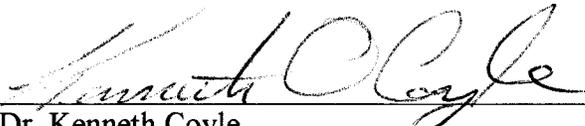


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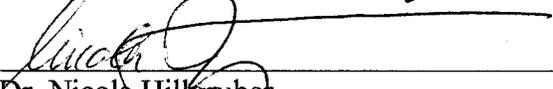
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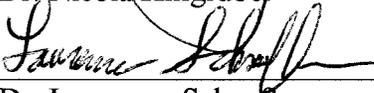
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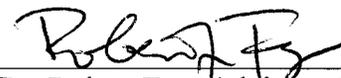
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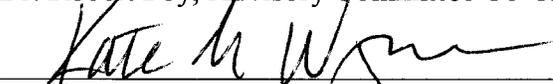
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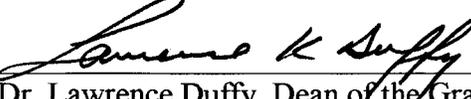


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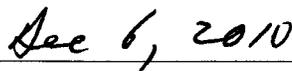
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KODIAK ARCHIPELAGO, ALASKA

A
DISSERTATION

Presented to the Faculty
of the University of Alaska Fairbanks
in Partial Fulfillment of the Requirements
for the Degree of
DOCTOR OF PHILOSOPHY

By
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Abstract

Assessing the availability of forage fishes is key to understanding fluctuations in populations of apex predators that prey upon them, including pinnipeds and seabirds in the Gulf of Alaska. In this study, multiple aspects of forage fish availability were measured in coastal waters of the Kodiak Archipelago, Alaska, in May (2004 & 2005), August (2004 & 2005), November (2006), and April (2007). Efforts were focused on four pelagic species that consistently dominated midwater trawl catches and have been described as important prey for upper trophic level predators around the Archipelago: walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), and eulachon (*Thaleichthys pacificus*). Fatty acid and stomach content analyses were combined to estimate the diet composition of these forage fishes as a means of identifying the immediate source of energy they transfer to upper trophic level taxa. Values of copepod-originated fatty acids indicated underestimation of dietary copepods by stomach content analysis, which suggests that fatty acid analysis should be used to supplement conventional methodologies in forage fish field studies. Lipid content and fatty acid composition were highly variable within species, suggesting that the use of average values at the species level should be avoided in fine-scale ecological investigations. Mesoscale horizontal distribution and energy density of forage fishes were measured in May and August (2005) to assess the prey fields available to local apex predators over critical periods of their life history. Dense post-spawning aggregations formed seasonal energetic “hotspots”, exemplified by herring schools on the northwest side of the Archipelago in May and capelin schools on the northeast side in August. Results presented in this dissertation offer key information needed to identify energetic pathways of significance to upper trophic level consumers in the Kodiak Archipelago. Understanding local trophic interactions and their role in regional apex predator population fluctuations will improve efforts to develop trophodynamic models and ecosystem-based fishery management plans in the North Pacific Ocean.

Table of Contents

	Page
Signature Page	i
Title Page	ii
Abstract	iii
Table of Contents	iv
List of Figures	vii
List of Tables	x
List of Appendices	xiii
Acknowledgements	xiv
Chapter 1: General Introduction	1
BACKGROUND.....	1
FORAGE FISHES AS ENERGY CONVEYERS.....	2
FORAGE FISH AVAILABILITY	2
DISSERTATION OBJECTIVES AND ORGANIZATION	4
LITERATURE CITED.....	5
Chapter 2: Underestimation of Dietary Copepods by Stomach Content Analysis: Using Fatty Acid Analysis to Refine Estimation of Forage Fish Diet Composition..	12
ABSTRACT.....	12
INTRODUCTION.....	13
MATERIALS AND METHODS.....	16
RESULTS.....	19

DISCUSSION	22
LITERATURE CITED	30
TABLES AND FIGURES	38
Chapter 3: Intra-Species Variation in Lipid Content and Fatty Acid Composition of Forage Fishes in Embayments of the Kodiak Archipelago, Alaska.....	48
ABSTRACT	48
INTRODUCTION.....	49
MATERIALS AND METHODS.....	51
RESULTS.....	53
DISCUSSION	56
LITERATURE CITED.....	61
TABLES AND FIGURES	69
Chapter 4: Measuring Mesoscale Horizontal Distribution Characteristics and Energy Density of Pelagic Forage Fishes in Coastal Waters of the Kodiak Archipelago, Alaska	84
ABSTRACT.....	84
INTRODUCTION.....	85
MATERIALS AND METHODS.....	86
Sampling.....	86
Acoustics analyses.....	87
Biochemical analyses.....	88
Statistical analyses	89
RESULTS.....	91

DISCUSSION	93
Distribution characteristics	93
Biomass as a proxy for energy density	95
Potential errors.....	96
Implications for local apex predators.....	97
Summary.....	99
LITERATURE CITED.....	99
TABLES AND FIGURES.....	106
Chapter 5: General Conclusion.....	119
LITERATURE CITED.....	122
Appendices.....	125

List of Figures

	Page
Figure 2.1 Locations of Uganik, Tonki, Perenos, and Paramanof Bays around the Kodiak Archipelago, Alaska.	46
Figure 2.2 Stomach fullness (% of whole-body wet weight) plotted against total length of walleye pollock (A, n = 389), Pacific herring, (B, n = 250), capelin (C, n = 242), and eulachon (D, n = 147) collected from embayments around the Kodiak Archipelago, Alaska.....	47
Figure 3.1 Locations of Uganik, Tonki, Perenos, and Paramanof Bays around the Kodiak Archipelago, Alaska.	74
Figure 3.2 Scatterplots of lipid content vs. total length of walleye pollock from embayments of the Kodiak Archipelago, Alaska, by sampling month and year.....	75
Figure 3.3 MDS ordination of walleye pollock fatty acid composition (n = 120) sampled from embayments of the Kodiak Archipelago, Alaska.....	76
Figure 3.4 Scatterplots of lipid content vs. total length of Pacific herring from embayments of the Kodiak Archipelago, Alaska, by sampling month and year.....	77
Figure 3.5 MDS ordination of Pacific herring fatty acid composition (n = 57, of which one sample considered as outlier) sampled from embayments of the Kodiak Archipelago, Alaska....	78
Figure 3.6 Contents (% of the total quantified fatty acids by weight) of four fatty acids plotted against total length of Pacific herring (n = 36) sampled from Uganik Bay, Alaska, in November 2006.....	79

Figure 3.7 Scatterplots of lipid content vs. total length of capelin from embayments of the Kodiak Archipelago, Alaska, by sampling month and year.	80
Figure 3.8 Content (% of the total quantified fatty acids by weight) of fatty acid 22:1n-11 plotted against total length of capelin sampled from embayments of the Kodiak Archipelago, Alaska, in May (2005, n = 20) and August (2004 and 2005 combined, n = 36).	81
Figure 3.9 MDS ordination of capelin fatty acid composition (n = 56) sampled from embayments of the Kodiak Archipelago, Alaska.....	82
Figure 3.10 Scatterplots of lipid content vs. total length of eulachon sampled from embayments of the Kodiak Archipelago, Alaska.	83
Figure 4.1 The five survey regions in waters off the northern part of the Kodiak Archipelago, Alaska.	113
Figure 4.2 Acoustic transects (black line) in survey regions (A) on the northeastern side of the Kodiak Archipelago and (B) in Uganik Bay, with the 100-m depth isobath (gray line).	114
Figure 4.3 Area units (black dot) where species-combined energy density was $\geq 10\%$ of the maximum values in (A & B) May and (C & D) August, when area units from all regions were compared within each month.....	115
Figure 4.4 Areal mean (A) fish density ($\times 10^4 \text{ km}^{-2}$), (B) biomass ($\times 10^3 \text{ kg km}^{-2}$), (C) lipid density ($\times 10^2 \text{ kg km}^{-2}$), and (D) energy density ($\times 10^7 \text{ kJ km}^{-2}$) of the four fish species in the five regions in May 2005.....	116
Figure 4.5 Areal mean (A) fish density ($\times 10^6 \text{ km}^{-2}$), (B) biomass ($\times 10^3 \text{ kg km}^{-2}$), (C) lipid density ($\times 10^3 \text{ kg km}^{-2}$), and (D) energy density ($\times 10^8 \text{ kJ km}^{-2}$) of the four fish species in the five regions in August 2005.....	117

Figure 4.6 Frequency distributions (one percent interval) of proportional differential (PD) between standardized values of species-combined (Pacific herring, eulachon, capelin, and walleye pollock) biomass (SB) and energy density (SED) in waters off the northern part of the Kodiak Archipelago, Alaska, in (A) May and (B) August 2005. 118

List of Tables

	Page
Table 2.1 20:1n-11/9 and 22:1n-11 fatty acid contents (% of total quantified fatty acids) in four fish species collected from embayments around the Kodiak Archipelago, Alaska.	38
Table 2.2 20:1n-11/9 and 22:1n-11 fatty acid contents (% of total quantified fatty acids) in four zooplankton groups collected from embayments around the Kodiak Archipelago, Alaska.	40
Table 2.3 Overall stomach content composition in four fish species collected from embayments around the Kodiak Archipelago, Alaska, in mean numerical percentage (No., %), percentage frequency of occurrence (FO, %), and mean prey-specific numerical percentage (SNo., %).	41
Table 2.4 Mean numerical percentage (No., %) and percent frequency of occurrence (FO, %) of copepods and euphausiids (adults and juveniles) in stomach contents of four fish species collected from embayments around the Kodiak Archipelago, Alaska.	42
Table 3.1 Lipid content (% of whole-body wet mass, means \pm SD) of four forage fish species from embayments of the Kodiak Archipelago, Alaska, by sampling month and year.	69
Table 3.2 Content (% of the total quantified fatty acids by weight, means \pm SD) of the 11 most abundant fatty acids in walleye pollock from embayments of the Kodiak Archipelago, Alaska, by sampling month and year.	70
Table 3.3 Lipid content (% of whole-body wet mess, means) and three fatty acid contents (% of the total quantified fatty acids by weight, means) of seven walleye pollock sample groups (based on year, embayment, and total length range) collected from embayments of the Kodiak Archipelago, Alaska, in August 2004 and 2005.	71

Table 3.4 Content (% of the total quantified fatty acids by weight, means \pm SD) of the 11 most abundant fatty acids in Pacific herring, capelin, and eulachon sampled from embayments of the Kodiak Archipelago, Alaska.....	72
Table 3.5 Lipid content (% of whole-body wet mess, means) and four fatty acid contents (% of the total quantified fatty acids by weight, means) of nine capelin sample groups (based on month, embayment, and total length range) collected from embayments of the Kodiak Archipelago, Alaska, in May (2005) and August (2004 and 2005 combined).....	73
Table 4.1 Descriptions of length classes of four forage fish species from embayments of the Kodiak Archipelago, Alaska.....	106
Table 4.2 Horizontal distribution parameters of four forage fish species (post-kriging, length classes combined) in five regions around the Kodiak Archipelago, Alaska, in May 2005.	107
Table 4.3 Horizontal distribution parameters of four forage fish species (post-kriging, length classes combined) in five regions around the Kodiak Archipelago, Alaska, in August 2005.....	108
Table 4.4 Lipid, protein, and energy content in whole-body wet mass of four forage fish species from embayments of the Kodiak Archipelago, Alaska, in May and August 2005.	109
Table 4.5 Species-combined (Pacific herring, eulachon, capelin, and walleye pollock) areal mean biomass (kg km^{-2}), lipid density (kg km^{-2}), protein density (kg km^{-2}), energy density (kJ km^{-2}), lipid content (%), protein content (%), and energy content (kJ g^{-1}) in five regions around the Kodiak Archipelago, Alaska, in May and August 2005.	110
Table 4.6 Index of aggregation ($\times 10^{-3} \text{ km}^{-2}$) of four forage fish species (pre-kriging, length classes combined) in five regions around the Kodiak Archipelago, Alaska, in May and August 2005, based on acoustic estimates from transect lines.	111

Table 4.7. Overall percentage frequency of occurrence (FO), mean numerical percentage (No), and mean prey-specific numerical percentage (SNo) of Pacific herring, eulachon, capelin, walleye pollock, Pacific sand lance (*Ammodytes hexapterus*), Pacific salmon (*Oncorhynchus* spp.), and Pacific sandfish (*Trichodon trichodon*) in Steller sea lion scats collected from sites in the Kodiak Archipelago (1999 to 2005), excerpted from McKenzie & Wynne (2008), with SNo values calculated as $No/FO \times 100\%$112

List of Appendices

	Page
Appendix A Fishing Permits.....	126
Appendix B IACUC Certificate	134

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Chapter 1: General Introduction

BACKGROUND

Since the 1970s, major population declines in pinnipeds and seabirds have been observed in the Gulf of Alaska and Bering Sea. Regional decreases by up to 85% were reported in Steller sea lions *Eumetopias jubatus* (Merrick et al. 1987, Trites & Larkin 1996), northern fur seals *Callorhinus ursinus* (York 1990, Towell et al. 2006), harbor seals *Phoca vitulina richardsi* (Pitcher 1990, Womble et al. 2010), and several species of murre and kittiwakes (Byrd et al. 2008, Slater & Byrd 2009). A variety of hypotheses have been brought forward to explain the declines, several of which are concerned with prey availability and quality (Merrick et al. 1997, Trites & Donnelly 2003): for example, the lack of high-quality prey was proposed to have negative effects on Steller sea lion reproductive success of adult females and the survival of their young (Calkins et al. 1998, Rosen & Trites 2005). Coincident with the declines in pinniped and seabird populations, significant decreases in forage fishes have occurred in the North Pacific Ocean since the 1970s (Alverson 1992, Anderson & Piatt 1999), along with abrupt climatic changes (Mantua et al. 1997, Hare & Mantua 2000). Because forage fishes constitute a major prey source for piscivorous pinnipeds and seabirds (Piatt et al. 2006, McKenzie & Wynne 2008), the declines in apex predators are considered to be partially attributed to the decreases in forage fishes and further to climate changes (Trites et al. 2007), although specific mechanisms of trophic interactions between forage fishes and their predators are still unclear. Therefore, refining our knowledge about forage fishes is one critical step toward explaining historical and current fluctuations in apex predators, and predicting future trends in relation to climate change (Springer & Speckman 1997, Trites et al. 2007).

FORAGE FISHES AS ENERGY CONVEYERS

Forage fishes form the main energy passageways between zooplankton and piscivorous fishes, marine mammals and seabirds (Springer & Speckman 1997). Forage fishes consume a wide range of holo- and mero-zooplankton taxa, including copepods, euphausiids, and crab larvae (Grover 1990, Merati & Brodeur 1996, Wilson et al. 2006). They are also consumed by a variety of piscivorous predators, including groundfishes (Yang & Nelson 2000, Yang et al. 2006), marine mammals (Sinclair & Zeppelin 2002, McKenzie & Wynne 2008), and seabirds (Hatch & Sanger 1992, Golet et al. 2000). It has been noticed that a small number of forage fish species, typically less than ten, transfer most of the energy that is conveyed from zooplankton to piscivorous predators in a given marine ecosystem (Springer & Speckman 1997, Ayon et al. 2008). These forage fish species are characterized by extremely high abundances and serve as the energetic intermediates between numerous species of zooplankton prey and piscivorous predators (Cury et al. 2000, Freon et al. 2009). As a result, each forage fish species is linked with a high number of prey and predator taxa through direct trophic interactions and can be an important driving factor for ecosystem dynamics (Hunt & McKinnell 2006, Bakun et al. 2009).

FORAGE FISH AVAILABILITY

Information on the availability of forage fishes as prey is a key to understanding distribution and population changes in piscivorous predators (Springer & Speckman 1997). For example, variations in capelin (*Mallotus villosus*) availability led to population fluctuations of Atlantic cod (*Gadus morhua*) off eastern Newfoundland, Canada, in the 1980s (Methven & Piatt 1989); the low availability of capelin and Atlantic herring (*Clupea harengus*) was a major factor contributing to the acute adult mortality and subsequent population decline of common murre (*Uria aalge*) in Norwegian waters in mid-1980s (Anker-Nilssen et al. 1997). Thus, understanding forage fish availability is an effective approach in our efforts towards a more thorough understanding of

marine ecosystems and ecosystem-based fisheries management of upper trophic levels (Pikitch et al. 2004, Bogetveit et al. 2008).

Availability of forage fishes is defined by several aspects, including size range, horizontal and vertical distribution patterns, biomass, and energy content. Size range and distribution patterns affect the accessibility of a prey field, because different predators have different thresholds for prey size (Sinclair et al. 2008, Young et al. 2010), horizontal foraging distance (Milette & Trites 2003, Davis et al., 2006, Fauchald 2009), and diving depth (Mitani et al. 2004, Bearhop et al. 2006, Cornick et al. 2006). Biomass and energy content measure the quantity and quality of available prey fields (Adams et al. 2008, Winter et al. 2009).

Various aspects of forage fish availability, such as horizontal and vertical distribution patterns, are often correlated to attributes of their zooplankton prey (Schabetsberger et al. 2000, Swartzman et al. 2002). These associations allow us to use zooplankton prey as a link to connect variations in forage fish availability with climate changes, because zooplankton are typically more quickly and directly affected by environmental parameters than forage fishes (Verheye & Richardson 1998, Ayon et al. 2008). However, these efforts first require the correct identification of important zooplankton prey, which demands an accurate description of forage fish diet composition. Therefore, deriving a reliable method to estimate forage fish diets is integral to better understanding forage fish availability.

In the western Gulf of Alaska, refining our knowledge of forage fish availability is in urgent need for investigating ecological questions of immediate biological and economic concerns. As a result of a severe decline, the western stock of Steller sea lions (in areas west of 144°W longitude) was listed as “endangered” under the US Endangered Species Act in 1997. Groundfish management in Alaska since the 1990s has been largely influenced by the listing. In order to address this issue, the Gulf Apex Predator-Prey Program was established to study trophic relationships between Steller sea lions, their prey, competitors, and predators in the regions

around the Kodiak Archipelago, Alaska. My dissertation project is part of the program and focuses on forage fishes in the coastal waters of the Archipelago. The results of this project are not only valuable to the Steller sea lion issue, but also applicable to investigations of other apex predators in the western Gulf of Alaska.

DISSERTATION OBJECTIVES AND ORGANIZATION

The overall goal of this project was to define forage fish availability in coastal waters of the Kodiak Archipelago, Alaska. These coastal waters are essential feeding and spawning habitats for forage fishes (Pahlke 1985, Loewen 2007), which constitute critical food sources for local apex predators (McKenzie & Wynne 2008, Witteveen et al. 2008). I focused on the northeastern and western sides of the Archipelago; both areas are primarily influenced by the near-shore buoyancy-driven Alaska Coastal Current (Stabeno et al. 1995). Hydrographic features in these waters are highly variable at relatively small spatial and temporal scales, resulted from the interactions among the prevalent Alaska Coastal Current, a large number of freshwater runoffs into embayments, and complex topography (Stabeno et al. 2004). Sampling in these waters provided an opportunity to examine fine-scale variations in forage fish availability in a highly dynamic setting.

In this dissertation, different aspects of forage fish availability were addressed in three studies, which are described in the following three chapters:

In Chapter Two, results on forage fish diet composition are presented. The objective was to combine fatty acid and stomach content analyses in order to refine the estimation of forage fish diet composition. The hypothesis was that dietary copepods are underestimated by stomach content analysis. The hypothesis was conceived based the following: 1) copepods and euphausiids are evacuated from forage fish stomachs at different rates due to differences in body size and exoskeleton fragility, and 2) copepods and euphausiids are often found in the same

individual stomachs in stomach content analysis. Copepod-originated fatty acids were used to estimate the proportions of dietary copepods, which were compared with the proportions derived from stomach content results. Discrepancies between the two datasets were discussed. The use of fatty acid analysis as a supplementary tool to stomach content analysis in studying forage fish feeding ecology was evaluated.

Chapter Three describes intra-species variations in forage fish lipid dynamics. Lipid content and fatty acid composition offer insights into forage fish life history and plankton production, and are important aspects in defining forage fish availability to upper trophic level predators. The objective was to improve the resolution of intra-species lipid dynamics in local forage fishes. Variations in lipid content and fatty acid composition related to month, fish length, and location were examined. Potential reasons for and implication of these variations were discussed.

In Chapter Four, horizontal distribution and energy density of forage fishes were measured to assess mesoscale variations in forage fish availability. The hypotheses were that 1) patchiness of forage fishes is species specific and these patchy distributions form seasonal “hotspots” of feeding grounds for apex predators, and that 2) biomass of forage fish assemblages is an inadequate proxy for the amount of energy available to predators. Distribution parameters of four forage fish species, computed based on acoustic-trawl survey data and geostatistics, were compared among five study regions and between two months in the Kodiak Archipelago. Spatial variations in species-specific and species-combined energy density were described. The use of biomass as a proxy for energy density was evaluated at two spatial scales. Implications of the results on local apex predators were discussed.

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Chapter 2:
**Underestimation of Dietary Copepods by Stomach Content Analysis: Using
Fatty Acid Analysis to Refine Estimation of Forage Fish Diet Composition¹**

ABSTRACT

Understanding of forage fish feeding ecology requires an accurate description of diet composition. Fatty acid and stomach content analyses were combined to estimate diet composition in walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), and eulachon (*Thaleichthys pacificus*) collected in embayments around the Kodiak Archipelago, Alaska. Comparisons between copepod-originated fatty acids and stomach contents in the four forage fish species indicated the underestimation of dietary copepods by stomach content analysis. The magnitudes of copepod underestimation could have profound effects on estimation of forage fish prey consumption. A “copepod-snacking” hypothesis was developed to account for the sharp contrast between fatty acid and stomach content results. As a valuable supplement to conventional stomach content analysis, fatty acid analysis should be included in field studies to better our understanding of forage fish feeding ecology.

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INTRODUCTION

Effectiveness of ecosystem-based fishery management relies on our knowledge of the key processes in a given ecosystem (Pikitch et al. 2004). In the Gulf of Alaska (GOA), such a key process is the energy transfer from zooplankton to small fishes of high abundance (Mundy & Hollowed 2005, Spies 2007). These small fishes, often referred to as forage fishes, play a critical role in sustaining productive fisheries as adults or as prey of commercially exploited species (Springer & Speckman 1997). In addition, forage fishes are the main energy conveyor between zooplankton and piscivorous fishes, marine mammals, and seabirds (Mundy & Hollowed 2005, Spies 2007). Therefore, understanding the feeding ecology of forage fishes in the GOA is an essential step to relate population fluctuations of upper trophic level taxa to variability of plankton production and further to changing climatic forces (Springer & Speckman 1997).

An accurate description of diet composition is required for many aspects of fish feeding ecology, such as prey selectivity, seasonal or ontogenetic patterns, and inter-species competition (Gerking 1994). When describing diet composition, stomach content analysis has long been employed as the standard practice, which quantifies ingested food items temporarily stored in stomachs prior to their evacuation into intestines. Each type of food item remains in a stomach for a certain duration, typically measured in gastric evacuation time or rate (Elliott 1972). Food items with shorter gastric evacuation time tend to be underestimated compared to those with longer gastric evacuation time, which is a potential error source of stomach content analysis (Hyslop 1980).

The potential bias induced by differential gastric evacuation rates can be problematic in analyzing forage fish stomachs containing taxa of such diverse sizes as copepods and euphausiids. In subarctic waters, copepods and euphausiids are usually the two most abundant constituents of forage fish stomach contents (Astthorsson & Gislason 1997, Brodeur et al. 2000). Forage fishes start ingesting euphausiids when they attain adequate gape width and swimming speed to capture

these relatively large and evasive prey taxa (Huse & Toresen 1996, Brodeur 1998). As fish grow larger while remaining zooplanktivorous, the relative importance of copepods as prey generally decreases, whereas the importance of euphausiids increases; over this stage, copepods and euphausiids commonly co-occur in the same individual stomach (O'Driscoll et al. 2001, Wilson et al. 2006). Co-occurring prey of differential volumes and exoskeletal chitinization are digested and passed through fish alimentary tracts at different rates (Hopkins & Larson 1990, Salvanes et al. 1995, Andersen 1999, 2001), potentially leading to the underestimation of small- and soft-bodied prey (Gannon 1976, Sutela & Huusko 1994). Copepods are considered to be evacuated from stomachs more rapidly than euphausiids (LeBrasseur & Stephens 1965), which is in agreement with results from laboratory studies. Brodeur & Percy (1987) reported that 90% (by weight) of ingested euphausiids were evacuated in 28.4 h from stomachs of sub-yearling coho salmon (*Oncorhynchus kisutch*) fed to satiation at 11.4°C. The same amount of evacuation took 20.9 h in adult Arctic charr (*Salvelinus alpinus*) fed *ad libitum* at 10.0°C (Amundsen & Klemetsen 1988). In both experiments, euphausiids were frozen and defrosted in advance, which can cause exoskeleton degradation and accelerate euphausiid evacuation by various degrees (Temming & Herrmann 2003). In contrast, the estimated time to evacuate 90% of copepod from stomachs of juvenile Atlantic herring (*Clupea harengus*) is 4 – 5 h at 14.9°C (Szypuła & Zalachowski 1984), which is equivalent to 6 – 8 h at 10.0°C if calculated with temperature-dependent functions obtained from two experiments in which euphausiids were fed to adult Arctic charr (Amundsen & Klemetsen 1988) and whiting (*Merlangius merlangus*, Andersen 1999). Thus, the gastric evacuation time of euphausiids is expected to be distinctly longer than that of copepods, although a direct comparison of gastric evacuation rates between the two groups fed to the same fish species under the same laboratory settings has not been reported. Consequently, the proportions of ingested copepods can be underestimated in copepod-and-euphausiid mixed stomach contents in forage fishes. Due to the inherent nature of this bias, alternative methodologies are needed to

supplement stomach content analysis in order to achieve a more reliable estimate of forage fish diet composition.

An alternative methodology is to measure copepod-originated fatty acids in forage fishes as a semi-quantitative means to evaluate the underestimation of copepods by stomach content analysis. Fatty acids are structural moieties in most lipid molecules (Christie 2003): fatty acids are typically esterified to alcohol groups (e.g., in glycerides) or amino groups (e.g., in sphingolipids). In marine plankton and fishes, fatty acids are commonly composed of 14 to 24 carbon atoms and up to six double bonds (see previous reviews for details of fatty acid structures, functions, and metabolism, e.g., Ackman & McLachlan 1968, Sargent & Henderson 1986, Tocher 2003). To date, calanoid copepods are the only known marine organisms capable of *de novo* biosynthesis of considerable amounts of 20:1 (20 carbon atoms and one double bond) and 22:1 fatty acids and fatty alcohols (Sargent & Henderson 1986; also as a reference for structures, functions, and biosynthesis of fatty alcohols in copepods). Several high latitude species of calanoid copepods deposit lipids predominately as wax esters, where 20:1 and 22:1 fatty acids and fatty alcohols account for up to half of the total lipid weight (Sargent & Henderson 1986, Saito & Kotani 2000). In zooplanktivorous fishes, dietary fatty alcohols are efficiently oxidized into fatty acids while dietary fatty acids are directly absorbed with little alteration (Patton & Benson 1975, Sargent et al. 1979). As a result, both 20:1 and 22:1 fatty alcohols and fatty acids from copepods are deposited as 20:1 and 22:1 fatty acids in fishes (Tocher 2003). Furthermore, 22:1 fatty acids are catabolized faster than 20:1 fatty acids and both are catabolized faster than other fatty acids in fishes (Pascall & Ackman 1976, Sargent 1976). For example, in capelin, selective oxidation of 20:1 and 22:1 fatty acids during sexual maturation resulted in only trace amounts of these fatty acids in roe lipids in contrast to the high concentrations in the lipids of parental fish (Henderson et al. 1984a,b). Preferential utilization of 20:1 and 22:1 fatty acids reduces the relative abundance of these fatty acids in predator lipids compared to in prey lipids; in other words, the relative

abundance of 20:1 and 22:1 fatty acids and fatty alcohols in consumed zooplankton should be greater than that of 20:1 and 22:1 fatty acids in zooplanktivorous fish. Thus, the presence and relative abundance of 20:1 and 22:1 fatty acids in forage fishes serve as indirect evidence for the importance of calanoid copepods as prey items for these fish species (Sargent & Henderson 1986, Dalsgaard et al. 2003).

In this study, we compared results of fatty acids and stomach contents in four forage fish species, walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), and eulachon (*Thaleichthys pacificus*), collected from embayments around the Kodiak Archipelago, Alaska. Specifically, copepod-originated fatty acids in forage fishes were measured to deduce the proportions of dietary copepods, which were then used to evaluate the underestimation of copepods through stomach content analysis. We hypothesized that copepod proportions in copepod-and-euphausiid mixed stomach contents would be lower than those derived from fatty acid analysis, because of differential gastric evacuation rates between copepods and euphausiids. By combining the two methodologies, our goal was to refine the understanding of forage fish feeding ecology in order to better discriminate trophic connections and therefore elucidate ecosystem functioning.

