.026) however relative ROMs did not differ among periods (H = 3.88, df = 2, p =0.143). Between species comparisons of ROMs among diel periods showed significant differences for day (Kruskal-Wallis ANOVAs, H = 4.83, df=1, p 0.028) and crepuscular (H = 4.34, df=1, p = 0.037) periods but not for night (H = 2.10, df=1, p = 0.148) (Figure 3.6). Analysis of ROMs by tidal phase showed significant differences among phases for both species (Kruskal Wallis ANOVAs, *G. morhua*: H = 16.9, df = 3, p = 0.001; *G. ogac*: H = 36.9, df = 3, $p < 0.001$) with the highest rates occurring during low and flood tides. Comparisons between species showed significant differences for all tidal phases (Kruskal-Wallis ANOVAs, low: H = 15.1, df=1, $p < 0.001$; flood: H = 37.2, df=1, $p < 0.001$; high: H = 51.8, df=1, $p < 0.001$;

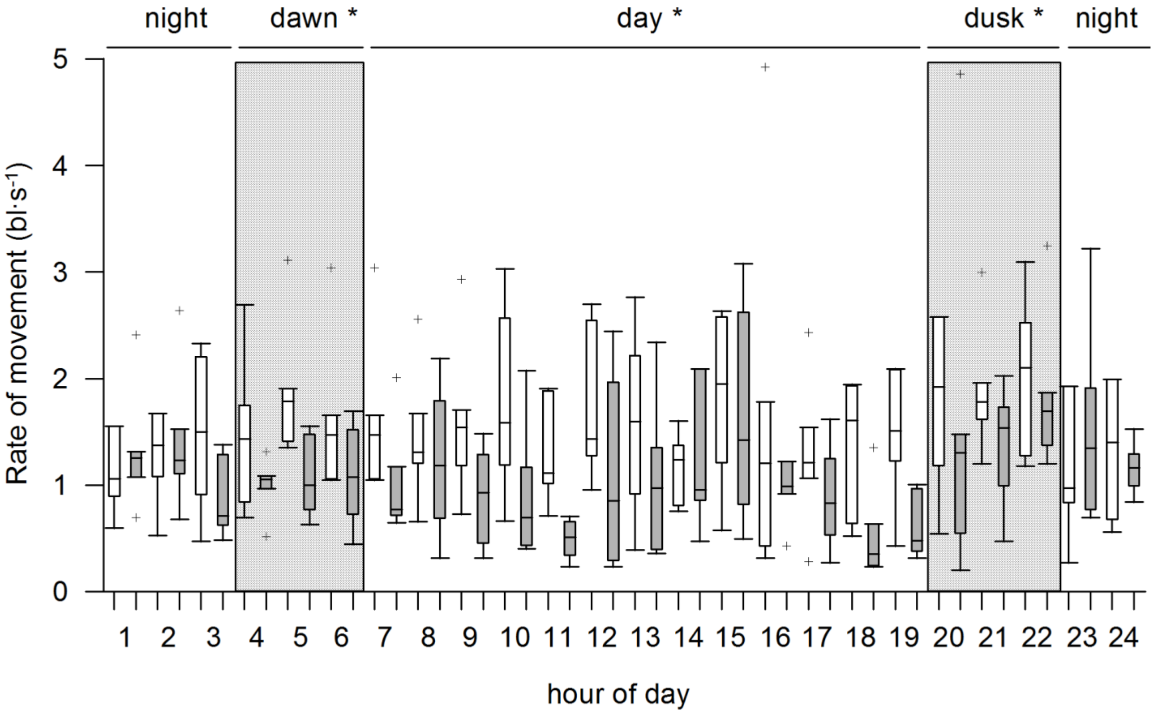

Figure 3.6 Box-Whisker plots of hourly movement rate (bl·s^{-1}) for *G. morhua* (open boxes) and *G. ogac* (shaded boxes) over a diel cycle. The box is defined by the lower and upper quartiles, also shown are the median and caps delimiting extreme values (with outliers). Shaded areas represent approximate mean crepuscular times (1 hour before and after mean sunrise and sunset for the study duration). Asterisks indicate significant differences between species for a given diel period ($p < 0.05$; Kruskal-Wallis ANOVAs). Note - dawn and dusk periods combined (crepuscular) for statistical testing.

ebb: H = 8.7, df=1, p = 0.003). Mean distance traveled per day ranged from 507 to 2180 m and from 675 to 2689 m for *G. ogac* and *G. morhua*, respectively (Table 3.1). Distance traveled per day was not significantly higher for *G. morhua* (Kruskal-Wallis ANOVA, H = 0.54, df = 1, p = 0.462) and was not related to fish size for either species (Kruskal-Wallis ANOVAs, *G. ogac*: $r_s(9) = 0.367$, p = 0.332 0.05; *G. morhua*: $r_s(9) = -0.280$, p = 0.434).

3.3.4 Acoustic Observations

Acoustic data from the echosounder-equipped vessel indicated loose schools of juvenile *G. morhua*, likely 3 and 4 year-olds based on target strength to length conversions (Rose and Porter, 1996). These fish were typically outside the array on the seafloor slope at depths from 15-40 m. Individual larger Atlantic cod (target strengths in the negative low-30s, hence >50 cm) were occasionally and sporadically detected and caught in deeper water (> 40 m). Pelagic fish schools, notably those of capelin, were rarely observed within or outside the study area in either year.

3.4 Discussion

The behavioural differences demonstrated by our data between the sympatric congenerics, *G. morhua* and *G. ogac*, suggest that spatial and temporal separation occurs during the summer season. Although both species showed high site fidelity, *G. morhua* occupied larger home ranges and core areas, moved at faster rates and were more active throughout the diel cycle than *G. ogac* of the same size. Hence, hypotheses that no difference would occur in their characteristics are rejected. The present results are consistent with previous studies indicating that spatial and temporal partitioning plays an important role in facilitating the coexistence of closely related fish species (e.g., Baker and Ross 1981; Ross 1986; Jepsen et al. 1997; Weston et al. 2010). The summer period is a key growth period for gadoids at these latitudes (Mello and Rose 2005), hence summer separation is likely key to co-existence. We note that spatial and temporal overlap between these two species may be greater at other times of the year, but less important to co-existence.

3.4.1 Residency

The present results indicate a high degree of site fidelity in both species with the majority captured and released within the study area staying there for the duration of the study. High site fidelity may be beneficial if an area encompasses optimal habitat and an adequate food supply since ranging behaviour should result in increased energy costs and predation risk (Dodson 1997). Site fidelity may enable an individual to learn the locations of productive feeding areas and resting sites (Helfman et al. 2009), and to avoid predation. In coastal Newfoundland, older juvenile *G. morhua* prefer structured habitat and areas with moderate to high bathymetric relief (Gregory and Anderson 1997; Cote et al. 2001; 2004; Knickle and Rose unpublished). Reports of habitat associations for *G. ogac* are generally lacking, however Morin et al. (1991) found this species preferred shallow (2-5 m) coastal waters, characterized by patches of eelgrass (*Zostera marina*) and laminarian kelp. Knickle and Rose (unpublished), in an allied study, reported structurally complex habitat (i.e., dense kelp patches interspersed with rocky outcroppings) and areas with high bathymetric relief throughout the study area. Furthermore, all tagged fish were caught by angling, indicating that fish were actively feeding at the time of the study. These observations suggest that site fidelity in both species was a result of individuals remaining within or in close proximity to preferred habitat that provided food and protection from predators.

Residency was lower and the number of detections outside the hydrophone array higher in 2009 than in 2010, particularly for *G. morhua*, which may have been related to warmer water conditions in 2009 (Figure 3.7). As cod at these latitudes typically avoid water > 8.5°C (Rose and Leggett 1989), higher water temperatures in 2009 likely resulted in less movement with fish exploiting cooler bottom waters. Lower overall water temperatures in 2010 likely resulted in more movement in and out of the hydrophone array.

Our results are consistent with single species tagging studies of juvenile *G. morhua* that reported limited summertime movements (Pihl and Ulmestrand1993; Svendsen 1995) but contrast with results in Clark and Green (1990) in which juveniles left the study site after being released in summer and moved extensively (> 3 km/day). The latter authors did report high site fidelity and limited movements by all (n = 11) fish during the fall (mid-Sept to Dec). They attributed the seasonal shift in behaviour to the disappearance of the summer thermocline and concluded that summer movements were associated with energetic benefits accrued by foraging in warm, shallow areas and resting in deeper, cooler waters. Similarly, Cote et al. (2004) found juvenile *G. morhua* showed

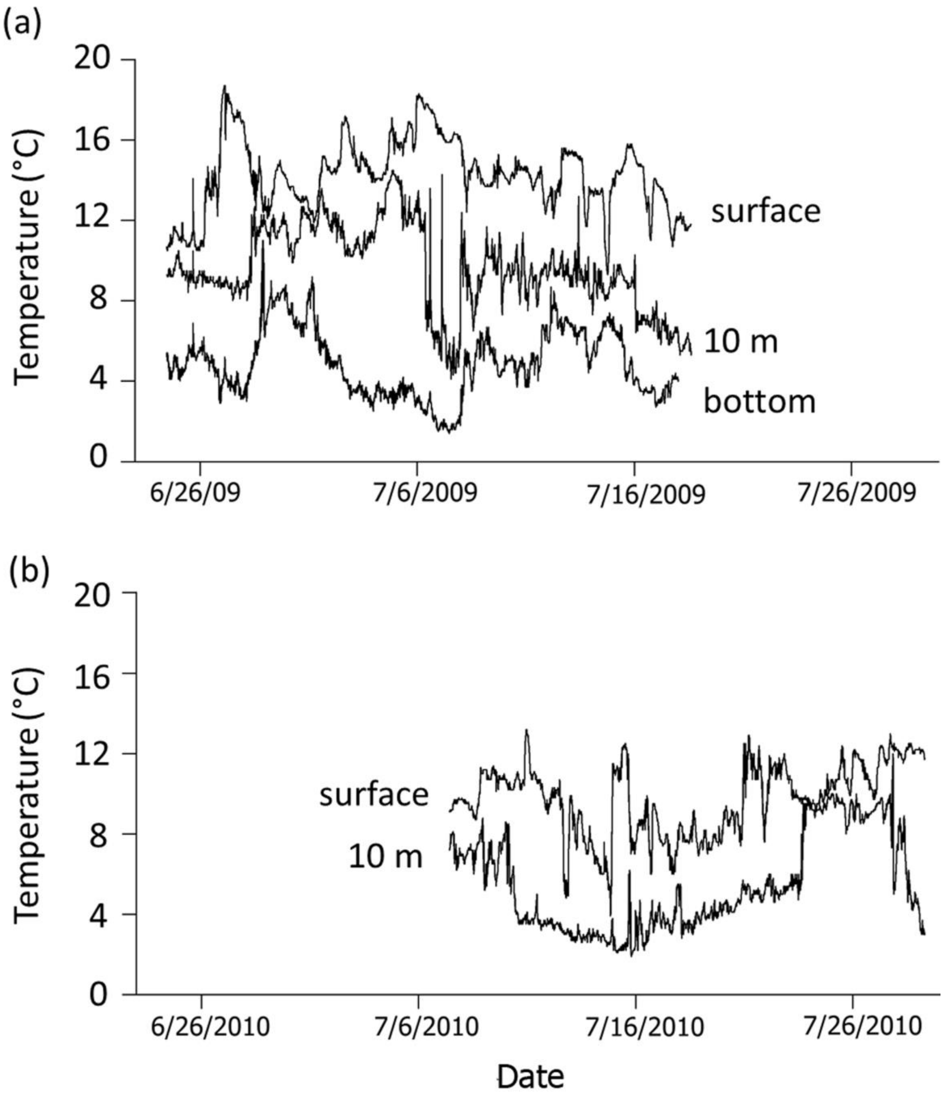

Figure 3.7 Water temperature at the study site in (a) 2009 and (b) 2010. (Note – no data for bottom temperatures in 2010).

strong site-fidelity in the fall, prior to winter migration which was precipitated by the water column becoming isothermal. In the present study, however, site fidelity was high in summer despite a strong thermocline during both years (Figure 3.7). Alternative explanations for discrepancies between studies remain speculative but may be related to the larger detection radius of the hydrophone array used in the present study (~300 m) that was roughly twice that (4 times the area) of the system used by Clark and Green (1990). However, this would not account for the considerable distances traveled the night of release by several fish in the previous study. Differences in observed behavioural patterns may relate to small sample sizes and different habitats. Sample sizes for high-resolution tracking studies are limited by technological constraints of the positioning system (e.g., Løkkeborg et al. 2002). It is noteworthy that while most fish in the present study showed strong site fidelity, a few moved several kilometers from the release site (i.e., fish #29, Figure 3.3) similar to summer movements reported by Clark and Green (1990). Furthermore, the maximum distance from the tagging site recorded for any fish was ~4 km (fish #21 and #29) but manual tracking was not performed beyond 5 km, therefore it is possible that some fish moved greater distances, similar to those reported for summer by Clark and Green (1990).

For *G. ogac*, this study corroborates other studies reporting limited movements (Mikhail and Welch 1989; Morin et al. 1991). Nevertheless, two individuals (fish #s 20 and 21) were relocated > 4 km from the release point, demonstrating that *G. ogac* is capable of moving considerable distances. This notion is supported by Morin et al. (1992)

who suggested that Greenland cod moved seasonally between estuarine and coastal waters (Morin et al. 1991).

3.4.2 Spatial Utilization/Home Range

The larger home ranges and core activity areas of *G. morhua* provide evidence of differential use of space between species which we suggest is related to differences in foraging strategies and/or prey selection. Recent studies from coastal Newfoundland have shown differences in dietary habits with *G. morhua* consuming more pelagic items and *G. ogac* consuming mainly benthic organisms (Knickle and Rose 2013). Hence, it is plausible that the larger home ranges and greater daily distances traveled by *G. morhua* reflect a more active foraging strategy (i.e., searching behaviour) and preference for more mobile and pelagic prey. Conversely, the smaller ranges and shorter daily distances traveled by *G. ogac* may indicate more of an ambush strategy and preference for more sedentary prey. In support of this hypothesis, recent stomach content studies showed a high proportion of bottom-dwelling polychaetes and pelagic hyperiid amphipods in the stomachs of *G. ogac* and *G. morhua,* respectively (Knickle and Rose 2013).

While general patterns were evident, we found considerable individual variation in space use in both species. The reasons for this are unknown but may be related to size, sex, or food availability. Sex could not be determined prior to tagging and prey distribution was not assessed. In contrast to Pihl and Ulmestrand (1993) who reported a positive relationship between distance traveled and body size for *G. morhua* in Swedish waters, we found no relationship between body size and area occupied (home range). For

G. ogac, however, larger fish had larger home ranges, perhaps reflecting a need for additional space and resources (Kramer and Chapman 1999).

