ATLANTIC COD (*GADUS MORHUA*) FEEDING FOR ECOSYSTEM-BASED MANAGEMENT AND SUSTAINABILITY IN NEWFOUNDLAND AND LABRADOR MARINE ECOSYSTEMS

by

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ABSTRACT

The purpose of this study is to challenge long-standing assumptions on Atlantic cod (*Gadus morhua*) feeding around Newfoundland and Labrador, Canada, and provide information that will be useful for the next generation of ecosystem-based models. Using stomach content analysis and published cod stomach data I address two primary questions: Do cod cease feeding during spawning? Does the cod diet reflect changes in prey assemblages in the ecosystem? Spatial and temporal diet variation was additionally analyzed. Regional variation was paramount such that diet diversity, mirroring ecosystem diversity, increased with decreasing latitude. Contrary to current assumptions, feeding continued through spawning. The stomach content contribution of shrimp reflect environmental trends in these prey assemblages over the past 65 years, while crab, a minor part of the cod diet, does not reflect abundance changes. Capelin appeared preferably consumed when encountered. Cod are not complete generalist feeders but select for certain energy rich prey.

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Table of Contents

Conclusion

List of Tables

List of Figures

List of Symbols, Nomenclature or Abbreviations

Abbreviation	**Definition**
BIC	Bayesian Information Criterion: Closely related to AIC (Akaike Information Criterion), BIC is a criterion for model selection which penalized for additional terms.
D	Simpson's Diversity Index. Consult Chapter III for definition.
FO	Frequency of Occurrence. The total number of stomachs containing a specified prey item over the total number of stomachs multiplied by 100.
IRI	Index of Relative Importance. An index of a prey item defined by the sum of the percentage of stomach contents by weight and the percent by number multiplied by the frequency of occurrence.
NAFO	Northwest Atlantic Fisheries Organization. An intergovernmental fisheries science and management body.
PFI	Partial Fullness Index. The sum of a portion of the stomach contents defined by a general group of prey items divided by the cubed length of the cod and multiplied by 10000.
TFI	Total Fullness Index. The sum of the stomach contents divided by the cubed length of the cod multiplied by 10000.

List of Appendices

Introduction and Overview

In recent decades, fishery science and management has sought to expand beyond traditional resource management techniques to include ecological and environmental considerations as single-species approaches to the sustainable use of fish stocks have often failed and the ocean ecosystem state continues to decline (Slocombe, 1993; Grumbine, 1994; Pikitch *et al*., 2004; Hassan *et al*., 2005). Current managing of human activities by sector (shipping, coastal development, etc.) without consideration of the cumulative impact of human activities on the environment have caused further damage (Guerry, 2005). Ecosystem based management seeks to broaden traditional management with the inclusion of interactions between fishery resources and their ecosystem, such as predation and impacts of increasing ocean temperatures on fish communities, as well as consideration of biotic (such as species interactions and distribution changes), abiotic (such as habitat differences and climate change), and anthropogenic components (such as fishing activities and habitat destruction) of the ecosystem to create an integrated ecological approach to fisheries (FAO, 2003, Guerry, 2005). Human activities such as shipping, fisheries, energy exploration, and coastal development place pressures on the ecosystem, each having been managed individually. In order to provide a more accurate representation of human pressures on the ecosystem, these components should be considered together as a collective impact.

The ecosystem is viewed as a complex adaptive system and by assessing the impacts of various components we may better predict how specific species and populations will behave (Levin, 1998). While ecosystem management does not require inclusion of every aspect of human activities or all aspects of the ecosystem, it should take ecosystem considerations and the impacts of multiple fisheries into consideration (Rice 2005). At the minimum qualitatively assessing possible impacts of human activities on the bios can be enough to guide management but increased ecological understanding can further feed into policies that impact assessments (Murawski, 2007). An integral part of generating and parameterizing fishery ecosystem models is an understanding of the food web dynamics (Gaichas *et al.*, 2010). The energy input to top predators in the ecosystem is a key aspect of this understanding as the removal of these predators has altered trophic interactions and worked to reduce the ecosystem's resilience (Folke *et al.*, 2004). Therefore, as a contribution to both food web dynamics and as a component of ongoing efforts to increase the application of ecosystem-based approaches within fishery management, this thesis focuses on the spatio-temporal feeding dynamics of a key marine predator in Newfoundland and Labrador in order to investigate two questions: Do Atlantic cod (*Gadus morhua*) feed during the spawning period? Do the contents of cod stomachs reflect the abundance of prey in the ecosystem?

The Atlantic cod stocks off Newfoundland and Labrador, including the Grand Banks, were formally the largest cod stocks in the world, being estimated at approximately 6-7 million tonnes of biomass (Rose, 2007). Rapid declines in cod biomass in the second half of the 20th century were resulted from overfishing during a period of low cod productivity due to changes in the ecosystem driven by changing conditions such as current patterns, variation in temperatures, salinity, and food availability (Rose *et* al., 2000; Robichaud & Rose, 2004; Rose, 2005; Lilly *et al.*, 2008). These factors have resulted in reduced stock productivity (Hilborn & Litzinger, 2009). It has become apparent that these depleted cod stocks have not performed the same as they did historically. Diverse responses have been observed in adjacent stocks around Newfoundland and Labrador such that some stocks have responded positively to fishery closures while other stocks have not. For example, cod groups in southern Newfoundland (Northwest Atlantic Fishery Organization Division 3Ps, see Figure 1.1) have exhibited historical pre-collapse population growth rates with no unexplained mortality or reduced condition (Rose, 2003; DFO, 2012a), while those on the Grand Bank (3L) and the continental shelf north to Labrador (3K & 2J) have exhibited little to no population growth (Lilly *et* al., 2000; DFO, 2012b) (Figure 1.1). There have also been major life history changes post-collapse in stocks outside of Division 3Ps, such as lowered age of maturity, elevated mortality rates, and poor recruitment in some populations, all contributing to the lack of recovery (Hutchings,1999; Lilly *et al.*, 2000; Anderson & Rose, 2001; Bundy, 2001; Olsen *et al.*, 2005).

These fish live in dynamic ecosystems such that environmental and fishery factors interact in complex ways (Rose, 2005). For example, climate change have undoubtedly impacted plankton and fish populations directly within recent decades (e.g. deYoung & Rose, 1993; Frank *et al*., 1996; Richardson & Shoeman, 2004), and many impacts remain uninvestigated. Changes in fish and plankton populations influence many elements of the ecosystem through species interactions (such as predation and competition). Factors that have been hypothesized to contribute to lower productivity than was predicted from traditional models include increased natural mortality, decreased body growth, reduced recruitment rates, and continued fishing mortality, both directed and as bycatch within other fisheries (Rice *et al.*, 2003; Shelton *et al.*, 2006).

While the collapse of the cod stocks around Newfoundland and Labrador are well known, numerous changes in various other fish species have also occurred in response to environmental changes (deYoung & Rose, 1993, Frank *et al*., 1996; Richardson & Shoeman, 2004; Windle *et al*., 2012). Of particular concern to the diet of the cod have been observed decreases in capelin and increases in shrimp and crab (Lilly *et al*., 2000; O'Driscoll *et al.*, 2000; Carscadden *et al.,* 2001; Dawe *et al*., 2012) During the 1990s a stark southward shift of the capelin distribution was observed (Frank *et al*., 1996). Within locations where capelin remained abundant and a dominant prey item such off the southern coast of Newfoundland (Division 3Ps), cod have fared reasonably well (with little impacts on cod weight at age) presumably due to the presence of this lipid-rich prey (Yaragina & Marshall, 2000; Mello & Rose, 2005). Although alternative prey may be utilized by Newfoundland and Labrador cod, many populations appear fairly dependent on capelin availability for growth (Pardoe *et al*., 2008). Correlations between cod growth and capelin consumption have been demonstrated in multiple North Atlantic stocks (Vilhjálmsson, 1997; Rose & O'Driscoll, 2002; Mullowney & Rose, 2014). During the late 1990's, the range of the capelin shifted south, corresponding with declining ocean temperatures, from the Newfoundland and Labrador shelf (2J and 3KL) towards the southern coast of Newfoundland (including 3Ps) and the Flemish Cap (Frank *et al.*, 1996). The loss of a primary lipid rich prey item in combination with size-specific fishing pressure are thought to have resulted in the low growth rates of northern cod on the

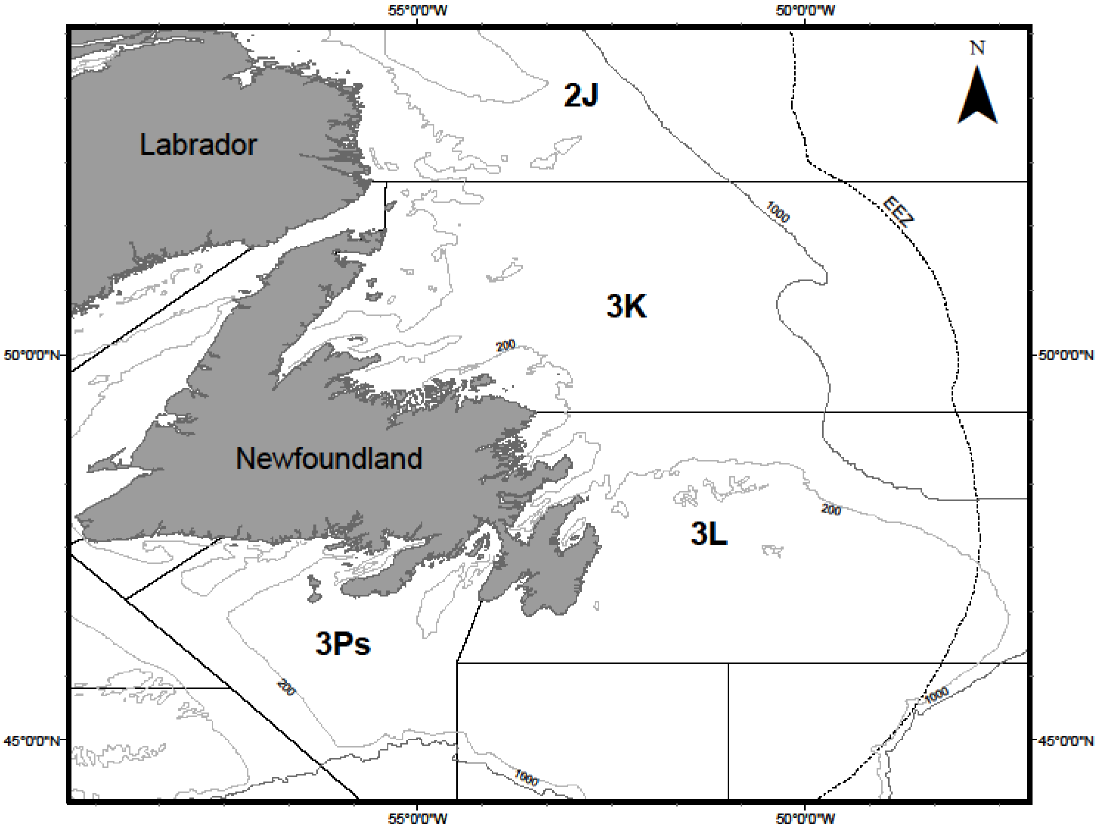
Grand Banks and northward to Labrador (Krohn *et al.*, 1997). Declining ocean temperatures not only affect food assimilation, but may alter food availability, digestion rates, satiation time, and maximum meal size (Waiwood *et al.*, 1991; Mello & Rose, 2005). The condition, growth rates, reproductive schedules and geographic distributions of cod are likely influenced by spatial and temporal changes in feeding (Rose & O'Driscoll, 2002). The various areas where cod are found around Newfoundland and Labrador do not have the same feeding opportunities which will impact their feeding behaviour.

Cod are thought to exhibit an opportunistic generalist feeding style (Link & Almeida, 2000) but with heterogeneity in their trophic role among stocks in the North Atlantic related to regional and seasonal availability of prey (Link *et al*., 2009). Predation on forage species appears to be related to gape size rather than the density of prey. Within Newfoundland and Labrador stocks, at fork lengths under 30 centimeters, diets consisted of pelagic prey, primarily zooplankton (mysids, euphausiids, and amphipods), shrimp, and squid (Lilly & Fleming, 1981; Sherwood *et al*., 2007). As the cod matures, the diet generally becomes more benthic or piscivorous to include more capelin (*Mallotus villosus*), herring (*Clupea harengus*), sandlance (*Ammodytes* sp.), and crab (*Chionocetes opilio*, *Hyas* sp., etc) (Popova, 1962; Methven & Piatt, 1989; Smith *et al.*, 2007). These changes in prey preference may be driven by increased energetic requirement in larger individuals (Kerr, 1971). Capelin is an important energy-rich prey item for cod as they are an oily fish and historically dominated the cod stomach contents of cod that followed the capelin migration inshore to their spawning grounds (Cormack, 1832; Thompson, 1943; Popova, 1962; Templeman, 1965; Turuk, 1968; Lilly & Fleming, 1981; Methven & Piatt, 1989; Link & Almeida, 2000; Mello & Rose, 2005). Cannibalism does occur by cod, but in the Newfoundland region only accounts for a small portion of the stomach contents (Popova, 1962; Templeman, 1965; Stanek, 1973; Waiwood & Majkowski, 1984; Lilly, 1991; Uzars & Plikshs, 2000).

In this thesis I investigate two primary questions provide new insights characterizing the variability in feeding behaviour of cod and its role as a key predator in the ecosystem. The first chapter of this thesis analyzes a longstanding assumption regarding cod feeding during their prolonged spawning period during the spring and summer. The current assumption states that cod cease feeding during the spawning period (Brawn, 1961; Templeman, 1965; Fordham & Trippel, 1999). This chapter challenges this assumption utilizing stomach analysis techniques to quantify cod feeding and cod maturity stages with contemporary data. The second chapter analyzes cod feeding behaviour over broad spatial and temporal scales. It has been established that the stomach contents of cod may be utilized in approximating prey biomass (Fahrig *et al*., 1993; Cook & Bundy, 2012). Stomach analysis techniques are utilized to demonstrate that this finding can be extended to utilize cod stomachs to diagnose and quantify changes in prey assemblages over longer time scales.

This research serves to extend the scope of ecosystem-based analyses to include interactions involving key predators in marine ecosystems. A number of simplifying assumptions regarding how fish populations should behave following a stock collapse were made in the past, including the assumption that stock dynamics can be predicted without consideration of the dynamics of prey species and environmental conditions necessary to promote historical species distributions, feeding relationships, and population growth rates of the cod stocks around Newfoundland and Labrador. Through the inclusion of new data and interpretations as presented in this thesis, traditional fisheries models can be expanded to include ecosystem considerations and thus provide a more complete picture of the role of cod as a top predator in its environment. Though the project is centered off the coast of Newfoundland and Labrador, the implications of the results can be useful towards managing other depleted fish stocks. With continued studies of the interactions between human activities and environmental factors we can hope to understand the ecological basis for sub-Arctic ecosystems capable of sustaining numerous commercial fish stocks.

Figures



Introduction Figure 1: Map of Newfoundland and Labrador with North Atlantic Fishery Organization (NAFO) divisions analyzed in this study identified.

Co-authorship Statement

I am the primary author of all research papers in this thesis. My work concentrated on utilizing biological samples obtained during ecosystem surveys as part of research programs of the Natural Sciences and Engineering Research Council of Canada (NSERC) Chair in Fisheries Conservation (CFC) and the Centre for Fisheries Ecosystems Research (CFER). I conducted all analysis with support from Dr. George A. Rose. Furthermore, I conducted a substantial amount of the lab work presented in this thesis, though the contributions of former members of Fisheries Conservation are hereby noted, particularly Susan Fudge. Finally, I conceived and wrote all manuscripts with generous amounts of analytical and editorial comments from Dr. George A. Rose, who co-authors all manuscripts produced from this thesis.

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Chapter 1. Atlantic cod (*Gadus morhua*) feed during spawning off Newfoundland and Labrador.

1.1 Abstract

I test a current assumption that Atlantic cod (*Gadus morhua*) off Newfoundland and Labrador, Canada do not feed during the protracted spawning season (March to September). Stomach contents were analyzed from 10,473 cod from four NAFO subdivisions (2J, 3K, 3L, and 3Ps) over 9 years from which gonads were also analyzed to determine sex and maturity status. Adult cod in spawning condition did feed in all regions, in most cases at rates equivalent to or even greater than non-spawning fish and juveniles. Both sexes fed during spawning, though females consumed lesser amounts. Regional differences were evident. Total fullness (TFI) was greater in the northern (2J) than southern (3Ps) region, with no consistent differences between spawners and non-spawners. The most southerly region (3Ps) exhibited the greatest prey diversity, the northern region (2J) the least. Shrimp was the major dietary item in the northern regions. Capelin, zooplankton, crab, and other fish increased in importance to the south. Differences in prey items between non-spawning and spawning individuals of both sexes were possibly related to spawning behaviour. Models using consumption rates should not assume that cod do not feed during the protracted spawning season in these waters.

1.2 Introduction

Knowledge of diet and consumption of dominant predatory species such as Atlantic cod (*Gadus morhua*) is pivotal to ecosystem models and approaches to fisheries management (Bundy & Fanning, 2005). Much of the information on diet has been derived from stomach contents studies, many limited to a single season within one or more years with assumptions of how this relates to annual consumption (Popova, 1963; Lilly & Fleming, 1981; Methven & Piatt, 1989; Casas & Paz, 1996; Gerasimova & Kiseleva, 1998; Adlerstein & Welleman, 2000). More comprehensive information on annual cod feeding has been obtained from studies utilizing data over entire years (Turuk, 1971; Daan, 1973; Klemetsen, 1982; Albikovskaya & Gerasimova, 1993; Schwalme & Chouinard, 1999; Mello & Rose, 2005; Link *et al*., 2009).

In the Newfoundland-Labrador area, cod spawning is protracted over 40-50 days, typically occuring between March and August (Templeman & Fleming, 1962; Templeman & May, 1965; Fitzpatrick & Miller, 1979; Hutchings & Myers, 1993; Myers *et al*., 1993). Female cod release eggs in batches over spawning intervals of 2 or more days (Kjesbu, 1989; Fordham & Trippel, 1999). Known spawning locations around Newfoundland and Labrador are widespread, including outer portions of the Labrador shelf (notably the Hamilton Bank and Hawke Channel), northeast Newfoundland Shelf, northern and southern Grand Banks, Halibut Channel and St. Pierre Bank, as well as several inshore areas, such as Trinity and Placentia Bays, though spawning may also occur at varying locations during migration (Templeman & May, 1965; Serebrayakov, 1967; Fitzpatrick & Miller, 1979; Hutchings *et al.*, 1993; Rose, 1993; Smedbol & Wroblewski, 1997).

A prevailing assumption for northwest Atlantic cod, in particular the stocks of Newfoundland and Labrador, is that these fish do not feed during the protracted spawning period. This assumption has been based largely on studies conducted on captive fish in which feeding appeared to cease during spawning (Brawn, 1961; Templeman, 1965; Fordham & Trippel, 1999). Numerous models and findings relating to cod consumption and growth have incorporated this assumption (Hutchings, 1999; Skjæraasen *et al*., 2004; Jørgensen & Fiksen, 2006). The same assumption has been made for northeast Atlantic cod, but was recently shown to be invalid (Michalsen *et al.*, 2008). North Sea cod have long been known to feed during spawning (Daan, 1973). These findings led to a questioning of the assumption that cod off the coasts of Newfoundland and Labrador cease feeding during spawning.

In this study I test a base hypothesis that spawning cod cease feeding in Newfoundland and Labrador waters. I also tested four null hypotheses relating to feeding behaviour during the spawning period. Specifically I test for no difference in: 1) feeding amount in spawning, non-spawning, and juvenile fish; 2) prey species; 3) diversity of prey; and 4) prey consumption between sexes. These hypotheses are assessed using data for cod populations in four Northwest Atlantic Fisheries Organization (NAFO) subdivisions off Newfoundland and Labrador.

1.3 Methods

1.3.1 Stomach Analysis

A total of 10,473 cod stomachs were collected between March and September from trawl (Campelen 1800 and Yankee 36) and handline catches during surveys from 1997 to 2003, 2008, and 2011 in NAFO subdivisions 2J, 3K, 3L, and 3Ps off Newfoundland and Labrador (Tables 1 & 2, Figure 1.1). Spawning occurs in each of these regions (Myers *et el.,* 1993). I compared the diets of cod on this geographical basis, recognizing that within these regions a number of cod spawning groups exist. The broadscale geographic basis of our comparisons is thought to have maximized the likelihood that any small scale differences in diet, or small sample sized, would not overly influence the large scale questions posed here.

