

The role of cephalopods in the Canadian Arctic – an examination of their distribution,
biogeography and trophic interactions within the Canadian eastern Arctic

by

Kathleen Gardiner

A thesis submitted to the Faculty of Graduate Studies of
The University of Manitoba
in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

Department of Science – Biological Sciences

University of Manitoba

Winnipeg

Copyright © 2015 by Kathleen Gardiner

Abstract

This thesis establishes baseline information on the distribution, biogeographical variability, habitat preference and trophic interactions for the most common Canadian Arctic cephalopod species: *Gonatus fabricii*, *Rossia moelleri*, *R. palpebroso*, *Bathypolypus* species complex and *Cirroteuthis muelleri*. Records of Arctic cephalopods and their predators were compiled and areas of interest within the Canadian Arctic were identified. Morphometric analyses of *G. fabricii* and *R. palpebroso* identified potential populations and described the key morphometric characters associated with each population. *G. fabricii* separated into four groupings: Hudson Strait, Ungava Bay, Baffin Bay/Greenland and Disko Bay, while St. Lawrence *R. palpebroso* were distinguishable from Arctic samples. Principal component analysis (PCA) was the preferable multivariate method for population analyses. Stable isotope analyses of $\delta^{13}\text{C}$ identified cephalopod habitat preferences and potential ontogenetic habitat shifts while stomach content analyses, $\delta^{15}\text{N}$ values and mixing models provided trophic information, including the first descriptions of *R. palpebroso* and *C. muelleri* prey items.

Acknowledgements

This thesis would not have been possible without the support and guidance of many people. First, I would like to thank my mom and aunt who not only supported me through all the trials of graduate school but who were also there to help clean dishes and take notes whenever I needed them. I would also like to thank the department of Biological Sciences for their support throughout this degree. I thank Dr. N. Kenkel for his patience and advice on statistical analyses and Drs. G. Goldsborough, J. Markham and S. Renault for laboratory space. Many thanks also to J. Matley, D. Kamada, O. Friesen, E. Spice, R. Wastle and Dr. W. Walkusz for their help and advice on statistical and stable isotope analyses, genetic analyses, and invertebrate identification. I would also thank my committee members (Drs. R. Baydack, A. Fisk and M. Docker) for their support and input throughout this degree. Support from the Department of Fisheries and Oceans Canada (DFO, Winnipeg and Quebec) for the collection of samples from the eastern and western Canadian Arctic and the Gulf of St Lawrence was essential to the success of this thesis. We are indebted to Dr. Michael Papst (DFO) for his extensive support throughout the project. Thank you also to Claude Nozères (Maurice Lamontagne Institute - DFO Québec) and Rasmus Nygaard (Greenland Institute of Natural Resources) for additional specimens. I would also like to thank Arctic Net and the Faculty of Science for graduate student support. Thanks to the Natural Sciences and Engineering Research Council (NSERC) operating grant and Northern Research Chair funding to T. Dick for support towards this thesis research. Finally, I would like to thank my supervisor, T. Dick for all the support, advice and help he provided throughout these past years. I could not have accomplished this without him. Thank you.

This thesis is dedicated to my Nan who taught me to always persevere.

Table of Contents

Abstract	ii
Acknowledgements	iii
Dedication	iv
Table of Contents	v
List of Tables	xii
List of Figures	xiii
Manuscript Claims	xvii
CHAPTER 1 General Introduction	1
1.1 Introduction	1
1.1.1 The global ecological and economic role of cephalopods	2
1.1.2. Ecological role of Canadian Arctic cephalopods	4
Objectives	5
CHAPTER 2 Literature Review	7
2.1 Arctic Oceanography	7
2.1.1 Introduction	7
2.1.2 Comparison of Eurasian/North American Arctic oceanography.....	8
2.1.2.1 Bathymetry	8
2.1.2.2 Water masses	10
2.1.2.3 Water circulation patterns	11
a) Eurasian Arctic	12
b) North American Arctic	13
2.1.2.4 Current formation	15
a) Temperature / salinity interactions	15
b) Atmospheric interactions	16
2.1.3 Oceanography of sample locations	17
2.1.3.1 Hudson Strait	17
2.1.3.2 Ungava Bay.....	18
2.1.3.3 Baffin Bay.....	19
2.1.3.4 Davis Strait	20
2.1.3.5 Disko Bay.....	20
2.1.3.6 St. Lawrence	21

2.1.4 Impact of climate change on the Arctic ocean	22
2.2. Arctic Cephalopods	26
2.2.1 Introduction	26
2.2.1.1. Evolution and systematics of Class Cephalopoda	27
2.2.1.2. General life history of Class Cephalopoda	29
a) Distribution	29
b) Life history strategies	32
c) General trophic interactions	35
2.2.1.3. Ecological importance of global cephalopods	36
2.2.1.4. Economic importance of global cephalopods	37
2.2.1.5. Potential impacts of climate change on cephalopod populations	38
2.2.2. Review of the basic biology of common Canadian Arctic cephalopod species	39
2.2.2.1. <i>Gonatus fabricii</i>	40
a) Distribution	40
b) Life history	43
c) Morphometrics, systematics and populations	46
d) Trophic relationships	48
2.2.2.2. <i>Rossia</i> spp.	51
a) Distribution	51
b) Life history	53
c) Morphometrics, systematics and populations	56
d) Trophic relationships	58
2.2.2.3. <i>Bathypolypus</i> spp.	59
a) Distribution	59
b) Life history	61
c) Morphometrics, systematics and populations	63
d) Trophic relationships	65
2.2.2.4. <i>Cirroteuthis muelleri</i>	66
a) Distribution	66
b) Life history	68
c) Morphometrics, systematics and populations	69
d) Trophic relationships	70

2.2.3. Population analysis	71
2.2.3.1. Morphometric (character) analysis	72
2.2.3.2. Genetic analysis	75
2.3. Trophic Analyses	77
2.3.1. Introduction	77
2.3.2. Technique overview	77
2.3.2.1. Stomach content analysis	78
2.3.2.2. Stable isotope analysis (SIA)	78
2.3.3. Overview of stable isotope analyses (SIA)	79
2.3.3.1. Background	79
2.3.3.2. Common isotopes used in trophic analyses	81
a) $\delta^{15}\text{N}$	81
b) $\delta^{13}\text{C}$	83
2.3.4. Methodology	84
2.4. Literature conclusion	86
Figures	87
CHAPTER 3 Study site descriptions, general and chapter specific methods	89
3.1. Sample areas	89
3.1.1. Hudson Strait.....	89
3.1.2. Baffin Bay.....	90
3.1.3. Western Greenland.....	91
3.1.4. St. Lawrence estuary and Gulf.....	91
3.2. Specimen preservation.....	92
3.3. Chapter specific methods	92
Figures	93
CHAPTER 4 Arctic cephalopod distributions and their associated predators with an emphasis on determining Canadian Arctic foci	96
4.1 Introduction	97
4.2 Materials and methods	98
4.3 Results	99
4.3.1 Distributions	100
a) <i>Gonatus fabricii</i>	100

b) <i>Rossia moelleri</i>	100
c) <i>Rossia palpebrosa</i>	101
d) <i>Bathypolypus arcticus</i>	101
e) <i>Cirroteuthis muelleri</i>	102
f) Unidentified cephalopods	102
g) Rare species of the Canadian Arctic Ocean and adjacent areas.....	102
4.3.2 Cephalopod-predator interactions	103
4.4 Discussion	104
4.4.1 Arctic cephalopod range extensions	104
a) <i>Gonatus fabricii</i>	104
b) <i>Rossia moelleri</i>	105
c) <i>Rossia palpebrosa</i>	105
d) <i>Bathypolypus arcticus</i>	106
e) <i>Cirroteuthis muelleri</i>	106
f) Additional Arctic cephalopod distributions	107
4.4.2 Predator-prey relationships	107
4.4.3 Oceanographic variables and distributions	108
4.4.4 Predator-prey distribution relative to ocean variables	109
4.5 Summary	110
Tables and Figures	111
CHAPTER 5 Biogeographic variation of Canadian Arctic cephalopods	132
5.1 Introduction	133
5.2 Materials and Methods	136
5.2.1 Sampling	136
5.2.2 Morphometric measurements	137
5.2.3 Genetic/Barcode analyses	138
5.2.4 Statistical analysis	139
5.3 Results	143
5.3.1 Environmental data vs. sample location	143
5.3.2 <i>G. fabricii</i> morphometric analyses	144
5.3.3 <i>G. fabricii</i> morphometric variables vs. environmental data	147
5.3.4 <i>R. palpebrosa</i> morphometric analyses	147
5.3.5 <i>R. palpebrosa</i> morphometric variables vs. environmental data	149

5.4 Discussion	150
5.4.1 Arctic cephalopod biogeography	150
a) <i>G. fabricii</i> biogeography	150
(i) Overview	150
(ii) Hudson Strait	151
(iii) Ungava Bay	152
(iv) Baffin Bay/ Greenland	153
(v) Disko Bay	154
(vi) Environmental impacts on morphometric characteristics of <i>G. fabricii</i>	155
b) <i>R. palpebroso</i> biogeography	156
(i) Overview	156
(ii) St. Lawrence	157
(iii) Environmental impacts on morphometric characteristics of <i>R. palpebroso</i>	158
5.4.2. Statistical methodology	158
5.4.3. Genetic analyses	159
5.5 Summary	160
Tables and Figures	162

CHAPTER 6 Habitat and trophic studies using stable isotope (SI) and stomach content

analyses of cephalopod tissues and SIA of prey items	193
6.1 Introduction	194
6.2. Material and Methods	200
6.2.1. Specimen collection	200
6.2.2. Stable isotope analysis	201
6.2.2.1. Methodology	201
6.2.2.2. Statistical analyses	203
6.2.3. Prey identification	203
6.2.3.1. Stomach content analyses	203
6.2.3.2. SIAR mixing models	204
6.3. Results	205
6.3.1. Habitat variability ($\delta^{13}\text{C}$) of the common cephalopods from the Canadian Arctic and St. Lawrence regions	205

6.3.1.1. General differences between locations	205
a) Arctic vs. St. Lawrence regions	205
b) Arctic region	205
c) St. Lawrence region	206
6.3.1.2. Habitat variability between life stages of the common cephalopod species	206
a) <i>G. fabricii</i>	206
b) <i>R. palpebrosa</i>	207
c) <i>Bathypolypus</i> spp.	209
d) <i>C. muelleri</i>	210
6.3.2. Trophic role of the common Canadian Arctic cephalopods ($\delta^{15}\text{N}$)	211
6.3.2.1. General differences in $\delta^{15}\text{N}$ between the cephalopod groups .	211
a) Arctic region overview	211
b) St. Lawrence region overview	213
6.3.2.2. Interspecific variability of $\delta^{15}\text{N}$ by location and size range	
/maturity stage	213
a) <i>G. fabricii</i>	213
b) <i>R. palpebrosa</i>	214
c) <i>Bathypolypus</i> spp.	216
d) <i>C. muelleri</i>	217
6.3.3. Arctic cephalopod prey differentiation	218
6.3.3.1. <i>G. fabricii</i>	218
a) Stomach contents	218
b) Mixing models	219
6.3.3.2. <i>R. palpebrosa</i>	221
a) Stomach contents	221
b) Mixing models	222
6.3.3.3. <i>Bathypolypus</i> spp.	224
a) Stomach contents	224
b) Mixing models	224
6.3.3.4. <i>C. muelleri</i>	225

a) Stomach contents	225
b) Mixing models	225
6.4. Discussion	226
6.4.1. Delta ¹³ C values as indicators of habitat and feeding ground preferences of eastern Canadian Arctic cephalopods	226
6.4.1.1. Arctic vs. St. Lawrence variations in δ ¹³ C	226
6.4.1.2. Intra-Arctic δ ¹³ C variability	228
a) Interspecific variations in δ ¹³ C	228
b) Variability of δ ¹³ C by size range and maturity stage	230
6.4.2. Trophic interactions of eastern Canadian Arctic cephalopods	231
6.4.2.1. Variability of δ ¹⁵ N within the eastern Canadian Arctic	232
a) <i>G. fabricii</i>	232
b) <i>R. palpebrosa</i>	233
c) <i>Bathypolypus</i> spp.	234
d) <i>C. muelleri</i>	235
6.5 Conclusion	236
Tables and Figures	238
THESIS SUMMARY	275
REFERENCES	279
APPENDIX I – A concentration of large forms of five common cephalopods from the Canadian Arctic	304
Introduction	304
Materials and Methods	305
Results	307
Discussion	308
Tables and Figures	313
References	315

List of Tables

- Table 4.1. Additional reported cephalopod species from the circumpolar Arctic.
- Table 4.2. Percentages of cephalopod prey items reported from the stomachs of Arctic predators.
- Table 4.3. Percentage occurrences of cephalopod prey items from the stomachs of Arctic predators (percentages of predators sampled with cephalopods in their stomachs).
- Table 4.4. Anecdotal accounts of cephalopods as prey species from the Arctic.
- Table 5.1. Survey sample locations and their summarized environmental variables.
- Table 5.2. Standard cephalopod morphometric measurements and their associated codes.
- Table 5.3. Ontogenetic size ranges for *G. fabricii* and maturity stages of *R. palpebroso*.
- Table 5.4. Size measurements of *G. fabricii* and *R. palpebroso* used for PCA and Discriminant Analyses per location and maturity stage.
- Table 5.5 Barcode of Life (IBoL/BOLD) sequence reference numbers for DNA analyses
- Table 5.6. MANOVA results (Pillai's Trace) for all *G. fabricii* and *R. palpebroso* using principal component scores from PCA.
- Table 6.1. Literature stable isotope values used in mixing models.
- Table 6.2. Literature stable isotope values of defined taxa used for detailed mixing models.
- Table 6.3. Kruskal-Wallis results of comparisons of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ by location and species.
- Table 6.4. Habitat descriptors and means (standard deviations) of the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of the common Canadian Arctic cephalopods by size range/maturity stage in comparison to those from the St. Lawrence region.

List of Figures

- Figure 2.1. Circumpolar bathymetric map of the Arctic region. (Image reproduced from the GEBCO website http://www.gebco.net/data_and_products/gebco_world_map).
- Figure 2.2 General circulation patterns in the Canadian Arctic Archipelago (modified from LeBlond, 1980 and Michel et al. 2006).
- Figure 3.1 Sample locations of cephalopods collected during the annual GINR groundfish survey (—), DFO shrimp and groundfish surveys (---), and the DFO Gulf of St. Lawrence survey (- - -).
- Figure 3.2 Percent of total tows per 200 m depth increments during DFO and GINR fishery and shrimp surveys.
- Figure 3.3 Mean temperatures (and standard deviations) per 200 m depth increments of DFO and GINR surveys where cephalopods were collected.
- Figure 4.1. Circumpolar records of *Gonatus fabricii*.
- Figure 4.2. Distribution of *Gonatus fabricii* in the western European Arctic with reference to potential spawning locations, areas of 500+ juveniles per haul caught between June and August 1978–1981 and a region where 8000 juveniles per haul were recorded in July 1980 (Wiborg et al. 1982).
- Figure 4.3. Occurrence records of *Gonatus fabricii* specimens, including remains in the stomach contents of predators.
- Figure 4.4. Circumpolar records of *Rossia moelleri*.
- Figure 4.5. Circumpolar records of *Rossia moelleri* specimens, including remains in the stomach contents of predators.
- Figure 4.6. Circumpolar records of *Rossia palpebrosa*.

- Figure 4.7. Circumpolar records of *Bathypolypus arcticus*.
- Figure 4.8. Circumpolar records of *Bathypolypus arcticus* specimens, including remains in the stomach contents of predators.
- Figure 4.9. Circumpolar records of *Cirroteuthis muelleri*.
- Figure 4.10. Canadian records of unidentified cephalopods.
- Figure 5.1. Sample zones used for morphometric analyses.
- Figure 5.2. Standard morphometric measurements of **a)** *Gonatus fabricii* and *Rossia* spp. (dorsal - **b** and ventral - **c**) as described in Table 5.2.
- Figure 5.3. PCA results of environmental data from the sample locations.
- Figure 5.4. Comparison between sampling years 2007 (open symbols) and 2009 (filled symbols) for the Hudson Strait region.
- Figure 5.5. Principal component (PCA) results and loading plot for all size ranges of *G. fabricii*.
- Figure 5.6. Discriminant analysis results (without FLA) of all *G. fabricii* specimens using principle component scores to remove any correlations.
- Figure 5.7. PCA results and loading scores of *G. fabricii* by size range.
- Figure 5.8. Discriminant analysis results of *G. fabricii* by size range.
- Figure 5.9. Genetic taxonomic tree based on COI barcode results of *G. fabricii* (IBoL, BOLD, University of Guelph).
- Figure 5.10. Redundancy analysis (500 permutations; $p < 0.0001^*$) of all size ranges of *G. fabricii*'s morphometric characters to environmental variables.
- Figure 5.11. Redundancy analysis (500 permutations) of *G. fabricii*'s morphometric characters per size range to the collected environmental variables.
- Figure 5.12. PCA results of *R. palpebroso* per maturity stages.

Figure 5.13. Discriminant analyses of *R. palpebroso* per maturity stage.

Figure 5.14. Discriminant analysis based on principal component scores of *R. palpebroso* (all maturity stages).

Figure 5.15. Genetic taxonomic tree based on COI barcode results of *R. palpebroso* (IBoL, BOLD, University of Guelph).

Figure 5.16. Redundancy analysis (500 permutations) of *R. palpebroso*'s morphometric characters per maturity stage to the collected environmental variables.

Figure 6.1. Analysis of stable isotope values (with standard deviations) of four different tissues and stomach content from five Hudson Strait (2007) *G. fabricii* to determine the best tissue to use for the remaining analyses.

Figure 6.2. Mean and standard deviations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for *G. fabricii* by size range and location.

Figure 6.3. Mean and standard deviations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for *R. palpebroso* by maturity stage and location.

Figure 6.4. Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for *Bathypolypus* spp. by maturity stage and location.

Figure 6.5. Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and their standard deviations for *C. muelleri* by maturity stage.

Figure 6.6. Percent occurrence of prey items in the stomachs of *G. fabricii* per sample location and size range.

Figure 6.7. Boxplots of general and detailed mixing model results of potential prey of size 2 *G. fabricii* by location.

- Figure 6.8. Boxplots of general and detailed mixing model results of potential prey of size 3 *G. fabricii* by location.
- Figure 6.9. Boxplots of general and detailed mixing model results of potential prey of size 4 and 5 *G. fabricii* by location.
- Figure 6.10. Percent occurrence of prey items in the stomachs of *R. palpebroso* per sample location and maturity stage.
- Figure 6.11. Boxplots of mixing model results of potential prey of Arctic *R. palpebroso* by maturity stage and location.
- Figure 6.12. Boxplots of mixing model results of potential prey of St. Lawrence region *R. palpebroso* by maturity stage.
- Figure 6.13. Percent occurrence of prey items in stomach contents of *B. bairdii* per sample location and maturity stage.
- Figure 6.14. Boxplots of mixing model results of potential prey of Arctic *Bathypolypus* spp. by species, location and maturity stage.
- Figure 6.15. Boxplots of mixing model results of potential prey of St. Lawrence *Bathypolypus* spp. by species and maturity stage.
- Figure 6.16. Percent occurrence of prey items in the stomachs of *C. muelleri* from Baffin Bay by maturity stage.
- Figure 6.17. Boxplots of mixing model results of potential prey of *C. muelleri* by maturity stage.

Manuscript Claims

Chapters 4, 5 and 6 of this thesis are presented in manuscript format with their own introduction, materials and methods, results and discussion sections. All references per chapter, however, have been combined at the end of the thesis. Appendix I has been included as a complete manuscript at the end of the thesis.

Manuscript references are as follows:

Chapter 4 (pg. 96): Gardiner, K. and T. A. Dick. 2010. Arctic cephalopod distributions and their associated predators. *Polar Research*. **29**(2): 209-227.

Kathleen Gardiner compiled the data, created the maps, and wrote the manuscript with guidance from T.A. Dick. Authors of *Polar Research* articles retain their copyright, so no permission is required for reproduction.

Appendix I (pg. 302): Gardiner, K. and T.A. Dick. 2010. A concentration of large forms of five common cephalopods from the Canadian Arctic. *Marine Biodiversity Records*. **3**(e37): 1-6.

Kathleen Gardiner collected and analyzed the data and wrote the manuscript under the supervision of T.A. Dick. © Reproduced with permission from Cambridge University Press.

Chapter 1

General Introduction

1.1. Introduction

Climate change and the resulting loss of sea ice have unlocked the Arctic for exploration and exploitation. The impacts that anthropogenic pressures will have on the ecosystem, especially in combination with continued climate change (i.e. increasing surface temperatures and stratification, acidification from CO₂ absorption, pollutants from lower latitudes (Pierce et al. 2008, Belkin 2009, Gruber 2011, Guerra et al. 2011, Overland et al. 2011)) are difficult to predict due to the lack of baseline information, particularly concerning local marine biodiversity (André et al. 2010, Darnis et al. 2012, Snelgrove et al. 2012). This lack of information prompted a national meeting of scientists to address this issue for the Canadian Arctic (Snelgrove et al. 2012).

Complexities of the Arctic region hinder comparisons between the European and Canadian polar zones. The Canadian Arctic is subject to polar currents, whereas, the European Arctic is primarily affected by warmer North Atlantic waters (WHOI 2006, Coachman and Aagaard 1974, Rudels 1986). The Canadian continental shelf is also narrower (50 to 180 km) in comparison to the European shelf (800 km) (Coachman and Aagaard 1974, Weber 1989) resulting in more diverse habitats close to shore. Therefore any inferences between the Canadian and the European Arctic must be viewed with caution.

1.1.1. The global ecological and economic role of cephalopods

Cephalopods are found in all marine ecosystems, from the surface to deep-sea hydrothermal vents (González et al. 1998, Wood and O'Dor 2000, Forsythe 2004, Albertin et al. 2012, Coll et al. 2013). They reside in both pelagic and neritic habitats with ranges extending to both poles (Wood and O'Dor 2000, Forsythe 2004, Albertin et al. 2012, Coll et al. 2013). Cephalopods play an important role in global marine ecosystems; providing high-energy food sources for a variety of marine predators, including sharks, whales and commercial fish species (Rodhouse and Nigmatullin 1996, Lawson et al. 1998, Piatkowski et al. 2001, Boyle and Rodhouse 2005c, Hunsicker et al. 2010, Coll et al. 2013). Their diurnal migrations in search of prey also help to cycle nutrients between the surface and benthos (Sennikov et al. 1989, Nesis 2003c, Chambers and Dick 2007), effectively increasing nutrient availability at less productive depths.

Cephalopods are typically short-lived (1 to 2 years), fast growing and exhibit semelparous life cycles, making them easily impacted by ecological and anthropogenic shifts (Rodhouse and White 1995, Boyle and Boletzky 1996, Agnew et al. 2002, Zuev and Nesis 2003, Pierce et al. 2008, Rodhouse 2010, Coll et al. 2013). Deep sea and Arctic species, however, are thought to be longer lived due to slower maturation and growth rates in cold habitats but are still sensitive to environmental changes (Rodhouse and Nigmatullin 1996, Wood and O'Dor 2000, Arkhipkin 2004, Collins and Villanueva 2006, Zumholz and Frandsen 2006). Cephalopods are also highly stenohaline (30 to 39 ‰), with salinity acting as a strong influence on their dispersal and survival (Zuev and Nesis 2003). Temperature, depth and oceanic currents also impact their life histories with the main impacts on the developmental stage of the population (Pierce et al.

2008). These sensitivities make cephalopods excellent indicator species for observing the effects of climate change on marine ecosystems (André et al. 2010, Coll et al. 2013), in particular, the Arctic region.

Class Cephalopoda can be divided into two subclasses: Nautiloidea, the last of the primitive shelled cephalopods, and Coleoidea consisting of all other living species and characterized by a reduced, internalized or complete lack of a shell (Carlini 1998, Boyle and Rodhouse 2005a, i). Arctic coleoides can be further divided into: Sepiolida (represented by bobtail squids), Teuthida (conventional squids) and Octopoda (ITIS, Carlini 1998, Boyle and Rodhouse 2005a). Teuthida consists of two sub-orders, Myopsida and Oegopsida, with only oegopsids (pelagic species lacking corneal coverings) present within the polar region (GBIF, ITIS, Carlini 1998, Boyle and Rodhouse 2005a). Octopoda consists of Incirrata, the stereotypical ‘octopus’; and Cirrata, the deep-sea winged gelatinous form, with both suborders represented in the Arctic fauna (Dunning et al. 1998, Carlini 1998, Boyle and Rodhouse 2005a). Each of these groups (with the exception of the deep-dwelling cirrates) includes species that are exploited globally (Dunning et al. 1998, Roper et al. 1983, Boyle and Rodhouse 2005e, De Angelis 2012).

As global finfish stocks become depleted, commercial interest has shifted to cephalopods, with cephalopods becoming a larger component of commercial landings (Caddy and Rodhouse 1998, Rodhouse et al. 1998a, Jackson et al. 2000, Piatkowski et al. 2001, Boyle and Rodhouse 2005e, Hunsicker et al. 2010). Cephalopod catches have been on the increase for 25 years (Piatkowski et al. 2001) with a total global catch of more than 4 million tons in 2007 (Oosterwind et al. 2010). Although there is no cephalopod fishery within the Canadian Arctic, it

has been noted that the oegopsid *Gonatus fabricii* has the potential for commercial exploitation off of southwestern Greenland and Baffin Bay (Wiborg et al. 1982, Kristensen 1983, Roper et al. 1983, Piatkowski and Wieland 1993, Frandsen and Wieland 2004, Zumholz and Frandsen 2006). Both *Rossia moelleri* and *Bathypolypus* spp. are also mentioned as potential fishery species off of Greenland (Frandsen and Wieland 2004). These potential new fisheries, along with the changing environmental conditions at the poles, make collecting baseline biological data from the Canadian Arctic imperative for future stock management and monitoring of environmental shifts (Jackson et al. 2000, Wood and O'Dor 2000, Jackson 2004).

1.1.2. Ecological role of Canadian Arctic cephalopods

Cephalopods have long been overlooked in the Canadian Arctic with regard to distribution, biology, and their role in the ecosystem. Research examining the trophic structure of Arctic marine fish has provided evidence that cephalopods are important contributors to Arctic food chains (Sennikov et al. 1989, Nesis 2003c, Chambers and Dick 2007, Gardiner and Dick 2010) and are frequently reported from the stomach contents of many of the Arctic marine mammals and birds, as well as many commercially important fish species such as cod, haddock and Greenland halibut; suggesting a contributing role to the overall financial and cultural sustainability of the Arctic region (Hjort and Ruud 1929, Nesis 1965, Finley and Gibb 1982, Sennikov et al. 1989, Barrett et al. 1997, Orr and Bowering 1997, Dawe et al. 1998, Bjørke 2001, Loeng et al. 2005, Zumholz and Frandsen 2006, Chambers and Dick 2007).

The four common Arctic genera reflect the various habitats available in the Arctic realm. *Gonatus fabricii* is a pelagic squid typically found over deep water (Kristensen 1983, Frandsen and Wieland 2004) while both *Rossia* spp. (Sepioidea) and *Bathypolypus* spp. (Incirrate octopus)

are benthic (Frandsen and Wieland 2004, Frandsen and Zumholz 2004). *Rossia* spp. (consisting of *R. palpebrosa*, *R. megaptera* and *R. moelleri*) are typically found in shallow coastal waters (~70 to 500 m) while *Bathypolypus* spp. are found in deep water (down to 1600 m) except at high latitudes suggesting temperature plays a greater role in habitat selection than depth (Mercer 1968b, O'Dor and Macalaster 1983, Vecchione et al. 1989, Nesis 2001, Frandsen and Wieland 2004, Frandsen and Zumholz 2004, Zumholz and Frandsen 2006). *Cirroteuthis muelleri* (cirrate octopus) is also found in deep water but is abyssal-pelagic (Nesis 2001). Only *G. fabricii* exhibits planktonic life stages and diurnal migrations (Kristensen 1983).

Because the common species each inhabit different niches, their responses to environmental and anthropogenic shifts will provide insight into how the Canadian Arctic, as a whole, is responding to the new pressures being imposed on it. But first, baseline information is required.

This thesis increases the understanding of **the ecological role that cephalopods play within the Canadian Arctic**, by: **1)** providing baseline information regarding the circumpolar distribution of Arctic cephalopods, with an emphasis on identifying concentrations of the most common Canadian species (CHAPTER 4); **2)** identifying biogeographic variations through morphometric analyses, and comparing and contrasting life stages within the Canadian and adjacent Arctic regions (CHAPTER 5); and **3)** examining the habitat preferences and trophic roles of the most common species in relation to maturity through stable isotope (SI) and stomach content analyses (CHAPTER 6). A detailed literature review was undertaken (CHAPTER 2) and overall methodologies are discussed (CHAPTER 3).

Increasing our understanding of Arctic cephalopods is another piece of the Arctic ecosystem puzzle. Deciphering the general biology of these intriguing creatures aids in their direct management, provides insights to the management of key Arctic predators and identifies indicators of environmental shifts. This thesis provides baseline data that will ultimately contribute to the Arctic economy.

Chapter 2

Literature Review

2.1. Arctic Oceanography

2.1.1. Introduction

The Arctic Ocean is a complex ecosystem spanning 14.5 million km² with ~7.25 million km² covering productive continental shelves (Gradinger 1995, Carmack and Macdonald 2002, Michel et al. 2006). The ocean is further divided into deep basins separated by large oceanic ridges, islands and channels, which help control the flow of water (Fig. 2.1) (Metcalf 1954, Coachman and Aagaard 1974, Rudels 1986) and thereby the dispersal of marine organisms. Arctic circulation is driven by wind, large-scale atmospheric events (i.e. El Nino, Arctic Oscillation (AO)) and sea level slope between the fresher Pacific and saltier Atlantic Oceans (Proshutinsky and Johnson 1997, Loeng et al. 2005, McLaughlin et al. 2005, Serreze et al. 2006, Overland et al. 2011). Sea ice formation and melt, along with outflow from large rivers such as the Mackenzie (Northwest Territories, Canada), modify the coastal surface salinity, creating haloclinic circulation (Carmack and Macdonald 2002, McLaughlin et al. 2005). Wind and heat advection also help to create predictable areas of open water, known as polynyas, which provide surface access to the marine ecosystem for most of the year (Stirling 1980, Dunbar 1981, Smith and Rigby 1981, Williams et al. 2007). Each of these processes, in combination with biological interactions, create a diverse and complex region; ultimately impacting the distribution and abundance of Arctic marine organisms.

Climate change is most pronounced within the Arctic region, impacting the extent of sea ice, altering circulation patterns, modifying temperature regimes and influencing the productivity

of the region (Gradinger 1995, Overland et al. 2011, Richter-Menge et al. 2011). Prominent oceanographic differences (e.g. temperature, continental shelf features) between the Eurasian and North American Arctic make any assumptions as to the effects of climate change from one region to another, difficult. Therefore, any extrapolation from known climate impacts in other parts of the Arctic region to the Canadian Arctic should be examined cautiously.

2.1.2. Comparison of Eurasian vs. North American Arctic oceanography

For the purposes of this thesis, the Eurasian Arctic refers to the Arctic Ocean extending from eastern Greenland to eastern Siberia and north to the North Pole. The North American Arctic begins with the Aleutian Islands and extends to the western coast of Greenland, encompassing the Canadian Arctic Archipelago, north to the North Pole. This thesis will only focus on the eastern Canadian Arctic region, hereafter referred to as the Canadian Arctic and western Greenland.

2.1.2.1. Bathymetry

The Arctic Ocean has limited connectivity to other marine sources and consists of a variety of canyons, sills, ridges and shelves controlling the flow of Atlantic, Pacific and Arctic water through the region (Fig. 2.1) (Coachman and Aagaard 1974, Rudels 1986, Tomczak and Godfrey 2003). These connections consist of the Bering Strait (Pacific input), Fram Strait and the Barents Sea (Atlantic inflow) (Rudels 1986). The majority of inflow from the Atlantic is through the Barents Sea while half of the polar outflow is through the Canadian Arctic Archipelago (Figs. 2.2 and 2.3) (Rudels 1986).

The Polar Ocean's primary basin is surrounded by continental shelves and made up of two smaller basins; the Canada and the Eurasian, which can be further subdivided by a series of ridges: Alpha, Mendeleev and Lomonosov (Fig. 2.1) (Metcalf 1954, Coachman and Aagaard 1974, Tomczak and Godfrey 2003, Michel et al. 2006). These ridges help to control water movement throughout the Arctic basin (Metcalf 1954, Coachman and Barnes 1961, Coachman and Aagaard 1974, Tomczak and Godfrey 2003, Michel et al. 2006). The Lomonosov Ridge, in particular, acts as a barrier, preventing deep, cold (> -0.4 °C) bottom water from entering the Canada Basin (Tomczak and Godfrey 2003).

Continental shelves of varying widths surround the Polar basin (Fig. 2.1) (Coachman and Aagaard 1974). The Eurasian side is characterized by nearly 800 km wide shelves while the North American shelves average 50 to 90 km in width (Coachman and Aagaard 1974). At the widest point, the North American shelf reaches 180 km and is narrowest off the shores of Banks and Queen Elisabeth Islands (400 to 600 m) (Weber 1989). The European shelf is divided into five shallow seas: the Barents, Kara, Laptev, East Siberian and Chukchi, which are greatly influenced by river outflow (Coachman and Aagaard 1974). Circulation within the Eurasian seas is dependent on deep-sea canyons in the Kara and Chukchi Seas (Coachman and Aagaard 1974). These canyons allow the warm, dense Atlantic water to enter and mix with shelf water (Coachman and Aagaard 1974).

Although narrow, the North American shelf is comprised of the Canadian Arctic Archipelago (Fig. 2.1). This archipelago consists of sixteen interconnecting passages of varying depths (< 700 m) and is found from 68°N to 82°N and 60°W to 130°W (Coachman and Aagaard 1974, Fissel et al. 1984, Michel et al. 2006). These passages and their associated sills also help

control the flow of water through the region (Fig. 2.2), however, large areas remain unsurveyed (Coachman and Aagaard 1974, Fissel et al. 1984, McLaughlin et al. 2005). Of the sixteen channels, Nares Strait and Lancaster Sound appear to be the most important for water exchange (Figs. 2.2 and 2.3) (Coachman and Aagaard 1974).

Continental shelves are unique habitats for marine biota, especially in the Arctic. Due to their relative shallow depths, they are subject to extreme annual and inter-annual variations in flow, freshwater input and ice cover, resulting in increased mixing and increased productivity (Carmack and Macdonald 2002, Zuev and Nesis 2003).

2.1.2.2. Water masses

Water sources can be identified through comparisons of temperature and salinity signatures at different depths to adjoining regions (Coachman and Barnes 1961). Arctic water by definition is cold (0 °C to -1.8 °C) with salinities of 31 to 34 ‰, while Atlantic water is typically warmer and more saline (0 °C to 2 °C and 34.2 to 34.5 ‰) (Fissel et al. 1981). Pacific water is warmer, more saline and has more nutrients than the surface water but is less saline than Atlantic water (Treshnikov and Baranov 1972, Coachman and Aagaard 1974). From these characteristics, three main water masses can be determined in the Arctic Ocean: 1) cold, dilute surface water (Arctic origin – ice and river runoff); 2) warmer (0 °C), saltier (34.5 to 35‰) Atlantic Water (150 to 900 m) and 3) colder, high saline bottom water (also of Atlantic origin) (Treshnikov and Baranov 1972, Coachman and Aagaard 1974).

2.1.2.3. Water circulation patterns

Oceanic circulation plays a vital role in nutrient dispersal and ventilation of the Arctic Ocean and is essential for controlling the global climate (Drinkwater 1986, Aksenov and Coward 2001, Stow 2006). Many planktonic organisms, including larval fish and squid, and even some adult cephalopods (i.e. *Illex illecebrosus*) rely on oceanic circulation for distribution and to minimize energy expenditures during large-scale migrations (O'Dor 1988, Bakun and Csirke 1998, Arkhipkin and Bjørke 1999, Semmens et al. 2007). Circulation can be affected by bathymetry, topography, temperature and salinity gradients, among other factors, and consists of vertical and horizontal movement (Coachman and Aagaard 1974, Rudels et al. 1999). Current flow is prone to offshoots and divergences, only to re-join with other currents later on; while cooling creates transient plumes that flow off the shelf to the deeper depths (Rudels 1995, Rudels et al. 1999).

The major Arctic circulation patterns can be viewed on the Woods Hole Oceanographic Institute's Polar Discovery website (<http://polardiscovery.whoi.edu/arctic/circulation.html>; WHOI 2006). Warm Atlantic water is only able to enter the Arctic region through two main channels, Fram Strait and Barents Sea, and exit through the narrow channels of the Canadian Arctic Archipelago, western Baffin Bay and the West Greenland Sea via the Baffin Bay and East Greenland currents respectively (Coachman and Aagaard 1974, Rudels 1986). Overall water movement is predominantly cyclonic (Tang et al. 2004). The majority of currents are interconnected, however, there are more interactions of water circulation within the Eurasian Arctic than within the North American Arctic. The following are brief descriptions of some of the major currents affecting the: a) Eurasian Arctic and b) North American Arctic.

a) Eurasian Arctic

The circumpolar boundary current begins as Atlantic water and enters the Norwegian Sea via the Greenland-Scotland Ridge (Rudels et al. 1999). The current splits near Bear Island Channel, with the majority of its water continuing north as the relatively warm and saline West Spitsbergen Current (WSC) (Rudels et al. 1999). The small portion of the WSC that enters the Arctic Basin via Fram Strait and Barents Sea, flows eastward along the Eurasian slope (sinking as it goes), only to rejoin the larger circumpolar boundary current in the Kara Sea (Treshnikov and Baranov 1972, Rudels 1995, Rudels et al. 1999). This boundary current continues east until it splits again near the Lomonosov Ridge with part flowing into the Canada Basin (Rudels 1995, Rudels et al. 1999). The remaining current follows the bathymetric contours, with a narrow portion (≤ 100 km) cooled by high latitudes, flowing along the continental shelves (Rudels 1995, Rudels et al. 1999, Aksenov and Coward 2001). The Arctic boundary current exits through Fram Strait, rejoins the WSC and flows south as the East Greenland Current (EGC) (Treshnikov and Baranov 1972, Rudels 1995, Rudels et al. 1999, Aksenov and Coward 2001).

The EGC is seasonally variable with semi-periodical oscillations every ~ 50 days during February to August (Aksenov and Coward 2001). The origin of these oscillations is still not well understood but it has been speculated that it may be the result of wind conditions or recirculation between the WGC and the EGC (Aksenov and Coward 2001).

The North Pacific Current (NPC) impacts the local Eurasian Arctic as well as the North American Arctic regions. The NPC enters the Chukchi Sea via the shallow (45 m) Bering Strait and splits in two (Treshnikov and Baranov 1972, Coachman and Aagaard 1974). The first fraction mixes with Siberian shelf water by a pair of vortices and then flows back to the Chukchi

Sea; while the second, larger branch, follows the shore of Alaska only to turn northwest near Point Barrow (Coachman and Barnes 1961, Treshnikov and Baranov 1972, Aksenov and Coward 2001). This current combines with freshwater outflow from the local rivers and begins to cool, promoting ice formation (Treshnikov and Baranov 1972), which in turn, can clog the narrow strait during the cold winter months limiting inflow (Coachman and Aagaard 1974). Pacific flow is also limited in winter by strong northern winds that halt the formation of the current (Treshnikov and Baranov 1972). Pacific water deeper than 50 m is protected from localized cooling and can persist in the environment for extended periods of time (Treshnikov and Baranov 1972). Some of this current even persists as part of the central Arctic surface water (Treshnikov and Baranov 1972).

b) North American Arctic

The West Greenland Current (WGC; $\sim 5\text{ }^{\circ}\text{C}$) enters Davis Strait and flows along the west coast of Greenland, north to Baffin Bay (Fig. 2.2) (Rudels 1986, Jørgensen et al. 2005). The WGC current is the product of both the warm Irminger Current ($4\text{ to }6\text{ }^{\circ}\text{C}$) and cold EGC mixing near shore before looping around Cape Farewell (Jørgensen et al. 2005). Even after mixing, the Irminger Current is strong at deeper depths off of western Greenland (Jørgensen et al. 2005). At the top of the bay, the current turns around, is amplified with Arctic water inflow (i.e. Polar Current), and begins to flow along the eastern shore of Baffin Island only to exit into the Labrador Sea (Fig. 2.2) (Rudels 1986, Jørgensen et al. 2005). Because this current system brings warmer Atlantic water up along the western shelf of Greenland and carries colder Arctic water along the shores of Baffin Island, distinct habitats are created on each side of Baffin Bay

and Davis Strait (Chambers and Dick 2007). These oceanographic differences will likely impact the local biodiversity and productivity of the region (Chambers and Dick 2007).

The Baffin Current has a strong cyclonic surface flow (0.2 to 0.3m/s off of Devon Island) and consists of the rejoined branches of the WGC that flow from northern Baffin Bay to Davis Strait (Fissel et al. 1981, Ingram et al. 2002). The current flows along the shores of Jones and Lancaster Sounds and finally exits into the bay along the southern shores of the islands (Ingram et al. 2002).

Although not part of the major Arctic currents, the Canadian Arctic Archipelago, in particular the Northwest Passage, is a key pathway for ocean flow (Fig. 2.2) (McLaughlin et al. 2005). This passage has a limiting sill (125 m) east of Barrow Strait but quickly descends to 500 m in Lancaster Sound where the water exits into Baffin Bay (< 2000 m) (Fissel et al. 1981, Aksenov and Coward 2001, McLaughlin et al. 2005). The flow originates from both the Pacific and Arctic Oceans and is driven by the higher Pacific sea level, the result of Pacific water being fresher and therefore lighter than Atlantic water (McLaughlin et al. 2005).

The shallow, narrow channels of the archipelago help control the unidirectional outflow of Arctic water, however, oceanographic models have shown that there is sufficient room in some of the channels to allow bidirectional flow (Fig. 2.2) (LeBlond 1980, McLaughlin et al. 2005). Barrow Strait, for example, has fresher surface water flowing towards Baffin Bay while deeper water flows towards the Canada Basin (McLaughlin et al. 2005). This is also the region where most of the Pacific water exits the Arctic Ocean (Rudels et al. 1999).

The impact that ice has on flow through the archipelago is also significant. According to computer modeling, when Nares Strait is open, there is a sevenfold increase in water transport through the islands towards Labrador Sea than when it is iced in (Aksenov and Coward 2001).

Gyres are also important components of marine circulation. They are caused by the Coriolis Effect which deflects surface currents to the right of prevailing winds/currents (Stow 2006). One of the largest gyres is found on the Beaufort shelf and is known as the Beaufort Gyre (Coachman and Barnes 1961; WHOI 2006). The Beaufort shelf has strong winds (caused by high pressure systems typically blowing from the northeast), variable salinity (Mackenzie River outflow and Pacific inflow) and deep ocean circulation, affecting the entire water column (Rudels 1995, Aksenov and Coward 2001, Dunton et al. 2006).

2.1.2.4 Current formation

Arctic currents are formed by a variety of forces and although depth independent, bathymetry is known to have an impact, especially within narrow channels (e.g. Hell Gate – Cardigan Polynya) (Dickson 1999). Friction caused by water flowing over the sediment or under the ice can affect fluidity, causing the flow to be reduced (McLaughlin et al. 2005, Stow 2006). Gravity also has an impact on circulation (i.e. geostrophic currents) as it influences the Coriolis Effect (Metcalf 1954, Stow 2006). Other driving forces include density and wind.

a) Temperature/salinity interactions

Temperature and salinity are closely linked in the Arctic Ocean and produce thermo- and halocline currents. As Atlantic water enters into the Arctic Basin, its salinity decreases due to increased freshwater input (i.e. precipitation, river outflow, glacial runoff); and coupled with

surface cooling, create an unstable stratification that helps to initiate ice production and brine rejection (Rudels 1995, Wells et al. 1996). As the salt is rejected from the ice crystals, the underlying water becomes denser causing it to sink, eventually forming plumes that flow off the continental shelves (Rudels 1995). As the water sinks, it is replaced by less saline water which continues the freeze/sink cycle, effectively mixing the surface layers (Rudels 1995). The plumes created by the dense brine water eventually join the Atlantic deep current and become part of the global deep water circulation which helps to ventilate the abyssal waters (Rudels 1995).

b) Atmospheric interactions

Atmospheric conditions are closely linked to ocean circulation (Stow 2006). Wind is a principal factor controlling permanent currents within the Arctic Basin (Treshnikov and Baranov 1972). Anticyclonic air circulation is common between 70 °N and 75 °N, especially around Greenland, the Beaufort Sea and the Canadian Archipelago (Reed and Kunkel 1960). Cyclonic activity is also common in the central Arctic, especially along the southern tip of Greenland, Iceland and Baffin Bay, where they coincide with low-pressure systems in the area (Reed and Kunkel 1960).

The highly variable North Atlantic Oscillation (NAO) affects the strength and direction of the winds over the North Atlantic and Arctic Oceans, thereby affecting the surface currents (Mysak 2001). When the NAO is positive, lows over Iceland create strong western winds over the Atlantic and south winds through the Norwegian Sea (Mysak 2001). This same system produces northerlies along the Labrador Sea (Mysak 2001). When the NAO is negative, winds are weakened (Mysak 2001).

A similar oscillation, the Arctic Oscillation (AO), in combination with the NAO, can shift wind direction and affect marine transport (Mysak 2001). When both the AO and NAO are positive, winds are cyclonic in the Eurasian Basin, which help to create the transpolar drift carrying ice and 'fresher' water from the Laptev Sea to Fram Strait and the Atlantic (Mysak 2001, National Snow and Ice Data Centre). When both oscillations are negative, strong high-pressure systems develop which results in anticyclonic drift in the Eurasian Basin towards Fram Strait (missing the Canada Basin completely) (Mysak 2001). This increase in AO is possibly linked to climate change and has a significant effect on the distribution of pollutants (Mysak 2001, Stow 2006).

2.1.3. Oceanography of sample locations

2.1.3.1. Hudson Strait

Hudson Strait is 760 km long and an average of 150 km across (Drinkwater 1986, Allard 1990). It connects Hudson Bay and Foxe Basin to the Labrador Sea and Davis Strait (Drinkwater 1986). On average the Straits' depth is 300 to 400 m with a deep 1000 m basin at the eastern edge (Drinkwater 1986). A 400 m sill separates the Strait from Labrador Sea (Drinkwater 1986).

Currents in this region flow in three directions (Fig. 2.2): 1) low salinity water from Hudson Bay and Foxe Basin flows along the southern shore; 2) higher salinity water from Labrador Sea flows westerly along the north shore; and 3) a cross current also flows from the Labrador sea along the north shore and cuts across the Strait just by the western edge of Ungava Bay (not shown in Fig. 2.2) (Drinkwater 1986, Allard 1990). Flow through the region is

regulated by salinity differences between the low saline Hudson Bay and Foxe Basin and the oceanic salinity of the Labrador Sea (Drinkwater 1986). This mixture of both Atlantic and Arctic water masses allow for a high level of biodiversity within the region (National Marine Conservation Areas of Canada website).

Salinity varies from 29 to 32 ‰ (or less with ice melt) along the southern shore and 32 to 33 ‰ along the north shore (Drinkwater 1986). Temperatures also vary, with the southern shore having warmer water (0 to 5 °C) compared to the north coast (0 to 2 °C) (Drinkwater 1986). There is even a shift in water masses between the western portion of the Strait which is almost exclusively polar water with little stratification, compared to the eastern side with a Labrador Sea water mass influencing the 400 m depth (2 °C) (Drinkwater 1986). These opposing currents, along with large tidal fluctuations within the region help increase vertical mixing, and ultimately increase productivity in the region (Drinkwater 1986).

2.1.3.2. Ungava Bay

Ungava Bay is located along the south shore of Hudson Strait (Drinkwater 1986). It is a relatively shallow bay, with depths less than 150 m and a channel of 200 to 400 m running through it (Drinkwater 1986). Ungava Bay is exposed to high volumes of freshwater runoff, but its lower layers remain marine, with the Labrador Sea flow maintaining its marine salinity and temperatures < -1 °C, however, this stratification eventually dissipates through mixing (Drinkwater 1986). This bay also has highly variable substrates, providing a variety of habitats for benthic organisms (Stewart et al. 1985).

2.1.3.3. Baffin Bay

Baffin Bay is a mediterranean sea with a large central abyssal plain (2300 m) and limited input from both the Arctic Ocean and Labrador Sea (Tang et al. 2004, Jørgensen et al. 2005). Arctic input is through three straits: Jones Sounds, Barrow and Nares Strait (Tang et al. 2004). Labrador Sea input is through Davis Strait (Tang et al. 2004). The sill depth of each entrance helps retain the deep-water layer (Baffin Bay Deep water) (Tang et al. 2004, Jørgensen et al. 2005).

The bay is composed of three water masses: 1) the Arctic water (or Polar/Cold layer) characterized by low salinity and colder temperatures near the surface; 2) West Greenland Intermediate water - warmer (> 0 °C) and more saline (> 34 ‰) waters from the WGC; and 3) Baffin Bay Deep water found below 1200 m (temperature ~ 0.5 °C and salinity ~ 34.5 ‰) with no direct access to Arctic or Atlantic waters (Tang et al. 2004, Jørgensen et al. 2005).

The west and east sides of Baffin Bay are exposed to different oceanographic processes. The eastern bay (Western Greenland) has wider shelves than the western (Baffin Island) side (Fig. 2.1, 2.3) (Chambers and Dick 2007). The eastern shore is exposed to the warmer WGC as it flows in from the North Atlantic; while the western shore is influenced by the Arctic amplified Baffin Current on its way to Davis Strait (Fig. 2.2) (Fissel et al. 1981, Rudels 1986, Munk et al. 2003, Tang et al. 2004). Current flow is faster near shore than towards the center of the bay (Fissel et al. 1981) and currents decrease in velocity with depth (Tang et al. 2004).

Temperature is at its minimum at ~100 m depth as a result of winter cooling through central and western Davis Strait and north Baffin Bay; and at its maximum (~ 2.2 °C) between 500 to 800 m throughout the bay (Tang et al. 2004, Jørgensen et al. 2005).

This region is also characterized by a recurring polynya known as the North Water (near the northern part of Baffin Bay) (Tang et al. 2004), which provides access to open water throughout much of the year.

2.1.3.4. Davis Strait

Davis Strait connects the North Atlantic to Baffin Bay and ranges in depth from 650 to 1000 m (Allard 1990). Warm (4 °C at surface), saline waters from the WGC flow north over the eastern edge of the strait, while cold (0.5 °C at surface), fresher (32 to 33.5 ‰) water from the Canadian Archipelago and Baffin Bay flow south along its western edge (Tang et al. 2004). The eastern edge of the strait is variable and dependent on variations in the WGC, resulting in the warmest temperatures in the winter and coldest in the summer (Tang et al. 2004). Circulation is dependent on bathymetry with flow speeds decreasing with depth and varying by season (winter and spring have slower currents than in the summer and fall) (Tang et al. 2004). A sill depth of 650 m helps control circulation to and from Baffin Bay (Tang et al. 2004, Jørgensen et al. 2005).

2.1.3.5. Disko Bay

Disko Bay is a highly productive region found midway up the west coast of Greenland (Hansen et al. 2012). More than 10 % of all Greenland ice output comes from the Jakobshavn glacier and flows through this small bay helping shape its bathymetry through scouring (Weinrebe et al. 2008, Hansen et al. 2012).

At its central point, Disko Bay is 800 m deep (Munk et al. 2003) with temperatures ranging from 1.5 °C to ~ 2 °C and an overall mean salinity of ~ 33 ‰ (Ribergaard 2009). It has been reported that August surface waters (0 to 50 m) can vary in temperature from -1.8 °C to 6.7 °C and salinities of 30.6 to 33.7 ‰ (dependent on distance from glacier outflow) (Hansen et al. 2012). Below 150 m, temperatures and salinity are more stable at -0.5 °C to 3.4 °C and 33.3 to 34.3 ‰, with a persistent cold water layer between 30 to 130 m throughout the bay (Hansen et al. 2012).

The stratification caused by glacial runoff, sea ice melt and atmospheric interactions, make this region highly productive (Frandsen and Wieland 2004, Hansen et al. 2012).

2.1.3.6. St. Lawrence

The St. Lawrence sample region (inclusive of Gulf of St. Lawrence and the eastern part of the St. Lawrence estuary) has a maximum depth of 520 m with a complex bathymetry of slopes, deep channels (100 to 200 m) and plateaus (Chouinard and Dutil 2011, Chouinard 2011). The water column is vertically stratified with low salinity waters of the surface (outflow from St. Lawrence River) overlaying either a cold intermediate layer or a mixture of Labrador Current and warm Gulf Stream, dependent on depth (Chouinard and Dutil 2011). Tidal flow and localized gyres add to the complex current system within the region (Chouinard and Dutil 2011). Its complex oceanography provides a wide range of habitats, allowing the region to maintain species from both Arctic and temperate environments (Chouinard and Dutil 2011).

2.1.4. Impact of climate change on the Arctic Ocean

The Arctic Ocean is a careful balance of temperature, salinity, ice formation, currents and wind, which control habitat formation, nutrient and biological distributions, and to an extent, global climate (Dickson 1999, Michel et al. 2006, Belkin 2009, Planque et al. 2010). Any changes to this balance could have long lasting ecological effects (Michel et al. 2006, Planque et al. 2010).

Global impacts to marine ecosystems as a result of climate change are expected to be: 1) an increase in temperature (increased heat absorption from atmosphere and solar energy), 2) an overall decrease in surface salinity (increased precipitation, ice melt, terrestrial runoff), 3) increased acidity (increased CO₂ absorption from the atmosphere), and 4) a decrease in oxygenation (decreased mixing and the lower O₂ solubility at higher temperatures) (Pierce et al. 2008, Belkin 2009, Gruber 2011, Guerra et al. 2011, Overland et al. 2011). These changes could result in shifts of global circulation systems, increased stratification (decreased nutrient mixing throughout the water column), an increase in climactic events (e.g. stronger El Niño's, more frequent flooding) as well as indirect impacts on marine organisms such as distributional changes, increased predation/competition, and added anthropogenic stresses (Pierce et al. 2008, André et al. 2010, Overland et al. 2010, Planque et al. 2010, Gruber 2011, Overland et al. 2011). All of these changes combine to push ecosystems beyond their tipping point and to a new state (André et al. 2010).

Initial models predicted that higher latitudes would be the first to be impacted by global climate shifts (Carmack and Macdonald 2002, Gruber 2011, Overland et al. 2011). These effects would then be magnified in northern regions (Arctic amplification) through loss of sea ice

(adding to temperature and salinity shifts, stratification, as well as changes to regional productivity) and poleward movement of the global heat transport (Carmack and Macdonald 2002, Gruber 2011, Overland et al. 2011). Several 'hotspots' have been identified where sea ice loss is predicted to be greater and include Baffin Bay and northeastern Canadian Arctic (Overland et al. 2011).

Over the past 30 years, records show a reduction in sea ice, impacting ocean circulation and water mass characteristics (Michel et al. 2006). 2011 was the second consecutive year that the Northwest Passage (both north and south routes) remained open (Overland et al. 2011). This loss of sea ice is due to increased atmospheric and marine temperatures (Overland et al. 2010). In 2011, the Arctic was in its warmest period in recorded history (Overland et al. 2011). Alaska reported an increase in its annual average temperature by 1.5 °C since 1985 with similar increases throughout most of the Arctic region (Gradinger 1995, Overland et al. 2011, Richter-Menge et al. 2011). The global ocean acts as a heat sink, absorbing in excess of 80 % of the atmospheric heat created by global warming (Gruber 2011, Guerra et al. 2011). Since much of the anthropogenic-produced heat is carried poleward (Overland et al. 2011), it is the Arctic (and Antarctic) oceans that will see the greatest influx. The result is an increase of 0.7 °C in sea surface temperatures (SST) over the last 100 years with a predicted further increase of 3 °C per century (Gruber 2011, Guerra et al. 2011). While most of the temperature increase affects surface waters, Guerra et al. (2011) predict increases of 3 to 5 °C for bottom water over continental shelves with temperature changes reported as deep as 3000 m (although these increases are likely to be miniscule (Gruber 2011)).

There is also evidence of changes to the water masses, such as a warmer than usual Atlantic layer and a shift between the boundary of Atlantic and Pacific water from the Lomonosov to the Mededeleyev Ridge in the past few decades (Michel et al. 2006). Changes to the water masses are likely the result of increased freshwater input through sea ice melt, increased precipitation and terrestrial runoff (Rudels 1995, 2011).

The loss of sea ice and changes in global marine circulation has caused a decrease in surface salinity (Overland et al. 2010, Overland et al. 2011). Continued desalinization of Arctic waters, in conjunction with increased temperatures, will intensify marine stratification, ultimately decreasing nutrient transport and local productivity (Overland et al. 2010, Gruber 2011). Such an increase in stratification would also decrease deep-water production, thermohaline circulation and the ventilation of the abyssal regions (Rudels 1995, Richter-Menge et al. 2011).

Much of the excess carbon in the atmosphere as a result of anthropogenic processes (i.e. global warming) is carried northward (similar to the heat transport) and is absorbed in the Arctic Ocean (Overland et al. 2011). This absorption has decreased pH values, impacting the biogeochemistry of the region and calcified (CaCO_3) marine organisms (Guerra et al. 2011, Overland et al. 2011). Overland et al (2011) reported that a CaCO_3 saturation of < 1 would have corrosive effects on such minerals as aragonite (key component in fish otoliths and cephalopod statoliths (Kristensen 1980, Rodhouse and Hatfield 1990, Bettencourt and Guerra 2000, Arkhipkin 2005)), calcite and increase magnesium calcite. This would be detrimental for organisms that require these compounds for their shells and sensory organs.

Climate change could also shift atmospheric circulation from anticyclonic to cyclonic (Mysak 2001) which could cause reversals of many of the surface currents, shifts in upwelling regions as well as increase the Atlantic input to the Arctic (Michel et al. 2006). Such changes would impact the biodiversity and distribution of marine species, including important fishery stocks, especially those that take advantage of ocean circulation for migrations and larval distributions (O'Dor 1988, Bakun and Csirke 1998, Rodhouse et al. 1998a, Arkhipkin and Bjørke 1999, Carmack and Macdonald 2002, Michel et al. 2006, Semmens et al. 2007).

Arctic organisms rely on the predictability of seasonal cycles for maturation, reproduction and migration (Overland et al. 2010). Any changes to the system that could impact the timing and intensity of processes such as phytoplankton blooms or current flow would have a detrimental effect on the productivity, distribution and biodiversity within the Arctic region. Increased temperatures and loss of sea ice could result in poleward shifts of temperate species (Overland et al. 2010), introducing further competition and an increase of predators to the region (Carmack and Macdonald 2002). Loss of sea ice also means a loss of hunting and birthing grounds of many marine mammals (Carmack and Macdonald 2002). Sea ice communities would also be affected which would alter nutrient availability to the rest of the food web (Gradinger 1995).

Understanding the impact of climate change on the biogeography and biology of Arctic organisms is vital due to the relative low species biodiversity of the region and low number of trophic links (Carmack and Wassmann 2006). Any change to the system could damage an already fragile ecosystem, potentially pushing the ecosystem past its tipping point (André et al. 2010).

2.2 Arctic Cephalopods

2.2.1. Introduction

Cephalopods are important components of all marine ecosystems (Sennikov et al. 1989, Clarke 1996, Takai et al. 2000, Piatkowski et al. 2001, Nesis 2003c, Zumholz and Frandsen 2006, Chambers and Dick 2007, André et al. 2010). Not only as avid predators on a variety of invertebrates, fish and other cephalopods (Rodhouse and Nigmatullin 1996), but also as high-energy prey species for a variety of marine mammals, fish and birds (Lawson et al. 1998, Hooker et al. 2001, Piatkowski et al. 2001, Frandsen and Wieland 2004, Boyle and Rodhouse 2005k, André et al. 2010, Albertin et al. 2012). Their central position within food webs help cycle nutrients between the surface and benthic habitats through diurnal migrations as well as on and off continental shelves via large-scale migrations (e.g. Ommastrephids) (Sennikov et al. 1989, Clarke 1996, Takai et al. 2000, Nesis 2003c, Chambers and Dick 2007). Cephalopod life cycles are also highly dependent on environmental variables; from juvenile and adult dispersal using oceanographic currents to temperature induced spawning events, as well as incubation and maturation rates (Boletzky 1994, Rodhouse and Nigmatullin 1996, Nesis 1999, Forsythe 2004, Boyle and Rodhouse 2005f, g, Leporati et al. 2007). Their dependence as prey items and opportunistic responses to environmental shifts, make cephalopods ideal indicator species for monitoring impacts of climate change (André et al. 2010, Rodhouse 2010, Coll et al. 2013, Navarro et al. 2013).

Cephalopods are a major component of marine fisheries, often filling the gap left by depleted finfish stocks (Caddy and Rodhouse 1998, Pauly 1998, Jackson et al. 2000, Wood and O'Dor 2000, Piatkowski et al. 2001, Hunsicker et al. 2010, Coll et al. 2013), and are ranked third

most lucrative behind tuna and shrimp (Rodhouse and White 1995, Clarke 1996). However, their short life spans, semelparous reproduction and reliance on environmental conditions for a variety of biological cues and metabolic processes (Rodhouse and White 1995, Boyle and Boletzky 1996, Rodhouse and Nigmatullin 1996, Boyle and Rodhouse 2005g, Rodhouse 2010, Gruber 2011) make cephalopod populations highly susceptible to potential collapse when conditions are not ideal or additional stresses are placed upon the system (i.e. anthropogenic impacts) (Lipinski et al. 1998, Rodhouse et al. 1998a, Rodhouse et al. 1998b, Pierce et al. 2008).

The ecological and economic importance of cephalopods, along with their potential as indicator species, highlight the need for baseline information regarding this group (Pauly 1998, Wood and O'Dor 2000, Piatkowski et al. 2001, André et al. 2010, Coll et al. 2013, Navarro et al. 2013), in particular for Arctic species where climate change is predicted to be the most pronounced (Gradinger 1995, Loeng et al. 2005, Overland et al. 2011, Richter-Menge et al. 2011).

2.2.1.1. Evolution and systematics of Class Cephalopoda

Cephalopods appeared during the Cambrian period and currently contain ~700 species found in every ocean, and include the largest invertebrate, *Architeuthis dux* (Steenstrup in Harting 1860), as one of its taxa (Clarke 1996, Carlini 1998, Wood 2000, Wood and O'Dor 2000, Albertin et al. 2012). The order Cephalopoda can be divided into two subclasses, Nautiloidea (Bather 1888) and Coleoidea (Agassiz 1847) (Carlini 1998, Strugnell et al. 2009), with coleoids representing 99% of extant taxa (Wood 2000). Nautiloidea contains the only living primitive shelled cephalopods and contains only two genera: *Nautilus* L. and *Allonautilus* (Ward and Saunders 1997) (ITIS), while Coleoidea are characterized by individuals lacking a shell (e.g.

most octopods) or those with reduced, internalized shells (e.g. squid and cuttlefish) (Carlini 1998, Strugnell et al. 2009). These coleoids also possess fusiform muscular mantles with a modified foot, a closed circulatory system and complex eye and lens (Carlini 1998, Strugnell et al. 2009). Coleoids are also known to undergo rapid growth and have a semelparous reproductive strategy (Carlini 1998) as opposed to the multiple spawnings of Nautiloids (Boyle and Rodhouse 2005g). Carlini (1998) suggests that it is these features that allowed coleoids to enter and thrive in the pelagic realm.

Within the coleoids, there are two superorders: Decabrachia (Boettger 1952), consisting of the orders Sepiida (Zittel 1895), Sepiolida (Fioroni 1981), Spirulida (Stolley 1919) and Teuthida (Naef 1916); and Octobrachia (Fioroni 1981), consisting of the orders Octopoda (Leach 1818) and Vampyromorphida (Pickford 1939) (ITIS). Within the Canadian Arctic, only Sepiolida (Family Sepiolidae, subfamily Rossinae (Appellöf 1898)), Teuthida and Octopoda are represented.

Teuthida can be divided into two suborders, Myposina (Orbigny 1841) and Oegopsina (D'Orbigny 1945) (ITIS, Carlini 1998, Arkhipkin 2004, Boyle and Rodhouse 2005a). Myopsids consist of a single family, the shelf-living Loliginidae (Lesueur 1821) (ITIS) and are characterized by a corneal eye cover (Boyle and Rodhouse 2005a) protecting their complex eyes from the turbulent shelf water (Clarke 1996). Oegopsid squid lack a cornea (Boyle and Rodhouse 2005a) but are found within the more stable and less debris-filled pelagic zone.

The order Octopoda can also be subdivided into suborders Incirrina (Grimpe 1916) and Cirrina (Grimp 1916) (ITIS). Incirrate octopuses represent the stereotypical eight armed, benthic octopods found throughout the deep sea to intertidal pools (Boyle and Rodhouse 2005a). Cirrate

octopuses, however, represent the oldest members of the group (Voss 1988) and are typically deep-sea, epibenthic species (Boyle and Rodhouse 2005a). Cirrate octopuses are distinguished from incirrates by the presence of cirri on their arms (rather than only suckers), their gelatinous texture, internal 'shell', and large fins and web used for locomotion (Voss 1988).

Cephalopoda is a highly diversified class with much confusion still occurring even at the higher taxonomic levels (Clarke 1996, Collins and Villanueva 2006). Lack of specimens, difficulty in capturing new samples (i.e. adults are more elusive of sampling gear) and few cephalopod taxonomists have all contributed to this poor understanding of cephalopod systematics (Roper and Young 1975, Clarke 1996, Boyle and Rodhouse 2005k). In addition to taxonomic confusion, there is a significant lack of understanding regarding the basic biology of most species, including many of commercial importance (Clarke 1996).

2.2.1.2. General life history of Class Cephalopoda

a) Distribution

Cephalopods are found in every ocean (Wood and O'Dor 2000, Boyle and Rodhouse 2005a, Albertin et al. 2012). The diversity of taxa within the class has allowed this group to invade all marine habitats, with species even adapted to harsh hydrothermal environments (Clarke 1996, González et al. 1998, Wood and O'Dor 2000, Boyle and Rodhouse 2005a, Rosa et al. 2005, Albertin et al. 2012).

Each species has different physical requirements dependent of their stage of development that dictates their preferred habitat (Benton and Werner 1974). Temperature, particularly the temperature necessary to spawn and facilitate incubation, is a primary requirement (Benton and

Werner 1974, Nesis 1999, Wood 2000, Wood and O'Dor 2000, Semmens et al. 2007). Some species, typically those that undergo large-scale migrations from feeding to spawning grounds, are considered eurythermal – able to withstand a wide range of temperatures (e.g. *Illex illecebrosus* (Lesueur 1821)) while others are stenothermal with a narrow temperature tolerance (e.g. *Bathypolypus arcticus* (Prosch 1847), *Rossia* spp. (Owen 1834)) (Mercer 1968b, Benton and Werner 1974, Nesis 2003c, Zumholz and Frandsen 2006, Laptikhovsky et al. 2008). Temperature has been described as a dispersal barrier to many marine organisms, especially with regards to reproduction (Benton and Werner 1974). Temperature also varies with depth. Species living near the surface or closer to shore where the water is shallower will experience greater temperature fluctuations within smaller geographical areas than those living at greater depths, therefore, deep-sea species are thought to have a wider distribution than their pelagic and neritic counterparts due to more consistent temperature regimes (Boyle and Rodhouse 2005a).

Salinity is another major dispersal barrier, particularly for cephalopods (Zuev and Nesis 2003). Few species are found in salinities below 30 ‰ (e.g. *Lolliguncula brevis* (Blainville 1823)) with the majority of species strictly marine stenohaline, preferring 30 to 39 ‰ (Zuev and Nesis 2003, Boyle and Rodhouse 2005a, f). Consequently, environmental impacts such as rainfall, river outflow and sea ice melt influence cephalopod dispersal and may even lead to isolated populations (Semmens et al. 2007).

Cephalopod distribution is also linked to the productivity within a region, with prime cephalopod fishing grounds found along frontal zones and regions of increased mixing (Voss 1988, Bakun and Csirke 1998, Dawe and Brodziak 1998, Zuev and Nesis 2003). Varied bathymetry, islands, vortices and water masses all contribute to the productivity of a region

(Zuev and Nesis 2003). While productivity of the region appears to be an important component, prey availability does not. Cephalopods, especially those undergoing extended migrations, will resort to cannibalism when prey items are in short supply (Rodhouse and Nigmatullin 1996, Bakun and Csirke 1998, Boyle and Rodhouse 2005b).

Many cephalopods utilize oceanic currents as a way to travel extended distances without expending much energy (Semmens et al. 2007). This method is also used by paralarvae (the planktonic young) of many species as a transport mechanism to move to productive nursery grounds (Zuev and Nesis 2003). Shifts in timing or direction of these currents will impact the distribution, survival and stability of the different cephalopod populations (Semmens et al. 2007).

A marine organisms' distribution is not only defined by its horizontal (latitudinal/longitudinal) distribution, but also by its vertical distribution throughout the water column. Cephalopods have been recorded from the intertidal zone to 5000 m; requiring unique adaptations to help them survive at a preferred depth (Clarke 1996, Boyle and Rodhouse 2005a). Shelf-living species and benthic dwellers have a variety of adaptations that help protect them from the volatile environment (Clarke 1996). Most shelf living species have a secondary skin over their eyes to protect them from debris (Clarke 1996). Other neritic species such as cuttlefish and octopus exhibit extensive camouflaging techniques, while bobtail squid bury themselves in the sediment during the day (Boyle and Rodhouse 2005d, Rodrigues et al. 2010), likely as protection from potential predators. Pelagic and deep-sea species (including some neritic species) have unique adaptations to help with buoyancy and maintaining their depth (Clarke 1996, Rosa et al. 2005). Cephalopod buoyancy techniques range from fish-like 'swim-

bladders', air filled shells, lighter ammonium ions in lieu of heavier ions (i.e. ammoniacal squids) and even squaline-like oils (i.e. Gonatidae) (Clarke 1996, Boyle and Rodhouse 2005h). Ommastrephid species, on the other hand, must swim to maintain their depth (Clarke 1996). Energy and calorific values of these species vary depending on their buoyancy mechanisms (Clarke 1996).

b) Life history strategies

The biotic and abiotic factors affecting cephalopod distribution, also impact their life histories. Understanding the general life history patterns of cephalopods from different habitats and locations is essential for developing environmental and fishery monitoring and management programs (Anderson and Rodhouse 2001, Boyle and Rodhouse 2005b, André et al. 2010).

Cephalopods are short-lived (1 to 2 years), fast-growing, with semelparous life cycles (excluding Nautiloids) (Rodhouse and White 1995, Boyle and Boletzky 1996, Rodhouse and Nigmatullin 1996, Boyle and Rodhouse 2005g, André et al. 2010, Rodhouse 2010), however, deep-sea and polar species are thought to be longer lived and slower to mature (Rodhouse and Nigmatullin 1996, Wood 2000, Wood and O'Dor 2000, Arkhipkin 2004, Collins and Villanueva 2006, Zumholz and Frandsen 2006). Although they are important components of the ecosystem, to date, research on their basic biology has been limited to commercially important (e.g. *Illex* spp. (Steenstrup 1880)) and near shore species (e.g. *Loligo* spp. (Lamarck 1798), *Sepia* spp. L.) (Clarke 1996, Wood 2000).

Cephalopods have a variety of life history patterns (Boyle and Rodhouse 2005g) which can be narrowed down to two major concepts: 1) individuals mature fast to avoid predators and

negative environmental influences, resulting in increased fitness through multiple generations over a short period of time; or 2) individuals mature slowly and risk predation to attain a larger size; but if they survive, fecundity is increased with a greater quantity of large eggs and increased yolk reserved for the hatchlings (Nesis 1999, Wood and O'Dor 2000). It has been established that species that lay large eggs typically produce precocious young while smaller eggs produce paralarvae (planktonic young) (Voss 1988, Nesis 1999). Arctic species appear to favour the second life history pattern.

Within the Arctic, maturation is slowed due to lower temperatures (Rodhouse and Nigmatullin 1996, Nesis 1999, Wood 2000, Wood and O'Dor 2000, Zumholz and Frandsen 2006). The cold water also benefits the hatchlings by decreasing the absorption rate of their yolk sac, allowing early hatchlings to survive without feeding until sufficient prey items are available (Boletzky 1994, Nesis 1999). In warmer regions, juveniles hatch as soon as their yolk sac has been absorbed (Boletzky 1994), suggesting that an increase in Arctic temperatures could result in a misalignment of available nutrients (i.e. yolk sac vs. plankton blooms) for the hatchlings. Temperature is also thought to be the cue for sexual maturation and determines the duration of egg incubation per species (Boletzky 1994, Boyle and Rodhouse 2005f).

Both cirrate and sepiolid females are polytelic with eggs present in the ovary at varying stages of development, suggesting extended spawning events (Mercer 1968b, Boyle and Rodhouse 2005g, Zumholz and Frandsen 2006, Laptikhovsky et al. 2008, Morov and Sabirov 2009). They also both produce large eggs with rigid casings that resist fouling or degradation over time (Boletzky 1994). In contrast, most incirrate octopuses lay all their eggs at once and protect their juveniles by physically brooding over them until hatch, providing constant aeration

via water flow (Boletzky 1994, Nesis 1999, Muus 2002). Squid, however, typically lay their eggs in gelatinous masses which can either be attached to a substrate or be free floating (Boletzky 1994). These masses are quickly colonized and if free floating, risk stranding on shorelines or transported to sub-optimal hatching grounds, therefore, habitat selection is vital (Boletzky 1994). The squid *Gonatus onyx* (Young 1972) has been observed brooding their eggs, an unusual behaviour for teuthids, however, it is thought that this behaviour may also be found in other Gonatids (Lindgren et al. 2004, Lindgren et al. 2005, Seibel et al. 2005). Similar to *G. onyx*, female *G. fabricii* (Lichtenstein 1818) also undergo tissue degradation upon maturation which is thought to add buoyancy to help during brooding, and large masses of planktonic mature females have been observed floating in the Norwegian Sea (Arkhipkin and Bjørke 1999, Hooker et al. 2001, Frandsen and Wieland 2004, Lindgren et al. 2005).

Temperature also impacts the size range of cephalopods available in a region (Forsythe 2004, Leporati et al. 2007). The Forsythe effect (Forsythe 2004) describes how cephalopods from the same cohort produce individuals of varying sizes depending on when they hatch (Leporati et al. 2007). Early hatching individuals are exposed to colder temperatures and therefore grow slower than those that hatch a few weeks later when the water is warmer (Forsythe 2004, Leporati et al. 2007). Temperature increases of 1 °C are reported to triple the weight of *Loligo forbesii* (Steenstrup 1856) in laboratory experiments, with a 2 °C increase resulting in an animal five times as large (Wood and O'Dor 2000, Forsythe 2004). This results in larger, 'younger' individuals from the same cohort within the same region (Forsythe 2004, Leporati et al. 2007).

c) General trophic interactions

Prey items of cephalopods are not well known (Piatkowski et al. 2001). All cephalopods are carnivores (Boyle and Rodhouse 2005b) with the exception of *Vampyroteuthis infernalis* (Chun 1903), which has recently been discovered to be a detritivore (Hoving and Robison 2012), however, detailed prey items for all other taxa remain elusive (Piatkowski et al. 2001).

Cephalopods eat by catching their prey with their arms (and tentacles when available) and manoeuvring it towards their beak where they dismember it with small bites (Piatkowski et al. 2001, Boyle and Rodhouse 2005b). Bite size is important because their brain encircles the esophagus, so any food item too large could have detrimental effects (Boyle and Rodhouse 2005b). Also, hard body tissues are often rejected, making identification of prey species based on stomach contents difficult (Piatkowski et al. 2001).

All cephalopods (with the exception of *V. infernalis*) are voracious, opportunistic predators, feeding on any prey they can catch (Boyle and Rodhouse 2005b, Hoving and Robison 2012). As the cephalopods grow, they are able to take larger prey items but continue to eat by removing pieces of tissue rather than consuming the whole organism (Boyle and Rodhouse 2005b). Species, such as octopods, produce toxins from their salivary glands that aid in immobilizing their prey but also contain chitinase that helps remove the carapace from the tissue for easier digestion (Rodhouse and Nigmatullin 1996, Mangold and Young 1998). Oegopsid squid likely feed multiple times a day but have fast digestion rates, adding to the difficulty of prey identification (Kristensen 1984, Mangold and Young 1998).

2.2.1.3. Ecological importance of global cephalopods

Cephalopods are important components in marine ecosystems, helping cycle nutrients throughout the food web and between the surface and benthic habitats via their migrations (Sennikov et al. 1989, Clarke 1996, Takai et al. 2000, Nesis 2003c, Chambers and Dick 2007). Estimated total biomass of cephalopods is approximately 193 to 375 Mt (Rodhouse and Nigmatullin 1996), which provides a large quantity of high quality prey to other marine predators while also putting significant pressure on lower trophic levels (Caddy and Rodhouse 1998). Their wet weight conversion efficiencies have been estimated to be between 13 (active squid) and 69 % (sedentary octopods) with a conservative estimate of 10 % energy transfer between trophic levels (Wood and O'Dor 2000, Boyle and Rodhouse 2005k). Cephalopod feeding rates are controlled by both temperature and individual size (Agnew et al. 2002, Boyle and Rodhouse 2005j).

Arctic cephalopods such as *G. fabricii*, are frequently found in the stomachs of marine mammals, birds, commercially fished and culturally important Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum 1792)) and cod (*Boreogadus saida* (Lepechin 1774)) (Nesis 1965, Wiborg et al. 1982, Bjørke 2001, Zumholz and Frandsen 2006, Chambers and Dick 2007). Hooker et al. (2001) and Frandsen and Wieland (2004) noted the high presence of marine predators in areas of large concentrations of cephalopods, in particular *G. fabricii*; with Hooker et al. (2001) suggesting that bottlenose whales (*Hyperoodon ampullatus* (Forster 1770)) were targeting mature female *G. fabricii*.

2.2.1.4. Economic importance of global cephalopods

Cephalopods play an important role in commercial fishing. As traditional finfish stocks are depleted, cephalopod landings have increased (Clarke 1996, Caddy and Rodhouse 1998, Jackson et al. 2000, Piatkowski et al. 2001, Boyle and Rodhouse 2005e, Hunsicker et al. 2010). Their total global catch exceeded 4 million tons in 2007 (Oesterwind et al. 2010) but these values may be underestimates as many artisanal fisheries go unreported and more than half of the species caught are listed as ‘unidentified cephalopods’ (Boyle and Rodhouse 2005e, André et al. 2010). Regardless of underreporting, this increase in cephalopod catches may be the result of climate change (Piatkowski et al. 2001) due to increased prey availability and accelerated maturation (i.e. decrease in generation time and quicker development of eggs), or simply the result of decreased teuthophagus predators (Caddy and Rodhouse 1998, Navarro et al. 2013). Unfortunately, most biological and fishery research has had limited scope, focusing on in-shore or commercial species (i.e. octopods, cuttlefish, loliginid squids and select Ommastrephidae), with little known about Arctic species (Clarke 1996, Navarro et al. 2013).

Currently there is no cephalopod fishery within the Canadian Arctic and western Greenland, however, *G. fabricii* has the potential for commercial exploitation off of southwestern Greenland and Baffin Bay (Wiborg et al. 1982, Kristensen 1983, Roper et al. 1983, Kristensen 1984, Piatkowski and Wieland 1993). Both *Rossia moelleri* (Steenstrup 1856) and *Bathypolypus* spp. (Grimpe 1921) are also thought to have the potential to support a local fishery off Greenland (Frandsen and Wieland 2004).

2.2.1.5. Potential impacts of climate change on cephalopod populations

Climate change scenarios indicate that the Arctic region will be impacted by increasing sea surface temperatures (SST), decreasing salinity from increased terrestrial runoff and ice melt, decreased pH due to CO₂ uptake and de-oxygenation caused by poor thermal oxygen coupling (Pierce et al. 2008, Belkin 2009, Gruber 2011, Guerra et al. 2011, Overland et al. 2011). The effects of these changes on cephalopod distributions and abundance are difficult to predict without baseline information (Sims et al. 2001, Agnew et al. 2002).

Predicted SST increases of 1 to 5.8 °C (with increases predicted as deep as 3000 m) over the next century (Gruber 2011, Guerra et al. 2011) are expected to not only impact the growth and maturation of cephalopods (Wood and O'Dor 2000, Boyle and Rodhouse 2005j), but also affect their distribution and the timing of peak abundances (Sims et al. 2001). These changes will directly impact many Arctic predators. Off of Plymouth, UK, a 1.5 °C increase in SST resulted in a shift in the peak *L. forbesii* abundance by four months (Sims et al. 2001). One of the largest cephalopod fisheries, *I. argentinus* (Castellanos 1960), is also highly correlated with SST (Agnew et al. 2002). Increasing temperatures will also allow for temperate species to shift their distribution north (Overland et al. 2010, Węśławski et al. 2011), ultimately increasing competition and/or predation for Arctic cephalopods (Carmack and Macdonald 2002, Golikov et al. 2013). These range extensions are already occurring, with Humboldt squid (*Dosidicus gigas* (D'Orbigny 1835)) extending their range from Baja, Mexico to the North Pacific, with individuals reported as far north as Alaska (Zeidberg and Robison 2007).

With most cephalopods being stenohaline (Zuev and Nesis 2003, Boyle and Rodhouse 2005a, e), shifts in salinity, even at the surface will impact their distributions and migrations

(Semmens et al. 2007). Salinity will also increase stratification within the Arctic region (Overland et al. 2010, Gruber 2011), making the nutrient transport trophic function of cephalopods even more important.

Increased terrestrial outflow and glacial melting will also impact benthic species by increasing the amount of siltation within the region (Węśławski et al. 2011)

Shifts in both temperature and salinity, along with atmospheric changes, will contribute to shifts in oceanic surface currents (O'Dor 1988, Bakun and Csirke 1998, Rodhouse et al. 1998a, Arkhipkin and Bjørke 1999, Carmack and Macdonald 2002, Michel et al. 2006, Semmens et al. 2007). These changes will impact the distribution of cephalopods that rely on currents for migration and distribution of the paralarval stage (Zuev and Nesis 2003, Semmens et al. 2007).

Shifts in pH within the marine system will impact calcified support structures and sensory organs of marine species (Guerra et al. 2011). Cephalopods rely on aragonite statoliths (similar to fish otoliths) to acquire information regarding position and velocity within the water column (Budelmann 1990, Arkhipkin 2005, Zumholz et al. 2007). However, Arrington and Winemiller (2002) state that decreasing CaCO_3 will cause corrosive effects on such minerals, ultimately impacting cephalopod orientation.

2.2.2. Review of the basic biology of common Canadian Arctic cephalopod species

Eight cephalopod species are common in the Canadian Arctic and reflect the heterogeneous habitats of the region. The species are: *G. fabricii* (a pelagic fast-swimming squid), *R. moelleri*, *R. palpebrosa* (Owen 1834), *R. megaptera* (Verrill 1881) (benthic, shallow water bobtail squids), *B. arcticus*, *B. bairdii*, *B. pugniger* n. sp. (deep-water, benthic octopuses

whose taxonomy has recently undergone revision (Muus 2002)) and *Cirroteuthis muelleri* (Eschricht 1836) (a benthic-pelagic finned octopus (Collins and Villanueva 2006)). The following sections summarize the known literature for each of these common species.

2.2.2.1 *Gonatus fabricii*

Gonatus fabricii is a member of the family Gonatidae (Hoyle 1886), consisting of medium sized oceanic squids with distinctive four sucker and/or hook armature, simple funnel cartilage grooves (funnel locking apparatus) and hooks on the tentacular clubs of some species (Zuev and Nesis 2003, Lindgren et al. 2004). This family is comprised of four genera and 19 species: *Berryteuthis* (Naef 1921) (two species), *Eogonatus* (Nesis 1972) (one species), *Gonatopsis* (Sasaki 1920) (five species) and *Gonatus* (Gray 1849) (11 species) (ITIS). Gonatidae are also notable for containing the only squids that exhibit post-spawning egg brooding (Lindgren et al. 2004, Lindgren et al. 2005).