MATERIALS AND METHODS

Forage fishes were collected during acoustic-trawl surveys in four embayments of the Kodiak Archipelago, Alaska: Uganik, Tonki, Perenosa, and Paramanof Bay (Fig. 2.1). A total of 81 midwater trawls were conducted in May and August of 2004 and 2005, November 2006, and April 2007 (Fish Resource Permits authorized by Alaska Department of Fish and Game were held for all sample collections and are documented in Appendix A). The trawl net was equipped with a modified codend of 10 cm mesh and 2.5 cm mesh liner. Sample length ranges were targeted to include stages in which fishes are expected to feed on both copepods and euphausiids, which

would allow us to test the hypothesis that copepods are underestimated in the presence of co-existing euphausiids by conventional stomach content analysis. Trawls were deployed during daylight hours to groundtruth acoustic data collected to estimate fish biomass. For this study, we focused on four species that consistently dominated net catches: walleye pollock, Pacific herring, capelin, and eulachon. For fatty acid analysis, specimens of whole fish were placed in air-tight containers and stored at -20°C on board; after each survey, samples were vacuum-packed and stored at -30°C until analysis. For stomach content analysis, samples were preserved in 10% seawater-buffered formalin solution. Stomachs of fish larger than 30 cm in total length (TL) were excised between esophagus and pylorus and preserved individually in nylon bags; fish of 15 – 30 cm TL were immersed in formalin solution with abdominal incisions to expose stomachs; and whole bodies of fish smaller than 15 cm were directly immersed into formalin solution.

Zooplankton samples were collected concurrently for fatty acid analysis to ensure that copepod-originated fatty acids were not present in large amounts in other zooplankton taxa, particularly in euphausiids. Sampling gears included a triple-net Tucker Trawl (1 m² opening, 300 μm mesh), a bongo trawl (both 0.75 m diameter opening, 500 and 1000 μm mesh), and a ring net (0.75 m diameter opening, 130 μm mesh). The Tucker and bongo trawls were employed opportunistically and towed obliquely while the ring net was employed systematically at pre-designated stations and towed vertically. On board, net contents were sorted into four groups: copepods, euphausiids including adults and juveniles, chaetognaths, and pteropods, which are known important prey taxa of forage fishes in the GOA (Brodeur 1998, Wilson et al. 2006). Samples were preserved the same way as fish samples for fatty acid analysis.

Copepod-originated fatty acids were quantified for both fish and zooplankton samples. Lipids were extracted from individually homogenized whole fish, following the modified Folch method (Folch et al. 1957, Ways & Hanahan 1964). In brief, lipids in aliquots of 1.5 g homogenates were extracted with the solvent mixture of 20 mL chloroform and 10 mL methanoi.

Lipid content was calculated gravimetrically as percentage of whole-body wet weight. Lipids in zooplankton samples of the four groups were extracted the same way as in fish samples. After lipid extraction, a total of 252 fish and 80 zooplankton samples were further analyzed for fatty acid composition. Hilditch reagent was used to catalyze the transesterification of extracted lipids in aliquots of ~ 0.3 mg at 55 – 60 °C for 18 h and the resulting fatty acid methyl esters were washed with 5% NaCl and extracted with hexane (Christie 2003). Using a Varian Saturn 2200 GC/MS, a total of 37 fatty acids were quantified to the nearest nanogram against calibration curves established for each batch of transesterified lipid samples (8 – 20 samples for one batch). Three copepod-originated fatty acid isomers, 20:1n-11, 20:1n-9, and 22:1n-11 (Dalsgaard et al. 2003; n-11: double bond is between 11th and 12th carbon atoms, counting from terminal methyl group of the molecule) were reported in weight percentage of the 37 quantified fatty acids, referred to as content hereafter. The two isomers 20:1n-11 and 20:1n-9 were summed as 20:1n-11/9. Fatty alcohols, especially 20:1 and 22:1 isomers, were expected to occur in large amounts in copepod samples, while to be absent or negligible in samples of fish and the three other zooplankton groups collected (Sargent & Henderson 1986). Therefore, fatty alcohols were only qualitatively assessed for both fish and zooplankton samples to confirm that copepods were the sole group with 20:1 and 22:1 fatty alcohols.

Fish stomach content analysis was focused on the occurrence of copepods and euphausiids in order to compare with our fatty acid results. In the lab, fish were measured for TL to the nearest 0.1 cm and whole-body wet weight to the nearest 0.01 g. Excised stomach contents were weighed to the nearest 0.001 g, identified to the lowest taxonomic or developmental level possible and counted. Prey items that were unidentifiable due to digestion were not quantified. To facilitate comparison between stomach content and fatty acid results, prey were combined into broad taxonomic and developmental categories. Euphausiids of different developmental stages were reported in two groups: 1) adults and juveniles, and 2) furcilia stages, calyptopis stages, and eggs.

Copepods of various species and developmental stages were merged into a single copepod category. This taxonomic compromise conformed to the coarse level adopted in fatty acid analysis of concurrently collected zooplankton, which enabled direct comparisons of the two datasets.

For each fish species, month, and embayment, samples were grouped into length categories, which were based on length modes derived from length frequency histograms in respective months. The same length categories were applied to samples for both fatty acid and stomach content analyses. Each fish group, which is specific to species, month, embayment, and length category, was used as a unit for calculation. Statistical comparisons of copepod-originated fatty acid contents among groups were subjected to Mann-Whitney *U* or Kruskal Wallis test. Stomach content composition in each group was reported in terms of mean numerical percentage, percentage frequency of occurrence, and mean prey-specific numerical percentage. Calculation of mean prey-specific numerical percentage only involves stomachs containing the prey in question, instead of all stomachs (Amundsen et al. 1996). Stomach fullness (%) was calculated as the weight of stomach contents divided by fish whole-body wet weight. Correlations between stomach fullness and TL were measured by Spearman Rho values.

RESULTS

Fatty acid contents (% of total quantified fatty acids) of 20:1n-11/9 and 22:1n-11 varied in fish samples among species, months, embayments, and length categories (Table 2.1). For example, values in walleye pollock collected in August 2004 were higher in Uganik Bay than in those of similar TL in Tonki Bay ($p < 0.01$). In all fish samples, 20:1 or 22:1 fatty alcohols were negligible.

In zooplankton samples, fatty acid contents of 20:1n-11/9 and 22:1n-11 varied among taxonomic groups and months (Table 2.2). In particular, values in euphausiids were relatively low,

with a maximum of 3.15% for 20:1n-11/9 and 3.38% for 22:1n-11. In addition, 20:1 or 22:1 fatty alcohols were found in large amounts in copepods, while they were negligible in euphausiids, chaetognaths, or pteropods.

Both copepods and euphausiids were encountered in fish stomach contents (Table 2.3), which satisfied the premise of our hypothesis. Stomachs were empty in 2.5%, 3.4%, 2.8%, and 4.4% of sampled walleye pollock, Pacific herring, capelin, and eulachon, respectively. In 1,043 non-empty stomachs, adult and juvenile euphausiids (hereafter euphausiids) had the highest mean numeric percentage in all fish species, followed by copepods (Table 2.3). All adult herring, capelin, and eulachon were entirely zooplanktivorous.

Comparison between fatty acid and stomach content results displayed a re-occurring discrepancy: high contents of copepod-originated fatty acids were coupled with low numerical percentage of copepods in stomach contents. The scope and extent of the discrepancy varied among fish species. In walleye pollock, for example, fatty acid and stomach content results of most sample groups were in agreement. Exceptions were observed in samples of TL range 32.5 – 43.5 cm from Uganik Bay in August 2004 and of TL range 10.0 – 12.4 cm, 19.7 – 24.8 cm, and 26.0 – 41.0 cm from Uganik Bay in November 2006; in each of these cases, 20:1n-11/9 and 22:1n-11 fatty acid contents were higher than in other pollock groups ($p < 0.01$) and about three times higher than those in concurrent euphausiid samples (Tables 2.1 & 2.2). In contrast, stomach contents of corresponding groups were mostly composed of euphausiids and not of copepods (Table 2.4). In Pacific herring, the discrepancy was more widespread and profound than in pollock. In November, relatively large herring (25.7 – 29.3 cm TL) had significantly higher 20:1n-11/9 and 22:1n-11 fatty acid contents ($p < 0.01$) but fewer copepods in their stomachs compared to relatively small herring (13.6 – 22.3 cm TL). In April, 20:1n-11/9 and 22:1n-11 fatty acids combined accounted for 35.64% of herring lipids by weight; at the same time, copepods were not found in herring stomachs. In capelin, the discrepancy between fatty acid and stomach

content results was shown consistently in relatively large individuals (> 10.0 cm TL), which had high contents of copepod-originated fatty acids but few or no copepods in their stomachs. In eulachon, there was no disagreement between fatty acid and stomach content results.

The consistent discrepancy between fatty acid and stomach content results in large capelin (> 10.0 cm TL) was coupled with unique patterns in capelin stomach contents and fullness. As in pollock and herring, larger capelin contained fewer copepods and more euphausiids in stomachs than smaller capelin (≤ 10.0 cm TL); but unlike pollock or herring in which the change of prey composition was gradual, capelin abruptly shifted their stomach contents from a combination of Cirripedia (barnacle nauplii and cyprids) and copepods to stomach contents containing primarily euphausiids (Table 2.4). The ontogenetic pattern of stomach fullness in capelin was the opposite of other species (Fig. 2.2): stomach fullness was positively correlated with TL in capelin (Rho = 0.41), while the correlation was negative in other species (Rho = -0.52, -0.30, and -0.63 for pollock, herring, and eulachon, respectively, all $p < 0.05$). Samples collected in different months were combined.

Differences in diet composition among certain groups were indicated by fatty acid results but not displayed in stomach contents results. Significant differences in copepod-originated fatty acid content were found between groups of similar stomach contents. For example, in relatively large capelin (> 10.0 cm TL) collected in May 2005, 20:1n-11/9 and 22:1n-11 fatty acid contents were lower in Uganik Bay than in Tonki Bay ($p < 0.01$, Table 2.1), while stomach contents of both groups were identical (Table 2.4). In herring collected in April 2007, 20:1n-11/9 and 22:1n-11 fatty acid contents were lower in Uganik Bay than in Tonki Bay ($p \leq 0.02$), while stomach contents of both groups were not different (100% euphausiids in both groups). In both of the capelin and herring examples, the same spatial patterns were observed: 1) samples in Uganik Bay showed lower contents of copepod-originated fatty acids than in Tonki Bay; 2) lipid content was not different between comparing groups ($p \geq 0.36$). Different spatial patterns were found in

relatively large pollock (32.5 – 37.0 cm TL) collected in August 2004: 20:1n-11/9 and 22:1n-11 fatty acid contents, as well as lipid content, were higher in Uganik Bay than in Tonki Bay ($p < 0.01$).

DISCUSSION

It has been concluded that 20:1 and 22:1 fatty acids in planktivorous fishes, originated from 20:1 and 22:1 fatty acids and fatty alcohols in copepods, are catabolized at higher rates than other fatty acids (Pascall and Ackman 1976, Sargent 1976, Tocher 2003). In this study, we made an assumption that the four study species (walleye pollock, Pacific herring, capelin, and eulachon) are not exceptions to this conclusion. The rate differentials mean that the contents (% of total fatty acids) of 20:1 and 22:1 fatty acids in forage fishes cannot be higher than those in their diets; in other words, relatively high contents of 20:1 and 22:1 fatty acids in forage fishes cannot be obtained from diets of relatively low 20:1 and 22:1 contents (either fatty acids or fatty alcohols).

The recurring discrepancy between high contents of copepod-originated fatty acids and low numerical percentages of copepods in stomach contents of the four forage fish species suggests that dietary copepods were underestimated by stomach content analysis. An alternative explanation for the discrepancy would be that 20:1 and 22:1 fatty acids in fish were obtained from consuming euphausiids that had fed on copepods, because the discrepancy typically co-occurred with a dominance of euphausiids in stomach contents. In other words, euphausiids could have served as an intermediate between copepods and fish. However, concurrent euphausiid samples showed fairly low contents of 20:1 and 22:1 fatty acids and no 20:1 and 22:1 fatty alcohols. It is possible that we may have under-sampled the portion of euphausiids that may have specialized on consuming copepods, because our euphausiid samples included adults and juveniles of various species. Nevertheless, it is still unlikely that copepod-eating euphausiids would have such high 20:1 and 22:1 fatty acid contents. Due to size restriction, euphausiids typically consume copepod

eggs, nauplii, and early stages of copepodites (Bamstedt & Karlson 1998, Nakagawa et al. 2003), which have negligible to low contents of 20:1 and 22:1 fatty acids and fatty alcohols compared to later stages of copepodites and adults (Sargent & Henderson 1986, Saito & Kotani 2000). Local copepod species rich in 20:1 and 22:1 fatty acids and fatty alcohols are of the genus *Neocalanus* and *Calanus* (Sargent & Henderson 1986, Saito & Kotani 2000), of which the late stages of copepodites and adults are considerably larger than copepods found in euphausiid stomachs (Bamstedt & Karlson 1998, Nakagawa et al. 2003). Because 20:1 and 22:1 fatty acid content cannot be enriched from the low levels observed in euphausiids, it is unlikely that euphausiids as an intermediate could account for the large amounts of copepod-originated fatty acids in fish samples. Therefore, the discrepancy between fatty acid and stomach content results must be viewed as indirect evidence that copepods were underestimated by stomach content analysis.

The magnitudes of copepod underestimation by stomach content analysis displayed large ranges and varied by sample groups that were formed based on different fish species, months, and embayments. In sample groups in which 20:1 and 22:1 fatty acid contents were similar to those in concurrent euphausiid samples, the underestimation was negligible. In contrast, in sample groups where 20:1 and 22:1 fatty acid contents were much higher than those in concurrent euphausiid samples, the magnitude of copepod underestimation could be enormous. For example, in herring of 15.9 – 16.8 cm TL in Uganik Bay in April 2007, the weight ratio between ingested copepods (W_C) and euphausiids (W_E) was estimated through the formula

$$(W_C \times L_C \times FA_C + W_E \times L_E \times FA_E) / (W_C \times L_C + W_E \times L_E) = 31.29\%,$$

where L is lipid content (%), FA is the sum of 20:1n-11/9 and 22:1n-11 fatty acid and fatty alcohol content (%), subscript letters C and E represent copepods and euphausiids, respectively, and 31.3% is the sum of mean 20:1n-11/9 and 22:1n-11 fatty acid content of the herring group. We assumed that 20:1 and 22:1 fatty acids in herring were exclusively from copepods and euphausiids. Values for L_C and FA_C are 5.3% and 54.5% (calculation based on *Neocalanus*

cristatus of the 4th copepodite stage in Saito & Kotani 2000, assuming 90% as moisture content); values of L_E and FA_E are 2.9% and 4.1%. The ratio of W_C to W_E was calculated to be 0.63:1. If the weight of juvenile *Thysanoessa inermis* was used to represent euphausiids, which are on average 9.1 times heavier than an individual *Neocalanus cristatus* of the 4th copepodite stage (K. Coyle, *unpubl. data*), the weight ratio was 5.7:1. This calculation suggests that 5.7 times more copepods than euphausiids were consumed by herring; this estimation is in sharp contrast to our observation of no copepods in herring stomach contents. Unfortunately, similar calculations in other months were impossible due to the lack of copepod fatty acid data. However, we did observe a sharp contrast between the fatty acid contents and stomach contents in several sample groups of herring and capelin; these results clearly indicate a large magnitude of copepod underestimation by standard stomach content analysis.

The underestimation of dietary copepods by stomach content analysis can have profound effects on estimating prey consumption of forage fishes. Two different sets of models, one based on bioenergetics and the other based on gastric evacuation rates, have been widely applied to estimate prey consumption (Hansen et al. 1993, Bromley 1994). Models based on bioenergetics require at least ten different physiological parameters (Ney 1993), which are only available for a limited number of fish species. Models based on gastric evacuation rates rely on the accuracy of these estimated rates. After sampling fish stomachs at different time intervals, weight changes in stomach contents over a certain period, mostly 24 h, are fit into four primary models and their derivatives (Richter et al. 2002). However, if the proportions of ingested copepods are underestimated by stomach content analysis, these underestimates will propagate through subsequent calculations of gastric evacuation rates, daily ration, and prey consumption. Our calculation showed that the magnitude of copepod underestimation can be substantial. Therefore, stomach content analysis for forage fishes should be used with caution before we know more about in-situ feeding behavior, especially when this method is used to estimate prey consumption.

Different temporal scales associated with fatty acid and stomach content analysis may partially explain copepod underestimation by stomach content analysis, but cannot fully account for the large magnitudes of underestimation in certain groups. Fatty acid composition of fish tissues is an integrated result of dietary lipids consumed over the past one to several weeks (Anderson & Arthington 1989, Kirsch et al. 1998, Jobling 2004), depending on fatty acid turnover rates in tissues, which can be affected by multiple factors, such as fish size and temperature (Sargent et al. 1999, Jobling & Bendiksen 2003). In contrast, stomach contents of zooplanktivorous fishes represent a snap-shot of prey items ingested over the previous several hours to several days (Szypuia & Zalachowski 1984, Brodeur & Percy 1987). The difference in the temporal scales between these two methodologies leads to the possibility that potential copepod-eating phases were missed during stomach sampling but captured with fatty acid analysis. Because we only sampled in daylight hours and for periods of two to three days in each embayment, the discrepancy could have resulted from nocturnal ingestion of copepods or from a sudden prey switch from copepods to euphausiids during our sampling periods by local forage fishes. However, neither of these scenarios were reported in previous studies; to the contrary, euphausiids were more important prey than copepods at night and in all sampling periods for fishes of similar lengths (Brodeur & Percy 1987, Merati & Brodeur 1996, Brodeur 1998, Brodeur et al. 2000, Wilson et al. 2006, Adams et al. 2007). In addition, the high levels of 20:1 and 22:1 fatty acids in several sample groups of herring and capelin would have required these fish to ingest substantial amounts of copepods, outnumbering euphausiids by multiple factors. It is unlikely that such large quantities of copepods could have been ingested at night but would have not been detectable at all during the day or in any of the previous studies. Therefore, time of day or length of sampling alone cannot account for the large magnitudes of copepod underestimation by stomach content analysis.

To explain the sharp contrast between fatty acid and stomach content results, we developed a hypothesis based on observed prey-specific numerical percentages and reported internal dynamics of fish stomachs. Prey-specific numerical percentages of euphausiids ranged on average from 70.78% to 97.37% for the four forage fish species (Table 2.3), which are similar to those presented by Wilson et al. (2006). These values indicate that in stomachs containing euphausiids, euphausiids on average outnumbered the sum of all other prey taxa. The number of euphausiids in a single stomach was typically less than ten; therefore, the number of copepods in a single stomach would have averaged less than ten whenever euphausiids were present. Because the gastric evacuation rate of a single prey type will not be affected by the presence of other prey types in the same stomach (Macdonald et al. 1982, Sutela & Huusko 1994, Singh-Renton & Bromley 1996), an individual adult copepod is expected to be evacuated faster than an individual adult euphausiid from the same fish stomach (LeBrasseur & Stephens 1965, Szypuia & Zalachowski 1984, Brodeur & Percy 1987). Since a higher number of individual prey take longer to be evacuated (Persson 1981, Bromley 1994, Andersen 1998), the coexistence of copepods in small quantities and euphausiids in large quantities in fish stomachs should amplify the differences in gastric evacuation rates between these two prey groups. In addition, internal dynamics of stomachs may further widen the differences. Specifically, Bernreuther et al. (2008) reported that when a copepod was ingested by a juvenile Atlantic herring (*Clupea harengus*) with a relatively full stomach, the newly-ingested copepod was pushed directly toward the intestine instead of being pushed to the back of the stomach where previously ingested prey items were stored. Thus, if a small number of copepods are ingested into a stomach mostly occupied by euphausiids, it is possible that these copepods are directly pushed toward the intestine and preferentially evacuated from the stomachs.

The small quantities and fast gastric evacuation rates of copepods led us to develop a “copepod-snacking” hypothesis. Specifically, we suggest that local forage fishes may capture

copepods on multiple occasions within 24 h, but in relatively small quantities on each occasion. These ingested copepods would then be quickly evacuated from fish stomachs, while euphausiids are broken down more slowly in the same stomachs. Because the numbers of copepods do not accumulate over time, the ratio of copepods to euphausiids present in the stomachs at any given moment will lead to an underestimation of the ratio of total copepods to total euphausiids ingested over a 24-h period. This could explain the sharp contrast we observed between fatty acid and stomach content results.

If such a “copepod-snacking” behavior occurred, it is more likely to happen during daylight hours. Although feeding activities of many forage fishes peak at night or during twilight hours (Vesin et al. 1981, Wilson et al. 2006), numerical percentages of copepods in stomach contents are often the highest during daylight hours (Merati & Brodeur 1996, Brodeur et al. 2000). If both are consumed at night, copepods are unlikely to outlast euphausiids throughout the duration of digestion; hence, increased numerical percentages of copepods during daylight hours indicate copepod consumption beyond peak feeding time. In addition, because copepods are less pigmented than euphausiids, capturing copepods during daylight hours is more feasible for visual predators and more energetically efficient than during nighttime. For Atlantic herring, for example, prey capture by biting individual copepods requires better light condition but costs less energy per captured prey than by filter feeding (Gibson & Ezzi 1992).

Such a “copepod-snacking” behavior would have multiple advantages. When reaching adequate size, local forage fishes typically ingest euphausiids at night or twilight hours until stomachs become relatively full (Merati & Brodeur 1996, Wilson et al. 2006), exemplified by capelin in this study. We noticed that capelin stomachs that contained euphausiids were more stretched when compared visually to those that contained no euphausiids. This was also the reason why larger capelin showed higher stomach fullness (Fig. 2.2), an ontogenetic pattern different from most fish species (Brett 1971, Hyslop 1980). Gill & Hart (1998) reported that

relatively large prey were consumed by three-spined stickleback (*Gasterosteus aculeatus*) until their stomachs were full; afterwards, prey of similar sizes were rejected while smaller prey were still consumed. It is probable that fishes in our study, after consuming euphausiids, switched to copepods due to the constraint imposed by remaining stomach storage space (Hart & Ison 1991). In addition, copepods are more abundant and richer in lipids than euphausiids. In local waters and adjacent areas, copepods are considered more available to forage fishes than euphausiids (Incze et al. 1997, Brodeur 1998, Coyle & Pinchuk 2003). In late copepodite stages, which dominated our copepod samples, lipids generally comprise more than half of whole-body dry mass (Hakanson 1984, Sargent & Henderson 1986, Miller et al. 2000, Irigoien 2004); in contrast, the maximum lipid content of whole-body dry mass in local euphausiids is 20% (L. Guo & R. Foy, *unpubl. data*). Therefore, when euphausiids can no longer be accommodated due to stomach storage constraints, it is energetically beneficial for fishes to switch to more readily-available and lipid-rich copepods, which are also smaller and accordingly less evasive than euphausiids (Okubo 1987, Vogel 1996). Compared to the conventional dichotomy of feeding vs. non-feeding periods within 24 h, intermittent ingestion of copepods after intensive ingestion of euphausiids enables zooplanktivorous fishes to maximize their energetic gain in a much larger time frame.

The extent of “copepod-snacking” is specific to fish species and area. In this study, capelin displayed the most consistent discrepancy between stomach content and fatty acid results, followed by herring. These two species are expected to frequently “snack” on copepods. In contrast, pollock and eulachon appear less likely to engage in such a behavior, based on their generally low 20:1 and 22:1 fatty acid content. A key aspect of this behavior is large quantities of euphausiids present in stomachs, which requires relatively high euphausiid availability. Merati & Brodeur (1996) reported that age-0 pollock near the Kodiak Archipelago consumed more euphausiids than those from other nearshore areas of the western GOA, with the latter mainly consuming larvaceans. It is possible that such a “copepod-snacking” behavior is not significant in

areas of low euphausiid availability, where other prey such as copepods have to be consumed in large amounts during peak feeding periods.

In forage fish field studies, fatty acid analysis is a valuable supplement to conventional stomach content analysis, especially when survey frequency or length is restricted. Compared to stomach contents, fatty acid composition infers dietary information on a larger temporal scale and therefore is less affected by temporal oceanographic events. An event common in embayments is the pulsed elevation of meroplankton abundance, with each of these pulses typically lasting one to several days (Shanks 1986, Shanks & Wright 1987, Farrell et al. 1991, Alexander & Rougharden 1996). In this study, stomach contents showed that barnacle nauplii were the major prey of small capelin from Tonki Bay in August 2004, while fatty acid compositions indicated a major consumption of copepods. These conflicting results suggest that, since barnacle nauplii are generally not positively selected by forage fishes (Brodeur 1998, Wilson et al. 2006), our two-day sampling effort in Tonki Bay may have overlapped with temporally high abundance of barnacle nauplii, which was, however, not representative of the previous weeks. In addition, since stomach content analysis is only a snap-shot of the consumed prey items, it is impossible to capture dietary differences beyond the immediate sampling periods. In this study, differences in diet composition were suggested in several cases by significant inter-embayment differences in 20:1 and 22:1 fatty acid contents, while stomach contents were identical between the compared embayments. On the other hand, it has to be noted that the costs of fatty acid analysis are considerably higher than stomach content analysis. However, the gain of using this method is apparent from the results of this study. In addition, we were able to make statistical comparisons and detect significant differences with relatively small sample sizes, because individual variation in fatty acid composition within sample groups was relatively small.

In conclusion, the results of this study demonstrate the need to use fatty acid analysis, in concert with stomach content analysis, to provide more diversified and reliable results on diet composition in order to refine our understanding of forage fish feeding ecology.

