

VARIATION IN THE TROPHIC POSITION OF SPINY DOGFISH (*SQUALUS*
ACANTHIAS) IN THE NORTHEASTERN PACIFIC OCEAN: AN APPROACH USING
CARBON AND NITROGEN STABLE ISOTOPES

By

Alexander George Andrews III

RECOMMENDED:

Dr. Gordon H. Kruse

Dr. Matthew J. Wooller

Dr. Nicola Hillgruber, Advisory Committee Co-Chair

Dr. Robert J. Foy, Advisory Committee Co-Chair

Dr. Trent M. Sutton, Program Head, Fisheries Division

APPROVED:

Dr. Michael A. Castellini
Dean, School of Fisheries and Ocean Sciences

Dr. Lawrence K. Duffy, Dean of the Graduate School

Date

VARIATION IN THE TROPHIC POSITION OF SPINY DOGFISH (*SQUALUS*
ACANTHIAS) IN THE NORTHEASTERN PACIFIC OCEAN: AN APPROACH USING
CARBON AND NITROGEN STABLE ISOTOPES

A
THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By

Alexander G. Andrews III

Fairbanks, Alaska

December 2010

Abstract

Spiny dogfish (*Squalus acanthias*) are among the most abundant shark species in the Gulf of Alaska (GOA). An increase in relative biomass of spiny dogfish in 2003 and 2007 inspired interest in this species as a commercial resource. However, very little was known about the ecology of this species in the GOA. This study investigated the trophic role of spiny dogfish in the GOA, British Columbia (BC), and Washington using stable isotope analysis of carbon and nitrogen. Specifically, we examined the trophic position (TP) of spiny dogfish in relation to length, sex, and geographic region. Weathervane scallops (*Patinopecten caurinus*) were used as a stable isotopic baseline organism. Spiny dogfish between 52 to 113 cm length had $\delta^{15}\text{N}$ values that ranged geographically from 10.8‰ to 15.6‰; $\delta^{15}\text{N}$ was linearly related to length. In contrast, lipid-normalized $\delta^{13}\text{C}$ values ranged from -21.2‰ to -16.8‰ and were not linearly related to length. In the GOA, TP of spiny dogfish ranged from 3.3 to over 4.1, with Kodiak having the highest TPs for spiny dogfish of a given length. Our results indicated that size-based ontogenetic changes in TP of spiny dogfish are important and should be incorporated into mass-balance, food-web models such as Ecopath.

Table of Contents

	Page
Signature Page	i
Title Page	ii
Abstract	iii
Table of Contents	iv
List of Figures	vii
List of Tables	viii
List of Appendices	ix
Acknowledgements	x
General Introduction	1
Chapter 1	11
1.1 Abstract	11
1.2 Introduction	13
1.3 Methods	17
1.4 Results/Discussion	18
1.4.1 Isotopic differences between sexes in Yakutat Bay	18
1.4.2 Isotopic differences among sites	19
1.4.3 Trophic level and diet implications	20
1.4.4 Food-web and habitat implications	21
1.4.5 Spatial gradients in other ecosystems	23
1.5 Conclusion	23

	Page
1.6 Acknowledgements.....	25
1.7 References.....	30
Chapter 2.....	37
2.1 Abstract.....	37
2.2 Introduction.....	39
2.3 Materials and Methods.....	45
2.3.1 Sample collection.....	45
2.3.2 Sample processing and stable isotope analysis.....	46
2.3.3 Trophic position calculation	48
2.3.4 Lipid normalization.....	48
2.3.5 Statistical analysis.....	49
2.3.5.1 Weathervane scallops.....	49
2.3.5.2 Spiny dogfish	50
2.3.5.2.1 Interannual variation	50
2.3.5.2.2 Linear relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and length	51
2.3.5.2.3 Differences between sexes.....	51
2.3.5.2.4 Differences among sites.....	51
2.4 Results.....	52
2.4.1 Weathervane scallops.....	52
2.4.2 Spiny dogfish	53
2.4.2.1 Summary of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$	53

	Page
2.4.2.2 Interannual variation of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$	54
2.4.2.3 Relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and length.....	54
2.4.2.4 $\delta^{15}\text{N}$ differences between sexes	55
2.4.2.5 Isotopic differences among sites.....	55
2.4.2.6 Adjusted trophic position.....	56
2.5 Discussion.....	56
2.6 Acknowledgements.....	68
2.7 References.....	85
Appendices.....	98
General Conclusions	103

List of Figures

	Page
1.1 Sampling locations.....	26
1.2 Mean (SE) $\delta^{13}\text{C}$ values and $\delta^{15}\text{N}$ values for male and female spiny dogfish	27
1.3 Mean (SE) $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ values of male spiny dogfish	28
2.1 Number and location of spiny dogfish sampled in the Gulf of Alaska.....	69
2.2 Approximate locations of weathervane scallop samples	70
2.3 Weathervane scallop $\delta^{15}\text{N}$ values for 2004 and 2005	71
2.4 Weathervane scallop $\delta^{15}\text{N}$ values in the Gulf of Alaska.....	72
2.5 Weathervane scallop $\delta^{15}\text{N}$ values in the pooled NMFS regulatory areas.....	73
2.6 Spiny dogfish $\delta^{13}\text{C}'$ (lipid-normalized $\delta^{13}\text{C}$) values.....	74
2.7 Linear relationship between spiny dogfish $\delta^{15}\text{N}$ and length.....	75
2.8 Linear relationship between spiny dogfish $\delta^{13}\text{C}$ and length	76
2.9 Linear relationship between spiny dogfish $\delta^{13}\text{C}'$ (lipid normalized) and length.	77
2.10 $\delta^{15}\text{N}$ differences between sexes	78
2.11 Boxplot of $\delta^{13}\text{C}'$ (lipid-normalized $\delta^{13}\text{C}$) values.....	79
2.12 Fitted linear relationships.....	80

List of Tables

	Page
1.1 Mean (SD) of stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of spiny dogfish	29
2.1 Spiny dogfish sample sizes (N) at each site.....	81
2.2 Sample site and region, date, bottom depth, and mean $\delta^{15}\text{N}$	82
2.3 Parameters, test statistics, and sample sizes (N) for linear relationships.....	83
2.4 Pairwise comparisons of $\delta^{13}\text{C}'$ (lipid-normalized $\delta^{13}\text{C}$) values among sites.....	84

List of Appendices

	Page
A.1 Sampling site, date, gear, and sample location	98
A.2 Specimen ID number, carbon and nitrogen ratio (C:N), and isotopes.....	100

Acknowledgements

I thank my co-advisors Dr. Nicola Hillgruber and Dr. Robert Foy for providing advice and guidance throughout this process. I wish to express my deepest gratitude to Dr. Nicola Hillgruber. She joined my committee at a key point in time and encouraged me to persevere and write. Additionally, she provided excellent editing assistance and promoted my ability to think critically. I could not have completed this thesis without her help. I thank Dr. Robert Foy for the numerous memorable discussions on topics ranging from sample sizes to food-webs; these conversations were crucial and guided my design of this study. My committee members Dr. Matthew Wooller and Dr. Gordon Kruse provided keen scientific acumen. I value Dr. Matthew Wooller's enthusiasm regarding the use of stable isotope techniques in ecology as well as his eye for simple yet telling experimental design. I thank Dr. Gordon Kruse for sharing both his vast knowledge of fisheries in Alaska and his insights into what types of biological information are important.

A number of people helped with sample collections. First and foremost, I thank Cindy Tribuzio (NOAA-ABL) for graciously offering spiny dogfish samples and data collected in her concurrent doctorate study at the UAF-SFOS. Thanks to ADFG-Kodiak, Greg Bargmann (WA-WDFW), Dean Courtney (NOAA-ABL), Vince Gallucci (UW), Jackie King (DFOS), and Nicole Vega (UW) for providing and assisting with spiny dogfish sample collection. Thanks to Jeff Barnhart (ADFG-Kodiak) for assisting with the collection of weathervane scallops. Also, my great appreciation to NOVA Fisheries Inc. for providing weathervane scallop samples. Tremendous thanks to Mr. Tom Minio (F/V

Provider), and Mr. John Lemar and Mr. Glenn Mikkelson (F/V Ocean Hunter); these captains voluntarily collected scallop samples at no cost.

I am grateful for the statistical advice provided by Franz Mueter (UAF-SFOS) and Terry Quinn (UAF-SFOS). This project would not have been possible without the expertise of Norma Haubenstock and Tim Howe at the UAF-Alaska Stable Isotope Facility. They welcomed me to the lab and guided me through the process of prepping samples. I valued lab meetings with fellow graduate students and especially appreciated discussions with Jen Marsh, Andrew Eller, Ashwin Sreenivasan, and Wes Strasburger. Also, thanks to Gabrielle Hazelton and Louisa Hayes at UAF-SFOS for all the administrative support that they have provided over the years. Funding was provided by the Cooperative State Research, Education and Extension Service, U.S. Department of Agriculture. I would also like to thank my colleagues at NOAA-ABL for supporting me during the writing stage of this project.

I truly would not have been able to achieve this goal without the unfaltering support and patience of my wife, Ellen Andrews. I am extremely grateful (and indebted) to my parents Alex and Joanne Andrews for supporting me during this endeavor; they have always believed in me and my abilities.

General Introduction

In 2005 at the onset of this project, total biomass estimates of spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska (GOA) based on the 2003 National Marine Fisheries Service trawl survey data peaked at an all-time high of 99,000 metric tons (mt). After declining in 2005, biomass estimates in 2007 again increased to a new peak of 162,000 mt (Tribuzio et al. 2009). Although surrounded by a large degree of uncertainty, these biomass estimates still generated interest in the commercial harvest of this species in the GOA. In addition, many fishing communities in the GOA voiced concerns about increasing catches of spiny dogfish and the potential impact this species might exert on fish species targeted by the sport and commercial fisheries. Yet, little was known about spiny dogfish in the waters of the GOA. Most of the biological information available on this species was collected from outside the GOA from studies in British Columbia, Washington, or even farther away in the Atlantic Ocean (Bonham 1954; Jones and Geen 1977; Bowman et al. 1984). Consequently, it was apparent that a better understanding of this species in the GOA was needed to address questions about potential commercial harvest or predatory impact of spiny dogfish in the GOA.

Spiny dogfish are distributed throughout temperate and subarctic latitudes in the Pacific and Atlantic oceans occurring at depths to 675 m (Castro 1983). Along the west coast of North America, spiny dogfish range from Baja California to the Bering Sea, west along the Aleutians to Russia, and south to Japan (Castro 1983). As generalist opportunists, spiny dogfish predate upon a variety of prey items that include fishes, mollusks, and crustaceans (Bonham 1954; Jones and Geen 1977; Tribuzio 2010). As

spiny dogfish grow and mature, they shift from diets of predominantly pelagic to more demersal prey items (Beamish and Sweeting 2009), target larger prey items, and ingest primarily fishes (Bowman et al. 1984; Alonso et al. 2002; Tribuzio 2010). These include some of the key forage species in the North Pacific ecosystem, such as Pacific herring (*Clupea pallasii*) and capelin (*Mallotus villosus*) that many piscivorous fishes, seabirds, and marine mammals also depend upon (Jones and Geen 1977).

The life-history parameters of spiny dogfish likely influence the vulnerability of this species to commercial fishing. They are slow growing, late maturing, and long lived (McFarlane and Beamish 1987). In the GOA, the age and length at 50% maturity for females (males) is 36 (21) years and 97 (75) cm (total length extended), respectively (Tribuzio 2010). In British Columbia, maximum ages are in excess of 80 years (McFarlane and Beamish 1987). Spiny dogfish also have a low fecundity (1-15 pups) and a 22-24 month gestation period (Holden 1977; Tribuzio 2004). Management must carefully consider these life-history parameters to insure the sustainability of a potential commercial fishery targeting this species.

Targeted fisheries for spiny dogfish have occurred in both the North Atlantic and North Pacific Oceans. In the northwestern Atlantic Ocean, U.S. commercial catches increased five-fold in the late eighties and early nineties (Rago et al. 1998), peaking at 27,000 mt in 1996 (NMFS 2001). In 1998, this fishery was declared over-fished and a fishery management plan that reduced catch limits was adopted in early 2000 (ASMFC 2002). Early in the 20th century, development of fisheries on the west coast of North America was driven primarily by the need for spiny dogfish liver oil, which was used in a

variety of applications, including machine oil, illumination, and tanning (Castro 1983). By World War II, intense fisheries along the west coast targeted spiny dogfish for vitamin A found in their liver. By the late 1940s, these fisheries declined due to reduced numbers of spiny dogfish, importation of vitamin A, and the production of synthetic vitamin A (Castro 1983; Ketchen 1986). In the mid-1970s, west coast fisheries began again harvesting spiny dogfish for food for export to Europe (Ketchen 1986). At present, spiny dogfish fisheries in British Columbia and Washington continue, although there is evidence that some of the stocks targeted in Washington's inland marine waters have declined (Palsson 2009).

Alaska has no directed fisheries for spiny dogfish, however, this species can be retained as bycatch in both state and federally managed waters. An exception to this is the availability of an Alaska Department of Fish and Game Commissioner's Permit for the Cook Inlet region, which allows a small-scale targeted spiny dogfish fishery; however, to date, this has not attracted much interest. In federal waters of the GOA, spiny dogfish are managed as part of the combined shark complex that includes Pacific sleeper sharks (*Somniosus pacificus*), salmon sharks (*Lamna ditropis*), and spiny dogfish. On average, spiny dogfish comprise 53% of the total shark catch (Tribuzio et al. 2010). Decreases or increases in the abundance and biomass of one or several species can upset the balance in the ecosystem and may lead to a re-structuring of ecological communities (Fogarty and Murawski 1998; Frank et al. 2005). Understanding catches of predators, such as sharks, are particularly important as their abundance can influence the GOA ecosystem through top-down processes (Myers et al. 2007). Clearly, there is a need to improve our

understanding of the biology of spiny dogfish in the GOA before a targeted fishery may be implemented; research into the life-history of spiny dogfish should include, but not be limited to, the trophic role of these sharks in the northeastern Pacific Ocean.

Nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) stable isotope ratios have been used as a tool to describe food-web linkages, trophic status, and source of primary production (DeNiro and Epstein 1978; DeNiro and Epstein 1981; Rau et al. 1992). It is possible to construct food-webs and determine trophic status using the enrichment properties of ^{15}N , as there is typically an enrichment between prey and consumer of $3.4 \pm 1.1\text{‰}$ (Minagawa and Wada 1984). Also, planktonic phytoplankton is depleted in ^{13}C relative to benthic sources and therefore, $\delta^{13}\text{C}$ can be used to distinguish between different sources of primary productivity at the base of the food-web (France 1995). Sources of primary productivity provide the initial $\delta^{15}\text{N}$ values that are propagated up the food chain; therefore, it is important to understand how $\delta^{15}\text{N}$ values vary at the base of the food chain and to determine an isotopic baseline (Cabana and Rasmussen 1996; Post 2002). This is especially important when a study encompasses a large geographic area. Trophic roles of elasmobranchs are often explored using TP based on gut content analysis (Cortes 1999); however, a number of studies have established that nitrogen stable isotope analysis is a useful tool in determining the TP of elasmobranchs as a reliable alternative method to gut content analysis (Rau et al. 1983; Fisk et al. 2002; Estrada et al. 2003; MacNeil et al. 2005).

Potential changes in spiny dogfish biomass and the relative lack of biological information specific to the GOA provided the impetus for this thesis and a companion study (Tribuzio 2010). In addition, findings of a panel exploring ecosystem-based management practices have provided specific data requirements needed for improving fishery management. These recommendations included developing a conceptual model of the food-web at each life-history stage over time and describing how removals will affect the trophic structure (NMFS 1999). The findings demonstrate the necessity of studies that explore the trophic role of marine species of a range of size classes. In Chapter 1, I focus on assessing the large-scale geographical variation in TP of spiny dogfish in the northeastern Pacific Ocean. In an effort to limit the variables affecting the results, this initial work focused on a narrow size range of mostly males from several sites in Washington, British Columbia, and the eastern Gulf of Alaska. In Chapter 2, I broadened my sampling to include a large size range of both males and females from sampling sites ranging from Kodiak Island to British Columbia. Specifically, my objectives for this chapter were (1) to examine the effects of length and sex on the TP of spiny dogfish and (2) to assess large-scale geographical differences in TP of spiny dogfish in the Alaskan waters of the GOA. My results demonstrate the importance of size-based ontogenetic changes in TP of spiny dogfish in the northeastern Pacific Ocean.

References

Alonso, M. K., E. A. Crespo, N. A. Garcia, S. N. Pedraza, P. A. Mariotti, and N. J. Mora. 2002. Fishery and ontogenetic driven changes in the diet of the spiny dogfish,

- Squalus acanthias*, in Patagonian waters, Argentina. *Environmental Biology of Fishes* 63(2):193-202.
- ASMFC (Atlantic States Marine Fisheries Commission). 2002. Interstate fishery management plan for spiny dogfish. Atlantic States Marine Fisheries Commission. Washington, DC.
- Beamish, R. J., and R. M. Sweeting. 2009. Spiny dogfish in the pelagic waters of the Strait of Georgia and Puget Sound. Pages 101-118 in V. F. Gallucci, G. A. McFarlane, and G. G. Bargmann, editors. *Biology and management of dogfish sharks*. American Fisheries Society, Bethesda, Maryland.
- Bonham, K. 1954. Food of the dogfish *Squalus acanthias*. *Fisheries Research Papers* 1(2):25-36.
- Bowman, R., R. Eppi, and M. Grosslein. 1984. Diet and consumption of spiny dogfish in the Northwest Atlantic. ICES C.M.1984/G:27, Copenhagen, Denmark.
- Cabana, G., and J. B. Rasmussen. 1996. Comparison of aquatic food chains using nitrogen isotopes. *Proceedings of the National Academy of Sciences* 93(20):10844-10847.
- Castro, J. I. 1983. *The sharks of North American waters*. Texas A&M University Press, College Station.
- Cortes, E. 1999. Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science* 56(5):707-717.
- 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(3):341-351.
- Estrada, J. A., A. N. Rice, M. E. Lutcavage, and G. B. Skomal. 2003. Predicting trophic position in sharks of the north-west Atlantic Ocean using stable isotope analysis. *Journal of the Marine Biological Association of the United Kingdom* 83(6):1347-1350.
- Fisk, A. T., S. A. Tittlemier, J. L. Pranschke, and R. J. Norstrom. 2002. Using anthropogenic contaminants and stable isotopes to assess the feeding ecology of Greenland sharks. *Ecology* 83(8):2162-2172.
- Fogarty, M. J., and S. A. Murawski. 1998. Large-scale disturbance and the structure of marine systems: Fishery impacts on Georges Bank. *Ecological Applications* 8(1, supplement):S6-S22.
- France, R. L. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Marine Ecology Progress Series* 124(1-3):307-312.
- Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308:1621-1623.
- Holden, M. J. 1977. Elasmobranchs. Pages 187-215 in A. Gulland, editor. *Fish population dynamics*. J. Wiley and Sons, New York.
- Jones, B. C., and G. H. Geen. 1977. Food and feeding of spiny dogfish (*Squalus acanthias*) in British Columbia waters. *Journal of the Fisheries Research Board of Canada* 34(11):2067-2078.

- Ketchen, K. S. 1986. The spiny dogfish (*Squalus acanthias*) in the Northeast Pacific and a history of its utilization. Canadian Special Publication of Fisheries and Aquatic Sciences 88:78 p. Ottawa
- MacNeil, M. A., G. B. Skomal, and A. T. Fisk. 2005. Stable isotopes from multiple tissues reveal diet switching in sharks. Marine Ecology Progress Series 302:199-206.
- McFarlane, G. A., and R. J. Beamish. 1987. Validation of the dorsal spine method of age determination for spiny dogfish. Pages 287-300 in R. C. Summerfelt, and G. E. Hall, editors. The Iowa State University Press, Ames.
- 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.
- Myers, R. A., J. K. Baum, T. D. Shepherd, S. P. Powers, and C. H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315(5820):1846-1850.
- NMFS (National Marine Fisheries Service). 1999. Ecosystem-based fishery management: a report to Congress by the ecosystem principles advisory panel. National Marine Fisheries Service, Washington DC.
- NMFS (National Marine Fisheries Service). 2001. United States National Plan of Action for the Conservation and Management of Sharks, Silver Spring, Maryland.

- Palsson, W. A. 2009. The status of spiny dogfish in Puget Sound. Pages 53-65 in V. F. Gallucci, G. A. McFarlane, and G. G. Bargmann, editors. Biology and management of dogfish sharks. American Fisheries Society, Bethesda, Maryland.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83(3):703-718.
- Rago, P. J., K. A. Sosebee, J. K. T. Brodziak, S. A. Murawski, and E. D. Anderson. 1998. Implications of recent increases in catches on the dynamics of Northwest Atlantic spiny dogfish (*Squalus acanthias*). *Fisheries Research* 39:165-181.
- Rau, G. H., D. G. Ainley, J. L. Bengtson, J. J. Torres, and T. L. Hopkins. 1992. $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. *Marine Ecology Progress Series* 84:1-8.
- Rau, G. H., and coauthors. 1983. Animal $^{13}\text{C}/^{12}\text{C}$ correlates with trophic level in pelagic food webs. *Ecology* 64(5):1314-1318.
- Tribuzio, C. A. 2004. An investigation of the reproductive physiology of two North Pacific shark species: spiny dogfish (*Squalus acanthias*) and salmon shark (*Lamna ditropis*). Master's thesis. University of Washington, Seattle.
- Tribuzio, C. A. 2010. Life history, demography, and ecology of the spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska. Doctoral dissertation. University of Alaska Fairbanks, Fairbanks.
- Tribuzio, C. A., K. Echave, C. Rodgveller, J. Heifetz, and K. Goldman. 2010. Gulf of Alaska Stock Assessment and Fishery Evaluation Report. North Pacific Fishery Management Council, Seattle, Washington.

Tribuzio, C. A., C. Rodgveller, J. Heifetz, and K. Goldman. 2009. Gulf of Alaska Stock Assessment and Fishery Evaluation Report. North Pacific Fishery Management Council, Seattle, Washington.

Chapter 1

Geographical variation in the carbon and nitrogen stable isotope ratios in spiny dogfish in the northeastern Pacific Ocean¹

1.1 Abstract

Spiny dogfish *Squalus acanthias* biomass has increased in the Gulf of Alaska, yet little is known about the ecological niche that dogfish fill in this ecosystem. Trophic position is an important indicator of the ecological role of an organism. To explore the trophic position of dogfish, we analyzed the nitrogen and carbon stable isotope ratios of 60 dogfish from five locations between Washington and the Gulf of Alaska. The mean $\delta^{15}\text{N}$ values for dogfish ranged from 12.0‰ (central Gulf of Alaska) to 13.4‰ (Howe Sound, British Columbia) and the mean $\delta^{13}\text{C}$ values ranged from -21.3‰ (Yakutat Bay, Alaska) to -17.9‰ (Puget Sound, Washington). Sites to the north tended to be significantly depleted in the heavy isotopes of both nitrogen and carbon. The differences in nitrogen isotope ratios among sites were attributed to potential changes in dogfish feeding behavior and trophic position. Differences in carbon isotope ratios suggested that dogfish utilize different food-webs along the northeastern Pacific Ocean shelf.

Additionally, it was hypothesized that feeding differentially in offshore versus inshore food-webs or targeting pelagic versus benthic prey species may explain the isotopic

¹Andrews, A. G. III and R. J. Foy. 2009. Geographical variation in the carbon and nitrogen stable isotope ratios in spiny dogfish in the northeastern Pacific Ocean. Pages 269-276 in V. F. Gallucci, G. A. McFarlane, and G. G. Bargmann, editors. Biology and management of dogfish sharks. American Fisheries Society, Bethesda, Maryland.

variability. These results are preliminary and require additional tests before conclusions can be made about the trophic position of dogfish in this region. Future work will explore stable isotope variability at lower trophic levels to test the hypothesis that entire food-webs are isotopically shifted owing to differences in isotopic fractionation at the base of the food-web. Also, trophic level differences among dogfish size classes and between sexes will be explored among a greater diversity of locations to better describe the ecological consequences of increased biomass of dogfish in the northeastern Pacific Ocean.