Gonatus fabricii is of ecological and cultural importance with the potential of commercial harvest and are typically caught as by-catch in the polar shrimp (*Pandalus borealis* (Krøyer 1838)) and groundfish fisheries of western Greenland and the Norwegian Sea (Wiborg et al. 1982, Kristensen 1983, Roper et al. 1983, Kristensen 1984, Piatkowski and Wieland 1993, Frandsen and Wieland 2004, Lindgren et al. 2004, Zumholz and Frandsen 2006).

a) Distribution

The family Gonatidae is thought to have originated in the north Pacific, where most of the extant species are still found (Nesis 2003b, Lindgren et al. 2004). A few species, in

particular *G. fabricii*, radiated north through the Bering Sea into the Polar Basin and down into the North Atlantic during the Pliocene (Nesis 2003b).

Gonatus fabricii represents the most abundant and widely distributed Arctic squid (Kristensen 1984, Piatkowski and Wieland 1993, Bjørke 2001, Frandsen and Wieland 2004, Zumholz and Frandsen 2006, Golikov et al. 2013) and one of the two circumpolar and panpolar Arctic cephalopods (Nesis 2001, Zuev and Nesis 2003). Three *G. fabricii* were reported from drifting stations in the high Arctic by Nesis (2003c), extending their range from the boreal North Atlantic to the North Pole (Nesis 2001, 2003b). *G. fabricii* are common off of western Greenland, with greater abundances near Disko Bay (400 to 600 m) and Fyllas Bank (southern Greenland) (Kristensen 1984, Piatkowski and Wieland 1993, Bjørke 2001, Frandsen and Wieland 2004). These squid are also abundant in the Norwegian and Greenland seas and south to Flemish Cap Bank in the North Atlantic, with a southern range of Cape Cod (Nesis 2003b, Zuev and Nesis 2003, Golikov et al. 2013). Their polar range extends from Baffin Bay to Davis Strait, around Greenland to the Irminger Sea, Svalbard (Norway) through to the Bering Sea (Clarke 1966, Nesis 2003b, Golikov et al. 2013). Zuev and Nesis (2003) describe their distribution as rarely being found in the Barents Sea and only in the Siberian and Beaufort seas accidentally, however, recent surveys extend the range of *G. fabricii* to the eastern Barents (Novaya Zemlya) and the western Kara seas (Svyataya Anna Trough) with the speculation that this extension is likely due to increasing temperature of the Atlantic water layer (Golikov et al. 2013). Individuals are unlikely to be found in the southeastern Barents Sea due to lowered salinity (< 25 ‰) from river runoff (Golikov et al. 2013), which may also explain their rarity in the Beaufort Sea where the outflow of the Mackenzie Delta impacts the salinity of the surrounding area. Individual *G. fabricii* are also reported from Northern Japan, California and

the Mediterranean (Clarke 1966) but these records are likely misidentifications (Wiborg et al. 1982).

Two morphologically distinct populations have been identified within close proximity along western Greenland: Disko Bay and Amerdloq Fjord (Holsteinsborg), however, the geographic reason(s) for these populations is not yet understood (Kristensen 1982, 1984). Descriptions of their morphological differences are outlined in section 2.2.2.1.c.

G. fabricii are eurybathic, with their vertical distribution within the water column primarily associated with their maturity level (Zuev and Nesis 2003). Juveniles are typically found closer to the surface (0 to 500 m with most found near 80 m) over deep water (≥ 200 m) and descend to deeper depths as they mature (beginning their descent once 50 to 70 mm mantle length (ML)) (Clarke 1966, Wiborg et al. 1982, Kristensen 1983, 1984, Piatkowski and Wieland 1993, Zuev and Nesis 2003, Frandsen and Wieland 2004). Adults are thought to live near the ocean bottom with peak numbers near 400 to 600 m but can extend to 1000 m (one source reports a maximum depth of 2000 m), however, these adults rarely ascend to the surface (Kristensen 1984, Piatkowski and Wieland 1993, Zuev and Nesis 2003, Frandsen and Wieland 2004). Both adults and juveniles are found within the same region, suggesting no spawning migrations (Nesis 1965, Clarke 1966, Zuev and Nesis 2003).

Most of the Gonatidea are considered cold-water stenotherms (Zuev and Nesis 2003), and *G. fabricii* follows the deep-water layer within the Polar Basin, preferring deeper, colder water in their more southern range (Clarke 1966). *G. fabricii* also prefers areas of high productivity, such as regions with variable bathymetries, converging water masses and continental slopes (Zuev and Nesis 2003).

A closely related species, *G. steenstrupi* (Kristensen 1981), is also found within the North Atlantic, extending into the Arctic realm but its distribution is limited to warmer water than *G. fabricii*. *G. steenstrupi* is found off of eastern Greenland to the European sub-arctic south to the eastern Mid-Atlantic Ridge (Nesis 2003b).

b) Life history

Gonatus fabricii hatch at ~ 3.0 mm pen length (PL), with under-developed mantles, short-stubby arms and are incapable of active locomotion (Clarke, 1966, Kristensen 1983, 1984, Sweeney et al. 1992, Arkhipkin and Bjørke 2000). Juveniles (≤ 30.0 mm PL) are planktonic and often found in large shoals near the surface (most at ~ 80 m) (Kristensen 1983, Arkhipkin and Bjørke 1999, Zuev and Nesis 2003). As they mature, the mantle becomes more muscular and arms begin to extend (Kristensen 1983, Sweeney et al. 1992, Arkhipkin and Bjørke 2000). Hooks develop on the tentacular clubs at approximately 25.0 to 30.0 mm PL and increases hunting success and the ability to handle larger and higher quality prey species (Nesis 1965, Kristensen 1983, 1984). By 50.0 to 70.0 mm ML (herein ML and PL will be used interchangeably), the juveniles have developed into active miniature adults and begin to descend to deeper depths (Nesis 1965, Clarke 1966, Wiborg et al. 1982, Kristensen 1983, 1984, Piatkowski and Wieland 1993, Zuev and Nesis 2003, Frandsen and Wieland 2004, Zumholz and Frandsen 2006). Arkhipkin and Bjørke (1999) further refined the maturity stages based on specimens from the Norwegian Sea, Nigmatullin's (1989) maturity scale and the observed ontogenetic distribution of the specimens. Their maturity scale is as follows:

3.5 to 15.0 mm PL	“Planktonic epipelagic paralarvae”
15.0 to 65.0 mm PL	“Mesonektonic epipelagic juveniles”
65.0 to 130.0 mm PL	“Nektonic mesopelagic immature squid”
130.0 to 200.0 mm PL	“Meso- and bathypelagic immature females and maturing males”
> 160.0 mm PL	“Nektonic bathypelagic mature males”
> 200.0 mm PL	“Planktonic bathypelagic maturing, mature and spent females”

(Note: modified from Arkhipkin and Bjørke 1999)

Research has examined growth rates from both the Norwegian Sea and western Greenland, with individuals from the colder western Greenland locations growing slower than those from the warmer Norwegian Sea (Kristensen 1984, Frandsen and Wieland 2004, Zumholz and Frandsen 2006). Growth rates of juveniles collected from Disko Bay and Davis Strait (1984 and 2004) showed growth rates of ~ (4.0) 8.0 to 9.0 mm PL per month with individuals reaching upwards of 11.0 cm PL during the first year (Kristensen 1984, Frandsen and Wieland 2004), however, Zumholz and Frandsen (2006) suggest that growth rates off western Greenland are closer to 6.0 cm ML per year. Individuals collected from the Norwegian Sea, had accelerated growth, with juveniles reaching 14.0 mm ML per month (~ 17.0 cm ML per year) (Frandsen and Wieland 2004).

Testes begin to develop at 8.0 to 10.0 cm PL and individuals reach maturity at 20.0 to 25.0 cm PL (Kristensen 1984) but Arkhipkin and Bjørke (1999) suggest that males may reach

maturity at 16.0 cm PL. Ovaries begin to develop at 6.0 cm PL (Disko Bay) and 8.0 cm PL (Davis Strait) (Kristensen 1984). Females > 20.0 cm PL are thought to be mature (Arkhipkin and Bjørke 1999), however, some specimens > 25.0 cm PL were not mature (Kristensen 1984). Sexual dimorphism occurs at maturity (Kristensen 1983).

Male *G. fabricii* are believed to mate over two consecutive years (during years 2 and 3) with a maximum life span of 3 years (Kristensen 1983, Frandsen and Wieland 2004). Females live a maximum of 3 years but are limited to a single spawning event and undergo morphological deterioration at the onset of sexual maturity (2 to 2.5 years) (Kristensen 1981, 1983, 1984, Arkhipkin and Bjørke 1999, Nesis 1999, Lindgren et al. 2004; Lindgren et al. 2005). Once gravid, females lose their tentacles and arm suckers (Kristensen 1981, Nesis 1999). Their mantle and arm tissues become watery, their nidamental gland expands to nearly a third of their PL and their oviducal gland becomes distended in preparation for expelling 10 000 (~ 5.0 mm diameter) eggs (Kristensen 1981, 1984, Arkhipkin and Bjørke 1999, Nesis 1999, Frandsen and Wieland 2004, Lindgren et al. 2004). This loss of muscle increases buoyancy, which may be a brooding adaptation to allow females to carry and protect the eggs until hatch (Arkhipkin and Bjørke 1999). Female *G. onyx* were the first recorded squid to brood their eggs (Seibel et al. 2005) and it is thought that *G. fabricii* may behave similarly due to their observed tissue deterioration (Lindgren et al. 2004, Lindgren et al. 2005). Nesis (1999) estimated eggs require 112 days at -0.5 °C (central Polar Basin) to incubate and during this time the females cease to feed, relying instead on their energy stores within their digestive glands (Nesis 1999, Lindgren et al. 2004). Nesis (1999) speculated that the fatty digestive glands would provide adequate nutrients for nine months without external feeding.

Gonatus fabricii are thought to spawn in the pelagic layer with spawning commencing at the beginning of biological spring (Zuev and Nesis 2003); however spawning times vary by region. Kristensen (1984) estimated that hatching occurs in Davis Strait in the early spring and summer and in October to January for Disko Bay. The early hatch of Davis Strait juveniles may be the result of Davis Strait being ~ 4 °C warmer at 200 to 600 m depth range than Disko Bay, allowing individuals to develop faster and decrease their incubation time (Kristensen 1984). This temperature difference could also explain the occurrence of two morphologically distinct populations within the region. In the European Arctic, Wiborg et al. (1982) suggested that *G. fabricii* spawned during December to April between Norway, Spitsbergen, Iceland and Jan Mayen but spawning may extend over five to seven months.

c) Morphometrics, systematics and populations

Gonatus fabricii are identifiable by their simple funnel cartilage, hooks on the tentacular clubs of maturing-mature specimens and distinctive four-rowed armature with hooks replacing the middle two rows of suckers with maturation (Zuev and Nesis 2003, Lindgren et al. 2004). These arm hooks are the result of modified suckers, where the chitinous teeth of the sucker begin to recede leaving the central tooth to become enlarged and develop into the distinctive hooks (Zuev and Nesis 2003). While alive, the dorsal skin of *G. fabricii* is dark purple, lightening to reddish brown along the sides (Zuev and Nesis 2003), however, their skin is frequently damaged during collection and cannot be relied on for identification. This species attains a size up to 35.0 cm ML and 60.0 cm total length (TL) but are typically smaller (~ 20.0 cm ML) (Zuev and Nesis 2003). Sennikov et al. (1989) reported a mature female with a mantle length of 385 mm from the Norwegian Sea.

Two morphologically distinct, yet geographically close, populations of *G. fabricii* have been identified along the western coast of Greenland (Kristensen 1982, Zumholz and Frandsen 2006). Kristensen (1982) utilized ten morphometric characters and multivariate analyses to identify potential populations and determine which characters best distinguished between the locations. Utilizing discriminant function analysis and multivariate F-tests for log transformed indices, two groups in the western Arctic were identified: Disko Bay and Amerdloq Fjord (Kristensen 1982). Nuchal cartilage length and arm lengths 1 and 3 were determined to be important characters separating these locations (Kristensen 1982).

While these populations are geographically close, it is unclear what causes the formation of the distinct populations (Kristensen 1982). It is speculated that environmental variation may play a role but the impact of environmental variability on cephalopod morphometric characters has only been shown for gill size in relation to oxygen concentration (Kristensen 1982). This study also highlights the importance of population identification for future stock assessments (Kristensen 1982).

Genetic analyses have also been conducted on the family Gonatidae, however, emphasis was on evolutionary relationships rather than population determination (Lindgren et al. 2004, Lindgren et al. 2005). Lindgren et al. (2005) utilized 12 sRNA, 16 srRNA and Cytochrome c Oxidase subunit I (COI) to identify two key evolutionary linkages showing a relationship between mantle musculature (in late maturity stages) and the number of rows of radular teeth to the likelihood of exhibiting egg brooding behaviour. Prior research found monophyly for the family Gonatidae but not for individual genera within the clade, and did not distinguishing among potential populations (Lindgren et al. 2004).

d) Trophic relationships

Based on stomach content analyses, *G. fabricii* prey can be divided into four main groups: crustaceans, fish, cephalopods (including their own species) and “unidentified hyaline mass” (Kristensen 1984). Prey choice is correlated with maturity stage as a result of their ability to actively hunt and hold their prey (Kristensen 1984). Both adults and juveniles select the largest prey they can handle (Nesis 1965, Kristensen 1983).

Juveniles lack hooks on their tentacular clubs and arms (Zuev and Nesis 2003) making catching and holding larger prey difficult and their body structure is not conducive for hunting highly mobile prey (Clarke, 1966, Kristensen 1983, 1984, Sweeney et al. 1992, Arkhipkin and Bjørke 2000). Zuev and Nesis (2003) stated that most juvenile *G. fabricii* stomachs tend to be empty and Kristensen’s (1984) research corroborates this point with 51 % of examined juvenile stomachs void of prey. Such results may be caused by fast digestion rates (Kristensen 1984). When prey was found in juvenile (1 to 2 months old) *G. fabricii* stomachs, common items included: young *Calanus* spp. (Leach 1819) (56% frequency) and larval euphausiids (35% frequency) (Nesis 1965, Kristensen 1983, Zuev and Nesis 2003). Other prey items include: amphipods, pteropods and chaetognaths (9% combined frequency) (Nesis 1965, Kristensen 1983, Zuev and Nesis 2003). Nesis (1965) further identified copepods *C. finmarchicus* (Gunner 1765), *C. hyperboreus* (Krøyer 1838), *Paraeuchaeta norvegica* (Boeck 1872), *Metridia* sp. (Boeck 1865), along with the euphausiid *Thysanoessa longicaudata* (Krøyer 1846), and amphipods *Hyperia galba* (Montagu 1813), and *Pseudabrotus* sp., as important prey species. Within the Norwegian Sea, Wiborg et al. (1982) also identified the amphipod *Parathemisto* sp. (Boeck 1870) as a dominant food item, along with *Pasiphaea* sp. (Savigny 1816), *Limacina* sp.

(Bosc 1817), in addition to the previously mentioned copepods, chaetognaths, euphausiids and pteropods. There are no records of juveniles preying on fish or other *G. fabricii* (Kristensen 1984).

With the development of tentacular hooks (at ~25.0 mm ML), prey selection becomes greater with sub-adult and adult *G. fabricii* able to catch larger and higher quality prey (Nesis 1965, Clarke 1966, Zuev and Nesis 2003). Lipids from the higher quality prey stored in the squid's digestive gland aid buoyancy (Nesis 1965, Clarke 1996, Boyle and Rodhouse 2005h) and are used as energy during egg brooding (Nesis 1999, Lindgren et al. 2004, Lindgren et al. 2005). Primary prey of mature specimens include: amphipods, isopods, decapods, pteropods, chaetognaths, fish larvae (e.g. lanternfish) and squid (including the occasional octopus), along with the potential of prawns and mysids (Kristensen 1984, Zuev and Nesis 2003), but not copepods or euphausiids (Kristensen 1983, 1984, Zuev and Nesis 2003). Nesis (1965, 2003c), however, found adults were feeding on large copepods (primarily *Paraeuchaeta* sp. (Scott 1909)), chaetognaths (*Eukrohnia hamate* (Mobius 1875)) and to a lesser extent euphausiids. This suggests that sub-adults and adults will feed on copepods and euphausiids, but only when larger prey is unavailable. Sub-adults and adult *G. fabricii* may become cannibalistic, something not observed among juveniles (Wiborg et al. 1982, Kristensen 1984, Nesis 2003c). As *G. fabricii* grow, a greater percent of their prey is fish (Kristensen 1984). Wiborg et al. (1982) noted that Norwegian *G. fabricii* (> 60.0 mm ML) were feeding on redfish (*Sebastes* sp. (Cuvier 1829)) fry and pearlsides (*Maurolicus muelleri* (Gmelin 1789)), while Kristensen (1983) reported capelin (*Mallotus villosus* (Müller 1776)) and redfish (*Sebastes* sp.) in adult *G. fabricii* stomachs. Kristensen's (1983) observation suggests that *G. fabricii* are not only hunting near the surface (capelin) but also near the bottom (redfish).

Gonatus fabricii are also important high quality prey. Analysis of their nutritional value found that adult *G. fabricii* from western Greenland had muscle protein levels of 12.5 % and muscle lipids of 1 % (Kristensen 1984). The majority of lipids were found within the digestive glands (63 %, double that found in cod) (Kristensen 1984). These lipids give *G. fabricii* a high energy density (kJg^{-1}) similar to capelin (Kristensen 1984, Lawson et al. 1998, Frandsen and Wieland 2004). Examination of whole specimen *G. fabricii* collected around Newfoundland and Labrador found lower lipid (10.9 ± 3.80 %) and protein content (13.7 ± 2.70 %) compared to capelin (lipid: 13.7 ± 7.87 %; protein: 16.1 ± 4.97 %) and Atlantic herring (lipid: 13.7 ± 3.90 %; protein: 20.1 ± 1.28 %). However, the energy density of *G. fabricii* (6.9 ± 1.76 kJg^{-1}) was comparable to the two north Atlantic prey species (capelin: 8.4 ± 3.28 kJg^{-1} ; herring: 9.4 ± 1.40 kJg^{-1}) (Lawson et al. 1998). *G. fabricii* also had higher energy density than *I. illecebrosus* (5.9 kJg^{-1}) (Lawson et al. 1998) suggesting that migration of this species into the Arctic will not only impact *G. fabricii* through competition and predation, but also the teuthophagus predators that require the high energy *G. fabricii* to survive the harsh Arctic environment.

Gonatus fabricii's high metabolic efficiency provides higher trophic levels with increased nutrients which makes them a preferred prey for a variety of fish, birds and marine mammals, including those of cultural and commercial importance (Cephbase, Kristensen 1983, Rodhouse and Nigmatullin 1996, Bjørke 2001, Nesis 2001, Laidre et al. 2002, Nesis 2003c). A list of *G. fabricii* predators includes bottlenose whales (*H. ampullatus* (Forster 1770)), sperm whales (*Physeter catodon* L.), narwhals (*Monodon monoceros* L.), bearded seals (*Erignathus barbatus* (Erxleben 1777)), northern Fulmars (*Fulmarus glacialis* L.), Greenland halibut (*R. hippoglossoides* (Walbaum 1792)), cod (*Gadus morhua* L.), redfish (*S. marinus* L.) and *I. illecebrosus* (Cephbase, Kristensen 1983, 1984, Bjørke 2001, Nesis 2001, Laidre et al. 2002,

Zuev and Nesis 2003). Both Bjørke (2001) and Hooker et al. (2001) proposed that the distribution of sperm whales and bottlenose whales within the Norwegian Sea was a direct result of the presence of mature *G. fabricii*, ultimately resulting in a region known as the “Bottlenose Grounds” (Kristensen 1984). When in large shoals, juvenile *G. fabricii* are also targeted by baleen whales (e.g. fin, sei) (Kristensen 1984, Zuev and Nesis 2003).

2.2.2.2. *Rossia* spp. (Owen, 1834)

Rossia are members of the Sepiolidae family and are distinguished by their squat bodies, retractable tentacles and free mantle (Berry 1912, Mercer 1968b). *Rossia* also lack a light organ on their ink sacs and have suckers elevated on stalks with chitinous rings (Vecchione et al. 1989). There are ten *Rossia* species, which combined, have a global distribution (Brocco 1971). Four species have been collected from coastal Greenland: *R. macrosoma* (Chiaie 1830), *R. megaptera* (Verrill 1881), *R. moelleri* and *R. palpebrosa* (Owen 1834) with only *R. moelleri*, *R. palpebrosa* and *R. megaptera* common in the Canadian Arctic.

a) Distribution

Rossia spp. are thought to have originated in the North Atlantic and migrated to the Pacific via the Arctic Ocean and Bering Strait (Nesis 2003b). *Rossia* spp. are nektobenthic and frequently caught on mud and sandy substrates along continental shelves and slopes (typically at depths of 200 to 2000 m); there are no known pelagic species (Brocco 1971, Rosa et al. 2005, Laptikhovsky et al. 2008). The three Canadian species have regionally overlapping distributions (Mercer 1968b, Vecchione et al. 1989, Nesis 2001, 2003b, Laptikhovsky et al. 2008).

Rossia moelleri is considered the only true endemic Arctic cephalopod, associated with the Arctic water mass (Mercer 1968b, Nesis 2001) and has the most northern distribution of the three Canadian Arctic species, extending to 82°N (Nesis 2003b, Laptikhovskiy et al. 2008). It has been reported from Franklin Bay, Canada, extending east to the East Siberian Sea and also from the Hebron Fjord off of northern Labrador where it is thought to be a glacial relic population (Mercer 1968b, Nesis 2001, 2003b, Laptikhovskiy et al. 2008). Because *R. moelleri* is only associated with the Arctic water mass, it is absent in areas where warmer Atlantic water is more pronounced, such as southwest Greenland, Iceland, Barents Sea and also Ungava Bay; as well as the Pacific influenced Chukchi Sea and northern Alaskan waters (Mercer 1968b). It prefers cold water, with all specimens examined by Mercer (1968b) caught below -1.0 °C but Nesis (2001) suggests a broader temperature range of -1.37 to 5.83 °C within depths of 50 to 700 m. Similar to the other species, *R. moelleri* can be found in shallow water at higher latitudes (Nesis 2001), indicating that temperature is likely of greater influence than depth. During surveys off western Greenland, *R. moelleri* was the most abundant in areas < 250 m depth (Zumholz and Frandsen 2006).

Rossia palpebrosa is an “Arcto-Atlantic” species, with a range extending north to Ellesmere Island and northern Greenland and south to South Carolina (western Atlantic) and Ireland (eastern Atlantic) (Mercer 1968b, Vecchione et al. 1989, Nesis 2001, 2003b). This species has been reported from Baffin Bay and the eastern Canadian Arctic Archipelago to Iceland, the North Sea and Spitsbergen, as well as the East Siberian Sea, including the Barents and Kara seas (Mercer 1968b, Vecchione et al. 1989, Nesis 2001, 2003b). Unlike *R. moelleri*, *R. palpebrosa* is found in Ungava Bay (Mercer 1968b). During groundfish surveys of the eastern United States, *R. palpebrosa* specimens were found at depths of 88 to 175 m along the outer

shelf but are also known from depths < 600 m and temperature ranges of -1.36 to 4.89 °C (Mercer 1968b, Vecchione et al. 1989, Frandsen and Wieland 2004). Individuals from the high Arctic, however, have been found at depths of 6 to 8 m (Nesis 2001).

R. megaptera is sometimes caught at the same time as *R. palpebrosa*, however, its distribution is more restricted than the previous two species (Mercer 1968b). Its range extends from Davis Strait to western Greenland and south to Massachusetts (Mercer 1968b); it is not known to have a circumpolar distribution. It has the deepest range, extending from 179 to 1536 m depth with the majority caught ~ 299 m and is typically found in areas of 1.67 to 5.38 °C water temperature (Mercer 1968b).

b) Life history

Four maturity stages for *Rossia* spp. were described by Mercer (1968b) and Laptikhovskiy et al. (2008): immature, maturing, mature and spent. Immature specimens have no visible gonads (Laptikhovskiy et al. 2008), however, Mercer (1968b) describes immature females as possessing small opaque eggs, likely referring to individuals of a later but still immature stage. Maturing females have noticeably pale white to yellow nidamental glands with the presence of large, but not yet ripe, eggs (Mercer 1968b, Laptikhovskiy et al. 2008). It is during the maturing stage that females typically mate (Laptikhovskiy et al. 2008). Maturing males have only a few spermatophores in Needham's sac with sperm in the spermaduct (Mercer 1968b, Laptikhovskiy et al. 2008), therefore, mating may be restricted to mature males only. Female nidamental glands turn red when mature and a few ripe (clear) eggs will be in the oviduct ready for deposit (Mercer 1968b, Laptikhovskiy et al. 2008). The size ranges of mature eggs for the three common species are: *R. moelleri* 7.4 to 8.5 mm; *R. palpebrosa* 5.9 to 8.1 mm; and *R. megaptera* 5.6 to 7.5 mm;

with larger females of each species producing larger eggs (Mercer 1968b, Laptikhovskiy et al. 2008). Female *Rossia* spp. are polytelic with eggs of varying maturity stages present within the ovary (Mercer 1968b, Zumholz and Frandsen 2006, Laptikhovskiy et al. 2008, Morov and Sabirov 2009). This allows females to lay small batches over an extended period of time, adding them to previously laid eggs from other females, resulting in egg masses of varying embryonic development (Mercer 1968b, Zumholz and Frandsen 2006, Laptikhovskiy et al. 2008). Mature males are noted as having their Needham's sac densely packed with spermatophores (Mercer 1968b, Laptikhovskiy et al. 2008). There are a small number of large spermatophores produced, a feature conducive to species living in cold and/or deep water (Golikov and Sabirov 2009). Once spent, both males and female gonads appear shrunken with only a few ova or spermatophores remaining (Mercer 1968b, Laptikhovskiy et al. 2008).

Spawning is thought to occur over an extended period of time, with *R. moelleri* from western Greenland described as spawning during their third or fourth summers (late summer) followed by senescence (Zumholz and Frandsen 2006, Laptikhovskiy et al. 2008). Therefore, it has been suggested that *R. moelleri* may live in excess of four years (Zumholz and Frandsen 2006).

The first description of a *Rossia* egg mass was by Aldrich and Lu (1968) off of Newfoundland, Canada. The egg mass consisted of ~100 to 150 eggs of varying maturities surrounded by benthic sponge (Aldrich and Lu 1968). *Rossia* eggs are protected by the substrate (e.g. shells or sponges) but also have added protection from their own outer shell (Aldrich and Lu 1968, Mercer 1968b, Boletzky 1994, Nesis 1999, Laptikhovskiy et al. 2008). Aldrich and Lu (1968) speculated that by laying the eggs within a sponge, they have additional benefits of

camouflage, a buffer to debris and predators, and access to nutrients through currents created by the sponge.

Rossia palpebrosa and *R. moelleri* eggs take 122 and 124 days, respectively, to incubate, at temperatures between 0 to 2 °C (Nesis 1999). In western Greenland incubation time for *R. moelleri* is up to six months (Nesis 1999, Zumholz and Frandsen 2006). *R. palpebrosa* hatch at 8.0 mm ML with the precocious juveniles hatching from large eggs (> 10 % of ML; 7.0 to 12.0 mm length) (Mercer 1968b, Laptikhovsky et al. 2008) with yolk sacs intact (Boletzky 1994, Nesis 1999). The yolk sac allows the hatchlings to survive in cold conditions when prey resources are minimal (Boletzky 1994, Nesis 1999). For example, *R. macrosoma* is known to survive up to three months without an external food source at 8 to 9 °C (Boletzky 1994, Nesis 1999). Additional research has shown that the size of the egg, and in turn the size of the ‘mother’, is directly proportional to the size of the offspring (Mercer 1968b, Laptikhovsky et al. 2008), with larger hatchlings having a greater survival rate.

Daytime burying behaviour has been observed for various Sepioids, including *Sepioida atlantica* and *R. pacifica* (a close relative to *R. moelleri*), and is likely a common behaviour for the whole group (Mercer 1968b, Brocco 1971, Boletzky 1996, Rodrigues et al. 2010, Anderson 2012). During daylight hours, bobtail squid use their funnels to flush sand from beneath them, while using their dorsal arms and fins to cover the remaining exposed areas and remain motionless until night (Rodrigues et al. 2010, Anderson 2012). This behaviour may be a defensive strategy against visual predators. During the night, when visibility is limited, they can be found sitting on top of the sediment unprotected (Rodrigues et al. 2010, Anderson 2012). It is unclear whether Arctic *Rossia* utilize this strategy and what the benefits would be in a region that

has continuous daylight during the summer months and 24-hour night during the winter. Arctic specimens have, however, been collected from benthic trawls and sediment surveys (e.g. DFO Beaufort Sea survey 2008), suggesting burying behaviour, at least in the Beaufort Sea.

c) Morphometrics, systematics and populations

The genus *Rossia* can be distinguished from other cephalopods by their pouch-like shape, reduced gladius, presence of a funnel valve and dorsal web on the tentacular clubs (Mercer 1968b). Males of this genus are also typically smaller and lighter than females; with mature males reported to be 17.0 g to 55.7 g lighter than mature females of the same species (Mercer 1968b, Brocco 1971). Several morphological features are useful to identify the three common *Rossia* species within the Canadian Arctic (Mercer 1968b).

Rossia moelleri are up to 7.0 cm ML with a maximum weight for mature males reported at 33.3 g and females between 79.0 to 89.0 g (Mercer 1968b). This species differs from the other two common Arctic *Rossia* spp. by having several suckers on the distal portion of the tentacular club greatly enlarged (Mercer 1968b, Frandsen and Zumholz 2004). Armature is biserial at the distal end and suckers on the tentacular club are in seven to ten rows (Mercer 1968b) but Frandsen and Zumholz (2004) report four to six sucker rows with four on the proximal portion of the club and six on the distal end. Their anal palps are described as large and bladed, similar to those observed in *R. palpebrosa* (Mercer 1968b). *R. moelleri* differs from *R. palpebrosa* by having smooth skin (Mercer 1968b). *R. moelleri* also has a long funnel, extending beyond the base of the ventral arms and has a pronounced dorsal web (Mercer 1968b).

Rossia palpebrosa is the smallest of the three species with a maximum mantle length \leq 5.0 cm ML (Mercer 1968b, Frandsen and Zumholz 2004). Mature males have been reported from 4.0 to 31.6 g with mature females reported to weigh 11.4 to 48.6 g (Mercer 1968b). Although this species is found south into the North Atlantic, the largest specimens collected were from the coldest regions (Mercer 1968b). The head and dorsal mantle of *R. palpebrosa* is covered in distinct small papillae but number, size and distribution are highly variable (Mercer 1968b, Nesis 2001). Club suckers are in six to ten rows but, unlike *R. moelleri*, are similar in size (Mercer 1968b, Frandsen and Zumholz 2004). As with *R. moelleri*, the anal palps are large and bladed but the funnel of *R. palpebrosa* does not extend beyond the base of the ventral arms (Mercer 1968b). The fins of *R. palpebrosa* do not extend beyond the mantle collar (Mercer 1968b, Vecchione et al. 1989). Both *R. glaucopsis* Loven 1845 and *R. sublaevis* Verrill 1878 are considered junior synonyms of *R. palpebrosa* (Mercer 1968b, Vecchione et al. 1989).

Rossia megaptera, the largest of the three species, reaches \leq 8.0 cm ML and rarely is 10.0 cm ML (Mercer 1968b, Frandsen and Zumholz 2004). Weights of mature individuals are reported as 7.9 to 16.7 g for males and 14.6 to 32.6 g for females (Mercer 1968b). This species has large eyes with a larger head width than *R. palpebrosa* (Mercer 1968b). Its skin is smooth with biserial armature, similar to *R. moelleri*, but *R. megaptera* has distinctive tentacular clubs covered in small suckers of similar sizes arranged in eight or more rows (Mercer 1968b, Frandsen and Zumholz 2004). Their clubs are not expanded like in the other species (Mercer 1968b, Frandsen and Zumholz 2004). *R. megaptera*'s funnel does not extend to the base of the ventral arms and unlike *R. palpebrosa*, the anterior portions of the fins do extend beyond the mantle collar (Mercer 1968b, Frandsen and Zumholz 2004). The anal palps of this species are distinctly short and simple (Mercer 1968b). Originally, Grimpe (1933; *in* Mercer 1968b) thought

R. megaptera was a poorly preserved *R. palpebroso* but it has since been given its own valid taxonomic designation.

While these morphometric characters are useful for identification between the species, care is required as the specimens are easily distorted due to fixation and preservation (including freezing) (Mercer 1968b, Voight 1993, Muus 2002). For example, if stressed prior to preservation, contraction of the arms can result in a biserial sucker armature appearing to be in threes or four to a row and may also affect the position of the fins (Mercer 1968b). These types of distortions may explain much of the variation found within these three species (Mercer 1968b).

Little is known about population structure of this genus. Lack of a planktonic stage (neither egg nor larval) and limited distribution is thought to produce localized *Rossia* spp. populations (e.g. glacial relic population of *R. moelleri* in the Hebron Fjord) (Mercer 1968b). Isolation has been suggested as the cause of *R. moelleri*'s differentiation from its close relative *R. pacifica* during their migration through the Bering Strait (Mercer 1968b). Golikov and Sabirov (2009) were able to show heterogeneity of *R. palpebroso* spermatophores within the Barents Sea and suggested potential populations apart from those of eastern Svalbard, Novaya Zemlya and the shallow water around Murmansk, Russia.

d) Trophic relationships

Rossia spp. are opportunistic feeders, preying on benthic and nektobenthic organisms (Brocco 1971, Nesis 2001). Rossinae feed primarily on crustaceans but also on fish, echinoderms, anemones (Mercer 1968b, Nesis 2001), amphipods, mysids, *Pandalus* sp. (Leach

1814) and *Lithodes* sp. (Latreille 1806) (Mercer 1968b). The closely related *R. pacifica*'s diet consists of crustaceans (86.6%), fish (16.6%), with the occasional bivalve, cephalopod and ostracod (Brocco 1971). It is likely that Arctic *Rossia* spp. will have similar diets. To date, only Takai et al. (2000) has attempted to look at the stable isotopes of *R. pacifica* from the Japan Sea ($12.0 \pm 0.5 \delta^{15}\text{N}$ and $-18.6 \pm 0.5 \delta^{13}\text{C}$).

Sepiolidae are prey to a variety of predators but their remnants are not found in large quantities within stomachs (Rosa et al. 2006). Predators, including marine mammals such as walrus (*Odobenus rosmarus* L.) and fish species such as haddock (*Melanogrammus aeglefinus* L.) and cod (*G. morhua* L.), have been reported for *R. moelleri* (Cephbase, Rosa et al. 2006). I assume that the other two Arctic species have similar predators.

2.2.2.3. *Bathypolypus* spp. Grimpe 1921

Bathypolypus arcticus is a species complex consisting of three separate incirrate octopuses: the Arctic *B. arcticus sensu lato*, the arcto-boreal *B. bairdii*, and *B. pugniger* n. sp. (Muus 2002). Prior to Muus' (2002) re-descriptions, all three species were lumped together as highly variable *B. arcticus*, highlighting the need for careful comparisons of biological attributes.

a) Distribution

Bathypolypus arcticus' distribution was previously described as circumpolar, extending north into the Polar Basin and south to the Strait of Florida (Muus 2002). Upon further investigation, Muus (2002) determined that *B. arcticus* is actually a stenothermal species, limited to the Arctic region, or areas occasionally exposed to cold Arctic waters. Muus (2002), based on examined specimens and published descriptions, suggested that the *B. arcticus* specimens

attributed to warmer Atlantic waters were likely *B. bairdii*; making *B. arcticus* and *B. bairdii* thermally separated allopatric species. *Bathypolypus arcticus* are found between 15 and 1600 m depth (typically deeper than 400 m) with decreasing depth in response to increasing latitudes (Muus 2002) but it has been reported from as shallow as 6 to 8 m depth from western Arctic fjords.

Bathypolypus bairdii's range is limited to 'warm' (2 to 8 °C) currents, the influence of Atlantic water, and the upper 180 to 1000 m of the North Atlantic continental shelves and slope (Muus 2002). The warm Norwegian Current allows *B. bairdii* to extend from Greenland to the Barents Sea and south to North Sea, while the Irminger Current increases its distribution along western Greenland (Muus 2002). This species is common around the Davis Strait/Baffin Bay ridge as well as the Iceland-Greenland ridge (Muus 2002). A gap in their distribution near Cape Farewell, Southern Greenland is thought to indicate cold water, especially due to the presence of *B. arcticus* (Muus 2002). *B. bairdii*'s range extends to the Greenland-Scotland Ridge and south to Florida, US where it is considered the most abundant octopod in the Northeast United States (Muus 2002). *B. bairdii*'s preferred depth (20 to 1545 m) also depends on latitude, with the deepest specimen caught at the most southern location (29° 45'N 30° 09'W) (Muus 2002). Specimens caught off of Greenland were collected at 1100 m (Muus 2002).

Bathypolypus pugniger's (Muus 2002) distribution is not entirely known. Muus (2002) suggested this species was found in warmer Atlantic water but unlike *B. bairdii*, could tolerate slight exposure to Arctic overflow. All specimens described by Muus (2002) were from the Faroe Island Ridge, with one specimen from western Greenland. Frandsen and Zumholz (2004) extended this range by suggesting *B. pugniger* could be found from Davis Strait, south around

Greenland and south Icelandic waters, ending at the Faroe Islands. Temperature preference is unknown but their depth ranges are speculated to be 200 to 1000 m (Frandsen and Zumholz 2004).

b) Life history

This section will discuss what little is known on the life histories of the species complex.

Bathypolypus spp. hatch as relatively large sized (6 mm ML; ~ 0.2 g) precocious young and their subsequent growth is dependent on temperature and prey availability (O'Dor and Macalaster 1983, Wood 2000). Unlike other benthic octopuses, *Bathypolypus* lack a planktonic dispersal stage (Rodhouse and Nigmatullin 1996, Wood 2000, Muus 2002). Although they hatch without an external yolk sac, *B. arcticus* hatchlings can survive up to 68 days without food, a vital adaptation enabling survival in regions with seasonal prey (Wood 2000).

Bathypolypus spp. are relatively common with both juveniles and adults evenly spaced throughout their habitat (O'Dor and Macalaster 1983, Muus 2002). This genus does not use dens like other octopods (with the exception of gravid females). *B. bairdii* have been observed resting in unprotected shallow depressions along muddy/sandy sediments (Muus 2002).

Laboratory experiments found that individuals reached maturity within six years when reared at 4 °C, however, in the wild they may live 10+ years dependent on water temperature and prey availability (O'Dor and Macalaster 1983, Wood 2000). This extended life history creates an overlap between generations, with a certain number of individuals spawning each year (Wood 2000). This type of life history strategy provides a buffer to the population against environmental variability (Wood 2000). O'Dor and Macalaster (1983) found that with

acclimation, *B. arcticus* (most likely *B. bairdii*) could tolerate a short exposure to 11 °C but without acclimation, exposure to 10+ °C was fatal (Wood 2000).

Mating occurs several months prior to egg laying (Wood 2000). Males use the ligula on their modified third left arm (hectocotylus) to transfer spermatophores to the females (O’Dor and Macalaster 1983). Wood (2000) also speculated that the ligula could remove competitors’ spermatophores from the female. Since individuals are sparsely distributed, spawning appears to be opportunistic; males are known to mate with any octopod, including other males (Wood 2000). Females retain the spermatophores until they are ready to lay eggs, however, they have been observed removing spermatophores to eat, a behaviour thought to be a way of determining paternity (Wood 2000).

Once gravid, females build a den and glue the eggs to the walls (Wood 2000). Brooding consists of jetting water over the eggs to remove debris and guarding them from potential predators (Wood 2000). Rarely will the female eat, instead living off of energy reserves (Nesis 1999, Wood 2000). The female *Bathypolypus* sp. leaves the den just prior to egg hatch (Wood 2000). This may be a mechanism to lure predators away from the eggs and hatchlings or to keep their dead body from fouling the eggs (Wood, 2000). Unlike the females, males are able to spawn more than once (Wood 2000).

Bathypolypus spp. have the longest brooding of any incirrate octopus, extending ≥ 400 days at 7.5 °C (Wood 2000), with Nesis (1999) suggesting as long as 737 days when exposed to 3.5 °C water. However, when exposed to exterior stressors such as light, changes in salinity and excessive motion, early hatching may occur (Wood 2000). Such a reaction is thought to be an escape mechanism for the hatchlings from negative conditions (Wood 2000).

c) Morphometrics, systematics and populations

Octopus morphology reflects their biogeography, with tropical octopuses tending to be elongate compared to the more squat appearance of those from the Arctic or deep-sea (Voight 1993). All three Arctic *Bathypolypus* species agree with this description, each possessing short mantles and arms (Muus 2002). In addition, *Bathypolypus* spp. lack an ink sac (Voss 1988, Muus 2002), a feature typically found in species living in low to no light environments (e.g. deep-sea) (Voight 1993). Detailed morphometric descriptions for each species as well as the geographic variation observed in male *B. bairdii* are available through Muus' (2002) taxonomic review of the species complex. This section will highlight only those characteristics that help differentiate among the species. Key features include: ligula shape/size (and laminae count) in males, presence of a crop diverticulum, skin texture, funnel organ and radula (Muus 2002).

Bathypolypus arcticus is a small (< 229.4 mm TL) egg-shaped species and the only species in the complex with a true crop diverticulum (Appendix I, Muus 2002). Skin has a stellate pattern, with a large dot encircled by smaller dots, often light yellow in colour (Muus 2002). The radula is described as “irregular multicuspid” and the funnel organ is a distinctive VV but is fragile and can be misidentified as comprising two bars (II) if damaged (Muus 2002). The ligula, a spoon-shaped organ on the third right arm (hectocotylus) used to transfer spermatophores to the female, is small, with 11 to 17 laminae (Muus 2002). The sides of the ligula are rolled inwards, resembling a fist (Muus 2002).

B. bairdii are square bodied octopods (< 210 mm TL), with random papillae typically grey in colour (Appendix I, Muus 2002). It lacks a crop and the radula has a central simple homodont tooth (Muus 2002). The variable funnel organs range from pad-like to two bars (II)

(Muus 2002). Males of the species are easily distinguished by their large, rectangular ligula with 7 to 13 laminae, a feature evident in specimens as small as 11 mm ML (Muus 2002). Geographic variation has been noted for this feature, with more southern specimens, in particular those from the eastern United States, having larger ligulas than those of western Greenland and samples from the North Atlantic (Muus 2002).

Bathypolypus pugniger has similar morphometric characters to the previous two species, and is speculated to be a hybrid of *B. arcticus* and *B. bairdii* (Muus 2002). *B. pugniger* is smaller than the previous two species (< 201 mm TL) with short arms (Appendix I, Muus 2002). Their skin has pronounced papillae similar to *B. arcticus*, only more pointed (Gardiner unpublished). This species lacks a true crop but can have swelling down part of its esophagus (Muus 2002). Similar to *B. bairdii*, the radula has a single homodont tooth that is much broader than *B. bairdii* (Muus 2002). Its funnel organ also varies from pad-like to distinct bars, only smaller in size than observed in *B. bairdii* (Muus 2002). The ligula of this species is small and fleshy with only 4 to 6 laminae (Muus 2002).

Unlike most benthic octopuses (Rodhouse and Nigmatullin 1996), this genus lacks a planktonic stage, limiting their dispersal ability (Muus 2002). Therefore, distinct populations are expected (Muus 2002). Geographic variations in *B. bairdii* have already been noted with the number of laminae on the ligula increasing and the number of hectocotylus suckers decreasing on specimens found below 45 °N compared to those of western Greenland (Muus 2002). The reason(s) for this variation are still unknown (Muus 2002). At the time of Muus' (2002) revision, there were too few identified specimens of true *B. arcticus* and *B. pugniger* to determine any geographic variation within the species (Muus 2002).

d) Trophic relationships

Bathypolypus spp. are opportunistic predators (O'Dor and Macalaster 1983), preferring a sit and wait strategy to active hunting (Wood 2000). They have even been known to sift through the sediment in search of prey (Wood 2000). Not much research has been conducted regarding prey items for the three species, however, brittlestars (Ophiuroidea Gray) are known to be the most common prey source based on stomach content analyses (Wood 2000). O'Dor and Macalaster (1983) report 58 % of adult *Bathypolypus* spp. had brittlestars in their stomachs, even though they are low in nutritional value (Wood 2000). To add to this, it appears that only the arms are eaten, leaving the higher caloric disk containing the gonads behind (Wood 2000). Such a low quality diet would impact their growth rates and delay maturation (Wood 2000). In laboratory studies, however, when presented with a higher quality prey item, *Bathypolypus* specimens would readily choose the more nutritious prey over brittlestars, suggesting that the ophiroids may simply be a last resort (Wood 2000). Crustaceans were the second most common prey group (Wood 2000) with O'Dor and Macalaster (1983) reporting their presence in 25 % of stomachs. Other prey species were (in order of the percent of stomachs found) polychaetes (23.1 %), bivalves (21 %), gastropods (12.1 %), foraminiferans (7.1 %), siphunculids (6.7 %) and cumaceans (4.9 %) (O'Dor and Macalaster 1983). Fish scales were also noted in some stomachs, suggesting that *Bathypolypus* spp. may also scavenge dead prey (Macalaster (1976) in Wood 2000).

Wood (2000) states that *Bathypolypus* spp. make up < 0.5 % of the stomach contents of predators but Finley and Gibb (1982) reports the presence of *B. arcticus* beaks in 16 % of the narwhal stomachs examined. Unfortunately, only a few reported had flesh still attached,

indicative of recent ingestion (Finley and Gibb 1982). Other predators include *G. morhua* L., haddock, wolfish (*Anarhichadidae* Bonaparte), beluga (*Delphinapterus leucas* Pallas) and halibut (O'Dor and Macalaster 1983). Decreased predation is likely the result of their sparse distribution, making them a less targeted prey species (Wood 2000).

To date, no stable isotope analyses have been examined for these species.

2.2.2.4. *Cirroteuthis muelleri* (Eschricht, 1836)

There are three cirrate octopuses found in the western Arctic: *Stauroteuthis syrtensis* Verrill 1879, *Opisthoteuthis* sp. Verrill 1883 and *Cirroteuthis muelleri*, with *C. muelleri* the most common and diverse throughout the Canadian Arctic (Nesis 2001, Collins 2002, Frandsen and Zumholz 2004). Cirrates are considered primitive octopods and are distinguished by their gelatinous texture, cartilaginous support structure and their well-developed fins and webs used in locomotion (Berry 1912, Roper and Brundage 1972, Voss 1988, Collins et al. 2001, Collins 2002). Due to their gelatinous nature, this group is easily damaged during collection, which has resulted in few, usually poor quality specimens used for taxonomic and biological analyses (Piertney et al. 2003, Collins and Villanueva 2006). Luckily, recent forays into deep-sea commercial fishing have provided much needed access to additional specimens (Collins et al. 2001). But further research into their general biology and distribution is required (Collins 2002, Collins and Villanueva 2006).

a) Distribution

Cirrates are found in all oceans and are typically the dominant taxa throughout the benthopelagic region (500 – 5000 m) (Collins 2002, Piertney et al. 2003, Collins and Villanueva

2006). *Cirroteuthis muelleri* (Cirroteuthidae family) is the second of the circumpolar cephalopods species (along with *G. fabricii*), with a range extending from the polar basin (relatively common) to the Porcupine Seabight in the North Atlantic as well as into the northern Pacific Basin (Voss 1988, Nesis 2001, Collins 2002). *C. muelleri* has also been reported from New Zealand (Voss and Percy 1990, O'Shea 1999) but due to their poor dispersal abilities, this record is questionable (Collins 2002).

Cirroteuthis muelleri are benthic-pelagic species, typically found in deep waters (> 500 m) but can also be found at shallower depths at higher latitudes (Collins et al. 2001, Collins 2002, Collins and Villanueva 2006). For example, specimens were collected from 4846 m off the Porcupine Seabight in the North Atlantic while others were found near the surface off Greenland (Collins 2002, Collins and Villanueva 2006). This broad bathymetric range with obvious latitudinal correlations, suggests that temperature is likely the driving environmental variable rather than depth (Collins 2002, Collins and Villanueva 2006).

C. muelleri, is considered pelagic but is typically found just above the sea floor (Collins and Villanueva 2006). Most cirrates are collected from soft sediments but this habitat preference may be a result of gear selection (Collins and Villanueva 2006). Gear selection may also explain the unequal male to female ratios in the samples (Collins and Villanueva 2006). Females are thought to lay their eggs on hard substrates that may keep them out of reach of the sampling gear (Collins and Villanueva 2006). Observations from submersibles corroborate this with *Cirroteuthis* sp. individuals found on both soft and rocky substrates (Roper and Brundage 1972, Collins and Villanueva 2006).

b) Life history

Cirroteuthis muelleri, typically, has a unique life history (Collins and Villanueva 2006). Unlike other cephalopods, cirrates do not undergo seasonal spawning but instead are thought to have continuous gonad production and spawn throughout their life (Boyle and Rodhouse 2005g, Collins and Villanueva 2006).

Developing ova are surrounded by a sheath that remains in the ovary once the egg is expelled (Collins and Villanueva 2006). Quantitative reproductive studies have only examined the shallow water *Opisthoteuthis* sp., however, the presence of these sheaths in other genera suggests continuous gonad development (i.e. more sheaths with increasing specimen size) for the group as a whole (Collins and Villanueva 2006). These sheaths also allow highly accurate fecundity 'estimates' (Collins and Villanueva 2006). Male cirrates expend less energy than females for gonad development, suggesting that they are multiple spawners (Collins and Villanueva 2006).

Female cirrates lay individual large eggs encased in protective chitinous shells on rocky benthic substrates (Voss 1988, Nesis 1999, 2001, Collins and Villanueva 2006). This protection suggests the lack of post-spawning care (Collins and Villanueva 2006). Although cirrate development time is unknown, estimates based on egg size and water temperature suggest that *C. muelleri* may take up to 2.6 years (964 days) to develop in -0.8 °C (Nesis 1999). As with the previously discussed genera (e.g. *Rossia* spp. and *Bathypolypus* spp.), large eggs typically represent direct development and precocious hatchlings (Voss 1988, Collins and Villanueva 2006).

The length of time between hatch and onset of spawning is unknown, however, researchers speculate that due to their habitat preference (deep and cold), cirrates live longer than their shelf inhabiting and pelagic relatives (Boyle and Rodhouse 2005f, Collins and Villanueva 2006).

Observations from submersibles noted that cirrates were primarily solitary, with no evidence of schooling (Collins and Villanueva 2006). Despite being solitary, cirrates are still common within the ecosystem, with abundance estimates indicating up to 2000 cirrates per km² in the Arctic (Collins and Villanueva 2006).

Cirrate mobility is either by medusoid contraction of their web, jet propulsion from their funnel, using their fins or a combination of the three methods (Voss 1988). Morphologically, young cirrates have proportionally longer fins than adults, suggesting that swimming may be an important component of early life stages (Collins and Villanueva 2006). These longer fins may improve hunting success during critical growth periods or be used for limited dispersal.

c) Morphometrics, systematics and populations

Care must be taken when examining the morphology of cirrates as various preservation techniques (including freezing) affect different species in different ways (Collins and Villanueva 2006).

The presence of a secondary web (used in locomotion and to increase arm mobility (Frandsen and Zumholz 2004)) is a key feature distinguishing Cirroteuthidae (*Cirroteuthis* spp., *Cirrothauma* spp. and *Stauroteuthis* spp.) from the other three cirrate families (Piertney et al. 2003, Collins and Villanueva 2006). Shell morphology and optic nerve arrangement can also be

used (Piertney et al. 2003). This observation was supported by 16 S rDNA analyses, however, confusion still remains regarding the systematics of the cirrates in general (Piertney et al. 2003, Collins and Villanueva 2006). To add to the confusion, most of their features are difficult to distinguish and their internal organs are not well studied (Voss 1988).

Cirroteuthis sp. have rounded gelatinous bodies with large fins supported by a large, distinctive “saddle-shaped” cartilaginous internal shell (Berry 1912, Collins and Villanueva 2006). Their armature alternates between a single sucker and a long (> 50 % ML) cirri on the mid to proximal portion of the arm (Berry 1912, Collins and Villanueva 2006). These cirri are thought to be sensory organs (Collins and Villanueva 2006). Cirroteuthids lack a radula and only possess anterior salivary glands (Collins and Villanueva 2006). The digestive gland of *Cirroteuthis* sp. is only a single lobe as opposed to the double lobed digestive glands of *Opisthoteuthis* spp. and *Luteuthis* spp. (Collins and Villanueva 2006).

Due to the scarcity of quality specimens, much of the cirrate research has focused on resolving their taxonomic statuses. To my knowledge, there have been no population analyses for *C. muelleri*.

d) Trophic relationships

Benthic-pelagic cirrates are thought to be more specialized hunters than their incirrate relatives (Rodhouse and Nigmatullin 1996). It is believed that their cirri function as sensory probes to find prey within the upper layers of the soft sediments (Roper and Brundage 1972) while also exploiting slow moving epibenthic prey such as copepods, amphipods, other small crustaceans and polychaetes (Rodhouse and Nigmatullin 1996, Nesis 2001, Collins and

Villanueva 2006). Prey species for Cirroteuthids are unknown but the shallow water *Opisthoteuthis* spp. are known to prey on *Gammarus* spp., amphipods, polychaetes as well as mysids, ostracods, decapods and copepods (Collins and Villanueva 2006). Observations from submersible surveys noted Cirroteuthids showing pumping action of their web near the sediment, a behaviour conducive to prey capture (Collins and Villanueva 2006). This suggests that Cirroteuthids are likely feeding on suprabenthic prey (Collins and Villanueva 2006). Collins and Villanueva (2006) also noted that *C. muelleri* has a deeply pigmented digestive tract, indicative of bioluminescent prey.

Unlike the previous muscular cephalopods, the gelatinous cirrates have low protein levels as well as low lipid content (*Opisthoteuthis* spp.: protein 53 %; lipid 3.4 %), likely a result of low metabolic processes and slow swimming (Collins and Villanueva 2006).

Cirrate predators are poorly known but some evidence of their predation have been found in the stomachs of sharks, fish, fur seals and sperm whales (Collins and Villanueva 2006). The lack of predators is likely the result of difficulty in distinguishing among the beaks of the various species and limited deep-sea studies of potential teuthophagus predators (Collins and Villanueva 2006).

2.2.3. Population analysis

Increasing knowledge of Arctic cephalopod biology and their role within the ecosystem is the first step to improve monitoring of anthropogenic and environmental impacts as well as to aid in the management of current and future Arctic fisheries. For this information to be useful it

is imperative to identify potential populations in order to assess their individual responses to variable environmental stimuli (Boyle and Rodhouse 2005k).

Populations are traditionally defined as intraspecific breeding groups from the same geographic regions that develop through physical isolation (e.g. large freshwater input restricting contact among groups) or variable breeding times, among other influences (Boyle and Rodhouse 2005k). These isolations result in genetic differentiation (Carvalho et al. 1992) that can ultimately lead to speciation. Populations, however, are complex and highly variable in location and numbers, often consisting of smaller micro-cohorts caused by life history and/or environmental variability, and large meta-populations from immigration/emigration among neighbouring groups (Boyle and Rodhouse 2005k). Populations can also be divided into stocks, referring to the portion of the population available to the fishery (Boyle and Rodhouse 2005k). Cephalopod populations are particularly difficult to study due to lack of sufficient numbers of specimens (i.e. much of the research relies on fishery catches biased to adults and often not identified to species) (Brocco 1971, Carlini 1998, Boyle and Rodhouse 2005k) and their susceptibility to environmental change (André et al. 2010).

Two methods that are frequently used to identify populations are: 1) morphometric analysis of physical characteristics, and 2) genetic analysis.

2.2.3.1. Morphometric (Character) analysis

Morphometric analysis is the traditional method used to describe species and distinguish between populations. Variations in physical characteristics identified two populations of *L. forbesii*, one from near the Azores and a second population along the European mainland (Pierce

et al. 1994), while Kristensen (1982) used the method to distinguish between two geographically close populations of *G. fabricii* off western Greenland.

Morphometric analyses require precise measurements of polarized physical characters in order to determine significant variations between different regions and/or age classes (Carlini 1998, Vecchione 1998). These measurements, especially for soft-bodied animals, must be based on definitive definitions to maintain continuity (Vecchione 1998, Boyle and Rodhouse 2005k). However, these definitions were not available until Voss (in 1963) and Roper and Voss (1983) compiled and described standardized measurements to improve comparisons between various studies (Vecchione 1998, Voss et al. 1998, Boyle and Rodhouse 2005k). Morphometric analyses also require a good understanding of allometric changes within the characters (Brocco 1971, Carlini 1998, Vecchione 1998, Lindgren et al. 2004) as size alone may account for the majority of variability, highlighting differences in maturity stages rather than populations. Care must also be taken to avoid any potential artifacts resulting from collection, predation or various fixation techniques that can impact different tissues (Mercer 1968b, Brocco 1971, Muus 2002, Lindgren et al. 2005).

Once morphometric measurements have been obtained, multivariate statistical analyses help to summarize trends (Somers 1986). The two different analyses that have been shown to be useful are principal component analysis (PCA) and discriminant analysis.

PCA utilizes matrix algebra to condense the morphometric variables into a few useful components (axes) and component scores (data points) summarizing the variability of the original data (Gotelli and Ellison 2004). The resulting component scores are uncorrelated (unlike the original data) and normally distributed which allows for further analysis (Gotelli and

Ellison 2004). The PC1 axis (principal component one) accounts for the majority of variability within the data and is often associated with size (Somers 1986, Voight 1993, Gotelli and Ellison 2004). The subsequent PC2 axis is perpendicular to PC1 and describes the second largest amount of variation (Gotelli and Ellison 2004). Each successive component axis is perpendicular to the one before and defines the remaining variability within the component scores, with the last few axes representing random variability (Somers 1986, Gotelli and Ellison 2004). By plotting the component scores, overall relationships (i.e. clustering) based on all of the morphometric variables collected from different sample sites become apparent (Gotelli and Ellison 2004). Eigenvalues (and eigenvectors) help identify the variables exerting the greatest impact on each axis; variables with the highest eigenvalues have the greatest impact (Gotelli and Ellison 2004). These values and vectors are derived from the linear matrix calculations of:

$$Ax = \lambda x \quad (\text{Eqn 2.1})$$

where x is the column vector (eigenvector) and A is the square matrix; λ is the associated eigenvalue (Gotelli and Ellison 2004). Characters with negative eigenvalues are not biologically defined (Somers 1986) but can show inverse relationships to those with positive values.

Care must be taken when interpreting PCA results as they are easily impacted by ontogeny, size and shape (Mosimann 1970, Somers 1986). Somers (1986) describes size as the extent of a given character while shape is defined as the “relationship between two or more characters”. When multiple size ranges are present, the exclusion of PC1 can decrease the number of relationships that are solely size-based, however, some shape variation is lost in the process (N. Kenkel pers. comm., Jolicoeur (1963) in Somers 1986, Voight 1993). The remaining components describe shape variability, with PC2 and PC3 providing the most information

(Voight 1993), however, size is never fully removed from the analysis (N. Kenkel pers. comm.). Logarithmic transformation of the raw data also helps to simplify shape components resulting in stronger relationships (Somers 1986).

Discriminant analysis utilizes linear correlations to maximize separation between pre-defined groups (e.g. sample locations) based on combined morphometric characters (Kristensen 1982, Voight 1993, Gotelli and Ellison 2004). The resulting relationships are assessed based on the accuracy of the observed (i.e. given) to the predicted (i.e. calculated from within group distances) classifications (Gotelli and Ellison 2004). Values that are located off the diagonal represent classification errors and decrease the distance between the groups (Gotelli and Ellison 2004). Non-overlapping groups can then be assumed to be morphologically distinct and are likely distinct populations. As with PCA, this method assumes multivariate normal distribution (Gotelli and Ellison 2004) but it is more sensitive to this assumption than PCA (N. Kenkel pers. comm.). Discriminant analysis can also be used as a posteriori test for the results of other methods (e.g. PCA) if the MANOVA is rejected (Voight 1993, Gotelli and Ellison 2004).

2.2.3.2. Genetic analysis

Molecular techniques have helped to shed light on systematic questions not easily answered by typical morphological analyses (Hillis 1987; Lindgren et al. 2005; Layton et al. 2014). This methodology is of particular interest for species that lack a solid fossil record such as cephalopods (Carlini 1998, Strugnell and Nishiguchi 2007). Genetic analysis, however, still requires some refining when applied to population analysis (Boyle and Rodhouse 2005k).

Previous molecular analyses examined 12S RNA, 16S rRNA, Actin I and II, and cytochrome C oxidase subunits (I, III) as potential markers for systematic analysis of cephalopods but most lack the refinement required to define local populations (Bonnaud et al. 1997, Carlini 1998, Lindgren et al. 2004, Boyle and Rodhouse 2005k). Microsatellite analyses have been successful in identifying populations but requires taxa specific (or related) primers for amplification (An et al. 2014, Liu et al. 2014, Lin et al. 2015). Expanding cephalopod fisheries and recent interest in cephalopod genomics, in particular the formation of the CephSeq Consortium and the first description of the octopus genome (*O. bimaculoides*) has resulted in an increase in the development of primers (Albertin et al. 2012, An et al. 2014, Liu et al. 2014, Albertin et al. 2015, Lin et al. 2015). Further development is still required, especially for Arctic species. Until such a time, cytochrome C oxidase subunit I (COI) has been shown to be the most conserved gene of those assayed, with sufficient variability in the third codon position to distinguish between recently diverged taxa (Carlini 1998, Ratnasingham and Hebert 2007). Unlike 12S rRNA, COI uses universal primers for amplification, aiding in its popularity as the primary barcode gene (Carlini 1998, Ratnasingham and Hebert 2007). Ibáñez et al. (2011) were able to utilize COI for population analyses by examining haplotype diversity, rather than taxonomic relationships, within jumbo squid (*D. gigas*) caught along the Pacific coast.

Understanding the genetic variation within a species or population will not only be beneficial for potential fisheries management, but will provide insights into their ability to tolerate environmental change, either through movement patterns or increased genetic variability (Carvalho et al. 1992, Ibáñez et al. 2011, An et al. 2014, Liu et al. 2014, Lin et al. 2015). Morphometric and genetic analyses each have analytical issues but a combination of the two methods provides a more stable, complete picture of cephalopod population interactions (Hillis

1987). This picture will only become clearer with the development of more cephalopod-specific primers and microsatellites for analyses.

2.3 Trophic Analyses

2.3.1. Introduction

Trophic analysis utilizes various methods to identify and describe energy pathways throughout an ecosystem. These pathways illustrate, not only the movement of nutrients through the system, but also inter- and intra-specific interactions among species (i.e. food webs), and variations in life history traits (e.g. habitat preference, mobility, migration) (Sennikov et al. 1989, Clarke 1996, Takai et al. 2000, Nesis 2003c, Rosa et al. 2005, Chambers and Dick 2007, Hobson and Norris 2008). By examining the trophic preference of keystone species, such as cephalopods (André et al. 2010), these interactions can provide insight as to the extent potential environmental and/or anthropogenic shifts may impact the ecosystem as a whole (Santos et al. 2001, Hobson and Cherel 2006).

2.3.2. Technique Overview

A variety of methods can be utilized to identify trophic interactions. A few examples include stomach content analyses, direct observation of feeding events (both in the field and within laboratory settings), serological analysis (expensive but provides a wider window into prey preference than other methods), lipid analysis, DNA analysis and stable isotope analysis (SIA) (Michener and Schell 1994, Rodhouse and Nigmatullin 1996, Boyle and Rodhouse 2005b, Deagle et al. 2005, Michener and Kaufman 2007, Field et al. 2013). Of these methods, stomach content analysis and SIA are the most frequently used.

2.3.2.1. Stomach content analysis

The simplest method for alimentary analysis is to directly examine the stomach contents of the species of interest and identify to the lowest possible taxa. This method allows for a quantitative comparison between ages, sexes and even species (Clarke 1987) but it only provides limited information based on a single (or narrow) feeding event (Jackson et al. 2007). Trophic interactions determined through stomach content analysis are problematic when feeding methods of cephalopods are taken into account (Rodhouse and Nigmatullin 1996, Piatkowski et al. 2001, Boyle and Rodhouse 2005b). Cephalopods have rapid digestion rates often resulting in empty stomachs or stomachs containing only highly digested and unidentifiable contents upon examination (Rodhouse and Nigmatullin 1996, Boyle and Rodhouse 2005b). The undigested prey structures often lack discernable characters required for identification because cephalopods expel the hard structures of their prey prior to ingestion (Rodhouse and Nigmatullin 1996, Boyle and Rodhouse 2005b, Jackson et al. 2007). Cephalopods are also known to continue feeding after capture, therefore, their stomach contents may reflect artificial trophic interactions rather than natural prey preferences (Rodhouse and Nigmatullin 1996, Boyle and Rodhouse 2005b).

These potential sources of error suggest the need to apply other tools to trophic analyses.

2.3.2.2. Stable isotope analysis (SIA)

In recent years, SIA has become a useful tool to study energy flow through various systems (Lajtha and Michener 1994, Michener and Schell 1994, Hobson et al. 2002, Post 2002, McCutchan et al. 2003, Navarro et al. 2013). It has also been useful to provide insight into other ecological questions, such as large-scale migrations (Hobson and Norris 2008).

In contrast to stomach content analyses, SIA can provide trophic information over a longer time frame, with tissue selection the primary limiting factor (i.e. turnover rates) (Tieszen et al. 1983, Lesage et al. 2001, Jackson et al. 2007). This method, however, does not distinguish between different prey species (Lesage et al. 2001), suggesting a multi-analytical approach (stomach contents and SIA) would be best to gain a more complete trophic picture for this keystone group (Navarro et al. 2013).

2.3.3. *Overview of Stable Isotope Analyses (SIA)*

2.3.3.1. Background

Stable isotopes are useful tools to determine how matter cycles through a system (DeNiro and Epstein 1978, 1981, Lajtha and Michener 1994, Takai et al. 2000, Boyle and Rodhouse 2005b, Michener and Kaufman 2007). Stable isotopes are naturally occurring identical atoms, differing only in the number of neutrons and, therefore, mass (i.e. light vs. heavy) (Sulzman 2007). Similar numbers of neutrons and protons prevent decay, adding in their stability (Sulzman 2007). Elements ideal for SIA have a single isotope with one much heavier than the other, have a low atomic mass and occur in more than one oxidative state (modified from (Sulzman 2007)). It is also important that the rare isotope (typically the heavier of the two) not occur in great quantities naturally (Sulzman 2007).

SIA relies on this heavy (e.g. ^{15}N) to light (e.g. ^{14}N) ratio compared to a standard to examine such interactions as predator/prey (i.e. food webs), large-scale migrations, and carbon fluxes (Lajtha and Michener 1994, Lesage et al. 2001, Post 2002, Dawson and Siegwolf 2007, Michener and Kaufman 2007, Hobson and Norris 2008, Navarro et al. 2013). Comparing the

ratio to a known standard helps to minimize the variability and fluctuations within the SIA results (Lajtha and Michener 1994). The ratios are expressed in delta (δ) notation and are calculated by finding the *per mil* (‰) value of the difference between the samples and standard values:

$$\delta^{15}\text{N} = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000 \quad \text{Eqn 2.2}$$

where R is the ratio of $^{15}\text{N}/^{14}\text{N}$ (for example) (Ehleringer et al. 1986, Lajtha and Michener 1994, Takai et al. 2000, Dawson and Siegwolf 2007, Sulzman 2007).

In relation to trophic analysis, SIA utilizes these ratios to assess the isotopic values of digested prey (McCutchan et al. 2003, Ruiz-Cooley et al. 2004). As an individual feeds, the heavier isotopic signatures of the prey (or plant) are assimilated into the predators' tissues, while the lighter isotopes are lost through respiration (^{12}C) and excretion (^{14}N) (Minagawa and Wada 1984, McCutchan et al. 2003, Ruiz-Cooley et al. 2004). These isotopic signatures can then be measured using a mass spectrometer (Minagawa and Wada 1984, Sulzman 2007) and compared to determine their trophic role (Rodhouse and Nigmatullin 1996, Post 2002, Ruiz-Cooley et al. 2004). For example, the higher the δ value, the higher the trophic level (Rodhouse and Nigmatullin 1996, Post 2002, Ruiz-Cooley et al. 2004). Since a body's isotopic composition must be balanced through turnover and fractionation, tissue selection is an important component of SIA, and must reflect the question being asked (DeNiro and Epstein 1978, Tieszen et al. 1983, Lajtha and Michener 1994, Michener and Kaufman 2007, Post et al. 2007). Metabolically active tissues, such as the liver, have a fast turnover in elemental composition in relation to diet and should be restricted for use regarding short-term trophic questions (Hobson and Welch 1992a, Michener and Schell 1994). While the usefulness of this method requires a certain predictable

understanding of how the isotopes are taken up, care must still be taken when interpreting the results as individual and species biochemistry may vary (Lajtha and Michener 1994, McCutchan et al. 2003). Since not all isotopes are evenly distributed or easily absorbed, understanding geographic variations, incorporation rates of prey, and the turnover and fractionation rates for the tissues and species in question all help piece together the trophic puzzle (Tieszen et al. 1983, Hobson and Welch 1992a, Takai et al. 2000, McCutchan et al. 2003).

2.3.3.2. Common isotopes used in trophic analyses

Various isotopes can be utilized for trophic analysis, however, the most common are $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Lajtha and Michener 1994). Delta ^{13}C is also useful for identifying carbon sources and potential migrations (Michener and Schell 1994, Takai et al. 2000, Post 2002, Ruiz-Cooley et al. 2004, Barnes et al. 2009, Navarro et al. 2013).

a) $\delta^{15}\text{N}$

Nitrogen isotopes are useful in constructing food webs when sufficient isotopic variation exists within the food consumed (DeNiro and Epstein 1981, Minagawa and Wada 1984, Takai et al. 2000, Post 2002). Delta ^{15}N ratios reflect those of their prey, showing a steady increase with trophic levels (Hobson and Welch 1992b, Michener and Schell 1994, Takai et al. 2000, Ruiz-Cooley et al. 2004). As a rule of thumb, a change of 3 to 4 ‰ represents a trophic shift (DeNiro and Epstein 1981, Minagawa and Wada 1984, Peterson and Fry 1987, Michener and Schell 1994, Post 2002), however, Hobson and Welch (1992a) found that an enrichment factor of 3.8 ‰ per trophic shift was appropriate for higher trophic levels within the Arctic.

Delta ^{15}N values can vary between the same sample tissue of individuals of the same species eating the same food (DeNiro and Epstein 1981). This variation may be the result of the individuals' unique metabolic processes (Minagawa and Wada 1984), different uptake rates (DeNiro and Epstein 1978), quality of prey (McCutchan et al. 2003) or seasonal and/or environmental variability (Michener and Schell 1994). Also, $\delta^{15}\text{N}$ enrichment is often associated with increased nitrogen excretion through urea or urine (i.e. waste consisting of lighter ^{14}N rather than the heavier ^{15}N isotope) (Minagawa and Wada 1984, Michener and Schell 1994, McCutchan et al. 2003, Ruiz-Cooley et al. 2004), which can occur from exposure to a variety of salinities (e.g. diurnal/ontogenetic migrations, ice melt). Elevated $\delta^{15}\text{N}$ levels have also been associated with starving individuals and could serve as a possible indicator of body condition (Michener and Schell 1994, McCutchan et al. 2003).

Delta ^{15}N values are uncorrelated with latitude, even when higher latitude regions contained areas of upwellings, increasing the nitrogen input (Takai et al. 2000). Instead, Takai et al. (2000) suggests that $\delta^{15}\text{N}$ values are related to regional nitrogen metabolism. Benthic organisms, however, are enriched compared to their pelagic counterparts, suggesting $\delta^{15}\text{N}$ is correlated with depth (Michener and Schell 1994). This enrichment may also be caused by longer food webs than pelagic systems or meiofauna interactions (Michener and Schell 1994, Iken et al. 2005).

Delta ^{15}N is also independent of body size (Cherel et al. 2009). Cherel et al. (2009) analyzed the $\delta^{15}\text{N}$ values of 19 cephalopod species' beaks from a wide range of habitats and found that the giant squid (*Architeuthis dux* (Steenstrup in Harting 1860) = 6.4 ‰) fed at the mid-trophic range and had $\delta^{15}\text{N}$ values less than *G. steenstrupi* (~ 10.7 ‰). The highest $\delta^{15}\text{N}$

cephalopod values were from *Taningia danae* (Joubin 1931) and were similar to those of sperm whales; the lowest values belonged to *V. infernalis*, a filter feeding detritivore (Cherel et al. 2009, Hoving and Robison 2012, Navarro et al. 2013). Cherel et al. (2005, 2009) also found that based on standard chitinization progression, examining individual beak structures (e.g. rostrum, lateral wall, wing) would provide information on the trophic levels of previous life stages.

Navarro et al. (2013) compiled published literature values for cephalopods from around the world and compared trophic levels based on local oceans and ecozones (e.g. Arctic Shelf/Slope). Although large variations were initially present within each dataset (likely caused by variable isotopic compositions of seawater affecting the values of phytoplankton/macrophytes, zooplanktons, etc.), once adjusted for environmental variability, trends became apparent (Navarro et al. 2013). Cephalopods exploit a wide range of trophic resources with Arctic cephalopods 7.5 ‰ enriched over zooplankton and on par with individuals from the Pacific Ocean (~ 12.5 ‰) (Navarro et al. 2013). Arctic cephalopods from the shelf ecozone also had higher $\delta^{15}\text{N}$ values (~ 12.5 ‰) compared to those from the Antarctic shelf, open ocean and temperate coast/shelf (Navarro et al. 2013).

b) $\delta^{13}\text{C}$

Carbon ($\delta^{13}\text{C}$) composition also reflects the diet of an individual, however, only in small increments (~ 1 ‰) (Michener and Schell 1994). This is because of the loss of light ^{12}C through metabolic fractionation, respiration and uptake by various tissues (Michener and Schell 1994, Cherel and Hobson 2005). Tissues with higher metabolic activity, such as lipids, also have faster turnover rates and will be naturally depleted in $\delta^{13}\text{C}$, thereby producing false low readings (Hobson and Welch 1992a, Michener and Schell 1994, Post 2002, McCutchan et al. 2003). A

strong correlation between $\delta^{13}\text{C}$ and diet was not reported in cephalopods, however, it is positively correlated to specimen size (Cherel et al. 2009).

Delta ^{13}C values are also used to identify resident water masses (Hooker et al. 2001). Coastal and benthic ecosystems tend to have high $\delta^{13}\text{C}$ values compared to pelagic regions and $\delta^{13}\text{C}$ has a negative relationship with increasing latitude (Hobson and Welch 1992a, Takai et al. 2000, Hooker et al. 2001, Cherel et al. 2009). Phytoplankton is known to decrease by -0.015‰ $\delta^{13}\text{C}$ for each degree north (Rau et al. 1983, Takai et al. 2000), which may explain the isotopes' negative association with latitude. Water temperature and dissolved CO_2 may also have an impact on $\delta^{13}\text{C}$ levels (Takai et al. 2000). Migration and drifting patterns can therefore be derived from $\delta^{13}\text{C}$ values.

2.3.4. Methodology

Stable isotope analysis compares the ratio of heavy to light isotopic compounds such as $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ to a known standard (Lajtha and Michener 1994, Sulzman 2007). The known sample is then converted to a pure gas that is read by a mass spectrometer (Lajtha and Michener 1994, Sulzman 2007). The isotope ratios are then compared to a standard to mitigate variation and fluctuation caused by sample preparation and analysis (Lajtha and Michener 1994, Sulzman 2007). The standards for each isotope come from a variety of sources, e.g. carbon standard is from marine limestone Vienna Pee Dee Belemnite (PDB) while atmospheric nitrogen is the standard for nitrogen (DeNiro and Epstein 1978, 1981, Lajtha and Michener 1994, Takai et al. 2000, Sulzman 2007).

Methods of collection and analysis vary depending on the isotope in question (Lajtha and Michener 1994). Tissue selection should reflect the specific question being asked (DeNiro and Epstein 1978, Tieszen et al. 1983, Lajtha and Michener 1994, Michener and Kaufman 2007, Post et al. 2007). For example, high metabolic tissues (e.g. liver, lipids) with quick isotopic turnover rates can represent recent feeding activities while those with low metabolic rates (e.g. hair and chitin) present a wider trophic picture (DeNiro and Epstein 1978, Tieszen et al. 1983, Cherel and Hobson 2005, Hobson and Cherel 2006). For a more complete trophic representation, a variety of different tissues should be analyzed (DeNiro and Epstein 1978, Tieszen et al. 1983, Michener and Schell 1994).

Once collected, samples are dried by oven (70 °C) or freeze dryer and then ground to powder (Lajtha and Michener 1994, Carabel et al. 2006). Grinding allows for thorough mixing of all the components, decreasing variability (Lajtha and Michener 1994). If contaminants such as carbonates still remain within the sample, acidification with HCl, for example, will remove unwanted compounds (Lajtha and Michener 1994). It is important to remove impurities since heavy carbonates (for example) may affect the results (Lajtha and Michener 1994). High levels of lipids also cause a negative shift in $\delta^{13}\text{C}$ because they are isotopically lighter, therefore, should be removed prior to further analysis (Hobson and Welch 1992a, Michener and Schell 1994, McCutchan et al. 2003). Lipids can be removed by rinsing the powder with a 2:1 chloroform:methanol solution (Takai et al. 2000) or by choosing a sample tissue low in lipids (e.g. mantle tissue (Kristensen 1984)). Once purified, samples are then ready for analysis or storage in sealed containers at -20 °C to decrease further fractionation and degradation (DeNiro and Epstein 1978, Lajtha and Michener 1994).

2.4. Literature conclusion

Cephalopods are important components of all marine ecosystems and are impacted by environmental and anthropogenic pressures. They are of particular importance within the Arctic ecosystem, a region experiencing growing environmental and anthropogenic pressures, and where cephalopods serve as high quality prey for a variety of Arctic fish and mammal species. The loss of sea ice, increased land runoff and shifts in water circulation among other environmental shifts, will impact the distribution and abundance of Arctic cephalopods which in turn will have an impact on teuthophagus predators, including those of cultural and commercial importance.

In order to better monitor these changes, a strong biological baseline must be established. This literature review has provided a foundation of what is known for Arctic cephalopods and the Arctic region as a whole, but it has also highlighted areas where basic information is lacking. Questions still remain about the trophic preference of some of the common species, the overall distribution of cephalopod species within the Canadian Arctic and whether they form distinct populations or whether the Canadian Arctic consists of a large, interconnected metapopulation. The following chapters will attempt to answer some of these questions.

Figure 2.1. Circumpolar bathymetric map of the Arctic region. (Image reproduced from the GEBCO website http://www.gebco.net/data_and_products/gebco_world_map).

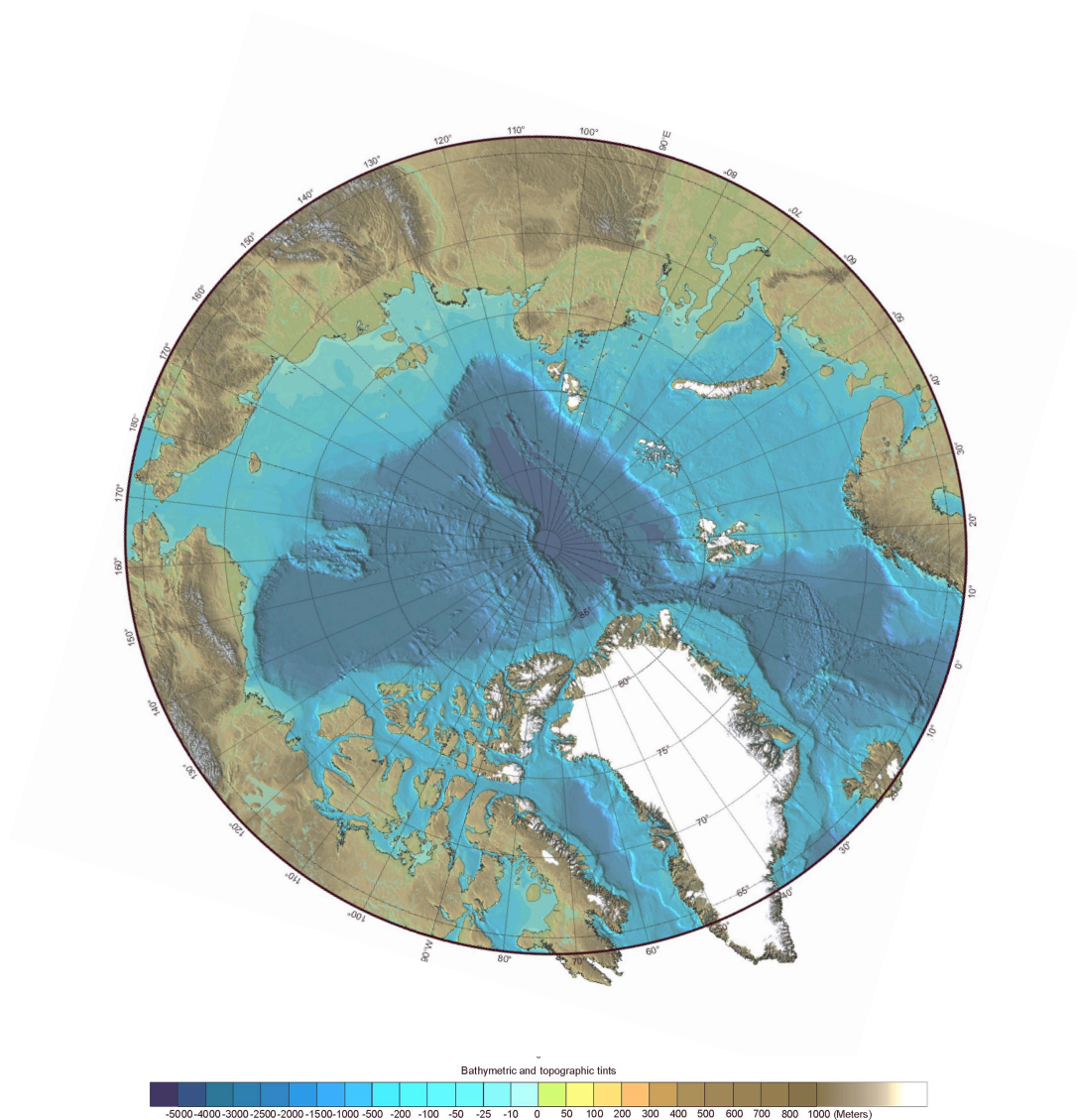
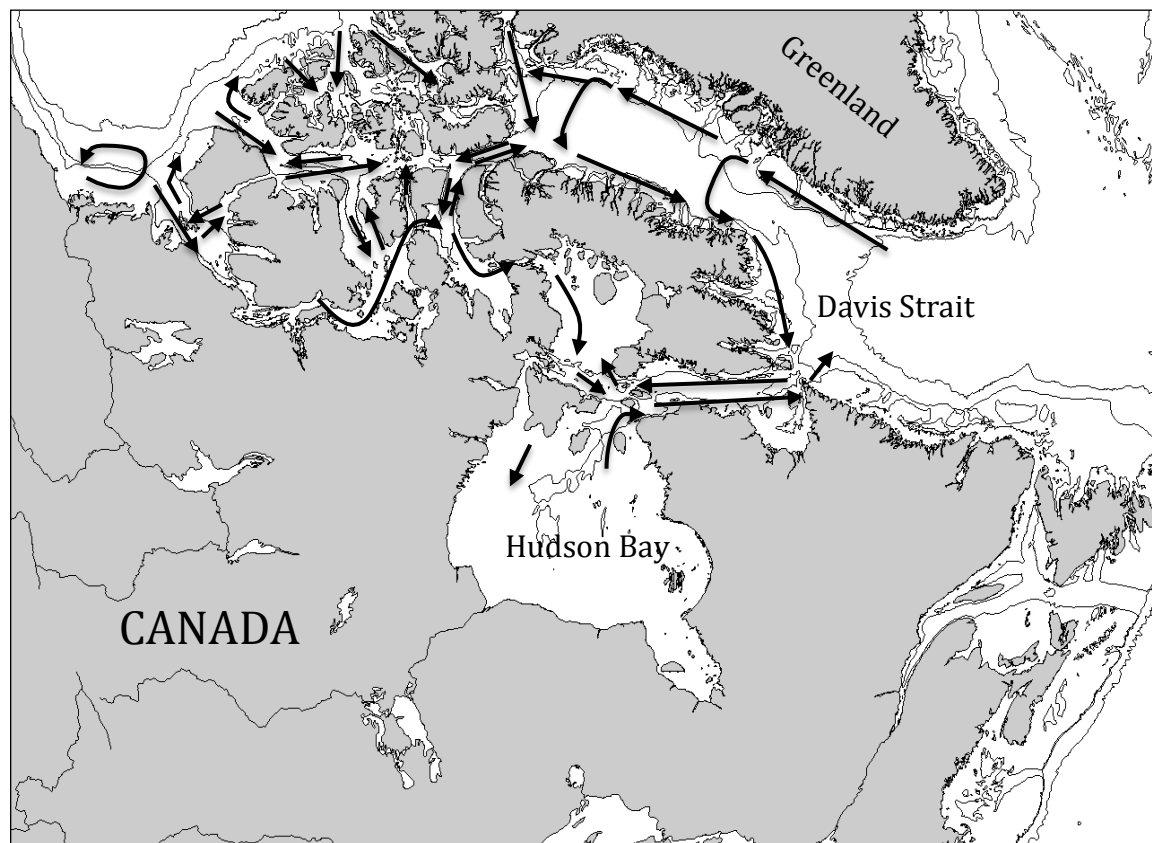


Figure 2.2. General circulation patterns in the Canadian Arctic Archipelago (modified from LeBlond 1980 and Michel et al. 2006).