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TABLES AND FIGURES

Table 2.1 20:1n-11/9 and 22:1n-11 fatty acid contents (% of total quantified fatty acids) in four fish species collected from embayments around the Kodiak Archipelago, Alaska. n: sample size; lipid content: % of whole-body wet mass; 20:1n-11/9: the sum of fatty acid isomer 20:1n-11 and 20:1n-9; values = means \pm SD

species	Month	year	embayment	total length range (cm)	n	lipid content (%)	20:1n-11/9 (%)	22:1n-11 (%)	
walleye pollock	May	2004	Uganik	14.1-15.2	5	1.41 \pm 0.33	0.47 \pm 0.16	0.33 \pm 0.15	
				21.8-26.1	5	1.18 \pm 0.23	3.02 \pm 2.33	2.84 \pm 2.31	
				35.5-41.6	5	1.59 \pm 0.63	0.75 \pm 0.53	1.26 \pm 1.72	
	August	2004	Uganik	32.5-37.0	5	4.39 \pm 1.12	9.21 \pm 2.96	8.99 \pm 2.93	
				7.7-9.1	5	3.50 \pm 0.81	1.93 \pm 0.66	1.74 \pm 0.64	
			Tonki	34.0-35.0	5	4.58 \pm 1.93	1.27 \pm 0.66	1.11 \pm 0.65	
				Paramanof	8.2 -10.5	6	6.17 \pm 1.84	1.76 \pm 0.51	1.62 \pm 0.50
			2005	Uganik	7.1-9.1	9	4.03 \pm 2.02	2.54 \pm 2.74	2.38 \pm 2.69
					20.3-24.4	10	5.35 \pm 1.50	3.25 \pm 1.39	3.07 \pm 1.36
					30.5-39.8	10	2.63 \pm 1.68	1.74 \pm 1.48	1.57 \pm 1.45
November	2006	Uganik	10.0-12.4	20	5.46 \pm 0.86	5.83 \pm 2.59	5.63 \pm 2.56		
			19.7-24.8	20	4.91 \pm 1.73	7.18 \pm 2.27	6.92 \pm 2.13		
			26.0-41.0	15	3.18 \pm 1.36	6.98 \pm 2.60	6.78 \pm 2.58		

Table 2.1 (continued)

species	month	year	embayment	total length range (cm)	n	lipid content (%)	20:1n-11/9 (%)	22:1n-11 (%)
Pacific herring	May	2005	Uganik	19.1-23.8	5	3.97 ± 1.10	2.51 ± 0.50	3.20 ± 0.75
	August	2004	Uganik	17.5-21.0	5	4.32 ± 5.15	3.84 ± 1.64	5.50 ± 2.84
	November	2006	Uganik	13.6-22.3	23	10.32 ± 2.57	6.05 ± 2.29	11.57 ± 5.93
				25.7-29.3	14	18.28 ± 3.24	8.74 ± 2.83	26.55 ± 6.84
	April	2007	Uganik	15.9-16.8	5	14.44 ± 1.39	13.35 ± 1.76	17.94 ± 1.18
			Tonki	17.0-18.2	5	13.22 ± 2.85	15.21 ± 0.33	24.12 ± 1.51
capelin	May	2005	Uganik	8.2-8.7	5	15.85 ± 1.48	1.93 ± 0.18	2.06 ± 0.61
			Uganik	11.9-13.3	5	7.06 ± 2.32	1.57 ± 0.53	2.67 ± 1.93
			Tonki	11.2-13.2	10	5.96 ± 1.01	3.21 ± 0.53	11.94 ± 3.60
		2004	Tonki	8.4-9.8	5	6.47 ± 1.17	6.06 ± 0.96	14.13 ± 5.62
				10.7-12.8	5	10.18 ± 0.87	6.72 ± 0.85	26.55 ± 2.05
	August	2005	Uganik	7.9-9.2	5	6.08 ± 1.71	1.95 ± 0.29	3.16 ± 1.23
			Perenosa	7.9-9.5	12	7.07 ± 2.32	4.91 ± 1.76	7.67 ± 4.98
				10.1-12.9	8	14.24 ± 6.53	4.23 ± 1.95	11.92 ± 4.66
eulachon	November	2006	Uganik	13.9-17.7	10	21.02 ± 1.94	1.69 ± 0.17	3.83 ± 1.29
				20.4-23.3	10	20.56 ± 0.87	1.80 ± 0.32	5.51 ± 1.80

Table 2.2 20:1n-11/9 and 22:1n-11 fatty acid contents (% of total quantified fatty acids) in four zooplankton groups collected from embayments around the Kodiak Archipelago, Alaska. n: sample size; 20:1n-11/9: the sum of fatty acid isomer 20:1n-11 and 20:1n-9

group	month	n	20:1n-11/9 (%)		22:1n-11 (%)	
			mean	maximum	mean	maximum
copepods	May	10	5.24	10.89	9.37	15.76
	August	8	8.19	10.65	11.15	16.23
	November	5	8.15	11.38	8.60	12.04
	April	4	5.67	6.23	8.86	13.10
euphausiids (adults & juveniles)	May	7	1.01	1.38	0.81	1.39
	August	19	1.30	3.15	1.32	3.38
	November	3	2.07	2.60	1.87	2.28
	April	4	1.85	3.10	1.42	2.67
chaetognaths	May	3	4.95	7.87	4.09	5.98
	August	6	6.32	7.32	5.32	7.61
	November	2	9.35	9.70	5.89	6.20
	April	3	9.13	11.46	5.91	7.19
pteropods	May	4	3.52	4.22	2.04	2.64
	August	2	4.16	4.30	0.48	0.64

Table 2.3 Overall stomach content composition in four fish species collected from embayments around the Kodiak Archipelago, Alaska, in mean numerical percentage (No., %), percentage frequency of occurrence (FO, %), and mean prey-specific numerical percentage (SNo., %). n: number of non-empty stomachs analyzed; a + j: adult + juvenile; f + c + e: furcilia + calyptopis + egg

n	walleye pollock			Pacific herring			capelin			eulachon		
	404			250			242			147		
taxonomic group	No.	FO	SNo.	No.	FO	SNo.	No.	FO	SNo.	No.	FO	SNo.
Amphipoda	1.77	7.67	23.05	4.38	10.80	40.59	0.10	0.41	25.00	2.66	4.76	55.78
Chaetognatha	0	0	0	0.28	0.40	70.83	0	0	0	0	0	0
Cirripedia	0.08	0.25	33.33	2.38	5.00	47.60	21.58	33.47	64.48	0	0	0
Copepoda	14.93	23.02	64.84	26.49	34.00	77.92	32.37	47.52	68.13	5.79	8.16	70.95
Euphausiacea, a + j	73.07	87.13	83.87	59.04	82.00	70.78	44.66	45.87	97.37	89.83	100	89.83
Euphausiacea, f + c + e	0.54	4.21	12.90	0	0	0	0.86	4.55	19.01	0	0	0
Larvacea	3.18	11.63	27.34	0	0	0	0	0	0	1.72	2.72	63.10
Decapoda	0.75	2.48	30.20	7.67	13.60	56.42	0	0	0	0	0	0
Pteropoda	1.45	3.47	41.91	0.04	0.40	10.00	0	0	0	0	0	0
others	4.23	7.43	56.92	0	0	0	0.41	0.41	100	0	0	0

Table 2.4 Mean numerical percentage (No., %) and percent frequency of occurrence (FO, %) of copepods and euphausiids (adults and juveniles) in stomach contents of four fish species collected from embayments around the Kodiak Archipelago, Alaska. n: number of non-empty stomachs analyzed

species	month	year	embayment	total length range (cm)	n	copepods		euphausiids		all others
						No.	FO	No.	FO	No.
walleye pollock	May	2004	Uganik	13.6-15.5	15	75.45	100	7.33	20.00	17.22
				23.6-28.9	15	25.74	86.67	10.27	40.00	63.99
				35.0-43.0	15	8.06	33.33	69.26	100	22.68
		2005	Uganik	13.0-24.2	20	63.77	80.00	27.40	65.00	8.83
				43.0-48.5	10	14.78	30.00	66.44	100	18.78
				Uganik	10	0	0	97.89	100	2.11
	August	2004		Tonki	20	0	0	100	100	0
				Perenosa	20	0	0	100	100	0
				Paramanof	10	0	0	100	100	0
				Uganik	30	41.44	60.00	44.90	73.33	13.66
		2005		Uganik	25	0.31	4.00	91.09	92.00	8.60
				Tonki	15	95.85	100	2.61	73.33	1.54
				Perenosa	14	11.75	21.43	66.92	100	21.33
				Perenosa	15	7.65	33.33	79.72	100	12.63

Table 2.4 (continued)

species	month	year	embayment	total length range (cm)	n	copepods		euphausiids		all others
						No.	FO	No.	FO	No.
walleye pollock	November	2006	Uganik	10.5-12.1	20	0	0	100	100	0
				16.4-23.6	40	0	0	92.50	92.50	7.50
				26.0-42.0	25	0	0	69.00	84.00	31.00
				48.0-76.0	10	0	0	61.67	80	38.33
	April	2007	Uganik	19.0-30.1	21	0	0	100	100	0
				34.0-76.0	24	0	0	88.75	91.67	11.25
				Tonki	15	0	0	100	100	0
				Perenosa	15	0	0	97.33	100	2.67
Pacific herring	May	2004	Uganik	9.7 -11.3	12	87.26	100	11.91	50.00	0.83
				26.0-30.1	17	8.35	23.53	88.12	100	3.53
		2005	Uganik	10.4-12.8	11	47.47	90.91	19.15	63.64	33.39
				19.0-23.6	8	22.20	62.50	27.14	100	50.66
	August	2004	Uganik	16.0-23.0	30	0.80	6.67	37.93	93.33	61.27
				Tonki	10	0	0	92.59	100	7.41
			Perenosa	16.6-27.0	18	0	0	100	100	0
				2005	Perenosa	40	2.46	10.00	70.03	85.00

Table 2.4 (continued)

species	month	year	embayment	total length range (cm)	n	copepods		euphausiids		all others
						No.	FO	No.	FO	No.
Pacific herring	November	2006	Uganik	15.9-21.8	40	92.09	95.00	7.61	40	0.30
				23.1-29.0	14	66.32	78.57	33.68	71.43	0
	April	2007	Uganik	16.6-21.6	15	0	0	100	100	0
				26.7-32.6	15	0	0	100	100	0
			Tonki	13.9-19.1	20	0	0	100	100	0
				8.0-9.5	15	18.25	46.67	0	0	81.75
capelin	May	2005	Uganik	10.7-13.2	24	0	0	95.83	95.83	4.17
				7.3-8.5	15	10.65	33.33	0	0	89.35
			Tonki	11.3-12.9	25	0	0	100	100	0.00
				7.1-8.7	10	37.89	100	0	0	62.11
			Perenosa	11.4-13.4	10	0	0	100	100	0.00
				7.9-9.9	20	19.43	95.00	0	0	80.57
August	2004	Tonki	11.4-13.0	10	5.83	20	91.67	100	2.50	
			7.6-9.0	20	98.33	100	1.67	5.00	0	
		Paramanof								

Table 2.4 (continued)

species	month	year	embayment	total length range (cm)	n	copepods		euphausiids		all others
						No.	FO	No.	FO	No.
capelin	August	2005	Uganik	8.0-9.2	15	77.93	90	10.56	20	11.52
				5.2-6.0	9	81.11	100	0	0	18.89
			Tonki	8.0-9.0	15	90.16	100	0	0	9.84
				10.3-12.7	15	0	0	100	100	0
			Perenosa	7.8-9.2	15	90.48	100	0	0	9.52
				10.9-13.1	10	0	0	100	100	0
			November	2006	Uganik	9.1 -11.0	14	0	0	100
eulachon	May	2005	Uganik	14.2-18.6	20	0	0	87.56	100	12.44
			Tonki	12.7-19.9	20	20.95	30.00	66.43	100	12.62
	August	2004	Tonki	10.7-18.4	14	0	0	100	100	0
			Perenosa	15.9-21.5	18	0	0	100	100	0
		2005	Uganik	8.6 -21.5	30	0	0	100	100	0
	November	2006	Uganik	15.1-20.0	10	14.67	20.00	85.33	100	0
				20.3-24.6	20	14.29	25.00	78.63	100	7.08
April	2007	Uganik	17.2-25.6	15	0	0	100	100	0	

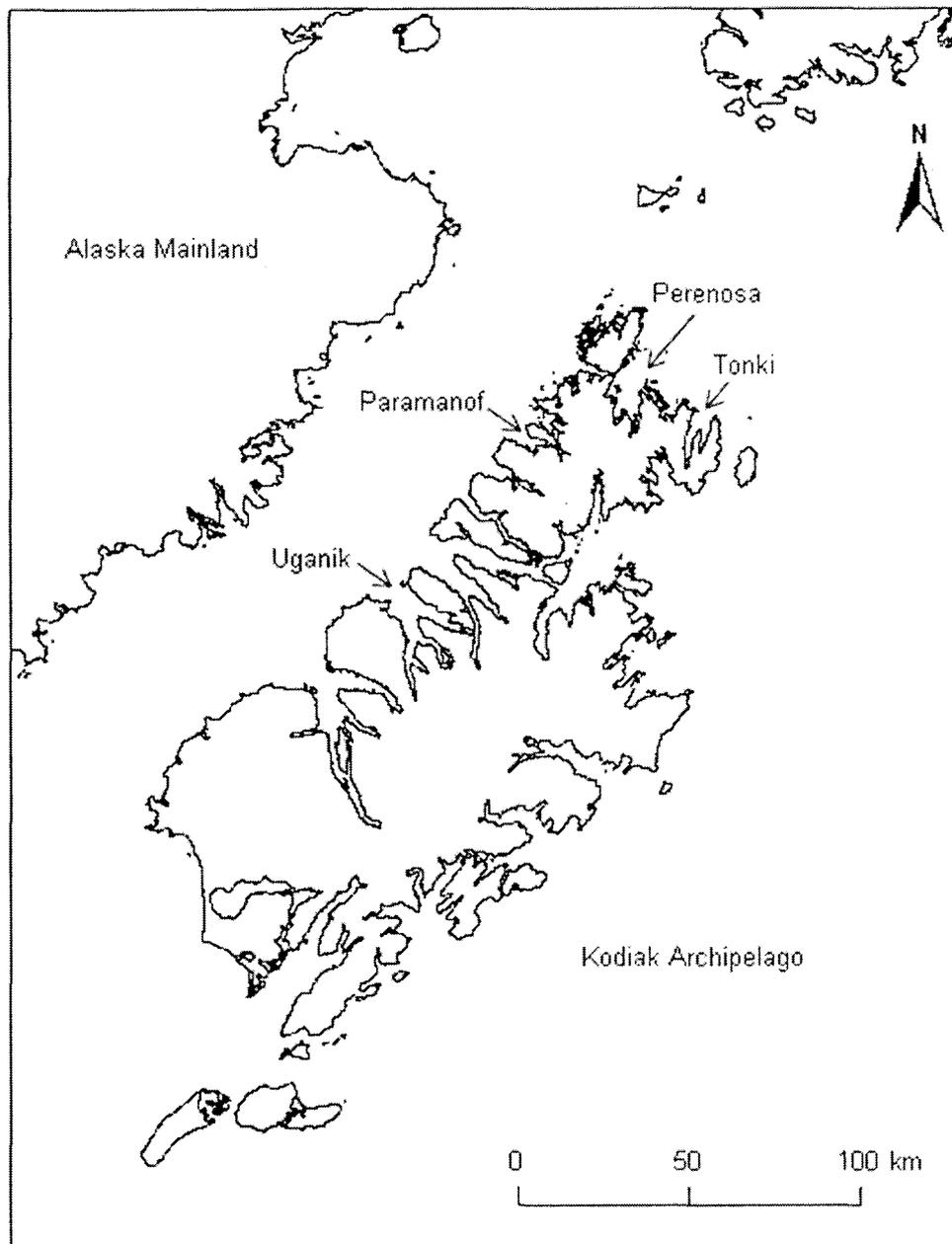


Figure 2.1 Locations of Uganik, Tonki, Perenosa, and Paramanof Bays around the Kodiak Archipelago, Alaska.

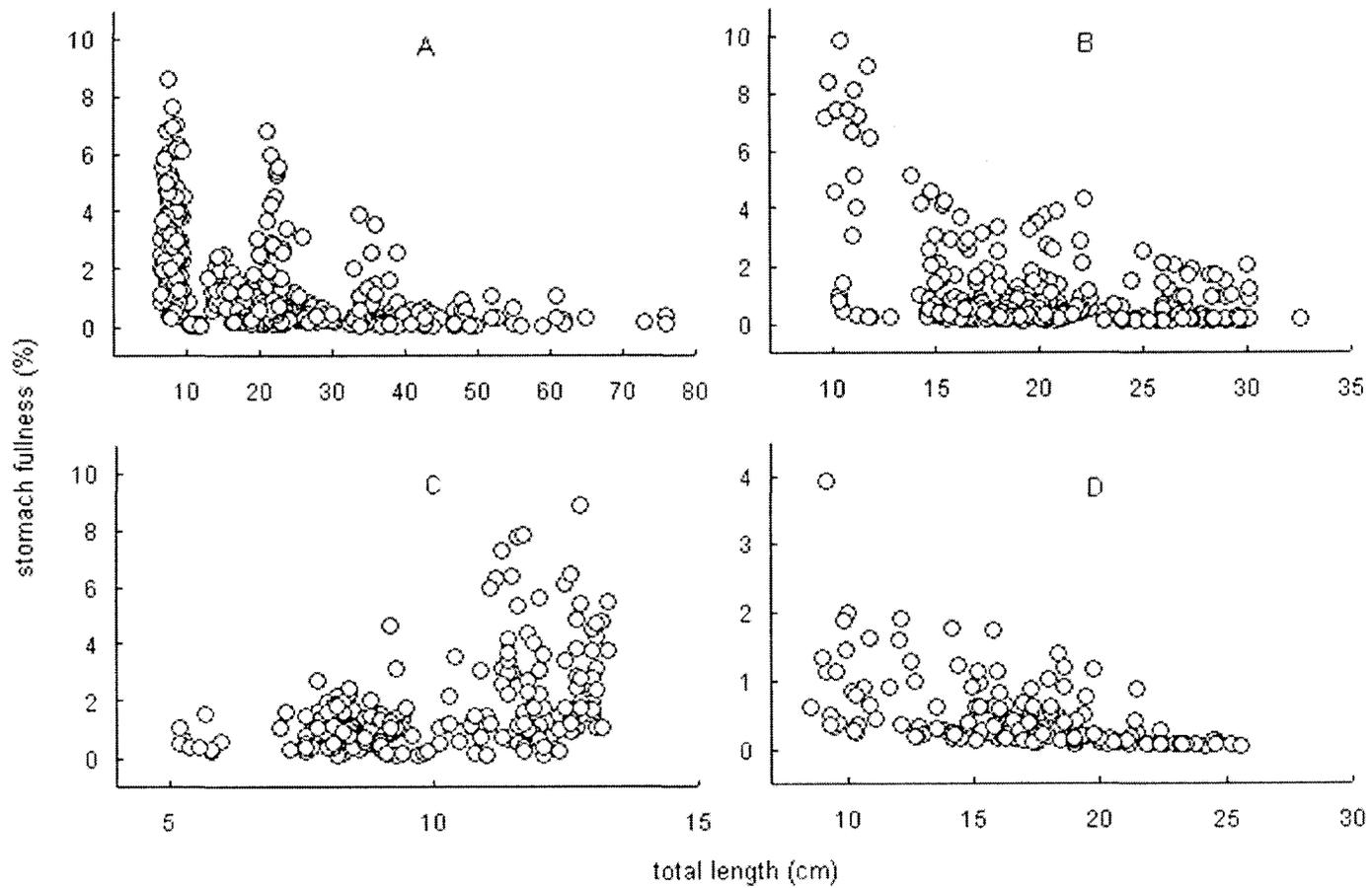


Figure 2.2 Stomach fullness (% of whole-body wet weight) plotted against total length of walleye pollock (A, n = 389), Pacific herring, (B, n = 250), capelin (C, n = 242), and eulachon (D, n = 147) collected from embayments around the Kodiak Archipelago, Alaska.

Chapter 3:
**Intra-Species Variation in Lipid Content and Fatty Acid Composition
of Forage Fishes in Embayments of the Kodiak Archipelago, Alaska¹**

ABSTRACT

Forage fish lipid content and fatty acid composition can offer insights into forage fish life history and local plankton production, and largely define the nutritional values of prey for upper trophic level predators. In this study, we analyzed lipid content and fatty acid composition of four forage fish species, walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*) and eulachon (*Thaleichthys pacificus*), that were systematically sampled (n = 816) from four embayments of the Kodiak Archipelago, Alaska. Lipid content varied significantly by month and fish length; inter-month variations did not strictly mirror the annual cycle of zooplankton production; ontogenetic patterns were specific to fish species and month. Fatty acid composition varied significantly by month, fish length, and embayment; contents of certain fatty acids were significantly correlated with lipid content. The large magnitudes of intra-species variations suggest against the use of average values at a species level when applying lipid data to ecological studies. Results also demonstrated that fatty acid analysis can be a valuable approach to refining our knowledge in forage fish feeding ecology.

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INTRODUCTION

Refining our knowledge in forage fish lipid dynamics is a necessary and effective step to improve the understanding of marine ecosystem functioning (Rosa et al. 2010, Spitz et al. 2010). Forage fishes serve as the main energy passageways between zooplankton and piscivorous fishes, marine mammals, and seabirds (Springer & Speckman 1997), and a significant portion of the conveyed energy is in the form of lipids (Van Pelt et al. 1997, Ball et al. 2007). Variations in forage fish lipid content and fatty acid composition not only offer insights into forage fish life history and local plankton production (Henderson et al. 1984, Litz et al. 2010), but also have profound implications on upper trophic level species (Montevecchi & Piatt 1984, Iverson et al. 1997, Rosen & Trites 2000a). For these reasons, information on forage fish lipid dynamics has been used to investigate a variety of ecological questions, from fish community reorganization to marine mammal population decline (Rosen & Trites 2000b, Iverson et al. 2004, Litzow et al. 2006).

Lipid content in forage fishes is known to be highly variable (Van Pelt et al. 1997, Ball et al. 2007). Efforts to assess variations in forage fish lipid content have increased in recent years, propelled primarily by the rising need for better understanding the potential implications of different prey qualities on marine mammals and seabirds (Schaufler et al. 2006, Spitz et al. 2010). Earlier studies have focused on inter-species variations (Payne et al. 1999, Bando 2002), since forage fish remains in stomachs or scats of apex predators were typically identified to the species level (Lowry et al. 1989, Merrick et al. 1997). More recent work examined intra-species variations and these variations were attributed to multiple factors, such as sampling month and fish length (Iverson et al. 2002, Vollenweider 2005). It has been noticed that the magnitudes of intra-species variations can match those of inter-species variations (Ball et al. 2007, Rosa et al. 2010); these observations indicate that the use of average lipid content values at the species level for fine-scale ecological studies must be viewed with caution. Currently, forage fish lipid content

data are scarce and most existing data are based only on opportunistic sampling. As a result, applications of published lipid content results are often limited to the compromised use of species-specific average values, which severely reduces the resolution of calculated results. It has been strongly recommended that individual variations be incorporated in calculations when investigating fish bioenergetics (Hartman & Brandt 1993, Ney 1993, Wuenschel et al. 2006); however, this recommendation requires a systematical examination of intra-species variations.

Fatty acids have long been used as natural biomarkers in marine ecosystems, because most dietary fatty acids are deposited in predator tissues with little modification (Sargent et al. 1987, Dalsgaard & St. John 2004). Fatty acid composition, measured by the relative contributions of various fatty acids to the total (Christie 2003), offers specific diet information that can be difficult to acquire through stomach content analysis (Iverson et al. 2004, Stevens et al. 2004). Fatty acid composition of forage fishes provides indirect evidence regarding the importance of calanoid copepods as prey (Sargent & Henderson 1986, Dalsgaard et al. 2003, Tocher 2003) and can be quantitatively traced in marine mammals and seabirds (Iverson et al. 1997, Iverson et al. 2004, Williams & Buck 2010). Unfortunately, baseline data on forage fish fatty acids are currently lacking in most marine ecosystems. The lack of background information that new data could be compared with severely limits the scope and certainty of ecological conclusions derived from isolated fatty acid dataset (Litzow et al. 2006, Litz et al. 2010, Williams & Buck 2010). Therefore, the construction of a baseline database is key to using fatty acid analysis as a promising biochemical approach to studying forage fishes and their trophic interactions.

In this study, we assess lipid content and fatty acid composition of four locally important forage fish species, walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), and eulachon (*Thaleichthys pacificus*), systematically sampled from embayments of the Kodiak Archipelago in the Gulf of Alaska (GOA). Forage fishes utilize these embayments as feeding and spawning habitats, and constitute critical food sources of local

piscivorous fishes, marine mammals and seabirds (Pahlke 1985, McKenzie & Wynne 2008). Historical population fluctuations of forage fishes in the GOA (Anderson & Piatt 1999), along with their predators (Merrick et al. 1987), and projected climate change prompted our efforts to better understand local forage fishes through their lipid dynamics. The first step was to establish a baseline database by describing the intra-species variations in lipid content and fatty acid composition. We hypothesized that lipid content and fatty acid composition would vary significantly by month, fish length, and embayment. Results of this study will enable us to better understand forage fish lipid dynamics and ecosystem functioning in the coastal waters of the Kodiak Archipelago.

MATERIALS AND METHODS

Forage fishes were collected from Uganik, Tonki, Perenosia, and Paramanof Bays of the Kodiak Archipelago (Fig. 3.1) in May and August of 2004 and 2005, November 2006, and April 2007 (Fish Resource Permits authorized by Alaska Department of Fish and Game were held for all sample collections and are documented in Appendix A). Samples were captured using a midwater trawl (DanTrawl Bering Billionaire) with a codend of 10 cm mesh and 2.5 cm mesh liner. We focused on four forage fish species that consistently dominated the net catches: walleye pollock, Pacific herring, capelin, and eulachon. Samples were stored in air-tight containers at -20°C on board and, after each survey, vacuum-packed and stored in the lab at -30°C until analysis.

Lipids were extracted from whole-body homogenates of 816 samples following Folch et al. (1957) with modifications by Ways & Hanahan (1964). Each sample was one individual fish, except for seven samples that consisted of five or ten fish pooled together. In the lab, total length was measured to the nearest 0.1 cm and whole-body wet weight to the nearest 0.01 g. Lipids in aliquots of 1.5 g homogenates were extracted with the solvent mixture of 20 mL chloroform and

10 mL methanol. Lipid content (%) was calculated as the weight of extracted lipids divided by whole-body wet weight. Extraction of the first 140 samples was conducted in duplicates and averages were reported. Because differences between replicates were negligible (less than 5% of the averages for 95% of samples), the remaining 676 samples were extracted with one replicate.

Extracted lipids from 252 samples were analyzed for fatty acid composition. Hilditch reagent was used to catalyze the transesterification of extracted lipids in aliquots of ~ 0.3 mg at 55-60 °C for 18 h and the resulting fatty acid methyl esters were washed with 5% NaCl and extracted with hexane (Christie 2003). Using a Varian Saturn 2200 GC/MS, a total of 37 fatty acids were quantified to the nearest nanogram against calibration curves established for each batch of transesterified lipid samples (8 – 20 samples for one batch). Weight values of the 37 fatty acids were standardized into compositional values, which were percentages of the total; these standardized values are hereafter referred to as fatty acid contents. Fatty acid nomenclature follows the standard “n” system (Christie 2003): for example, 20:1n-11 means that the fatty acid molecule has 20 carbon atoms and one double bond that is between carbon atom 11 and 12 counting from the terminal methyl group (CH₃).

Differences in lipid content among fish species, months, and embayments were subjected to Mann-Whitney *U* or Kruskal Wallis tests. Correlations among lipid content, fatty acid contents, and total length were measured by Spearman Rho values. Fatty acid composition was represented by the 37 fatty acid contents and examined with multivariate statistics. Dissimilarity matrices of fatty acid composition among samples were calculated based on Bray-Curtis coefficient. Ordination of samples was carried out using non-metric multidimensional scaling (MDS) and presented in two dimensions; stress values were calculated to measure how well the two-dimensional plots represent the true ordination, with values < 0.1 considered good representations (Kruskal & Wish, 1981). Differences in fatty acid composition were tested by permutation-based analysis of similarity (ANOSIM) using the ANOSIM routine in PRIMER

(version 6, PRIMER-E Ltd). Pollock and capelin samples in certain months were divided into length groups based on length modes derived from length frequency histograms in respective months. Differences in lipid content and specific fatty acid contents among groups were subjected to Mann-Whitney *U* or Kruskal Wallis tests; inter-group dissimilarity in fatty acid composition was decomposed by similarity percentage analysis using the SIMPER routine in PRIMER to determine the relative contribution of each fatty acid to the total dissimilarity. Correlations between the dissimilarity coefficient of fatty acid composition among samples and the differential in lipid content or total length were measured by Spearman Rho values using the BEST routine in PRIMER.

RESULTS

Walleye pollock lipid content ranged from 0.62% to 9.86%. Samples in April and May had lower lipid content than those in August and November ($p < 0.01$, Table 3.1). Correlations between lipid content and total length were positive in April and negative in November ($p < 0.01$, Fig. 3.2). Fatty acid composition was different among months (ANOSIM, $p < 0.001$; Fig. 3.3). Within each month, contents of four to eight of the 11 most abundant fatty acids were significantly correlated with lipid content ($p < 0.05$, Table 3.2). Dissimilarity coefficient of fatty acid composition among samples was moderately correlated with the differential in lipid content ($p < 0.01$, $Rho = 0.26$), while weakly correlated with the differential in total length ($p = 0.01$, $Rho = 0.08$). Significant differences in fatty acid composition were not detected among pollock collected from different areas within Uganik Bay (ANOSIM, $p > 0.10$), but were found among those collected from different embayments (ANOSIM, $p < 0.01$). In August 2004, for example, fatty acid composition in large pollock (30.0 – 40.0 cm) in Uganik Bay differed significantly from that in Tonki Bay (ANOSIM, $p = 0.008$). Differences in 18:1n-9 and 22:1n-11 contents between these two groups made up 40.72% of the dissimilarity in fatty acid composition; pollock in

Uganik Bay had lower 18:1n-9 content but higher 22:1n-11 content than those in Tonki Bay (Mann-Whitney U , $p < 0.001$, Table 3.3: group A and B). In the same month, fatty acid composition in small pollock (7.0 – 11.0 cm) in Tonki Bay was different from that in Paramanof Bay (ANOSIM, $p = 0.006$). Differences in 18:1n-9 and 22:6n-3 contents contributed to 44.29% of the dissimilarity; samples in Tonki Bay showed lower 18:1n-9 content but higher 22:6n-3 content than those in Paramanof Bay (Mann-Whitney U , $p < 0.001$, Table 3.3: group C and D). Ontogenetic variation was specific to embayment and month. In Uganik Bay in August 2005, fatty acid composition was not different among three pollock length groups (ANOSIM, $p = 0.06$, Table 3.3: group E, F, and G), while in Tonki Bay in August 2004, fatty acid composition was different between two length groups (ANOSIM, $p = 0.008$, Table 3.3: group B and C); differences in 18:1n-9 and 22:6n-3 contents accounted for 47.73% of the dissimilarity in fatty acid composition between the two groups. Interannual difference in fatty acid composition was noticed in Uganik Bay in August between large pollock (30.0 – 40.0 cm) collected in 2004 and 2005 (ANOSIM, $p < 0.001$, Table 3.3: group A and E); differences in 18:1n-9, 22:1n-11, and 22:6n-3 contents made up 47.64% of the dissimilarity in fatty acid composition.

Pacific herring lipid content ranged from 0.53% to 26.62%. Samples in April 2007, August 2005, and November 2006 were of higher lipid content than those in May 2004, May 2005, and August 2004 ($p < 0.01$, Table 3.1). Correlations between lipid content and total length were negative in May 2004 and positive in August 2005 and November 2006 ($p < 0.01$, Fig. 3.4). Fatty acid composition was different among months (ANOSIM, $p < 0.001$, Fig. 3.5). When samples from different months were combined, contents of all the 11 most abundant fatty acids were significantly correlated with lipid content ($p < 0.05$, Table 3.4). Dissimilarity coefficient of fatty acid composition among all the samples was significantly correlated with the differential in both lipid content and total length ($p < 0.01$, $Rho = 0.50$ and 0.33 , respectively). In November 2006, when lipid content was strongly correlated with total length ($Rho = 0.78$, Fig. 3.4), contents of all

the 11 most abundant fatty acids were significantly correlated with total length (Spearman Rho, $p < 0.001$), among which 14:0, 20:1n-11, 22:1n-11, and 18:4n-3 were positively correlated (Rho = 0.58, 0.59, 0.67, and 0.67, respectively, Fig. 3.6). Significant differences in fatty acid composition were not detected among different areas within Uganik Bay (ANOSIM, $p > 0.08$), but were found between different embayments. Specifically, in April 2007, herring in Uganik Bay had different fatty acid composition from those in Tonki Bay (ANOSIM, $p = 0.008$); the two sample groups were clustered separately in MDS ordination based on fatty acid composition (Fig. 3.5). Samples from Uganik Bay had higher 18:1n-9 content but lower 22:1n-11 content than those from Tonki Bay (Mann-Whitney U , $p = 0.01$); these two fatty acids accounted for 42.45% of the dissimilarity in fatty acid composition between the two embayments.

