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THE GREENLAND HALIBUT OF CUMBERLAND SOUND: TRENDS IN CATCH RATES AND PREFERENCES IN DIET

by

Susan T. Dennard

A Thesis Submitted to the Faculty of Graduate Studies through the Great Lakes Institute for Environmental Research in Partial Fulfillment of the Requirements of the Degree of Master of Science at the University of Windsor

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DECLARATION OF CO-AUTHORSHIP

I hereby declare that this thesis incorporates material that is the result of joint research, as follows: Chapter 2 contains material from a manuscript entitled "Hiearchical analysis of a remote, Arctic, artisanal, longline fishery" that has been submitted to the ICES Journal of Marine Science. The manuscript is co-authored by S.T. Dennard, M.A. MacNeil, S. Campana, M. Treble, and A.T Fisk. Chapter 3 contains material from a manuscript entitled "Using stable isotope analysis to assess the feeding ecology of Greenland halibut in Cumberland Sound" that will be submitted to Polar Biology. This manuscript is co-authored by S.T. Dennard, B.C. McMeans, A.T. Fisk. In all cases, key ideas, primary contributions, data analysis, and interpretation were performed by the author, and the contribution of the co-authors was through modeling and/or lab work guidance. I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work. Additionally, I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from each of the co-authors to include the above materials in my thesis.

ABSTRACT

Inaccessibility and harsh conditions of the Arctic frequently limit research on local fish and ecosystems. Cumberland Sound on southern Baffin Island houses a remote, winter fishery for Greenland halibut (*Reinhardtius hippoglossoides*) and presented a unique site for evaluating Arctic fish stock trends and feeding behavior from limited data. Relative abundance through time, 1987-2003, of the Greenland halibut stock was modeled hierarchically from catch per unit effort (CPUE) data with multiple fixed effects and location and fisherman as random effects. Month and the North Atlantic Oscillation were important predictors of CPUE. Additionally, fisherman behavior influenced CPUE, breaking the assumption that CPUE is proportionate to fish abundance. A second study using stable isotopes found pelagic feeding of the Greenland halibut and a dietary preference for capelin, consistent with studies in other systems. The combination of these studies is the first incorporation of fishery and ecological information to assess Cumberland Sound Greenland halibut.

DEDICATION

I dedicate this to my grandparents Robert and Merle Dennard who instilled the importance of knowledge and academic excellence in me, and to my parents, Dave and Sue Dennard, for their unconditional support and love.

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I thank the fishermen of Pangnirtung for keeping records of their catch as well as the Pangnirtung Hunters and Trappers Association for provision of and permission to use their logbooks; Joe Akpalialuk and Jesse Eesemaile for their help conducting field work; Government of Canada International Polar Year Project CC144 for funding this project; Bailey McMeans for her help with sample provision, preparation, and guidance; Jaclyn Brush for her help with sample preparation and processing.

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CHAPTER ONE

INTRODUCTION

The Arctic and sub-Arctic oceans are seasonally productive marine ecosystems subject to heavy levels of biological resource exploitation (Usher et al. 2005). However, because Arctic species are typically long-lived and slow-growing, they can be sensitive to even modest harvest levels (Usher et al. 2005) and stocks of almost all commercially harvested marine species assessed in the North Atlantic and Barents Sea have declined since the Second World War (Bernes 1996). Additionally, increasing sea surface temperatures, a rise in global sea levels, and decreasing persistence of sea-ice will affect biological productivity in these ecosystems, in turn influencing fishery productivity and distribution of marine resources (Everett et al. 1995). Fish stocks are predicted to move towards the North or South Pole, shifting distributions of stocks and leading to the expansion of some fisheries and collapse of others (Everett et al. 1995). Studies of Arctic/Antarctic systems, where harsh conditions limit methods for evaluating deep-water fisheries, often suffer from a lack of data to assess stock status—effectively preventing assessment of the impact from increased fishing pressure and/or changes in climate. Thus, establishing baseline knowledge for the status of both stocks and ecosystems in Arctic systems is highly desirable.

Cumberland Sound on southern Baffin Island, Nunavut houses a seasonal Inuit fishery for Greenland halibut (*Reinhardtius hippoglossoides*). As a commercially popular fish, Greenland halibut has been heavily harvested throughout the North Atlantic (Nedreaas and Smirnov 2004) and has been potentially overfished in some areas (ICES 1998). Peak catches for Cumberland Sound reached greater than 400 tonnes in the early 1990s, but recent years have shown reduced total catch (e.g. 2007 yielded only 3 tonnes) caused by warmer, shorter winters and reduced formation of landfast sea ice (Treble 2008). Though several reports have assessed the Greenland halibut catch rates in Cumberland Sound (e.g. Pike 1994, Mathias and Keast 1996, Treble 2008), no studies have addressed the ecosystem—specifically, what environmental processes are driving catch trends and what is the structure of the Cumberland Sound food web. The remote, artisanal, and self-reporting nature of the Greenland halibut longline fishery in Cumberland Sound made it a unique site for evaluating a cold-water fish stock from sparse data. Additionally, a current interest by local fisherman and Fisheries and Oceans Canada (DFO) to expand the fishery requires further ecosystem and stock research in order to most effectively manage the local Greenland halibut.

Fishery Stock Assessment

The ultimate goal of fisheries managers is to promote sustainable production of fish stocks over time via regulatory and enhancement actions (Hilborn and Walters 1992). As such, predicting stock fluctuations to direct management has motivated much of marine fisheries research. Stock assessments based on available data (e.g. fishery logbooks, fishery surveys, tagging studies, etc.) provide a means of assessing fish populations under potential management strategies through statistical and mathematical methods (Hilborn and Walters 1992). Stock management is then based on the stock assessment as well as the social, political, and economic context of the fishery. Evaluating population status for a population that is not directly observable forces stock assessments to rely on statistical models that represent the population (Hilborn and Mangel 1997). To create stock assessment models requires harvest/catch rate data and a measure of relative abundance (Maunder and Punt 2004). Ideally, this data would be

collected independently of the fishery—for example, via trawl survey—but fishery-independent data is often impractical and cost-inefficient to collect. Thus, data collected by the fishery, i.e. fishery-dependent data, is often the main source of abundance data on which to base stock assessments (Maunder et al. 2006).

The most available and frequently used fishery-dependent data is information on catch and effort—catch being the amount of target species harvested and effort being the amount of time/gear used to harvest (Maunder and Punt 2004). Catch-per-unit-effort (CPUE) reflects fishing success, and because fishing success is linked closely with fish abundance, CPUE is frequently used as an indicator of change in a fish stock's relative abundance (Hilborn and Walters 1992). CPUE is written as a ratio,

<u>Fish Quantity</u> (1)

Effort

where fish quantity could be total weight or total number of fish harvested and effort could be the time spent fishing, number of hooks, number of boats, etc. On small spatial scales, CPUE assumes that catch is proportional to fish abundance (Maunder and Punt 2004), but studies using Virtual Population Analysis have shown there is often little correlation between CPUE and estimated stock size (Ultang 1976, Garrod 1977). Even when CPUE and abundance are related, however, the relationship is often nonlinear and changes in stock size are not reflected proportionally by changes in CPUE (Pope and Garrod 1975).

One assumption that is often not met when assessing CPUE is that catchability is constant (Cooke and Beddinton 1984). The catchability coefficient, q, is the portion of the stock captured by one unit of effort, and if q is constant over time, then CPUE will be proportional to abundance (Maunder et al. 2006). However, q is seldom constant through time. For example, catchability

can increase if the fishing fleet's efficiency increases (e.g. new technology). Environment can also affect catchability (e.g. *El Niño* reduces catchability of yellowfin tuna for purse-seine fisheries in the eastern Pacific; Maunder et al. 2006). Essentially, where fishing occurs, when fishing occurs, and who is fishing can all change q (Cooke and Beddington 1984). Additionally, catchability is often linked to abundance, so if abundance changes with time then catchability will change with time (Maunder et al. 2006), as fewer fish are harder to find.

Another requirement for CPUE to be proportional to abundance is random distribution of fishing effort relative to the fish. Yet, fishermen do not fish at random. For example, information sharing allows fishermen/fleets to harvest in optimal locations and thereby reduce fishing time (i.e. the q or Effort), so CPUE remains high while fish abundance declines (Branch et al. 2006). CPUE is also the metric most heavily influenced by individual fisherman behavior (Branch et al. 2006). Gillis and Peterman (1998) showed that exploitative competition among fishermen in a fishery that allows movement in response to changing catch rates causes the relationship between CPUE and local abundance to break down.

To deal with all the assumptions and various factors that can affect or bias catch rates, a process called standardization is used (Maunder and Punt 2004). Standardization of catch and effort data attempts to remove/explain annual variation in the data unrelated to changes in fish abundance (Maunder and Punt 2004), and the most common approach is the use of generalized linear models (GLMs; Nelder and Wederburn 1972). The statistical distribution of the response variable, typically catch rate, and how various explanatory variables relate to the response define the GLM—thereby assuming that the relationship between the expected response and explanatory variable is linear (Maunder and Punt 2004). In GLMs of CPUE, year is always an

explanatory variable since the main objective of CPUE standardization is to evaluate trends in relative abundance through time (Maunder and Punt 2004).

Generalized linear mixed models (or hierarchical model) (Pinheiro and Bates 2000) build on GLMs by including both fixed effects and random effects. Fishery-dependent data is inherently hierarchical because predictors are either non-independent (i.e. fishing fleets) or multi-level through time. Inclusion of fixed effects in a model allows for comparison among different levels, but random effects allow for generalization of conclusions from the fixed effects to the population associated with the random effect (Maunder and Punt 2004). For example, if random changes exist in the distribution of a fish population through time, it is possible to create a random effect of location (Maunder and Punt 2004). Thus, a hierarchical model created with a location random effect would predict CPUE for each location but take other location's CPUE into consideration, rather than predicting CPUE independently for each location. The assumption is that then one can predict the relationship of explanatory variables to CPUE for all similar locations (Zuur et al. 2007). Essentially, by developing hierarchical models that share information based on simple, localized relationships, the resulting models capture the broader, regional processes that drive CPUE.

Even if all known or available factors relating to the fish stock are included in the CPUE standardization, there is still the possibility that CPUE is not linearly proportional to relative abundance (Maunder and Punt 2004). Essentially, no model is ever correct, but some models are more useful for specific applications and represent a system well enough to improve management decisions (Hilborn and Walters 1992). For example, data limitations such as those from the Cumberland Sound fishery (e.g. reliance on voluntarily recorded catch records, lack of fishery-independent surveys, no understanding of the local Greenland halibut catchability, and

no estimates of total abundance) often restrict stock assessments that directly estimate population abundance. Instead, models can focus on determining the processes driving CPUE trends, such environmental or social factors. Assessing the mechanisms that influence catch rates is crucial for appropriate management decisions since teasing apart effects from the mediated by the environment versus those mediated by humans can be difficult; there is growing evidence that a considerable component in fish stock declines is caused by the environment rather than overfishing (Caddy and Gulland 1983, Hilborn and Walters 1992). Additionally, changes in fish population health and abundance (e.g. overfishing) usually go undetected until problems are severe, but reducing fishing pressure once problems have been identified is economically and socially difficult (Hilborn and Walters 1992). Thus, it is important to focus on not only fishing catch rates and abundance, but also to realize that fisheries are dynamic interactions of the fish population, the fishermen, and the environment.