Daily home ranges for *G. morhua* were comparable to reports from previous summer (Hawkins et al. 1980) and fall (Clark and Green 1990) studies. Total period home range estimates were similar to those reported for late and early winter by Cote et al. (2004) and comparable but somewhat larger than those reported for fall by Clark and Green (1990).

Home range results for *G. ogac* are in accordance with other studies that suggest that *G. ogac* has a relatively sedentary inshore distribution (Jensen 1948; Mikhail and Welch1989; Nielsen and Andersen 2001). Our results contrast with those of Morin et al. (1991) who concluded that *G. ogac* has a large and diffuse home range.

3.4.3 Rates of movement

The overall higher rates of movement for *G. morhua* suggest greater mobility than for *G. ogac*. Diel patterns of movement also differed, with *G. ogac* being more nocturnally active and *G. morhua* active throughout the diel cycle. Rates of movement for fish are normally indicative of foraging, anti-predator, or spawning behaviour. Since all *G. morhua* in this study were almost certainly immature based on size and any mature *G. ogac* would have spawned in late-winter or early spring (Scott and Scott 1988; Cohen et al. 1990), any effect of reproduction on fish activity is unlikely. Predator avoidance also seems unlikely as large (> 60 cm) Atlantic cod that can prey on smaller conspecifics and *G. ogac* (Chaput 1981; Nielsen and Andersen 2001; Knickle and Rose 2013) were rarely observed within the hydrophone array during echosounding observations during daylight hours and near dusk when both species were active. The observed movements of tracked fish were most likely related to searching for and consuming food. *G. morhua* prefer food in the water column over food on the bottom (Brawn 1961) and comparative diet studies have revealed a higher proportion of pelagic prey items for *G. morhua* (Chaput 1981; Knickle and Rose 2013). Conversely, *G. ogac* is an opportunistic benthic feeder (Jensen 1948; Chaput 1981; Mikhail and Welch 1989; Knickle and Rose 2013).

Rates of movement for *G. morhua* were somewhat higher but comparable to those from similar studies (Løkkeborg et al. 2002, Fernö et al. 2011), with differences consistent with swimming speeds increasing with rises in ambient water temperatures (Peck et al. 2006). For example, Fernö et al. (2011) studied deeper Norwegian waters (50 to 70 m) at temperatures from 5 to 6 °C whereas much of our study took place in < 10 m of water at mean temperatures of 6 to 12 °C. Earlier field studies of tracked cod (Hawkins et al. 1980; Hawkins et al. 1985; Løkkeborg 1998; Løkkeborg and Fernö 1999; Svendsen 1995, Cote et al. 2002) reported much lower rates of movement but these results almost certainly underestimated swimming speeds, as these studies did not account for the bias associated with large position fixing intervals (Lagardère et al. 1990; Løkkeborg et al. 2002). This study provides the first reports of swimming speeds for *G. ogac* which were higher than those reported for other gadiformes (Sarno et al. 1994; Løkkeborg et al. 2000).

3.4.4 Activity Patterns

Although differences in diel patterns were evident, both species showed increased activity during the crepuscular period; a pattern that has been shown for *G. morhua* (Løkkeborg et al. 2002). Crepuscular activity is thought to increase the probability of encountering and capturing prey (Helfman 1986). Alternatively, Clark and Green (1990) suggested that diel activity patterns for juvenile *G. morhua* were related to predator avoidance from larger cod. While adult *G. morhua* are present in Smith Sound during the summer months (Rose 2007; Knickle and Rose 2011) they pose a predation risk to both species of young gadids (Nielsen and Andersen 2001; Knickle and Rose 2013). If activity patterns of juvenile *G. morhua* were related to predator avoidance, juvenile *G. ogac* might be expected to have shown a similar diel pattern. Our data do not support this, but are consistent with the hypothesis that diel activity relates to temporally different prey availability or selection by these two species (Helfman 1986). Data on prey availability and selection would be needed to address this hypothesis.

Our results for *G. morhua* are consistent with those from Cote et al. (2002) who reported juvenile fish were active throughout the diel cycle but differ from data obtained by Clark and Green (1990) who found juveniles were most active at night. Although no significant difference in movement rates between diel periods was observed for *G. morhua*, movement rates were generally higher during the day than at night; an observation that is consistent with other juvenile and adult cod studies from coastal areas that suggest this species is more diurnally active (Hawkins et al. 1980; Løkkeborg 1998; Løkkeborg and Fernö 1999; Løkkeborg et al. 2002). The present results for *G. ogac* are consistent with Morin et al. (1991) who suggested lower daytime activity levels for this species.

Explanations for the high rates of movements by both species during the low and rising (flood) tidal phases are speculative, however, fish may be exploiting food resources made available by the incoming tides or actively foraging at low tide when prey may be more concentrated in shallow waters.

In conclusion, *G. morhua* and *G. ogac* show different spatial and temporal distributions and behaviours. We conclude that differences in home ranges, rates of movement and diel activity is consistent with spatial and temporal partitioning during the key summer growth period and that such partitioning likely facilitates co-existence of these closely related species in coastal waters of the North Atlantic.

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Chapter 4. Microhabitat use and vertical habitat partitioning of juvenile Atlantic (*Gadus morhua*) and Greenland (*Gadus ogac*) cod in coastal Newfoundland

Abstract

Twenty co-occurring juvenile gadids (10 *Gadus ogac* and 10 G*adus morhua*) were surgically implanted with ultrasonic transmitters with depth sensors and continuously monitored for up to 23 days in the summers of 2009 and 2010 to test fine-scale habitat use and vertical distribution overlap in coastal Newfoundland (>18700 positional fixes). A habitat map with 8 substrate and 3 slope classes (low (<5°), moderate (5-10°), and high (>10°)) was generated from acoustic data and coincident video data using seabed mapping software (QTC). Fish locations were integrated with a habitat map to assess and quantify habitat preference. Both species avoided fine gravel/sand substrates with little vegetation and selected for large particle (cobble and boulder) substrates with moderate or dense vegetation, and spent the majority of time in < 10 m of water. Nevertheless, species differences in habitat use were evident. *G. ogac* typically remained in close proximity to the seafloor whereas *G. morhua* was often distributed more pelagically and showed greater variation in vertical distribution. Habitat use and vertical distribution patterns were consistent across the diel period. Our results suggest that despite high overlap in habitat use, *G. morhua* and *G. ogac* often segregate vertically in the water column, which may reduce competitive interference. We suggest that these patterns are related to differences in diet.

4.1 Introduction

Divergent habitat selection is a common attribute of closely related species that may reduce competition and promote coexistence (Pianka 1973; Schoener 1974; Ross 1986; Morris 2003). Atlantic cod (*Gadus morhua*) and Greenland cod (*Gadus ogac*) are two congeneric species of gadids that co-occur as juveniles in coastal areas of Newfoundland and Labrador and more northern areas to Greenland (Scott and Scott 1988; Rose 2007). It has been suggested that competition for resources between the two species is likely (Cohen et al. 1990), however few studies on their interactions exist.

Recent studies suggest that sympatry of these species is facilitated primarily through partitioning of food resources, with *G. morhua* pursuing more pelagic prey (Knickle and Rose 2013) and to a lesser extent by differences in activity patterns (Knickle and Rose unpublished). However, microhabitat partitioning could also be an enabler of sympatry but has not been studied in these species. Competition for habitat can negatively impact fitness components such as growth and survival by forcing individuals to use habitats that offer less protection from predators or poorer foraging opportunities (Kramer et al. 1997).

Despite being an important commercial species for 500 years (Rose 2007), habitat associations of age 2-4 juvenile *G. morhua* in coastal Newfoundland remain uncertain. Several studies have shown juveniles preferred areas with macroalgae and/or coarse substrates and generally avoided fine substrates (Keats et al. 1987; Gotceitas et al. 1997; Gregory and Anderson 1997; Cote et al. 2001; 2003; 2004). Other studies reported that juveniles did not associate with macroalgae (Keats 1990; Gregory and Anderson 1997) or typically occurred over sand (Clark and Green 1990). No studies of habitat utilization by *G. ogac* have been reported from Newfoundland waters. In other regions, adult and juvenile *G. ogac* occupied shallow (2-5 m) coastal waters characterized by belts of eelgrass (*Zostera marina*) during summer in southern Hudson’s Bay (Morin et al. 1991) and were observed in slightly deeper water (< 35 m) more northerly (Mikhail and Welch 1989)

In this study, we combined acoustic habitat mapping with radio-acoustic positioning of individual fish to compare fine-scale habitat utilization of co-occurring juvenile *G. morhua* and *G. ogac* in coastal Newfoundland. Based on previous studies, we hypothesized that both species would select for similar habitat types and show a preference for coarse substrates and areas with macroalgae while avoiding open areas and fine substrates. We also hypothesized that *G. morhua* but not *G. ogac* would show a preference for areas of high bathymetric relief and that *G. ogac* would be more benthically distributed as compared to more pelagic distributions of *G. morhua*.

4.2 Methods

4.2.1 Study Area

The study was carried out in a small cove located in Smith Sound on the western side of Trinity Bay, Newfoundland, Canada (48°10'N, 53°44' W) (Figure 4.1). Water depth at the site ranged from < 1 m to > 50 m. The site comprised various habitat types ranging from flat, open areas to structured rock formations to densely vegetated (*Laminaria sp*) areas. Juvenile *G. ogac* and *G. morhua* are known to co-occur in this area and were commonly

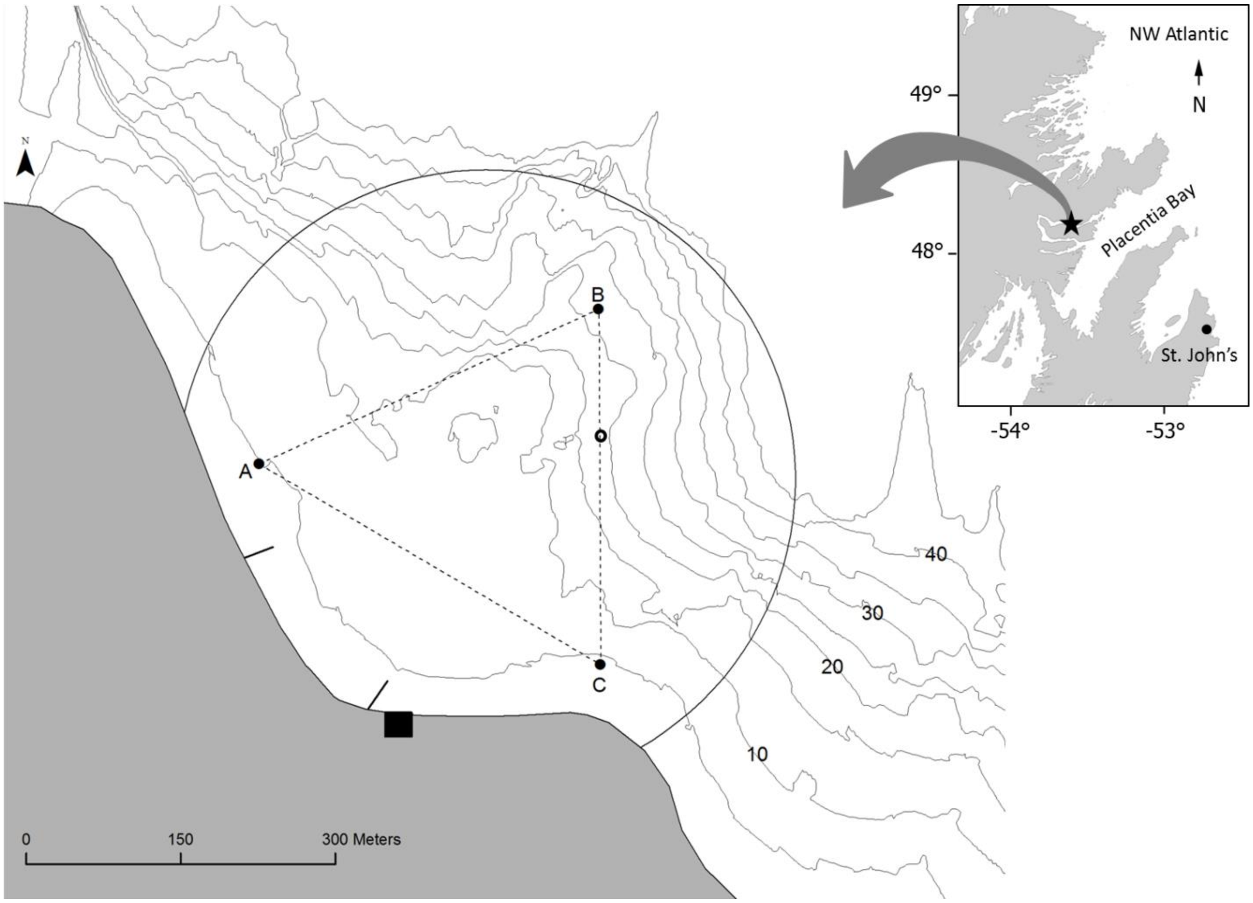

Figure 4.1 Map of study area. Inset shows study site relative to the eastern portion of Newfoundland. Enlarged area shows position of hydrophone array (• - radio-acoustic buoys A-C), base station (■), position of temperature loggers (○), wharves (—), positional range (circular black line - 300 m radius from array centre) and depth contours from acoustic recordings from the present study.

encountered during previous unrelated studies (e.g., Knickle and Rose 2010). The hydrophone array of the acoustic positioning system used to monitor individuals covered an area approximately 5.7 ha while the detection range of the system encompassed roughly 25 ha (Figure 4.1).

4.2.2 Habitat Mapping

A combination of acoustic remote sensing and underwater video were used to create a map of the study area. Repeated acoustic surveys were conducted over 2 days in July of 2009 using a calibrated (Foote et al. 1987) Biosonics DT-X digital echosounder system (Biosonics Inc., Seattle, WA, USA) with 120 kHz single beam (6º) and 200 kHz split-beam (6.5º) transducers, mounted in close proximity on the RV "Gecho" (6 m). The transducers transmitted 0.4 ms pulses alternately at the rate of 5 pulses s^{-1}, with an internal digitizing depth increment of approximately 1.4 cm. The vessel performed a series of overlapping transects spanning the detection range of the positioning system at a speed of 3-4 knots (Figure 4.2). The vessel drew < 0.5 m of water and was able to survey very close to shore to water depths less than the beam forming range of the transducers (approximately 3 m). Substrate composition was semi-quantitatively verified with video footage *in situ* using a submersible video camera (Sea-Drop 950, Sea Viewer Cameras, Inc., Tampa, FL) deployed from the vessel. Date/time stamps and GPS data enabled acoustic data and video to be matched closely. Substrate composition was verified at 125 locations (Figure 4.2).