Capelin lipid content ranged from 1.09 to 20.48% and was not significantly different among months ($p = 0.27$, Table 3.1). Correlations between lipid content and total length were positive in August 2004 and 2005 and negative in May 2005 ($p < 0.01$, Fig. 3.7). Large capelin (10.0 – 14.0 cm) had lower lipid content in May 2005 than those in August of both 2004 and 2005, while small capelin (7.0 – 9.9 cm) exhibited the opposite pattern ($p < 0.001$). Fatty acid composition in May was different (ANOSIM, $p < 0.001$) from that in August (2004 & 2005 combined). Contents of four and seven fatty acids were significantly correlated with lipid content in May and August, respectively ($p < 0.05$, Table 3.4). Content of 22:1n-11 was positively correlated with total length in both May and August ($p \leq 0.03$, Rho = 0.48 and 0.72, respectively, Fig. 3.8). Dissimilarity coefficient of fatty acid composition among all the samples was significantly correlated with the differential in both lipid content and total length ($p < 0.01$, Rho = 0.36 and 0.15, respectively). Fatty acid composition in large capelin was always different from that in small ones when samples from the same embayment and month were compared (ANOSIM, $p \leq 0.008$, Table 3.5, Fig. 3.9). Fatty acid composition among embayments was different for both large and small capelin (ANOSIM, $p \leq 0.008$, Table 3.5, Fig. 3.9). In all cases

where the difference in fatty acid composition between sample groups was significant, differences in contents of four fatty acids, 18:1n-9, 22:1n-11, 20:5n-3, and 22:6n-3, accounted for 55.34 to 75.41% of inter-group dissimilarities.

Eulachon lipid content ranged from 5.34% to 27.86%. Samples in April and May had lower lipid content than those in August and November ($p < 0.01$, Table 3.1). Lipid content was positively correlated with total length in both May and August ($p < 0.01$, Fig. 3.10). Fatty acid composition was assessed for 20 eulachon collected in Uganik Bay in November 2006; only 20:5n-3 content was significantly correlated with lipid content ($p < 0.05$, Table 3.4); 18:1n-9 was the most abundant fatty acid with its content averaging 39.34%.

At the species level, lipid content in pollock was the lowest and in eulachon the highest among the four species (Mann-Whitney U , $p < 0.001$); there was no difference in lipid content between herring and capelin (Mann-Whitney U , $p = 1.00$). In comparison, fatty acid composition in the four species, pollock, herring, capelin, and eulachon, was different from each other (ANOSIM, $p < 0.001$).

DISCUSSION

Results of this study demonstrated relatively large intra-species variations in forage fish lipid content and fatty acid composition. The wide ranges of lipid content and fatty acid contents within each species were similar to or slightly larger than those reported from other areas in the GOA (Worthy & Miculka 1997, Iverson et al. 2002, Vollenweider 2005, Williams et al. 2009). Both lipid content and fatty acid composition varied significantly by month and fish length, while only fatty acid composition differed among embayments.

Seasonal variations in forage fish lipid content did not strictly mirror the annual cycle of prey availability, since they are expected to reflect changes in species-specific energy budgets that incorporate life history events (Robards et al. 1999, Kitts et al. 2004, Eder & Lewis 2005). From

April to May, lipid content in walleye pollock did not change, while it decreased in Pacific herring; over the same period, zooplankton biomass is known to increase in the waters of the GOA (Incze et al. 1997, Coyle & Pinchuk 2003). The different temporal trends between lipid content and zooplankton biomass are likely attributed to differences in growth rates and maturity stages of the two forage fishes between the two months. Juvenile pollock and herring have higher growth rates in May than in April (Salveson 1984, Brodeur & Wilson 1996, Stokesbury et al. 1999), which requires more energy expenditure in May. In addition, spawning of herring peaks in late April in the Kodiak waters (based on sac roe harvest dates in Spalinger & Gretsich 2007), while our samples were collected in early April. Thus, lipid depletion during spawning (Henderson et al. 1984, Robards et al. 1999) may have also contributed to the differences in lipid content observed between April and May. In November, lipid content in pollock and herring was higher than in May, despite lower concurrent zooplankton biomass (Incze et al. 1997, Coyle & Pinchuk 2003). However, growth rates of pollock and herring in November transition from positive to zero or negative (Salveson 1984, Brodeur & Wilson 1996, Stokesbury et al. 1999); accordingly most of the energy intake at this time is believed to be stored as lipids for overwintering (Paul et al. 1998, Foy & Paul 1999, Sogard & Olla 2000), which might explain the higher lipid content at this time.

Ontogenetic patterns in lipid content were species specific. In November, larger pollock had lower lipid content than smaller ones, while larger herring showed higher lipid content. These opposite patterns indicate differences in winter-feeding levels between the two species. Previous studies have demonstrated that energy content increases or does not change over winter months in juvenile pollock (Paul et al. 1998), while it continually decreases in juvenile herring (Foy & Paul 1999), suggesting that energy input through winter-feeding is able to meet metabolic demands in juvenile pollock but not in juvenile herring. In addition, both adult pollock and herring require considerable amounts of energy during the winter months for the development of their gonads.

Thus active winter-feeding in adult pollock is necessary to supplement their low lipid content in November in order to accommodate all the energetic expenditures; in comparison, adult herring can rely mainly on energy storage instead of winter feeding to meet their metabolic demands.

Ontogenetic patterns in lipid content were also specific to month, exemplified by the opposite patterns in capelin between May and August (Fig. 3.7). For capelin, the spawning period in local waters begins in May (Pahlke 1985, Doyle et al. 2002); accordingly, most samples of large female capelin (10.0 – 14.0 cm) had visible oocytes, while small capelin (7.0 – 9.9 cm) did not. These oocytes are typically considered rich in lipids (Henderson et al. 1984, Harris et al. 1986) and were not removed before homogenizing samples. Surprisingly, large capelin had lower lipid content than small ones. In contrast, Anthony et al. (2000) reported that whole-body lipid content in both female and male capelin decreased by ~ 40% when maturing from “developing” to “ripe” stage. Most female samples of large capelin in this study were in “ripe” stage, which may explain their relatively low lipid content. Similarly, “ripe” female eulachon collected in May 2005 also showed significantly lower lipid content than non-spawning eulachon. It is possible that eulachon, which spawn slightly earlier than capelin in the GOA (Marston et al. 2002), deplete lipids in manners similar to capelin when maturing. In August, the low lipid content in small capelin is likely due to the high energy demand for growth. Knoth & Foy (2008) reported that arrowtooth flounder near the Kodiak Archipelago consumed significantly more capelin in August than in May, suggesting a high predation pressure for capelin in August. Therefore, small capelin may have to invest more energy in growth than large ones in order to more quickly out-grow the risk of size-dependent predation (Lundvall et al. 1999).

Fatty acid analysis can be a valuable supplement to conventional stomach content analysis for estimating forage fish diet composition. A parallel stomach content study was conducted on samples concurrently collected (L. Guo & R. Foy, *unpubl. data*). Comparisons with stomach content results showed that fatty acid composition increased the temporal or spatial resolution of

forage fish diets: significant differences in fatty acid composition were found even if no difference in stomach content composition was observed, but not vice versa. This discrepancy may be attributed to different temporal scales associated with the two methodologies. Fatty acid composition of fish tissues is an integrated result of dietary lipids ingested over the past one to several weeks (Anderson & Arthington 1989, Kirsch et al. 1998, Jobling 2004); in contrast, stomach contents of zooplanktivorous fishes are snap-shots of ingested prey over the previous several hours to several days (Szypuła & Zalachowski 1984, Brodeur & Percy 1987). Therefore, fatty acid composition may be able to capture dietary differences from a larger temporal scale and these differences may not be reflected by a snap-shot of stomach contents. In addition, the temporal difference between the two methodologies makes fatty acid results less affected by short-term oceanographic events and differential gastric evacuation rates among various prey types (Dalsgaard et al. 2003, Iverson et al. 2004), which enables fatty acid analysis to compensate for some of the inherent limitations of stomach content analysis (Hyslop 1980).

In particular, significant inter-embayment differences in fatty acid composition were detected among sample groups of the same month and length range. In comparison, no significant difference was found in stomach content composition between these groups (L. Guo & R. Foy, *unpubl. data*). Distances among sampling embayments ranged from ~20 km to ~100 km; variations in physical and biological parameters among these embayments have been described in previous studies (Loewen 2007, Mueter & Norcross 2000), but often observations are difficult to test statistically due to sampling limitations. The highly sensitive response of forage fish fatty acid composition demonstrated in this study may be one way to detect ecosystem differences that are otherwise difficult to measure, especially considering field studies are often restricted in survey frequency and length.

An unexpected ontogenetic pattern was found in herring and capelin, namely the positive correlation between 20:1n-11 and/or 22:1n-11 content and total length (Fig. 3.6 & 3.7). Isomers

of 20:1 and 22:1 fatty acids have been extensively used as natural biomarkers to quantify the importance of calanoid copepods as prey for zooplanktivorous predators: higher 20:1 and 22:1 fatty acid contents indicate higher proportions of calanoid copepods in the diets (Sargent & Henderson 1986, Dalsgaard et al. 2003, Tocher 2003, Springer et al. 2007). It has been repeatedly reported that the relative importance of calanoid copepods as prey decrease as forage fishes grow larger (Huse & Toresen 1996, Brodeur 1998, O'Driscoll et al. 2001, Wilson et al. 2006). The same trend was observed in the parallel stomach content study (L. Guo & R. Foy, *unpubl. data*). Hence we had expected that larger fish herein would have lower 20:1n-11 or 22:1n-11 contents than smaller ones; however, our results showed the opposite pattern. This discrepancy suggests that fatty acid analysis may offer insights into forage fish feeding ecology that might be missed by stomach content analysis. It needs to be noted that our current knowledge of fatty acid metabolism in fishes is based on a small number of species and on particular life stages (Tocher 2003); therefore, interpretations of fish fatty acid data are largely based on the assumption that differences in lipid metabolism among species or life stages are not substantial.

This study described intra-species variations in lipid content and fatty acid composition of four important forage fish species in relation to month, fish length, and embayments; these results will serve as a baseline database for ecosystem investigations in local waters. Considering the magnitudes of observed variations, it is apparent that the use of average values at the species level should be avoided when applying lipid data to ecological studies. The construction of forage fish lipid content and fatty acid databases, which are currently in great demand, should incorporate factors including, but not limited to, month, fish length, and location. We also demonstrated that fatty acid analysis can be used as a sensitive and informative tool, in combination with stomach content analysis, to refine our knowledge of forage fish feeding ecology.

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TABLES AND FIGURES

Table 3.1 Lipid content (% of whole-body wet mass, means \pm SD) of four forage fish species from embayments of the Kodiak Archipelago, Alaska, by sampling month and year. Superscript letters indicate significant inter-month differences within species (Kruskal Wallis, $p < 0.01$) and values with superscript letter “a” are significantly higher than values with “b”; n: sample size; na: not available

	April 2007	May 2004	May 2005	August 2004	August 2005	November 2006
walleye pollock	1.28 ^b \pm 0.43 (n = 40)	1.67 ^b \pm 0.68 (n = 30)	1.96 ^b \pm 0.91 (n = 25)	4.36 ^a \pm 1.55 (n = 80)	4.48 ^a \pm 2.02 (n = 95)	4.42 ^a \pm 1.61 (n = 65)
Pacific herring	12.54 ^a \pm 3.16 (n = 37)	4.97 ^b \pm 2.85 (n = 20)	3.94 ^b \pm 1.66 (n = 36)	5.82 ^b \pm 4.63 (n = 43)	12.07 ^a \pm 5.63 (n = 55)	13.33 ^a \pm 4.81 (n = 37)
capelin	na	na	8.00 \pm 3.58 (n = 45)	7.84 \pm 3.37 (n = 56)	8.98 \pm 5.89 (n = 21)	9.52 \pm 1.09 (n = 7)
eulachon	16.75 ^b \pm 1.41 (n = 25)	na	15.00 ^b \pm 4.90 (n = 50)	na	19.14 ^a \pm 3.01 (n = 29)	20.79 ^a \pm 1.48 (n = 20)

Table 3.2 Content (% of the total quantified fatty acids by weight, means \pm SD) of the 11 most abundant fatty acids in walleye pollock from embayments of the Kodiak Archipelago, Alaska, by sampling month and year. n: sample size; Spearman Rho values in parentheses indicate significant correlations ($p < 0.05$) between fatty acid contents and lipid content (% of whole-body wet mass)

	May 2004	August 2004	August 2005	November 2006
n	15	21	29	55
14:0	1.59 \pm 0.59 (0.68)	2.44 \pm 0.47 (0.74)	2.88 \pm 0.42 (0.83)	2.81 \pm 0.30 (0.51)
16:0	9.37 \pm 0.91	8.76 \pm 1.53	8.50 \pm 1.47 (0.51)	8.39 \pm 1.10
18:0	2.90 \pm 0.66 (0.82)	2.62 \pm 0.36	2.67 \pm 0.73	2.58 \pm 0.37
16:1n-7	3.92 \pm 1.78 (0.91)	5.30 \pm 1.03 (0.64)	5.66 \pm 1.30 (0.81)	4.71 \pm 0.58 (0.75)
18:1n-9	17.42 \pm 4.68 (0.90)	18.92 \pm 3.58 (0.52)	20.59 \pm 4.83 (0.66)	15.83 \pm 1.96
18:1n-7	7.79 \pm 2.39 (0.88)	7.58 \pm 1.17	8.2 \pm 1.92 (0.37)	5.87 \pm 0.81
20:1n-11	1.65 \pm 0.53	1.84 \pm 0.86	2.11 \pm 0.75	5.19 \pm 2.08 (0.31)
22:1n-11	1.26 \pm 1.72	2.34 \pm 1.93	3.28 \pm 3.56	6.41 \pm 2.45
18:4n-3	1.00 \pm 0.65	1.73 \pm 0.56	2.00 \pm 1.01 (0.53)	3.72 \pm 0.71 (0.29)
20:5n-3	19.65 \pm 2.30 (-0.79)	21.26 \pm 1.77	20.8 \pm 2.23 (0.46)	17.04 \pm 1.81 (0.28)
22:6n-3	24.47 \pm 6.60 (-0.80)	18.13 \pm 4.75 (-0.51)	14.83 \pm 4.22 (-0.87)	17.27 \pm 3.13 (-0.72)

Table 3.3 Lipid content (% of whole-body wet mess, means) and three fatty acid contents (% of the total quantified fatty acids by weight, means) of seven walleye pollock sample groups (based on year, embayment, and total length range) collected from embayments of the Kodiak Archipelago, Alaska, in August 2004 and 2005. n: sample size

group	A	B	C	D	E	F	G
n	5	5	5	6	10	10	9
year	2004	2004	2004	2004	2005	2005	2005
embayment	Uganik	Tonki	Tonki	Paramanof	Uganik	Uganik	Uganik
total length range (cm)	32.5-37.0	34.0-35.0	7.7-9.1	8.2-10.5	30.5-39.8	20.3-24.4	7.1-9.1
lipid content	4.39	4.58	3.50	6.17	2.63	5.35	4.03
18:1n-9 content	18.00	26.15	15.78	22.11	19.18	19.24	18.27
22:1n-11 content	8.99	1.11	1.74	1.62	1.57	3.07	2.38
22:6n-3 content	13.42	11.11	19.37	15.31	19.10	15.82	19.61

Table 3.4 Content (% of the total quantified fatty acids by weight, means \pm SD) of the 11 most abundant fatty acids in Pacific herring, capelin, and eulachon sampled from embayments of the Kodiak Archipelago, Alaska. n: sample size; Spearman Rho values in parentheses indicate significant correlations ($p < 0.05$) between fatty acid contents and lipid content (% of whole-body wet mass)

	Pacific herring	----- capelin -----		eulachon
	n	56	May (2005) 20	August (2004 & 2005) 36
14:0	4.17 \pm 0.90 (0.56)	4.11 \pm 0.60	4.06 \pm 0.7	4.33 \pm 0.41
16:0	8.10 \pm 1.92 (-0.60)	7.84 \pm 2.00	7.12 \pm 1.83 (-0.35)	7.84 \pm 1.29
18:0	1.21 \pm 0.63 (-0.77)	1.63 \pm 0.63	1.53 \pm 0.51 (-0.65)	1.59 \pm 0.27
16:1n-7	5.35 \pm 0.92 (-0.39)	7.26 \pm 0.70	6.52 \pm 1.16	7.78 \pm 0.54
18:1n-9	14.65 \pm 4.60 (-0.64)	22.75 \pm 15.96 (0.62)	16.2 \pm 4.11	39.34 \pm 3.53
18:1n-7	3.26 \pm 1.95 (-0.80)	5.17 \pm 2.36	3.76 \pm 1.69	8.64 \pm 0.45
20:1n-11	7.34 \pm 4.15 (0.66)	2.19 \pm 0.87	4.31 \pm 2.09 (0.38)	1.50 \pm 0.25
22:1n-11	15.73 \pm 9.61 (0.79)	7.15 \pm 5.58	11.32 \pm 8.24 (0.60)	4.67 \pm 1.76
18:4n-3	4.10 \pm 1.85 (0.63)	3.36 \pm 1.90 (-0.49)	3.97 \pm 1.22 (0.39)	2.47 \pm 0.53
20:5n-3	12.95 \pm 3.59 (-0.50)	16.10 \pm 4.75 (-0.49)	14.71 \pm 2.61 (-0.33)	7.10 \pm 1.62 (0.51)
22:6n-3	13.67 \pm 4.59 (-0.74)	13.21 \pm 4.23 (-0.81)	14.53 \pm 4.76 (-0.72)	6.52 \pm 1.02

Table 3.5 Lipid content (% of whole-body wet mess, means) and four fatty acid contents (% of the total quantified fatty acids by weight, means) of nine capelin sample groups (based on month, embayment, and total length range) collected from embayments of the Kodiak Archipelago, Alaska, in May (2005) and August (2004 and 2005 combined). n: sample size; *: five individual fish were combined as one sample

group	A	B	C	D	E	F	G	H	I
n	5	5	10	5	5	5	1*	8	12
month	May	May	May	August	August	August	August	August	August
embayment	Uganik	Uganik	Tonki	Uganik	Tonki	Tonki	Tonki	Perenosa	Perenosa
total length range (cm)	11.9-13.3	8.2-8.7	11.2-13.2	7.9-9.2	10.7-12.8	8.4-9.8	5.7	10.1-12.9	7.9-9.5
lipid content	7.06	15.85	5.96	6.08	10.18	6.47	1.09	14.24	7.07
18:1n-9 content	26.70	46.09	9.09	16.84	9.94	15.95	13.25	19.29	16.84
22:1n-11 content	2.67	2.06	11.94	3.16	26.55	14.13	0.95	11.92	7.67
20:5n-3 content	18.66	8.89	8.42	17.11	11.14	13.07	17.49	14.64	15.69
22:6n-3 content	11.74	7.54	6.77	19.30	8.79	13.76	27.97	10.83	16.61

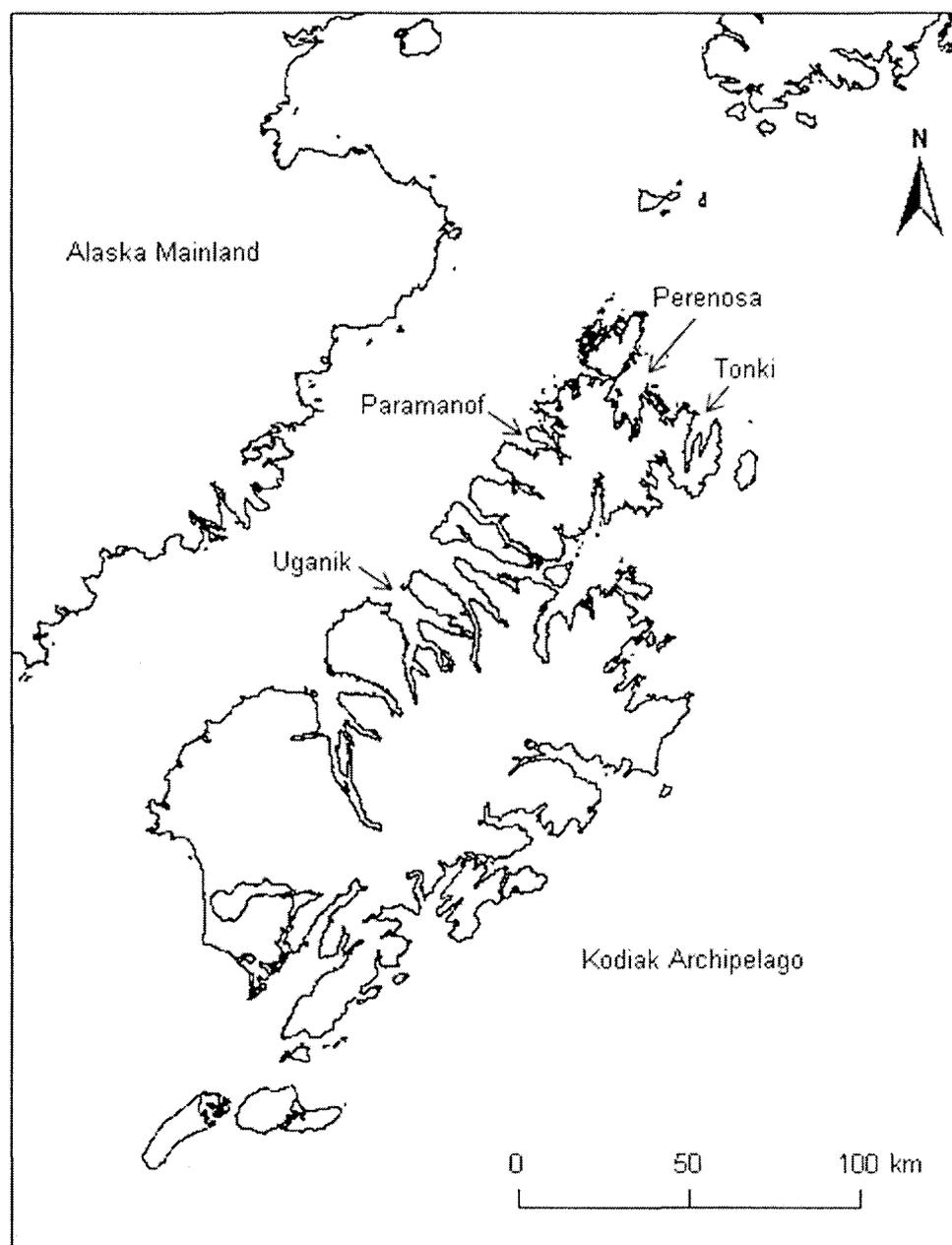


Figure 3.1 Locations of Uganik, Tonki, Perenosa, and Paramanof Bays around the Kodiak Archipelago, Alaska.

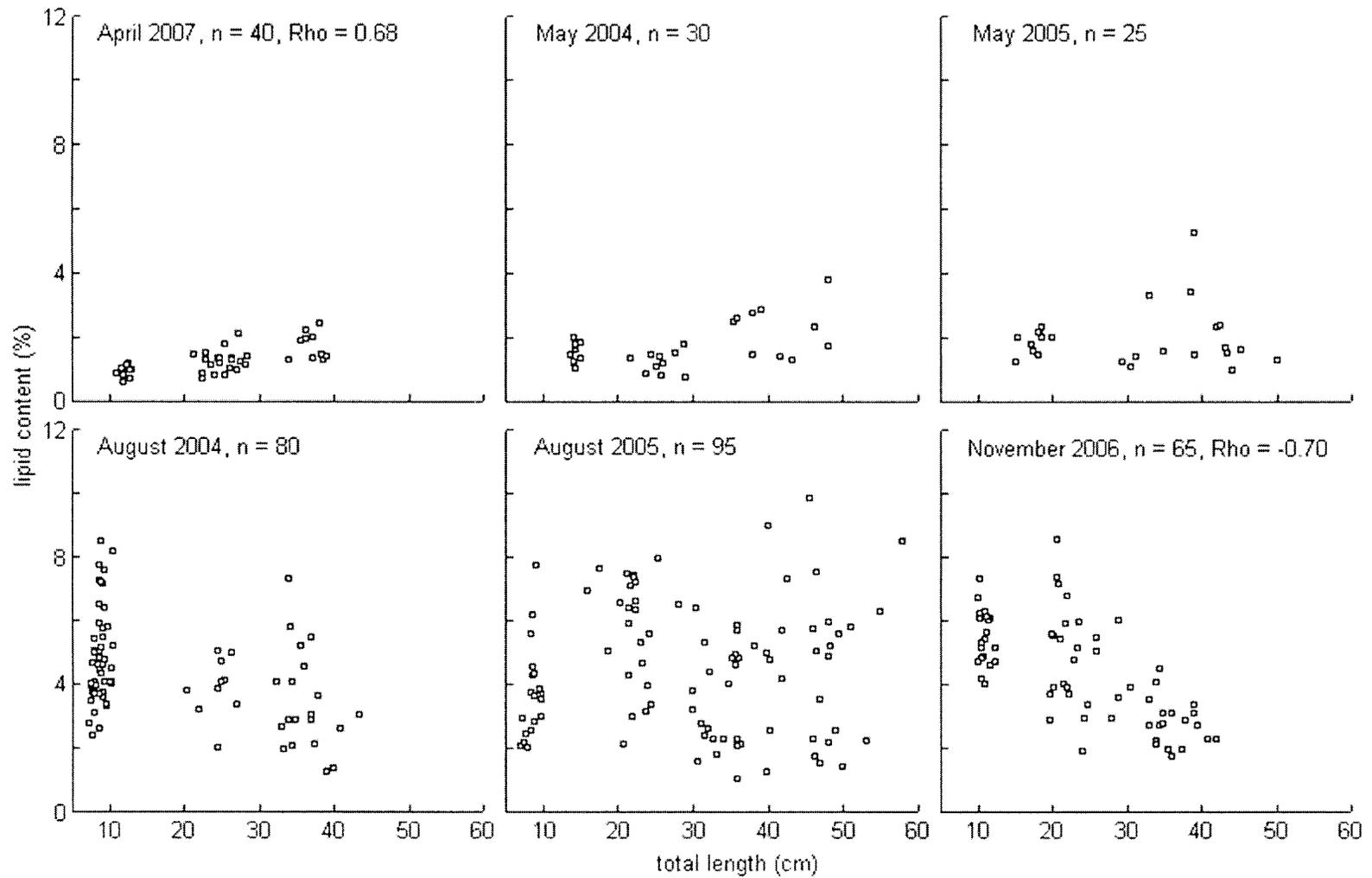


Figure 3.2 Scatterplots of lipid content vs. total length of walleye pollock from embayments of the Kodiak Archipelago, Alaska, by sampling month and year. n: sample size; Spearman Rho values indicate significant correlations ($p < 0.01$) between lipid content and total length

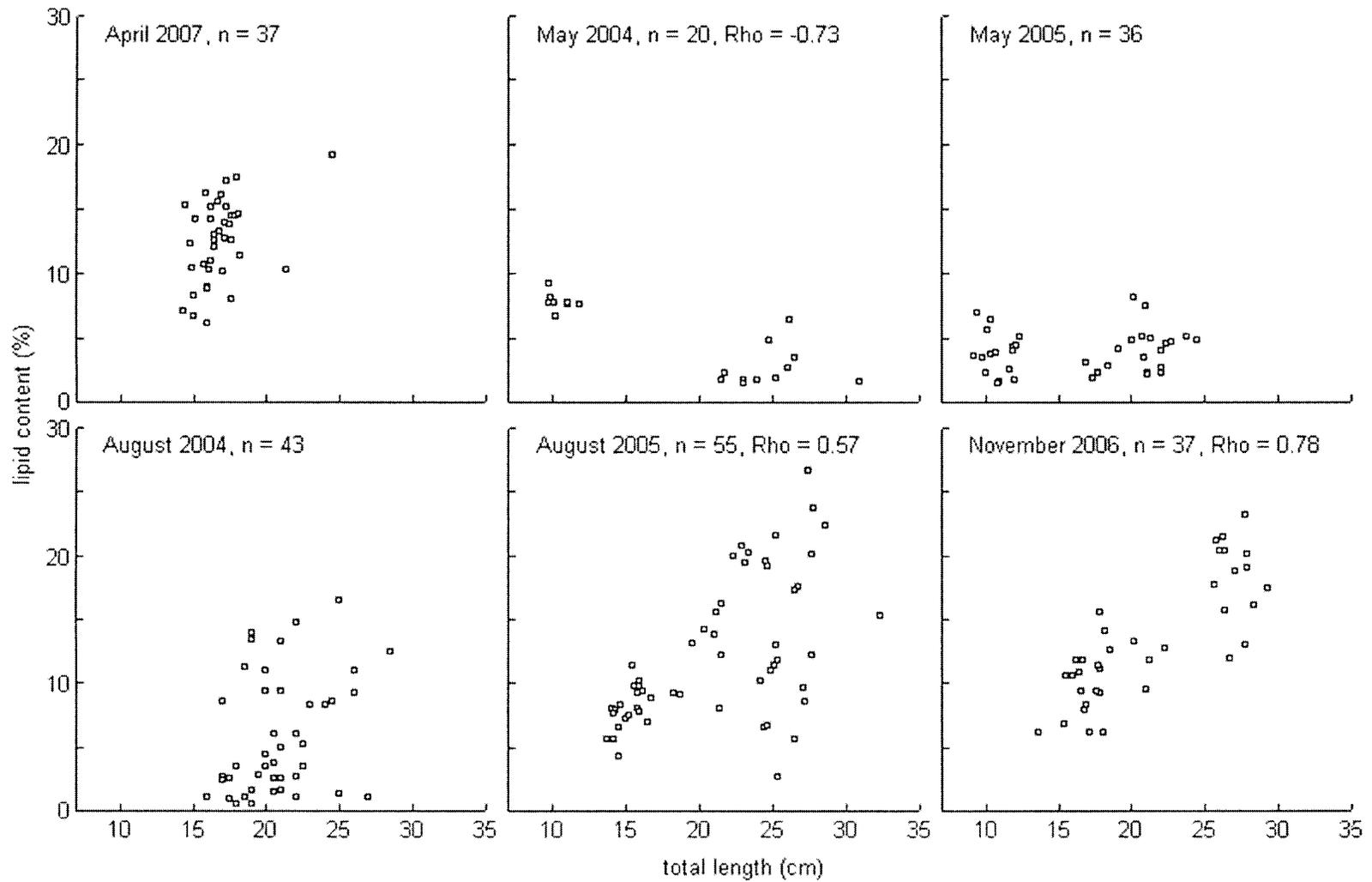


Figure 3.4 Scatterplots of lipid content vs. total length of Pacific herring from embayments of the Kodiak Archipelago, Alaska, by sampling month and year. n: sample size; Spearman Rho values indicate significant correlations ($p < 0.01$) between lipid content and total length