Ecosystem-based fisheries management

The most important biological feature of a fishery is the fish population. Single-species assessment models aim to address status and productivity of a specific fish stock, often relying on single-species historical data (Walters and Martell 2004). However, because of multiple indirect effects of fishing (i.e. habitat destruction, bycatch, evolutionary effects on population demographics, and changes in the function and structure of ecosystems; Pikitch et al. 2004) more than just the population must be considered. There is a critical need for understanding ecological interactions and the effects of fishing on these relationships. Fisheries management has historically been ineffective because of a focus on the single target species and frequent disregard for ecosystem aspects such as habitat, predators, or prey (Pikitch et al. 2004), leading

to fishery collapses despite attentive and seemingly effective stock assessments. Additionally, flawed management has stemmed from an imperviousness of fisheries managers to scientific invalidation of particular policies—essentially, many fisheries managers have ignored empirical evidence and past experience in favor of dogmatic assumptions (Walters and Martell 2004).

Ecosystem management is a popular concept in current fisheries management (Maunder et al. 2006)—essentially, ecosystem-based fishery management reverses the order of management priorities, starting with the ecosystem rather than the target species (Pikitch et al. 2004). Based on single-species models, multiple species models consider predation, food supply, and environment (Hilborn and Walters 1992) while ecosystem models allow single-species process errors to be explained, at least partially, by trophic-interaction effects (Walters and Martell 2004).

Ecosystem-based fisheries management does not replace stock assessments but rather incorporates them into ecosystem models. To develop ecosystem models requires information on bioenergetics and trophic relationships, knowledge of spatial distribution based on species behavior and interactions, and awareness of large-scale, long-term ecosystem events (Walters and Martell 2004). Considerable effort has been devoted to developing trophic mass-balancing models that describe status and trophic interactions in aquatic ecosystems, allowing for predictions of ecosystem state changes under various harvest levels (Christensen and Pauly 2004). However, the main limitation to ecosystem-based management implementation has been lack of data on species linkages relative to commercially important species (Charles 2001); often not all information is available, forcing ecosystem-based management to be applied in varying degrees.

Although a rare occurrence, data and knowledge on a fish stock's biology, population dynamics, and environment should be accumulated prior to the commencement or expansion of a fishery, making the separation of fishing and natural mortality rates clearer for subsequent stock assessments. Data-poor situations for target species and ecosystem processes demand using information on natural history and developing precautionary methods (e.g. reduced catch limits or large closed areas; Piketch et al. 2004). Christensen and Pauly (2004) indicate that research should be focused on analyses and management of exploited ecosystems rather than just management of their components.

Currently, a growing body of public support exists for fisheries that have long-term sustainability and protect the capability of ecosystems to support diverse creatures (Walters and Martell 2004). Charles (1994) considered the most important component of sustainability for individual stocks to be maintaining or enhancing the capacity or quality of the ecosystem, while Pitcher and Pauly (1998) indicate that rebuilding ecosystems should be the goal of fisheries managers. Thus, fisheries managers should focus on providing not only stock assessments but also food web structure studies—thereby setting the stage for ecosystem-based management strategies.

Stable isotopes as tracers of food web structure

One method frequently used to estimate food web linkages in marine ecosystems is stable isotope analysis. Isotopes are atoms of a chemical element that form the same bonds but have differing atomic masses; their nuclei have the same number of protons but not neutrons. Stable isotopes do not exhibit radioactive decay and either possess extra neutrons, referred to as "heavy," or fewer neutrons, referred to as "light." Typically, heavier isotopes are less common in the environment (Ehleringer and Rundel 1989) and form stronger bonds in chemical compounds (Sacks 1953, Peterson and Fry 1987). As such, heavier isotopes react at slower rates than the lighter isotopes (Sacks 1953, Peterson and Fry 1987), resulting in changes in their relative abundances. This process, called fractionation, can cause an organism's tissue to possess different isotope ratios relative to that organism's food (Minagawa and Wada 1984, Peterson and Fry 1987). An increased proportion of heavy (e.g., ¹⁵N) to light isotopes (e.g., ¹⁴N) is referred to as ¹⁵N enrichment (Fry 2006).

Because fractionation occurs at the 5th or 6th decimal point of an isotope's concentration, the notation delta (δ) is used to amplify, by 1000, the changes from fractionation. δ -notation expresses stable isotopes as the ratio of heavy to light isotopes in a sample relative to a standard material,

$$\delta X = [Rsample/Rstandard) - 1] \times 1000$$
⁽²⁾

where X is ¹⁵N or ¹³C and R is the corresponding ratio of ¹⁵N/¹⁴N or ¹³C/¹²C. The difference between an organism's and its food's relative stable carbon or nitrogen isotope ratios is called the isotopic discrimination factor, denoted Δ ,

$$\Delta \delta X = \delta X_{\text{predator}} - \delta X_{\text{prey}} \tag{3}$$

where X is the stable isotope. Nitrogen, ¹⁵N, or carbon, ¹³C, stable isotopes are those most commonly used in food web ecology.

 $\Delta \delta^{13}$ C is relatively conserved, compared to $\Delta \delta^{15}$ N, with increased trophic position in aquatic food webs. Fractionation averages at ±1‰ (Peterson and Fry 1987), and because of this the isotope can often be used to distinguish benthic/inshore food webs from pelagic/offshore food webs—stable-carbon isotope values being more enriched in the benthic/inshore systems (Hobson and Welch 1992, Hobson et al. 1994, France 1995). Benthic/inshore algae have more positive δ^{13} C values than pelagic algae because they possess thicker stagnant boundary layers that resist diffusion of CO₂, resulting in depleted CO₂ (or HCO₂⁻) and less subsequent assimilation of normally discriminated ¹³C (France 1995).

For nitrogen, ¹⁵N, enrichment occurs with trophic level at a relatively constant rate of 3-4‰, allowing derivation of relative trophic positions from δ^{15} N values (Minagawa and Wada 1984, Michener and Schell 1994, Post 2002). This occurs because a consumer becomes enriched in ¹⁵N relative to its diet from excretion of isotopically light nitrogenous wastes and retention of isotopically heavy amino acids (Minagawa and Wada 1984). Relative trophic position can be inferred by comparing δ^{15} N of a consumer to the δ^{15} N of an organism from a known trophic level (e.g. a primary producer would be assigned a trophic level of 1). The equation for calculating trophic position states:

$$TP_{1} = \lambda + (\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{baseline}}) / \Delta \delta^{15}N$$
(4)

where $\delta^{15}N_{\text{consumer}}$ is the $\delta^{15}N$ of the species of interest, $\delta^{15}N_{\text{baseline}}$ is the $\delta^{15}N$ of the known baseline species, and λ is the trophic position the known baseline species. However, Jennings et al. (2002) found that decreasing $\delta^{15}N$ values for small herring reflected decreasing trophic level, so averaging a species' $\delta^{15}N$ values can hide the variation among individuals of different sizes. Also, because a disproportionately high amount of the light isotopes are absorbed by an organism during fasting (i.e. ¹⁵N or ¹³C enrichment), parts of isotopic variation will include differences in feeding rate and metabolic state (Olive et al. 2003).

Recently, the development of stable isotope mixing models has allowed quantitative assessment of relative contributions of different potential dietary sources in a mixture, i.e. the minimum to maximum proportion of a prey species in a predator's diet (Phillips and Gregg 2003, Moore and Semmes 2008). These mass-balance models can quantitatively assess contribution of

different sources to the mixture by assuming that stable isotopes are conserved over time and change at a predictable rate during biological processes (Peterson and Fry 1987, Phillips and Gregg 2001, Phillips and Gregg 2003, Schindler and Lubetkin 2004, Martínez del Rio and Wolf 2005). Mass-balance models are often written as,

$$\delta_{M} = f_{1} * (\delta_{1} + \gamma_{1}) + f_{2} * (\delta_{2} + \gamma_{2}) \dots + f_{n} * (\delta_{n} + \gamma_{n})$$
(5)

where f_i is the proportional contribution of the *i*th source to the mixture, δ_i is the isotopic signature of the *i*th source, and γ_i is the isotopic fractionation of the *i*th source. However, to calculate fractional contributions, the reverse process is used: δ values are used to calculate source contributions, and then a ratio-based approach is used to calculate total amount of material contributed to each source (Fry 2006). Statistical models (e.g. IsoSource; Phillips and Gregg 2003) can solve for the range of possible source contributions, defining minimum and maximum potential contributions for each source. Other models (e.g. MixSIR, Semmens and Moore 2008) can determine probability distributions for proportional source contributions to the mixture of interest.

Thus, stable isotopes can provide information on feeding location (e.g. benthic or pelagic) and trophic relationships, while mixing models can identify potential proportions of dietary items. However, stable isotopes are plagued by the fact that they rely on underlying but largely unstated assumptions (Gannes et al. 1997; Jardine et al. 2006). For example, unless fractionation has been investigated for a specific species, $\delta^{15}N$ and $\delta^{13}C$ is assumed to change 3-4‰ and 1‰, respectively, between trophic levels, although numerous controlled studies have shown this value to vary with species (e.g. Overmyer et al. 2008) and environmental conditions (e.g. temperature; Power et al. 2003). Additionally, baseline values of $\delta^{15}N$ and $\delta^{13}C$ can vary among ecosystems, forcing trophic position and relative source calculations to be based on an

isotopic baseline unique to every ecosystem of interest (Post 2002, Jardine et al. 2006). And, because the relative trophic position is calculated from the baseline $\delta^{15}N$ value, the selected baseline species must be able to account for temporal variation in all energy sources (e.g. primary producers, detritus; Post 2002). Another concern is that $\delta^{15}N$ and $\delta^{13}C$ ratios are variable among sampling conditions (Power et al. 2003), tissue type (Hobson and Clark 1992), and species (Macko et al. 1982, Hobson and Clark 1992, Vander Zanden and Rasmussen 2001).

Nonetheless, stable isotopes still provide useful tools for assessing carbon sources and food web structure, particularly when combined with other trophic assessment methods such as stomach content analysis. Stomach content analysis relies on the assumption that prey items present in an organism's stomach represent its diet and can therefore be used to estimate trophic position. However, different foods are absorbed at different rates in the gut, preventing examination of various source contributions in the consumer's diet (Stoner and Zimmerman 1988), but stable isotope analysis integrates short-term variation in diet and is therefore less temporally biased (Pinnegar and Polunin 2000). Additionally, indiscernible stomach contents can be clarified by stable isotopes (Malej et al. 1993). Thus, combining stable isotopes with stomach content data can be an effective approach to analyze diet: stable isotopes can clarify trophic position, trophic similarities, and food-chain lengths while stomach contents can clarify specific dietary components (Pinnegar and Polunin 2000).

Stable isotopes can also be used to assess potential trophic structure changes caused by fishing. Fishing is known to affect size and community species composition due to selectivity of larger individuals. As fishing increases, the mean size of individuals has been observed to decrease (e.g. Gislason 1994, Jennings and Kaiser 1998). Jennings et al. (2002) found the trophic level of North Sea demersal fish decreased between 1982 and 2000 in response to fishing, but

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they emphasized the importance of historical trophic data to accurately observe the impacts fishing can have on food webs. Walters and Martell (2004) designated the need for information on trophic linkages early in the development of a fishery in order to understand changing exploitations rates. Therefore, establishing current trophic position of Greenland halibut in Cumberland Sound and assessing other trophic linkages are important requirements prior to the fishery's expansion.

Greenland halibut

Greenland halibut are right eye flatfish inhabiting deep waters more than 2200 m (Boje and Hareide 1993). Mainly found in waters with temperatures from 1-4°C (Jørgensen 1998), it has a circumpolar distribution (Nielsen 1986). Although a flatfish, Greenland halibut possess muscles developed equally on both sides, and these fish are known as vigorous and vertical swimmers (de Groot 1970). Also, unlike other fish in its family, the left eye does not fully migrate to the right side, but rather sits on the dorsal ridge of the forehead, likely providing a wider peripheral vision (Stenberg 2007).