Chapter 3

Study site descriptions, general and chapter specific methods

3.1. Sample areas

Cephalopod specimens were collected by otter trawls on board the M/Tr ‘Pâmiut’ during Fisheries and Oceans Canada (DFO; Freshwater Institute, Winnipeg, Canada) and the Greenland Institute of Natural Resources’ (GINR; Nuuk, Greenland) annual groundfish and shrimp surveys. Specimens were collected from Hudson Strait (DFO 2007 and 2009), Davis Strait (DFO 2007 and 2008), Baffin Bay (DFO 2008 and GINR 2009) and western Greenland (GINR 2009) (Fig. 3.1; T. Siferd and M. Treble, Winnipeg, Manitoba (FWI-DFO); R. Nygaard (GINR)). Additional specimens were obtained from the CCGS ‘Teleost’ during the 2010 annual DFO fishery survey of the Gulf of St. Lawrence (Fig. 3.1; C. Nozères, Maurice Lamontagne Institute (MLI-DFO; Mont-Joli, Quebec)). All cephalopods collected were by-catch.

3.1.1. Hudson Strait

Hudson Strait was sampled during the 2007 and 2009 Fisheries and Oceans Canada shrimp surveys by the M/Tr. ‘Pâmiut’, a 53 m long 722 GRT stern trawler (Treble 2009) rigged with a Cosmos bottom otter trawl and a 20 mm cod end liner. Sampling extended from 62°58’16.09”N 77°56’2.69”W to 60°55’31.80”N 63°56’35.88”W (Fig. 3.1). The 2007 survey extended south into Ungava Bay and east into Davis Strait. The 2009 survey sampled as far west as Nottingham Island where Hudson Strait connects to Foxe Basin and east to Resolution Island. Depths sampled range from 134 m to 968 m (Fig. 3.2). Hudson Strait is relatively shallow with the majority of samples being collected from the 201 to 400 m depth range; the 2007 survey extending into Davis Strait also sampled some deeper water (968 m; Fig. 3.2). Bottom

temperature ranged from $-0.28\text{ }^{\circ}\text{C}$ to $3.79\text{ }^{\circ}\text{C}$ in 2007 but was colder ($-1.14\text{ }^{\circ}\text{C}$ to $2.95\text{ }^{\circ}\text{C}$) during the 2009 survey (Fig. 3.3).

Sampling occurred 24 hours a day during the month of October in both years. Trawls were typically 15 minutes (range of 6 to 45 minutes) in length, with 85 stations sampled in 2007 and 151 stations in 2009. Cephalopod samples obtained represent a sub-sample of the total cephalopod catch observed during the surveys.

3.1.2. Baffin Bay

The Davis Strait-Baffin Bay survey (herein referred to as simply the Baffin Bay survey) was part of the DFO annual (2008) groundfish survey (Fig. 3.1). Again, the GINR trawler, M/Tr. 'Pâmiut', was used to survey the areas between $66^{\circ}16'5.87''\text{N}$ $61^{\circ}9'55.08''\text{W}$ to $66^{\circ}45'53.80''\text{N}$ $57^{\circ}46'56.65''\text{W}$ and $71^{\circ}31'2.26''\text{N}$ $70^{\circ}23'53.85''\text{W}$. Depths sampled ranged from 11 m to 1474 m with temperatures ranging from $-1.64\text{ }^{\circ}\text{C}$ to $4.16\text{ }^{\circ}\text{C}$ (Fig. 3.2 and 3.3). An Alfredo III bottom otter trawl was used with a 30 mm liner at the cod end and rock hoppers attached (Treble 2009). Towing speed was approximately 3.0 knots and lasted on average 15 to 30 minutes (range 10.4 to 52.5 minutes) (Treble 2009).

The survey was conducted during October and early November of 2008 and samples were collected 24 hours per day. A total of 183 tows were sampled. As with the Hudson Strait surveys, cephalopods collected for necropsies were only a subsample of the total cephalopod catch.

3.1.3. *Western Greenland*

The Greenland combination shrimp and groundfish survey (Nygaard et al. 2008) was conducted over three cruises on the M/Tr 'Pâmiut' with 161 tows during the first cruise, 89 tows in the second cruise and 117 tows during the third cruise. Areas sampled extended from 58°37'50.16"N 45°18'12.54"W to 72°21'12.15"N 60°39'22.44"W and included Disko Bay, Greenland (Fig. 3.1).

As with the Hudson Strait surveys, a Cosmos bottom otter trawl was used with a 20 mm mesh cod end liner (Nygaard et al. 2008). Towing speed was approximately 2.5 knots for an average of 15 minute sets (Nygaard et al. 2008) (range 1.8 minutes to 49.998 minutes). Sampling took place between June and the end of August 2009 with samples collected 24 hours per day. Depths sampled ranged from 51 m to 950 m with temperatures warmer than observed on the Canadian side of Davis Strait and Baffin Bay (0.679 °C to 5.131 °C; Figs. 3.2 and 3.3).

3.1.4. *St. Lawrence estuary and Gulf*

The St. Lawrence is sampled annually as part of the DFO shrimp surveys on board the CCGS 'Teleost'. Cephalopods obtained represent a subsample of the actual cephalopod catch during the survey. Samples were obtained between 48°20'18.58"N 69°7'59.72"W and 50°5'11.97"N 58°40'55.02"W using a Campelen 1800 four faced shrimp trawl with rock hopper gear attached and 12.7 mm mesh cod end liner (Bourdages et al. 2007). Fifteen-minute trawls at an average speed of 3.0 knots (Bourdages et al. 2007) were conducted 24 hours a day between August 8 and 30, 2010. Depth ranges sampled were 87 m to 436 m (Fig. 3.2) with no temperatures collected.

3.2. Specimen preservation

Whole cephalopods were sub-sampled from the total catch per tow, and represent the full size range observed. These individuals were sorted into groups of similar appearance and bagged by tow number. The cephalopods were then placed in -20 °C freezers and transported to the University of Manitoba for further morphometric, genetic and trophic analyses.

3.3. Chapter specific methods

Methods utilized throughout this thesis consist of: **1)** location integration of historical literature, museum specimens and fishery records to identify areas of cephalopod concentrations and predator interactions (Chapter 4); **2)** multivariate analysis of standard morphometric measurements (Mercer 1968b, Roper and Voss 1983, Muus 2002) to identify biogeographic variations and potential populations of cephalopods within the Canadian and Greenland Arctic with verification from DNA barcoding and the Barcode of Life online database (Chapter 5); and **3)** SIA in conjunction with alimentary analysis to describe habitat preferences and trophic characteristics of common Arctic species, in particular, the lesser studied *Rossia* spp. and *C. muelleri* (Chapter 6). Detailed methodologies are outlined in their respective chapters.

Figure 3.1. Sample locations of cephalopods collected during the annual GINR groundfish survey (—), DFO shrimp and groundfish surveys (---), and the DFO Gulf of St. Lawrence survey (- . - . -).

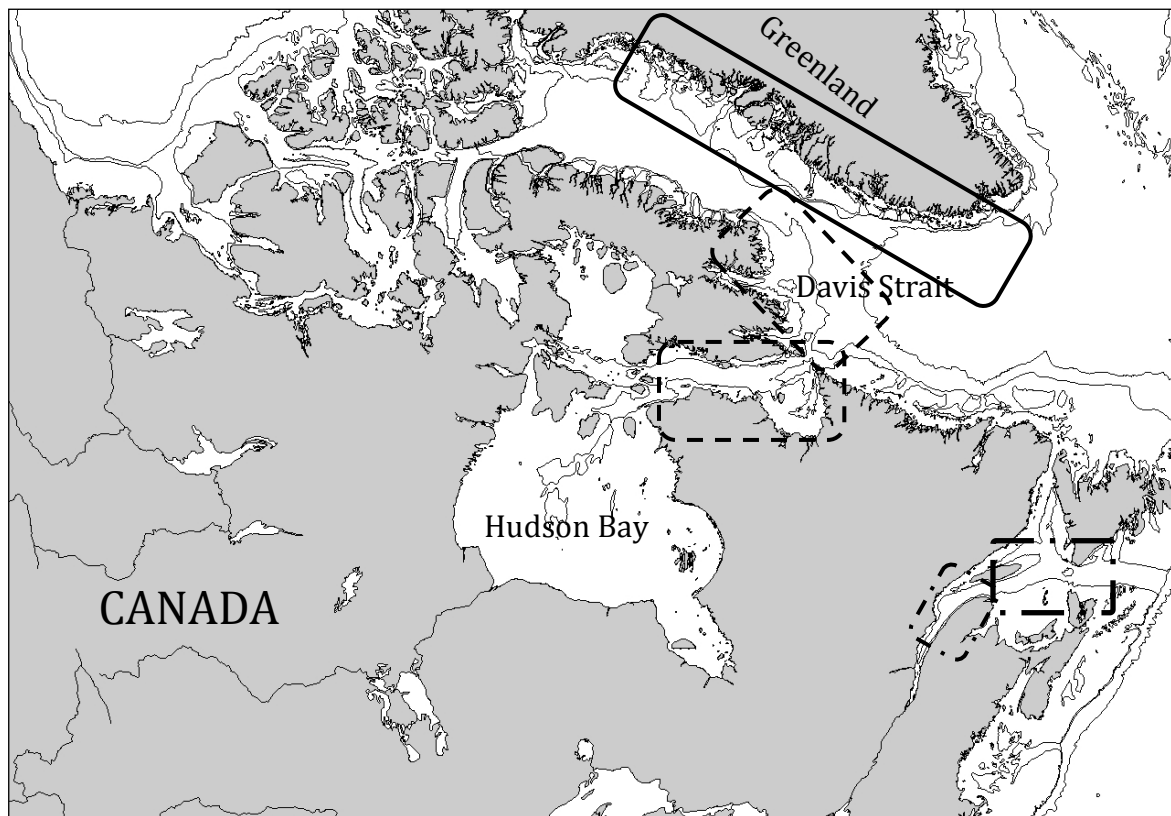


Figure 3.2. Percent of total tows per 200 m depth increments during DFO and GINR fishery and shrimp surveys.

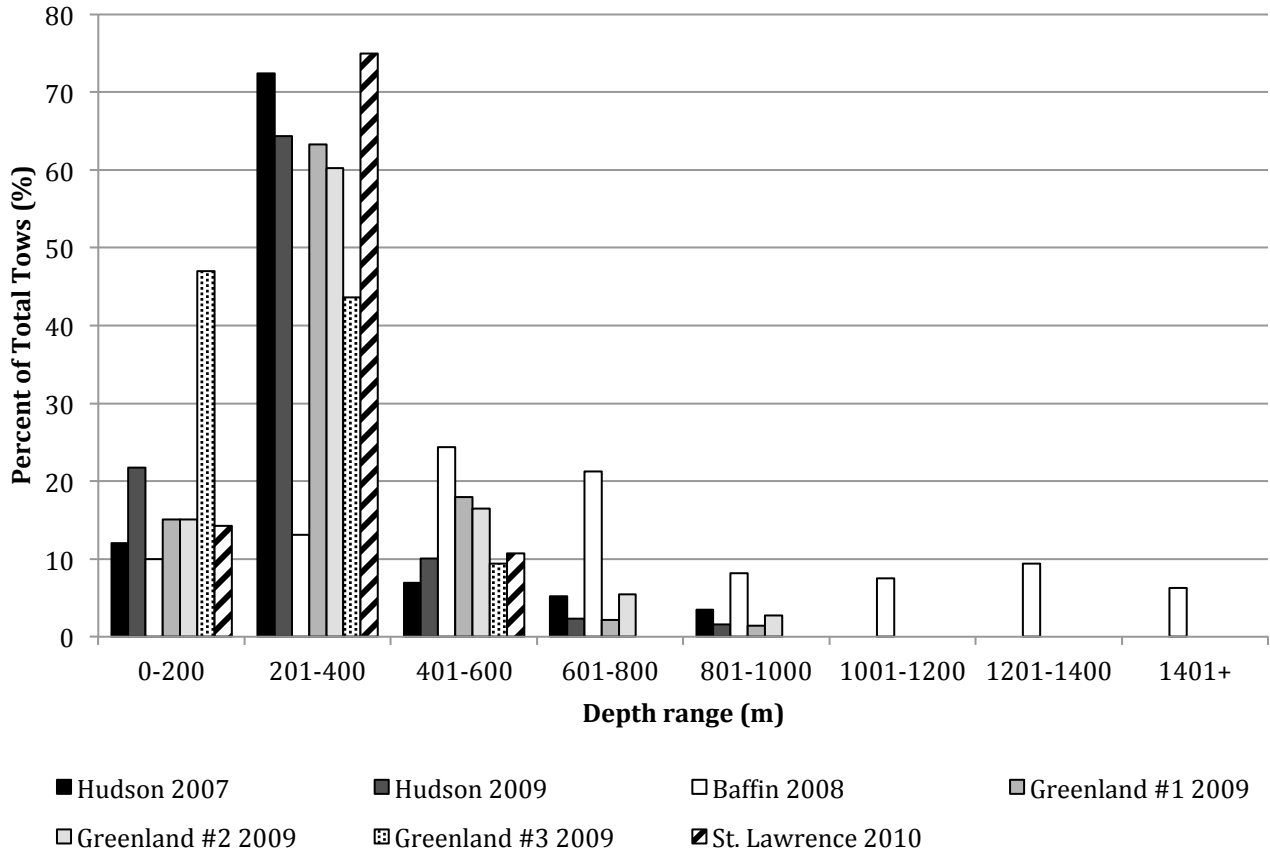
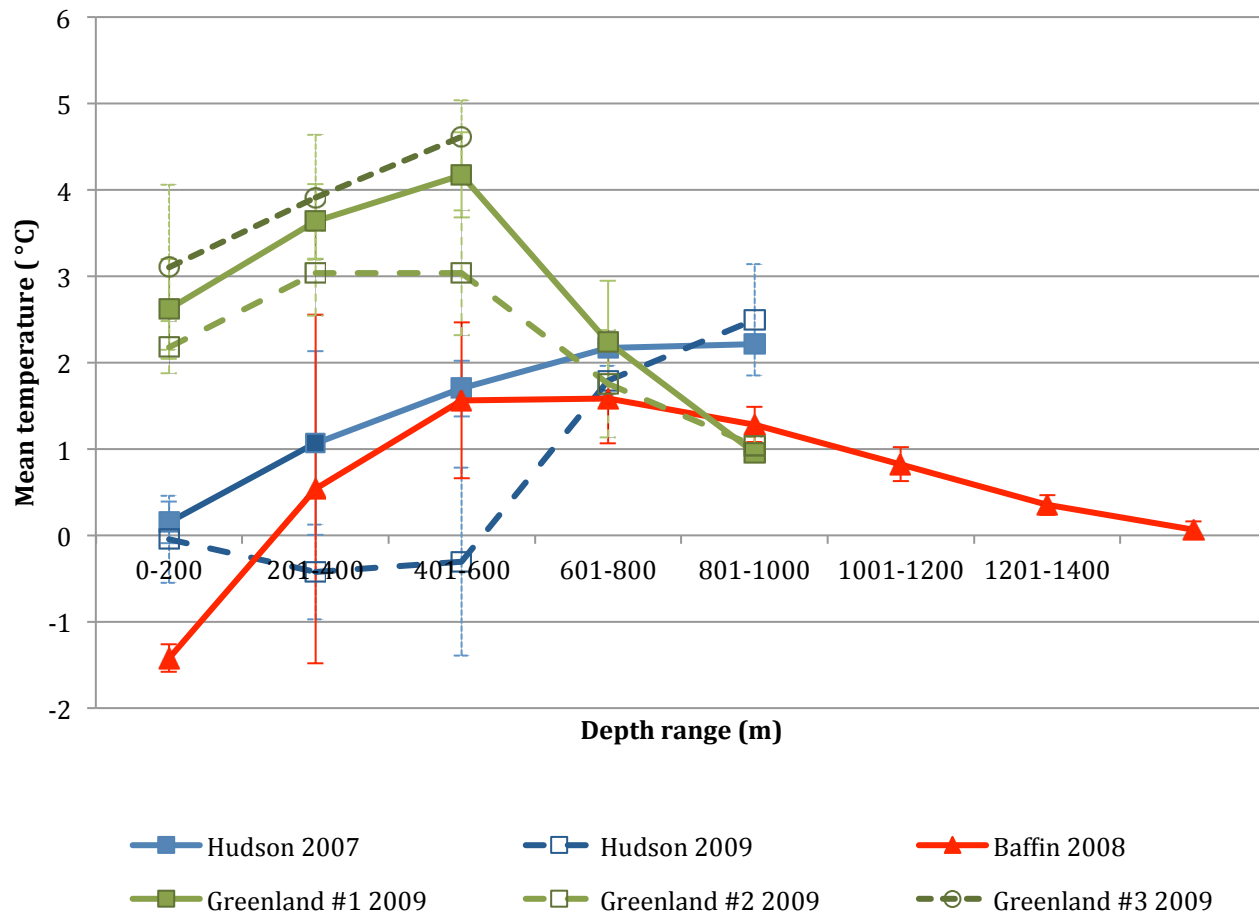


Figure 3.3. Mean temperatures (and standard deviations) per 200 m depth increments of DFO and GINR surveys where cephalopods were collected.



Chapter 4

Arctic cephalopod distributions and their associated predators with an emphasis on

determining Canadian Arctic foci

(Published in Polar Research, 2010, **29**(2): 209-227, co-author T.A. Dick; articles originally cited as 'in press' have been updated)

*Note: The NAFO surveys discussed in this chapter were conducted by Fisheries and Oceans Canada.

Abstract

Cephalopods are key species of the eastern Arctic marine food web, both as prey and predator. Their presence in the diets of Arctic fish, birds and mammals illustrates their trophic importance. There has been considerable research on cephalopods (primarily *Gonatus fabricii*) from the north Atlantic and the west side of Greenland, where they are considered a potential fishery and are taken as a by-catch. By contrast, data on the biogeography of Arctic cephalopods are still incomplete. This study integrates most known locations of Arctic cephalopods in an attempt to locate potential areas of interest for cephalopods, and the predators that feed on them. International and national databases, museum collections, government reports, published articles and personal communications were used to develop distribution maps. Species common to the Canadian Arctic include: *G. fabricii*, *Rossia moelleri*, *R. palpebrosa* and *Bathypolypus arcticus*. *Cirroteuthis muelleri* is abundant in the waters off Alaska, Davis Strait and Baffin Bay. Although distribution data are still incomplete, groupings of cephalopods were found in some areas that may be correlated with oceanographic variables. Understanding species distributions and their interactions within the ecosystem is important to the study of a warming Arctic Ocean and the selection of marine protected areas.

4.1. Introduction

Cephalopods are found in all marine habitats of the world, and are prey for a variety of commercial and culturally significant species. Cephalopod distributions are correlated (Hjort and Ruud 1929, Bjørke 2001) with predators such as narwhals (*Monodon monoceros* L.) (Finley and Gibb 1982, Bjørke 2001) and Greenland halibut (*Reinhardtius hippoglossoides* Walbaum) (Orr and Bowering 1997, Dawe et al. 1998, Bjørke 2001). A species of interest is the squid *Gonatus fabricii* Lichtenstein, which is considered a keystone species in several Arctic food webs (Chambers and Dick 2007). *Gonatus fabricii* are high in lipids and an excellent source of energy (Hooker et al. 2001, Frandsen and Wieland 2004). These squid are also predatory on a variety of fish and other marine invertebrates (e.g., Nesis 1965), enabling a transfer of energy from the productive epipelagic zone to benthic waters through ontogenetic migrations (Sennikov et al. 1989).

A significant body of research has been conducted on cephalopods around Greenland (e.g. Collins 2002, Zumholz and Frandsen 2006), Norwegian (Kristensen 1977, Wiborg et al. 1982) and Russian waters (e.g., Nesis 1965, 2001). However, cephalopods of the Canadian Arctic (above 60°N) are not well known. Most reports (e.g., Clarke 1966, Kristensen 1983, O'Dor and Macalaster 1983, Nesis 2001) have focused on potential commercial species (e.g., *G. fabricii*) and their presence or absence in an area, whereas others have been general surveys.

The objectives of this work are to: (1) consolidate all distributional data to a single source; (2) present maps to identify areas of biodiversity interest and potential feeding areas (i.e., predator–prey interactions); and (3) establish a baseline for future comparisons, including climate change effects in the Arctic.

4.2. Materials and Methods

Initial queries into Arctic cephalopods were conducted using the Global Biodiversity Information Facility website (<http://www.gbif.org/>). All cephalopod records for areas north of 60°N were acquired, and five taxa were determined to be the most abundant. Of those taxa, records were obtained through contacts with museums (the Canadian Museum of Nature [CMNML] in Ottawa, Ontario, and the Atlantic Reference Centre [ARC] in St. Andrew's, New Brunswick), organizations such as Arctic Ocean Diversity (ArcOD, at the University of Alaska Fairbanks) and the US National Oceanic and Atmospheric Administration (NOAA) Ocean Explorer project, and unpublished data of one of the authors (TAD) as well as unpublished data provided in 2007 by L. Harwood, B. Bluhm and D. Hardie. Data and locations were also obtained from published literature (Wiborg et al. 1982, Nesis 2001, Muus 2002, Raskoff et al. 2010). The GeoNames website was used to determine the most likely latitude and longitude in lieu of the given place name. All samples listed from Arctic communities were assumed to be caught at the nearest marine location. Additional locations were identified from published, geo-referenced maps (Nesis 1965, Kristensen 1977, 1982, Wiborg et al. 1982, Sennikov et al. 1989). If the identification from a location was questionable (e.g., fishery survey) the specimens were listed as unidentified. If a specimen was described from a broad region (e.g., bay, sea, ocean), it was not mapped but was listed in Table 4.1. Specific sites were averaged from start and end trawl locations. Sample numbers were denoted with incrementally larger markers.

All specimens from the Northwest Atlantic Fisheries Organization (NAFO) survey of 2007 (M. Treble, pers. comm.) were identified by one of the authors (KG). Specimens from the CMNML collection from Frobisher Bay (CMNML 35058) and Cape Parry (CMNML 37887, 37897, 37891) were examined to verify the original identification, and were found to be correct.

The identification of ARC specimens, primarily from the Mercer collection, was previously verified by the senior author (KG). Although location data were only used from reputable sources, there is the chance of misidentifications, especially with *Bathypolypus arcticus* Prosch. Holdings of this particular species should be re-examined to verify its speciation. The names of all species were validated, and those considered invalid were listed as their synonym in accordance with the Integrated Taxonomic Information System (ITIS).

Beaks and specimens from stomach content analyses were recorded as such in the data set. Locations were obtained from published literature, government documents, surveys, Arctic expeditions (e.g., Wacasey et al. 1979, Nesis 2001, Cepibase) and unpublished data (T.A. Dick; L. Harwood, pers. comm. 2007) (Tables 4.1 - 4.4). Each predator species was identified with a unique symbol that differed from specimens recovered from trawls. Again, if a location was described from a broad region, it was not mapped. Predators and capture locations are listed in Tables 4.2 - 4.4.

All locations were mapped using ARCMAP 9 (ESRI GIS mapping software).

4.3. Results

Specimens described in this paper were collected between 1856 and 2007. The five most prominent species from the Canadian Arctic are *G. fabricii*, *Rossia moelleri* Steenstrup, *R. palpebrosa* Owen, *B. arcticus* and *Cirroteuthis muelleri* Eschricht.

4.3.1. Distributions

a) *Gonatus fabricii*

Gonatus fabricii has a circumpolar distribution, extending from Alaska north to the high Arctic (Fig. 4.1). The Canadian range extends from the Dolphin and Union Strait, Northwest Territories (NWT), north to Cape Vera, Nunavut (NU), and Pond Inlet, NU, and south through the Hudson Strait (Fig. 4.1). *G. fabricii* also extends along the coasts of Greenland, through the Denmark Strait, Norwegian Sea, off the Norwegian shore, around the Faroe Islands and Svalbard, and into the Barents Sea (Figs. 4.1, 4.2).

Because of the number of groundfish and shrimp surveys in the Norwegian Sea and west coast of Greenland, there are numerous records of *G. fabricii* (Nesis 1965, Kristensen 1977, Wiborg et al. 1982, Sennikov et al. 1989). Other areas of interest include Cape Vera (190 specimens) and Pond Inlet (46 specimens) (Figs. 4.1, 4.2). Wiborg et al. (1982) also identified potential spawning sites in the Norwegian Sea (Fig. 4.2).

Distributions around Greenland and Hudson Strait are based on samples collected in trawls, whereas those from Cape Vera and Pond Inlet are from stomach contents of northern fulmars (*Fulmarus glacialis* L.) and narwhals, respectively (Fig. 4.3). Several Hudson Strait locations are from the stomachs of thick-billed murres (*Uria lomvia* L.), whereas most of the locations in the eastern Arctic are based on stomach contents from commercially fished haddock (*Melanogrammus aeglefinus* L.), Greenland halibut and cod (*Gadus* sp. L.) (Fig. 4.3).

b) *Rossia moelleri*

Rossia moelleri has a circumpolar distribution, with a range extending from Cape Parry,

NWT, through the Dolphin and Union Strait, NWT, to Foxe Basin, Frobisher Bay and north to Slidre Fjord, Ellesmere Island (Fig. 4.4). It was also recorded from western Greenland and Denmark Strait (Fig. 4.4). There are records from the Norwegian Sea north to Svalbard, with one specimen reported from the Laptev Sea (Fig. 4.4).

Cape Parry (12 records) and Slidre Fjord (nine records) have the greatest number of recorded specimens (Fig. 4.4). Most records are from trawls. One beak was collected from a walrus (*Odobenus rosmarus* L.) off the north-west tip of Greenland (Fig. 4.5). Records from the Norwegian Sea and Denmark Strait are primarily from the stomachs of cod. One was from the stomach of a haddock (Fig. 4.5).

c) *Rossia palpebrosa*

Most records of *R. palpebrosa* are reported from the junction of the East Siberian and Laptev seas and the Laptev Sea proper (Fig. 4.6). Individuals were recorded from Svalbard, the Kara and Barents seas, as well as from the northern tip of Greenland to Disko Bay, across Davis to the Hudson Strait (Fig. 4.6). Individuals were also collected from Slidre Fjord, Ellesmere Island, Frobisher Bay and the east coast of Somerset Island (Fig. 4.6).

There are no records of predators for this species.

d) *Bathypolypus arcticus*

The Arctic range of *B. arcticus* extends from Frobisher Bay north through Davis Strait to Pond Inlet, Devon Island and Lady Ann Strait, and along the west coast of Greenland (Fig. 4.7). Records exist from the middle of the east coast of Greenland through Denmark Strait to Iceland, and down to the Faroe Islands (Fig. 4.7). *Bathypolypus arcticus* is also found offshore of

Norway and in the Norwegian Sea to Svalbard (Fig. 4.7). There are also reports from the Kara and Laptev seas (Fig. 4.7). The most western distribution is from the Canada Basin, north of Alaska (Fig. 4.7). Areas of interest are Kap Powlett, Greenland and the Laptev Sea (Fig. 4.7).

Specimens are typically recovered from trawls. One was found in the stomach of a narwhal caught at Pond Inlet (Fig. 4.8). The specimen from Lichtenauvfjord, Greenland, was from the stomach contents of a Greenland halibut (Fig. 4.8).

e) *Cirroteuthis muelleri*

The majority of *C. muelleri* specimens are from Baffin Bay, and the Norwegian and Greenland seas, with a few records from the Laptev Sea (Fig. 4.9). *C. muelleri* is also reported from the deep water of the Canada Basin (Raskoff et al. 2010; B. Bluhm, pers. comm. 2007), and from Davis Strait and Baffin Bay (Fig. 4.9).

f) Unidentified cephalopods

Although not much cephalopod research has been conducted in the Canadian Arctic, there are records of unidentified cephalopods (typically from fishery or bird surveys) from areas such as Pond Inlet, Arctic Bay, Cape Vera, Somerset Island and Peel Sound, NU, with other records from Liverpool Bay, southern Banks and Victoria islands, NWT (Fig. 4.10).

g) Rare species of the Canadian Arctic Ocean and adjacent areas

Deep-sea squid like the giant squid (*Architeuthis* sp. Steenstrup) and temperate species such as *Illex illecebrosus* Lesueur and *Sepiolo atlantica* D'Orbigny have been reported from Greenland (Berry 1925, Grimpe 1933, Nesis 1987) (Table 4.1). *Architeuthis* sp. have also been

reported from Iceland and the Norwegian coastline, whereas *Loligo forbesi* Steenstrup has been reported from the Norwegian Sea (Table 4.1). *Rossia glaucopsis* Loven is reported along the eastern shore of Greenland, and its presence was noted in Svalbard, the Faroe Islands, and the Barents and Kara seas (Table 4.1). *Bathypolypus bairdii* Verrill and Muus's (2002) proposed species *Bathypolypus pugniger* were found through the Denmark Strait and around Greenland, with *B. bairdii* extending west into the Davis Strait (Table 4.1). Both were reported (Treble 2007) from Baffin Bay in the 2006 NAFO fishery survey (Table 4.1). Numerous *Gonatus* sp., *Bathypolypus* sp. and *Rossia* sp. were also collected throughout the Hudson Strait (Table 4.1).

4.3.2. Cephalopod–predator interactions

The percentage of diets comprising cephalopods of various Arctic species is listed in Table 4.2. Cephalopods comprised ca. 90% of the diet of Bering Sea beaked (*Mesoplodon stejnegeri* True) and Baird's beaked (*Berardius bairdii* Stejneger) whales (Table 4.2). The diet of sperm whales is ca. 72–96% cephalopods (Table 4.2). Santos et al. (2001) reported that 96% (by weight) of prey items in stranded sperm whale stomachs from Norwegian waters were *Gonatus* sp.. Other mammalian predators from the Bering Sea, such as northern fur seals (*Callorhinus ursinus* L.) and Dall's porpoise (*Phocoenoides dalli* True), have 33–50% of their diets made up of squid (Table 4.2). Thick-billed and common murrens (*Uria* spp.) off Bjørnøya and Bleiksøy, Norway, have 30% and 40% of their diets represented by squid and *G. fabricii* (Table 4.2).

The percentage occurrence of indigestible cephalopod parts (mostly beaks) and flesh from the stomachs of sampled predators is listed in Table 4.3. These records indicate cephalopod remains, but not the relative proportion in the diets. All bottlenose whales

(*Hyperoodon ampullatus* Forster) sampled around Iceland had squid remains in their stomachs, and 92% of narwhals caught off Pond Inlet in 1978 had *G. fabricii* parts in their digestive tracts (79% in 1979) (Table 4.2). Cephalopods comprised 67–71% of the diet of bearded seals (*Erignathus barbatus* Erxleben) from Grise Fjord (Table 4.2), and 69.4% of the diet was unidentified octopods near Barrow, Alaska (Table 4.3). Of the sperm whales collected off Andenes, Norway, in 1971, 83% had squid beaks in their stomachs (Table 4.3).

More than 50% of the anecdotal accounts of diets of Arctic predators list *Gonatus* sp. (likely to be *G. fabricii* based on locations) in the diets, indicating its importance as a prey species (Table 4.4).

4.4. Discussion

Recent studies have shown that cephalopods, specifically the high-energy keystone species *G. fabricii*, are important prey for a variety of Arctic predators (Frandsen and Wieland 2004, Chambers and Dick 2007). With increasing water temperatures, more temperate species, such as *I. illecebrosus* and *L. forbesi*, are likely to become more common, thereby increasing the competition for prey and adding to the predation pressure on such species as *G. fabricii* (O'Dor 1983). It is unknown what impact these potential shifts in predator–prey interactions might have on the overall food web.

4.4.1. Arctic cephalopod range extensions

a) Gonatus fabricii

We extend the range of *G. fabricii* from that described by Clarke (1966). This new distribution includes the eastern Siberia Sea, the Beaufort Sea (Canada Basin) (Raskoff et al.

2010, B. Bluhm, pers. comm. 2007), Pond Inlet (stomach contents of narwhals) and the most northern Canadian Arctic location, Cape Vera (T.A. Dick, unpubl. data; Fig. 4.1). Although not reported by Nesis (2001), specimens from the Dolphin and Union Strait (ARC; Fig. 4.1) give validity to Nesis's description of a circumpolar species.

Discrepancies have been noted between the range described in this study and previously reported distributions, especially from the Pacific Ocean. Other regions of the Pacific Ocean probably represent a different species of gonatid (Wiborg et al. 1982).

b) *Rossia moelleri*

Nesis (2001) noted that *R. moelleri* is not typically found south of 75°N, although a “questionable” specimen from Franklin Bay was reported. The present range includes specimens collected south of 75°N near Cape Parry and Coronation Gulf, and extending into waters around Iceland (Fig. 4.4). The range also extends to the interior of Frobisher Bay and Melville Island (Fig. 4.4).

c) *Rossia palpebrosa*

With a distribution throughout most of the Arctic Ocean (Nesis 2001), *R. palpebrosa* has a similar range to *R. moelleri*. The present distribution reflects that described by Nesis (2001), with the exception of no records from Iceland or the Danish Strait (Fig. 4.6). The range is extended in the Canadian Arctic to Hudson Strait, the mouth of Cumberland Sound, Frobisher Bay, and Somerset and Ellesmere islands (Fig. 4.6).

d) *Bathypolypus arcticus*

Muus's (2002) redescription of the *B. arcticus* complex requires most museum specimens to be re-examined and identified under the new criteria. Based on current museum records, our map shows a distribution south from Hudson Strait to Frobisher Bay, southern Davis Strait and north to Lady Ann Strait (Fig. 4.7). The species identification of samples collected around the United Kingdom, Norway and southern Greenland are questionable, as they occur in areas of potential overlap between *B. arcticus*, *B. bairdii* and *B. pugniger* n. sp. (Fig. 4.7) (Muus 2002).

A specimen from Cape Parry (CMNML) (Fig. 4.7) was confirmed as the westernmost Canadian distribution of *B. arcticus*, however, records extend the range further west to Point Barrow, Alaska, and the Canada Basin (Fig. 4.7). These locations extend the range west from Muus' (2002) original description. Only two specimens were recorded by Muus (2002) from Canadian waters, one from Devon Island and the other just off the Cumberland Peninsula, Baffin Island. The current map extends the species to Pond Inlet and Frobisher Bay. Our distribution re-affirms O'Dor and Macalaster's (1983) and Nesis's (2001) claim of a western Canadian distribution.

e) *Cirroteuthis muelleri*

Nesis (2001) described *C. muelleri* as a circumpolar species found in deep water (500–3786 m), and our range agrees, with the exception of specimens from the shallower Laptev Sea (Fig. 4.9). Additional locations were identified from the Canada Basin, based on plankton samples and remotely operated vehicle surveys by ArcOD and the NOAA Ocean Explorer (Raskoff et al. 2010, B. Bluhm, pers. comm. 2007; Fig. 4.9). The greatest number of samples caught in one location (n = 63) were caught in northern Baffin Bay (Fig. 4.9).

f) Additional Arctic cephalopod distributions

Several other species have been reported from the Arctic (Table 4.1), and of these *B. bairdii* and *R. glaucopsis* were the most abundant (Table 4.1). The remaining species are listed in Table 4.1.

4.4.2. Predator–prey relationships

Arctic predators of cephalopods are often large and mobile. Consequently, the source of samples collected needs to be considered when designating an “area of interest”. Areas with large numbers of recorded specimens may indicate a greater abundance of cephalopods or may be associated with an active sampling program of a nearby field station or traditional hunting grounds. The latter may also indirectly reflect an abundance of prey in that particular region.

Cape Vera and Pond Inlet are areas where northern fulmars are studied and narwhals are traditionally hunted. Records from both locations indicate that more than 100 samples of *G. fabricii* were collected from individual fulmar and narwhal stomachs (Figs. 4.1, 4.3). This distribution may indicate areas of greater cephalopod concentrations where predators congregate to feed. However, cephalopod beaks can accumulate in stomachs over time, with unknown expulsion rates (Lowry et al. 1986), which could result in an overestimation of predation pressure (Santos et al. 2001). Arctic predators are also migratory, and beaks collected from a sample from one location may be acquired from a different region. In the case of Cape Vera, the northern fulmars were believed to not travel great distances to forage, but a recent survey of the area found only a few individuals hunting in the nearby Hell Gate polynya, suggesting foraging trips of greater distances (Mallory and Gilchrist 2005). However, as Cape Vera is a breeding colony, it is unlikely that the birds would venture too far in search of food while caring for their

young. Also, beaks may indirectly enter a predator's stomach when the animal feeds on a teuthophagus predator (Santos et al. 2001).

Increased sample numbers from a region may also reflect an active commercial fishery with a substantial bycatch. Large numbers of *G. fabricii* are reported from trawls along the south-west coast of Greenland (Fig. 4.1), and are frequently recovered as bycatch in the shrimp fishery (Kristensen 1983, Piatkowski and Wieland 1993, Zumholz and Frandsen 2006). Similarly, *B. arcticus* distribution is frequently reported from trawls (Stewart et al. 1993) (Figs. 4.7, 4.8).

4.4.3. Oceanographic variables and distributions

Many species of cephalopod have planktonic life stages, and ocean currents influence dispersal and local retention. Reports from the Norwegian Sea (between Jan Mayen and Vesterålen) indicate high densities of cephalopods, particularly *G. fabricii*, in areas with eddies (Figs. 4.2, 4.3; Wiborg et al. 1982). Larval *G. fabricii* cannot contract mantle muscles to drive active locomotion (e.g., Nesis 1965, Kristensen 1983, Arkhipkin and Bjørke 1999), and, similarly, mature females lose musculature and revert back to a planktonic way of life (e.g., Clarke 1966, Kristensen 1983, Arkhipkin and Bjørke 1999). By contrast, *B. arcticus* and *Rossia* species lack a planktonic stage, and are not greatly influenced by currents (Sweeney et al. 1992, Wood 2000).

Depth is another key variable, as *C. muelleri* is typically limited to deep water regions in the Arctic Ocean and Baffin Bay (Fig. 4.9).

Polynyas, regions with wind-induced upwellings and direct access to sunlight, have

increased productivity (Brown and Nettleship 1981). The Canadian Arctic has several polynyas, including the large North Water in Baffin Bay (Michel et al. 2006). The distributions of some cephalopod species may correlate with these open water areas. An example is cephalopods from Cape Parry, a potential “hotspot” affected by the Cape Bathurst flaw lead (Michel et al. 2006). This lead creates higher productivity and, in turn, provides greater quantities of prey for cephalopods. Large numbers of *B. arcticus* were also collected off Greenland near the North Water Polynya. Nesis (2003c) suggested that cephalopods caught in the High Arctic through holes in the ice from drifting stations may have been responding to increased light. If this is the case, polynyas are likely to be the areas with most light during the winter months in the Arctic Ocean, and may explain, at least in part, the occurrences of greater numbers of cephalopods and their predators.

4.4.4. Predator–prey distributions relative to ocean variables

Predators are often reported in areas with an abundance of cephalopods (Hjort and Ruud 1929). Table 4.4 lists predators found in the Norwegian Sea near retention areas with strong circular currents (Wiborg et al. 1982, Dommasnes et al. 2001), where planktonic cephalopods (e.g., larvae) are likely to become concentrated. Narwhals feeding near Pond Inlet may be responding to greater prey abundance caused by currents in Baffin Bay and the local polynya (WHOI 2006, Barber and Massom 2007). Belugas have also been reported from the Amundsen Gulf (L. Harwood pers. comm. 2007), which is an area of cephalopod aggregations (Figs. 4.1–4.10), possibly as a result of eddies formed by the influx of water from the Bering Sea (WHOI 2006) or by the retention from the Cape Bathurst polynya flaw lead (Barber and Massom 2007).

4.5. Summary

In summary, cephalopods play an important role in Arctic food webs, and are highly dependent on oceanographic processes for distribution. Further research on the collection of quantitative trawl data in biologically sensitive areas, in areas of active ocean currents and remote regions of the Canadian Arctic are urgently needed. Furthermore, a comprehensive compilation of community-based data on the diets of the commonly harvested marine predators will substantially increase the knowledge of this important group of invertebrates. Equally important is information on the physiological requirements of Arctic animals and climate change. Portner and Farrel (2008) discuss poleward shifts in the geographical distributions of animals, population collapses, changes in seasonal timing of biological events and changes in food-web structure, all of which are influenced by environmental temperatures. Cephalopods inhabit both deep and shallow waters, and some of their larvae are dispersed by surface waters, which make them vulnerable to temperature changes at all depths. Data are needed on cephalopod optimum temperature ranges and oxygen requirements. These baseline data are essential to clarify the importance and distribution of this nutrient-rich food source in Arctic marine food webs in the context of ice loss, warming waters, altered ocean currents, salinity and alien species invasions, including the large cephalopod predators.

Table 4.1. Additional reported cephalopod species from the circumpolar Arctic.

Species	Locations
<i>Architeuthis</i> sp. ^{a,b,c}	Iceland, Norwegian coast, south-west Greenland
<i>Bathypolypus</i> sp. ^{d,e,f}	Baffin Bay, Hudson Strait, south-west Greenland
<i>Bathypolypus bairdii</i> ^{d,e,g,h}	Baffin Bay, Davis Strait, Denmark Strait, east Greenland, south-west Greenland, Iceland, Norwegian coast, south of Svalbard
<i>Bathypolypus pugniger</i> sp. ^{e,h}	Baffin Bay, Denmark Strait, Faroe Islands, Iceland, south-west Greenland
<i>Benthoctopus</i> sp. ^{b,i,j,k}	Faroe–Shetland Strait, Kara Sea, Norwegian coast, Resolute Bay (Nunavut), east Svalbard
<i>Benthoctopus hokkaidensis</i> ^l	Point Barrow, Alaska
<i>Benthoctopus profundorum</i> ^l	Point Barrow, Alaska
<i>Benthoctopus sibericus</i> ^{b,j}	east Siberian and Laptev seas
<i>Brachiooteuthis riiseri</i> ^b	Faroe Islands, Norwegian coast, Norwegian Sea, south Iceland
<i>Eledone cirrhosa</i> ^{b,m}	Iceland, Norwegian coast, Norwegian sea, Svalbard
<i>Gonatus</i> sp. ^{d,e,f,i,n,o}	Baffin Bay, east Baffin Island, Cumberland Strait (mouth), Foxe Basin, southern tip of Greenland, south-west Greenland, Hudson Strait, Point Barrow (Alaska)
<i>Graneledone verrucosa</i> ^b	south of Iceland
<i>Grimpoteuthis</i> sp. ^{i,p}	Denmark Strait
<i>Illex illecebrosus</i> ^{a,b}	south Greenland (Frederikshaab), Iceland
<i>Loligo forbesii</i> ^{q,r}	North Sea, Norwegian coast, Norwegian Sea
<i>Moroteuthis robusta</i> ^s	Gulf of Alaska
<i>Ommastrephes bartrami</i> ^b	north-east Greenland, Norwegian Sea
<i>Onychoteuthis banski</i> ^b	south of Iceland, north coast of Norway
<i>Opisthoteuthis</i> sp. ^{t,u}	Davis Strait, Gulf of Alaska, south Iceland
<i>Opisthoteuthis borealis</i> ^v	south-west Greenland, south Iceland
<i>Rossia</i> sp. ^{e,f,w}	Baffin Bay, Denmark Strait, Hudson Strait, north Somerset Island (Nunavut)
<i>Rossia glaucopsis</i> ^{b,g,m,n,q,r,x}	Barents Sea, around the Faroe Islands, east Greenland, Kara Sea, Iceland, North Sea, Svalbard
<i>Rossia macrosoma</i> ^b	Faroe Islands, Norwegian coast
<i>Rossia megaptera</i> ^{a,y}	Davis Strait
<i>Semirossia tenera</i> ^b	Laptev Sea, Norwegian coast
<i>Sepiolo atlantica</i> ^{b,m}	South of Iceland, Iceland

Table 4.1. Cont'd

Species Cont'd	Locations Cont'd
<i>Sepiola rondeletti</i> ^y	Ellesmere Island, Jones Sound
<i>Stauroteuthis syrtensis</i> ^t	Davis Strait, Denmark Strait
<i>Teuthowenia megalops</i> ^{b,g,i,z}	Denmark Strait, south-west Greenland, south Iceland
<i>Todarodes sagittatus</i> ^{b,m}	Faroe Islands, Iceland, north coast of Norway
<i>Todaropsis elbanae</i> ^{aa}	North Sea, Norway

^aBerry 1925; ^bGrimpe 1933; ^cNesis et al. 2003; ^dNorthwest Atlantic Fisheries Organization (NAFO) fishery survey of 2004 (M. Treble, pers. comm.); ^eTreble 2007; ^fNAFO survey of 2007 (M. Treble, pers. comm.); ^gMuus 1962; ^hMuus 2002; ⁱSmithsonian National Museum of Natural History Invertebrate Zoology Collections; ^jNesis 2001; ^kMuus (2002) reported that the *Benthoctopus* type specimen is actually a *Bathypolypus* spp. Therefore any mention of *Benthoctopus piscatorum* has been listed as *Benthoctopus* sp.; ^lMercer 1968a; ^mTaxonomic Information System for the Belgian Coastal Area database; ⁿAtlantic Reference Centre database; ^oPiatkowski and Wieland 1993; ^pReferred to in this article as *Opisthoteuthis megaptera*, an invalid species name according to the Integrated Taxonomic Information System (2008); ^qHistorical Benthic Dredge Samples from the Southern Baltic and the North Sea database; ^rKondakov 1937; ^sNorth Pacific Groundfish Observer database; ^tCollins 2002; ^uNesis 2003a; ^vCollins 2005; ^wD. Hardie (pers. comm. 2007); ^xAtlantic Reference Centre; ^yAcademy of Natural Sciences Malacology Database; ^zNesis 1965; ^{aa}Swedish Museum of Natural History: Invertebrates database.

Table 4.2. Percentages of cephalopod prey items reported from the stomachs of Arctic predators

Location	Predators	Cephalopod Prey	% of diet (weight)
Bering Sea	Baird's beaked whale (<i>Berardius bairdii</i>) ^a	cephalopods	90%
	Baird's beaked whale (<i>Berardius bairdii</i>) ^a	octopods	<1%
	beluga whale (<i>Delphinapterus leucas</i>) ^a	cephalopods	2%
	Bering Sea beaked whale (<i>Mesoplodon stejnegeri</i>) ^a	cephalopods	90%
	Dall's porpoise (<i>Phocoenoides dalli</i>) ^a	squid	50%
	fin whale (<i>Balaenoptera physalus</i>) ^a	cephalopods	2%
	harbour porpoise (<i>Phocoena phocoena</i>) ^a	squid	1%
	harbour seal (<i>Phoca vitulina</i>) ^a	squid	4%
	humpback whale (<i>Megaptera novaeangliae</i>) ^a	cephalopods	1%
	killer whale (<i>Orcinus orca</i>) ^a	cephalopods	20%
	minke whale (<i>Balaenoptera acutorostrata</i>) ^a	cephalopods	1%
	northern fur seal (<i>Callorhinus ursinus</i>) ^a	squid	33%
	northern sea lion (<i>Eumetopias jubatus</i>) ^a	squid	3%
	Pacific walrus (<i>Odobenus rosmarus</i>) ^a	octopods	1%
	ribbon seal (<i>Histiophoca fasciata</i>) ^a	squid	1%
	sperm whale (<i>Physeter macrocephalus</i>) ^a	cephalopods	82%
	spotted seal (<i>Phoca largha</i>) ^a	squid	<1%
	Bjørnøya and Bleiksøy islands	thick-billed murre (<i>Uria lomvia</i>) ^b	squid
common murre (<i>Uria aalge</i>) ^b		<i>Gonatus fabricii</i>	40%
Clyde	bearded seal (<i>Erignathus barbatus</i>) ^{c,d}	<i>Bathypolypus arcticus</i>	<1%
		<i>Gonatus</i> sp.	<1%
Grise Fjord	bearded seal (<i>Erignathus barbatus</i>) ^{c,e}	<i>Bathypolypus arcticus</i>	<1%
		<i>Gonatus</i> sp.	<1%
Iceland	hooded seal (<i>Cystophora cristata</i>) ^f	<i>Gonatus</i> sp.	79%
		<i>Gonatus</i> sp.	96%
Norwegian waters	sperm whale (<i>Physeter macrocephalus</i>) ^g	<i>Haliphron</i>	1.60%
		<i>Histioteuthis</i>	1.20%
		<i>Teuthowenia</i>	0.34%
		<i>Todarodes</i>	0.43%
		Cranchiidae	25%
eastern Norwegian waters	sperm whale (<i>Physeter macrocephalus</i>) ^f	<i>Gonatus</i> sp.	9%
		<i>Histioteuthis</i>	38%
		<i>Bathypolypus arcticus</i>	<1%
Pond Inlet	bearded seal (<i>Erignathus barbatus</i>) ^{c,h}	<i>Gonatus</i> sp.	<1%
		<i>Bathypolypus arcticus</i>	<1%
		narwhal (<i>Monodon monoceros</i>) ^{i,j,k}	squid

^aPerez 1990; ^bBarrett et al. 1997; ^cFinley and Evans 1983; ^dFinley and Evans (1983) reported that bearded seals from the Clyde had a 57% occurrence of *B. arcticus* and *Gonatus* sp. in their stomachs. ^eFinley and Evans (1983) also reported bearded seals from Grise Fjord, NU, had a 67% occurrence of *B. arcticus* and a 71% occurrence of *Gonatus* sp. in their stomachs. ^fBjørke 2001; ^gSantos et al. 2001; ^hFinley and Evans (1983) described an occurrence of 85% *B. arcticus* and 77% *Gonatus* sp. in the stomachs of bearded seals caught off Pond Inlet, NU. ⁱFinley and

Gibb 1982; ^jEstimates from Pond Inlet in 1978 described a 92% occurrence of *G. fabricii* and a 16% occurrence of *B. arcticus* in the stomachs of narwhals caught. In 1979, 79% of narwhals had *G. fabricii* and 17% had *B. arcticus* remains in their stomachs (Finley and Gibb 1982).

^kFinley and Gibb (1982) reported that narwhals in Pond Inlet were feeding on cephalopods, in particular, *G. fabricii*.

Table 4.3. Percentage occurrences of cephalopod prey items from the stomachs of Arctic predators (percentages of predators sampled with cephalopods in their stomachs).

Location	Predators	Cephalopod Prey	% occurrence in stomachs
Andenes	sperm whale (<i>Physeter macrocephalus</i>) ^a	squid	83.3
Baffin Bay, Greenland	narwhal (<i>Monodon monoceros</i>) ^b	<i>Gonatus fabricii</i>	35
Barrow (Alaska)	bearded seal (<i>Erignathus barbatus</i>) ^c	<i>Octopus</i> spp.	69.4
Barrow (Alaska), Holman (Canada)	ringed seal (<i>Pusa hispida</i>) ^c	cephalopods	2.6
Davis Strait	Greenland halibut (<i>Reinhardtius hippoglossoides</i>) ^{d,e}	cephalopods	2
Greenland Sea pack ice	harp seal (<i>Phoca groenlandica</i>) ^f	<i>Gonatus</i> sp.	40
	hooded seal (<i>Cystophora cristata</i>) ^f	<i>Gonatus</i> sp.	82
Hendrickson Island	beluga whale (<i>Delphinapterus leucas</i>) ^g	cephalopods	3
Jan Mayen	northern bottlenose whale (<i>Hyperoodon ampullatus</i>) ^a	cephalopods	75
Kendall Island Bird Sanctuary	beluga whale (<i>Delphinapterus leucas</i>) ^g	cephalopods	3
Little Diomede Island (Alaska)	spotted seal (<i>Phoca largha</i>) ^c	squid	2.6
north-east Iceland	northern bottlenose whale (<i>Hyperoodon ampullatus</i>) ^a	<i>Gonatus</i> sp.	100

^aBjørke 2001; ^bLaidre et al. 2004; ^cDehn et al. 2007; ^dOrr and Bowering, 1997; ^eOrr and Bowering (1997) also commented that Greenland halibut preyed on *Gonatus* sp. in the Davis Strait; ^fHaug et al. 2004; ^gL. Harwood (pers. comm. 2007).

Table 4.4. Anecdotal accounts of cephalopods as prey species from the Arctic.

Location	Predators	Cephalopod prey
Admiralty Inlet	narwhal (<i>Monodon monoceros</i>) ^a	squid
Akpatok Island	thick-billed murre chicks (<i>Uria lomvia</i>) ^b	<i>Gonatus fabricii</i>
Arctic/sub-Arctic waters of North America and Eurasia	beluga whale (<i>Delphinapterus leucas</i>) ^c	cephalopods
Atlantic side of Arctic	narwhal (<i>Monodon monoceros</i>) ^d	squid
Barents Sea	harp seal (<i>Phoca groenlandica</i>) ^c	squid
	hooded seal (<i>Cystophora cristata</i>) ^c	<i>Gonatus</i> sp.
Barrow (Alaska)	bearded seals (<i>Erignathus barbatus</i>) ^e	<i>Octopus</i> sp.
Barrow (Alaska), Holman (Canada)	ribbon seal pups (<i>Histiophoca fasciata</i>) ^e	cephalopods
	spotted seals (<i>Phoca largha</i>) ^e	cephalopods
	walrus (<i>Odobenus rosmarus</i>) ^e	<i>Octopus</i> sp.
Barrow Strait	narwhal (<i>Monodon monoceros</i>) ^a	squid
Canadian Arctic	bearded seals (<i>Erignathus barbatus</i>) ^e	<i>Octopus</i> sp.
Coats Island	thick-billed murre chicks (<i>Uria lomvia</i>) ^b	<i>Gonatus fabricii</i>
Digges Island	thick-billed murre chicks (<i>Uria lomvia</i>) ^b	<i>Gonatus fabricii</i>
east coast of Greenland, Denmark Strait	harp seal (<i>Phoca groenlandica</i>) ^f	<i>Gonatus fabricii</i>
	hooded seal (<i>Cystophora cristata</i>) ^f	<i>Gonatus fabricii</i>
eastern Bering Sea	beluga whale (<i>Delphinapterus leucas</i>) ^d	cephalopods
	Greenland halibut (<i>Reinhardtius hippoglossoides</i>) ^d	squid
	harp seal (<i>Phoca groenlandica</i>) ^d	squid
	hooded seal (<i>Cystophora cristata</i>) ^d	squid
	sperm whale (<i>Physeter macrocephalus</i>) ^d	squid
Eclipse Sound	narwhal (<i>Monodon monoceros</i>) ^a	squid
Greenland	beluga whale (<i>Delphinapterus leucas</i>) ^g	cephalopods
Hantzsch Island	thick-billed murre chicks (<i>Uria lomvia</i>) ^b	<i>Gonatus fabricii</i>
High Arctic	northern bottlenose whale (<i>Hyperoodon ampullatus</i>) ^h	<i>Gonatus</i> sp.
	long-finned pilot whale (<i>Globicephala melas</i>) ⁱ	<i>Gonatus</i> sp.
	sperm whale (<i>Physeter macrocephalus</i>) ⁱ	<i>Gonatus</i> sp.
Iceland–Faroe Ridge	cod (<i>Gadus</i> sp.) ^h	<i>Gonatus</i> sp.
	halibut sp. ^h	Ommastrephidae
		<i>Gonatus</i> sp.
		Ommastrephidae
Irminger Sea, south Iceland	northern bottlenose whale (<i>Hyperoodon ampullatus</i>) ^j	<i>Gonatus</i> sp.
Lancaster Sound	narwhal (<i>Monodon monoceros</i>) ^a	squid
Navy Board Inlet	narwhal (<i>Monodon monoceros</i>) ^a	squid
northern Bering and Chukchi seas	beluga whale (<i>Delphinapterus leucas</i>) ^g	<i>Gonatus</i> sp.
		<i>Octopus</i> sp.
Norwegian Sea	beluga whale (<i>Delphinapterus leucas</i>) ^j	<i>Gonatus</i> sp.
	blue ling (<i>Molva dypterygia</i>) ^j	<i>Gonatus</i> sp.
	cod (<i>Gadus</i> sp.) ^j	<i>Gonatus</i> sp.
	Greenland halibut (<i>Reinhardtius hippoglossoides</i>) ^j	<i>Gonatus</i> sp.
	Greenland shark (<i>Somniosus microcephalus</i>) ^j	<i>Gonatus</i> sp.
	grenadier fish sp. ^j	<i>Gonatus</i> sp.
	harp seal (<i>Phoca groenlandica</i>) ^{i,k}	<i>Gonatus</i> sp.
		squid
	hooded seal (<i>Cystophora cristata</i>) ^{j,k}	<i>Gonatus</i> sp.
		<i>Gonatus</i> sp.
	narwhal (<i>Monodon monoceros</i>) ^j	<i>Gonatus</i> sp.
	northern bottlenose whale (<i>Hyperoodon ampullatus</i>) ^j	<i>Gonatus</i> sp.
	long-finned pilot whale (<i>Globicephala melas</i>) ^j	<i>Gonatus</i> sp.

Table 4.4 Cont'd

Location Cont'd	Predators Cont'd	Cephalopod prey Cont'd
Norwegian Sea Cont'd	saithe (<i>Pollachius virens</i>) ^j sea perch sp. ^j seabirds ^j Sowerby's beaked whale (<i>Mesoplodon bidens</i>) ^j sperm whale (<i>Physeter macrocephalus</i>) ^j	<i>Gonatus</i> sp. <i>Gonatus</i> sp. <i>Gonatus</i> sp. <i>Gonatus</i> sp. <i>Gonatus</i> sp.
Peel Sound	narwhal (<i>Monodon monoceros</i>) ^a	squid
Pond Inlet, Eclipse Sound, Admiralty Inlet	narwhal (<i>Monodon monoceros</i>) ^l	squid
Prince Regent Inlet	narwhal (<i>Monodon monoceros</i>) ^a	squid
southern Greenland	Greenland halibut (<i>Reinhardtius hippoglossoides</i>) ^m	squid
Tremblay Sound, Creswell Bay	narwhal (<i>Monodon monoceros</i>) ⁱ	<i>Gonatus</i> sp.
Uummannaq (north-west Greenland)	narwhal (<i>Monodon monoceros</i>) ⁿ	<i>Gonatus fabricii</i>
western Alaska	beluga whale (<i>Delphinapterus leucas</i>) ^g	<i>Gonatus</i> sp. <i>Octopus</i> sp.
Within the predators' natural range	harbour seal (<i>Phoca vitulina</i>) ^{d,o} ribbon seal (<i>Histiophoca fasciata</i>) ^{d,o} spotted seal (<i>Phoca largha</i>) ^{d,o} narwhal (<i>Monodon monoceros</i>) ^{d,o}	squid squid squid <i>Gonatus fabricii</i>

^aWelch et al. 1992; ^bGaston 1985; ^cStewart and Stewart 1989; ^dLoeng et al. 2005; ^eDehn et al. 2007; ^fHaug et al. 2004; ^gDahl et al. 2000; ^hHjort and Ruud 1929; ⁱLaidre et al. 2004; ^jBjørke 2001; ^kDommasnes et al. 2001; ^lHay and Mansfield 1989; ^mWoll and Gundersen 2004; ⁿCOSEWIC 2004; ^oTomilin 1967 (1957).

Figure 4.1. Circumpolar records of *Gonatus fabricii*. Sources: Berry (1925); Hjort & Ruud (1929); Grieg (1930) and Kubodera & Tsuchiya (1993), as cited in Cephbase; Grimpe (1933); Muus (1962); Nesis (1965, 2001, 2003c); Young (1973); Kristensen (1977, 1982); Finley and Gibb (1982); Wiborg et al. (1982); Gaston (1985); Sennikov et al. (1989); Piatkowski and Wieland (1993); Barrett et al. (1997); B. Bluhm (pers. comm. 2007); Zumholz et al. (2007); Atlantic Reference Centre collection; Canadian Museum of Nature collection; Atlantic Reference Centre online database; Smithsonian National Museum of Natural History online database; Northwest Atlantic Fisheries Organization (NAFO) fishery survey of 2004 (M. Treble, pers. comm.); NAFO survey of 2007 (M. Treble, pers. comm.); Raskoff et al. 2010; and T.A. Dick (unpubl. data). Forty-two specimens were collected during the NAFO trawl surveys in 2006. They were caught along the west side of Baffin Bay between depths of 425.5 and 1482.5 m (Treble 2007).

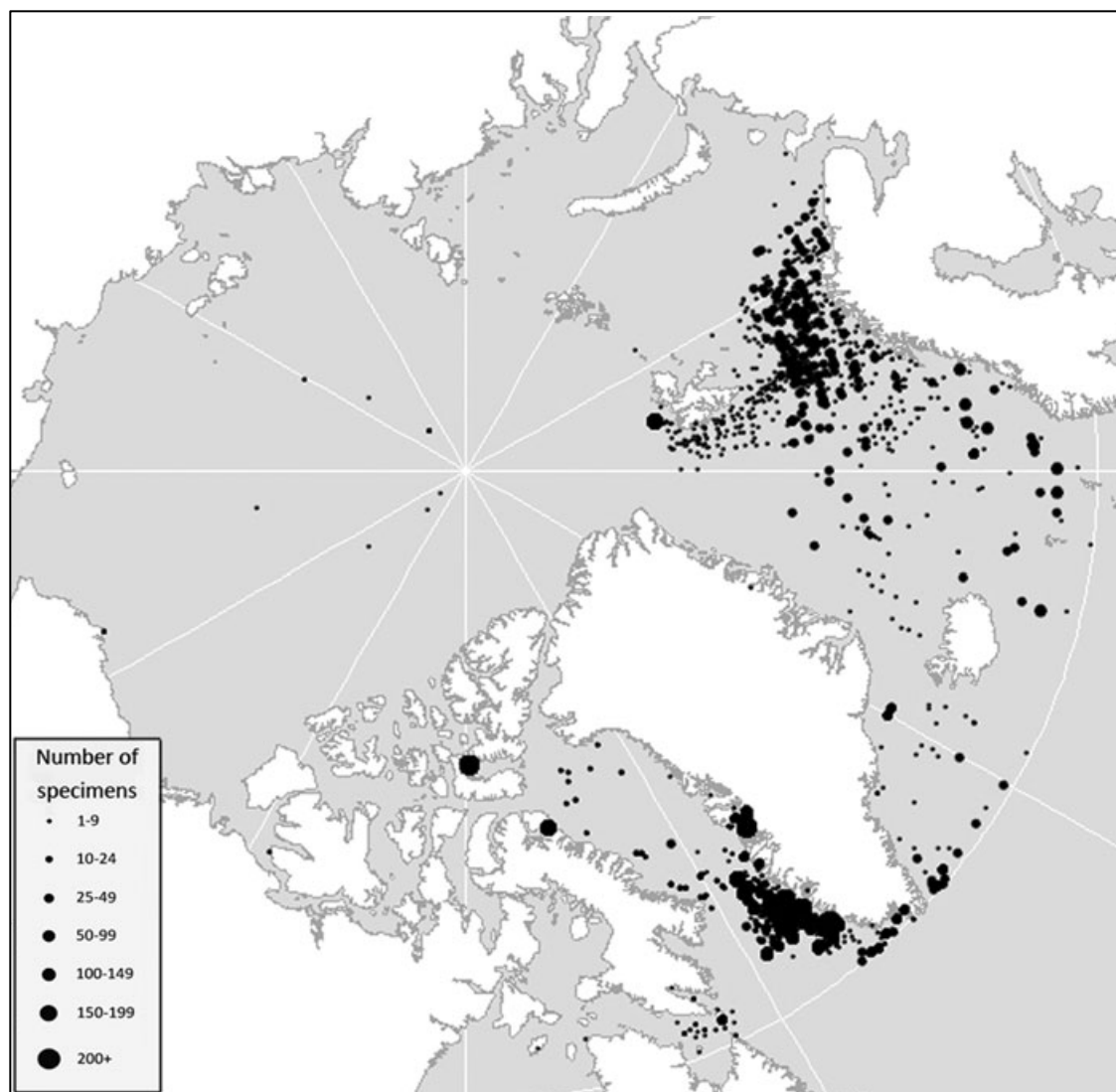


Figure 4.2. Distribution of *Gonatus fabricii* in the western European Arctic with reference to potential spawning locations, areas of 500+ juveniles per haul caught between June and August 1978–1981 and a region where 8000 juveniles per haul were recorded in July 1980 (Wiborg et al. 1978–1981 and a region where 8000 juveniles per haul were recorded in July 1980 (Wiborg et al. 1982). For a more accurate representation of the juvenile distribution of *G. fabricii*, see Wiborg et al. (1982: fig. 1).

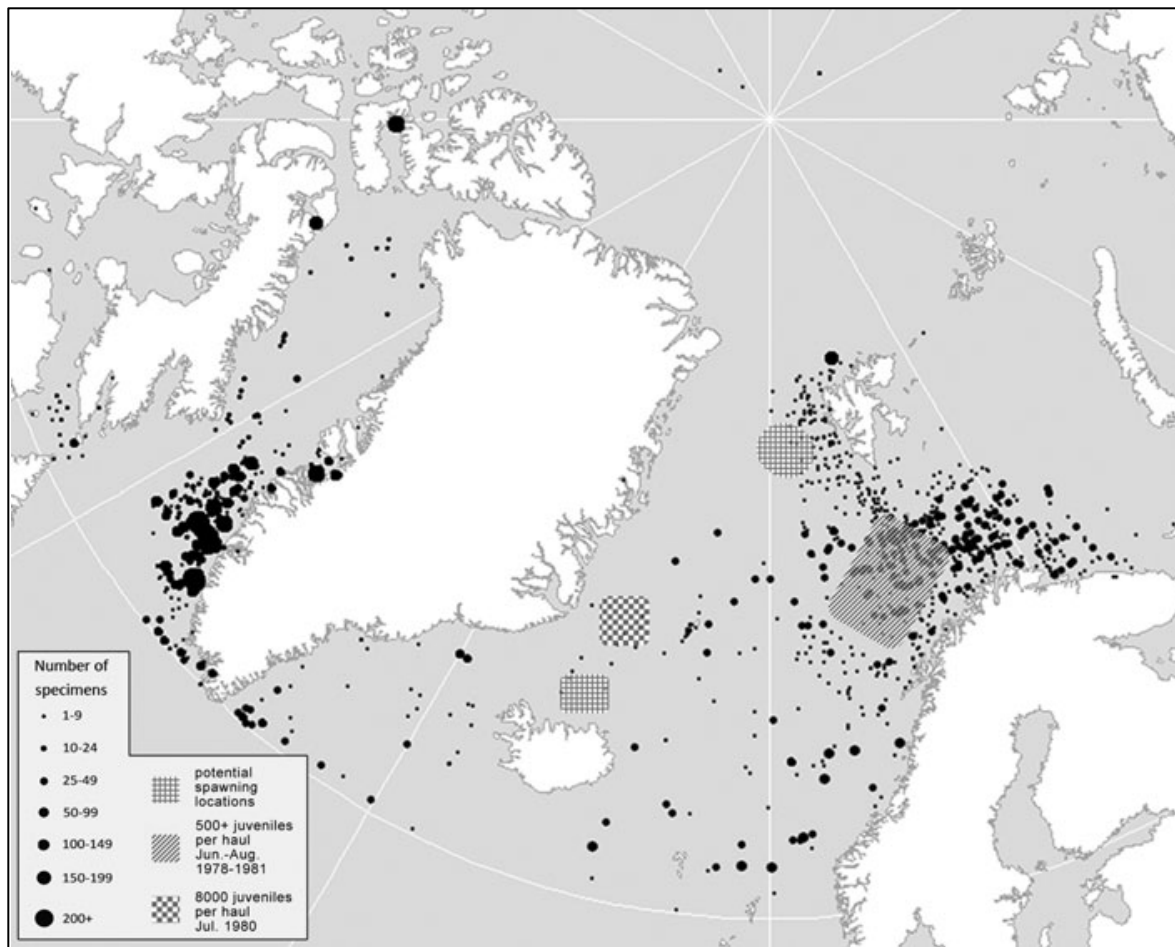


Figure 4.3. Occurrence records of *Gonatus fabricii* specimens, including remains in the stomach contents of predators. Sources: Berry (1925); Hjort and Ruud (1929); Grieg (1930) and Kubodera & Tsuchiya (1993), as cited in Cepibase; Grimpe (1933); Muus (1962); Nesis (1965, 2001, 2003c); Young (1973); Kristensen (1977, 1982); Wiborg et al. (1982); Finley and Gibb (1982); Gaston (1985); Sennikov et al. (1989); Piatkowski and Wieland (1993); Barrett et al. (1997); B. Bluhm (pers. comm. 2007); Zumholz et al. (2007); Atlantic Reference Centre collection; Canadian Museum of Nature collection; Atlantic Reference Centre online database; Smithsonian National Museum of Natural History online database; Northwest Atlantic Fisheries Organization (NAFO) (M. Treble pers. comm.); NAFO survey of 2007 (M. Treble, pers. comm.); Raskoff et al. 2010; and T.A. Dick (unpubl. data).

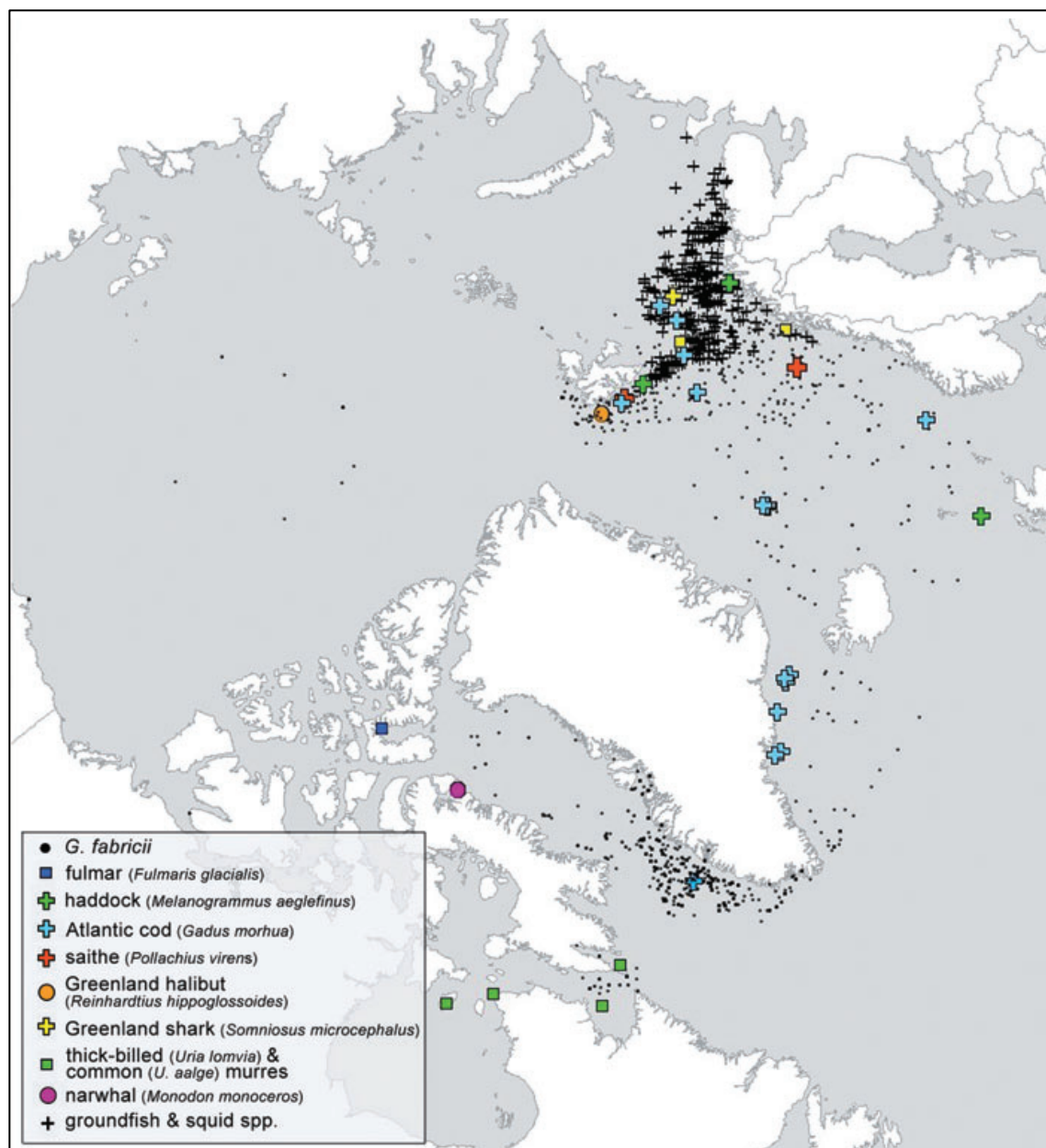


Figure 4.4. Circumpolar records of *Rossia moelleri*. Sources: Grieg(1930), as cited in Cephbase; Grimpe (1933); Kondakov (1937); Muus (1962); Wacasey et al. (1979); Atkinson and Wacasey (1989); Nesis (2001); Canadian Museum of Nature collection; and Atlantic Reference Centre online database. One specimen of *R. moelleri* was caught between a depth of 139 and 150.5 m from the western side of Baffin Bay during Northwest Atlantic Fisheries Organization trawl surveys in 2006 (Treble 2007).

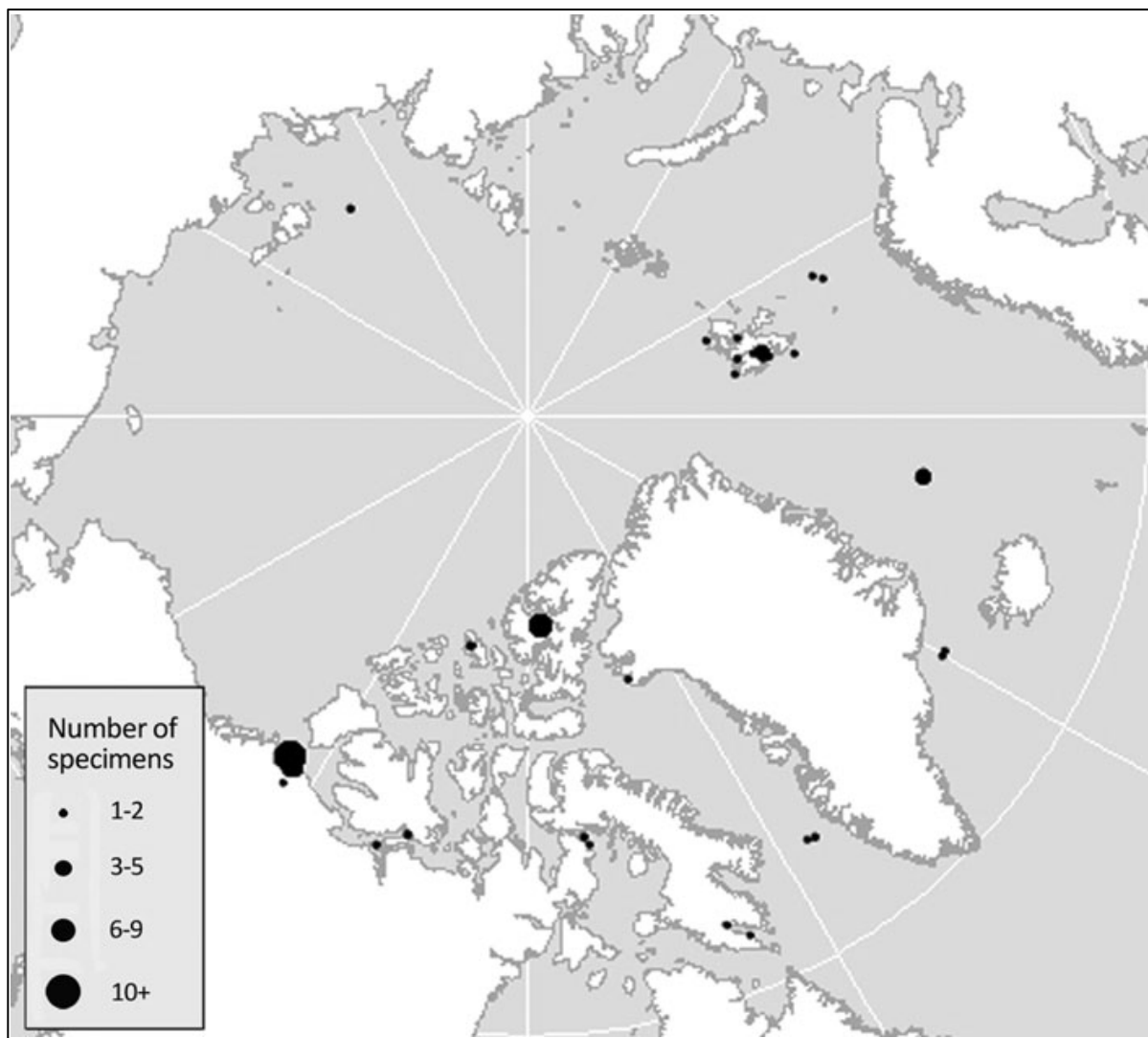


Figure 4.5. Circumpolar records of *Rossia moelleri* specimens, including remains in the stomach contents of predators. Sources: Grieg (1930), as cited in Cephbase; Grimpe (1933); Kondakov (1937); Muus (1962); Wacasey et al. (1979); Atkinson and Wacasey (1989); Nesis (2001); Canadian Museum of Nature collection; and Atlantic Reference Centre online database.

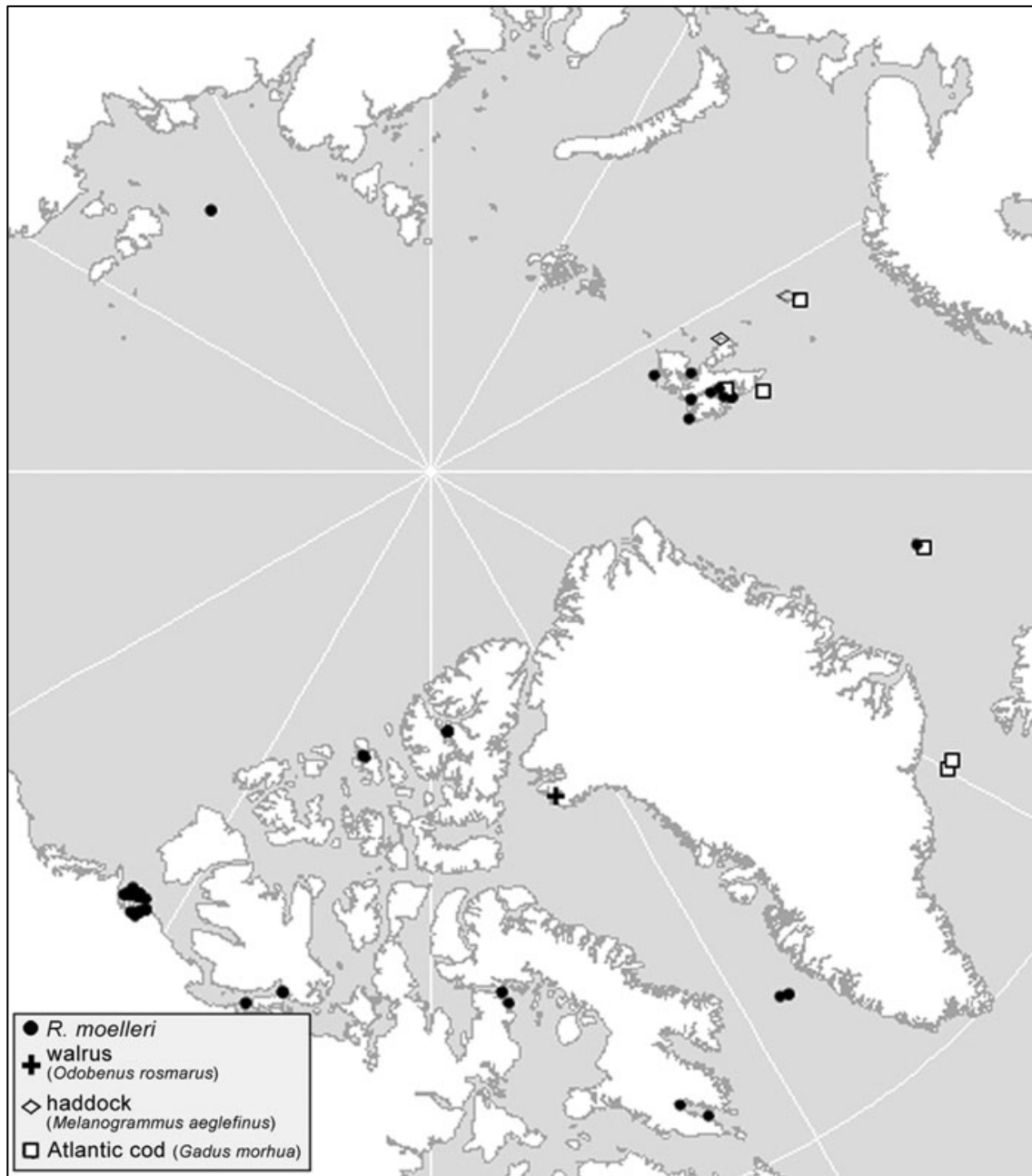


Figure 4.6. Circumpolar records of *Rossia palpebrosa*. Sources: Grimpe (1933); Kondakov (1937); Wacasey et al. (1979); Nesis (2001); Canadian Museum of Nature collection; and Atlantic Reference Centre online database. Seven specimens were collected from the western side of Baffin Bay during Northwest Atlantic Fisheries Organization trawl surveys in 2006. They were all caught between depths of 123 and 611.5 m (Treble 2007).