1.2 Introduction

Spiny dogfish *Squalus acanthias* have been one of the most abundant and economically important species of shark in North American waters (Castro 1983). Dogfish are distributed throughout temperate and subarctic latitudes in the Pacific and Atlantic Oceans occurring at depths to 1,244 m (Castro 1983; Mecklenburg et al. 2002). Fisheries catches in British Columbia suggest that a greater proportion of dogfish occur at 20 m in the summer and 100 m in the winter (Ketchen 1986). Along the west coast of North America, dogfish range from Baja California to the Bering Sea, west along the Aleutians to Russia, and south to Japan (Castro 1983).

Shark populations throughout the world have received a great deal of attention because of their relative trophic position and the effects of fishing on population biomass (Kitchell et al. 2002). In the Gulf of Alaska (GOA), spiny dogfish biomass estimates are variable and have shown an increasing trend in recent years. Biomass estimates from groundfish surveys have ranged from 19,000 to 162,000 metric tons (mt) between 1990 and 2007 (Courtney et al. 2006; Conrath and Foy 2009). The incidental catch in commercial fisheries over a similar period from 1997 to 2006 was variable yet increased substantially from 117 mt in 2002 to 1,324 mt in 2006. Estimates of abundance from stock-assessment models based on incidental catch were also variable and much higher than estimates based only on survey or catch per unit effort (CPUE) (Rice et al. 2009). The apparent increasing biomass trend and the spike in incidental catch have led to interest by some commercial groups in developing dogfish fisheries in Alaska.

While increasing numbers of spiny dogfish may suggest a targeted fishery could

be viable, the vulnerability of sharks to overfishing (Walker 1998; Musick et al. 2000) makes it imperative that managers proceed with caution. Dogfish are slow growing, late maturing, and long lived (McFarlane and Beamish 1987). In British Columbia, the age and length at 50% maturity for females is 35.5 years and 93.9 cm (total length extended) (Saunders and McFarlane 1993) and maximum ages are in excess of 80 years (McFarlane and Beamish 1987). Dogfish have a low fecundity (1–15 pups) and a 22–24 month gestation period (Holden 1977; Tribuzio et al. 2009). Management should carefully consider these life-history characteristics along with the ecological role of dogfish to ensure sustainability of potential fisheries and appropriate conservation of the species.

To better understand the effects of increased spiny dogfish biomass on the North Pacific ecosystem, studies should be focused on the ecological niche that dogfish fill. Specifically, little is known about the trophic role of dogfish in the northeastern Pacific Ocean. In many marine systems, sharks are considered top predators (Hinman 1998; Cortés 1999) that have an important role in structuring the community (Frank et al. 2005). During the 1970s, 1980s, and 1990s off the coast of New England, the Georges Bank fish community changed significantly from a gadid and flatfish dominated system to a system dominated by skates and small sharks, including dogfish (Fogarty and Murawski 1998; Collie and DeLong 1999). In the 1990s, increasing dogfish fisheries and their subsequent collapse contributed to additional ecosystem level reorganizations of the marine community occupying the Georges Bank. Although sharks are an important consumer and considered to be a top predator in marine food-webs, the trophic position of many sharks is unknown (Cortés 1999).

Spiny dogfish are opportunistic feeders that consume a wide range of prey items that include: small schooling fishes, hake, cod, flatfishes, juvenile salmon, crabs, shrimp, euphausiids, jellyfish, ctenophores, octopus, and squid (Bonham 1954; Jones and Geen 1977). Independent studies in the Atlantic and Pacific oceans have indicated that diet compositions are dependent on the availability of different prey (Jones and Geen 1977; Bowman et al. 1984; Alonso et al. 2002). Furthermore, diet shifts have been correlated with ontogenetic changes. In British Columbia, larger dogfish had a greater proportion of fishes in their diet and tended to feed more demersally than smaller dogfish (Jones and Geen 1977). Seasonal variation in the diet and the diversity of prey items consumed (Jones and Geen 1977) suggest that increased spiny dogfish biomass and subsequent total consumption by dogfish might impact numerous northeastern Pacific species.

Effective management of spiny dogfish and their commercially important prey will require ontogenetic and spatially specific data on their diet and trophic position. Trophic levels of sharks have been calculated by combining diet analyses with published data on the trophic level of each prey category (Cortés 1999). Alternatively, stable isotope analysis has been used to predict the trophic level of sharks including blue shark *Prionace glauca*, shortfin mako *Isurus oxyrinchus*, thresher shark *Alopias vulpinus*, basking shark *Cetorhinus maximus* (Rau et al. 1983; Estrada et al. 2003), Greenland shark *Somniosus microcephalus* (Fisk et al. 2002), and spiny dogfish (Fry 1988). Estimation of shark trophic level based on stable isotope values was not different from direct observations of stomach contents (Estrada et al. 2003). Stable isotope analyses integrate feeding patterns over longer periods and are thus more appropriate for trophic

level assessment than other methods (Polunin and Pinnegar 2000). This suggests that stable isotope analysis is appropriate to quantify the diet and trophic position of dogfish (also see Hazlett et al. 2009).

Stable isotopes of nitrogen and carbon are used to describe food-webs and to determine the source of primary production (DeNiro and Epstein 1978; DeNiro and Epstein 1981; Fry and Sherr 1984; Fry 1988; Rau et al. 1992). Typically, there is an average 3.4‰ enrichment of ^{15}N from prey to consumer (Minagawa and Wada 1984) due to the preferential loss of the lighter isotope in metabolic processes (Rau et al. 1983). Enrichment of ^{13}C between trophic levels is more conservative ($\Delta\delta^{13}\text{C} = 0\text{--}1\text{‰}$) and can be used to assess different sources of carbon at the base of food-webs, including sources of primary productivity (DeNiro and Epstein 1978). This fractionation and consistent enrichment of ^{15}N and ^{13}C make it possible to describe food-webs and determine trophic linkages (Peterson and Fry 1987; Rau et al. 1992; Post 2002). For example, marine phytoplankton is typically depleted in ^{13}C relative to benthic sources (e.g., macroalgae, seagrasses), thus providing potential discrimination between the two food-webs (Fry and Sherr 1984).

The goal of this study was to investigate the ecological role that spiny dogfish have in the North Pacific ecosystem. The objective to accomplish this goal was to assess nitrogen and carbon isotope values from dogfish sampled at several sites in the northeastern Pacific Ocean. Trophic level, food-web, and habitat implications were discussed and further analyses were suggested. Hazlett et al. (2009) investigated sampling along the dogfish spine at different ages for similar isotopic ratios.

1.3 Methods

Spiny dogfish were opportunistically collected in June, July, and August 2005 from five distinct sites in the northeastern Pacific Ocean: Puget Sound, Washington; Howe Sound, British Columbia; Dixon Entrance, Alaska; Yakutat Bay, Alaska; and central GOA (Figure 1.1). Ten males of similar size (overall range: 72–87 cm) were collected from each region using either baited longlines or trawls. In addition, ten females from the same size range were collected from Yakutat Bay, Alaska.

The second dorsal spine with attached dorsal muscle tissue was removed from each individual, frozen (0°C) in plastic bags, and transported to laboratory facilities for further processing. In the laboratory, samples were partially thawed at ambient temperature and a clean piece of white muscle tissue was excised from an area near the base of the spine. Tissue samples were placed in glass vials, freeze dried for 24 h, and homogenized.

Stable nitrogen and carbon isotopes were analyzed at the Alaska Stable Isotope Facility, University of Alaska Fairbanks. Samples were processed in a Costech ECS4010 elemental analyzer (EA) that is interfaced through a CONFLO III to a Finnigan Delta^{plus} XP isotope ratio mass spectrometer. All samples were run in duplicate. Each sample was weighed (0.2–0.4-mg subsamples) and placed in a tin capsule. Based on replicates of peptone, analytical errors were 0.15‰ and 0.13‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively. Results are presented in delta (δ) notation calculated using the following formula:

$$\delta X\text{‰} = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \cdot 1,000,$$

where R is ratio of the heavy isotope to the light isotope (e.g., $^{15}\text{N}/^{14}\text{N}$, and $^{13}\text{C}/^{12}\text{C}$) for a given element. Recognized standards of Vienna-PeeDee Belemnite (VPDB) for carbon and atmospheric air (AIR) for nitrogen were used for comparison with sample ratios.

Means and standard deviations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were calculated for males from each of the regions and for males and females from Yakutat Bay. Statistical differences between males and females from Yakutat Bay were assessed with a t -test. Statistical differences among stations were assessed with an analysis of variance (ANOVA) followed by posthoc Tukey tests for equal sample sizes.

1.4 Results/Discussion

1.4.1 *Isotopic differences between sexes in Yakutat Bay*

No significant differences were found for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between female and male spiny dogfish collected from Yakutat Bay ($\delta^{15}\text{N}$: $t = 0.99$, $P = 0.333$; $\delta^{13}\text{C}$: $t = 0.91$, $P = 0.353$). Mean $\delta^{15}\text{N}$ values were 12.1‰ and 12.4‰ for females and males, respectively (Figure 1.2a). Mean values for $\delta^{13}\text{C}$ were -21.5‰ for females and -21.3‰ for males (Figure 1.2b). In contrast, diets of mature male and female spiny dogfish off the coast of Argentina were significantly different based on the specific overlap index (Alonso et al. 2002). In that study, mature females had higher numbers of squid in their diet. Since spiny dogfish are known to form schools that are segregated by size and sex (Ketchen 1986), future work in the northeastern Pacific Ocean will explore the variation between males and females across a range of size classes.

1.4.2 *Isotopic differences among sites*

Mean $\delta^{15}\text{N}$ values for spiny dogfish ranged from 12.0‰ (central GOA) to 13.4‰ (Howe Sound, British Columbia) and were significantly different among sites (Table 1.1 ; $F = 10.72$, $P < 0.001$). Specifically, $\delta^{15}\text{N}$ values for spiny dogfish from the central GOA and Yakutat Bay were significantly lower than from Dixon Entrance, Howe Sound, or Puget Sound (Figure 1.3). Mean $\delta^{13}\text{C}$ values ranged from -21.3‰ (Yakutat Bay, Alaska) to -17.9‰ (Puget Sound, Washington) and were also significantly different among sites (Table 1.1 ; $F = 24.05$, $P < 0.001$). Values of $\delta^{13}\text{C}$ from the central GOA were not significantly different than those for Yakutat Bay, Dixon Entrance, or Howe Sound. However, $\delta^{13}\text{C}$ of Yakutat Bay samples were significantly lower than values from all sites south of Yakutat Bay. Mean $\delta^{13}\text{C}$ of dogfish from Dixon Entrance and Howe Sound were not significantly different. Values of $\delta^{13}\text{C}$ from Puget Sound, Washington, were significantly higher than from all other sites, possibly indicating that the pelagic system has less of an influence on these fish (Figure 1.3).

Isotopic values of spiny dogfish on the Georges Bank in the Atlantic Ocean were lower than in this study; mean (SD) $\delta^{15}\text{N}$ values were 11.2 (0.8‰) and mean (SD) $\delta^{13}\text{C}$ values were -17.4 (0.6‰) (Fry 1988). In the Celtic Sea, isotopic values of dogfish (length: 60–66 cm; $n = 6$) were similar to those on the Georges Bank; mean (SD) $\delta^{15}\text{N}$ values were 11.6 (0.6‰) and mean (SD) $\delta^{13}\text{C}$ values were -17.0 (0.4‰) (Domi et al. 2005). The lower N and C isotopic values in Atlantic dogfish might suggest that they occupy a lower trophic level and different feeding niche than spiny dogfish in the north

Pacific. However, the Celtic Sea dogfish were smaller than those in this study so differences may be related to ontogenetic changes in feeding behavior. Also, differences between upper trophic levels from these two ecosystems may reflect differences in fractionation during primary production at the base of the food-web (France 1995; Cabana and Rasmussen 1996; Post 2002).

1.4.3 *Trophic level and diet implications*

Differences in $\delta^{15}\text{N}$ among sites suggested that spiny dogfish occupy different trophic positions in the northeastern Alaska region than further south along the Alaskan and Canadian coast. On average, a $\delta^{15}\text{N}$ increase of 3.4‰ occurs between a predator and consumer and represents a single trophic level (Minagawa and Wada 1984). The largest difference in mean $\delta^{15}\text{N}$ observed in this study was 1.4‰ between Central GOA and British Columbia. This difference could indicate that dogfish have a different role and fill different feeding niches in the ecosystem at these sites. In addition, interannual differences in $\delta^{15}\text{N}$ of 2.7‰ have been observed in annuli of dogfish spines (Hazlett et al. 2009). Their results indicate that individual dogfish display temporal variability in trophic positions. These findings coupled with our results provide further evidence that dogfish are capable of taking advantage of different prey sources and of occupying different habitats throughout their lifespan. These changes may be correlated to growth and ontogeny.

Differences in $\delta^{13}\text{C}$ among sites suggested that spiny dogfish diets can be categorized based on three regions: the northeastern Alaska region, central region of the

northeastern Pacific, and Washington. Puget Sound, Washington, samples had the most enriched values of all the sites, suggesting an even more unique diet for dogfish from this site.

1.4.4 *Food-web and habitat implications*

Variability in carbon and nitrogen isotopic ratios may indicate differences in production and initial nitrogen and carbon fixing during primary production among the study sites. Baseline isotope values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ indicate the variability at the base of the food-web and can vary between distinct ecological systems (Cabana and Rasmussen 1996; Post 2002). Patterns of variation for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values found in zooplankton collected from the Bering, Chukchi, and Beaufort seas were linked to variability in the growth rates of primary producers (Schell et al. 1998). Enriched $\delta^{13}\text{C}$ have also been correlated with faster growth rates in diatoms (Fry 1991).

Variability in both the nitrogen and carbon stable isotopes indicated that spiny dogfish are feeding in different food-webs and in potentially different habitats over the spatial range of this study. Depleted amounts of ^{13}C in the Yakutat and central GOA dogfish may indicate participation in a more pelagic food-web based on phytoplankton at the base of the food-web, whereas enriched ^{13}C in the dogfish from southern sites may indicate that a higher proportion of prey originates from benthic communities. Marine benthic algae isotopes tends to be more enriched than isotopes of marine phytoplankton and benthic food-webs tend to have more trophic links (McConnaughey and McRoy 1979; France 1995).

Differences in the type of food-web used by spiny dogfish may be correlated to

the difference between inshore and offshore habitats. The Yakutat samples, and to a greater extent the Central GOA samples, may represent a population of dogfish that predominantly feed on pelagic prey items and are strongly tied to the phytoplankton-based food-web typical of offshore systems. The potential increased use of benthic food-webs in the southern sites may be indicative of feeding closer to shore in shallower waters. Specifically, the samples from Puget Sound, Washington, were more enriched than any other site, indicating a unique food-web. Interestingly, the isotopic values from dogfish in Howe Sound do not indicate the same change to a benthic food-web. Possible foraging in inshore and offshore waters by the shortfin mako shark in the Northwest Atlantic Ocean led to a large range of $\delta^{15}\text{N}$ (12.2–15.2‰) and $\delta^{13}\text{C}$ values (–17.1 to –15.9‰) (Estrada et al. 2003).

To account for variation at the base of the food-web that can propagate up the food-web and lead to variation at higher trophic levels, indicator species are often used in studies with high spatial extent. Bivalve mollusks, including mussels and scallops, have been used successfully in both freshwater and marine systems to measure the variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at the base of the food-web (Cabana and Rasmussen 1996; Vander Zanden et al. 1997; Vander Zanden and Rasmussen 1999; Post 2002; Jennings and Warr 2003; Howard et al. 2005). Future studies to assess the spatial variability in the trophic structure of spiny dogfish in the northeastern Pacific Ocean will incorporate analyses of weathervane scallops *Patinopecten caurinus* to gain insight into possible baseline isotopic variation among ecosystems. Weathervane scallops are a widely available primary consumer whose distribution overlaps with dogfish in the northeastern Pacific

Ocean.

1.4.5 *Spatial gradients in other ecosystems*

Spatial gradients of species-specific isotopic values exist over large distances in other ecosystems similar to those investigated in this study. Higher $\delta^{13}\text{C}$ values were found at lower latitudes in the Southern Ocean in seabirds and their prey (Quillfeldt et al. 2005). Isotope ratios ($\delta^{13}\text{C}$) of *Neocalanus cristatus* copepods are enriched by 4‰ in Prince William Sound (PWS) compared to the GOA (Kline 1996). Gradients of $\delta^{13}\text{C}$ in particulate organic matter (0.5–3.5‰), zooplankton (3.1–3.7‰), and larvae fish (4.3‰) were found between continental shelf and slope/deep ocean waters that were within 40–45 km of each other off the coast of Vancouver Island (Perry et al. 1999). Therefore, similar processes are likely to drive $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variability over large spatial areas and may lend insight into the latitudinal differences found in this study of spiny dogfish from the northeastern Pacific Ocean.

1.5 Conclusion

This study provides a preliminary assessment of the diet and trophic position of spiny dogfish in the northeastern Pacific Ocean. The significant range of nitrogen and carbon stable isotope values provides evidence that dogfish are occupying different trophic positions and potentially different habitats in this region. These data may indicate that dogfish range from a more pelagic, lower trophic position in the GOA and Yakutat to having a greater reliance on benthically derived prey of a higher trophic position in the more southern and, in some cases, enclosed habitats of Dixon Entrance, Howe Sound,

and Puget Sound. Diet studies have shown that dogfish are opportunists that prey on seasonally abundant prey (Jones and Geen 1977). This opportunistic feeding behavior coupled with the results of this study suggest that dogfish may be capable of filling a wide range of feeding niches as their population increases. However, further data are needed on baseline isotope values from each ecosystem and food-web to accurately assess trophic position.

Finally, it is not known whether the spiny dogfish population in the North Pacific is increasing due to actual population increases or to a distributional shift from southern latitudes. Evidence for some migration potential in the British Columbia dogfish population exists (McFarlane and King 2003). Further research into the trophic role of spiny dogfish should continue to explore geographic variation, size-class, and sex comparisons, and baseline variation. Understanding the geographic variation of the trophic position of an organism could play an increasingly important role in developing ecosystem-modeling approaches to fisheries management. Spatially explicit data on trophic position will provide necessary data for the complex food-web models necessary to adequately assess the fluctuations in dogfish-stock size and potential commercial fishery interactions.

1.6 Acknowledgments

We thank M. Wooller for his insight into stable isotope analyses and for sharing his breadth of knowledge of the ecological applications of these techniques. We thank C. Tribuzio for graciously sharing samples and data collected for her doctorate work on spiny dogfish at the University of Alaska Fairbanks and to G. Kruse for his support. G. Bargmann, D. Courtney, V. Gallucci, J. King, and N. Vega assisted with sample collections. J. Marsh and J. Nash contributed to discussions on methods and objectives. We also thank N. Haubenstein and T. Howe at the Alaska Stable Isotope Facility for their assistance and expertise processing samples. Funding was provided by the Cooperative State Research, Education and Extension Service, U.S. Department of Agriculture.

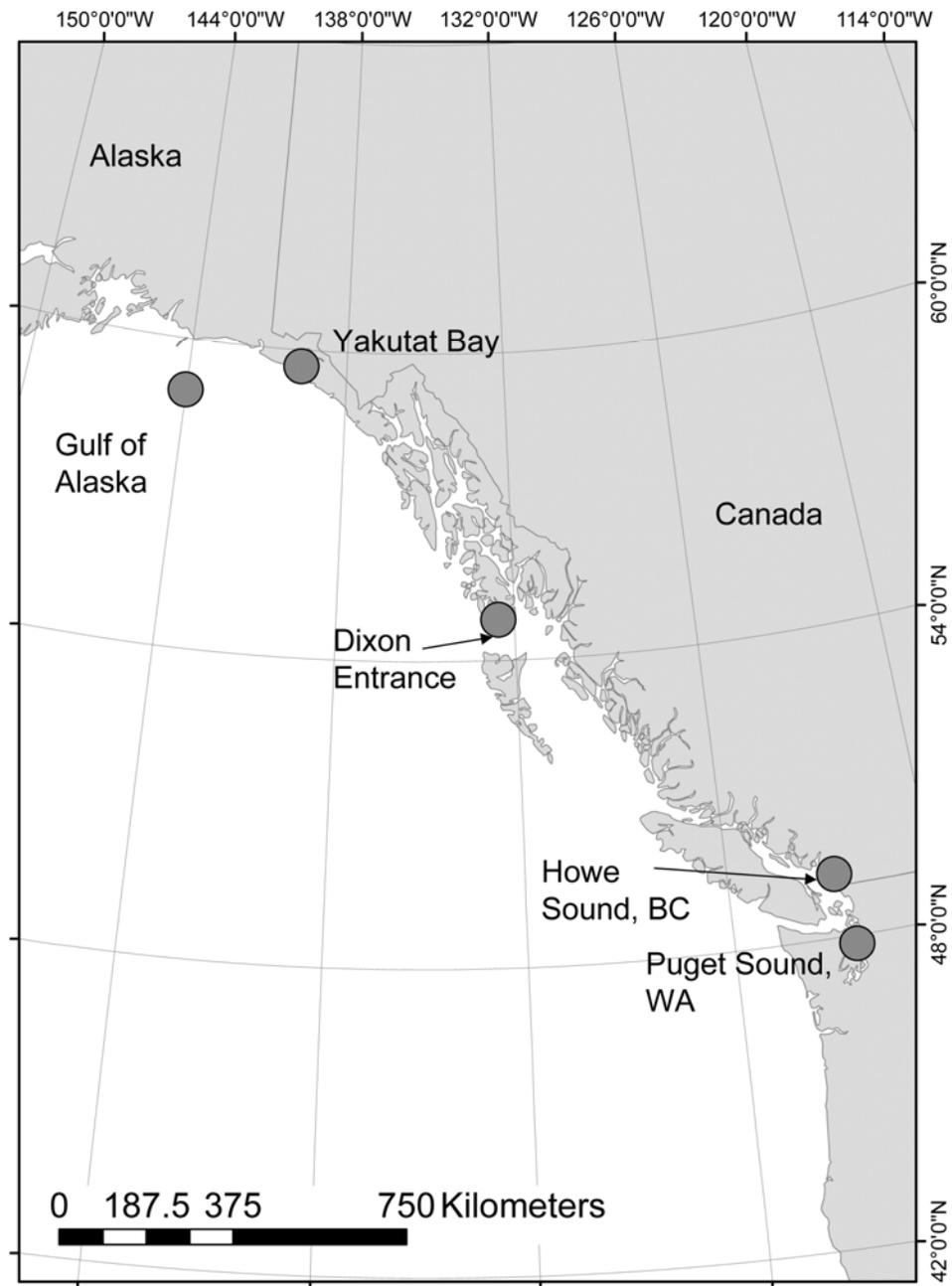


Figure 1.1. Sampling locations in Puget Sound (Washington); Howe Bay (British Columbia, Canada); and Gulf of Alaska, Yakutat Bay, and Dixon Entrance (Alaska).