Age and maturation of Greenland halibut are currently under debate, but small halibut typically inhabit shallower depths (0-600 m) while the abundance of older, larger fish increases with depth (Atkinson et al. 1982, Bowering 1982, Atkinson and Bowering 1987, Crawford 1992, Jørgensen 1998). Spawning is thought to occur in early winter in the deep waters of Davis Strait with pelagic larvae drifting with the West Greenland current along the west coast of Greenland (Stenberg 2007). Small juveniles, < 20 cm, undertake vertical migrations during night, feeding on pelagic crustaceans (Jørgensen 1997). Stomach analysis of individuals approximately 20-69 cm indicate a primarily piscivorous diet (e.g. capelin) with some predation on cephalopods

(Bowering and Lilly 1992, González et al. 2006). Individuals \geq 70 cm tend to consume demersal, large fish (e.g. redfish ;Bowering and Lilly 1992).

Population delineation has been determined by studies on meristics (Templeman 1970, Misra and Bowering 1984, Riget et al. 1992, Rasmussen et al. 1999), parasites (Khan et al. 1982, Boje et al. 1997), genetics (Fairbairn 1981, Riget et al. 1992, Vis et al. 1997), and tagging (Smidt 1969, Bowering 1984, Boje 2002). Results indicate populations in the Norwegian and Barents Sea, the waters of East Greenland, Iceland, and the Faroe Islands, Newfoundland, the Grand Banks, Labrador, West Greenland, and the Gulf of St. Lawrence. Knutsen et al. (2007) indicated significant genetic structure, i.e. genetic divergence in separate stocks, in the North Atlantic, mediated by drifting larvae and eggs on ocean currents.

Commercially, the Greenland halibut has been a popular fish species since the beginning of the 20th Century (Bernes 1996). Originally caught on a subsistence basis in Greenland waters, it is now the most important fish species for the Greenland fishing industry (Bernes 1996). Canadian catches, mainly taken via gillnets focused in the deepwater channels near the Newfoundland and Labrador coasts, peaked in the 1980s (Bowering and Brodie 1995). The decline of these Greenland halibut resources in the 1990s along with declines in other groundfish resources led the Canadian government to encourage harvest of Greenland halibut in other areas (e.g. Davis Strait, Cumberland Sound) as "developmental fisheries" (Bowering and Brodie 1995). However, these fisheries have been typically assigned one quota, such as 500 tonnes in Cumberland Sound (Treble 2008), and then are considered "stable" when the quotas are not exceeded (Bowering and Brodie 1995). Despite actions to increase regulations, management units have requested increased research activity (Stenberg 2007), and effective ecosystem-based management demands basic information on food-web structure, trophic interactions, and stock/population status.

Objectives and Rationale

Commercial popularity of Greenland halibut and potential expansion of the Cumberland Sound artisanal fishery demand a basic understanding of the factors affecting Greenland halibut relative abundance and its trophic role in the Cumberland Sound system. In the context of both restricted access for research and limited historical focus on the Cumberland Sound system, this project pursued two objectives:

- To assess the fishery-mediated and environmentally-mediated mechanisms driving trends in Greenland halibut catch rates in Cumberland Sound by establishing models built from fisherman logbooks.
- To establish the trophic position and carbon sources for the Greenland halibut stock in Cumberland Sound.

Each of these goals is addressed individually, 1) as Chapter 2, *Hierarchical modeling of a remote, Arctic, artisanal, longline fishery*, and 2) as Chapter 3, *Using stable isotope analysis to assess the feeding ecology of Greenland halibut in Cumberland Sound.* The implications and conclusion of both sections are discussed in Chapter 4, *Ecosystem management approaches in Cumberland Sound.*

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CHAPTER TWO

HIERARCHICAL ANALYSIS OF A REMOTE, ARCTIC, ARTISANAL LONGLINE FISHERY*

[•] This manuscript is co-authored by S.T Dennard, M.A. MacNeil, S. Campana, M. Treble, and A.T. Fisk.

Introduction

Despite the commercial fishing importance of the Greenland halibut *Reinhardtius hippoglossoides* to indigenous communities, stocks in the Eastern Canadian Arctic have been relatively unstudied to date—in part due to the remoteness characterizing such fisheries. The Greenland halibut is a deepwater flatfish, found up to 1500 m deep in the Davis Strait off Baffin Island (Templeman 1973) and as deep as 2200 m off West Greenland (Boje and Hareide 1993). Small halibut typically inhabit shallower depths (0-600 m) while the abundance of older, larger fish often increases with depth (Atkinson et al. 1982, Bowering 1982, Atkinson and Bowering, 1987). Davis Strait is considered an important spawning area for Greenland halibut in the Northwest Atlantic (Jørgensen 1997, Simonsen and Gundersen 2005). Because the pelagic eggs and larvae disperse via currents, their distribution has been linked to the North Atlantic Oscillation (NAO; Adlandsvik et al. 2004). The NAO is an atmospheric pressure difference controlling the North Atlantic Current, and variations in the NAO lead to changes in ocean circulation and conditions in the North Atlantic (Dickson et al. 1999, Dickson et al. 2000); increased Greenland halibut commercial landings in West Greenland waters have coincided with periods of colder water temperature (Buch et al. 2004).

Studies of Arctic/Antarctic systems, where harsh conditions limit methods for evaluating deep-water fisheries, often suffer from a lack of data to assess stock status. Although the ultimate goal of fisheries managers is to promote the sustainable production of fish stocks through formal stock assessment, it is often impractical to collect fishery-independent data in remote environments, meaning data collected by a fishery is the main (or only) source of abundance data available (Maunder et al. 2006). A remote, artisanal, and self-reporting longline fishery in Cumberland Sound, Nunavut presented a unique site for evaluating trends in cold-water fish

stocks from limited data since CPUE data were recorded by individual fishermen and collected by the Fisheries and Oceans Canada (DFO) since 1987. Characterized by winter landfast ice, Cumberland Sound contains an ice-dependent seasonal Inuit fishery for Greenland halibut that is accessible from the town of Pangnirtung. Peak catches, in the early 1990s, reached greater than 400 tonnes, but recent years have shown reduced total catch (e.g. 2007 yielded only 3 tonnes), potentially due to increasingly shorter sea ice seasons, less stable ice conditions, and fewer fishermen participating in the fishery.

In this study, we evaluate catch per unit effort data (CPUE) from 1987 to 2003 within the fished areas of Cumberland Sound to determine how social and environmental factors have affected the observed catch trends. Past reports assessing Cumberland Sound Greenland halibut stocks have suggested over-harvest as a potential explanation for decreased CPUE (Pike 1994) and shrinking weight-at-age (Mathias and Keast 1996). Treble (2008) indicated that decline in mean length and reduced catch rates could be attributed to the commencement of a new fishery, changes in fishing location, or growth over-fishing. Though these explanations are potentially driving reduced CPUE, other factors may have affected local catch rates, including NAO or fishing characteristics of individual fishermen.

The process of data collection presented a unique opportunity to study the effects of fisherman behavior in Cumberland Sound because catch records were kept specific to individual fisherman. Of all fishery dependent data, CPUE is the most influenced by fisherman behavior—for example, through information sharing or increased fishing power (*sensu* Branch et al. 2006). Allen and McGlade (1986) indicated the importance of identifying the "actors" in a fishery and including their subjective responses/actions in a model rather than assuming a global desire of fishermen for optimal efficiency. Their analysis suggested two forms of fisherman

behavior relevant to Arctic fisheries: *Stochasts* who are willing to take new directions and risks in the fishery and are typically the more skilled, highlining individuals and *Cartesians* who simply follow the leaders (Allen and McGlade 1986). We suggest that CPUE trends in Cumberland Sound reflect these aspects of fisherman behavior while changes in the true abundance and distribution of Greenland halibut in Cumberland Sound result from variations in the physical environment.

Materials and Methods

Fishery characteristics

Cumberland Sound is an inlet on the southeastern side of Baffin Island, approximately 250 km long and 80 km wide (Fig. 1). The bottom topography, though variable, generally consists of shallow margins with central depths greater than 1500 m. Characterized by the formation of seasonal land-fast sea ice, the timing and extent of ice development varies annually based on latent heat of surface water and weather conditions (Treble 2008). The observed fishing locations from 1987 to 2003 were generally dependent on sea ice conditions and therefore catch locations varied annually Overall, fishing has been concentrated in the northern portion of the sound, within 70 km of Pangnirtung.

The Cumberland Sound halibut fishery is dependent on the formation of land-fast ice for travel to the deep-water fishing grounds and as a substructure for fishing. The fishery uses bottom longlines set through a hole in the ice and stretched along the bottom via a metal kite. On average, 100 hooks are placed at ~ 2 m intervals using gangions placed along the line; the longline is tied to a groundline approximately 2000 m long. Between 1987 and 1995, the fishery shifted from hand-operated to power winches, making it easier to fish multiple lines from one
location. However, the time required to bait and set additional lines was generally longer than the 2-3 hr set time when a single line was used, leading to an increase in the average duration of long-line sets. Because of the increase in abundance of larger halibut with depth, fishing effort was focused between 800-1200 m in Cumberland Sound when ice conditions allowed. Fishermen were also aware of halibut preference for mud substrates, and as such, directed their fishing in such areas. No offshore gill netting or trawling are permitted in the Sound.

Beginning in 1987, voluntary logbooks were offered to fisherman by DFO and catcheffort trends have been monitored since the formation of the fishery. Logbook data included longline soak time, number of hooks deployed, number of fish caught, bycatch species, fishing locations, and fisherman identification (all terms defined in Appendix 1). We used a monthly North Atlantic Oscillation (NAO) index taken from the Climate Analysis Section of the U.S. National Center for Atmospheric Research (Hurrell 1995). Additionally, we utilized logbook information to generate several additional covariates: 1) annual number of fisherman, 2) a pre/post storm dummy variable representing a storm in February of 1996 that caused 70% of fishermen to lose their gear and quit fishing (and used to examine annual trend changes pre/post storm), 3) a dummy variable representing presence of shark bycatch and 4) a categorical variable for each surname reported in the logbook data representing individual fishermen, used to structure a random-effects distribution of fisherman effects. The response variable was CPUE = number of Greenland halibut caught/100 hooks/hour.

Model structure

Following data exploration and organization, we established candidate models of CPUE based on available explanatory data, knowledge of the system, and awareness of highly

correlated parameters. All candidate models (Appendix 2) were run as generalized linear models (GLM) or generalized mixed-effects (hierarchical) models.

After log transformation of the response, all candidate models assumed a normal distribution of errors, e_i , run in the following form:

$$log(CPUE)_{i} = b_{0} + b_{i}x_{i} + e_{i}$$
, (1)

with β_0 as the model intercept, β_i as the model slope for any given covariate x_i . From the basic GLMs, we established an additional set of hierarchical models with location or fisherman included as random effects. This approach accounted for the non-independence of observations (e.g. individual fishermen) in predictors representing multiple levels through time (Zuur et al. 2007). Because only a subset of the data had precise location or fisherman records, we created two separate sets of hierarchical models. Essentially, we built hierarchical models from localized, simple relationships available from the logbook data in order to capture the broader, regional processes driving CPUE. Thus, we modeled a distribution of location and fisherman in hierarchical models that accounted for within-location and within-fisherman dependence. Because not all years were represented in the subsets, shark bycatch records were too rare to include in the hierarchical models. Additionally, the fisherman hierarchical model did not include the number of fishermen variable since a high correlation between the number of fishermen and the storm dummy variable existed in the fisherman subset.

The candidate mixed-effects models were formed from:

$$\log(\text{CPUE})_{it} = b_0 + b_i x_{it} + e_{it} + a_i,$$
(2)

where a₁ represents the random effect for either location or fisherman, modeled as an independent and normally distributed variable. All candidate models were run using the glm and nlme packages in the statistical package R (R Development Core Team, 2008). Evidence from

the data supporting individual models were compared using Akaike's Information Criteria (AIC; Burnham and Anderson, 2002) and model goodness-of-fit (GOF) was assessed using likelihood ratio tests (LRT) of each fitted model relative to a null (intercept-only) model (Zurr et al. 2007).