All stomachs were collected whole and frozen. Everted stomachs resulting from an inflated swim bladder were discarded and not utilized in this study. In the lab, stomach contents were weighed and identified to the lowest taxon feasible. Slow-dissolving morphological prey components, such as otoliths, exoskeletons, and squid beaks, were frequently utilized for identification. Components of the prey items are often found several days after consumption, depending on the prey item (Tyler, 1970; dos Santos & Jobling, 1991; Temming & Herrmann, 2003). Prey items of particular interest were capelin (*Mallotus villosus*), cod (*Gadus morhua*), sand lance (*Ammodytes* sp.), herring (*Clupea harengus*), other gadids, shrimp (*Pandalus* sp., *Crangon* sp., etc.), crab, eggs and zooplankton. Additional categories for remaining benthic prey and any additional fish species consumed were also established. These classifications represent the dominant prey items with categories such as benthic prey covering a range of species. Each prey item was quantified by weight.

1.3.2 Analysis of maturity

Gonads were analyzed at the time of sampling to determine maturity and spawning status. Males were classified as immature, maturing (no milt but gonads turgid), partially spent (spawning with milt present, gonads turgid) and spent (gonads non-turgid but developed). Females were classified as immature, maturing with no hydrated eggs, spawning with less than 50% hydrated eggs, spawning with over 50% hydrated eggs, or spent (deflated gonads) according to Morrison (1990).

1.3.3 Data analysis

The frequency of occurrence was calculated for each prey item was:

$$F_i = \frac{N_i}{N} 100 \tag{1}$$

where N_i is the number of stomachs containing the specified prey item and N the total number of stomachs in a given sample.

The partial fullness index (PFI) was calculated for each prey type to allow comparison of prey quantities over various sizes of cod (Lilly & Fleming, 1981):

$$PFI_i = \frac{w_i}{f_l^3} 10^4 \tag{2}$$

The average PFI is defined as the sum of the PFIs in a given sample divided by the sample size (Lilly & Fleming, 1981).

As was the total fullness index (TFI):

$$TFI = \sum_i PFI_i = \sum_{i=1}^{s} \frac{w_i}{f_l^3} 10^4 \quad (3)$$

where w_i is the weight of the prey type *i* in grams, f_l is the length of the fish in centimeters, and *s* is the number of prey items present in the stomach.

Diversity of the prey items was determined using Simpson index of diversity (Simpson, 1949), defined as:

$$D = 1 - \sum_{i=1}^{s} \frac{n_i(n_i - 1)}{n(n-1)} \quad (4)$$

where n_i is the number of times in which prey type *i* appears in the total number of stomachs, *n* is the number of times in which all prey types appear in all stomachs, and s the number of prey types.

The stomach contents data always exhibited non-normal error structure, thus nonparametric analysis was used to examine differences between groups. The Mann-Whitney or Wilcoxon test was used to test differences between two samples such as between spawning states or males and females. Testing of regional variation among groups employed the Kruskal-Wallis one-way analysis of variance. Percentages of empty stomachs were compared using a logistic link function with binomial error. Diversity was analyzed using a mixed effects model with Poisson error structure. All analyses were done in R statistical software. Both the percentage of empty stomachs and the Simpson's Diversity Index were run with the explanatory variables of spawning status, maturity, sex, and NAFO subdivision.

1.4 Results

1.4.1 Prevalence of spawning individuals

Spawning individuals were present in all regions during the months sampled (Table 1). Handline catches had a higher frequency of spawning individuals than did trawl catches, likely because they more closely targeted active spawning areas. The most complete sampling occurred in 3Ps where spawning fish were present from March to September (7 months). The proportions of spawning fish across regions could only be compared in March and June and in both these months were higher in 3Ps than the other regions (5% in March while 0-2% in other regions and 15% in June with 4-8% in other regions). These differences are not thought to represent differences in the proportions spawning in the different regions but reflect more focused sampling on spawning fish in 3Ps.

1.4.2 Differences in Feeding Amount

The percentage of empty stomachs ranged from 0% to 36% among the various region-maturity stage groups (Table 1.1) with region being the most significant explanatory factor ($p < 0.001$) (Table 1.2). The northern regions had lower percentages of empty stomachs than did southern regions (2J: 21.6%; 3K: 19.9%; 3L: 30.4%; 3Ps: 26.3%). Spawning state was found to be important for explaining the proportion of empty stomachs ($p=0.003$), but interaction between spawning status and region was significant ($p=0.007$). In the northern regions, 3K and 2J, spawning fish had slightly higher percentages of empty stomachs than did non-spawning fish (16.0% vs. 11.4% for 3K and 25.2% vs. 21.1% for 2J), while the reverse was true for the southern regions of 3L and

3Ps (16.0% vs. 24.3% for 3L and 23.3% vs. 25.9% for 3Ps). Hence there was no consistent difference in the proportion of empty stomachs between spawning and non-spawning cod.

Mean TFIs also varied among regions (0.613 for 2J, 0.753 for 3K, 0.429 for 3L, and 0.592 for 3Ps, p=<0.001) with the northern regions showing higher total gut contents (Table 1.3). TFIs of spawning and non-spawning fish within each region did not differ except in 3Ps where non-spawning individuals had a higher TFI (0.709) than did spawning individuals (0.584) (p=<0.001). In all other regions spawning individuals had higher TFIs than did non-spawners, although these differences were not significant (p=0.055 for 2J, 0.651 for 3K, 0.143 for 3L).

1.4.3 Prey Differences

A total of 103 different prey items were identified in cod stomachs. A general linear model with the explanatory variables of NAFO subdivision and gear type demonstrated prey composition and intensity of feeding did not vary consistently between gear types. Overall the dominant prey species were capelin (31.6% by weight), shrimp (21.3%), other fish (11.0%), crab (10.5%), and zooplankton (10.0 %). Regional differences were paramount (Table 1.3). In the most northern region, 2J, the diet was dominated by shrimp (87.1%) and other fish (7.4%), whereas in 3K, shrimp (78.1%), capelin (13.5%), and other fish (5.3%) were dominant. In 3L, capelin (61.3%), shrimp (12.0%), other fish (9.0%), and cod (5.3%) were consumed. In the most southerly region studied 3Ps, the diet was more diverse and comprised of capelin (33.5%), zooplankton (14.9%), crab (14.4%), other fish (12.6%), sand lance (6.7%), benthic organisms (5.7%), and shrimp (5.2%). The frequency of occurrence of each prey type parallels the regional variations in the amounts of prey in the stomachs (Figure 1.2).

Spawning fish tended to consume more lipid-rich prey, especially capelin ($p<0.001$), than did non-spawners that consumed more crab and sand lance (Table 1.3). While spawning individuals were on average 2.92 centimeters larger than non-spawning individuals (53.36 cm and 56.28 cm for non-spawning and spawning, respectively), the difference in prey eaten is not likely related to size differences. Regional differences were again apparent. Spawning individuals in 2J consumed more sand lance, whereas capelin was more common in spawners from 3K ($p=0.024$), shrimp in 3L, and shrimp and sand lance in 3Ps.

1.4.4 Differences Between Sexes

No consistent differences were evident between the percentage of empty stomachs in males and females or in interactions with region, maturity state and spawning state (Table 1.2). For fish that had fed, spawning males had higher TFIs than did spawning females in all regions (Table 1.3). In contrast, non-spawning females had higher TFIs than did males in all regions except 2J. Immature fish TFIs did not differ between males and females. Higher TFIs in spawning males reflected PFIs of the dominant prey items: in 2J and 3K largely shrimp; in 3L capelin and shrimp; and in 3Ps capelin, sand lance and most other diet items, with the notable exception that spawning females consumed more small cod. As in spawning fish, the higher TFIs of non-spawning females reflected higher PFIs of shrimp in 2J and 3K, capelin in 3L, and capelin, shrimp, and crab in 3Ps. Diets of immature fish were for the most part near identical, with only minor differences evident.

1.4.5 Immature vs. Adult Diet

The overall percentage of empty stomachs did not differ between immature and mature individuals although some regional variation was evident (Table 1.2). Regions 3L and 3Ps varied in amount fed between immature and mature individuals. Mature cod from regions 3L and 3Ps had reduced TFIs when compared to immature individuals ($p < 0.001$ for both regions). Immature cod in southern regions were therefore found to reduce the frequency of feeding on greater quantities of prey, while northern regions fed at the same frequency on approximately the same amounts of prey.

As expected, immature cod typically consumed greater quantities of zooplankton, shrimp, and sand lance whereas mature individuals consumed more crab, cod, and other fish (Table 1.3), though the frequency of occurrence shows immature individuals had a lower occurrence of such prey in their stomachs (Figure 1.2). Regional variation was observed. In 2J mature individuals consumed more benthic prey and shrimp while immature cod consumed more gadids (most often Arctic cod, *Boreogadus saida*). Mature individuals consumed more shrimp and zooplankton in 3K, more zooplankton, shrimp, other fish, and sand lance in 3L, and more shrimp in 3Ps, than did immature in their respective regions.

1.4.6 Diversity of prey

Region was the only significant factor explaining the variation observed in the diversity index (Table 1.2). The diversity of prey items was highest in southern regions 3L and 3Ps (Table 1.1, Figure 1.3), and lowest in 2J where shrimp dominated the diet (Figure 1.2). No interactive effects were evident.

1.5 Discussion

1.5.1 Base hypothesis

Our results indicate that spawning cod around eastern Newfoundland and Labrador continue to feed during spawning. The presence of food in the stomachs of spawning cod in addition to the lack of any consistent increase in the percentage of empty stomachs among spawners indicates that feeding persists throughout the spawning period. Hence the base hypothesis that cod cease feeding during spawning can be rejected.

1.5.2 Differences in Feeding Amount

Feeding amounts differed between spawning and non-spawning fish but in diverse ways. TFIs were elevated in males during spawning in all regions. Females in one region (3Ps) showed decreased food consumption during spawning. Juvenile TFIs did not differ from those of adults. In the more northern regions (2J and 3K), the higher percentages of empty stomachs suggests that spawning cod will feed less frequently than non-spawning cod, but often consume more. This difference was not evident in southern regions and may reflect the wider availability of potential food items in the southern regions.

The cod at higher latitudes were found to have higher average TFIs than those of southern populations. Despite these elevated amounts present in the stomachs, the growth rates are lower in the northern NAFO subdivisions than in southern ones (Olsen *et al.*, 2005), which is counter to the counter-gradient effects suggested by Billerbeck *et al.* 2001. Low temperatures will negatively influence the growth of cod (Björnsson *et al.*, 2007), hence the increased consumption and fewer empty stomachs may counter the lower-quality shrimp prey available in the north. It appears from these results that prey quality and energy content, capelin rich and shrimp poor (see Rose & O'Driscoll, 2002 for summary), trumps latitude in terms of gradients in growth.

1.5.3 Prey Species

Our PFI data show that the types of food consumed differed among regions. Northern fish (2J and 3K), both mature and immature, spawning and not spawning, fed primarily on shrimp. In the southern regions (3L and 3Ps), the diet included large quantities of capelin, sand lance, and many other prey. These regional differences are consistent with the southerly shift in capelin that occurred in the early 1990s and has endured over the period of the present study (Frank *et al.*, 1996). Differences in diet between spawning and non-spawning fish in all regions except 3Ps were infrequent and mostly related to total feeding (TFI).

Spawning individuals were found to consume more lipid-rich prey, particularly capelin. As the sizes of spawning and non-spawning individuals were approximately the same as non-spawning ones (56.2 cm and 53.2 cm, respectively), the increase in lipid-rich prey consumption is likely not the result of gape size. The foraging behaviour may therefore not be limiting. It seems likely that energetic needs during spawning may explain the need to pursue better-quality prey.

The primary prey of cod around Newfoundland and Labrador has been reported to be capelin, zooplankton, crab, and shrimp (*Pandalus* sp.) (Popova, 1963; Turuk, 1971; Methven & Piatt, 1989; Lilly, 1991; Mello & Rose, 2005). While these species comprise the majority of the overall cod diet, regional variation was quite large. Capelin predation depends on their migration (Lilly & Fleming, 1981; Methven & Piatt, 1989; Rose & Leggett, 1990), leading to a large observed variation in the capelin PFI in northern regions. Consistent with our results, spatial variation in prey items has been observed off the coast of Newfoundland such that northern populations consume greater quantities of shrimp while southern populations consume greater quantities of fish and crab (Gerasimova & Kiseleva, 1998). Prey consumed by northern populations was overall of lower energy content than the food consumed by the southern populations. This fact is likely representative of the prey as availability rather than cod selectivity. Cod in northern regions do not have the same access to the lipid-rich prey the southern populations do, which likely contributes to observed low growth and survival rates (Olsen *et al.*, 2005).

1.5.4 Diversity

Our data indicate that prey diversity differed among regions and increased with decreasing latitude, as expected with increased diversity of potential prey in southern regions. Casas & Paz (1996) and Powles (1958) observed an increase in diet diversity with increased age in cod from the Flemish Cap stock (NAFO 3M) and the Gulf of St. Lawrence, respectively, but this was not observed in the present study. Our results indicate that mature cod had higher consumption of benthic or fish prey, primarily oil-rich fish such as capelin (*Mallotus villosus*), herring (*Clupea harengus*), and sand lance (*Ammodytes* sp.) than immature fish, but comparable diet diversity. Neither spawning status nor sex was a significant factor in describing the observed variation in diet.

1.5.5 Differences Between Sexes

Our data suggest that variation may exist between male and female cod diets, though differences between regions were of greater magnitude. Explanations for sex differences include possible prey selectivity or spatial variation of cod residency on the spawning grounds (Robichaud & Rose, 2003), which could result in different food availability.

1.5.6 Conclusion

Our goal was to test the hypothesis that Atlantic cod do not feed during spawning in Newfoundland and Labrador waters. This hypothesis has been rejected. In brief, although some region-sex variations were evident in the amount and frequency of feeding, cod do not restrict their feeding during the protracted spawning season in Newfoundland and Labrador waters. This finding has important implications for bioenergetics and ecosystem-based models based on consumption of key predators such as Atlantic cod.

1.6 Tables

Table 1.1: Sample size, percentage of empty stomachs, mean Total Fullness Index (TFI), and Simpson's Diversity Index (D) of sampled cod divided by region, spawning status, and sex.

Region	**Spawning Status**	**Sex**	**Sample size *n***	**% Empty Stomachs**	**TFI**	**D**
2J	Immature	M	335	26.3	.686	0.393
		F	760	19.9	.696	0.347
	Non-spawning	M	875	17.5	.713	0.389
		F	802	25.0	.624	0.404
	Spawning	M	150	27.5	.581	0.356
		F	73	20.4	.471	0.304
3K	Immature	M	215	25.1	.807	0.655
		F	355	22.1	.731	0.485
	Non-spawning	M	96	10.5	.845	0.600
		F	96	12.4	1.056	0.582
	Spawning	M	38	13.2	.988	0.543
		F	12	25.0	.421	0.333
3L	Immature	M	395	34.6	.749	0.747
		F	636	35.7	.775	0.690
	Non-spawning	M	309	28.2	.461	0.634
		F	337	20.8	.552	0.627
	Spawning	M	49	12.2	.588	0.601
		F	26	23.0	.360	0.620
3Ps	Immature	M	588	35.0	.778	0.650
		F	887	24.0	.794	0.646
	Non-spawning	M	1518	29.6	.607	0.632
		F	1266	21.5	.790	0.633
	Spawning	M	406	23.4	.768	0.631
		F	238	29.0	.422	0.612

Table 1.2: Mutli-way ANOVA of Percentage of Empty Stomachs and Simpson’s Diversity Index

Parameter	**Percentage of Empty Stomachs F (p)**	**Simpon’s Diversity Index F (p)**
Region	15.11 (<0.001)	36.87 (<0.01)
Spawning/Non-spawning	8.82 (0.003)	0.11 (0.74)
Mature/ Immature	0.32 (0.57)	0.22 (0.64)
Sex	0.27 (0.61)	0.14 (0.71)
Region*Spawning	7.37 (0.01)	0.33 (0.80)
Region*Mature	0.20 (0.65)	0.41 (0.75)
Region*Sex	2.30 (0.13)	1.55 (0.20)
Spawning*Sex	3.93 (0.15)	3.22 (0.07)
Mature*Sex	1.05 (0.31)	1.24 (0.27)

Table 1.3: Mean PFI and TFI values for each prey species across the regions, sexes, and spawning status.

NAFO	**Spawning Status**	**Sex**	**Mean PFI**											**TFI**
			Capelin	Sand Lance	Cod	Herring	Gadids	Other Fish	Shrimp	Zooplankton	Crab	Benthic Prey	Other	
2J	Immature	M	.030	0	0	0	0	.033	.594*§	.005	.010	.014§	<.001	.686
		F	.010	0	0	0	.006	.024§	.635*	.005	.005	.011	<.001	.696§
	Non-spawning	M	.017	0†	<.001	0	0	.049	.625†*	.005	.008	.008	<.001	.713*
		F	.006	0	0	0	0	.050	.540*	.006	.014	.005	.001	.624*
	Spawning	M	.004	.007†	0	0	0	.039	.514†	.003	.004	.009	0	.581
		F	0	0	0	0	0	.036	.431	.003	.001	.002	<.001	.471
3K	Immature	M	.147	0	0	0	0	.113*	.487	.017 §	.016	.026	.001	.807
		F	.074	0	0	0	0	.030*	.586§	.014§	.005	.023	.003§	.731
	Non-spawning	M	.137	0	0	0	0	.076*	.618	.008	.001	.003	<.001	.845
		F	.069	0	0	0	<.001	.011*	.951	.008	.007	.008	.001	1.056
	Spawning	M	.151	0	0	0	0	.020	.788	.004	0	.025	0	.988
		F	.166	0	0	0	0	0	.249	.002	0	.004	0	.421
3L	Immature	M	.378	0§	0	0	0	.054	.197§	.035§	.045*§	.038	.002	.749§
		F	.412	<.001§	0	0	.004	.063	.220§	.020§	.030*	.023	.003	.775§
	Non-spawning	M	.278	.003	0	.001	.002	.064	.056†	.027	.002	.027	.001†	.461
		F	.378	.003	.021	.001	.004	.039	.054	.022	.014	.013	.002	.552
	Spawning	M	.345	0	0	0	0	.051	.106†	.072	.001	.003	.009†	.588
		F	.176	0	0	0	0	.032	.055	.046	.046	<.001	.001	.360
3Ps	Immature	M	.288	.13§	<.001	.003	0	.075	.046	.151	.032§	.039	.006	.778§
		F	.315	.095§	.002	.006	0	.744	.042§	.195§	.020§	.038	.005§	.794
	Non-spawning	M	.200†*	.033	.006	.004	<.001	.072	.038†*	.106	.093*	.043	.007†	.607*
		F	.268*	.039†	.017	.006	0†	.084	.055†*	.111†	.154†*	.047†	.009 †	.790†*
	Spawning	M	.319†	.013	0*	0	0	.080	.102†*	.184*	.034*	.021*	.015†*	.768*
		F	.139	.002†	.051*	0	.012†	.034	.006†*	.140†*	.023†*	.012†*	.004†*	.422†*

† 95% significant differences in PFI between spawning and non-spawning within sex for each region.

* 95% significant difference in PFI between male and female for each region and spawning group.

§ 95% significant in PFI difference between immature and mature individuals within sex for each region.