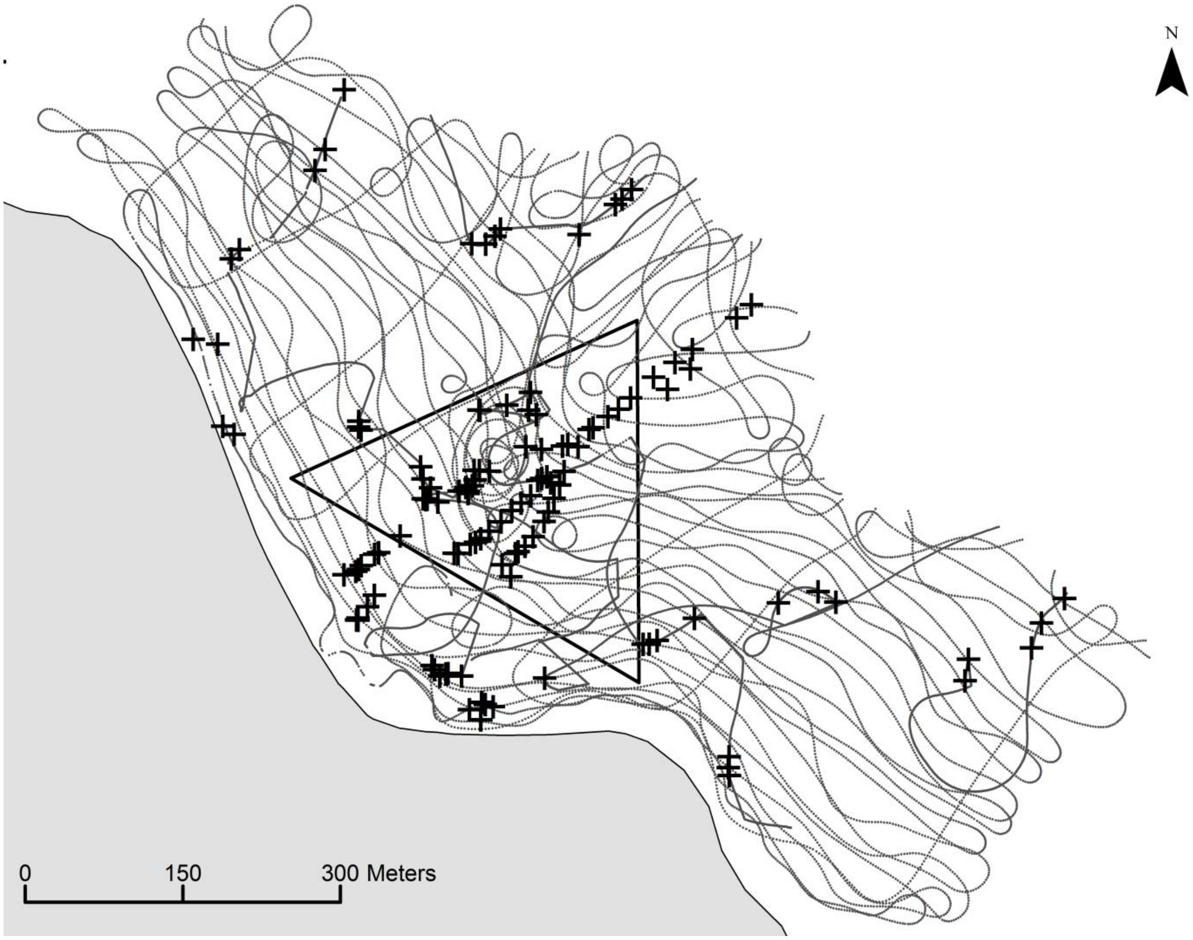

Figure 4.2 Acoustic survey tracks (dotted lines) (15-17 Jul, 2009) and seabed video locations (+).

Acoustic data was analyzed and integrated using QTC IMPACT (acoustic seabed classification for echo sounders) (Quester Tangent Corporation, Saanichton, BC, CAN). This software system analyses return echoes from the seafloor and groups them into classes based on similarities in vertical patterns and strengths of the backscatter. We used the software's automated clustering function to determine an optimal number of classes. We subsequently grouped several classes based on similar acoustic properties and video images to reduce the total number of substrate classes to within the range (8 – 12) usually produced with higher resolution sidescan acoustics (J.T. Anderson, DFO, ST. John's, NL, personal communication, 2012). Finally, derived classes were interpolated between tracks using the inverse distance weighting (IDW) method in ArcMap 9.3 (ESRI, Redlands, CA, USA). Although biotic habitat features (namely macrophyte distribution) may vary seasonally, we observed no notable changes in macrophyte distribution between years therefore the final map generated was assumed to be representative of the habitat in both years of the study. Substrate particle size was estimated by keeping the camera a fixed distance (~1 m) from the bottom to maintain a consistent field of view. As well, objects of known size (i.e., from anthropogenic sources) on the substrate provided an additional means to approximate particle size.

To generate a bathymetric profile of the study area, acoustic estimates of depth to the seafloor were edited in Echoview 4.8 (Myriax Pty Ltd., Hobart, Tasmania, AUS), then corrected for tidal amplitude and plotted on a geo-referenced map of the study area and interpolated by inverse distance weighting (IDW) in ArcMap 9.3 (ESRI, Redlands, CA, USA). The slope tool in ArcMap was used to calculate the slope (°) of the seabed within the study area and create three classes of bathymetric relief: low (<5° slope), moderate (5-10° slope), and high (>10° slope). Surface (~1 m), mid-water (~10 m) and bottom (~20 m) water temperatures were recorded at 5 minute intervals at a fixed location within the study area (Figure 4.1) using Minilog data loggers (VEMCO Division, AMIRIX Systems Inc., NS, CAN).

4.2.3 Tagging and Tracking

Juvenile (~30-45 cm TL) Atlantic and Greenland cod were caught within the study area by angling using single, barbless hooks and selected for tagging to provide a comparable size range between species. Fish were placed in an anaesthetic solution of MS-222 and sea water (~0.1 g of per L) until equilibrium was lost. Fish were then measured and a continuous acoustic transmitter (VEMCO V9P-1H, 9 x 40 mm, 5.2 g in air) equipped with a pressure sensor was implanted in the body cavity through a small (ca. 1 cm) incision made in the belly anterior to the vent and slightly offset from the mid-ventral line. A single suture was used to close the wound and fish were placed in fresh sea water to recover. Once recovered, fish were released at or near the point of capture. Tagged fish were tracked on a continuous basis using an acoustic positioning system (VEMCO VRAP, Vemco, Bedford, NS, CAN) consisting of three fixed hydrophone buoys equipped with radio antennas arranged in a triangle over the study area (Figure 4.1). Buoy hydrophones received acoustic pulses from transmitters and relayed the information via radio signal to a land-based station where the data was viewed and stored on computer disc. The exact position of each transmitter was triangulated autonomously by the system based on the time delay in pulses arriving at each buoy. Tags set at three different frequencies (63, 75, and 81 kHz) transmitted every 15-35 s. The system could potentially record an individual’s position in 3 dimensions approximately once every 180 s. The accuracy of the system was tested by mooring a stationary transmitter at a known location within the study area. Mean (± SE) positional accuracy was 2.48 m ± 0.25 m inside the buoy array and 6.53 ± 0.17 m outside the array and was similar to other studies (Sauer et al. 1997; O’Dor et al. 1998; Klimley et al. 2001; Barnett et al. 2010). To determine the acoustic range of the system, a single transmitter was lowered to a depth of ~10 m from a research vessel at increasing 50 m intervals from the centre of the array. Range tests showed successful detections beyond 450 m, however, a conservative 300 m effective detection range was used because positional accuracy is known to decrease with distance from the array (e.g., O’Dor et al. 1998; Klimley et al. 2001; Espeland et al. 2007). The accuracy of the pressure sensor within transmitters was tested by anchoring a stationary transmitter for an extended period of time during calm conditions and examining the statistical dispersion of depth measurements. Mean (± SE) depth for a transmitter moored at approximately 12.5 m was 12.66 ± 0.04 m (n = 295).

4.2.4 Habitat Associations

Tracking data obtained within the first 24 hours after tagging and release were omitted from analyses to remove any potential effect of surgical implantation on fish behaviour (see Cote et al. 1999). Past 24 h post-released there was no indication of lethargic behaviour that differed from the remainder of the study period. The remaining positional fixes were plotted on the geo-referenced habitat map of the study area and a small number (< 1%) of invalid fixes (i.e., detections on land, detections from unrecognized transmitter IDs, etc.) were removed. The proportion of fixes occurring within each habitat type was determined using Hawth's Analysis Tools for ArcMap (Beyer 2004). To test whether each species used habitats in proportion to their availability or were selecting for certain habitats, log-likelihood chi-square tests with fish as sampling units were used (Manly et al. 2002; Rogers and White 2007). The first test determined whether selection for specific habitats was occurring while the second determined whether individuals were utilizing habitats similarly. The difference between the two chi-squares defined whether on average, habitat types were used in proportion to their availability. Where non-proportional use was determined, habitat preference and avoidance was assessed using selection ratios defined as habitat utilization (proportion of fixes in a certain habitat) divided by habitat availability (proportion that particular habitat type available within the 300 m detection range). Bonferroni-adjusted 95% confidence intervals were calculated for each selection ratio and intervals encompassing the value 1 indicated proportional habitat use based on availability. Intervals where the lower limit > 1 indicated selection for a given habitat while those where the upper limit < 1 indicated avoidance (Manly et al. 2002). Selection ratios and confidence intervals were calculated for total, day and night periods. To quantify overlap in habitat use between species the proportional use of each habitat class for each species was determined and compared using the following equations from 1) Pianka (1973): $O = \sum_i^n p_{ij} \, p_{ik} / \sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}$, and 2) Schoener (1970): $O = 1 - 0{\cdot}5 \left(\sum | p_{ij} - p_{ik} |\right)$, where p_{ij} and p_{ik} represent the proportional use of habitat class *i* by species *j* and *k*, respectively. Index values ranged from 0 (no overlap) to 1 (complete overlap) with values ≥ 0.6 generally considered to be biologically significant (Wallace 1981).

4.2.5 Depth Distribution

To examine the vertical distribution of tagged individuals relative to bottom depth, we integrated bathymetry and fish depth data based on spatial location then subtracted fish depth from bottom depth to obtain a measure of altitude. Welch's t-tests were used to test for differences in depth and altitude between species for total, day and night periods defined as the time between sunrise and sunset and sunset and sunrise, respectively. F-tests were used to test for differences in variances in depth and altitude between species while regressions were used to test whether fish size was related to depth and altitude.

4.3 Results

Twenty fish (10 *G. morhua* and 10 *G. ogac*) were tracked continuously for periods up to 23 days resulting in > 18 700 detections with the VRAP system between 24 June and 17 July, 2009 and 7-28 July, 2010 (Table 4.1). All fish survived the implantation and were detected with the VRAP system except for fish 21 (*G. ogac*, 49.0 cm) which left the study area immediately after release and was detected manually 13 days later, approximately 4 km from the release point. Mean (± SE) fish length did not differ between years (ANOVAs, $p > 0.05$), therefore telemetry data for both years were pooled by species.

Table 4.1 Data summary for all fish monitored in Smith Sound, 2009-2010 (*- omitted from analyses).

Fish ID	Species	Year	TL (cm)	No. detections	No. days tracked	Mean (± SE) Depth (m)	Mean (± SE) Altitude (m)
1	*G. ogac*	2009	34	635	23	8.34 ± 0.079	0.27 ± 0.121
2	*G. ogac*	2009	41	847	22	7.11 ± 0.064	0.53 ± 0.119
3	*G. ogac*	2009	29.5	744	21	8.52 ± 0.073	0.55 ± 0.108
4	*G. morhua*	2009	42.5	1742	23	7.30 ± 0.040	1.08 ± 0.054
5	*G. ogac*	2009	35.5	1702	23	6.56 ± 0.058	1.13 ± 0.134
6	*G. ogac*	2009	44	296	14	10.87 ± 0.314	1.75 ± 0.216
7	*G. morhua*	2009	41	582	10	6.60 ± 0.155	3.11 ± 0.148
8	*G. morhua*	2009	38.5	136	15	10.81 ± 0.276	0.75 ± 0.208
9	*G. morhua*	2009	35.5	1589	21	7.54 ± 0.048	0.83 ± 0.084
10	*G. morhua*	2009	33.5	1707	21	8.55 ± 0.026	0.45 ± 0.034
20	*G. ogac*	2010	35	1159	13	7.24 ± 0.035	1.05 ± 0.050
21*	*G. ogac*	2010	49	0	0	-	-
22	*G. ogac*	2010	37	2932	22	7.12 ± 0.038	1.89 ± 0.047
23	*G. ogac*	2010	32	1399	19	6.90 ± 0.051	2.12 ± 0.069
24	*G. ogac*	2010	31.5	876	20	5.75 ± 0.045	2.89 ± 0.067
25	*G. morhua*	2010	45	1053	22	6.38 ± 0.059	2.98 ± 0.074
26*	*G. morhua*	2010	47	8	1	23.87 ± 2.540	5.58 ± 1.170
27	*G. morhua*	2010	38.5	56	6	8.05 ± 0.929	8.41 ± 0.769
28	*G. morhua*	2010	29	731	14	7.74 ± 0.216	7.03 ± 0.145
29	*G. morhua*	2010	37	609	8	5.88 ± 0.088	9.27 ± 0.157

Total Period Mean	*G. ogac*	7.60 ± 0.496	1.35 ± 0.289
	G. morhua	7.65 ± 0.485	3.77 ± 1.180
Daytime Mean	*G. ogac*	7.74 ± 0.375	1.23 ± 0.314
	G. morhua	7.92 ± 0.476	3.75 ± 1.050
Nighttime Mean	*G. ogac*	7.31 ± 0.848	1.70 ± 0.319
	G. morhua	7.17 ± 0.562	4.49 ± 1.600

4.3.1 Habitat Mapping

Seafloor substrate identified by video footage varied from solid rock and boulders to fine gravel and sand (Figure 4.3). Cabbage kelp (*Laminaria longicruris*) was the dominant macrophyte and was abundant in areas < 10 m deep, often creating narrow, maze-like pathways between the vegetation (Figure 4.3a). Red seaweeds (rhodoliths, *Porphyra* sp.) and brown algae (*Desmarestia viridis*) were also present (Figure 4.3b). Kelp patches were generally dense, often prohibiting the visual identification of substrate particles. Closer to the center of the array, a shallow rocky outcropping comprised mainly of solid rock (Figure 4.3c) and boulders was evident in both video and acoustic data. Deeper areas (> 30m) were generally characterized by little or no vegetation and fine gravel substrate (Figure 4.3d). Based on dominant substrate particle size and degree of macrophyte coverage determined from video footage, the unsupervised seabed classification derived by the QTC software was selected to represent: 1) fine gravel/sand (< 0.3 cm diameter), 2) fine gravel/sand with moderate (25-50%) coverage, 3) coarse gravel (0.3-10 cm) with moderate coverage, 4) coarse gravel with dense (> 50%) coverage, 5) small cobble (10-15 cm) with dense coverage, 6) large cobble (15-20 cm) with dense coverage, 7) boulders (>20 cm) with moderate coverage and 8) solid rock (Figure 4.4).