Results

Data exploration

Pairwise plotting of explanatory variables showed no collinearity in the full data set or location subset, but in the fisherman subset, a strong correlation existed between the number of fishermen and the storm term (cor = -0.91). A plot of raw log(CPUE) data through time for Cumberland Sound indicated a major drop in Greenland halibut abundance since 1990-1992 (Fig. 2a) with a steady decline in CPUE from the start of the fishery in 1987 to the lowest CPUE in 1999 followed by an apparent rapid increase in catch rates until 2002. A comparison of the raw CPUE plot to a plot of annual NAO index (Fig. 2b) showed no obvious similarities but comparison of a monthly NAO index plot for all years to a monthly CPUE plot for all years showed a parallel trend (Fig. 2c). Declines or increases in the NAO monthly index appeared to correspond with a decrease or increase in Cumberland Sound catch rates. A plot of fisherman participation (Fig. 2d) showed an increasing number entering the fishery after its onset, a peak participation in 1995, followed by a sharp drop after the storm of 1996.

Generalized Linear Model results

The top-ranked GLM (MS11; Appendix 2) included all fixed effects. The selected GLM and top-ranked hierarchical models all included the effects of year and NAO (Table 1); all three selected models showed a strong ability to predict log(CPUE) when predicted log(CPUE) values

were plotted against observed log(CPUE) values (Fig. 3). Model goodness-of-fit (GOF) likelihood ratio tests and quantile-quantile plots for all top-ranked models showed adequate model fits for the assumed normally-distributed errors.

For GLM MS11, the year effect (Fig. 4) indicated a general decrease in catch rates over time, suggesting reduced abundance of Greenland halibut in the Sound through time. NAO had a positive effect on log(CPUE); an increased index was associated with increased catch rates. Categorical month variables showed February through May had higher log(CPUE) than January with the greatest catch rates occurring in February and March. The interaction term between storm and year, shared by the best-fitting GLM and fisherman hierarchical models, captured an increase in the predicted catch rate slope after the 1996 storm, where the annually decreasing trend in catch rates changed to an increasing trend in catch through time.

Because of the rarity of shark records within the data, only the GLM models could include the shark presence/absence variable, and it was identified as an important predictor of log(CPUE). The negative value for shark presence indicated that the presence of a shark on the line reduced the predicted log(CPUE). Only the GLM models identified the number of fishermen variable as important, having a negative effect on catch rates. More fisherman in the industry reduced log(CPUE). Thus, when a GLM alone was used to model CPUE (i.e. location and fishermen were not accounted for), the number of fishermen appeared to be an important factor in predicting CPUE.

Location Hierarchical Model

Based on AIC values, the best location model included the fixed effects of NAO and the categorical month variable (LM7; Appendix 2). The year effect (Fig. 4), like the GLM, showed a

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decrease in catch rates through time, suggesting reduced Greenland halibut abundance through time. The NAO effect on catch rates was positive, but the effect size was larger in the location hierarchical model than the GLM, suggesting that when location is accounted for, the estimated NAO effect on Greenland halibut increases. The categorical month variables showed greatest catch rates during March, followed by February. However, the magnitude of the effect of April was reduced in the location hierarchical model from the GLM while the effect of May became negative. The reduced month effect size indicates that the ability to capture Greenland halibut in later months was unrelated to the fishing location.

Fisherman Hierarchical Model

The AIC-ranked best model for the fisherman data included the fixed effect of NAO, month, and the interaction term of storm and year (FM7; Appendix 2). Year was negatively associated with log(CPUE) (Fig. 4), but the magnitude of the year effect for FM7 was larger than both the GLM and LM7; a decline in relative abundance was most pronounced when individual fisherman were accounted for. A positive NAO paralleled positive log(CPUE), but the NAO effect size was largest for the fisherman model. Thus, when individual fishermen are considered, the potential importance of NAO in driving catch rates and relative abundance increases still further. The categorical month variable mirrored the location hierarchical model with a negative effect of May, but the highest catch rates were predicted log(CPUE) increased relative to the no-interaction model. The fisherman model's storm effect size increased relative to a positive catch rate slope when individual fishermen effects are modeled directly.

Discussion

When modeling CPUE, annual trends typically reflect changes in annual abundance (Maunder and Punt 2004), and negative values are thought to represent decreases in relative abundance through time. However, the fact that CPUE is oftentimes not proportional to abundance (Ultang 1976, Garrod 1977) demands explanatory data to standardize CPUE and deal with the associated assumptions (Maunder and Punt 2004). Despite the data limitations in Cumberland Sound, we have shown that changes in relative abundance may not have been fishery driven and trends in CPUE represented an inconsistent index of Greenland halibut relative abundance. Environmental factors such as NAO and season appear to be driving trends in fish abundance while aspects of the fishery—particularly individual fishermen characteristics—are affecting reported catch rates. Importantly, the magnitude of environmental effect sizes was compromised when catch differences among fishermen were ignored. Thus, we were able to provide an informative analysis of the Cumberland Sound catch rate trends in the context of data restrictions.

In the GLM analysis of the full dataset, all available covariates were identified as important predictors of Greenland halibut catch rates. The presence of Greenland sharks as bycatch, a variable only included in the GLM, negatively affected catch rates, indicating that sharks either prey on unhooked fish, scavenge hooked fish before being hooked themselves, or sever the longline. The tendency of Greenland sharks to entangle themselves in and/or break the longline is a major source of time and gear loss to Cumberland Sound fishermen (Pike 1994). The ability of a species to survive, escape, or avoid scavengers once hooked determines the catch actually brought to the surface, and amount of time a baited hook is available to fish will influence how many fish are captured (Ward et al, 2004). Though typically greater soak time allows for greater catch rates, the risk of bycatch or scavenging also increases. Additionally, Greenland halibut may trade food for safety (McNamara and Houston 1990), avoiding longlines where sharks are present. The positive correlation between shark catch rates and set duration suggests that reducing set time would reduce Greenland shark bycatch, but since the transition to a power winch, set times have actually increased.

The number of fisherman present in the fishery was only identified by the GLM analysis as significant. This variable represents a measure of resource competition, defined as use of the same resource by several foragers (*sensu* Birch 1957). Interference competition occurs when foraging success is reduced by interactions among foragers or between forager activities, and exploitative competition occurs when limited resources are shared (Park 1954)—potentially leading to a tragedy of the commons in which individuals receive the economic benefits associated with resource exploitation while the consequences of stock depletion are shared by all resource users (Hardin 1968).

The parameter estimate for number of fisherman in our GLM was negative, indicating that greater fishery participation was correlated with an overall reduced efficiency of the fishery. In fact, as the number of fisherman participating increased, the CPUE associated with individual fisherman decreased. However, the Cumberland Sound fishermen work in clusters—they fish near each other in one general location, suggesting that location is tied to the effect of fishermen density. The top-ranked location hierarchical model did not find the number of fishermen as a significant effect, meaning that when recorded location is considered a sample of all locations, catch rates did not actually decline as more fishermen participated. However, although the location hierarchical model suggests that it is unlikely overfishing occurred through either exploitative or interference competition, it is also possible the model could simply not detect an effect.

Both hierarchical models and the GLM identified two physical factors strongly associated with catch rates: NAO index and month. The monthly North Atlantic Oscillation (NAO) index had a significant positive effect on log(CPUE) of Greenland halibut, consistent with other fisheries in the North Atlantic (Bøgstad and Gjøster 1994, Friedland et al. 1998, Dickson and Turrell 1999). The NAO index is measured as the difference between the subtropic high-pressure zone over the Azores and the polar low-pressure zone over Iceland (Hurrell 1995). A positive NAO index represents an increased pressure difference, i.e. an Azores High and an Icelandic Low, and shifts in the NAO mediate changes in temperature, ocean circulation, and winter storms (Ottersen et al. 2001). The Davis Strait and Labrador Sea are mixing sites of both Arctic and sub-Arctic waters (Dunbar 1951, Bailey 1957), and changes in the boundaries of these waters influence the distribution of marine fauna in Cumberland Sound (Aitken and Gilbert 1989). An increased monthly NAO index represented a change in Arctic and sub-Arctic currents, and it was strongly associated with increased monthly catch rates in Cumberland Sound. In the Norwegian Sea, distribution of Greenland halibut was related to the hydrographic front between surface Atlantic water and colder, deeper waters (Bakken et al. 1975, Bergstad and Isaksen 1987, Bergstad 1990), and in the Faroe-Shetland Channel, the best Greenland halibut catch rates were in intermediate waters originating in the Arctic (Bullough et al. 1998). Thus, NAO-mediated temperature changes could affect the distribution of Greenland halibut within Cumberland Sound.

The increased NAO effect in the mixed-effect models indicates that a high NAO index is associated with higher CPUE, independent of fisherman or catch location. Thus, NAO-mediated

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environmental changes were likely affecting Greenland halibut distribution since parallel trends in NAO index and CPUE were unrelated to fishery aspects such as fisherman or location. Distribution changes have been observed in other fish as well, such as Atlantic salmon (*Salmo salar*) whose thermal habitat size shrunk during years of positive NAO index and expanded during negative phases (Friedland et al. 1998, Dickson and Turrell 1999). A high NAO could expand thermal habitat size for Greenland halibut in Cumberland Sound and make them more available to fisherman, thereby increasing the catchability coefficient.

Separate from the monthly NAO index, both hierarchical models and the GLM contained an effect from the categorical variable month, i.e. different months affected CPUE differently. We included the months January-May as factors, and in both models, February and March had the highest CPUE relative to January. Some variation among months could likely be attributed to the NAO, but the correlation coefficient (cor=-0.58) suggests only a partial influence of NAO on monthly conditions. Fishing location varied monthly based on formation and break-up of sea ice, but when fishing location was included as a random effect, the variation in monthly CPUE became more pronounced. In fact, the change of May to a negative effect from the GLM and hierarchical models suggests that accessibility of fisherman to halibut through season and change of fisherman through season were not affecting catch rates. Rather, the likely mechanism was an environmental effect associated with month. This is consistent with previous findings for summer longline catches in Cumberland Sound where catch rates were reduced relative to winter longline catches (Northlands Consulting 1994, Mathias and Keast 1996) and only trawl and gillnet gear fished at deepwater stations within Cumberland Sound produced catches (Northlands Consulting 1994). Observed changes in catchability with season and between gears suggest environmental factors could be influencing fish distribution.

One possible reason for a change in behavior could be migration associated with the onset of maturity in Greenland halibut. Distribution and size data from a trawl survey suggest a late summer movement of Greenland halibut to spawning grounds in the deep waters (>1000 m) of Davis Strait (*Jø*rgensen 1997). Additionally, seasonal migration between feeding and spawning areas has been observed for Greenland halibut in the Gulf of St. Lawrence (Bowering 1982) and Icelandic waters (Sigurdsson 1979). However, if Greenland halibut are migrating seasonally, catches between Cumberland Sound and Davis Strait would be expected; an exploratory fishery in Cumberland Sound caught no Greenland halibut at the Sound's mouth during August/September of 1994 (Northlands Consulting 1994). This absence suggests that if the fish leave, they do so before late summer or their behavior reduces their catchability to near zero. Additionally, reduced catch could also result from a general dispersal within Cumberland Sound as opposed to an out-migration to Davis Strait. Nonetheless, parasite fauna on Cumberland Sound fish could not be discriminated from Hawke Channel in the Labrador Sea, implying movement to/from the Sound (Arthur and Albert 1993).

The most widely applicable conclusion from the present analysis is that individual fishermen characteristics can be a critical factor in understanding trends in fishery-dependent CPUE data. Because fishermen report CPUE themselves, it is the data source most likely to be influenced by their behavior (Branch et al. 2006); teasing apart the effects of behavior from other potential covariates is an important, but not often possible, step in analysis of fishery-dependent data. The unique nature of this dataset allowed us to explore fisherman behavior and demonstrate that, at a small scale, individuals can substantially affect reported fishery trends.