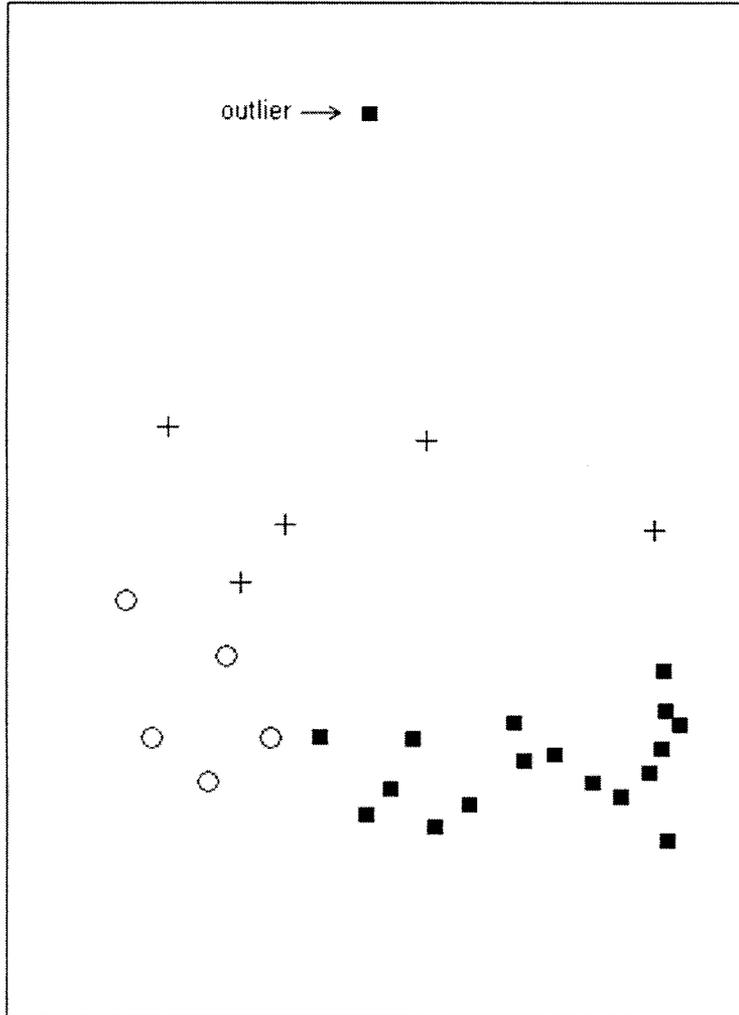
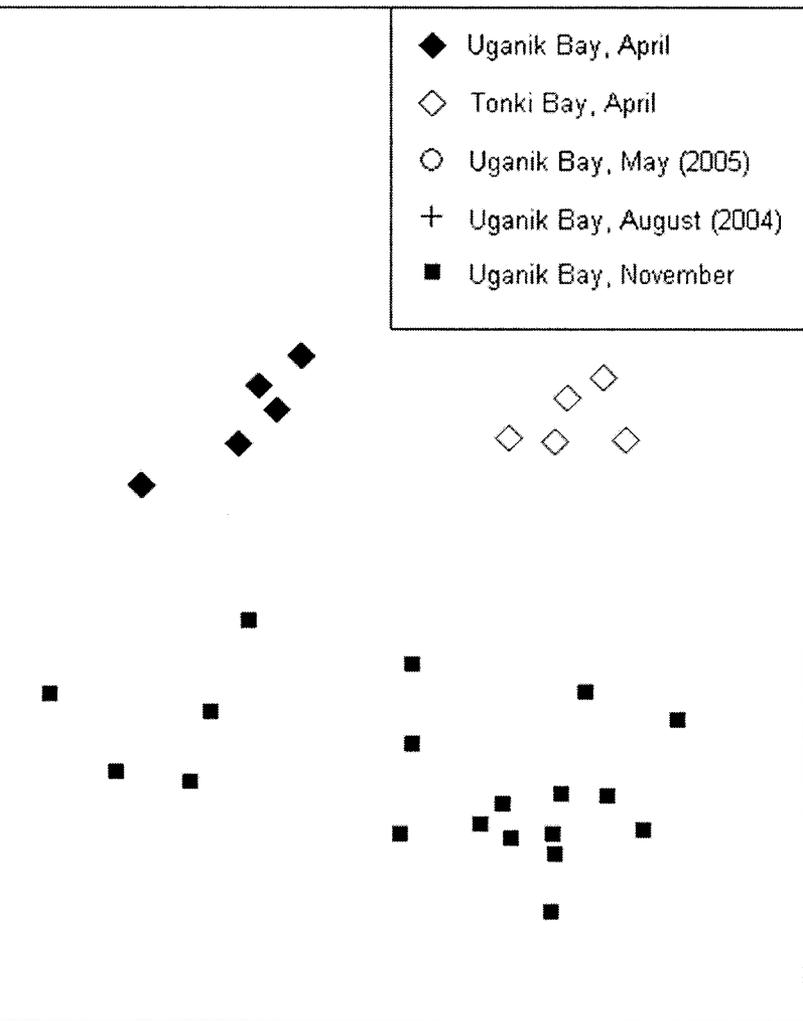


Figure 3.5 MDS ordination of Pacific herring fatty acid composition (n = the Kodiak Archipelago, Alaska. MDS two-dimensional stress = 0.059



57, of which one sample considered as outlier) sampled from embayments of

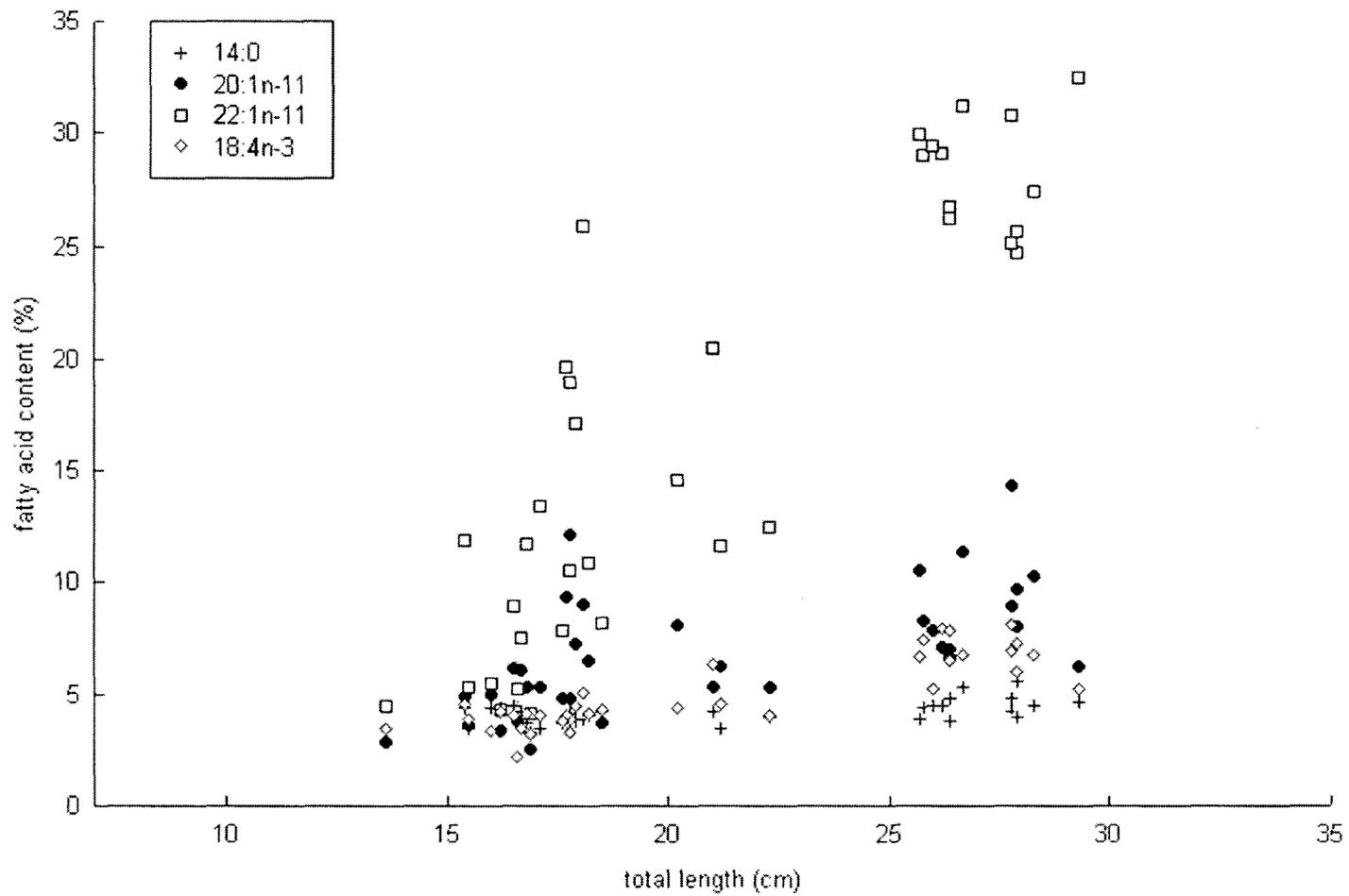


Figure 3.6 Contents (% of the total quantified fatty acids by weight) of four fatty acids plotted against total length of Pacific herring (n = 36) sampled from Uganik Bay, Alaska, in November 2006.

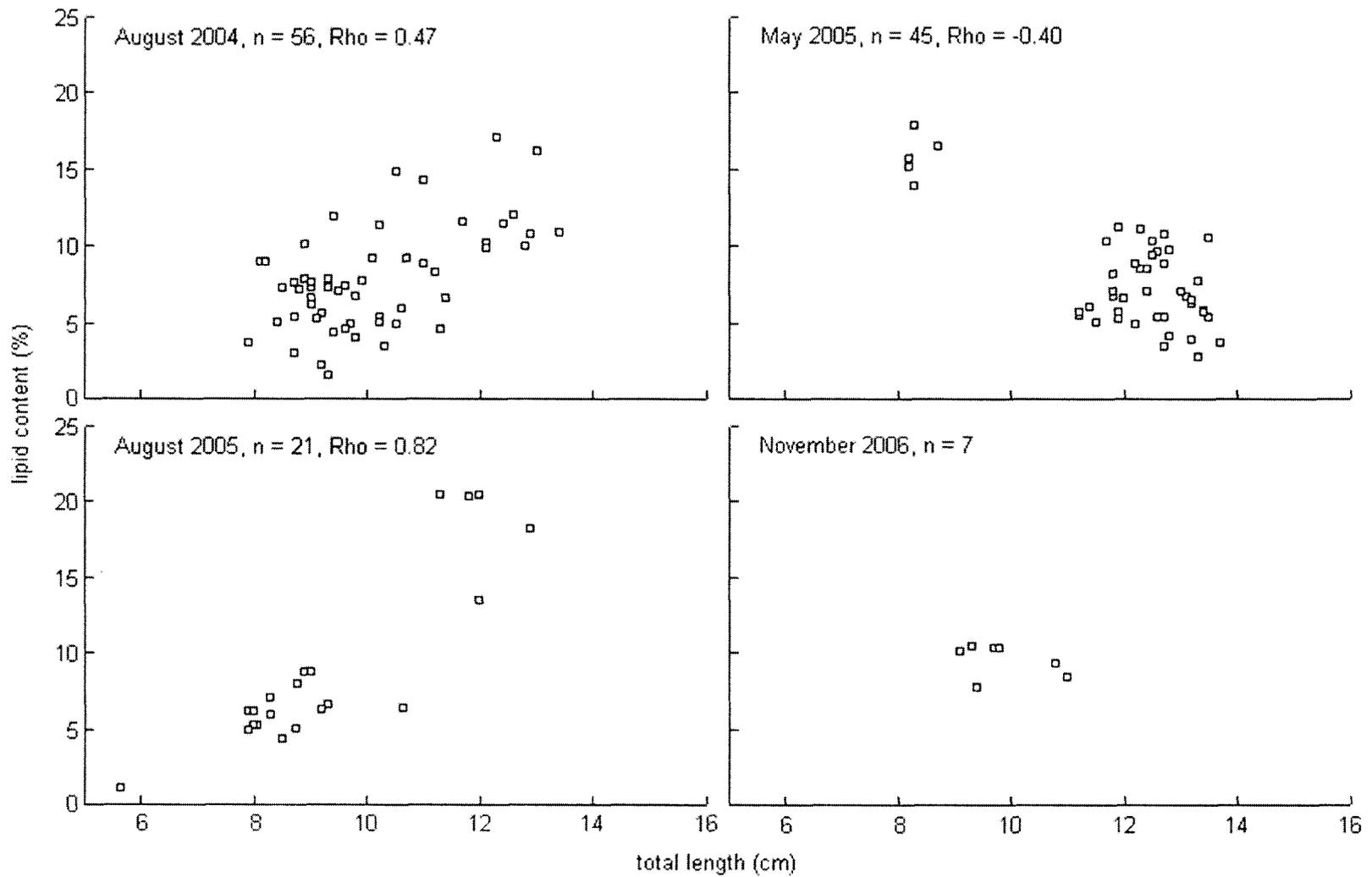


Figure 3.7 Scatterplots of lipid content vs. total length of capelin from embayments of the Kodiak Archipelago, Alaska, by sampling month and year. n: sample size; Spearman Rho values indicate significant correlations ($p < 0.01$) between lipid content and total length

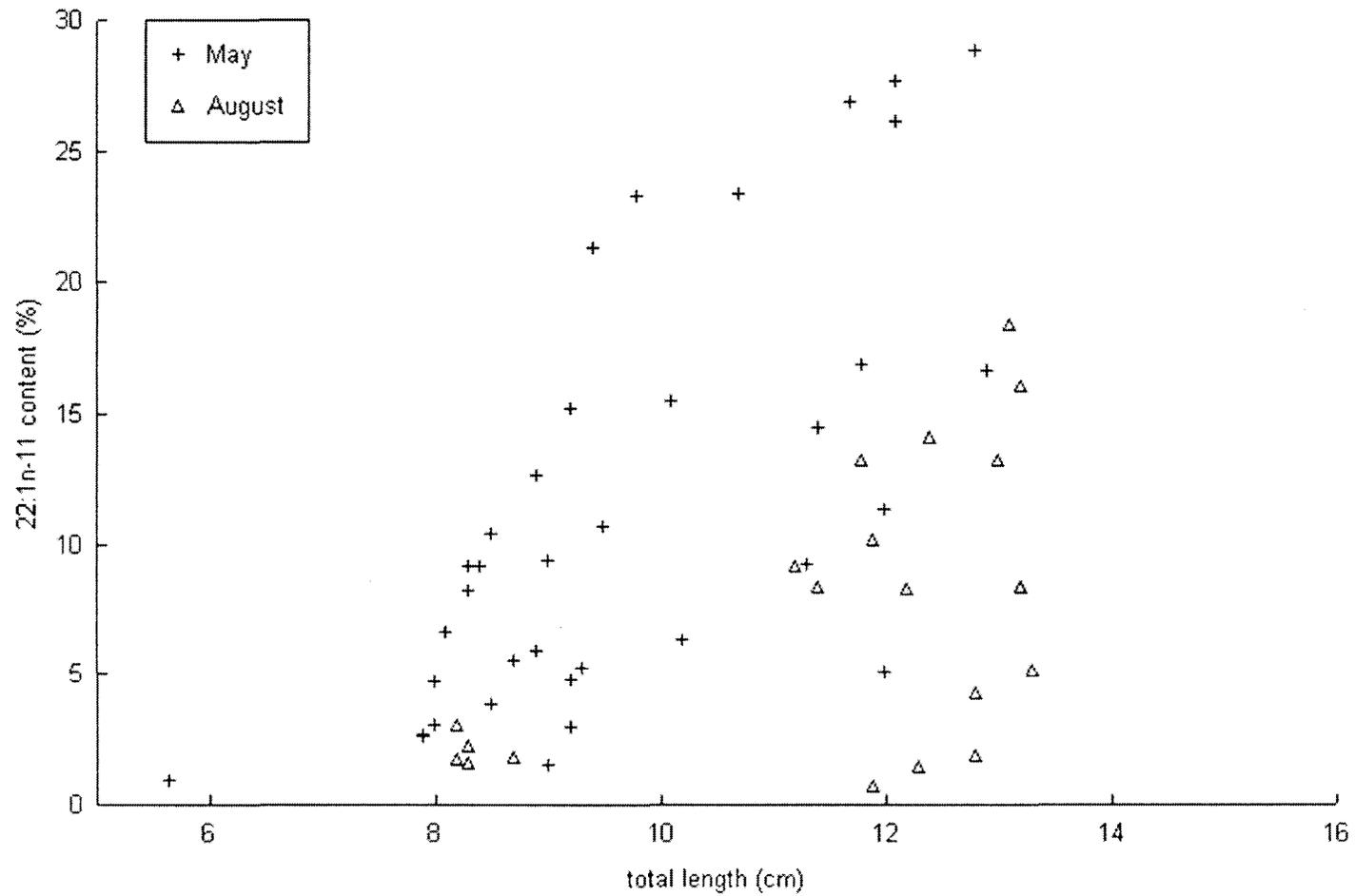


Figure 3.8 Content (% of the total quantified fatty acids by weight) of fatty acid 22:1n-11 plotted against total length of capelin sampled from embayments of the Kodiak Archipelago, Alaska, in May (2005, n = 20) and August (2004 and 2005 combined, n = 36).

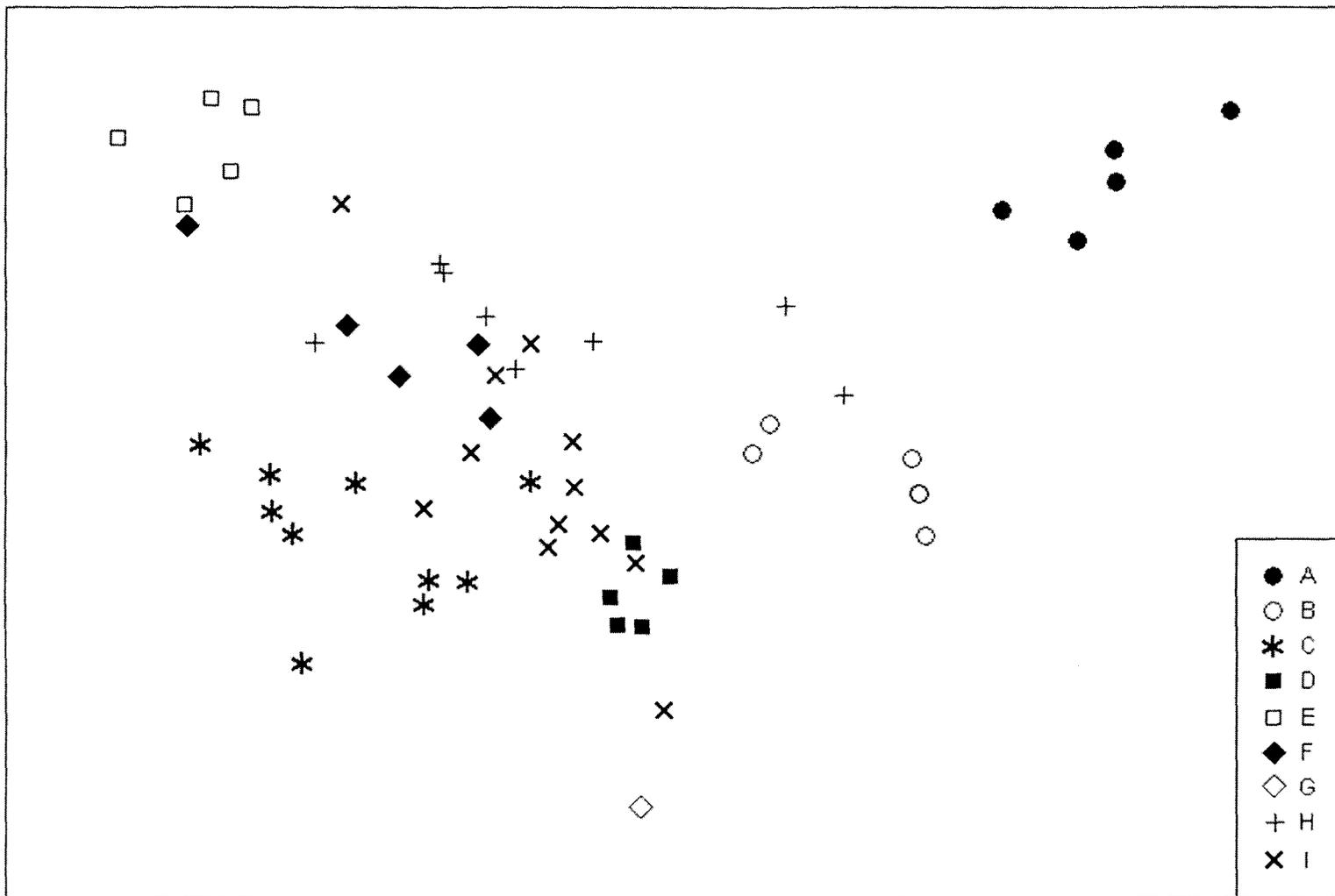


Figure 3.9 MDS ordination of capelin fatty acid composition (n = 56) sampled from embayments of the Kodiak Archipelago, Alaska. Sample group A to I described in Table 3.5; MDS two-dimensional stress = 0.081

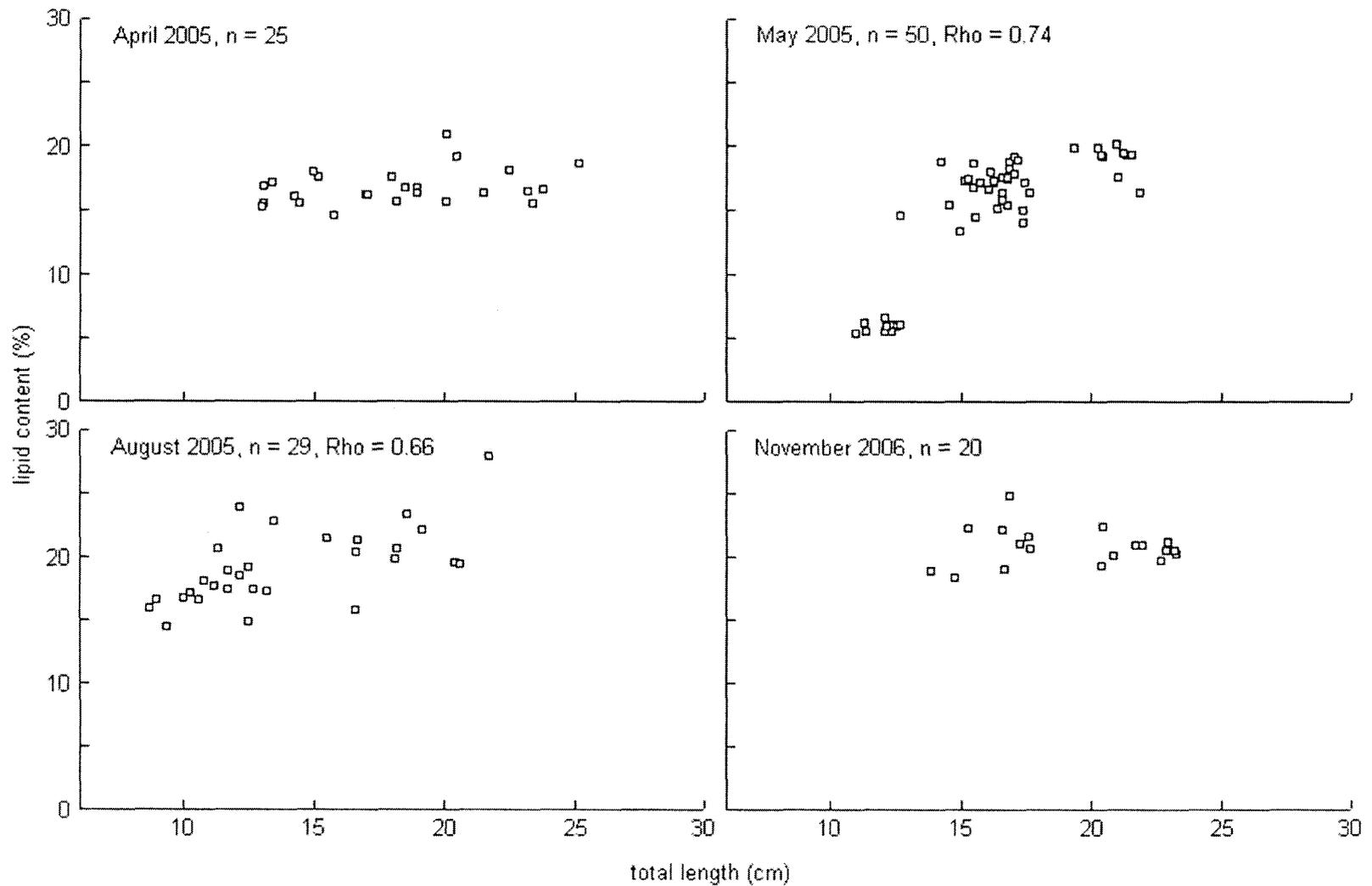


Figure 3.10 Scatterplots of lipid content vs. total length of eulachon sampled from embayments of the Kodiak Archipelago, Alaska. n: sample size; Spearman Rho values indicate significant correlations ($p < 0.01$) between lipid content and total length.

Chapter 4:

Measuring Mesoscale Horizontal Distribution Characteristics and Energy Density of Pelagic Forage Fishes in Coastal Waters of the Kodiak Archipelago, Alaska¹

ABSTRACT

The quality of prey fields available to piscivorous predators is largely defined by mesoscale (0.1's – 10's km) attributes of forage fish aggregations. To better understand forage fish availability to local apex predators, we measured mesoscale horizontal distribution characteristics and energy density of four pelagic forage fishes, Pacific herring (*Clupea pallasii*), eulachon (*Thaleichthys pacificus*), capelin (*Mallotus villosus*), and walleye pollock (*Theragra chalcogramma*), in coastal waters off the Kodiak Archipelago, Alaska, in May and August 2005. Distribution parameters, including area of occupation, aggregation size, and index of aggregation, varied considerably among fish species and month. Patchiness was consistently higher in narrower embayments than wider ones or open areas. Biomass of forage fish assemblages was found to be a reasonable proxy for energy content at the scales of 10's to 100's km². Dense aggregations formed seasonal energetic “hotspots” of prey fields for piscivorous predators, exemplified by herring schools on the west side of the Archipelago in May and capelin schools on the northeast side in August. The spatial patterns of seasonal “hotspots” may have profound implications for prey choice and feeding success of local apex predators, which could affect predator bioenergetics at the population level.

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INTRODUCTION

Attributes of mesoscale (0.1's – 10's km) forage fish aggregations are key aspects in defining the quality of prey fields for apex predators (Suryan et al. 2002, Bogetveit et al. 2008). It is at these scales that many interactions between pelagic prey and predators take place (Schneider 1989, Winter et al. 2009). Aggregation attributes, such as patchiness and energy density, affect predator feeding behavior and efficiency (Schneider & Piatt 1986, Womble et al. 2005, Womble & Sigler 2006). Therefore, information on mesoscale forage fish aggregations is valuable to understand both short-term and long-term fluctuations in apex predator populations.