4.3.2 Habitat Utilization

Both species exhibited strong selection for certain types of substrate and bathymetric relief (Log likelihood chi-square tests; Table 4.2). Over the entire diel cycle, both species avoided fine gravel/sand substrates with little vegetation and selected for small and large

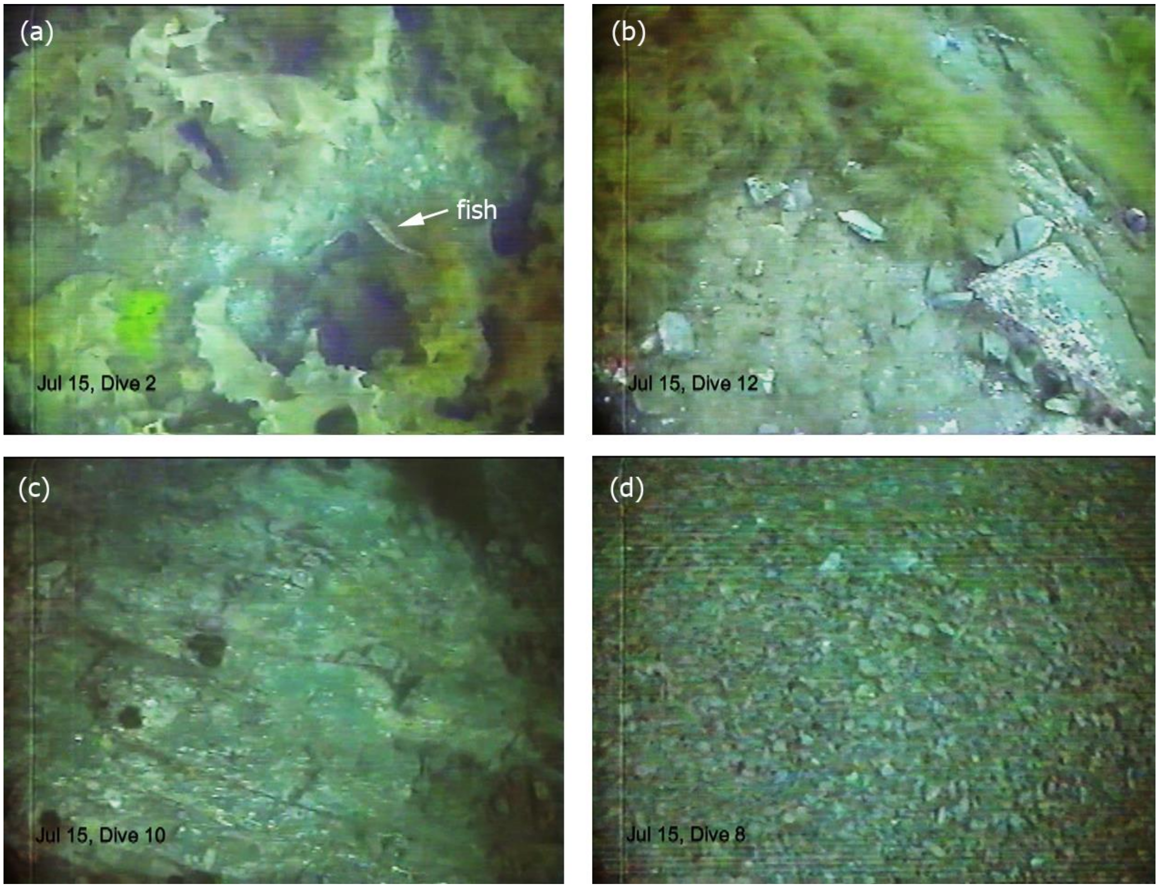

Figure 4.3 Example images from video ground-truthing observations of the seafloor: (a) coarse gravel with > 50% vegetation (*Laminaria sp*) coverage (with unknown fish), (b) large cobble and boulders with 50% vegetation (*Desmarestia viridis*), (c) solid rock, and (d) fine gravel.

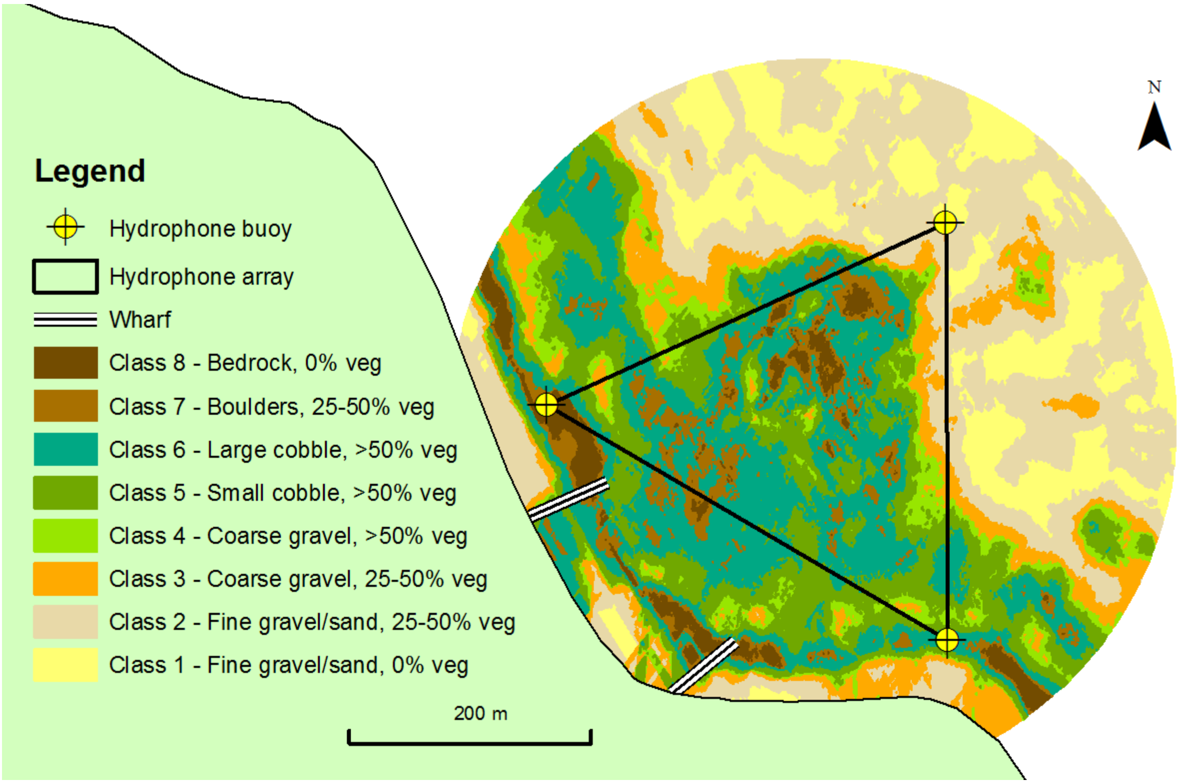

Figure 4.4 Results of the seabed substrate unsupervised classification.

Table 4.2 Results of log-likelihood chi-square tests comparing habitat use and proportion of availability for tagged *G. ogac* and *G. morhua*. The results of the first tests indicate that both species were selective in the types of habitat while the second tests establish that fish used habitats very differently from one another. The difference between the chi-square tests demonstrates strong selection for certain habitat types within species.

			Substrate			Slope		
	Fish #	**N**	**DF**	**Chi-Sq**	**P-Value**	**DF**	**Chi-Sq**	**P-Value**
G. ogac	1	635	7	884	<0.001	2	658	<0.001
	2	847	7	785	<0.001	2	398	<0.001
	3	744	7	960	<0.001	2	744	<0.001
	5	1702	7	1528	<0.001	2	785	<0.001
	6	296	7	159	<0.001	2	80	<0.001
	20	1159	7	1524	<0.001	2	918	<0.001
	22	2932	7	3011	<0.001	2	1331	<0.001
	23	1399	7	1981	<0.001	2	979	<0.001
	24	876	7	1533	<0.001	2	464	<0.001
	Total	**10590**	**63**	**12368**	**<0.001**	**18**	**6361**	**<0.001**
	Fish*Habitat		**56**	**1202**	**<0.001**	**16**	**259**	**<0.001**
	Difference		**7**	**11165**	**<0.001**	**2**	**6101**	**<0.001**
	Fish #	**N**	**DF**	**Chi-Sq**	**P-Value**	**DF**	**Chi-Sq**	**P-Value**
G. morhua	4	1742	7	1895	<0.001	2	1387	<0.001
	7	582	7	544	<0.001	2	14	<0.001
	8	136	7	87	<0.001	2	3	0.149
	9	1589	7	1417	<0.001	2	521	<0.001
	10	1707	7	2357	<0.001	2	1964	<0.001
	25	1053	7	703	<0.001	2	179	<0.001
	27	56	7	5	0.5562	2	2	0.262
	28	731	7	148	<0.001	2	116	<0.001
	29	606	7	76	<0.001	2	86	<0.001
	Total	**8213**	**63**	**7235**	**<0.001**	**18**	**4276**	**<0.001**
	Fish*Habitat		**56**	**1821**	**<0.001**	**16**	**2272**	**<0.001**
	Difference		**7**	**5414**	**<0.001**	**2**	**2004**	**<0.001**

cobble and boulder substrates with moderate or dense vegetation (Figure 4.5a). *G. ogac* also avoided coarse gravel with moderate vegetation whereas *G. morhua* neither selected nor avoided this substrate (Figure 4.5a). In daytime, both species avoided fine gravel/sand substrates with little vegetation and selecting for cobble and boulders with moderate or dense vegetation (Figure 4.5b). In addition, *G. morhua* selected for coarse gravel with moderate vegetation and both species avoided areas with boulders and no vegetation (Figure 4.5b). At night, as in daytime, both species avoided fine gravel/sand substrates with little vegetation and coarse gravel with moderate vegetation and selected for small and large cobble with moderate and dense vegetation (Figure 4.5c). Bedrock with no vegetation was also avoided at night by both species (Figure 4.5c). Preference and avoidance for the same habitat was generally stronger in *G. ogac* (Figure 4.5). Both species showed strong selection for low (0-5° slope) relief areas and avoidance of moderate (5-10° slope) and high (>10° slope) relief areas both day and night (Figure 4.6). Selection for and avoidance was generally stronger for *G. ogac* except for at night when selection ratios were similar (Figure 4.6). Both overlap indices showed high overlap for substrate (Pianka: O = 0.98; Schoener: O = 0.87) and slope (Pianka: O = 0.98; Schoener: O = 0.88).

4.3.3 Depth and Altitude Distribution

Mean depth and altitude for each fish as well as for each species by diel period are shown in Table 4.1. Overall, 78% of detections for *G. morhua* were between 5 and 10 m, 13.6% were at depths less than 5m and 8.2% were at depths greater than 10 m. For *G. ogac*, 80.2

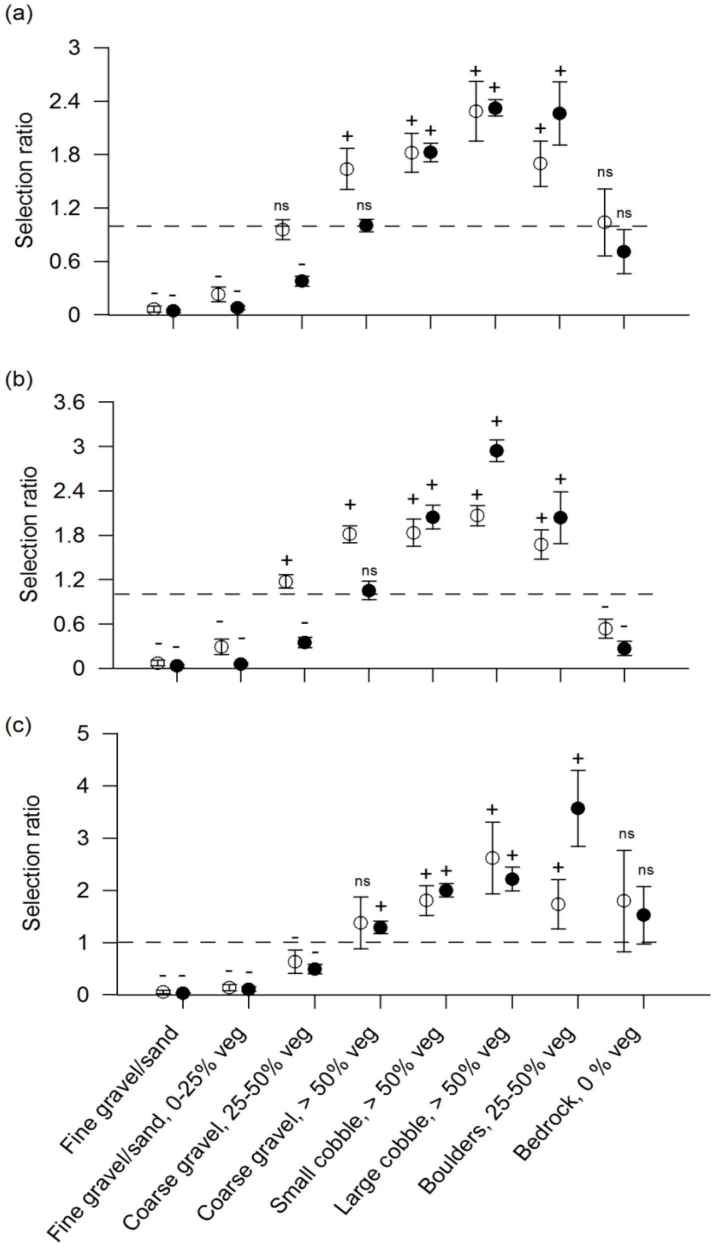

Figure 4.5 Selection ratios with Bonferroni-adjusted 90% CIs by substrate class for *G. ogac* (●) and *G. morhua* (○) calculated for (a) total, (b) daytime and (c) nighttime periods. In each panel, the horizontal dashed line indicates an index value of 1 (proportional use of habitat). Symbols indicate selection for (+), proportional use (ns) and avoidance (-) of habitat types.