For Cumberland Sound, participation in the fishery rapidly increased after the initial successful years. High payoffs and the introduction of power winches to increase fishing

efficiency attracted new individuals each year until a storm in 1996 prevented subsequent return. Consistent with predictions from behavior theory (Branch et al. 2006), differences in longlining skill varied widely among fisherman, causing distorted trends in GLM environmental covariates (Fig. 5). Despite the fact that fishermen are individuals with different skills, backgrounds, fishing behavior, and honesty in reporting, consideration of fisherman dynamics remains relatively unemployed in fishery modeling—particularly for artisanal fisheries. The application of hierarchical modeling provides a cohesive approach for incorporating and understanding the behavioral effect in fishery-dependent data, and in this study, the fixed effect for storm actually embodied effects from individual fisherman behavior.

The presence of risk-taking stochasts versus low-risk cartesians emerged in the fisherman hierarchical model as the pre/post storm factor. Included as a dummy variable in both the GLM and the fisherman mixed effects models, the effect of the 1996 storm changed model-predicted CPUE from negative to positive, i.e. CPUE increased after the storm, most likely due to changes in which fishermen were participating. Essentially, the fishermen who most likely remained or re-entered the fishery after a gear loss of 70% were stochasts because their behavior was not influenced by fishing conditions (Allen and McGlade 1986). Because stochasts are also typically risk-taking highliners who are more efficient at catching fish (Allen and McGlade 1986, Holland and Sutinen 2000), CPUE through time increased when the high-quality fishermen remained and caused a reduced overall fishery effort. In fact, the top-ranked hierarchical fisherman model shows an increasing trend in CPUE for those highliners who remained in the fishery after 1996 (Fig. 6), but the model predicts a decrease in CPUE for the fishermen who dropped out, implying that those who left were also less skilled. Thus, because the quality of individual fishermen in the

Cumberland Sound fishery is tied so closely to catch rates, the assumption that CPUE represents relative fish abundance was not met.

These effects are evident from the change in the storm effect size between the GLM and the fishermen hierarchical model: the storm term in both models decreased the intercepts but increased predicted CPUEs per year, yet the size of the effect was increased in the hierarchical model. If the pre/post storm variable represents a change in the skill of the average fisherman in the fishery, then the increase in its effect size from the GLM to the mixed-effects model suggests those remaining in the fishery were in fact more skilled. Thus, despite accounting for variation among fisherman with the inclusion of a random effect, the importance of the storm remained—fitting our a priori expectations of fisherman influence on reported CPUE.

Conclusion

We suggest that trends in the abundance and distribution of Greenland halibut, as represented by catch rates, result from variations in the physical environment rather than the fishery since the self-reported CPUE in the Cumberland Sound fishery reflects a considerable influence of individual fisherman behavior and location. Increased effect sizes and trends from the GLM to the hierarchical models show the importance of accounting for fishery characteristics that increase observation error in catch rates to more accurately assess relative fish abundance. The time-series, multi-level, and random nature of fishery-dependent data make it inherently hierarchical and therefore the utilization of random effects in a hierarchical model is a more appropriate approach to structure fishery-dependent data analysis than regular GLMs. Despite limited data availability on this remote, self-reporting fishery, our understanding of the mechanisms affecting catch rates of Greenland halibut in Cumberland Sound strongly implicate local, environmental processes rather than human-mediated effects.

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Parameter	GLM ± 1SE	LM7 ± 1SE	FM7 ± 1SE	
Intercept	1.4461 ± 0.050	0.7109 ± 0.125	0.7894 ± 0.452	
Year	-0.1178 ± 0.005	-0.1146 ± 0.051	-0.2447 ± 0.018	
NAO	0.0111 ± 0.006	0.0541 ± 0.009	0.0603 ± 0.008	
Storm	-0.9804 ± 0.084		-1.1551 ± 0.071	
Storm*Year	0.2179 ± 0.014		0.3719 ± 0.018	
Month(February)	0.2900 ± 0.048	0.3077 ± 0.067	0.3417 ± 0.457	
Month(March)	0.3708 ± 0.048	0.1751 ± 0.066	0.2106 ± 0.455	
Month(April)	0.2214 ± 0.054	0.0710 ± 0.069	0.1758 ± 0.455	
Month(May)	0.1636 ± 0.066	-0.6930 ± 0.088	-0.0416 ± 0.458	
Shark Presence	-0.1970 ± 0.034			
Number of Fisherman	-0.0029 ± 0.0002			
Explained Deviance	0.283	0.317	0.348	

Table 2.1. Parameter estimates and standard errors for the Generalized Linear Model (GLM MS11) and hierarchical models.



Figure 2.1. Location of the Inuit commercial fishery targeting Greenland halibut in Cumberland Sound, Nunavut, Canada.

Figure 2.2. Trends in response and covariates. A) Annual average catch per unit effort measured as log(# Greenland halibut/100 hooks/hour) through time, 1987-2003; catch rates declined during1990s. B) Number of fishermen participating in the Cumberland Sound fishery each year; most fishermen withdrew after a 1996 storm destroyed 70% of all gear. C) Average annual NAO index through time, 1987-2003. D) Monthly NAO index averaged for all years, 1987-2003; monthly NAO indexes paralleled monthly Greenland halibut catch rates.



Figure 2.3. Comparison of predicted log(CPUE) against observed log(CPUE) for Greenland halibut in Cumberland Sound from the best AIC-ranked GLM (MS11), location hierarchical model (LM7), and fisherman hierarchical model (FM7).



Figure 2.4. Observed log(CPUE) through time with the predicted log(CPUE) through time for the GLM (MS11), location hierarchical model (LM7), and fisherman hierarchical model (FM7). The catch rates predicted in the hierarchical models more closely follow observed catch rates than the GLM predicted values.







Figure 2.6. Predicted catch per unit effort measured as log(# Greenland halibut/100 hooks/hour) for each fisherman in the Greenland halibut commercial fishery of Cumberland Sound as derived from the fisherman hierarchical model. Lines are predicted catch rates while points are observed catch rates. For the fishermen who remained in the fishery after 1996, a general increasing trend in catch is predicted, while those who dropped out have a predicted general decline in catch rates.



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Appendix 2.1. Variables recorded (taken from Pangnirtung fishermen voluntary logbooks and other sources).

YEAR	Year of catch observation
JDAY	Jday of catch observation
DATE	Date of catch observation
MONTH	Month of catch observation
	1 = January, 2 = February,
	3 = March, $4 =$ April, $5 =$ May
SET	Time of day line was set
HAULED	Time of day line was hauled
DURATION	Soak time (in hours)
HSET	# Hooks set on line
HLOST	# Hooks lost during soak
HFISHED	# Hooks returned when line hauled
TURBOT	# of Turbot caught
Turb/100hk	(TURBOT/HFISHED)*100
Turb/100hk/hr	Turb/100hk/DURATION
SHARK	# Greenland Sharks caught
Shark/100hk	(SHARK/HFISHED)*100
Shark/100hk/hr	Shark/100hk/DURATION
RAY	# Skates or Rays caught
LOCATION	Sites fished, A-H
FISHERMAN	Full name of fisherman for observation

FAMILY	Surname of fisherman for observation
NAO	North Atlantic Oscillation index (monthly)
STORM	Dummy variable:
	0 = before Feb. 1996 storm
	1 = after Feb. 1996 storm
SHARKPRES	Dummy variable:
	0 = shark not captured
	1 = shark(s) captured
NUMFISH	Total # of fisherman for year of observation

Appendix 2.2. All candidate models run to predict catch per unit effort of Greenland halibut in Cumberland Sound.

Origin. M0	al Candidate (log(CPUE)	General Linear Models = b ₀
M1		$= b_0 + b_1$ Year
M2		$= b_0 + b_1$ Month
M3		$= b_0 + b_1$ Fisherman
M4		$= b_0 + b_1$ NumberFishermen
M5		$= b_0 + b_1$ Storm
M6		$= \mathbf{b}_0 + \mathbf{b}_1 \mathbf{NAO}$
M7		$= b_0 + b_1$ Location
M8		$= b_0 + b_1 Location + b_2 NAO$
M9		$= b_0 + b_1$ Storm $+ b_2$ NAO
M10		$= b_0 + b_1 Year + b_2 Month$
M11		$= b_0 + b_1 Year + b_2 NAO$
M12		$= b_0 + b_1$ Storm $+ b_2$ Month
M13		$= b_0 + b_1$ NumberFishermen+ b_2 Fisherman
M14		$= b_0 + b_1$ Storm $+ b_2$ NAO $+ b_3$ Fisherman
M16		$= b_0 + b_1$ Storm + b_2 Month + b_5 Fisherman
M16		$= b_0 + b_1$ NumFish + b_2 Year + b_3 NAO
M17		$= b_0 + b_1$ NumFish + b_2 Year + b_3 Month
M18		$= b_0 + b_1$ NumFish + b_2 Year + b_3 NAO + b_4 Fisherman
M19		$= b_0 + b_1$ NumFish + b_2 Year + b_3 Month+ b_4 Fisherman
M20		$= b_0 + b_1 Location + b_2 NAO + b_3 Fisherman$

M21	$= b_0 + b_1 Location + b_2 Month + b_3 Fisherman$
M22	$= b_0 + b_1 Location + b_2 NAO + b_3 NumFish$
M23	$= b_0 + b_1 Location + b_2 Month + b_3 NumFish$
M24	$= b_0 + b_1 Location + b_2 NAO + b_3 NumFish + b_4 Fisherman$
M25	$= b_0 + b_1Location + b_2Month + b_3NumFish + b_4Fisherman$
M26	$= b_0 + b_1$ Year $+ b_2$ Month $+ b_3$ Fisherman
M27	$= b_0 + b_1$ Year $+ b_2$ NAO $+ b_3$ Fisherman
Candidate CPUE Ge	eneral Linear Models for all years, 1987-2003
MS0 log(CPUE)	$= b_0 + e_1$
MS1	$= b_0 + b_1 Year + e_1$
MS2	$= b_0 + b_1 Year + b_2 Month + e_1$
MS3	$= b_0 + b_1 Year + b_2 Month*NAO + e_1$
MS4	$= b_0 + b_1 Y ear + b_2 Month + b_3 NAO + e_1$
MS5	$= b_0 + b_1 Year + b_2 SharkPres + e_1$
MS6	$= b_0 + b_1$ Year + b_2 Month*NAO + b_3 SharkPres + e_1
MS7	$= b_0 + b_1 Year + b_2 Month + b_3 SharkPres + e_1$
MS8	$= b_0 + b_1 Y ear + b_2 Storm + b_3 Y ear^* Storm + b_4 Month + e_1$
MS9	$= b_0 + b_1 Year*Storm + b_2 Month*NAO + b_3 SharkPres + e_1$
MS10	$= b_0 + b_1 Year*Storm + b_2 Month*NAO + b_3 SharkPres +$
	b₄NumFish + e₁
MS11	$= b_0 + b_1 Storm + b_2 Month + b_3 NAO + b_4 SharkPres + b_5 NumFish +$
	e,
MS12	$= b_0 + b_1 Year^*NAO + e_1$