Patchiness is an important feature of pelagic forage fish distributions due to schooling behaviors (Shaw 1961, Springer & Speckman 1997). Highly dense schools of forage fishes often develop during pre-spawning and spawning periods (Marston et al. 2002, Davoren et al. 2006), or over regions of relatively high zooplankton prey availability (Winter & Swartzman 2006, Hollowed et al. 2007). These aggregations form ideal prey fields and typically attract large numbers of piscivorous predators (Piatt 1990, Sigler et al. 2004, Bogetveit et al. 2008). Hence measuring the patchiness of forage fish distributions is essential to reveal the heterogeneity of prey fields available to apex predators.

The major parameters for describing the quality of prey fields include density (number per unit), biomass (mass per unit), and energy density (energy per unit) (Willson & Womble 2006, Winter et al. 2009). While density and biomass are relatively easy to estimate with standard survey data, energy density values are more widely applicable because they incorporate differences in weight and energy content among species (Ney 1993, Ball et al. 2007). However, energetic measurements are logistically difficult and therefore more expensive to carry out, which explains why prey availability is most often described using biomass instead of energy, despite the relatively large variability of energy content among and within species (Anthony et al. 2000, Vollenweider et al. 2006, Spitz et al. 2010).

In this study, we measured distribution parameters and energy density of mesoscale aggregations of forage fishes to describe pelagic prey fields for apex predators in coastal waters of the Kodiak Archipelago, Alaska. We hypothesized that 1) patchiness of local forage fishes is species specific and these patchy distributions form seasonal “hotspots” of prey fields for upper trophic level predators, and that 2) biomass of forage fish assemblages is an inadequate proxy for the amount of energy available to predators.

MATERIALS AND METHODS

Sampling

Vessel surveys were conducted to sample nearshore waters off the northern part of the Kodiak Archipelago in May (05/21 – 06/04) and August (08/06 – 08/21), 2005. Fish Resource Permits authorized by Alaska Department of Fish and Game were held for all sample collections and are documented in Appendix A. We selected five regions, three on the northeastern side of the Archipelago and two on the western side (Fig. 4.1). The five regions are hereafter referred to as Tonki (Tonki Bay), Shelf (the shelf area northeast of Tonki and Perenosa Bay), Perenosa (Perenosa Bay), Uganik North (the northern part of Uganik Bay), and Uganik South (the southern part of Uganik Bay). The division of Uganik Bay into two regions was based on differences in fish species composition (Loewen 2007) and the degree of transect coverage. Unlike in Tonki, Shelf, and Perenosa, where the degrees of transect coverage within regions were similar (Fig. 4.2A), the degree of transect coverage in Uganik Bay was much lower in the northern part than in the southern part as the bay narrows southward (Fig. 4.2B). These differences required the two regions in Uganik Bay to be processed separately in the subsequent geostatistical analysis (Rivoirard et al. 2008). The boundary of each region (Fig. 4.1) was based on the extent of transects (Fig. 4.2). Because transects in embayments rarely covered waters shallower than 20 m, the 20-m depth isobath (based on bathymetric data from Alaska Department of Natural Resources)

was selected as the boundaries for region Tonki, Perenosa, Uganik North, Uganik South, except for the mouths of respective embayments where no area is shallower than 20 m. Consequently, results presented herein may not apply to the shallow waters between region boundaries and the landmass in the embayments.

Acoustic-trawl surveys were conducted during daylight hours on the chartered stern trawler *F/V Alaskan*, equipped with a Simrad EK60 echo-sounder system. Active acoustic backscatter data were collected through a hull-mounted 38 kHz split-beam transducer (calibrated for gain parameters and beam pattern characteristics), while the vessel followed transects (Fig. 4.2) at a nominal speed of 14.8 km hr⁻¹ (8.0 knots). A midwater trawl net (DanTrawl Bering Billionaire) with a modified codend of 10 cm mesh and 2.5 cm mesh liner was opportunistically deployed along transects to corroborate species and length composition of aggregations identified by the acoustic backscatter. A total of 18 and 20 trawls were conducted in May and August, respectively; targeted depths ranged from 30 m to 200 m. Net catches in each trawl were sorted by species, counted, and systematically sub-sampled for measurements of total length (hereafter referred to as length) and weight. In the following analyses, we focused on four forage fish species that dominated our catches: Pacific herring (*Clupea pallasii*), eulachon (*Thaleichthys pacificus*), capelin (*Mallotus villosus*), and walleye pollock (*Theragra chalcogramma*). For each species, a length-frequency distribution was constructed for each trawl to generate length modes. The four species were systematically sub-sampled for energy content assessment; samples were frozen at -20°C upon capture and stored at -30°C in the lab after each survey until processing.

Acoustics analyses

Acoustic backscatter data were processed using Echoview 4.80 (Myriax Software) to estimate fish density (km⁻²) and biomass (kg km⁻²) on transects. A standard bottom detection algorithm in Echoview was chosen to delineate the sea bottom, which was then examined visually and manual corrections were applied when the algorithm was considered to select an unrealistic

bottom. Fish target strength (TS) values were calculated from the standard regression equation (Simmonds & MacLennan, 2005):

$$TS = 20 \log L + b,$$

where L values (cm) were the modes of length-frequency distributions; b = -65.1, -84.5, -69.3, and -67.2 for herring, eulachon, capelin, and pollock, respectively (Gauthier & Horne 2004). Euphausiids and larval fishes, occasionally caught in net catches, were assigned -70 as their collective TS. Volume backscattering strength was echo-integrated through Echoview algorithms over horizontal bins of 185.2 m (0.1 nmi) between 8.5 m below sea surface (the transducer was at ~ 4 m below surface) and 0.5 m above corrected delineation of the sea bottom. The latitude and longitude of the center point in each horizontal bin were used as the coordinate of that bin in the subsequent geostatistical analysis. Based on net catch percentages and target strength values, Echoview apportioned the integrated backscatter to each length mode for each of the four species. Then the apportioned backscatter was converted to fish density and biomass, the latter incorporating length-weight regressions established for each species and each month.

Biochemical analyses

Lipid content (%) and protein content (%) in whole-body wet mass were measured in order to compute energy content. Lipids were extracted from homogenates with the modified Folch method (Folch et al. 1957, Ways & Hanahan 1964) and afterwards lipid content was calculated gravimetrically. To determine protein content, nitrogen content was quantified with a LecoTM - FP2000 Analyzer, in which triplicates of ~ 0.5 g homogenate were conveyed through a combusting chamber at 1000 °C and resulting nitrogen was measured before its content was computed gravimetrically. Protein content (%) was calculated as the product of nitrogen content (%) times 6.25 (Dowgiallo 1975). Because the amounts of carbohydrates are basically negligible in fish (Brett 1995), energy content was computed by the following equation:

$$\text{Energy content (kJ g}^{-1}\text{)} = (\text{lipid content} \times 36.43 \text{ kJ g}^{-1} + \text{protein content} \times 20.10 \text{ kJ g}^{-1}) / 100,$$

where 36.43 and 20.10 are the respective energetic equivalents for lipids and proteins, adopted from Brett (1995).

Statistical analyses

Ordinary kriging, a geostatistical interpolation method, was used to reproduce the stochastic processes of fish distribution across each survey region and to estimate off-transect density and biomass from on-transect values. By comparing different kriging methods, Simard et al. (1993) showed that ordinary kriging performed best for assessing pelagic fishes in coastal areas. To simplify calculations, length modes within species that were clustered together were grouped into length classes, referred to as Small, Medium, Large, and Very Large (Table 4.1). For each length class, biomass values were kriged separately from density to account for heterogeneity of length-mode composition among different locations within a given region. An anisotropic spherical semivariogram model was constructed for each length class of each fish species in each region from the respective experimental semivariogram. The lag size of all models was set at 190 m, which was aimed to be slightly larger than the distance between the centers of two neighboring echo-integration bins of 185.2 m (Isaaks & Srivastava 1989). In ArcGIS 9.3 (ESRI Inc.), models were parameterized with the goal of minimizing errors (in terms of root-mean-squared error) between predicted and measured on-transect values based on leave-one-out cross-validation. The parameterized models and ordinary point kriging in ArcGIS 9.3 were applied to predict off-transect values, which in combination with on-transect values form prediction surfaces of density and biomass (species- and length class-specific) in each of the five regions. The prediction surfaces by default are of rectangular shape, which unrealistically span over surrounding landmass. To solve this problem, the prediction surfaces were extracted using the predefined region boundaries (Fig. 4.1). The extracted prediction surfaces were then gridded into area units of $185.2 \text{ m} \times 185.2 \text{ m}$ (0.01 nmi^2). Within each area unit, values of each length class were averaged and the length-class means were summed for each species.

Horizontal distribution characteristics of the four fish species in each region were described with the following parameters: 1) proportion of area units with positive fish density (> 0) as a measurement of geographic occupation, 2) median of positive area-unit fish density, and 3) index of aggregation (Bez 2000), which measures the degree of aggregation or patchiness:

$$\text{Index of aggregation} = \sum_i z_i^2 / [S \times (\sum_i z_i)^2],$$

where z_i is density in area unit i and S is the total area of a given region. A larger value of the index means that distribution is patchier or less even. Values of positive area-unit density were subjected to Mann-Whitney U or Kruskal Wallis tests for inter-region comparison.

For each forage fish length class, lipid (protein) density (kg km^{-2}) was calculated as the product of biomass and lipid (protein) content (%), and energy density (kJ km^{-2}) was computed as the product of biomass and energy content (kJ g^{-1}).

We evaluated whether biomass of a fish assemblage was a reasonable quantitative proxy for its energy density, in other words, how well variations in biomass among area units or regions quantitatively represented the variations in energy density. The evaluation was carried out at two spatial scales: within regions and among regions. Within regions, species-combined biomass and energy density values in each area unit were standardized following the equation:

$$\text{Standardized value} = \text{area-unit value} / \text{sum} \times 100\%,$$

where sum is the summation of all area-unit values in the region. The differences between standardized biomass (SB) and standardized energy density (SED) were then further standardized into proportional differential (PD), calculated with the equation:

$$\text{PD} = \text{abs} (\text{SB} - \text{SED}) / \text{SED} \times 100\%,$$

where abs denotes absolute value. The frequency distribution of PD values measures how well variations in biomass among area units quantitatively represented the variations in energy density; if most PD values are close to zero, biomass is a good quantitative proxy on this scale. Among regions, biomass and energy density were standardized in the same way as within a region, except

that values were the means of regions instead of area units and the summation across regions were weighted by the area (km²) of regions.

RESULTS

In May, Pacific herring were not captured in Tonki, Shelf, and Perenosá, the three regions on the northeastern side of the Archipelago; eulachon were not encountered in Tonki and Uganik South; capelin and walleye pollock were found in all five regions. When encountered, the proportions of area units with positive fish densities varied considerably among regions (Table 4.2: n'/n). For example, capelin were found in 83.7% of area units in Perenosá but only in 23.3% in Shelf, and pollock occupied 91.8% of area units in Uganik North but only 34.7% in Shelf. Aggregation densities, measured by positive area-unit fish density values, were significantly different among regions for all species ($p < 0.05$, Table 4.2). The densest aggregations of herring and pollock were found in Uganik South, while the densest aggregation of eulachon and capelin were encountered in Uganik North and Tonki, respectively. Index of aggregation was consistently higher in Tonki and Uganik South than other regions for herring, capelin, and pollock (Table 4.2), indicating that distributions of these species were relatively patchier in Tonki and Uganik South compared to other regions.

In August, herring were not captured in Tonki and Shelf; eulachon, capelin, and pollock were encountered in all five regions. Compared to May (Table 4.2: n'/n), the proportions of area units with positive fish densities generally increased (Table 4.3: n'/n). In particular, herring occupied at least 85.3% of area units in the regions where encountered, and capelin were found in at least 69.9% of area units in all regions. Aggregation densities in different regions were significantly different from each other for all four species ($p < 0.05$, Table 4.3), except for eulachon in Uganik North and Uganik South. Similar to May, index of aggregation values were relatively high in Tonki and Uganik South compared to other regions (Table 4.3).

Herring demonstrated a seasonal relationship between aggregation density and geographic expansion or distribution patchiness. In both Uganik North and Uganik South, aggregation densities were significantly higher in May than in August (Mann-Whitney U , $p < 0.01$), while herring in May occupied fewer area units and were patchier than in August (Tables 4.2 & 4.3). This seasonal relationship was inconsistent in other species. For example, capelin occupied fewer area units in all regions in May than in August, but aggregation densities were not always lower in May.

Whole-body energy content of Large (pre-defined length class, Table 4.1) eulachon averaged 9.0 and 10.3 kJ g⁻¹ in May and August, respectively, both the highest among length classes of the four species (Table 4.4). Medium pollock had the lowest mean energy content in May (3.5 kJ g⁻¹) and Small capelin had the lowest in August (3.2 kJ g⁻¹) among length classes of the four species (Table 4.4).

There was a seasonal shift in the location of area units with the highest energy density ($\geq 10\%$ of the maximum area-unit energy density), when area units from all regions were compared. In May, most of the area units with the highest energy densities were located in Uganik South (Fig. 4.3A, B); this was primarily due to dense aggregations of herring (Table 4.2). In August, the majority of the area units with the highest energy densities were found in Shelf (Fig. 4.3C, D), primarily as a result of high densities of capelin (Table 4.3).

A large seasonal change in species composition was the increase of capelin from May to August (Fig. 4.4 & 4.5). The contribution of capelin to the species-combined energy densities of all regions rose from 11.2% (mean weighted by region area) in May to 66.0% in August. In Shelf, capelin biomass increased by 12,500% from May to August; in comparison, pollock biomass only increased by 28.7%.

Within regions, the mean species-combined area-unit energy content ranged from 3.5 to 9.0 kJ g⁻¹ in May and from 3.2 to 9.6 kJ g⁻¹ in August; these ranges were comparable to the energy

content range among length classes of the four species (Table 4.4). In contrast, the mean species-combined energy content of the five regions only ranged from 3.6 to 4.6 kJ g⁻¹ in May and from 5.0 to 6.1 kJ g⁻¹ in August (Table 4.5).

Within regions, species-combined biomass was not a good proxy for their energy density. About half (50.1% in May and 47.9% in August) of the standardized values of area-unit biomass underestimated or overestimated standardized energy density by more than 15.0% (Fig. 4.6). Among regions, however, biomass was a fairly good quantitative measure of energy density. The proportional differential between standardized biomass and energy density was 15.6% (overestimation) in Perenosa in May, 11.5% (underestimation) in Shelf in August, and less than 9.57% for the rest.

DISCUSSION

Distribution characteristics

Horizontal distribution was patchier in Tonki and Uganik South than in other regions for all four forage fish species in both months. Despite a marked difference in species composition and a relatively large geographic distance (among the five regions) between Tonki and Uganik South, the two regions differ from others by a higher degree of land enclosure (Fig. 4.1). In comparison, Giannoulaki et al. (2006) concluded that the relationship between the degree of land enclosure and the spatial structure of pelagic fishes was not consistent and varied with fish species and season.

The relatively high values of the index of aggregation in Tonki and Uganik South were not generated by ordinary kriging; instead, they reflected the actual spatial structure of fish schools observed from acoustic backscatter. Because kriging is known to “smooth” prediction surfaces (Isaaks & Srivastava 1989, Rivoirard et al. 2008), there was the potential that higher degrees of transect coverage in Tonki and Uganik South interacted with the kriging process and led to less

“smoothed” prediction surfaces than other regions. To test whether relatively high patchiness in Tonki and Uganik South was created during kriging, we calculated the index of aggregation based only on acoustic estimates from transect lines (Table 4.6), assuming that fish density in the 185.2-m horizontal bin of echo integration represented a square area of 185.2 m by 185.2 m. Although the absolute values of the index were different from those after kriging due to differences in total abundance and the potential smoothing effect of kriging, the relatively high values in Tonki and Uganik South were similar to the post-kriging results.

The consistently high patchiness of fish distribution in local embayments requires special consideration during survey planning. To retain reasonable precision for estimating fish density, a relatively high degree of transect coverage should be applied in narrow embayments or arms of embayments. In this study, we happened to have higher degrees of transect coverage in Tonki and Uganik South, not because we expected that fish distribution would be more patchy in the two regions, but because we adopted zig-zag transect lines to minimize vessel turning points and maximize transecting time in semi-enclosed areas (Simmonds & MacLennan 2005). At least in these embayments, zig-zag transecting has an additional advantage over other transect designs.

The higher degree of patchiness in more enclosed areas may be attributed to a collective anti-predator strategy by the four species. There is little evidence suggesting that oceanographic features in narrow areas of local embayments are more heterogeneous than those in relatively open areas (Loewen 2007); hence, habitat preference does not seem to be the driving force. In addition, the sampling periods did not coincide with the peak in spawning of the four species (Dougherty et al. 2007, Brown 2002, Marston et al. 2002), thus the observed pattern cannot be explained by site fidelity to spawning grounds. The patchy distribution in narrow embayments is most likely due to the shared strategy by forage fishes to extend the time needed for predators to search prey in relatively enclosed areas (Iwasa et al. 1981), considering the high variety and abundance of potential local predators (Wynne 2005, Witteveen et al. 2007, Knoth & Foy 2008).

The most noticeable seasonal change was the increase of capelin biomass in the Shelf region, where capelin in August not only occupied more area units but also aggregated in denser schools than in May. Capelin spawn between mid-May and late July (Pahlke 1985, Doyle et al. 2002) and school sizes in August are typically smaller than during spawning periods (Brown 2002). In this study, capelin in August formed highly dense schools, although none of the examined specimens were at the stage of pre-spawning or spawning. The densest aggregations were mostly along the 100-m isobath in the northeast part of Shelf where energy densities were the highest across all regions (Fig. 4.3C). A temperature and salinity front was observed along this 100-m isobath during our survey (L. Guo & R. Foy, *unpubl. data*). Therefore, these dense capelin aggregations were probably attracted by favorable oceanographic conditions and high zooplankton prey availability associated with the observed front (Brodeur et al. 2002, Coyle & Pinchuk 2002).

Biomass as a proxy for energy density

We demonstrated that biomass can be used as a proxy for energy density at certain spatial scales. Comparisons between standardized biomass and energy density values showed that biomass was a reasonable quantitative indicator of energy density among regions (region areas ranging from 51 to 508 km²), but not among area units within regions (each area unit being 0.034 km²). The reason standardized biomass was close to standardized energy density at the larger spatial scale was that mean energy content among regions had a relatively narrow range. This narrow range was largely attributed to the consistent level of mean protein content at this scale. Although fish lipids are nearly twice as energy dense as proteins (Brett 1995), the total amount of energy stored in proteins was still higher (1.98 times in May and 1.39 times in August, weighted by region areas) than that in lipids. As a result, the less variable protein content buffered the fluctuation of lipid content among regions (Table 4.5). At the smaller scale, however, inter-species differences in patchiness led to random species assemblages in various area units, which dictated that the mean energy content of each area unit fluctuated in an unpredictable

manner. In conclusion, the relative quantity of species-combined biomass was a reasonable quantitative measure of the relative energy density at the scale of 10's to 100's km².

Potential errors

The potential errors associated with the methodologies adopted in this study should be taken into consideration when interpreting our results. Since the surveys were conducted during daytime, schools of herring, eulachon, and pollock were often located close to the bottom. Echo integration tends to underestimate fish density within a few meters from the bottom due to the “dead zone” effect (Simmonds & MacLennan, 2005). Also, the chosen target strength (TS) values did not incorporate the seasonal variation of fish body composition, which could affect TS by 1-3 dB (Horne 2003, Gauthier & Horne 2004). In addition, the ordinary kriging method used to interpolate off-transect fish density and biomass tends to “smooth” predictions by overestimating when the true values are relatively low and underestimating when the true values are relatively high (Rivoirard et al. 2008). While these error sources will affect the absolute magnitude of density, biomass, or energy density estimates, it is unlikely that they will affect the relative order of those estimates and therefore our conclusions.

Different length classes of each fish species were combined to describe horizontal distribution characteristics at the species level. Differences among length classes in area-unit occupation and index of patchiness were occasionally detected when multiple length classes were encountered in the same region; there was no consistent ontogenetic pattern among regions for any species (L. Guo & R. Foy, *unpubl. data*). In addition, an ontogenetic trend in depth distribution was noticed in pollock: schools of Small pollock in August were distinctly above the bottom while Medium, Large and Very Large pollock were close to the bottom (L. Guo & R. Foy, *unpubl. data*), which is in agreement with findings from other areas in the Gulf of Alaska (McKelvey 1996, Brodeur & Wilson 1996). As a result, our focus on horizontal distribution

characteristics at the species level may have obscured the variations among length classes and depths.

Implications for local apex predators

The dense aggregations of capelin in August offer an ideal feeding opportunity for predators, which was supported by sightings of tens of thousands of piscivorous feeding seabirds in the northeast part of Shelf during the survey. In addition, co-occurring eulachon and pollock in the Shelf region happened to be of the lowest density among the five regions and were generally found in deeper waters than capelin; herring were not encountered in Shelf in August. The relative isolation from other species and dense aggregations over a large area make capelin potentially the dominate prey for apex predators. We used data from McKenzie & Wynne (2008) to compute the mean prey-specific numerical percentage (%) of capelin in Steller sea lion (*Eumetopias jubatus*) scats collected from sites around the Kodiak Archipelago from 1999 to 2005. Prey-specific numerical percentage measures the numeral percentage in samples that contain a specific prey taxa; samples that do not contain the given prey taxa are excluded in the computation (Amundsen et al. 1996). The prey-specific numerical percentage of capelin was 91.9%, only slightly lower than Pacific sand lance (*Ammodytes hexapterus*) among important prey (Table 4.7); in contrast, both percentage frequency of occurrence and mean numerical percentage of capelin were much lower than those of sand lance (Table 4.7). The high prey-specific value means that when encountered by sea lions, capelin are the preferred prey and tend to be consumed exclusively during the time frame representative of scat results, typically two to three days (Tollit et al. 1997, 2007). In comparison, herring, eulachon, and pollock were typically ingested in mixed diets (Table 4.7). Therefore, the aggregative patterns of capelin may be an important factor in their relative importance in Steller sea lion diets.

Capelin are also an important prey resource for humpback whales (*Megaptera novaeangliae*), a local apex predator that prefer capelin over co-occurring pollock of similar sizes (Witteveen et

al. 2008). In 2005, the humpback population feeding on the east side of the Kodiak Archipelago was estimated to be 192, based on the 2002 estimate of 157 (Witteveen et al. 2007) and a 6.8% annual increase in the North Pacific over the last four decades (Calambokidis et al. 2008). The population in 2005 required 5.29×10^{10} kJ of energy from prey during a five-month feeding season (Witteveen et al. 2006), assuming total energy requirement is proportional to population level. If 24.3% of the total required energy is met by feeding on capelin (based on a simplified diet composition derived from stable isotopes of the same humpback population, B. Witteveen, University of Alaska Fairbanks, pers. comm.), and 6.1 kJ g^{-1} is the energy content of capelin (the species average in the Shelf region in August, weighted by biomass of length classes), the humpback population in 2005 would consume 2.10×10^6 kg of capelin over five months. This estimate accounts for 13.0% of the total capelin biomass in the Shelf region and exceeds the total capelin biomass of all other regions in August. Therefore, the removal by humpback whales may cause significant localized reduction of capelin population, which would potentially limit the availability of capelin to other sympatric predators.

Forage fish aggregation density and distribution patchiness may be important factors influencing the utilization of haulout sites by Steller sea lions. Previous studies have suggested that sea lion counts in haulouts are correlated to forage fish abundance and energy density in surrounding waters (Womble & Sigler 2006, Winter et al. 2009). At Cape Ugat, a haulout ~ 15 km away from Uganik Bay, aerial counts of Steller sea lions decreased from May to August in most of the observation years (Wynne 2005). Because herring were the most common prey in Steller sea lion scats deposited from the same haulout (McKenzie & Wynne 2008), we expected that energy density of herring would have been higher in May than in August. In contrast, we found that the mean area-unit energy densities of herring in August were actually 14 and 1.3 times higher than in May for Uganik North and Uganik South, respectively; species-combined energy densities were also noticeably higher in August than in May. However, herring in May

occupied fewer area units and aggregated in denser schools than in August for both Uganik North and Uganik South. In addition, relatively low aerial counts of sea lion in August at Cape Ugat were corresponded to seasonal peaks of sea lion counts at Chief Cove, ~ 20 km south of Cape Ugat, where sea lions have been observed to prey on salmon at setnet sites (Wynne 2005). Therefore, highly aggregated prey over a relatively small area may shorten the mean time predators spend in capturing each prey (Orians & Pearson 1979), and may outweigh the benefit of a higher total energy available over a broader area.

Summary

This study presents a comprehensive description of mesoscale distribution characteristics and energy density of pelagic forage fishes in coastal waters of the Kodiak Archipelago. Distribution was highly variable but consistently patchier in narrower embayments for all species. Despite the marked difference in species composition, the mean energy content of forage fish assemblages was similar among regions. Thus biomass of forage fish assemblages was found to be an adequate proxy for energy density at the scales of 10's to 100's km². Dense aggregations were encountered after spawning periods and formed seasonal prey "hotspots" for piscivorous predators. The spatial patterns of forage fish "hotspots" may have profound implications for feeding behaviors of local apex predators, which could affect predator bioenergetics at the population level.

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TABLES AND FIGURES

Table 4.1 Descriptions of length classes of four forage fish species from embayments of the Kodiak Archipelago, Alaska. na: not available; values: total length in cm

	length class	Small	Medium	Large	Very Large
Pacific	length range	9.0 -12.9	13.0 -18.9	19.0-32.3	na
herring	length mode range	10.0-11.4	15.0 -17.6	20.2-28.1	na
eulachon	length range	na	8.0-14.9	15.0-29.3	na
	length mode range	na	10.1 -13.5	15.3-19.4	na
capelin	length range	5.2 -6.2	7.0 -9.9	10.0-13.8	na
	length mode range	5.6 -5.7	7.6 -9.2	10.3-13.2	na
walleye	length range	5.8 -12.9	13.0 -29.9	30.0-43.9	44.0-71.0
pollock	length mode range	7.5-9.3	14.3 -28.8	31.2-43.2	44.5-67.0

Table 4.2 Horizontal distribution parameters of four forage fish species (post-kriging, length classes combined) in five regions around the Kodiak Archipelago, Alaska, in May 2005. n: total number of area units; n': number of area units with positive fish density; median: median of positive area-unit fish density (number km⁻²); IA: index of aggregation; different superscript letters indicate significant inter-region differences within species (Mann-Whitney *U* or Kruskal Wallis, *p* < 0.05) and letter A indicate the highest values

		Tonki	Shelf	Perenosa	Uganik North	Uganik South
Pacific herring	n	1555	14825	2862	4523	1506
	n'	0	0	0	1205	668
	n'/n (%)	0	0	0	26.6	44.4
	median (×10 ³ km ⁻²)	na	na	na	1.60 ^B	35.7 ^A
	IA (×10 ⁻⁵ km ⁻²)	na	na	na	0.91	13.8
eulachon	n'	0	5032	1574	3939	0
	n'/n (%)	0	33.9	55.0	87.1	0
	median (×10 ³ km ⁻²)	na	15.5 ^B	0.15 ^C	21.3 ^A	na
	IA (×10 ⁻⁵ km ⁻²)	na	0.09	1.29	0.49	na
capelin	n'	363	8117	2395	1208	464
	n'/n (%)	23.3	54.8	83.7	26.7	30.8
	median (×10 ³ km ⁻²)	58.7 ^A	15.7 ^C	1.73 ^E	7.01 ^D	54.5 ^B
	IA (×10 ⁻⁵ km ⁻²)	42.0	0.27	0.81	6.04	11.3
walleye pollock	n'	1020	5141	1806	4150	1282
	n'/n (%)	65.6	34.7	63.1	91.8	85.1
	median (×10 ³ km ⁻²)	1.43 ^E	2.24 ^D	3.07 ^C	4.69 ^B	6.98 ^A
	IA (×10 ⁻⁵ km ⁻²)	3.89	0.09	1.15	0.70	3.78

Table 4.3 Horizontal distribution parameters of four forage fish species (post-kriging, length classes combined) in five regions around the Kodiak Archipelago, Alaska, in August 2005. n: total number of area units; n': number of area units with positive fish density; median: median of positive area-unit fish density (number km⁻²); IA: index of aggregation; superscript letters indicate significant inter-region differences within species (Kruskal Wallis, p < 0.05) and letter A indicate the highest values

		Tonki	Shelf	Perenosa	Uganik North	Uganik South
Pacific herring	n	1482	13446	2966	4506	1503
	n'	0	0	2529	3889	1473
	n'/n (%)	0	0	85.3	86.3	98.0
	median (×10 ³ km ⁻²)	na	na	16.9 ^A	0.25 ^C	5.91 ^B
	IA (×10 ⁻⁵ km ⁻²)	na	na	1.43	0.30	5.61
eulachon	n'	1101	3968	1470	3520	838
	n'/n (%)	74.3	29.5	49.6	78.1	55.8
	median (×10 ² km ⁻²)	18.2 ^C	0.22 ^D	28.9 ^B	825 ^A	500 ^A
	IA (×10 ⁻⁵ km ⁻²)	6.02	0.43	1.08	0.33	6.69
capelin	n'	1353	11450	2962	4495	1050
	n'/n (%)	91.3	85.2	99.9	99.8	69.9
	median (×10 ⁴ km ⁻²)	34.7 ^D	581 ^A	264 ^B	116 ^C	0.78 ^E
	IA (×10 ⁻⁵ km ⁻²)	4.81	0.07	0.80	0.44	4.23
walleye pollock	n'	1343	5679	2540	4312	1240
	n'/n (%)	90.6	42.2	85.6	95.7	82.5
	median (×10 ⁴ km ⁻²)	8.98 ^C	0.21 ^E	4.97 ^D	27.8 ^A	46.4 ^B
	IA (×10 ⁻⁵ km ⁻²)	4.74	0.30	0.91	0.54	4.23

Table 4.4 Lipid, protein, and energy content in whole-body wet mass of four forage fish species from embayments of the Kodiak Archipelago, Alaska, in May and August 2005. Numbers in parentheses: sample size for protein content analysis when different from that of lipid content analysis; na: not available; *: one or more samples consist of five or ten individual fish (as opposed to one); values of lipid and protein content: means \pm SD (when SD was available); values of energy content: calculated from means of lipid and protein content

	length class	-----May-----			-----August-----				
		sample size	lipid content (%)	protein content (%)	energy content (kJ g ⁻¹)	sample size	lipid content (%)	protein content (%)	energy content (kJ g ⁻¹)
Pacific herring	Small	25 (9)	5.2 \pm 2.2	17.7 \pm 0.5	5.5	0	na	na	na
	Medium	0	na	na	na	32	6.7 \pm 3.2	17.0 \pm 1.2	5.8
	Large	27 (11)	03.7 \pm 1.8	15.3 \pm 1.0	4.4	66	10.6 \pm 6.7	17.0 \pm 1.0	7.2
eulachon	Medium	13 (3)	08.2 \pm 4.7	12.8 \pm 0.1	5.7	18	18.0 \pm 2.5	13.2 \pm 0.7	9.2
	Large	37 (27)	17.4 \pm 1.7	13.0 \pm 0.3	9.0	11	21.0 \pm 3.0	13.2 \pm 0.4	10.3
capelin	Small	0	na	na	na	1*	1.1	14.0	3.2
	Medium	5 (1*)	15.8 \pm 1.5	15.0	8.8	44* (12*)	6.3 \pm 2.0	17.0 \pm 1.5	5.7
	Large	40 (20)	07.0 \pm 2.3	15.4 \pm 0.4	5.6		10.9 \pm 4.8	15.4 \pm 0.9	7.1
walleye pollock	Small	0	na	na	na	70* (61*)	4.5 \pm 1.5	17.1 \pm 1.8	5.1
	Medium	31	01.5 \pm 0.4	14.8 \pm 1.1	3.5	34	5.2 \pm 1.7	16.4 \pm 1.3	5.2
	Large & Very Large	21	02.2 \pm 1.0	14.1 \pm 2.0	3.6	71	4.0 \pm 2.0	15.4 \pm 1.2	4.5

Table 4.5 Species-combined (Pacific herring, eulachon, capelin, and walleye pollock) areal mean biomass (kg km⁻²), lipid density (kg km⁻²), protein density (kg km⁻²), energy density (kJ km⁻²), lipid content (%), protein content (%), and energy content (kJ g⁻¹) in five regions around the Kodiak Archipelago, Alaska, in May and August 2005.