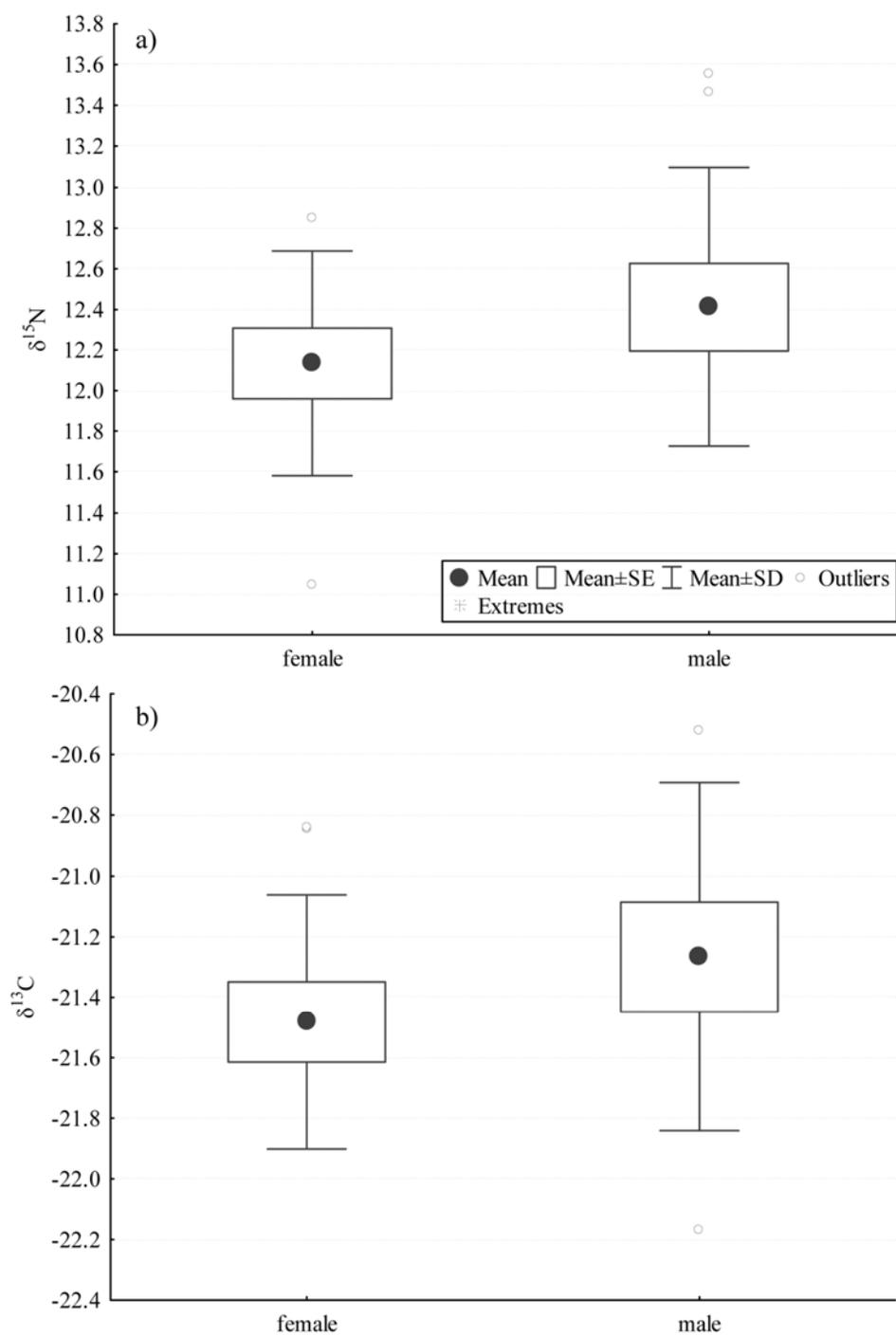


Figure 1.2. Mean (SE) $\delta^{13}\text{C}$ values and $\delta^{15}\text{N}$ values for male and female spiny dogfish

Squalus acanthias collected from Yakutat Bay, Alaska, during 2005.

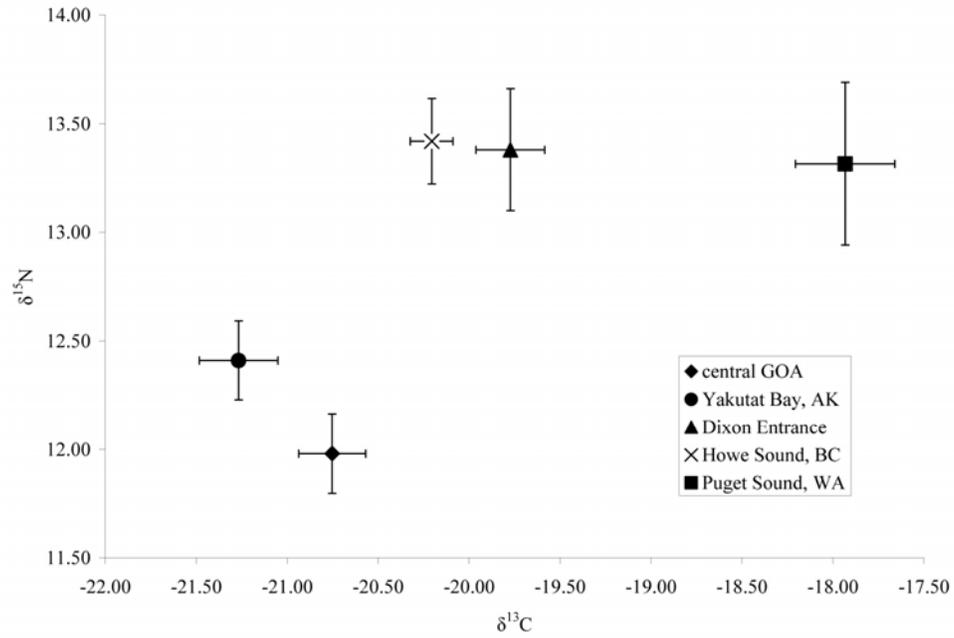


Figure 1.3. Mean (SE) $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ values of male spiny dogfish collected from five locations sampled during 2005 in the northeastern Pacific Ocean.

Table 1.1. Mean (SD) of stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of spiny dogfish collected during 2005 from five different sites in the northeastern Pacific Ocean.

Site	N	Sex	Month collected	Length range (cm)	Mean (SD) $\delta^{15}\text{N}$ (‰)	Mean (SD) $\delta^{13}\text{C}$ (‰)
Central Gulf of Alaska (GOA)	10	male	Aug	72.2 - 86.0	11.98 (0.58)	-20.75 (0.70)
Yakutat Bay, Alaska	10	male	June	74.5 - 87.0	12.41 (0.68)	-21.27 (0.57)
Yakutat Bay, Alaska	10	female	June	74.5 - 86.0	12.13 (0.55)	-21.48 (0.42)
Dixon Entrance	10	male	July	78.0 - 83.5	13.38 (0.60)	-19.77 (0.89)
Howe Sound, British Columbia	10	male	Aug	77.6 - 82.4	13.42 (0.37)	-20.21 (0.62)
Puget Sound, Washington	10	male	June	71.0 - 86.7	13.32 (0.86)	-17.93 (1.19)

1.7 References

- Alonso, M. K., E. A. Crespo, N. A. Garcia, S. N. Pedraza, P. A. Mariotti, and N. J. Mora. 2002. Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina. *Environmental Biology of Fishes* 63(2):193–202.
- Bonham, K. 1954. Food of the dogfish *Squalus acanthias*. *Fisheries Research Papers* 1(2):25–36.
- Bowman, R., R. Eppi, and M. Grosslein. 1984. Diet and consumption of spiny dogfish in the Northwest Atlantic. ICES C. M.1984/G:27, Copenhagen, Denmark.
- Cabana, G., and J. B. Rasmussen. 1996. Comparison of aquatic food chains using nitrogen isotopes. *Proceedings of the National Academy of Sciences, USA* 93(20):10844–10847.
- Castro, J. I. 1983. The sharks of North American waters. Texas A&M University Press, College Station.
- Collie, J. S., and A. K. DeLong. 1999. Multispecies interactions in the Georges Bank fish community. Pages 187–210 *in* *Ecosystem approaches for fisheries management. Proceedings of the 1998 Wakefield Fisheries Symposium: Ecosystem Considerations in Fisheries Management*. University of Alaska, Alaska Sea Grant Publication AK-SG-99-01, Fairbanks.
- Conrath, C. L., and R. J. Foy. 2009. A history of the distribution and abundance of spiny dogfish in Alaskan waters. Pages 119–126 *in* V. F. Gallucci, G. A. McFarlane, and G. G. Bargmann, editors. *Biology and management of dogfish sharks*.

American Fisheries Society, Bethesda, Maryland.

Cortés, E. 1999. Standardized diet compositions and trophic levels of sharks. ICES

Journal of Marine Science 56(5):707–717.

Courtney, D. L., C. A. Tribuzio, K. J. Goldman, and J. S. Rice. 2006. GOA Sharks. Pages

481–562 *in* North Pacific Groundfish Stock Assessment and Fishery Evaluation

Report. North Pacific Fishery Management Council (NPFMC), Anchorage,

Alaska.

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(3):341–351.

Domi, N., J. M. Bouquegneau, and K. Das. 2005. Feeding ecology of five commercial

shark species of the Celtic Sea through stable isotope and trace metal analysis.

Marine Environmental Research 60(5):551–569.

Estrada, J. A., A. N. Rice, M. E. Lutcavage, and G. B. Skomal. 2003. Predicting trophic

position in sharks of the north-west Atlantic Ocean using stable isotope analysis.

Journal of the Marine Biological Association of the United Kingdom 83(6):1347–

1350.

Fisk, A. T., S. A. Tittlemier, J. L. Pranschke, and R. J. Norstrom. 2002. Using

anthropogenic contaminants and stable isotopes to assess the feeding ecology of

Greenland sharks. *Ecology* 83(8):2162–2172.

Fogarty, M. J., and S. A. Murawski. 1998. Large-scale disturbance and the structure of

- marine systems: fishery impacts on Georges Bank. *Ecological Applications* 8(1, supplement):S6–S22.
- France, R. L. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: food web implications. *Marine Ecology Progress Series* 124(1–3):307–312.
- Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308:1621–1623.
- Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnology and Oceanography* 33(5):1182–1190.
- Fry, B., and S. C. Wainright. 1991. Diatom sources of ^{13}C -rich carbon in marine food webs. *Marine Ecology Progress Series* 76(2):149-157.
- Fry, B., and E. B. Sherr. 1984. $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science* 27:13–47.
- Hazlett, S., N. Misarti, A. G. Andrews, G. A. McFarlane, and M. J. Wooller. 2009. Stable isotopic variability along spiny dogfish spines: implications for retrospective ecological studies. Pages 259–267 in V. F. Gallucci, G. A. McFarlane, and G. G. Bargmann, editors. *Biology and management of dogfish sharks*. American Fisheries Society, Bethesda, Maryland.
- Hinman, K. 1998. Ocean roulette: conserving swordfish, sharks and other threatened pelagic fish in longline-infested waters. National Coalition for Marine Conservation, Leesburg, Virginia.
- Holden, M. J. 1977. Elasmobranchs. Pages 187–215 in A. Gulland, editor. *Fish population dynamics*. J. Wiley and Sons, New York.

- Howard, J. K., K. M. Cuffey, and M. Solomon. 2005. Toward using *Margaritifera falcata* as an indicator of base level nitrogen and carbon isotope ratios: insights from two California coast range rivers. *Hydrobiologia* 541(1):229–236.
- Jennings, S., and K. J. Warr. 2003. Environmental correlates of large-scale spatial variation in the $\delta^{15}\text{N}$ of marine animals. *Marine Biology* 142(6):1131–1140.
- Jones, B. C., and G. H. Geen. 1977. Food and feeding of spiny dogfish (*Squalus acanthias*) in British Columbia waters. *Journal of the Fisheries Research Board of Canada* 34(11):2067–2078.
- Ketchen, K. S., 1986. The spiny dogfish (*Squalus acanthias*) in the Northeast Pacific and a history of its utilization. *Canadian Special Publication of Fisheries and Aquatic Sciences* 88:78 p. Ottawa.
- Kitchell, J. F., T. E. Essington, C. H. Boggs, D. E. Schindler, and C. J. Walters. 2002. The role of sharks and longline fisheries in a pelagic ecosystem of the Central Pacific. *Ecosystems* 5:202–216.
- Kline, T. C., Jr. 1997. Confirming forage fish food web dependencies in Prince William Sound using natural stable isotope tracers. *In* Forage fishes in marine ecosystems. *Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems*. University of Alaska, Alaska Sea Grant Publication AK-SG-97-01, Fairbanks.
- McConnaughey, T., and C. P. McRoy. 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. *Marine Biology* 53(3):257–262.
- McFarlane, G. A., and R. J. Beamish. 1987. Validation of the dorsal spine method of age

- determination for spiny dogfish. Pages 287–300 in R. C. Summerfelt and G. E. Hall, editors. The age and growth of fish. The Iowa State University Press, Ames.
- McFarlane, G. A., and J. R. King. 2003. Migration patterns of spiny dogfish (*Squalus acanthias*) in the North Pacific Ocean. Fisheries Bulletin 101:358–367.
- Mecklenburg, C. W., T. A. Mecklenburg, and L. K. Thorsteinson. 2002. Fishes of Alaska. American Fisheries Society, Bethesda, Maryland.
- Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between delta ^{15}N and animal age. Geochimica et Cosmochimica Acta 48:1135–1140.
- Musick, J. A., G. Burgess, G. Cailliet, M. Camhi, and S. Fordham. 2000. Management of sharks and their relatives (Elasmobranchii). Fisheries 25(3):9–13.
- Perry, R. I., P. A. Thompson, D. L. Mackas, P. J. Harrison, and D. R. Yelland. 1999. Stable carbon isotopes as pelagic food web tracers in adjacent shelf and slope regions off British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences. 56:2477–2486.
- Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293–320.
- Polunin N. V. C., Pinnegar J. K. 2000. Trophic level dynamics inferred from stable isotopes of carbon and nitrogen. Pages 69–73 in Fishing down the Mediterranean food webs? The Mediterranean Science Commission (CIESM), CIESM Workshop Series 12, Kerkyra, Greece.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods,

- and assumptions. *Ecology* 83(3):703–718.
- Quillfeldt, P., R. A. R. McGill, and R. W. Furness. 2005. Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. *Marine Ecology Progress Series* 295:295–304.
- Rau, G. H., D. G. Ainley, J. L. Bengtson, J. J. Torres, and T. L. Hopkins. 1992. $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. *Marine Ecology Progress Series* 84:1–8.
- 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(5):1314–1318.
- Rice, J. S., V. F. Gallucci, and G. H. Kruse. 2009. Evaluation of the precision of age estimates for spiny dogfish. Pages 161–168 in V. F. Gallucci, G. A. McFarlane, and G. G. Bargmann, editors. *Biology and management of dogfish sharks*. American Fisheries Society, Bethesda, Maryland.
- Saunders, M. W., and G. A. McFarlane. 1993. Age and length at maturity of the female spiny dogfish, *Squalus acanthias*, in the Strait of Georgia, British Columbia, Canada. *Environmental Biology of Fishes* 38:49–57.
- Schell, D. M., B. A. Barnett, and K. A. Vinette. 1998. Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort seas. *Marine Ecology Progress Series* 162:11–23.
- Tribuzio, C. A., V. F. Gallucci, and G. G. Bargmann. 2009. Reproductive biology and

management implications for spiny dogfish in Puget Sound, Washington. Pages 181–194 *in* V. F. Gallucci, G. A. McFarlane, and G. G. Bargmann, editors. Biology and management of dogfish sharks. American Fisheries Society, Bethesda, Maryland.

Vander Zanden, M. J., G. Cabana, and J. B. Rasmussen. 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}\text{N}$) and literature dietary data. *Canadian Journal of Fisheries and Aquatic Sciences* 54(5):1142–1158.

Vander Zanden, M. J., and J. B. Rasmussen. 1999. Primary consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and the trophic position of aquatic consumers. *Ecology* 80(4):1395–1404.

Walker, T. I. 1998. Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Marine and Freshwater Resources* 49:553–72.

Chapter 2

Ontogenetic and spatial variation in the trophic position of spiny dogfish, *Squalus acanthias*, in the northeastern Pacific Ocean²

2.1 Abstract

Spiny dogfish *Squalus acanthias* are one of the most abundant shark species in the Gulf of Alaska (GOA) and are captured as bycatch in commercial and recreational fisheries. During the last decade, evidence of increasing numbers spurred interest in developing a commercial fishery on this species in the GOA. However, because very little is known about the ecology and abundance of this species in Alaskan waters and the trophic position (TP) of spiny dogfish is poorly understood, the effects of the removal of spiny dogfish biomass on the North Pacific Ocean ecosystem are unknown. This study investigated the feeding ecology of spiny dogfish in the GOA using stable isotope analysis of carbon and nitrogen to examine TP in relation to length, sex, and geographic region. Samples were collected from the GOA (n=410) to the inside waters of southwestern British Columbia (BC, n=81). Weathervane scallops *Patinopecten caurinus* were used as a stable isotopic baseline for estimation of TP of spiny dogfish in the GOA. Values of $\delta^{15}\text{N}$ from spiny dogfish of length 52 to 113 cm (total length extended) ranged from a minimum of 10.8‰ (Yakutat and northeastern GOA (NEGOA)) to a maximum of 15.6‰ (Kodiak), while $\delta^{13}\text{C}$ values ranged from -23.1‰ (Yakutat) to -16.3‰ (BC). Both

² Andrews, A. G. III, N. Hillgruber, R. J. Foy, G. H. Kruse, and M. J. Wooller. Transactions of the American Fisheries Society. To be submitted.

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were linearly related to length at most sites. However, to account for variation in lipid content in the muscle, we normalized lipids for $\delta^{13}\text{C}$; lipids are depleted in $\delta^{13}\text{C}$. Lipid-normalized $\delta^{13}\text{C}$ ' values ranged from -21.2‰ (Yakutat and NEG OA) to -16.8‰ (BC) and were not linearly related to length. In the GOA, where spiny dogfish TPs were adjusted for spatial variability in a baseline organism, TP ranged from 3.3 to over 4.1. Kodiak had the highest TPs in the GOA for spiny dogfish of a given length. In contrast, the lowest TPs were observed at sites in the eastern GOA. Our results improve our understanding of ontogenetic dietary changes, specifically how size-specific dietary patterns influence the role of spiny dogfish in the North Pacific ecosystem.

2.2 Introduction

The spiny dogfish *Squalus acanthias* is a circumglobal shark species that occurs in the temperate and subarctic waters of the Pacific and Atlantic Ocean (Castro 1983). This species inhabits waters from the surface to 675 m (Castro 1983; C. A. Tribuzio, NOAA, personal communication). Along the west coast of North America, spiny dogfish range from Baja California to the Bering Sea, west along the Aleutians to Russia, and south to Japan (Castro 1983). Spiny dogfish have been one of the most abundant and economically important shark species in North American waters (Castro 1983). Despite life-history characteristics, such as longevity, low natural mortality, and late maturity, that predispose this species to overfishing (Saunders and McFarlane 1993; King and McFarlane 2003), targeted fisheries for spiny dogfish have occurred in both the North Atlantic and North Pacific Oceans; in Alaska, regulations have been approved for a small-scale targeted fishery in Cook Inlet and a bycatch fishery in Yakutat. However, interest in commercial exploitation has remained low.

Spiny dogfish biomass estimates based on bottom trawl surveys in the GOA indicate an increasing trend from 1990 until 2007 (Courtney et al. 2006; Tribuzio et al. 2009), stemming increasing interest in a targeted commercial spiny dogfish fishery. However, biomass estimates for spiny dogfish in 2009 were the lowest since 1987 (Tribuzio et al. 2009), adding uncertainty as about the veracity of an increase in spiny dogfish abundance. These unpredictable changes or uncertainties in spiny dogfish biomass estimates clearly demonstrate the need for a better understanding of the ecology and life-history of this species. Not only is it important to understand the effects of a

large spiny dogfish biomass in the GOA, but it is important to understand the concomitant effects on the ecosystem that commercial fishing could have due to a reduction of biomass. Little is known about the ecology of spiny dogfish in the GOA ecosystem; only one study examined dietary patterns and trophic linkages of spiny dogfish in the GOA (Tribuzio 2010). However, because of the trophic connectivity between different species inhabiting a given ecosystem, some studies indicate that reduction in the abundance and biomass of one or several species can dramatically upset the balance in the ecosystem and lead to a re-structuring of ecological communities (Fogarty and Murawski 1998; Frank et al. 2005). Other studies however, have concluded that a reduction in predator abundance may not significantly benefit the prey (Stevens et al. 2000). In light of changes in spiny dogfish biomass in the GOA, a better understanding of the size-specific trophic role of this species is essential not only to better describe dynamics and functions of the GOA ecosystems but also to assess potential consequences for the GOA ecosystems as a result of fishery removals of this important predator.

Spiny dogfish are omnivorous opportunists that consume a wide range of prey items, including fishes, mollusks, and crustaceans (Bonham 1954; Jones and Geen 1977; Bowman et al. 1984; Ebert et al. 1992; Laptikhovskiy et al. 2001; Tribuzio 2010). Prey composition in spiny dogfish may be a function of size and vary with season, prey abundance, and geographical region (Bowman et al. 1984; Alonso et al. 2002; Tribuzio 2010). Spiny dogfish, particularly at larger sizes, are important piscivorous predators in the ecosystem; e.g., in British Columbian waters, forage fishes, such as Pacific herring

Clupea pallasii, eulachon *Thaleichthys pacificus*, and capelin *Mallotus villosus* made up more than half of the prey items ingested by spiny dogfish (Jones and Green 1977). The seasonal variation in their diet composition and the opportunistic nature of this species suggests that increased spiny dogfish biomass might significantly impact the food-web of the northeast Pacific Ocean. Trophic linkages of an organism can be examined with different techniques, such as gut content or stable isotope analysis. With a few exceptions (Hazlett et al. 2008; Andrews and Foy 2009) in the North Pacific Ocean, trophic studies on spiny dogfish have relied on gut content analysis. Gut content analysis is valuable in describing recent feeding patterns, but unless diets are collected throughout the year, may not be optimal for assessing the ecological role of a species that may switch its diet frequently, such as the spiny dogfish.

Stable nitrogen ($\delta^{15}\text{N}$) and carbon isotope ($\delta^{13}\text{C}$) ratios are another tool that can be used to describe food-web linkages and to determine the source of primary production (DeNiro and Epstein 1978; DeNiro and Epstein 1981; Fry and Sherr 1984; Fry 1988; Rau et al. 1992). Typically, there is an enrichment of the heavy isotope ^{15}N from prey to consumer of approximately 3.4 ± 1.1 ‰ (Minagawa and Wada 1984). Using the enrichment properties of ^{15}N , it is possible to construct food-webs and determine trophic linkages (Peterson and Fry 1987; Rau et al. 1992). In contrast to stable nitrogen isotope ratios, $\delta^{13}\text{C}$ can be used to distinguish between different sources of primary productivity at the base of the food-web. Typically, marine planktonic phytoplankton is depleted in ^{13}C relative to benthic sources in large part due to the boundary effect which restricts the diffusion of CO_2 creating a limiting step for benthic algae (e.g., macroalgae) (Fry and

Sherr 1984; France 1995). Therefore, $\delta^{13}\text{C}$ values are useful in differentiating habitat use of consumers during ontogenetic movements or seasonal migrations.

Isotopic values of primary producers may vary by geographic area or season and these variations can lead to variation in isotopic values of higher consumers (Hobson and Welch 1992; Cabana and Rasmussen 1996; Hoekstra et al. 2002). Therefore, isotopic values of consumers alone are misleading and need to be adjusted for baseline isotopic variation among sites and ecosystems to provide a more accurate estimate of an organism's absolute trophic position (TP)(Post 2002; Jennings and Warr 2003). Filter-feeding bivalve mollusks, including mussels and scallops, have been used successfully in freshwater and marine systems to measure the variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at the base of the food-web (Cabana and Rasmussen 1996; Vander Zanden et al. 1997; Vander Zanden and Rasmussen 1999; Post 2002; Jennings and Warr 2003; Howard et al. 2005).

Ecological roles of elasmobranchs are often explored using TP based on gut content analysis (Cortes 1999; Ebert and Bizzarro 2007). However, a mounting number of studies have established that nitrogen stable isotope analysis is a useful tool in determining the TP of elasmobranchs as a reliable alternative method to gut content analysis (e.g., blue shark *Prionace glauca*, shortfin mako *Isurus oxyrinchus*, thresher shark *Alopias vulpinus*, basking shark *Cetorhinus maximus*, and Greenland shark *Somniosus microcephalus*)(Rau et al. 1983; Fisk et al. 2002; Estrada et al. 2003; MacNeill et al. 2005). Fisk et al. (2002) hypothesized that elasmobranch nitrogen stable isotope values may lead to an underestimate of TP due to the presence of both urea and trimethylamine oxide (TMAO) in the tissues; as waste products, the urea and TMAO

were thought to contain isotopically, lighter nitrogen (Fisk et al. 2002). Evidence from a number of studies, however, suggests that the presence of nitrogenous wastes in elasmobranchs has no effect on their stable isotope values and that an accurate TP can be estimated based on their $\delta^{15}\text{N}$ values (Estrada et al. 2003; Logan and Lutcavage 2010).