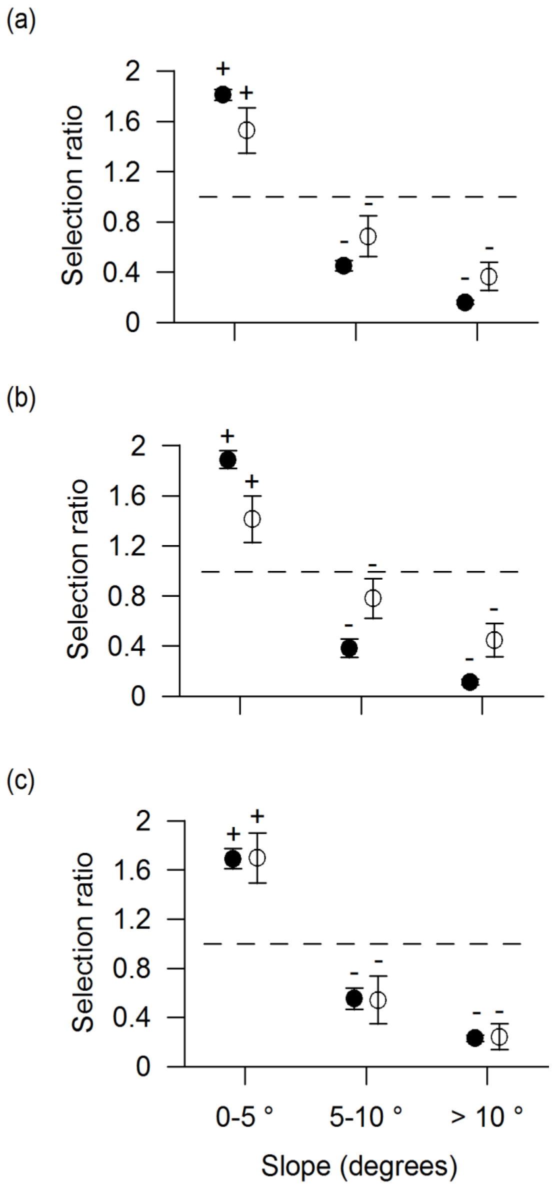

Figure 4.6 Selection ratios with Bonferroni-adjusted 90% CIs by bathymetric relief (slope) class for *G. ogac* (●) and *G. morhua* (○) calculated for (a) total, (b) daytime and (c) nighttime periods. In each panel, the horizontal dashed line indicates an index value of 1 (proportional use of habitat. Symbols indicate selection for (+), proportional use (ns) and avoidance (-) of habitat types.

% of detections were between 5 and 10 m, 14.8 % were at depths less than 5m and 5 % were at depths greater than 10 m. The maximum depths recorded were 28.5 m (fish 6) and 36.8 m (fish 28) for *G. ogac* and *G. morhua*, respectively. Mean depth occupied did not differ between species for total, daytime or nighttime periods (Welch's t-tests, $p > 0.05$). *G. ogac* was generally distributed closer to the bottom than *G. morhua* for all periods, however only mean daytime altitude was significantly different between species (Welch's t-test, $t = -2.30$, $p = 0.047$) (Figure 4.7). Variances for depth did not differ between species (F-test, $F_{(9,9)} = 1.04$, $p > 0.05$). *G. morhua* had a significantly greater variance in altitude than *G. ogac* (F-test, $F_{(9,9)} = 16.7$, $p < 0.01$) (Figure 4.7). A significant relationship between body size (TL) and maximum depth was observed for *G. ogac* ($r^2 = 55.1$, $p = 0.022$, $n=9$) but not *G. morhua* ($p = 0.207$). Body size was not significantly related to mean depth or altitude for either species ($p > 0.05$).

4.4 Discussion

Results from the present study suggest that juvenile *G. ogac* and *G. morhua* in coastal Newfoundland occupied the same habitats and were distributed at similar depths of < 10 m. Nevertheless, altitudes differed significantly with *G. morhua* on average located further from the seafloor both day and night and showing more variation in altitude. Both species selected for moderately to densely covered areas with large substrate particles and (cobble and boulders) and low bathymetric relief areas, while avoiding substrates having little or no vegetation and fine substrate particles and moderate to high bathymetric relief.

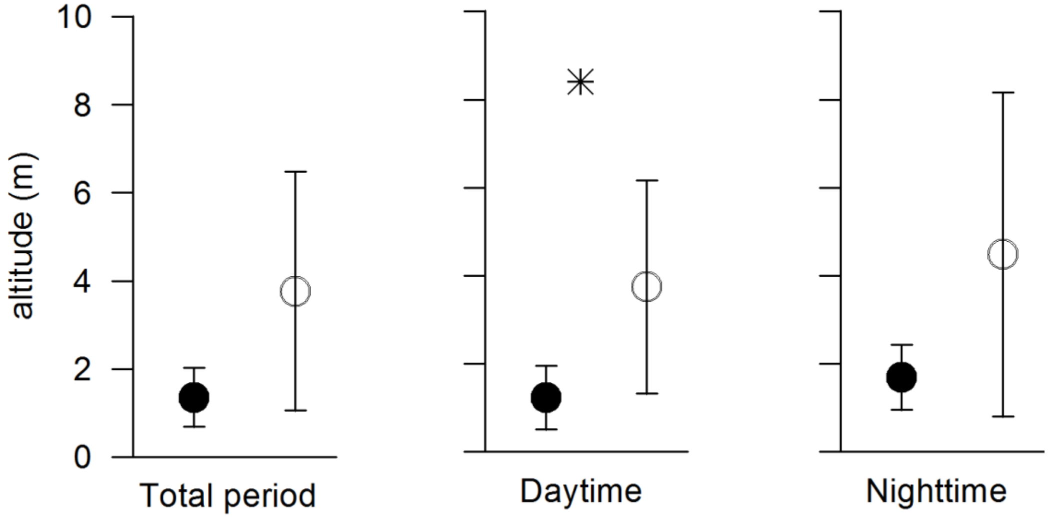

Figure 4.7 Plots of mean altitude (± CI) for *G. ogac* (●) and *G. morhua* (○) for total, daytime and nighttime periods. Asterisk indicates significant difference in mean altitudes (Welch's t-test, $p < 0.05$).

4.4.1 Habitat Use

A preference for areas with coarse substrates and dense aquatic vegetation habitat by both species was likely related to predator avoidance and/or foraging. Several single-species studies have shown that younger juvenile *G. morhua* (age 0-1+) selected coarse substrates and vegetated areas to reduce risk of predation (e.g., Gotceitas and Brown 1993; Gotceitas et al. 1995; 1997; Linehan et al. 2001). Other studies from coastal Newfoundland have shown that older (age 2-4) juvenile *G. morhua* were typically associated with macroalgae and/or coarse substrates (Keats et al. 1987; Gregory and Anderson 1997; Cote et al. 2001; 2003; 2004). Large (> 60 cm) cod are known to prey on smaller conspecifics as well as *G. ogac* (Chaput 1981; Nielsen and Andersen 2001; Knickle and Rose 2013), and were observed acoustically and caught by angling in close proximity to the study area. Hence, selection by both young gadids for complex substrates is consistent with an anti-predator strategy.

Our results are inconsistent with single-species studies that reported older juvenile *G. morhua* were not associated with macroalgae (Keats 1990; Gregory and Anderson 1997) or were typically observed over sand (Clark and Green 1990). Gregory and Anderson (1997) speculated that the lack of association with macroalgae in their study was due to seasonal differences in juvenile and adult (predator) distribution and suggested older juveniles may only associate with macroalgae in summer and fall. In our summertime study, juveniles of both species showed a strong selection for coarse substrates and areas with dense algae. Predator (large cod) abundance varies seasonally in Smith Sound (Rose 2003) and more generally in coastal waters of the northeast coast of

Newfoundland. Hence, if predator avoidance is the key factor in habitat selection by juvenile gadids, then their location and spatial overlap is likely to vary seasonally. Further studies are required to address this hypothesis.

It is also possible that juvenile gadids prefer complex and macrophyte habitats because of the availability of food (e.g., Morin et al. 1991 for *G. ogac*). Dietary overlap between juvenile *G. morhua* and *G. ogac* does occur, with both species feeding on organisms typically associated with inshore macroalgae beds such as polychaetes and benthic fish (e.g., shannys; *Stichaeidae*)) (Scott and Scott 1988; Christian et al. 2010). Nevertheless, there are key differences is the diets of these gadids (Chaput 1981; Knickle and Rose 2013) which might be expected to lead to different habitat use patterns if food is the key factor. The more benthic habits of *G. ogac* may be related to the more benthic diet of this species in comparison to the more pelagic behaviour of *G. morhua.*

The strong association with areas of low bathymetric relief by both species was not expected *a priori* and conflicts with single-species studies that have reported that older juvenile *G. morhua* select for areas of medium and high relief in coastal Newfoundland (Gregory and Anderson 1997; Cote et al. 2004). However, in both the latter studies, coarse substrate (cobble, rock/boulder) and high bathymetric relief were generally found together and whether juveniles were selecting for habitat based on substrate type or vertical relief remained unclear. Considering all the evidence, we suggest that juvenile habitat of both gadids in summer is largely determined by substrate type and macrophyte coverage and not bathymetric relief, although combinations of these features may be relevant (Gregory and Anderson 1997).

4.4.2 Vertical Distribution

Whereas many habitat preferences were shared by these co-occurring juvenile gadids, the most apparent difference was a propensity for *G. morhua* to be distributed higher in the water column and display greater variation in altitude as compared to *G. ogac.* Young *G. morhua* appear to adapt to a more pelagic existence while *G. ogac* is primarily demersal. We further suggest that even a small segregation along the vertical habitat dimension may assist coexistence between these two species and that this pattern is likely a component of differences in foraging behaviour. *G. morhua* tends to have a higher proportion of pelagic food items (Chaput 1981; Knickle and Rose 2013) and a more pelagic stable isotope signature than does *G. ogac* (Knickle and Rose 2013).

In the present study, both species maintained similar depth and altitude distributions across the diel cycle. These results differ from reports for *G. morhua* in summer by Clark and Green (1990) in which older juveniles rested in cooler, deep (> 30m) water during the day and moved to warmer, shallower water at night. Differences in water temperature regimes might explain these differences. In the present study, both species occupied deeper water and were positioned closer to the bottom in 2009 when bottom temperatures were considerably warmer than in 2010 (Figure 4.8). Temperature is well known to influence inshore cod distribution (e.g., Rose and Leggett 1988) and it is likely that this factor will influence selection for habitat as well as feeding opportunities.

In conclusion, our results suggest the co-occurring *G. morhua* and *G. ogac* are partitioning habitat by having different vertical distributions over the same grounds. These results are consistent with other studies with closely related fish species (e.g.,

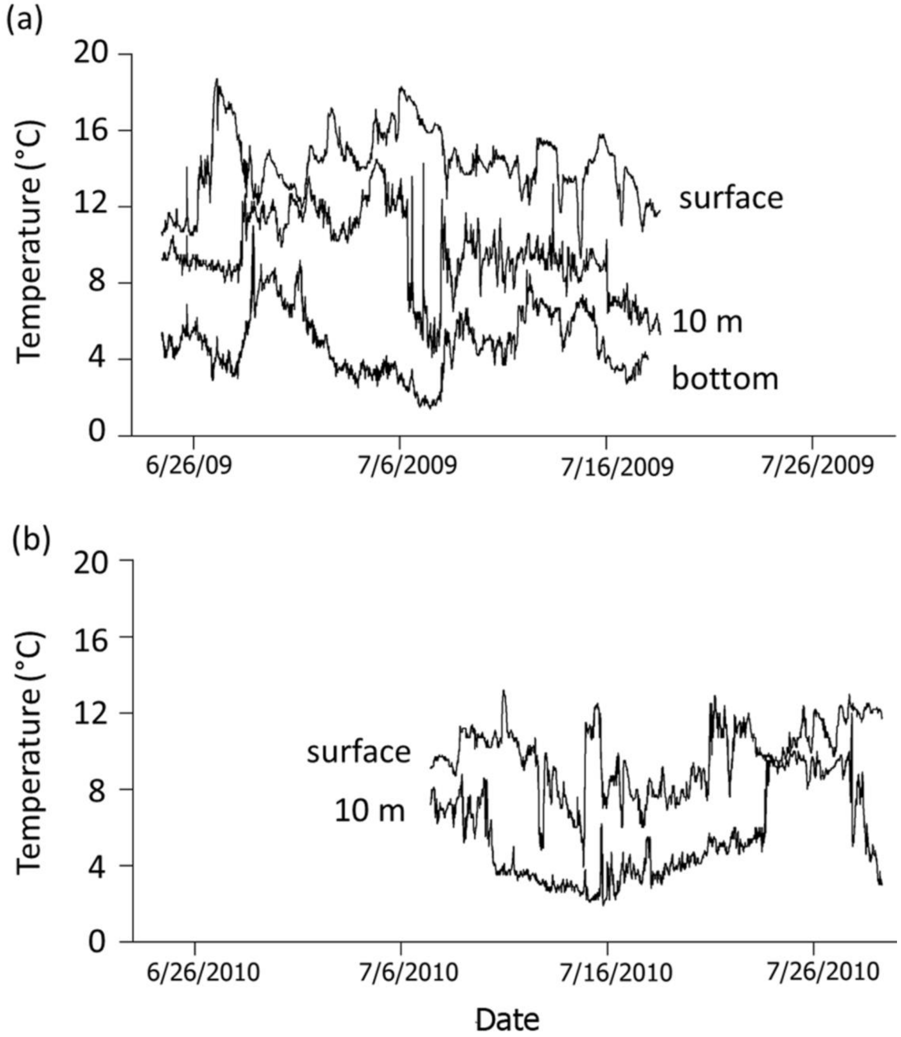

Figure 4.8 Water temperature data at the study site in (a) 2009 and (b) 2010. (Note – no data for bottom temperatures in 2010).

Baker and Ross 1981; Shpigel and Fishelson 1989; Goldschmidt et al. 1990; Albertson 2008). We suggest that this segregation is largely the *modus operandi* of differences in foraging strategies and prey selection.