	Tonki	Shelf	Perenosa	Uganik North	Uganik South	
May	region area (km ²)	53.34	508.48	98.16	155.13	51.65
	biomass	1.81×10 ³	2.18×10 ³	3.10×10 ³	4.08×10 ³	1.58×10 ⁴
	lipid density	6.27×10 ¹	1.03×10 ²	6.82×10 ¹	1.86×10 ²	4.60×10 ²
	protein density	2.59×10 ²	3.07×10 ²	4.36×10 ²	5.70×10 ²	2.31×10 ³
	energy density	7.48×10 ⁶	9.94×10 ⁶	1.12×10 ⁷	1.82×10 ⁷	6.31×10 ⁷
	lipid content	3.5	4.7	2.2	4.6	2.9
	protein content	14.3	14.1	14.1	14.0	14.6
	energy content	4.1	4.6	3.6	4.5	4.0
August	region area (km ²)	50.83	461.18	101.73	154.55	51.55
	biomass	1.16×10 ⁴	3.69×10 ⁴	2.14×10 ⁴	2.76×10 ⁴	2.21×10 ⁴
	lipid density	6.07×10 ²	2.79×10 ³	1.24×10 ³	1.39×10 ³	1.37×10 ³
	protein density	1.80×10 ³	6.06×10 ³	3.49×10 ³	4.43×10 ³	3.51×10 ³
	energy density	5.84×10 ⁷	2.24×10 ⁸	1.15×10 ⁸	1.40×10 ⁸	1.20×10 ⁸
	lipid content	5.2	7.6	5.8	5.0	6.2
	protein content	15.6	16.4	16.3	16.1	15.9
	energy content	5.0	6.1	5.4	5.1	5.4

Table 4.6 Index of aggregation ($\times 10^{-3} \text{ km}^{-2}$) of four forage fish species (pre-kriging, length classes combined) in five regions around the Kodiak Archipelago, Alaska, in May and August 2005, based on acoustic estimates from transect lines.

		Tonki	Shelf	Perenosa	Uganik North	Uganik South
May	Pacific herring	na	na	na	1.64	11.99
	eulachon	na	0.41	2.91	1.19	na
	capelin	87.30	4.43	3.09	14.16	21.08
	walleye pollock	4.37	0.41	2.58	1.65	4.16
August	Pacific herring	na	na	3.90	0.59	6.40
	eulachon	8.08	3.16	2.62	0.62	6.15
	Capelin	5.38	0.48	2.56	2.19	5.02
	walleye pollock	5.46	1.79	2.24	1.06	5.01

Table 4.7. Overall percentage frequency of occurrence (FO), mean numerical percentage (No), and mean prey-specific numerical percentage (SNo) of Pacific herring, eulachon, capelin, walleye pollock, Pacific sand lance (*Ammodytes hexapterus*), Pacific salmon (*Oncorhynchus* spp.), and Pacific sandfish (*Trichodon trichodon*) in Steller sea lion scats collected from sites in the Kodiak Archipelago (1999 to 2005), excerpted from McKenzie & Wynne (2008), with SNo values calculated as $No/FO \times 100\%$.

	FO (%)	No (%)	SNo (%)
Pacific herring	23.0	6.3	27.4
eulachon	1.1	0.2	18.2
capelin	8.6	7.9	91.9
walleye pollock	36.8	10.9	29.6
Pacific sand lance	41.7	38.6	92.6
Pacific salmon	26.3	4.3	16.3
Pacific sandfish	10.5	2.8	26.7

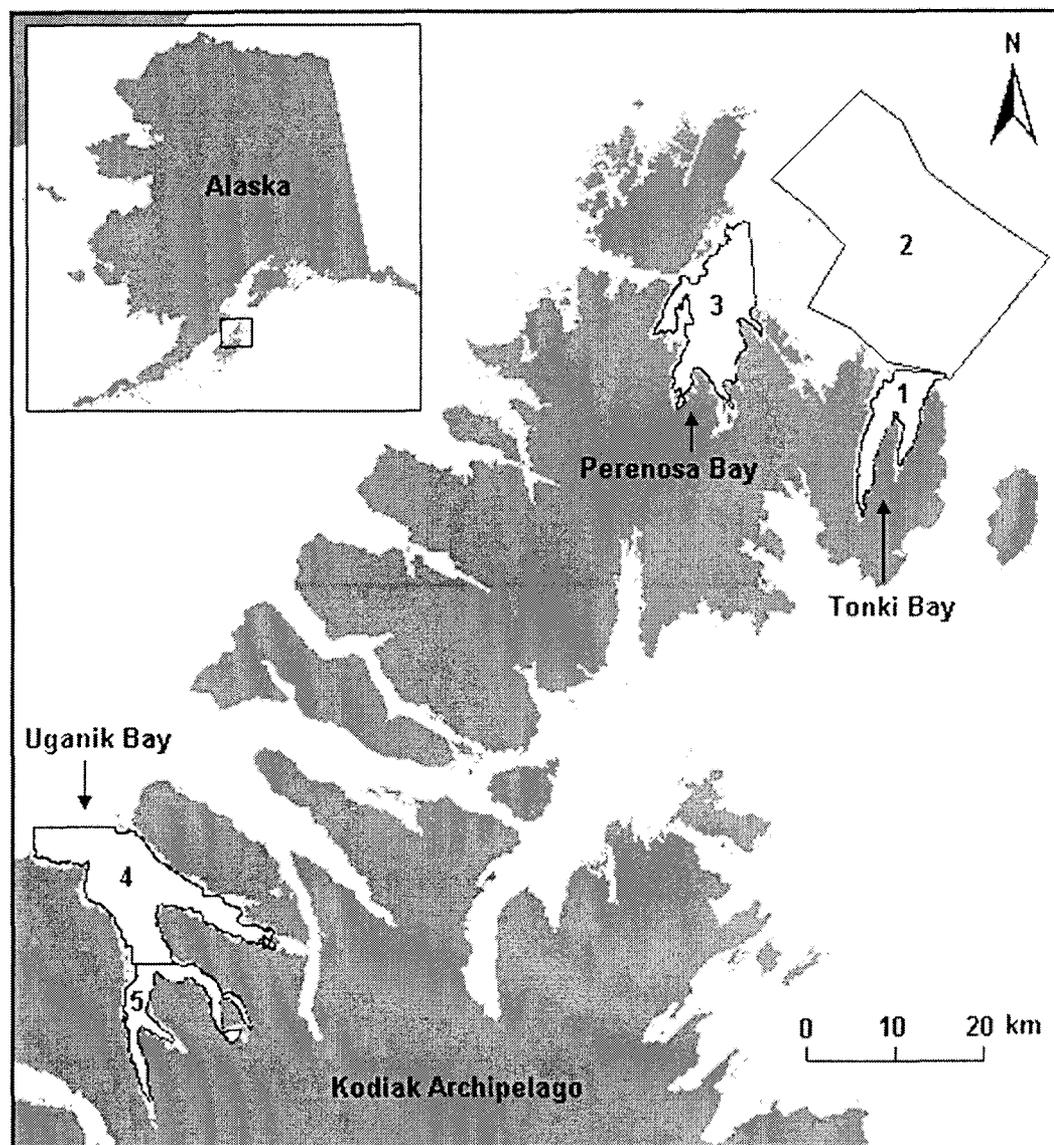


Figure 4.1 The five survey regions in waters off the northern part of the Kodiak Archipelago, Alaska. 1: Tonki; 2: Shelf; 3: Perenosa; 4: Uganik North; 5: Uganik South

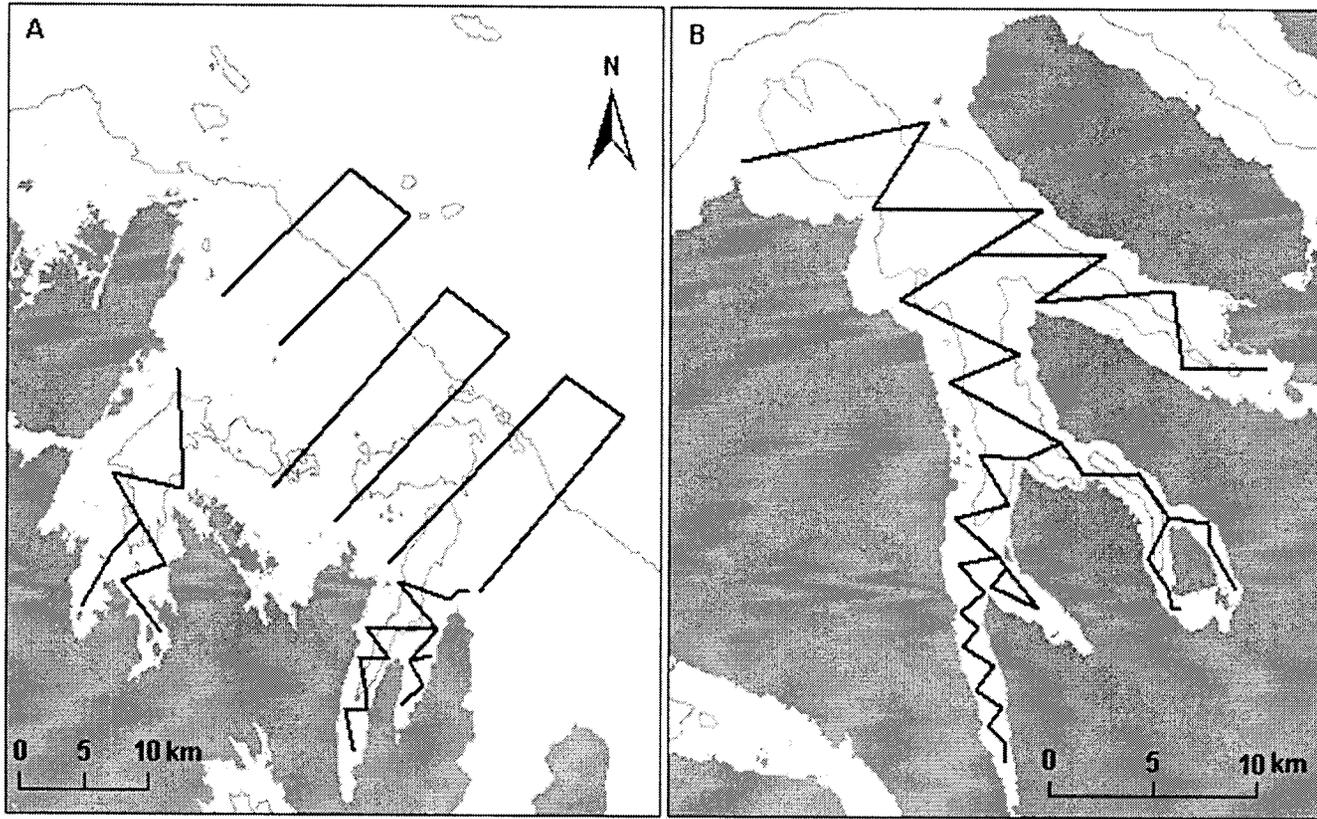


Figure 4.2 Acoustic transects (black line) in survey regions (A) on the northeastern side of the Kodiak Archipelago and (B) in Uganik Bay, with the 100-m depth isobath (gray line).

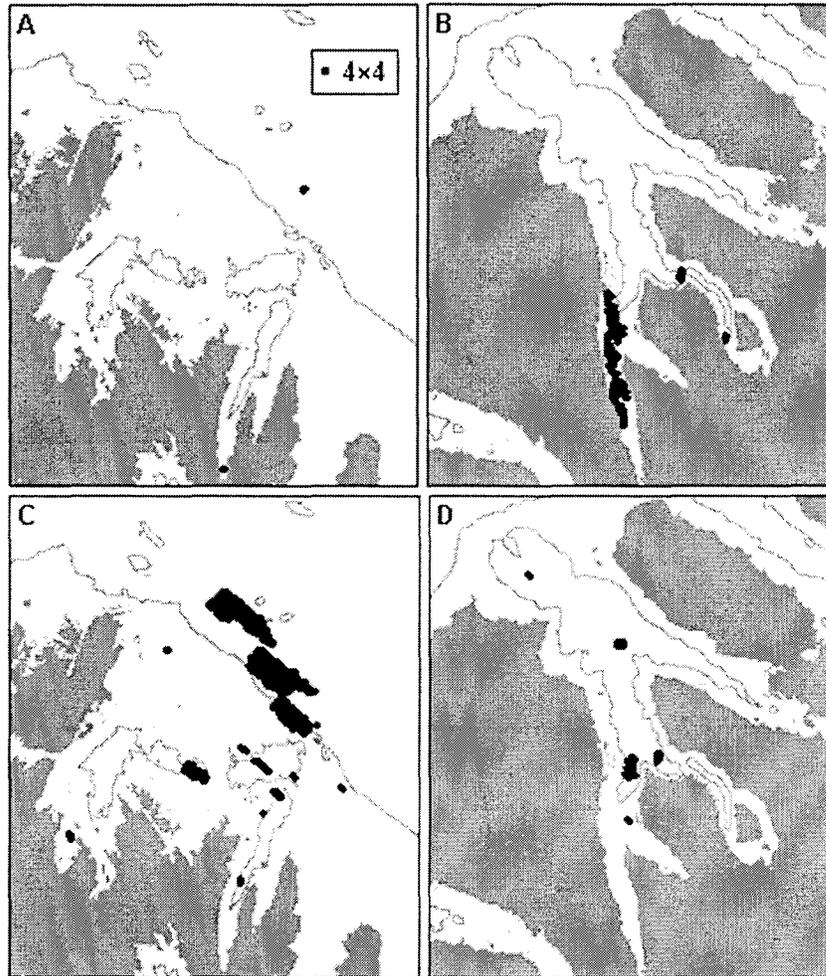


Figure 4.3 Area units (black dot) where species-combined energy density was $\geq 10\%$ of the maximum values in (A & B) May and (C & D) August, when area units from all regions were compared within each month. The size of each black dot was chosen so that each dot is large enough to be legible but not so large that dots cover surrounding landmass; the size of each dot does not represent the actual scale of one area unit (185 m \times 185 m); the size of the black square in the inserted panel within panel A represents 16 area units, arranged as 4 \times 4; gray line is the 100-m depth isobath

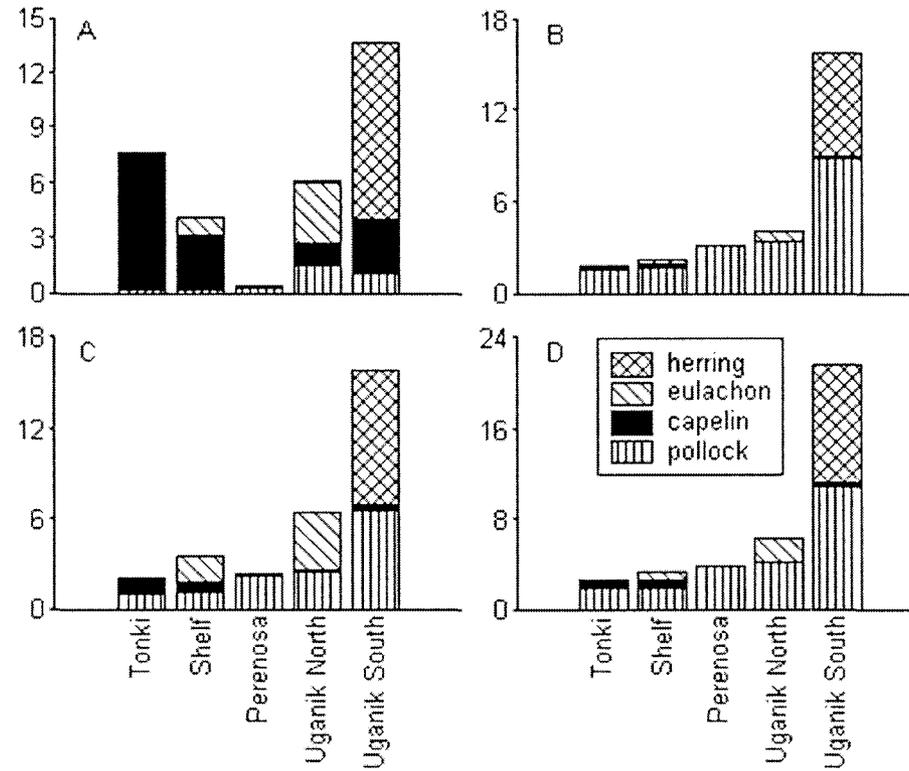


Figure 4.4 Areal mean (A) fish density ($\times 10^4 \text{ km}^{-2}$), (B) biomass ($\times 10^3 \text{ kg km}^{-2}$), (C) lipid density ($\times 10^2 \text{ kg km}^{-2}$), and (D) energy density ($\times 10^7 \text{ kJ km}^{-2}$) of the four fish species in the five regions in May 2005. Area units with zero values were included in calculation

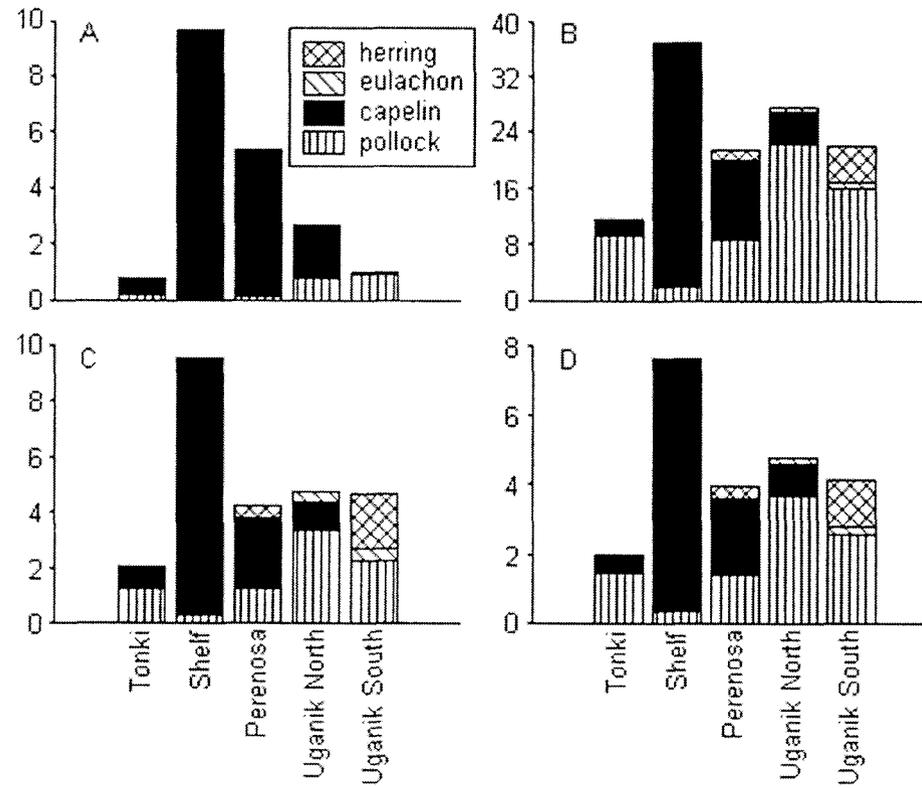


Figure 4.5 Areal mean (A) fish density ($\times 10^6 \text{ km}^{-2}$), (B) biomass ($\times 10^3 \text{ kg km}^{-2}$), (C) lipid density ($\times 10^3 \text{ kg km}^{-2}$), and (D) energy density ($\times 10^8 \text{ kJ km}^{-2}$) of the four fish species in the five regions in August 2005. Area units with zero values were included in calculation

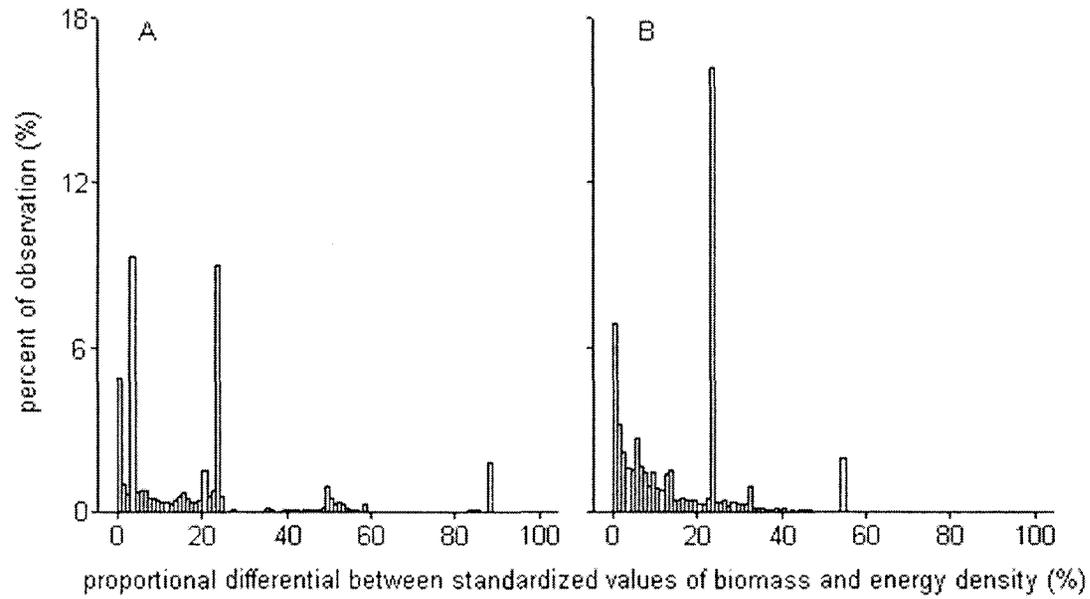


Figure 4.6 Frequency distributions (one percent interval) of proportional differential (PD) between standardized values of species-combined (Pacific herring, eulachon, capelin, and walleye pollock) biomass (SB) and energy density (SED) in waters off the northern part of the Kodiak Archipelago, Alaska, in (A) May and (B) August 2005. $PD = \text{abs}(SB - SED) / SED \times 100\%$, where abs denotes absolute value.

Chapter 5:

General Conclusion

This study examined multiple aspects of forage fish availability in the coastal waters of the Kodiak Archipelago, Alaska, as a key step to refine our knowledge on local trophic interactions and ecosystem functioning. I provided an improved estimation of diet composition, systematically described intra-species variations in lipid content and fatty acid composition, and measured mesoscale distribution characteristics and energy density of forage fish assemblages. The objectives were achieved through a multidisciplinary approach, involving biochemical, stomach content, acoustics, and geostatistical analyses. Major findings of this dissertation are summarized as follows.

- Comparisons between copepod-originated fatty acids and stomach contents in four forage fish species indicated the underestimation of dietary copepods by stomach content analysis.
- Lipid content of forage fishes varied significantly by month and fish length; inter-month variations did not strictly mirror the annual cycle of zooplankton production; ontogenetic patterns were specific to fish species and varied by month.
- Fatty acid composition of forage fishes varied significantly by month, fish length, and embayment; contents (weight percentages of total quantified fatty acids) of certain fatty acids were significantly correlated with lipid content.
- Mesoscale horizontal distribution parameters, including area of occupation, aggregation size, and index of aggregation, varied considerably among fish species and month.
- Patchiness of forage fish distribution was consistently higher in narrower embayments than wider ones or open areas.

- Dense post-spawning aggregations formed energetic “hotspots” for piscivorous predators, exemplified by herring schools on the west side of the Archipelago in May and capelin schools on the northeast side in August.
- Biomass of forage fish assemblages was found to be a reasonable proxy for energy content at the scales of 10’s to 100’s km², but not at smaller scales.

Large variations in measured parameters were demonstrated among study regions.

Significant differences in forage fish fatty acid composition were found between embayments that are only 10’s km apart, which indicates substantial localized differences in diet; abundance, biomass, energy density, and index of patchiness were highly variable among study regions. Spatial scales of sampling regimes influence our understanding of ecosystem functioning (Vlietstra 2005, Fauchald 2009). The high spatial variability in physical and biological parameters in waters around the Kodiak Archipelago presented in this and previous studies (Mueter & Norcross 2000, Loewen 2007, McKenzie & Wynne 2008) emphasizes the importance of mesoscale (0.1’s – 10’s km) assessment of forage fish availability.

My results demonstrated large intra-species variations in lipid content, fatty acid composition, and energy content. These findings and similar conclusions from other regions (Ball et al. 2007, Litz et al. 2010) affirm the need to incorporate intra-species variability in trophodynamic studies. Currently, average values at a species level are most widely used. For example, fatty acid models designed to delineate forage fish-predator relationships operate at the species level and frequently combine samples from different locations or months, which leads to model outputs that obscure spatial and temporal patterns (Iverson et al. 2004, Williams & Buck 2010). Furthermore, significant differences in lipid or energy content derived from inter-species comparison are often used to divide forage fishes into high- and low-quality prey, which grossly simplifies the natural variability and therefore is potentially misleading. For example, capelin (*Mallotus villosus*) are commonly referred to as “lipid-rich” or high-energy species (Abookire & Piatt 2005, Litzow et al. 2006); in this study, capelin of 5.2 – 6.2 cm total length in August had the lowest lipid and energy

content among all forage fish species studied, including walleye pollock (*Theragra chalcogramma*) that are typically considered a “lipid-poor” or low-energy species (Abookire & Piatt 2005, Litzow et al. 2006). For these reasons, intra-species variations in forage fish biochemical parameters need to be carefully considered in order to obtain a more realistic assessment of trophodynamics.

Spatial patterns of post-spawning forage fish aggregations may be a critical aspect of forage fish availability. The relationship between pre-spawning or spawning aggregations of forage fishes and their predators have been extensively studied (Sigler et al. 2004, Bogetveit et al. 2008); the locations of these aggregations are typically consistent interannually due to fidelity to spawning sites (Willson & Womble 2006, Womble & Sigler 2006). In contrast, the relationship between post-spawning aggregations and predators are more difficult to examine, partly because the locations of these aggregations are relatively unpredictable and more associated with oceanographic conditions (Hollowed et al. 2007). The abrupt climatic changes in the North Pacific Ocean over the last several decades (Mantua et al. 1997, Hare & Mantua 2000) may dramatically alter the spatial patterns of post-spawning aggregations of forage fishes (Anderson & Piatt 1999). The change in aggregation locations can have diverse effects on different types of predators. For example, central-place foragers, such as seabirds and pinnipeds that return from feeding forays to shore nests or haulouts, may switch to more dispersed prey when dense forage fish aggregations move out of their foraging distance, which will increase foraging costs. In comparison, predators that feed over relatively larger distances, such as cetaceans, may be able to follow and exploit these aggregations at different locations. This behavioral difference may partly explain the contrasting population trends between different types of apex predators, exemplified by the western stock of Steller sea lions (*Eumetopias jubatus*) and humpback whales (*Megaptera novaeangliae*): the former declined by 80% between the 1970s and 1990s (Trites & Larkin 1996, Loughlin 1998), while the latter increased by 6.8% annually over the last four decades (Calambokidis et al. 2008).