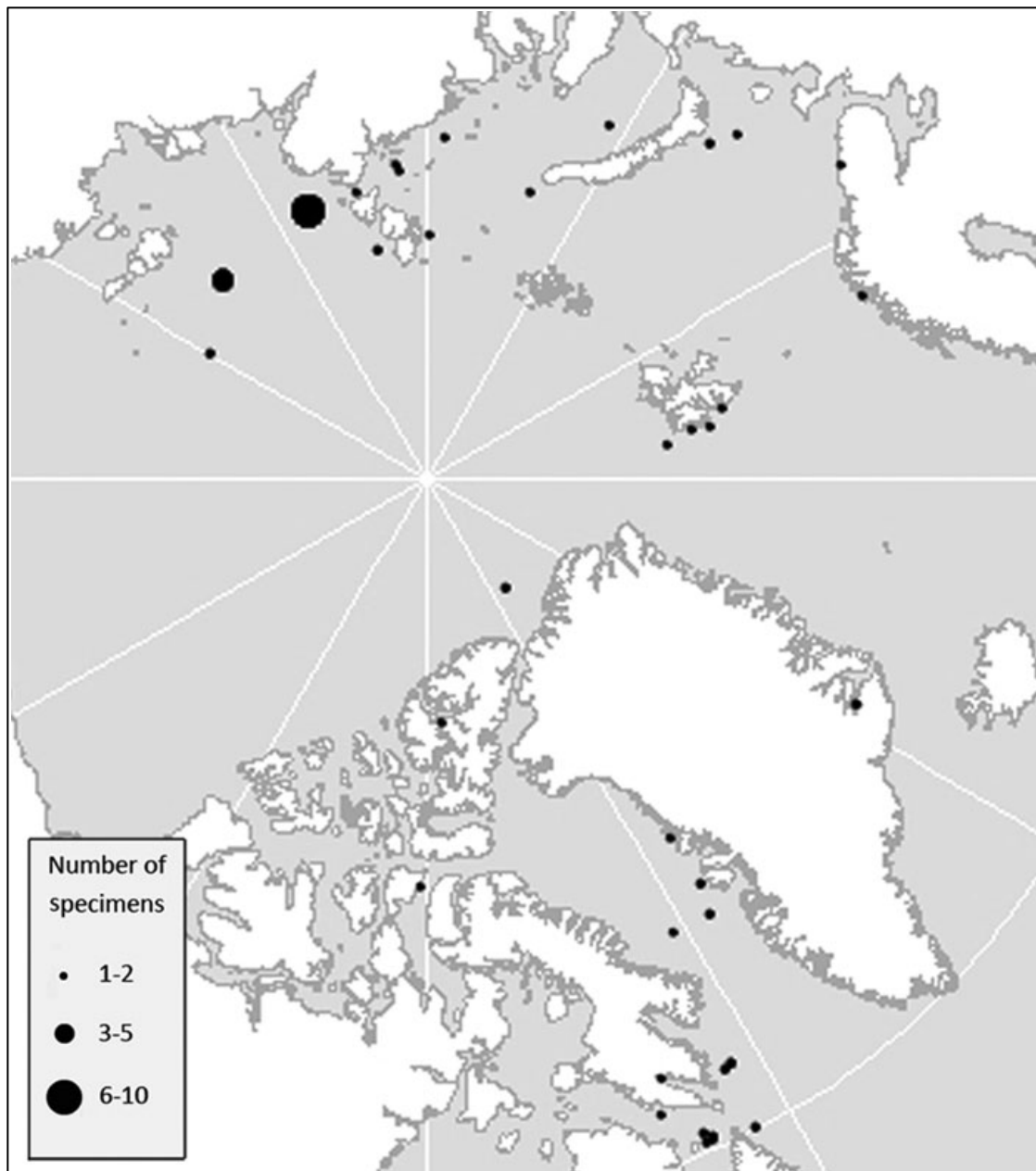


Figure 4.7. Circumpolar records of *Bathypolypus arcticus*. Not included is a record (Taxonomic Information System for the Belgian Coastal Area online database) from the centre of Iceland. Sources: Hoyle (1886), Grieg (1930), Robson (1931), Adam (1939) and Macalaster (1976), as cited in Cephbase; Grimpe (1933); Kondakov (1937); Muus (1962, 2002); Wacasey et al. (1979); Finley and Gibb (1982); Atkinson and Wacasey (1989); Stewart et al. (1993); Nesis (2001); Canadian Museum of Nature collection; Smithsonian National Museum of Natural History online database; Northwest Atlantic Fisheries Organization (NAFO) survey of 2004 (M. Treble, pers. comm.); and NAFO survey of 2007 (M. Treble, pers. comm.).

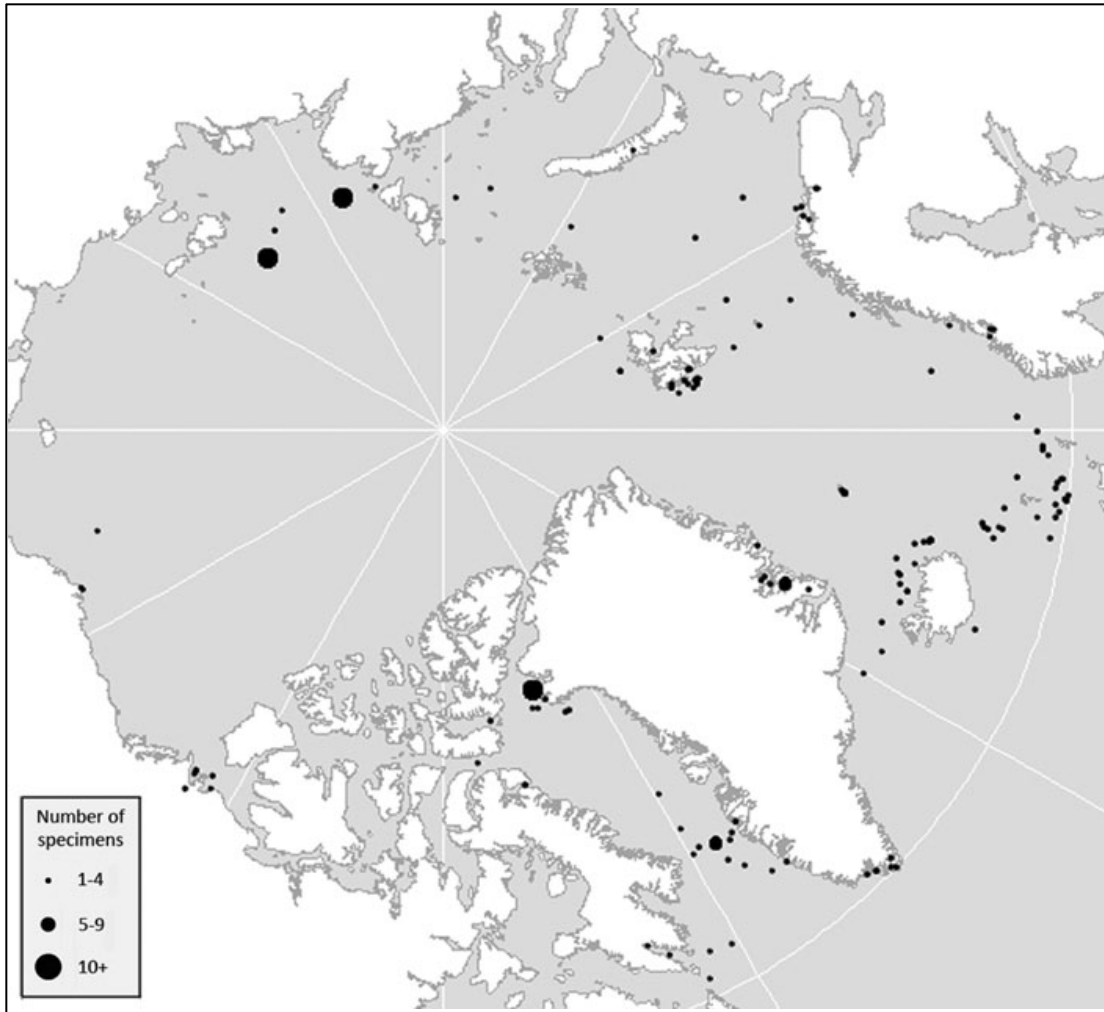


Figure 4.8. Circumpolar records of *Bathypolypus arcticus* specimens, including remains in the stomach contents of predators. Sources: Hoyle (1886), Grieg (1930), Robson (1931), Adam (1939) and Macalaster (1976), as cited in Cephbase; Grimpe (1933); Kondakov (1937); Muus (1962, 2002); Wacasey et al. (1979); Finley and Gibb (1982); Atkinson and Wacasey (1989); Stewart et al. (1993); Nesis (2001); Canadian Museum of Nature collection; Smithsonian National Museum of Natural History online database; Northwest Atlantic Fisheries Organization (NAFO) survey of 2004 (M. Treble, pers. comm.); and NAFO survey of 2007 (M. Treble, pers. comm.).

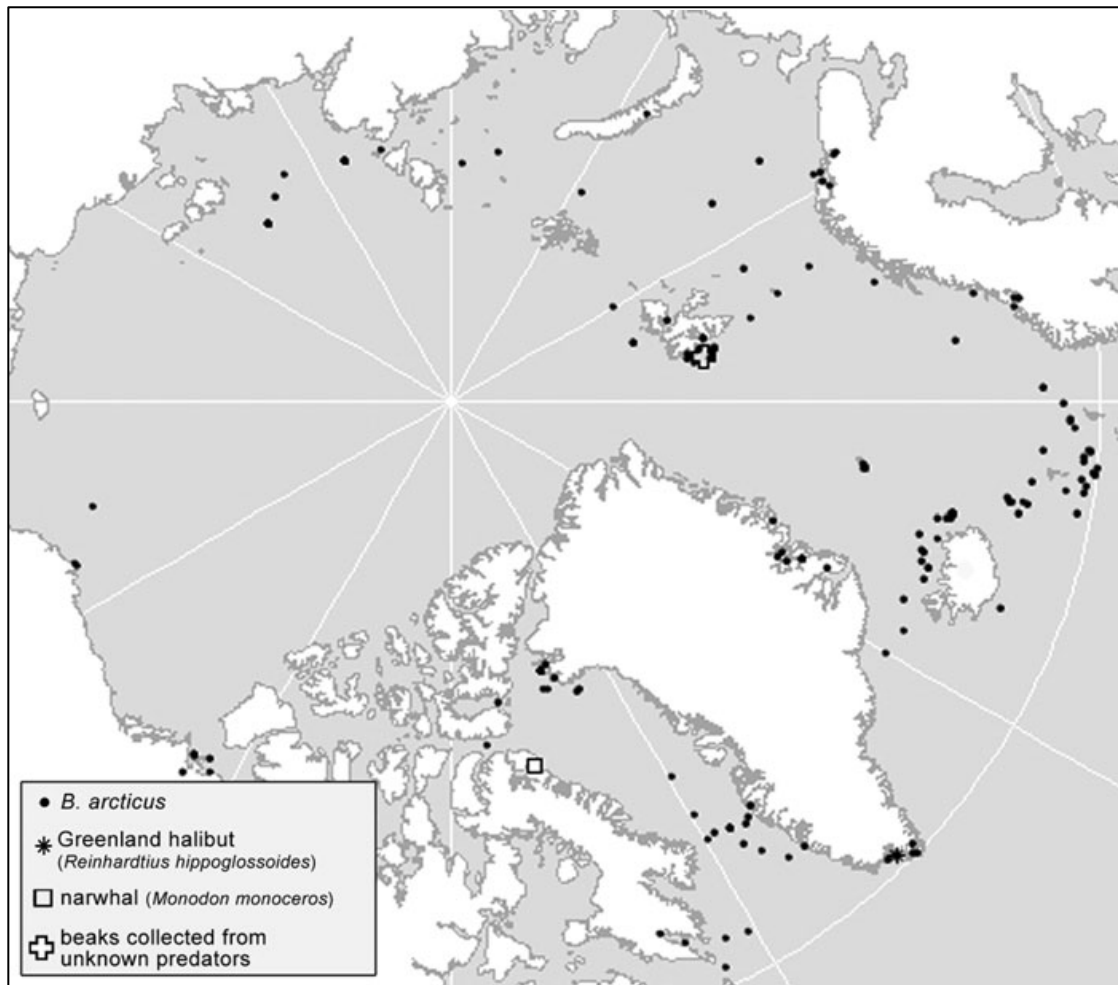


Figure 4.9. Circumpolar records of *Cirroteuthis muelleri*. Forty-five individuals were collected from the western side of Baffin Bay during the Northwest Atlantic Fisheries Organization (NAFO) trawl surveys in 2006. They were collected between the depths of 103 and 1482.5 m (Treble 2007). Sources: Grieg (1930) and Robson (1931), as cited in Cephbase; Grimpe (1933); Muus (1962); Nesis (1987, 2001); Collins (2002); B. Bluhm (pers. comm. 2007); Raskoff et al. 2010; Ifremer BIOCEAN database 2007; Smithsonian National Museum of Natural History online database; Swedish Museum of Natural History online database; and NAFO survey of 2004 (M. Treble, pers. comm.).

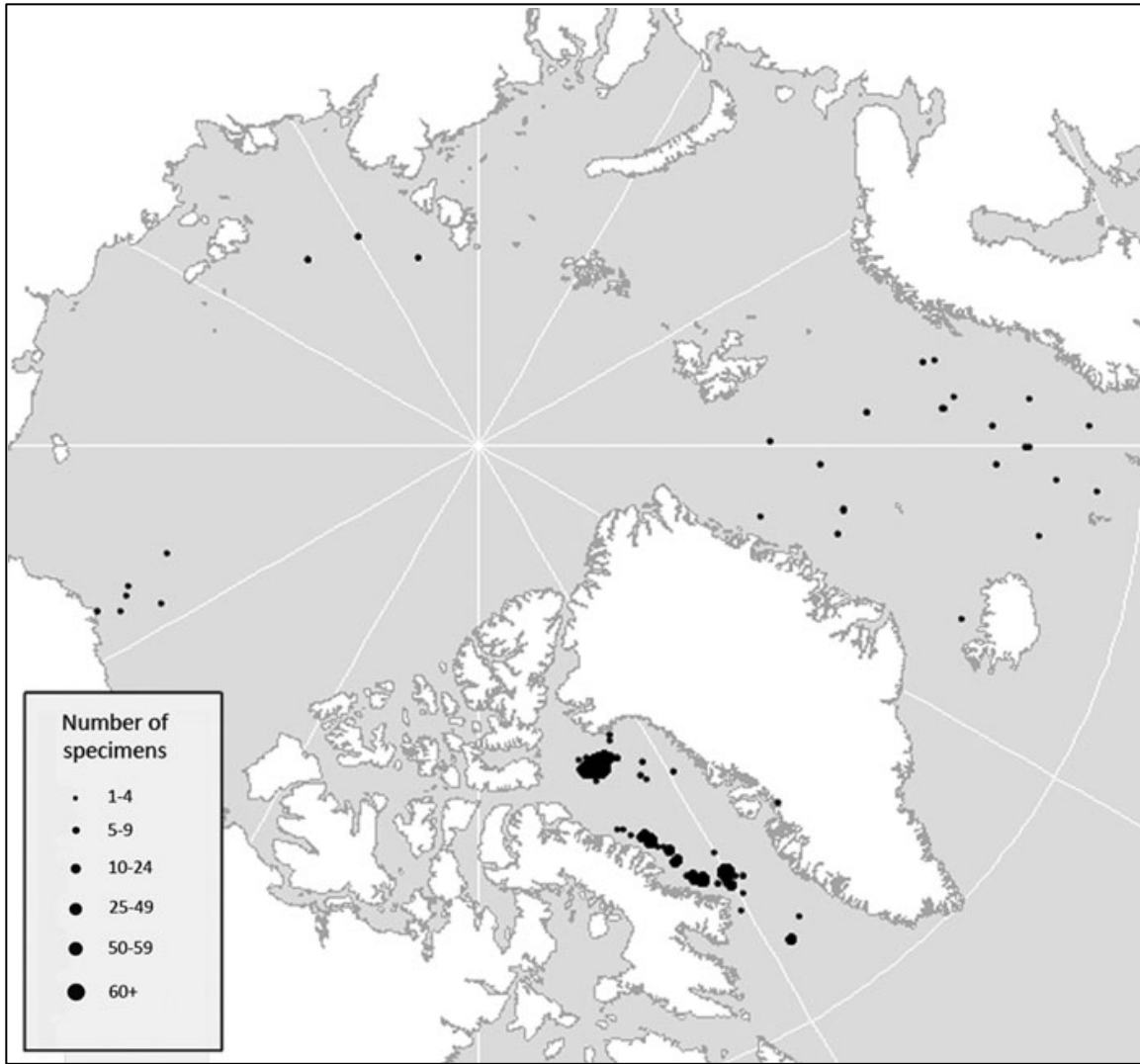
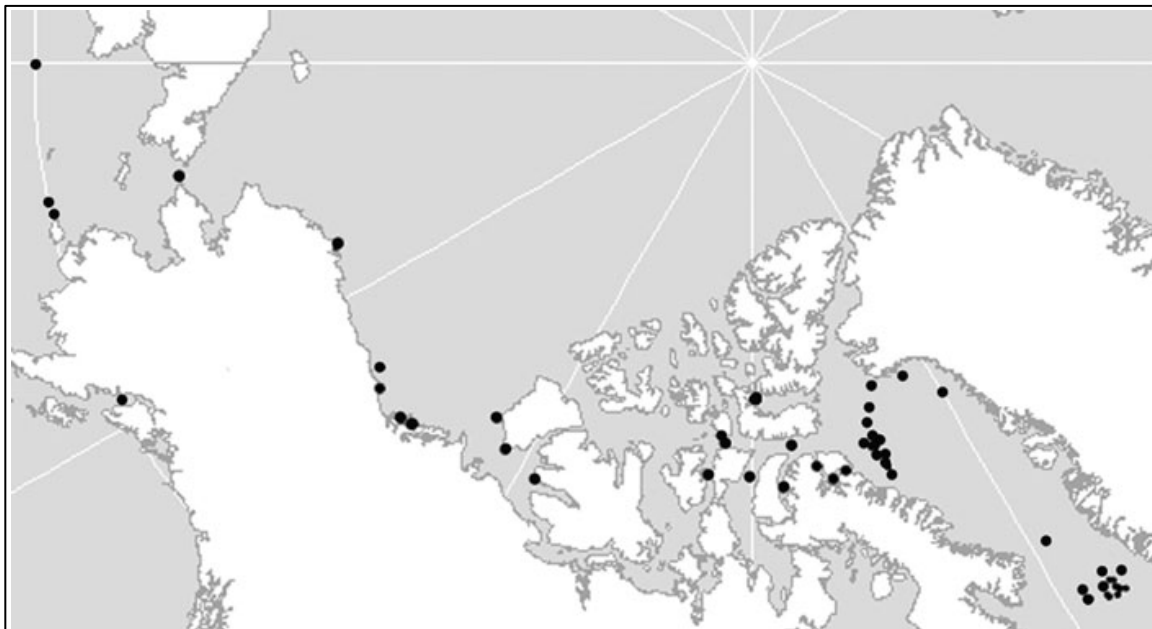


Figure 4.10. Canadian records of unidentified cephalopods. Not included are a record of an unidentified cephalopod from central Norway and one from Alaska (coordinates not accurate). Sources: Hay and Mansfield (1989); Welch et al. (1992); Stewart et al. (1993); Dehn et al. (2007); L. Harwood (pers. comm. 2007); Smithsonian National Museum of Natural History online database; Northwest Atlantic Fisheries Organization (NAFO) survey of 2004 (M. Treble, pers. comm.); NAFO survey of 2007 (M. Treble, pers. comm.); and T.A. Dick (unpubl. data).



Chapter 5

Biogeographic variation of Canadian Arctic cephalopods

Abstract

Morphometric measurements of two cephalopod species (*G. fabricii* and *R. palpebroso*) from distant habitats were compared using principal component analyses, discriminant analyses and Pillai's Trace (MANOVA) to determine potential populations within the eastern Canadian Arctic and western Greenland regions. Environmental variable interactions with morphometric characters were examined using redundancy analysis. Initial morphometric analyses of *G. fabricii* size ranges found four biogeographic groupings: Hudson Strait, Ungava Bay, western Greenland/Baffin Bay and Disko Bay. Specimens from Disko Bay, Greenland clustered within the larger Greenland/Baffin Bay network, suggesting a potential distinct population in agreement with Kristensen's (1982) original observations of a localized population. Limited *R. palpebroso* specimens also show separation between St. Lawrence and the Arctic region but this was only evident in maturing individuals. Genetic barcode (COI) data was obtained for verification of the observed populations but COI was unable to distinguish between sample regions for either species, even when large geographic ranges were included (e.g. *R. palpebroso* from the St. Lawrence compared to those from the Arctic). The environmental variables confirmed ontogenetic shifts to deeper water by *G. fabricii* and that northern *R. palpebroso* were smaller with larger eyes and less energy reserves than those from the St. Lawrence. Better collection techniques for *R. palpebroso* and future use of sensitive microsatellite analyses may provide further insights into the Arctic populations of these important species.

5.1 Introduction

The Arctic Ocean is undergoing environmental shifts including decreased salinity and increasing water temperature, stratification and acidification that will directly impact nutrient availability and influence ocean circulation within the region (Loeng et al. 2005, Pierce et al. 2008, Belkin 2009, André et al. 2010, Overland et al. 2010, Planque et al. 2010, Gruber 2011, Guerra et al. 2011, Overland et al. 2011). Climate change has also facilitated anthropogenic impacts such as natural resource exploration/exploitation and the potential development of new fisheries and shipping routes within the polar realm. These stressors are of concern as not much is known about the biodiversity within this region (André et al. 2010, Darnis et al. 2012, Snelgrove et al. 2012), or how these shifts will impact the Arctic flora and fauna.

Research is still establishing baseline information on a variety of Arctic marine species (Darnis et al. 2012, Snelgrove et al. 2012) but most of the research is focused on long-lived marine vertebrates, in particular, those of cultural and commercial importance, or their associated prey (Hop and Graham 1995, Lawson et al. 1998, Laidre et al. 2002, Munk et al. 2003, Haug et al. 2004, Laidre et al. 2004, Byers et al. 2010). Arctic cod (*B. saida*), a common prey species in Arctic marine food webs, has been of primary interest for researchers (Graham and Hop 1995, Hop and Graham 1995, Munk et al. 2003, Benoit et al. 2010, Thanassekos and Fortier 2012, Thanassekos et al. 2012), yet Arctic cephalopods, another vital prey source, have been overlooked.

Cephalopods play a central role within all marine ecosystems and are highly sensitive to environmental change, with many life history events, including the distribution of most species, dependent on oceanographic variables (Chapter 2, sections 2.2.1.3, 2.2.1.5 and 2.2.2.1a, d;

Tables 4.2 to 4.4). Their relative short life spans (in comparison to other Arctic species) and semelparous life cycles make cephalopods highly susceptible to any oceanographic, biological or anthropogenic variability (Boyle and Boletzky 1996, Wood and O'Dor 2000, Piatkowski et al. 2001, Agnew et al. 2002, Forsythe 2004, Zumholz and Frandsen 2006, Pierce et al. 2008, Rodhouse 2010).

Within the Arctic Ocean, there are 34 known cephalopod species (Chapter 4, Gardiner and Dick 2010) with two of the most prominent being, *Gonatus fabricii* and *Rossia palpebrosa*. Although neither species is of direct commercial importance, these taxa represent distinctive life histories and habitat preferences (pelagic and neritic respectively), play important roles within the ecosystem and are frequently caught as bycatch (Wiborg et al. 1982, Kristensen 1983, Roper et al. 1983, Kristensen 1984, Piatkowski and Wieland 1993, Frandsen and Wieland 2004, Lindgren et al. 2004, Zumholz and Frandsen 2006). Their reliance on oceanographic processes (e.g. temperature, salinity, current flow) for major life events (e.g. distribution, hatching times, maturation rates) also make cephalopods excellent indicator species for the study of Arctic climate change.

Gonatus fabricii is a high energy (Kristensen 1984, Lawson et al. 1998, Zumholz and Frandsen 2006), medium-sized pelagic oegopsid, with planktonic hatchlings (Zuev and Nesis 2003) and is a major component of the Arctic food web (Chambers and Dick 2007). While not of direct commercial importance, *G. fabricii* is often associated with the northern shrimp (*Pandalus* spp.) fishery, and is regularly brought in as bycatch (Zumholz and Frandsen 2006). No Canadian Arctic or western Greenland spawning sites are known for this species, however, large, immature individuals were recorded from a deep region within Davis Strait (Appendix I).

Kristensen (1982, 1984) speculated that spawning may occur throughout the Davis Strait-western Greenland region with Disko Bay individuals showing separate spawning times than nearby local populations. Disko Bay individuals were also morphologically distinct from the nearby Amerdloq Fjord specimens (Kristensen 1982). Reports from other regions indicate that both adults and juveniles were found together suggesting limited to no spawning migrations (Nesis 1965, Clarke 1966, Zuev and Nesis 2003, Zumholz and Frandsen 2006).

Rossia palpebroso are benthic sepiolids (bobtail squid), found along the continental shelf with depth preferences dependent on latitude (Nesis 2001). Females lay 'shelled' eggs in batches on sponges (Aldrich and Lu 1968, Mercer 1968b, Boletzky 1994, Nesis 1999, Laptikhovskiy et al. 2008) and juveniles hatch as precocious young (Mercer 1968b, Boletzky 1994, Nesis 1999, Laptikhovskiy et al. 2008) with minimal dispersal capabilities. Although a common species, there has been limited research into *R. palpebroso*'s life history (e.g. prey items, habitat/substrate preference) or the life history of other Arctic *Rossia* spp. (Mercer 1968b, Zumholz and Frandsen 2006) and consequently, it is unknown how environmental changes will impact this species.

This chapter will provide baseline information regarding cephalopod populations within the western Canadian Arctic by: **1)** identifying biogeographic differences among *G. fabricii* and *R. palpebroso* within the region, and **2)** examining how key environmental variables influence the morphology of these species at each life stage. Standard morphometric and multivariate analyses will be combined with DNA barcoding data (cytochrome C oxidase subunit I (COI); Barcode of Life, University of Guelph) for verification.

It is hypothesized (5.1) that due to oceanographic variability within the Canadian Arctic and adjoining regions (Chapter 2, section 2.1.2 and 2.1.3) cephalopods will have sufficient morphometric variations, indicative of distinct populations, due to environmental isolating factors (i.e. natural barriers to dispersal such as salinity or temperature differences) (Kristensen 1982). Specimens of *R. palpebrosa* collected from the St. Lawrence and Gulf of St. Lawrence region, in comparison to those from the Canadian Arctic, will show the greatest morphological differences due to the large geographic distance between sampling regions and the low mobility of the species; resulting in at minimum two distinct populations.

5.2. Materials and Methods

5.2.1. Sampling

Specimens of *G. fabricii* and *R. palpebrosa* were collected during the annual groundfish and shrimp surveys of Davis Strait/Baffin Bay (Nunavut; 2008) and Hudson Strait (Nunavut/Labrador; 2007 and 2009) by Fisheries and Oceans Canada (DFO - Margaret Treble and Tim Seford) and groundfish surveys of western Greenland by the Greenland Institute of Natural Resources (GINR - Rasmus Nygaard; 2009; Table 5.1, Fig. 5.1). Additional *R. palpebrosa* specimens were collected from the St. Lawrence (Quebec; DFO Maurice Lamontagne Institute - Claude Nozère; 2010) to provide a greater latitudinal separation between sample locations (Table 5.1, Fig. 5.1). No *G. fabricii* were collected from the ‘shallow’ St. Lawrence, as this species is pelagic and typically caught at depths in excess of 200 m (Kristensen 1984).

Individuals were randomly collected from otter trawl bycatch and placed in station-specific bags and frozen. Upon arrival to the laboratory, all specimens were separated into individual bags, labeled and counted.

5.2.2. Morphometric measurements

Seventeen variables were measured (standard ruler and digital callipers to 0.001 cm) and weighed (Mettler Toledo scale to 0.01 g) for each *G. fabricii*, with 32 obtained from each *R. palpebrosa* specimen (Table 5.2). Variables measured were as described by Roper and Voss (1983), Mercer (1968b) and Kristensen (1982) (Table 5.2, Fig 5.2). Any variation from the standard measurements were noted in table 5.2 and described in figure 5.2.

The funnel locking apparatus (FLA), as well as nuchal cartilage were additional measurements utilized by Kristensen (1982) to distinguish between the Amerdloq Fjord population and specimens from Disko Bay, the Irminger Sea and Newfoundland. Both FLA and nuchal cartilage length are not standard measurements and only FLA was measured for *G. fabricii* samples caught in 2008 to 2009 (nuchal cartilage was not measured). Upon initial analysis (PCA), it was observed that FLA was only an important character at PC6 (0.528% of the variation), indicating that it is not vital for distinguishing between potential populations. It was therefore excluded to increase *G. fabricii* sample numbers. The gladius length (GL) is typically used as the primary descriptor of size, however, it was determined that there was no significant difference between GL (or pen length PL) and mantle length (ML) ($R^2 = 0.98$). Therefore, ML was used as the size criterion for this thesis and GL was excluded from analyses.

Each specimen was also assigned a maturity stage (for *R. palpebrosa*) or size range (for *G. fabricii*) (Table 5.3). Only 63 *G. fabricii* had visible gonads but none were sexually mature, therefore, size categories associated with known ontogenetic shifts (Chapter 2 section 2.2.2.1b; Arkhipkin and Bjørke 1999) were used rather than maturity stages (Table 5.3).

Individuals were randomly selected for necropsy with effort to include all available size ranges from each survey. A minimum of 100 *G. fabricii* from each survey were sampled, with the exception of the Hudson Strait 2009 survey where only 33 individuals were sampled. All available *Rossia* spp. were necropsied, however, individuals collected during the Baffin 2008 survey were lost in a laboratory fire prior to measurement. Each survey was further subdivided into smaller sample regions (Tables 5.1 and 5.4) for statistical analyses.

5.2.3. Genetic/Barcode analyses

Fifty-three *G. fabricii* and 36 *R. palpebrosa* mantle tissue samples were collected for molecular analyses at the International Barcode of Life (IBoL; University of Guelph). The resulting sequence data is now part of the IBoL sequence database (Table 5.5; IBoL/BOLD; University of Guelph).

Microsatellites are a good method to use in population analyses, however, until recently specific primers (e.g. An et al. 2014, Liu et al. 2014, Lin et al. 2015) were unavailable (Albertin et al. 2012). In contrast, cytochrome C oxidase subunit I (COI), while missing the refinement of microsatellites (Bonnaud et al. 1997, Carlini 1998, Lindgren et al. 2004, Boyle and Rodhouse 2005k), is conservative enough to distinguish between ‘recently’ diverged taxa (Carlini 1998,

Ratnasingham and Hebert 2007). COI also utilizes a universal primer for amplification (Carlini 1998, Ratnasingham and Hebert 2007), eliminating the need for cephalopod specific primers.

The resulting nucleotide sequence data was made available on the BOLD Systems website (www.boldsystems.org; Table 5.5). Taxon trees were made for both *G. fabricii* and *R. palpebrosa* using the Kimura 2 Parameter distance model 1 with MUSCLE alignment provided by BOLD Systems (www.boldsystems.org) and then coded by sample region for better visual comparisons (Table 5.1; Figs. 5.1, 5.9 and 5.15).

5.2.4. Statistical analysis

Biological data are typically the result of multiple variables interacting (Gotelli and Ellison 2004). To adequately describe these interactions, multivariate analyses are required. For this chapter, morphometric characters for each species were analyzed using principal component analyses (PCA) to determine potential population clusters (Figs. 5.5, 5.7 and 5.12) followed by discriminant analyses and MANOVA (Pillai's trace) for verification (Table 5.6, Figs. 5.6, 5.8 and 5.13). Interactions between morphometric characters and available environmental variables were analyzed using redundancy analyses with 500 permutations (Figs. 5.10, 5.11 and 5.16).

A primary assumption of multivariate analyses is that the data conforms to multivariate normal distribution (Quinn and Keough 2002, Gotelli and Ellison 2004). While there are tests to determine multivariate normality, they are not readily used due to conflicting results and limited access to software (Gotelli and Ellison 2004). Researchers, instead, typically check each variable independently for normal distribution, even if this method does not guarantee true multivariate normality (Gotelli and Ellison 2004). To increase the probability of multivariate

normal distributions, all morphometric data were log transformed and standardized (Gotelli and Ellison 2004, N. Kenkel, University of Manitoba pers. comm.). This transformation/standardization also minimizes outliers and removes potential errors that may occur when axes are dominated by a few variables with large units (Gotelli and Ellison 2004, N. Kenkel, University of Manitoba, pers. comm.). Each transformed and standardized variable was then tested for normality using: Shapiro-Wilk, Anderson-Darling, Jarque-Bera and Lilliefors tests (XLSTAT). PCA, as an analytical method, is robust enough to tolerate slight variations from normality, however, errors do occur when empty or missing values are present in the data (N. Kenkel, University of Manitoba pers. comm.). Therefore, any individual with many missing characters were removed from the analysis and conversely, any variables with many missing data points were also removed to maintain sample size. This decreased the number of *G. fabricii* characters from 17 to 13 with gladius length and FLA removed along with the frequently damaged tentacle and club lengths. *R. palpebrosa* characters dropped from 32 to 30 with the loss of club length and arm weight.

PCA creates new uncorrelated variables (principal component scores) from the original data that characterize the majority of the variation with fewer variables (principal components – PCs) (Quinn and Keough 2002, Gotelli and Ellison 2004). This method is one of the simplest multivariate analyses but requires underlying correlations to work (Gotelli and Ellison 2004). When plotted, principal component 1 (PC1) axis is the linear function consisting of the largest amount of variation within the data, principal component 2 (PC2) is the axis orthogonal to PC1 and consists of the second largest amount of variation, and so on (Quinn and Keough 2002). The total number of PCs calculated are the same as the number of variables utilized in the initial analysis, however, only the first few components consisting of the largest amount of variation are

kept (Quinn and Keough 2002, Gotelli and Ellison 2004). The eigenvectors furthest from zero for each PC indicate which original variables are most directly impacting that particular axis (Quinn and Keough 2002). These eigenvectors can also be plotted against the component scores to determine which variables are impacting which potential population (i.e. cluster). It is important to note that if all the eigenvectors are positive in PC1, then size is the primary source of variation (N. Kenkel, University of Manitoba pers. comm.). Since this chapter describes the changes in shape regardless of size, PC1 was omitted from all the PCA analyses. Only correlated PCA's were used due to the different units of measure between the variables (i.e. weight vs. length measures) (Quinn and Keough 2002).

Unlike PCA, which generates unbiased clustering based on variability of the PCs, discriminant analysis maximizes the distances between pre-determined groups while minimizing the distance of within group observations (Quinn and Keough 2002, Gotelli and Ellison 2004). Individual observations are assigned to one of the *a priori* groups (Quinn and Keough 2002, Gotelli and Ellison 2004). If the *a priori* groups are statistically distinct, then the percentage of observations accurately assigned to each group will be high (i.e. percent of misclassifications will be low) (Quinn and Keough 2002). Post-hoc MANOVA (Pillai's trace) was used to verify if all samples were from a single group and whether any similarities are due to random differences (H_0) (Gotelli and Ellison 2004). Pillai's trace was chosen because it is the most robust of the MANOVA tests to any variation in multivariate normality (Quinn and Keough 2002, Gotelli and Ellison 2004).

While PCA is a robust analysis, able to withstand some slight multivariate non-normality, discriminant analysis is more sensitive to such variations in assumptions, therefore, principal

component scores obtained from the PCA were used in lieu of the transformed/standardized raw data to assure no inter-correlations and more normal distributions (N. Kenkel, University of Manitoba pers. comm.). Discriminant analysis also requires the number of component scores to not exceed the smallest number of individuals from a given sample location (N. Kenkel, University of Manitoba pers. comm.). Therefore, to maintain sufficient information (i.e. number of component scores), sample locations with only a couple of specimens were omitted from the analysis. The exception to this was the St. Lawrence estuary (s) and the Gulf of St. Lawrence (S) specimens. Only seven *R. palpebrosa* (all size ranges) were collected from those locations so they were combined into a single St. Lawrence category.

Redundancy analysis (RDA), a multi-regression analysis, is used when both predictor and response variables are multivariate (Gotelli and Ellison 2004). This analytical method is often used to study the impact of environmental variables (predictor variables) on biological data (e.g. species compositions; response variables) (Gotelli and Ellison 2004). Unlike the PCA, the first step in an RDA is to find linear relationships of the response to the predictor variables followed by the extraction of eigenvalues, eigenvectors and ordination (Quinn and Keough 2002). Monte Carlo simulations (i.e. permutations) can then be used to test the null hypothesis (H_0) that there is no relationship between the response and predictor variables (Gotelli and Ellison 2004). The resulting eigenvectors in combination with component loadings provide insight into how each predictor variable impacts the response variables (Quinn and Keough 2002).

5.3. Results

5.3.1. Environmental data vs. sample location

Initial PCA analysis of the environmental data collected from all sample locations show three distinct clusters: Hudson Strait (consisting of western and eastern Hudson Strait samples, Davis Strait individuals and those collected from Ungava Bay), Baffin Bay/west Greenland (herein referred to as Baffin Bay/Greenland) and the St. Lawrence cluster (inclusive of both the St. Lawrence estuary and the Gulf of St. Lawrence) (Fig. 5.3; see Table 5.1 for location code definitions). The average latitudes (eigenvector = 0.64746) and longitudes (eigenvector = 0.62233) account for the largest variation on PC1 (Fig. 5.3). Hudson Strait is also shallower than Baffin Bay/Greenland and its depth increases along an easterly trajectory (with the exception of Ungava Bay (U); Fig. 5.3). Both St. Lawrence and western Hudson Strait clusters have ~ similar depth characteristics (Fig. 5.3). Bottom temperature (eigenvector = 0.99184) was the most variable for PC2 and accounts for the distinctiveness of the St. Lawrence sample regions (i.e. warmer than the two Arctic clusters; Fig. 5.3).

No observable difference was found between sample years (2007 open symbols and 2009 filled-in symbols) for the Hudson Strait grouping, the only locations with multi-year sampling (Fig. 5.4). The observed difference in temperature by depth outlined in Fig. 3.3, where 2009 samples were colder than those collected in 2007 at similar depths, may be the result of 2009 sampling further west in the Strait and additional Ungava Bay samples during the 2007 survey (Fig. 5.4).

5.3.2. *G. fabricii* morphometric analyses

When all *G. fabricii* specimens are analyzed together, regardless of size range, eastern Hudson Strait (E) individuals separate into two distinct clusters, with one cluster (E1) highly correlated with lens diameter (8 (PC2 eigenvector -0.50417; PC3 eigenvector 0.72995)) and the other cluster (E2) highly correlated with beak weight (32 (PC2 eigenvector 0.64567) and 33 (PC2 eigenvector 0.48615; PC3 eigenvector 0.38458)) (Fig. 5.5; see Table 5.1 for location codes). Ungava (U) individuals also show slight clustering and are connected to the E1 grouping (Fig. 5.5). Ungava individuals are highly correlated to lens diameter but are negatively correlated with the third right arm length (20 (PC3 eigenvector -0.28217)) (Fig. 5.5). Baffin Bay/Greenland individuals are highly variable; but still showed slight clustering between the two E groupings, with Disko Bay individuals tightly clustered within the larger Baffin Bay/Greenland grouping (Fig. 5.5). Specimens from Baffin Bay/Greenland region (including Disko Bay) are negatively correlated with both the lens diameter (8) and beak weights (32 and 33) (Fig. 5.5).

The discriminant analysis of all *G. fabricii* specimens found similar clustering as the PCA with the exception of eastern Hudson Strait (EHS) maintaining only a single grouping (Fig. 5.6). Although all locations were highly variable, Ungava Bay (UB) and EHS formed a distinct grouping while Baffin Bay/Greenland formed another with Disko Bay (DB) slightly attached (Fig. 5.6). These groupings were found to be significant (Pillai's Trace, $p < 0.0001$, $\alpha = 0.05$) even though 50.88 % of the individuals were misclassified (Fig. 5.6).

Because specimens collected from different regions belonged to varying size ranges (e.g. Hudson Strait individuals tended to be smaller in comparison to those from western Greenland),

individual PCA analyses were conducted for each *G. fabricii* size range (see Table 5.3 for definitions). Figure 5.7a shows the juvenile (size range 2) *G. fabricii* separating into three clusters: Davis Strait, Ungava Bay and Baffin Bay/Greenland. The key characters separating the Davis Strait cluster from the Baffin Bay/Greenland cluster are the beak weights (32 (PC2 eigenvector 0.64567); 33 (PC2 eigenvector 0.48615)), with Baffin Bay/Greenland individuals positively correlated with beak weight and Davis Strait individuals were negatively correlated (Fig. 5.7a). Lens diameter (8 (PC3 eigenvector 0.62376)), third right arm (20 (PC3 eigenvector -0.40412) and liver weight (30 (PC3 eigenvector 0.38083) were the key characters separating Ungava individuals from the Baffin Bay/Greenland cluster (Fig. 5.7a). The discriminant analysis for this size range (Fig. 5.8a) does not verify these clusters (high misidentification (57.04 %) and has a lot of overlap among all *a priori* groupings), however, the MANOVA (Pillai's Trace) was found to be significant ($p < 0.0001$ $\alpha = 0.05$; Table 5.6).

Size range 3 (Table 5.3) PCA for *G. fabricii* shows that both Baffin Bay/Greenland and Hudson Strait clusters are highly variable, however, Disko Bay forms its own cluster within the larger Baffin Bay/Greenland grouping (Fig. 5.7b). Hudson Strait cluster is correlated with eye diameter (7 (PC2 eigenvector 0.40008)), lens diameter (8 (PC2 eigenvector 0.59994)) and fin width (13 (PC2 eigenvector 0.35054) but is negatively correlated with upper beak weight (32 (PC2 -0.42354)) (Fig. 5.7b). Baffin Bay/Greenland cluster is highly correlated to beak weights (32 (PC3 eigenvector 0.44501); 33 (PC3 eigenvector 0.55044) but negatively correlated to liver weight (30 (PC3 eigenvector -0.37420) (Fig. 5.7b). None of the variables associated with the Disko Bay cluster were found to have a significant impact on either PC2 or PC3 but specimens from this location have longer third right arms (20) and fin lengths (11) than individuals from the other two clusters (Fig. 5.7b). Disko Bay individuals also have heavier livers (30) and

consequently heavier total body weights (28) than individuals from Baffin Bay/Greenland and most of those from Hudson Strait (Fig. 5.7b). Discriminant analysis found two distinct clusters, eastern Hudson Strait (EHS) and Baffin Bay/Greenland (Fig. 5.8b). Disko Bay was not found to be distinct from the Baffin Bay/Greenland cluster but was associated with the geographically close specimens from central Greenland (CG) (Fig. 5.8b). MANOVA results confirm that there are significantly different groups (Pillai's Trace, $p = 0.0030$, $\alpha = 0.05$) with much less misidentifications (29.51 %) than observed in the previous analyses (Table 5.6).

Figure 5.7c shows highly variable component scores for *G. fabricii* size range 4 (Table 5.3) representing the only two locations available for that size range; Baffin Bay/Greenland and Disko Bay. Much of the variation in PC2 is explained by lens diameter (8 (eigenvector 0.74117)), fin width (13 (eigenvector 0.32317)), total weight (28 (eigenvector -0.36735)) and fin length (11 (eigenvector -0.29801)) (Fig. 5.7c). PC3 variation is explained by fin length (11 (eigenvector 0.67462)), eye diameter (7 (eigenvector -0.48914)) and liver weight (30 (eigenvector -0.32103)) (Fig. 5.7c). Although the discriminant analysis for this size range shows two distinct clusters (Disko bay (DB) and Central Greenland (CG)) (Fig. 5.8c), the MANOVA found these groupings to be insignificant (Pillai's trace, $p = 0.1373$, $\alpha = 0.05$) (Table 5.6).

Genetic analyses using COI barcoding data found no clustering of *a priori* groupings (see Table 5.1 and Fig. 5.1 for *a priori* group definitions; Table 5.5; Fig. 5.9).

5.3.3. *G. fabricii* morphometric variables vs. environmental data

Redundancy analyses were used to examine the impacts that the measured environmental variables had on the morphometric characters (Figs. 5.10, 5.11). When all *G. fabricii* specimens were utilized for analyses, liver weight (30) and upper beak weight (32) are negatively correlated with bottom temperature, along with dorsal mantle length (1), total length (4), fin length (11) and third right arm (20) (Fig. 5.10). These same variables were positively correlated with average longitude and latitude (Fig. 5.10). Fin width (13), lens diameter (8), buccal mass (i.e. muscle surrounding the beak, 31), lower beak weight (33), total weight (28) and arm weight (29) were all also positively correlated with average latitude and longitude as well as depth (Fig. 5.10).

When examining morphometric characters vs. environmental variables by size range for *G. fabricii*, a similar pattern was observed for individuals from size range 2 as when all size ranges were combined (Fig. 5.11a). Specimens of size range 3 have greater total weights (28) and liver weights (30) with increasing temperatures while the remaining characters are more correlated with depth and negatively correlated with average latitude (Fig. 5.11b). Both analyses for size ranges 2 and 3 were significant (size 2, $p = 0.002$, $\alpha = 0.05$; size range 3, $p = 0.014$, $\alpha = 0.05$), however the results for size range 4 were not significant ($p = 0.090$, $\alpha = 0.05$) (Fig. 5.11c).

5.3.4. *R. palpebrosa* morphometric analyses

PCA analyses of *R. palpebrosa* by maturity stage show wide variations within each stage (Fig. 5.12). The immature *R. palpebrosa* show a loose clustering of specimens from Ungava Bay (U) and only one individual from central Greenland (C) (Fig. 5.12a). The discriminant analysis for the immature specimens shows an association between the Hudson Strait (EHS and

WHS) and Ungava Bay (UB) (Fig. 5.13a) but there are no significant groupings (MANOVA, Pillai's Trace, $p = 0.3050$, $\alpha = 0.05$ with 41.67 % of individuals misclassified; Table 5.6).

Maturing *R. palpebrosa* is the only stage with a distinct cluster (i.e. St. Lawrence individuals) in the PCA (Fig. 5.12b). St. Lawrence individuals are positively correlated with the third (24) and fourth (25) left arm lengths (PC 2, eigenvector 0.35284 and 0.33381 respectively) and negatively correlated with sucker diameters on the tentacles (16, PC2, eigenvector -0.40444) (Fig. 5.12b). The associated discriminant analysis shows that Ungava Bay (UB) specimens are linked to east (EHS) and west Hudson Strait (WHS) individuals but those from St. Lawrence (SL) are only linked to WHS (Fig. 5.13b). The MANOVA, however, shows that there are no significant clustering and that any clusters are likely the result of random distributions (Pillai's Trace, $p = 0.0652$, $\alpha = 0.05$ with 31.25 % of individuals misclassified; Table 5.6).

The PCA result for mature individuals, similar to the immatures, has a loose clustering of Ungava Bay individuals (Fig. 5.12c). St. Lawrence individuals (S and s) show no clustering within this maturity stage (Fig. 5.12c). As with immatures, many variables contribute to the variation observed within PC2 and PC3, with none showing any strong correlations (Fig. 5.12c). The discriminant analysis for mature specimens agrees with the lack of groupings observed in the PCA (Fig. 5.13c), however, this is the only group with a significant MANOVA result (Pillai's Trace, $p = 0.0306$, $\alpha = 0.05$ with 31.58 % of individuals misclassified; Table 5.6) suggesting that potentially St. Lawrence individuals do belong to a distinct group.

When all maturity stages for *R. palpebrosa* were analyzed using a discriminant function, St. Lawrence individuals did separate out into a distinct group from individuals within the Hudson Strait clusters (Hudson Strait (HS), Ungava Bay (UB), east Hudson Strait (EHS) and

west Hudson Strait (WHS)) (Fig. 5.14). This distinct grouping was confirmed with a significant Pillai's Trace (MANOVA, $p < 0.0001$, $\alpha = 0.05$ with 52.94 % of individuals misclassified; Table 5.6).

Genetic barcode data does not show any separation between St. Lawrence (hollow arrows) individuals and those from the Arctic region, nor within the Arctic region itself (Table 5.5; Fig. 5.15).

5.3.5. *R. palpebrosa* morphometric variables vs. environmental data

Immature *R. palpebrosa* morphometric characters show negative correlations with all environmental variables (Fig. 5.16a). Dorsal mantle length (1), ventral mantle length (2), head length (6), lens diameter (8), sucker diameter on the tentacle clubs (16), FLA (26), total weight of specimen (28), liver weight (30) and buccal weight (31) are all negatively correlated with average latitude (Fig. 5.16a). The remaining characters are negatively correlated with average longitude (which is highly correlated with depth) and bottom temperature (Fig. 5.16a).

Relationships between environmental variables and the morphometric characters of the maturing *R. palpebrosa* were found to be insignificant (i.e. not linearly correlated) and cannot be interpreted (Fig. 5.16b).

Mature *R. palpebrosa* dorsal mantle length (1), total weight of specimen (28), liver weight (30) and buccal weight (31) are the most negatively correlated with average latitude, similar to observations of the immature specimens (Fig. 5.16a and c). Buccal weight (31) and beak weights (32 and 33) are the most negatively correlated with bottom temperature (Fig. 5.16c).

5.4. Discussion

Traditional morphometric analyses in conjunction with multivariate statistics were able to identify potential populations for the two cephalopod species.

5.4.1. Arctic cephalopod biogeography

a) *G. fabricii* biogeography: (i) Overview: Morphometric analyses of *G. fabricii* identified four main clusters throughout the eastern Canadian and Greenland Arctic in agreement with hypothesis 5.1 (page 136; Figs. 5.5 to 5.8). These clusters are: 1) Hudson Strait, 2) Ungava Bay, 3) Baffin Bay/Greenland and 4) Disko Bay (Figs. 5.5 to 5.8). The key morphometric characteristics separating the four locations are eye dimensions (lens diameter (8) and to a lesser extent eye diameter (7)), beak weights (32 and 33), fin dimensions (fin length (11) and fin width (13)), length of the third right arm (20) and liver weight (30) (Figs. 5.5 and 5.7).

Discriminant analysis and significant Pillai's Trace (MANOVA) verified these clusters, highlighting interactions between Baffin Bay/Greenland specimens and those from Disko Bay, as well a close connection between Ungava Bay and Hudson Strait specimens (Table 5.6; Figs. 5.6 and 5.8). The formation of a distinct Disko Bay cluster, even though it is within the more variable Baffin Bay/Greenland cluster, is in accordance with Kristensen's (1982, 1984) description of a localized population within that region (Fig. 5.5, 5.7b).

Unlike the PCA and discriminant (MANOVA) analyses, the COI results do not confirm the presence of distinct populations; most likely the result of insufficient elapsed time for genetic divergence (Fig. 5.9). Bonnaud et al. (1997), Carlini (1998), Lindgren et al. (2004) and Boyle and Rodhouse (2005k) all agree that COI lacks the refinement to identify populations, however,

until primers and microsatellites are developed for Arctic cephalopod species, or related species (Albertin et al. 2012), barcode data is the best genetic option.

(ii) Hudson Strait: Initially, Hudson Strait specimens split into two clusters, E1 and E2 when all size ranges were combined (PCA), with E2 having heavier beaks (32, 33) and E1 individuals distinguished by larger lenses (Fig. 5.5). Cephalopod beaks undergo chitinization with maturity (Cherel and Hobson 2005), resulting in older specimens (larger size ranges) having heavier, more chitinized beaks. Therefore, E2 may represent older/larger individuals than E1 (Fig. 5.5). This separation was not maintained when the morphometric characters were examined by distinct size range, reinforcing the argument that groupings E1 and E2 are likely based on size only (Table 5.3; Figs. 5.6 to 5.8).

The presence of the two different size ranges (E1 and E2) within the same region at the same time (Fig. 5.5) is indicative of either two distinct breeding populations which spawn at different times or early and late hatching specimens from a single breeding population (Kristensen 1982, 1984, Nesis 1999). Individuals that hatch earlier will have additional time to mature and grow, resulting in larger, more chitinized beaks, than those that hatched later. Varying water temperatures at hatch are also known to impact maturation and growth rates of individuals (Chapter 2, section 2.2.2.1b) (Kristensen 1984, Frandsen and Wieland 2004, Forsythe 2004, Zumholz and Frandsen 2006, Leporati et al. 2007). Water flowing along the northern shore of Hudson Strait is cooler (0 to 2 °C) than the southern shore (0 to 5 °C) (Chapter 2, section 2.1.2.3b), therefore, individuals found in the warmer southern water of the strait are expected to mature/grow faster than similar aged specimens from the cooler northern region. Further examination of statolith growth rings (Arkhipkin and Bjørke 2000) will help determine if

these individuals are actually different 'ages' or whether these groupings are the result of environmental factors.

Size 2 Hudson Strait *G. fabricii* were highly variable and showed no distinctive clustering, however, the size 3 cluster was defined by large eyes (and lenses) as well as wide fins compared to Baffin Bay/Greenland and Disko Bay specimens (Fig. 5.7b). Large eyes, in particular large lenses, suggest that Hudson Strait individuals have better vision than individuals from Baffin Bay/Greenland. Hudson Strait is relatively shallow (300 to 400 m), with counter-current water flow resulting in high production (Stewart et al. 1985, Drinkwater 1986, Allard 1990). It is therefore expected to be more turbid than the slower moving, deeper (2300 m) (Tang et al. 2004, Jørgensen et al. 2005) Baffin Bay/Greenland locations, thereby, necessitating better eyesight for prey detection and predator avoidance. Wider fins would also help the squid swim in faster moving water.

(iii) Ungava Bay: The Ungava Bay cluster in the initial PCA of all size ranges was closely associated with the E1 subgroup of Hudson Strait and also showed a positive correlation with lens diameter (8) (Fig. 5.5). This correlation was also observed for the size 2 Ungava Bay cluster, along with a positive correlation with eye diameter (7) (Fig. 5.7a). Ungava Bay is a shallow (150 m), but highly productive region where turbidity is expected to be high due to mixing (Drinkwater 1986), therefore, better vision would, again, be an asset.

Ungava Bay individuals were also found to have shorter third right arms (20) than Hudson Strait, Baffin Bay/Greenland and Disko Bay individuals (Fig. 5.5, 5.7a). Shorter arms may be indicative of maturity. Arm length may also be the result of another factor such as prey size. Perhaps Baffin Bay/Greenland and Disko Bay individuals require longer arms to handle

larger prey than Ungava Bay specimens. Ungava Bay individuals also had heavier liver weights (30) than the other regions, suggesting that they are feeding on higher quality (i.e. lipid) prey (Fig. 5.7a). This again points to the higher productivity of the region.

(iv) Baffin Bay/Greenland: Baffin Bay/Greenland individuals (size 2 and 3) have heavier beaks than those from Hudson Strait and Ungava Bay (Fig. 5.7a,b), suggesting that the majority of specimens are at the larger end of the size range compared to Hudson Strait/Ungava individuals (Cherel and Hobson 2005). The Baffin Bay/Greenland region is influenced by the relatively warm (~ 5 °C) West Greenland Current compared to the colder (0 to 5 °C) counter-current of Hudson Strait and the Labrador Sea (< -1 °C) influenced Ungava Bay (Chapter 2, section 2.1.2.3b). Therefore, even if hatch times were the same in all locations, the warmer Baffin Bay/Greenland region would allow for faster growth and maturation.

Even with larger beaks, Baffin Bay/Greenland individuals have lower liver weights (30) than the respective Ungava Bay (size 2) and Hudson Strait (size 3) specimens (Fig 5.7a,b). Lower liver weights suggest that even with larger/stronger beaks, Baffin Bay/Greenland individuals are not getting similar amounts of lipid in their diets as Hudson Strait (including Ungava Bay) individuals.

Size 4 Baffin Bay/Greenland individuals showed no significant difference between the sample locations (Table 5.6). Baffin Bay/Greenland individuals, however, had wider fins than those from Disko Bay (Fig. 5.7c). These wider fins may help to better propel individuals through the water, reducing the amount of energy required for diurnal or latitudinal/longitudinal migrations.

The large Baffin Bay/Greenland *G. fabricii* were also positively correlated with lens diameter. This species undergoes an ontogenetic shift to deeper depths (< 1000m) with size/maturity (Chapter 2, section 2.2.2.1a,b) (Clarke 1966, Wiborg et al. 1982, Kristensen 1983, 1984, Piatkowski and Wieland 1993, Arkhipkin and Bjørke 1999, Zuev and Nesis 2003, Frandsen and Wieland 2004), therefore, larger lens would be required due to the lack of light at the greater depths.

(v) Disko Bay: Kristensen (1982) identified this region as having a distinct population from the geographically close Amerdloq Fjord. This study also shows Disko Bay specimens clustering, for each size range, although each cluster is closely associated with the more variable Baffin Bay/Greenland grouping (Figs. 5.5, 5.6, 5.7 and 5.8).

Size 3 Disko Bay individuals show a positive correlation with fin length (11), arm length (3rd arm on the right side, 20) and liver weight (30) (Fig. 5.7b). The longer arms (also observed by Kristensen (1982)) may indicate that Disko Bay *G. fabricii* are feeding on larger prey than the other location, and their heavier livers point to higher quality prey (Fig. 5.7b). As with Hudson Strait and Ungava Bay, Disko Bay is thought to be highly productive (Frandsen and Wieland 2004, Hansen et al. 2012), therefore, their prey will also be benefiting from this productivity, adding to the available energy (i.e. lipids).

Contrary to Baffin Bay/Greenland size 3 individuals, Disko Bay specimens have longer, but narrower fins (Fig. 5.7b). This may provide a hydrodynamic advantage while not increasing the power generated by the fins. Therefore, Disko Bay specimens likely do not undergo large migrations that would require wide, muscular fins for propulsion.

Kristensen (1982) speculated that the Disko Bay population was the result of different spawning times than for populations from the adjoining regions. While this cannot be verified with this study, analysis of statoliths would provide information on hatch times by counting the lines back to the hatch mark (Arkhipkin and Bjørke 2000).

(vi) Environmental impacts on morphometric characteristics of *G. fabricii*: The main geographic clusters (i.e. potential populations) are in accordance with the regions determined by the environmental data, with the addition of Ungava Bay and Disko Bay (Fig. 5.3 and 5.5). Both Ungava and Disko Bay have similar environmental variables as the other locations but are exposed to excessive freshwater input (terrestrial runoff in Ungava Bay and glacial outflow in Disko Bay) (Drinkwater 1986, Hansen et al. 2012). This situation may help to isolate this pelagic species. Cephalopods are strictly stenohaline (Zuev and Nesis 2003, Boyle and Rodhouse 2005a, f), therefore, the decreased salinities within Disko and Ungava Bay could act as an isolating mechanism (Semmens et al. 2007), forcing the squid into the deeper and/or more central, saline water of the bays, allowing for morphometric differentiation.

Redundancy analyses found that most *G. fabricii* individuals tended towards larger individuals (dorsal mantle length (1), total length (4)) with larger energy stores (i.e. liver weight (30)) in colder environments (Figs. 5.10, 5.11a). This is in agreement with their known ontogenetic shift behaviour, where larger, more mature individuals migrate to deeper/colder realms (Clarke 1966, Wiborg et al. 1982, Kristensen 1983, 1984, Piatkowski and Wieland 1993, Arkhipkin and Bjørke 1999, Zuev and Nesis 2003, Frandsen and Wieland 2004). The opposite of this was found for size range 3 *G. fabricii* where a positive association with body and liver weight with bottom temperatures was found (Fig. 5.11b). For these individuals, warmer water

accounted for larger individuals with greater energy reserves. Disko Bay was the only location where size 3 individuals had a positive correlation with liver weight (Fig. 5.7b); Disko Bay's productivity could account for the increased liver weight. Disko Bay was also the warmest sample location for *G. fabricii*, in July, compared to October for the Hudson Strait and Ungava Bay surveys (Table 5.1).

Total weight (28), lens diameter (8), fin width (13), buccal mass (31), lower beak weight (33) and arm weight (29) were all positively correlated with depth (m) and location (latitude/longitude) for all size ranges (Figs. 5.10). Therefore, specimens caught at deeper depths were not only heavier with larger fins but had better eyesight (lens diameter) and more muscular mouths (buccal mass and beak weight) than those found in shallower, more southern locations. This also agrees with larger individuals undergoing ontogenetic shifts to deeper water.

b) *R. palpebroso* biogeography: (i) Overview:

The limited number of specimens collected for this species makes morphometric descriptions difficult. *R. palpebroso* is a benthic species whose relatives are known to burry in the sediment (Chapter 2, section 2.2.2.2.b) (Mercer 1968b, Boyle and Rodhouse 2005d, Rodrigues et al. 2010) making their collection difficult. The following descriptions are based on all of the complete *R. palpebroso* specimens collected from each sample location.

The discriminant analysis of all *R. palpebroso* specimens, regardless of maturity stage, found that St. Lawrence individuals were distinct from those collected in the Hudson Strait in agreement with hypothesis 5.1 (page 136; Table 5.6, Fig. 5.14), however, PCA analysis of specimens by maturity stage did not provide a clear clustering (Fig. 5.12). COI was also not

useful in determining separation among samples, even over a large geographical range (Fig. 5.15).

(ii) St. Lawrence: Only maturing individuals showed distinct clustering between St. Lawrence and Arctic specimens in the PCA (Fig. 5.12b) but this grouping was not confirmed by either the discriminant analysis or MANOVA (Table 5.6, Fig. 5.13b). The maturing St. Lawrence individuals had wider fins and longer arms than those in the Arctic (Fig. 5.12b). *Rossia* spp. are known to use their arms and fins to bury themselves in the sediment (Rodrigues et al. 2010, Anderson 2012). The reason for this behaviour is not yet known, however, it typically occurs during daylight hours, with individuals frequenting the sediment surface at night (Rodrigues et al. 2010, Anderson 2012). The St. Lawrence region is the only sample location in this study where night/day cycles are constant (i.e. Arctic has extended 24 hour days and 24 hour nights), therefore, this behaviour may be more common there than within the Arctic, thereby requiring more developed arms and fins.

The Pillai's Trace (MANOVA) of mature *R. palpebrosa* shows significant differences (the only significant result for *R. palpebrosa* by maturity stage) between the *a priori* groupings of the discriminant analysis, even though the groupings are not evident in the graphical output (Table 5.6; Fig 5.13). This significant result can only be explained by the tight St. Lawrence clustering around the centroid in the discriminant graph while still connected to the Hudson Strait/Ungava Bay groups (Fig. 5.13c). This cluster was not observed in the PCA; instead Ungava Bay individuals formed a variable cluster (Fig. 5.12c). Mature Ungava individuals have larger eyes and mantles compared to those from St. Lawrence, while Hudson Strait specimens

have fins attached lower on the mantle (further from the collar) than the other locations (Fig. 5.12c).

(iii) Environmental impacts on morphometric characteristics of *R. palpebrosa*: All neritic *R. palpebrosa* morphometric characters show some negative correlation with the environmental variables, with dorsal mantle weight (1), total weight (28), liver weight (30) and buccal mass (31) being the most negatively correlated to latitude and eye (8) and lens diameters (8) being the least negatively correlated (Fig. 5.16). This suggests that individuals found further north are smaller with better eyesight but lower energy stores than their southern counterparts. Larger eyes may be the result of 24 hours of darkness Arctic *R. palpebrosa* experience during the winter months thereby, improving vision in low light habitats for hunting and to evade predation. However, as previously mentioned, *Rossia* species from more southern locals are known to bury into the sediment during the daylight hours and hunt at night (Rodrigues et al. 2010, Anderson 2012). Therefore, these results may indicate that prey items are more difficult to find (i.e. needing larger eyes) in the northern regions, which might explain the lower lipid reserves, ultimately reducing growth.

5.4.2. Statistical methodology

The straight-forward discriminant analysis is the go-to statistical method for morphometric analyses as it maximizes the differences between *a priori* sample groups, minimizes within group variation and provides hypothesis testing via post-hoc MANOVAs (Quinn and Keough 2002, Gotelli and Ellison 2004). This was the method Kristensen (1982) used to identify Disko Bay as an isolated population of *G. fabricii* from the nearby Amerdloq Fjord. The method, however, is inherently biased as it utilizes *a priori* groupings and only

attempts to determine if these groups are statistically different rather than take into account any other potential clusters (e.g. the E1 and E2 clusters observed in the PCA of all size ranges of *G. fabricii*; Fig. 5.5). By contrast, PCA provides an unbiased review of the morphometric data. Although the data was labeled with sample location markers, PCA does not utilize this information but rather consolidates the majority of the variation into the least number of component scores (i.e. axis) possible (Quinn and Keough 2002, Gotelli and Ellison 2004). Consequently any observed clustering is related to morphometric character interactions, not pre-defined groupings. Eigenvectors obtained through the PCA also highlight the key morphometric characters that define each potential population. Because PCA's are unbiased and provide information regarding important morphometric characters, they are recommended for future population analyses.

5.4.3. Genetic analyses

Genetic analyses were unsuccessful in determining populations within the Canadian and Greenland Arctic region (Figs. 5.9 and 5.15). COI, while sensitive enough to identify various species, was not sensitive enough to identify populations. Ibáñez et al. (2011), however, was able to utilize COI sequence data based on haplotype diversity to examine populations of *D. gigas* within the Pacific Humboldt Current System. Examination of potential haplotypes for the Arctic species based on their COI sequences may help to further differentiate local populations within the region.

Increased interest in cephalopod fisheries, potential impacts of invasive species (e.g. jumbo squid), the establishment of CephSeq Consortium and with the recent description of the octopus genome, it is hoped that there will be an increase in familial/genera/species specific

microsatellites and their associated primers (Ibáñez et al. 2011, Albertin et al. 2012, An et al. 2014, Liu et al. 2014, Albertin et al. 2015, Lin et al. 2015). This should also increase our understanding of these Arctic species

5.5. Summary

Morphometric analyses identified potential populations within the Canadian and Greenland Arctic (Hypothesis 5.1 - page 136). *G. fabricii* specimens separated into four main clusters: Hudson Strait, Ungava Bay, Baffin Bay/Greenland and Disko Bay, with the Hudson Strait cluster consisting of two subgroups, E1 and E2 (Fig. 5.5). Key morphometric characters were identified for each location and provided insight into habitat preference and behavioural traits of *G. fabricii* at the varying size ranges. (Kristensen 1982, Drinkwater 1986, Allard 1990, Tang et al. 2004, Jørgensen et al. 2005, Hansen et al. 2012). Ungava Bay is exposed to high levels of terrestrial freshwater runoff while Disko Bay surface water is affected by glacial runoff (Drinkwater 1986, Hansen et al. 2012), relegating stenohaline cephalopods to the center of the bays and away from the surface. The addition of salinity levels from each sample site will help improve environmental descriptors.

Morphometric analyses of *R. palpebroso* were limited by small sample sizes resulting in highly variable results. Despite the small N, maturing individuals from St. Lawrence were distinguishable from the Arctic specimens based on wider fins and longer arms. It was postulated that these characters may help with the diurnal burying behaviour known for the genus.

Direct barcode analysis (COI) lacked sensitivity to distinguish among potential populations for both *G. fabricii* and *R. palpebrosa*, even with large geographic separations. With increased interest in cephalopod genomics, the availability of cephalopod specific microsatellites and their associated primers will become more common, allowing for a more detailed understanding of cephalopod populations (Ibáñez et al. 2011, Albertin et al. 2012, An et al. 2014, Liu et al. 2014, Albertin et al. 2015, Lin et al. 2015). Further investigation using physical and chemical tags might also provide insights into migration patterns of these species and help to determine potential spawning sites within the region.

Table 5.1. Survey sample locations and their summarized environmental variables.

Code	Full Name	Month/Yr Sampled	N Samples (<i>Gonatus</i> = G; <i>Rossia</i> = R)	Latitude (Range) DecDeg °N	Long (Range) DecDeg °W	Mean Temp (°C) ± StDev	Mean Bottom Depth (m) ± StDev
B	Baffin Bay	Oct 2008	G = 16 R = 0	67.451 – 69.825	-59.857 - -57.992	2.634 ± 1.148	615.6 ± 341.9
C	Central Greenland	Oct 2008 & 2009; June-July 2009	G = 82 R = 5	66.239 – 70.562	-59.418 - -54.000	3.554 ± 0.614	455.2 ± 132.7
d	Disko Bay	July 2009	G = 25 R = 1	68.887 – 69.849	-52.329 - -51.432	3.569 ± 0.070	451.7 ± 108.6
D	Davis Strait	Oct 2007 & 2009	G = 7 R = 1	60.923 – 61.445	-64.290 - -63.941	2.624 ± 1.066	372.6 ± 45.0
E	Eastern Hudson Strait	Oct 2007 & 2009	G = 73 R = 15	60.855 – 62.444	-69.726 - -65.011	1.309 ± 0.702	456.8 ± 237.0
S	Gulf of St. Lawrence	Aug 2010	G = 0 R = 7	48.912 – 49.555	-60.291 - -59.252		217.3 ± 25.7
G	Northern Greenland	July 2009	G = 20 R = 1	71.138 – 72.349	-60.661 - -56.359	1.783 ± 0.853	633.2 ± 305.9
g	Southern Greenland	June 2009	G = 2 R = 0	63.489	-52.276	3.682	479.5
s	St. Lawrence	Aug 2010	G = 0 R = 2	49.294 – 49.852	-65.098 - -64.675		158.0 ± 100.4
U	Ungava Bay	Oct 2007	G = 12 R = 26	59.353 – 60.899	-68.768 - -65.076	0.408 ± 0.616	239.3 ± 74.1
W	Western Hudson Strait	Oct 2009	G = 0 R = 14	62.541 – 64.004	-77.952 - -71.773	-0.676 ± 0.402	243.4 ± 85.6

Table 5.2. Standard cephalopod morphometric measurements and their associated codes. Only robust measurements (in **bold**) used for the multivariate analysis to maintain sample numbers.

*Measurements modified from standard descriptions, ** Kristensen (1982)

<i>Gonatus fabricii</i> (Roper & Voss, 1983)		Code	<i>Rossia</i> spp. (Mercer, 1968)	
Measure (mm) (Abbr.)	Description		Measure (unit) (Abbr.)	Description
Mantle Length (ML)	Dorsal length from tip of tail to mantle collar	1	Dorsal Mantle Length (DML)	Dorsal length from mantle collar to posterior body
		2	Ventral Mantle Length (VML)	Ventral length from mantle collar to posterior body
		3	Mantle Width (MW)	Widest width of mantle
Total Length* (TL)	Dorsal length from tip of tail to tip of the longest extended arm	4	Total Length (TL)	Dorsal length from the posterior mantle to tip of the longest extended arm
		5	Head Width (HW)	Distance from outer eye to outer eye
		6	Head Length (HL)	From the nuchal cartilage to the base of Arms 1
Eye Diameter (ED)	Diameter of eye bulbous	7	Eye Diameter (ED)	Diameter of eye bulbous
Lens Diameter (LD)	Diameter of hardened lens	8	Lens Diameter (LD)	Diameter of hardened lens
Tentacle Length (TentL)	Length of tentacle from insertion point to tip of club	9	Tentacle Length (TentL)	Length of tentacle from insertion point to tip of club
Club Length (ClubL)	Length of club (from first basal sucker)	10	Club Length (ClubL)	Length of club (from first basal sucker)
Fin Length (FL)	Length of fin along the mantle axis	11	Fin Length (FL)	Widest point of fin along the mantle axis
		12	Fin Width (FW)	Greatest width across both fins and body
Fin Width* (FW)	Distance from mantle to the tip (90° from mantle axis)	13	Fin Width Single* (FWs)	Distance from mantle to tip (90° from mantle axis) of a single fin
		14	Fin Position (FP)	Distance from mantle collar to insertion point of fin
		15	Fin Insertion Length (FIL)	Length of insertion line
		16	Sucker Diameter Tentacle (SDtent)	Diameter of largest suckers on the tentacles
		17	Sucker Diameter Sessile (SDsess)	Diameter of largest suckers on the 3 rd left arm

Table 5.2 Cont'd

<i>Gonatus fabricii</i> (Roper & Voss, 1983)			<i>Rossia</i> spp. (Mercer, 1968)	
Measure (mm) (Abbr.)	Description	Code	Measure (unit) (Abbr.)	Description
Arm Length (AR3)	From insertion point on head to tip of the 3 rd left arm	18-21	Right Arm Lengths (RA1-RA4)	Length of arms from insertion point on head to tip (right side)
		22-25	Left Arm Lengths (LA1-LA4)	Length of arms from insertion point on head to tip (left side)
Funnel Locking Apparatus** (FLA)	Length of funnel locking apparatus	26	Funnel Locking Apparatus** (FLA)	Length of funnel locking apparatus
Gladius Length (GL) or Pen Length (PL)	Total length of the chitin dorsal structure	27		
Wet Weights (g) (Abbr.)	Description		Wet Weights (g) (Abbr.)	Description
Total Weight (TotWW)	Total weight of specimen once thawed	28	Total Weight (TotWW)	Total weight of specimen once thawed
Arm Weight (ArmWW)	Wet weight of 3 rd left arm	29	Arm Weight (ArmWW)	Wet weight of 3 rd left arm
Liver Weight (LiverWW)	Total wet weight of liver	30	Liver Weight (LiverWW)	Total wet weight of liver
Buccal Mass Weight (BuccalWW)	Weight of buccal muscle removed from around the beaks	31	Buccal Mass Weight (BuccalWW)	Weight of buccal muscle removed from around the beaks
Upper Beak Weight (UpperBK_WW)	Weight of upper beak only (tissue removed)	32	Upper Beak Weight (UpperBK_WW)	Weight of upper beak only (tissue removed)
Lower Beak Weight (LowerBK_WW)	Weight of lower beak only (tissue removed)	33	Lower Beak Weight (LowerBK_WW)	Weight of lower beak only (tissue removed)

Table 5.3. Ontogenetic size ranges for *G. fabricii* and maturity stages of *R. palpebrosa*.

<i>Gonatus fabricii</i>		
Size Range (mm ML)	Code	Description (taken directly from Arkhipkin and Bjørke 1999)
3.5 – 14	1	Planktonic epipelagic paralarvae
15 – 64	2	Mesonektonic epipelagic juveniles
65 – 129	3	Nektonic mesopelagic immature
130 - 199	4	Nektonic meso- and bathypelagic immature and maturing *includes mature males ~ 160 mm ML
200+	5	Planktonic bathypelagic maturing, mature and spent females
<i>Rossia palpebrosa</i>		
Maturity Stage		Description (modified from Mercer 1968)
Paralarvae		No visible gonads
Immature		All eggs opaque; male gonads beginning to differentiate
Maturing		Some clearing in eggs; spermatophores developing
Mature		Clear eggs in ovary; spermatophores in Needham's sac

Table 5.4. Size measurements of *G. fabricii* and *R. palpebrosa* used for PCA and Discriminant Analyses per location and maturity stage.

Species	Locations	SizeRange / MaturityStage	N	Mean (ML mm) (± St. Dev)	Range (ML mm)
<i>G. fabricii</i>	Baffin Bay	2	12	47.40 (± 7.55)	(33.42 - 57.05)
		3	1	94.36	
		5	2	249.00 (± 1.41)	(248.00 - 250.00)
	Central Greenland	2	52	49.28 (± 8.14)	(33.17 - 62.72)
		3	18	92.08 (± 23.30)	(65.04 - 126.82)
		4	13	148.38 (± 19.62)	(131.08 - 192.33)
	Disko Bay	3	9	100.73 (± 19.52)	(66.74 - 120.20)
		4	14	152.89 (± 18.99)	(130.51 - 195.00)
		5	2	210.75 (± 15.20)	(200 - 221.50)
	Davis Strait	2	5	44.17 (± 6.08)	(36.00 - 51.70)
		3	2	102.53 (± 18.14)	(89.70 - 115.35)
	East Hudson Strait	2	54	42.30 (± 6.84)	(31.15 - 60.12)
		3	19	97.33 (± 9.60)	(83.40 - 115.45)
	Northern Greenland	2	4	59.31 (± 4.15)	(55.50 - 64.87)
		3	15	88.70 (± 18.33)	(66.11 - 124.55)
		5	1	216.72	
Southern Greenland	2	2	56.56 (± 9.84)	(49.60 - 63.51)	
Ungava Bay	2	9	48.46 (± 5.18)	(40.00 - 53.40)	
	3	3	78.51 (± 7.92)	(72.24 - 87.41)	
<i>R. palpebrosa</i>	Central Greenland	2	1	18.24	
		3	1	24.41	
	Davis Strait	4	1	42.15	
	East Hudson Strait	2	5	23.17 (± 1.57)	(21.44 - 25.55)
		3	2	39.67 (± 3.47)	(37.21 - 42.12)
		4	5	43.81 (± 4.19)	(38.40 - 41.33)
	Gulf of St. Lawrence	3	2	20.45 (± 3.35)	(18.08 - 22.82)
		4	2	28.89 (± 6.75)	(24.12 - 33.66)
	Hudson Strait	2	1	30.82	
		3	1	37.36	
		4	2	42.49 (± 2.36)	(40.82 - 44.16)
Northern Greenland	3	1	33.52		
St. Lawrence	3	1	29.45		
	4	1	43.34		

Table 5.4. Cont'd

Species	Locations	SizeRange / MaturityStage	N	Mean (ML mm) (± St. Dev)	Range (ML mm)
<i>R. palpebrosa</i> Cont'd	Ungava Bay	2	5	24.98 (± 2.84)	(21.70 - 27.84)
		3	6	36.19 (± 6.08)	(30.44 - 47.55)
		4	7	44.47 (± 3.58)	(40.71 - 51.55)
	West Hudson Strait	2	2	22.02 (± 1.63)	(20.86 - 23.17)
		3	5	27.64 (± 1.74)	(26.02 - 29.95)
		4	4	36.62 (± 3.40)	(33.23 - 40.97)

Table 5.5 Barcode of Life (IBoL/BOLD) sequence reference numbers for DNA analyses

Species (base pair range)	% Mean Within Species Distance (SE %)	Max Within Species Distance (%)	Reference code
<i>G. fabricii</i> (581 to 658 bp)	0.06 (0)	0.46	KGCAO 001-09 to 006-09 KGCAO 040-09 KGCAO 058-09 to 082-09 KGCAO 097-11 to 118-11
<i>R. palpebrosa</i> (340 to 658 bp)	0.06 (0)	0.51	KGCAO 037-09 to 039-09 KGCAO 041-09 to 057-09 KGCAO 120-11 to 121-11 KGCAO 123-11 KGCAO 128-11 KGCAO 132-11 KGCAO 136-11 to 142-11 KGCAO 172-11 KGCAO 175-11 KGCAO 177-11 to 178-11 KGCAO 180-11 to 181-11 KGCAO 185-11 to 187-11

Table 5.6. MANOVA results (Pillai's Trace) for all *G. fabricii* and *R. palpebroso* using principal component scores from PCA. Percentages are those misclassified by discriminant analysis. The smaller the percentage, the more distinct the groupings. P values denoted by an * are significant to $\alpha = 0.05$.

Species	Size Range	Value	Approx. F	Num. df	Den.df	Prob>F
<i>G. fabricii</i>	Size 2 (57.04 %)	0.4891061	3.5942	20	516	< 0.0001*
	Size 3 (29.51 %)	0.8049569	2.0781	27	153	0.0030*
	Size 4 (7.41 %)	0.6508129	1.8638	13	13	0.1373
	All Size Ranges (50.88 %)	0.9348418	3.7502	65	1060	0.0001*
<i>R. palpebroso</i>	Immature (41.67 %)	0.4501004	1.3068	4	18	0.3050
	Maturing (31.25 %)	0.7353205	2.3257	6	24	0.0652 [†]
	Mature (31.58 %)	0.9508381	2.3201	9	45	0.0306*
	All Maturity Stages (52.94 %)	0.9024235	3.3503	16	184	< 0.0001*

¹ No paralarval (size 1) *G. fabricii* were collected

² Due to the small sample size for Size 5 of *G. fabricii* (n = 5), this group was not included in the analysis.

³ Only one hatchling *R. palpebroso* was present therefore, it was excluded from the analyses.

[†] Significant difference found with the three other MANOVA tests: Wilks' Lambda, Hotelling-Lawley and Roy's Max Root; only Pillai's Trace showed no significance.

Figure 5.1. Sample zones used for morphometric analyses. Full names and associated codes listed in Table 5.1. All specimens collected within the deep trough between the Greenland and Baffin Island shelves were deemed 'Baffin Bay' (B) individuals.

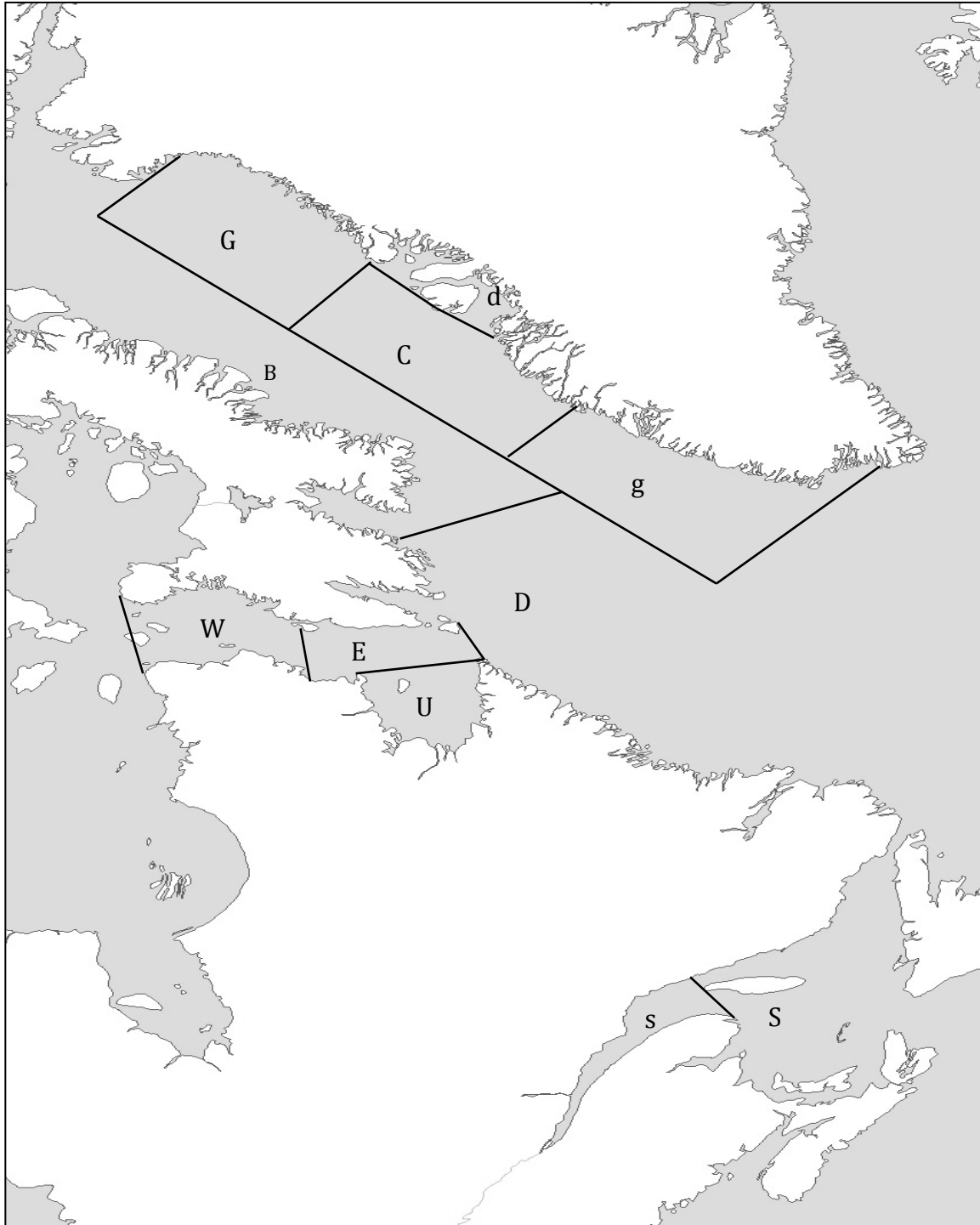


Figure 5.2. Standard morphometric measurements of **a)** *Gonatus fabricii* and *Rossia* spp. (dorsal - **b** and ventral - **c**) as described in Table 5.2.

