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Movement and depth and temperature preferences of benthic, deep water fish in an Arctic marine ecosystem

Iva Peklova

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MOVEMENT AND DEPTH AND TEMPERATURE PREFERENCES OF
BENTHIC, DEEP WATER FISH IN AN ARCTIC MARINE ECOSYSTEM

by

Iva Peklová

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

Windsor, Ontario, Canada
2012

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DECLARATION OF CO-AUTHORSHIP/PREVIOUS PUBLICATION

I. Co-Authorship Declaration

I hereby declare that this thesis incorporates material that is a result of a joint research, which was undertaken under supervision of Drs. Aaron Fisk and Nigel Hussey. The collaboration is covered in Chapter 2 of the thesis. This manuscript was coauthored by I. Peklova, N. Hussey, K. Hedges, M. Treble and A. Fisk. Throughout the thesis, main ideas, data analysis and interpretation were performed by the author, and the contribution of co-authors was through theoretical knowledge input, help with statistical analysis of the data and guidance through the writing process, including revisions of the drafts.

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-author(s) to include the above material(s) in my thesis.

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ABSTRACT

Given concerns about climate change and exploitation of Arctic marine resources, it is critical to elucidate the movements of deep-water Arctic marine species. This thesis analysed data from pop-off archival transmitting tags deployed on commercially exploited Greenland halibut (*Reinhardtius hippoglossoides*) and a bycatch species Arctic skate (*Amblyraja hyperborea*) in Cumberland Sound, Nunavut tagged in August 2010-2011. Data collected for 40-300 days defined the preferred depth and temperature ranges for halibut (800-1300m, 1.5-2.5°C) and skates (500-1300m, 1.5-3.0°C) and suggested differences in activity levels and behaviour. Greenland halibut were more sedentary compared to more active skates and displayed high site fidelity with no evidence for diel vertical migration, though they undertook seasonal movements to shallow water. The profiles of the active, relatively fast-swimming skates indicated that they may switch between benthic and pelagic foraging modes. Both species overlapped in spatial habitat use. This information will contribute to regional species-specific fisheries management plans.
DEDICATION

I dedicate this thesis to my parents Jan and Ivana Peklovi for their love, care, support and trust. It is wonderful to venture the world, if you have a home you can return to.
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1 GENERAL INTRODUCTION

This thesis aims to describe adult stage movement, considering diel and seasonal movement patterns, and behaviour (e.g. foraging) of two deep water, benthic, fish species; the Greenland halibut (*Reinhardtius hippoglossoides*) and Arctic skate (*Amblyraja hyperborea*), in an Arctic marine system. More specifically, this thesis will define depth and temperature preferences of these species. The following chapter will provide background information on movement of fish, technology used, the test system, study species and rationale and objectives of this study.

1.1. MOVEMENT OF FISH

Understanding the movements and depth and temperature preferences of fish throughout their life cycle is important in order to comprehend their ecology. Application of that knowledge is critical for conservation of species and ecosystems, for better management of economically significant fish species such as salmonids, gadids or groundfish, and for the protection of species that are negatively affected by commercial fishing efforts (i.e., bycatch). Movement patterns can define the depth and temperature ranges of a species, which represent a realized niche of a species. As oppose to fundamental niche, i.e. the complete set of suitable range of conditions where species can maintain stable or increasing population size (Hutchinson 1957), the realized niche reflects limiting factors including food and space, interspecific competition for these resources and presence of natural predators (Hutchinson 1957; MacArthur and Levins 1967; Jeffries and Lawton 1984). Thus, movement of fish will reflect the evolutionary-time responses to these factors, as well as shorter, ecological-time responses to changing ecological and environmental factors, such as food availability, avoidance of adverse
environmental conditions or predators (Gibson et al. 1996; Pittman and McAlpine 2001). Monitoring of the movement of fish provide insight into how fish react to these factors and ultimately it aims to increase knowledge about more general behaviours associated with particular movements. Once general rules in fish behaviour that determine movement (e.g. dispersal, migration or resource use) are identified, then movements can be modelled and used for better decision making in conservation and resource management efforts (MBA 2006).

Movement of fish during early life stages (i.e., movement of eggs and larvae) is usually passive, including wind-induced transport or dispersal due to tidal or large oceanic currents (Norcross and Shaw 1984; Pittman and McAlpine 2001; Albert and Høines 2003). However, some studies have shown that even as a larva, fish may actively affect their movement by positioning themselves in different levels of the water column in order to be transported into favourable habitats (Hardy 1953; Leis et al. 1996).