1.9 Figures

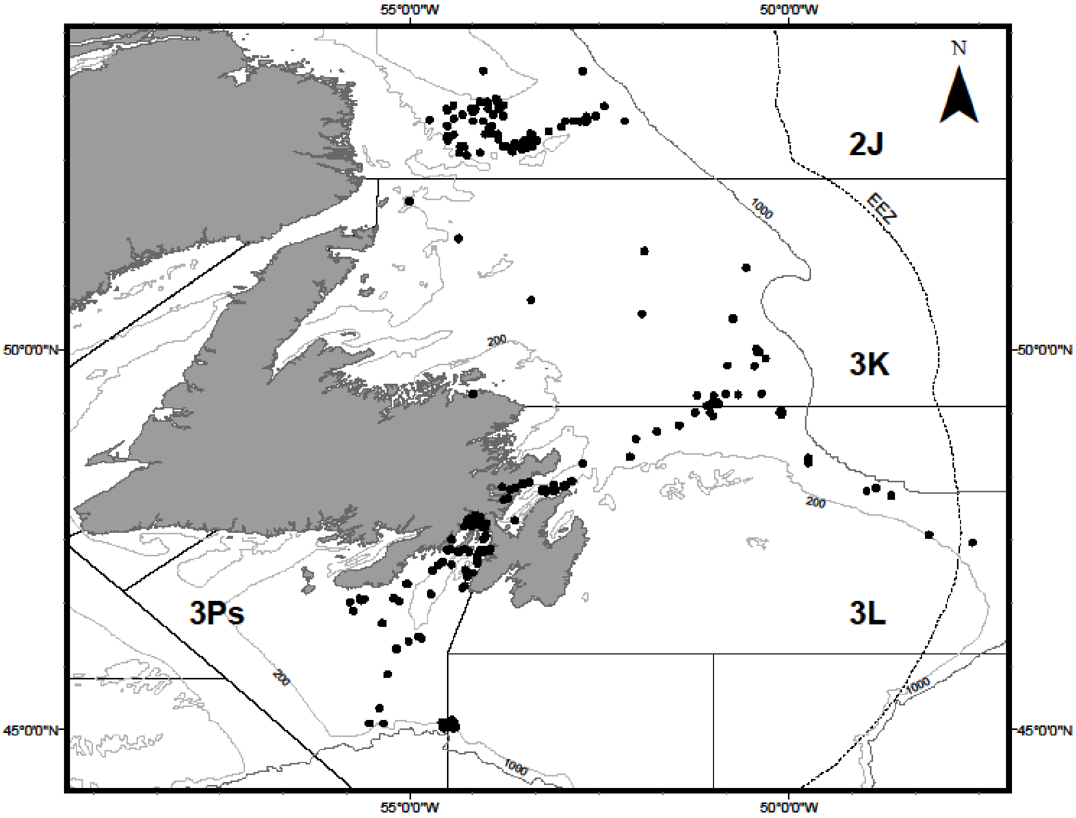


Figure 1.1: Sampling Location in the NAFO subdivisions surrounding Newfoundland and Labrador.

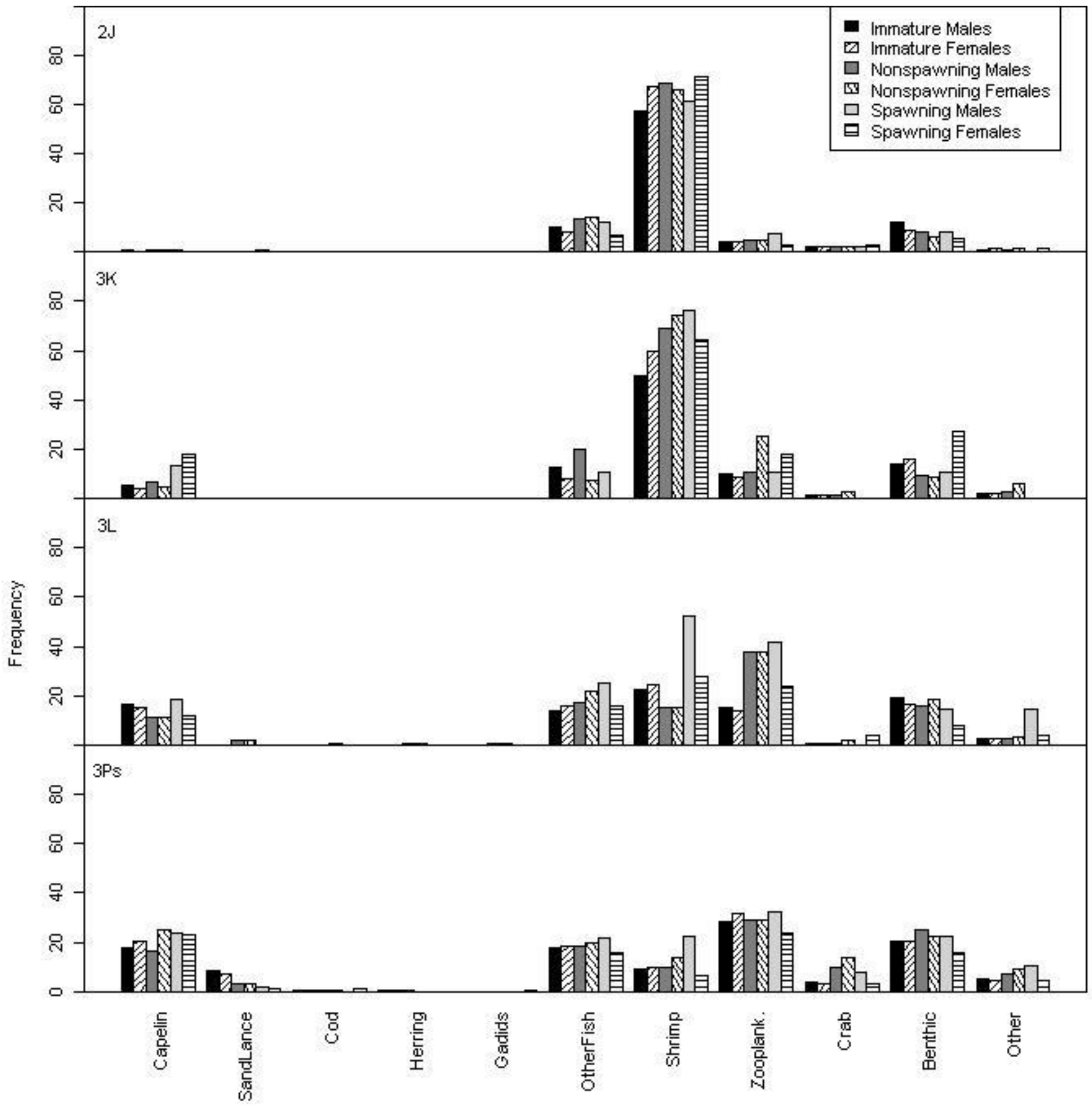


Figure 1.2: Frequency of occurrence of prey items for the four NAFO subdivisions by maturity stage and sex.

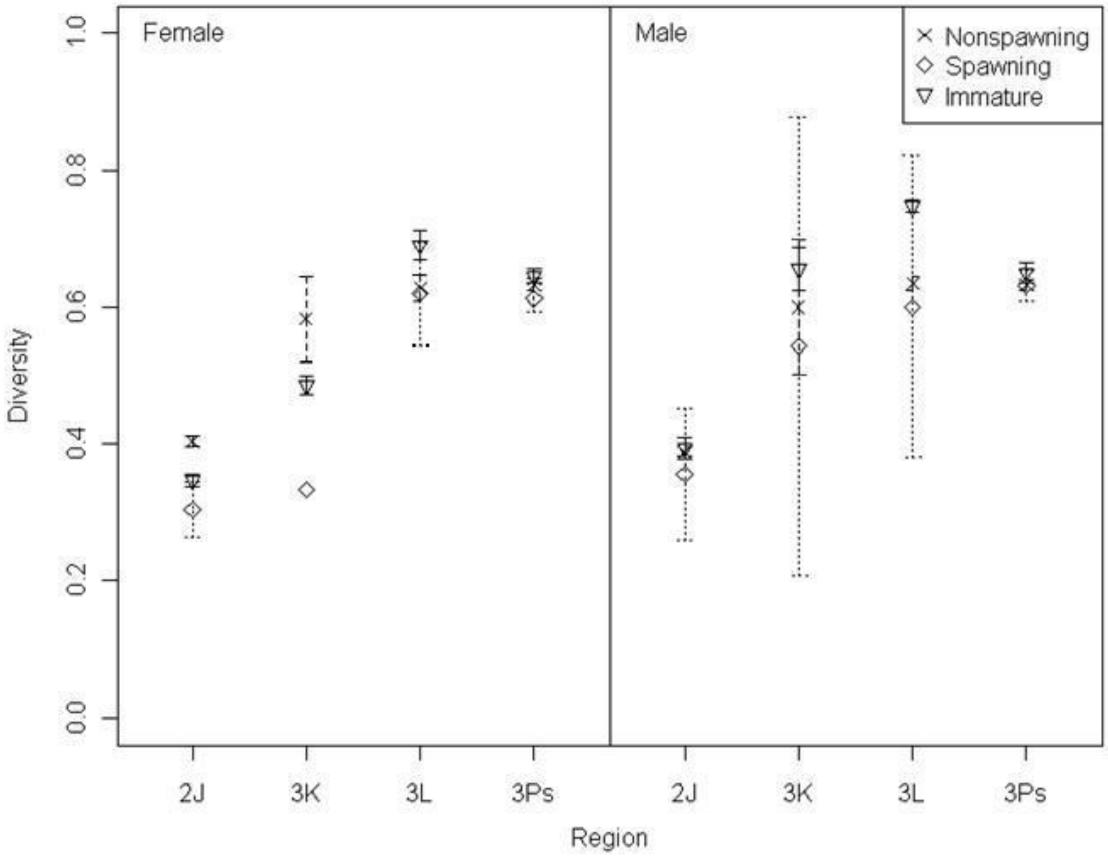


Figure 1.3: Simpson's Diversity Index by region, sex, and spawning status (error bars representing standard error).

Chapter 2: Does Atlantic cod feeding reflect spatial and temporal prey dynamics in Newfoundland waters?

2.1 Abstract

The Northwest Atlantic ecosystem underwent substantial changes in the early 1990s marked by the collapse of the cod stocks in northeast Newfoundland and Labrador. Parallel and subsequent changes occurred in numerous other fished and non-fished species that are less well documented. Diets of generalist feeders such as Atlantic cod (*Gadus morhua*) provide a means of assessing prey abundance, hence I hypothesize that the frequency of occurrence (FO) and percent weight (%W) of prey in cod stomachs would track changes in prey abundance at decadal scales. Through a combination of historical data from 1947 to the mid-1990s (91,750 stomachs) and original data from 1997 to 2011 (18,299 stomachs) from NAFO subdivisions 2J, 3KL, and 3Ps, I investigated whether cod stomach contents mirrored the documented abundance trends in three key prey species: shrimp (*Pandalus* sp.), capelin (*Mallotus villosus)* and crab (particularly snow crab, *Chionocetes opilio*). Shrimp FOC and % W directly reflected abundance. On the other hand, capelin did not decline in the cod diet in proportion to abundance, suggesting a preference. Crab comprised a minor portion of the stomach contents irrespective of the abundance. I conclude that cod are not solely generalist feeders. Some species were fed upon in proportion to their abundance, some species more than expected from their abundance, and some demonstrating no trend.

2.2 Introduction

Major changes associated with ocean climate dynamics have occurred in the ecosystems of the Northwest Atlantic in recent decades (Hurrel & Van Loon, 1997; Seager, 2000; Drinkwater *et al*, 2010). These changes have impacted distributions and abundances of organisms over multiple trophic levels (e.g., deYoung & Rose, 1993, Frank *et al*., 1996; Greene *et al*., 2008). The stock collapses of Atlantic cod (*Gadus morhua*) are well known (e.g., Rose, 2007), but less known are the spatial (and abundance) changes that occurred in many other species. Of particular note were rapid declines in capelin (*Mallotus villosus*) whose abundance was once estimated over a million tonnes in the Newfoundland and Labrador region (Winters & Carscadden, 1978; Carscadden & Nakashima, 1997; DFO, 2012; Obradovich *et al.*, 2013; Buren *et al*., 2014) and increases in snow crab (*Chionocetes opilio*) and Pandalid shrimp (Dawe *et al.*, 2012; Orr *et al.*, 2011; Mullowney *et al.*, 2014).

Atlantic cod are often considered generalist feeders, their diet reflecting prey abundance (Gotshall, 1969; Livingston, 1989; Fahrig *et al.*, 1993; Link & Almeida, 2000). In the Newfoundland and Labrador region, cod have long been known to be highly dependent on a single and formerly abundant forage species: capelin (Cormack, 1832; Templeman, 1965; Lilly & Fleming, 1981; Akenhead *et al.*, 1982; Mello & Rose, 2005). For cod in this region, recent ecosystem dynamics have resulted in rapid and extreme reductions in the distribution and abundance of capelin with near simultaneous increases in shrimp and crab, both potential prey. With cod at record low abundance, and the noted prey species and environmental changes, density dependent responses in predator-prey relationships were possible, as were asymmetrical changes in prey availability as a consequence of differing predator and prey responses to environmental changes (Hunsicker *et al.*, 2011). Both density dependence and abundance changes called into question whether cod would remain a generalist feeder in ecosystems subjected to major change. In simple words, would cod diet reflect the changing prey field, despite low densities and possible preferences for certain prey?

Foraging theory centers on the idea that foraging behavior of organisms has evolved in such a way to maximize energy intake (MacArthur & Pianka, 1966; Emlen, 1966). Numerous factors have been identified to impact foraging behavior, including prey availability, habitat structure, availability of thermoregulatory opportunities, reproductive state, and dietary preferences (Perry & Planka, 1997). As a sub-field of optimal foraging theory is optimal diet theory which is concerned of which kinds of food of the available food sources should a predator select in order to maximize net energy intake (Emlen, 1966). Original models were often designed to provide short-term descriptions of foraging behavior. It was observed, however, that these techniques do not accurately describe the long-term foraging behavior of predators (Katz, 1974; Craig *et al.*, 1979). We therefore need to make considerations of the long-term foraging behavior of a predator when we are working to describe an animal's feeding behaviors. Further developments changed the field from numeric formulae describing the system to implementing "decision rules" to describe how a predator will behave (Pyke, 1978; Krebs *et al.*, 1983). Optimal foraging theory allows for qualitative analysis of foraging decisions (Stephens & Krebs, 1986), but has been subject to numerous attacks due to the number of assumptions required, such as the assumption that the maximization of fitness will result in the maximization of foraging efficiency and that fitness will be maximized by natural selection (Heinrich, 1983; Porter *et al.*, 1983; Pierce & Ollasen, 1987; Gray, 1987). Stomach analysis of predators provides a useful sampling tool to assess the abundance and distribution of prey (Gotshall, 1969; Livingston, 1989; Fahrig *et al.*, 1993). If cod diet reflects prey abundance with no impact on cod density then feeding should parallel changes in the prey field. On the other hand, if there is some selection for a particular prey, or feeding depends on cod density, a simple relationship may not hold. For example, if cod show a preference for capelin, as some recent studies suggest (e.g. Dawe *et al.*, 2012), then capelin feeding by cod should have declined at a lower rate than abundance, at least above some prey threshold. However, if cod typically do not feed heavily on certain prey, such as snow crab (Dawe *et al.*, 2012), then predation on this prey should be low and stable irrespective of predator or prey abundance.

The objective in of this paper is to investigate the relationships between predator feeding and prey abundance over wide ranges in the abundance of both. I cannot address issues of local prey availability with the present abundance data, but have spatially resolved existing data as much as possible in comparisons, and rely on large changes in abundance and distribution to mask small-scale availability dynamics. In particular, I test the diet hypotheses in an ecosystem that experienced temporal and spatial changes in both predator and prey fields measured over orders of magnitude. Between 1947 and 2011 cod and capelin populations declined from millions to tens of thousands of tonnes while shrimp and snow crab increased from unknown but lower levels to hundreds of thousands of tonnes (Orr *et al.*, 2011; Dawe *et al.*, 2012).

2.3 Methods

2.3.1 Sample collection

A total of 18,299 cod stomachs were collected from trawl (Campelen 1800 and Yankee 36) and handline catches during surveys from 1997 to 2004, 2006, 2008, 2010, and 2011 in North Atlantic Fisheries Organization (NAFO) subdivisions 2J, 3KL, and 3Ps (Figure 2.1; Table 2.1). Samples were collected in both summer (March-August) and winter (September-February). Fish lengths ranged from 8 – 134 cm (Table 2.1) and are representative of the range of sizes in the population at the time of sampling.

2.3.2 Stomach Analysis

Stomachs were collected whole and promptly frozen (Table 2.1). Everted stomachs were discarded. In the lab, stomach contents were identified to the lowest taxon feasible and weighed. Stomach content data for capelin (*Mallotus villosus*), shrimp (*Pandalus* sp., *Crangon* sp., etc.), and crab (*Chionocetes opilio*, *Hyas* sp., etc) were utilized in this study as these represent important components of the cod diet and furthermore have ecosystem abundance estimates for the Newfoundland and Labrador region. Additional categories for remaining benthic invertebrate prey and any other fish species consumed were also established but no abundance data existed for these species to test the generalist feeding hypothesis.

2.3.3 Data analysis

Two indices were calculated to allow for comparison with historical cod diet data as well as provide a comprehensive description of the cod diet.

Percent weight (%W) provides a means of assessing the relative importance of prey groups to the nutrition of the fish (Bowen, 1983). The percent weight was defined as:

$$\%\,Weight = \frac{Weight\ of\ Individual\ Prey\ Type}{Weight\ of\ All\ Prey\ in\ Stomachs} \qquad (1)$$

The frequency of occurrence (FO) provides a means to assess how uniformly the cod behave in terms of prey selection (Bowen, 1983). The FO is calculated for each prey item as:

$$F_i = \frac{N_i}{N} 100 \qquad (2)$$

where N_i is the number of stomachs containing the specified prey item and N the total number of stomachs in a given sample. The proportion of empty stomachs was additionally calculated to provide an indication of the frequency of feeding events and is defined as the number of empty stomachs over the total number of collected stomachs. General linear models with a Gaussian error structure were constructed utilized both historical and contemporary data for the response variables of percent weight and frequency of occurrence against the explanatory variables of season, year, region, and their interactions. The months April-September were considered summer and October-March winter. The percentage of empty stomachs was analyzed using a logistic link function with binomial error. Bayesian Information Criterion (BIC) values were used to compare models and select the important explanatory variables for explaining the observed variablity. Calculation of BIC values is as follows:

$$BIC= -2*\text{Log-likelihood} + npar*\log(nobs) \quad (3)$$

Where npar is the number of parameters and nobs is the number of observations (Schwarz, 1978). The selected models exhibited the lowest BIC values. As the primary purpose of such model construction was to provide a descriptive rather than predictive representation of the data, BIC analysis was chosen over AIC to select the more important factors explaining the variability observed in the data. In scenarios where the Δ BIC between two models was less than or equal to 3, the models were considered equal quality and the simpler of the models was chosen (Kass & Raftery, 1995). All analyses were done in R statistical software (R Core Team, 2013).

2.4 Results

2.4.1 Regional, year and seasonal dependence

Twenty-five studies were used to temporally compare cod diets from 1947 to 2011 (Tables 2.2-2.4). The proportion of empty stomachs did not vary with region but increased in winter ($p<0.001$). Initial models selected by the BIC criteria indicated that time (year) was an important factor in explaining variation in the weights (%W) of capelin, shrimp and crab, and in the FO of capelin and shrimp (Table 2.5). Region was also a major determinant of capelin and shrimp %W but not of crab. No variables explained the variation in crab FO. Season was a contributor to the variation in the stomach content %W of capelin and crab, but not of shrimp, nor the FO of any of these species. Based on these results, all subsequent investigations of temporal trends were conducted by region.

2.4.2 NAFO Subdivision 2J- Hawke Channel/Hamilton Bank

According to the historical record (e.g. Templeman, 1965), capelin dominated the summer diet of large cod (length > 45 cm) in NAFO subdivision 2J prior to the 1960s, with smaller cod feeding on zooplankton (Table 2.2). In the 1960s, however, several quantitative studies indicated that capelin were infrequently consumed in summer (FO ranging from 1.7 to 6.3%, mean 6.1%, and 15%W as compared to winter FO of 1.7-45%, mean 30.8%, and 3.4%W; Figure 2.2). In the 1970s and 1980s winter diets contained 16 to 60% (mean 33.15%) capelin by weight (FO 9.9-45.1%, mean 21.3%) while summer diets contained between 0 and 31.7% (mean 20.3%) by weight (FO 0-30%, mean 8.2%). In contrast to the earlier data, capelin comprised only 0-3.4% (mean 1.3%) of stomach contents by weight in 0-1.8% (mean 0.6%) of stomachs during summer in the 1990s and 2000s, and 0-0.3% (mean <0.1%) of both in winter. Capelin FO and percent weight decreased over time ($p<0.001$ for both indices) (Table 2.5).

Both qualitative historical accounts and later estimates suggest that capelin were abundant seasonally in 2J prior to 1974 (Cormack, 1832; Jeffers, 1931; Thompson, 1943; Devold, 1971; Bakanev, 1983). During the late 1970s abundance decreased but quickly rebounded until the late 1980s (Carscadden *et* al, 1984a; Bakanev & Mamylov, 1988;

Carscadden *et al.*, 1988) (Figure 2.3), but in the early 1990s an abrupt decline occurred, coinciding with a southward shift of the capelin population as far as the Scotian Shelf and Flemish Cap (Frank *et al*., 1996). Capelin abundance in 2J has remained low since then. The decadal changes in capelin feeding mirror the changes in seasonal capelin abundance in 2J (Figures 2.2 and 2.3). Wintertime declines in both percent weight and FO of capelin in cod stomachs match a decline in capelin migration to 2J and resultant abundance. Summertime declines are also evident but of lesser magnitude (Figure 2.2).