Stable isotope signatures vary with the body tissue type used for analysis (Tieszen et al. 1983). Some tissues, such as liver, have a fast turnover rate of 30 d to 5 months (MacNeil et al. 2006). Other tissues, such as muscle tissue, are replaced more slowly. As a result, stable isotope signatures of muscle tissues in elasmobranchs, as with teleosts, may represent an average of a diet assimilated in the previous year or longer (Hesslein et al. 1993; MacNeil et al. 2006; Logan and Lutcavage 2010); thus, the use of muscle tissue can indicate only long-term shifts, such as ontogenetic habitat changes. In contrast, seasonal migrations can most likely not be resolved by using the stable isotope signatures of muscle tissue.

The trophic role of spiny dogfish in the Atlantic and Pacific Oceans has been studied using nitrogen and carbon stable isotopes (Fry 1988; Domi et al. 2005; Andrews and Foy 2009; Hazlett et al. 2009; Logan and Lutcavage 2010). In these studies, however, spiny dogfish were often only one of many fishes analyzed and sample sizes and length ranges were generally small. In the Pacific Ocean, stable isotope values collected along the length of spiny dogfish spines were examined providing evidence that spiny dogfish may change their feeding and habitat use with ontogeny (Hazlett et al. 2009). In the northeastern Pacific Ocean, differences in stable isotope values from wide ranging geographical regions were observed, suggesting geographical differences in feeding

patterns (Andrews and Foy 2009); the isotopic baseline variability among these sites, however, was unknown thus making it impossible to clearly assess the TP of these sharks by area.

The environmental structure of the northeastern Pacific Ocean likely plays an important role in the range of trophic linkages in the diverse food-webs. The northeastern Pacific Ocean is dominated by a counterclockwise circulation, the subarctic gyre (Weingartner 2007). The eastward flowing North Pacific Current bifurcates at a transition zone near the coast of British Columbia and continues northward as the Alaska Current and southward as the California Current (Stabeno et al. 2004). The shelf waters of the GOA are heavily influenced by the Alaska Coastal Current, which is driven by the predominant southerly winds and large input of freshwater. The Alaska Current is transformed into the Alaska Stream along the Alaska Peninsula; while parts of the Alaska Stream flows into the eastern Bering Sea, the majority of it continues southwesterly and back-circulates into the subarctic gyre. The Alaska Coastal Current follows the coastline of Alaska before being injected into the Bering Sea. The counterclockwise circulation of the GOA gyre results in upwelling at the center of the gyre and downwelling along the gyre margins (Weingartner 2007). In spite of the nearshore downwelling, the waters are surprisingly productive due in part to across-shelf nutrient transport (Stabeno et al. 2004). This productive system supports large abundances of economically important fish stocks including Pacific salmon *Oncorhynchus* spp., walleye pollock *Theragra chalcogramma*, Pacific cod *Gadus macrocephalus*, and Pacific halibut *Hippoglossus stenolepis*. Also, a number of elasmobranch species which take advantage of these productive waters, such

as the salmon shark *Lamna ditropis*, the Pacific sleeper shark *Somniosus pacificus*, and the spiny dogfish, are abundant in these waters.

The primary goal of this project was to describe patterns in the TP of male and female spiny dogfish in the northeast Pacific Ocean, from British Columbia to Kodiak Island, Alaska. Weathervane scallops *Patinopecten caurinus* were used to understand the underlying isotopic baseline variability allowing for an adjustment of spiny dogfish TPs between sites in the GOA. Specifically, our objectives for this study were (1) to examine the effects of length and sex on the TP of spiny dogfish and (2) to assess large-scale geographical differences in TP of spiny dogfish in the Alaskan waters of the GOA.

2.3 Materials and Methods

2.3.1 Sample collection

Spiny dogfish were collected in the northeastern Pacific Ocean off British Columbia and Alaska using baited longlines, trawls, set nets, and sportfishing gear (i.e., rod and reel) during April to September 2004-2006 (Table 2.1; Figure 2.1). Sampling closely followed a protocol approved by the University of Alaska Animal Care and Use Committee (IACUC no's 04-38 and 04-36). After capture, spiny dogfish were measured for length (total length extended) to the nearest 0.1 cm and weight to the nearest 0.1 kg. In addition, sex was determined and sampling depth was recorded for each specimen (Table A-1).

For the isotope analysis, the second dorsal spine with attached white muscle tissue was removed from each specimen. Spines with attached tissue were placed in plastic

bags, frozen at -20°C , and transported to laboratory facilities for additional processing. A total of 491 spiny dogfish were analyzed for stable isotope ratios. The majority of samples ($n=451$) were selected from 2005; however, in order to explore interannual variation in stable isotope signatures, additional samples from one site (Yakutat) from 2004 ($n=20$) and from 2006 ($n=19$) were processed.

In this study, we used weathervane scallops, a bivalve ranging from California to the southern Bering Sea (Foster 1991), to adjust for baseline isotopic variations. In 2005 and 2006, weathervane scallops were obtained from nine sites in the GOA (2005, $n=1$; 2006, $n=8$), ranging from Lituya Bay in the eastern GOA to the Shumagin Islands in the western GOA, and from two sites in the southeastern Bering Sea (2005, $n=1$; 2006, $n=1$) (Figure 2.2; Table 2.2; Table A-2). Immediately after capture, scallop adductor muscles were placed in plastic bags and frozen at -20°C for further processing in the lab. At each site, 10 scallops were analyzed for nitrogen and carbon stable isotopes. Weathervane scallop data from the GOA were used to determine the isotopic baseline of nitrogen and to explore interannual variation, while scallop data from the Bering Sea were used to explore interannual variation at one site.

2.3.2 Sample processing and stable isotope analysis

Spiny dogfish samples were partially thawed and a small, clean piece of white muscle tissue was excised from an area near the base of each spine and placed in a glass vial. The spine was retained for aging as part of a companion study (Tribuzio 2010). Tissue samples of spiny dogfish were refrozen prior to being freeze dried for

approximately 24 h. Freeze dried samples were pulverized in the glass vial using a quartz rod to homogenize tissue.

Weathervane scallop samples were partially thawed, weighed, and a small, clean piece of tissue was excised from the center of the adductor muscle and placed in a glass vial. Similar to the shark tissue samples, scallop tissue samples were freeze dried for approximately 24 h, after which they were pulverized to homogenize the tissue.

Stable nitrogen and carbon isotopes were analyzed at the Alaska Stable Isotope Facility, University of Alaska Fairbanks. Samples were processed in a Costech ECS4010 elemental analyzer that was interfaced through a CONFLO III to a Finnigan Delta^{plus}XP isotope ratio mass spectrometer. Of each sample, a subsample weighing 0.16-0.51 mg was taken, weighed to the nearest 0.01 mg, and placed in a tin capsule. A portion of spiny dogfish tissue (n=3) and scallop tissue samples (n=4) were run in replicates of five to determine the quality of sample homogenization. Due to the low standard deviations (SD) and coefficient of variations (CV), it was determined that running replicates on all samples would not be necessary (spiny dogfish: SD < 0.25 and CV < 2.0 % for $\delta^{15}\text{N}$ and SD < 0.24 and CV < 1.2 % for $\delta^{13}\text{C}$; scallops: SD < 0.16 for $\delta^{15}\text{N}$ and SD < 0.05 for $\delta^{13}\text{C}$). The analytical precision was based on the SD of the replicates of the internal standard peptone; SD < 0.18 for $\delta^{15}\text{N}$ and SD < 0.17 for $\delta^{13}\text{C}$.

Results are presented in delta (δ) notation and calculated using the following formula:

$$\delta X\text{‰} = [(R_{\text{sample}} - R_{\text{standard}}) / (R_{\text{standard}})] * 1,000, \quad (1)$$

where X is the stable isotope of interest and R is the ratio of the heavy isotope to the light isotope (e.g., $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$) for the given element. Recognized standards of atmospheric air for nitrogen and Vienna-PeeDee Belemnite for carbon were used for comparison with sample ratios.

2.3.3 Trophic position calculation

In this study, we used weathervane scallops, a primary consumer, to examine patterns in baseline variation of isotopic values by geographic areas and year. The following equation was used to adjust the isotopic values of spiny dogfish to account for baseline variability:

$$\text{Trophic Position (TP)} = \lambda + (\delta^{15}\text{N}_{\text{higher consumer}} - \delta^{15}\text{N}_{\text{base}}) / \Delta_n \quad (2)$$

where:

$$\lambda = \text{TP of the organism used to estimate } \delta^{15}\text{N}_{\text{base}};$$

$$\Delta_n = \text{enrichment in } \delta^{15}\text{N} \text{ per trophic level};$$

$$\text{TP}_{\text{spiny dogfish}} = 2.5 + (\delta^{15}\text{N}_{\text{spiny dogfish}} - \delta^{15}\text{N}_{\text{scallop}}) / 3.4.$$

2.3.4 Lipid-normalization

Compared to proteins, lipids are depleted in ^{13}C ; as a result, the lipid content of a given tissue can influence carbon stable isotope values of that tissue (DeNiro and Epstein

1977). Here, we used the C:N ratio as a proxy for lipid content to adjust for variable lipid content of samples. The C:N ratio was calculated from the %C and %N of each individual sample measured by the mass spectrometer. To correct $\delta^{13}\text{C}$ values measured in muscle tissues with varying amounts of lipids, a lipid-normalization based on the C:N ratios was conducted (McConnaughey and McRoy 1979). For the lipid-normalization, the following equations, which were developed and implemented by McConnaughey and McRoy (1979) and validated by Kline et al. (1998), were used:

$$L = 93 / [1 + (0.246 * \text{C:N} - 0.775)^{-1}] \quad (3)$$

$$\delta^{13}\text{C}' = \delta^{13}\text{C} + D[-0.207 + 3.90 / (1 + 287 / L)], \quad (4)$$

where:

$$\delta^{13}\text{C}' = \text{lipid-normalized } \delta^{13}\text{C};$$

$$L = \text{calculated lipid};$$

$$D = 6\text{‰} \text{ (isotopic difference between protein and lipid).}$$

2.3.5 Statistical analysis

2.3.5.1 Weathervane scallops

Geographic variation in scallop nitrogen stable isotopes between the Bering Sea and GOA was assessed using a Mann-Whitney test. For all tests, we confirmed that assumptions for normality (Anderson-Darling test) and equal variances were met (F-test or Bartlett's test for equal variances). The GOA was separated into the National Marine Fisheries Service (NMFS) regulatory areas of western GOA (WGOA), central GOA

(CGOA), and eastern GOA (EGOA). Interannual variation of $\delta^{15}\text{N}$ was assessed in the EGOA and the Bering Sea using either a Mann-Whitney test or a two sample t-test. Samples were pooled in each NMFS regulatory area (i.e., EGOA, CGOA, and WGOA) and overall differences were assessed with a one-way analysis of variance (ANOVA). If significant differences were found, a post-hoc Tukey test was performed to determine potential differences between sites. Mean $\delta^{15}\text{N}$ values were calculated for each of the NMFS regulatory areas if significant differences were found.

2.3.5.2 Spiny dogfish

Spiny dogfish samples were categorized into seven sites based on general location of capture. The seven sites range that from Kodiak Island to British Columbia and include: Kodiak, Cook Inlet, Prince William Sound (PWS), northeastern GOA (NEGOA), Yakutat Bay (Yakutat), southeastern GOA (SEGOA), and British Columbia (BC).

2.3.5.2.1 Interannual variation

Interannual variations of nitrogen and carbon stable isotopes in spiny dogfish were explored by examining samples collected in three years (2004 (n=20), 2005 (n=87), and 2006 (n=19)) at the Yakutat site. Analysis of covariance (ANCOVA) was used to explore differences in $\delta^{15}\text{N}$ among years. Length was used as a covariate based on the linear relationship between $\delta^{15}\text{N}$ and length. First, the model included an interaction term. If the interaction term was not significant, then the analysis was repeated excluding the interaction term to explore for differences in $\delta^{15}\text{N}$ among years. Due to the lack of a

linear relationship between $\delta^{13}\text{C}'$ and length an ANCOVA was not necessary and therefore an ANOVA was used to explore differences in $\delta^{13}\text{C}'$ among years.

2.3.5.2.2 Linear relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and length

The relationship between $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and $\delta^{13}\text{C}'$ (lipid-normalized) versus length was explored at each site. Significance of the linear relationship was determined using the p-values. The R^2 values were used as an indicator of the goodness of fit and to assess the influence of length on variations in $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and $\delta^{13}\text{C}'$.

2.3.5.2.3 Differences between sexes

Differences in $\delta^{15}\text{N}$ between male and female spiny dogfish were assessed with an ANCOVA at individual sites. Length was used as the covariate based on the linear relationship between $\delta^{15}\text{N}$ and length. Initially, an interaction term was included to assess whether the slopes were constant. If the interaction term was not significant, then the analysis was repeated excluding the interaction term to explore for differences in $\delta^{15}\text{N}$ among sexes. If no differences were determined between males and females, then all fish were pooled for further analyses.

2.3.5.2.4 Differences among sites

The analysis of difference in $\delta^{15}\text{N}$ among sites was confined to the GOA where weathervane scallops were collected to provide an isotopic baseline correction. Differences in $\delta^{15}\text{N}$ among sites in the GOA were assessed with ANCOVA using length as the covariate. Initially, an interaction term was included to assess whether the slopes were constant. If the interaction term was not significant, then the analysis was repeated

excluding the interaction term to explore for differences in $\delta^{15}\text{N}$ among sites. Multiple comparisons were performed with a post-hoc Tukey test.

Differences in $\delta^{13}\text{C}'$ (lipid-normalized) among sites were assessed with a one-way ANOVA. A post-hoc Tukey test was used to perform multiple comparisons among sites. Results were considered statistically significant at a p-value of <0.05 for all statistical analyses.

2.4 Results

2.4.1 *Weathervane scallops*

Weathervane scallop $\delta^{15}\text{N}$ values differed significantly between the Bering Sea and the GOA (Mann-Whitney test, $W = 1992.0$, $p < 0.001$). A non-parametric test was used because the data were not normally distributed (Anderson-Darling test for normality, $A^2 = 4.395$, $n = 110$, $p < 0.005$). Consequently, interannual variation of weathervane scallop $\delta^{15}\text{N}$ values was explored separately for only those areas with samples from multiple years, namely the Bering Sea and the EGOA for the years 2005 and 2006. For the Bering Sea, there was no significant difference in $\delta^{15}\text{N}$ between 2005 and 2006 (independent samples t-test, $t = -1.66$, d.f. = 18, $p = 0.115$; Figure 2.3A); these data were normally distributed (Anderson-Darling test for normality, $A^2 = 0.423$, $n = 20$, $p = 0.289$). For the EGOA, there was a significant difference in $\delta^{15}\text{N}$ between 2005 and 2006 (Mann-Whitney test, $W = 349.0$, $p = 0.023$; Figure 2.3B); these data were normally distributed but had unequal variances (Anderson-Darling test for normality, $A^2 = 0.327$, $n = 50$, $p = 0.512$; F-Test for equal variances, Test statistic = 0.08, $p < 0.001$). Despite the

differences in $\delta^{15}\text{N}$ between 2005 and 2006, for the purposes of this study it was assumed that in the GOA interannual variation was not a significant factor and these values represented the isotopic baseline for all years that spiny dogfish were sampled in this study, 2004 – 2006.

In the GOA, mean $\delta^{15}\text{N}$ values of weathervane scallops ranged from $8.3\text{‰} \pm 0.1$ (Mean \pm SE; NW of Icy Bay) to $9.3\text{‰} \pm 0.1$ (N of Lituya Bay (Table 2.2, Figure 2.4). Within the NMFS regulatory areas, the assumption of equal variance was not met. However, when sampling locations were pooled into the three regulatory areas, namely the WGOA, the CGOA, and the EGOA, the assumption of equal variance was met and there was no significant difference among sites (ANOVA $F_{2,87} = 1.74$, $p = 0.182$; Figure 2.5). Thus, a mean stable nitrogen value for the entire GOA ($n=90$) was calculated (mean $\delta^{15}\text{N} = 8.7 \pm 0.1 \text{‰}$) and used as the baseline nitrogen isotopic value to adjust spiny dogfish nitrogen values and calculate TP.

2.4.2 *Spiny dogfish*

2.4.2.1 Summary of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$

A total of 186 males and 305 females were sampled, ranging in length from 61 to 96 cm and 52 to 113 cm, respectively. These length ranges bracket the size at 50% maturity (75 cm for males; and 97 cm for females) found in the GOA (Tribuzio 2010); therefore, our samples represent both immature and mature fish. Given that age at 50% maturity is 21 and 36 years for males and females, respectively (Tribuzio 2010), our samples also include a large range of ages that encompass several decades. Individual

spiny dogfish $\delta^{15}\text{N}$ values ranged from a minimum of 10.8 ‰ (PWS, NEGOA, and Yakutat) to a maximum of 15.6 ‰ (Kodiak), while $\delta^{13}\text{C}$ values ranged from -23.1 ‰ (Yakutat) to -16.3 ‰ (BC). Lipid-normalized $\delta^{13}\text{C}'$ values ranged from -21.2 ‰ (Yakutat and NEGOA) to -16.8 ‰ (BC) (Table 2.1).

2.4.2.2 Interannual variation of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$

The interannual variation of nitrogen stable isotopes was explored using samples obtained from Yakutat in 2004 – 2006. There was no significant interaction between length and year (interaction term $F_{2,120} = 2.05$, $p = 0.133$). After excluding the interaction term, nitrogen stable isotope values did not differ significantly among years (ANCOVA $F_{2,122} = 2.00$, $p = 0.139$). Similarly, sampling year also had no significant effect on lipid-normalized carbon stable isotopes, $\delta^{13}\text{C}'$ values (ANOVA $F_{2,123} = 2.50$, $p = 0.086$) (Figure 2.6).

2.4.2.3 Relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and length

For spiny dogfish ranging in length from 52 to 113 cm (see Table 2.1 for length ranges for a given site), both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were linearly related to length at most sites (Figures 2.7 and 2.8). For $\delta^{15}\text{N}$, the regressions were significant for all sites except for Cook Inlet and SEGOA; however, the p-value for Cook Inlet was nearly significant (Table 2.3). The R^2 values ranged from a low of 0.01 (SEGOA) to as high as 0.50 (Kodiak). While regressions for $\delta^{13}\text{C}$ were significant at all sites (Table 2.3), results were quite different for lipid-normalized $\delta^{13}\text{C}'$ values; none of the regressions at the other sites were significant (Table 2.3, Figure 2.9).

2.4.2.4 $\delta^{15}\text{N}$ differences between sexes

The following sites had no significant interaction between sex and length: Kodiak (interaction term $F_{1,82} = 0.17$, $p = 0.678$), Cook Inlet (interaction term $F_{1,28} = 0.38$, $p = 0.543$), NEGOA (interaction term $F_{1,41} = 1.74$, $p = 0.195$), Yakutat (interaction term $F_{1,122} = 1.86$, $p = 0.175$), SEGOA (interaction term $F_{1,72} = 1.29$, $p = 0.260$), and BC (interaction term $F_{1,77} = 2.66$, $p = 0.107$). After excluding the interaction term, the analysis was repeated for these sites when length remained significant. Sex was found to not be a significant factor at these sites: Kodiak $F_{1,83} = 1.11$, $p = 0.294$; and Yakutat $F_{1,123} = 1.09$, $p = 0.299$. BC $F_{1,78} = 0.05$, $p = 0.818$ (Figure 2.10).

2.4.2.5 Isotopic differences among sites

Differences in $\delta^{15}\text{N}$ values were compared among all those GOA sites, where baseline data had been collected. Kodiak, PWS, NEGOA, and Yakutat had significant linear relationships between $\delta^{15}\text{N}$ and spiny dogfish length (Table 2.3). There was no significant interaction between length and site; interaction term $F_{3,294} = 2.44$, $p = 0.064$. When the analysis was repeated excluding the interaction term, $\delta^{15}\text{N}$ was found to differ significantly among sites ($F_{3,297} = 17.53$, $p < 0.001$). A pairwise comparison determined that PWS, NEGOA, and Yakutat were not significantly different from each other, but all three were significantly lower than Kodiak.

Because there was no significant linear relationship between $\delta^{13}\text{C}'$ and length, we explored differences among all sites using a one-way ANOVA. Lipid-normalized, $\delta^{13}\text{C}'$ differed significantly among sites (ANOVA $F_{6,484} = 71.00$, $p < 0.001$, Figure 2.11).

Overall, mean $\delta^{13}\text{C}'$ values from BC and SEGOA were more enriched than all other sites; -18.9 ± 0.1 ‰ and -19.4 ± 0.1 ‰ respectively (Mean \pm SE). Yakutat, NEGOA, and PWS were not significantly different from each other, and similarly, Kodiak and Cook Inlet were not significantly different from each other (Table 2.4).

2.4.2.6 Adjusted trophic position

Based on the results of the ANCOVA, we determined that the best fitting relationship between $\delta^{15}\text{N}$ and length had a constant slope. The fitted values were used to calculate a baseline adjusted TP. A value of 2.5 was used as the TP of weathervane scallops as it is unlikely that scallops selectively feed entirely on phytoplankton, which would give them a TP of 2.0. Instead it is more likely that, in addition to phytoplankton, weathervane scallops will ingest particulate organic matter and small zooplankton. Spiny dogfish ranging in length from 63 to 109 cm had a predicted TP that increased with length, ranging from 3.5 to 4.2 in Kodiak. In Yakutat, TP increased from 3.3 to 4.1 for spiny dogfish ranging in length from 61 to 113 cm. In summary, GOA spiny dogfish of a given length had the highest TP in Kodiak, while those sharks collected in Yakutat, NEGOA, and PWS had the lowest TP (Figure 2.12).

2.5 Discussion

This study demonstrated that there is a clear ontogenetic shift in spiny dogfish diet. Body size of fishes is very important in fish trophodynamics (Peters 1983) and can play a major role in how species interact within an ecosystem. Size-based ontogenetic changes in diet have been well documented in a variety of fishes including elasmobranchs (Lowe et al. 1996; Estrada et al. 2006; Ellis and Musick 2007; Menard et

al. 2007; Galvan et al. 2010; Nakazawa et al. 2010). In spite of the important and widely known effect of size on diet, it is to date still largely ignored (Werner and Gilliam 1984). At five of seven sites, spiny dogfish $\delta^{15}\text{N}$ values were linearly related to length supporting a positive association between TP and length. In the GOA, where spiny dogfish TPs were adjusted for the baseline, TP ranged from 3.3 to over 4.1. Extrapolating this relationship to the maximum size (130 cm; Ketchen 1972) of spiny dogfish, the TPs of spiny dogfish can be expected to increase by over 1 TP from immature to large mature fish. Therefore, it must be concluded that spiny dogfish are interacting with their ecosystem in significantly different ways during their transition to maturity in the GOA.

The results of this study support findings from diet analyses that spiny dogfish prey items are a function of size (Jones and Geen 1977; Bowman et al. 1984; Laptikhovsky et al. 2001; Alonso et al. 2002; Tribuzio 2010). In the northwest Atlantic Ocean, spiny dogfish appeared to switch to more abundant prey items and broadened their diets to include a wide variety of fishes with increasing size (Bowman et al. 1984). In the southern Atlantic Ocean, larger spiny dogfish were also found to consume larger prey items, such as octopods *Benthoctopus spp.* and *Enteroctopus megalocyathus* and hoki *Macruronus magellanicus* (Laptikhovsky et al. 2001). In Patagonian waters, immature spiny dogfish had a higher occurrence of ctenophores while mature females had ingested higher numbers of squid; a significant difference in the dorsal mantle length of squid was also observed between immature and mature female spiny dogfish (Alonso et al. 2002). In the Pacific Ocean, similar patterns have been observed where fishes become an increasingly important diet item for larger spiny dogfish (Jones and Geen

1977). Our results support the findings of a recent study from the GOA that larger spiny dogfish capitalized on larger prey and exhibited a diet of higher diversity, but that the prey items themselves were also of a higher trophic level (Tribuzio 2010). These studies were able to detect and document changes in the diet and more specifically the size of the prey items with an increase in spiny dogfish size. Our results provide further insight that spiny dogfish are not only expanding their diet to include larger prey items, but are clearly accessing prey items that are of a higher trophic level with increasing size. With increasing size, spiny dogfish in the GOA are significantly increasing their TP by consuming prey of a higher TP. In the GOA, these prey items include forage fish species such as Pacific herring and capelin, two forage fish species that are of importance to a variety of piscivorous predators (Jones and Geen 1977; Tribuzio 2010).