During the juvenile stage, fish experience different types of movement patterns associated with ontogenetic shifts in morphology and physiology. This is often associated with responses to different selection pressures from their environment or periodical home range movements (e.g. inshore-offshore and normal diel vertical movements) typically associated with foraging. Juveniles may also move away from their home as a consequence of change in environmental conditions, i.e. undergo relocation of their home range (Kramer and Chapman 1999).

As fish mature, reaching the adult stage, they continue to move, forage and react to changes in environmental conditions. For example, Sims et al. (2008) observed patterns in movements of sharks (Levy flights) and used it to explain how they forage effectively.
in patchy environments. Additionally, adult fish may undergo large-scale migrations (e.g., Block et al. 2001; Pittman and McAlpine 2001; Sepulveda et al. 2004; Seitz et al. 2008; Bernal et al. 2009). These migrations may occur due to changes in external environmental conditions, for example seasonal changes in temperature and productivity (Pittman and McAlpine 2001), or may be associated with maturity and reproduction. For example, Atlantic bluefin tuna (*Thunnus thynnus*) migrate across the ocean to reach their spawning grounds (Block et al. 2001) and various salmonid species travel thousands of kilometers to the ocean to feed before they comes back ready to spawn (Dittman and Quinn 1996; McCormick et al. 1998; Klementsen et al. 2003).

Each type of movement is associated with a different time and spatial scale and potentially coincides with diel, tidal, lunar and seasonal cycles (Levy 1990; Gibson et al. 1996; Pitman and Alpine 2001; Scheuerell and Schindler 2003). Thus, it is convenient to look for periodicities and patterns in movement of fish, because such patterns may be indicative of specific routine behaviours characteristic of a particular fish species or group of related species. These patterns can be studied using satellite telemetry tags and acoustic telemetry devices.

1.2. SATELLITE TELEMETRY

Satellite telemetry technology has been widely recognized as a useful tool to monitor movement patterns of fish (Wearmouth and Sims 2009; see review by Hammerschlag et al. 2010; Kaplan et al. 2010). It is suitable to track rare movements, large-scale spawning migrations (e.g., Hunter et al. 2003; Block et al. 2005; Sims 2008) and also periodical and home range associated movements related to, for example, foraging behaviour (e.g., Kitawaga et al. 2004; Loher 2008; Sims et al. 2008;
Viswanathan 2010). In the following section, I will introduce previous and concurrent technologies that have been used for tracking of the movement of fish, highlighting strengths and limitations of each of these technologies to provide a rationale for the choice of satellite telemetry as a tracking tool in this study.

Technologies to track movement of fish

In the past, movement of marine fish populations was conventionally monitored either by mark and recapture or fixed point sampling (e.g., research surveys, commercial catch reports) (Bowering 1984; Quinn and Brodeur 1991; Campana et al. 1999; Boje 2002). However, technical and analytical problems associated with these methods were significant, for example mark and recapture approach requires extensive fishing effort and is usually more effective in small-scale studies (i.e. lakes). Additionally, fixed point sampling induces inevitable bias by arbitrary experimental design. For these reasons both techniques are less effective to monitor rare species and wide-ranging species that undergo less frequent movements or are in areas were fishing pressure is low (i.e., chance of recapture is low) (Quinn and Brodeur 1991).

Recently, stable isotopes, carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N), in animal tissues have been used as markers for the assessment of feeding relationships, food web structure in natural environments and a tool for tracking movement between regions with distinct isotopic signatures (e.g., inshore versus offshore, marine versus freshwater). The use of stable isotopes assumes a predictable relationship between the isotopic composition of a tissue (e.g., muscle, liver) of the consumer and its diet and/or that the specific isotopic signature of one habitat is reflected and retained in a specific tissue (e.g., feather or
otolith) of the animal that records changes in habitat use through time (Peterson and Fry 1987; Hobson 1999).

This method has shown to be more practical (no need for recapture) and less time consuming compared to the conventional methods, yielding migration and movement data for various taxa including fish, marine mammals, birds and insects (Cherel et al. 2000; Kurle and Worthy 2002; Rubenstein and Hobson 2004; Pinela et al. 2010). However, it can be problematic in aquatic animals (e.g., unknown species-specific diet-tissue discrimination factors (DTDFs)) (Hussey et al. 2010).