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Chapter 5. Comparing growth and maturity of sympatric *Gadus morhua* and *Gadus ogac* in coastal Newfoundland

Abstract

Growth and maturity of two sympatric gadids were examined from 48 Atlantic cod (*Gadus morhua* L., 1758) and 42 Greenland cod (*Gadus ogac* Richardson, 1836) ranging from 17-74 cm in length collected from an inshore area of Trinity Bay, Newfoundland during 2009 and 2010. Ages estimated from otolith readings ranged from 2-7 for both species. Age and size at 50 % maturity differed between species, being 2.3 years and 28.2 cm for *G. ogac* and 4.6 years and 48.8 cm for *G. morhua*. Von Bertalanffy growth models did not differ between species with parameters L_∞ = 91 cm, k = 0.16 yr^{-1}, t_0 = -0.02 yr for *G. ogac* and L_∞ = 112 cm, k = 0.13 yr^{-1}, t_0 = 0.18 yr for *G. morhua*. Length-weight relationships differed; $W = 0.000005\ \text{kg}\cdot\text{cm}^{-b} * L^{3.17}$ for *G. ogac* and $W = 0.000011\ \text{kg}\cdot\text{cm}^{-b} * L^{2.91}$ for *G. morhua* suggested slightly positive and negative allometric growth, respectively. For *G. morhua*, growth curves, length-weight relationships and maturity rates did not differ between fish collected during this and earlier studies. Differences in maturity schedules and growth may decrease resource competition and help facilitate coexistence of these species.

5.1 Introduction

The coexistence of closely related fish species is often explained by partitioning, whereby niche components are differentially utilized along one or more axes (Schoener 1974; Ross 1986). Partitioning typically occurs along trophic, spatial or temporal axes, but sympatry may also be facilitated through differences in growth and maturation rates. Such rate differences can result in different trophic requirements and habitat use and decrease resource competition (Wilson 1975; Bengtson 1984; Barnes et al. 2011).

Gadus morhua (L., 1758) and *Gadus ogac* (Richardson, 1836) are two closely related gadids that occur together in most bays in coastal Newfoundland and Labrador (Scott and Scott 1988; Rose 2007). Recent studies have shown strong dietary niche partitioning between these two species as well as differences in space use and activity patterns (Knickle and Rose unpublished). It is also believed that *G. ogac* doesn't grow as large or live as long as *G. morhua* and matures at an earlier age (Scott and Scott 1988; Cohen et al. 1990), however few growth studies for *G. ogac* exist. Growth and maturity schedules have been examined in Hudson's Bay (Morin and Dodson 1986; Mikhail and Welch 1989; Morin et al. 1991) and at West Greenland (Jensen 1948; Nielsen 1992) but little information was available from Newfoundland waters (but see Nielsen et al. 2010). The objective of this study was to compare the growth and maturity characteristics of sympatric *G. ogac* and *G. morhua* in a coastal area of Newfoundland, as a potential factor contributing to the co-existence of these congeneric species. Working hypotheses were that *G. ogac* would: 1) grow at a slower rate, and 2) mature at an earlier age than *G. morhua*.

5.2 Methods

5.2.1 Study Area and Sampling

Sampling was conducted in a small cove located in Smith Sound on the western side of Trinity Bay, Newfoundland, Canada (Figure 5.1). Water depth at the site ranged from <1 to ~50 m and substrate types varied from fine gravel to bedrock. Vegetation was dominated by kelp (*Laminaria sp.*) and coverage ranged from dense to sparse. Fish were caught within 1-2 meters of the bottom by hook and line in July of 2009 and 2010 from a 9 m research vessel (*RV Gecho II*). Fish were selected to fulfill a size range (~25-45 cm) for older juveniles (age 2-4) however several adults of both species were caught and included in the analyses. All fish were put on ice immediately after capture and were later sampled for total length, whole weight, gutted weight, sex, and reproductive stage. The liver, gonads and stomach were individually weighed and sagittal otoliths were removed and stored in envelopes for ageing. Because of the bias associated with gear selectivity and scientific permit restrictions, we were unable to obtain the recommended number of samples to obtain unbiased parameters of age and growth (i.e., 7-10 samples per 2 cm length class) (Kritzer et al. 2001). However, recent studies have shown that reasonable estimates of age and growth can be attained from limited (i.e., n < 25) samples (Smart et al. 2013). For mean age and length, estimates can be confidently estimated with as few as 25 samples (Kritzer et al. 2001). Age-at-length and maturity data for *G. morhua* from previously collected samples from Smith Sound (n=255) were also used to supplement data collected during the study period. These were collected from trawl catches from the

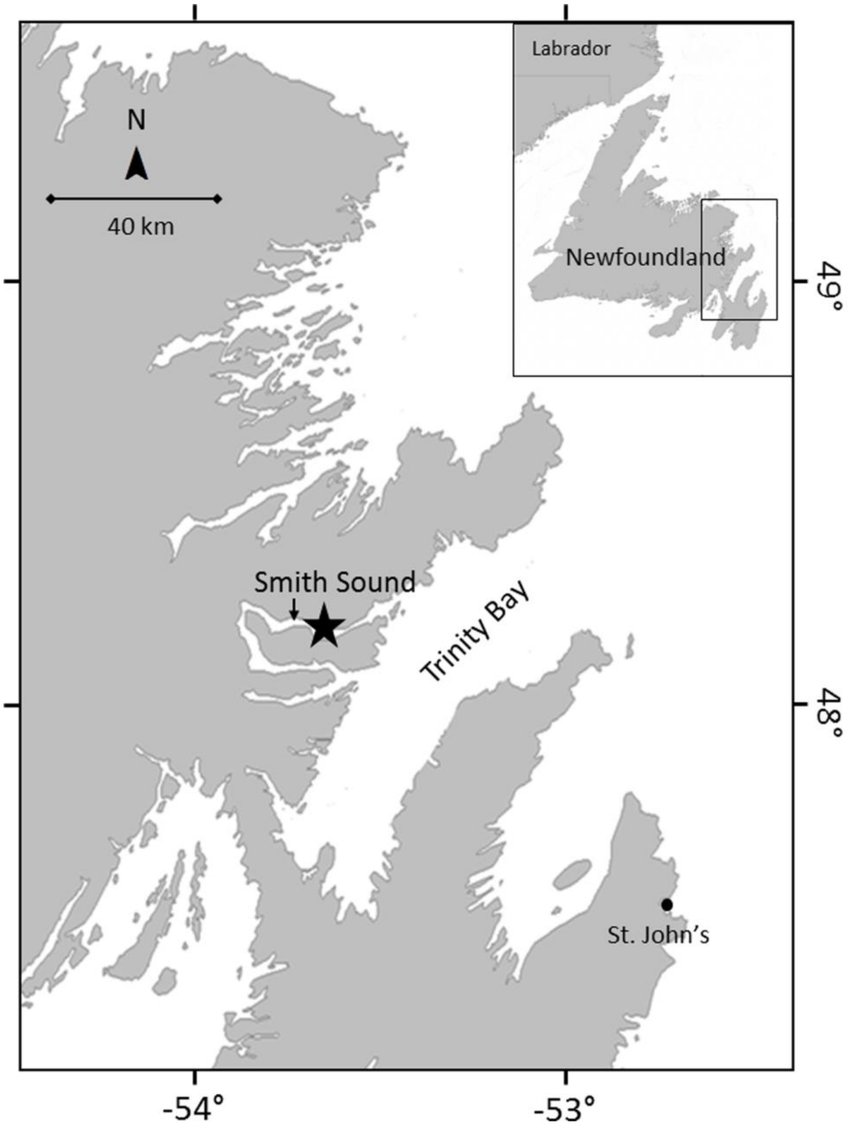

Figure 5.1 Map of the Eastern portion Newfoundland showing location of sampling area (black star) within Smith Sound. Inset shows position of enlarged map relative to the Island of Newfoundland.

CCGS Shamook (January 2006 and January and May 2007) and using hand lines from the *RV Coastal Explorer* (June 2006) as part of an unrelated study.

5.2.2 Age Determination

Stored otoliths were embedded in epoxy (Buehler Epothin resin and hardener in a 5:2 weight ratio) and allowed to cure for several days. An Isomet low-speed diamond bladed saw (Buehler IsoMet low speed saw, Pine Bluff, IL, USA) with two blades separated by a 1 mm spacer was used to section embedded otoliths. Sections were rinsed in ethanol and polished using 30 µm dry lapping film (Extec Corp., Enfield, CT, USA). After polishing, sections were photographed under reflected light with an Olympus SZX16 Research high class stereo microscope equipped with an Olympus DP72 microscope digital camera (Olympus Corporation, Tokyo, Japan). Images were enhanced with digital imaging software (Adobe Photoshop CS5 version 12.1, Adobe Systems Incorporated) to facilitate identification of annuli which were counted along two axes to estimate fish age a minimum of 3 times. A consensus age estimate was determined using the median counts for each otolith. The mean length at age for each species was then calculated and used to determine average growth rates. Ageing of previously collected samples was performed by Norman Batten, an ageing consultant and former specialist in gadoid ageing at the Department of Fisheries and Oceans (DFO), St. John’s, Newfoundland.

5.2.3 Life History Parameters

Growth was modelled using a von Bertalanffy growth model (VBGM): $L_t = L_\infty (1 - e (-k (t - t_0)))$, where L_t is the average length at age t, L_∞ is the asymptotic average length, k is the Brody growth coefficient (year^{-1}) and t_0 is the x-intercept (theoretically the age at which length = 0 cm). Starting values for L_∞ and k were estimated using the Ford-Walford plot method (Ford 1933; Walford 1946) and starting values for t_0 were subsequently determined by inserting starting values for L_∞ and k into the initial VBGF equation and algebraically solving for t_0. We tested for significant differences in growth curves between species and between data obtained during the study period and supplemental data from previous years for *G. morhua* by comparing residual sum of squares (ARSS) for non-linear models as described by Chen et al. (1992). In addition, *t*-tests were used to determine if size-at-age differed significantly between species and between study period and supplemental data for *G. morhua*. The number of samples collected during the study period was insufficient to obtain unbiased growth curves and parameter estimates for each sex. As a result, we tested for differences in length at age relationships between males and females for each species using ANCOVAs and compared mean lengths at age between sexes using *t*-tests. We tested for differences in growth curves between males and females for supplemental data using ARSS. Von Bertalanffy growth curves were fitted using Growth II software (Pisces Conservation Ltd, Hampshire, UK) and all other statistical analyses were conducted using Minitab 16.2.2 statistical program (Minitab Inc.).

Length-weight data were plotted for each species and fitted with a model for allometric growth: $Wt_g = a * L^b$, where Wt_g is gutted weight (kg), L is length (cm) and a and b are parameter estimates. Gutted weight was used rather than whole weight in order to avoid any potential bias of stomach fullness or maturity stage on the relationship. Starting values for a and b were 0.001 and 3 (isometric growth), respectively. Differences in length-weight relationships between species were evaluated using ARSS.

Maturity stage (mature or immature) was assigned by visual examination of gonads in the field following the classification scheme of Morrison (1990). Maturity curves were estimated using binary logistic regression and tested for differences between species using ARSS. The predicted age or length at 50% maturity was calculated as A (or $L)_{50} = -b_0/b_1$ where b_0 and b_1 are parameters that define the slope and position of the fitted curve.

5.3 Results

A total of 90 fish (48 *G. morhua* and 42 *G. ogac*) ranging from 2-7 years of age were sampled although few fish older than 5 years were caught (Table 5.1). Fish size ranged from 17-60 cm for *G. ogac* and 25-74 cm for *G. morhua*. Male to female ratios were 0.6 and 0.9 for *G. morhua* and *G. ogac*, respectively. No significant difference in the relationship between size and age was observed between males and females for either species (ANCOVAs, $p > 0.05$). In addition, mean size at age did not differ between sexes (when sample size was sufficient to perform tests) (*t*-tests, $p > 0.001$), hence for further analyses data were pooled by sex. Supplemental data for *G. morhua* showed no

Table 5.1 Number of samples (*n*) by age used to model growth curves.

	Age									
	2	3	4	5	6	7	8	9	10	Total
G. ogac	11	25	4	1	-	1	-	-	-	42
G. morhua	2	21	13	7	3	2	-	-	-	48
G. morhua (2005-2010)	11	15	31	47	65	35	17	16	18	255

significant difference in growth rates between sexes for fish < 7 yrs old (ARSS, $F_{3, 198} = 0.812$, $p = 0.488$), however a significant difference in growth rates between sexes was observed when fish > 7 yrs old (the maximum age observed in the present study) were included in the analysis (ARSS, $F_{3, 249} = 3.36$, $p = 0.019$).

Growth rates did not differ between species (ARSS, $F_{3, 84} = 0.437$, $p = 0.727$; Table 5.2, Figure 5.2), nor did mean size-at-age (ages 2-4 only) (*t*-tests, age 2: $t = -0.58$, $p = 0.666$; age 3: $t = -0.27$, $p = 0.790$; age 4: $t = 0.72$, $p = 0.509$). For *G. morhua* growth rates from supplemental data did not differ from those sampled during the study period (ARSS, $F_{3, 254} = 1.016$, $p > 0.05$). For all age classes except 3 year olds, mean lengths at age did not differ between *G. morhua* sampled during the study period and those collected in previous years (*t*-tests, ages 2-7, $p > 0.05$; for 3 year olds, $t = 4.73$, $p < 0.001$).

Length-weight relationships differed between species (ARSS, $F_{3, 84} = 107.2$, $p = 0.365$) (Figure 5.3). On average, *G. ogac* was heavier at length than *G. morhua*, particularly at lengths > 30 cm. The allometric growth coefficient *b* (95% CI) was 2.91 (0.08) for *G. morhua* and 3.17 (0.11) for *G. ogac* revealing slightly negative and positive allometric growth for *G. morhua* and *G. ogac*, respectively. Length-weight relationships did not differ between *G. morhua* collected in previous years and those collected during the study period (ARSS, $F_{3, 354} = 1.074$, $p = 0.360$) (Figure 5.3). For *G. morhua*, allometric growth coefficient *b* (95% CI) for supplemental data was 3.04 (0.07) and slightly higher and closer to isometric growth (i.e., $b = 3$) than for *G. morhua* sampled during the study period.

Table 5.2 Parameter estimates and 95% confidence intervals for modelled von Bertalanffy growth curves.