Candidate Location Hierarchical models

LM0	$log(CPUE) = b_0 + e_1 + Location$
LM1	$= \mathbf{b}_0 + \mathbf{b}_1 \mathbf{Y} \mathbf{ear} + \mathbf{e}_1 + \mathbf{Location}$
LM2	$= b_0 + b_1$ Year $+ b_2$ Month $+ e_1 +$ Location
LM3	$= b_0 + b_1 Year + b_2 NAO + e_1 + Location$
LM4	$= b_0 + b_1$ Year $+ b_2$ Storm $+ b_3$ Year *Storm $+ e_1$ + Location
LM5	$= b_0 + b_1$ Year $+ b_2$ NumFish $+ e_1$ + Location
LM6	$= b_0 + b_1$ Year $+ b_2$ NumFish $+ b_3$ Month $+ e_1$ $+$ Location
LM7	$= b_0 + b_1$ Year $+ b_2$ NAO $+ b_3$ Month $+ e_1 +$ Location
LM8	$= b_0 + b_1$ Year $+ b_2$ Month*NAO $+ e_1 + $ Location
LM9	$= b_0 + b_1$ Year $+ b_2$ NumFish $+ b_3$ NAO $+ e_1 + Location$
LM10	$= b_0 + b_1 Year + b_2 NumFish + b_3 Month*NAO + e_1 + Location$
LM11	$= b_0 + b_1 Year + b_2 NumFish + b_3 NAO + b_4 Month + e_1 + Location$
LM12	$= b_0 + b_1 Y ear + b_2 Storm + b_3 Y ear * Storm + b_4 NAO + e_1 + b_4 NAO + b_1 NAO + b_1 AO + b_1 AO + b_2 AO + b_2 AO + b_1 AO + b_2 AO + b_2 AO + b_2 AO + b_1 AO + b_2 AO + b_2$
	Location
LM13	$= b_0 + b_1 Year + b_2 Storm + b_3 Year^* Storm + b_4 Month + e_1 + b_4 Month + b_1 + b_4 Month + b_4 Month + b_1 + b_4 Month + b_$
	Location
LM14	$= b_0 + b_1 Y ear + b_2 Storm + b_3 Y ear * Storm + b_4 Month + b_5 NAO +$
	e_1 + Location
LM15	$= b_0 + b_1 Year + b_2 Storm + b_3 Year * Storm + b_4 NAO + b_5 NumFish$
	$+ e_1 + Location$
LM16	$= b_0 + b_1 Y ear + b_2 Storm + b_3 Y ear * Storm + b_4 Month + b_5 NumFish$
	$+ e_1 + Location$

LM17
$$= b_0 + b_1 Year + b_2 Storm + b_3 Year^* Storm + b_4 Month + b_5 NAO +$$

 b_6 NumFish + e_1 + Location

Candidate Fisherman Hierarchical models

FM0	$log(CPUE) = b_0 + e_1 + Fisherman$
FM1	$= b_0 + b_1 Year + e_1 + Fisherman$
FM2	$= b_0 + b_1 Year + b_2 Month + e_1 + Fisherman$
FM3	$= b_0 + b_1 Year + b_2 NAO + e_1 + Fisherman$
FM4	$= b_0 + b_1 Year + b_2 Storm + b_3 Year * Storm + b_4 NAO + e_1 +$
	Fisherman
FM5	$= b_0 + b_1 Year + b_2 Storm + b_3 Year * Storm + b_4 Month + e_1 +$
	Fisherman
FM6	$= b_0 + b_1$ Year $+ b_2$ Month $+ b_3$ NAO $+ e_1 +$ Fisherman
FM7	$= b_0 + b_1 Y ear + b_2 S torm + b_3 Y ear^* S torm + b_4 Month + b_5 NAO + e_1$
	+ Fisherman
FM8	$= b_0 + b_1 Y ear + b_2 S torm + b_3 Y ear * S torm + b_4 Month * NAO + e_1 + b_4 Month * NAO + b_1 + b_1 + b_2 Month * b_2 + b_1 + b_2 Month * b_1 + b_2 Month * b_2 + b_1 + b_2 Month * b_2 + b_1 + b_2 Month * b_2 b_2 $
	Fisherman
FM9	$= b_0 + b_1 Year + b_2 NumFish + e_1 + Fisherman$
FM10	$= b_0 + b_1$ Year $+ b_2$ NumFish $+ b_3$ Month $+ e_1 +$ Fisherman
FM11	$= b_0 + b_1$ Year $+ b_2$ NumFish $+ b_3$ NAO $+ e_1 +$ Fisherman
FM12	$= b_0 + b_1 Y ear + b_2 NumFish + b_3 NAO + b_4 Month + e_1 + Fisherman$
FM13	$= b_0 + b_1 Year + b_2 NumFish + b_3 Month*NAO + e_1 + Fisherman$

CHAPTER THREE

USING STABLE ISOTOPE ANALYSIS TO ASSESS THE FEEDING ECOLOGY OF GREENLAND HALIBUT IN CUMBERLAND SOUND*

^{*} This manuscript is co-authored by S.T. Dennard, B.C. McMeans, and A.T. Fisk.

Introduction

The use of naturally occurring stable isotopes of elements such as carbon (δ^{13} C) and nitrogen (δ^{15} N) has advanced the study of energy flow and trophic ecology (Michener and Schell 1994) since stable isotope ratios in consumer tissues can be related to the ratios in their diet (DeNiro and Epstein 1978, 1981). Little change between trophic positions occurs for δ^{13} C, but the differences can be used to distinguish benthic/inshore food webs from pelagic/offshore food webs— δ^{13} C values tend to be more enriched in benthic/inshore systems (Hobson and Welch 1992, Hobson et al. 1994, France 1995). However, enrichment of the heavy isotope of nitrogen occurs with trophic position at a relatively constant rate, allowing relative trophic positions to be derived from δ^{15} N (Michener and Schell 1994). Thus, stable isotopes can provide information on feeding location (e.g. benthic or pelagic) and trophic relationships, and when used in conjunction with other dietary analysis methods (e.g. stomach content) or previous knowledge, they can provide confirmation or clarification of feeding ecology.

The Greenland halibut is a commercially popular fish species with a circumpolar distribution (Nielsen 1986). In Cumberland Sound, Nunavut, the Greenland halibut are targeted by an artisanal, Inuit longline fishery. Although many studies have focused on Greenland halibut diet, they have been generally restricted to stomach content analysis with little use of stable isotopes. Efforts to assess the diet of the Cumberland Sound stock have placed them at a 4th trophic level with a pelagic carbon source (Fisk et al. 2002). Specific species in Greenland halibut diets vary geographically, but trends in feeding have been observed: juvenile Greenland halibut (< 20 cm) feed primarily on small crustaceans and cephalopods, individuals 20-69 cm predominately consume small fish (e.g. herring, capelin), and individuals >69 cm target demersal fish (e.g. redfish; Bowering and Lilly 1992, Dawe et al. 1998). Overall, stomach content and

visual observations show that despite being a flatfish, Greenland halibut tend to feed pelagically (Orr and Bowering 1997). However, Greenland halibut diet depends on many factors, and diet changes with area, depth, or predator size (Bowering and Lilly 1992, Sólmundsson 1993, Rodríguez-Marin et al. 1997). Pedersen and Riget (1993) suggest that Greenland halibut feed on the most abundant prey within its habitat, preventing assumptions of a Greenland halibut stock's dietary preferences in an unstudied system where potential prey items are unknown.

The Cumberland Sound Greenland halibut stock is of commercial importance to the Inuit of Cumberland Sound, but recent years have seen changes in climate: late formation of landfast sea ice and shorter ice seasons. Additionally, there are efforts to both expand the artisanal fishery and to extend it into summer months. Trophic dynamics are sensitive to environmentallymediated effects and human-mediated effects. Thus, to assess and predict potential stock responses to changes in the Cumberland Sound ecosystem requires an initial understanding of trophic position and carbon sources for the local Greenland halibut stock.

The purpose of this study was to provide preliminary information on the Greenland halibut diet in Cumberland Sound, focusing on two known potential prey items, capelin (*Mallotus villosus*) and shrimp (*Lebbeus polaris*), and to assess the utility of stable isotopes to define the feeding ecology of a large arctic fish. Capelin represent a pelagic, surface-feeding organism (Templeman 1948) while shrimp are known to be epibenthic feeders (Birkely and Gulliksen 2003)—thereby allowing these species to act as proxies of their respective habitats. Copepods (*Calanus hyperboreus*) and scallops (*Chlamys islandica*) were also included in this study; copepods and scallops represented the baseline for pelagic and benthic carbon sources, respectively, and a trophic position of 2 (i.e. primary herbivores; Hobson et al. 2002).

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Materials and Methods

Sampling

Greenland halibut (n = 26, 17 males, 7 females) were collected in April 2008 in the Cumberland Sound fishery via bottom longline. All halibut were measured for total length and assigned to size classes. Because of the current discrepancy in aging Greenland halibut (e.g. 50 cm Greenland halibut could grow ~1-5 cm/year depending on the aging method; Treble 2008), 6 size classes were created with 5 cm intervals: <55, 55-60, 60-65, 65-70, 70-75, >75. Samples of dorsal muscle tissue and liver tissue were collected, stored in plastic bags, and frozen until analysis. Stomach contents, if any, were identified as close to species level as possible. Shrimp and copepod samples were collected from Cumberland Sound in April 2008 and capelin and scallop samples were collected in August 2008. Shells of shrimp and scallops were removed prior to analysis.

Stable isotope analysis

Copepods were analyzed whole and multiple individuals were combined for each sample to achieve sufficient tissue weight. Soft tissue of individual scallops and shrimps were analyzed while capelin and Greenland halibut were subsampled to approximately 1 gram before freeze drying 48 hours. Tissue was ground using a ball mill grinder (SPEX CertiPrep 8000-D ball milling unit, SPEX CertiPrep, Metuchen, NJ, USA). Samples were homogenized in 5 ml of 2:1 chloroform:methanol with 30 seconds of vortexing, left 24 hours, and then decanted for gravimetric determination of lipids (Post et al. 2007). The process was repeated for thorough extraction and solvents were dried off the tissue via 24 hours in a fumehood. Between 400-600 µg of tissue was weighed into tin capsules and stable carbon and nitrogen isotope ratios were provided from a continuous flow isotope ratio mass spectrometer (IRMS, Finnigan MAT Delta^{plus}, Thermo Finnigan, San Jose, CA, USA).

Stable isotope abundances are expressed in delta (δ) values as the deviation from standards in parts per thousand (∞) from the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$
⁽¹⁾

where X is ¹⁵N or ¹³C and R is the ratio ¹⁵N/¹⁴N or ¹³C/¹²C. The standard reference material was Pee Dee Belemnite carbonate for CO₂ and atmospheric nitrogen N₂. The analytical precision for δ^{15} N was <0.22 and <0.24 for δ^{13} C, based on more than 100 analyses of NIST standard (bovine muscle) across multiple sample runs. Based on a recent single run of NIST standards sucrose (*n* = 13) and ammonium sulphate (*n* = 13), δ^{15} N was 0.14 and δ^{13} C was 0.05

Data analysis

Because the Greenland halibut were assigned to size classes, the relationship between Greenland halibut size, sex, and δ^{15} N (muscle tissue) was investigated using a generalized linear model (GLM). Confidence intervals at 95% were calculated to compare Greenland halibut tissue isotope values between size classes and to other food web species. All analyses were run in R (R Development Core Team 2008).

Trophic position (TP) was determined relative to the sampled copepod, which was assumed to be a primary herbivore occupying a trophic position of 2 (Hobson et al. 2002). Relative trophic positions of consumers were calculated based on muscle tissue δ^{15} N using:

Trophic position = 2 +
$$(\delta^{15}N_{consumer} - \delta^{15}N_{Calanus})/3.4$$
 (2)

and assuming an isotopic discrimination factor among trophic positions of 3.4‰ (Post 2002).

Isosource mixing model software (Philips and Gregg 2003) was used to assess dietary contributions of both prey species to the diet of the Greenland halibut. This model calculates feasible combinations of primary producer isotope signatures, $\delta^{15}N$ and $\delta^{13}C$, that explain observed consumer isotope signatures. Outputs are given as the range of all possible solutions indicating minimum and maximium contributions of each food source consistent with isotope mass balance (Urton and Hobson 2005, Inger et al. 2006). The model source increment was set at 1% and the tolerance at 0.7%. Isosource ouputs are reported here as median and 1-99th percentile range of solutions (Bernstead et al. 2006).