Alternatively, electronic tagging technologies have provided an opportunity for researchers to investigate fish behaviour and movement in a multidimensional space and in some cases in real time. Multiple types of tags, including acoustic, satellite, radio and GPS exist to accommodate different questions about fish movement and behaviour. Two types of tags are commonly used in marine systems – acoustic and satellite. These tags are equipped as time recorders and specific sensors to capture biological (location, swimming, diving, internal temperature, and heart rate) and physical (e.g. light, temperature, salinity) features of the fish and the environment they inhabit over time (Kaplan et al. 2010).

Acoustic telemetry tagging is a suitable technology to record the movement of fish from a relatively fine scale (~1 m) to a large spatial scale (1,000s km) (Heupel et al. 2006). The acoustic transmitter is secured to or in (external or internal) the fish body and emits an individual-specific acoustic pulse that can be recognized and recorded by a hydrophone to identify the fish is in range of the hydrophone and in some cases exact position. The hydrophone can be either active (done in real time, while following the
fish) or passive (fixed listening station/receiver placed onto the sea bottom). This method has been used in numerous projects, especially in coastal environments to precisely monitor smaller-scale movements within a defined study system using an acoustic grid of receivers (e.g., Heupel and Hueter 2001; Starr et al. 2002; Kerwath et al. 2009). Additionally, this method has been widely used to monitor migrations of for example anadromous fish, by setting curtains of receivers along a restrained pathway or a migration route (e.g., Block et al. 1997; Sepulveda et al. 2004; Bernal et al. 2009; Cartamil et al. 2010). However, this technology is restricted by the dissipation of sound (i.e., fish have to be relatively close to the hydrophone, in most cases < 1 km) in the water and maximum depth in which receiving monitors can be deployed (generally < 500 m). For these reasons, this technology is limited in the size of the area that can be effectively monitored and appears unsuitable for continual monitoring of large-scale spawning migrations. In addition, acoustic tags can induce increased mortality and decrease the rate of growth or result in expulsion of the tag (Lacroix et al. 2004; Welch et al. 2005). Thus, despite tags being previously deployed on variety of teleost, crustaceans, chondrichthyans and cephalopods (Heupel et al. 2006), sensitivity of the species and potential modifications to its behaviour caused by the transmitter shall be considered.

Satellite telemetry uses externally attached tags to collect, store and transmit data via Argos satellite system. Once tags are secured to the animal, they record data for a pre-programmed period of time (this can be anywhere from days to years, depending on the memory capacity of the tag and the objectives of the study) or until the animal is recaptured. At the end of the deployment period, tag has to be either be physically recovered (yields a full record, e.g., electronic data storage (DST) and temperature depth
recorder (TDR) tags, Wildlife Computers Inc., Redmont, WA, USA) or detaches from the animal, floats to the water surface (due to the buoyant body of the tag and corrodictible pin that releases it from the fish) and transmits the record via satellites (the record may be incomplete, e.g., pop-off archival transmitting (MiniPAT, PSAT) tags, Wildlife Computers Inc.). Some tags will uplink to the satellites during the deployment period every time the tag is in the contact with air, i.e. the animal comes to the surface (e.g., SPLASH and SPOT tags, Wildlife Computers Inc.).

Location of the animal in satellite tags can be either generated accurately by GPS positioning system in real time (e.g., SPLASH, SPOT) or estimated from light levels at sunrise and sunset, and the duration of the day (e.g., pop-off tags) (Kaplan et al. 2010). While the former is mainly used for fine scale studies and works better for species that come to sea surface periodically (e.g., reptiles, marine mammals), the latter is often used for longer deployment periods targeting larger scale migrations of animals, that do not spend enough time at the surface to allow for real time location estimation (Kaplan et al. 2010), such as Atlantic bluefin tuna (used in a study by Block et al. 2001; 2005) and Basking shark (Cetorhinus Maximus) (used in a study by Sims 2008). Apart from horizontal movement, satellite telemetry tags provide time series of detailed depth and temperature data to help investigate water column use, vertical movement patterns and whether these relate to periodic cycles (e.g. diel, tidal). Tags also provide depth and temperature histograms and summaries to address behavioural patterns (e.g., foraging, feeding, resting) (Loher and Seitz 2006; Loher 2008; Sims et al. 2008; Wearmouth and Sims 2009; Queiroz et al. 2010; Viswanathan 2010) and environmental data including depth-temperature profiles and sea surface temperature.
The main advantage of the satellite tags is that they do not require fishing effort and usually show much better recovery rate compared to conventional T-anchored tags used in mark and recapture studies (Bowering 1984; Boje 1994; Musyl et al. 2011). Coupled with their unique capacity to collect environmental and biological data over short or long term periods, satellite tags can yield important information about ecology, with potential use in conservation of species and management of fisheries (Hunter et al. 2003). More extensive use of the satellite telemetry tags is, however, restricted by a relatively high price for a single tag (e.g., $1000-4000) and a minimum size of the animal on which satellite tags can be deployed (~0.3 m).