	G. ogac		*G. morhua*		*G. morhua* (2005-2010)	
Parameter	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
L_∞ (cm)	91.21	5.106	112.03	10.46	99.45	0.714
k (yr^{-1})	0.160	0.014	0.131	0.021	0.194	0.003
t_0 (yr)	-0.021		0.181		1.144	
n	42		48		255	

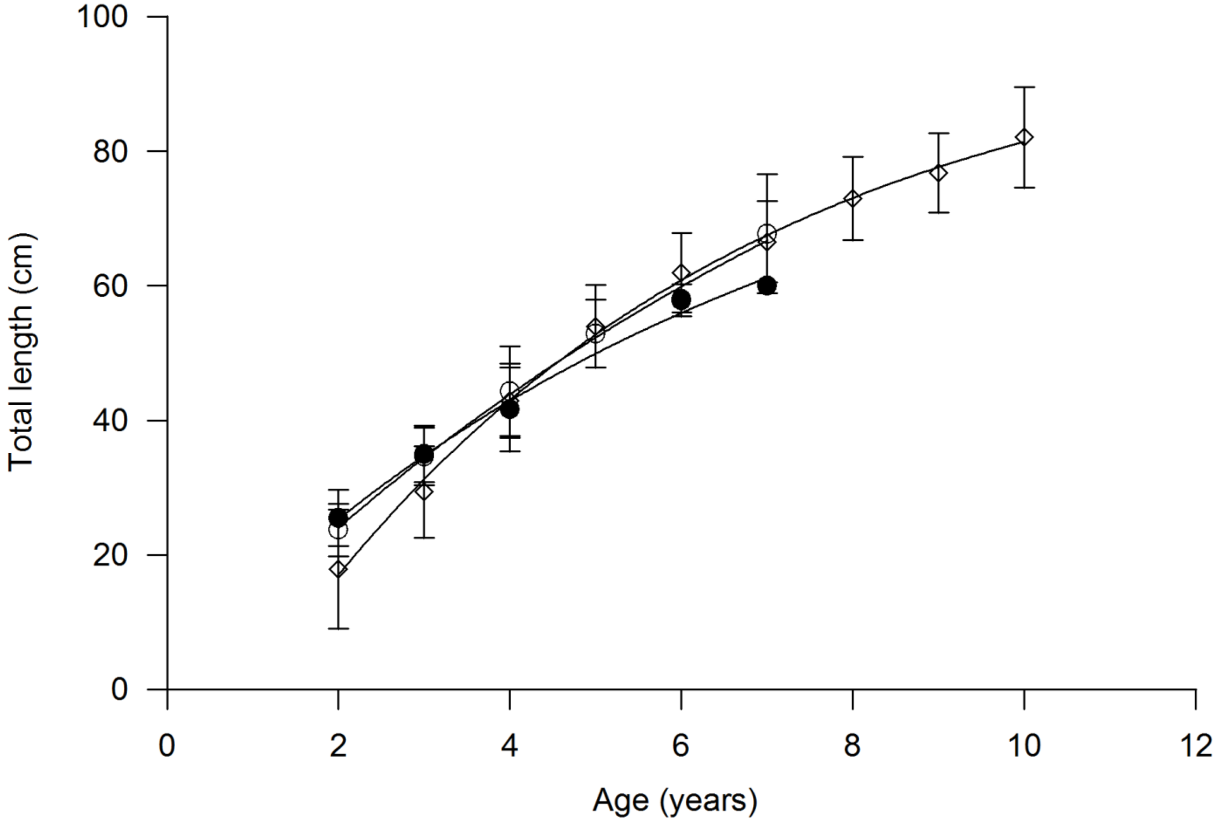

Figure 5.2 Modelled von Bertalanffy growth curves for *G. ogac* (●) and *G. morhua* (○) collected during the study period and for *G. morhua* (◊) collected from previous years in Smith Sound. Symbols are mean ± SD size at age. Parameter values for growth curves are listed in Table 5.2.

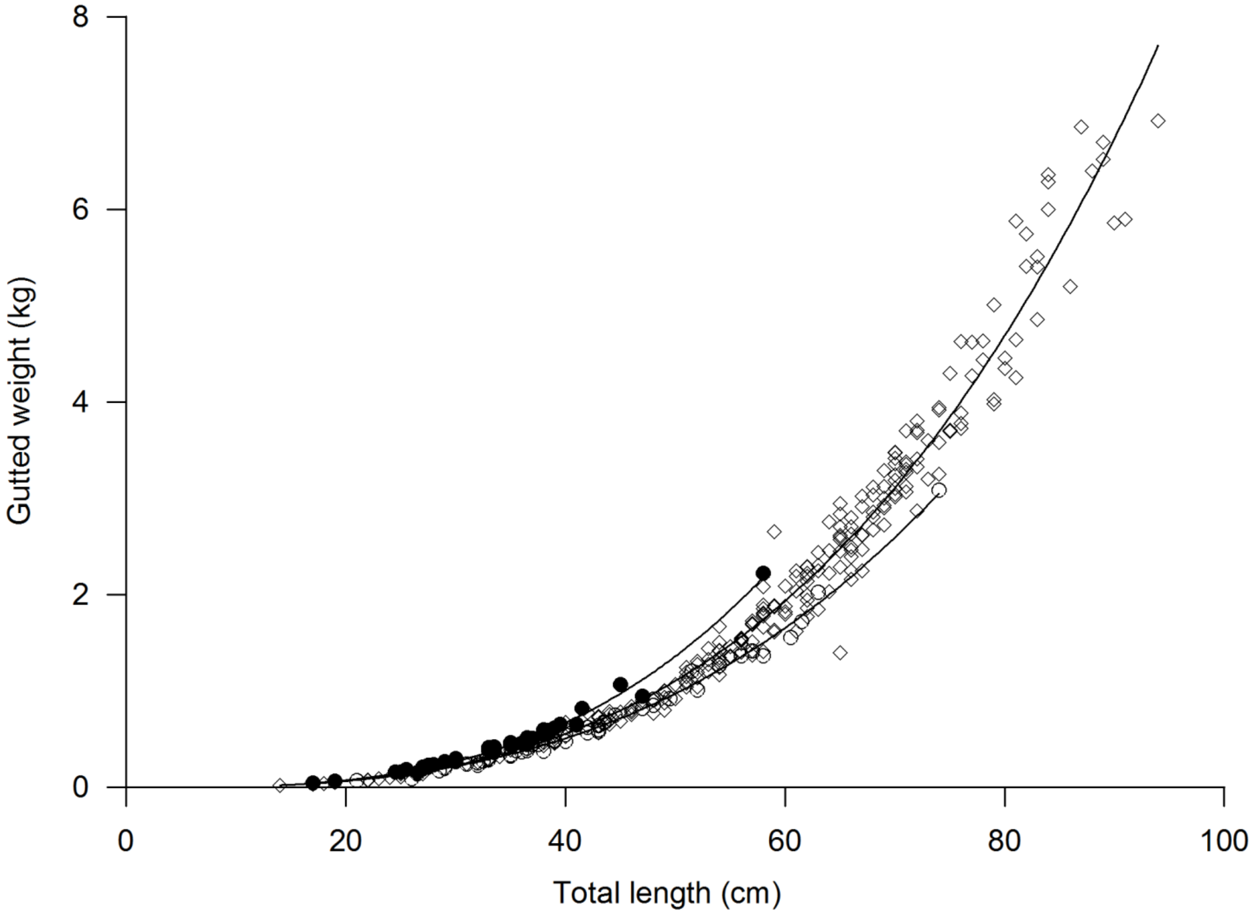

Figure 5.3 Modelled relationship between gutted weight and total length for *G. ogac* (●) ($W = 0.000005$ kg·cm$^{-b} * L^{3.17}$) and *G. morhua* (○) ($W = 0.000011$ kg·cm$^{-b} * L^{2.91}$) collected during the study period and for *G. morhua* (◊) ($W = 0.000010$ kg·cm$^{-b} * L^{3.04}$) collected from previous years in Smith Sound.

Estimated A_{50} and L_{50} was 2.31 years and 28.20 cm for *G. ogac* and 4.64 years and 48.8 cm for *G. morhua* (Figure 5.4). Maturity curves for both age and length differed significantly between species (ARSS, age: $F_{3, 84} = 345.93$, $p < 0.001$; length: ARSS, $F_{3, 84} = 138.03$, $p < 0.001$) (Figure 5.4). At age 4, 100 % of *G. ogac* were sexually mature whereas at age 7, all *G. morhua* were mature . The smallest mature *G. ogac* was a 27 cm male and the largest immature fish was a 33 cm female. The smallest mature *G. morhua* was a 49.5 cm female and the largest immature fish was a 48 cm female. A_{50} and L_{50} for *G. morhua* collected from previous years were consistent with data collected during the study period at 4.74 years and 49.10 cm, respectively (Figure 5.4).

5.4 Discussion

Our data indicate that *G. ogac* and *G. morhua* co-occur in Newfoundland coastal waters up to age 6 or 7. Over this period, these species exhibited similar growth rates. Hence, the hypothesis that *G. ogac* grows at a slower rate must be rejected. Nevertheless, parameter estimates suggest *G. ogac* grows more rapidly initially, approaching asymptotic length earlier in life and at a much smaller size than *G. morhua*. Growth rates in the present study for *G. ogac* were somewhat higher than previously reported (Jensen 1948; Morin and Dodson 1986; Mikhail and Welch 1989; Morin et al. 1991; Nielsen 1992). For *G. morhua*, however, growth rates were consistent with previous reports for this region (Fleming 1960; Brattey et al. 2008). The similar growth rates of these species were likely a consequence of shared environmental conditions. Recent work has shown juvenile *G. morhua* and *G. ogac* possess small home ranges and show high site fidelity in coastal

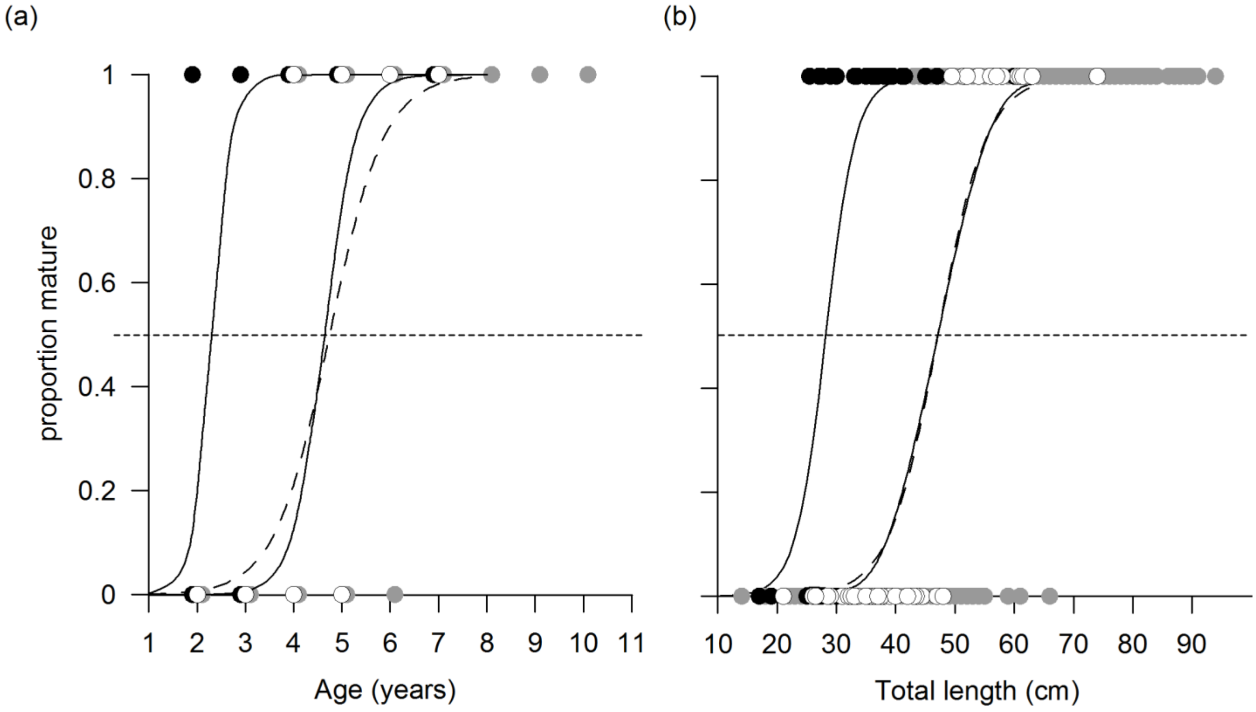

Figure 5.4 Maturity data and fitted curves for (a) maturity-at-age and (b) maturity-at-length for *G. ogac* (●) and *G. morhua* (○) collected during the study period and for *G. morhua* (X) collected from 2005-2010 (dashed curve). Horizontal line indicates 50% maturity.

Newfoundland (Knickle and Rose unpublished). Hence, it is likely that fish from this study would have maintained a limited range and been exposed to similar growth conditions such as temperature, photoperiod, and food availability. Overall, our results suggest that interspecific differences in growth are modest and unlikely to be a direct factor in niche separation.

Length-weight comparisons indicated that *G. ogac* gained weight more rapidly than did *G. morhua* with increases in length. This result is consistent with data from West Greenland (Nielsen et al. 2010), and likely a consequence of the earlier maturation and smaller maximum size of *G. ogac*. As gadids reach sexual maturity, somatic growth decreases as more energy is allocated to gonadal development (Roff 1983). Differences in length-weight relationships may also reflect divergent morphological characteristics which relate to habitat utilization. For example, recent work has shown that juvenile *G. morhua* consume a higher proportion of pelagic prey and are generally distributed further from the bottom than *G. ogac* which suggests differential use of habitat in the vertical dimension (Knickle and Rose unpublished). The slightly negative allometric growth shown by *G. morhua* results in a more streamlined body shape which may be interpreted as an adaptation to a more pelagic existence. In contrast, the positive allometric growth and stouter body shape of *G. ogac* may be an adaptation to more benthic habitat use.

Maturity data from the present study indicate a much earlier maturation for *G. ogac* than *G. morhua* and are consistent with previous reports for both species (Jensen 1948; Mikhail and Welch 1989; Morin et al. 1991; Nielsen 1992; Brattey 1996; Lilly et al. 1998; Olsen et al. 2005). Therefore, our hypothesis that *G. ogac* matures at an earlier age than *G. morhua* is supported. We propose that different maturation rates may facilitate coexistence between species by creating different energetic requirements for similar sized fish. Because fish need extra energy to be able to initiate the maturation process, the onset of maturation can result in an ontogenetic shift in feeding behaviour or dietary needs (e.g., Koen-Alonso et al. 2002). As such, it is possible that *G. ogac* feed more and select prey items that help with gonadal development while *G. morhua* of the same size maintain feeding levels and utilize prey optimal for somatic growth. The predominance of smaller and immature *G. morhua* compared to all ages of *G. ogac* in the coastal region could reflect a need for *G. morhua* to switch diets and habitats as they mature.