Understanding differences in the trophic roles between sexes can provide further insight into the trophic role of a species and the partition of resources (Box et al. 2010). For example, male and female pearly razorfish *Xyrichtys novacula* in the Mediterranean Sea differed in $\delta^{15}\text{N}$, possibly as a result of the larger more aggressive males (Box et al. 2010). In contrast, there was no difference between male and female piked spurdog *Squalus megalops*, a congener of the spiny dogfish, off the Australian coast (Braccini et al. 2005), while off the coast of Argentina differences in the diets were found among immature, mature male, and immature female spiny dogfish (Alonso et al. 2002). Spiny dogfish are known to form large schools segregated by size, sex, and maturity (Ketchen 1986); therefore, it is likely that males and females may be exposed to very different prey fields. Tribuzio (2010) found shrimp to be an important prey item in males, more so than

females; however, these results may have been influenced by size differences, because most sampled males tended to be smaller than females (Tribuzio 2010). In the current study, we used an ANCOVA to explore differences between sexes. For a given length, there was no significant difference in $\delta^{15}\text{N}$ between male and female spiny dogfish at Kodiak, Yakutat, and BC; these sites are considered to better represent the population than the other sites, which may have been under-sampled and had a combination of poor length distributions, skewed sex ratios, and low sample sizes, which may have led to an interaction between sex and length. The combination of stable isotope analysis and a statistical analysis that compensates for a wide range of lengths (i.e., ANCOVA) may lessen the confusion describing diet differences in males and females found in other studies. Our results lead us to conclude that in Alaskan waters of the GOA, male and female spiny dogfish of similar length were feeding at the same TP.

Exploration of the differences in TP among sites was limited to the GOA where we had weathervane scallop samples, which allowed us to determine the isotopic baseline. Isotopic values of consumers alone may poorly represent the TP of the organism. Adjusting for baseline isotopic variation among sites and ecosystems will allow for better estimates of the “absolute” TP of an organism (Post 2002; Estrada et al. 2003; Jennings and Warr 2003). Our initial study found significant regional variation in nitrogen stable isotopes among five sites ranging from Washington to the eastern GOA (Andrews and Foy 2009). However, this earlier work lacked data on the variation of the isotopic baseline among sites, thereby making it difficult to describe and discuss food-web or dietary changes among sites (Post 2002).

Weathervane scallops were selected as a baseline organism to measure the isotopic variability of primary production at the base of the food-web. Given that filter feeding bivalves primarily consume phytoplankton, they are useful as natural collectors of baseline nitrogen isotopic values. This and the spatial overlap between spiny dogfish and weathervane scallops in the GOA allowed for an adjustment of the TP of spiny dogfish and a comparison of spiny dogfish isotope values to be made across regions that may have had different isotopic baseline values (Vander Zanden et al. 1997; Vander Zanden and Rasmussen 1999; Jennings and Warr 2003). In the Bering Sea, the interannual variation was not a significant factor for samples collected opportunistically from 2005 and 2006. In the EGOA we also collected scallop samples in 2005 and 2006, and determined that there was a significant difference in $\delta^{15}\text{N}$ between years in this area and that the samples had unequal variances. However, our sampling design was somewhat flawed. Due to the difficulty obtaining samples from 2005, we were limited to comparing 2005 samples from a single site to 2006 samples from four sites. Given that the mean value of the single site from 2005 fell in the middle of the surrounding 2006 sites, for the purposes of this study we chose to make the assumption that our 2006 isotopic baseline data was representative of the 2005 isotopic baseline and therefore could be used to adjust our spiny dogfish isotopic values.

Overall, we found weathervane scallops $\delta^{15}\text{N}$ values to be relatively stable in the WGOA and CGOA, while in the EGOA they were more variable both in mean values and the sample variances among sites. This may be due to the influence of large inputs of freshwater and silt from the many glacial inlets along the coastline of the EGOA. In

general, the sampling depths in the EGOA were shallower than the sites in CGOA and WGOA. On Georges Bank in the northwestern Atlantic Ocean, scallop $\delta^{13}\text{C}$ values increased with decreasing depth, while $\delta^{15}\text{N}$ values showed no relationship to depth; however, in the same study, differences in $\delta^{15}\text{N}$ values of up to 1 ‰ were observed at a single site and this degree of variability was considered acceptable based on studies of animals feeding on similar diets in a laboratory setting (Fry 1988). However, there are important life-history characteristics of spiny dogfish that lead us to pooling the weathervane scallop into larger NMFS regulatory areas where unequal variance was no longer of statistical significance. Spiny dogfish are known to migrate several hundred nautical miles or more within a year, with rarer movements occurring between North America and Japan (Ketchen 1986; McFarlane and King 2003). In addition, recent evidence describes the turnover rate in muscle tissue of sharks to be greater than one year (Logan and Lutcavage 2010). Given the slow turnover rates in muscle tissue and the fact that this species is highly mobile and capable of travelling large distances within a year, we considered it necessary and appropriate to pool our isotopic baseline data into the relatively large NMFS regulatory areas. In the GOA, we found no difference in the isotopic baseline among WGOA, CGOA, and EGOA. Therefore, differences among sites for spiny dogfish $\delta^{15}\text{N}$ are assumed to represent actual differences in prey types and food-webs.

It has been well documented that spiny dogfish switch prey to take advantage of high abundances of a certain prey items (Bonham 1954; Beamish et al. 1992). Therefore,

one would expect to find regional differences in TP if one region has more abundant prey or if one region is comprised of different food-webs. Alternately, food chain length in different habitats can lead to differences in TP. The food-web of the continental shelf ecosystem of the northwestern Atlantic Ocean was found to contain a high number of links, possibly leading to higher $\delta^{15}\text{N}$ values found in small shortfin mako shark *Isurus oxyrinchus* frequenting inshore habitats (Link 2002; Estrada et al. 2003). Also, McConnaughey and McRoy (1979) hypothesized that the benthic food chain is likely to be longer due to the inclusion of bacteria and meiofauna; presumably, an omnivorous opportunist like the spiny dogfish would take advantage of benthic organisms to higher degree while nearshore than when offshore.

In the GOA, our Kodiak site had higher TPs for a given size than NEGOA, PWS, and Yakutat. As turnover rates are very slow in shark muscle (Logan and Lutcavage 2010), this may indicate a shift in prey items or feeding behavior that persists long enough to alter the stable isotope signatures. Spiny dogfish in the waters surrounding Kodiak Island may be capitalizing on abundant prey items found there or may have a longer residence time in nearshore waters. Based on carbon stable isotope ratios from marine planktonic and marine benthic sources found in the literature, the spiny dogfish sampled in this study display values that straddle these values possibly indicating that spiny dogfish are benefitting from both sources (France 1995). Our lipid-normalized $\delta^{13}\text{C}$ values provide some evidence that spiny dogfish from Kodiak may utilize nearshore or benthic habitats slightly more intensively than those from PWS, NEGOA, and Yakutat. The wider continental shelf surrounding Kodiak versus a much narrower

shelf off the NEGOA may provide a partial explanation. Furthermore, NEGOA, PWS, and Yakutat did not have significantly different TP to length relationships, nor did the $\delta^{13}\text{C}$ values differ significantly among these sites. These results suggest that spiny dogfish in this EGOA statistical area are feeding at the same TP and are likely participating in very similar food-webs. It is important to note that several studies have found a latitudinal versus $\delta^{13}\text{C}$ effect, where $\delta^{13}\text{C}$ is less enriched at higher latitudes (Quillfeldt et al. 2005; Menard et al. 2007). However, our data are more complicated than these previous studies and includes a larger range of both pelagic and benthic habitats.

Spiny dogfish $\delta^{13}\text{C}$ values were not linearly related to length (Table 2.3). The lack of a linear relationship of the lipid-normalized carbon isotope values to length provides evidence that there is not a significant habitat shift with ontogeny for spiny dogfish over the length range sampled. It has been noted, though, that our dataset did not include spiny dogfish pups or very young immatures, for which an ontogenetic habitat shift would have been expected because dogfish are thought to feed more pelagically as juveniles and become more demersal as adults (Jones and Geen 1977; Beamish and Sweeting 2009). Diet studies in British Columbia documented that the prey of younger spiny dogfish were primarily pelagic, while adults depended on pelagic prey to a lesser degree and become increasingly demersal (Jones and Geen 1977).

Stable isotope analysis can be useful in revealing ontogenetic diet changes over large temporal scales on the order of years to decades. Several studies have explored isotopic turnover rates in teleost fishes and elasmobranchs, demonstrating that it is unlikely that seasonal changes in diet can be revealed with stable isotopic analysis of

muscle tissue (Hesslein et al. 1993; MacNeil et al. 2005; MacNeil et al. 2006; Logan and Lutcavage 2010). As some of these studies conclude, it would be beneficial to perform stable isotope analysis on multiple tissues to elucidate seasonal diet changes (MacNeil et al. 2005; Logan and Lutcavage 2010). Muscle tissue can only reveal short-term diet changes in small, fast-growing fishes, such as larval and juvenile stages; in red drum *Sciaenops ocellatus* larvae, for example, a shift in diet was observed in $\delta^{15}\text{N}$ within 1-2 days and a complete turnover was accomplished in only 10 days (Herzka and Holt 2000). The lack of spiny dogfish pups and early immature stages in this study made it unlikely that we would observe any short-term diet changes. In Yakutat, we analyzed spiny dogfish from 2004-2006 and found no indication of diet change on an annual scale. These findings indicate that, at least over 2004 - 2006, there was no large-scale shift in the diets or feeding ecology of spiny dogfish in the Yakutat region. Regime shifts have been described by others by using changes in species composition and biomass (Anderson and Piatt 1999; Mueter and Norcross 2000). Stable isotope analysis could be developed as another technique for monitoring and documenting regime shifts. Furthermore, stable isotope analysis could prove to be an important tool in quantifying the effects of climate change on fishes and other marine organisms.

The need for understanding size-specific dietary needs and TP becomes more important with the increased interest in ecosystem-based fishery management (Marasco et al. 2007). Ecosystem models, such as Ecosim and Ecopath, can be improved with additional knowledge of the trophic role of different life-history stages of a species (Pauly et al. 2000). One study used ecosystem models to compare three large marine

ecosystems (i.e., Bering Sea, GOA, and Aleutian Islands), but used only a single TP of 4.3 for spiny dogfish potentially generating misleading results (Aydin et al. 2007). Based on our results, a TP of 4.3 would only represent the largest females in the population, which are typically more rare (Tribuzio et al. 2009). Stable isotope analysis can provide size-specific information on TPs for any number of species, and may provide more accurate TPs that are based on integrated diets over many months to a year.

Our estimates of spiny dogfish TP include a lower range of TPs than what were found in a concurrent diet study that examined spiny dogfish of similar lengths (Tribuzio 2010). Diet studies that are unable to collect specimens year round may be missing seasonally occurring prey items or prey items that are quickly digested and may therefore bias the TP estimate of the predator. Spiny dogfish, for example, are known to consume ctenophores, which break down quickly and are hard to preserve in stomach samples (Jones and Geen 1977). In the GOA, gelatinous prey items that are not observed in stomach samples and prey items of a lower TP may make up more of the diet of spiny dogfish in the under-sampled winter months and could be influencing the TPs calculated from stable isotopes. In a study using stable isotope analysis in the Celtic Sea in the northeast Atlantic Ocean, a TP of 3.4 was calculated for spiny dogfish of approximately 63 cm length (Pinnegar et al. 2002). In Yakutat, these results closely align with our results based, namely on a predicted TPs of 3.3 and 3.4 for spiny dogfish of 61 cm and 66 cm lengths, respectively. Another study using stable isotope analysis determined that spiny dogfish on the Georges Bank had stable nitrogen isotope values within the range of our values, although, they tended to be on the lower end of our ranges (Fry 1988). The

lengths of the spiny dogfish were not published, therefore, it is difficult to draw conclusions from this comparison.

On a final note, spiny dogfish biomass will continue to fluctuate in the northeastern Pacific Ocean, but it is unknown whether future physical and biological changes in the GOA ecosystem would support a long-term increase in the population of spiny dogfish. Studies focused on the effects of climate change and fisheries predict that fish distributions will move toward higher latitudes (Perry et al. 2005). The Pacific Decadal Oscillation (PDO) index has varied between positive and negative anomalies and most recently has been negative, although it was positive during the high abundance years of spiny dogfish. If the relative abundance of spiny dogfish in the GOA is linked to warmer sea surface temperatures, then spiny dogfish numbers may increase as temperatures rise. Competition between elasmobranchs (including spiny dogfish) and commercially important gadoids has been a concern on Georges Bank (Fogarty and Murawski 1998; Collie and DeLong 1999). Although, there is recent dietary evidence that predation by elasmobranchs is not a contributing factor (Link et al. 2002), the complexity of marine ecosystems in general makes it difficult to sort out the cause of trophic cascades. Our results demonstrate that spiny dogfish have a range of TPs from at least 3.3 to over 4.2 in the GOA. A TP on the lower end of this range would mean that spiny dogfish are occupying the same TP as many small schooling fishes (e.g., herring, and capelin), soles (e.g., rex sole *Glyptocephalus zachirus* and yellowfin sole *Limanda aspera*, and skates (e.g., Aleutian skate *Bathyraja aleutica* (Aydin et al. 2007); the middle range of TPs that spiny dogfish occupy would be in the range of salmon *Oncorhynchus*

spp., rockfish (Scorpaenidae), walleye pollock *Theragra chalcogramma*, and baleen whales (Aydin et al. 2007); while the upper range encompasses TPs that are occupied by some skates, sablefish *Anoplopoma fimbria*, Pacific cod *Gadus macrocephalus*, and piscivorous seabirds (Aydin et al. 2007). Therefore, large spiny dogfish are an important predator in the GOA ecosystem and share high TPs along with other top predators that include piscivorous seabirds and fishes. In an effort to understand species competition, future work should focus on direct interactions between spiny dogfish and other top predators and their prey to explore whether certain prey items are of a limited supply.

2.6 Acknowledgements

We thank C. Tribuzio for graciously sharing spiny dogfish samples collected for her doctorate at the University of Alaska Fairbanks. Thanks to ADF&G Kodiak, G. Bargmann, D. Courtney, V. Gallucci, J. King, and N. Vega for providing and assisting with spiny dogfish sample collection. Thanks to J. Barnhart for assisting with the collection of weathervane scallops. Also, we thank NOVA Fisheries Inc. for providing weathervane scallop samples. We thank N. Haubenstock and T. Howe at the Alaska Stable Isotope Facility for their assistance and expertise processing samples. We are grateful for the statistical advice offered by F. Mueter and T. Quinn II. Funding was provided by the Cooperative State Research, Education and Extension Service, U.S. Department of Agriculture.

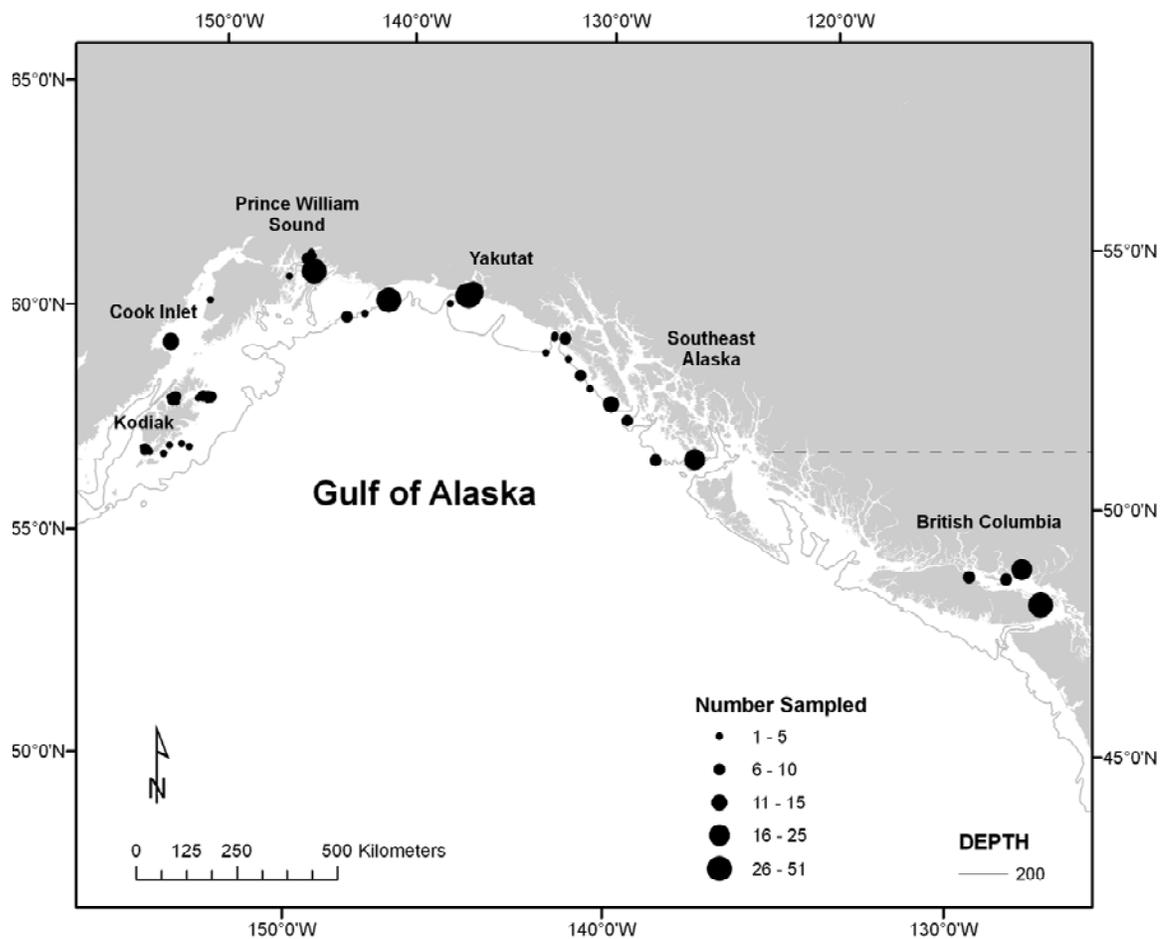


Figure 2.1. Number and location of spiny dogfish sampled in the Gulf of Alaska. For the purposes of our study, samples collected between Prince William Sound and Yakutat are considered northeastern Gulf of Alaska. Two hundred meter bathymetric line is indicated.

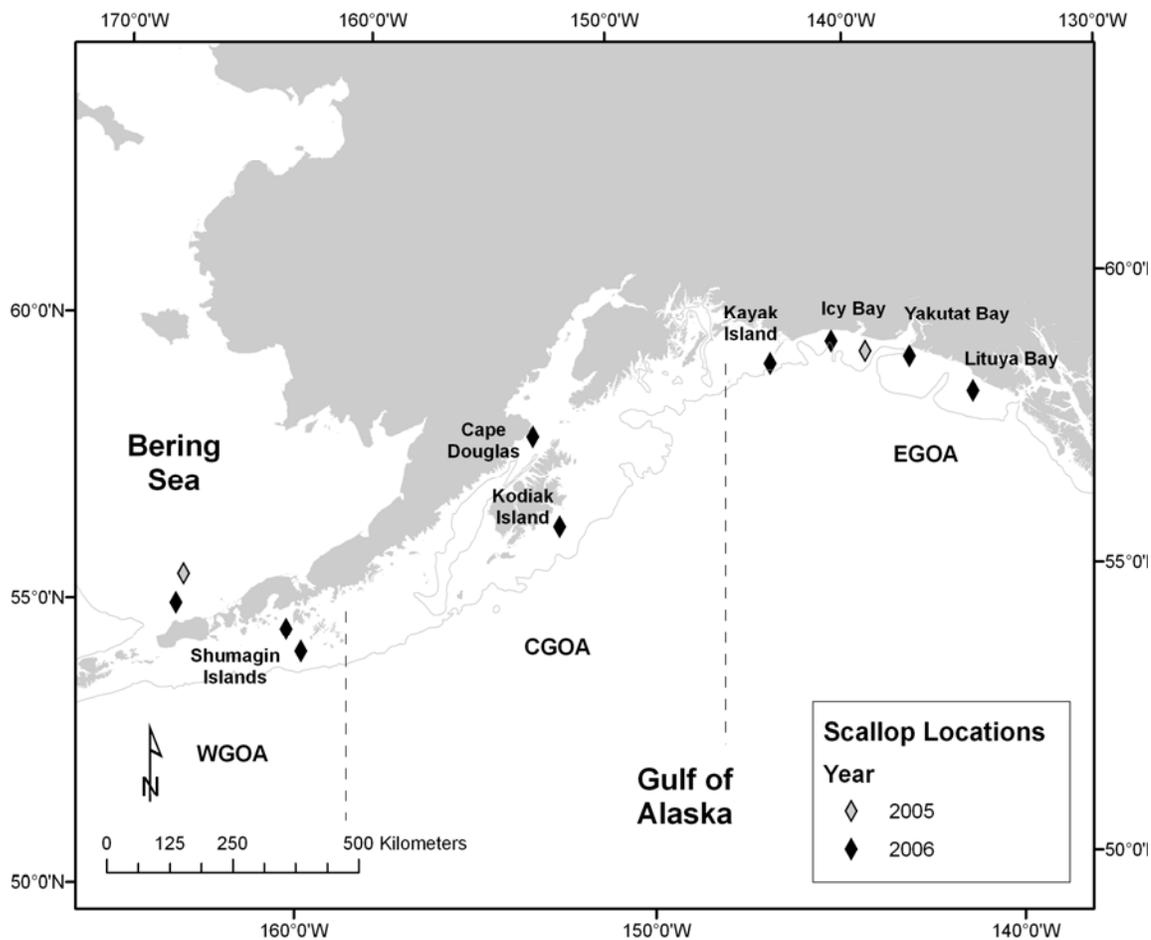


Figure 2.2. Approximate locations of weathervane scallop samples from the Gulf of Alaska. Scallops were pooled into the National Marine Fisheries Service regulatory areas of western Gulf of Alaska (WGOA), central GOA (CGOA), and eastern GOA (EGOA). Two hundred meter bathymetric line is indicated.