To date, most of the studies using satellite telemetry tags were conducted in tropical and temperate climates and have seldom been used in Polar Regions, with the exception of study conducted by Fisk et al. (2012). However, this methods may provide a powerful and especially suitable tool to study species that live in hard-to-study systems (cold, remote, dominated by the sea ice cover), such as the Arctic.

### 1.3. ARCTIC ECOSYSTEMS

The Arctic is often defined as a region that extends over the land (pertaining to eight countries including Canada, Denmark/Greenland, Finland, Iceland, Norway, Sweden, Russia and the United States) and the ocean northwards of the Arctic Circle (66°32’N). More precise delineations of the Arctic however incorporate important physical, geographical and ecological characteristics such as variation in air temperature, temperature and salinity of water or extent of the sea ice (Fig. 1.1) (Murray et al. 1998). For example, marine boundary of the Arctic runs along the convergence of cool, less saline surface waters from the Arctic Ocean and warmer, saltier waters coming from the
South (Fig. 1.1) (Murray et al. 1998). The majority of the Arctic consists of the Arctic Ocean, where sea ice is the most defining feature (Serreze et al. 2007).

Sea ice forms from the ocean water in three different areas: the drifting (perennial) pack ice, marginal ice zone (boundary between the pack ice and the open water) and land fast ice, which develops along the coast and between archipelagoes each winter, extending offshore (Murray et al. 1998). Borders of marginal and land fast ice zones with open water usually represent the most biologically productive areas in the seasonally production-limited Arctic ecosystems (Murray et al. 1998). The major limitations to primary production in the Arctic are extreme physical conditions such as reduced incoming solar radiation, wide range in the length of daylight, low temperatures and aforementioned sea ice, i.e. physical barrier to the energy penetration (Barrie et al. 1992). These conditions result in a seasonally-driven productivity and lower species diversity ecosystems with often short, but greatly interconnected foodwebs (e.g., phytoplankton-zooplankton-fish-seal-polar bear or phytoplankton-zooplankton-whale) (Barrie et al. 1992; Post et al. 2009). In general, Arctic species are highly reliant on their extremely variable seasonal habitats (e.g. the border sea ice) and also tightly adapted to effectively explore available resources of typical spatially and temporally patchy distributions (Barrie et al. 1992). Still, largely understudied Arctic ecosystems are expected to undergo rapid changes due to the warming of the global climate (ACIA 2005).

Warming (largely assigned to the increase of greenhouse gases in the atmosphere) (Rayner et al. 2003; Schrank et al. 2007) has been one of the most pronounced trends observed in the Arctic’s climate over the last century, which has contributed to the decline of sea ice cover in most parts of the region (Serreze et al. 2000; Serreze et al.
2007; Post et al. 2009). Some of the changes following the warming and the loss of the sea ice cover will be shifts in atmospheric circulation and precipitation patterns, disruption of the global thermohaline circulation and nutrient availability (for details see Serreze et al. 2007; Post et al. 2009). These factors will influence the overall biological dynamics, affecting especially those Arctic species such as the Pacific walrus (*Odobenus rosmarus divergens*), ringed seal (*Pusa hispida*), narwhal (*Monodon monoceros*), and polar bear (*Ursus maritimus*) (Laidre et al. 2008), whose life cycles and behaviour (e.g., feeding, reproduction and predator avoidance) are closely tied to the sea ice (Tynan and DeMaster 1997; Post et al. 2009). Such changes will also affect deep water species; however the extent of the impacts is largely unknown due to lack of research on these species. Additionally, these changes will have an effect on the exploration of Arctic natural resources by humans.