Qualitative historical data suggest that shrimp was only rarely consumed by cod in the late 1940s and early 1950s in 2J (Templeman, 1965). The earliest measures during the late 1950s and 1960s suggest that shrimp FO ranged between 0.5 and 34.5% (mean 20.5%; Table 2.3). The FO and %W of shrimp in the diet increased during the 1970s and 1980s to become the dominant prey group (5.9-65.8%W, mean 10.4%, with FOs of 18.1-85.2%, mean 38.8%). By the 1990s and 2000s shrimp dominated 2J cod stomach contents, comprising 82.0-99.2% (mean 87.2%) by weight in 52-95.1% (mean 66.7%) of stomachs during summer and 81.1-92% (mean 87.6%) and 37.5-67% (mean 53.2%), respectively, in winter. Both shrimp FO and %W increased with time from the 1950s to the early 2000s ($p<0.001$ for both indices).

Prior to the mid-1980s the shrimp biomass in 2J was thought to be low and declining (Parsons *et al.*, 1980; Parsons & Veitch, 1991). Around 1986 shrimp rapidly increased until 2007 but have since declined (Parsons, 2005; DFO, 2011) (Figure 2.5). The increase in shrimp consumption in both summer and winter as evident in both cod stomach indices parallels the increase in abundance of shrimp that occurred in the late 1980s.

Contrary to shrimp and capelin, the crab component of 2J cod stomach contents was consistently low and relatively stable over time (Figure 2.6). Qualitative data from the late 1940s and early 1950s suggest that crab was rarely consumed (Templeman, 1965). Later studies typically reported the crab portion of stomach contents to range from 0 to 15.3 % W (mean 7.6%) with FO between 0 and 10.7% (mean 7.0%), with the exception of a single study in 1975 that reported a larger consumption (Minet & Perodou, 1978). Data from the 1990s and 2000s indicated a continuation of low crab consumption, with a FO of 0.7-3.9 (mean 2.2%) and 0.1-3.2 %W (mean 1.9%) in summer, and 0.3-5.9% (mean 2.8%) and 0.1-5.6% (mean 2.8%), respectively, in winter.

Little is known of the historical snow crab abundance in 2J, but it is frequently assumed to have increased rapidly in the 1990s from historical levels (Dawe *et al.*, 2010; DFO, 2012). Since 2001, snow crab abundance in 2J has declined (Mullowney *et al*., 2013) (Figure 2.7). There is little evidence of parallel changes in crab consumption by cod in either of the indices (Figure 2.4).

2.4.3 NAFO Subdivision 3KL- Newfoundland Shelf

Historical accounts suggest that capelin was the dominant prey of cod during the summer months in this area in the 1940s (Thompson, 1943). Between 1947 and 1951, capelin accounted for 63.4-98.3% (mean 81.3%) of reported stomach contents in summer, declining to 1.2-37.3% in winter (mean 25.5%; Table 2.2). During the 1960s, capelin consumption remained high, with reported FO ranging from 12 to 45% (mean 26.1%) and 50.8-95%W (mean 81.7%) in summer and FO of 0-39% (mean 16.6%) and 0-3.1%W (mean 2.7%) in winter (Figure 2.2; Table 2.2). In the 1970s, the capelin portion of cod diet declined, with FOs ranging from 9.7-45% (mean 23.5%) comprising 15-36% W (mean 17.3%). By the 1990s, capelin consumption by weight had declined in summer but most recently has increased. In contrast, the FO of capelin in cod stomachs remained relatively stable through the 1980s and 1990s but has declined in the 2000s (Figure 2.2). In contrast to 2J, summer consumption of capelin was greater than in winter ($p<0.001$). Capelin has long been known to be abundant in this region (Cormack, 1832; Jeffers, 1931; Templeman, 1948; Devold *et al*., 1972). A well-recorded decline in abundance occurred in the late 1970s, resulting in an effective closure of the fishery (DFO, 1982; Carscadden *et al*., 1984a) (Figure 2.3). Nevertheless, in the 1980s capelin abundance was again high and stable both inshore and offshore (Carscadden *et al,* 1984b ; Bakanev & Mamylov, 1988; Lilly, 1991). In 1991 capelin abundance declined rapidly and has remained low since, although not as low as in 2J, and has increased to some extent since 2010 (Frank *et al*., 1996; Lilly *et al*., 2000; DFO, 2013).

The decadal changes in capelin feeding are generally consistent with the changes in capelin abundance in 2J and 3KL (Figure 2.2 and 2.3). Nevertheless, the declines in both %W and FO of capelin in cod stomachs appear to be less than declines in capelin abundance over the stock range (Figure 2.2). Declines in capelin consumption in winter are also evident but are of lower magnitude. In the 2000s, the mean %W appears to have rebounded somewhat, but the FO is remains low.

Shrimp were historically considered to be a secondary but important prey for cod in 3KL (Thompson, 1943). Between 1947 and 1951, shrimp accounted for 0.4-2.1% (mean 1.0%)

of the cod diet by weight in summer and 3.1-13.8% (mean 9.1%) in winter (Table 2.3). In the late 1950s and 1960s shrimp FO ranged from 8.5-30.6% (mean 13.5%) with greater representation in winter. In the 1970s and 1980s, shrimp occurred in 3.0 and 46% (mean 25.1%) of stomachs and 4-18.9% W (mean 8.4%). In the 1990s and 2000s, both indices of shrimp consumption increased over time (p=0.007), though not as rapidly as in 2J. During this later period, shrimp comprised 0.1-81.2% (mean 23.2%) of the diet by weight with a FO of 1.1-87.3% (mean 35.0%) during summer and 0.4-99.6 (mean 21.2%) and 1.8-100% (mean 52.9%), respectively, during winter.

Early research on shrimp in 3KL indicated low densities that were not commercially exploitable (Squires, 1961). Fishing began only in 1987, when populations had grown sufficiently to support a small fishery (Parsons *et al.*, 1988). The shrimp in region 3KL increased from 1986 to 2007 followed by declines as in 2J (Lilly *et al.*, 2000; Parsons, 2005; Orr *et al.*, 2011) (Figure 2.5). An increasing amount of shrimp was consumed by cod from the 1980s onward but not to the same extent as further north in 2J. The FO of shrimp in cod stomach has not increased during this period.

Historical anecdotes suggest that snow crab was a consistent part of the cod diet (Thompson, 1943). The first quantitative studies in the late 1940s and early 1950s indicated that crab consumption was highest during winter, ranging between 33.9% and 54% W (mean 45.7%) compared to 0.3-18.2% (mean 8.2%) in summer (Table 2.4). In the late 1950s and early 1960s, however, several studies reported that crab was rarely encountered in cod stomachs (<5%). Similar results were reported in studies from the 1960s and 1980s, in which crab occurred in less than 3.8-20.2% (mean 13.5%) of stomachs (1.3-27% W, mean 11.2%). In the 1990s and 2000s crab remained a minor portion of cod stomach contents (0-39.8% FO, mean 2.6%, and 0-22.7%W, mean 3.6%). Commercial concentrations of snow crab were present in 3KL when the fishery began in 1968, and although the abundance was unknown it was assumed to have remained stable until the 1980s (Watson & Simpson, 1969; Taylor & O'Keefe, 1981) The fishery declined in the early 1980s and collapsed in 1985 (Taylor *et al.,* 1990). In the early 1990s, however, both abundance and catch rates increased rapidly and without precedent (Dawe *et al*., 1996). Since 2001 the snow crab biomass has declined (Mullowney *et al.,* 2013) (Figure 2.7).

The relatively low crab consumption by cod appeared for the most part to be independent of crab abundance. Most strikingly, the crab consumed by weight declined and the modest FO in cod stomachs did not change significantly as crab abundance increased during the early 1990s (Figure 2.6; Table 2.1). Although difficult to quantify, the lack of large cod in the 1990s and until recent (DFO, 2014) may have influenced this result, as large cod are more effective predators of crab than are smaller cod.

2.4.4 NAFO Subdivision 3Ps- Placentia Bay and Halibut Channel

Historical stomach content data for 3Ps are sparse. Thompson (1943) reported that during the early 1900s, spawning capelin were a dominant prey of cod on the adjacent southern Grand Bank. In the 1960s, several studies in summer reported that capelin comprised 4.6-47% (mean 19.2%) of stomach contents by weight (FO of 9-51%, mean 24.7%; Table 2.2). During the 1970s to mid-1990s capelin were present in 10 to 85.7% (mean 27.3%)

of cod stomachs (Figure 2.2). More recently, capelin comprised 0-60.5% (mean 34.1%) of the stomach contents by weight (FO of 0-28.4%, mean 20.7%) during summer. Winter FO values were consistently low. Unlike in 2J and 3KL, no multi-decadal temporal trends in the data on capelin consumption in 3Ps were apparent, although a decline in the most recent years from higher consumption in the 1990s is evident.

Data on capelin abundance in 3Ps is also limited. Nevertheless, dense shoals of capelin in this region were widespread there in the late 1990s (Mello & Rose, 2005), and recently have declined (Rose, unpublished) although no consistent surveys or stock assessments have been conducted (Frank *et al.*, 1996; DFO). A decline in capelin abundance from the 1990s to 2000s is mirrored in both summer and winter diet indices (Figure 2.2).

Shrimp occurred in 10.6-38% (mean 13.1%) of cod stomachs in the 1960s, and during the 1970s to mid-1990s in 2-10% (mean 9.0%) of stomachs (Table 2.3). In the late 1990s and 2000s, shrimp was a minor part of the diet in most studies ranging between 0 and 18%W (mean of 4.6%). FO were similarly low in most studies (0-43.3, mean 9.1%).

Shrimp are not numerous in 3Ps and have never supported a commercial fishery (Brothers, 1971). There are no abundance indices. Shrimp consumption by cod is much lower than the more northern regions, with uncertain trends over time (some evidence of an increase from the 1990s to the 2000s).

Snow crab was a common constituent of the cod diet in the 1940s in 3Ps (Thompson, 1943). In the late 1950s and 1960s crab occurred in 15-45% of stomachs (mean 22.4%; Table 2.4) and in the 1970s in 2-15% (mean 13.5%; Figure 2.6). Crab were a relatively minor part of the stomach contents in the 1990s and early 2000s occurring in 0-40.7% (mean 6.2%) of stomachs and comprising 0-59.4% (mean 12.9%) by weight.

Snow crab has never been as abundant in 3Ps as in 2J or 3KL, but abundance was stable from 1985 to 1992 (Dawe *et al.*, 1996; Markle *et al.*, 1998). From 1992 to 1998 abundance increased but has since declined (Dawe *et al.*, 2009; DFO, 2012).

Discussion

Our data in general support the hypothesis that cod feeding assessed over large spatial scales depends on regional and seasonal prey availability. In Newfoundland and Labrador waters, the abundance of migratory capelin and more stationary shrimp was reflected in decadal changes in consumption as indicated by stomach contents. These relationships held despite changes in both cod and capelin abundance over orders of magnitude.

Regional and seasonal differences were extreme. For the most northerly region studied (2J), the historical fall-winter migration of capelin to this region, and the dependence of cod on this prey, was evident in both stomach indices. The near absence of capelin in 2J in the 1990s and 2000s and the increasing abundance of shrimp were mirrored in the cod diet. Further south (3Ps), the data, although sparse, are consistent with a southward movement of capelin in the 1990s (Frank *et al.*, 1996) and a subsequent decline in the 2000s. In 3Ps the lesser abundance of shrimp is also reflected in the cod diet.

Notwithstanding the general relationship between prey availability and cod diet, our data further suggest that cod are not simply feeding without preference on what is available seasonally in their habitat. Evidence for this comes from a lower decline in capelin feeding in 3KL than might be expected under a no-preference hypothesis. In addition, in the 2000s capelin comprised approximately 45% of the stomach contents but were found in <15% of stomachs, which might be predicted if encounter rates with schooling capelin were low but encounters resulted in heavy feeding. These results are supportive of the notion that cod prefer capelin as prey in these waters (Dawe, *et al.*, 2013). The hypothesis of generalist feeding is not supported. Our data for cod feeding on two dominant prey, capelin and shrimp, are consistent with this, but suggest that there are limits and possible preferences for prey, notably capelin. Snow crab has undergone similar changes in abundance as capelin and shrimp, yet there is no clear relationship between availability and feeding.

There is also evidence in the cod diet of an interaction between the abundance of alternative prey. The northern region of 2J provides the clearest example of a switch in prey that reflects the inverse availability of two alternative prey, capelin and shrimp. But cod may be more likely to consume shrimp as capelin abundance declines, independent of shrimp abundance. For example, in Subdivision 3Ps, despite low levels of shrimp abundance, cod fed more often on shrimp when capelin consumption decreased.

Our data indicate snow crab is a minor part of the cod diet in all regions studied and that feeding indices do not reflect the abundance of crab over time or region. Although catchability of snow crab is biased based on the crab size and bottom substrate type such that small crabs (≤ 40 mm) and hard substrates are underrepresented, observed trends are thought to representative of population fluctuations and frequently match trends in exploitable biomass (Dawe *et al.*, 2010). Cod feeding on crab appears to be episodic and relatively rare compared to the more consistent feeding on capelin and shrimp.

The diet composition of cod has been reported to reflect the marine environment at the time of sampling (e.g. Stanek, 1975; Lilly, 1986; Fahrig *et al.*, 1993). The close association of cod feeding with prey abundance indices has been reported in past studies (e.g. Fahrig *et al.*, 1993) and enables the use of stomach contents to describe the distribution of key prey species. The presence of a prey item in the stomachs should indicate presence and potentially abundance of that species in the ecosystem. This association does not appear to hold for all prey, however, as cod feeding on crab did not reflect abundance. These observations would indicate, in accordance to foraging theory, that while cod will utilize what resources are readily available, they will actively pursue prey to increase the net energy gain from their diet. Analysis of stomach contents provides a means to assess geographical distributions of primary prey species and changes therein. I demonstrate this point with capelin in the present study but these principles have been applied to other species, such as short-finned squid (*Illex illecebrosus*) (Lilly & Osborne, 1984). The decline in capelin abundance in Subdivisions 2J and 3KL was associated with a southward shift of capelin. The capelin abundance in 3PS, however, remained stable until recent observed declines. Additional changes in capelin distribution are also observed in our data due to the migratory nature of capelin, which historically migrate to the Newfoundland coast in summer and northward to Labrador in early fall to spawn (Cormack, 1832; Jeffers, 1931). These changes in capelin distribution, but long term and short term, can be observed in the stomach data.

Environmental changes have occurred in the Newfoundland and Labrador region over the last few decades resulting in dynamics of abundance and distribution of numerous species, many of which are common prey for cod (e.g. deYoung & Rose, 1993; Frank *et al.*, 1996; Richardson & Shoeman, 2004). These changes can have ecosystem-wide impacts. It has been proposed that food availability plays a key role in determining cod abundance, distribution, and condition (Templeman, 1965; Rose & O'Driscoll, 2002). The variability in cod recovery could therefore relate to changes in prey availability in the environment. Studies in how the cod diet has changed over time and how it reflects changes within the ecosystem provide essential information into how the environment will affect cod populations.

Our objective was to assess whether the variation observed in predator feeding reflected changes of prey abundance in the environment. For important prey items, such as capelin and shrimp for the Atlantic cod, this connection could be made. Prey preference could furthermore be established in cases where the percent weight changed without a change in the frequency of occurrence. While I demonstrated this relationship for cod, similar approaches may be applied to other predatory fish species to assess changes within the marine ecosystem. Historical data in combination with continued diet investigation can help researchers assess the impacts these changes are having on prey assemblages and monitor changes in trophic dynamics. Information on species interactions, impacts of environmental changes, and the results of human activities on the fish and invertebrate populations are essential to our understanding and managing of fish stocks from an ecosystem-based perspective.

2.6 Tables

Table 2.1: Sample sizes and percentage of empty stomachs for each region in summer and winter from 1997 to 2011.

NAFO Subdivision	Season	Length Range (cm)	Mean Length (±SD) (cm)	Stomach Sample Size	% Empty Stomachs
2J	Summer	13-100	39.8 (±7.1)	3041	13.2
	Winter	16-60	34.2 (±9.1)	1067	9.2
3KL	Summer	9-106	43.2 (±15.6)	2305	16.2
	Winter	9-122	48.3 (±18.2)	3979	34.0
3Ps	Summer	13-128	54.1 (±12.4)	5192	13.7
	Winter	22-107	52.2 (±11.9)	2715	17.1

Table 2.2: Capelin percent of stomach content weight (%W), frequency of occurrence (FO), and length range (cm) (L)

Year	Season	Area									Sample Size	Gear	Source
		2J			3KL			3Ps					
		% W	FO	L	% W	FO	L	% W	FO	L			
1947	Summer	-	-	-	63.4	-	41 -110	-	-	-	169	Trap, linetrawl	Templeman, 1965
	Winter	-	-	-	37.3	-	39 -140	-	-	-	212	Linetrawl	
1948	Summer	-	-	-	98.3	-	31 -80	-	-	-	171	Trap	
	Winter	-	-	-	30.1	-	31 -120	-	-	-	300	Linetrawl	
1949	Summer	-	-	-	67.1	-	31 -100	-	-	-	196	Trap, linetrawl	
	Winter	-	-	-	1.2	-	31 -150	-	-	-	161	Handline, linetrawl	
1951	Summer	-	-	-	97.4	-	31 -80	-	-	-	182	Trap	
1959	Summer	-	18	30-80	-	33	30 -130	-	4	50-80	330	Bottom trawl	Popova, 1962
1960	Summer	-	31	20-70	-	31	20 -130	-	9	50-80	492; not given	Bottom trawl	Popova, 1962; Templeman, 1965
1961	Summer	-	-	-	95	-	Not Given	-	-	-	Not given	Not given	Templeman, 1965
1962	Winter	-	-	-	0	0	31-80	-	-	-	156	Bottom trawl	Stanek, 1973; Stanek, 1975
1963	Winter	3.4	1.7	31-80	3.1	2.5	31-80	-	-	-	1435		
1964	Summer	15	1.9	21-70	51.3	19.7	21->100	4.6	26.9	21 ->100	2630		
1965	Summer	-	-	-	50.8	26.9	21->100	22.1	26.9	21->100	2359		
	Winter	-	-	-	-	39	36 -75	-	-	-	237	Bottom trawl	Turuk, 1976

1966	Summer	-	-	-	74	45	25 -75	-	-	-	80	Poundnet, gillnet	Lilly & Fleming, 1981
1964-1966	Summer	-	6.3	Not Given	-	26.2	Not Given	-	-	-	21297	Bottom trawl	Turuk, 1968
	Winter	-	25.7		-	18.8		-	-	-	19070		
1967	Summer	-	-	-	79.7	42.3	35-95	-	-	-	792	Poundnet, gillnet; bottom trawl	Lilly & Fleming, 1981; Turuk, 1976
	Winter	-	45	36-75	-	-	-	-	-	-	194	Bottom trawl	Turuk, 1976
1968	Summer	-	-	-	-	-	-	47	51	15-125	134	Poundnet and gillnet	Lilly & Fleming, 1981
1969	Summer	-	-	-	-	12	36 -75	-	-	-	571	Bottom trawl	Turuk, 1976
	Winter	-	-	-	-	-	-	-	0	36-75	180		
1971	Summer	-	-	-	-	23	36 -75	-	-	-	405		
1975	Summer	0.8	1.7	16 -105	33	36.0	16 -105	-	-	-	261	Bottom trawl	Minet & Perodou, 1978
	Winter	-	-	-	-	-	-	64.7	85.7	26 -115	98		
1976	Winter	55.3	45.1	16 -105	41.8	37.5	16 -105	-	-	-	267		
1973-1976	Summer	-	30	Not Given	-	30	Not Given	-	25	Not Given	2935	Bottom trawl	Turuk, 1978
	Winter	-	45		-	45		-	35				
1978	Summer	-	0	Not Given	-	27.5	Not Given	-	12	Not Given	14650	Bottom trawl	Turuk & Postolaky, 1980
1979	Summer	-	-	-	15.0	19.1	Not Given	-	-	-	1771	Bottom Trawl	Lilly & Rice, 1983