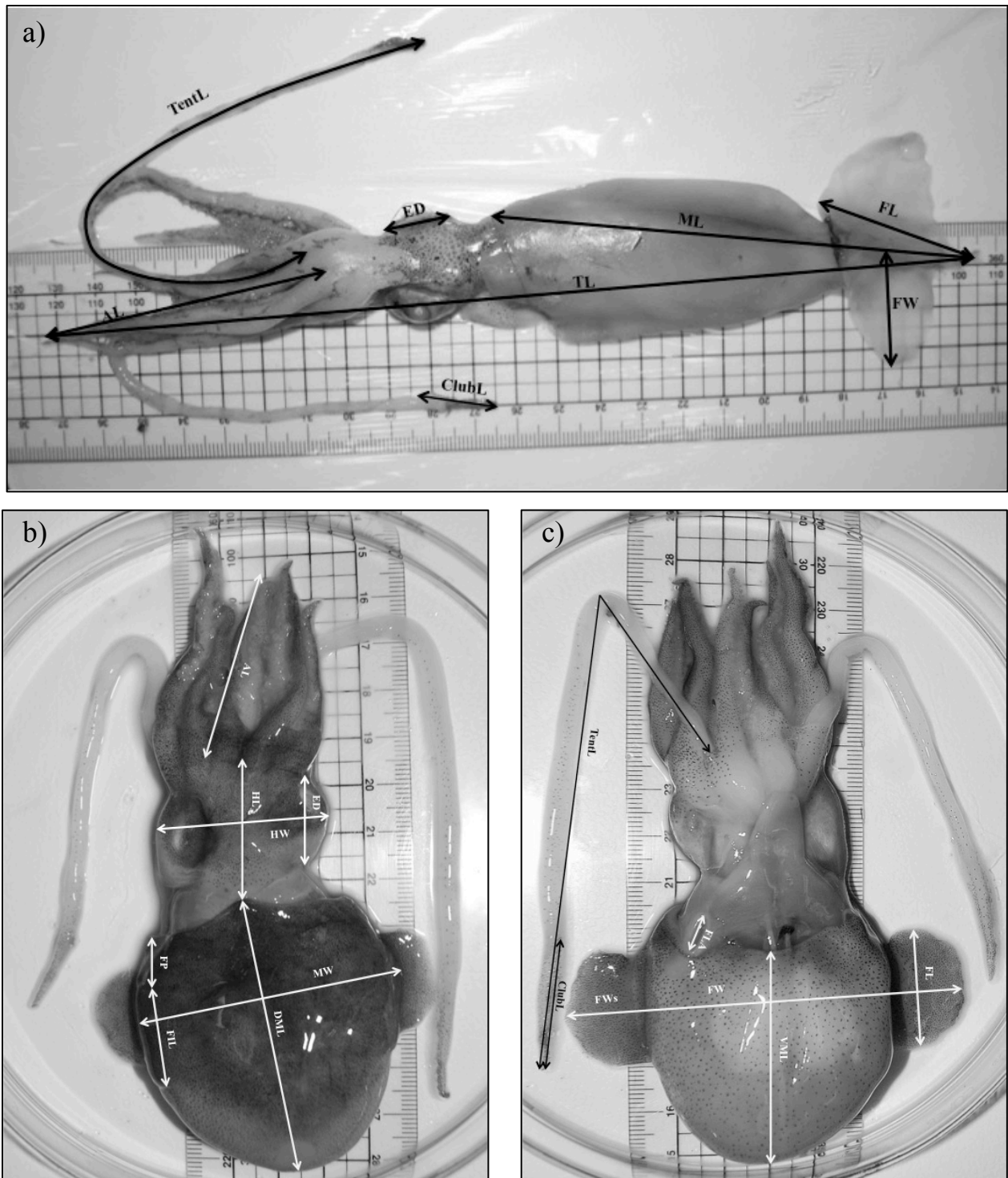


Figure 5.3. PCA results of environmental data from the sample locations. Components 1 and 2 account for 71.3 % of the observed variation. Three distinct clusters evident: Hudson Strait (—); Baffin Bay/Greenland (---); and St. Lawrence (...) (see Table 5.1 for location code definitions). MANOVA results show significant differences between the sampling regions (Pillai's trace = 1.338, $F_{33,780} = 19.021$, $p < 0.001$ for $\alpha = 0.05$).

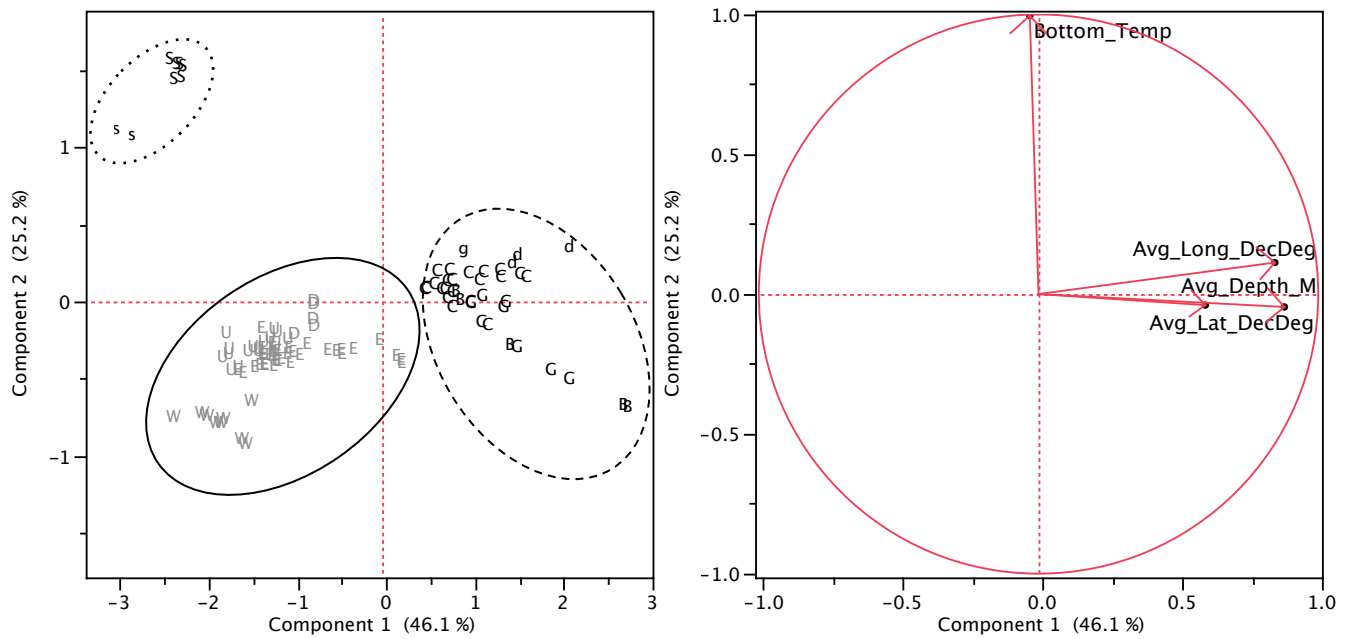


Figure 5.4. Comparison between sampling years 2007 (open symbols) and 2009 (filled symbols) for the Hudson Strait region (eastern Hudson Strait \triangle , western Hudson Strait \circ , Ungava Bay \square). The average longitudes (eigenvector = 0.55799) and bottom temperatures (eigenvector = 0.54070) account for most of the variation on PC1 (63.0 %) while average latitudes (eigenvector = 0.61721) and depths (eigenvector = 0.60328) were most variable for PC2 (28.2 %).

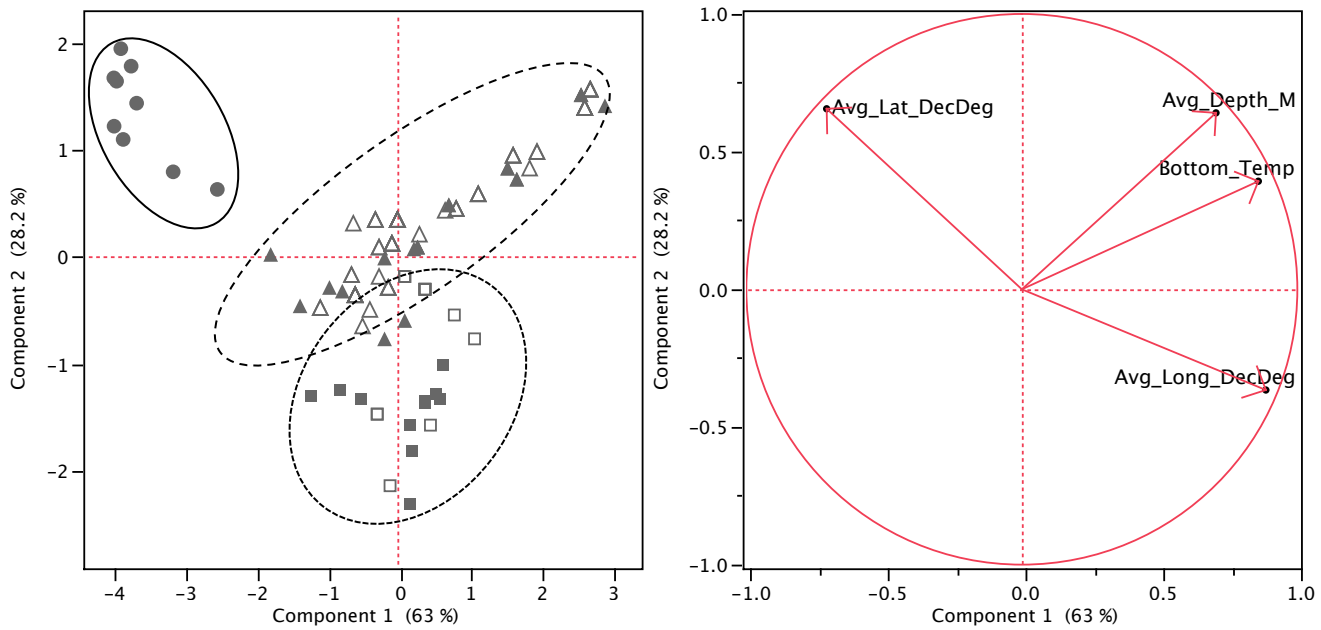


Figure 5.5. **a)** Principal component (PCA) results and **b)** loading plot for all size ranges of *G. fabricii*. The first three axes comprise 95.61 % of the variation. Five main clusters are evident: Hudson Strait region (___) formed two distinct groups; Ungava Bay (---); and Disko Bay (._._.) formed a tight cluster within the larger Baffin/Greenland central grouping (._._.). **b)** Loading plot of morphometric variables (see Table 5.1 for location codes and Table 5.2 for morphometric character codes).

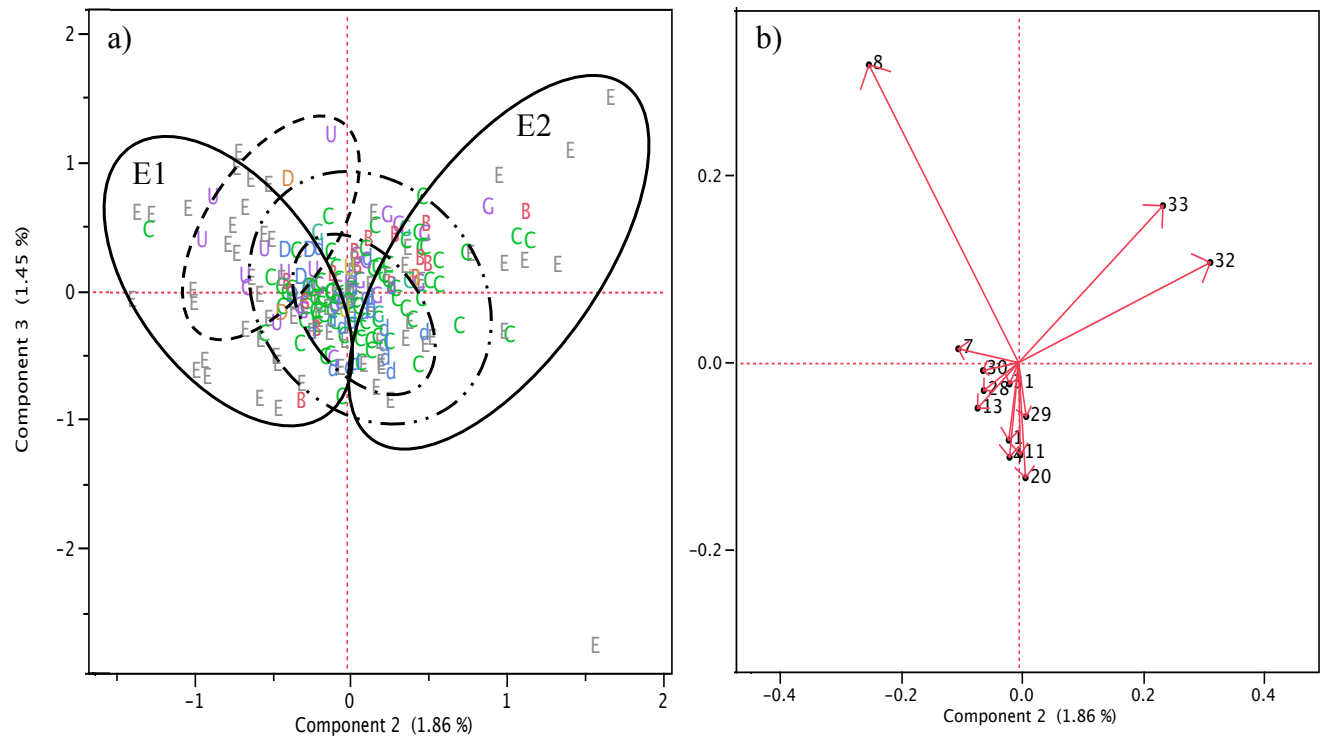


Figure 5.6. Discriminant analysis results (without FLA) of all *G. fabricii* specimens using principle component scores to remove any correlations. (Pillai's Trace = 0.9348418; $F_{65,1060} = 3.7502$, $p < 0.0001^*$; 50.88% misclassified)

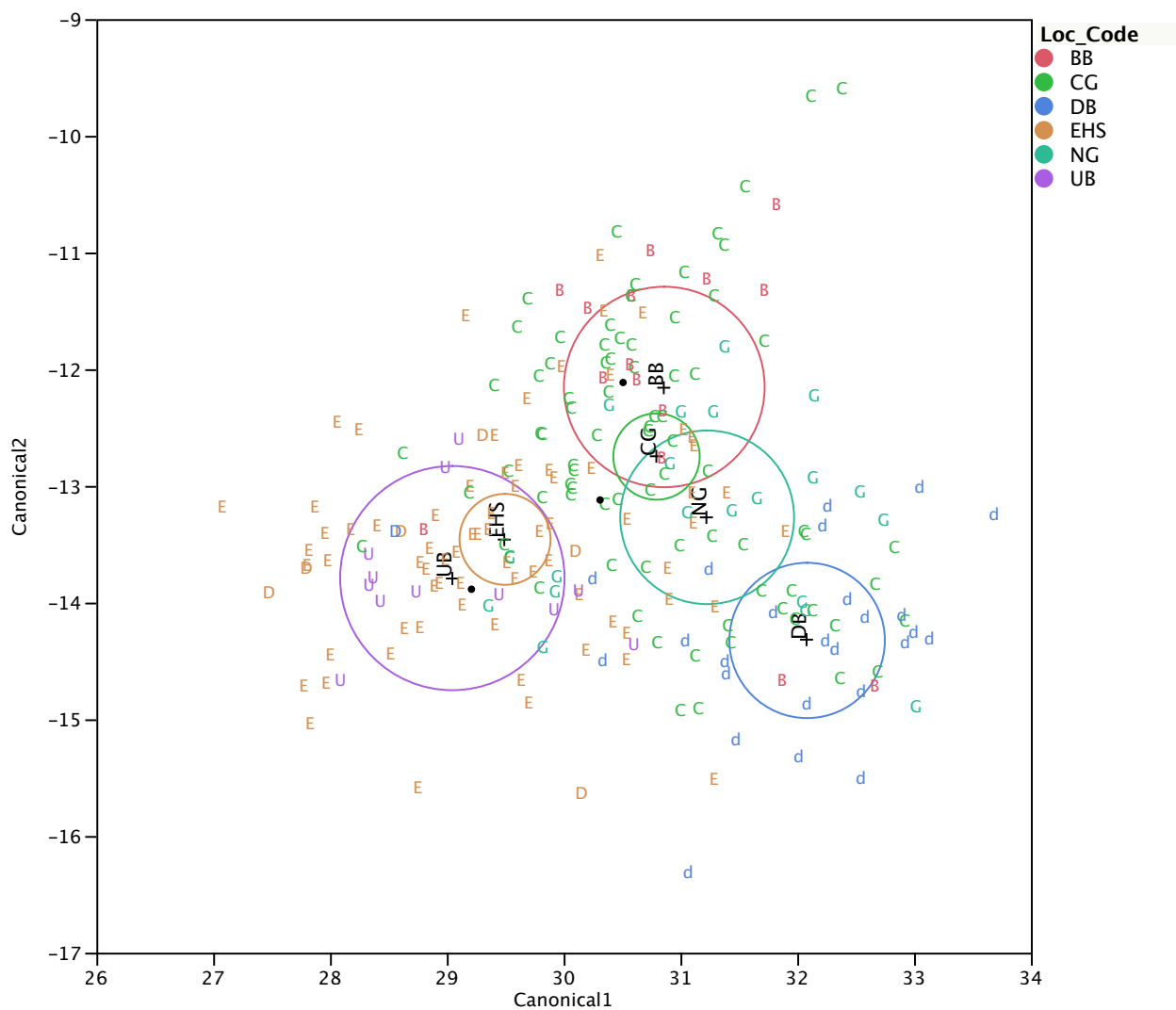


Figure 5.7. PCA results and loading scores of *G. fabricii* by size range (**a** = 2 (81.55 % of the variation), **b** = 3 (85.55 % of the variation), **c** = 4 (83.96 % of the variation); see Table 5.3 for size range code descriptions and Table 5.2 for morphometric character codes).

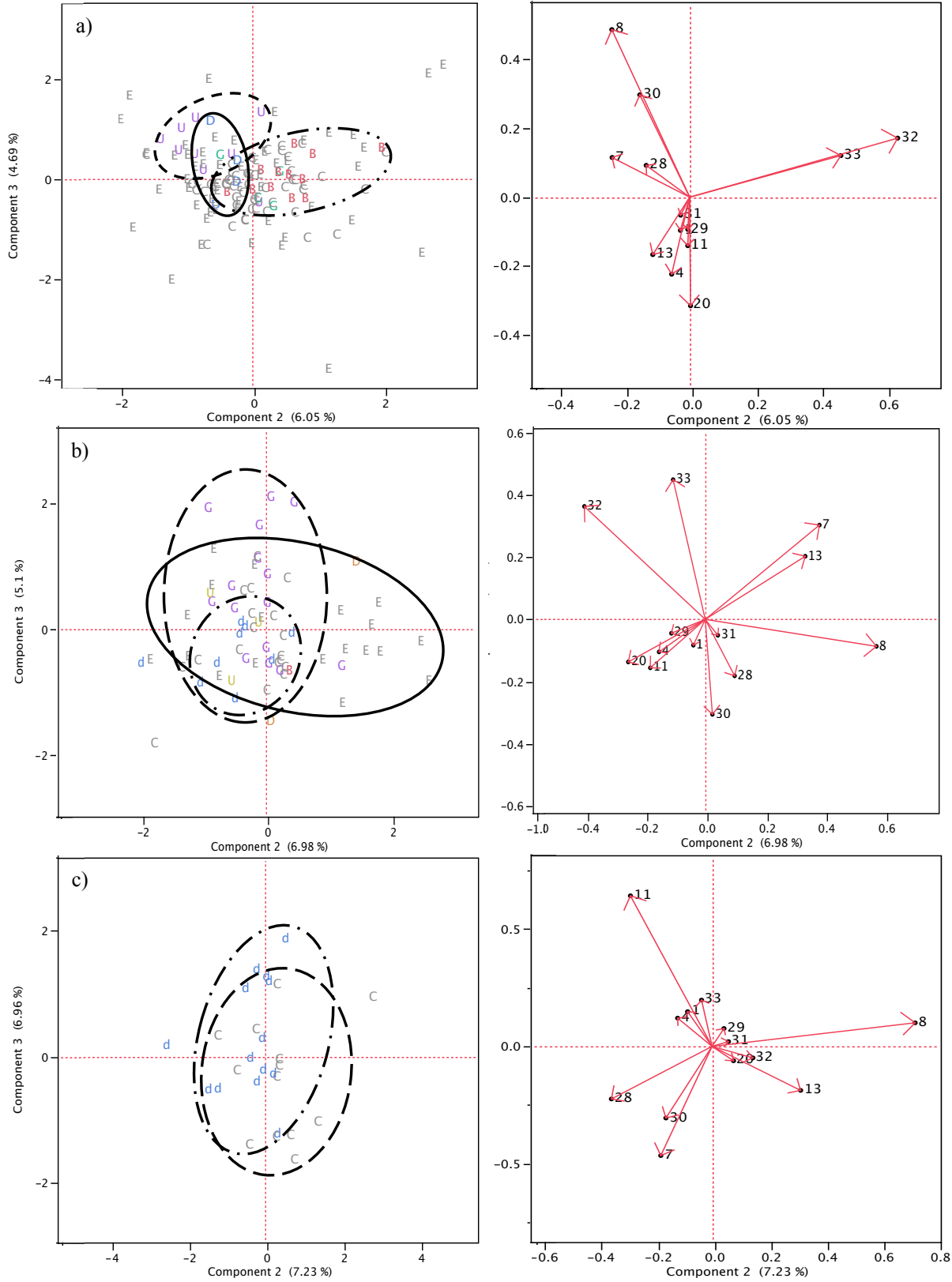


Figure 5.8. Discriminant analysis results of *G. fabricii* by size range (**a** = 2, **b** = 3, **c** = 4; see Table 5.3 for size range code descriptions). The analysis used the component scores from the PCA analyses to remove any potential inter-correlations.

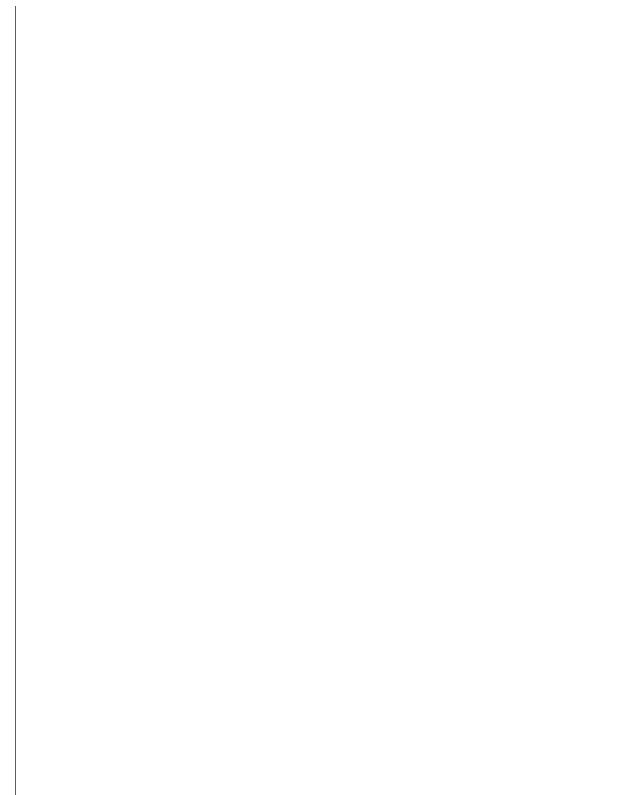
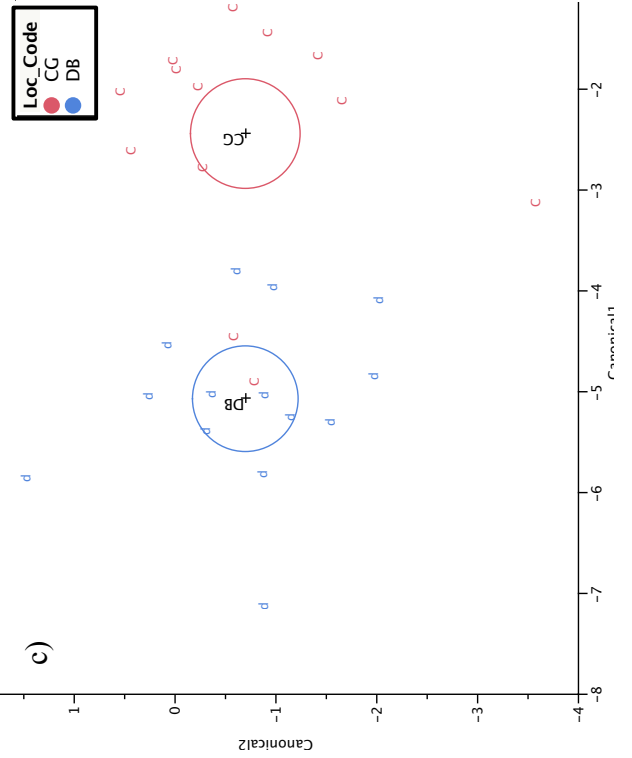
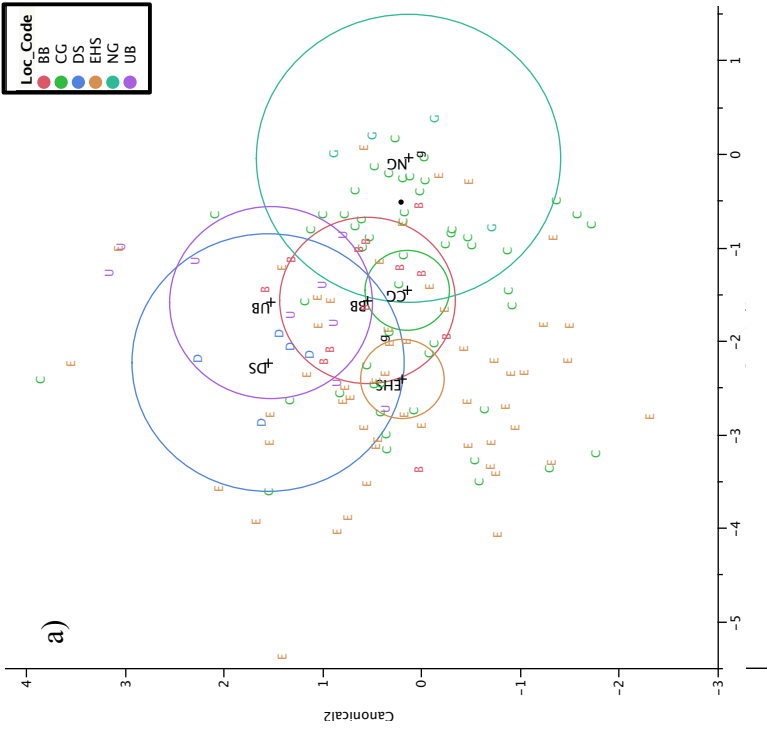
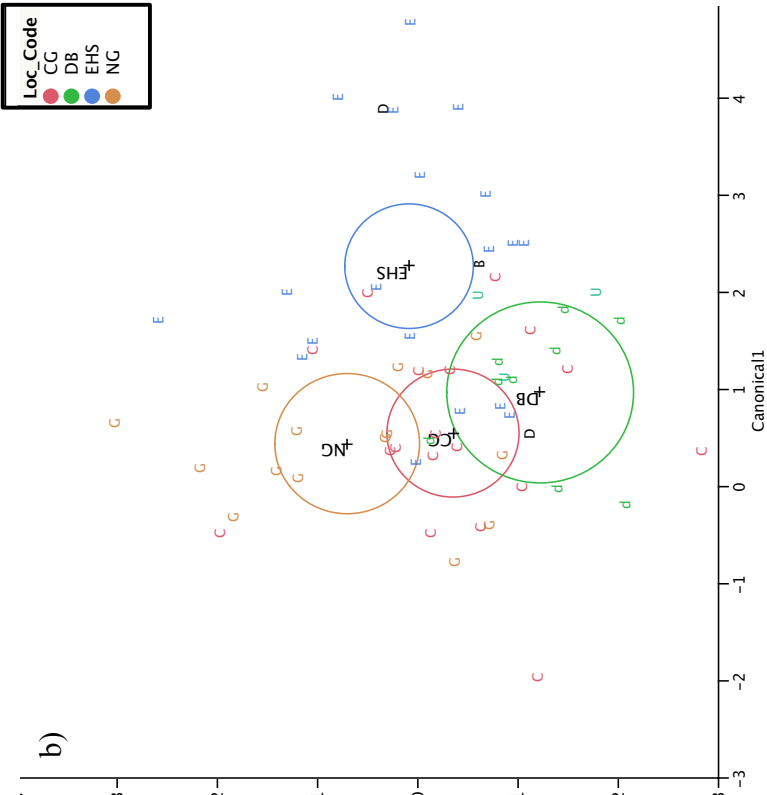


Figure 5.9. Genetic taxonomic tree based on COI barcode results of *G. fabricii* (IBoL, BOLD, University of Guelph). See Table 5.1 and Fig. 5.1 for the associated location codes. Grey arrows represent Hudson Strait specimens (Hudson Strait, Davis Strait and Ungava Bay).

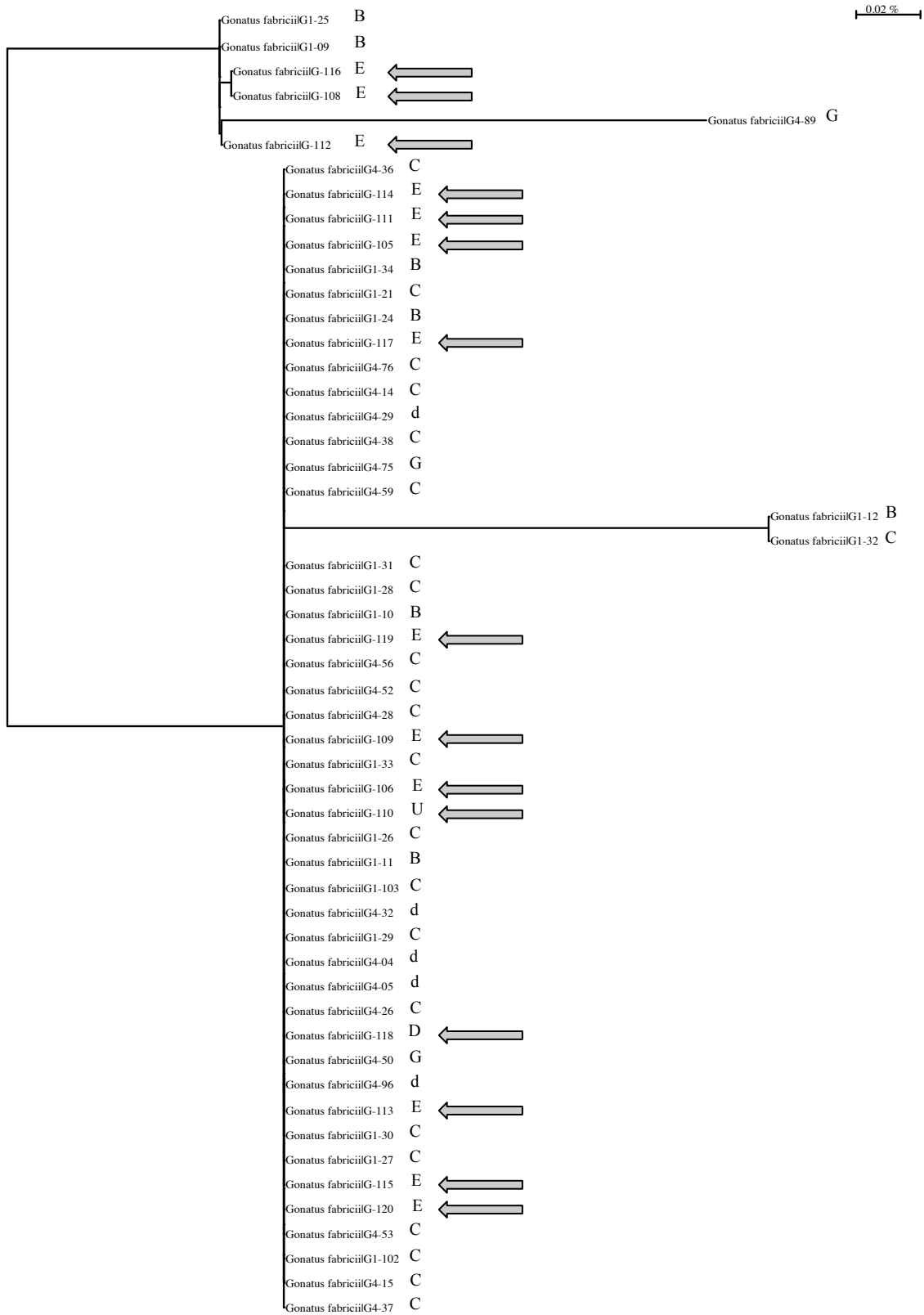


Figure 5.10. Redundancy analysis (500 permutations; $p < 0.0001^*$) of all size ranges of *G. fabricii*'s morphometric characters (see Table 5.2 for character codes) to the collected environmental variables. Note * denotes significant p values for $\alpha = 0.05$ which indicate that the axis are linearly related.

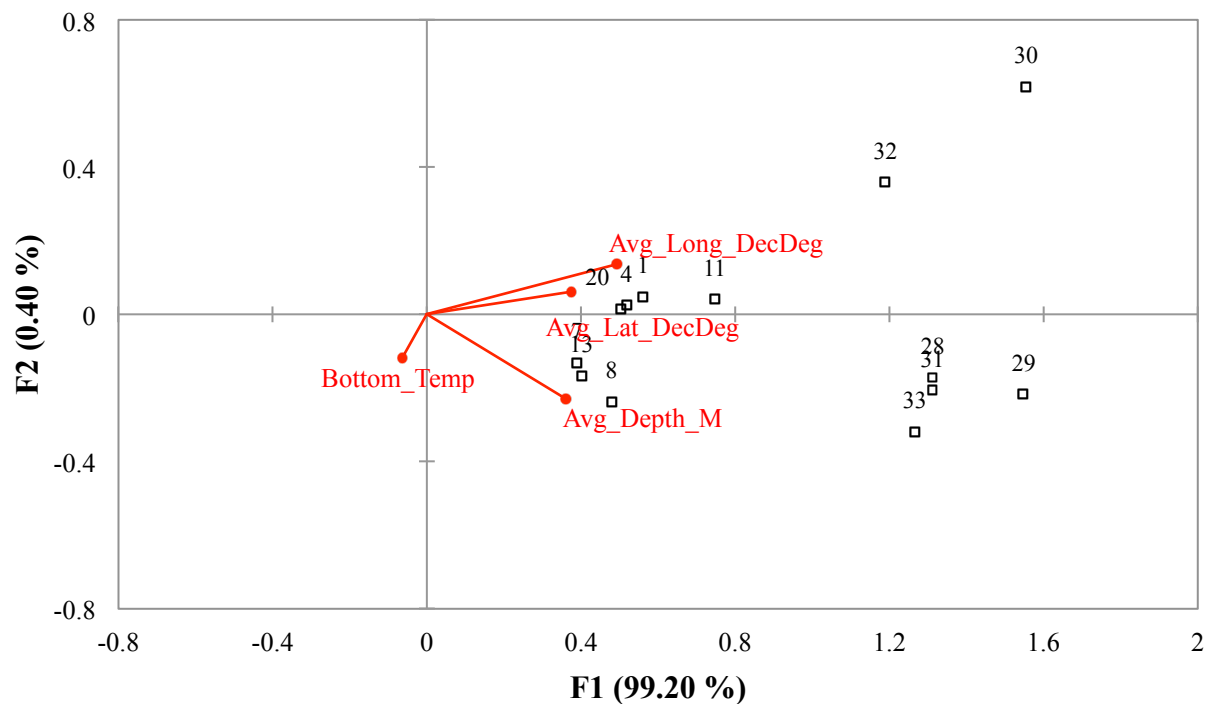


Figure 5.11. Redundancy analysis (500 permutations) of *G. fabricii*'s morphometric characters per size range to the collected environmental variables (see Table 5.2 for character codes and Table 5.3 for size ranges). **a)** RDA for size range 2 (500 permutations; $p = 0.002^*$); **b)** RDA for size range 3 (500 permutations; $p = 0.014^*$); and **c)** RDA for size range 4 (500 permutations; $p = 0.090$; not linearly related). Note * denotes significant p values for $\alpha = 0.05$ which indicate that the axis are linearly related.

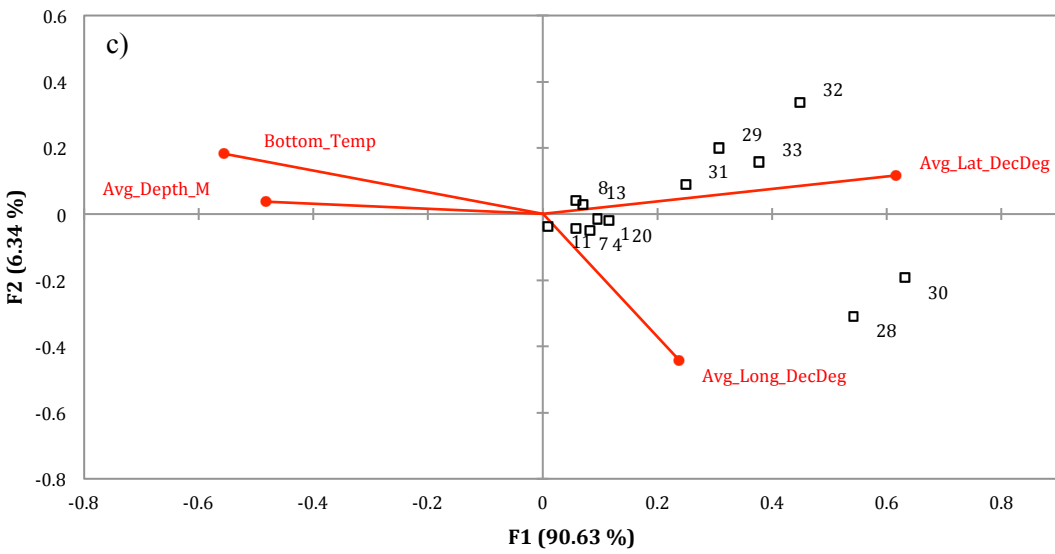
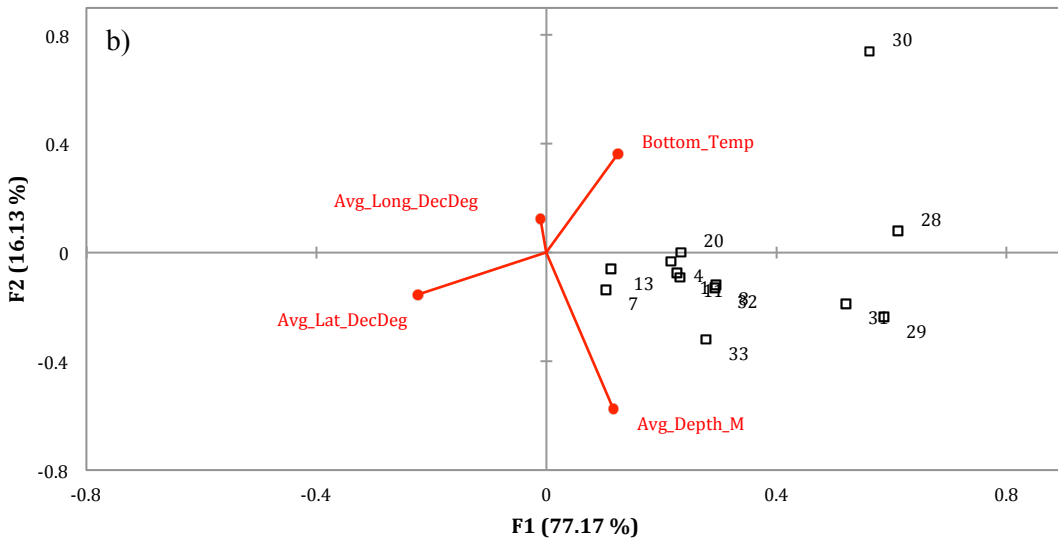
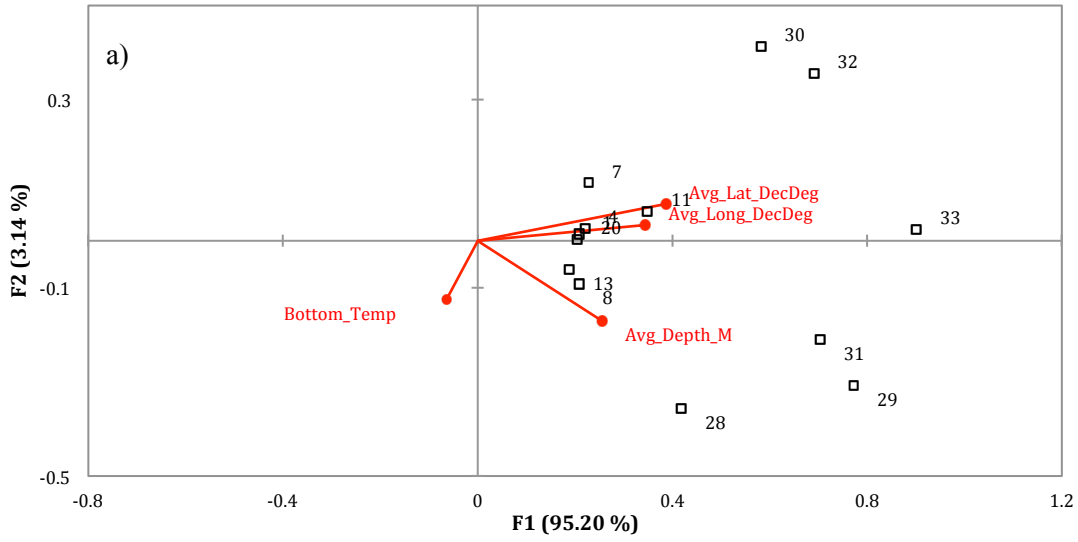


Figure 5.12. PCA results of *R. palpebrosa* per maturity stage (**a** = immature (78.77 % of the variation), **b** = maturing (83.79 % of the variation), **c** = mature (75.9 % of the variation); see Table 5.3 for size range code descriptions and Table 5.2 for morphometric character codes).

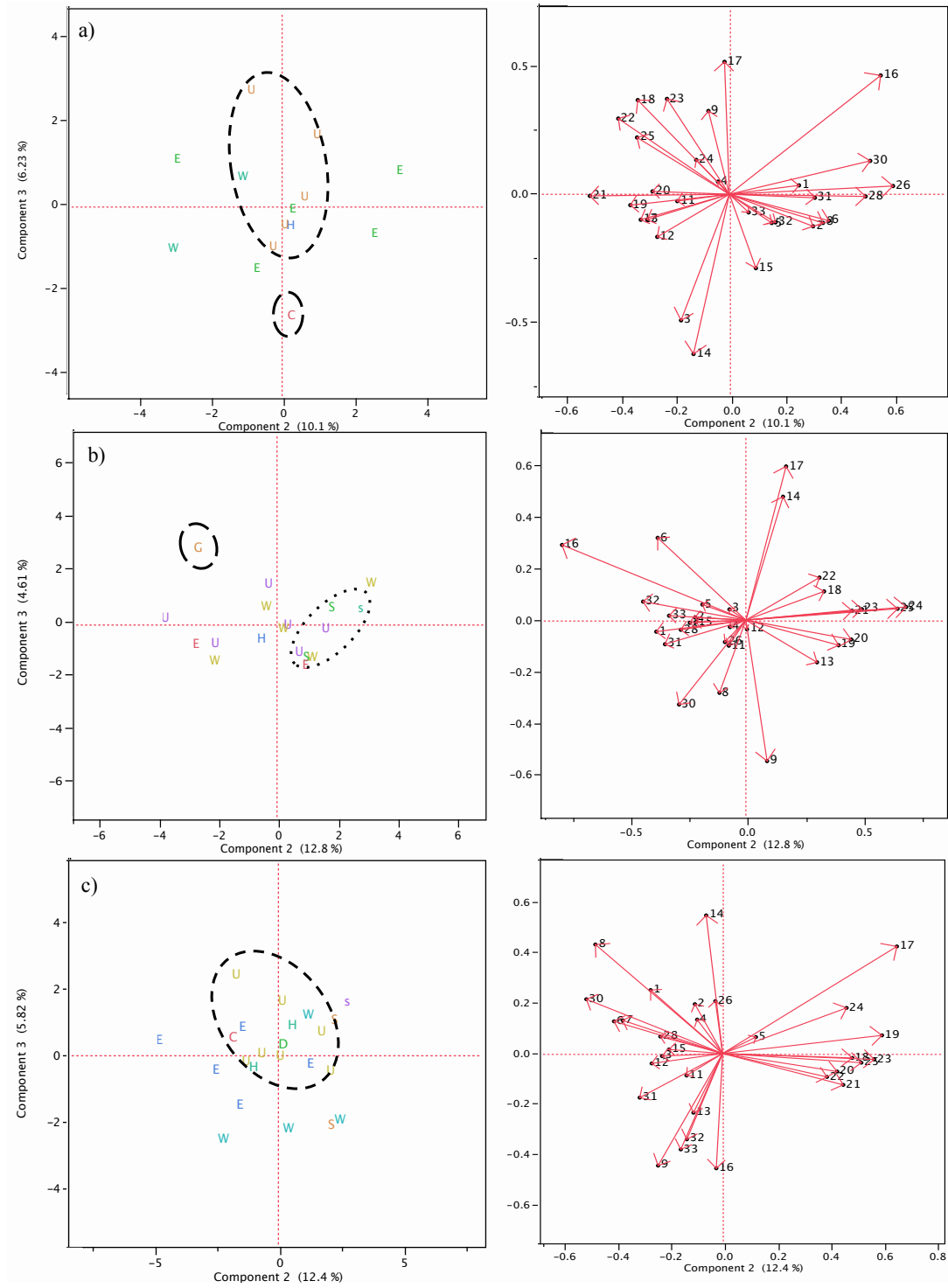


Figure 5.13. Discriminant analyses of *R. palpebrosa* per maturity stage (**a** = immature, **b** = maturing, and **c** = mature; see Table 5.3 for size ranges). See Table 5.6 for the corresponding MANOVA results.

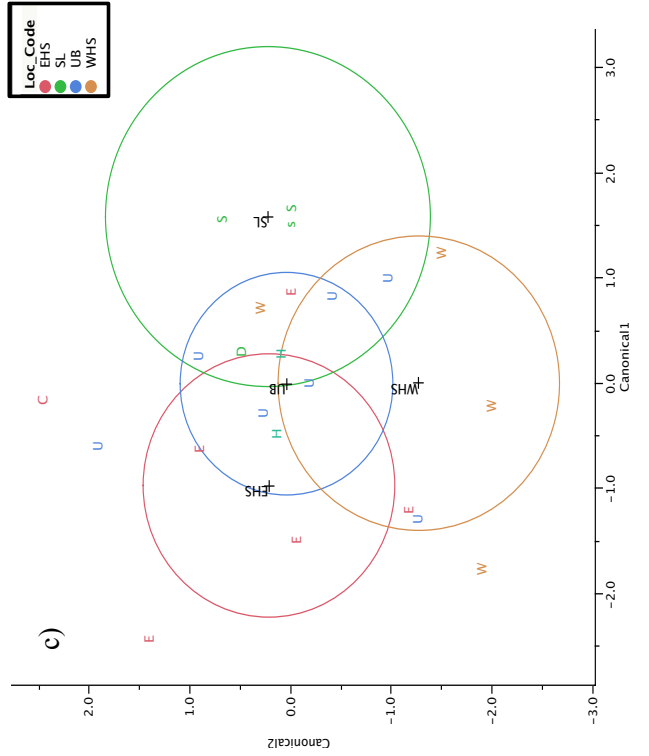
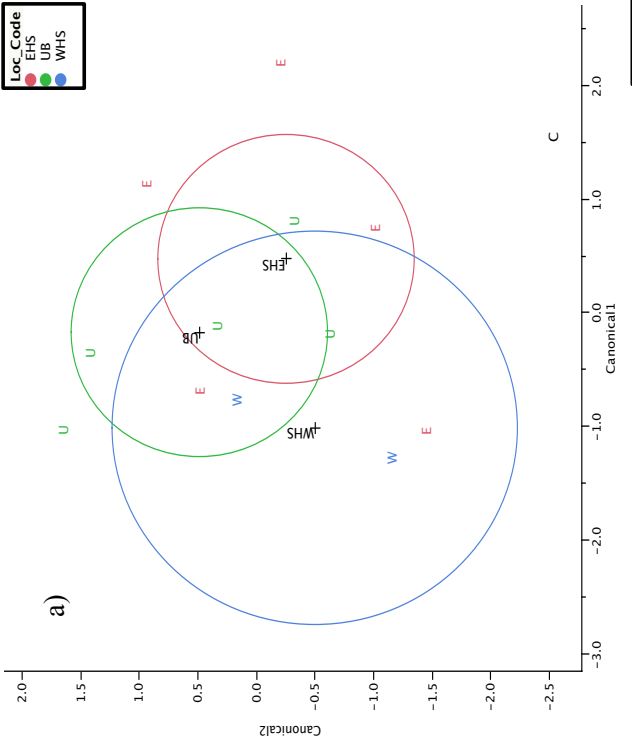
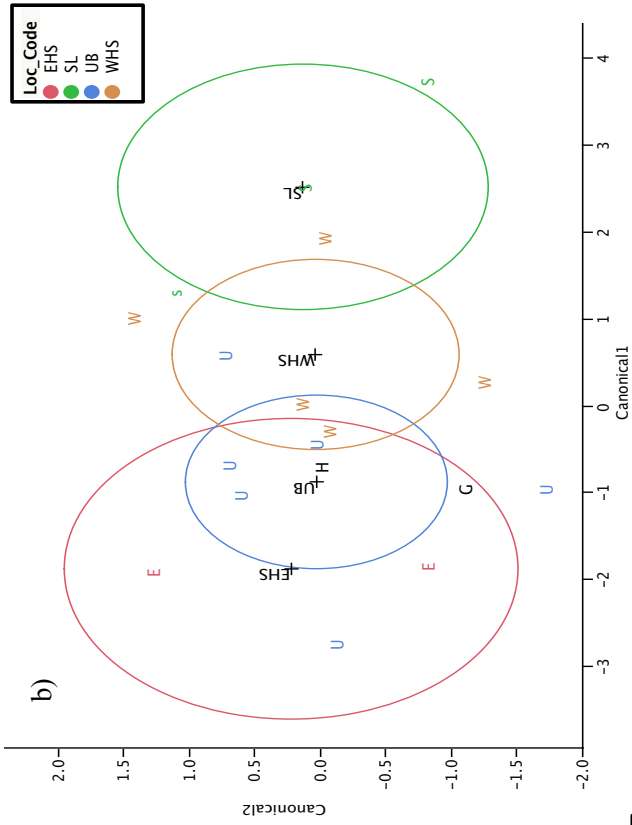


Figure 5.14. Discriminant analysis based on principal component scores of *R. palpebrosa* (all maturity stages).

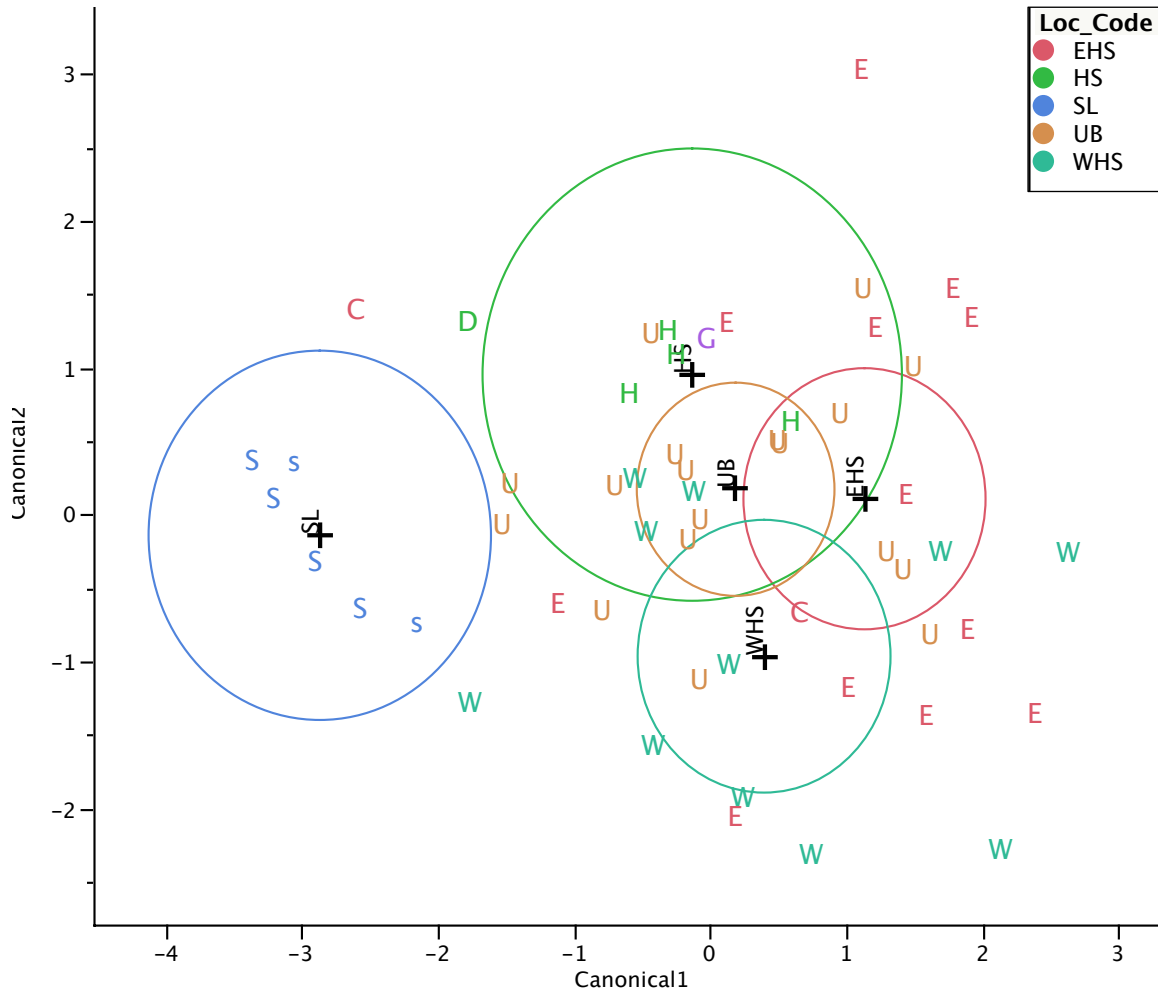


Figure 5.15. Genetic taxonomic tree based on COI barcode results of *R. palpebrosa* (IBoL, BOLD, University of Guelph). See Table 5.1 and Fig. 5.1 for descriptions of the associated location codes. No visible clustering between Baffin Bay/Greenland (solid arrows), Hudson Strait or St. Lawrence (hollow arrows) specimens indicating lack of sufficient time to diverge.

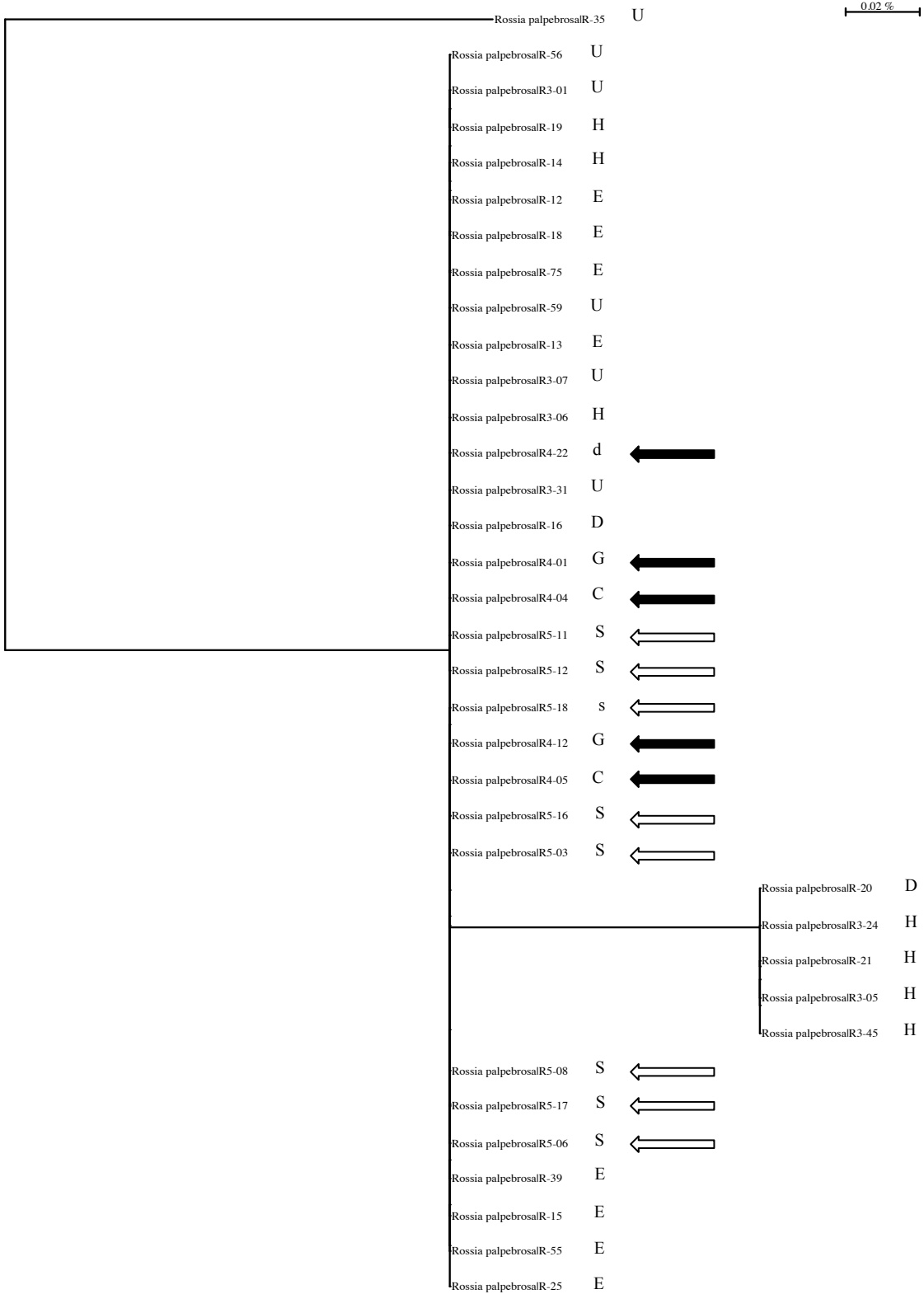
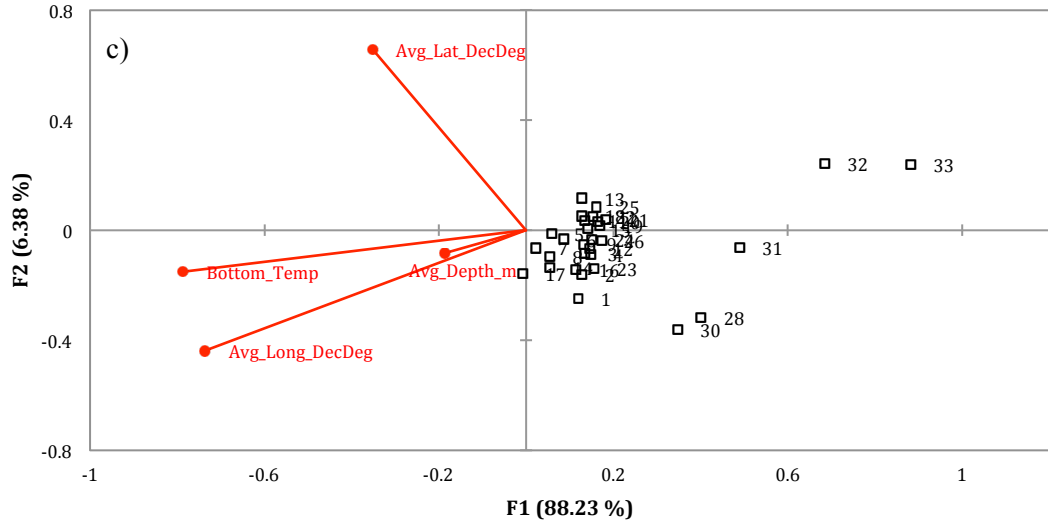
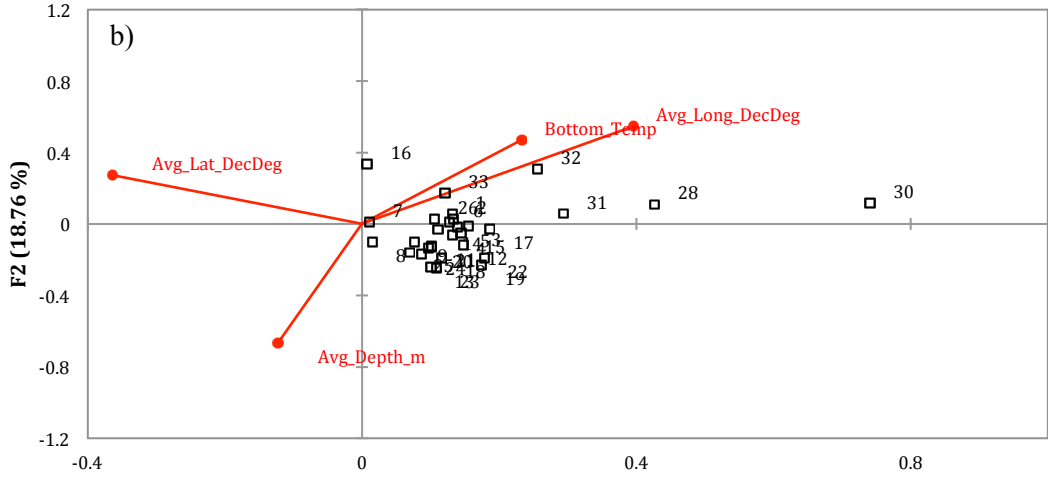
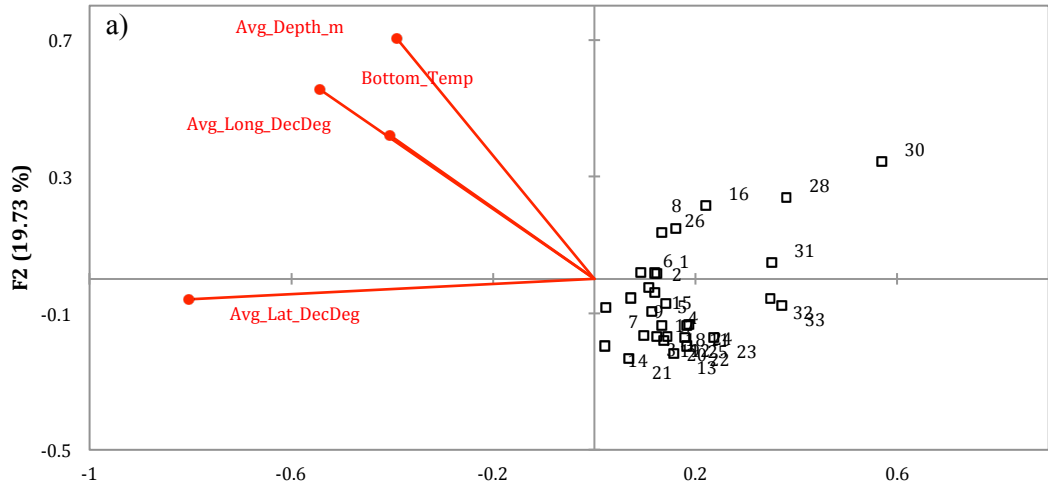


Figure 5.16. Redundancy analysis (500 permutations) of *R. palpebrosa*'s morphometric characters per maturity stage to the collected environmental variables (see Table 5.2 for character codes and Table 5.3 for maturity stage). **a)** RDA for immature individuals (500 permutations; $p = 0.018^*$); **b)** RDA for maturing individuals (500 permutations; $p = 0.226$; not linearly correlated); and **c)** RDA for mature individuals (500 permutations; $p = 0.002^*$). Note * denotes significant p values for $\alpha = 0.05$ which indicate that the axis are linearly related.



Chapter 6

Habitat and trophic studies using stable isotope (SI) and stomach content analyses of cephalopod tissues and SIA of prey items

Abstract

Cephalopods are an important trophic component throughout most marine ecosystems, transferring nutrients through the food web both as energy-rich prey items and notable predators. This chapter examines the trophic role of Arctic cephalopods within the polar region using stable isotope (SI) and traditional stomach content analyses, and statistical mixing models to: **1)** define potential feeding habitats and shifts in trophic structure throughout the life cycles of *G. fabricii*, *R. palpebrosa*, *Bathypolypus* spp. (species complex) and *C. muelleri* and **2)** identify potential primary prey species for the Arctic cephalopods. Delta ^{13}C values distinguished among distinct habitats of the four common species examined and also indicated a shift in habitat preference with maturity for both *Bathypolypus* spp. and *R. palpebrosa*, likely the result of mature individuals moving to spawning sites. Delta ^{15}N values added to the limited knowledge on the feeding habits and habitats of Arctic cephalopod species. Benthic species (including sit-and-wait predators) were more enriched than active pelagic hunters (*G. fabricii*). Statistical mixing models in conjunction with stomach content and stable isotope analyses provided insights into potential prey species and highlighted the importance of copepods in the diet of Arctic *G. fabricii* of all size ranges and intertidal mussels in the diet of *Bathypolypus* spp. from the St. Lawrence region. This is the first account of potential prey species for *C. muelleri*, which include polychaetes, decapods, ostracods and clams.

6.1. Introduction

The complex Arctic ecosystem relies on established timing of increased nutrient loads coinciding with plankton blooms to provide the necessary building blocks for the Arctic food web (Gradinger 1995, Overland et al. 2010). Shifts in ecological conditions (i.e. temperatures, salinity shifts) and timing, such as those predicted to occur with climate change, could upset this natural balance, altering the quantity and quality of available prey organisms (Michel et al. 2006, André et al. 2010, Planque et al. 2010). Such a shift would negatively impact many of the larger Arctic predators (Chapter 2, section 2.1.4, pg.30), including those of commercial and cultural importance to the Inuit of the region.

Within the Arctic ecosystem, cephalopods play a central role cycling nutrients throughout the depths (Sennikov et al. 1989, Clarke 1996, Takai et al. 2000, Nesis 2003c). They feed on a variety of invertebrates, fish and other cephalopods (including cannibalism) (Bakun and Csirke 1998, Boyle and Rodhouse 2005b) making them energy-rich prey for higher trophic level marine species (Chapter 2 section 2.2.1.3 and 2.2.2.1d; Tables 4.2, 4.3 and 4.4). Cephalopods are also sensitive to environmental shifts, with many of their life history components dependent on current environmental conditions (Chapter 2, sections 2.2.1.3 and 2.2.1.5) (Boletzky 1994, Rodhouse and Nigmatullin 1996, Nesis 1999, Forsythe 2004, Boyle and Rodhouse 2005f, g, Leporati et al. 2007). Understanding the trophic role Arctic cephalopods play within and between their respective habitats (e.g. pelagic, neritic) will provide baseline information for future studies on abiotic and biotic impacts to the Arctic marine ecosystem.

G. fabricii, the common, pelagic Canadian Arctic cephalopod, feed on the largest prey they can capture (based on Norwegian, Barents and Labrador Sea studies), targeting high lipid

species (e.g. crustaceans) when available and showing ontogenetic shifts in prey quality with size (i.e. larger *G. fabricii* are known to prey on finfish like Arctic cod (*Boreogadus saida*) and capelin (*Mallotus villosus*)) (Chapter 2, section 2.2.2.1.d) (Nesis 1965, Kristensen 1983, 1984, Sennikov et al. 1989, Zuev and Nesis 2003). In contrast, the benthic *Bathypolypus* species (spp.) complex (published as *B. arcticus*) feed primarily on nutritionally poor brittlestar arms (Ophiuroidea Gray) (Chapter 2, section 2.2.2.3d) (O'Dor and Macalaster 1983, Wood 2000). It was noted, however, that these octopods took more nutritious prey when offered under laboratory conditions (Wood 2000) suggesting a more opportunistic predation strategy than selective. Other reported *Bathypolypus* spp. prey (from the North Atlantic *Bathypolypus* spp.) include benthic worms (polychaetes and siphunculids), molluscs (bivalves and gastropods) and foraminiferans (O'Dor and Macalaster 1983). Aside from *G. fabricii* and *Bathypolypus* spp., little is known about the prey preference of other Canadian Arctic cephalopod species (Chapter 2 section 2.2.2).

A variety of methods provide insight into the trophic habits of this important intermediary group. Trophic analyses range from *in situ* observations to the classical stomach content analyses, and immunological methodologies to DNA identification (Chapter 2, section 2.3) (Michener and Schell 1994, Rodhouse and Nigmatullin 1996, Boyle and Rodhouse 2005b, Deagle et al. 2005, Michener and Kaufman 2007, Field et al. 2013). Traditional stomach content analyses are difficult for cephalopods because: a) feeding is done by ripping bite-sized pieces of tissue from their prey, b) hard structures required for identification are often expelled; c) they have rapid digestion rates resulting in most of the contents being highly digested; d) stomach contents only represent the most recent feeding events; and e) they continue to feed after capture resulting in potentially biased prey interactions (Chapter 2, sections 2.2.1.2.c and 2.3.2.1) (Nesis

1965, Rodhouse and Nigmatullin 1996, Piatkowski et al. 2001, Boyle and Rodhouse 2005b, Deagle et al. 2005, Jackson et al. 2007, Field et al. 2013). Therefore, alternative methods or combination of methods are required (Field et al. 2013).

Stable isotope analysis (SIA), the ratio of heavy (e.g. ^{15}N) to light (^{14}N) isotopic values for an unknown compound compared to a standard (Lajtha and Michener 1994), is a useful and less invasive tool for determining trophic interactions and provides insight over a longer period of time (Chapter 2, section 2.3.2.2). The two most common compounds used in trophic analyses are $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Chapter 2, section 2.3.3.2). As an individual feeds, the heavy isotopic signature (^{13}C , ^{15}N) of the food is amplified within the consumers' tissue while the lighter isotope (^{12}C , ^{14}N) is lost through respiration (^{12}C) or excretion (^{14}N) (Minagawa and Wada 1984, McCutchan et al. 2003, Ruiz-Cooley et al. 2004). Because tissues are metabolically active, the appropriate tissue for the question being asked is vital (i.e. highly metabolic liver tissues are best for short-term questions while lower metabolic muscle tissues provides a longer trophic window) (DeNiro and Epstein 1978, Tieszen et al. 1983, Lajtha and Michener 1994, Michener and Kaufman 2007, Post et al. 2007). Takai et al. (2000) noted that the $\delta^{15}\text{N}$ of cephalopods increased significantly with a single feeding event and an increase of 3.4 ± 1 ‰ was sufficient to show an increased trophic level. Delta ^{15}N values for cephalopods also reflect the type of nitrogen metabolism of the region but are thought to be uncorrelated with latitude (Takai et al. 2000). Unlike stomach content analyses, SIA of $\delta^{15}\text{N}$ does not identify the prey to taxa, only their isotopic signatures, therefore, combining SIA and traditional stomach content analyses provides a more complete trophic picture (Lesage et al. 2001, Navarro et al. 2013).

Carbon ($\delta^{13}\text{C}$) (Chapter 2 section 2.3.3.2.b.) also reflects the diet of an individual with a significant increase of only 1 ‰ from a single feeding (Michener and Schell 1994, Takai et al. 2000); but this has not been observed in cephalopods (Cherel et al. 2009). Delta ^{13}C also becomes depleted in high lipid tissues, making false low readings problematic (Hobson and Welch 1992a, Michener and Schell 1994, Post 2002, McCutchan et al. 2003). Delta ^{13}C , however, can identify resident water masses based on the source of primary production (e.g. benthic, pelagic, terrestrial) (Takai et al. 2000, Hooker et al. 2001). Coastal and benthic ecosystems are enriched in $\delta^{13}\text{C}$ compared to pelagic regions and there is a negative relationship with increasing latitudes (Takai et al. 2000, Hooker et al. 2001). Delta ^{13}C can, therefore, help determine potential feeding grounds of the Arctic cephalopods.

This chapter provides insight into the habitat interactions of the most common Canadian Arctic cephalopods based on SIA results, describe their trophic roles, and discern potential prey preferences for some of the lesser-studied species (*R. palpebrosa*, *Bathypolypus* spp. and *C. muelleri*). This will be accomplished by: **1)** describing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ shifts between cephalopod species by sample region (as described in Chapter 5 – Hudson Strait, Ungava Bay, Baffin Bay/Greenland, Disko Bay and St. Lawrence) and size or maturity ranges; and **2)** utilize isotopic mixing models to estimate primary prey preferences of each cephalopod species by maturity (or size range) in comparison with stomach content observations.

Five hypotheses are as follows:

1. Delta ^{13}C reflects habitat preference and feeding grounds of the common Arctic cephalopod species (Hypothesis 6.1; Chapter 2 sections 2.2.2.1a, 2.2.2.2a, 2.2.2.3a, 2.2.2.4a; Takai et al. 2001, Hooker et al. 2001). Delta ^{13}C values will become less enriched (more negative) with

- increasing latitude due to the well-documented phytoplankton-latitude relationship (Hypothesis 6.1a) (Takai et al. 2000, Hooker et al. 2001). *G. fabricii*, a pelagic cephalopod preferring water depths in excess of 200 m extending to < 1000 m with age (Chapter 2 section 2.2.2.1a) will be less enriched in $\delta^{13}\text{C}$ than the benthic-neritic *R. palpebrosa* that are frequently found on muddy or sandy substrates of the continental shelves and slopes (Hypothesis 6.1b; Chapter 2 section 2.2.2.2a; Takai et al. 2000, Hooker et al. 2001). *Bathypolypus* spp., while similar to *Rossia*'s association with the benthos and preference of shallower water at higher latitudes, are also widely distributed and are not restricted to the shelf region (Chapter 2.2.2.3a) and are therefore expected to have highly variable $\delta^{13}\text{C}$ values reflective of both neritic and benthic primary production sources (Hypothesis 6.1c; Takai et al. 2000, Hooker et al. 2001). *C. muelleri* are benthic-pelagic and are typically found at deep depths where they feed just above the sea floor (Collins and Villanueva 2006) (Chapter 2.2.2.4a). Although associated with the benthos (the same as *Rossia* and *Bathypolypus* spp. and therefore expected to be more enriched in $\delta^{13}\text{C}$), they share the same primary carbon source as *G. fabricii* (i.e. marine snow) and are expected to have a $\delta^{13}\text{C}$ value more reflective of the pelagic habitat. (Hypothesis 6.1d).
2. It is also hypothesized (6.2) that both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ will vary based on maturity stage or size ranges, reflecting ontogenetic shifts in habitat preference and each species' ability to capture larger, more nutritious prey (e.g. paralarval *G. fabricii* compared to large fish-eating adults; Chapter 2, section 2.2.2).
 3. There is no known relationship between $\delta^{15}\text{N}$ and latitude (Takai et al. 2000) but the highly productive North Water Polynya (Stirling 1980, 1997) is located at the northern extent of the Baffin Bay/Greenland region. Hypothesis 6.3 proposes that specimens collected from more

northern regions (Baffin/Greenland) will have enriched $\delta^{15}\text{N}$ values than those from Hudson Strait or Ungava Bay because of the proximity to this polynya and access to higher quality and quantities of prey. Specimens from Disko Bay are also expected to be enriched in $\delta^{15}\text{N}$ because of that region's increased productivity (Frandsen and Wieland 2004, Hansen et al. 2012). There will also be a distinct difference between the $\delta^{15}\text{N}$ values of *R. palpebrosa* and *Bathypolypus* spp. from the Arctic compared to those from the St. Lawrence because of regional differences in prey species.

4. The $\delta^{15}\text{N}$ values of each cephalopod species will also reflect their respective hunting styles (Hypothesis 6.4). *G. fabricii* are active hunters, known to feed on higher trophic level prey (e.g. Arctic cod) while *Bathypolypus* spp. and *Rossia* spp. are thought to be sit-and-wait predators, opportunistically feeding on whatever prey they encounter (Chapter 2, sections 2.2.2.1.d, 2.2.2.2.d, and 2.2.2.3.d). Cirrate octopods, while more specialized hunters than their incirrate relatives (i.e. feeding on suprabenthic prey), lack the musculature and speed to capture larger, higher trophic level prey (e.g. fish; Chapter 2, section 2.2.2.4.d), therefore, *G. fabricii* will be the most enriched in $\delta^{15}\text{N}$ of the Arctic cephalopods.
5. Finally, it is hypothesized (6.5) that the prey species highlighted in the isotopic mixing models will reflect the stomach contents of each cephalopod species. Further, isotopic mixing models will identify prey items to a lower taxa than was noted in the stomach contents.

6.2. Material and Methods

6.2.1. Specimen collection

Cephalopods collected represent pelagic, benthic and abyssal-pelagic species. All individuals collected were bycatch of the annual shrimp and groundfish surveys conducted by Fisheries and Oceans Canada (Freshwater Institute, Winnipeg, Manitoba and Maurice Lamontagne Institute, Mont-Joli, Quebec) and the Greenland Institute of Natural Resources (Nuuk, Greenland) as outlined in Chapter 3 and Chapter 5 section 5.2.1. Greenland samples were collected between June and July while the remaining samples were collected between October and early November (Table 5.1).

Specimens sampled (for both SIA and stomach contents) represent the total available size ranges observed for each species per survey location (Table 6.1). Pre-determined size ranges for *G. fabricii* and the maturity scale used for *R. palpebroso* are as described in Chapter 5 (Table 5.3). Observed *Bathypolypus* spp. and *C. muelleri* maturities were designated based on a modified *R. palpebroso* maturity scale (Table 5.3): *immature* individuals had undeveloped and transparent gonads, *maturing* individuals had underdeveloped opaque gonads and *mature* individuals had fully developed gonads. Because *C. muelleri* are polytelic (Boyle and Rodhouse 2005g, Collins and Villanueva 2006) with gonads at varying stages of maturity, the presence of a single mature ova or spermatophore was sufficient to designate the individuals as mature.

6.2.2. Stable isotope analysis

6.2.2.1. Methodology

Several tissues types were initially collected and analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Fig. 6.1). Mantle tissue was chosen for the remainder of the analyses because it had the least variation (Fig. 6.1) and the lowest lipid (1%) values (Kristensen 1984).

Mantle tissue and stomach content samples (when available) were collected from each individual. Small tissue samples were collected from the collar region of the ventral mantle with the exception of *C. muelleri*, where tissue samples were collected from the arms due to excess debris on the mantle. Any evident debris or ink was rinsed off of the samples with distilled water to limit contamination. If any other organism was found attached to the cephalopod or in the same bag as the cephalopod, they were also collected as reference SI samples (noted as “smp1” in the mixing models). Mantle tissues (including reference samples) were then placed in a 70 °C oven for a minimum of 48 hours until dry.

The samples were analyzed at two different laboratories, the University of Winnipeg Isotope Laboratory (*UWIL*, University of Winnipeg, Manitoba, Canada) and the Great Lakes Institute for Environmental Research (*GLIER*, University of Windsor, Ontario, Canada). Each lab followed similar methodologies with the dried samples ground and placed into tin capsules for carbon and nitrogen analysis (Isinguzo 2009, Hussey et al. 2010). Samples were analyzed using continuous flow ion ratio mass spectrometry (CF-IRMS) (Isinguzo 2009, Hussey et al. 2010). Samples sent to UWIL were analyzed using a GV-Instruments® IsoPrime with peripheral temperature controlled EuroVector® elemental analyzer (Isinguzo 2009) and those

sent to GLIER were analyzed by a Finnigan MAT Delta V IRMS (Thermo Finnigan, San Jose, CA, USA) also equipped with an elemental analyzer (Costech, Valencia, CA, USA; Hussey et al. 2010). The samples were placed in the elemental analyzer along with internally calibrated standards of carbon (Vienna Pee Dee Belemnite) and nitrogen (1 AEA-N-1, UWIL, Isinguzo 2009; atmospheric nitrogen, GLIER; Hussey et al. 2010).

Every fifth sample analyzed at UWIL was duplicated and every 15th analyzed in triplicate. Samples sent to GLIER were randomly tripled to assure accuracy. In addition, twenty ‘blind’ samples of known isotope values were also sent for analysis to validate the results. No significant difference in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were found between the laboratories (*G. fabricii* specimens from the Baffin Bay 2008 survey, t-test $p > 0.05$).

Stable isotope ratios (δ) were calculated by determining the *per mil* (‰) difference between the samples and standard values (eq. 6.1; (Sulzman 2007)).

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000 \quad (\text{Eq. 6.1})$$

where R is the ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$

GLIER precision (n=29), based on Bovine muscle (NIST 8414) and Tilapia muscle (internal standard), was 0.03 and 0.06 respectively for $\delta^{13}\text{C}$ and 0.14 and 0.22 respectively for $\delta^{15}\text{N}$ based on standard deviations. The analysis of NIST standards (8573 and 8414; n=5) was between 0.0 and 0.03 standard deviation from the certified values for $\delta^{13}\text{C}$ and 0.01 standard deviation for $\delta^{15}\text{N}$.

6.2.2.2. Statistical analyses

Based on Goodness-of-Fit tests (JMP-10) for each species per sample location and maturity stage/size range, much of the SIA data did not conform to normal distributions. Therefore, non-parametric Kruskal-Wallis tests (JMP-10) were used to determine interspecific significance between the means ($\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰)) of species (per size/maturity range) caught in the Arctic and St. Lawrence, as well as any significant within-species differences based on the detailed sampling locations. The means and their associated standard deviations were then plotted by size range/maturity stage per locations.

6.2.3. Prey identification

6.2.3.1. Stomach content analyses

Stomach contents from each individual were examined and a subsample (when available) was taken for identification. Any prey items were identified to the lowest possible taxon (i.e. often only pieces of carapace available, therefore, prey were designated as ‘arthropods’). If distinctive pieces were present, they were saved and identified by a zooplankton expert (W. Walkusz pers. comm.).

Once identified, the presence or absence of a prey item was recorded and its percent occurrence in relation to all other prey species observed for that cephalopod species by size range/maturity stage was plotted by location. To determine if there were more regional differences in prey preference, the original (narrower) survey locations were used (Table 5.1, Figure 5.1) rather than those determined by PCA in Chapter 5 (i.e. Northern Greenland, Central Greenland, Baffin Bay rather than the all encompassing Baffin/Greenland).

6.2.3.2. SIAR Mixing models

General mixing models (SIAR - R statistical program) compared the cephalopod stable isotope data to literature values of potential prey (Tables 6.1 and 6.2). The results provide an estimate of prey species proportions, highlighting potential prey sources (Moore and Semmens 2008). The mixing model results were compared to the observed stomach content data and SIA results to provide a more complete trophic picture of these northern cephalopods.

Mixing model datasets were separated by species collected from the Arctic and St. Lawrence habitats. Literature values of potential prey species reflect the actual sampling regions as closely as possible (Arctic: Hobson and Welch (1992a), Fisk et al. (2003) and Pomerleau et al. (2011); St. Lawrence: Lesage et al. (2001)) (Table 6.1). Published standard deviations were used when available, but if not, a standard deviation of 0.1 was used in the model. When more than one value for an overall taxa was found in the literature (i.e. more than one species of copepod), the average was used (along with the average standard deviations). If one of these 'averaged' groups were found to be significant for one of the cephalopod species (via the model), the program was re-run using the original species values to help discern the primary prey to the lowest possible taxa (Table 6.2). Trophic enrichment factors (TEF) for the Arctic models were from Hobson and Welch (1992a) and Iken et al. (2005) ($N = 3.8 \pm 0.4$ and $C = 1 \pm 0.4$) and the St. Lawrence models from Ben-David and Flaherty (2012) ($N = 3.4 \pm 0.4$ and $C = 0 \pm 0.4$).

6.3. Results

6.3.1. Habitat variability ($\delta^{13}\text{C}$) of the common cephalopods from the Canadian Arctic and St. Lawrence regions

6.3.1.1. General differences between locations

a) Arctic vs. St. Lawrence regions: Only *Bathypolypus* spp. and *R. palpebrosa* were collected from both the Arctic and St. Lawrence regions (Table 6.3 and 6.4). No significant difference (Kruskal-Wallis $p > 0.05$) in $\delta^{13}\text{C}$ was observed between Arctic and St. Lawrence specimens of the same maturity stages (Table 6.3). However, in general, St. Lawrence specimens were more depleted in $\delta^{13}\text{C}$ than those from the Arctic (Table 6.4). The only exceptions being immature and mature *Bathypolypus* spp. from Baffin Bay/Greenland (0.65 ‰ and 0.04 ‰ more depleted respectively), maturing *Bathypolypus* spp. from Ungava Bay (0.44 ‰ more depleted than St. Lawrence conspecifics) and maturing *R. palpebrosa* from both Baffin Bay/Greenland and Baffin Island (0.14 ‰ and 0.04 ‰ more depleted respectively) (Table 6.4).

b) Arctic region: Within the Arctic, the most depleted specimens ($\delta^{13}\text{C}$) were the small (size 2) *G. fabricii* (-20.90 ± 0.59 ‰) from Baffin Bay/Greenland and the least depleted were mature *Bathypolypus* spp. from Ungava Bay (-14.97 ‰) (Table 6.4).