The Arctic has been long known for plentiful natural resources including oil, gas, minerals, fresh water, forest and fish (Bakke et al. 1998; Murray et al. 1998; Vilhjálmsson et al. 2005; Gautier et al. 2009), which now have an increased potential to be further developed and explored as the global climate continues to warm (ACIA 2005). For example, more fisheries may be able to operate in the Arctic regions, which are no longer sheltered by the sea ice for most of the year. Historically, fishing and whaling has had a long tradition in the open water regions of the Arctic. Commercial whaling was practiced across the Arctic since the 16th century, however, whale stocks were usually depleted due to unsustainable harvest (Ross 1993; Vilhjálmsson et al. 2005), which later led into controlled harvest with strict quotas often allocated to indigenous hunters (Vilhjálmsson et al. 2005). Similarly, Arctic marine fish resources such as herring
(Melanogrammus aeglefinus), or capelin (Mallotus villosus) have been explored by subsistence fisheries for centuries, especially in open water regions such as Barents Sea (Hamre 1994; Gjosaeter 1995). After the 1950s some of the subsistence fisheries turned into commercial fleets. Inevitably, collapse of the local fish stock followed; after 15 years of severe overfishing, the Norwegian herring stock was depleted (Vilhjálmsson et al. 2005). With the ongoing decline in all of the fish stocks experienced in tropical and temperate climates, fish resources in the Arctic (especially seasonally covered regions) have received more attention. One of the Arctic systems that had recently developed commercial fishery for groundfish is Cumberland Sound - the study system of this project.

Cumberland Sound

Cumberland Sound is a westward extension of the Labrador Sea (65.22 N, -65.75 W) and one of the largest inlets of Baffin Island located in the Southeast part of the Island, extending above the Arctic Circle (Figure 2.1). Typical conditions in Cumberland Sound are characterized by winter land fast ice that extends seawards from the shallow margins (Treble 2003; Dennard et al. 2009b) and summer melting events, dividing the year into two seasons – ice covered and ice free. With bottom topography of shallow margins surrounding a deep central basin that descends to ~1500 m (Treble 2003; Dennard et al. 2009a), the Sound supports a wide range of marine fauna including numerous fish (e.g., anadromous Arctic Char (Salvelinus alpinus), pelagic capelin, Greenland halibut, grenadier (Coryphaenoides spp.), wolfish (Anarchichas spp.), Greenland shark (Somniosus microcephalus), Arctic skate and thorny skate (Raja radiata)) (Pike 1994; Dennard 2009a), marine mammals such as beluga (Delphinapterus
leucas), bowhead whale (Balaena mysticetus), killer whale (Orcinus orca), harp (Pagophilus groenlandicus) and ringed seals (Pusa hispida) and polar bear (Ursus maritimus) and seabirds such as Black guillemots (Cepphus grylle), Common eiders (Somateria mollissima borealis), Glaucous gull (Larus hyperboreus) and Iceland gull (Larus glaucoides) (Diemer et al. 2011). This plentiful marine biodiversity of the Sound has supported local communities for centuries. Traditionally, whaling was an important source for subsistence and as a material for arts, until it became a commercial practice in the middle of 19th century (Kekerten Island area) (Moshenko et al. 2003). However, due to over-harvesting, tight quotas are now placed on whale hunting in Cumberland Sound. For example, traditionally targeted bowhead whale is currently the only whale species allowed to be harvested in Eastern Canadian Arctic waters. Bowhead whales from Cumberland Sound are a part of the Baffin Bay/Davis Strait population. Inuit hunters are allocated one hunt every 13 years for subsistence (Moshenko et al. 2003).

As commercial whaling ceased, emphasis was put on other natural resources including seals and fish, also abundant in the Sound. One of the most important fish resources is Greenland halibut. Winter commercial fishery for Greenland halibut was opened in 1986 and was operated by the Inuit fishermen from Pangnirtung community, who adopted long-line, through-ice fishing technique (DFO 2008b, Dennard 2009b). Winter fishing has been successful, however, it is highly dependent on the quality and duration of the land fast ice in the Sound (DFO 2008b), marking some years with poor or zero catches. Approximately 20 years later, in 2007, the fish resource potential of Cumberland Sound resulted into an expansion into a summer, vessel operated fishery. Currently, two commercial fisheries for Greenland halibut (summer, winter) and one for
Arctic Char (*Salvelinus alpinus*) (summer), exist in the Sound. Fishery for Greenland halibut was divided into two separate stock management units with specific, non-transferrable quotas (NAFO 2004). The inshore Cumberland Sound management zone has a quota of 500 t per year and is managed by the Nunavut Wildlife Management Board. The traditional winter fishing grounds are located along the coast of the inshore Cumberland Sound management areas, whereas the summer fishing occurs mostly in central deep waters on the inner boundary between the inshore Cumberland Sound and the Division 0B NAFO management zones (Fig. 2.1) (DFO 2008a). Greenland halibut is one of the two study species in this project, mainly because of its economic importance and poorly understood movement patterns.