1979	Winter	-	-	-	11.0	9.7	35 -95	-	-	-	1348	Poundnet, gillnet, handline	Lilly & Osborne, 1984
1981	Summer	0	0	25 -85	-	60	Not Given	-	-	-	854	Sputnik 1600 Shrimp Trawl; Gillnet	Bowering et al, 1983; Methven & Piatt, 1989
1982	Summer	0	9.3	25 -85	-	95	Not Given	-	-	-	704		
	Winter	16.0	9.9	9 -98	16.0	9.9	9 -98	-	-	-	3075	Bottom trawl	Lilly, 1984; Lilly, 1986
1978-1982	Summer	12.9	-	Not Given	18.5	-	Not Given	-	-	-	1296	Bottom trawl	Lilly et al, 1984
1983	Summer	-	-	-	-	87.9	Not Given	-	-	-	182	Gillnet	Methven & Piatt, 1989
1984	Summer	-	-	-	-	78.5	Not Given	-	-	-	248	Gillnet	Methven & Piatt, 1989
1985	Winter	36.2	26.6	Not Given	36.2	26.6	Not Given	-	-	-	2437	Bottom trawl	Lilly, 1986
1986	Winter	40.2	18.7	18 -89	40.2	18.7	18 -89	-	-	-	2125	Bottom trawl	Lilly, 1991
1987	Summer	-	-	-	-	29.6	27 -80	-	-	-	744	Bottom trawl	Gerasimova et al, 1992
1988	Summer	-	-	-	-	32.8	27 -89	-	-	-	825		
1989	Summer	-	-	-	-	30.6	27 -89	-	-	-	1671		
1990	Summer	-	-	-	-	20.5	27 -89	-	-	-	1059		
1991	Summer	-	-	-	-	41.0	18 -98	-	-	-	1054		
1978-1997	Summer	-	-	-	-	25-50	Not Given	-	10-25	Not Given	1541	Bottom trawl	Geraximova & Kiseleva, 1998

1992	Summer	-	-	-	3.5	-	21 -79	-	-	-	846	Diamond IX, Engels 145 high-rise & Western IIA trawls	DeBlois & Rose, 1996
1997	Summer	-	-	-	-	-	-	47.0	1.9	29 -93	214	Handline, Yankee 36	Present Study
	Winter	-	-	-	-	-	-	1.5	0.6	30 -92	327	Handline, Campelen 1800	
1998	Summer	2.5	0.5	21 -61	-	-	-	47.4	28.4	14 -112	1685	Handline, Campelen 1800	
	Winter	0	0	18 -58	-	-	-	13.3	3.7	22 -107	1590	Handline, Campelen 1800, Igypt	
1999	Summer	0.8	0.7	20 -100	54.5	5.5	9 -95	60.5	31.1	13 -128	2340	Handline, Campelen 1800	
	Winter	0	0	16 -60	0	0	13 -82	29.8	1.4	30 -89	871	Handline, Campelen 1800, Igypt	
2000	Summer	0.4	0.4	17 -60	42.6	9.2	13 -85	28.3	19.3	22 -101	657	Handline, Campelen 1800, Yankee 36	
	Winter	0	0	21 -59	0.3	0.2	12 -101	-	-	-	618	Campelen 1800	

2001	Summer	1.3	0.5	13 -73	12.3	5.4	12 -91	28.2	19.0	19.5 - 100	2364	Handline, Campelen 1800, Igypt, Yankee 36	Present Study
2002	Summer	3.4	1.8	16 -61	71.0	13.6	15 -74	29.2	8.2	22 -86	1805	Handline, Campelen 1800, Yankee 36	
	Winter	-	-	-	25.4	12.3	12 -108	0.2	0.1	24 -61	1923	Campelen 1800	
2003	Summer	0.4	0.5	22 -63	19.5	7.9	17 -61	2.6	3.8	32 -91	1124	Handline, Campelen 1800, Yankee 36	
	Winter	-	-	-	6.3	1.8	9 -110	-	-	-	872	Campelen 1800	
2004	Winter	-	-	-	0	0	21 -115	-	-	-	920	Campelen 1800	
2006	Summer	-	-	-	54.3	49.2	43 -106	-	-	-	61	Handline	
	Winter	-	-	-	0	0	53 -122	-	-	-	65	Yankee 36	
2008	Summer	0	0	21 -44	3.2	1.6	20 -84	-	-	-	206	Campelen 1800	
	Winter	-	-	-	0	0	26 -44	-	-	-	8		
2011	Summer	-	-	-	60.0	15.7	17 -50	-	-	-	83	Campellen 1800, GOV	
	Winter	0.1	0.3	19 -57	10.6	3.1	19 -77	-	-	-	568		

Table 2.3 : Shrimp percent of stomach content weight (%W), frequency of occurrence (FO), and length range (cm) (L)

Year	Season	Area									Sample Size	Gear	Source
		2J			3KL			3Ps					
		% W	FO	L	% W	FO	L	% W	FO	L			
1947	Summer	-	-	-	2.1	-	41 -110	-	-	-	169	Trap, linetrawl	Templeman, 1965
	Winter	-	-	-	13.8	-	39 -140	-	-	-	212	Linetrawl	
1948	Summer	-	-	-	0.4	-	31 -80	-	-	-	171	Trap	
	Winter	-	-	-	8.9	-	31 -120	-	-	-	300	Linetrawl	
1949	Summer	-	-	-	1.5	-	31 -100	-	-	-	196	Trap, linetrawl	
	Winter	-	-	-	3.1	-	31 -150	-	-	-	161	Handline, linetrawl	
1951	Summer	-	-	-	0.1	-	31 -80	-	-	-	182	Trap	
1959	Summer	-	13.2	30-80	-	10	30 -130	-	0	50-80	330	Bottom trawl	Popova, 1962
1960	Summer	-	0.5	20-70	-	10	20 -130	-	38	50-80	492	Bottom trawl	Popova, 1962; Templeman, 1965
1962	Winter	-	-	-	-	30.6	31-80	-	-	-	156	Bottom trawl	Stanek, 1973; Stanek, 1975
1963	Winter	-	17.7	31-80	-	22.9	31-80	-	-		1435		
1964	Summer	-	13.6	21-70	-	11.4	21- >100	-	10.6	21 - >100	2630		
1965	Summer	-	-	-	-	10.6	21- >100	-	10.6	21- >100	2359		
1964-1966	Summer	-	34.5	Not Given	-	8.5	Not Given	-	-	-	21297	Bottom trawl	Turuk, 1968
	Winter	-	8.4		-	19.2		-	-	-	19070		

1975	Summer	23.9	53.4	16 -105	7.5	26.4	16 -105	-	-	-	261	Bottom trawl	Minet & Perodou, 1978
	Winter	-	-	-	-	-	-	0.5	2.0	26 -115	98		
1976	Winter	10.0	33.3	16 -105	4.0	24.0	16 -105	-	-	-	267		
1978	Summer	-	50	Not Given	-	46	Not Given	-	10	Not Given	14650	Bottom trawl	Turuk & Postolaky, 1980
1979	Summer	-	-	-	2.4	8.0	Not Given	-	-	-		Bottom Trawl	Lilly & Rice, 1983
	Winter	-	-	-	12.9	35.3	35 -95	-	-	-	1348	Poundnet, gillnet, handline	Lilly & Osborne, 1984
1981	Summer	65.8	85.2	25 -85	-	3	Not Given	-	-	-	854	Sputnik 1600 Shrimp Trawl; Gillnet	Bowering et al, 1983; Methven & Piatt, 1989
1982	Summer	65.8	69.9	25 -85	-	6	Not Given	-	-	-	704		
	Winter	9.3	24.4	9 -98	9.3	24.4	9 -98	-	-	-	3075	Bottom trawl	Lilly, 1984; Lilly, 1986
1978-1982	Summer	22.4	-	Not Given	18.9	-	Not Given	-	-	-	1296	Bottom trawl	Lilly et al, 1984
1983	Summer	-	-	-	-	12	Not Given	-	-	-	182	Gillnet	Methven & Piatt, 1989
1984	Summer	-	-	-	-	8	Not Given	-	-	-	248	Gillnet	Methven & Piatt, 1989
1985	Winter	7.3	18.1	Not Given	7.3	18.1	Not Given	-	-	-	2437	Bottom trawl	Lilly, 1986
1986	Winter	7.1	40.3	18 -89	7.1	40.3	18 -89	-	-	-	2125	Bottom trawl	Lilly, 1991
1987	Summer	5.9	-	9 -116	5.9	-	9 -116	-	-	-	Not given	Bottom trawl	Lilly *et al.*, 2000

1978-1991	Summer	-	-	-	-	<25	Not Given	-	<25	Not Given	1541	Bottom trawl	Geraximova & Kiseleva, 1998
1992	Summer	-	-	-	50.2	-	21 -79	-	-	-	846	Diamond IX, Engels 145 high-rise and Western IIA trawls	DeBlois & Rose, 1996
1997	Summer	-	-	-	-	-	-	0.1	1.4	29 -93	214	Handline, Yankee 36	Present Study
	Winter	-	-	-	-	-	-	0.7	2.8	30 -92	327	Handline, Campelen 1800	
1998	Summer	82.0	52.0	21 -61	-	-	-	0.4	1.5	14 -112	1685	Handline, Campelen 1800	
	Winter	88.7	48.9	18 -58	-	-	-	1.2	5.4	22 -107	1590	Handline, Campelen 1800, Igypt	
1999	Summer	85.2	54.0	20 -100	0.1	1.1	9 -95	0.3	1.7	13 -128	2340	Handline, Campelen 1800	
	Winter	88.7	37.5	16 -60	11.5	3.75	13 -82	1.1	2.9	30 -89	871	Handline, Campelen 1800, Igypt	

2000	Summer	97.0	81.6	17 -60	55.9	64.8	13 -85	17.7	34.3	22 -101	657	Handline, Campelen 1800, Yankee 36	Present Study
	Winter	92.0	60.7	21 -59	20.9	23.4	12 -101	-	-	-	618	Campelen 1800	
2001	Summer	82.4	58.0	13 -73	68.2	59.1	12 -91	17.8	43.3	19.5 - 100	2364	Handline, Campelen 1800, Igypt, Yankee 36	
2002	Summer	90.2	80.6	16 -61	11.4	14.8	15 -74	1.9	5.2	22 -86	1805	Handline, Campelen 1800, Yankee 36	
	Winter	-	-	-	47.8	35.6	12 -108	3.0	10.9	24 -61	1923	Campelen 1800	
2003	Summer	88.3	83.5	22 -63	71.8	87.3	17 -61	1.2	6.1	32 -91	1124	Handline, Campelen 1800, Yankee 36	
	Winter	-	-	-	30.4	18.0	9 -110	-	-	-	872	Campelen 1800	
2004	Winter	-	-	-	0.4	1.8	21 -115	-	-	-	920	Campelen 1800	
2006	Summer	-	-	-	0.3	14.8	43 -106	-	-	-	61	Handline	
	Winter	-	-	-	2.8	100	53 -122	-	-	-	65	Yankee 36	
2008	Summer	99.2	95.1	21 -44	81.2	69.3	20 -84	-	-	-	206	Campelen 1800	
	Winter	-	-	-	99.6	100	26 -44	-	-	-	8		

2011	Summer	-	-	-	14.2	30.1	17 -50	-	-	-	83	Campellen 1800, GOV	Present Study
	Winter	81.1	67.0	19 -57	36.2	36.3	19 -77	-	-	-	568		

Table 2.4 : Crab percent of stomach content weight (%W), frequency of occurrence (FO), and length range (cm) (L)

Year	Season	Area									Sample Size	Gear	Source
		2J			3KL			3Ps					
		% W	FO	L	% W	FO	L	% W	FO	L			
1947	Summer	-	-	-	11.6	-	41 -110	-	-	-	169	Trap, linetrawl	Templeman, 1965
	Winter	-	-	-	33.9	-	39 -140	-	-	-	212	Linetrawl	
1948	Summer	-	-	-	0.3	-	31 -80	-	-	-	171	Trap	
	Winter	-	-	-	54.0	-	31 -120	-	-	-	300	Linetrawl	
1949	Summer	-	-	-	18.2	-	31 -100	-	-	-	196	Trap, linetrawl	
	Winter	-	-	-	45.6	-	31 -150	-	-	-	161	Handline, linetrawl	
1951	Summer	-	-	-	1.6	-	31 -80	-	-	-	182	Trap	
1959	Summer	-	13	30-80	-	5	30 -130	-	45	50-80	330	Bottom trawl	Popova, 1962
1960	Summer	-	1.5	20-70	-	5	20 -130	-	15	50-80	492	Bottom trawl	Popova, 1962; Templeman, 1965
1962	Winter	-	-	-	-	17.3	31-80	-	-	-	156	Bottom trawl	Stanek, 1973; Stanek, 1975
1963	Winter	-	7.2	31-80	-	15.7	31-80	-	-		1435		
1964	Summer	-	2.0	21-70	-	14.3	21->100	-	20.2	21 ->100	2630		
1965	Summer	-	-	-	-	20.2	21->100	-	20.2	21->100	2359		
1975	Summer	40.9	31.0	16 -105	1.3	3.8	16 -105	-	-	-	261	Bottom trawl	Minet & Perodou, 1978
	Winter	-	-	-	-	-	-	0.1	2.0	26 -115	98		
1976	Winter	0	0	16 -105	1.8	4.8	16 -105	-	-	-	267		

1978	Summer	-	0	Not Given	-	16	Not Given	-	15	Not Given	14650	Bottom trawl	Turuk & Postolaky, 1980
1979	Summer	-	-	-	27.0	13.5	Not Given	-	-	-	1771	Bottom Trawl	Lilly & Rice, 1983
	Winter	-	-	-	4.2	12.9	35 -95	-	-	-	1348	Poundnet, gillnet, handline	Lilly & Osborne, 1984
1981	Summer	3	-	25 -85	-	5	Not Given	-	-	-	854	Sputnik 1600 Shrimp Trawl; Gillnet	Bowering et al, 1983; Methven & Piatt, 1989
1982	Summer	3	-	25 -85	-	5	Not Given	-	-	-	704		
	Winter	10.7	15.3	9 -98	10.7	15.3	9 -98	-	-	-	3075	Bottom trawl	Lilly, 1984; Lilly, 1986
1978-1982	Summer	0.2	-	Not Given	2.0	-	Not Given	-	-	-	1296	Bottom trawl	Lilly et al, 1984
1983	Summer	-	-	-	-	4	Not Given	-	-	-	182	Gillnet	Methven & Piatt, 1989
1984	Summer	-	-	-	-	5	Not Given	-	-	-	248	Gillnet	Methven & Piatt, 1989
1985	Winter	-	5.3	Not Given	-	5.3	Not Given	-	-	-	2437	Bottom trawl	Lilly, 1986
1986	Winter	4.8	8.7	18 -89	4.8	8.7	18 -89	-	-	-	2125	Bottom trawl	Lilly, 1991
1978-1997	Summer	-	-	-	-	<25	Not Given	-	50<	Not Given	1541	Bottom trawl	Geraximova & Kiseleva, 1998

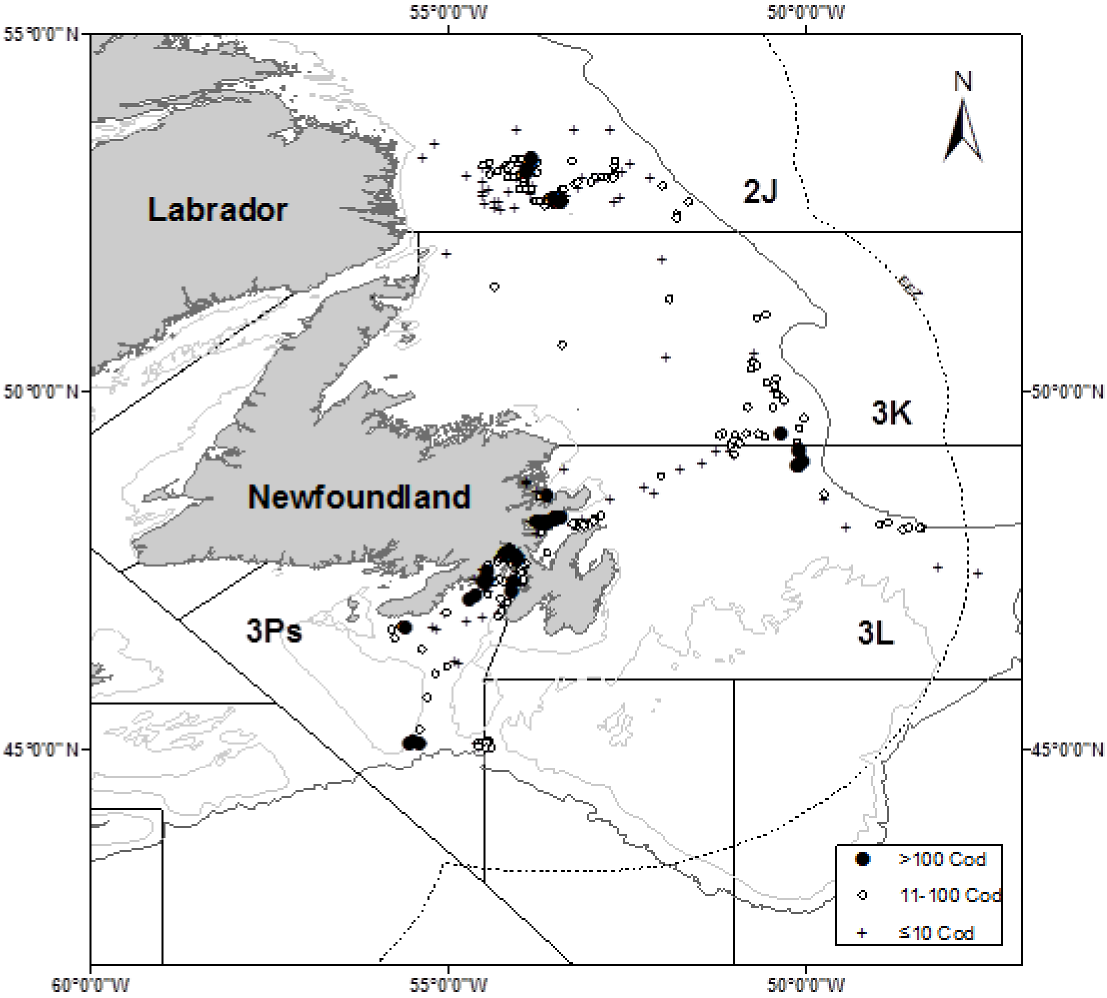
1992	Summer	-	-	-	17.2	-	21 -79	-	-	-	846	Diamond IX, Engels 145 high-rise, Western IIA trawls	DeBlois & Rose, 1996
1997	Summer	-	-	-	-	-	-	0.6	0.5	29 -93	214	Handline, Yankee 36	Present Study
	Winter	-	-	-	-	-	-	0.1	0.3	30 -92	327	Handline, Campelen 1800	
1998	Summer	1.3	1.9	21 -61	-	-	-	0.1	0.5	14 -112	1685	Handline, Campelen 1800	
	Winter	0.1	0.3	18 -58	-	-	-	6.5	1.1	22 -107	1590	Handline, Campelen 1800, Igypt	
1999	Summer	1.6	0.7	20 -100	5.0	1.5	9 -95	0.8	0.6	13 -128	2340	Handline, Campelen 1800	
	Winter	3.5	3.1	16 -60	5.7	0.8	13 -82	2.3	2.9	30 -89	871	Handline, Campelen 1800, Igypt	
2000	Summer	1.7	3.9	17 -60	0.1	0.5	13 -85	4.8	1.3	22 -101	657	Handline, Campelen 1800, Yankee 36	

	Winter	2.3	1.7	21 -59	1.3	0.7	12 -101	-	-	-	618	Campelen 1800	Present Study
2001	Summer	1.0	1.4	13 -73	6.4	2.2	12 -91	14.0	13.4	19.5 - 100	2364	Handline, Campelen 1800, Igypt, Yankee 36	
2002	Summer	0.9	2.8	16 -61	0.1	0.4	15 -74	3.5	2.0	22 -86	1805	Handline, Campelen 1800, Yankee 36	
	Winter	-	-	-	2.2	2.9	12 -108	0.2	2.3	24 -61	1923	Campelen 1800	
2003	Summer	3.2	2.9	22 -63	0	0	17 -61	59.4	40.7	32 -91	1124	Handline, Campelen 1800, Yankee 36	
	Winter	-	-	-	22.7	1.0	9 -110	0	0	-	872	Campelen 1800	
2004	Winter	-	-	-	4.6	4.5	21 -115	-	-	-	920	Campelen 1800	
2006	Summer	-	-	-	2.6	16.4	43 -106	-	-	-	61	Handline	
	Winter	-	-	-	1.5	100	53 -122	-	-	-	65	Yankee 36	
2008	Summer	0.1	2.4	21 -44	1.7	6.8	20 -84	-	-	-	206	Campelen 1800	
	Winter	-	-	-	0	0	26 -44	-	-	-	8		
2011	Summer	-	-	-	14.6	39.8	17 -50	-	-	-	83	Campellen 1800, GOV	
	Winter	5.6	5.9	19 -57	5.7	5.7	19 -77	-	-	-	568		

Table 2.5: Resulting model selected by BIC stepwise analysis for six response variables. The Δ BIC shows the change in BIC values between the null model and the resulting model.