The Baffin Bay/Greenland region was the only sampling location where all species were represented (Table 6.3 and 6.4). No significant difference was observed between the immature/size 3 species of the region, however, the maturing/size 4 and mature/size 5 individuals of each species were significantly different (Table 6.3). Of the maturing species, the benthic *Bathypolypus* spp. were the least depleted in $\delta^{13}\text{C}$ (-17.76 ± 1.30 ‰) while the pelagic *G.*

fabricii were the most depleted (-20.20 ± 0.54 ‰) (Table 6.4). Maturing neritic *R. palpebrosa* were 0.22 ‰ more depleted than the abyssal-pelagic *C. muelleri* of the same maturity (Table 6.4). As with the maturing species, mature *Bathypolypus* spp. again were the least depleted but had highly variable $\delta^{13}\text{C}$ values (-18.27 ± 3.01 ‰) (Table 6.4). Also, size 5 *G. fabricii* were again the most depleted (-20.53 ± 0.45 ‰) of the ‘mature’ Baffin Bay/Greenland species (Table 6.4). It should be noted that no sexually mature *G. fabricii* were collected throughout the study and that size 5 individuals simply represent the largest (200+ mm ML) individuals described (Table 5.3).

c) St. Lawrence region: Within the St. Lawrence, *R. palpebrosa* specimens (regardless of maturity stage) were on average 1.17 ‰ more depleted than the *Bathypolypus* specimens (Table 6.4). The immature individuals of both species were the most depleted in $\delta^{13}\text{C}$ of the maturities (Table 6.4).

6.3.1.2. Habitat variability between life stages of the common cephalopod species

a) *G. fabricii*: (i) Variability in $\delta^{13}\text{C}$ per size range by sample location: Within each sample site, *G. fabricii* specimens from Baffin Bay/Greenland (Kruskal-Wallis: χ^2 16.1834, df 3, $p = 0.0010^*$), Hudson Strait (Kruskal-Wallis: χ^2 23.2905, df 1, $p < 0.0001^*$) and Ungava Bay (Kruskal-Wallis: χ^2 7.3846, df 1, $p = 0.0066^*$) showed significant differences between the size ranges, with the smallest individuals being the most depleted in $\delta^{13}\text{C}$ and the larger individuals, less depleted (Tables 6.3 and 6.4). It should be noted that size 4 Baffin Bay/Greenland specimens were less depleted from that location than the size 5 individuals (Table 6.4; Fig. 6.2). Only specimens from Disko Bay showed no significant difference in $\delta^{13}\text{C}$ between the maturity stages (Kruskal-Wallis: χ^2 4.8044, df 2, $p = 0.0905$) (Table 6.3).

(ii) Variability in $\delta^{13}\text{C}$ between sample locations for each size range: Size 2 *G. fabricii* showed significant differences between sample locations (Kruskal-Wallis: χ^2 10.6448, df 3, $p = 0.0138^*$) with a maximum range of 1.48 ‰ difference between the least depleted Ungava Bay specimens and the most depleted Baffin Island individuals (Table 6.4; Fig. 6.2a).

A significant difference (Kruskal-Wallis: χ^2 45.5160, df 3, $p < 0.0001^*$) was also noted between size 3 *G. fabricii* collected from the least depleted region, Ungava Bay (-19.07 ± 0.48 ‰) and Baffin Bay/Greenland (-20.71 ± 0.60 ‰), the most depleted of the sample locations (Table 6.4; Fig. 6.2b)

No significant difference was observed among the size 4 *G. fabricii* specimens collected from Baffin Bay/Greenland and Disko Bay (Kruskal-Wallis: χ^2 0.0642, df 1, $p = 0.8000$) (Fig. 6.2c). However, the size 5 individuals from the same regions were significantly different (Kruskal-Wallis: χ^2 5.3571, df 1, $p = 0.0206^*$) with Baffin Bay/Greenland being 1.11 ‰ more depleted than individuals from Disko Bay (Fig. 6.2 d).

b) *R. palpebrosa*: (i) Variability in $\delta^{13}\text{C}$ per maturity stage by sample location: No significant differences in the $\delta^{13}\text{C}$ values were apparent when comparing the maturity stages of *R. palpebrosa* within the same sample location (Kruskal-Wallis $p > 0.05$) (Table 6.3). However, as with *G. fabricii*, $\delta^{13}\text{C}$ values were generally less depleted with increasing maturity when comparing specimens from the same sample location (Table 6.4; Fig. 6.3).

(ii) Variability in $\delta^{13}\text{C}$ between sample locations for each maturity stage: *R. palpebrosa* $\delta^{13}\text{C}$ values ranged from -20.04 ‰ (immature individuals from the St. Lawrence region) to -16.73 ‰

(maturing Ungava Bay individual) with immature and maturing life stages showing the most variation between sample regions (Table 6.4; Fig. 6.3).

A difference of 2.24 ‰ $\delta^{13}\text{C}$ was observed between the least depleted (Ungava Bay) and the most depleted (Baffin Bay/Greenland) immature *R. palpebrosa* specimens caught within the eastern Canadian Arctic region (Fig. 6.3b). Immature specimens showed a close relationship (0.56 ‰ difference) between the $\delta^{13}\text{C}$ values of Ungava Bay and Hudson Strait (Table 6.4; Fig. 6.3b). A single immature specimen collected from the Beaufort Sea had a $\delta^{13}\text{C}$ value of -21.95 ‰, 2.22 ‰ more depleted than the most depleted specimen from the eastern Canadian Arctic (immature Baffin Bay/Greenland individual) (Table 6.4; Fig. 6.3b).

Maturing *R. palpebrosa* had a difference of 2.68 ‰ $\delta^{13}\text{C}$ among eastern Arctic specimens, however, Ungava Bay and Hudson Strait individuals were not as closely related (1.09 ‰ difference) as was observed with the immature specimens (Table 6.4; Fig. 6.3c). Conversely, only a 0.10 ‰ difference separated the Baffin Bay/Greenland and Baffin Island specimens (Table 6.4; Fig. 6.3c).

Mature *R. palpebrosa* from the eastern Canadian Arctic only had a difference of 0.73 ‰ $\delta^{13}\text{C}$ but also only consisted of specimens from Hudson Strait and Baffin Island (Table 6.4; Fig. 6.3d).

While highly variable, no significant difference (Kruskal-Wallis: $p > 0.05$) was observed between specimens of the same maturity stage collected from different sample regions (Table 6.3).

St. Lawrence specimens, present in the immature, maturing and mature stages showed no significant difference in $\delta^{13}\text{C}$ values from what was observed within the eastern Arctic specimens (Table 6.4; Fig. 6.3). In fact, immature specimens from the St. Lawrence and Baffin Bay/Greenland showed only a 0.31 ‰ difference in $\delta^{13}\text{C}$ (Table 6.4; Fig. 6.3b). This difference decreased to 0.14 ‰ for maturing specimens from the same regions, with Baffin Island individuals found between the Baffin Bay/Greenland and St. Lawrence $\delta^{13}\text{C}$ values (Table 6.4; Fig. 6.3c). No mature Baffin Bay/Greenland specimens were collected but the difference between the mature Baffin Island and St. Lawrence individuals was only 0.40 ‰, with the St. Lawrence being the most depleted of the mature specimens (Table 6.4; Fig. 6.3d).

When available, Ungava Bay individuals were always the least depleted in $\delta^{13}\text{C}$ regardless of the maturity stage (Table 6.4; Fig. 6.3).

c) *Bathypolypus* spp.: (i) Variability in $\delta^{13}\text{C}$ per maturity stage by sample location: As with the *R. palpebrosa* specimens, no significant difference was observed for *Bathypolypus* spp. of different maturity stages regardless of sample location (Kruskal-Wallis $p > 0.05$) (Table 6.3). However, unlike the previous species, only *Bathypolypus* spp. from Ungava Bay had less depleted $\delta^{13}\text{C}$ values with increasing maturity stages; the remaining $\delta^{13}\text{C}$ values per maturity stage were highly variable (Table 6.3 and 6.4).

(ii) Variability in $\delta^{13}\text{C}$ between sample locations for each maturity stage: No significant difference in $\delta^{13}\text{C}$ was observed between the *Bathypolypus* species per maturity stages in either the Arctic or the St. Lawrence regions, therefore, non-parametric analyses combined all species from the same maturity stages and locations (Table 6.3). Graphical analysis, however, examined the difference between not only location but also species per maturity stage (Fig. 6.4).

Immature specimens were only collected from Baffin Bay/Greenland and the St. Lawrence regions, with no significant difference in $\delta^{13}\text{C}$ noted (Kruskal-Wallis: χ^2 1.5000, df 1, $p = 0.2207$; Table 6.4; Fig. 6.4a). Regardless of significance, immature *Bathypolypus* sp. (i.e. female specimens of *Bathypolypus*) from Baffin Bay/Greenland were 0.65 ‰ more depleted than those from the St. Lawrence (Table 6.4; Fig. 6.4a).

No significant difference was observed between maturing *Bathypolypus* spp. from Baffin Bay/Greenland, Hudson Strait, Ungava Bay and St. Lawrence (Kruskal-Wallis: χ^2 2.5425, df 3, $p = 0.4677$), however, there was a high interspecific variability in $\delta^{13}\text{C}$ (Fig. 6.4b). A 2.34 ‰ range was observed between the different species and their sample locations with the greatest difference between maturing *B. bairdii* from Baffin Bay/Greenland (-16.84 ‰) and the same species/maturity stage from the St. Lawrence (-17.97 \pm 0.53 ‰) (Fig. 6.4b). *B. arcticus* from Hudson Strait was also 1.02 ‰ more enriched than the same species from the nearby Ungava Bay (Fig. 6.4b).

Mature individuals had the largest $\delta^{13}\text{C}$ range of -14.94 to -19.33 (\pm 4.31) ‰ (Fig. 6.4c) but again were not significantly different between sample locations (Kruskal-Wallis: χ^2 4.0788, df 3, $p = 0.2531$). Female *Bathypolypus* sp. from Ungava Bay were 2.12 ‰ more enriched than specimens collected from the nearby Hudson Strait and were 3.80 ‰ more enriched than female specimens from the St Lawrence (Fig. 6.4c).

d) *C. muelleri*: All *C. muelleri* were collected within the Baffin Bay/Greenland sample region (Table 6.3 and 6.4). No significant difference in $\delta^{13}\text{C}$ was observed between the life stages of *C. muelleri* (Kruskal-Wallis: χ^2 2.3805, df 2, $p = 0.3042$) even with a 622.5 m depth difference between the immature and the mature capture sites (Table 6.3 and 6.4). A range of

-19.11 to -20.43 ‰ was present with only 1.32 ‰ difference between the most depleted immature specimens and the least depleted the mature *C. muelleri* individuals (Table 6.4; Fig. 6.5). This range is less depleted than what was observed for the pelagic *G. fabricii* (Fig. 6.2).

6.3.2. Trophic role of the common Canadian Arctic cephalopods ($\delta^{15}\text{N}$)

6.3.2.1. General differences in $\delta^{15}\text{N}$ between the cephalopod groups

No significant difference (Kruskal-Wallis: $p > 0.05$) was observed between similar species found within the Arctic and the St. Lawrence regions, however, on average, Arctic species were more enriched in $\delta^{15}\text{N}$ with the exception of immature *R. palpebrosa* (Tables 6.3 and 6.4). Within the Arctic, the immature *C. muelleri* was the most enriched with 15.99 ‰ $\delta^{15}\text{N}$ while the small size 2 *G. fabricii* were the least enriched (10.70 ± 0.87 ‰) (Table 6.4). Mature *Bathypolypus* spp. were the most enriched in $\delta^{15}\text{N}$ (13.32 ± 0.56 ‰) while immature *R. palpebrosa* were the least enriched (11.38 ‰) among the St. Lawrence specimens (Table 6.4). Non-parametric analyses showed no significant difference (Kruskal-Wallis: $p < 0.05$) between *Bathypolypus* species of the same maturity stage for both the Arctic region and the St. Lawrence (Table 6.3). No significant difference (Kruskal-Wallis: $p > 0.05$) was also noted for *R. palpebrosa* specimens of the same maturity stage when comparing these two latitudinal extremes (Table 6.3).

a) Arctic region overview: Only *G. fabricii* specimens from Baffin Bay/Greenland and Hudson Strait *R. palpebrosa* specimens had SI values for each of the four size ranges/maturity stages (Table 6.4).

A steady enrichment in $\delta^{15}\text{N}$ was observed for *G. fabricii*, however, from the least enriched (size 2 individuals; 10.70 ± 0.87 ‰) to the most enriched (size 5; 13.48 ± 1.41 ‰), the difference did not indicate a trophic shift ($\delta^{15}\text{N}$ difference = 2.78 ‰) (Table 6.4).

Mature *R. palpebrosa* were the most enriched in $\delta^{15}\text{N}$ (13.63 ± 1.43 ‰) from Hudson Strait while the immature specimens were the least (12.71 ± 0.95 ‰) (Table 6.4). The largest difference in $\delta^{15}\text{N}$ between the maturity stages did not exceed 0.92 ‰ (Table 6.4).

When all species from Baffin Bay/Greenland were analyzed by maturity stage, there was no significant difference in $\delta^{15}\text{N}$ between immature individuals (and size 3 *G. fabricii*) (Kruskal-Wallis: χ^2 6.4092, df 3, $p = 0.0933$) (Table 6.3). Older and larger individuals (i.e. maturing (size 4 for *G. fabricii*) and mature (size 5 for *G. fabricii*)) did show significant differences in $\delta^{15}\text{N}$ between the species (Kruskal-Wallis: $p < 0.05$) (Table 6.3). Abyssal-pelagic maturing *C. muelleri* were the most enriched in $\delta^{15}\text{N}$ (15.44 ± 1.24 ‰) while pelagic size 4 *G. fabricii* were the least enriched (12.01 ± 0.59 ‰) of the four taxa from the Baffin Bay/Greenland region (Table 6.4). On average, the benthic *Bathypolypus* spp. were 0.77 ‰ less enriched than the neritic *R. palpebrosa* (Table 6.4), however, *Bathypolypus* spp. values were highly variable (11.23 to 15.59 ‰) compared to the single *R. palpebrosa* representative (14.18 ‰) (Figs. 6.3c and 6.4b).

As with the maturing individuals, the mature abyssal-pelagic *C. muelleri* specimens were the most enriched (15.44 ± 1.06 ‰) of the species found within the Baffin Bay/Greenland region and size 5 *G. fabricii* were the least enriched (13.48 ± 1.41 ‰) (Table 6.4). Mature *Bathypolypus* spp. were only 0.28 ‰ more enriched than the *G. fabricii* specimens (Table 6.4). No mature *R. palpebrosa* were collected from this region.

b) St. Lawrence region overview: Benthic *Bathypolypus* species (spp.) collected from the St. Lawrence region were more enriched in $\delta^{15}\text{N}$ than their neritic *R. palpebrosa* equivalents (Table 6.4). Both species showed increased $\delta^{15}\text{N}$ values with maturity, with the exception of the immature *Bathypolypus* spp. that were 0.34 ‰ more enriched in $\delta^{15}\text{N}$ than the maturing individuals (Table 6.4). Neither species showed a significant increase in $\delta^{15}\text{N}$ to indicate a trophic shift (Table 6.4).

6.3.2.2. Interspecific variability of $\delta^{15}\text{N}$ by location and size range/maturity stage

a) *G. fabricii*: (i) Variability in $\delta^{15}\text{N}$ per size range by sample location: Significant differences in $\delta^{15}\text{N}$ enrichments were observed between the size ranges of *G. fabricii* from each location (Kruskal-Wallis: $p < 0.05$) with the exception of Ungava Bay (Kruskal-Wallis: χ^2 1.8462, df 1, $p = 0.1742$) (Table 6.3). The remaining locations show an increase in $\delta^{15}\text{N}$ with increasing size, however, none of the increases are equal to a full trophic shift (Table 6.4). The largest observable shift in $\delta^{15}\text{N}$ was a 2.78 ‰ enrichment between size 2 and size 5 of specimens caught in Baffin Bay/Greenland (Table 6.4).

(ii) Variability in $\delta^{15}\text{N}$ between sample locations for each size range: Significant differences were observed among the sample locations for size 2 (Kruskal-Wallis: χ^2 10.5028, df 3, $p = 0.0147^*$) and 4 (Kruskal-Wallis: χ^2 4.9915, df 1, $p = 0.0255^*$) but not sizes 3 (Kruskal-Wallis: χ^2 2.8797, df 3, $p = 0.4106$) and 5 (Kruskal-Wallis: χ^2 0.8571, df 1, $p = 0.3545$).

Size 2 *G. fabricii* from Baffin Bay/Greenland were the least enriched in $\delta^{15}\text{N}$ (10.7 ± 0.87 ‰) while individuals from Baffin Island were the most enriched (11.88 ± 1.06 ‰) for the size range (Table 6.4; Fig. 6.2a).

Only a 0.5 ‰ difference in the $\delta^{15}\text{N}$ values was observed for size 3 *G. fabricii* with the least enriched being individuals from Disko Bay (11.67 ± 0.66 ‰) and the most enriched, those from Baffin Bay/Greenland (12.17 ± 0.96 ‰) (Table 6.4; Fig. 6.2b).

Size 4 and 5 individuals were only collected from Disko Bay and Baffin Bay/Greenland sample locations (Table 6.4). Unlike the size 3 individuals, size 4 specimens from Disko Bay were 0.70 ‰ enriched in $\delta^{15}\text{N}$ than those from Baffin Bay/Greenland (Table 6.4; Fig. 6.2c). Conversely, size 5 individuals from Baffin Bay/Greenland were 0.29 ‰ more enriched in $\delta^{15}\text{N}$ than those from Disko Bay (Table 6.4; Fig. 6.2d).

b) *R. palpebrosa*: (i) Variability in $\delta^{15}\text{N}$ per maturity stage by sample location:

Delta¹⁵N values of *R. palpebrosa* showed enrichment with maturity at each sample location but these differences were not significant (Kruskal-Wallis: $p < 0.05$) (Table 6.3 and 6.4). The largest observed difference between maturity stages was between the immature and maturing *R. palpebrosa* from Baffin Bay/Greenland (2.88 ‰) but did not equal a trophic shift (Table 6.4; Fig. 6.3).

(ii) Variability in $\delta^{15}\text{N}$ between sample locations for each maturity stage:

Although highly variable, none of the sample locations for *R. palpebrosa* showed any significant difference in $\delta^{15}\text{N}$ enrichment (Kruskal-Wallis: $p > 0.05$) within each size range (Fig. 6.3).

Only three *R. palpebrosa* hatchlings were sampled and were all from Hudson Strait (Table 6.4; Fig. 6.3a). These individuals were the least enriched of the Hudson Strait specimens,

however, an immature *R. palpebrosa* from Baffin Bay/Greenland (11.30 ‰) was found to have the lowest $\delta^{15}\text{N}$ value of all the specimens examined (Table 6.4; Fig. 6.3a,b).

As with the $\delta^{13}\text{C}$ range, the immature *R. palpebrosa* specimens had the most variable $\delta^{15}\text{N}$ values with the Hudson Strait specimens (12.88 ± 0.60 ‰) being the most enriched for that maturity stage for the eastern Canadian Arctic and the Baffin Bay/Greenland individual being the least (Table 6.4; Fig. 6.3b). Ungava Bay specimens had $\delta^{15}\text{N}$ values similar to those from Hudson Strait (0.31 ‰ difference) (Table 6.4; Fig. 6.3b). The single Beaufort Sea specimen was the most enriched of all the immature specimens, exceeding the Hudson Strait individuals by 0.58 ‰ (Table 6.4; Fig. 6.3b).

Maturing *R. palpebrosa* specimens showed a wide variability in $\delta^{15}\text{N}$ values in relation to their sample region (Fig. 6.3c). The largest difference within the Canadian Arctic was 0.98 ‰ between Hudson Strait individuals and those from Baffin Island (Table 6.4; Fig. 6.3c). The maturing specimens from Baffin Island had similar $\delta^{15}\text{N}$ values as those from Baffin Bay/Greenland (difference of 0.11 ‰) (Table 6.4; Fig. 6.3c).

The only mature Arctic specimens were collected from Hudson Strait and Baffin Island (Table 6.4; Fig. 6.3d). The Baffin Island individual was 1.16 ‰ more enriched in $\delta^{15}\text{N}$ than the Hudson Strait individuals (Table 6.4; Fig. 6.3d).

St. Lawrence individuals (where available) were on average less enriched in $\delta^{15}\text{N}$ than most of the Arctic individuals with the exception of the immature Baffin Bay/Greenland specimen which was only slightly less enriched (0.08 ‰) (Table 6.4; Fig. 6.3).

c) *Bathypolypus* spp.: (i) Variability in $\delta^{15}\text{N}$ per maturity stage by sample location: No significant differences between maturity stages were observed within each sample location for the *Bathypolypus* spp. (Table 6.3). Unlike the previous species, no trend in $\delta^{15}\text{N}$ enrichment was observed with increasing maturity (Table 6.4).

(ii) Variability in $\delta^{15}\text{N}$ between sample locations for each maturity stage:

Delta ^{15}N of the *Bathypolypus* spp. show high variability between species and locations per maturity stages; however non-parametric analyses show no significant difference between the sample regions when the species were combined, regardless of maturity stage (Kruskal-Wallis: $p > 0.05$) (Table 6.3 and 6.4; Fig. 6.4).

The immature *Bathypolypus* spp. are represented by the female *Bathypolypus* sp. and although not significantly different (Kruskal-Wallis: χ^2 1.5000, df 1, $p = 0.2207$), the Baffin Bay/Greenland specimen was 1.82 ‰ more enriched in $\delta^{15}\text{N}$ than those collected from the St. Lawrence region (Fig. 6.4a).

No significant difference was noted for the combined maturing *Bathypolypus* species from the same location (Kruskal-Wallis: χ^2 1.2190, df 3, $p = 0.7485$), however, when the different species were plotted, the results showed more variability (Fig. 6.4). The most enriched individual, of the maturing specimens, was a *B. pugniger* from Baffin Bay/Greenland with a value of 15.59 ‰ while the least enriched was a *Bathypolypus* sp. from Ungava Bay ($\delta^{15}\text{N} = 11.20$ ‰) (Fig. 6.4b). The *B. pugniger* specimen from Baffin Bay/Greenland was 4.36 ‰ (in excess of a trophic shift) more enriched in $\delta^{15}\text{N}$ than the similarly maturing *B. bairdii* from the same sample region (Fig. 6.4b). A comparable shift of 3.43 ‰ was noted between the female

Bathypolypus sp. and the more enriched *B. arcticus* from Ungava Bay (Fig. 6.4b). St. Lawrence *B. bairdii* were 0.83 ‰ more enriched in $\delta^{15}\text{N}$ than female specimens from the same region (Fig. 6.4b). Although less enriched in $\delta^{15}\text{N}$ than their male counterparts, the female *Bathypolypus* sp. from the St. Lawrence were more enriched than both the *Bathypolypus* sp. from Ungava Bay and the *B. bairdii* from Baffin Bay/Greenland (Fig. 6.4b).

The largest range in $\delta^{15}\text{N}$ values for mature *Bathypolypus* specimens was 3.99 ‰ with *Bathypolypus* sp. from Ungava Bay being the most enriched (15.07 ‰) and *B. arcticus* from Hudson Strait being the least enriched in $\delta^{15}\text{N}$ (11.08 ‰) (Fig. 6.4c). Unlike the maturing individuals, the female *Bathypolypus* sp. from Hudson Strait was 1.94 ‰ more enriched in $\delta^{15}\text{N}$ than its male counterpart (*B. arcticus*) from the same sample location (Fig. 6.4c). St. Lawrence *B. bairdii* were 0.31 ‰ less enriched than those from Baffin Bay/Greenland and *Bathypolypus* sp. (St. Lawrence) were 1.81 ‰ less enriched than females from Ungava Bay (but 0.24 ‰ more enriched than Hudson Strait females) (Fig. 6.4c). Although variations were observed, when all of the species were combined, there was no significant difference between the $\delta^{15}\text{N}$ values for the mature *Bathypolypus* spp. (Kruskal-Wallis: χ^2 3.1891, df 3, p = 0.3634) (Fig. 6.4c)

d) *C. muelleri*: No significant difference in $\delta^{15}\text{N}$ was observed between maturity stages for *C. muelleri* (Kruskal-Wallis: χ^2 1.1225, df 2, p = 0.5705), however, the immature specimen was 0.55 ‰ more enriched than either the maturing or mature individuals (Table 6.4; Fig. 6.5). The maturing and mature *C. muelleri* have equal $\delta^{15}\text{N}$ values (Table 6.4; Fig. 6.5).

All *C. muelleri* were collected from Baffin Bay/Greenland region, so no variation in sample locations could be determined (Fig. 6.5).

6.3.3. Arctic cephalopod prey differentiation

6.3.3.1. *G. fabricii*

a) Stomach contents

The majority of the stomachs examined for all size ranges of *G. fabricii* (see Table 5.3 for the description of the size ranges) were either empty, contained highly digested material, or consisted of small pieces of arthropods, in particular crustaceans (Fig. 6.6).

Size 2 *G. fabricii* had the most variable stomach contents of the four size ranges, with no prey item dominating any particular survey location (Fig. 6.6a). Prey able to be identified to a more refined taxon than ‘arthropod’ or ‘crustacean’ consisted of: amphipods (overall 26.81 %), copepods (overall 25.53 %), decapods (overall 24.71 %), and cephalopods (overall 19.33 %) with individuals from Ungava Bay also having evidence of mysids (3.85 %) and sponge (3.85 %) in their stomachs (Fig. 6.6a). Polychaetes were reported from the stomachs of 0.57 % of Hudson Strait individuals while unidentified eggs were reported from 0.51 % of stomachs from Central Greenland (Fig. 6.6a). All of the size 2 Baffin Bay specimens had empty stomachs (Fig. 6.6a). No prey item dominated a particular survey location for the size 3 individuals either (Fig. 6.6b). Prey items were similar to those observed in size 2 individuals: decapods (overall 48.51 %), amphipods (26.90 %), copepods (overall 13.80 %), fish (overall 6.89 %) and cephalopods (5.98 %), however, there was no evidence of mysids, sponges or polychaetes in the size 3 stomachs (Fig. 6.6b). Unlike the size 2 specimens, 5.56 % of the stomachs had evidence of potential nudibranchs (Fig. 6.6b).

Size 4 *G. fabricii* stomach contents were only from Disko Bay (white bars) and Central Greenland (black bars) specimens (Fig. 6.6c). The majority (overall 86.27 %) of the stomachs contained highly digested material while the remaining stomachs contained remnants of arthropods and/or crustaceans (overall 28.42 %; Fig. 6.6c). Central Greenland individuals had 5.88 % (overall) of stomachs containing copepods and 5.88 % (overall) containing unknown eggs (Fig. 6.6c). Alternatively, Disko Bay had remnants of decapods (overall 6.67 %), cephalopods (overall 3.33 %) and fish (overall 3.33 %; Fig. 6.6c).

Most of the size 5 *G. fabricii* stomachs were full of highly digested material but individuals from central Greenland contained mysids (overall 50 %) and isopods (overall 50 %; Fig. 6.6d).

b) Mixing models

Copepods are the dominant (highest proportion) prey group for all the *G. fabricii* size ranges with the exception of mature Disko Bay specimens (Figs. 6.7, 6.8 and 6.9). More detailed mixing models were then able to differentiate between the different species of copepods as well as other specific invertebrate prey species (e.g. *Anonyx nugax*, *Onisimus glacialis* and *Themisto libellula* rather than simply ‘amphipods’; Figs. 6.7, 6.8 and 6.9). The following describe the results of the overall mixing models per size range and sample location for *G. fabricii* and the detailed models.

Copepods have the highest proportions for all the mixing models for size 2 *G. fabricii* (Fig. 6.7a, c, e). Hudson Strait and Ungava Bay individuals also had a higher proportion of pteropods (*Clione limacine*) (Fig. 6.7c, e). More detailed mixing models were able to determine

that for size 2 *G. fabricii* from Baffin Bay/Greenland region, only *Calanus hyperboreus* showed any significance (Fig. 6.7b). Hudson Strait individuals also had a high proportion of *C. hyperboreus* but *C. glacialis*, the amphipod *T. libellula* and the copepod *Metridia longo* were also prominent (Fig. 6.7d). Ungava Bay individuals also had elevated *C. hyperboreus* proportions, but *M. longo* was more prominent (Fig. 6.7f). The copepod *C. glacialis* and amphipods *A. nugax* and *T. libellula* also had elevated proportions for size 2 Ungava Bay specimens (Fig. 6.7f).

Copepods remained the dominant estimated prey for size 3 *G. fabricii* (Fig. 6.8a, c, e), however, the proportions are much reduced for specimens from Ungava Bay (Fig. 6.8g). Size 3 specimens from Baffin Bay/Greenland had the highest proportion of *C. hyperboreus* but also had an elevated proportion of *C. glacialis* (Fig. 6.8b). Detailed mixing models of Disko Bay specimens show similar elevated *C. hyperboreus* and *C. glacialis* proportions as Baffin Bay/Greenland, but also had elevated *M. longo*, *Cl. limacine* (pteropod) and *T. libellula* (Fig. 6.8d). *C. hyperboreus* was also elevated for the mixing models of size 3 Hudson Strait individuals but to a much reduced level (Fig. 6.8f). The detailed mixing model for the Hudson Strait individuals showed that all prey species were elevated with the exception of the amphipod *Onisimus glacialis* (Fig. 6.8f). Copepods and pteropods show slightly elevated proportions for Ungava Bay specimens as well as amphipods and Mysidae (Fig. 6.8g), however, detailed mixing models failed to identify the dominant species (Fig. 6.8h).

Copepods remained the dominant prey species identified by the mixing models for the larger *G. fabricii* from Baffin Bay/Greenland (size 4 and 5) and Disko Bay (size 4) (Fig. 6.9a,c,e). *C. hyperboreus* and *C. glacialis* had the highest proportions for size 4 individuals from

Baffin Bay/Greenland, followed by *M. longo*, *Cl. limacina* and *T. libellula* (Fig. 6.9b). Size 4 Disko Bay mixing model had elevated amphipod and pteropod values, in addition to the copepod proportions (Fig. 6.9c) but the more detailed model showed that *C. hyperboreus* followed by *C. glacialis* were the most dominant prey species followed by *O. glacialis* (Fig. 6.9d). Size 5 *G. fabricii* from Baffin Bay/Greenland, again show an extremely high proportion of copepods with *C. hyperboreus* and *M. longo* being the most dominant followed by *C. glacialis* (Fig. 6.9e, f). *T. libellula* and *Cl. limacina* were also elevated (Fig. 6.9f). The mixing models for size 5 Disko Bay specimens showed no differentiation between the potential prey items (Fig. 6.9g, h).

6.3.3.2. *R. palpebroso*

a) Stomach contents

Many of the *R. palpebroso* specimens examined, of all maturity stages, had highly digested stomach contents with arthropods and crustaceans being the most prominent prey items when present (Fig. 6.10).

Western Hudson Strait hatchlings fed on unidentified eggs (50 %) while eastern Hudson Strait and Hudson Strait individuals preyed on arthropods (overall 64.29 %), crustaceans (overall 64.29 %), amphipods (14.29 %), mysids (14.29 %) and polychaetes (14.29 %) (Fig. 6.10a).

Immature *R. palpebroso* had the most diverse stomach contents of all the maturity stages (Fig. 6.10b). Aside from arthropods and crustaceans, other prey items included: decapods (overall 29.09 %), amphipods (overall 29.09%), copepods (overall 19.09 %), unidentified eggs (19.09 %), mysids (10.00 %), cephalopods (10.00 %), polychaetes (10.00 %), nudibranchs (9.09 %) and snails (9.09 %) (Fig. 6.10b).

Maturing *R. palpebrosa* from Central Greenland showed a high percentage of unidentified eggs in their stomachs (100 %) with North Greenland, west Hudson Strait, east Hudson Strait and Ungava Bay individuals also having eggs within their stomach contents (overall 45.17 %) (Fig. 6.10c). Other prey items include: decapods (overall 85.76 %), fish (overall 36.87 %), polychaetes (overall 23.61 %), cephalopods (overall 21.59 %), mysids and ostracods (each overall 16.67 %), amphipods (11.11 %) and copepods (9.09 %) (Fig. 6.10c).

Mature *R. palpebrosa* were the only maturity stage to have remnants of the shrimp *Pandalus* sp. (overall 48.58 %) in their stomachs (Fig. 6.10d). Decapods (overall 74.34 %), unidentified eggs (71.16 %), snails (overall 37.67 %) and polychaetes (overall 36.87 %) make up the majority of the remaining prey items (Fig. 6.10d). Fish (11.11 %), amphipods (9.09 %) and an Ophioroid (9.09 %) were also preyed upon (Fig. 6.10d).

Many specimens had peach coloured, coral-like hard substance within their stomachs and ceaca (Fig. 6.10). While not able to identify or even determine if this substance was actual prey or possibly sediment residue, it was still included in the analysis (Fig. 6.10).

No sample location specific prey preferences were observed with the exception of maturing central Greenland individuals with a high percentage of eggs in their stomachs (Fig. 6.10c).

b) Mixing models

Mixing models for hatchling *R. palpebrosa* showed slight increased estimated proportions for echinoderm, basketstar, mollusc and fish1 (*Boreogadus saida*) as well as pteropods and mysids (Fig. 6.11a).

Mixing models for immature *R. palpebroso* from Baffin Bay/Greenland showed no differentiation between prey species (Fig. 6.11b) while those for immature individuals from Hudson Strait and Ungava Bay showed elevated proportions of echinoderms, molluscs, basketstar, fish1, decapod and polychaete (Fig. 6.11c, d). The models for immature Hudson Strait prey items also show an elevated proportion of pteropods and mysids (Fig. 6.11c).

No difference was obtained through isotopic mixing models for maturing Baffin Bay/Greenland and Ungava Bay *R. palpebroso*, however, slight elevated proportions of basketstar, fish1, pteropod and mysids were obtained for models of Baffin Island and Hudson Strait (Fig. 6.11e, f, g, h). Echinoderms and molluscs were also elevated in the Hudson Strait models (Fig. 6.11g).

No difference in prey proportions was noted for the isotopic mixing models of mature Baffin Island *R. palpebroso* (Fig. 6.11i). Mature Hudson Strait *R. palpebroso*, however, showed a similar prey proportion to earlier maturity stages with fish1, mollusc, echinoderm, pteropod, decapod and basketstar showing slightly elevated results (Fig. 6.11j).

Mixing models for St. Lawrence *R. palpebroso* showed no significant difference in prey proportions among the immature individuals (Fig. 6.12a). With increasing maturity, copepods, sea spiders, fish1 as well as mysids, amphipods and bivalves become more predominant (Fig. 6.12b, c). Echinoderms, polychaetes, crabs nor shrimp had much influence on the mixing model (Fig. 6.12).

6.3.3.3. *Bathypolypus* spp.

a) Stomach contents

Only *B. bairdii* from the St. Lawrence and the Gulf of St. Lawrence had stomach contents analyzed (Fig. 6.13). No immature or hatchling *B. bairdii* were available from the region for analyses (Table 6.3; Fig. 6.13). Arthropods and crustaceans were found in all maturing and mature individuals' stomachs, except mature individuals from the St. Lawrence, which had a high percentage of clams (66.7 %; Fig. 6.13). Clams were also present in the stomachs of St. Lawrence maturing (33.3 %), Gulf of St. Lawrence maturing (25 %) and Gulf of St. Lawrence mature (22.2 %) octopods (Fig. 6.13). Mature St. Lawrence individuals also had eggs (33.3 %) present in their stomachs (Fig. 6.13). Brittlestars (Ophioroids) were only reported from mature Gulf of St. Lawrence octopods (Fig. 6.13).

b) Mixing models

Mixing models of the Arctic *Bathypolypus* spp. showed no significant difference in prey proportion for any of the potential prey items (Fig. 6.14).

The mixing models for the St. Lawrence region combined SI samples collected from individuals from both St. Lawrence and the Gulf of St. Lawrence (Fig. 6.15). No differentiation in estimated prey proportions were observed for immature *Bathypolypus* sp. (i.e. female specimens), however, *Mytilus edulis* (blue mussels) and sea spider had elevated proportions compared to *Chlamys islandica*. (scallop), crab, shrimp, and the gastropods *Littorina* sp. (periwinkle) and *Buccinum undulatum* (common whelk) (Tables 6.1 and 6.2; Fig. 6.15a).

Both maturing *B. bairdii* and *Bathypolypus* sp. showed elevated proportions of *M. edulis*, amphipod, mysids and polychaetes (Fig. 6.15b and c). Maturing *B. bairdii* had elevated sea spider proportions not observed in maturing *Bathypolypus* sp. (Fig. 6.15b and c).

The mature *B. bairdii* mixing model shows a high proportion of amphipods, polychaetes and *M. edulis* and to a lesser extent mysids and sea spiders (Fig. 6.15d). No discernable prey preferences were evident from the mature *Bathypolypus* sp. mixing model (Fig. 6.15e).

6.3.3.4. *C. muelleri*

a) Stomach contents

Immature *C. muelleri* stomachs contained 49 % polychaete setae, 2 % arthropod carapace and 49 % unknown tissues (49 %) (Fig. 6.16). Maturing *C. muelleri* had the most diverse stomach contents with arthropods (30 %), crustaceans (27 %), decapods (22 %), ostracods (17 %) and even clams present (5 %) (Fig. 6.16). Polychaete setae were also present but to a lesser extent (10 %) than observed in the immature stomachs (Fig. 6.16). Fifty percent of the mature specimens had empty stomachs with the remaining 50 % only containing highly digested material (Fig. 6.16).

b) Mixing model

No proportional difference was noted between potential prey species of immature *C. muelleri* (Fig. 6.17a). Maturing individuals had proportionally elevated responses to basketstar, Mysidae, ostracod and molluscs but had low proportional responses to benthic fish2 (snailfish

Liparis sp. and sculpin *Myoxocephalus scorpioides*), octopus (*B. bairdii*) and brittlestars (Table 6.1; Fig. 6.17b).

Basketstars were the highest proportional prey for mature *C. muelleri* with mysids, ostracods and molluscs to a lesser extent (Fig. 6.17c).

6.4. Discussion

The combination of stable isotope and traditional stomach content analyses for the four most common Arctic cephalopod species provided a window into both the habitat and prey preferences of these important species as well as insight into ontogenetic shifts with maturity.

6.4.1. Delta¹³C values as indicators of habitat and feeding ground preferences of eastern Canadian Arctic cephalopods

Delta ¹³C values described habitat preferences between the Arctic cephalopod species in accordance with hypothesis 6.1 (page 196).

6.4.1.1. Arctic vs. St. Lawrence variations in δ¹³C

Previous studies have described a negative relationship between δ¹³C and latitude attributed to the well documented 0.015 ‰ poleward decrease in phytoplankton δ¹³C (Rau et al. 1983, Hobson and Welch 1992a, Takai et al. 2000, Hooker et al. 2001, Cherel et al. 2009). Such a relationship was not observed between Arctic *Bathypolypus* spp. and *R. palpebrosa* when compared with their St. Lawrence conspecifics (Table 6.3). Although not significantly different, St. Lawrence specimens were generally more depleted than their Arctic counterparts, the opposite of what was expected (Hypothesis 6.1a: δ¹³C will be depleted with increasing latitudes

due to phytoplankton-latitude inter-relationship; (Takai et al. 2000, Hooker et al. 2001)). Such a difference may be explained by examining the sample locations in question.

The majority of the St. Lawrence specimens were collected from the Gulf of St. Lawrence or near the boundary of where the St. Lawrence estuary transitions into the Gulf (Fig. 5.1). Unlike the estuary where much of the carbon comes from terrestrial runoff and freshwater phytoplankton, the Gulf of St. Lawrence is considered an inland sea where most of its carbon source is marine based (Lesage et al. 2001). Therefore, $\delta^{13}\text{C}$ values of the St. Lawrence region would be reflective of a pelagic system as opposed to coastal. The $\delta^{13}\text{C}$ values of the Arctic specimens, however, were averaged from all locations north of 60° including the pelagic Baffin Bay as well as the coastal Hudson Strait. Hudson Strait, in particular, is a mixture of low salinity Hudson Bay water flowing out along the southern shore and high salinity North Atlantic water (Labrador Sea) flowing in along the north shore (Fig. 2.2; Drinkwater 1986, Allard 1990), resulting in two different carbon sources (one marine and one neritic macrophyte). This mixture of both pelagic and coastal carbon input likely contributed to the less depleted $\delta^{13}\text{C}$ values observed in the Arctic specimens (Table 6.4). Baffin Bay/Greenland (pelagic C source) immature *Bathypolypus* spp. and maturing *R. palpebrosa*, however, were more depleted than their St. Lawrence counterparts (in agreement with Hypothesis 6.1a - page 198) (Table 6.4), giving validity to the above argument. Maturing *R. palpebrosa* from Baffin Island were also more depleted than the St. Lawrence specimens, and although from a coastal sample site, water flowing along the eastern edge of Baffin Island originated in Baffin Bay and would likely be dominated by pelagic carbon signatures (Fig. 2.2). Maturing *Bathypolypus* spp. from Ungava Bay were also more depleted than the St. Lawrence specimens (Table 6.4). The shallow Ungava Bay is fed by a cross current of marine water from the Labrador Sea which is then covered by

freshwater land runoff resulting in a highly stratified region (until mixing) (Drinkwater 1986). The benthic *Bathypolypus* spp. would therefore, be exposed primarily to marine carbon sources resulting in depleted $\delta^{13}\text{C}$ values.

6.4.1.2. Intra-Arctic $\delta^{13}\text{C}$ variability

a) Interspecific variations in $\delta^{13}\text{C}$: Each cephalopod species examined for this chapter represent a distinct marine habitat. *G. fabricii* are pelagic, preferring 200+ m of water, descending to deeper depths with size, while *R. palpebrosa* (based on what is known for other *Rossia* species) are neritic, typically found along the continental shelf (Chapter 2, 2.2.2.1a; 2.2.2.2a). The incirrate *Bathypolypus* spp. are also benthic, however, its habitat preference depends on which species in the complex is being examined. *B. arcticus* is limited to the Arctic region or areas exposed to cold Arctic water while *B. bairdii* prefers areas influenced by warmer North Atlantic water – typically along continental shelves (Chapter 2, 2.2.2.3a). *B. pugniger*'s habitat preference is unclear but Muus (2002) suggested that it is an Atlantic species which can tolerate exposure to Arctic water (Chapter 2, 2.2.2.3a). It should be noted that although the descriptions of the preferred habitats vary for each *Bathypolypus* species, especially in relation to water mass and temperature, no significant differences were observed between the species per maturity stage, from $\delta^{13}\text{C}$ values. Consequently, all species were combined for analyses (Table 6.3). *C. muelleri* represents the abyssal-pelagic habitat and are typically found at deep depths just above the sediment (Chapter 2, 2.2.2.4a). Based on these known habitat preferences, it was hypothesized (6.1) that the $\delta^{13}\text{C}$ values for each species would reflect their preferred habitats (i.e. coastal/benthic species will be less depleted in $\delta^{13}\text{C}$ than pelagic regions (Hobson and Welch 1992a, Takai et al. 2000, Hooker et al. 2001, Cherel et al. 2009)).

Baffin Bay/Greenland was the only sample location where all of the species were collected (Table 6.3; 6.4). While no significant difference was observed between the immature/size 3 specimens, significant differences in $\delta^{13}\text{C}$ values were apparent between the species at greater maturity/size levels (Table 6.3). Maturing and mature individuals (from least to most depleted in $\delta^{13}\text{C}$) were *Bathypolypus* spp., *C. muelleri*, *R. palpebrosa* and *G. fabricii* (Table 6.4), indicating that habitat preference could be determined from $\delta^{13}\text{C}$ values as hypothesized (6.1 - page 197).

Rossia palpebrosa, a benthic coastal cephalopod, (Chapter 2, 2.2.2.2a) was more enriched in $\delta^{13}\text{C}$ than the pelagic *G. fabricii* in accordance with hypothesis 6.1b (page 198) but were less enriched than the deeper benthic octopods (*Bathypolypus* spp. and *C. muelleri*) (Table 6.4).

The largest variation in $\delta^{13}\text{C}$ values was found in the mature *Bathypolypus* spp. from Baffin Bay/Greenland (Table 6.4). This was as hypothesized (6.1c - page 198) indicating a wider habitat range for this genus compared to the other Baffin Bay/Greenland taxa.

It was also hypothesized (6.1d - page 198) that because the benthic *C. muelleri* was exposed to primarily pelagic carbon sources (i.e. marine snow), it would have similar $\delta^{13}\text{C}$ values to *G. fabricii*. But hypothesis 6.1d (page 198) was rejected as the *C. muelleri* $\delta^{13}\text{C}$ signature, was instead similar to that of *Bathypolypus* spp. (Table 6.4). This association is likely due to both octopods (cirrate and incirrate) being benthic and benthic $\delta^{13}\text{C}$ undergoes greater bacterial and meiofaunal turnover compared to terrestrial runoff and macrophyte sources (Iken et al. 2005, Michener and Kaufman 2007). Temperature also plays a role in the amount of carbon available

to a system, with greater availability at lower temperatures (i.e. deeper regions) (Michener and Kaufman 2007).

b) Variability of $\delta^{13}\text{C}$ by size range and maturity stage: Further insight into cephalopod habitat preference was obtained through comparisons of sampling locations per maturity/size ranges (in agreement with Hypothesis 6.2 - $\delta^{13}\text{C}$ will reflect ontogenetic shifts in habitat of the various species; Table 6.3 and 6.4; Figs. 6.2 to 6.5). A shift from depleted to less depleted $\delta^{13}\text{C}$ values could indicate a shift from a pelagic/offshore region to more inshore habitats as the cephalopod matures. This trend, although not statistically significant, was observed for both *R. palpebrosa* from the Arctic and St. Lawrence regions and *Bathypolypus* spp. from Ungava Bay (Tables 6.3 and 6.4). While both of these taxa are benthic, the $\delta^{13}\text{C}$ values indicate a potential shift from offshore feeding locations to near-shore spawning sites. Perhaps the offshore regions have sufficient prey for larger individuals while the near-shore spawning sites provide better prey availability for the precocious hatchlings. Mature *R. palpebrosa* from Hudson Strait were found at deeper depths (Table 6.4) suggesting that these individuals may be moving to deeper regions to find sheltered spawning sites away from highly turbulent, shallow strait waters.

G. fabricii also showed a significant increase in $\delta^{13}\text{C}$ values with size (Tables 6.3 and 6.4; Fig. 6.2). Unlike *Bathypolypus* spp. and *Rossia* spp., *G. fabricii* are believed to brood their eggs while floating near the surface, negating the need to find suitable spawning substrates (Chapter 2, 2.2.2.1b). None of the specimens examined were sexually mature ruling out a potential shift due to spawning behaviour. Since *G. fabricii* undergo an ontogenetic shift to deeper water as they

mature (Chapter 2, 2.2.2.1b), the increase in $\delta^{13}\text{C}$ (Table 6.4) could be the result of larger specimens frequenting the benthic habitat more than the pelagic realm.

No significant difference in $\delta^{13}\text{C}$ values were noted for *C. muelleri* of different maturity stages (Table 6.3), suggesting that both the adult and juveniles occur within the same habitat.

6.4.2. Trophic interactions of eastern Canadian Arctic cephalopods

While $\delta^{13}\text{C}$ values describe changing cephalopod habitats based on carbon sources, $\delta^{15}\text{N}$ describe trophic interactions throughout the Arctic region and at various life stages.

No significant shift in $\delta^{15}\text{N}$ was observed with increasing latitude (Table 6.3) but Arctic specimens were on average more enriched than those from the St. Lawrence (Table 6.4). Contrary to what was expected (Hypothesis 6.3 - $\delta^{15}\text{N}$ values will increase with latitude due to proximity to the productive North Water polynya), there was no evidence that the northern specimens (i.e. those from Baffin Bay/Greenland and Disko Bay) were more enriched in $\delta^{15}\text{N}$ than those from the more southern Arctic locals (i.e. Hudson Strait and Ungava Bay) (Table 6.4; Figs. 6.2 to 6.5). Therefore, northern and southern conspecifics are likely feeding on organisms of the same trophic level regardless of sample location.

Significant differences in $\delta^{15}\text{N}$ between species were observed for the maturing and mature specimens (Hypothesis 6.4 - $\delta^{15}\text{N}$ values will reflect each cephalopods respective hunting style; Table 6.3). *C. muelleri* were the most enriched of the Arctic species followed by *R. palpebrosa*, *Bathypolypus* spp. and *G. fabricii* (Table 6.4). This is not as expected (Hypothesis 6.4 - page 199). While both *Rossia* spp. and *Bathypolypus* spp. are thought to be more passive hunters (sit-and-wait predators), *G. fabricii* is known to be a voracious predator, often feeding on

the same fish that are trying to feed on them – they are also cannibalistic (Chapter 2, 2.2.2.1d; 2.2.2.2d; 2.2.2.3d; (Nesis 1965, Kristensen 1983, Wood 2000)). Because *G. fabricii* feed on the largest prey they can capture, they should be the most enriched in $\delta^{15}\text{N}$ of the Arctic species but this is not the case (Table 6.4). Instead, benthic cephalopod species show the most $\delta^{15}\text{N}$ enrichment (Table 6.4), again highlighting the impact of nutrient recycling (and amplification) through benthic food chains, specifically through meiofauna, unselective deposit feeders, and benthic predators (e.g. polychaetes) (Michener and Schell 1994, Iken et al. 2005).

6.4.2.1. Variability of $\delta^{15}\text{N}$ within the eastern Canadian Arctic

Delta ^{15}N values do not show full trophic shifts between maturity stages/size ranges of the Arctic and St. Lawrence cephalopods, however, ontogenetic shifts were observed for *G. fabricii* and *R. palpebrosa* (in agreement with Hypothesis 6.2 - $\delta^{15}\text{N}$ will reflect ontogenetic shifts in species ability to capture higher quality prey).

a) *G. fabricii*: SIA found that there was a steady enrichment in $\delta^{15}\text{N}$ values with increasing size of *G. fabricii* but the overall increase did not indicate a trophic shift (2.78 ‰) (Table 6.4; Fig. 6.2). This was not surprising as stomach content analyses revealed that most size 2 to size 4 individuals fed on the same prey items: arthropods, crustaceans, decapods, amphipods and copepods (Fig. 6.6). However, evidence of fish were also present in the stomachs of even the smallest group of squid (size 2) as well as evidence of potential cannibalism (i.e. cephalopod structures); prey items not previously reported for the juveniles of this species (Fig. 6.6). *G. fabricii* is one of the best studied cephalopod species, with a variety of sources describing the observed prey items by size/maturity range. Kristensen (1984) clearly states that juveniles do not feed on fish while Wiborg et al. (1982) and Nesis (2003c) added that

cannibalism was not observed in juveniles. The intake of such high-energy prey items would increase the $\delta^{15}\text{N}$ values of the smaller size ranges, ultimately obscuring any notable trophic shifts.

Nesis (1965, 2003c) also states that larger *G. fabricii* rarely feed on copepods and euphausiids, unless no other prey is available. By contrast, in this study, copepods, in particular *Calanus hyperboreus*, appear to be prominent prey species for Canadian/Greenland Arctic *G. fabricii* (with the exception of size 5 specimens from Disko Bay) (Figs. 6.7 to 6.9). Other copepod species include *C. glacialis* and *Metridia longo* (Figs. 6.7 to 6.9). Within the Arctic, it is predicted that environmental shifts in ice cover and temperature, for example, will result not only in cyclical changes in zooplankton abundance within the region but will also favour smaller species (Persson et al 2012). It is possible that these shifts are already occurring. Additional prey species relatively consistent throughout the life cycle of *G. fabricii* include the pteropod *Clione limacine* and the amphipod, *Themisto libellula* (Figs 6.7 to 6.9).

b) *R. palpebrosa*: *Rossia* species are opportunistic predators, preferring the sit-and-wait strategy over actively hunting for prey (Brocco 1971, Nesis 2001). To my knowledge, there are no reports on the trophic interactions of *R. palpebrosa*, but prey species for Rossinae are highly variable and include crustaceans, fish, echinoderms, anemones, amphipods and even decapods like *Lithodes* sp. and *Pandalus* sp. (Mercer 1968a). Such a variable diet would contribute to the opportunistic predator theory. *R. palpebrosa* stomach contents revealed a similar diet with prey species consisting of amphipods, mysids, nudibranchs, snails, cephalopods, polychaetes, ostracods, fish, decapods and unknown eggs (Fig. 6.10). Based on these observations, the diet of *R. palpebrosa* is similar to the other Rossinae species.

The mixing models emphasized molluscs, echinoderms and basketstars as Arctic prey species, with increasing proportions of fish i.e. larger proportions of *B. saida* in larger individuals from Hudson Strait region (Table 6.1; Fig. 6.11). This explains the $\delta^{15}\text{N}$ enrichment from immature to mature individuals, even though there was not a full trophic shift (Table 6.4). A similar $\delta^{15}\text{N}$ enrichment was evident for the St. Lawrence *R. palpebrosa*, however, the mixing models only showed a slight increase in the proportion of sea spiders with maturity and a decrease in echinoderm and polychaete prey (Fig. 6.12).

c) *Bathypolypus* spp.: *Bathypolypus* spp. are also thought to be opportunistic predators (Wood 2000), however, unlike *R. palpebrosa* and *G. fabricii*, *Bathypolypus* spp. show no significant $\delta^{15}\text{N}$ enrichment with maturity (Tables 6.3 and 6.4).

North Atlantic *Bathypolypus* spp. feed primarily on brittlestars but will readily accept higher quality food when available (O'Dor and Macalaster 1983, Wood 2000). Based on the stomach contents of the St. Lawrence specimens, ophioroids (brittlestars) were only a small portion of the diet of mature *B. bairdii* while 'clams' (based on pieces of shell), arthropods/crustaceans and unidentified eggs made up the majority of the diet for both the maturing and mature individuals from the St. Lawrence and Gulf of St. Lawrence region (Fig. 6.13). Mixing models highlighted other potential prey species such as mysids and amphipods in maturing *B. bairdii* and *Bathypolypus* sp. and mature *B. bairdii* (Fig. 6.16). Polychaetes also appeared to be important prey species for mature *B. bairdii* (Fig. 6.15). The most interesting finding based on the mixing models for *Bathypolypus* spp. was the importance of *Mytilus edulis* for all the life stages (with the exception of mature *Bathypolypus* spp.) (Table 6.2; Fig. 6.15). *Mytilus* is typically an intertidal species (Zagata et al. 2008) and *Bathypolypus* spp. are thought

to be found in deeper water, especially at more southern latitudes where the water is cooler (Muus 2002). The fact that the $\delta^{15}\text{N}$ signature of an intertidal species would register as prey for a benthic octopod suggests that *Bathypolypus* spp. migrate inshore to feed within the St. Lawrence region or that the $\delta^{15}\text{N}$ signature of *M. edulis* is similar to clams found at deeper depths (i.e. feeding at approximately the same trophic levels). This later explanation is unlikely, as a deep water scallop, *Chlamys islandica* (Sarabia and Zymans 2013) was also included in the mixing model and no association was found (Fig. 6.15).

No prey species were identified through mixing models for Arctic *Bathypolypus* spp. (Fig. 6.14). Even brittlestars did not appear as a potential prey source (Fig. 6.14).

d) *C. muelleri*: This is the first time *C. muelleri* prey are reported (Chapter 2, 2.2.2.4d) due to the difficulty to acquire samples of these solitary individuals from deep sea habitats (Chapter 2, 2.2.2.4 a, b). Based on submersible surveys *Cirroteuthis* sp. likely prey on suprabenthic invertebrates but direct feeding has not been observed, only an instance of extended web movement near the substrate (Collins and Villanueva 2006).

SI analyses found immature *C. muelleri* to be the most enriched in $\delta^{15}\text{N}$ of the maturity stages (although not a trophic shift (Hobson and Welch 1992a, Hobson et al. 2002)) (Table 6.4; Fig. 6.5). Initial stomach content analyses showed that the immature specimen fed primarily on polychaetes and a small portion of arthropods (Fig. 6.16). The remaining immature stomach contents were unidentifiable (Fig. 6.16). The mixing model was also unable to distinguish potential primary prey species with all potential prey species showing similar proportions (Fig. 6.17a).

Both maturing and mature *C. muelleri* had similar $\delta^{15}\text{N}$ values and they appear to have similar prey preferences (Table 6.4; Fig. 6.5). This was not apparent from the stomach contents analysis since maturing individuals fed on prey which included decapods, ostracods, amphipods and clams, while mature individuals only had empty stomachs or were filled with highly digested material (Fig. 6.16). The mixing models, however, showed a preference for mysids, ostracods, basketstars and some molluscs (clams: *Hiatella arctica*, *Macoma calcarea*, *Mya truncate*, *Serripes groenlandica*) for both maturity stages (Table 6.1; Fig. 6.17b and c). The presence of molluscs as a primary prey item suggests that *C. muelleri* are opportunistic predators feeding on a variety of benthic invertebrates, as Cirroteuthids lack a radula required to drill through a molluscs' shell and must instead rely on compounds secreted from their anterior salivary gland to help open it (Collins and Villanueva 2006). It is believed that the cirri on the octopods arms are used to find prey within the sediment (Collins and Villanueva 2006). This was verified as some of the preferred species in the mixing model were infaunal (e.g. *Macoma calcarea*, *Serripes groenlandica* (Voronkov 2010a, b)).

Based on the above comparisons, isotopic mixing models were useful in providing confirmation of stomach content analyses and provided increased taxonomic identification of potential prey species for most of the Arctic cephalopods examined. The findings support [hypothesis 6.5](#) (page 199).

6.5 Conclusion

The Arctic Ocean is a complex ecosystem with cephalopods as one of its primary prey species. Although a vital component in all marine ecosystems, trophic studies of cephalopods have proven to be inherently difficult. Stable isotope analyses provided new insights on habitat

preference and trophic interactions for the various Canadian Arctic cephalopod species, particularly those for which there is little published information (e.g. *R. palpebrosa* and *C. muelleri*). Delta ^{13}C values distinguished among habitat preferences of several species (Hypothesis 6.1 – page 197) while $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ provided evidence of ontogenetic shifts in habitat and prey selection for the Arctic cephalopods (Hypothesis 6.2 – page 198). Changes in $\delta^{15}\text{N}$ (Hypothesis 6.3 – page 198) did not increase with latitude, indicating that similar trophic level prey are available in all habitats. Delta ^{15}N varied based on cephalopod species but the values were more representative of their habitat than the types of prey consumed (Hypothesis 6.4 – page 199). Sit-and-wait predators (e.g. *C. muelleri* and *Bathypolypus* spp.) had higher $\delta^{15}\text{N}$ values than the energetic *G. fabricii* and highlight the trophic importance of the benthic ecosystem. Finally, isotopic mixing models provided taxonomic insight into the prey of the Arctic cephalopods (Hypothesis 6.5 – page 199) particularly *R. palpebrosa* and *C. muelleri*.

Large sample sizes and data from other regions of the Arctic may help to reduce the variability observed in some $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Furthermore, there needs to be a much better understanding of the vertical distribution of all prey items, at the local scale, as temperatures shift upward and salinity levels change in Arctic waters.

Table 6.1. Literature stable isotope values used in mixing models.

Arctic Prey						
Major Group	Taxa	Location	Mean $\delta^{13}\text{C}$	StDev $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	StDev $\delta^{15}\text{N}$
Amphipod ^{1,2}	<i>Anonyx nugax/Onisimus glacialis/Themisto libellula</i>	Hudson Strait/Davis Strait/Baffin Bay	-19.49	0.9	9.85	1.022
Cnidaria ³	<i>Anemone urticina/Mertensia ovum</i>	Lancaster Sound	-19.35	0.5	13.95	0.45
Copepod ^{1,2}	<i>Calanus glacialis/Calanus hyperboreus/Metridia longo</i>	Hudson Strait/Davis Strait/Baffin Bay	-21.83	0.55	8.3	0.59
Decapod ³	<i>Lebbeus polaris</i>	Lancaster Sound	-16	0.3	14.5	0.3
Pandalus sp. ¹	<i>Pandalus</i> sp.	Hudson Strait	-17.8		12.7	
Basketstar ¹	<i>Gorgoncephalus arcticus</i>	Hudson Strait	-21.5	0.8	13	0.3
Brittlestar ⁴	<i>Ophiura sarsi</i>	North Water Polynya	-11.3	0.5	9.7	0.3
Echinoderm ^{1,3}	<i>Ctenodiscus crispatus/Gorgonocephalus arcticus/Strongylocentrotus droebachiensis/unidentified cucumber</i>	Hudson Strait/Lancaster Sound	-18	0.75	10.6	0.5
Fish ^{0,4}	<i>Boreogadus saida</i> larvae	North Water Polynya	-20	0.5	10.7	0.8
Fish ^{1,2,4}	<i>Boreogadus saida</i>	Davis Strait/Baffin Bay/North Water Polynya	-19.9	0.53	11.87	0.4
Fish ^{2,3}	<i>Liparis</i> sp./ <i>Myoxocephalus scorpioides</i>	Lancaster Sound	-17.75	0.3	15.1	0.25
Isopod ¹	<i>Saduria entamon</i>	Hudson Strait	-20.6	0.3	14.3	0.5
Mollusc ^{1,2,3}	<i>Hiatella arctica/Macoma calcarea/Mya truncata/Serripes groenlandica</i>	Lancaster Sound	-18.53	0.53	9.25	0.5
Mysidae ^{1,2}	<i>Mysid</i> sp./ <i>Mysis oculata</i>	Hudson Strait/Davis Strait/Baffin Bay	-21.4	0.2	10.7	0.1
Ostracod ²	<i>Conchoecinae</i> sp.	Davis Strait/Baffin Bay	-20.6		12.9	
Pteropod ²	<i>Clione limacina</i>	Davis Strait/Baffin Bay	-20.67	1.19	9.44	1.34
Polychaeta ⁴	<i>Lumrineris</i> sp./ <i>Phyllodoce mucosa</i>	North Water Polynya	-17.9	0.6	13.2	0.45

Table 6.1 Cont'd

St. Lawrence Prey						
Major Group	Taxa	Location	Mean $\delta^{13}C$	StDev $\delta^{13}C$	Mean $\delta^{15}N$	StDev $\delta^{15}N$
Amphipod ⁵	<i>Gammarus</i> sp.	St. Lawrence	-17.8		9.1	
Mysid ⁵	<i>Caprella</i> sp./ <i>Mysis</i> sp.	St. Lawrence	-19.15		8.45	
Copepod ⁵	<i>Calanus hyperboreus</i> / <i>Calanus</i> sp./ <i>Metridia</i> sp.	St. Lawrence	-20.4	0.2	11	1.1
Crab ⁵	<i>Cancer irroratus</i>	St. Lawrence	-16.5	0.4	12.7	1
Shrimp ⁵	<i>Pandalus</i> sp.	St. Lawrence/Gulf of St. Lawrence	-17.9	0.4	13.55	0.5
Bivalvia ⁵	<i>Mytilus edulis</i> / <i>Chlamys islandica</i>	St. Lawrence/Gulf of St. Lawrence	-18.5		8.83	
Fish1 ⁵	<i>Boreogadus saida</i> / <i>Clupea harrengus</i> / <i>Mallotus villosus</i>	St. Lawrence/Gulf of St. Lawrence	-19.38	0.6	13.46	0.41
Fish3 ⁵	<i>Reinhardtius hippoglossoides</i>	St. Lawrence/Gulf of St. Lawrence	-19.3	0.3	12.95	0.4
Echinoderm ⁵	<i>Strongylocentrotus droebachiensis</i>	St. Lawrence	-14.6	0.2	7.7	0.7
Polychaeta ⁵	<i>Nereis</i> sp.	St. Lawrence	-16.2		10.6	
POM ⁵	Particulate Organic Matter	St. Lawrence	-22.9	1.7	4.5	0.9

¹ Fisk et al. 2003, ² Pomerleau et al. 2011, ³ Hobson and Welch 1992a, ⁴ Hobson et al. 2002 and

⁵ Lesage et al. 2001

Table 6.2. Literature stable isotope values of defined taxa used for detailed mixing models.

Major Group	Detailed Taxa	Location	Mean $\delta^{13}\text{C}$	StDev $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	StDev $\delta^{15}\text{N}$
Amphipod	<i>Anonyx nugax</i> ¹	Hudson Strait	-19.3	0.5	13.5	3.4
	<i>Onisimus glacialis</i> ²	Davis/Baffin	-15.37	2.8	8.64	0.71
	<i>Themisto libellula</i> ^{1,2}	Hudson Strait/Davis Strait/Baffin Bay	-20.93	0.4	9.03	0.33
Copepod	<i>Calanus glacialis</i> ²	Davis Strait/Baffin Bay	-20.7	1	8.05	0.75
	<i>Calanus hyperboreus</i> ^{1,2}	Hudson Strait/Davis Strait/Baffin Bay	-22.1	0.37	7.6	0.3
	<i>Metridia longo</i> ^{1,2}	Hudson Strait/Davis Strait/Baffin Bay	-22.55	0.36	9.6	0.85
Mysidae	<i>Caprella</i> sp. ⁵	St. Lawrence	-17.9		6	
	<i>Mysis</i> sp. ⁵	St. Lawrence	-20.4		10.9	
Bivalvia	<i>Mytilus edulis</i> ⁵	St. Lawrence	-19.4		7.35	
	<i>Chlamys islandica</i> ⁵	St. Lawrence	-16.2		11.8	
Gastropoda	<i>Littorina</i> sp. ⁵	St. Lawrence	-14.8	0.1	8.6	0
	<i>Buccinum undatum</i> ⁵	St. Lawrence	-17.6	0.5	11.1	0.3

¹Fisk et al. 2003, ²Pomerleau et al. 2011, ³Hobson and Welch 1992a, ⁴Hobson et al. 2002 and

⁵Lesage et al. 2001

Table 6.3. Kruskal-Wallis results of comparisons of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ by location and species.

* refers to significant values. Note size 5 *G. fabricii* does not signify that the individuals were mature, only that they were in the largest size range sampled. No mature *G. fabricii* were collected.

Location	Species	Size Range/ Maturity Stage	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
			χ^2	df	p value	χ^2	df	p value
Bathypolypus species								
Arctic	<i>B. arcticus</i> <i>B. bairdii</i> <i>B. pugniger</i> <i>Bathypolypus</i> sp.	Maturing	2.2000	3	0.5319	3.8000	3	0.2839
	<i>B. arcticus</i> <i>B. bairdii</i> <i>B. pugniger</i> <i>Bathypolypus</i> sp.	Mature	3.0444	3	0.3848	1.3556	3	0.7160
St. Lawrence	<i>B. bairdii</i> <i>Bathypolypus</i> sp.	Maturing	0.1154	1	0.7341	3.4904	1	0.0617
	<i>B. bairdii</i> <i>Bathypolypus</i> sp.	Mature	0.2500	1	0.6171	0.0000	1	1.0000
Arctic vs. St. Lawrence								
	<i>Bathypolypus</i> spp.	Immature	1.5000	1	0.2207	1.500	1	0.2207
		Maturing	0.0333	1	0.8551	0.0333	1	0.8551
		Mature	0.3231	1	0.5698	0.1648	1	0.6847
	<i>R. palpebrosa</i>	Immature	1.0000	1	0.3173	1.0000	1	0.3173
		Maturing	0.2000	1	0.6547	1.8000	1	0.1797
Baffin Bay/Greenland species								
	<i>Bathypolypus</i> spp. <i>C. muelleri</i> <i>G. fabricii</i> <i>R. palpebrosa</i>	Size 3 Immature	5.6103	3	0.1322	6.4092	3	0.0933
	<i>Bathypolypus</i> spp. <i>C. muelleri</i> <i>G. fabricii</i> <i>R. palpebrosa</i>	Size 4 Maturing	15.3651	3	0.0015*	21.3214	3	< 0.0001*
	<i>Bathypolypus</i> spp. <i>C. muelleri</i> <i>G. fabricii</i>	Size 5 Mature	8.9159	2	0.0116*	7.2239	2	0.0270*
Between life stages per location								
Baffin Bay/Greenland	<i>Bathypolypus</i> spp.		1.4000	2	0.4966	0.2000	2	0.9048
Hudson Strait			0.0000	1	1.0000	1.5000	1	0.2207
Ungava Bay			1.5000	1	0.2207	1.5000	1	0.2207
St. Lawrence			1.2022	2	0.5482	5.0816	2	0.0788
Baffin Bay/Greenland	<i>C. muelleri</i>		2.3805	2	0.3042	1.1226	2	0.5705
Baffin Bay/Greenland	<i>G. fabricii</i>		16.1834	3	0.0010*	48.2937	3	< 0.0001*
Disko Bay			4.8044	2	0.0905	10.9009	2	0.0043*
Hudson Strait			23.8498	1	< 0.0001*	11.3932	1	0.0007*
Ungava Bay			7.3846	1	0.0066*	1.8462	1	0.1742
Baffin Bay/Greenland	<i>R. palpebrosa</i>		1.0000	1	0.3173	1.0000	1	0.3173
Baffin Island			1.8000	1	0.1797	0.2000	1	0.6547
Hudson Strait			0.7165	3	0.8693	1.9468	3	0.5835
Ungava Bay			1.8000	1	0.1797	1.8000	1	0.1797
St. Lawrence			1.4400	2	0.4868	2.0444	2	0.3598

Table 6.4. Habitat descriptors and means (standard deviations) of the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of the common Canadian Arctic cephalopods by size range/maturity stage in comparison to those from the St. Lawrence region.

LOCATION	Taxa	Size/Maturity Range	N	Latitude Range	Longitude Range	Depth Range (m)	Bottom Temp Range (°C)	ML Range (mm)	Mean $\delta^{13}\text{C}$ (\pm stdev)	Mean $\delta^{15}\text{N}$ (\pm stdev)
Arctic	<i>Bathypolypus</i> spp.	immature	1	66.87	-58.08	871.00	1.13	27.85	-19.22	14.64
		maturing	2	66.83 to 67.68	-58.44 to -58.89	647.50 to 871.50	1.16 to 3.79	47.45 to 60.60	-17.76 (\pm 1.3)	13.41 (\pm 3.08)
		mature	6	66.27 to 67.85	-58.51 to -59.12	376.00 to 773.50	1.34 to 4.00	42.05 to 71.45	-18.27 (\pm 3.01)	13.76 (\pm 2.96)
		hatchling	0							
		immature	1	67.08	-57.58	839.50	0.92	17.42	-20.43	15.99
		maturing	17	66.66 to 68.09	-57.27 to -60.03	428.50 to 1462.00	-0.02 to 3.82	20.38 to 78.78	-19.19 (\pm 0.69)	15.44 (\pm 1.24)
	<i>C. muelleri</i>	mature	7	67.69 to 67.89	-59.66 to -59.86	1452.00 to 1462.00	-0.02 to 0.04	42.80 to 68.36	-19.11 (\pm 0.83)	15.44 (\pm 1.06)
		2	43	61.73 to 72.35	-52.28 to -67.49	225.00 to 948.50	0.51 to 4.52	33.42 to 64.87	-20.9 (\pm 0.59)	10.7 (\pm 0.87)
		3	34	63.49 to 72.49	-52.58 to -60.66	187.50 to 948.50	0.96 to 4.52	65.04 to 126.82	-20.71 (\pm 0.6)	12.17 (\pm 0.96)
		4	13	68.39 to 70.56	-54.00 to -56.00	238.50 to 574.50	3.15 to 4.52	131.08 to 192.33	-20.2 (\pm 0.54)	12.01 (\pm 0.59)
		5	9	67.69 to 71.19	-56.82 to -59.86	285.50 to 1462.00	-0.02 to 2.95	201.00 to 330.00	-20.53 (\pm 0.45)	13.48 (\pm 1.41)
	<i>R. palpebrosa</i>	immature	1	67.63	-58.15	280.00	3.31	18.85	-19.73	11.30
		maturing	1	68.43	-64.37	366.50	-0.20	18.90	-19.41	14.18
	BI	<i>G. fabricii</i>	2	66.27	-61.16	190.50	-1.28	30.35 to 39.87	-21.66 (\pm 0.67)	11.88 (\pm 1.06)
			3	61.52 to 68.32	-63.48 to -65.26	262.50 to 586.00	-1.06 to 0.79	33.60 to 36.10	-19.31 (\pm 0.85)	14.29 (\pm 2.02)
<i>R. palpebrosa</i>		1	67.59	-63.52	567.50	2.47	36.5	-18.71	14.79	
DB	3	9	68.89 to 69.85	-51.43 to -52.33	373.50 to 598.00	3.50 to 3.63	66.74 to 120.20	-20.26 (\pm 0.35)	11.67 (\pm 0.66)	
		15	68.89 to 69.85	-51.43 to -52.33	373.50 to 598.00	3.50 to 3.63	130.51 to 195.00	-20.12 (\pm 0.41)	12.71 (\pm 0.83)	
	4	4	68.89 to 69.85	-51.43 to -51.47	373.50 to 598.00	3.63	200.00 to 256.00	-19.42 (\pm 0.75)	13.19 (\pm 0.4)	
		1	61.62	-68.37	285.00	1.08	50.94	-17.02	13.21	
	HS	<i>Bathypolypus</i> spp.	maturing	2	60.98 to 62.10	-64.10 to -69.05	242.50 to 390.50	0.41 to 2.38	36.21 to 47.50	-17.38 (\pm 0.74)
mature			72	60.85 to 62.22	-63.94 to -69.89	225.00 to 901.00	-0.76 to 2.38	24.60 to 60.12	-20.57 (\pm 1.23)	11.26 (\pm 1.38)
<i>G. fabricii</i>		3	60.41 to 61.33	-63.94 to -68.05	249.80 to 965.60	0.67 to 3.74	65.97 to 115.45	-19.51 (\pm 0.73)	11.99 (\pm 1.19)	
		3	61.30 to 61.75	-66.17 to -68.06	243.00 to 245.50	0.86	15.12 to 20.31	-18.42 (\pm 0.89)	12.71 (\pm 0.95)	
<i>R. palpebrosa</i>		immature	5	61.31 to 62.10	-66.21 to -69.66	242.50 to 285.00	0.01 to 1.08	15.65 to 37.70	-18.05 (\pm 0.49)	12.88 (\pm 0.6)
	maturing	6	59.28 to 61.62	-64.10 to -68.37	187.00 to 390.50	0.05 to 2.38	17.55 to 38.90	-17.82 (\pm 0.92)	13.31 (\pm 0.56)	
	mature	7	61.02 to 61.75	-64.18 to -68.18	220.50 to 617.50	0.50 to 3.79	33.50 to 53.41	-17.98 (\pm 0.56)	13.63 (\pm 1.43)	
UB	<i>Bathypolypus</i> spp.	maturing	2	59.76 to 60.77	-65.75 to -66.95	189.00 to 384.50	0.18 to 1.64	30.73 to 62.89	-18.56 (\pm 0.88)	12.92 (\pm 2.43)
		mature	1	59.56	-66.99	272.00	-0.23	71.75	-14.94	15.07
	<i>G. fabricii</i>	2	60.61 to 60.90	-66.74 to -68.42		0.04 to 1.64	40.00 to 61.00	-20.18 (\pm 0.44)	11.37 (\pm 0.54)	
		3	60.41 to 60.65	-65.33 to 68.20	249.80	-0.09 to 0.67	67.00 to 87.41	-19.07 (\pm 0.48)	12.04 (\pm 0.87)	
<i>R. palpebrosa</i>	immature	3	59.56 to 60.61	-65.62 to -66.99	183.50 to 272.00	-0.23 to -0.40	11.95 to 24.20	-17.49 (\pm 0.54)	12.57 (\pm 0.7)	
	maturing	1	59.58908332	-67.42	175.50	-0.17	25.5	-16.73	13.62	
Beaufort	<i>Bathypolypus</i> spp.	hatchling	1	71.26	-127.19	56.06	-1.02	15.00	-20.69	13.54
	<i>R. palpebrosa</i>	immature	1	70.42	-123.11	66.08	0.61	9.42	-21.95	13.46
St. Lawrence	<i>Bathypolypus</i> spp.	immature	2	49.48	-64.98	360.00		14.92 to 26.17	-18.57 (\pm 0.11)	12.82 (\pm 1.09)
		maturing	12	48.34 to 49.48	-61.09 to -69.13	229.00 to 436.00		21.91 to 38.59	-18.12 (\pm 0.54)	12.48 (\pm 0.84)
	<i>R. palpebrosa</i>	mature	7	48.34 to 49.56	-59.74 to -69.13	209.00 to 357.00		26.20 to 49.09	-18.23 (\pm 0.73)	13.32 (\pm 0.56)
		immature	1	49.56	-60.29	209.00		22.08	-20.04	11.38
	<i>R. palpebrosa</i>	maturing	3	49.29 to 49.56	-60.15 to -65.10	209.00 to 260.00		18.08 to 29.45	-19.27 (\pm 0.89)	12.33 (\pm 0.95)
mature	5	49.03 to 49.85	-59.25 to -64.68	87.00 to 215.00		24.12 to 43.34	-19.11 (\pm 1.03)	12.99 (\pm 0.7)		

Figure 6.1. Analysis of stable isotope values (with standard deviations) of four different tissues and stomach content from five Hudson Strait (2007) *G. fabricii* to determine the best tissue to use for the remaining analyses.

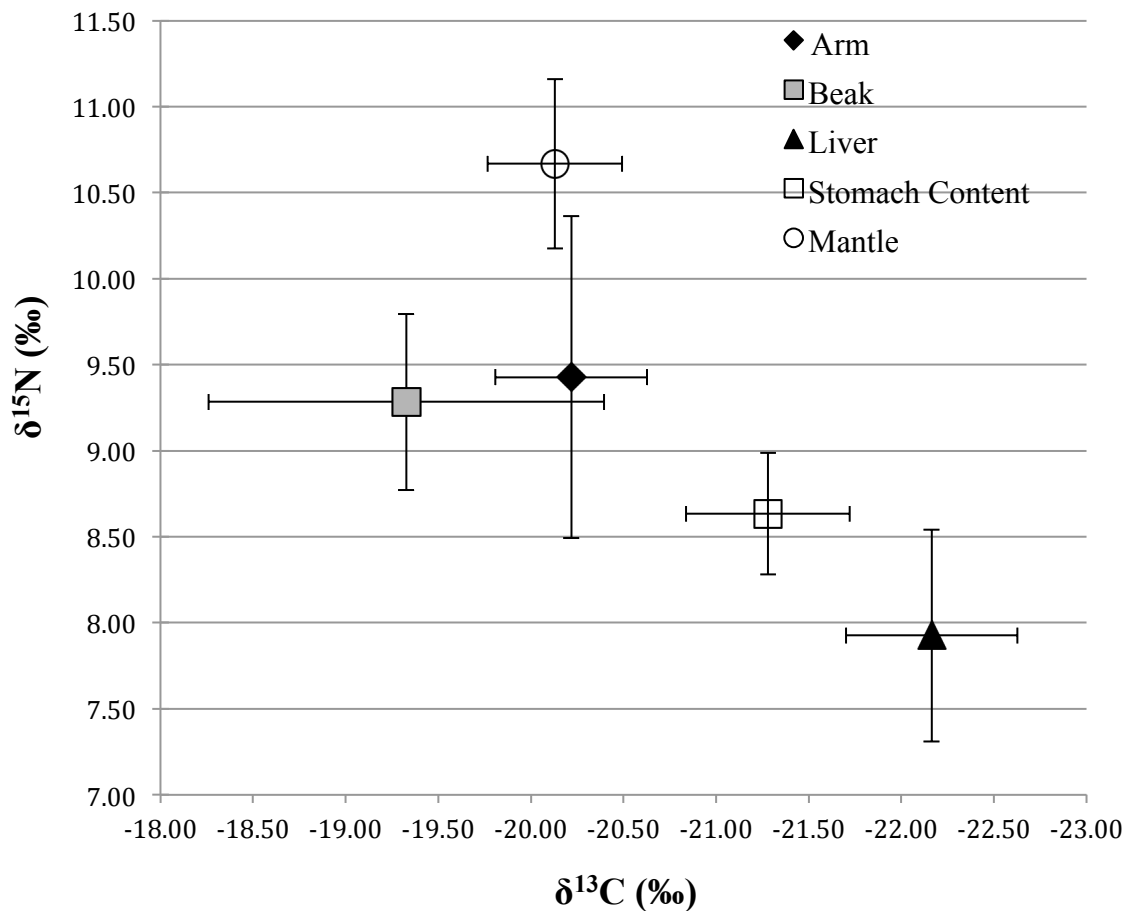


Figure 6.2. Mean and standard deviations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for *G. fabricii* by size range: (a) 2, (b) 3, (c) 4 and (d) 5. Symbols represent locations as described by PCA analysis in Chapter 5 (\diamond Baffin Bay/Greenland, - Baffin Island (new location), \triangle Hudson Strait, \times Ungava Bay, and \circ Disko Bay).

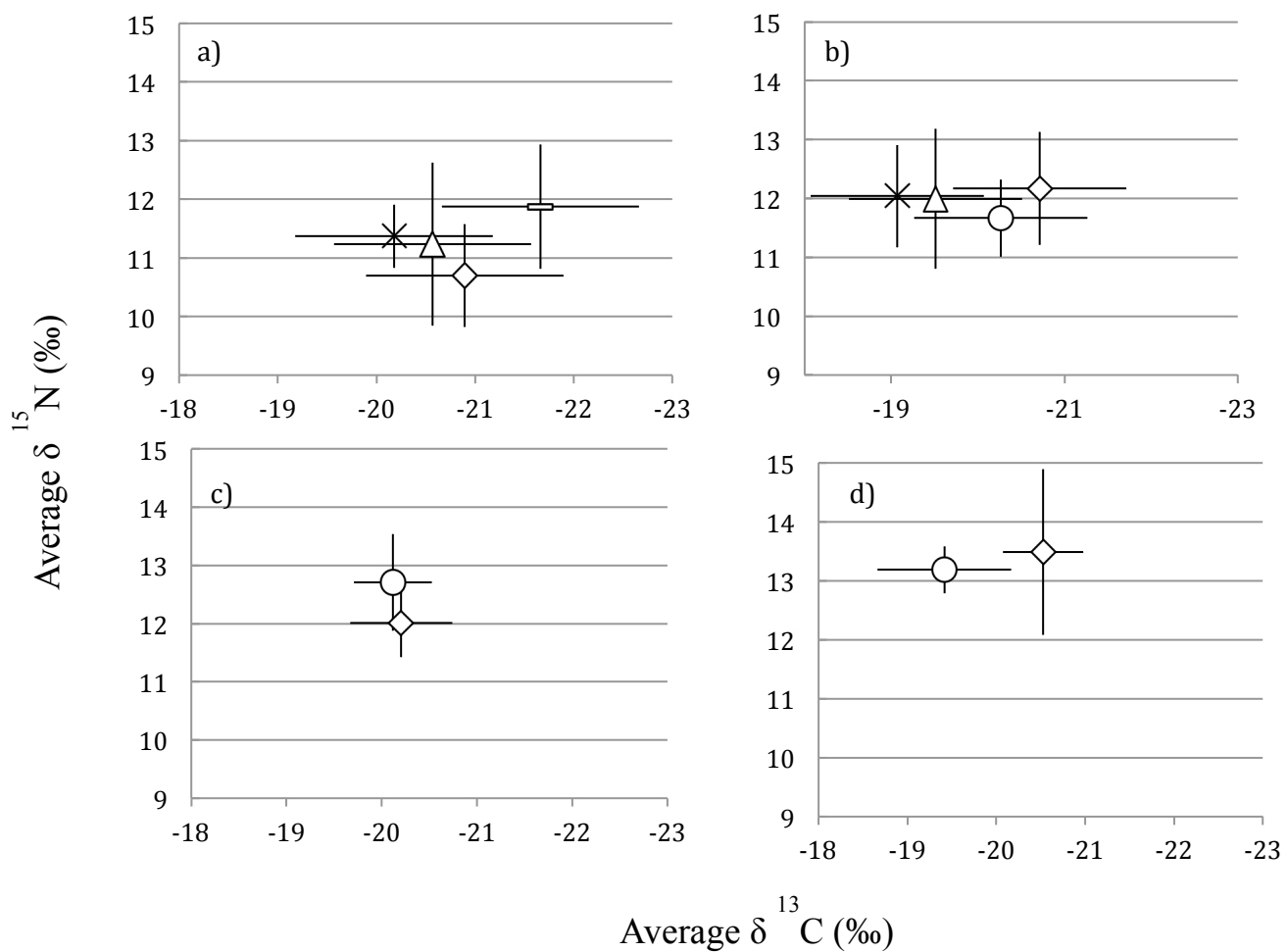


Figure 6.3. Mean and standard deviations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for *R. palpebrosa* by maturity stage: (a) hatchling, (b) immature, (c) maturing and (d) mature. Symbols represent locations as described in Chapter 5 (\diamond Baffin Bay/Greenland, - Baffin Island (new location), \triangle Hudson Strait, \times Ungava Bay, \square St. Lawrence, and Beaufort Sea $*$).