Life history theory further suggests that early maturation is an adaptation to high mortality rates associated with unpredictable and typically harsh environmental conditions and has been proposed as an explanation for early maturation for *G. ogac* in coastal waters of arctic seas (Morin et al. 1991). Both species occur near shore as juveniles, but adult *G. morhua* transition to deeper, more stable offshore waters as they mature. In contrast, *G. ogac* remain coastal for their lifespan and are likely subjected to more erratic environmental conditions as adults which may in turn, exert selective pressure for earlier maturation. Differences in maturation no doubt are related to the maximum size and age for each species; *G. ogac* is not thought to live beyond 11 years and grow to more than 77 cm (Jensen 1948; Nielsen 1992) whereas *G. morhua* may reach > 20 years in age and > 140 cm in length (Scott and Scott 1988; Rose 2007).

Another key life history difference between these species is that *G. morhua* is a pelagic spawner both inshore and offshore whereas *G. ogac* spawns demersally and only in the coastal zone (Scott and Scott 1988; Cohen et al. 1990; Rose 2007). Despite these differences, age 0 juveniles of both species end up in the same habitats inshore (Methven et al. 2001; Laurel et al. 2004). Moreover, the difference in spawning mode does separate the species at spawning, but does not necessarily explain the earlier maturation schedule of *G. ogac*. Demersal spawning is consistent with this species spending its entire life in shallow coastal waters, but does not explain early maturation and short life cycle, as other demersal and coastal spawning species (e.g., Atlantic herring, *Clupea harengus*) have much more protracted life cycles. Addressing these aspects of the life history of *G. ogac* is beyond the scope of the present study, but we suggest that the spawning differences between these species is not the main life history trait that mollifies competition.

In conclusion, this study shows that sympatric *G. ogac* and *G. morhua* in coastal areas of Newfoundland have similar growth rates up to age 6 or 7. At the same time, these species exhibit very different maturation rates that may result in a decrease in direct resource competition and assist coexistence. To the best of our knowledge this study provides the first age and growth data for Greenland cod and the first comparative study with *G. morhua* in Newfoundland waters.

5.5 Acknowledgements

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Chapter 6. Summary

The comparative study of closely related, coexisting species can provide insight into the underlying ecological principles structuring natural communities as well as the evolutionary history of a species. In this thesis, I compared niche parameters between two sympatric gadid species in coastal Newfoundland by concurrently measuring resource use along multiple niche dimensions to determine the degree of resource overlap and the sources of niche partitioning between species. I began by examining trophic niche overlap using stomach content analysis and stable isotopes (Chapter 2). Next, I investigated spatio-temporal niche partitioning using fine-scale movement patterns determined from acoustic radio-positioning (Chapter 3). I then examined habitat partitioning using acoustic positioning and habitat mapping in Chapter 4. Finally, I compared growth and maturity characteristics using size at age and maturity data (Chapter 5). In this concluding chapter, I integrate the key findings and conclusions from previous chapters, examine study limitations and identify future research directions.

6.1 Evidence of Niche Partitioning

The findings from Chapter 2 showed clear differences and minimal overlap in the diets of the *G. ogac* and *G. morhua*. Stomach analyses indicated differing prey and a higher proportion of benthic items for *G. ogac* and pelagic items for *G. morhua*. Polychaetes, fish and small crustaceans were predominant in the stomachs of *G. ogac* while small crustaceans, in particular hyperiid amphipods and fish, dominated those of *G. morhua*. Isotopic signatures for *G. ogac* were significantly more enriched in ^{13}C, indicating more benthic feeding, whereas signatures for *G. morhua* were relatively depleted in ^{13}C, indicative of more pelagic feeding (Davenport and Bax 2002; Hobson et al. 2002; Sherwood and Rose 2005). Dietary overlap was not significant in both stomach and stable isotope analyses. I conclude that these species segregate along the trophic dimension and that interspecific competition for food is low.

The results from Chapter 3 demonstrated important behavioural differences in space use between species during the key summer growth period. Although both species showed high site fidelity, *G. morhua* occupied significantly larger home ranges and core areas, moved at faster rates and were more active throughout the diel cycle than *G. ogac* of the same size. I hypothesize that differences in movement patterns relate to differences in prey selection and morphology between species.

The results from Chapter 4 showed that, despite similar use of substrate habitat classes, vertical distributions differed significantly between species with *G. morhua* on average located further from the seafloor and showing more variation in vertical position. Both species avoided fine gravel/sand substrates with little vegetation and selected for large particle (cobble and boulder) substrates with moderate or dense vegetation. However, *G. ogac* typically remained in close proximity to the seafloor whereas *G. morhua* was often distributed more pelagically and showed greater variation in vertical distribution. I conclude that these species often segregate vertically in the water column, which may help to reduce competitive interactions. I further suggest that these patterns are related to differences in diet morphological characteristics.

Chapter 5 revealed similar growth rates but very different maturation rates for *G. ogac* and *G. morhua*. This chapter also provides the first age and growth data for Greenland cod in Newfoundland waters. G. ogac matured at 2-3 years and ~30 cm as compared to 4-5 years and ~50 cm for *G. morhua*, respectively. Length-weight relationships suggested slightly positive growth for *G. ogac* and negative allometric growth for *G. morhua*. I conclude that differences in maturity schedules may help to decrease resource competition and assist coexistence of these species.

6.2 Mechanisms of Niche Partitioning

Based on the findings from previous chapters, I contend that *G. ogac* and *G. morhua* differentiate habitat in the vertical dimension which leads to differences in prey availability and diet composition - a pattern of resource use that has been demonstrated in many fish assemblages (e.g., Baker and Ross 1981; Shpigel and Fishelson 1989; Helland et al. 2008). This hypothesis is strongly supported by results from chapters 2 and 4 which demonstrate clear differences in dietary habits and vertical habitat utilization, and is further substantiated by reported morphological differences between species (Scott and Scott 1988; Cohen et al. 1990); the more slender body and lighter colouration of *G. morhua,* is suggestive of more pelagic behaviour, whereas the stouter form and darker colouration of *G. ogac* is consistent with more demersal habits (Figure 1.2). Moreover, the larger home ranges and faster movement rates for *G. morhua* demonstrated in chapter 3 are congruent with the observed differences in vertical habitat distributions, prey selection and morphologies. Because *G. morhua* consumes more pelagic items and *G.*

ogac consumes mainly slower-moving benthic organisms (chapter 2), it is reasonable that larger home ranges, greater daily distances traveled and faster movements by *G. morhua* reflect a more active foraging strategy (i.e., searching behaviour) and preference for more mobile and pelagic prey. Likewise, the smaller home ranges, shorter daily distances traveled and slower rate of movement by *G. ogac* may reflect more of an ambush strategy and preference for more sedentary prey. Differences in length-weight relationships observed in chapter 5 add further support to this notion; the slightly negative allometric growth shown by *G. morhua* will result in a sleeker body shape which can be interpreted as an adaptation to a more pelagic lifestyle. In contrast, the positive allometric growth and plumper body shape of *G. ogac* can be seen as an adaptation to a more benthic existence.

I propose that differences in maturation rates between these two species (chapter 5) is likely not a major factor contributing to coexistence but may help to reduce interspecific competition by creating different energetic requirements for similar sized fish. Since fish need additional energy to be able to initiate the maturation process, the onset of maturation can result in an ontogenetic shift in feeding behaviour or dietary needs (e.g., Koen-Alonso et al. 2002). In this way, it is possible that *G. ogac* feed more and select prey items that help with gonadal development as they near maturation while *G. morhua* of the same size maintain feeding levels and utilize prey optimal for somatic growth.

6.3 Implications for Fisheries Conservation

For *G. morhua*, interspecific competition with *G. ogac* has the potential to influence stock levels which may in turn, affect fishery resources. The results of this study indicate that interspecific competition between these two species in coastal Newfoundland is low and thus should not be a major factor affecting the population structure and dynamics of either species. Nevertheless, interspecific competition for food and space may exist in other areas (see Nielsen and Andersen 2001) and further examination of potential resource competition at other times of the year or in other geographic locations may be warranted (see section 6.5).

The ecological importance of coastal habitats to commercially exploited marine fish such as Atlantic cod is well known (e.g., Keats et al. 1987; Gotceitas et al. 1997; Gregory and Anderson 1997; Christian et al. 2010). The degradation of coastal habitats can result in the loss of nurseries or other critical habitats necessary for feeding or reproduction and lead to population declines (Sietz et al. 2013). The preference for coarse substrates and vegetated areas and an avoidance of open areas with sand and/or fine gravel for both species (chapter 4), further demonstrates the importance of structurally complex habitats and marine vegetation to these two gadids and other aquatic species and emphasizes the need to protect sensitive coastal areas in Newfoundland and other areas.

6.4 Study Limitations

Radio-acoustic positioning systems represent a powerful means of studying animal movements in the wild (O'Dor et al. 1998; Klimley et al. 2001). However there is a tradeoff between the high quality data that can be obtained by these systems, the maximum number of individuals that can be tracked and the temporal scale of the study. Because the present study was designed to examine microhabitat utilization and the movement patterns of individuals at high-resolution (± 1 m every 2-3 minutes), it limited the number of individuals that were able to be tagged and effectively monitored (i.e., the VRAP system is unable to simultaneously monitor high pulse-rate transmitters on multiple frequencies). As a result, sample sizes for tracking data were less than optimal. Furthermore, the high powered transmitters and high pulse frequency used in this study restricted the duration of the study to approximately 3 weeks. A system that is able to monitor multiple individuals over a larger geographical area for a greater amount of time such as the Vemco Positioning System (VPS) (http://vemco.com/products/vps/), which can run automated and cover vast areas for up to a year (and was under design at the time of this study), could potentially alleviate these challenges and provide researchers with longer-term information on space use over a larger proportion of a species natural range.

In addition to distance range, acoustic transmitter detection is hampered by environmental conditions, namely sea state and physical obstructions that may block transmitter pulses from being received by hydrophones. This was apparent in the present study as detections were highest during times of low wind stress (Figure 6.1). Additional range testing under varying field conditions could aid researchers in evaluating the effect of environmental conditions on detection rates and may provide a more accurate interpretation of acoustic data.

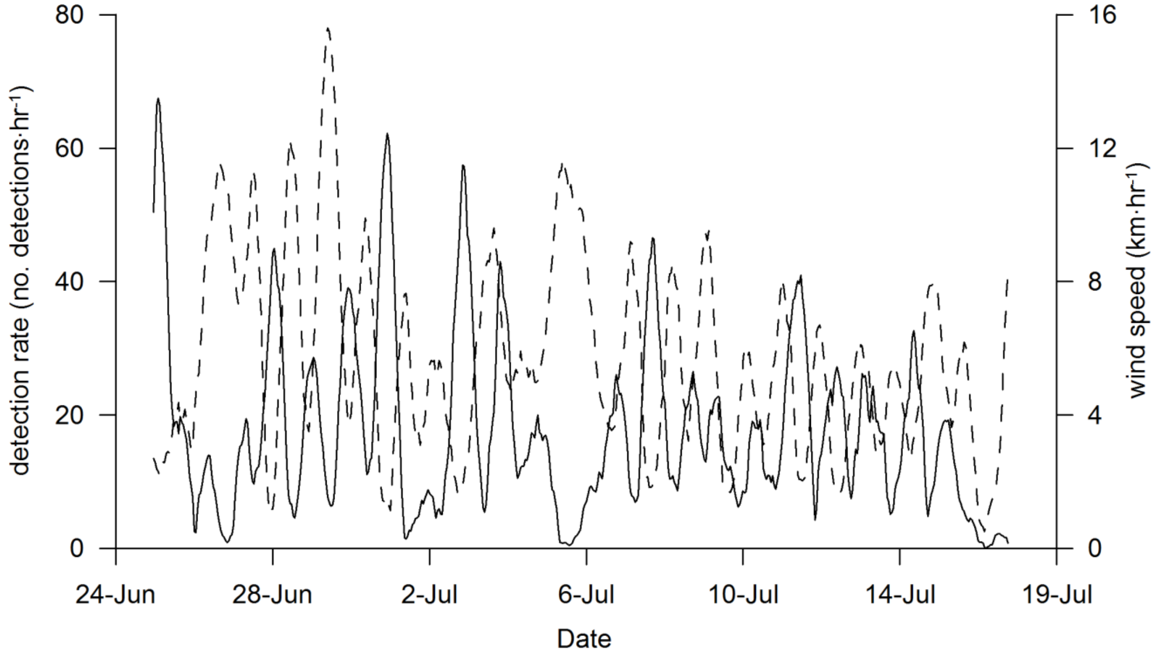

Figure 6.1 Effect of wind speed (km·hr^{-1}) (dashed line) on detection rate (no. detections hr^{-1}) (solid line) recorded by the VRAP system for the 2009 study period. Data are fitted using a running average function.

While the results of this study clearly indicate that niche partitioning occurs between these two species at the late-juvenile and early adult life stages, they do not allow the assertion that niche partitioning patterns are consistent across all life stages. These two species also co-occur as virtually indistinguishable young (0-1+) juveniles in coastal Newfoundland (e.g., Methven and McGowan 1998; Methven et al. 2001; Laurel et al. 2004). Whether they partition resources as newly settled juveniles remains unknown and would be an interesting question for future research (see section 6.5). Similarly, conclusions drawn from the current study are restricted by the relatively short temporal scale of the investigation. Although the present study shows that niche partitioning occurs during the key summer growing season, it doesn’t examine partitioning at other times of the year. Resource use and the degree of resource overlap between co-occurring species can vary seasonally in some fish assemblages (e.g., see Ross 1986; Jepsen et al 1997; Høines and Bergstad 1999). Thus, increasing the scope of the current study through ecological comparisons across several seasons and years would undoubtedly improve the current study design.

6.5 Future Research

Several new questions emerge from the present work that could lead to future research endeavors. First most, an in-depth examination of differences in functional morphology could be used to further test the ‘pelagic-benthic’ ecomorphological niche hypothesis presented in this thesis. Numerous studies have shown niche partitioning through differences in functional morphology in fishes (e.g., Gatz 1979; Sibbing 2001; Lujan et al

2011; Faye et al 2012). Despite their similar appearance (Figure 1.2), morphological differences are known to exist between *G. ogac* and *G. morhua* with the former generally having a darker colouration, broader head, larger interorbital space, larger eye, and narrower caudal peduncle (Jensen 1948; Scott and Scott 1988; Cohen et al 1990). Results from an ecomorpohological study comparing variations in ecological (i.e., dietary habits, vertical habitat utilization, movement rates, etc.) and morphological characteristics (i.e.,body depth, orbital length, oral gape size, caudal peduncle depth , etc) could be used to evaluate whether these two species have evolved different morphological adaptations to specific habitats and/or food types.

As mentioned in the previous section, extending comparisons of resource use to include multiple seasons and other life stages would be an appropriate and important step in developing a more comprehensive understanding of the ecological interactions and resource use patterns of these two species.

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