Response Variable	**Resulting Model**	**Δ BIC**
% Weight Capelin	Region*Season+ Year	-21.9
% Weight Shrimp	Region*Year	-61.0
% Weight Crab	Year*Season	-9.9
FO Capelin	Year	-16.9
FO Shrimp	Region*Year	-30.8
FO Crab	None	0

2.7 Figures



2.1: Sampling locations around Newfoundland and Labrador with location sample sizes.

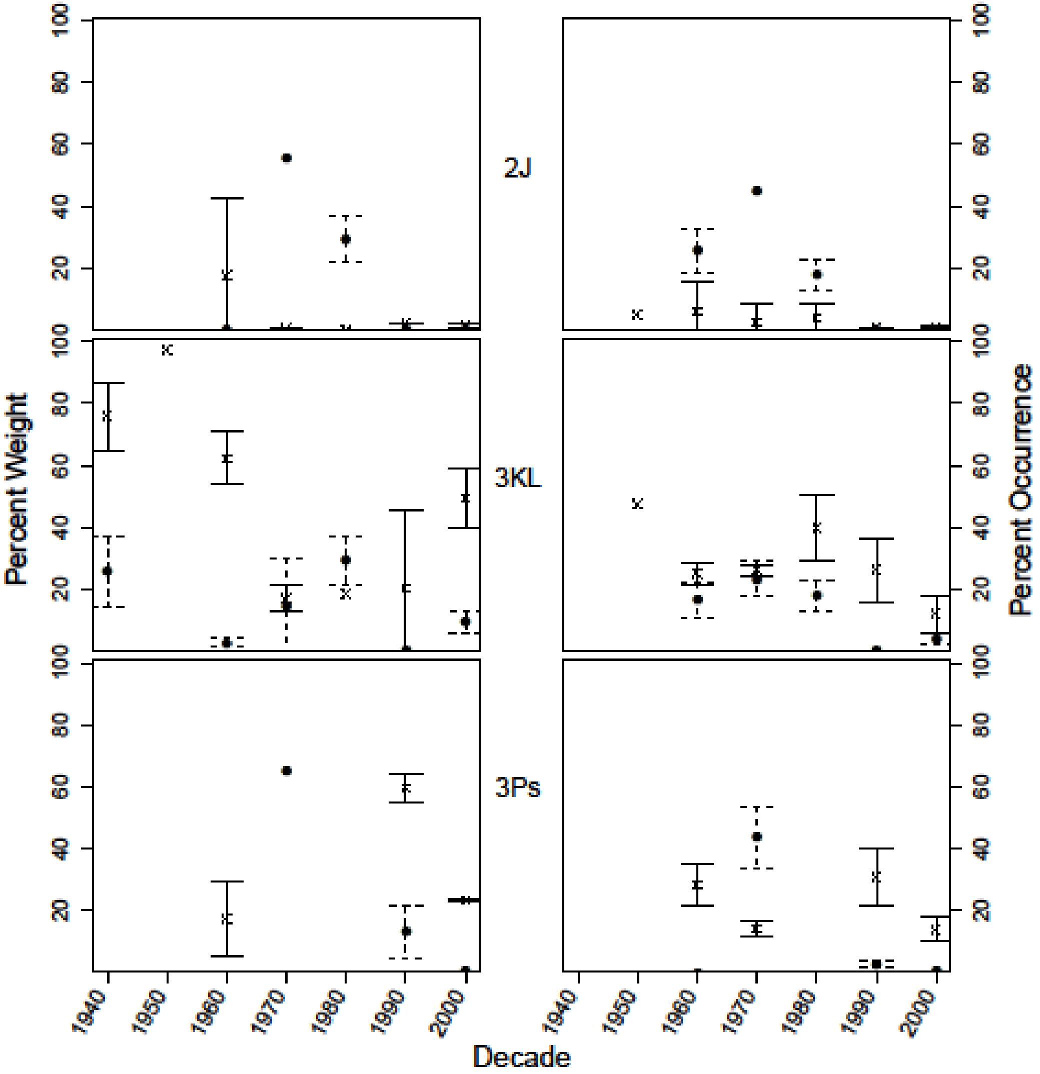


Figure 2.2: Percent weight and frequency of occurrence of capelin in cod stomachs by decade (error bars representing standard error between studies). Summer months are represented by x and solid error bars and winter months by circles with dashed error bars.

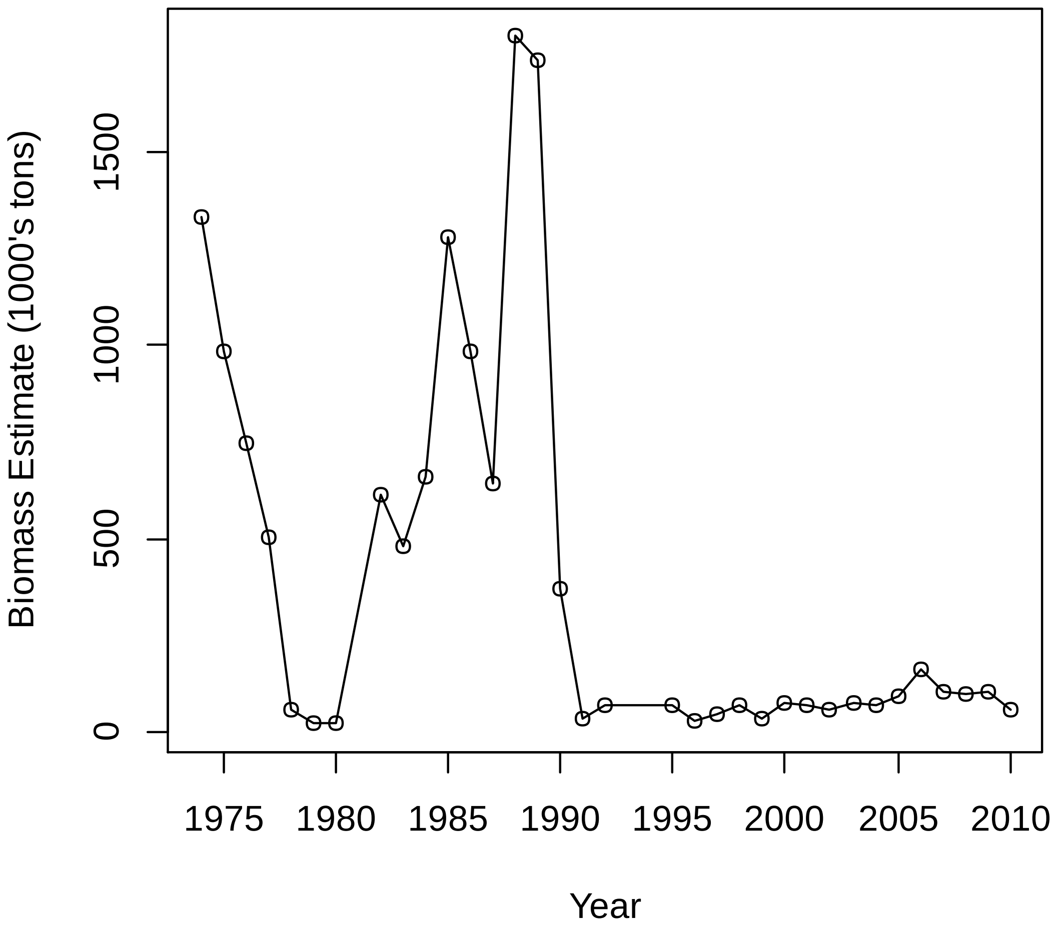


Figure 2.3: Capelin biomass estimates (1000’s of tons) for 2J+3KL from 1975 to 2010. Combined data contributed from Miller (1992), DFO (2008), and DFO (2010).

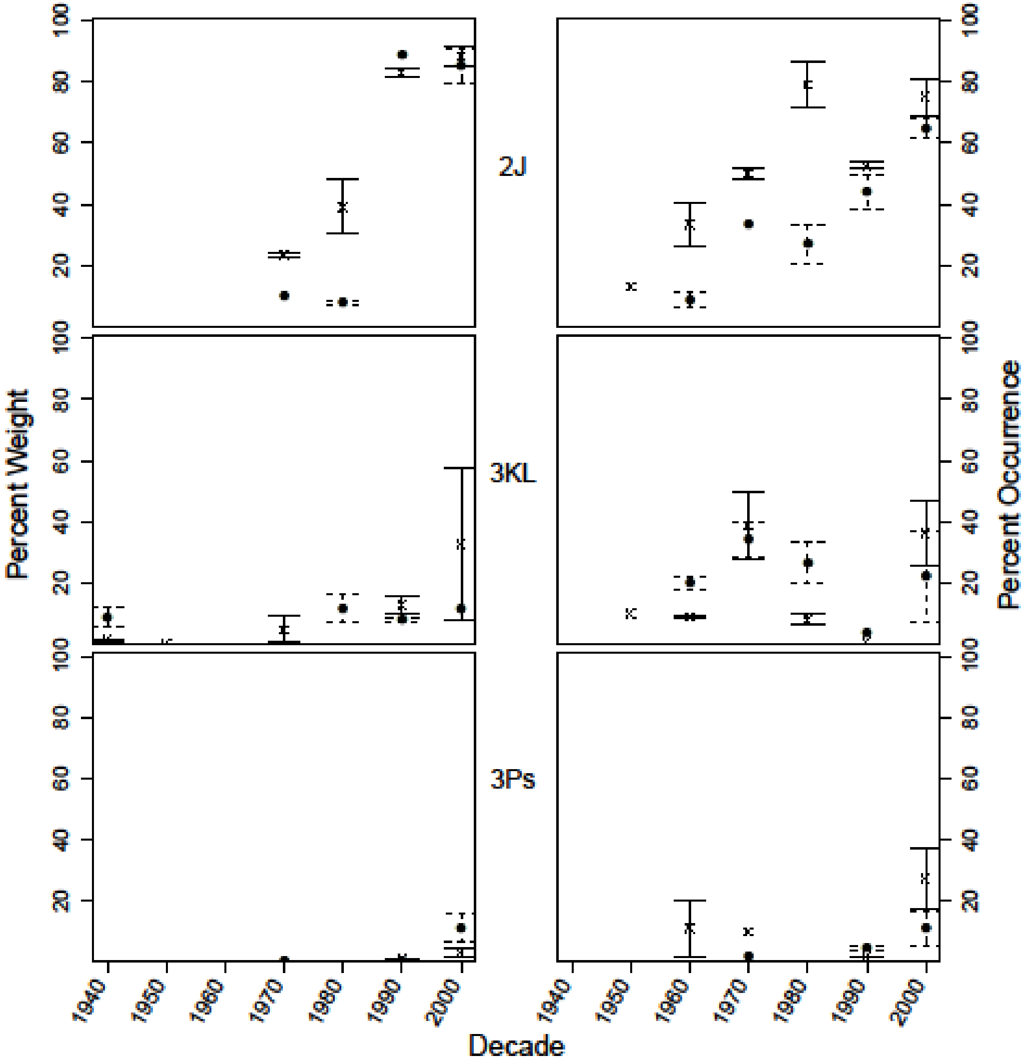


Figure 2.4: Percent weight and frequency of occurrence of shrimp in cod stomachs by decade (error bars representing standard error). Summer months are represented by x and solid error bars and winter months by circles with dashed error bars.

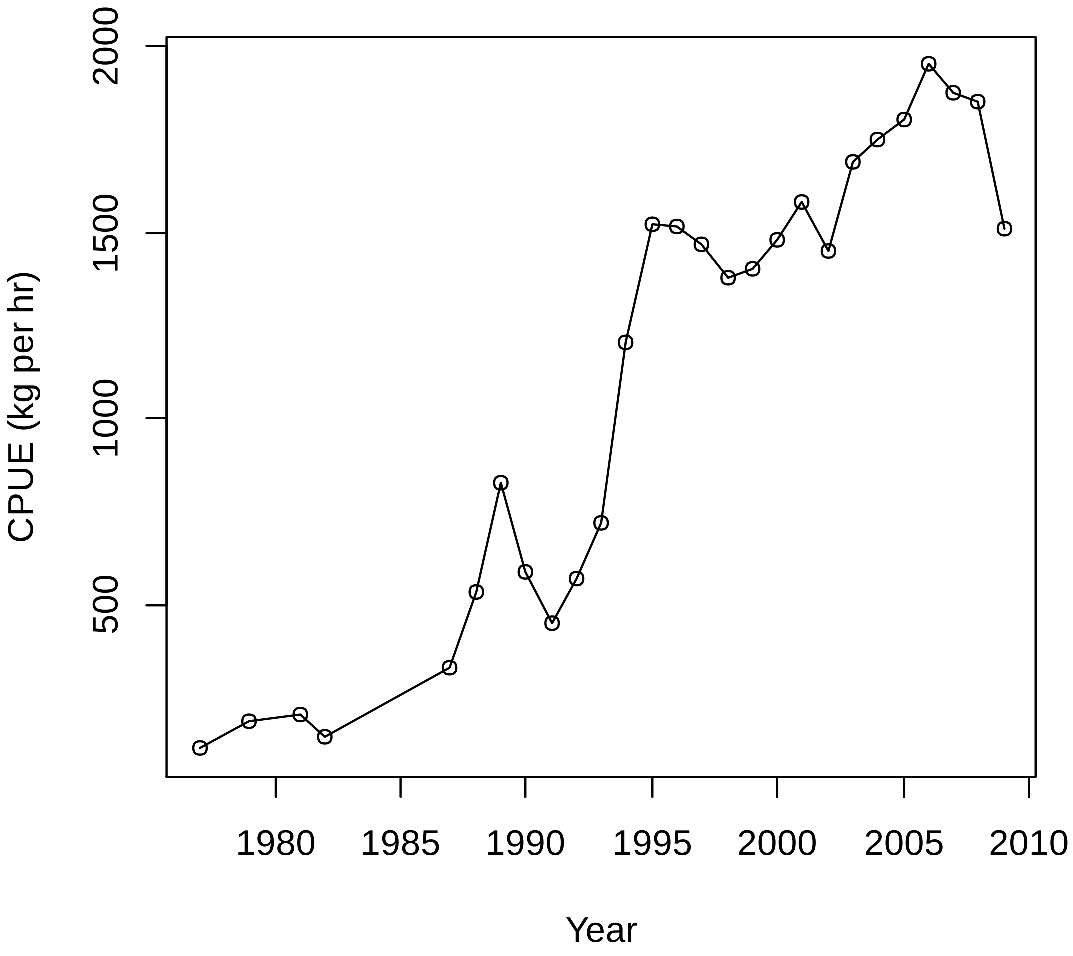


Figure 2.5: Shrimp catch per unit effort (kilograms per hour) for 2J+3KL from 1977 to 2009, considered an approximation of shrimp abundance. Combined data contributed from Parsons *et al.* (1999) and Orr *et al.* (2011).

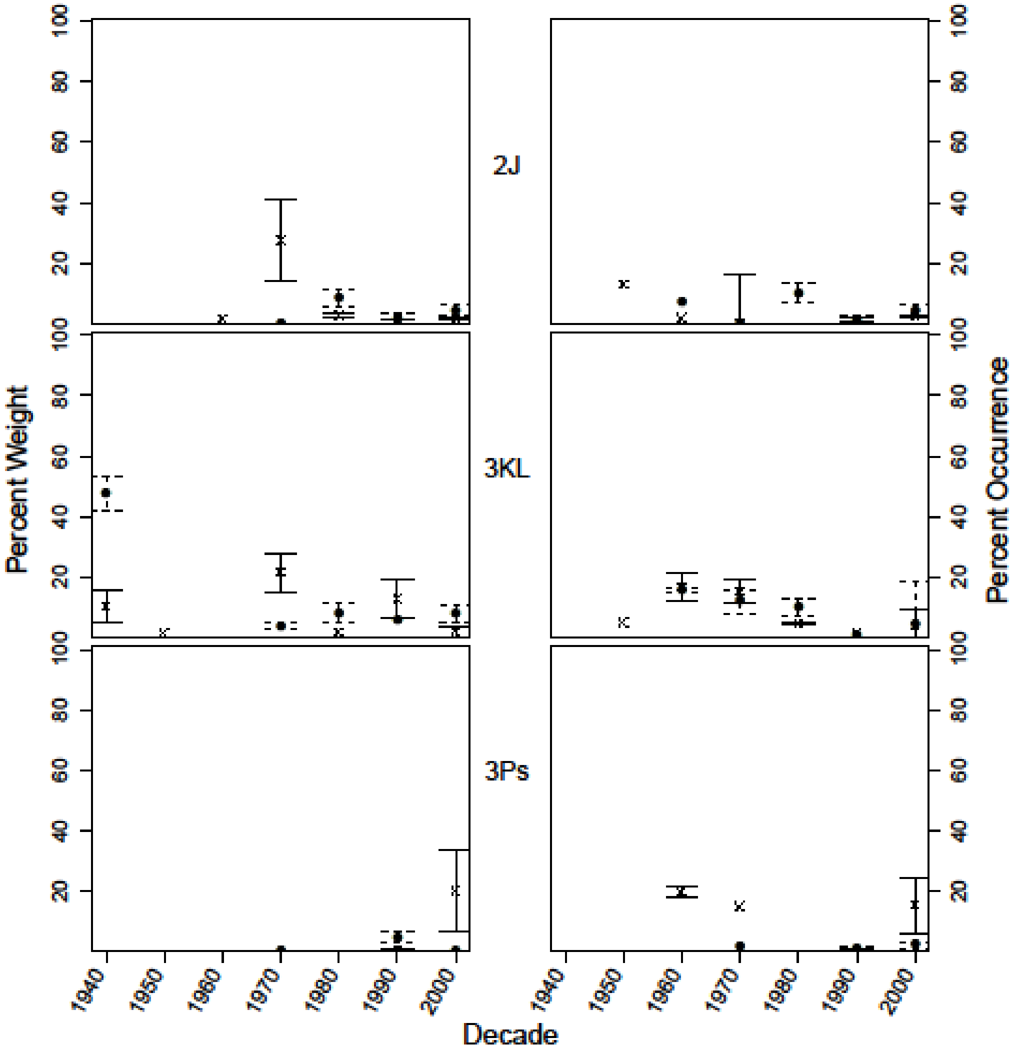


Figure 2.6: Percent weight and frequency of occurrence of crab in cod stomachs by decade (error bars representing standard error). Summer months are represented by x and solid error bars and winter months by circles with dashed error bars.

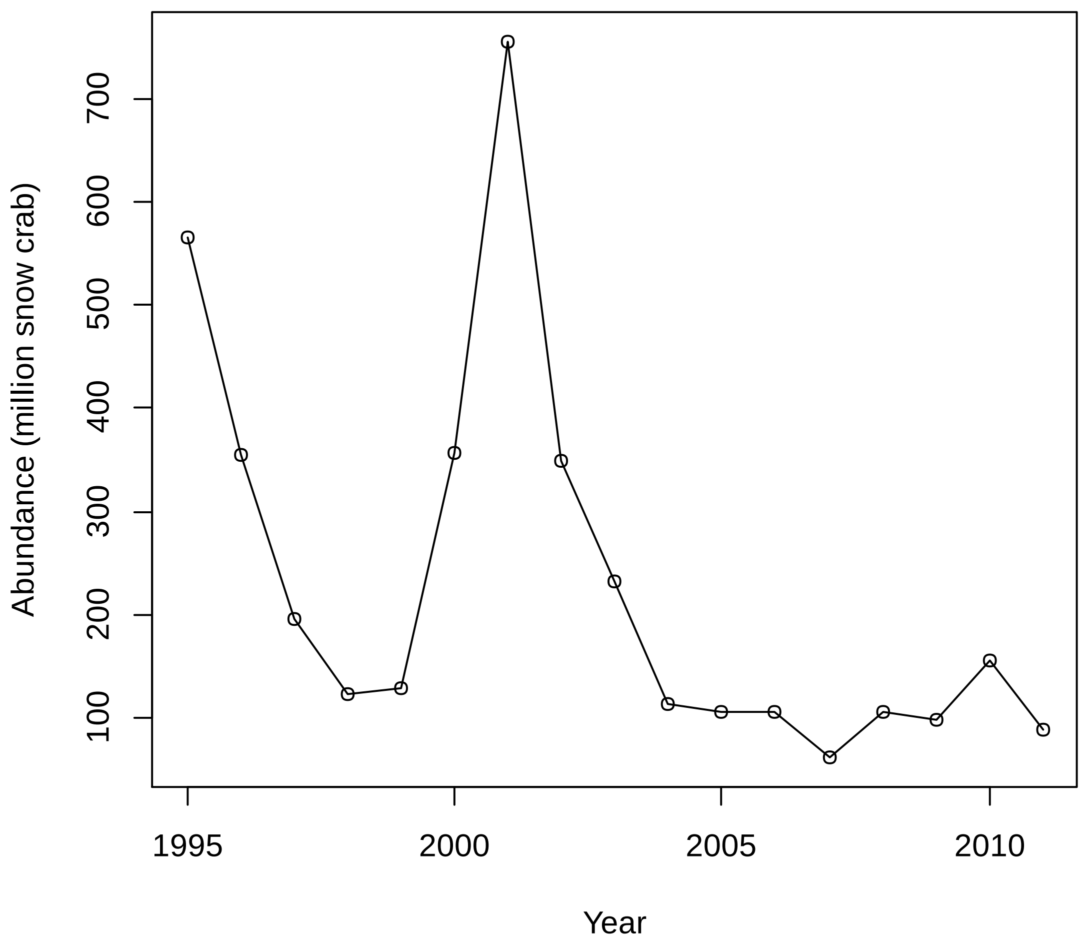


Figure 2.7: Snow crab abundance estimates (millions of crab) for crab ≤40 mm for 2J+3KLNO from 1995 to 2010. Crab in this size range are an appropriate prey size for Atlantic cod. Data summarized from Mullowney *et al.* (2013).