Another stable isotope mixing model, MixSIR, (Semmens and Moore 2008) was also applied to assess relative contributions of different prey to the consumer. Unlike Isosource, MixSIR uses a Bayesian framework to estimate probability distributions of source contributions to a mixture while accounting for uncertainty associated with multiple sources, fractionation, and isotope signatures. We used previously published fractionation values of $1.0 \pm 0.4\%$ for δ^{13} C and $3.4 \pm 1.1\%$ for δ^{15} N. The maximum importance ratio was below 0.001, indicating model effectiveness in estimating true posterior density (Moore and Semmens 2008). MixSIR results are presented as median, 5th, and 95th percentiles.

Results

Total length ranged in size from 51.4 cm to 85.6 cm with a mean \pm 95% confidence interval (CI) of 62.44 \pm 2.95 cm. The majority of stomachs were empty (89%) with three stomachs containing shrimp, mysids, or unidentifiable fish.

Of species analyzed from the Cumberland Sound food web for Greenland halibut feeding, Greenland halibut size class 6, >75 cm, had the highest $\delta^{15}N$ (17.13) and scallops the

lowest δ^{15} N (8.58 ± 0.18) (Table 1, Fig. 1). The lowest δ^{13} C belonged to copepods (-20.52 ± 0.82) and highest δ^{13} C to scallop (-18.55 ± 0.38) (Table 1). The mean δ^{13} C value for Greenland halibut was -18.95 ± 0.16%, with little variation across sizes (Table 1).

Trophic positions were calculated for each species using equation (2) and are listed in Table 1. The Greenland halibut was calculated at a trophic position of approximately 4.0 for all size classes (Table 1). Only the largest size class, >75 cm and for which n = 1, had a different trophic position (TP=4.3). Assessment of size in the GLM found length as a significant predictor of Greenland halibut $\delta^{15}N$ (p = 0.0022), but when a sex effect was also included in the GLM, neither effect was significant (sex p = 0.9124, length p = 0.0893). Overlapping 95% confidence interval bars indicated no significant difference in $\delta^{15}N$ across Greenland halibut size classes, but because the largest size class was only n = 1, a confidence interval could not be calculated. Thus, by assessing length as categorical variable in the GLM, i.e. six size classes, only the largest size class was a significant predictor of $\delta^{15}N$.

Capelin was identified as the main component of the Greenland halibut's diet by both IsoSource and MixSIR (Table 2). Capelin and shrimp were the only potential prey items included in the models, although other prey items that were not sampled also likely contributed to the Greenland halibut's diet. Nonetheless, the mixing models confirmed that Greenland halibut with a length of 50 - 85 cm depend on a pelagic food source.

Discussion

Greenland halibut are primarily harvested in Cumberland Sound during winter and early spring months, and stomach content analysis has proven ineffective due to the high percentage of empty stomachs during this season. Attempts in this study to capture Greenland halibut in
Cumberland Sound in summer/fall months were unsuccessful, indicating the usefulness and necessity of stable isotope data to elucidate the prey preferences of Greenland halibut in Cumberland Sound.

Values of δ^{13} C across the sampled species from Cumberland Sound suggested two carbon sources, pelagic and benthic. Benthic organisms in this study were ¹³C enriched, more negative in δ^{13} C relative to the pelagic species, consistent with others studies of arctic ecosystems (Hobson and Welch 1992, Hobson et al. 1995, Hobson et al. 2002). Consistent with known habitat and feeding preferences of these organisms, the invertebrates and fish increased on a gradient of δ^{13} C from pelagic habitat species (copepods, capelin; Templeman 1948, Hirche 1997) to epibenthic (shrimp; Birkely and Gulliksen 2003) to benthic habitat species (scallops; Wiborg 1963). Scallops were the most ¹³C enriched, suggesting a primarily benthic carbon source. Copepods and capelin, as the most ¹³C depleted samples, indicated pelagically feeding species. Shrimp exhibited an intermediate δ^{13} C, suggesting that they feed between both habitats. The Greenland halibut δ^{13} C values across all size classes grouped them with the offshore pelagic species. Despite being a flatfish, pelagic feeding behavior of Greenland halibut in Cumberland Sound is consistent with body morphology (de Groot 1970) and stomach content studies (Bowering and Lilly 1992, Gonzalez et al. 2006). The mixing models, which were based on both δ^{13} C and δ^{15} N, also indicated pelagic behavior by identifying capelin as the main component (relative to shrimp) in the Cumberland Sound Greenland halibut diet.

Relative values of δ^{15} N for the species in this study were also consistent with prior knowledge of their feeding ecology. Capelin are a foraging pelagic fish found throughout the Arctic and sub-Arctic zones of the Atlantic and Pacific oceans (Templeman 1948), and a relative trophic position of 3.0 is consistent with their position as secondary consumers (O[•]Driscoll et al. 2001). Greenland halibut across all sizes were a trophic position of 3.8, consistent with a known dietary preference in other ecosystems for capelin (TP = 3.0) or shrimp (TP = 3.1).

The mixing models identified capelin as the main prey item for the 50 – 85 cm Greenland halibut sampled in Cumberland Sound, also consistent with previous observations on diet with size: individuals 20-69 cm predominately consume small fish (e.g. herring, capelin). However, it is important to note that not all possible prey species were included in this study but rather common species representing pelagic fish and meso-benthic invertebrates. Other species (e.g. Arctic cod; Bowering and Lilly 1992) would share similar stable isotopes signatures to capelin/shrimp and likely be important components of the Cumberland Sound Greenland halibut diet. In fact, capelin represent a relatively new food source to the Greenland halibut of Cumberland Sound and have only been observed in the ecosystem in recent years. Fisk et al. (2002) found similar stable isotope signatures in 1999 that indicated a pelagic carbon source and 4th trophic position, thereby verifying the importance of other, unknown prey items in 1999 and suggesting other prey items currently. Although MixSIR (which incorporates multiple sources of uncertainty; Moore and Semmens 2008) still emphasized capelin as important, the systems modeled were incredibly simplified with only two source items included. The addition of other species to the mixing models could reduce the success and/or agreement of the models.

The tendency of Greenland halibut to change diet with growth as suggested by previous studies was reflected in the GLM results. Length was a significant predictor of δ^{15} N in the GLM, implying a change in diet with size. However, most Greenland halibut individuals in this study were 50 – 75 cm, and, according to other studies, such a range in size would share a similar diet. Thus, the significance of length was driven by the one individual > 75 cm—therefore suggesting

a consistent diet (TP = 3.9 - 4.0) prior to a certain size and then a change in prey preference (TP > 75 cm = 4.3).

The indication of pelagic feeding from the δ^{13} C values, the identification of capelin as the main prey item by the mixing models, and the implication by the GLM of transitions in diet with size are all characteristics observed in other studies of Greenland halibut. However, the diet of Greenland halibut can be extremely variable in prey preferences and seasonal diets, such that dietary assumptions cannot be made for Greenland halibut in an unstudied ecosystem. Nonetheless, the variability in diet preferences has been well-documented and can direct small-scale research in unstudied areas.

The usefulness of this study lies in its potential use for future research. Despite the concerted efforts of Fisheries and Oceans Canada (DFO) and the Pangnirtung Hunters and Trappers Association to determine the independence of the Greenland halibut of Cumberland Sound stock (Kabva Marine Services et al. 2003, Treble 2003), there has been limited research focusing on the ecology of this fish stock. Basic fisheries management requires single species models, and prior to this study, there have been none developed for the Cumberland Sound Greenland halibut. This study provides the starting point on which to base future studies by confirming the pelagic feeding of the Cumberland Sound Greenland halibut and indicating the importance capelin may represent in the diet. Additionally, this study indicates the usefulness of stable isotopes for assessing Greenland halibut feeding behavior in unstudied ecosystems. Focusing the direction of stable isotope studies on dietary assessments from other systems provides a straightforward method for structuring diet and trophic relationships with small sample size demands.

Because trophic dynamics are sensitive to both environmentally-mediated effects and human-mediated effects, establishing baseline information is crucial for predicting potential stock responses to changes in the Cumberland Sound ecosystem and fishery. Future research must focus on the importance capelin play in the local ecosystem and Greenland halibut diet. Additionally, identification of other important prey items is necessary. This study provides the starting point for more elaborate Cumberland Sound research on the local Greenland halibut feeding ecology by confirming pelagic feeding, establishing its relative trophic position, and specifying the importance of capelin as prey.

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Species	Size Class	n	δ ¹⁵ N (‰)	δ ¹³ C (‰)	Relative Trophic Position
Copepods		4 bulk	9.47 ± 0.26	-20.52 ± 0.82	2
Scallop		5	8.58 ± 0.18	-18.55 ± 0.38	benthic
Shrimp		5	13.24 ± 0.12	-18.74 ± 0.16	3.1
Capelin		7	12.92 ± 0.13	-19.25 ± 0.05	3.0
G. Halibut 1	< 55	6	15.85 ± 0.10	-19.05 ± 0.09	3.9
2	55 - 60	3	16.25 ± 0.10	-18.94 ± 0.01	4.0
3	60 - 65	8	16.00 ± 0.21	-19.01 ± 0.21	4.0
4	65 - 70	5	16.35 ± 0.20	-18.93 ± 0.09	4.0
5	70 - 75	3	16.50 ± 0.29	-18.62 ± 0.39	4.1
6	> 75	1	17.13	-18.91	4.3

components of the Cumberland Sound ecosystem and derived relative trophic position*

Table 3.1. Stable-nitrogen and stable-carbon isotope values (mean \pm SE) for several food web

* Trophic position = 2 + $(\delta^{15}N_{consumer} - \delta^{15}N_{Calanus})/3.4$

Table 3.2. Model estimates of prey contributions to the diet of Greenland halibut, *Reinhardtius hippoglossoides*, as provided by IsoSource (median, 1st and 99th percentiles) and MixSIR (median, 5th and 95th percentiles) using isotopic discrimination factors 3.4‰ and 1.0‰ for δ^{15} N and δ^{13} C, respectively.

Prey Species	IsoSource	MixSIR	
Shrimp	0.0 (0.0 – 0.01)	0.001 (0.0 – 0.002)	
Capelin	0.99 (0.99 – 1.0)	0.999 (0.998 – 1.0)	

Figure 3.1. Stable-nitrogen and stable-carbon isotope values (mean \pm SE) of 6 size classess of Greenland halibut, likely prey species (capelin and shrimp) of the Greenland halibut and two baseline species from the Cumberland Sound ecosystem.



CHAPTER FOUR

CONCLUSION: ECOSYSTEM MANAGEMENT APPROACHES IN CUMBERLAND SOUND

Conclusion

The overall goal of this research was to determine which social and environmental factors have affected the observed catch per unit effort (CPUE) trends in the Cumberland Sound fishery for Greenland halibut and to investigate basic feeding ecology of the Cumberland Sound Greenland halibut stock. The combination of these two studies provides the basis for understanding the social, physical, and biological mechanisms driving Greenland halibut catch rates in Cumberland Sound as well as establishing the starting point for an ecosystem-based management approach in the Cumberland Sound fishery. Despite data restrictions, these studies show some mechanisms driving catch rate trends can be developed through hierarchical modeling while carbon sources and trophic position can be established through stable isotope analysis.