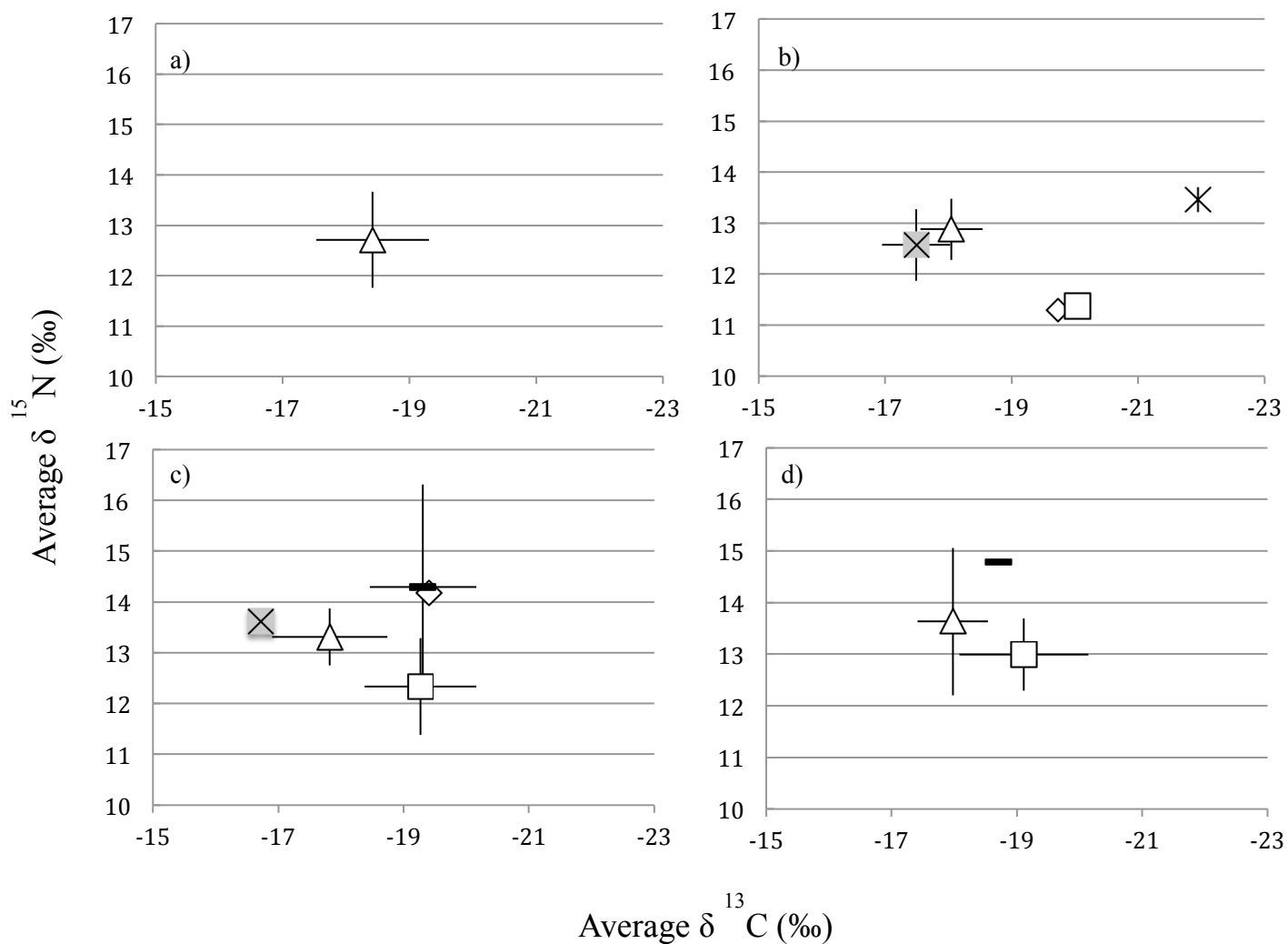


Figure 6.4. Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for *Bathypolypus* spp. by maturity stage: (a) immature, (b) maturing and (c) mature; and by species (*B. arcticus* = black symbols, *B. pugniger* = light grey symbols, *B. bairdii* = dark grey symbols and *Bathypolypus* sp. = open symbols). Symbols represent locations as described in Chapter 5 (\diamond Baffin Bay/Greenland, \triangle Hudson Strait, \times Ungava Bay, and \square St. Lawrence).

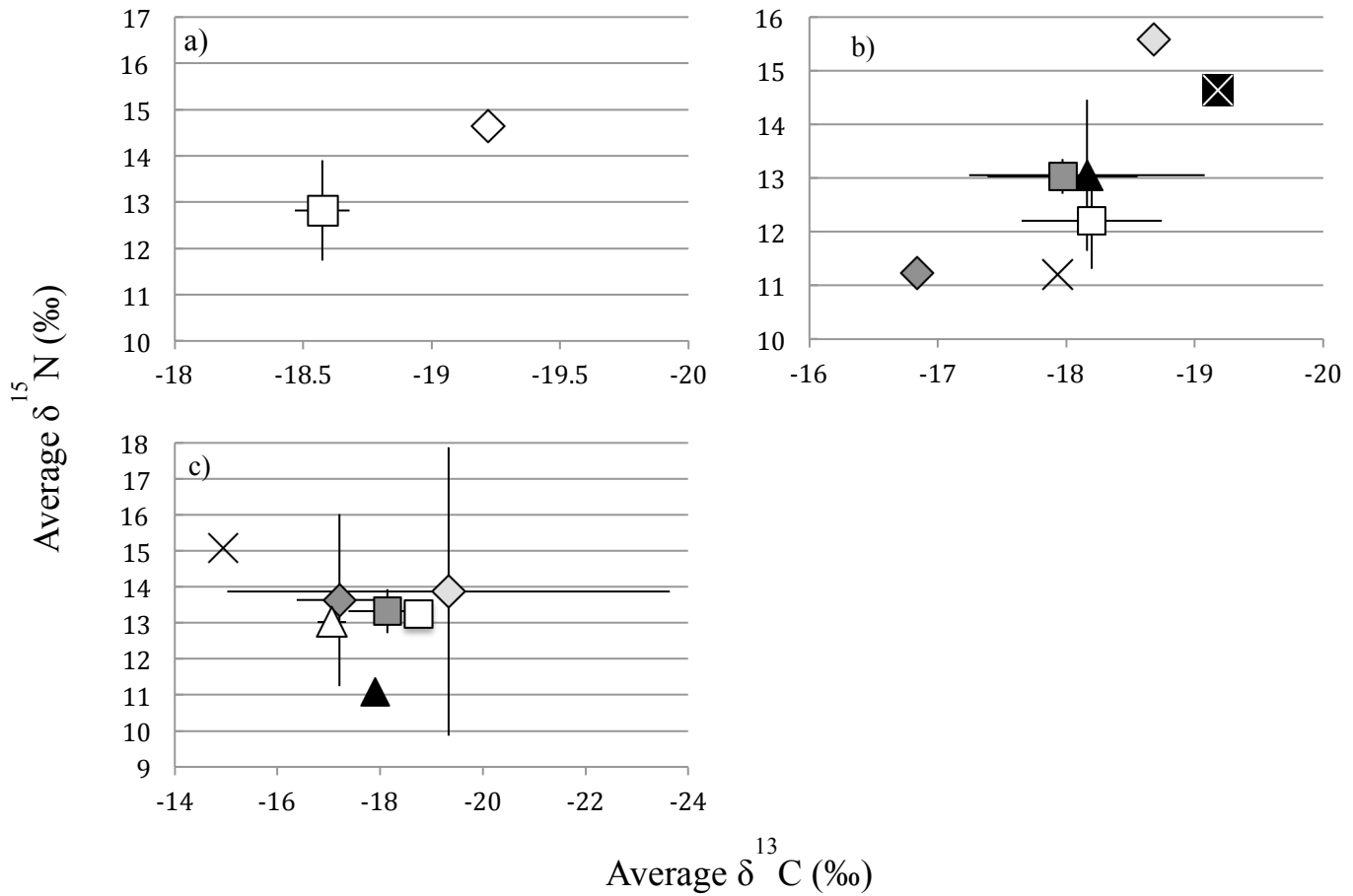


Figure 6.5. Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and their standard deviations for *C. muelleri* by maturity stage (\diamond immature, \triangle maturing and \square mature). Note: *C. muelleri* was only caught in the Baffin Bay/Greenland location.

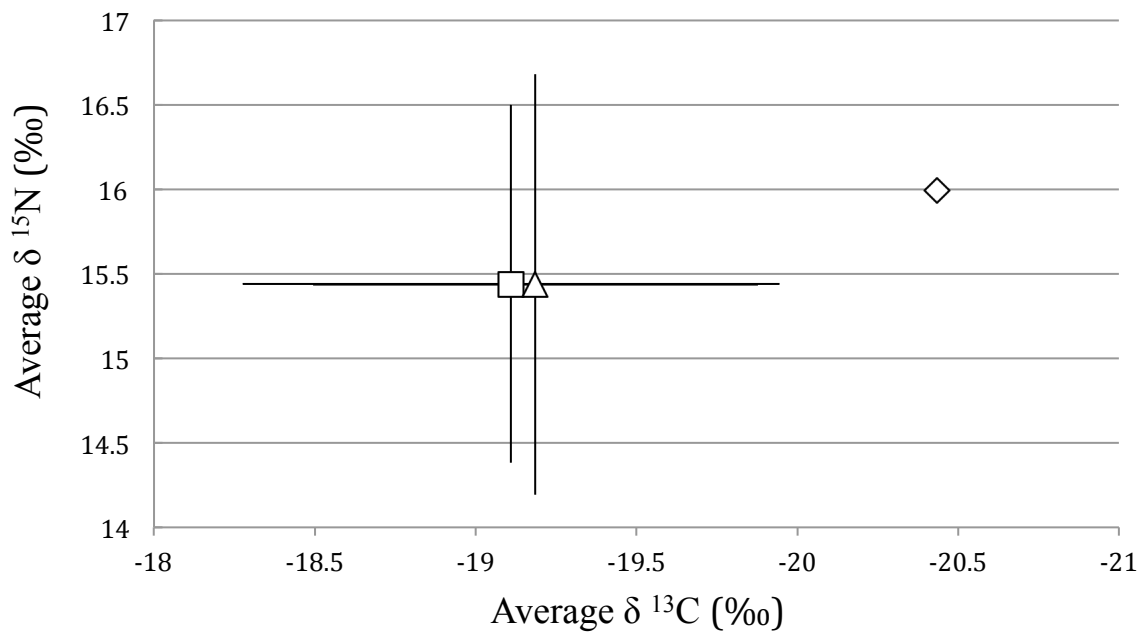
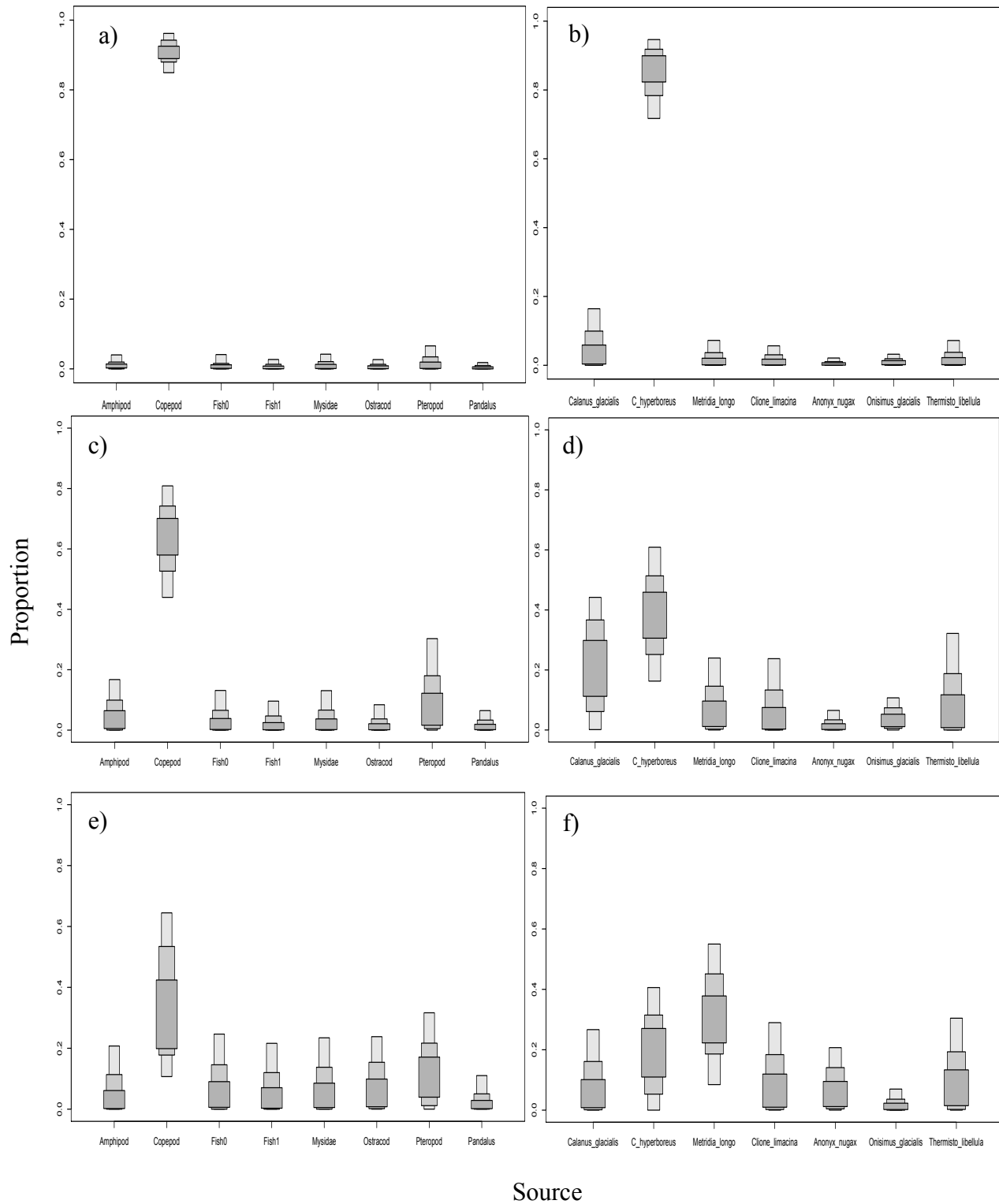


Figure 6.6. Percent occurrence of prey items in the stomachs of *G. fabricii* per sample location and size range (a = 2, b = 3, c = 4 and d = 5).

Figure 6.7. Boxplots of mixing model results of potential prey of size 2 *G. fabricii*: a) Baffin/Greenland general prey groups, b) Baffin/Greenland detailed prey species, c) Hudson Strait general prey groups, d) Hudson Strait detailed prey species, e) Ungava Bay general prey groups and f) Ungava Bay detailed prey species.



Source

Figure 6.8. Boxplots of mixing model results of potential prey of size 3 *G. fabricii*: a) Baffin/Greenland general prey groups, b) Baffin/Greenland detailed prey species, c) Disko Bay general prey groups, d) Disko Bay detailed prey species, e) Hudson Strait general prey groups, f) Hudson Strait detailed prey species, g) Ungava Bay general prey groups and h) Ungava Bay detailed prey species.

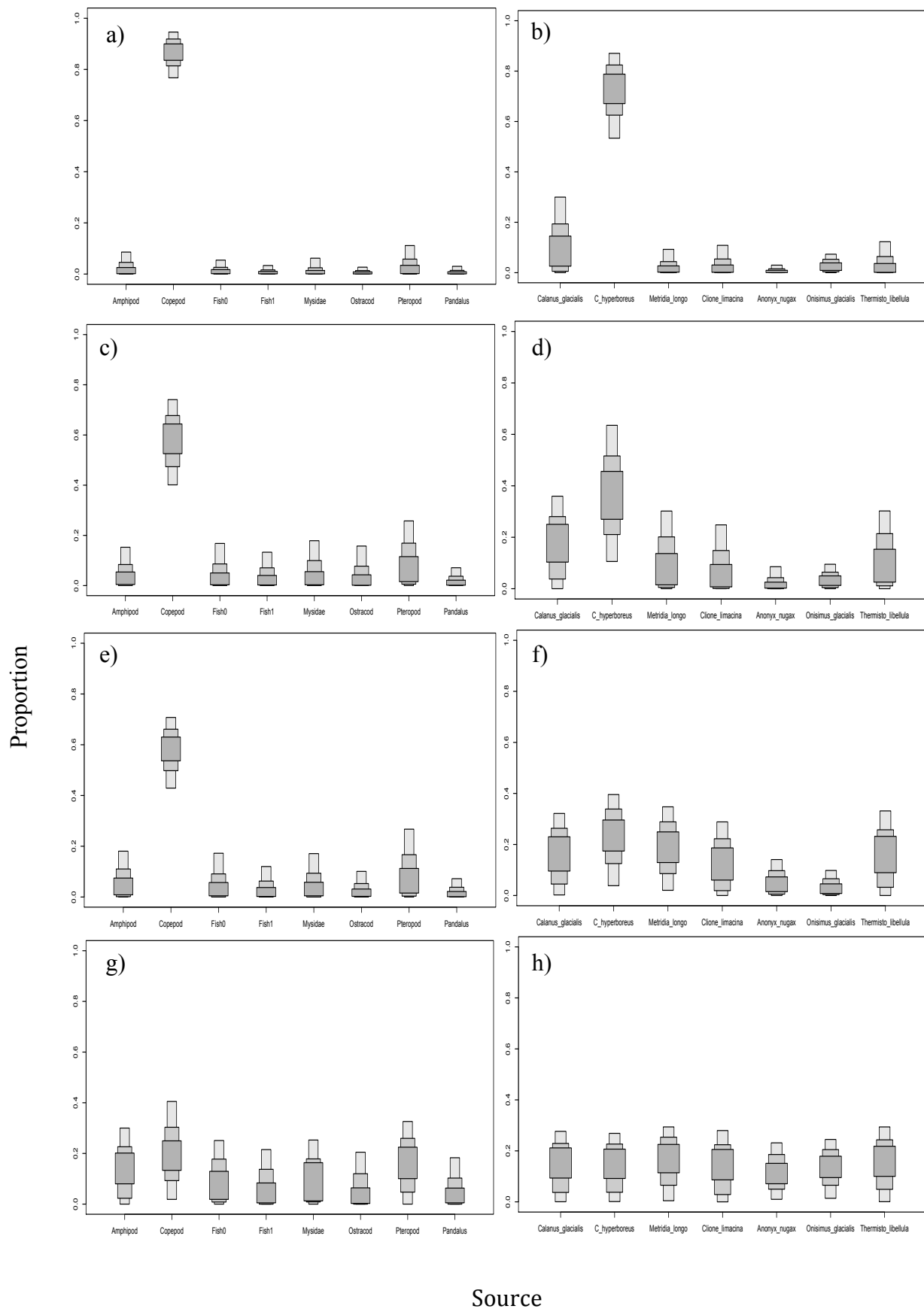


Figure 6.9. Boxplots of mixing model results of potential prey of *Gonatus fabricii* from a) Baffin/Greenland (size 4) general prey, b) Baffin/Greenland (size 4) detailed prey species, c) Disko Bay (size 4) general prey, d) Disko Bay (size 4) detailed prey species, e) Baffin/Greenland (size 5) general prey, f) Baffin/Greenland (size 5) detailed prey species, g) Disko Bay (size 5) general prey and h) Disko Bay (size 5) detailed prey species.

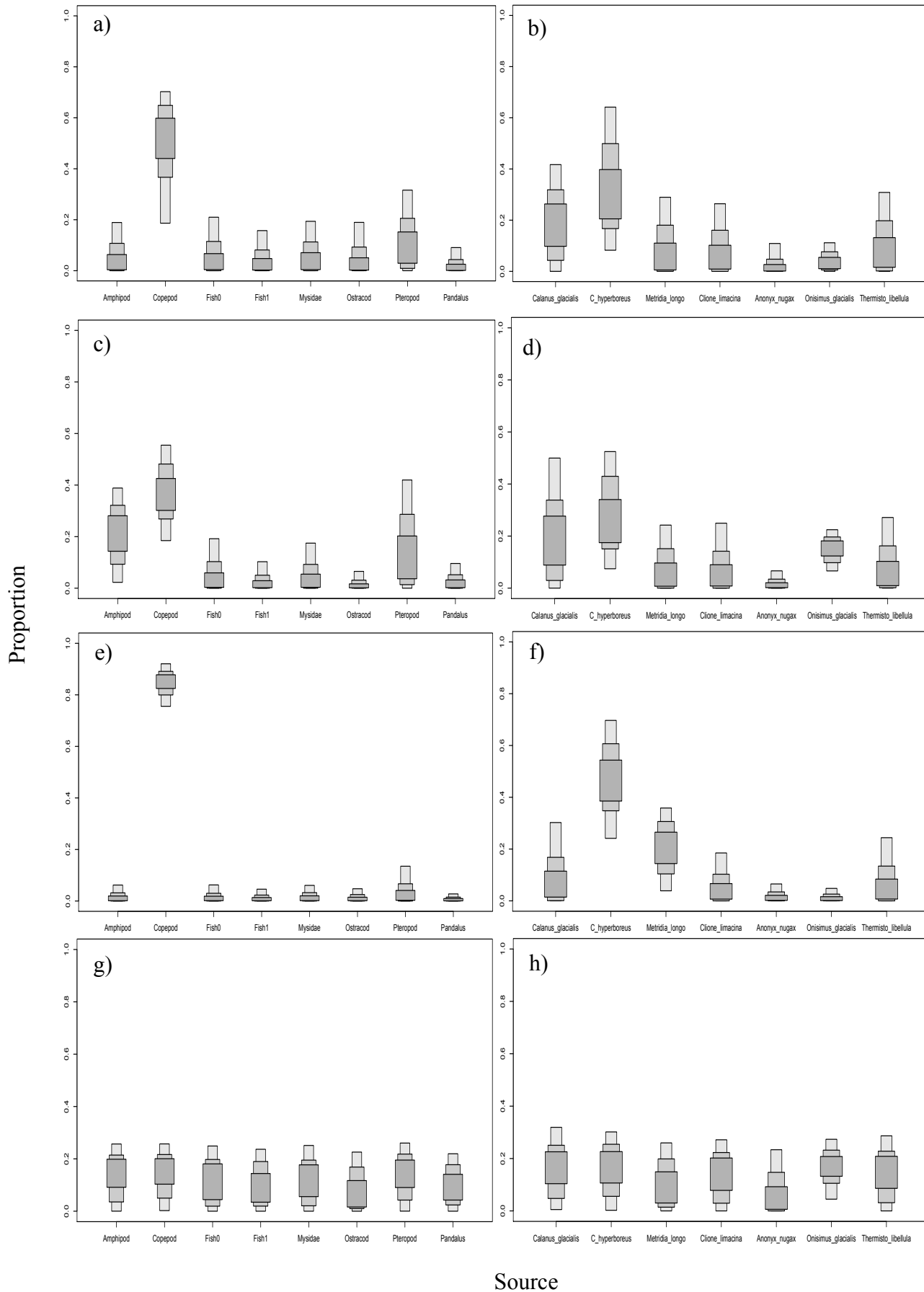


Figure 6.10. Percent occurrence of prey items in the stomachs of *R. palpebrosa* per sample location and maturity stage (a = hatchling, b = immature, c = maturing, d = mature)

Figure 6.11. Boxplots of mixing model results of potential prey of Arctic *R. palpebrosa*: a) Hudson Strait (hatchling), b) Baffin/Greenland (immature), c) Hudson Strait (immature), d) Ungava Bay (immature), e) Baffin/Greenland (maturing), f) Baffin Island (maturing), g) Hudson Strait (maturing), h) Ungava Bay (maturing), i) Baffin Island (mature) and j) Hudson Strait (mature).

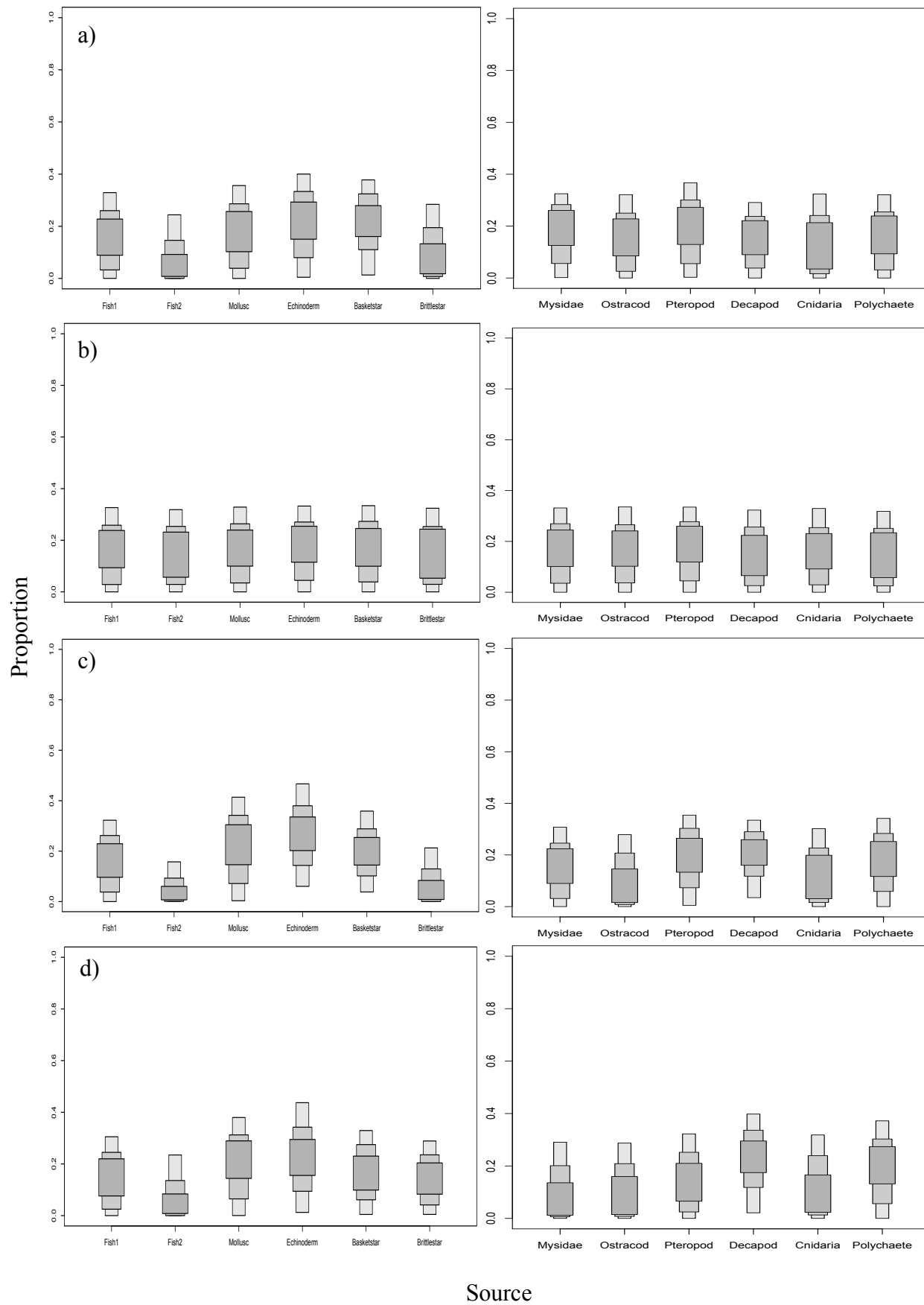
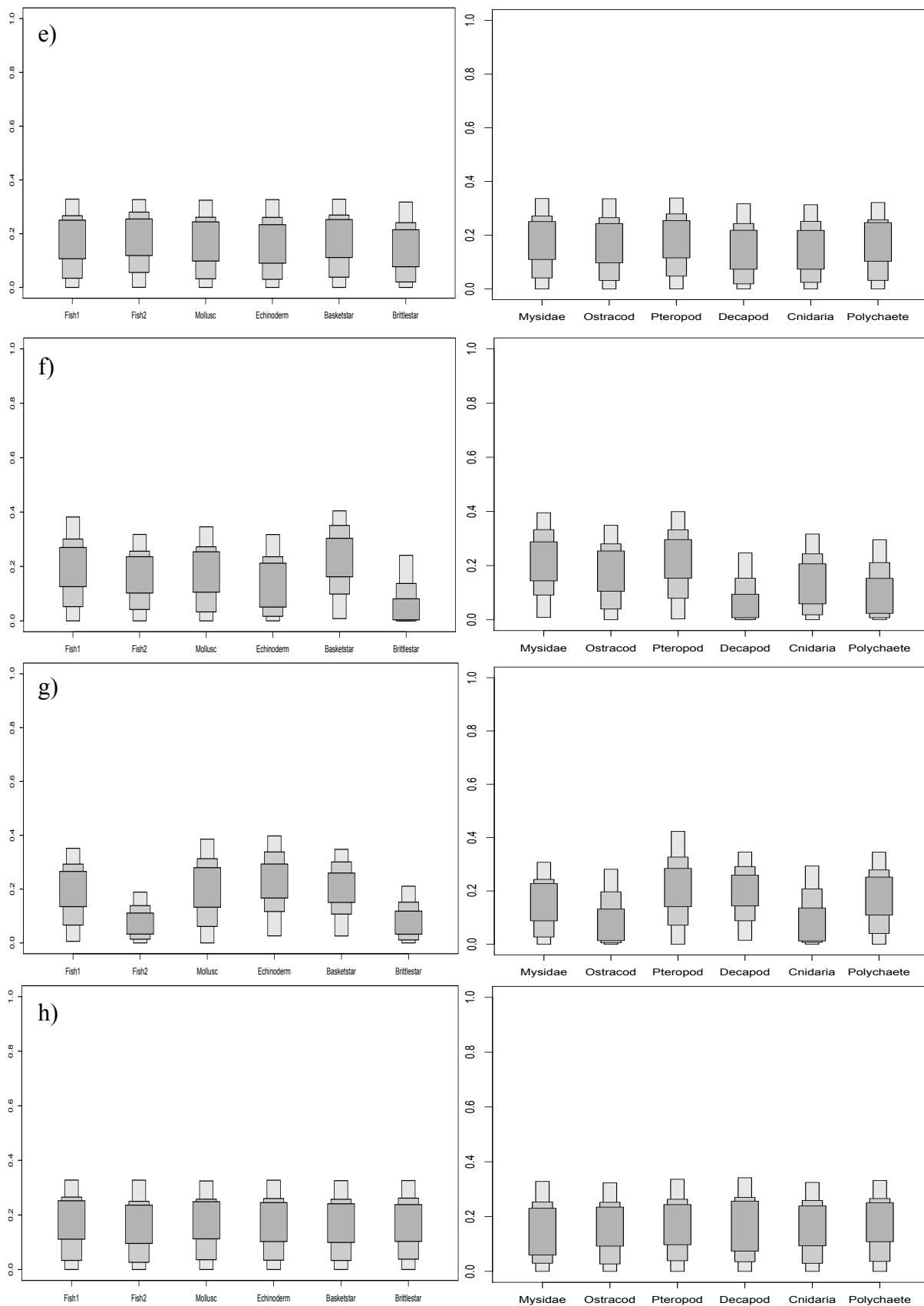


Figure 6.11 (Cont'd)

Proportion



Source

Figure 6.11 (Cont'd)

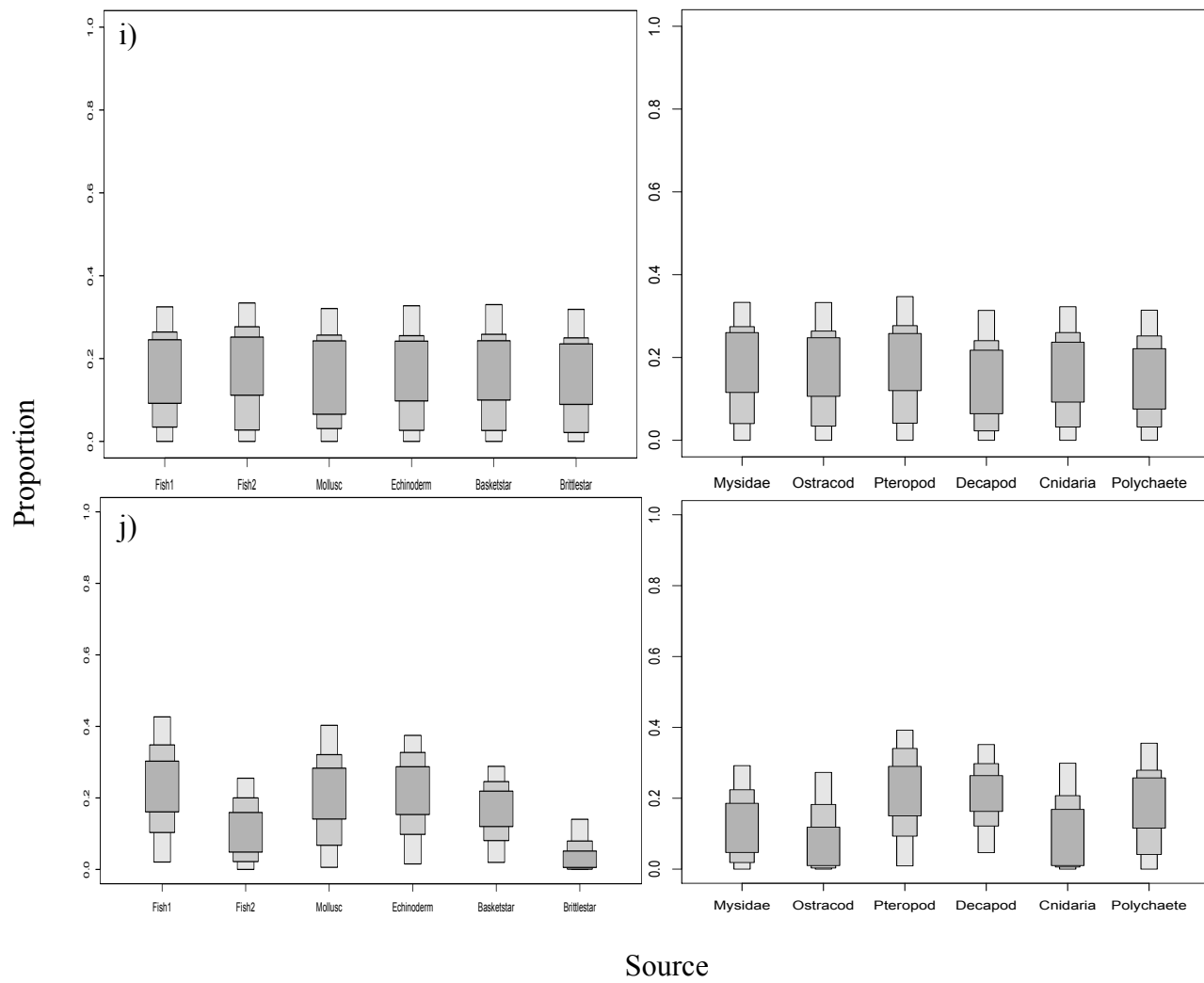


Figure 6.12. Boxplots of mixing model results of potential prey of St. Lawrence region *R. palpebrosa*: a) immature, b) maturing and c) mature.

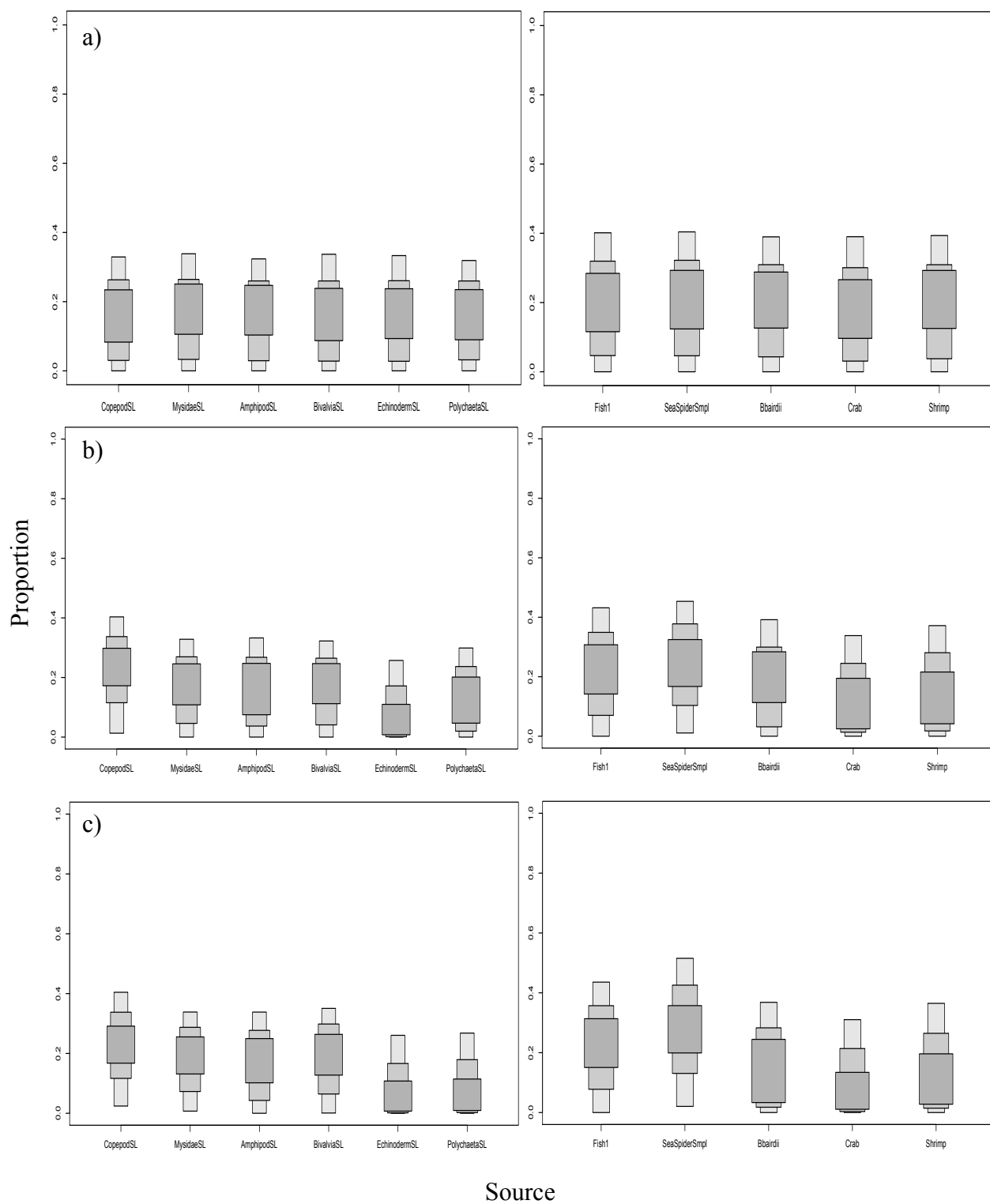


Figure 6.13. Percent occurrence of prey items in stomach contents of *B. bairdii* per sample location and maturity stage.

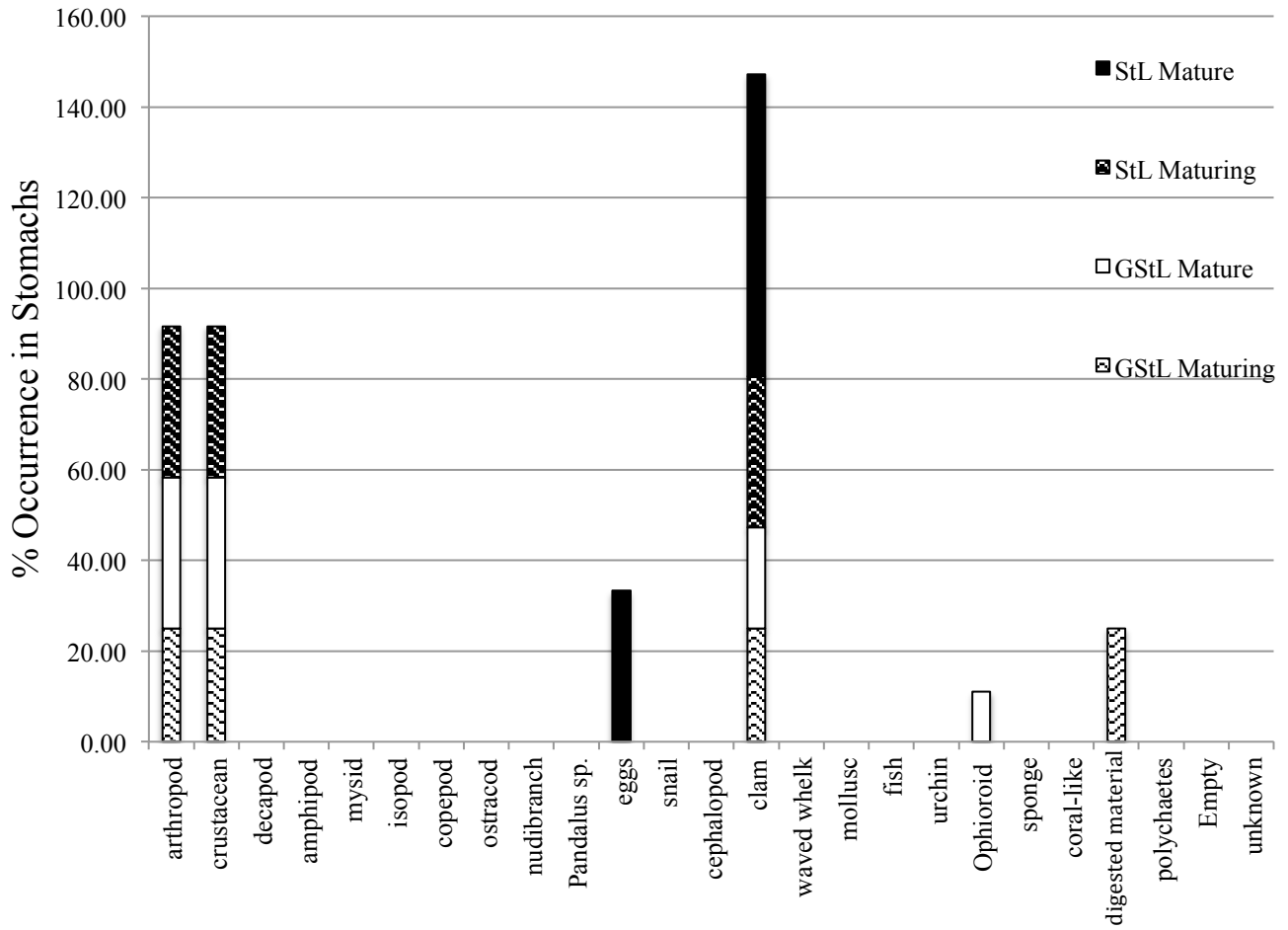


Figure 6.14. Boxplots of mixing model results of potential prey of Arctic *Bathypolypus* spp.: a) immature *Bathypolypus* sp. (Baffin/Greenland), b) maturing *B. bairdii* (Baffin/Greenland), c) maturing *B. pugniger* (Baffin/Greenland), d) maturing *B. arcticus* (Ungava Bay), e) maturing *Bathypolypus* sp. (Ungava Bay), f) mature *B. bairdii* (Baffin/Greenland), g) mature *B. pugniger* (Baffin/Greenland), h) mature *Bathypolypus* sp. (Hudson Strait) and i) mature *Bathypolypus* sp. (Ungava Bay).

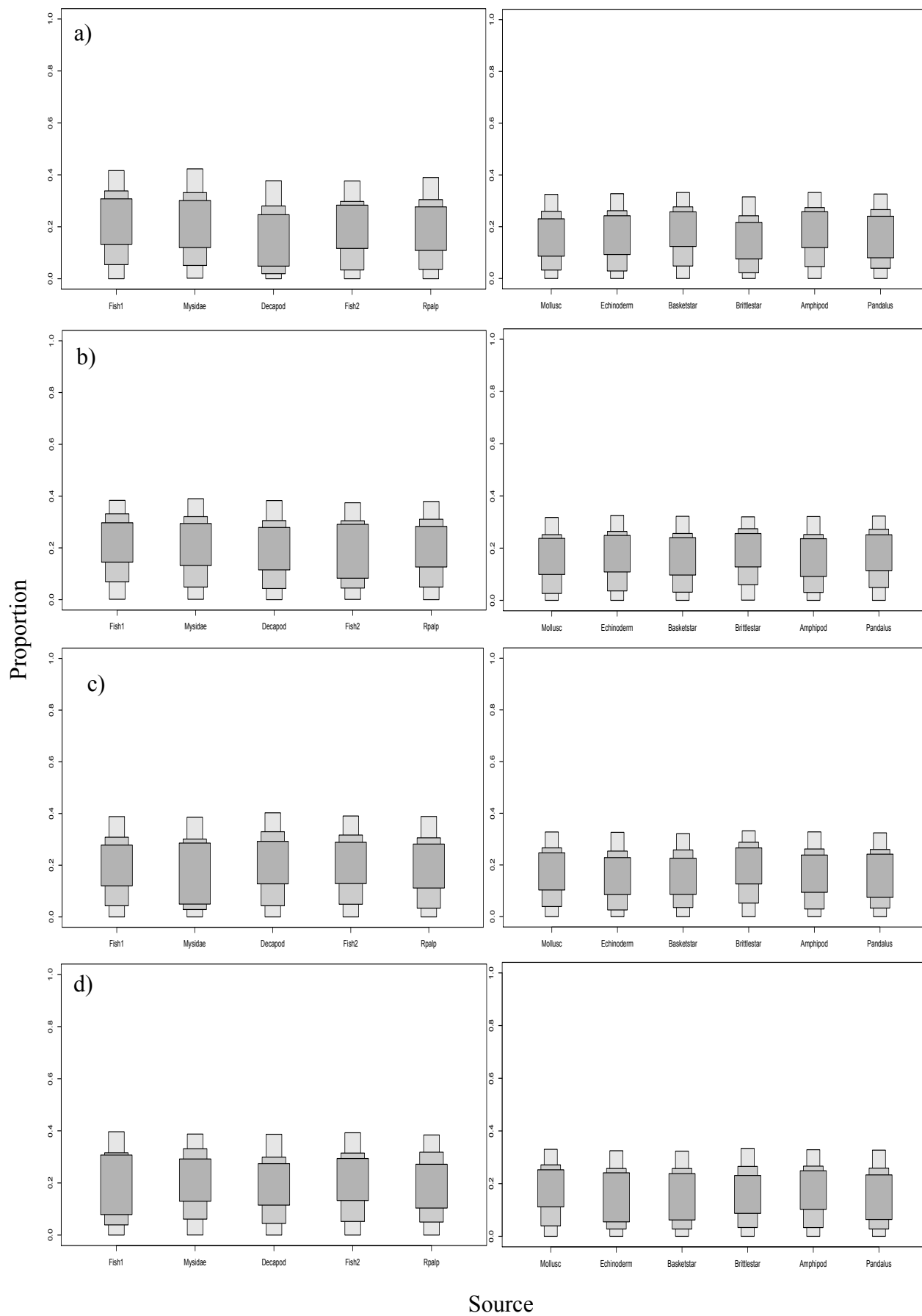


Figure 6.14 (Cont'd)

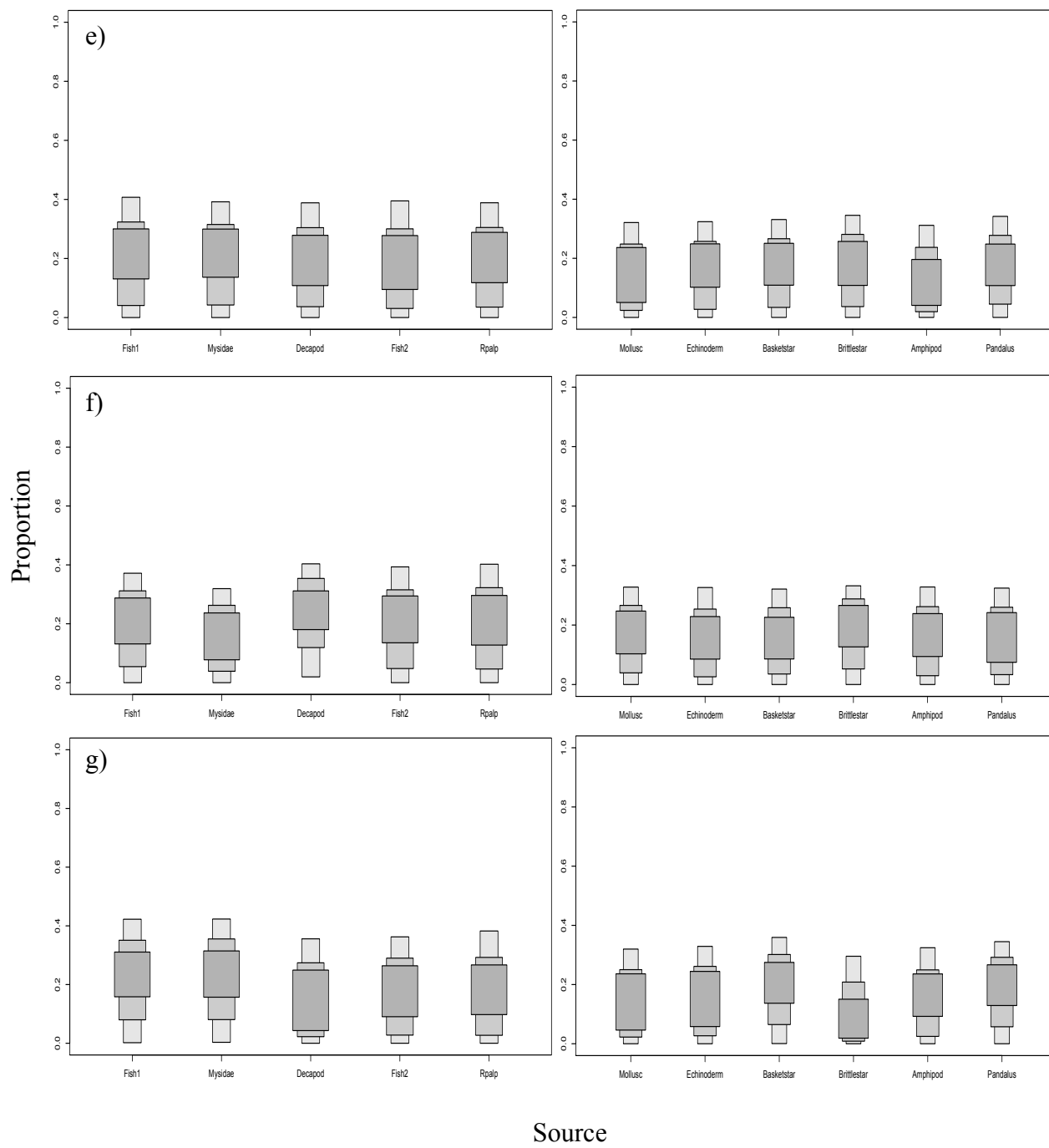


Figure 6.14 (Cont'd)

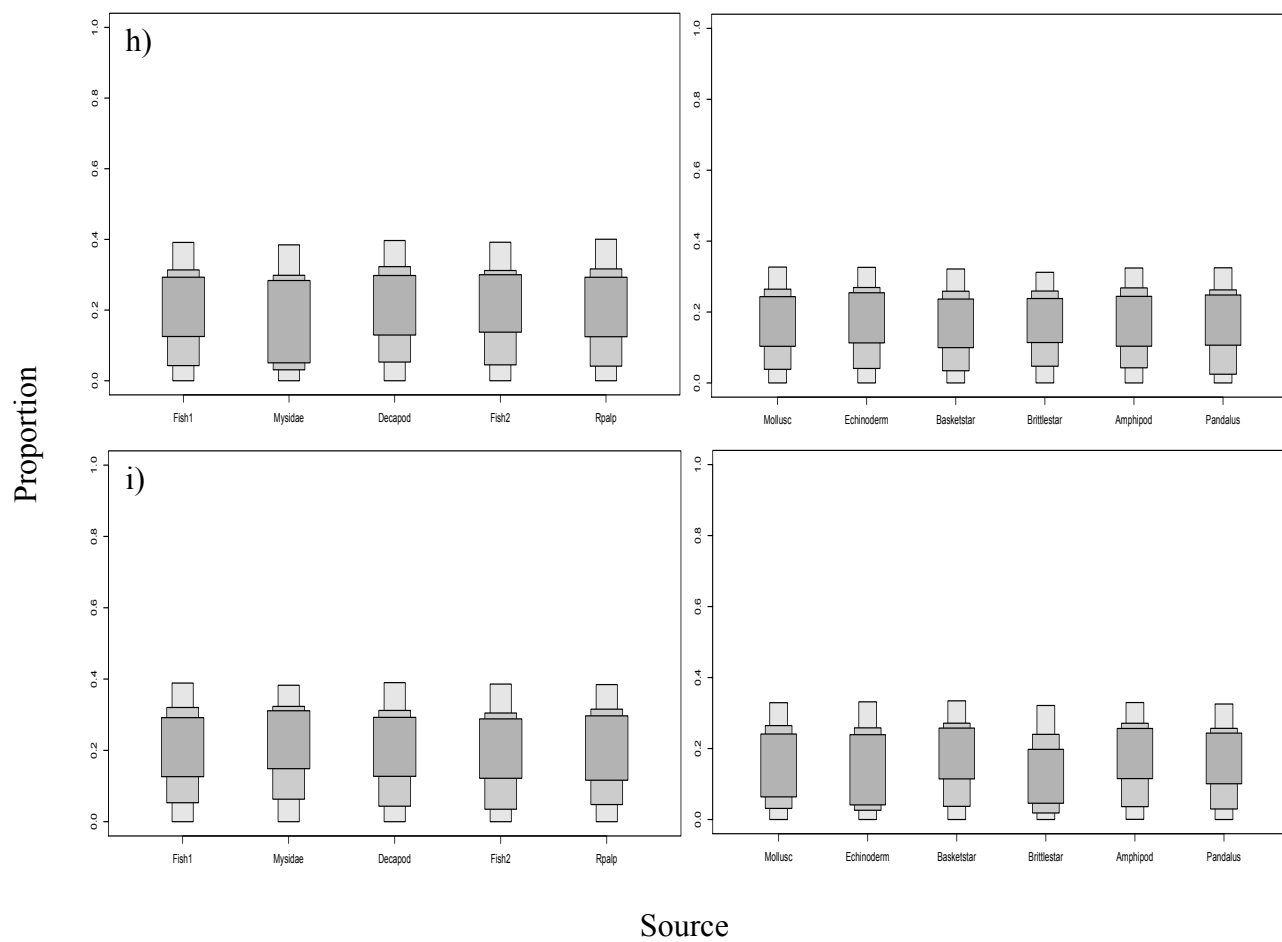


Figure 6.15. Boxplots of mixing model results of potential prey of St. Lawrence *Bathypolypus* spp.: a) *Bathypolypus* sp. immature, b) *B. bairdii* maturing, c) *Bathypolypus* sp. maturing, d) *B. bairdii* mature and e) *Bathypolypus* sp. mature.

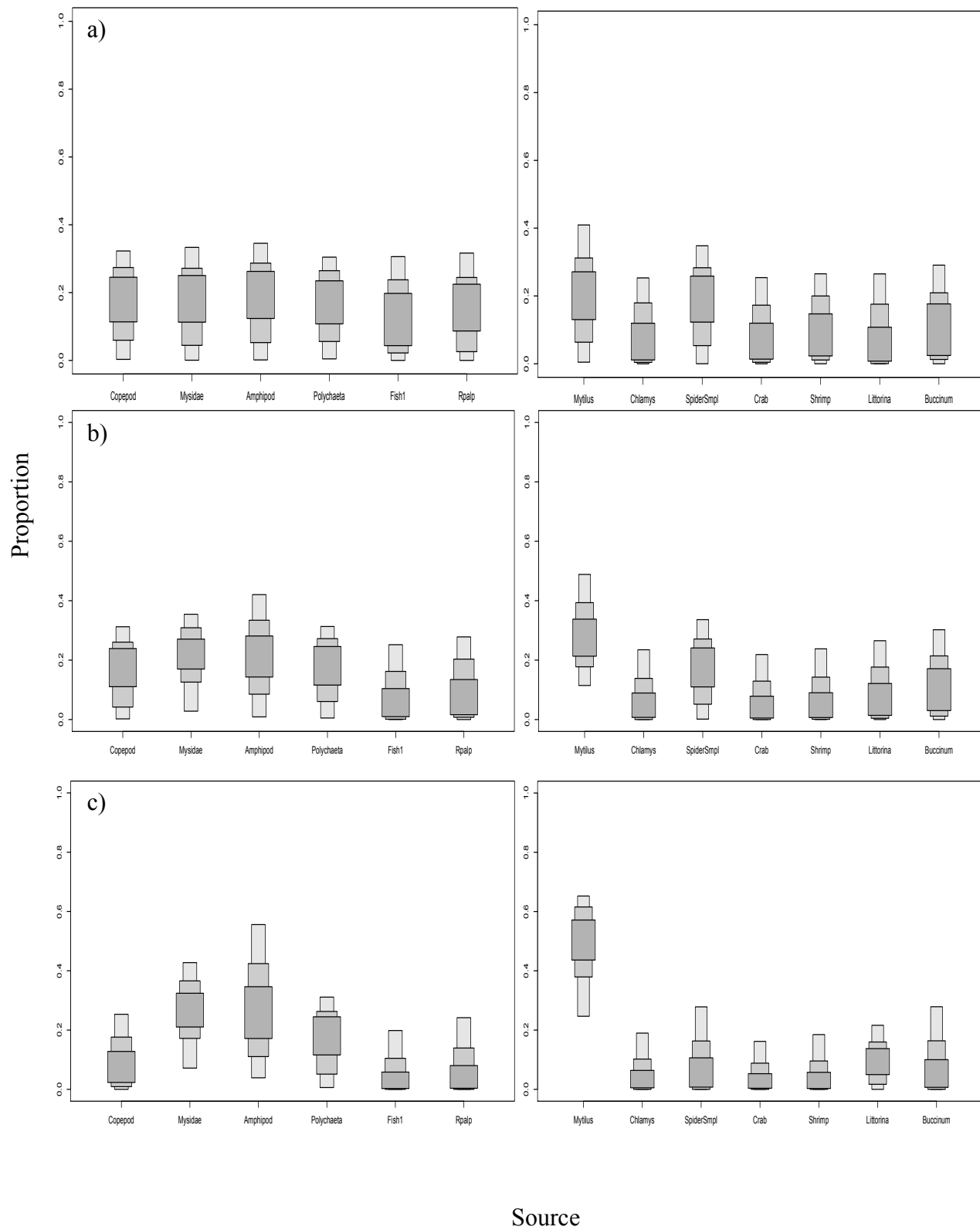


Figure 6.15 (Cont'd)

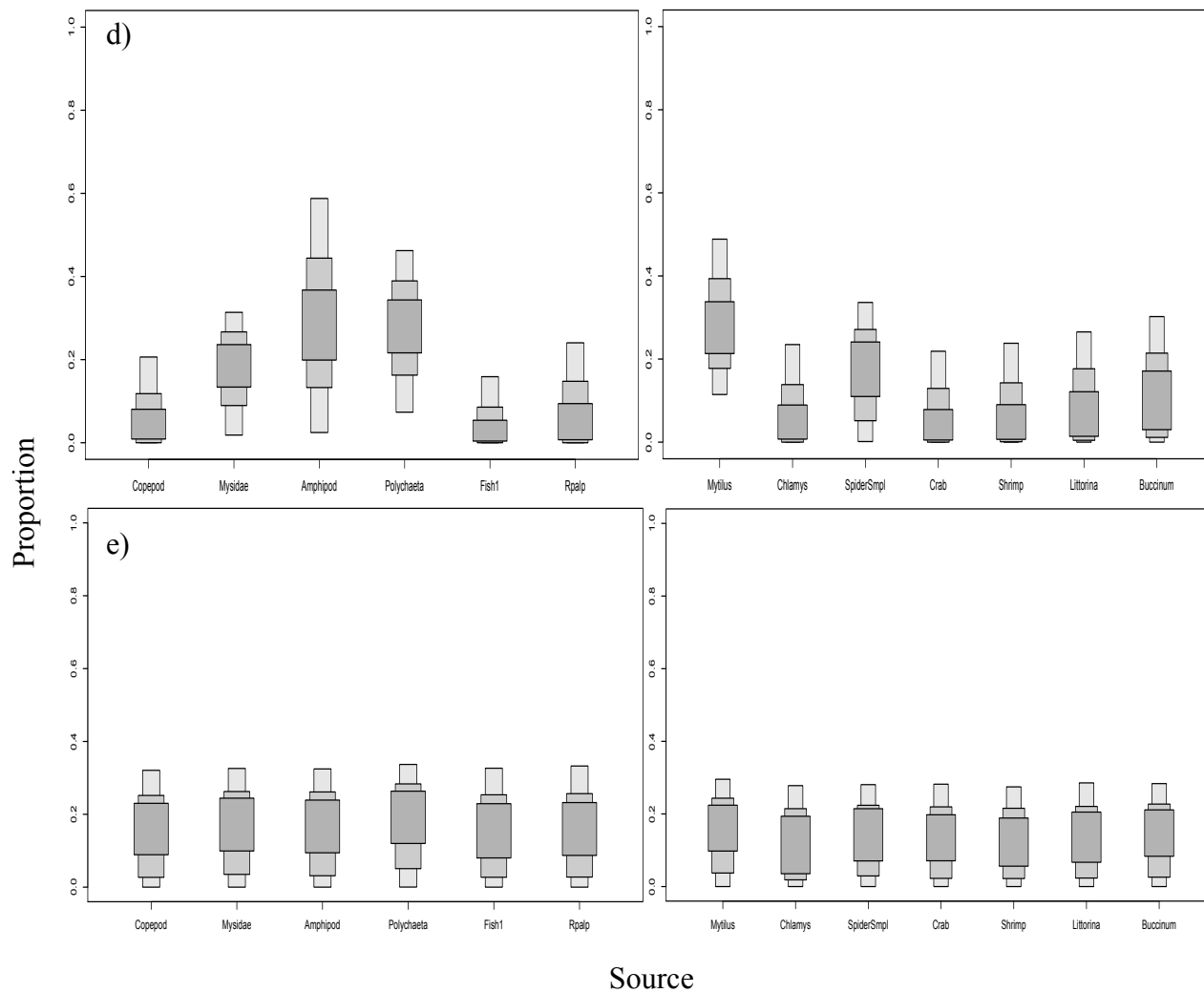


Figure 6.16. Percent occurrence of prey items in the stomachs of *C. muelleri* from Baffin Bay by maturity stage (□ immature, ■ maturing, and ■ mature).

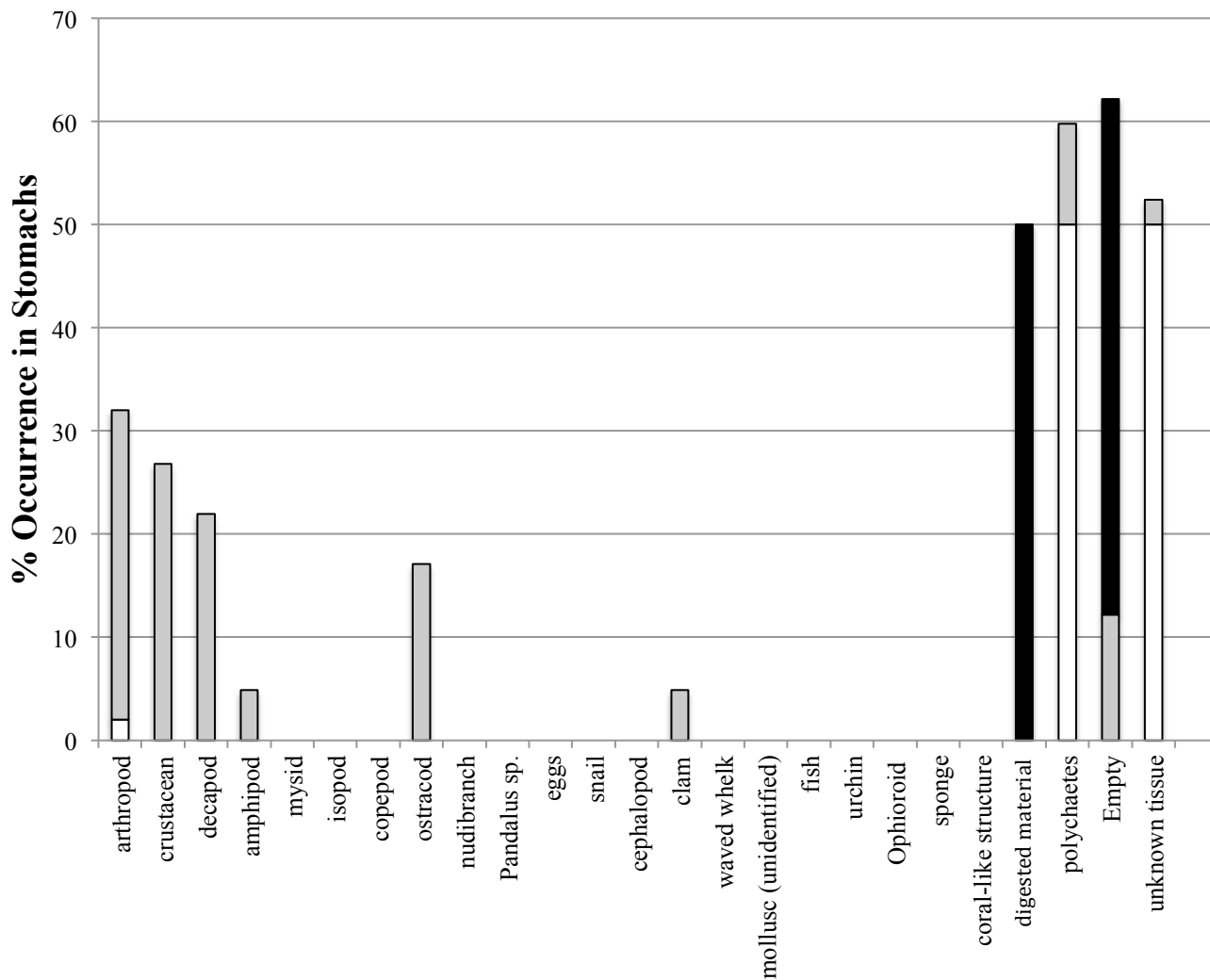
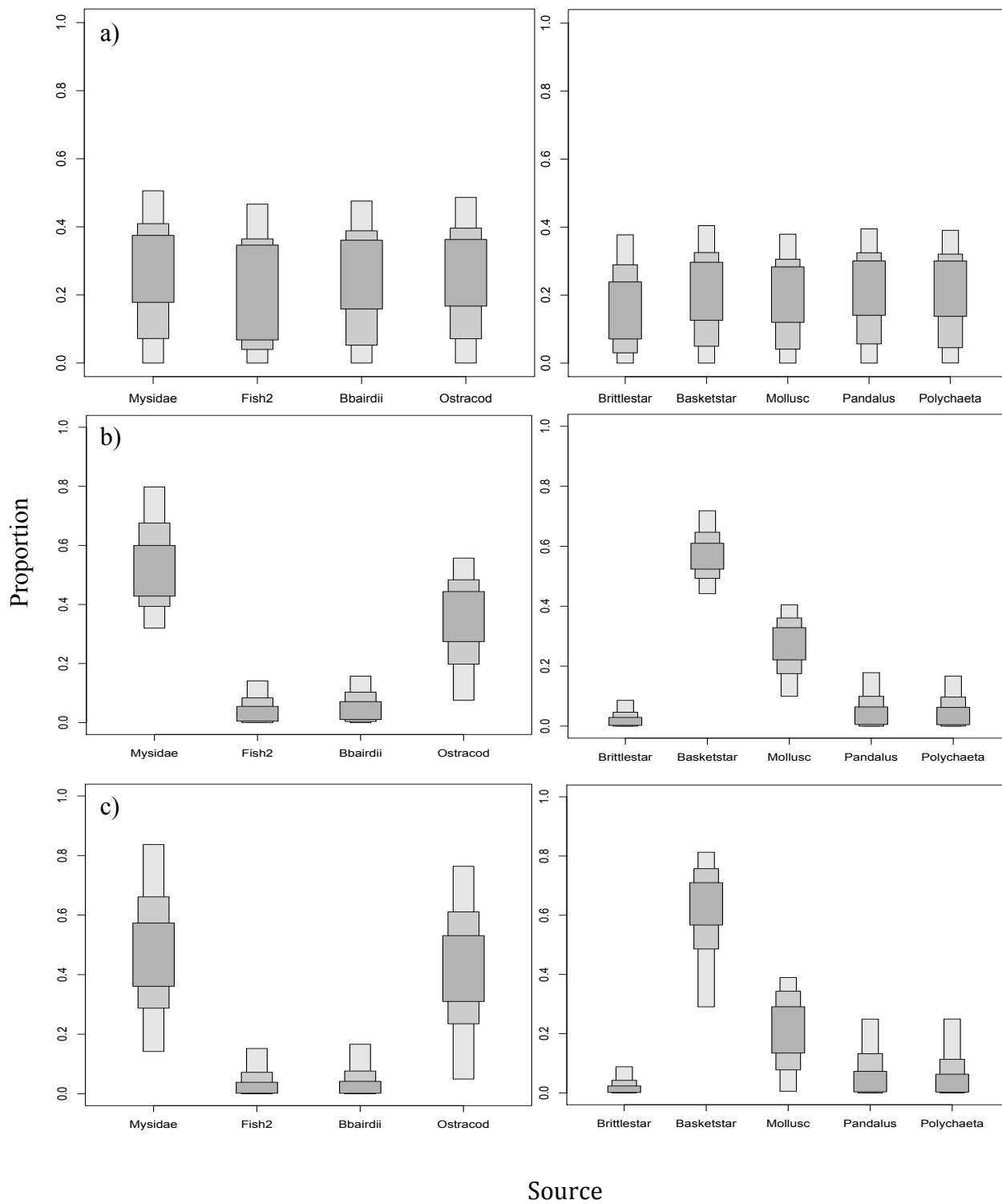


Figure 6.17. Boxplots of mixing model results of potential prey of *C. muelleri*: a) immature, b) maturing and c) mature *Cirroteuthis muelleri*.



Thesis Summary

This thesis examined the ecological role of cephalopods within the Canadian Arctic. The distribution of cephalopods throughout the circumpolar region with an emphasis on the Canadian Arctic was determined, the most common species identified and areas of historically high concentrations documented (Chapter 4). Data was acquired from a variety of sources including historical literature, refereed journals, fishery surveys and museum collections. The five most common species to the Canadian Arctic were the pelagic *G. fabricii*, the neritic *R. moelleri* and *R. palpebrosa*, the benthic-neritic octopus *B. arcticus* (considered a species complex including two additional species: *B. bairdii* and *B. pugnifer*) and the abyssal-pelagic cirrate octopus *C. muelleri*. Areas of interest included southwest Greenland, Disko Bay (Greenland), Hell's Gate polynya (separating Devon and Ellesmere Islands), Pond Inlet (NU) and eastern Hudson Strait for *G. fabricii*; Ellesmere Island and Franklin Bay (Beaufort Sea) for *R. moelleri*; Hudson Strait and Davis Strait for *R. palpebrosa*; north and southern extents of Baffin Bay for *B. arcticus*; and northern Baffin Bay and along the eastern edge of Baffin Island for *C. muelleri*. Chapter 4 also compiled data from literature records of all Arctic teuthophagous predators, highlighting the species most reliant on cephalopods.

Traditional morphometric measurements in conjunction with multivariate analyses and DNA barcoding (COI) was used to examine biogeographic variation within two of the most common eastern Canadian Arctic species, *G. fabricii* and *R. palpebrosa* (Chapter 5). Principal component analyses (PCA) of the physical characteristics of *G. fabricii* identified four potential Canadian and Greenland Arctic populations: Hudson Strait, Ungava Bay, Baffin Bay/Greenland and Disko Bay (Greenland); with Hudson Strait individuals dividing further into two subgroups, E1 and E2 (hypothesis 5.1 - page 136). Although based on a small sample size, morphometry

was also useful in describing differences between *R. palpebrosa* from the St. Lawrence region to those from the Canadian/Greenland Arctic. The PCA results also provided insight into which morphometric characters were most associated with each grouping, which was then used to explain habitat and certain behavioural preferences of the species. By contrast, barcode DNA (COI) analyses for both species were unable to identify potential populations, highlighting the need for further development of cephalopod specific microsatellites and their associated primers, with an emphasis on Arctic species, to obtain a more precise analysis. Redundancy analyses (RDA) described how morphometric characters were impacted by the environmental variables of the different regions. For example, the RDA of *G. fabricii* corroborates that larger individuals are likely found offshore in deeper, colder water masses, which correlates with known vertical ontogenetic migrations. Potential isolating mechanisms were also discussed with Hudson Strait and Baffin Bay samples likely being separated by oceanographic currents (Hudson Bay and Labrador cross-current flow within Hudson Strait compared to West Greenland Current flow along western Baffin Bay/Greenland) and Ungava Bay and Disko Bay individuals likely isolated by salinity differences caused by terrestrial and glacial freshwater inputs. More refined genetic analyses along with potential tagging experiments will provide further insights into whether these groupings are true populations.

Stable isotope (SI) and traditional stomach content analyses were used to further define habitat and prey preferences of four of the common Arctic species: *G. fabricii*, *R. palpebrosa*, *Bathypolypus* spp. (all species combined) and *C. muelleri* ([Chapter 6](#)). Shifts in $\delta^{13}\text{C}$ indicated four distinct habitats of the species examined i.e. pelagic, neritic, bentho-neritic and abyssal-pelagic ([hypothesis 6.1](#) – page 197). Delta ^{13}C values also became less enriched with latitude ([hypothesis 6.1a](#) – page 198) and were lower in the pelagic regions than the neritic or benthic

zones (hypothesis 6.1b – page 198). *Bathypolypus* spp. had highly variable $\delta^{13}\text{C}$ values suggesting a wider distribution compared to the neritic *R. palpebroso* (hypothesis 6.1c – page 198). *C. muelleri* specimens, however, were found to have higher $\delta^{13}\text{C}$ values than the pelagic *G. fabricii* indicating a benthic carbon source (i.e. increased carbon values caused by bacterial and meiofaunal turnover) rather than the hypothesized pelagic marine snow source (6.1d – page 198). Changes in $\delta^{13}\text{C}$ highlighted ontogenetic shifts in habitat preferences while changes in $\delta^{15}\text{N}$ were associated with ontogenetic increases in prey quality (i.e. higher trophic level; hypothesis 6.2 – page 198). $\Delta^{15}\text{N}$ did not increase with latitude (i.e. with proximity to the North Water Polynya) (contrary to hypothesis 6.3 – page 198) but did provide insight into how habitats impact nitrogen enrichment (hypothesis 6.4 – page 199). Active *G. fabricii* had lower $\delta^{15}\text{N}$ values than the sit-and-wait octopuses, again highlighting the importance of the benthic ecosystem. Although stomach content analyses are difficult for cephalopods, several prey items could be discerned. Prey items for *G. fabricii* were similar regardless of size range with even the smallest *G. fabricii* size range (size 2) feeding on fish and showing potential cannibalism. *R. palpebroso* had the most varied stomach contents of the species examined, with evidence of mysids, nudibranchs, snails, fish and again, cephalopods noted. *Bathypolypus* spp. were initially thought to feed solely on ophiroids but those collected from the St. Lawrence showed a preference for clams, arthropods/crustaceans and unidentified eggs. While the mature *C. muelleri* specimens had highly digested stomach contents or empty stomachs all together, the sole maturing *C. muelleri* from Baffin Bay had evidence of decapods, ostracods, amphipods and clams in its stomach. Isotopic mixing models were applied in conjunction with stomach content analyses to gain a better insight into prey preferences of Arctic species, in particular lesser-studied species such as *R. palpebroso* and *C. muelleri*. The models were able to not only identify

known stomach contents, but also additional prey species, and often to a lower taxonomic designation than was possible from the initial stomach content observations (e.g. copepods in *G. fabricii* stomachs were likely *C. hyperboreus*; [hypothesis 6.5](#) – page 199). The mixing models also highlighted the importance of copepods throughout the life history of *G. fabricii* and the occurrence of intertidal mussels in the diet of St. Lawrence *Bathypolypus* spp. The first account of potential prey species for *C. muelleri* is also presented.

This thesis has shown that cephalopods are important components within the Canadian Arctic, provides significant baseline information on cephalopod species distributions and contributes to the knowledge of Arctic food webs. Shifts in species compositions, habitat preference, prey selection or overall distributions from the baseline data documented within this thesis may be used to help understand changes in a warming Arctic region.

References

- Academy of Natural Sciences Malacology Database. Online database accessed through Global Biodiversity Information Facility (GBIF) Data Portal at <http://data.gbif.org/datasets/resource/175> on 5 November 2007.
- Agnew, D. J., J. R. Beddington, and S. L. Hills. 2002. The potential use of environmental information to manage squid stocks. *Canadian Journal of Fisheries and Aquatic Science* **59**:1851-1857.
- Aksenov, Y. and A. C. Coward. 2001. The Arctic Ocean circulation as simulated in a very high-resolution global ocean model (OCCAM). *Annals of Glaciology* **33**:567-576.
- Albertin, C. B., L. Bonnaud, C. T. Brown, W. J. Crookes-Goodson, R. R. da Fonseca, C. Di Cristo, B. P. Dilkes, E. Edsinger-Gonzales, R.M. Jr. Freeman, R. T. Hanlon, K. M. Koenig, A. R. Lindgren, M. Q. Martindale, P. Minx, L. L. Moroz, M.-T. Nödl, S. V. Nyholm, A. Ogura, J. R. Pungor, J. J. C. Rosenthal, E. M. Schwarz, S. Shigeno, J. M. Strugnell, T. Wollesen, G. Zhang, and C. W. Ragsdale. 2012. Cephalopod genomics: A plan of strategies and organization. *Standards in Genomic Sciences* **7**:175-188.
- Albertin, C.B., O. Simikov, T. Mitros, Z.Y. Wang, J.R. Pungor, E. Edsinger-Gonzales, S. Brenner, C.W. Ragsdale, and D.S. Rokhsar. 2015. The octopus genome and the evolution of cephalopod neural and morphological novelties. *Nature* **524**: 220-224.
- Aldrich, F. A. and C. C. Lu. 1968. Report on the larva, eggs, and egg mass of *Rossia* sp. (Decapoda, Cephalopoda) from Bonavista Bay, Newfoundland. *Canadian Journal of Zoology* **46**:369-371.
- Allard, M. R. 1990. "Kinguk survey": exploratory survey for marine groundfish and invertebrates in Western Hudson Strait, Northern Hudson Bay: project report. Farocan Inc. and Unaaq Fisheries Inc.
- An, H.S., E.M. Kim, J.I. Myeong, and C.M. An. 2014. Isolation and characterization of polymorphic microsatellite markers from the Korean common squid *Todarodes pacificus* (Ommastrephidae). *Genes and Genomics* **36**(6): 727-732.
- Anderson, C. I. H. and P. G. Rodhouse. 2001. Life cycles, oceanography and variability: ommastrephid squid in variable oceanographic conditions. *Fisheries Research* **54**:133-143.
- Anderson, R. C. 2012. *Rossia pacifica*, Stubby Squid. The Cephalopod Page. Accessed at <http://www.thecephalopodpage.org/Rpacificapacific.php>.
- André, J., M. Haddon, and G. Pecl. 2010. Modelling climate-change-induced nonlinear thresholds in cephalopod population dynamics. *Global Change Biology* **16**:2866-2875.

- Arkhipkin, A. and H. Bjørke. 1999. Ontogenetic changes in morphometric and reproductive indices of the squid *Gonatus fabricii* (Oegopsida, Gonatidae) in the Norwegian Sea. *Polar Biology* **22**:357-365.
- Arkhipkin, A. I. 2004. Diversity in growth and longevity in short-lived animals: squid of the suborder Oegopsina. *Marine and Freshwater Research* **55**:341-355.
- Arkhipkin, A. I. 2005. Statoliths as 'black boxes' (life recorders) in squid. *Marine and Freshwater Research* **56**:573-583.
- Arkhipkin, A. I. and H. Bjørke. 2000. Statolith shape and microstructure as indicators of ontogenetic shifts in the squid *Gonatus fabricii* (Oegopsida, Gonatidae) from the Norwegian Sea. *Polar Biology* **23**:1-10.
- Arrington, D. A. and K. O. Winemiller. 2002. Preservation effects on stable isotope analysis of fish muscle. *Transactions of the American Fisheries Society* **131**:337-342.
- Atlantic Reference Centre. Online database accessed through Global Biodiversity Information Facility (GBIF) Data Portal at <http://data.gbif.org/datasets/resource/341> on 5 November 2007.
- Atkinson, E. G. and J. W. Wacasey. 1989. Benthic invertebrates collected from the western Canadian Arctic, 1951 to 1985. Canadian Data Report of Fisheries and Aquatic Sciences **745**. Department of Fisheries and the Environment, Fisheries and Marine Service, Winnipeg.
- Bakun, A. and J. Csirke. 1998. Environmental processes and recruitment variability. FAO Fisheries Technical Paper. **376**: 105-124.
- Barber, D. G. and R. A. Massom. 2007. The role of sea ice in Arctic and Antarctic polynyas. Pages 1-54 in W. O. Smith and D. G. Barber, editors. *Polynyas - Windows to the World*. Elsevier Oceanography Series, Amsterdam.
- Barnes, C., S. Jennings, and J. T. Barry. 2009. Environmental correlates of large-scale spatial variation in the $\delta^{13}\text{C}$ of marine animals. *Estuarine, Coastal and Shelf Science* **81**:368-374.
- Barrett, R. T., V. Bakken, and J. V. Krasnov. 1997. The diets of common and Brunnich's guillemots *Uria aalge* and *U. lomvia* in the Barents Sea region. *Polar Research* **16**:73-84.
- Belkin, I. M. 2009. Rapid warming of large marine ecosystems. *Progress in Oceanography* **81**:207-213.
- Ben-David, M. and E. A. Flaherty. 2012. Stable isotopes in mammalian research: a beginner's guide. *Journal of Mammology* **93**:312-328.

- Benoit, D., Y. Simard, J. Gagne, M. Geoffroy, and L. Fortier. 2010. From polar night to midnight sun: photoperiod, seal predation, and the diel vertical migrations of polar cod (*Boreogadus saida*) under landfast ice in the Arctic Ocean. *Polar Biology* **33**:1505-1520.
- Benton, A. H. and W. E. J. Werner. 1974. Ecological energetics: The flow of energy through ecosystems. Page 564 *Field Biology and Ecology*. McGraw-Hill Book Company, New York.
- Berry, S. S. 1912. A review of the cephalopods of western North America. *Bulletin of the Bureau of Fisheries* **30**:269-336.
- Berry, S. S. 1925. The cephalopoda collected by the Canadian Arctic Expedition, 1913-18. *Report of the Canadian Arctic Expedition 1913-18* **8B**:3-8.
- Bettencourt, V. and A. Guerra. 2000. Growth increments and biomineralization process in cephalopod statoliths. *Journal of Experimental Marine Biology and Ecology* **248**:191-205.
- Bjørke, H. 2001. Predators of squid *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea. *Fisheries Research* **52**:113-120.
- Boletzky, S. 1994. Embryonic development of cephalopods at low temperatures. *Antarctic Science* **6**:139-142.
- Boletzky, S. v. 1996. Cephalopods burying in soft substrata: agents of bioturbation? *Marine Ecology* **17**:77-86.
- Bonnaud, L., R. Boucher-Rodoni, and M. Monnerot. 1997. Phylogeny of cephalopods inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* **7**:44-54.
- Bourdages, H., L. Savard, D. Archambault, and S. Valois. 2007. Results from the August 2004 and 2005 comparative fishing experiments in the northern Gulf of St. Lawrence between the CCGS Alfred Needler and the CCGS Teleost. *Canadian Technical Report of Fisheries and Aquatic Sciences* **2750**: ix +57p.
- Boyle, P. and P. Rodhouse. 2005a. Biodiversity and zoogeography. Pages 63-79 *in* P. Boyle and P. Rodhouse, editors. *Cephalopods, Ecology and Fisheries*. Blackwell Science Ltd, Oxford.
- Boyle, P. and P. Rodhouse. 2005b. Cephalopods as predators. Pages 222-233 *in* P. Boyle and P. Rodhouse, editors. *Cephalopods, Ecology and Fisheries*. Blackwell Science Ltd, Oxford.
- Boyle, P. and P. Rodhouse. 2005c. *Cephalopods, Ecology and Fisheries*. Blackwell Science Ltd., Oxford. Pp. 452.