Conclusion

Summary

The goal of this study was to provide information on cod feeding behaviour which could later feed into the next generation of ecosystem-based models. An understanding of the energy flow toward important predators within an ecosystem, such as cod in the north Atlantic, is an essential input into such models. Furthermore, this knowledge and the generated models provide an indication in how the ecosystem has changed over time and allow predictions for future changes.

Samples were collected from 1997 to 2011 with representative samples for each month in offshore NAFO subdivisions 2J, 3K, 3L, and 3Ps and inshore 3L and 3Ps. A total of 18,301 stomachs were collected and were analyzed to the lowest feasible taxonomic level. Prey contents were later placed into the following categories: capelin, sand lance, cod, herring, gadoids, other fish, shrimp, crab, zooplankton, benthic prey, and other.

The first topic presented in this thesis addresses an assumption regarding cod feeding during the prolonged spawning period. The assumption for the Newfoundland and Labrador region was that cod ceased to feed during spawning. To address this question, the gonads maturity of sampled cod was determined. Actively spawning cod fell under the categories of matb and matc females and partly spent males. Spawning cod stomachs contained comparable amounts of prey as their non-spawning counterparts with the exception of 3Ps females, which were found to have reduced amounts of prey in the stomachs. No consistent differences in the percentage of empty stomachs were found. Furthermore, no differences were found in the diversity of stomach prey among spawning groups. Cannibalism was found to occur, sometimes in great quantities, primarily in females. Other sex differences in prey consumption were observed and likely represent variable spatial usage of the spawning grounds.

The second topic addressed in this thesis investigates the potential use of cod stomachs for tracking fluctuations in prey abundances. Cod are considered generalist feeders and the presence of prey in the stomachs has been noted to be a tool to assess prey biomass (Fahrig *at al*., 1993). Given a more extensive time series one may extend these biomass estimations to allow for estimation of prey population dynamics. The economically important species crab, shrimp, and capelin were selected for their dominant presence in the cod stomachs, economic importance and respective abundance estimates present in the literature. The percent by weight and the frequency of occurrence were found to approximately mirror the recorded population biomass changes presented in the literature for capelin and shrimp. The southward shift of capelin in the early 1990s is fairly clearly shown in the stomach data, as well as the increase in shrimp representation mirroring increases in shrimp biomass in northern regions. Crab has always been a relatively minor part of the stomach contents (typically less than 10% by weight) and as a result was not found to effectively reflect changes in abundance. Our results further indicate that cod are not complete generalist feeders as there appears to be a preference for high energy prey such as capelin. The cod therefore show a more opportunistic feeding style.

Numerous studies present data from a single season with the assumption that it remains constant over the course of a year (Popova, 1963; Lilly & Fleming, 1981; Methven & Piatt, 1989; Casas & Paz, 1996; Gerasimova & Kiseleva, 1998; Adlerstein & Welleman, 2000). By splitting the data by season I have additionally demonstrated that this assumption is invalid for cod feeding around Newfoundland and Labrador and emphasized the need for sampling in multiple seasons to provide an accurate representation of annual diet.

Regional differences in the stomach contents were found to be the primary factors explaining the variability in cod feeding. Northern regions were defined by increased shrimp and zooplankton consumption, while the southern cod exhibited a more varied diet incorporating higher quality prey including a wide selection of fish. These regional differences are not likely to represent variable preference but reflect prey availability. The regional variability observed in the feeding behaviour helps explain the differences previously observed in cod growth, survival, and population recovery rates (Olsen *et al*., 2005). The northern cod, which I observed to have a relatively energy-depleted diet, was found to have the lowest estimates for all three rates, while off the southern coast of Newfoundland the cod were found to recover and prosper.

Variability in energy input determined by prey availability may provide another facet in describing the diverse responses in the recovery of cod populations observed around Newfoundland and Labrador. Recent environmental changes are occurring which are impacting elements of the ecosystem including trophic structure. Studies such as these relating to the feeding of top predators not only provide information which may be input for ecosystem models, but additionally provides insight into the current trophic dynamics of the ecosystem to provide a stepping stone to link changes which have been observed in the past to future changes to come in this region.

Limitations of This Approach

The hypotheses and questions addressed in this thesis were answered primarily through the use of stomach content analysis. This approach to analyzing feeding behaviour, while offering a simple and relatively inexpensive means of assessing what exactly an animal has been feeding on, results in a large degree of variability in the obtained data. Furthermore, the contents of a stomach represent a snapshot in time into what the animal fed upon and may not be representative of their long-term feeding habits. In order to combat this limitation, a large sample size was analyzed. In theory if you obtain enough snapshots you should be able to reconstruct the entire picture. Samples were also collected at various times of year such as to accommodate any seasonal variation in feeding habits. Heavily digested prey items often would be difficult to identify. A cautious approach was taken in the analysis of the difficult to identify items through the creation of “unknown material” categories. However, most items could be identified to a broad taxonomic level. Given funding and time this category could have been avoided through genetic analysis of the unknown material. Finally the data obtained through the use of stomach content analysis could have been verified through the use of chemical techniques, such as stable isotope analysis for carbon and nitrogen. This technique would allow approximations of diet composition on the scale of months rather than on the scale of hours from stomach content analysis.

The fourth chapter used not only stomach content data but environmental data. One of the major challenges encountered in the writing of this chapter is the fact that population abundance data was simply lacking. Of the major prey groups of cod, only three have a historical record of abundance in Newfoundland and Labrador waters: crab, capelin, and shrimp. Oftentimes qualitative data was presented but population biomass estimates not provided. There was furthermore regional heterogeneity in the coverage of surveys. For example, NAFO subdivision 3Ps has not had a survey conducted for these species and therefore was confined to qualitative data. Furthermore the stomach content data obtained from the literature for this chapter were sometimes patchy.

Despite these limitations, overall trends and variation in the feeding behaviour of the Atlantic cod could be observed. Changes on spatial and temporal scales were readily observed despite the large degree of variability inherent with the utilized techniques. The findings of this work strengthen our understanding of the trophic ecology of the Atlantic cod and provides information for the current questions regarding the recovery potential of cod in the Newfoundland and Labrador region.

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Appendices

Appendix 1: Trip details

Supplementary Table 1: Trip details for stomach samples included in this study.

Trip	Start Date	End Date	Subdivisions	Number of Sets	Number of Fish
INN9706	29/06/1997	30/06/1997	3Ps	15	19
INN9708	05/08/1997	12/08/1997	3Ps	13	195
MAR9709	27/09/1997	10/10/1997	3Ps	9	91
MAR9711	01/11/1997	22/11/1997	3Ps	18	236
TEL59	06/01/1998	17/01/1998	2J, 3Ps	27	909
TEL60	30/03/1998	02/04/1998	3Ps	29	237
MAR9807	01/07/1998	01/07/1998	3Ps	2	38
TEL65	11/07/1998	25/07/1998	2J, 3Ps	60	1409
MAR9809	12/09/1998	12/09/1998	3Ps	1	30
MAR9810	22/10/1998	27/11/1998	3Ps	38	652
TEL77	05/01/1999	15/01/1999	2J, 3L, 3Ps	32	760
SH285	07/04/1999	22/04/1999	3Ps	16	387
MAR9905	04/05/1999	10/05/1999	3Ps	9	124
TEL79	31/05/1999	17/06/1999	2J, 3L, 3Ps	40	1664
MAR9907	15/07/1999	27/07/1999	3Ps	16	165
MAR9910	22/10/1999	07/11/1999	3Ps	17	111
TEL89	05/01/2000	12/01/2000	2J, 3KL	17	618
SH325	03/04/2000	19/04/2000	3L, 3Ps	5	48
MAR0005	21/05/2000	28/05/2000	3Ps	14	19
TEL304	31/05/2000	16/06/2000	2J, 3KL, 3Ps	46	590
SH377	05/04/2001	15/04/2001	3Ps	7	544
TEL355	07/06/2001	21/06/2001	2J, 3KL, 3Ps	59	1820
TEL363	11/01/2002	19/01/2002	3L, 3Ps	15	1923
SH432	09/04/2002	23/04/2002	3Ps	10	426
TEL406	12/06/2002	22/06/2002	2J, 3KL, 3Ps	25	1379
TEL416	19/01/2003	27/01/2003	3KL	22	872
SH490	03/04/2003	15/04/2003	3Ps	13	506
TEL464	31/05/2003	11/06/2003	2J, 3KL	22	618
TEL474	06/02/2004	11/02/2004	3KL	9	920
SH653	15/01/2006	15/01/2006	3L	10	65
CO0606	15/06/2006	29/06/2006	3L	3	61
TEL756	28/02/2008	08/03/2008	2J, 3KL	14	214
CE1103	12/03/2011	02/04/2011	2J, 3KL	24	628
TEL98	11/2011	11/2011	3K	1	23

Appendix 2: Stomach sample sizes for data presented in thesis.

Supplementary Table 2: Sample sizes of cod stomachs for each region, spawning status, and sex by year for summer cod.

Region	Spawning Status	Sex	Year									Totals
			1997	1998	1999	2000	2001	2002	2003	2008	2011	
2J	Immature	M		105	38	52	83	37	1	19		335
		F		205	48	84	120	176	110	17		760
	Non-spawning	M		249	78	41	142	189	172	4		875
		F		198	115	26	190	58	214	1		802
	Spawning	M		48	19	14	32	36	1	0		150
		F		24	4	11	11	10	13	0		73
3K	Immature	M				53	110	23	0	29		215
		F				73	160	40	41	41		355
	Non-spawning	M				0	54	1	6	35		96
		F				7	58	0	2	29		96
	Spawning	M				6	31	1	0	0		38
		F				0	9	2	0	1		12
3L	Immature	M			34	64	46	193	0	13	45	395
		F			51	86	78	367	9	12	33	636
	Non-spawning	M			153	18	37	97	0	1	3	309
		F			217	14	55	48	0	2	1	337
	Spawning	M			14	3	23	7	1	1	0	49
		F			12	3	2	8	0	1	0	26
3Ps	Immature	M	16	145	174	19	119	88	27			588
		F	27	216	257	24	194	107	62			887
	Non-spawning	M	92	193	492	14	346	152	229			1518
		F	98	157	431	11	291	107	171			1266
	Spawning	M	26	68	115	14	125	47	11			406
		F	4	99	79	5	37	10	4			238
Totals	Immature	M	16	250	246	188	358	341	28	61	45	1533
		F	27	421	356	267	552	690	222	70	33	2638
	Non-spawning	M	92	442	723	73	579	439	407	40	3	2814
		F	98	355	763	58	594	213	387	32	1	2506
	Spawning	M	26	116	148	37	211	91	13	1	0	643
		F	4	123	95	19	59	30	17	2	0	349
	Total		263	1707	2331	642	2353	1804	1074	206	82	10462

Supplementary Table 3: Sample sizes of summer cod stomachs for each region, spawning status, and sex by month

Region	Spawning Status	Sex	Month						
			3	4	5	6	7	8	9
2J	Immature	M	19			316			
		F	17			743			
	Non-spawning	M	4			871			
		F	1			801			
	Spawning	M	0			150			
		F	0			73			
3K	Immature	M	29			186			
		F	41			314			
	Non-spawning	M	35			75			
		F	29			67			
	Spawning	M	0			38			
		F	1			11			
3L	Immature	M	58	0	0	337			
		F	45	0	7	584			
	Non-spawning	M	4	5	0	301			
		F	3	8	0	329			
	Spawning	M	1	0	0	48			
		F	1	1	0	24			
3Ps	Immature	M	27	208	13	305	19	15	1
		F	36	325	15	462	21	24	4
	Non-spawning	M	15	787	53	498	64	62	40
		F	15	481	65	556	56	71	24
	Spawning	M	1	134	3	221	19	20	8
		F	4	96	5	107	21	3	2
Totals	Immature	M	133	208	13	1144	19	15	1
		F	139	325	22	2103	21	24	4
	Non-spawning	M	58	792	53	1745	64	62	40
		F	48	489	65	1753	56	71	24
	Spawning	M	2	134	3	457	19	20	8
		F	6	97	5	215	21	3	2
	Total		386	2045	161	7417	200	195	79

Supplementary Table 4: Sample sizes of cod stomachs by year

Region	Season	Year											Totals
		1997	1998	1999	2000	2001	2002	2003	2004	2006	2008	2011	
Hawke Channel	Summer	-	829	302	228	578	506	557	-	-	41	-	3041
	Winter	-	327	261	173	-	-	-	-	-	-	306	1067
Offshore 3KL	Summer	-	-	-	175	434	788	61	-	-	165	83	204
	Winter	-	-	61	1	-	446	414	39	-	8	262	32
Inshore 3L	Summer	-	-	456	21	62	-	-	-	61	-	-	600
	Winter	-	-	339	444	-	568	452	881	65	-	-	2749
Inshore 3Ps	Summer	214	336	1301	232	1290	511	506	-	-	-	-	4390
	Winter	327	1263	210	-	-	275	6	-	-	-	-	2081
Offshore 3Ps	Summer	-	520	281	1	-	-	-	-	-	-	-	802
	Winter	-	-	-	-	-	634	-	-	-	-	-	634
Totals	Summer	214	1685	2340	635	2364	1805	1124	-	61	206	83	18301
	Winter	327	1590	871	618	-	1923	872	920	65	8	568	

Supplementary Table 5: Sample sizes for cod stomachs by month (darkened months representing the winter months).

Region	**Month**												**Totals**
	1	2	3	4	5	6	7	8	9	10	11	12	
Hawke Channel	761	306	41	-	-	3000	-	-	-	-	-	-	4108
Offshore 3KL	922	286	248	-	7	1451	-	-	-	-	23	-	2937
Inshore 3L	1868	881	-	14	-	586	-	-	-	-	-	-	3349
Inshore 3Ps	961	-	-	1897	146	1949	203	195	82	115	893	30	6471
Offshore 3Ps	634	-	100	137	8	557	-	-	-	-	-	-	1436
Totals	5146	1473	389	2048	161	7543	203	195	82	115	916	30	18301

Appendix 3: Complete list of identified prey species with DFO prey codes and prey group in which they were placed.

Supplementary Table 6: Complete List of Identified Prey Species

DFO Prey Codes	Common Name	Scientific Name	Group
132	Sturgeons (NS)	Acipenseridae	Other Fish
150	Herring, atlantic	Clupea harengus	Herring
187	Capelin	Mallotus villosus	Capelin
213	Anglemouth, longtooth	Gonostoma elongatum	Other Fish
272	Lanternfishes (NS)	Myctophidae	Other Fish
275	Lanternfish, kroyer's	Notosco oyeri	Other Fish
290	Lanternfish, glacier	Benthosema glaciale	Other Fish
320	Lancetfish, scaled	Notolepis rissoi kroyeri	Other Fish
422	Sticklebacks (NS)	Gasterosteidae	Other Fish
436	Gadoids (NS)	Gadidae	Gadoid
437	Cod (NS) Gadus sp.	Gadus sp.	Gadoid
438	Cod, atlantic	Gadus morhua	Gadoid
445	Hake, red (squirrel)	Urophycis chuss	Gadoid
447	Hake, white (common)	Urophycis tenius	Gadoid
450	Hake, (NS) Mer.SP.	Merluccius sp.	Gadoid
451	Cod, arctic	Boreogadus saida	Gadoid
453	Threebeard rockling (NS)	Gaidropsarus sp.	Other Fish
454	Threebeard rockling (NS)	Gaidropsarus ensis	Other Fish
471	Grenadiers (NS)	Macrouridae	Other Fish
474	Grenadier, roughhead	Macrourus berglax	Other Fish
530	John Dory	Zenopsis ocellata	Other Fish
591	Sea basses (NS)	Serranidae	Other Fish
600	Grouper, snowy	Epinephelus niveatus	Other Fish
630	Scad, bigeye	Selar crumenophthalmus	Other Fish
693	Sand lances (NS)	Ammodytidae	Sand Lance
697	Blennies (NS)	Blennioidea (SUBORDER)	Other Fish
698	Wolffishes (NS)	Anarhichadidae	Other Fish
700	Wolffish, striped	Anarhichas lupus	Other Fish
709	Pricklebacks (NS)	Stichaeidae	Other Fish
711	Fourline snakeblenny	eumesogrammus praecisus	Other Fish
714	Blennies (NS)	Lumpenus sp.	Other Fish
716	Snake blenny	Lumpenus lumpretaeformis	Other Fish
717	Shanny	Lumpenus maculatus	Other Fish
721	Wrymouth	Cryptacanthodes maculatus	Other Fish
725	Eelpouts (NS)	Zoarcidae	Other Fish

726	Eelpout (NS)	Lycodes sp.	Other Fish
746	Ocean pout, green	Gymnelis viridis	Other Fish
790	Rockfishes (NS)	Scorpaeniformes (ORDER)	Other Fish
792	Redfish (NS) SEB.SP.	Sebastes sp.	Other Fish
793	Redfish, golden(marinus)	Sebastes marinus	Other Fish
794	Redfish, deepwater	Sebastes mentella	Other Fish
796	Redfish, bank	Sebastes fasciatus	Other Fish
802	Searobin, shortwing	Prionotus stearnsi	Other Fish
808	Sculpins (NS)	Cottidae	Other Fish
810	Hookear sculpin (NS)	Artediellus sp.	Other Fish
811	Hookear sculpin, atlantic	Artediellus atlanticus	Other Fish
813	Mailed sculpins (NS)	Triglops sp.	Other Fish
814	Sculpin, moustache	Triglops murrayi	Other Fish
815	Mailed sculpin, arctic	Triglops nybelini	Other Fish
817	Sculpin, ribbed (horned)	Myoxocephalus sp.	Other Fish
819	Sculpin, shorthorn	Myoxocephalus scorpius	Other Fish
821	Sculpin, fourhorn	Myoxoce quadricornis	Other Fish
824	Muddler (NS)	Cottus sp.	Other Fish
829	Deepsea sculpin, arctic	Cottunculus microps	Other Fish
830	Twohorn sculpin (NS)	Icelus sp.	Other Fish
831	Sculpin, twohorn	Icelus bicornis	Other Fish
832	Sculpin, spatulate	Icelus spatula	Other Fish
835	Alligatorfish (NS)	Agonidae	Other Fish
836	Alligatorfish, northern	Agonus decagonus	Other Fish
842	Lumpfishes (NS)	Cyclopteridae	Other Fish
844	Lumpfish, spiny	Eumicrotremus spinosus	Other Fish
849	Lumpfish, common	Cyclopterus lumpus	Other Fish
853	Seasnails (NS)	Liparidae	Other Fish
857	Seasnails (NS) LIP.SP.	Liparis sp.	Other Fish
862	Seasnail, dusky	Liparis gibbus	Other Fish
882	Flatfish	Pluerone omata) (ORDER)	Other Fish
887	Righteye flounders	Pleuronectidae	Other Fish
889	American plaice	Hoppoglossoides platessoides	Other Fish
890	Witch flounder	Glyptocephalus cynoglossus	Other Fish
892	Greenland halibut	Reinhardtius hippoglossoides	Other Fish
895	Flounder, winter	Pseudopleuronectes americanus	Other Fish
965	Goosefishes (NS)	Lophidae	Other Fish
998	Redfish, large	Sebastes sp.	Other Fish
999	Unidentified fish	Unidentified fish	Other Fish
1100	Invertebrate (NS)	Invertebrata	Invertebrate
1101	Sponge	Porifera	Benthic
1340	Cnidarian	Cnidaria	Benthic