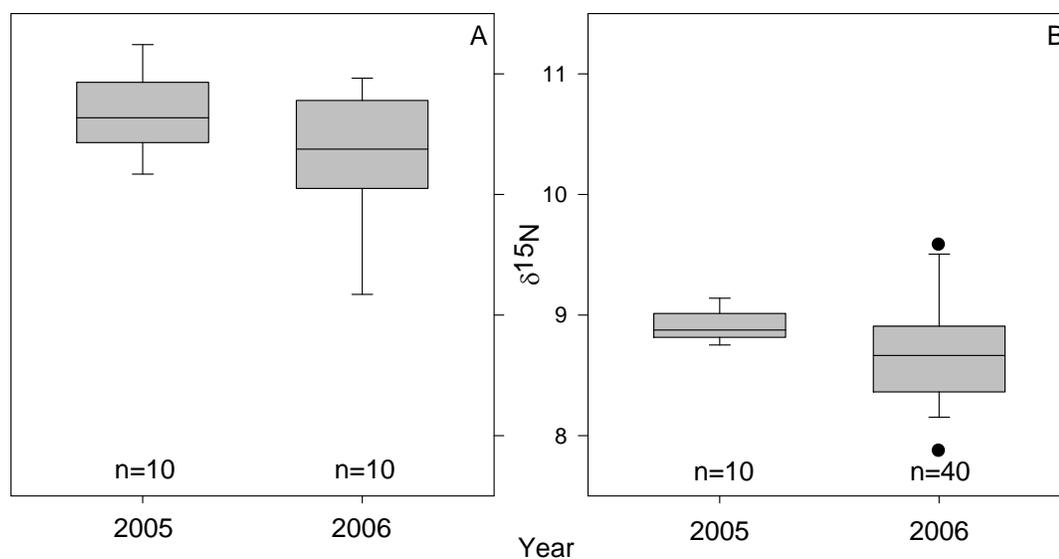


Figure 2.3. Weathervane scallop $\delta^{15}\text{N}$ values for 2004 and 2005 in the (A) Bering Sea and (B) eastern Gulf of Alaska (EGOA). In the Bering Sea, there was no significant difference in $\delta^{15}\text{N}$ values between 2005 and 2006 (independent samples t-test, $t = -1.66$, d.f. = 18, $p = 0.115$). In the EGOA, there was a significant difference in $\delta^{15}\text{N}$ values between 2005 and 2006 (Mann-Whitney test, $W = 349.0$, $p = 0.023$). Boxes represent the 5th and 95th percentiles, whiskers represent the 10th and 90th percentiles, and black dots represent the 5th and 95th percentiles. Horizontal bars represent the medians. Sample sizes are reported.

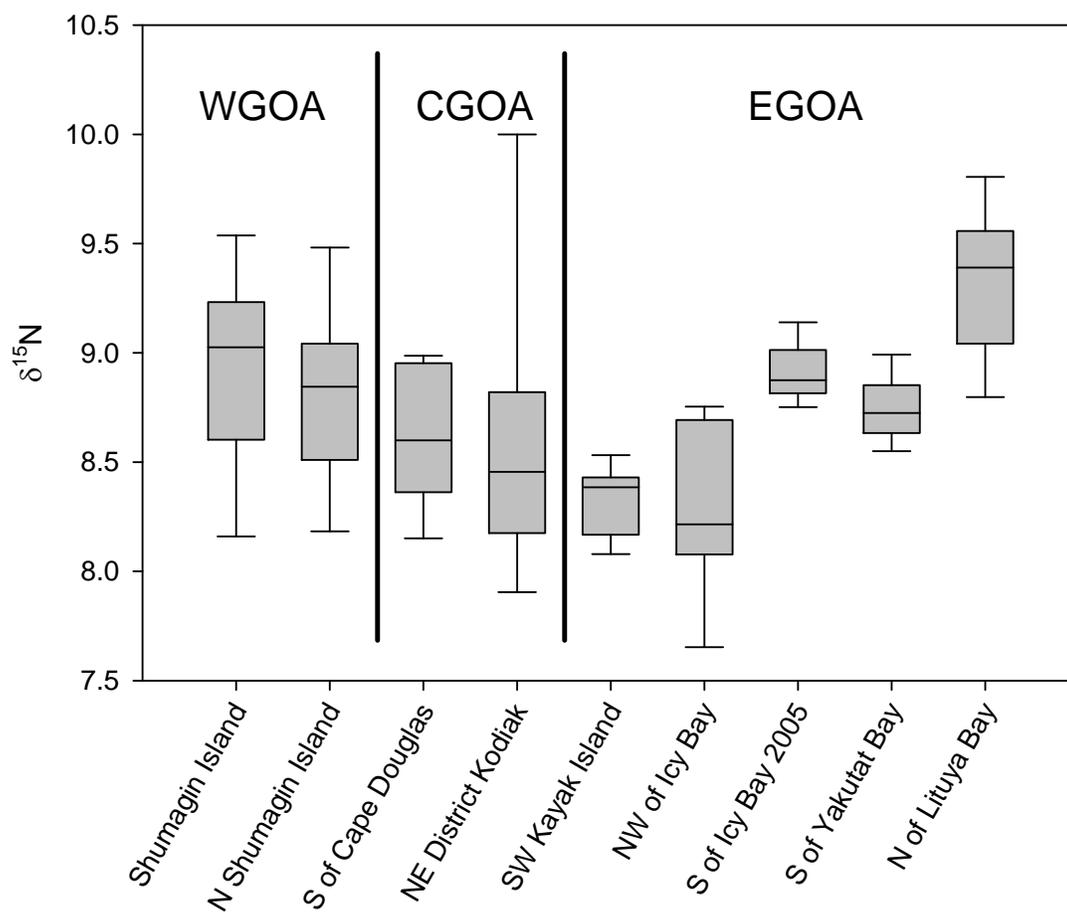


Figure 2.4. Weathervane scallop $\delta^{15}\text{N}$ values in the Gulf of Alaska. All scallops were collected in 2006 except S of Icy Bay (2005). Each site represents a sample size of ten. Compass headings that precede sites provide additional information on the location of the sampling area. National Marine Fisheries Service (NMFS) regulatory areas are shown for western GOA (WGOA), central GOA (CGOA) and eastern GOA (EGOA). Boxes represent the 25th and 75th percentile and whiskers represent the 10th and 90th percentiles. Horizontal bars represent the medians.

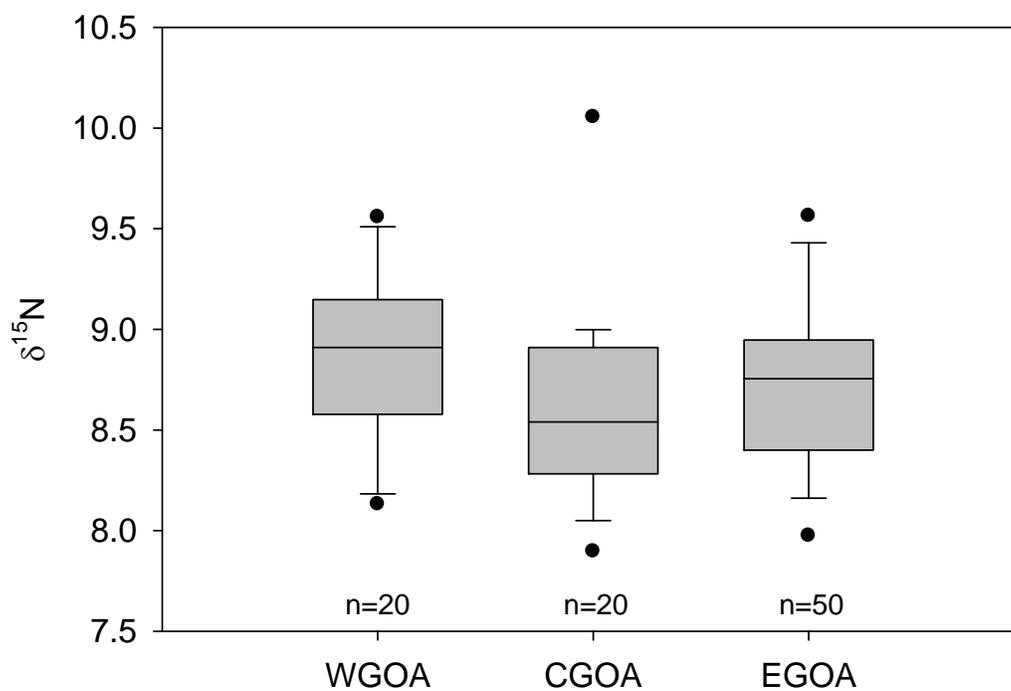


Figure 2.5. Weathervane scallop $\delta^{15}\text{N}$ values in the pooled NMFS regulatory areas; eastern Gulf of Alaska (EGOA), central GOA (CGOA), and western GOA (WGOA). There was no significant difference among areas (ANOVA $F_{2,87} = 1.74$, $p = 0.182$). Boxes represent the 25th and 75th percentile, whiskers represent the 10th and 90th percentiles, and black dots represent the 5th and 95th percentiles. Sample sizes are indicated below the box plots.

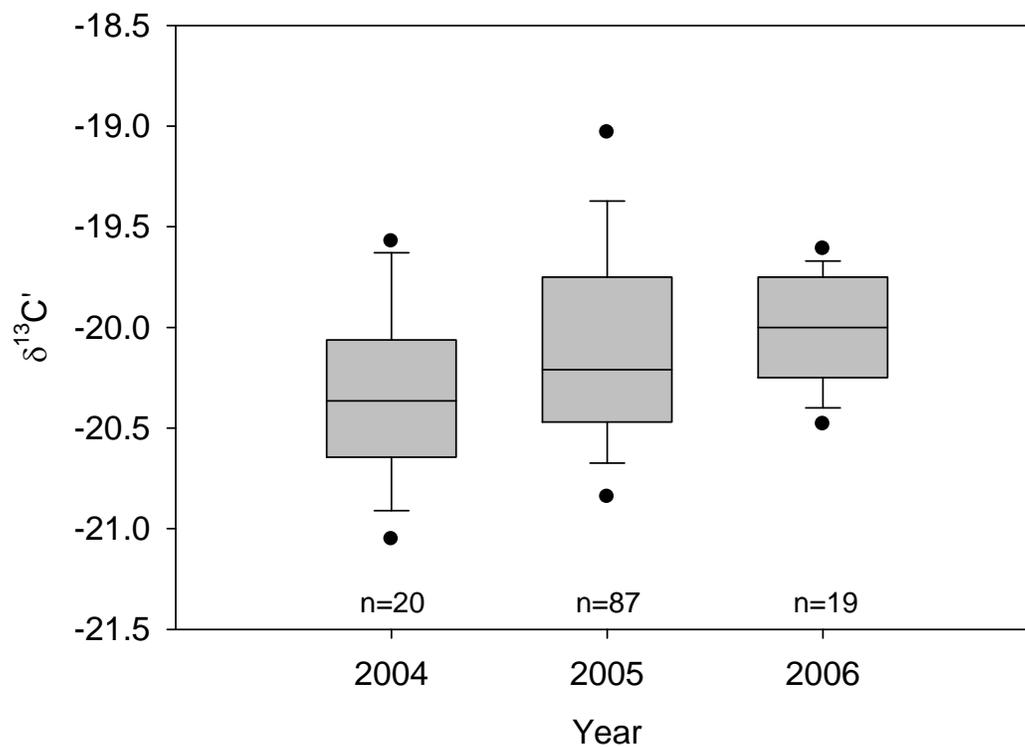


Figure 2.6. Spiny dogfish $\delta^{13}\text{C}'$ (lipid-normalized) values from samples collected from Yakutat in 2004, 2005, and 2006. Sampling year had no significant effect on $\delta^{13}\text{C}'$ values (ANOVA $F_{2,123} = 2.50$, $p = 0.086$). Boxes represent the 25th and 75th percentile, whiskers represent the 10th and 90th percentiles, and black dots represent the 5th and 95th percentiles. Sample sizes are indicated below the box plots.

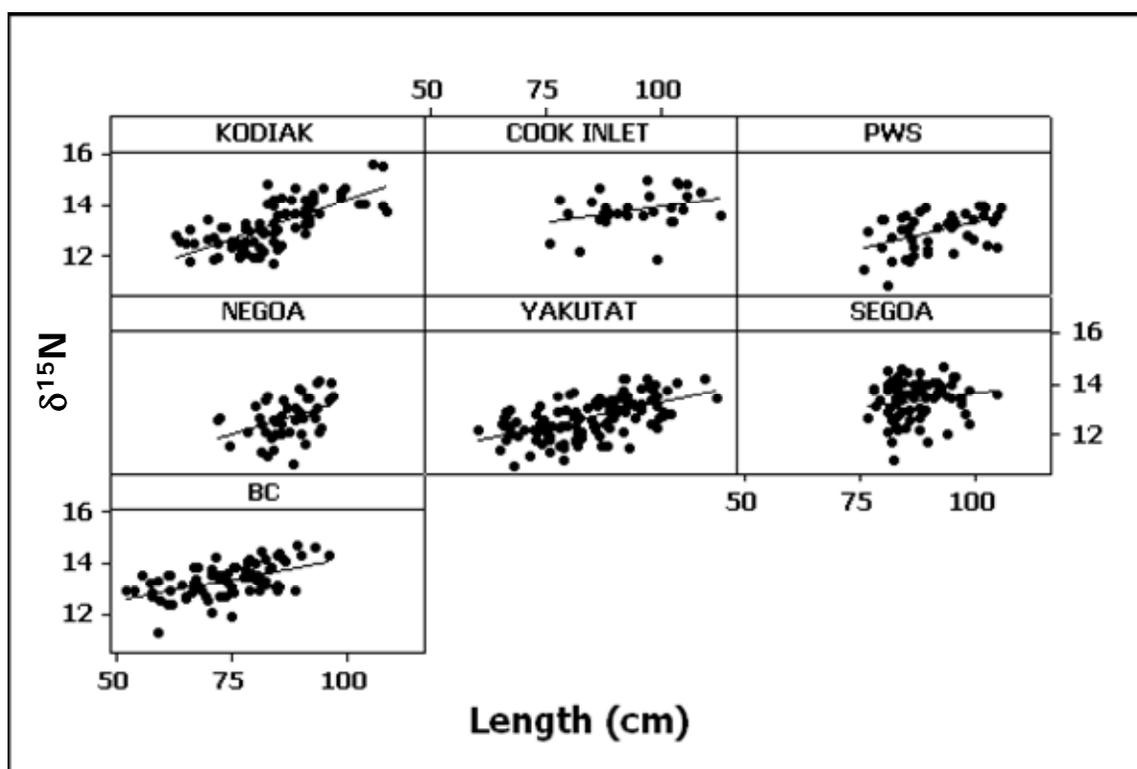


Figure 2.7. Linear relationship between spiny dogfish $\delta^{15}\text{N}$ and length (cm) at all sites including Kodiak, Cook Inlet, Prince William Sound (PWS), northeastern Gulf of Alaska (NEGOA), Yakutat Bay (Yakutat), southeastern GOA (SEGOA), and British Columbia (BC). All sites have a significant ($p < 0.05$) linear relationship except SEGOA ($p = 0.175$) and Cook Inlet ($p = 0.055$) (Table 2.3).

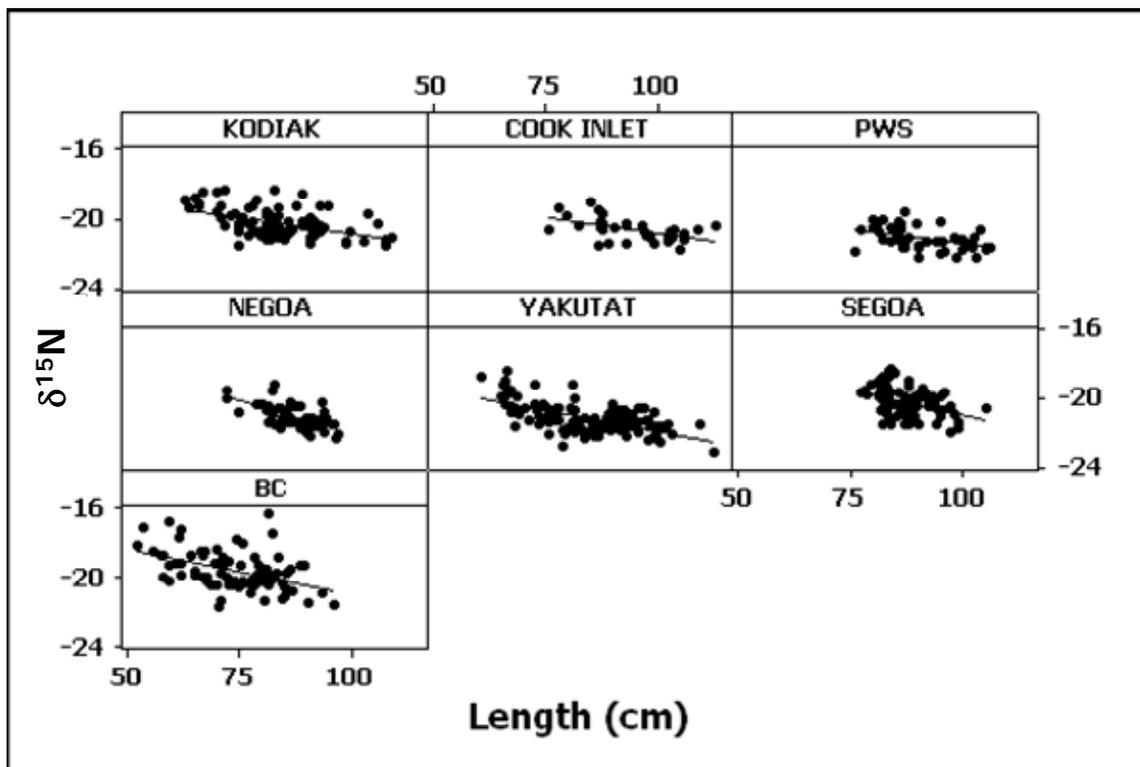


Figure 2.8. Linear relationship between spiny dogfish $\delta^{13}\text{C}$ and length (cm) at all sites including Kodiak, Cook Inlet, Prince William Sound (PWS), northeastern Gulf of Alaska (NEGOA), Yakutat Bay (Yakutat), southeastern GOA (SEGOA), and British Columbia (BC). All sites have a significant ($p < 0.05$) linear relationship (Table 2.3).

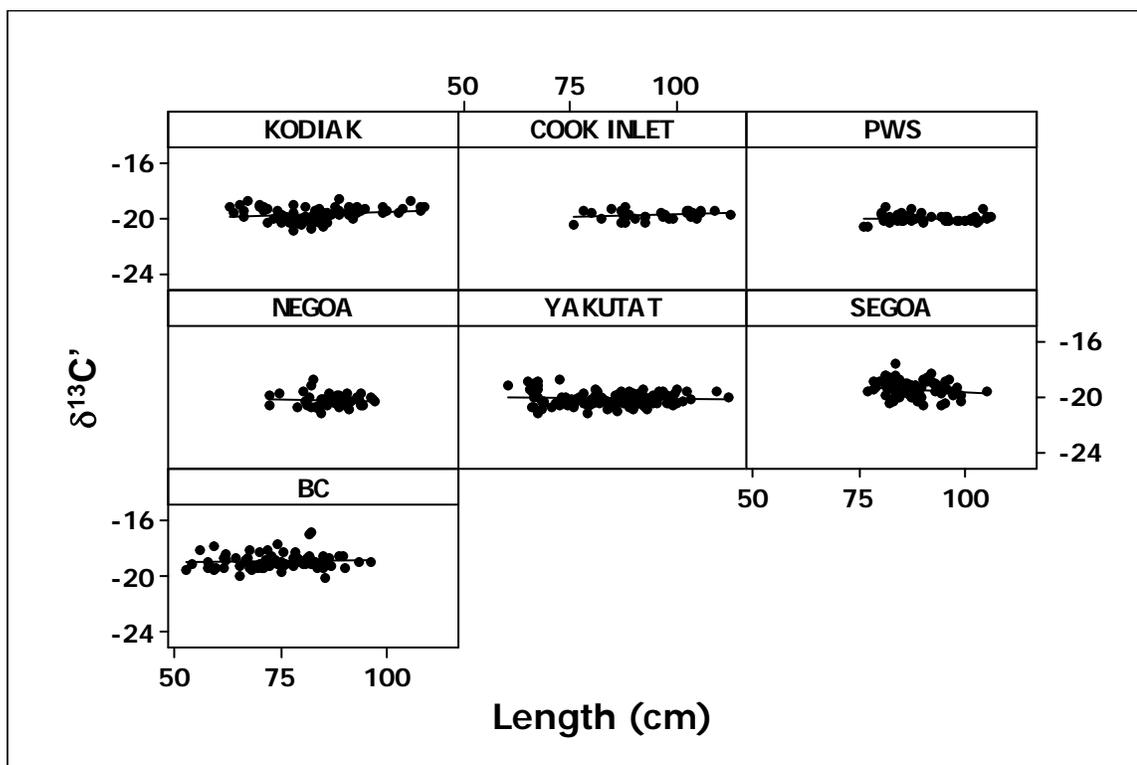


Figure 2.9. Linear relationship between spiny dogfish $\delta^{13}C'$ (lipid-normalized $\delta^{13}C$) and length (cm) at all sites including Kodiak, Cook Inlet, Prince William Sound (PWS), northeastern Gulf of Alaska (NEGOA), Yakutat Bay (Yakutat), southeastern GOA (SEGOA), and British Columbia (BC). None of these sites have a significant ($p < 0.05$) linear relationship.

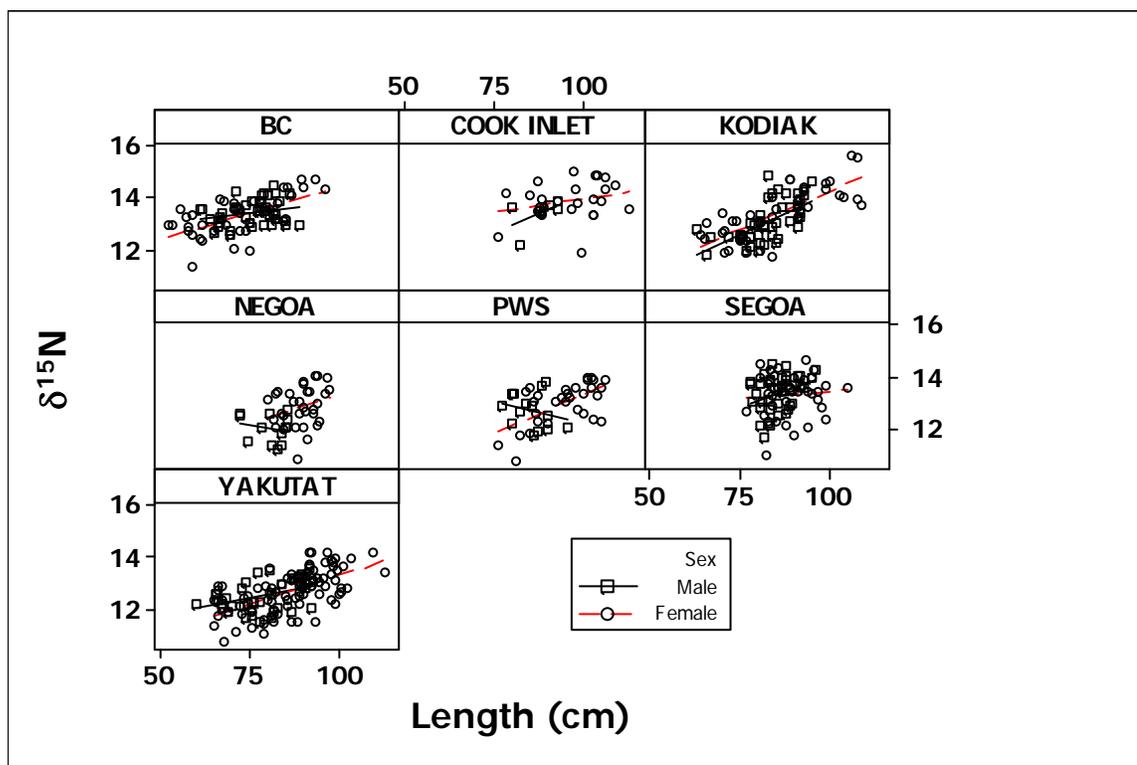


Figure 2.10. $\delta^{15}\text{N}$ differences between sexes. Linear relationship between spiny dogfish $\delta^{15}\text{N}$ and length (cm) at all sites including Kodiak, Cook Inlet, Prince William Sound (PWS), northeastern GOA (NEGOA), Yakutat Bay (Yakutat), southeastern GOA (SEGOA), and British Columbia (BC). Males are depicted with squares and females are depicted with circles. Sex could not be tested as a factor at all sites. Sex was not significant ($p < 0.05$) at the following sites: Kodiak $F_{1,83} = 1.11$, $p = 0.294$; and Yakutat $F_{1,123} = 1.09$, $p = 0.299$. BC $F_{1,78} = 0.05$, $p = 0.818$.