- Boyle, P. and P. Rodhouse. 2005d. Coastal and shelf species. Pages 161-175 *in* P. Boyle and P. Rodhouse, editors. *Cephalopods, Ecology and Fisheries*. Blackwell Science Ltd., Oxford.
- Boyle, P. and P. Rodhouse. 2005e. Fishery Resources. Pages 277-295 *in* P. Boyle and P. Rodhouse, editors. *Cephalopods, Ecology and Fisheries*. Blackwell Science Ltd, Oxford.
- Boyle, P. and P. Rodhouse. 2005f. Form and Function. Pages 7-35 *in* P. Boyle and P. Rodhouse, editors. *Cephalopods, Ecology and Fisheries*. Blackwell Science Ltd, Oxford.
- Boyle, P. and P. Rodhouse. 2005g. Life Cycles. Pages 80-100 *in* P. Boyle and P. Rodhouse, editors. *Cephalopods, Ecology and Fisheries*. Blackwell Science Ltd, Oxford.
- Boyle, P. and P. Rodhouse. 2005h. Oceanic and deep-sea species. Pages 176-204 *in* P. Boyle and P. Rodhouse, editors. *Cephalopods, Ecology and Fisheries*. Blackwell Science Ltd, Oxford.
- Boyle, P. and P. Rodhouse. 2005i. Origin and evolution. Pages 36-49 *in* P. Boyle and P. Rodhouse, editors. *Cephalopods, Ecology and Fisheries*. Blackwell Science Ltd., Oxford.
- Boyle, P. and P. Rodhouse. 2005j. Physiological ecology. Pages 116-130 *in* P. Boyle and P. Rodhouse, editors. *Cephalopods, Ecology and Fisheries*. Blackwell Science Ltd, Oxford.
- Boyle, P. and P. Rodhouse. 2005k. Population Ecology. Pages 205-221 *in* P. Boyle and P. Rodhouse, editors. *Cephalopods, Ecology and Fisheries*. Blackwell Science Ltd, Oxford.
- Boyle, P. R. and S. v. Boletzky. 1996. Cephalopod populations: definition and dynamics. *Philosophical Transactions of the Royal Society B - Biological Sciences* **351**:985-1002.
- Brocco, S. L. 1971. Aspects of the biology of the sepiolid squid *Rossia pacifica* Berry. M.Sc. Thesis. University of Victoria, Victoria.
- Brown, R. G. B. and D. N. Nettleship. 1981. The biological significance of polynyas to arctic colonial seabirds. Pages 59-65 *in* I. Stirling and H. Cleator, editors. *Polynyas in the Canadian Arctic*. Canadian Wildlife Service **Occasional Paper 45**. Ottawa.
- Budelmann, B. U. 1990. Statocysts. Pages 421-436 *in* D.L. Gilbert, J. Adelman, and J.M. Arnold, editors. *Squid as Experimental Animals*. Springer Science and Business Media. New York.
- Byers, T., A. Smith, and M. L. Mallory. 2010. Diet of black guillemots and northern fulmars breeding beside a High Arctic polynya. *Polar Biology* **33**:457-467.
- Caddy, J. F. and P. G. Rodhouse. 1998. Cephalopod and groundfish landings: evidence for ecological change in global fisheries? *Reviews in Fish Biology and Fisheries* **8**:431-444.

- Carabel, S., E. Godínez-Domínguez, P. Verísimo, L. Fernández, and J. Freire. 2006. An assessment of sample processing methods for stable isotope analyses of marine food webs. *Journal of Experimental Marine Biology and Ecology* **336**:254-261.
- Carlini, D. B. 1998. The phylogeny of coleoid cephalopods inferred from molecular evolutionary analyses of the cytochrome C oxidase I, muscle actin, and cytoplasmic actin genes. PhD Thesis. The College of William and Mary in Virginia.
- Carmack, E. and P. Wassmann. 2006. Food webs and physical–biological coupling on pan-Arctic shelves: Unifying concepts and comprehensive perspectives. *Progress in Oceanography* **71**:446-477.
- Carmack, E. C. and R. W. Macdonald. 2002. Oceanography of the Canadian Shelf of the Beaufort Sea: A setting for marine life. *Arctic* **55**:29-45.
- Carvalho, G. R., A. Thompson, and A. L. Stoner. 1992. Genetic diversity and population differentiation of the shortfin squid *Illex argentinus* in the south-west Atlantic. *Journal of Experimental Marine Biology and Ecology* **158**:105-121.
- Cephbase. National Resource Centre for Cephalopods, Galveston, TX. Online database. Accessed at <http://www.cephbase.utmb.edu/> December 2007.
- Chambers, C. A. and T. A. Dick. 2007. Using environmental variables to predict the structure of deep-sea Arctic fish communities: Implications for food web construction. *Arctic, Antartic and Alpine Research* **39**:2-8.
- Cherel, Y. and K. A. Hobson. 2005. Stable isotopes, beaks and predators: a new tool to study the trophic ecology of cephalopods, including giant and colossal squids. *Proceedings of the Royal Society B* **272**:1601-1607.
- Cherel, Y., V. Ridoux, J. Spitz, and P. Richard. 2009. Stable isotopes document the trophic structure of a deep-sea cephalopod assemblage including giant octopod and giant squid. *Biology Letters* **5**:364-367.
- Chouinard, P.-M. and J.-D. Dutil. 2011. Structure of demersal fish assemblages in a cold, highly stratified environment. *ICES Journal of Marine Science* **68**(9) 1-13.
- Chouinard, P.-M. S. 2011. Analyse de la communauté ichthyologique du nord du golfe et de l'estuaire du Saint-Laurent en lien avec son habitat: Approche multispecificque. M.Sc. Thesis. Université du Québec à Rimouski, Rimouski.
- Clarke, M. R. 1966. A review of the systematics and ecology of oceanic squids. *Advances in Marine Biology* **4**:91-300.

- Clarke, M. R. 1987. Cephalopod Biomass - Estimation from predation. Pages 221-238 in Anonymous, editor. Cephalopod Life Cycles: Comparative Review. Academic Press, London.
- Clarke, M. R. 1996. The role of cephalopods in the world's oceans: an introduction. Philosophical Transactions Royal Society London B **351**:979-983.
- Coachman, L. K. and K. Aagaard. 1974. Physical oceanography of arctic and subarctic seas. Office of Naval Research:72.
- Coachman, L. K. and C. A. Barnes. 1961. Contribution of Bering Sea water to the Arctic Ocean. Arctic **14**:147-161.
- Coll, M., J. Navarro, R. J. Olson, and V. Christensen. 2013. Assessing the trophic position and ecological role of squid in marine ecosystems by means of food-web models. Deep-Sea Research II **95**: 21-36.
- Collins, M. A. 2002. Cirrate octopods from Greenland and Iceland waters. Journal of the Marine Biological Association of the United Kingdom **82**:1035-1036.
- Collins, M. A. 2005. *Opisthoteuthis borealis*: a new species of cirrate octopod from Greenland waters. Journal of the Marine Biological Association of the United Kingdom **85**:1475-1479.
- Collins, M. A. and R. Villanueva. 2006. Taxonomy, ecology and behaviour of the cirrate octopods. Oceanography and Marine Biology: An Annual Review **44**:277-322.
- Collins, M. A., C. Yau, L. Allcock, and M. H. Thurston. 2001. Distribution of deep-water benthic and benthic-pelagic cephalopods from the north-east Atlantic. Journal of the Marine Biological Association of the United Kingdom **81**:105-117.
- COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2004. COSEWIC assessment and update status report on the *Monodon monoceros* in Canada. Ottawa.
- Dahl, T. M., C. Lydersen, K. M. Kovacs, S. Falk-Petersen, J. Sargent, I. Gjertz, and B. Gulliksen. 2000. Fatty acid composition of the blubber in white whales (*Delphinapterus leucas*). Polar Biology **23**:401-409.
- Darnis, G., D. Robert, C. Pomerleau, H. Link, P. Archambault, R. J. Nelson, M. Geoffroy, J.-E. Tremblay, C. Lovejoy, S. H. Ferguson, B. P. V. Hunt, and L. Fortier. 2012. Current state and trends in the Canadian Arctic marine ecosystems: II. Heterotrophic food webs, pelagic-benthic coupling, and biodiversity. Climatic Change **115**:179-295.
- Dawe, E. G., W. R. Bowering, and J. B. Joy. 1998. Predominance of squid (*Gonatus spp.*) in the diet of Greenland halibut (*Reinhardtius hippoglossoides*) on the deep slope of the northeast Newfoundland continental shelf. Fisheries Research **36**:267-273.

- Dawe, E. G. and J. K. T. Brodziak. 1998. Trophic relationships, ecosystem variability and recruitment. Pages 125-156 *in* P. G. Rodhouse, E. G. Dawe, and R. K. O'Dor, editors. Squid recruitment dynamics. The genus *Illex* as a model. The commercial *Illex* species. Influences on variability. FAO Fisheries Technical Paper, Rome.
- Dawson, T. E. and R. T. W. Siegwolf. 2007. Using stable isotopes as indicators, tracers and recorders of ecological change: some context and background. Pages 3-18 *in* T. E. Dawson and R. T. W. Siegwolf, editors. Stable Isotopes as Indicators of Ecological Change. Academic Press, Amsterdam.
- Deagle, B.E., S.N. Jarman, D. Pemberton, and N.J. Gales. 2005. Genetic screening for prey in the gut contents from a giant squid (*Architeuthis* sp.). *Journal of Heredity* **96**(4): 417-423.
- De Angelis, P. 2012. Assessing the impact of international trade on chambered nautilus. *Geobios* **45**:5-11.
- Dehn, L. A., G. G. Sheffield, E. H. Follmann, L. K. Duffy, and D. L. Thomas. 2007. Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. *Polar Biology* **30**:167-181.
- DeNiro, M. J. and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* **42**:495-506.
- DeNiro, M. J. and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* **45**:341-351.
- Dickson, B. 1999. All change in the Arctic. *Nature* **397**:389-391.
- Dommasnes, A., V. Christensen, B. Ellertsen, C. Kvamme, W. Melle, L. Nøttestad, T. Pedersen, S. Tjelmeland, and D. Zeller. 2001. An Ecopath model for the Norwegian Sea and Barents Sea. *in* S. Guénette et al. (eds.): Fisheries impacts on North Atlantic ecosystems: models and analyses. Fisheries Centre Research **9**: 213-240.
- Drinkwater, K. F. 1986. Physical oceanography of Hudson Strait and Ungava Bay. Elsevier Oceanography Series **44**:237-264.
- Dunbar, M. J. 1981. Physical causes and biological significance of polynyas and other open water in sea ice. Polynyas in the Canadian Arctic. Occasional Paper Number 45 Canadian Wildlife Service:29-44.
- Dunning, M. C., M. D. Norman, and A. L. Reid. 1998. Cephalopods. Pages 687-826. *in* K.E. Carpenter and V.H. Niem editors. FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Vol. 2. Cephalopods, crustaceans, holothurians and sharks. FAO. Rome

- Dunton, K. H., T. Weingartner, and E. C. Carmack. 2006. The nearshore western Beaufort Sea Ecosystem: circulation and importance of terrestrial carbon in Arctic coastal food webs. *Progress in Oceanography* **71**:362-378.
- Ehleringer, J. R., P. W. Rundel, and K. A. Nagy. 1986. Stable isotopes in physiological ecology and food web research. *TREE* **1**:42-45.
- Field, J.C., C. Elliger, K. Baltz, G.E. Gillespie, W.F. Gilly, R.I. Ruiz-Cooley, D. Pearce, J.S. Stewart, W. Matsubu, and W.A. Walker. 2013. Foraging ecology and movement patterns of jumbo squid (*Dosidicus gigas*) in the California Current System. *Deep-Sea Research II* **95**:37-51.
- Finley, K. J. and C. R. Evans. 1983. Summer diet of the Bearded seal (*Erignathus barbatus*) in the Canadian High Arctic. *Arctic* **36**:82-89.
- Finley, K. J. and E. J. Gibb. 1982. Summer diet of the narwhal (*Monodon monoceros*) in Pond Inlet, northern Baffin Island. *Canadian Journal of Zoology* **60**:3353-3363.
- Fisk, A. T., P. F. Hoekstra, J.-M. Gagnon, J. Duffe, R. J. Norstrom, K. A. Hobson, M. Kwan, and D. C. G. Muir. 2003. Influence of habitat, trophic ecology and lipids on, and spatial trends of, organochlorine contaminants in Arctic marine invertebrates. *Marine Ecology Progress Series* **262**:201-214.
- Fissel, D. B., D. D. Lemon, and J. R. Birch. 1981. The physical oceanography of western Baffin Bay and Lancaster Sound. *Environmental Studies* **25**:293.
- Fissel, D. B., D. D. Lemon, and D. N. Knight. 1984. An oceanographic survey of the Canadian Arctic archipelago, March 1983. Canadian contractor report of hydrography and ocean sciences **16**:355.
- Forsythe, J. W. 2004. Accounting for the effect of temperature on squid growth in nature: from hypothesis to practice. *Marine and Freshwater Research* **55**:331-339.
- Frandsen, R. P. and K. Wieland. 2004. Cephalopods in Greenland Waters. Technical Report. Technical Report 57, Greenland Institute of Natural Resources, Pinngortitaleriffik.
- Frandsen, R. P. and K. Zumholz. 2004. Cephalopods in Greenland waters A field guide. Greenland Institute of Natural Resources, Pinngortitaleriffik, Greenland.
- Gardiner, K. and T. A. Dick. 2010. Arctic cephalopod distributions and their associated predators. *Polar Research* **29**:209-227.
- Gaston, A. J. 1985. The diet of Thick-billed Murre chicks in the eastern Canadian Arctic. *The Auk* **102**:727-734.
- GeoNames. Online database accessed at <http://www.geonames.org> in December 2007.

GBIF. Global Biodiversity Information Facility Data Portal. Accessed at <http://www.gbif.org>

GEBCO. General Bathymetric Charts of the Ocean (GEBCO). Accessed at http://www.gebco.net/data_and_products/gebco_world_map

Golikov, A. V. and R. M. Sabirov. 2009. Functional morphology of reproductive system in males of Sepiida and Sepiolida orders (Cephalopoda) (*In Russian*). Pages 164-167 in Proceedings of the conference and achieving biochemical education. University of Kazan, University of Kazan.

Golikov, A. V., R. M. Sabirov, P. A. Lubin, and L. L. Jørgensen. 2013. Changes in distribution and range structure of Arctic cephalopods due to climate changes of the last decades. *Biodiversity* **14**:28-35.

González, A., A. Guerra, S. Pascual, and P. Briand. 1998. *Vulvanoctopus hydrothermalis* gen. et sp. nov. (Mollusca, Cephalopoda): an octopod from a deep-sea hydrothermal vent site. *Cahiers de Biologie Marine* **39**:169-184.

Gotelli, N. J. and A. M. Ellison. 2004. *A Primer of Ecological Statistics*. Sinauer Associates Inc., Sunderland, MA.

Gradinger, R. 1995. Climate change and biological oceanography of the Arctic Ocean. *Philosophical Transactions: Physical Sciences and Engineering* **352**:277-286.

Graham, M. and H. Hop. 1995. Aspects of reproduction and larval biology of Arctic Cod (*Boreogadus saida*). *Arctic* **48**:130-135.

Grimpe, G. 1933. Die cephalopoden des arktischen Gebietes. (Cephalopods of the Arctic) *Fauna Arctica* **6**:491-514.

Gruber, N. 2011. Warming up, turning sour, losing breath: ocean biogeochemistry under global change. *Philosophical Transactions of the Royal Society A - Mathematical, Physical and Engineering Sciences* **369**:1980-1996.

Guerra, Á., Á. F. González, S. Pascual, and E. G. Dawe. 2011. The giant squid *Architeuthis*: an emblematic invertebrate that can represent concern for the conservation of marine biodiversity. *Biological Conservation* **144**:1989-1997.

Hansen, M. O., T. G. Nielsen, C. A. Stedmon, and P. Munk. 2012. Oceanographic regime shift during 1997 in Disko Bay, Western Greenland. *Limnology and Oceanography* **57**:634-633.

Haug, T., K. T. Nilssen, and L. Lindblom. 2004. Feeding habits of harp and hooded seals in drift ice waters along the east coast of Greenland in summer and winter. *Polar Research* **23**:35-42.

- Hay, K. A. and A. W. Mansfield. 1989. Narwhal, *Monodon monoceros* Linnaeus 1758. Pages 145-176 in S. H. Ridgeway and R. J. Harrison, editors. Handbook of marine mammals Vol. 4. Academic Press, London.
- Hillis, D. M. 1987. Molecular Versus Morphological Approaches to Systematics. Annual Review of Ecology and Systematics **18**:23-42.
- Historical Benthic Dredge Samples from the Southern Baltic and the North Sea. Online database accessed through Global Biodiversity Information Facility (GBIF) Data Portal at <http://data.gbif.org/datasets/resource/407> on 5 November 2007.
- Hjort and Ruud. 1929. Whales and plankton in the North Atlantic - A contribution to the work of the whaling committee and of the North Eastern area committee. Conseil Permanent International pour l'Exploration de la Mer, Copenhagen.
- Hobson, K. A. and Y. Cherel. 2006. Isotopic reconstruction of marine food webs using cephalopod beaks: new insight from captively raised *Sepia officinalis*. Canadian Journal of Zoology **84**:766-770.
- Hobson, K. A., A. Fisk, N. Karnovsky, M. Holst, J.-M. Gagnon, and M. Fortier. 2002. A stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. Deep-Sea Research II **49**:5131-5150.
- Hobson, K. A. and D. R. Norris. 2008. Animal migration: a context for using new techniques and approaches. Pages 1-20 in K. A. Hobson and L. I. Wassenaar, editors. Tracking Animal Migration with Stable Isotopes. Elsevier Inc., Amsterdam.
- Hobson, K. A. and H. E. Welch. 1992a. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. Marine Ecology Progress Series **84**:9-18.
- Hobson, K. A. and H. E. Welch. 1992b. Observing the foraging northern fulmars (*Fulmarus glacialis*) in the Canadian High Arctic. Arctic **45**:150-153.
- Hooker, S. K., S. J. Inverson, P. Ostrom, and S. C. Smith. 2001. Diet of the northern bottlenose whales inferred from fatty-acid and stable-isotope analyses of biopsy samples. Canadian Journal of Zoology **79**:1442-1454.
- Hop, H. and M. Graham. 1995. Respiration of juvenile Arctic cod (*Boreogadus saida*): effects of acclimation, temperature, and food intake. Polar Biology **15**:359-367.
- Hoving, H. J. T. and B. H. Robison. 2012. Vampire squid: detritivores in the oxygen minimum zone. Proceedings of the Royal Society B Biological Sciences:1-9.

- Hunsicker, M. E., T. E. Essington, R. Watson, and U. R. Sumaila. 2010. The contribution of cephalopods to global marine fisheries: can we have our squid and eat them too? *Fish and Fisheries* **11**:421-438.
- Hussey, N. E., J. Brush, I. D. McCarthy, and A. T. Fisk. 2010. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ diet-tissue discrimination factors for large sharks under semi-controlled conditions. *Comparative Biochemistry and Physiology, Part A* **155**:445-453.
- Ibáñez, C.M., L.A. Cubillos, R. Tafur, J. Argüelles, C. Yamashiro and E. Poulin. 2011. Genetic diversity and demographic history of *Dosidicus gigas* (Cephalopoda: Ommastrephidae) in the Humboldt Current System. *Marine Ecology Progress Series* **431**:163-171.
- Ifremer BIOCEAN, Deep Sea Benthic Fauna. Online database accessed through Global Biodiversity Information Facility (GBIF) Data Portal at <http://data.gbif.org/datasets/resource/358> on 5 November 2007.
- Iken, I., B. A. Bluhm, and R. Gradinger. 2005. Food web structure in the high Arctic Canada Basin: evidence from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Polar Biology* **28**:238.
- Ingram, R. G., J. Backle, D. G. Barber, Y. Gratton, and H. Melling. 2002. An overview of physical processes in the North Water. *Deep-Sea Research* **49**:4893-4906.
- Isinguzo, I. C. 2009. The feeding habits of anadromous Arctic char, (*Salvelinus alpinus* L.) in Frobisher Bay, Baffin Island in the Eastern Canadian Arctic: diet, parasites and stable isotopes. PhD Thesis. University of Manitoba, Winnipeg.
- ITIS. Integrated Taxonomic Information System on-line database (ITIS). Accessed at <http://www.itis.gov/> in 2008
- Jackson, G. D. 2004. Cephalopod growth: historical context and future directions. *Marine and Freshwater Research* **55**: 327-329.
- Jackson, G. D., R. A. Alford, and T. H. Choat. 2000. Can length frequency analysis be used to determine squid growth? - An assessment of ELEFAN. *ICES Journal of Marine Science* **57**:948-954.
- Jackson, G. D., P. Bustamante, Y. Cherel, E. A. Fulton, E. P. M. Grist, C. H. Jackson, P. D. Nicholas, H. Pethybridge, K. Phillips, R. D. Ward, and J. C. Xavier. 2007. Applying new tools to cephalopod trophic dynamics and ecology: perspectives from the Southern Ocean Cephalopod Workshop, February 2-3, 2006. *Reviews in Fish Biology and Fisheries* **17**:79-99.
- Jørgensen, O. A., C. Hvingel, R. R. Møller, and M. A. Treble. 2005. Identification and mapping of bottom fish assemblages in Davis Strait and southern Baffin Bay. *Canadian Journal of Fisheries and Aquatic Science* **62**:1833-1852.

- Kondakov, N. N. 1937. Golovonogie molljuski (Cephalopoda) Karskogo morja. (The Cephalopoda of the Kara Sea). Transactions of the Arctic Institute **1**:61–67.
- Kristensen, T. K. 1977. Hatching, growth, and distribution of juvenile *Gonatus fabricii* (Mollusca: Cephalopoda) in Greenland waters. *Astarte* **10**:21-28.
- Kristensen, T. K. 1980. Periodical growth rings in cephalopod statoliths. *Dana* **1**:39-51.
- Kristensen, T. K. 1981. First record of a mature female of the squid *Gonatus fabricii* (Lichtenstein, 1818) (Cephalopoda: Teuthoidea). *Steenstrupia* **7**:101-108.
- Kristensen, T. K. 1982. Multivariate statistical analysis of geographic variation in the squid *Gonatus fabricii* (Lichtenstein, 1818) (Mollusca: Cephalopoda). *Malacologia* **22**:581-586.
- Kristensen, T. K. 1983. *Gonatus fabricii*. Pages 159-173 in P. R. Boyle, editor. *Cephalopod Life Cycles*. Academic Press, London.
- Kristensen, T. K. 1984. Biology of the squid *Gonatus fabricii* (Lichtenstein, 1818) from West Greenland waters. *Meddelelser om Grønland, Bioscience* **13**:3-17.
- Laidre, K. L., M. P. Heide-Jørgensen, and R. Dietz. 2002. Diving behaviour of narwhals (*Monodon monoceros*) at two coastal localities in the Canadian High Arctic. *Canadian Journal of Zoology* **80**:624-635.
- Laidre, K. L., M. P. Heide-Jørgensen, R. Dietz, O. A. Jørgensen, and M. A. Treble. 2004. Deep-ocean predation by a high Arctic cetacean. *ICES Journal of Marine Sciences* **61**:430-440.
- Lajtha, K. and R. H. Michener. 1994. Introduction. Pages xi-xix in K. Lajtha and R. H. Michener, editors. *Stable Isotopes in Ecology and Environmental Science*, Oxford.
- Laptikhovskiy, V. V., C. M. Nigmatullin, H. J. T. Hoving, B. Onsoy, A. Salman, K. Zumholz, and G. A. Shevtsov. 2008. Reproductive strategies in female polar and deep-sea bobtail squid genera *Rossia* and *Neorossia* (Cephalopoda: Sepiolidae). *Polar Biology* **31**:1499-1507.
- Lawson, J. W., A. M. Magalhaes, and E. H. Miller. 1998. Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density. *Marine Ecology Progress Series* **164**:13-20.
- Layton, K.K.S., A.L Martel, and P.D.N Hebert. 2014. Patterns of DNA barcode variation in Canadian marine molluscs. *PLOSone* **9**(4):e95003.
- LeBlond, P. H. 1980. On the surface circulation in some channels of the Canadian Archipelago. *Arctic* **33**:189-197.

- Leporati, S. C., G. T. Pecl, and J. M. Semmens. 2007. Cephalopod hatchling growth: the effects of initial size and seasonal temperatures. *Marine Biology* **151**:1375-1383.
- Lesage, V., M. O. Hammill, and K. M. Kovacs. 2001. Marine mammals and the community structure of the Estuary and Gulf of St. Lawrence, Canada: evidence from stable isotope analysis. *Marine Ecology Progress Series* **210**:203-221.
- Lin, L., C. Li, Z. Chen, S. Xu, and Y. Liu. 2015. Development and characterization of twenty-three microsatellite markers for the purpleback flying squid (*Symplectoteuthis oualaniensis*). *Conservation Genetic Resource* **7**:161-163.
- Lindgren, A. R., O. N. Katugin, M. K. Nishiguchi, and E. Amezcuita. 2004. Phylogenetic relationships among the Gonatidae (Cephalopoda, Teuthida, Oegopsida) based on DNA sequence data. Page 89 - 92 in Abstracts of the conference "Mollusks of the Northeastern Asia and Northern Pacific: Biodiversity, Ecology, Biogeography and Faunal History", Vladivostok, Dalnauka.
- Lindren, A.R., O.N. Katugin, E. Amezcuita, and M.K. Nishiguchi. 2005. Evolutionary relationships among squids of the family Gonatidae (Mollusca: Cephalopoda) inferred from three mitochondrial loci. *Molecular Phylogenetics and Evolution* **36**: 101-111.
- Lipinski, M. R., D. S. Butterworth, C. J. Augustyn, J. K. T. Brodziak, G. Christy, S. Des Clers, G. D. Jackson, R. K. O'Dor, D. Pauly, L. V. Purchase, M. J. Roberts, B. A. Roel, Y. Sakurai, and W. H. H. Sauer. 1998. Cephalopod fisheries: a future global upside to past overexploitation of living marine resources? Results of an international workshop, 31 August - 2 September 1997, Cape Town, South Africa. *South African Journal of Marine Science* **20**:463-469.
- Liu, L., X. Chen, Q. Xu, S. Tian, and B. Liu. 2014. Development of 39 polymorphic microsatellite markers for the jumbo squid *Dosidicus gigas* using Illumina paired-end sequencing. *Conservation Genetic Resources* **6**: 673-676.
- Loeng, H., K. Brander, E. Carmack, S. Denisenko, K. Drinkwater, B. Hansen, K. Kovacs, P. Livingston, F. McLaughlin, and E. Sakshaug. 2005. Marine Systems. Pages 439-538 in C. Symon and et. al., editors. Arctic Climate Impact Assessment. Cambridge University Press, Cambridge.
- Lowry, L. F., K. J. Frost, and G. A. Seaman. 1986. Investigations of belukha whales in coastal waters of western and northern Alaska, III: food habits. Fairbanks: Alaska Department of Fish and Game.
- Mallory, M. L. and H. G. Gilchrist. 2005. Marine birds of the Hell Gate polynya, Nunavut, Canada. *Polar Research* **24**:87-93.

- Mangold, K. M. and R. E. Young. 1998. The systematic value of the digestive organs. Pages 21-30 in N. A. Voss, M. Vecchione, R. B. Toll, and M. J. Sweeney, editors. Systematics and Biogeography of Cephalopods. Smithsonian Institution Press, Washington.
- McCutchan, J. H. J., W. M. J. Lewis, C. Kendall, and C. C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* **102**:378-390.
- McLaughlin, F. A., E. C. Carmack, R. G. Ingram, and W. J. Williams. 2005. Oceanography of the Northwest Passage. Pages 1213-1244 in A. R. Robinson and K. H. Bring, editors. The Sea: The Global Coastal Ocean - Interdisciplinary Regional Studies and Synthesis. Harvard University Press.
- Mercer, M. C. 1968a. A synopsis of the recent Cephalopoda of Canada. Pages 265-276 Proceedings of the Symposium on Mollusca held at Cochin from January 12 to 16, 1968. Part I. Marine Biological Association of India Symposium Series 3. Marine Biological Association of India, Madapam.
- Mercer, M. C. 1968b. Systematics and biology of the sepiolid squids of the genus - *Rossia*. Owen, 1835, in Canadian waters with preliminary review of the genus. MSc. Thesis. Memorial University of Newfoundland, St. John's.
- Metcalf, W. E. 1954. A note on Arctic oceanography and the Lomonosov range. *Arctic* **7**:108-109.
- Michel, C., R. G. Ingram, and L. R. Harris. 2006. Variability in oceanographic and ecological processes in the Canadian Arctic Archipelago. *Progress in Oceanography* **71**:379-401.
- Michener, R. H. and L. Kaufman. 2007. Stable isotope ratios as tracers in marine food webs: An update. Pages 238-282 in R. H. Michener and K. Lajtha, editors. Stable Isotopes in Ecology and Environmental Science. Blackwell Publishing, Malden, MA.
- Michener, R. H. and D. M. Schell. 1994. Stable isotope ratios as tracers in marine aquatic food webs. Pages 138-157 in K. M. Lajtha, R.H., editor. Methods in Ecology: Stable Isotopes in Ecology and Environmental Science. Blackwell Publishing.
- Minagawa, M. and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica et Cosmochimica Acta* **48**:1135 - 1140.
- Moore, J. W. and B. X. Semmens. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. *Ecology Letters* **11**:470-480.
- Morov, A. R. and R. M. Sabirov. 2009. Maturing's regularities of reproductive system and fecundity of females *Rossia pelpebrosa* (Cephalopoda: Sepiolida) on the eastern shelf of archipelago Spitsbergen (*In Russian*). Pages 168-171 in Proceedings of the conference and achieving biochemical education Univesity of Kazan, University of Kazan.

- Mosimann, J. E. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. *Journal of American Statistical Association* **65**:930-945.
- Munk, P., B. W. Hansen, T. G. Nielsen, and H. A. Thomsen. 2003. Changes in plankton and fish larvae communities across hydrographic fronts off West Greenland. *Journal of Plankton Research* **25**:815-830.
- Muus, B. J. 1962. Cephalopoda. The Godthaab Expedition 1928. *Meddelelser om Grønland* **81** (5). Copenhagen: Committee on Scientific Research in Greenland
- Muus, B. 2002. The *Bathypolypus-Benthoctopus* problem of the North Atlantic (Octopodidae, Cephalopoda). *Malacologia* **44**:175-222.
- Mysak, L. A. 2001. Patterns of Arctic circulation. *Science* **293**:1269-1270.
- National Marine Conservation Areas of Canada. Parks Canada. Accessed at http://www.pc.gc.ca/progs/amnc-nmca/intro_e.asp
- National Snow and Ice Data Center. All about sea ice: Processes: Dynamics: Circulation. Accessed at <http://nsidc.org/cryosphere/seaice/index.html>.
- Navarro, J., M. Coll, C. J. Somes, and R. J. Olson. 2013. Trophic niche of squids: insights from isotopic data in marine systems worldwide. *Deep-Sea Research II: Topical Studies in Oceanography* **95**:93-102.
- Nesis, K. N. 1965. The distribution and nutrition of young squid *Gonatus fabricii* (Licht.) in the Labrador Sea and the Norwegian Sea. *Oceanology* **5**:102-108.
- Nesis, K. N. 1987. Golovonogie molljuskij Severnogo Ledovitogo okeana i ego morej. (Cephalopod molluscs of the Arctic Ocean and its seas). Pages 115-136 in A. I. Kafanov, editor. *Fauna i raspredelenie molljuskov: Severnaja Pacifika i Poljarnyj Bassejn*. (Fauna and distribution of molluscs: North Pacific and Arctic Basin). Vladivostok: Far Eastern Scientific Center of the USSR Academy of Sciences.
- Nesis, K. N. 1999. The duration of egg incubation in high-latitude and deep-sea cephalopods. *Russian Journal of Marine Biology* **25**:499-506.
- Nesis, K. N. 2001. West-Arctic and East-Arctic distributional ranges of cephalopods. *Sarsia* **86**:1-11.
- Nesis, K. N. 2003a. Cephalopods from open waters of the Okhotsk Sea: general distribution and zoogeography. Pages 763-772 in M. J. Sweeney, editor. *English translations of selected publications on cephalopods by Kir N. Nesis*. Smithsonian Institution Libraries, Washington, DC.

- Nesis, K. N. 2003b. Distribution of recent cephalopoda and implications for Plio-pleistocene events. *Berliner Palaobiol. Abh* **3**:199-224.
- Nesis, K. N. 2003c. The squid *Gonatus fabricii* (Licht.) in the center of the Arctic Basin. Pages 71-75 in M. J. Sweeney, editor. English Translations of Selected Publications of Cephalopods by Kir N. Nesis. Smithsonian Institution Libraries, Washington.
- Nesis, K. N., A. M. Amelekhina, A. R. Boltachev, and G. A. Shevtsov. 2003. Records of giant squid of the genus *Architeuthis* in the north Pacific and south Atlantic. Pages 685-697 in M. J. Sweeney, editor. English translations of selected publications on cephalopods by Kir N. Nesis. Smithsonian Institution Libraries, Washington, DC.
- Nigmatullin, C. M. 1989. Las especies del calamar mas abundantes del Atlantico Sudoeste y synopsis sobre la ecologia del calamar (*Illex argentinus*). *Frente Marit* **5A**:71-81.
- North Pacific Groundfish Observer. Online databse accessed through Global Biodiversity Information Facility (GBIF) Data Portal at <http://data.gbif.org/datasets/resource/331> on 5 November 2007.
- Nygaard, R., K. Sunksen, and O. A. Jørgensen. 2008. Biomass and abundance of demersal fish stocks off West Greenland estimated from the Greenland shrimp survey, 1988 - 2007. Scientific Council Meeting. Northwest Atlantic Fisheries Organization. NAFO SCR Doc 08/28.
- O'Dor, R. 1983. *Illex illecebrosus*. Pages 175-199 in P. R. Boyle, editor. Cephalopod life cycles. Academic Press, London.
- O'Dor, R. K. 1988. The energetic limits on squid distributions. *Malacologia* **29**:113-119.
- O'Dor, R. K. and E. G. Macalaster. 1983. *Bathypolypus arcticus*. Pages 401-410 in P. R. Boyle, editor. Cephalopod Life Cycles. Academic Press, London.
- O'Shea, S. 1999. The marine fauna of New Zealand: Octopoda (Mollusca: Cephalopoda). NIWA Biodiversity Memoir **112**:1-280.
- Oosterwind, D., R. ter Hofstede, B. Harley, H. Brendelberger, and U. Piatkowski. 2010. Biology and meso-scale distribution patterns of North Sea cephalopods. *Fisheries Research* **106**:141-150.
- Orr, D. C. and W. R. Bowering. 1997. A multivariate analysis of food and feeding trends among Greenland halibut (*Reinhardtius hippoglossoides*) sampled in Davis Strait, during 1986. *ICES Journal of Marine Sciences* **54**:819-829.
- Overland, J., U. Bhatt, J. Key, Y. Liu, J. Walsh, and M. Wang. 2011. Temperature and clouds. Arctic Report Card for 2011 - Tracking recent environmental change. Accessed at www.arctic.noaa.gov/reportcard 2011.

- Overland, J. E., J. Alheit, A. Bakun, J. W. Hurrell, D. L. Mackas, and A. J. Miller. 2010. Climate controls on marine ecosystems and fish populations. *Journal of Marine Systems* **79**:305-315.
- Pauly, D. 1998. Why squid, though not fish, may be better understood by pretending they are. Pages 47-58 in A. I. L. Payne, M. R. Lipinski, M. R. Clarke, and M. A. C. Roeleveld, editors. *South African Journal of Marine Science*. South African Journal of Marine Science.
- Perez, M. A. 1990. Review of marine mammal population and prey information for Bering Sea ecosystem studies. NOAA Technical Memorandum NMFS F/NWC-186. US Department of Commerce, Washington, DC.
- Persson, J., L.C. Stige, N.C. Stenseth, N. Usov, D. Martynova. 2012. Scale-dependent effects of climate on two copepod species, *Calanus glacialis* and *Pseudocalanus minutus*, in an Arctic-boreal sea. *Marine Ecology Progress Series* **468**: 71-83.
- Peterson, B. J. and B. Fry. 1987. Stable Isotopes in Ecosystem Studies. *Annual Review of Ecology and Systematics* **18**:293-320.
- Piatkowski, U., G. J. Pierce, and M. Morais da Cunha. 2001. Impact of cephalopods in the food chain and their interaction with the environment and fisheries: an overview. *Fisheries Research* **52**:5-10.
- Piatkowski, U. and K. Wieland. 1993. The Boreoatlantic gonate squid *Gonatus fabricii*: distribution and size off West Greenland in summer 1989 and in summer and autumn 1990. *Aquatic Living Resources* **6**:109-114.
- Pierce, G. J., R. S. Thorpe, L. C. Hastie, A. S. Brierley, A. Guerra, P. R. Boyle, R. Jamieson, and P. Avila. 1994. Geographic variation in *Loligo forbesi* in the Northeast Atlantic Ocean: analysis of morphometric data and tests of causal hypotheses. *Marine Biology* **119**:541-547.
- Pierce, G. J., V. D. Valavanis, A. Guerra, P. Jereb, L. Orsi-Relini, J. M. Bellido, I. Katara, U. Piatkowski, J. Pereira, E. Balguerias, I. Sobrino, E. Lefkaditou, J. Wang, M. Santurtun, P. R. Boyle, L. C. Hastie, C. D. MacLeod, J. M. Smith, M. Viana, A. González, and A. F. Zuur. 2008. A review of cephalopod-environment interactions in European Seas. *Hydrobiologia* **612**:49-70.
- Piertney, S. B., C. Hudelot, F. G. Hochberg, and M. A. Collins. 2003. Phylogenetic relationships among cirrate octopods (Mollusca: Cephalopoda) resolved using mitochondrial 16S ribosomal DNA sequences. *Molecular Phylogenetics and Evolution* **27**:348-353.
- Planque, B., J.-M. Fromentin, P. Cury, K. F. Drinkwater, S. Jennings, R. I. Perry, and S. Kifani. 2010. How does fishing alter marine populations and ecosystems sensitivity to climate? *Journal of Marine Systems* **79**:403-417.

- Pomerleau, C., G. Winkler, A. R. Sastri, R. J. Nelson, S. Vagle, V. Lesage, and S. H. Ferguson. 2011. Spatial patterns in zooplankton communities across the eastern Canadian sub-Arctic and Arctic waters: insights from stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios. *Journal of Plankton Research* **33**:1779-1792.
- Portner, H.-O. and A. P. Farrel. 2008. Physiology and climate change. *Science* **322**:690-692.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83**:703-718.
- Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, and C. G. Montaña. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152**:179-189.
- Proshutinsky, A. Y. and M. A. Johnson. 1997. Two circulation regimes of the wind-driven Arctic Ocean. *Journal of Geophysical Research Oceans* **102**:12493-12514.
- Quinn, G. P. and M. J. Keough. 2002. Introduction to multivariate analyses. Page 537 *Experimental Design and Data Analysis for Biologists*. Cambridge, Cambridge.
- Raskoff, K. A., R. R. Hopcroft, K. N. Kosobokova, J. E. Purcell, and M. J. Youngbluth. 2010. Jellies under ice: ROV observations from the Arctic 2005 Hidden Ocean Expedition. *Deep-Sea Research II* **57**(1-2): 111-126.
- Ratnasingham, S. and P. D. N. Hebert. 2007. BOLD: The Barcode of Life Data System (<http://www.barcodinglife.org>). *Molecular Ecology Notes* **7**:355-364.
- Rau, G. H., A. J. Mearns, D. R. Young, R. J. Olson, H. A. Schafer, and I. R. Kaplan. 1983. Animal $^{13}\text{C}/^{12}\text{C}$ correlates with trophic level in pelagic food webs. *Ecology* **64**:1314-1318.
- Reed, R. J. and B. A. Kunkel. 1960. The Arctic circulation in summer. *Journal of Meteorology* **17**:489-506.
- Ribergaard, M. H. 2009. Oceanographic investigations off West Greenland 2008. Danish Meteorological Institute centre for Ocean and Ice. 1-49.
- Richter-Menge, J., M. O. Jeffries, and J. E. Overland. 2011. Arctic Report Card 2011 *in* J. Richter-Menge, M. O. Jeffries, and J. E. Overland, editors. Arctic Report Card 2011. NOAA.
- Rodhouse, P. G. 2010. Effects of environmental variability and change on cephalopod populations: an Introduction to the CIAC '09 Symposium special issue. *ICES Journal of Marine Science* **67**:1311-1313.

- Rodhouse, P. G., E. G. Dawe, R. K. O'Dor, and (eds). 1998a. Squid recruitment dynamics. The genus *Illex* as a model. The commercial *Illex* species. Influences on variability. FAO, Rome.
- Rodhouse, P. G. and E. M. C. Hatfield. 1990. Age determination in squid using statolith growth increments. *Fisheries Research* **8**:323-334.
- Rodhouse, P. G., E. J. Murphy, and M. L. Coelho. 1998b. Impact of fishing on life histories. Page 273 in P. G. Rodhouse, E. G. Dawe, and R. K. O'Dor, editors. Squid recruitment dynamics. The genus *Illex* as a model, the commercial *Illex* species and influences on variability. FAO.
- Rodhouse, P. G. and C. M. Nigmatullin. 1996. Role as consumers. *Philosophical Transactions: Biological Sciences* **351**:1003-1022.
- Rodhouse, P. G. and M. G. White. 1995. Cephalopods occupy the ecological niche of epipelagic fish in the Antarctic polar frontal zone. *The Biological Bulletin* **189**:77-80.
- Rodrigues, M., M. E. Garci, J. S. Troncoso, and A. Guerra. 2010. Burying behaviour in the bobtail squid *Sepiola atlantica* (Cephalopoda: Sepiolidae). *Italian Journal of Zoology* **77**:247-251.
- Roper, C. F. E. and W. L. J. Brundage. 1972. Cirrate octopods with associated deep-sea organisms: new biological data based on deep benthic photographs (Cephalopoda). *Smithsonian Contributions to Zoology* **121**:46.
- Roper, C. F. E., M. J. Sweeney, and C. E. Nauen. 1983. FAO Species Catalogue. Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. *FAO Fisheries Synopsis* **125**:1-277.
- Roper, C. F. E. and G. L. Voss. 1983. Guidelines for taxonomic descriptions of cephalopod species. *Memoirs of the National Museum of Victoria* **44**:49-63.
- Roper, C. F. E. and R. E. Young. 1975. Vertical distribution of pelagic cephalopods. *Smithsonian Contributions to Zoology* **209**:1-51.
- Rosa, R., J. Pereira, P. R. Costa, and M. L. Nunes. 2006. Distribution, abundance, biology and biochemistry of the stout bobtail squid *Rossia macrosoma* from the Portuguese coast. *Marine Biology Research* **2**:14-23.
- Rosa, R., J. Pereira, and M. L. Nunes. 2005. Biochemical composition of cephalopods with different life strategies, with special reference to a giant squid, *Architeuthis* sp. *Marine Biology* **146**:739-751.
- Rudels, B. 1986. The outflow of polar water through the Arctic Archipelago and the oceanographic conditions in Baffin Bay. *Polar Research* **40**:161-180.

- Rudels, B. 1995. The thermohaline circulation of the Arctic Ocean and the Greenland Sea. *Philosophical Transactions of the Royal Society London A* **352**:287-299.
- Rudels, B., H. J. Friedrich, and D. Quadfasel. 1999. The Arctic Circumpolar Boundary Current. *Deep-Sea Research II* **46**:1023-1062.
- Ruiz-Cooley, R. I., D. Gerdrón, S. Aguiniga, S. Mesnick, and J. D. Carriquiry. 2004. Trophic relationships between sperm whales and jumbo squid using stable isotopes of C and N. *Marine Ecology Progress Series* **277**:275-283.
- Santos, M. B., M. R. Clarke, and G. J. Pierce. 2001. Assessing the importance of cephalopods in the diets of marine mammals and other top predators: problems and solutions. *Fisheries Research* **52**:121-139.
- Sarabia, A. and C. Zymans. 2013. *Chlamys opercularis*. Animal Diversity Web. University of Michigan - Museum of zoology. Accessed at http://animaldiversity.org/accounts/Chlamys_opercularis/
- Seibel, B. A., B. H. Robison, and S. D. H. Haddock. 2005. Post-spawning egg-care by a squid. *Nature* **438**:929.
- Semmens, J. M., G. T. Pecl, B. M. Gillanders, C. M. Waluda, E. K. Shea, D. Jouffre, T. Ichii, K. Zumholz, O. N. Katugin, S. C. Leporati, and P. W. Shaw. 2007. Approaches to resolving cephalopod movement and migration patterns. *Reviews in Fish Biology and Fisheries* **17**:401-423.
- Sennikov, A. M., S. G. Mukhin, and T. E. Bliznichenko. 1989. Distribution and trophic importance of juvenile squid (*Gonatus fabricii* Lichtenstein) in the Norwegian and Barents Seas in 1986-1988. *International Council for the Exploration of the Sea, Copenhagen*. 1989/K, 15.
- Serreze, M. C., A. P. Barrett, A. G. Slater, R. A. Woodgate, K. Aagaard, R. B. Lammers, M. Steele, R. Moritz, M. Meredith, and C. M. Lee. 2006. The large-scale freshwater cycle of the Arctic. *Journal of Geophysical Research Oceans* **111**:1-19.
- Sims, D. W., M. J. Genner, A. J. Southward, and S. J. Hawkins. 2001. Timing of squid migration reflects North Atlantic climate variability. *Proceedings of the Royal Society London B*. **268**:2607-2611.
- Smith, M. and B. Rigby. 1981. Distribution of polynyas in the Canadian Arctic. Polynyas in the Canadian Arctic. **Occasional Paper Number 45** Canadian Wildlife Service:7-28.
- Smithsonian National Museum of Natural History Invertebrate Zoology Collections. Online database accessed through Global Biodiversity Information Facility (GBIF) Data Portal at <http://data.gbif.org/datasets/resource/1834> on 22 May 2008.

- Snelgrove, P. V. R., P. Archambault, S. K. Juniper, P. Lawton, A. Metaxas, P. Pepin, J. C. Rice, and V. Tunnicliffe. 2012. Canadian Healthy Oceans Network (CHONe): An academic-government partnership to develop scientific guidelines for conservation and sustainable usage of marine biodiversity. *Fisheries* **37**:296-304.
- Somers, K. M. 1986. Multivariate allometry and removal of size with principal components analysis. *Systematic Zoology* **35**:359-368.
- Stewart, B. E. and E. A. Stewart. 1989. *Delphinapterus leucas*. *Mammalian Species* **336**. American Society of Mammologists.
- Stewart, D. B., R. A. Ratynski, L. M. J. Bernier, and D. J. Ramsey. 1993. A fishery development strategy for the Canadian Beaufort Sea–Amundsen Gulf Area. Department of Fisheries and Oceans, Winnipeg.
- Stewart, P. L., P. Pocklington, and R. A. Cunjak. 1985. Distribution, abundance and diversity of benthic macroinvertebrates on the Canadian continental shelf and slope of southern Davis Strait and Ungava Bay. *Arctic* **38**:281-291.
- Stirling, I. 1980. The biological importance of polynyas in the Canadian Arctic. *Arctic* **33**:303-315.
- Stirling, I. 1997. The importance of polynyas, ice edges, and leads to marine mammals and birds. *Journal of Marine Systems* **10**:9-21.
- Stow, D. 2006. *Oceans - an illustrated reference*. University of Chicago Press.
- Strugnell, J. M., A. R. Lindgren, and A. L. Allcock. 2009. Cephalopod mollusks (Cephalopoda). Pages 242-246 in S. B. Hedges and S. Kumar, editors. *The Timetree of Life*. Oxford University Press, Oxford.
- Strugnell, J. and M.K. Nishiguchi. 2007. Molecular phylogeny of coleoid cephalopods (Mollusca:Cephalopoda) inferred from three mitochondrial and six nuclear loci: a comparison of alignment, implied alignment and analysis methods. *Journal of Molluscan Studies* **73**:399-410.
- Sulzman, E. W. 2007. Stable isotope chemistry and measurement: a primer. Pages 1-22 in R. H. Michener and K. Lajtha, editors. *Stable Isotopes in Ecology and Environmental Science - 2nd Edition*. Blackwell Publishing, Malden, MA.
- Swedish Museum of Natural History: Invertebrates. Online database accessed through Global Biodiversity Information Facility (GBIF) Data Portal at <http://data.gbif.org/datasets/resource/1027> on 5 November 2007.

- Sweeney, M. J., C. F. E. Roper, K. M. Mangold, M. R. Clarke, S. v. Boletzky, and (eds). 1992. "Larval" and juvenile cephalopods: a manual for their identification. Smithsonian Contributions to Zoology **513**. Washington, DC: Smithsonian Institution Press.
- Takai, N., S. Onaka, Y. Ikeda, A. Yatsu, H. Kidokoro, and W. Sakamoto. 2000. Geographical variations in carbon and nitrogen stable isotope ratios in squid. Journal of the Marine Biological Association of the UK **80**:675-684.
- Tang, C. C. L., C. K. Ross, T. Yao, B. Petrie, B. M. DeTracey, and E. Dunlap. 2004. The circulation, water masses and sea ice of Baffin Bay. Progress in Oceanography **63**:183-228.
- Taxonomic Information System for the Belgian Coastal Area. Online database accessed through Global Biodiversity Information Facility (GBIF) Data Portal at <http://data.gbif.org/datasets/resource/361> on 22 May 2008.
- Thanassekos, S. and L. Fortier. 2012. An individual based model of Arctic cod (*Boreogadus saida*) early life in Arctic polynyas: I. Simulated growth in relation to hatch date in the Northeast Water (Greenland) and the North Water (Baffin Bay). Journal of Marine Systems **93**:25-38.
- Thanassekos, S., D. Robert, and L. Fortier. 2012. An individual based model of Arctic cod (*Boreogadus saida*) early life in Arctic polynyas: II. Length-dependent and growth-dependent mortality. Journal of Marine Systems **93**:39-46.
- Tieszen, L. L., T. W. Boutton, K. G. Tesdahl, and N. A. Slade. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for $\delta^{13}\text{C}$ analysis of diet. Oecologia **57**:32-37.
- Tomczak, M. and J. S. Godfrey. 2003. Arctic oceanography: the path of North Atlantic Deep Water. Pages 83-104 in Regional oceanography: An introduction. Daya Publishing House, Delhi.
- Tomilin, A. G. 1967 (1957). Mammals of the U.S.S.R. and adjacent countries. Cetacea **9**. Jerusalem: Isreal Program for Scientific Translations.
- Treble, M. A. 2007. Analysis of data from the 2006 trawl surveys of NAFO division OA. Scientific Council Meeting. Northwest Atlantic Fisheries Organization, NAFO SCR Doc. 07/41.
- Treble, M.A. 2009. Report on Greenland halibut caught during the 2008 trawl surveys in NAFO Division OA. Scientific Council Meeting. Northwest Atlantic Fisheries Organization. NAFO SCR Doc 09/26.
- Treshnikov, A. F. and G. I. Baranov. 1972. The structure of water circulation in the Arctic Basin. Leningrad, Gidrometeoizdat:158.

- Vecchione, M. 1998. Character analysis: introductory comments. Pages 3-6 in N. A. Voss, M. Vecchione, R. B. Toll, and M. J. Sweeney, editors. Systematics and Biogeography of Cephalopods. Smithsonian Institution Press, Washington.
- Vecchione, M., C. F. E. Roper, and M. J. Sweeney. 1989. Marine Flora and Fauna of the Eastern United States Mollusca: Cephalopoda. NOAA Technical Report NMFS **73**:1-30.
- Voight, J. R. 1993. The association between distribution and octopodid morphology: implications for classification. Zoological Journal of the Linnean Society **108**:209-223.
- Voronkov, A. 2010a. *Macoma calcarea* Gmelin 1791. Arctic Ocean Diversity (ArcOD). Accessed at http://www.arcodiv.org/seabottom/bivalves/Macoma_calcarea.html.
- Voronkov, A. 2010b. *Serripes groenlandicus* Bruguiere 1789. Arctic Ocean Diversity (ArcOD). Accessed at http://www.arcodiv.org/seabottom/bivalves/Serripes_groenlandicus.html
- Voss, G. L. 1988. The biogeography of the deep-sea octopoda. Malacologia **29**:295-307.
- Voss, G. L. and W. G. Percy. 1990. Deep-water octopods (Mollusca: Cephalopoda) of the Northeastern Pacific. Proceedings of the California Academy of Sciences **47**:47-94.
- Voss, N. A., M. Vecchione, R. B. Toll, and M. J. Sweeney. 1998. Systematics and biogeography of cephalopods - Introduction. Pages 1-2 in N. A. Voss, M. Vecchione, R. B. Toll, and M. J. Sweeney, editors. Systematics and Biogeography of Cephalopods. Smithsonian Institution Press, Washington.
- Wacasey, J. W., E. G. Atkinson, and L. Glasspoole. 1979. Zoobenthos data from Upper Frobisher Bay 1967–1973. Department of Fisheries and Oceans, Ste. Anne de Bellevue, QC.
- Weber, J. R. 1989. Physiography and bathymetry of the Arctic Ocean seafloor. Pages 797-828 in Y. Herman, editor. The Arctic Seas: Climatology, Oceanography, Geology and Biology. Van Nostrand Reinhold Company, New York.
- Weinrebe, W., A. Kuijpers, I. Klaucke, M. Fink, J. B. Jensen, and N. Mikkelsen. 2008. High-Resolution Bathymetry of Disko Bay and Ilulissat Icefjord, West-Greenland (abstract) in American Geophysical Union Fall Meeting. #C31E-0563
- Welch, H. E., M. A. Bergmann, T. D. Siferd, K. A. Martin, M. F. Curtis, R. E. Crawford, R. J. Conover, and H. Hop. 1992. Energy flow through the marine ecosystem of the Lancaster Sound region, Arctic Canada. Arctic **45**:343–357.
- Wells, N. C., W. J. Gould, and A. E. S. Kemp. 1996. The role of ocean circulation in the changing climate. Pages 41-58 in C. P. Summerhayes and S. A. Thorpe, editors. Oceanography: an illustrated guide. John Wiley & Sons, New York.

- Węśławski, J. M., M. A. Kendall, M. Włodarska-Kowalczyk, K. Iken, M. Kędra, J. Legezynska, and M. K. Sejr. 2011. Climate change effects on Arctic fjord and coastal macrobenthic diversity - observations and predictions. *Marine Biodiversity* **41**:71-85.
- WHOI. 2006. Polar Discovery: Arctic circulation. Woods Hole Oceanographic Institute. Accessed at <http://polardiscovery.whoi.edu/arctic/circulation.html> on 7 January 2008.
- Wiborg, K. F., J. Gjørseter, and I. M. Beck. 1982. The squid *Gonatus fabricii*: Investigations in the Norwegian Sea and Western Barents Sea. ICES CM 1984/K: 19. Copenhagen. International Council of the Exploration of the Sea.
- Williams, W. J., E. C. Carmack, and R. G. Ingram. 2007. Physical oceanography of polynyas. Pages 55-85 in W. O. Smith and D. G. Barber, editors. *Polynyas - Windows to the World*. Elsevier Oceanography Series, Amsterdam.
- Woll, A. K. and A. C. Gunderson. 2004. Diet composition and intra-specific competition of young Greenland halibut around southern Greenland. *Journal of Sea Research* **51**:243-249.
- Wood, J. B. 2000. The natural history of *Bathypolypus arcticus* (Prosch), a deep-sea octopus. PhD Thesis. Dalhousie University, Halifax.
- Wood, J. B. and R. K. O'Dor. 2000. Do larger cephalopods live longer? Effects of temperature and phylogeny on interspecific comparisons of age and size at maturity. *Marine Biology* **136**:91-99.
- Young, R. E. 1973. Evidence for spawning by *Gonatus* species (Cephalopoda: Teuthoidea) in the High Arctic Ocean. *Nautilus* **87**:53-58.
- Zagata, C., C. Young, J. Sountis, and M. Kuehl. 2008. *Mytilus edulis* Animal Diversity Web. University of Michigan - Museum of Zoology. Accessed at http://animaldiversity.org/accounts/Mytilus_edulis/
- Zeidberg, L. D. and B. H. Robison. 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. *Proceedings of the National Academy of Sciences of the United States of America* **104**:12948-12950.
- Zuev, G. V. and K. N. Nesis. 2003. Squid (Biology and Fishing). Selected Translations of Publications on Cephalopods by Kir N. Nesis. Volume II. Smithsonian Washington, DC: Smithsonian Institution Libraries.
- Zumholz, K. and R. P. Frandsen. 2006. New information on the life history of cephalopods off west Greenland. *Polar Biology* **29**:169-178.

Zumholz, K., A. Klügel, T. Hansteen, and U. Piatkowski. 2007. Statolith microchemistry traces the environmental history of the boreoatlantic armhook squid *Gonatus fabricii*. *Marine Ecology Progress Series* **333**:195-204.

Appendix I

A concentration of large forms of five common cephalopods from the Canadian Arctic.

(Published 2010 Marine Biodiversity Records, Vol. 3; e37, co-author T.A. Dick; reproduced with permission from © Cambridge University Press; May 27, 2015)

*Note: The NAFO surveys discussed in this Appendix were conducted by Fisheries and Oceans Canada.

Abstract

Nine specimens belonging to four separate species and two genera from Davis Strait and Hudson Strait exceeded the known maximum recorded sizes for their associated species. New size records are given for *Bathypolypus pugniger*, *B. bairdii*, *B. arcticus* and *Cirroteuthis muelleri*. All individuals were found within the same basin (532 to 1453 m) within Davis Strait with the exception of *B. arcticus* which was found along the trench (284 to 388 m) that runs through the middle of Hudson Strait. Six large sized *Gonatus fabricii* were also found in the same region of Davis Strait, but did not exceed the maximum size of 385 mm, a female caught in the Norwegian Sea. Since these two regions are the only areas where such large individuals were found, we speculate that these areas are of particular interest as potential spawning sites and are oceanographically and biologically favourable for the maintenance of large individuals.

Introduction

Recent fishing and resource exploration in the Arctic Ocean has increased the need for a better understanding of the polar ecosystem and the interactions amongst the resident species. Cephalopods play an important role both as predator and prey to a variety of species including those of commercial importance to the Arctic region (Gardiner and Dick in press). As part of an ongoing study examining the biology and distribution of Canadian Arctic cephalopods (Gardiner

and Dick in press), three species of *Bathypolypus* Grimpe (*B. arcticus* Prosch, *B. bairdii* Verrill, and *B. pugniger*) and one *Cirroteuthis muelleri* Eschricht were found with individuals exceeding the normal size-range. Six large specimens of *Gonatus fabricii* Lichtenstein were also collected from Davis Strait. Fast growing, semelparous cephalopods are easily impacted by major marine ecological perturbations, i.e. increasing water temperatures and commercial fishing (Boyle and Boletzky 1996), and as a result, could conceivably collapse within a single year (Rodhouse and White 1995). Such impacts would also affect both their predators and prey (Boyle and Boletzky 1996) and may alter the exponential growth rates of their larval and juvenile stages (Wood and O'Dor 2000). This would then impact their size-at-maturity and thus their reproductive success (Wood and O'Dor 2000).

This note augments the current knowledge of the size and distribution of these Arctic cephalopods as well as speculates on the reasons why they are found in the same region.

Materials and Methods

Samples were obtained from by-catch of the NAFO Groundfish Surveys of the Hudson Strait and Davis Strait in 2007 and 2008 respectively. All cephalopods captured in Hudson Strait were brought back to the laboratory for morphometric analysis while only specimens from the southern extent of the 2008 Davis Strait – Baffin Bay survey were collected. Individuals collected from Davis Strait – Baffin Bay represented the size spectrum of the various species observed during the survey (M.A. Treble, personal communication, 2008).

In total, 101 stratified 25 minute bottom otter trawls produced 330 cephalopods in Hudson Strait from 14 October to 28 October 2007 (NAFO unpublished 2007). These 330

individuals represented three species (*Gonatus fabricii*, *Rossia palpebrosa* Owen and *Bathypolypus arcticus*), and were dominated by juvenile *G. fabricii*. The mean depth of the samples was 313.40 m with a range of 108 to 968 m and the average temperature was 1.26 °C with a range of –0.89 to 3.79 °C (NAFO 2007).

One hundred and eighty-three bottom otter trawls were conducted between 8 October and 4 November 2008 in Davis Strait – Baffin Bay and recovered 603 cephalopods, although not all individuals were collected for further study. The cephalopods sampled represented six species common to Canadian waters (*G. fabricii*, *B. bairdii*, *B. pugnifer*, *R. moelleri* Steenstrup, *R. palpebrosa* and *Cirrotheuthis muelleri*), with *G. fabricii*, again, the dominant species (Mercer 1968). The average bottom temperature was 0.86 °C with a range of –1.64 to 4.16 °C and a mean depth of 694.75 m with a range of 11 to 1474 m (NAFO unpublished 2008).

Maximum sizes were determined based on measurements from the most recent sources for the particular species. Historical metrics of *Bathypolypus* were based on the accounts of Muus (2002) while *Cirrotheuthis* was based on descriptions by Nesis (2001). All species measures for octopods (both cirrate and incirrate) are listed and include total length (TL) and mantle length (ML) as mantles can be distorted, while those of the decapods (i.e. *G. fabricii*) are listed as dorsal mantle length (ML) as per standard measures (Table 1).

Photographs and morphometric measurements were taken of the largest specimens (Figure 1). The specimens were preserved as museum vouchers, but were destroyed in a laboratory fire. However, smaller representative samples are preserved and will be placed in the Atlantic Reference Centre (ARC), St Andrew's, New Brunswick, Canada (accession numbers pending).

Results

Four large male *Bathypolypus pugniger* specimens were recorded from Davis Strait with the largest reaching 201 mm TL (Figure 1A; Table 1). All were collected between depths of 532 to 875 m at bottom temperatures ranging from 1.16 °C to 1.82 °C (Table 2).

The largest *B. bairdii* specimen from Davis Strait was a male with a TL of 210 mm and weighted 128.7 g (Figure 1C; Table 1). The female, although shorter (TL = 209 mm) was heavier, weighing 196 g (Table 1). Both *B. bairdii* specimens were collected at the same location from depths of 669 to 680 m and a bottom temperature of 1.4 °C (Table 2).

Two large specimens of *B. arcticus* (one male and one female) were collected from Hudson Strait (Figure 1D; Table 1). The largest (the female) had a TL of 229.4 mm (Table 1). The two individuals were collected at depths of 284 to 388 m (\bar{x} = 336 m) and at a mean bottom temperature of 1.36 °C (range 1.08 °C to 1.64 °C; Table 2). An additional female specimen, tentatively identified as *B. arcticus* based on external characteristics (Gardiner, unpublished) had a TL of 252.2 mm. This individual was collected between 270 and 274 m and at a temperature of -0.23 °C.

A single *Cirroteuthis muelleri* was collected in Davis Strait at ~1450 m depth (Table 2). It had a TL of 381 mm (Figure 1E; Table 1).

Six large *Gonatus fabricii* (Figure 1F) were collected from Davis Strait and had an average ML of 267.71 mm. The largest had a ML of 330 mm and was not sexually mature (Table 1).

Four specimens of *Bathypolypus pugniger* surpassed its known size-range of 150 mm TL by 51 mm (Table 1). Two *B. bairdii* specimens were collected nearby with the largest recorded at 210 mm TL, 10 mm greater than Muus (2002) described (Table 1). The largest *B. arcticus* specimen was 229.4 mm TL and exceeded the literature value of 200 mm TL (Table 1). One *Cirroteuthis muelleri* specimen from Baffin Bay was 381 mm and exceeded the literature value of 350 mm TL (Table 1).

Gonatus fabricii specimens were not larger than the maximum ML of 385 mm (Table 1) but were larger than those reported from a known breeding population in Disko Bay, Greenland (Zumholz and Frandsen 2006). The largest record from Disko Bay was a sexually mature male (257 mm pen length) (Zumholz and Frandsen 2006); while the largest, reported from the Norwegian Sea, was a mature female (385 mm ML; Table 1). The specimen in our study from Davis Strait, was 55 mm ML smaller than reported from the Norwegian Sea (Table 1) but 73 mm greater than described from Disko Bay (Zumholz and Frandsen 2006).

Discussion

The size of four cephalopod species across two genera exceeded the maximum size reported and the ubiquitous *G. fabricii* was near the maximum size. We speculate that further surveys in the high Arctic will produce even larger specimens of *Bathypolypus* spp., *C. muelleri* and especially *G. fabricii* since our samples did not have mature gonads. Perhaps *G. fabricii* exhibit similar maturation to *Moroteuthis ingens* from New Zealand waters that were reported to reach a certain mantle length before rapid gonadal development (Jackson 1997).

Since little information is available for *B. pugniger* and *C. muelleri* it was not surprising

that larger specimens would eventually be collected. *Gonatus fabricii* exceeded the largest size reported for breeding individuals from the adjacent, well-studied Disko Bay population (Kristensen 1982, Zumholz and Frandsen 2006). The addition of six large *G. fabricii* adds to the interest of the area. Previous work has identified two separate populations of this species; one in Amerdloq Fjord and the other in Disko Bay (Kristensen 1982). Although it is unclear why there are morphological differences (Kristensen 1982) it is possible, that the individuals caught in Davis Strait may also be a separate population as they were caught at >1000 m (Table 1) compared to a depth of < 541 m from Disko Bay (Zumholz and Frandsen 2006) and in water temperatures colder than 1 to 3 °C in Amerdloq Fjord (Kristensen 1982).

It is generally accepted that ectotherms become larger in cold conditions (Atkinson and Sibly 1997) but to find the largest specimens of four species, reported to date, from a relatively localized area of the Canadian Arctic is unexpected. Various factors may contribute to the large sizes, such as temperature, depth, cyclonic upwellings (food availability and productivity), latitude/longitude, response to predators and delayed sexual maturation and reproduction.

Bathypolypus bairdii and *B. pugniger* were found at similar depths and temperatures but *B. pugniger* was collected over a broader environmental range than *B. bairdii* (Table 2). *Bathypolypus pugniger* has been collected from Arctic overflow water (approximately -0.9 °C; Table 2) and may be able to tolerate colder temperatures than *B. bairdii*. By contrast, *B. bairdii* are usually recovered from waters with temperatures of 2 °C to 8 °C (Table 2). However, *B. bairdii* specimens recovered in Davis Strait were at temperatures of 1.4 °C (Table 2). Clearly *B. bairdii* has a wider thermal tolerance than previously thought and its range may extend further into the Arctic Ocean.

Bathypolypus arcticus specimens were found in relatively shallow, but colder waters than the other species (Table 2). These values agree with Muus (2002) who reported samples collected at -1.7 °C to 3 °C at 37 to 1210 m. This species, as with the other *Bathypolypus* species, is only found in shallow water at high latitudes where the temperature remains cold (Muus 2002). O'Dor and Macalaster (1983) established a maximum temperature of 12 °C for *B. arcticus* but also stated that it is rarely found above 6 °C. However, they were likely studying the more southern ranging *B. bairdii* as the study was done prior to the description by Muus (2002) of the *Bathypolypus* complex. If this genus behaves similarly to the southern ocean octopods examined by Strugnell et al. (2008), *Bathypolypus* spp. may move to deeper water if Arctic waters become warmer, altering its present distribution. The depth and temperatures at which *C. muelleri* specimens were collected are within the reported range (Table 2). *Cirroteuthis muelleri* has been reported from depths of 4846 m (Table 2) but Davis Strait does not exceed 1500 m in the more southern portion of the Strait (Jørgensen et al. 2005). It has been reported at temperatures of 0.04 °C (Table 2).

The *G. fabricii* specimens from Davis Strait were found at deeper depths (\bar{x} = 1335 m) than those reported from West Greenland (200–400 m) but not as deep as < 2700 m in the Norwegian Sea (Table 2). No references were found describing the preferred temperature range for *C. muelleri* and adult *G. fabricii* (Table 2).

Discovering large cephalopods specimens from the Canadian Arctic requires comment, albeit cautiously. Temperature, depth, hatch time, and high productivity (food) have been proposed to contribute to large size. Temperature is considered to be more important for distribution (Stewart et al. 1985, Strugnell et al. 2008), and size, than depth (Boyle and Boletzky

1996). For example squid adjust their depth to remain in their preferred temperature-range, as temperature decreases with depth and latitude. The Norwegian Sea is warmer and squid move deeper to find cooler water but the shallow water off West Greenland meets their temperature requirements (Kristensen 1983, Gyory et al. 2008). Similarly, *Bathypolypus* species occupy shallow waters at high latitudes (Nesis 2001).

Typically, warmer water promotes fast growth and maturation (Wood and O'Dor 2000). Perhaps cold Arctic waters slow maturation causing individuals to be older when they reach sexual maturity than those in warmer water. This allows more time to attain greater size before switching their energy to the production of gametes (Moltzchaniwskyi 2004). In laboratory rearing experiments, *Bathypolypus arcticus* (likely *B. bairdii*) was shown to speed up its maturation with increasing temperatures, producing a decrease in size and lifespan (Wood and O'Dor 2000). Our samples were recovered from cold deep water which is affected by the cold West Greenland Current and Baffin Island Current (Gyory et al. 2008). We speculate that sexual maturation takes several years rather than the typical 1–2 years expected for most cephalopods (Wood and O'Dor 2000), resulting in larger, older individuals. Large size could also be influenced by hatch time with late hatched individuals growing at a more rapid rate than those hatched earlier (Wood and O'Dor 2000). Perhaps these large specimens represent individuals that hatched later in the season when temperatures and food availability were optimal for growth.

Productivity is a factor of upwelling or water mixing from currents and eddies which provides greater nutrient flux and thereby greater quantities of food (Zuev and Nesis 2003). The sample locations are influenced by the West Greenland Current, some of which is deflected westward and mixes with the south flowing cold Baffin Current (Jørgensen et al. 2005). This

area of mixing and upwellings with increased productivity would be ideal for cephalopod feeding and dispersal (Zuev and Nesis 2003), especially for *G. fabricii*.

Clearly we are in the very early stages of understanding cephalopod biology and distribution in the Canadian and western Arctic Ocean, and it is likely that larger specimens of these and other cephalopod species will be discovered in the future.

Acknowledgements

The authors would like to thank Ms Margaret Treble and Mr Tim Siford (DFO—Winnipeg) for their help in the collection of samples on the North Atlantic Fisheries Organization (NAFO) surveys. T.A. Dick acknowledges financial support from a NSERC Northern Research Chair. We thank the referees for their constructive comments.

Table 1. Location, depth, sex, total length (TL) and mantle length (ML) of three *Bathypolypus* species, *Cirroteuthis muelleri* and *Gonattus fabricii* from Hudson Strait and Davis Strait, Canada.

Scientific name	Location	Latitude/longitude	Depth (m)	Sex	TL (mm) ¹	ML (mm) ²	Maximum values (Literature)
<i>Bathypolypus arcticus</i>	Hudson Strait	60.7705°N 66.9652°W	381–388	F	229.4 ($\mu = 217.67 \pm 16.59$) ³	62.89 ($\mu = 56.92 \pm 8.45$)	TL rarely over 200 mm ML rarely over 60–70 mm ^c
		61.6239°N 68.35892°W	284–286	M			
<i>Bathypolypus bairdii</i>	Davis Strait	66.4076°N 58.7193°W	669–680	M	210 ($\mu = 209.5 \pm 0.71$)	71.45 ($\mu = 63.75 \pm 10.89$)	TL rarely over 200 mm ML information not available ^c
		66.4076°N 58.7193°W	669–680	F			
<i>Bathypolypus pugniger</i>	Davis Strait	66.5753°N 57.7770°W	584–588	M	201 ($\mu = 185.25 \pm 13.23$)	60.6 ($\mu = 55.6 \pm 6.01$)	TL rarely over 150 mm ML rarely over 50 mm ^c
		66.8282°N 58.4714°W	868–875	M			
		66.2685°N 58.5336°W	532–565	M			
		66.5997°N 58.6365°W	720–725	M			
<i>Cirroteuthis muelleri</i>	Davis Strait	67.6992°N 59.6730°W	1451–1453	F	381	97.35	TL < 350 mm ML up to 150 mm ^b ML = 385 mm ^a
<i>Gonattus fabricii</i>	Davis Strait	67.6992°N 59.6730°W	1451–1453	F	526 ($\mu = 471.5 \pm 57.16$)	330 ($\mu = 293.17 \pm 40.37$)	
		67.5797°N 58.9948°W	1234–1239	F			
		67.8963°N 59.7932°W	1431–1436	F			

¹Largest individual total length (TL) for each species. ²Largest individual mantle length (ML) for each species. ³A single tentatively identified *B. arcticus* was recorded from Hudson Strait with a TL of 252.2 mm (59.56267°N 66.98367°W; 270–274 m depth).

^aSennikov *et al.* (1989); ^bNesis (2001); ^cMuus (2002).

Table 2. Temperature and depth-ranges for five Arctic cephalopod species comparing observed depth and temperatures to literature values.

Scientific name	N	Mean depth (m) ¹	Mean depth (m) (Literature)	Mean temperature (°C)	Mean temperature (°C) (Literature)
<i>Bathypolypus arcticus</i>	3	329 (284–388)	37–1210 m ⁸ (shallow water further north)	0.71 (–0.23–1.64)	Norwegian Sea DeepWater ^b (–1.7 to –1°C) ^d or Arctic Intermediate Water ^d (0 to 3°C) ^d
<i>Bathypolypus bairdii</i>	2	674.5 (669–680)	20–1545 m ⁸	1.4 ²	2°C–8°C ⁸
<i>Bathypolypus pugniger</i>	4	703.5 (532–875)	200–1000 m ⁸	1.42 (1.16–1.82)	Positive temperatures, occasional overflow of Arctic water ^a (–0.8 to –0.9°C) ⁸
<i>Cirroteuthis muelleri</i>	1	1452 (1451–1453)	500–4846 m; rarely at the surface ^{e,f}	0.04 ³	Range unknown; prefer cold water ^b
<i>Gonattus fabricii</i> (adult)	6	1335 (1234–1436)	Adults: 200–400 (West Greenland) ⁸ ; down to 2700 m (Norwegian Sea) ^a	0.135 (0.01–0.26)	1–5°C (West Greenland) ^b
(juvenile)		80–100 m ⁴			Juvenile 0.1°C–7.36°C surface temperatures ⁴

¹Combined depth-range from Table 1 values. ²Both *B. bairdii* were caught in the same location. ³Both *C. muelleri* were caught at the same depth.

⁴Surface temperatures warmer than at the depths they were caught.

^aKristensen (1983); ^bPiatkowski & Wieland (1993); ^cTomczak & Godfrey (2003); ^dBaum (2001); ^eCollins *et al.* (2001); ^fNesis (2001); ⁸Muus (2002); ^hCollins & Villanueva (2006).

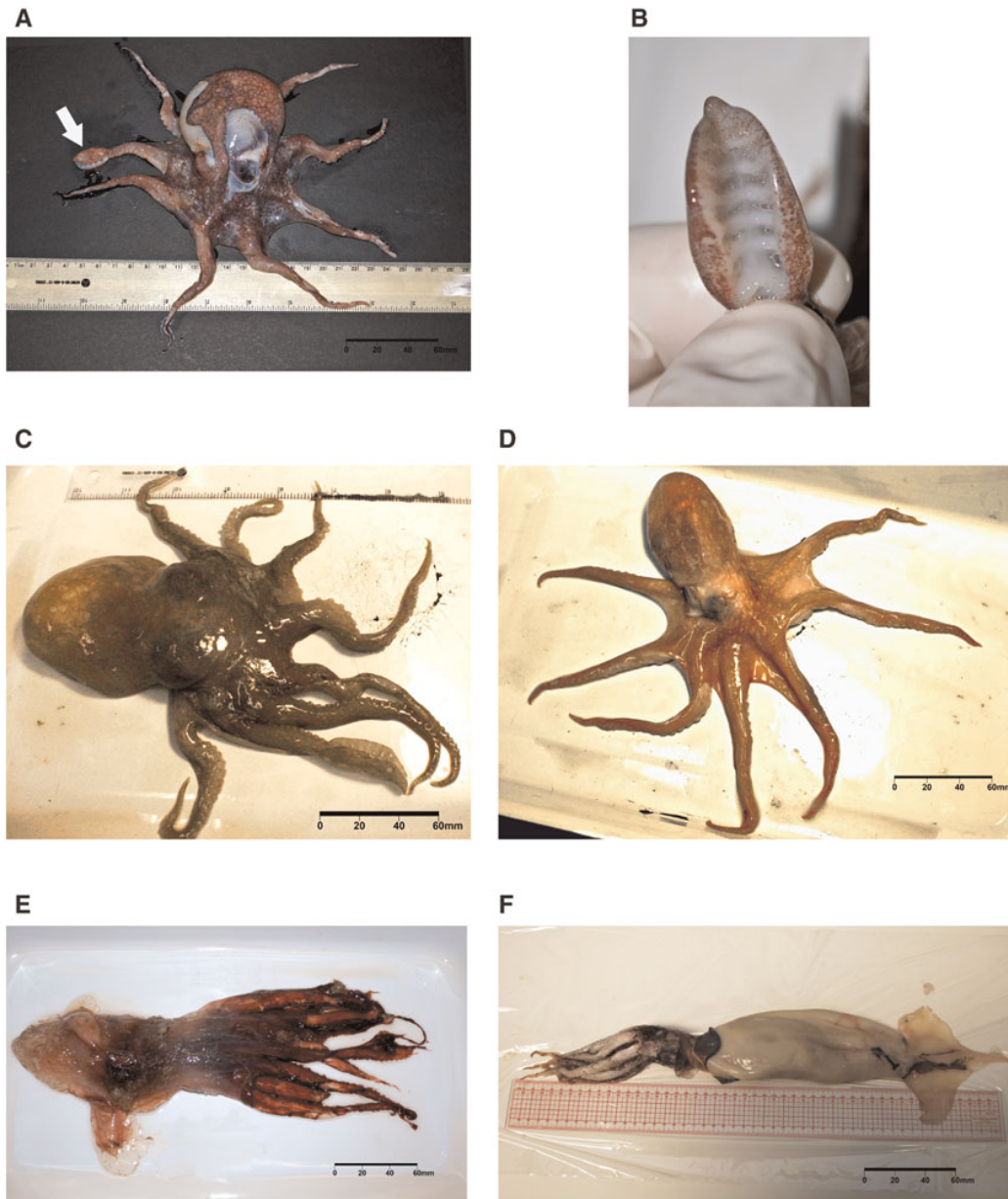


Fig. 1. The largest specimens of *Bathypolypus* spp. (A–D) collected in the eastern Canadian Arctic. (A) *B. pugniger*, arrow points to the ligula (enlarged in B); (C) *B. bairdii*; (D) *B. arcticus*; (E) *Cirroteuthis muelleri*; and (F) *Gonatus fabricii*. All specimens were collected during the NAFO fishery surveys in 2007 (Hudson Strait) and 2008 (Davis Strait).

References

Atkinson D. and Sibly R.M. (1997) Why are organisms usually bigger in cold environments? Making sense of a life history puzzle. *Trends in Ecology and Evolution* 12, 235–239.

Baum S.K. (2001) Glossary of oceanography and the related geosciences with references. <http://stommel.tamu.edu/~baum/paleo/ocean/ocean.html> (accessed May 2009).

Boyle P.R. and Boletzky S.v. (1996) Cephalopod populations: definition and dynamics. *Philosophical Transactions of the Royal Society, London: Biological Sciences* 351, 985–1002.

Collins M.A., Yau C., Allcock L. and Thurston M.H. (2001) Distribution of deep-water benthic and benthic-pelagic cephalopods from the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 81, 105–117.

Collins M.A. and Villanueva R. (2006) Taxonomy, ecology and behaviour of the cirrate octopods. *Oceanography and Marine Biology: an Annual Review* 44, 277–322.

Gardiner K. and Dick T.A. (in press) Arctic cephalopod distributions and their associated predators. *Polar Research*.

Gyory J., Mariano A.J. and Ryan E.H. (2008) The Norwegian and North Cape Currents. *Ocean Surface Currents*. <http://oceancurrents.rsmas.miami.edu/atlantic/norwegian.html> (accessed April 2009).

Jackson G.D. (1997) Age, growth and maturation of the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in New Zealand waters. *Polar Biology*, 17, 268–274.

Jørgensen O.A., Hvingel C., Møller P.R. and Treble M.A. (2005) Identification and mapping of bottom fish assemblages in Davis Strait and southern Baffin Bay. *Canadian Journal of Fisheries and Aquatic Science* 62, 1833–1852.

Kristensen T.K. (1982) Multivariate statistical analysis of geographic variation in the squid *Gonatus fabricii* (Lichtenstein, 1818) (Mollusca: Cephalopoda). *Malacologia* 22, 581–586.

Kristensen T.K. (1983) *Gonatus fabricii*. In Boyle P.R. (ed.) *Cephalopod life cycles: Volume 1 species accounts*. London: Academic Press, pp. 159–173.

Mercer M.C. (1968) A synopsis of the recent cephalopoda of Canada. *Proceedings of the Symposium on Mollusca. Marine Biological Association of India* 1, 265–276.

Moltzchanivskyi N.A. (2004) Understanding the process of growth in cephalopods. *Marine and Freshwater Research* 55, 379–386.

Muus B.J. (2002) The Bathypolypus – *Benthooctopus* problem of the North Atlantic (Octopodidae, Cephalopoda). *Malacologia* 44, 175–222.

Nesis K.N. (2001) West-Arctic and East-Arctic distributional ranges of cephalopods. *Sarsia* 86, 1–11.

O’Dor R. and Macalaster E. (1983) *Bathypolypus arcticus*. In Boyle P.R. (ed.) Cephalopod life cycles. Volume 1: species accounts. London: Academic Press, pp. 401–410.

Piatkowski U. and Wieland K. (1993) The Boreoatlantic gonate squid *Gonatus fabricii*: distribution and size off West Greenland in summer 1989 and in summer and autumn 1990. *Aquatic Living Resource* 6, 109–114.

Rodhouse P.G. and White M.G. (1995) Cephalopods occupy the ecological niche of epipelagic fish in the Antarctic polar frontal zone. *Biological Bulletin. Marine Biological Laboratory, Woods Hole* 189, 77–80.

Sennikov A.M., Mukhin S.G. and Bliznichenko T.E. (1989) Distribution and trophic importance of juvenile squid (*Gonatus fabricii* Lichtenstein) in the Norwegian and Barents Seas in 1986–1988. *ICES CM* 1989/K, 15.

Stewart P.L., Pocklington P. and Cunjak R.A. (1985) Distribution, abundance and diversity of benthic macroinvertebrates on the Canadian continental shelf and slope of southern Davis Strait and Ungava Bay. *Arctic* 38, 281–291.

Strugnell J.M., Rogers A.D., Prodohl P.A., Collins M.A. and Allcock A.L. (2008) The thermohaline expressway: the Southern Ocean as a centre of origin for deep-sea octopuses. *Cladistics* 24, 853–860.

Tomeczak M. and Godfrey J.S. (2003) Arctic oceanography; the path of North Atlantic Deep Water. In *Regional oceanography: an introduction*. 2nd edition, pp. 83–103.
<http://www.es.flinders.edu.au/~mattom/regoc/pdfversion.html>

Wood J.B. and O’Dor R.K. (2000) Do larger cephalopods live longer? Effects of temperature and phylogeny on interspecific comparisons of age and size at maturity. *Marine Biology* 136, 91–99.

Zuev G.V. and Nesis K.N. (2003) Squid (biology and fishing). Selected Translations of Publications on Cephalopods by Kir N. Nesis. Volume II. Washington, DC: Smithsonian Institution Libraries.

Zumholz K. and Frandsen R.P. (2006) New information on the life history of cephalopods off West Greenland. *Polar Biology* 29, 169–178.