1341	Hydrozoan	Hydrozoa	Benthic
2100	Anthozoan	Anthozoa	Benthic
2165	Sea anemone	Actinaria	Benthic
2280	Flatworm	Platyhelminthes	Benthic
2520	Rotifer	Rotifera	Zooplankton
2585	Nematode	Nematoda	Benthic
2642	Arrow worm SAG.ELEG.	Sagitta elegans	Zooplankton
2670	Bryozoan	Ectoprocta	Benthic
3080	Lamp shell Brach.	Brachiopoda	Benthic
3110	Mollusc	Mollusca	Benthic
3125	Chiton	Polyplacophora	Benthic
3175	Gastropod GAST.	Gastropoda	Benthic
3190	Gastropod	Acmaeidae	Benthic
3212	Gastropod	Margarites sp.	Benthic
3238	Gastropod	Lacuna vincta	Benthic
3248	Gastropod	Littorina sp.	Benthic
3383	Gastropod	Turbonilla sp.	Benthic
3392	Gastropod	Pyramidella fusca	Benthic
3437	Gastropod	Lunatia sp.	Benthic
3995	Bivalve	Bivalvia	Benthic
4019	Bivalve NUC.SP.	Nuculana sp.	Benthic
4022	Bivalve	Nuculana tenuisulcata	Benthic
4074	Bivalve YOL.SP.	Yoldia sp.	Benthic
4120	Mussel MYT.	Mytilidae	Benthic
4165	Scallop (NS)	Pectinidae	Benthic
4167	Scallop, islandic	Chlamys islandica	Benthic
4268	Bivalve CYCLO.BOR.	Cyclocardia borealis	Benthic
4416	Bivalve	Solenidae	Benthic
4425	Clam myidae	Myidae	Benthic
4426	Clam MYA.SP.	Mya sp.	Benthic
4427	Clam, soft shell	Mya arenaria	Benthic
4545	Cephalopod (NS)	Cephalopoda	Squid
4751	Squid ILLEX.SP.	Illex sp.	Squid
4753	Squid, short-fin	Illex illecebrosus	Squid
4846	Octopus OCTOPODA	Octopoda	Squid
4950	Polychaete	Polychaeta	Benthic
5001	Polychaete	Aphrodita sp.	Benthic
5232	Polychaete	Nereis sp.	Benthic
5614	Polychaete	Terebellida	Benthic
5900	Sipunculid	Sipunculida	Benthic
5951	Sea spider	Pycnogonida	Benthic
6000	Crustacean	Crustacea	Benthic
6020	Ostracod	Ostracoda	Zooplankton
6080	Copepod	Copepoda	Zooplankton

6081	Copepod Calanoid	Calanoida	Zooplankton
6580	Barnacle	Cirripedia	Benthic
6760	Isopod	Isopoda	Benthic
6930	Amphipod	Amphipoda	Zooplankton
6960	Hyperiid (FAMILY)	Hyperiidae	Zooplankton
6980	Gammarid (SUBORDER)	Gammaridea	Zooplankton
6996	Gammarid	Ampelisca sp.	Zooplankton
6998	Gammarid	Ampelisca macrocephala	Zooplankton
7025	Gammarid	Byblis gaimardi	Zooplankton
7278	Gammarid	Maera danae	Zooplankton
7741	Gammarid	Pontogeneia inermis	Zooplankton
7880	Caprellid	Caprellidea	Zooplankton
7881	Caprellid	Caprellidae	Zooplankton
7890	Caprellid	Aeginina longicornis	Zooplankton
7925	Mysid	Mysidacea	Zooplankton
7952	Mysid AMBL.ABB.	Amblyops abbreviata	Zooplankton
7967	Mysid MYSIS.SP.	Mysis sp.	Zooplankton
7973	Mysid MYSIS.STE.	Mysis stenolepis	Zooplankton
7986	Mysid NEOM.AME.	Neomysis americana	Zooplankton
7991	Euphausiid	Euphausiacea	Zooplankton
7994	Euphausiid MEGA.NOR.	Meganyctiphanes norvegica	Zooplankton
8000	Euphausiid THYSA.SP.	Thysanoessa sp.	Zooplankton
8019	Decapod, Crustacean	Decapoda	Benthic
8020	Shrimp NATA.	Natantia	Shrimp
8057	Shrimp PASIP.MUL.	Pasiphaea multidentata	Shrimp
8074	Shrimp EUAL.SP.	Eualus sp.	Shrimp
8075	Shrimp EUAL.FAB.	Eualus fabricii	Shrimp
8077	Shrimp EUAL.MAC.	Eualus macilentus	Shrimp
8079	Shrimp EUAL.GAI.	Eualus gaimardii	Shrimp
8080	Shrimp EUAL.GAI.GAI.	Eualus gaimardii gaimardii	Shrimp
8081	Shrimp EUAL.GAI.BEL.	Eualus Gaimardii belcheri	Shrimp
8084	Shrimp SPIRO.SP.	Spirontocaris sp.	Shrimp
8085	Shrimp SPIRO.SPI.	Spirontocaris spinus	Shrimp
8086	Shrimp SPIRO.PHI.	Spirontocaris phippsi	Shrimp
8087	Shrimp SPIRO.LIL.	Spirontocaris lilljeborgi	Shrimp
8091	Shrimp LEBB.SP.	Lebbeus sp.	Shrimp
8092	Shrimp LEBB.GRO.	Lebbeus groenlandicus	Shrimp
8093	Shrimp LEB.POL.	Lebbeus polaris	Shrimp
8095	Shrimp LEB.MIC.	Lebbeus microceros	Shrimp
8110	Shrimp PANDALUS.SP.	Pandalus sp.	Shrimp
8111	Shrimp PAND.BOR.	Pandalus borealis	Shrimp
8112	Shrimp PAND.MON.	Pandalus montaguii	Shrimp
8117	Shrimp CRANG.	Crangonidae	Shrimp
8119	Shrimp SCLE.BOR.	Sclerocrangon boreas	Shrimp

8127	Shrimp SAB.SP.	Sabinea sp.	Shrimp
8128	Shrimp SAB.SEP.	Sabinea septemcarinata	Shrimp
8129	Shrimp SAB.SAR.	Sabinea sarsi	Shrimp
8138	Shrimp ARG.DEN.	Argis dentata	Shrimp
8140	Malacostracan REP.	Reptantia	Crab
8177	Hermit crab PAG.	Paguridae	Crab
8203	Crab BRACH.	Brachyura	Crab
8204	Crab CANCR.	Cancridae	Crab
8211	Crab spider	Majidae	Crab
8212	Crab CHIO.SP.	Chionoecetes sp.	Crab
8213	Crab, snow or queen	Chionoecetes opilio	Crab
8216	Crab, toad HYAS.SP.	Hyas sp.	Crab
8217	Crab, toad HYAS.ARA.	Hyas araneus	Crab
8218	Crab, toad HYAS.COAR.	Hyas coarctatus	Crab
8260	Echinoderm	Echinodermata	Benthic
8290	Sea Cucumber HOL.	Holothuroidea	Benthic
8295	Sea Cucumber PSOL.FAB.	Psolus fabricii	Benthic
8318	Sea Cucumber	Stereoderma unisemita	Benthic
8360	Sea Urchin ECH.	Echinoidea	Benthic
8363	Sea Urchin STRO.SP.	Strongylocentrotus sp.	Benthic
8373	Sand Dollar ECH.PAR.	Echinarachnius parma	Benthic
8390	Sea Star	Asteroidea	Benthic
8407	Sea Star CTENO.CRISP.	Ctenodiscus crispatus	Benthic
8444	Sea Star SOLAS.SP.	Solaster sp.	Benthic
8530	Brittle Star	Ophiuroidea	Benthic
8539	Basket Star GORGO.	Gorgonocephalidae	Benthic
8552	Brittle Star OPH.ROB.	Ophiura robusta	Benthic
8553	Brittle Star OPH.SAR.	Ophiura sarsi	Benthic
8679	Chordate	Chordata	Benthic
8680	Tunicate, sessile	Ascidiacea	Benthic
8790	Tunicate, sessile	Pyuridae	Benthic
9980	Unid material	Unidentified material	Other
9981	Sand	Sand	Other
9982	Stone	Stone	Other
9984	Eggs, fish (SPAWN)	Fish Eggs (SPAWN)	Eggs
9986	Eggs, unidentified	Unidentified eggs	Eggs
9987	Plant material	Plant material	Other
9990	Gelatinous zooplank	Gelatinous zooplankton	Zooplankton
9992	Bryozoan ECT. Or ENT.	Bryozoa (Toprocta)	Benthic
9994	Offal, fish	Fish offal	Other
9997	Everted	Everted	Empty
9998	Empty	Empty	Empty

Appendix 4: Index of Relative Importance

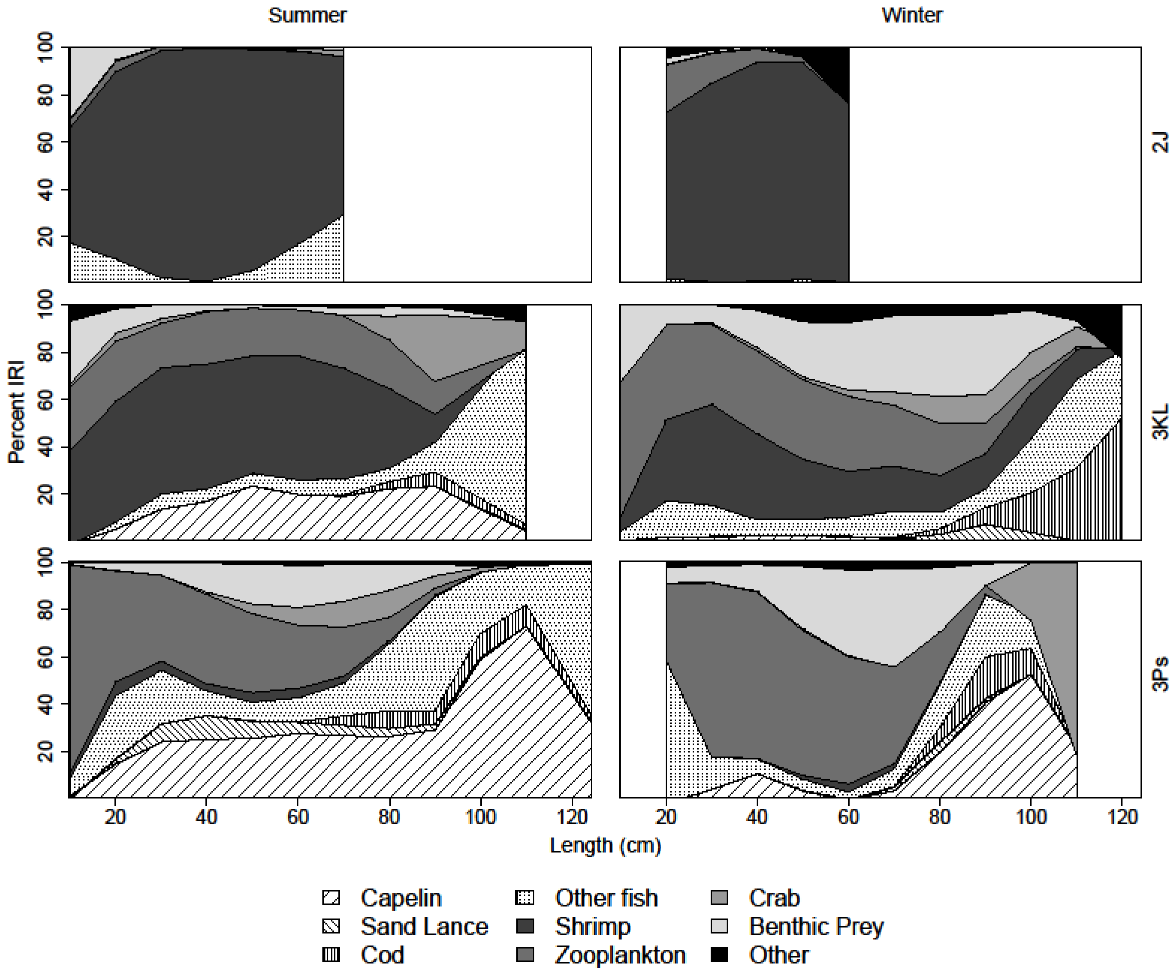
Originally included in Chapter 2, this data was later removed due to the inability to compare it to historical data. It does provide an effective index for describing the current cod diet.

The index of relative importance (IRI; Pinkas *et al.*, 1971) was given by:

IRI= $(N_i+W_i) \cdot F_i$

where N_i is the percentage of the number of specimens of a prey item over the total number of prey items, W_i the percentage of the weight of a prey item over the total weight of the stomach contents, and F_i being the frequency of occurrence being the percentage of stomachs with the the prey item present over the total number of stomachs. For simplicity of comparison, the %IRI was utilized, given by:

$$\% \, \mathbf{IRI}_{\boldsymbol{i}} = \mathbf{100} \, \mathbf{IRI}_{\boldsymbol{i}} / \sum_{\boldsymbol{i}=\mathbf{1}}^{\boldsymbol{n}} \mathbf{IRI}_{\boldsymbol{i}}$$

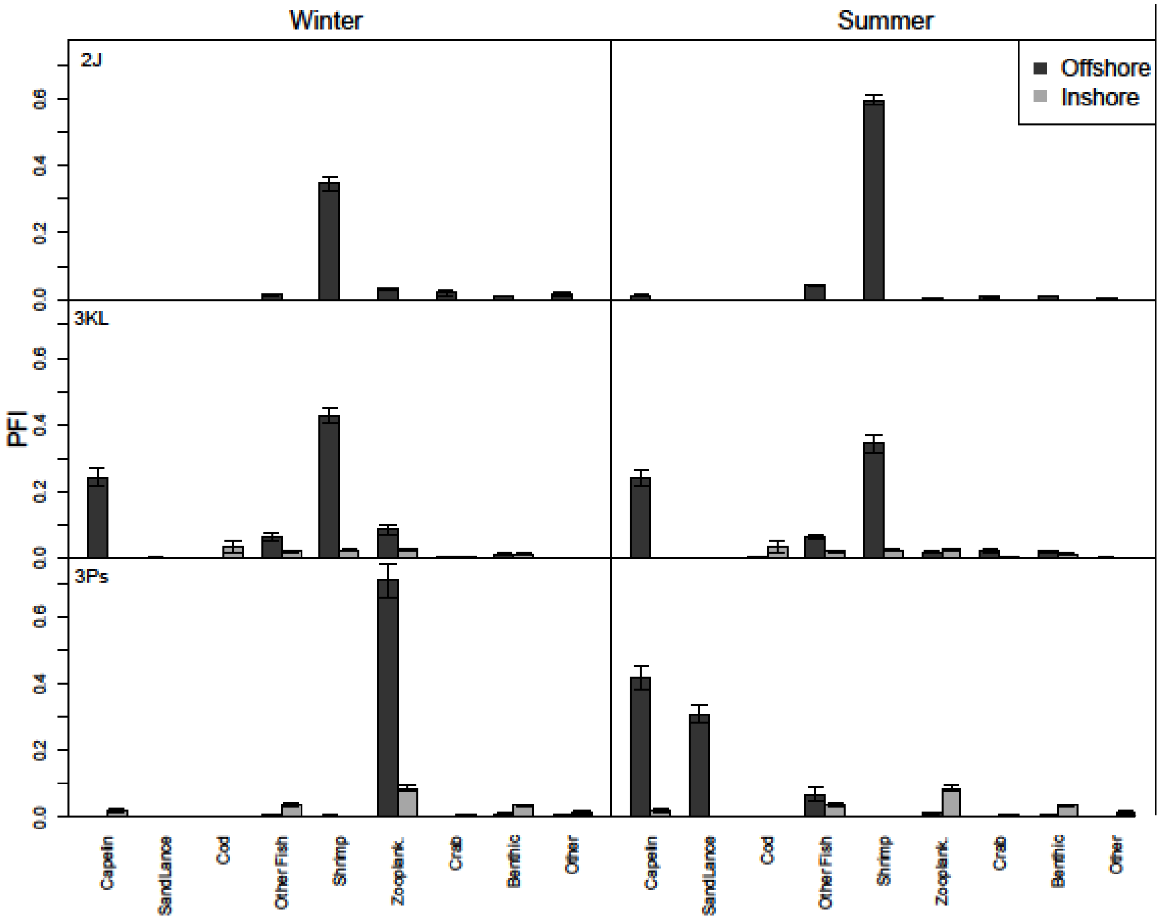


Supplementary Figure 1: Percent IRI over the length classes of caught fish.

Supplementary Table 6: BIC model selection of % Empty Stomachs, TFI, and IRI

Response Variable	Resulting Model	Δ AIC
% Empty Stomachs	Season	-5.55
TFI	Region*Year + Region*Season + Length*Season+ Year*Season	-1104.4
IRI Capelin	Length*Year + Season	-33.35
IRI SL	Year	-0.14
IRI Cod	Length*Year	-25.18
IRI Other fish	Length + Year	-9.49
IRI Shrimp	Region + Season + Year	-260.72
IRI Crab	Length + Year	-22.87
IRI Zooplankton	Region*Year + Length+ Season	-110.07
IRI Benthic	Region + Season	-26.14
IRI Other	Season	-7.8

Appendix 5: Frequency of occurrence, percent weight, and PFI data with different seasons and distinction between inshore and offshore data.



Supplementary Figure 2: Mean PFI (±SE) for inshore and offshore cod in 2J, 3KL, and 3Ps of the major prey categories

Supplementary Table 8: Mean PFI by subdivision, season, and inshore vs. offshore of the major prey categories.

NAFO	In/Offshore	Season	Mean PFI								
			Capelin	Sand Lance	Cod	Other Fish	Shrimp	Zooplankton	Crab	Benthic Prey	Other
2J	Offshore	Summer	0.013	<0.001	<0.001	0.013	0.596	0.005	0.009	0.008	0.001
		Winter	<0.001	0	0	0.013	0.347	0.031	0.020	0.009	0.002
3K	Offshore	Summer	0.104	0	0	0.054	0.610	0.013	0.007	0.020	0.002
		Winter	0.142	0.008	0	0.048	0.189	0.243	0.007	0.030	0.002
3L	Inshore	Summer	0.402	0.002	0.008	0.050	0.171	0.040	0.007	0.024	0.002
		Winter	0.001	0.001	0.020	0.024	0.017	0.0067	0.006	0.010	0.002
	Offshore	Summer	0.367	0.001	0.011	0.074	0.096	0.025	0.039	0.026	0.003
		Winter	0.303	0	0.001	0.071	0.543	0.020	0.003	0.008	0.002
3Ps	Inshore	Summer	0.228	0.005	0.011	0.082	0.058	0.152	0.097	0.044	0.009
		Winter	0.023	0.002	0.003	0.037	0.004	0.086	0.006	0.036	0.011
	Offshore	Summer	0.377	0.340	0	0.074	0.003	0.014	0.001	0.005	0.002
		Winter	0.003	0	0	0.008	0.005	0.722	0.002	0.009	0.004

Supplementary Table 9: Frequency of Occurrence (%) of major prey categories in each subdivision, season, and inshore vs. offshore.

NAFO	In/Offshore	Season	Frequency of Occurrence (%)								
			Capelin	Sand Lance	Cod	Other Fish	Shrimp	Zooplankton	Crab	Benthic Prey	Other
2J	Offshore	Summer	0.512	0.029	0.03	11.90	65.08	5.37	2.17	8.34	1.04
		Winter	0.144	0	0	8.74	53.93	26.93	3.04	11.12	5.58
3K	Offshore	Summer	5.208	0	0	10.56	60.54	17.32	1.94	14.65	2.78
		Winter	4.167	0.480	0	14.00	37.99	55.25	3.72	13.21	16.09
3L	Inshore	Summer	13.45	1.47	0.23	17.04	25.88	36.61	1.02	16.16	2.60
		Winter	2.40	2.40	3.28	4.62	11.64	21.06	5.18	24.87	12.24
	Offshore	Summer	17.04	0.22	0.78	20.31	17.15	16.81	5.01	18.82	4.57
		Winter	15.80	0	0.24	11.92	49.82	16.16	0.49	10.45	2.19
3Ps	Inshore	Summer	18.61	0.75	0.57	19.32	13.71	33.86	9.94	25.47	7.53
		Winter	2.91	0.33	0.23	16.94	4.59	27.40	1.12	25.00	6.99
	Offshore	Summer	27.33	23.66	0	19.33	1.25	5.19	0.87	6.83	5.28
		Winter	0.16	0	0	3.15	2.35	62.80	3.35	9.02	5.56