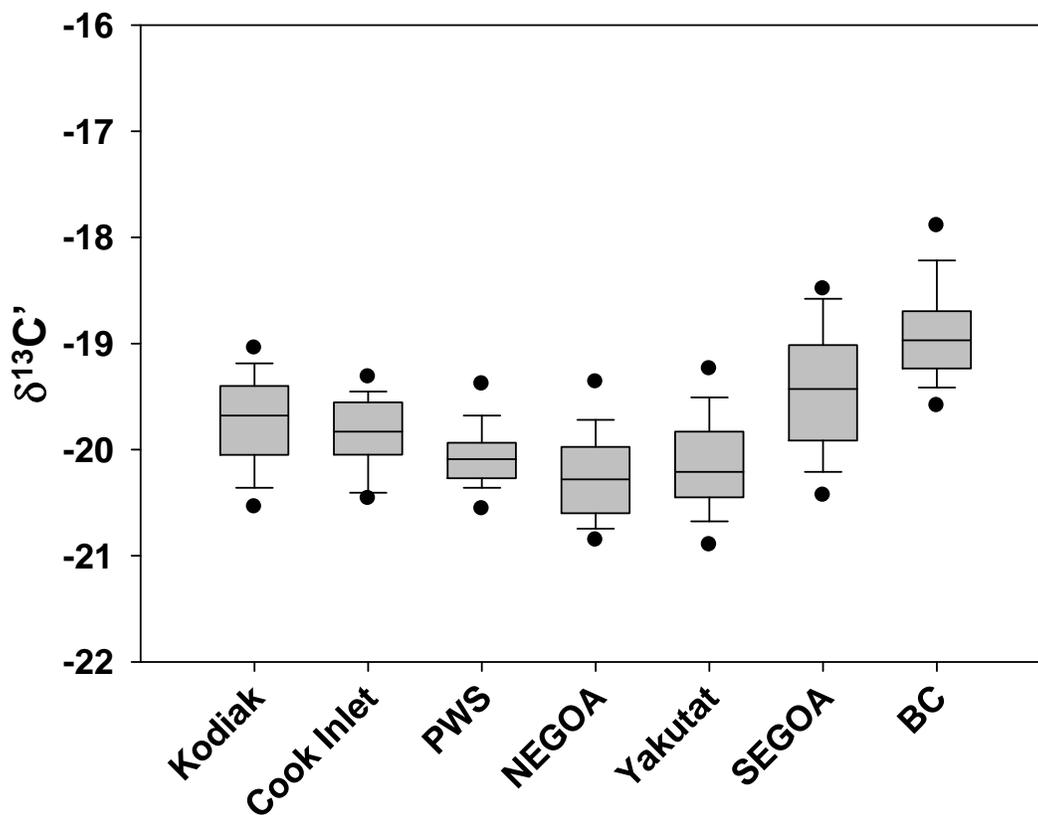


Figure 2.11. Boxplot of $\delta^{13}C'$ (lipid-normalized $\delta^{13}C$) values in the northeastern Pacific Ocean. Lipid-normalized, $\delta^{13}C'$, differed significantly among sites (ANOVA $F_{6,484} = 71.00$, $p < 0.001$). See Table 2.4 for results of pairwise comparison. Boxes represent the 25th and 75th percentile, whiskers represent the 10th and 90th percentiles, and black dots represent the 5th and 95th percentiles.

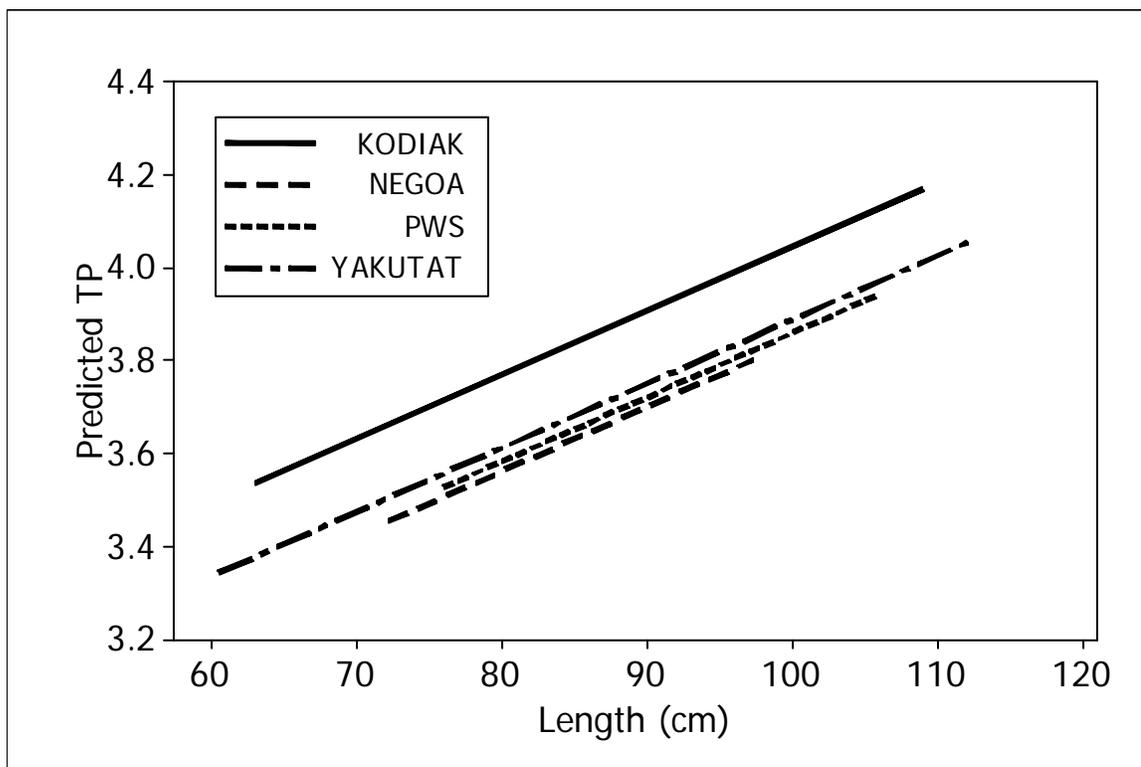


Figure 2.12. Fitted linear relationships between spiny dogfish trophic position (TP) to length (cm) for each site: Kodiak, Prince William Sound (PWS), northeastern Gulf of Alaska (NEGOA), and Yakutat.

Table 2.1. Spiny dogfish sample sizes (N) at each site for males (M) and females (F) with mean values and standard deviation (SD) for lengths (total length extended), $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, $\delta^{13}\text{C}'$, and carbon to nitrogen ratios (C:N). Indicated are the sampling areas of this study, Kodiak, Cook Inlet, Prince William Sound (PWS), northeastern Gulf of Alaska (NEGOA), Yakutat, southeastern Gulf of Alaska (SEGOA), and British Columbia (BC).

Site	Sex			Length (cm)		$\delta^{15}\text{N}$		$\delta^{13}\text{C}$		$\delta^{13}\text{C}'$		C:N
	N	M	F	Range	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD	Mean \pm SD
KODIAK	86	41	45	63.0 - 109	84.1 \pm 10.5	11.7 - 15.6	13.2 \pm 0.9	-21.6 - -18.4	-20.3 \pm 0.8	-20.9 - -18.7	-19.7 \pm 0.5	4.7 \pm 1.0
COOK INLET	32	6	26	76.0 - 113.1	94.3 \pm 9.5	11.8 - 15.0	13.8 \pm 0.7	-21.8 - -19.0	-20.7 \pm 0.7	-20.5 - -19.3	-19.8 \pm 0.3	5.0 \pm 0.8
PWS	45	14	31	76.0 - 106	91.6 \pm 8.6	10.8 - 14.0	12.9 \pm 0.8	-22.3 - -19.6	-21.2 \pm 0.7	-20.6 - -19.3	-20.1 \pm 0.3	5.5 \pm 1.0
NEGOA	45	12	33	72.2 - 97.3	87.0 \pm 6.1	10.8 - 14.1	12.6 \pm 0.8	-22.3 - -19.2	-21.0 \pm 0.7	-21.2 - -18.8	-20.3 \pm 0.5	5.0 \pm 1.0
YAKUTAT	126	35	91	60.5 - 112.6	84.3 \pm 11.1	10.8 - 14.2	12.7 \pm 0.7	-23.1 - -18.4	-21.1 \pm 0.9	-21.2 - -18.8	-20.1 \pm 0.5	5.4 \pm 1.3
SEGOA	76	37	39	77.0 - 105.0	87.5 \pm 5.8	11.0 - 14.7	13.4 \pm 0.8	-21.9 - -18.3	-20.2 \pm 0.9	-20.6 - -17.6	-19.4 \pm 0.6	5.0 \pm 0.9
BC	81	41	40	52.3 - 96.2	74.0 \pm 9.9	11.3 - 14.7	13.3 \pm 0.6	-21.7 - -16.3	-19.6 \pm 1.1	-20.2 - -16.8	-18.9 \pm 0.5	5.0 \pm 1.3

Table 2.2. Sample site and region, date, bottom depth, and mean $\delta^{15}\text{N} \pm$ standard error (SE) values for weathervane scallops collected for isotopic baseline. Sampling sites are Bering Sea, Shumagin Islands, north of (N) Shumagin Islands, south of (S) Cape Douglas, northeast (NE) District Kodiak, southwest of (SW) Kayak Island, northwest of (NW) Icy Bay, south of (S) Icy Bay, south of (S) Yakutat Bay, and north of (N) Lituya Bay. Sampling regions are Bering Sea (BS), western Gulf of Alaska (WGOA), central Gulf of Alaska (CGOA), and eastern Gulf of Alaska (EGOA).

Site	Region	N	Date	Year	Depth (m)	$\delta^{15}\text{N}$ (mean \pm SE)
Bering Sea	BS	10	11/15/2006	2006	95	10.3 \pm 0.2
Bering Sea	BS	10	12/23/2005	2005	95	10.7 \pm 0.1
Shumagin Island	WGOA	10	10/25/2006	2006	86	8.9 \pm 0.1
N Shumagin Island	WGOA	10	10/28/2006	2006	117	8.8 \pm 0.1
S of Cape Douglas	CGOA	10	8/2/2006	2006	110	8.6 \pm 0.1
NE District Kodiak	CGOA	10	11/1/2006	2006	91	8.6 \pm 0.2
SW Kayak Island	EGOA	10	7/3/2006	2006	77	8.3 \pm 0.1
NW of Icy Bay	EGOA	10	9/28/2006	2006	64	8.3 \pm 0.1
S of Icy Bay 2005	EGOA	10	10/1/2005	2005	68	8.9 \pm 0.0
S of Yakutat Bay	EGOA	10	9/5/2006	2006	69	8.7 \pm 0.1
N of Lituya Bay	EGOA	10	8/24/2006	2006	73	9.3 \pm 0.1

Table 2.3. Parameters, test statistics, and sample sizes (N) for linear relationships between length (cm) and $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and $\delta^{13}\text{C}'$ for spiny dogfish for all sampling sites, Kodiak, Cook Inlet, Prince William Sound (PWS), northeastern Gulf of Alaska (NEGOA), Yakutat, southeastern Gulf of Alaska (SEGOA), and British Columbia (BC).

$\delta^{15}\text{N}$	α	β	R^2	$R^2_{\text{adj.}}$	F-value	p-value	N
Kodiak	8.1	0.0612	50.6%	50.0%	86.14	< 0.001	86
Cook Inlet	11.3	0.0261	11.8%	8.8%	4.00	0.055	32
PWS	9.1	0.0418	21.7%	19.8%	11.89	0.001	45
NEGOA	8.0	0.0534	16.8%	14.9%	8.70	0.005	45
Yakutat	9.4	0.0388	33.4%	32.8%	62.09	< 0.001	126
SEGOA	11.6	0.0204	2.5%	1.1%	1.87	0.175	76
BC	10.8	0.0347	28.3%	27.4%	31.12	< 0.001	81
$\delta^{13}\text{C}$	α	β	R^2	$R^2_{\text{adj.}}$	F-value	p-value	N
Kodiak	-17.0	-0.0386	24.1%	23.2%	26.74	< 0.001	86
Cook Inlet	-17.3	-0.0361	26.5%	24.1%	10.83	0.003	32
PWS	-17.9	-0.0359	21.5%	19.7%	11.77	0.001	45
NEGOA	-14.6	-0.0743	40.0%	38.6%	28.66	< 0.001	45
Yakutat	-17.1	-0.0484	39.8%	39.3%	81.89	< 0.001	126
SEGOA	-15.0	-0.0602	16.9%	15.7%	15.00	< 0.001	76
BC	-15.7	-0.0526	20.9%	19.9%	20.87	< 0.001	81
$\delta^{13}\text{C}'$	α	β	R^2	$R^2_{\text{adj.}}$	F-value	p-value	N
Kodiak	-20.5	0.0092	4.5%	3.4%	3.97	0.050	86
Cook Inlet	-20.5	0.0074	4.7%	1.5%	1.46	0.236	32
PWS	-20.1	0.0001	0.0%	0.0%	0.00	0.986	45
NEGOA	-19.9	-0.0035	0.2%	0.0%	0.10	0.754	45
Yakutat	-19.9	-0.0032	0.6%	0.0%	0.69	0.407	126
SEGOA	-18.0	-0.0164	2.5%	1.2%	1.91	0.171	76
BC	-19.3	0.0051	0.8%	0.0%	0.67	0.415	81

2.7 References

- Alonso, M. K., E. A. Crespo, N. A. Garcia, S. N. Pedraza, P. A. Mariotti, and N. J. Mora. 2002. Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina. *Environmental Biology of Fishes* 63(2):193-202.
- Anderson, P. J., and J. F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189:117-123.
- Andrews, A. G., and R. J. Foy. 2009. Geographical variation in the carbon and nitrogen stable isotope ratios in spiny dogfish in the northeastern Pacific Ocean. Pages 269-276 in V. F. Gallucci, G. A. McFarlane, and G. G. Bargmann, editors. *Biology and management of dogfish sharks*. American Fisheries Society, Bethesda, Maryland.
- Aydin, K., S. Gaichas, I. Ortiz, D. Kinzey, and N. Friday. 2007. A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands large marine ecosystems through food web modeling. U.S. Department of Commerce. NOAA Tech Memo. NMFS-AFSC-178, 298p.
- Beamish, R. J., and R. M. Sweeting. 2009. Spiny dogfish in the pelagic waters of the Strait of Georgia and Puget Sound. Pages 101-118 in V. F. Gallucci, G. A.

- McFarlane, and G. G. Bargmann, editors. Biology and management of dogfish sharks. American Fisheries Society, Bethesda, Maryland.
- Beamish, R. J., B. L. Thomson, and G. A. McFarlane. 1992. Spiny dogfish predation on chinook and coho salmon and the potential effects on hatchery-produced salmon. Transactions of the American Fisheries Society 121(4):444-455.
- Bonham, K. 1954. Food of the dogfish *Squalus acanthias*. Fisheries Research Papers 1(2):25-36.
- Bowman, R., R. Eppi, and M. Grosslein. 1984. Diet and consumption of spiny dogfish in the Northwest Atlantic. ICES C. M.1984/G:27, Copenhagen, Denmark.
- Box, A., S. Deudero, A. Blanco, A. M. Grau, and F. Riera. 2010. Differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes in the pearly razorfish *Xyrichtys novacula* related to the sex, location and spawning period. Journal of Fish Biology 76(10):2370-2381.
- Braccini, J. M., B. M. Gillanders, and T. I. Walker. 2005. Sources of variation in the feeding ecology of the piked spurdog (*Squalus megalops*): implications for inferring predator-prey interactions from overall dietary composition. ICES Journal of Marine Science 62(6):1076-1094.
- Cabana, G., and J. B. Rasmussen. 1996. Comparison of aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Sciences 93(20):10844-10847.

- Castro, J. I. 1983. The sharks of North American waters. Texas A&M University Press, College Station.
- Collie, J. S., and A. K. DeLong. 1999. Multispecies interactions in the Georges Bank fish community. Pages 187-210 *in* Ecosystem approaches for fisheries management. Proceedings of the 1998 Wakefield Fisheries Symposium: Ecosystem Considerations in Fisheries Management. University of Alaska, Alaska Sea Grant Publication AK-SG-99-01, Fairbanks.
- Cortes, E. 1999. Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science* 56(5):707-717.
- Courtney, D. L., C. A. Tribuzio, K. J. Goldman, and J. S. Rice. 2006. Gulf of Alaska Stock Assessment and Fishery Evaluation Report. North Pacific Fishery Management Council, Seattle, Washington.
- DeNiro, M. J., and S. Epstein. 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. *Science* 197:261-263.
- 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(3):341-351.

- Domi, N., J. M. Bouquegneau, and K. Das. 2005. Feeding ecology of five commercial shark species of the Celtic Sea through stable isotope and trace metal analysis. *Marine Environmental Research* 60(5):551-569.
- Ebert, D. A., and J. J. Bizzarro. 2007. Standardized diet compositions and trophic levels of skates (Chondrichthyes : Rajiformes : Rajoidei). *Environmental Biology of Fishes* 80(2-3):221-237.
- Ebert, D. A., L. J. V. Compagno, and P. D. Cowley. 1992. A preliminary investigation of the feeding ecology of squaloid sharks off the west coast of southern Africa. Pages 601-609 in A. I. L. Payne, K. H. Brink, K. H. Mann, and R. Hilborn, editors. *Benguela Trophic Functioning*. Cape Town, South Africa.
- Ellis, J. K., and J. A. Musick. 2007. Ontogenetic changes in the diet of the sandbar shark, *Carcharhinus plumbeus*, in lower Chesapeake Bay and Virginia (USA) coastal waters. *Environmental Biology of Fishes* 80(1):51-67.
- Estrada, J. A., A. N. Rice, M. E. Lutcavage, and G. B. Skomal. 2003. Predicting trophic position in sharks of the north-west Atlantic Ocean using stable isotope analysis. *Journal of the Marine Biological Association of the United Kingdom* 83(6):1347-1350.
- Estrada, J. A., A. N. Rice, L. J. Natanson, and G. B. Skomal. 2006. Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. *Ecology* 87(4):829-834.

- Fisk, A. T., S. A. Tittlemier, J. L. Pranschke, and R. J. Norstrom. 2002. Using anthropogenic contaminants and stable isotopes to assess the feeding ecology of Greenland sharks. *Ecology* 83(8):2162-2172.
- Fogarty, M. J., and S. A. Murawski. 1998. Large-scale disturbance and the structure of marine systems: Fishery impacts on Georges Bank. *Ecological Applications* 8(1, supplement):S6-S22.
- Foster, N. R. 1991. Intertidal bivalves: a guide to the common marine bivalves of Alaska. University of Alaska Press, Fairbanks.
- France, R. L. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Marine Ecology Progress Series* 124(1-3):307-312.
- Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308:1621-1623.
- Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnology and Oceanography* 33(5):1182-1190.
- Fry, B., and E. B. Sherr. 1984. $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science* 27:13-47.
- Galvan, D. E., C. J. Sweeting, and W. D. K. Reid. 2010. Power of stable isotope techniques to detect size-based feeding in marine fishes. *Marine Ecology Progress Series* 407:271-278.

- Hazlett, S. D., N. Misarti, A. G. Andrews, G. A. McFarlane, and M. J. Wooller. 2009. Stable isotopic variability along spiny dogfish spines: implications for retrospective ecological studies. Pages 259-267 in V. F. Gallucci, G. A. McFarlane, and G. G. Bargmann, editors. *Biology and management of dogfish sharks*. American Fisheries Society, Bethesda, Maryland.
- Herzka, S. Z., and G. J. Holt. 2000. Changes in isotopic composition of red drum (*Sciaenops ocellatus*) larvae in response to dietary shifts: potential applications to settlement studies. *Canadian Journal of Fisheries and Aquatic Sciences* 57(1):137-147.
- Hesslein, R. H., K. A. Hallard, and P. Ramlal. 1993. Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}\text{S}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$. *Canadian Journal of Fisheries and Aquatic Sciences* 50(10):2071-2076.
- Hobson, K. A., and H. E. Welch. 1992. 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.
- Hoekstra, P. F., and coauthors. 2002. Trophic ecology of bowhead whales (*Balaena mysticetus*) compared with that of other Arctic marine biota as interpreted from carbon-, nitrogen-, and sulfur-isotope signatures. *Canadian Journal of Zoology* 80(2):223-231.

- Howard, J. K., K. M. Cuffey, and M. Solomon. 2005. Toward using *Margaritifera falcata* as an indicator of base level nitrogen and carbon isotope ratios: insights from two California coast range rivers. *Hydrobiologia* 541(1):229-236.
- Jennings, S., and K. J. Warr. 2003. Environmental correlates of large-scale spatial variation in the $\delta^{15}\text{N}$ of marine animals. *Marine Biology* 142(6):1131-1140.
- Jones, B. C., and G. H. Geen. 1977. Food and feeding of spiny dogfish (*Squalus acanthias*) in British Columbia waters. *Journal of the Fisheries Research Board of Canada* 34(11):2067-2078.
- Ketchen, K. S. 1972. Size at maturity, fecundity, and embryonic growth of the spiny dogfish (*Squalus acanthias*) in British Columbia waters. *Journal of the Fisheries Research Board of Canada* 29(12):1717-1723.
- Ketchen, K. S. 1986. The spiny dogfish (*Squalus acanthias*) in the Northeast Pacific and a history of its utilization. *Canadian Special Publication of Fisheries and Aquatic Sciences* 88:78 p. Ottawa.
- King, J. R., and G. A. McFarlane. 2003. Marine fish life history strategies: applications to fishery management. *Fisheries Management and Ecology* 10(4):249-264.
- Laptikhovsky, V. V., A. I. Arkhipkin, and A. C. Henderson. 2001. Feeding habits and dietary overlap in spiny dogfish *Squalus acanthias* (*Squalidae*) and narrowmouth

catshark *Schroederichthys bivius* (*Scyliorhinidae*). *Journal of the Marine Biological Association of the United Kingdom* 81(6):1015-1018.

Link, J. 2002. Does food web theory work for marine ecosystems? *Marine Ecology Progress Series* 230:1-9.

Link, J. S., L. P. Garrison, and F. P. Almeida. 2002. Ecological interactions between elasmobranchs and groundfish species on the northeastern US continental shelf. I. Evaluating predation. *North American Journal of Fisheries Management* 22(2):550-562.

Logan, J. M., and M. E. Lutcavage. 2010. Stable isotope dynamics in elasmobranch fishes. *Hydrobiologia* 644(1):231-244.

Lowe, C. G., B. M. Wetherbee, G. L. Crow, and A. L. Tester. 1996. Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Environmental Biology of Fishes* 47(2):203-211.

MacNeil, M. A., K. G. Drouillard, and A. T. Fisk. 2006. Variable uptake and elimination of stable nitrogen isotopes between tissues in fish. *Canadian Journal of Fisheries and Aquatic Sciences* 63(2):345-353.

MacNeil, M. A., G. B. Skomal, and A. T. Fisk. 2005. Stable isotopes from multiple tissues reveal diet switching in sharks. *Marine Ecology Progress Series* 302:199-206.

- MacNeill, M. A., G. B. Skomal, and A. T. Fisk. 2005. Stable isotopes from multiple tissues reveal diet switching in sharks. *Marine Ecology Progress Series* 302:199-206.
- Marasco, R. J., and coauthors. 2007. Ecosystem-based fisheries management: some practical suggestions. *Canadian Journal of Fisheries and Aquatic Sciences* 64(6):928-939.
- McConnaughey, T., and C. P. McRoy. 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. *Marine Biology* 53(3):257-262.
- McFarlane, G. A., and J. R. King. 2003. Migration patterns of spiny dogfish (*Squalus acanthias*) in the North Pacific Ocean. *Fishery Bulletin* 101(2):358-367.
- Menard, F., A. Lorrain, M. Potier, and F. Marsac. 2007. Isotopic evidence of distinct feeding ecologies and movement patterns in two migratory predators (yellowfin tuna and swordfish) of the western Indian Ocean. *Marine Biology* 153(2):141-152.
- 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.