1.4. **GREENLAND HALIBUT**

*Pleuronectiformes*

Flatfishes (order Pleuronectiformes) are “deep bodied, laterally compressed fishes” (Munroe 2005a). The most common remarkable feature of all flatfishes is that during metamorphosis one eye migrates from one side of the head to the other, determining the blind and the ocular (two-eyed) side (Brewster 1987). With this change, further external and internal changes in morphology, deviating from a bilaterally symmetrical body plan to a dorsally compressed body plan, occur (e.g. jaw shape, lateral body musculature, coloration of either side) (Munroe 2005a). This metamorphosis also causes a significant change in the lifestyle of the fish turning once pelagic larvae (as most species produce pelagic eggs, Russel 1976) into newly settled benthic juveniles. As they mature, most flatfish continue with a benthic or demersal lifestyle, involving frequent periods when fish lie on the bottom (on top of the substratum or partially buried in it) on their blind side.
There, near the bottom, flatfish can play an important ecological role as a predator and prey (Munroe 2005a) as they convert benthic production into a source for higher trophic levels including top predators such as sharks, whales and humans (Link et al. 2005).

Apart from commonalities across the flatfish order listed above, flatfish are a very diverse order that include over 700 species (Munroe 2005a). These are known to occupy marine, estuarine and to a lesser extend freshwater environments. Being present in all of the world’s oceans, flatfish species differ in “size, shape, trophic ecologies and habitats” (Munroe 2005a). Most of the marine flatfish species occupy inner or outer continental shelf, but some also reside on the continental slope. Additionally, numerous flatfish represent a significant resource for commercial fisheries (e.g., yellowfin sole (*Limanda aspera*), Pacific halibut (*Hippoglossus stenolepis*), Greenland halibut and American plaice (*Hippoglossoides platessoides*)) (Miller et al. 2005, Wilderbuer et al. 2005).

**Greenland halibut**

Greenland halibut is a deepwater flatfish with wide distribution across cold Arctic-boreal waters of the Pacific and Atlantic Oceans (Munroe 2005b). Greenland halibut may reach a maximum size of 130 cm (female total length); however, common length of male/unsexed fish is ~56 cm. The maximum weight ever reported was 45 kg and maximum age was 30 years (Luna and Binohlan 2011).

As a larva, Greenland halibut may travel large distance as it is usually transported by oceanic currents (Albert and Høines 2003). During juvenile stages, Greenland halibut stay in the pelagic realm until it completes the metamorphosis and settle to the sea bottom. Compared to other flatfish, Greenland halibut do not undergo complete
metamorphosis. For example, the eye only migrates to the side of the head instead of the top (Anonymous 1993). Because of this incomplete transformation, this flatfish is believed to be an unusually mobile species and an effective hunter as it possesses a greater field of vision (Anonymous 1993, DFO 2005).

Mark and recapture study confirmed that adult Greenland halibut can migrate vast distances to spawn (Boje 2002; Simonsen and Gundersen 2005). Considering its migratory capacity, it is not surprising that the Northern Atlantic population of Greenland halibut is genetically homogeneous (Vis et al. 1997), even though two stocks in Northwest and Northeast Atlantic were previously considered. As far as the movement along the vertical axis is considered, depth regimes of fish change with age; older fish tend to move into greater depths (reaching depths >2000 m) compared to younger individuals (Atkinson et al. 1982; Bowering 1982; Atkinson and Bowering 1987; Jørgensen 1997). Preference for bottom temperatures varied from 0-4°C and 2-6°C in halibut from the Northeast and Northwest Atlantic populations, respectively (Bowering and Nedreeas 2000). Optimum temperature range thus depends on the region; narrower range of temperatures may be expected during the reproductive phase (Bowering 1984).

Greenland halibut is a generalist feeder, whose diet consists of plankton and shrimp-like crustaceans when young, with a shift towards bony fish (capelin (Mallotus villosus), cod (Gadus spp.), redfish (Sebastes spp.)) and squids (Gonatus spp.), complemented by benthic and pelagic crustaceans and molluscs when adult (Bowering and Lilly 1992; Dennard et al. 2009a). It was suggested that the variability in diet records may reflect the most abundant prey within its habitat at a particular location and time of a year (Pedersen and Riget 1993).
Greenland halibut as a fish resource