This dissertation provides the most comprehensive description of forage fish availability in coastal waters of the Kodiak Archipelago, Alaska. As one part of the larger Gulf Apex Predator-Prey Program, this project offers a key piece that will be integrated with results from other trophic levels, especially apex predators, to better delineate local trophic interactions. The final products will provide us with a more holistic view of the local ecosystems and with valuable references for fisheries management in the North Pacific Ocean.

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Appendices

Appendix A Fishing Permits



Montrose

**STATE OF ALASKA
DEPARTMENT OF FISH AND GAME**

P.O. Box 115526
JUNEAU, ALASKA 99811-5526

Permit No. CF-07-024

Expires 12/31/2007

**FISH RESOURCE PERMIT
(For Scientific/Educational Purposes)**

This permit authorizes Robert Foy (*whose signature is required on page 2 for permit validation*)
person

of UAF Fishery Industrial Technology Center at 118 Trident Way, Kodiak, AK 99615
agency or organization address

to conduct the following activities from February 15, 2007 to December 31, 2007 in accordance with AS 16.05.330
and AS 16.05.340(b)

Purpose: To examine the material and energy transfer process between the zooplankton community and forage fish in embayments around Kodiak Archipelago.

Location: All nearshore areas on the west side of Kodiak from Uganik Bay north to Shuyak, Afognak Bays, Tenik Bay, and Perenosa Bay.

Species Collected: 100,000 Walleye Pollock, 1,000 arrowtooth flounder, 50,000 eulachon, 1,000 Pacific cod, 50,000 capelin, 50,000 Pacific sand lance, 50,000 Pacific herring, 20,000 various additional groundfish and pelagic fish. Adult and juvenile fish will be identified, measured and released. 100 from each species will be sacrificed to be used for energetic/diet analysis. (see Stipulations section).

Method of Capture: JanTrawl midwater trawl with modified research codend liner of 1 inch mesh. (see Stipulations section)

REPORT DUE January 31, 2008. The report shall include species, numbers, dates, and locations of collection and disposition, and if applicable, sex, age, and breeding condition, and lengths and weights of fish. The report shall also include other information as may be required under the stipulations section.

GENERAL CONDITIONS, EXCEPTIONS AND RESTRICTIONS

1. This permit must be carried by person(s) specified during approved activities who shall show it on request to persons authorized to enforce Alaska's fish and game laws. This permit is nontransferable and will be revoked or renewal denied by the Commissioner of Fish and Game if the permittee violates any of its conditions, exceptions or restrictions. No redelegation of authority may be allowed under this permit unless specifically noted.
2. No specimens taken under authority hereof may be sold or bartered. All specimens must be deposited in a public museum or a public scientific or educational institution unless otherwise stated herein. Subpermittees shall not retain possession of live animals or other specimens.
3. The permittee shall keep records of all activities conducted under authority of this permit available for inspection at all reasonable hours upon request of any authorized state enforcement officer.
4. Permits will not be renewed until detailed reports, as specified above, have been received by the department.
5. UNLESS SPECIFICALLY STATED HEREFIN, THIS PERMIT DOES NOT AUTHORIZE the exportation of specimens or the taking of specimens in areas otherwise closed to hunting and fishing; without appropriate licenses required by state regulations; during closed seasons; or in any manner, by any means, at any time not permitted by those regulations.

[Signature]
Division of Commercial Fisheries

[Signature]
Deputy Director
Division of Commercial Fisheries
Alaska Department of Fish and Game

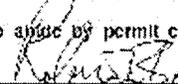
CF-07-024 continued (page 2 of 2)

Authorized Personnel: The following personnel may participate in collecting activities under terms of this permit:

Robert J. Foy, Lei Guo, Iluni Schimelko, Mike Trussel, Shannon Hanna.

Contingencies:

- 1) **Steve Schrof** (Division of Commercial Fisheries, Kodiak, (907) 486-1852) or **Wayne Donaldson** (Division of Commercial Fisheries, Kodiak (907) 486-1842) **must be contacted prior to you engaging in collecting activities.** They have the authority to restrict access to any area for conservation purposes or user conflicts. Division of Commercial Fisheries Area Management Biologists have the authority to specify methods for collecting, as well as limiting the collections of any species, and the number of specimens collected by time and area. **Jeff Wadle** (Division of Commercial Fisheries, Kodiak Area Finfish Biologist (907) 486-1807) **must be contacted prior to the collection of herring.**
- 2) Permits will indicate the number of specimens that may be taken by species and life stage. Sampling or collecting activities must stop when the maximum allowable number of specimens is obtained. All life fish, shellfish, and aquatic plants collected in excess of the number specified on the permit must be released immediately and unharmed at the capture location.
- 3) Fish not kept for energetic/diet analysis should be released unharmed back into the water, if possible. Samples saved for identification or diet analysis will be either disposed of or preserved for future reference at Kodiak lab facilities.
- 4) Fishing must cease immediately on any tow that catches more than 50 salmon. Permittee is expected to relocate before another tow is made. In addition, permittee is expected to relocate fishing activities if more than 1,000 juvenile salmon are present in any tow.
- 5) For all tows inside Kodiak and Afognak Bay, a maximum of 150 adult salmon and ~5 tons of herring may be captured (kept or released) in each bay. Area biologists request that the permittee seriously watch tows inside these bays and limit the time of tows, or if necessary, leave these bays to avoid excessive catches of salmon and herring.
- 6) Summarize catch data following each survey, and separated by gear or trawl type. List species (common name and scientific name) and numbers caught per gear type and disposition ('released alive', 'released dead' or 'taken back to lab') for all specimens. Please include a geographic descriptor in addition to
- 7) **Halibut may NOT be collected or retained under the authority of this permit. Please contact the International Pacific Halibut Commission at (206) 634-1838, P.O. Box 90009, Seattle, WA 98145-2009 to obtain permission for halibut collection.**
- 8) No person may transport, possess, export from the state, or release into the waters of the state, any live fish unless the person holds a valid fish transport permit (FTP), and the person is in compliance with all conditions of the permit and the provisions of 5 AAC 41.005 - 41.060. A fish transport permit may be issued by the Commissioner. A fish transport permit must be obtained prior to any exportation of non-preserved specimens. Please contact Sara Larsen at (907) 465-4724 for more information.
- 9) *A copy of this permit, including any amendments, must be made available at all field collection sites and project sites for inspection upon request by a representative of the department or a law enforcement officer.*
- 11) Issuance of this permit does not absolve the permittee from compliance in full with any and all other applicable federal, state, or local laws, regulations, or ordinances.
- 12) **A report of collecting activities, referencing this fish resource permit, must be submitted to the Alaska Department of Fish and Game, Division of Commercial Fish, PO Box 115526, Juneau, AK 99811-5526, attention Sara Larsen (465-4724; sara_larsen@fishgame.state.ak.us), within 30 days after the expiration of this permit.** For each tow, this report should summarize the date, time, and location of tow (name of general location and latitude/longitude of the beginning of tow), the duration of tow and towing speed, the estimated total catch by species (in approximate numbers of fish or approximate numbers of pounds), the number sampled or retained by species, and the fate of the remaining fish. Anecdotal information on the size and condition of all fish captured is encouraged. A report is required whether or not collecting activities were undertaken.
- 11) **PERMIT VALIDATION requires permittee's signature agreeing to abide by permit conditions before beginning collecting activities:**



 Signature of Permittee
- 12) Failure to comply with the conditions of this permit will result in the loss of future permitting privileges.

cc Steve Schrof
Wayne Donaldson

CF Division Files
Alaska Bureau of Wildlife Enforcement-Kodiak



STATE OF ALASKA
DEPARTMENT OF FISH AND GAME

P.O. Box 25526
JUNEAU, ALASKA 99802-5526

Permit No. CF-06-054

Expires 12/31/2006

FISH RESOURCE PERMIT
(For Scientific/Educational Purposes)

This permit authorizes Robert Foy (whose signature is required on page 2 for permit validation)
person

of UAF School of Fisheries and Ocean Sciences at 118 Trident Way, Kodiak, AK 99615
agency or organization address

to conduct the following activities from May 10, 2006 to December 31, 2006 in accordance with AS 16.05.930 and AS 16.05.340(b).

Purpose: To examine the material and energy transfer process between the zooplankton community and forage fish in embayments around Kodiak Archipelago and to develop 'habitat capability models' that appraise the value of nearshore habitats in terms of forage fish success.

Location: All nearshore areas on the west side of Kodiak from Ugalik Bay north to Shuyak, A'ognak Bays, and Chiniak and Marmot Bays.

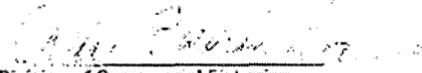
Species Collected: 50,000 Walleye Pollock, 1,000 arrowtooth flounder, 10,000 eulachon, 1,000 Pacific cod, 50,000 capelin, 50,000 sand lance, 50,000 Pacific herring, 10,000 various additional groundfish and pelagic fish. Adult and juvenile fish will be identified, measured and released. 100 from each species will be sacrificed to be used for energetics/diel analysis. (see Contingencies section)

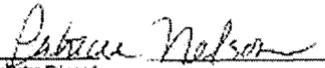
Method of Capture: Dan Trawl midwater trawl with modified research codend liner of 1/2 inch mesh for distribution and abundance studies in May, August and November, small mesh beach seine, mini purse seine for use in monthly surveys at 10 beaches in Chiniak Bay (see Contingencies section).

REPORT DUE January 31, 2007. The report shall include species, numbers, dates and locations of collection and disposition, and if applicable, sex, age, and breeding condition, and lengths and weights of fish. The report shall also include other information as may be required under the contingencies section.

GENERAL CONDITIONS, EXCEPTIONS AND RESTRICTIONS

1. This permit must be carried by person(s) specified during approved activities who shall show it on request to persons authorized to enforce Alaska's fish and game laws. This permit is nontransferable and will be revoked or renewal denied by the Commissioner of Fish and Game if the permittee violates any of its conditions, exceptions or restrictions. No reassignment of authority may be allowed under this permit unless specifically noted.
2. No specimens taken under authority hereof may be sold or bartered. All specimens must be deposited in a public museum or a public scientific or cultural and institution unless otherwise stated herein. Permittees shall not retain possession of live animals or other specimens.
3. The permittee shall keep records of all activities conducted under authority of this permit, available for inspection at reasonable hours upon request of any authorized state enforcement officer.
4. Permits will not be renewed until detailed reports, as specified above, have been received by the department.
5. **UNLESS SPECIFICALLY STATED HEREIN THIS PERMIT DOES NOT AUTHORIZE** the exportation of specimens or the taking of specimens in areas otherwise closed to hunting and fishing, without appropriate licenses required by state regulations, during closed seasons; or in any manner, by any means, at any time not permitted by these regulations.


Division of Commercial Fisheries


Deputy Director
Division of Commercial Fisheries
Alaska Department of Fish and Game

CF-06-054 continued (page 2 of 2)

Authorized Personnel: The following personnel may participate in collecting activities under terms of this permit:

Robert J. Foy, Lei G.-c. Ikuhi Schimatzka, Mike Trussel

Contingencies:

- 1) **Steve Schrof** (Division of Commercial Fisheries, Kodiak, (907) 486-1852) or **Wayne Donaldson** (Division of Commercial Fisheries, Kodiak (907) 486-1842) must be contacted prior to you engaging in collecting activities. They have the right to restrict access to any area for conservation purposes or user conflicts. Division of Commercial Fish Area Management Biologists have the right to specify methods for collecting, as well as limiting the collections of any species, and the number of specimens collected by time and area. **Jeff Waddle** (Division of Commercial Fisheries, Kodiak Area Fishery Biologist (907) 486-1807) must be contacted prior to the collection of herring.
- 2) Fish not kept for energetic/diet analysis should be released unharmed back into the water, if possible.
- 3) Fishing must cease immediately on any tow that catches more than 50 salmon. Permittee is expected to relocate before another tow is made. In addition, permittee is expected to relocate fishing activities if more than 1,000 juvenile salmon are present in any tow.
- 4) For all tows inside Kodiak and Adigrak Bays, a maximum of 150 adult salmon and ~5 tons of herring may be captured (kept or released) in each bay. Area biologists request that the permittee seriously watch tows inside these bays and limit the time of tows, or if necessary, leave these bays to avoid excessive catches of salmon and herring.
- 5) Summarize catch data following each survey, and separate by gear or trawl type. List species (common name and scientific name) and numbers caught, gear type and disposition ('released alive', 'released dead', or 'taken back to lab') for all specimens. Please include a geographic descriptor in addition to latitude/longitude when identifying the areas fished.
- 6) Samples saved for identification or diet analysis will be either disposed of or preserved for future reference at Kodiak lab facilities.
- 7) *Habitus* may NOT be collected or retained under the authority of this permit. Please contact the International Pacific Halibut Commission at (206) 634-1836, P.O. Box 55509, Seattle, WA 98145-2059 to obtain permission for *habitus* collection.
- 8) No person may transport, possess, export from the state, or release into the waters of the state, any live fish unless the person holds a valid fish transport permit (FTP), and the person is in compliance with all conditions of this permit and the provisions of 5 AAC 41.005. A fish transport permit may be issued by the Commissioner. A fish transport permit must be obtained prior to any exportation of non-preserved specimens. Please contact Sara Larsen at (907) 465-4724 for more information.
- 9) All unsentended collecting gear must be labeled with the permittee's name, telephone number, and permit number.
- 10) A copy of this permit, including any amendments, must be made available at all field collection sites and project sites for inspection upon request by a representative of the department or a law enforcement officer.
- 11) Issuance of this permit does not absolve the permittee from compliance in full with any and all other applicable federal, state, or local laws, regulations, or ordinances.
- 12) A report of collecting activities, referenced to this fish resource permit number, must be submitted to the Alaska Department of Fish and Game, Division of Commercial Fish, PO Box 115526, Juneau, AK 99811-5526, attention Sara Larsen (465-4724; sara_larsen@fishgame.state.ak.us), within 30 days after the expiration of this permit.
For each tow, this report should summarize the date, time, and location of tow (name of general location and latitude/longitude of the beginning of tow), the duration of tow and towing speed, the estimated total catch by species (in approximate numbers of fish or approximate numbers of pounds), the number sampled or retained by species, and the fate of the remaining fish (see attached example). Anecdotal information on the size and condition of all fish captured is encouraged. A report is required whether or not collecting activities were undertaken.

11) **PERMIT VALIDATION** requires permittee's signature agreeing to abide by permit conditions before beginning collecting activities:

Signature of Permittee

cc: Steve Hornold
Wayne Donaldson
Alaska Bureau of Wildlife Enforcement-Kodiak
CF Division Files



STATE OF ALASKA
DEPARTMENT OF FISH AND GAME
P.O. Box 25528
JUNEAU, ALASKA 99802-5526

Permit No. CF-05-045

Expires 12/31/2006

FISH RESOURCE PERMIT
(For Scientific/Educational Purposes)

This permit authorizes Robert Foy (*whose signature is required on page 2 for permit validation*)
person

of Fishery Industrial Technology Center; UAF at 118 Trident Way, Kodiak, AK 99615
agency or organization address

to conduct the following activities from March 15, 2006 to December 31, 2006 in accordance with AS 16.05.930 and AS 16.05.340(i);

Purpose: To take, possess, sample and release, tag and release, or sacrifice marine fish as part of ongoing surveys and new research projects. Survey data will be used to assess fish distribution, fisheries oceanography, and trophic interactions in the Kodiak Archipelago.

Location: All waters of the Kodiak Archipelago extending from the beach to the shelf break. Waters from Lower Cook Inlet to Portlock Bank and south to Criniak Gully, nearshore areas on the west side from Uganik Bay north to Shuyak as well as Chinik and Marmol Bays.

Species Collected: 100,000 Walleye Pollock, 20,000 arrowtooth flounder, 20,300 flathead sole, 40,000 eulachin, 8,000 Pacific cod, 5,000 rock sole, 100,000 capelin, 1,000 Pacific halibut, 100,000 sand lance, 50,000 Pacific herring, 20,000 various additional groundfish and pelagic fish. Adult and juvenile fish will be identified, measured and released. 100 from each species will be sacrificed to be used for energetic and otolith analysis. (see Contingencies section)

Method of Capture: DanTrawl bottom trawl, DanTrawl midwater trawl with modified research code id liners of 1-inch mesh, longline commercial seine, jigging gear, small mesh beach seine, mini purse seine (see Contingencies section)

REPORT DUE January 31, 2006. The report shall include species, numbers, dates, and locations of collection and disposition and if applicable, sex, age, and breeding condition and lengths and weights of fish. The report shall also include other information as may be required under the contingencies section.

GENERAL CONDITIONS, EXCEPTIONS AND RESTRICTIONS

1. This permit must be carried by person(s) specified during approved activities who shall show it on request to persons authorized to enforce Alaska's fish and game laws. This permit is non-transferable and will be revoked or renewal denied by the Commissioner of Fish and Game if the permittee violates any of its conditions, exceptions or restrictions. No redelegation of authority may be allowed under this permit unless specifically noted.
2. No specimens taken under authority hereof may be sold or bartered. All specimens must be deposited in a public museum or a public scientific or educational institution unless otherwise stated herein. Permittees shall not retain possession of live animals or other specimens.
3. The permittee shall keep records of all activities conducted under authority of this permit, available for inspection at all reasonable hours upon request of any authorized state enforcement officer.
4. Permits will not be renewed until detailed reports, as specified above, have been received by the department.
5. UNLESS SPECIFICALLY STATED HEREIN, THIS PERMIT DOES NOT AUTHORIZE the exportation of specimens or the taking of specimens in areas otherwise closed to hunting and fishing without appropriate licenses required by state regulations; during closed seasons; or in any manner, by any means, at any time not permitted by those regulations.

Ray Barringer
Division of Commercial Fisheries

Debra Bunn
Deputy Director
Division of Commercial Fisheries
Alaska Department of Fish and Game

CF-05-045 continued (page 2 of 2)

Authorized Personnel: The following personnel may participate in collecting activities under terms of this permit:

Robert J. Fry, Ashwin Sreenivasan, Mary Beth Loewen, Cory Williams, Brian Knott, Lei Guo.

Contingencies:

- 1) **Steve Honnold** (Division of Commercial Fisheries, Kodiak, (907)486-1873) or **Wayne Donaldson** (Division of Commercial Fisheries, Kodiak, (907)486-1842) **must be contacted prior to you engaging in collecting activities.** They have the right to restrict access to any area for conservation purposes or user conflicts. Division of Commercial Fish Area Management Biologists have the right to specify methods for collecting as well as limiting the collections of any species, and the number of specimens collected by time and area.
- 2) Fish not kept for energetic/diet analysis should be released unharmed back into the water, if possible.
- 3) Fishing must cease immediately on any tow that catches more than 50 salmon. Permittee is expected to relocate before another tow is made. In addition, permittee is expected to relocate fishing activities if more than 1,000 juvenile salmon are present in any tow.
- 4) For all tows inside Kodiak and Afognak Bays, a maximum of 150 adult salmon and 45 tons of herring may be captured (kept or released) in each bay. Area biologists request that the committee seriously watch tows inside these bays and limit the time of tows, or if necessary, leave these bays to avoid excessive catches of salmon and herring.
- 5) Summarize catch data following each survey, and separate by gear or trawl type. List species (common and scientific name) and numbers caught per gear type and disposition (released alive, released dead, or taken back to lab) for a specimens. Please include a geographic descriptor in addition to latitude/longitude when identifying the areas fished.
- 6) Samples saved for identification or diet analysis will be either disposed of or preserved for future reference at Kodiak lab facilities.
- 7) Herring may NOT be collected or retained under the authority of this permit. Please contact the International Pacific Halibut Commission at (206) 634-1638, P.O. Box 55009, Seattle, WA 98145-2009 to obtain permission for halibut collection.
- 8) No person may transport, possess, export from the state, or release into the waters of the state, any live fish unless the person holds a valid fish transport permit (FTP) and the person is in compliance with all conditions of the permit and the provisions of 5 AAC 41.005. A fish transport permit may be issued by the Commission. A fish transport permit must be obtained prior to any exportation of non-preserved specimens. Please contact Sara Larsen at (907)485-4724 for more information.
- 9) A unattended collecting gear must be labeled with the permittee's name, telephone number, and permit

- number:
- 10) A copy of this permit, including any amendments, must be made available at all field collection sites and project sites for inspection upon request by a representative of the department or a law enforcement officer.
 - 11) Issuance of this permit does not absolve the permittee from compliance in full with any and all other applicable federal, state, or local laws, regulations, or ordinances.
 - 12) A report of collecting activities, referenced to this fish resource permit number, must be submitted to the Alaska Department of Fish and Game, Division of Commercial Fish, PO Box 25526, Juneau, AK 99802-5526, attention Sara Larson (465-4724; sara_larson@fishgame.state.ak.us), within 30 days after the expiration of this permit.

For each tow, this report should summarize the date, time, and location of tow (name of general location and latitude/longitude of the beginning of tow), the duration of tow and towing speed, the estimated total catch by species (in approximate numbers of fish or approximate numbers of pounds), the number sampled or retained by species, and the fate of the remaining fish (see attached example). Anecdotal information on the size and condition of all fish captured is encouraged. A report is required whether or not collecting activities were undertaken.

- 11) **PERMIT VALIDATION** requires permittee's signature agreeing to abide by permit conditions before beginning collecting activities:

Signature of Permittee

cc: Steve Honnold
Wayne Donaldson
Kevin Brennan
Alaska Bureau of Wildlife Enforcement-Kodiak
CF Division Files



STATE OF ALASKA
DEPARTMENT OF FISH AND GAME

P.O. Box 25526
JUNEAU, ALASKA 99802-5526

Permit No. CF-04-031

Expires 12/31/2004

FISH RESOURCE PERMIT
(For Scientific/Educational Purposes)

This permit authorizes Robert Foy (whose signature is required on page 2 for permit validation)
person

of Fishery Industrial Technology Center, UAF at 11B Trident Way, Kodiak, AK 99615
agency or organization address

to conduct the following activities from March 15, 2003 to December 31, 2003 in accordance with AS 16.05.930 and AS 16.05.340(b):

Purpose: To take, possess, sample and release, tag and release, or sacrifice marine fish or invertebrates as part of ongoing surveys and new research projects. Survey data will be used in determining abundance, distribution, and biological characteristics of marine fish and invertebrates.

Location: Marine waters in the vicinity of Kodiak Island and Afognak Island.

Species Collected: Aquatic fish (finfish, invertebrates) in any of their life stages. All specimens encountered during surveys, including walleye Pollock, flathead sole, cutthroat Pacific cod, rock sole, rex sole, Pacific sand lance, capelin, etc. (see Contingencies section)

Method of Capture: Kodiak midwater trawl, DanTrawl Fiska II bottom trawl, DanTrawl Berling Billionaire midwater trawl with modified research vessel liners of 1-inch mesh beach seine, small purse seine (see Contingencies section)

-Continued on Back-

REPORT DUE January 31, 2005 The report shall include species, numbers, dates, and locations of collection and disposition, and if applicable, sex, age, and breeding condition, and lengths and weights of fish. The report shall also include other information as may be required under the contingencies section.

GENERAL CONDITIONS, EXCEPTIONS AND RESTRICTIONS

1. This permit must be carried by person(s) specified during approved activities who shall allow it on request to persons authorized to enforce Alaska's fish and game laws. This permit is nontransferable and will be revoked or renewal denied by the Commissioner of Fish and Game if the permittee violates any of its conditions, exceptions or restrictions. No redelegation of authority may be allowed under this permit unless specifically noted.
2. No specimens taken under authority hereof may be used in commerce. All specimens must be deposited in a public museum or a public scientific or educational institution unless otherwise stated herein. Subsequent to collection, the permittee shall not retain possession of live animals or other specimens.
3. The permittee shall keep records of all activities conducted under authority of this permit, available for inspection at all reasonable hours upon request of any authorized state enforcement officer.
4. Permits will not be renewed until detailed reports, as specified above, have been received by the department.
5. UNLESS SPECIFICALLY STATED HEREIN, THIS PERMIT DOES NOT AUTHORIZE the exportation of specimens or the taking of specimens in areas otherwise closed to hunting and fishing without appropriate licenses required by state regulations, during closed seasons, or in any manner, by any means, at any time not permitted by those regulations.


Division of Commercial Fisheries


Deputy Director
Division of Commercial Fisheries
Alaska Department of Fish and Game

CF-04-031 continued (page 2 of 2)

Authorized Personnel: The following personnel may participate in collecting activities under terms of this permit:

Robert J. Foy; students and technicians TBA.

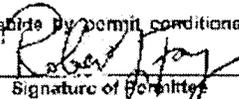
Contingencies:

- 1) Steve Honnold (Division of Commercial Fisheries, Kodiak, (907)458-1873) or Wayne Donaldson (Division of Commercial Fisheries, Kodiak (907)486-1842) must be contacted prior to you engaging in collecting activities. They have the right to restrict access to any area for conservation purposes or user conflicts. Division of Commercial Fish Area Management Biologists have the right to specify methods for collecting, as well as limiting the collectors of any species, and the number of specimens collected by time and area.
- 2) Fish not kept for energetic/diet analysis should be released unharmed back into the water, if possible.
- 3) Fishing must cease immediately on any tow that catches more than 50 salmon. Permittee is expected to relocate before another tow is made. In addition, permittee is expected to relocate fishing activities if more than 1,000 juvenile salmon are present in any tow.
- 4) For all tows inside Kodiak and Afognak Bays, a maximum of 150 adult salmon and ~5 tons of herring may be captured (kept or released) in each bay. Area biologists request that the permittee seriously watch tows inside these bays and limit the time of tows, or if necessary, leave these bays to avoid excessive catches of salmon and herring.
- 5) Summarize catch data following each survey, and separate by gear or trawl type. List species (common name and scientific name) and numbers caught per gear type and dispatcher (released alive, released dead, or taken back to lab) for all specimens. Please include a geographic descriptor in addition to latitude/longitude when identifying the areas fished.
- 6) Samples saved for identification or diet analysis will be either disposed of or preserved for future reference at Kodiak lab facilities.
- 7) Halibut may NOT be collected or retained under the authority of this permit. Please contact the International Pacific Halibut Commission at (206) 634-1938, P.O. Box 95009, Seattle, WA 98145-2009 to obtain permission for halibut collection.
- 8) No person may transport, possess, export from the state, or release into the waters of the state, any live fish unless the person holds a valid fish transport permit (FTP) and the person is in compliance with all conditions of the permit and the provisions of 5 AAC 41.005. A fish transport permit may be issued by the Commissioner. A fish transport permit must be obtained prior to any exportation of non-preserved specimens. Please contact Sheila Martin at (907)465-6149 for more information.
- 9) All unattended collecting gear must be labeled with the permittee's name, telephone number, and permit number.
- 10) A copy of this permit, including any amendments, must be made available at all field collection sites and project sites for inspection upon request by a representative of the department or a law enforcement officer.
- 11) Issuance of this permit does not absolve the permittee from compliance in full with any and all other applicable federal, state, or local laws, regulations, or ordinances.
- 12) A report of collecting activities, referenced to this fish resource permit number, must be submitted to the Alaska Department of Fish and Game, Division of Commercial Fish, PO Box 25526, Juneau, AK 99802-5526, attention Sheila Martin (465-6149; sheila_martin@fishgame.state.ak.us), within 30 days after the expiration of this permit.

SARA - 10/22/24

For each tow, this report should summarize the date, time, and location of tow (name of general location and latitude/longitude at the beginning of tow), the duration of tow and towing speed, the estimated tow water by species (in approximate numbers of fish or approximate numbers of pounds), the number sampled or retained by species, and the fate of the remaining fish (see attached example). Anecdotal information on the size and condition of all fish captured is encouraged. A report is required whether or not collecting activities were undertaken.

- 11) **PERMIT VALIDATION** requires permittee's signature agreeing to abide by permit conditions before beginning collecting activities:


Signature of Permittee

- cc: Steve Honnold
Fish & Wildlife Enforcement
Wayne Donaldson
Div. Comm. Fish files HQ
Kevin Brennan

Appendix B IACUC Certificate

Institutional Care and Use Committee

PO Box 757560, 206 Eielson Building

University of Alaska Fairbanks

Fairbanks, Alaska 99775-7560

(907) 474-7800

IACUC Web Page: <http://www.uaf.edu/iacuc>

IACUC e-mail: fyiacuc@uaf.edu

May 11, 2004

Subject: Completion of IACUC Humane Animal Care and Use Training

Dear Lei Guo:

The record indicates that the following modules of the University of Alaska Fairbanks Institutional Animal Care and Use Committee training program have been successfully completed:

Module 1: Introduction to Animal Care Issues

Module 5: Field Biology

Part 1- Fish

Teresa Lyons

Research Committee Coordinator

Office of Research Integrity