- Mueter, F. J., and B. L. Norcross. 2000. Changes in species composition of the demersal fish community in nearshore waters of Kodiak Island, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 57:1169-1180.
- Nakazawa, T., and coauthors. 2010. Is the relationship between body size and trophic niche position time-invariant in a predatory fish? First stable isotope evidence. *Plos One* 5(2):e9120.
- Pauly, D., V. Christensen, and C. Walters. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES Journal of Marine Science* 57(3):697-706.
- Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. *Science* 308(5730):1912-1915.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge, Massachusetts.
- Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18:293-320.
- Pinnegar, J. K., S. Jennings, C. M. O'Brien, and N. V. C. Polunin. 2002. Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. *Journal of Applied Ecology* 39(3):377-390.

- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83(3):703-718.
- Quillfeldt, P., R. A. R. McGill, and R. W. Furness. 2005. Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. *Marine Ecology Progress Series* 295:295-304.
- Rau, G. H., D. G. Ainley, J. L. Bengtson, J. J. Torres, and T. L. Hopkins. 1992. $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. *Marine Ecology Progress Series* 84:1-8.
- Rau, G. H., and coauthors. 1983. Animal $^{13}\text{C}/^{12}\text{C}$ correlates with trophic level in pelagic food webs. *Ecology* 64(5):1314-1318.
- Saunders, M. W., and G. A. McFarlane. 1993. Age and length at maturity of the female spiny dogfish, *Squalus acanthias*, in the Strait of Georgia, British Columbia, Canada. *Environmental Biology of Fishes* 38:49-57.
- Stabeno, P. J., and coauthors. 2004. Meteorology and oceanography of the northern Gulf of Alaska. *Continental Shelf Research* 24:859-897.
- Stevens, J. D., R. Bonfil, N. K. Dulvy, and P. A. Walker. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* 57(3):476-494.

- 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.
- Tribuzio, C. A. 2010. Life history, demography, and ecology of the spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska. Doctoral dissertation. University of Alaska Fairbanks, Fairbanks.
- Tribuzio, C. A., C. Rodgveller, J. Heifetz, and K. Goldman. 2009. Gulf of Alaska Stock Assessment and Fishery Evaluation Report. North Pacific Fishery Management Council, Seattle, Washington.
- Vander Zanden, M. J., G. Cabana, and J. B. Rasmussen. 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}\text{N}$) and literature dietary data. *Canadian Journal of Fisheries and Aquatic Sciences* 54(5):1142-1158.
- Vander Zanden, M. J., and J. B. Rasmussen. 1999. Primary consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and the trophic position of aquatic consumers. *Ecology* 80(4):1395-1404.
- Weingartner, T. J. 2007. The physical environment of the Gulf of Alaska. Pages 12-44 in R. Spies, editor. Long-term ecological change in the northern Gulf of Alaska. Elsevier, Oxford, United Kingdom.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size structured populations. *Annual Review of Ecology and Systematics* 15:393-425.

Appendices

Table A-1. Sampling site, date, gear and sample location (latitude, longitude) for sample size (N) of male and female spiny dogfish collected for this study. Indicated are the sampling areas of this study, Kodiak, Cook Inlet, Prince William Sound (PWS), northeastern Gulf of Alaska (NEGOA), Yakutat, southeastern Gulf of Alaska (SEGOA), and British Columbia (BC). Gear used for shark collection included, sport (i.e., rod and reel), setnet (SN), baited longlines (LL), midwater trawl (MT), and bottom trawl (BT).

Region	Site	Date	Gear	N	Males	Females	Latitude	Longitude
Alaska	COOK INLET	6/26/2005	sport	13	3	10	59.23	153.34
Alaska	COOK INLET	6/27/2005	sport	12	1	11	59.20	153.33
Alaska	COOK INLET	6/28/2005	sport	6	2	4	59.20	153.33
Alaska	COOK INLET	6/27/2006	SN	1	0	1	60.14	151.53
Alaska	CROSS SOUND	4/21/2005	LL	1	0	1	58.19	136.84
Alaska	CROSS SOUND	4/22/2005	LL	2	0	2	58.15	136.87
Alaska	CROSS SOUND	4/23/2005	LL	6	0	6	58.08	136.44
Alaska	CROSS SOUND	4/24/2005	LL	5	1	4	58.07	136.42
Alaska	EGOA	7/9/2005	LL	21	16	5	54.65	132.84
Alaska	EGOA	7/11/2005	LL	6	3	3	54.90	134.29
Alaska	EGOA	7/14/2005	LL	6	2	4	55.93	134.90
Alaska	EGOA	7/16/2005	LL	14	7	7	56.38	135.35
Alaska	EGOA	7/17/2005	LL	5	4	1	56.85	136.00
Alaska	EGOA	7/18/2005	LL	8	3	5	57.19	136.23
Alaska	EGOA	7/19/2005	LL	1	0	1	57.62	136.54
Alaska	EGOA	7/22/2005	LL	1	1	0	57.88	137.38
Alaska	EGOA	7/28/2005	LL	1	1	0	59.42	140.94
Alaska	EGOA	8/1/2005	LL	34	7	27	59.75	143.59
Alaska	EGOA	8/1/2005	LL	1	1	0	59.68	143.37
Alaska	EGOA	8/4/2005	LL	1	1	0	59.52	144.71
Alaska	EGOA	8/5/2005	LL	8	2	6	59.50	145.53
Alaska	KODIAK	6/21/2005	MT	2	1	1	57.91	151.81
Alaska	KODIAK	6/21/2005	MT	9	3	6	57.97	151.67
Alaska	KODIAK	6/21/2005	MT	8	5	3	57.98	151.78
Alaska	KODIAK	6/21/2005	MT	8	4	4	57.99	151.99
Alaska	KODIAK	6/21/2005	MT	2	1	1	57.97	152.09
Alaska	KODIAK	6/21/2005	MT	1	1	0	57.94	152.20
Alaska	KODIAK	6/21/2005	MT	2	1	1	57.94	151.99
Alaska	KODIAK	7/5/2005	MT	1	0	1	56.93	152.93
Alaska	KODIAK	7/5/2005	MT	2	2	0	56.86	152.63
Alaska	KODIAK	7/6/2005	MT	3	1	2	56.91	153.42
Alaska	KODIAK	7/8/2005	MT	4	1	3	56.72	153.66
Alaska	KODIAK	7/10/2005	MT	3	2	1	56.81	154.33
Alaska	KODIAK	7/10/2005	MT	2	2	0	56.84	154.39

Table A-1, continued.

Alaska	KODIAK	7/10/2005	MT	3	3	0	56.78	154.48
Alaska	KODIAK	7/10/2005	MT	3	1	2	56.86	154.42
Alaska	KODIAK	7/10/2005	MT	3	1	2	56.76	154.40
Alaska	KODIAK	7/10/2005	MT	1	0	1	56.76	154.48
Alaska	KODIAK	7/10/2005	MT	1	1	0	56.85	154.50
Alaska	KODIAK	7/11/2005	MT	2	2	0	56.76	154.24
Alaska	KODIAK	9/6/2005	MT	7	3	4	57.99	153.16
Alaska	KODIAK	9/7/2005	MT	3	1	2	57.86	153.12
Alaska	KODIAK	9/7/2005	MT	7	2	5	57.92	153.25
Alaska	KODIAK	9/7/2005	MT	4	3	1	57.94	153.30
Alaska	KODIAK	9/7/2005	MT	5	0	5	57.97	153.39
Alaska	PWS	9/5/2005	LL	2	2	0	60.94	146.89
Alaska	PWS	9/5/2005	LL	2	1	1	61.03	146.76
Alaska	PWS	9/6/2005	LL	8	4	4	60.90	146.98
Alaska	PWS	9/7/2005	LL	1	0	1	60.94	146.70
Alaska	PWS	9/7/2005	LL	1	1	0	60.54	147.88
Alaska	PWS	9/8/2005	LL	31	6	25	60.59	146.74
Alaska	YAKUTAT	7/28/2004	sport	10	0	10	59.60	139.85
Alaska	YAKUTAT	7/28/2004	sport	3	0	3	59.59	139.81
Alaska	YAKUTAT	7/29/2004	sport	7	0	7	59.65	139.99
Alaska	YAKUTAT	6/28/2005	LL	51	20	31	59.51	140.06
Alaska	YAKUTAT	6/29/2005	LL	10	4	6	59.60	139.83
Alaska	YAKUTAT	6/30/2005	LL	26	11	15	59.52	140.10
Alaska	YAKUTAT	7/18/2006	SN	19	0	19	59.56	139.84
British Columbia	BC	7/28/2005	BT	29	13	16	48.64	123.35
British Columbia	BC	8/5/2005	BT	2	2	0	49.86	125.09
British Columbia	BC	8/5/2005	BT	2	0	2	49.91	125.16
British Columbia	BC	8/5/2005	BT	9	6	3	49.92	125.15
British Columbia	BC	8/5/2005	BT	7	7	0	49.91	125.14
British Columbia	BC	8/6/2005	BT	10	0	10	49.50	124.03
British Columbia	BC	8/25/2005	LL	22	13	9	49.55	123.40

Table A-2. Specimen ID number, carbon to nitrogen ratio (C:N), and isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) for weathervane scallops collected from four different sites, Bering Sea (BS), eastern Gulf of Alaska (EGOA), central GOA (CGOA), and western GOA (WGOA). Sampling locations within sites were, Bering Sea, Shumagin Islands, north of (N) Shumagin Islands, south of (S) Cape Douglas, northeast (NE) District Kodiak, southwest of (SW) Kayak Island, northwest of (NW) Icy Bay, south of (S) Icy Bay, south of (S) Yakutat Bay, and north of (N) Lituya Bay.

ID	C:N	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Location	Site	Date	Depth (m)
1	3.39	10.74	-17.32	Bering Sea	BS	11/15/2006	95
2	3.39	10.40	-17.81	Bering Sea	BS	11/15/2006	95
3	3.45	9.91	-17.42	Bering Sea	BS	11/15/2006	95
4	3.56	10.10	-17.49	Bering Sea	BS	11/15/2006	95
5	3.40	10.33	-17.97	Bering Sea	BS	11/15/2006	95
6	3.36	10.55	-17.57	Bering Sea	BS	11/15/2006	95
7	3.54	9.09	-17.54	Bering Sea	BS	11/15/2006	95
8	3.33	10.35	-17.76	Bering Sea	BS	11/15/2006	95
9	3.33	10.90	-17.53	Bering Sea	BS	11/15/2006	95
10	3.40	10.97	-17.52	Bering Sea	BS	11/15/2006	95
11	3.71	8.79	-16.80	S of Cape Douglas	CGOA	8/2/2006	110
12	3.81	8.14	-17.05	S of Cape Douglas	CGOA	8/2/2006	110
13	3.67	8.99	-16.78	S of Cape Douglas	CGOA	8/2/2006	110
14	3.55	8.97	-16.98	S of Cape Douglas	CGOA	8/2/2006	110
15	3.55	8.63	-17.03	S of Cape Douglas	CGOA	8/2/2006	110
16	3.90	8.25	-16.92	S of Cape Douglas	CGOA	8/2/2006	110
17	3.61	8.58	-17.10	S of Cape Douglas	CGOA	8/2/2006	110
18	3.70	8.49	-16.97	S of Cape Douglas	CGOA	8/2/2006	110
19	3.65	8.95	-16.87	S of Cape Douglas	CGOA	8/2/2006	110
20	3.72	8.40	-17.03	S of Cape Douglas	CGOA	8/2/2006	110
21	3.50	8.66	-16.71	Shumagin Island	WGOA	10/25/2006	86
22	3.65	8.13	-16.72	Shumagin Island	WGOA	10/25/2006	86
23	3.30	8.97	-16.53	Shumagin Island	WGOA	10/25/2006	86
24	3.40	8.79	-16.37	Shumagin Island	WGOA	10/25/2006	86
25	3.29	8.43	-16.60	Shumagin Island	WGOA	10/25/2006	86
26	3.55	9.56	-16.46	Shumagin Island	WGOA	10/25/2006	86
27	3.47	9.33	-16.79	Shumagin Island	WGOA	10/25/2006	86
28	3.55	9.17	-16.59	Shumagin Island	WGOA	10/25/2006	86
29	3.64	9.20	-16.92	Shumagin Island	WGOA	10/25/2006	86

Table A-2, continued.

30	3.53	9.08	-16.82	Shumagin Island	WGOA	10/25/2006	86
31	3.17	7.63	-17.56	NW of Icy Bay	EGOA	9/28/2006	64
32	3.63	7.86	-17.92	NW of Icy Bay	EGOA	9/28/2006	64
33	3.30	8.17	-17.80	NW of Icy Bay	EGOA	9/28/2006	64
34	3.32	8.22	-17.64	NW of Icy Bay	EGOA	9/28/2006	64
35	3.24	8.76	-17.83	NW of Icy Bay	EGOA	9/28/2006	64
36	3.27	8.70	-17.63	NW of Icy Bay	EGOA	9/28/2006	64
37	3.36	8.15	-17.96	NW of Icy Bay	EGOA	9/28/2006	64
38	3.14	8.69	-17.73	NW of Icy Bay	EGOA	9/28/2006	64
39	3.32	8.53	-18.01	NW of Icy Bay	EGOA	9/28/2006	64
40	3.40	8.21	-17.91	NW of Icy Bay	EGOA	9/28/2006	64
41	3.16	9.10	-17.55	N of Lituya Bay	EGOA	8/24/2006	73
42	3.24	9.55	-18.02	N of Lituya Bay	EGOA	8/24/2006	73
43	3.19	9.83	-17.95	N of Lituya Bay	EGOA	8/24/2006	73
44	3.17	9.51	-17.72	N of Lituya Bay	EGOA	8/24/2006	73
45	3.08	9.44	-17.76	N of Lituya Bay	EGOA	8/24/2006	73
46	3.26	9.58	-18.00	N of Lituya Bay	EGOA	8/24/2006	73
47	3.19	9.16	-17.92	N of Lituya Bay	EGOA	8/24/2006	73
48	3.29	9.34	-17.78	N of Lituya Bay	EGOA	8/24/2006	73
49	3.17	8.80	-18.08	N of Lituya Bay	EGOA	8/24/2006	73
50	3.30	8.87	-18.24	N of Lituya Bay	EGOA	8/24/2006	73
51	3.47	8.66	-17.99	S of Yakutat Bay	EGOA	9/5/2006	69
52	3.29	8.55	-17.94	S of Yakutat Bay	EGOA	9/5/2006	69
53	3.39	8.55	-17.90	S of Yakutat Bay	EGOA	9/5/2006	69
54	3.44	8.68	-18.07	S of Yakutat Bay	EGOA	9/5/2006	69
55	3.48	8.79	-17.75	S of Yakutat Bay	EGOA	9/5/2006	69
56	3.40	8.77	-17.80	S of Yakutat Bay	EGOA	9/5/2006	69
57	3.44	8.92	-18.07	S of Yakutat Bay	EGOA	9/5/2006	69
58	3.37	9.00	-17.99	S of Yakutat Bay	EGOA	9/5/2006	69
59	3.43	8.83	-17.91	S of Yakutat Bay	EGOA	9/5/2006	69
60	3.52	8.67	-17.96	S of Yakutat Bay	EGOA	9/5/2006	69
61	3.52	8.55	-16.87	N Shumagin Island	WGOA	10/28/2006	117
62	3.54	9.05	-17.04	N Shumagin Island	WGOA	10/28/2006	117
63	3.36	8.84	-16.63	N Shumagin Island	WGOA	10/28/2006	117
64	3.36	8.16	-16.71	N Shumagin Island	WGOA	10/28/2006	117
65	3.37	8.85	-16.72	N Shumagin Island	WGOA	10/28/2006	117
66	3.29	8.73	-16.57	N Shumagin Island	WGOA	10/28/2006	117
67	3.23	8.39	-16.71	N Shumagin Island	WGOA	10/28/2006	117
68	3.57	9.53	-16.97	N Shumagin Island	WGOA	10/28/2006	117
69	3.43	8.98	-16.96	N Shumagin Island	WGOA	10/28/2006	117
70	3.56	9.04	-16.66	N Shumagin Island	WGOA	10/28/2006	117
71	3.41	8.42	-18.47	SW Kayak Island	EGOA	7/3/2006	77
72	3.36	8.16	-18.40	SW Kayak Island	EGOA	7/3/2006	77
73	3.37	8.17	-18.40	SW Kayak Island	EGOA	7/3/2006	77

Table A-2, continued.

74	3.33	8.40	-18.59	SW Kayak Island	EGOA	7/3/2006	77
75	3.31	8.40	-18.17	SW Kayak Island	EGOA	7/3/2006	77
76	3.20	8.37	-18.23	SW Kayak Island	EGOA	7/3/2006	77
77	3.34	8.54	-18.45	SW Kayak Island	EGOA	7/3/2006	77
78	3.30	8.36	-18.44	SW Kayak Island	EGOA	7/3/2006	77
79	3.47	8.46	-18.52	SW Kayak Island	EGOA	7/3/2006	77
80	3.37	8.07	-18.58	SW Kayak Island	EGOA	7/3/2006	77
81	3.63	10.88	-18.14	Bering Sea 2005	BS	12/23/2005	95
82	3.43	10.62	-17.51	Bering Sea 2005	BS	12/23/2005	95
83	3.40	11.26	-17.46	Bering Sea 2005	BS	12/23/2005	95
84	3.53	10.74	-17.51	Bering Sea 2005	BS	12/23/2005	95
85	3.40	11.08	-17.39	Bering Sea 2005	BS	12/23/2005	95
86	3.32	10.46	-17.29	Bering Sea 2005	BS	12/23/2005	95
87	3.36	10.15	-17.31	Bering Sea 2005	BS	12/23/2005	95
88	3.51	10.56	-17.49	Bering Sea 2005	BS	12/23/2005	95
89	3.42	10.65	-17.38	Bering Sea 2005	BS	12/23/2005	95
90	3.36	10.34	-17.50	Bering Sea 2005	BS	12/23/2005	95
91	3.27	8.85	-18.28	S of Icy Bay 2005	EGOA	10/1/2005	68
92	3.25	9.14	-18.31	S of Icy Bay 2006	EGOA	10/1/2005	68
93	3.29	8.83	-18.05	S of Icy Bay 2007	EGOA	10/1/2005	68
94	3.43	8.90	-18.03	S of Icy Bay 2008	EGOA	10/1/2005	68
95	3.24	9.14	-18.10	S of Icy Bay 2009	EGOA	10/1/2005	68
96	3.46	8.77	-18.35	S of Icy Bay 2010	EGOA	10/1/2005	68
97	3.34	8.75	-17.83	S of Icy Bay 2011	EGOA	10/1/2005	68
98	3.39	8.94	-17.84	S of Icy Bay 2012	EGOA	10/1/2005	68
99	3.29	8.97	-18.26	S of Icy Bay 2013	EGOA	10/1/2005	68
100	3.32	8.85	-18.01	S of Icy Bay 2014	EGOA	10/1/2005	68
101	3.70	8.76	-17.79	NE District Kodiak	CGOA	11/1/2006	91
102	3.67	8.38	-17.48	NE District Kodiak	CGOA	11/1/2006	91
103	3.43	8.68	-17.73	NE District Kodiak	CGOA	11/1/2006	91
104	3.40	8.22	-17.69	NE District Kodiak	CGOA	11/1/2006	91
105	3.47	10.11	-17.61	NE District Kodiak	CGOA	11/1/2006	91
106	3.44	9.00	-17.55	NE District Kodiak	CGOA	11/1/2006	91
107	3.60	8.04	-17.98	NE District Kodiak	CGOA	11/1/2006	91
108	3.51	7.89	-17.96	NE District Kodiak	CGOA	11/1/2006	91
109	3.70	8.51	-17.51	NE District Kodiak	CGOA	11/1/2006	91
110	3.54	8.40	-17.52	NE District Kodiak	CGOA	11/1/2006	91

General Conclusions

Relatively high spiny dogfish biomass estimates and anecdotal evidence from fishing communities has provided an impetus for this and other studies investigating the biology of spiny dogfish in the Gulf of Alaska (GOA). Although, trends in spiny dogfish biomass estimates remain unclear, it is apparent there is an urgent need to acquire a better understanding about life-history patterns and parameters of this species in the GOA. This study was initiated to explore the feeding ecology of spiny dogfish using stable isotope techniques in order to elucidate their trophic role in the GOA and therefore better understand potential impacts of this species on the GOA ecosystem through trophic connections.

In Chapter 1, my initial work on spiny dogfish, I demonstrated that large-scale geographic variation exists in both carbon and nitrogen stable isotopes of spiny dogfish muscle. These results led me to conclude that spiny dogfish are capable of occupying a variety of habitat niches in both pelagic and nearshore environments and may feed at higher trophic positions (TPs) in some of these nearshore habitats. However, these results were based on only small sample sizes ($n = 60$) and were mostly males ($n = 50$). In addition, there was no information available on the baseline variability of stable isotopes throughout the study area, so any conclusions on the TP of spiny dogfish by region have to be viewed with caution.

It was apparent that in order to examine differences in TP among regions, a better understanding of the underlying baseline variability in stable nitrogen isotopes had to be analyzed. As part of Chapter 2, I collected weathervane scallops (*Patinopecten caurinus*)

a primary consumer in the GOA to adjust the TP of spiny dogfish. In the GOA, I found that although variability existed within some regions mean values were not significantly different between the western, central, and eastern GOA. Therefore in the GOA, differences among spiny dogfish nitrogen stable isotope values were interpreted as representing actual difference in their TPs.

Based on results from my initial work, I also expanded my sampling to include spiny dogfish males (n = 186) and females (n = 305) from a broader geographical range in the GOA (western Kodiak to British Columbia) and a larger range in lengths (i.e., 52 to 113 cm). I found differences in TPs of spiny dogfish from different regions of the GOA, providing stronger evidence that spiny dogfish are flexible in their feeding behavior and are capable of feeding at higher or lower TPs in different parts of their geographic range. Specifically, spiny dogfish fed at a higher TP in the Kodiak area, while they fed at a lower TP at sites in the eastern GOA (i.e., Prince William Sound, northeastern GOA shelf, and Yakutat Inlet). Evidence from our lipid-normalized $\delta^{13}\text{C}$ values suggests that spiny dogfish in Kodiak may utilize nearshore or benthic habitats slightly more intensively than spiny dogfish in the eastern GOA. Therefore, the width of the continental shelf may be contributing to the TP at which spiny dogfish feed because the shelf surrounding Kodiak Island is wider than the narrower shelf in the eastern GOA.

In addition, spiny dogfish increase their TP as they increase in length. This ontogenetic change in TP associated with diet changes was found at all sites explored in this study demonstrating a common and widespread trait in the feeding ecology of spiny dogfish (Jones and Geen 1977; Alonso et al. 2002; Tribuzio 2010). For the length ranges

I explored, I found an increase of almost a full TP. Thus, spiny dogfish at the lower end of the length examined may be feeding on lower TP organisms (e.g., euphausiids) while those at the upper length may focus on forage fishes (e.g., Pacific herring (*Clupea pallasii*)). Furthermore, males and females of similar sizes appear to have very similar TPs in the northeastern Pacific Ocean.

The results of this study help increase our understanding of the trophic role of spiny dogfish in the GOA. Size-based ontogenetic changes in diet appear to be important factors and should be incorporated into mass balance food-web models (e.g., Ecopath) to provide more realistic output. The sex of spiny dogfish on the other hand, appeared to be less important for feeding patterns. Also, we observed notable differences in the TP of spiny dogfish by geographic regions. While not fully understood at the moment, these geographical differences are important and should be further investigated. My research demonstrates that the combination of stable isotope analysis, together with some of the statistical methods used here, could be applied to elucidate the trophic role of other fishes in the GOA and may lead to the improvement of our understanding of this complex ecosystem and its food-webs.

References

- Alonso, M. K., E. A. Crespo, N. A. Garcia, S. N. Pedraza, P. A. Mariotti, and N. J. Mora. 2002. Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina. *Environmental Biology of Fishes* 63(2):193-202.

Jones, B. C., and G. H. Geen. 1977. Food and feeding of spiny dogfish (*Squalus acanthias*) in British Columbia waters. *Journal of the Fisheries Research Board of Canada* 34(11):2067-2078.

Tribuzio, C. A. 2010. Life history, demography, and ecology of the spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska. Doctoral dissertation. University of Alaska Fairbanks, Fairbanks.