Greenland halibut belongs to the pool of 51 flatfish species in Northwest Atlantic Ocean and is one of eight commercially important flatfish species in this part of the Atlantic (Munroe et al. 2005b). Fishery for Greenland halibut has had a well established tradition in Northwest Atlantic Ocean ever since the depletion of Atlantic cod (Gadus morhua) stock in 1950s. Initially, the Greenland halibut fishery was developed in the Grand Banks area off Newfoundland coast. Over time, it has expanded northwards to Baffin Island and Davis Strait in the Arctic (Munroe et al. 2005b). In 1998, Greenland halibut landings dominated the fish market, showing its value as an important resource. That year, the total landings (Greenland halibut together with American plaice (Hippoglossoides platessoides) and common sole (Solea solea)) exceeded 50 % of the total flatfish landings in Northeast Atlantic (Munroe et al. 2005b).

1.5. ARCTIC SKATE

Arctic skate is the second study species in this project. Arctic skate have a circumpolar distribution, often inhabit deep waters of continental slopes, and their habitat overlaps the range of Greenland halibut. For this particular reason, Arctic skate appear to be prone to bycatch in fisheries for Greenland halibut.

Rajiformes

Rays (subclass Elasmobranchii, order Rajiformes) is an order that consists of mostly marine species. These elasmobranchs are easily distinguished by a strongly dorsoventrally flattened body, ventral position of gill openings and dorsal position of the eyes (oxfordreference.com). This order is comprised of eight families including Rajidae, which is a large family comprised of 120 species with world-wide distribution. The
typical body of a ray has an angular, disc shape that ends in a pointed snout (rostrum). In males, the dorsal side is usually covered in enlarged denticles (thorny back), females lay eggs in rectangular, horny capsules (oxfordreference.com). Rajidae typically move by undulation of their pectoral fins called rajiform swimming (Froese et al. 2011). One of the common Rajidae is Arctic skate.

**Arctic skate**

Arctic skate (*Amblyraja hyperborea*) is a largely unstudied, deep water skate (max length of 106 cm) with a wide distribution at higher latitudes towards both poles (Stevens and Last 1994, Kulka et al. 2007). It can occur at depths from 260 to ~2500 m (RAS 2000; Kulka et al. 2007), but most often is found between 300 to 1500 m (Skjæraasen and Bergstad 2001) in waters below 4°C (Bigelow and Schroeder 1953). Arctic skate is thought to be a benthic feeder, which mostly targets teleost fish and variety of benthic invertebrates (Last and Stevens 1994, Kulka et al. 2007).

IUCN Red List of Threatened Species lists Arctic skate as a species of least interest because it is common around both poles and outside of range of current fishing activities (Kulka et al. 2007). However, more recently Arctic skate has been reported as a growing bycatch in Barents Sea trawl and long line fisheries for cod, haddock, redfish and Greenland halibut (Dolgov et al. 2005) as well as Greenland halibut and shrimp fisheries in Davis Strait (Kulka et al. 2007). Moreover, life history of this medium to large skate species is currently poorly understood, but it may exhibit similar characters to other unproductive deepwater skates.
1.6. RATIONALE AND OBJECTIVES

This thesis intends to increase the current knowledge of the movement and behaviour of two hard-to-study, deepwater, Arctic marine species - Greenland halibut and Arctic skate. Each species will be allocated a data chapter to summarize the data obtained by satellite tags. This thesis is part of a larger Ocean Tracking Network (OTN) initiative (http://oceantrackingnetwork.org) that, as one of its goals, aims to improve our understanding of movements and migrations of marine macrofauna on various spatial and temporal scales. Subsequently, the goal is to implement such knowledge in the management of commercial species and conservation of endangered species. To do so, OTN has supported deployment of tracking technologies such as satellite and acoustic tags on numerous commercial and endangered marine species. For example, with the knowledge of specific migratory routes of fish, decisions about designation of protected areas, setting of shipping routes or exploration of oil and gas, will be much more effective (see OTN website for details).

Greenland halibut is an economically important species. Some of the Greenland halibut migration patterns were previously described by conventional methods, such as mark and recapture tagging and research or commercial surveys. However, these methods were difficult to conduct and inherently prone to a large bias, leaving major gaps in our knowledge of the movement patterns of this fish. Satellite telemetry tags provide a unique opportunity to monitor vertical movement patterns of Greenland halibut in seasonally ice covered Cumberland Sound. Detailed vertical movement patterns will, in turn, elucidate some of the feeding behaviours of a species known as a vigorous hunter and previously considered as a pelagic feeder. Additionally, this technology will enable to describe depth
and temperature preferences of these fish in relation to the ice-cover/season. Lastly, satellite and acoustic telemetry will allow verifying the anecdotal knowledge regarding seasonal movement between winter (operating in shallower waters) and summer (deeper waters) fisheries in Cumberland Sound, reported by Inuit fishermen. I hypothesize that adult Greenland halibut will undergo normal diel vertical migration because it was shown to feed on pelagic prey such as capelin and redfish (based on stomach content and stable isotope analyses) (Bowering and Lilly 1992; Dennard et al. 2009a). I also hypothesize, based on previous fishing records, that seasonal movement into shallow (“winter fishing”) grounds will occur with the onset of land fast sea ice.