Chapter two focused on reported declining catch rates observed in the mid-1990s. We found that changes in abundance and distribution of Greenland halibut likely resulted from variations in the physical environment and fisherman behavior rather than the fishery itself. By modeling fishing location and individual fisherman as random effects with multiple fixed effects in two hierarchical models of CPUE, we found the months (January through May) and the North Atlantic Oscillation (NAO) index were significant predictors of catch rate. The month effect showed greatest catch rates during February and March, but declining catch rates during May. The NAO index was positively associated with catch rates, i.e. high catch rates mirrored a high NAO index. In the fisherman hierarchical model, the significance of the storm variable, which represented a change after 1996 from decreasing to increasing CPUE, was linked to reduced fishery participation following a large storm that caused a gear loss of 70%. In fact, the storm variable was found to represent a switch in the quality of fisherman remaining in the fishery after

the large storm: the more skilled fishermen remained after such losses while the less skilled dropped out—effectively changing CPUE. Additionally, a generalized linear model (GLM) identified negative relationships of CPUE with shark bycatch and with increased fisherman participation. Reduced catch in the presence of Greenland shark bycatch was expected since the sharks are known to tangle or destroy lines and scavenge hooked Greenland halibut. However, the negative effect from increased fisherman participation was not identified in the location hierarchical model, indicating that when location is considered random (i.e. fished locations are only a sample of all potential locations), the number of fisherman participating is not affecting CPUE. Also, the fact that fisherman behavior influenced CPUE records illustrates the potential break down of the CPUE assumption that catch rates are proportional to true fish abundance. As such, using hierarchical models to predict CPUE is a more appropriate method than generalized linear models.

Chapter three used nitrogen (δ^{15} N) and carbon (δ^{13} C) stable isotope data to provide preliminary information on the Greenland halibut diet in Cumberland Sound, focusing on two known potential prey items. Capelin (*Mallotus villosus*) represent a purely pelagic organism while shrimp (*Lebbeus polaris*) are known to be partially benthic feeders—thereby allowing these prey species to act as proxies of their respective habitats. Despite being a flatfish, Greenland halibut are known water column feeders (Bowering and Lilly 1992, González et al. 2006), and δ^{13} C for the Greenland halibut stock indicated a pelagic carbon source in Cumberland Sound as well. Additionally, stable isotope mixing models, IsoSource and MixSIR, indicated a 99% dietary composition of capelin relative to the shrimp, further confirming a pelagic feeding behavior. This study provides the starting point for more elaborate Cumberland Sound research on the local Greenland halibut feeding ecology by confirming pelagic feeding, establishing

relative trophic position, and specifying the importance of capelin as prey. Additionally, this study confirms that stable isotopes are reliable and useful indicators of Greenland halibut feeding.

In summary, the main results of this work indicate that it is unlikely reduced catch rates were driven by the Cumberland Sound fishery. Rather, physical variables (e.g. month or NAO) are affecting distribution or abundance of Greenland halibut within the system and social variables (e.g. fisherman behavior) are affecting observed trends in CPUE. The time-series, multi-level, and random nature of fishery-dependent data makes it inherently hierarchical and therefore the utilization of random effects in a hierarchical model is a more appropriate approach to structure fishery-dependent data analysis than regular GLMs. Additionally, assessment of Greenland halibut stable isotopes provide the first evidence of pelagic feeding behavior in Cumberland Sound. Consequently, the combination of these studies is the first attempt to incorporate both fishery and ecological information to study the Cumberland Sound Greenland halibut.

Research Needs for the Cumberland Sound Greenland Halibut Fishery

The Cumberland Sound fishery for Greenland halibut is still new and small relative to other Greenland halibut fisheries. As an artisanal fishery with limited gear and participation, the fishery has yet to reach an assigned quota (Treble 2008). Recent years have seen a decline in fishery participation due to unstable ice conditions and shorter ice seasons. However, there has been interest in the formation of a summer fishery for Greenland halibut in Cumberland Sound in addition to an expansion of the commercial nature of the fishery. Prior to such steps, though, more information on the Cumberland Sound ecosystem and Greenland halibut stock is crucial for

predicting future trends and establishing appropriate management strategies. For example, conducting fishery-independent surveys would strengthen stock assessment models. Additionally, we must understand the distribution and abundance of the capelin stock, a recent species present in Cumberland Sound, as well as establish the importance capelin play in the Cumberland Sound Greenland halibut diet. Because Cumberland Sound is receiving attention for future research, our identification of these important knowledge gaps can help direct research efforts.

Seasonal/monthly effects on catch rates

Cumberland Sound is a relatively pristine system; fishing is limited to certain areas and longlining only occurs several months of the year. Previous exploratory surveys have had limited success longlining in summer months, but trawling yields low catches (Northlands Consulting 1994). Before development of a summer fishery, understanding why catch models show a monthly effect is crucial—essentially, why do catch rates decline as the season changes? The decrease in longline effectiveness from winter/spring to summer/fall suggests either a change in catchability (i.e. a change in fishing power or seasonal change in fish behavior), migration of Greenland halibut out of the Sound, or redistribution of the fish within Cumberland Sound.

One suggested mechanism for reduced longlining success in summer months and the significance of a month effect in the hierarchical model is a change in summer fishing power. Although catchability refers to the interaction of the animal's behavior and the fishing gear, the concept is often blurred with fishing power (Ward 2008), which actually refers to the property of the fishing gear and practices. In the case of Cumberland Sound, gear restrictions dictate fishing

power—trawling is prohibited in the winter fishing grounds. An exploratory survey in summer/fall of 1994 used longlining in addition to otter trawling, gill netting, and traps (Northlands Consulting 1994). Summer longlining with gear and fishing location similar to the winter methods proved unsuccessful. The highest catch rates were at a water depth of ~900 m and took an average of 63 hours for 300 hooks to catch 100kg of Greenland halibut (Northlands Consulting 1994). The winter fishery, which is spread out over shallower waters, needed an average of 4 hours for 300 hooks to catch 100 kg of Greenland halibut (Pike 1994). While otter trawling proved moderately successful when targeting waters >400m deep in Cumberland Sound (Northlands Consulting 1994), the fishing was not focused in the winter fishing grounds. Thus, a change in fishing power was not causing the observed summer catch rate decline.

Another possible cause of reduced summer catch is a change in behavior that reduced catchability: Greenland halibut may have begun feeding in the water column. As our stable isotope study showed, the Greenland halibut of Cumberland Sound feed pelagically and, consistent with other systems (Bowering and Lilly 1992), capelin likely form a main component of the diet. Capelin are migratory fish, moving in large schools to inshore waters for spawning in late spring and early summer, only inhabiting Cumberland Sound during summer months. If Greenland halibut do remain in Cumberland Sound year-round, they are possibly moving within the water column, targeting the summer capelin source. Thus, managing the Cumberland Sound fishery from ecosystem point of view demands assessment of Cumberland Sound capelin and other potential prey items. However, capelin have only been observed in Cumberland Sound in recent years, suggesting that they have either replaced the previous pelagic feeder or else represent a new food source for Greenland halibut in the ecosystem. Thus, a change in

Greenland halibut behavior to specifically target capelin would not explain the reduced summer catches in years prior to capelin arrival.

Migration of the fish out of the system or redistribution of Greenland halibut within Cumberland Sound could also explain reduced summer catches and the significance of a month effect in the hierarchical models. Distribution and size data from a trawl survey conducted in Davis Strait suggest a late summer movement of local Greenland halibut to spawning grounds in the deep waters (>1000 m; Jørgensen 1997), similar to seasonal migrations of Greenland halibut between feeding and spawning areas in the Gulf of St. Lawrence (Bowering 1982) and Icelandic waters (Sigurdsson 1979). However, if Greenland halibut are migrating seasonally, catches between Cumberland Sound and Davis Strait would be expected, but the 1994 exploratory fishery in Cumberland Sound caught no Greenland halibut at the Sound's mouth (Northlands Consulting 1994). Rather than an out-migration from the Sound, reduced catch could also result from a general dispersal within Cumberland Sound. Trawling in areas of Cumberland Sound not targeted during winter fishing yielded concentrations of Greenland halibut in waters >350m. Yet, parasite fauna on Cumberland Sound Greenland halibut imply movement to/from the Sound since the parasites could not be discriminated from those found in the Hawke Channel of the Labrador Sea (Arthur and Albert 1993).

One potential method for elucidating summer movement is the use of satellite tags on large Greenland halibut individuals. A study with Atlantic bluefin tuna using pop-up satellite archival tags provided insight into migrations and environmental preferences (Block et al. 2001)—information also needed for Cumberland Sound Greenland halibut. The satellite tag is attached externally to a fish, and after release at a preprogrammed time, it floats to the surface and transmits recorded data to satellites (Block et al. 1998). The tags record temperature and

depth data as well as daily geographic position of the fish as determined by light intensity records (Block et al. 1998). Thus, movements and behaviors determined from satellite tags could clarify if the Greenland halibut move within the water column during summer/fall months, redistribute within Cumberland Sound, or migrate into Davis Strait.

Ecosystem-based Management in Cumberland Sound

Because these studies suggest that changes in the abundance and distribution of Greenland halibut in Cumberland Sound resulted from variations in the physical environment and fisherman behavior rather than the fishery itself, understanding the ecology and behavior of the target species and its food web prior to developing a summer fishery is crucial. Although past models of fish populations have often ignored environment (Hilborn and Mangel 1997), there is growing evidence that a considerable component in fish stock declines is caused by the environment rather than overfishing (Caddy and Gulland 1983, Hilborn and Walters 1992). If a fishery develops with little or no conservation and regulation, though, overfishing is the likely cause of reduced CPUE (e.g. Namibian hake fishery; Hilborn and Mangel 1997).

With the realization that single species operate within an ecosystem and the failure of past attempts to manage fisheries as a single population (e.g. for maximum sustainable yield), fisheries management has turned its focus to the ecosystem level (Browman and Stergiou 2004). Because our understanding of the mechanisms affecting catch rates of Greenland halibut in Cumberland Sound strongly implicate local, environmental processes, and because trophic dynamics are sensitive to environmentally-mediated effects, placing the Greenland halibut within a food web structure is crucial—multiple species models require both accurate assessment of trophic linkages and single species models (Beverton and Holt 1957). Even when years of

fishery data are available, some key assessment calculations will depend on data that can only be gathered in the early stages of a fishery's development (e.g. behavior of a species; Hilborn and Walters 1992). Walters and Martell (2004) designated the need for information on trophic linkages early in the development of a fishery in order to understand changing exploitations rates. Therefore, establishing current trophic position of Greenland halibut in Cumberland Sound and assessing other trophic linkages is needed prior to the fishery's expansion in order to understand possible changes in future trophic structure in Cumberland Sound.

The importance of pelagic food sources in the Greenland halibut diet suggests that feeding behavior could also be driving stock distribution and fishery catch rates. However, stable isotopes can only pinpoint relative trophic level, and because of limitations in sampling and accessibility, the only potential prey we assessed were capelin and shrimp. To build an effective ecosystem-based management strategy before commercial exploitation is expanded within Cumberland Sound, other important food items must be identified and studied. The incorporation of CPUE into stable isotope modeling could be a powerful tool, showing how fishing can affect food web structures. However, stable isotope data spanning multiple years are required—Jennings et al. (2002) emphasized the importance of historical trophic data to accurately observe the impacts fishing can have on food webs.

Though the size of the data sets and variety of ecosystem knowledge needed to create large scale ecosystem studies is outside the scope of this project, future research within Cumberland Sound can focus its efforts in the direction needed for effective ecosystem-based management strategies. Essentially, determining reasons for reduced catch rates during summer/fall months (i.e. are the fish within the Sound or not), identifying the Cumberland Sound Greenland halibut dietary components (in addition to capelin), and also establishing a full

Cumberland Sound food web structure are all studies needed prior to the expansion of the Cumberland Sound fishery. Such information provides the basis for effective and appropriate ecosystem-based management as well as for understanding future CPUE trends in the face of changing climate and increased fishery effort.

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VITA AUCTORIS

Susan Towers Dennard was born in 1984 in Roanoke, Virginia, USA. She grew up in Dalton, Georgia, graduating from Dalton High in 2002 with an International Baccalaureate diploma. After receiving a B.S.F.R. in Fisheries and Aquaculture and a minor in Statistics from the University of Georgia in 2007, she moved to Windsor, Ontario, Canada. Currently, she is a candidate for the Master's degree in Environmental Science at the Great Lakes Institute for Environmental Research at the University of Windsor.