Arctic skate has a wide geographic range and is known to occupy wide range of depths, sharing similar depth range with commercially important Greenland halibut. For this reason, Arctic skate may become an important bycatch in Arctic fisheries. Satellite telemetry will be used to provide first ever insight into activity levels and detailed vertical movement patterns to reveal some of the life history traits of this species. Depth and temperature preferences will be described. I hypothesize that Arctic skate will not undergo normal diel vertical migration because of its preference for benthic prey (Last and Stevens 1994).

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Figure 1.1 Arctic boundaries defined by temperature (light grey line) (after Stonehouse 1989), the oceanographic properties (thin, dark grey line) and the Arctic Monitoring and Assessment Programme (AMAP) (thick, dark grey line) (after Murray (Ed) 1998)
2 DEPTH AND TEMPERATURE PREFERENCES OF THE DEEPWATER FLATFISH, GREENLAND HALIBUT (*Reinhardtius hippoglossoides*) IN AN ARCTIC MARINE ECOSYSTEM

2.1 INTRODUCTION

Much of the Arctic has been protected from major exploitation by commercial fisheries because of the climate and the extent of sea ice, which have also likely contributed to the lack of studies on movement and behaviour of Arctic marine fish species. The reduction in sea ice and the increase in temperature in polar regions that have occurred over the past two decades (Serreze *et al.* 2000; Rayner *et al.* 2003), along with global declines in temperate and tropical commercial fish stocks (Botsford 1997; Christensen *et al.* 2003; Hilborn *et al.* 2003), have resulted in a growing interest in Arctic resources and an associated increase in commercial fishing pressure on Arctic marine fishes in seasonally ice-covered areas (Schrank 2007). Limited knowledge on the movement of Arctic fish is of concern given the additional stressors that are now impacting fish populations, namely changes in water temperature and ocean currents caused by climate change and their consequent effects on the movement patterns of marine fishes, e.g., distribution and maturation of larvae (Gibson 1997; Sohn *et al.* 2010). Understanding how the characteristics of Arctic marine ecosystems relate to fish movement patterns (i.e., linking environmental parameters with the distribution and abundance of fishing resources) is of critical importance for the management and conservation of Arctic marine fish stocks (Schick *et al.* 2008).

*modified from: Peklova I, Hussey NE, Hedges KJ, Treble MA and Fisk AT. Depth and temperature preferences of the deepwater flatfish, Greenland halibut (*Reinhardtius hippoglossoides*) in an Arctic marine ecosystem. Accepted by the Marine Ecology Progress Series, doi: 10.3354/meps09899
Satellite telemetry has been used to study the movement, behaviour and environmental preferences of a wide range of aquatic species, including sharks (Sims et al. 2003; Teo et al. 2004; Sims et al. 2008, Brunnschweiler et al. 2010), and many teleostei including tuna (Block et al. 2001; Kitagawa et al. 2004; Schaefer and Fuller 2004) and flatfishes (Seitz et al. 2003; Loher and Seitz 2006; Loher and Blood 2009). These tags are attached externally to the fish, record depth, temperature and light, and release after a specified length of time, thus providing insight into horizontal and vertical movements and habitat use over different spatial and temporal scales (Block et al. 2001; Wearmouth and Sims 2009; Humphries et al. 2010). There is no requirement to recapture tagged individuals, making this technology particularly useful for studying fish in deepwater habitats and extreme environments such as the Arctic, where daily fieldwork or observations are impractical. Despite the apparent advantages of this technology, it has received little use in such environments to date.

Greenland halibut (Reinhardtius hippoglossoides) have become an important commercial fish species, particularly in the Northwest Atlantic (Bowering and Brodie 1995; DFO 2008a). This benthic flatfish inhabits deep (typically 400 to 1000 m and as deep as 2200 m) (Vis et al. 1997; Bowering and Nedreaas 2000) and cold (~0 to 6°C) (Bowering and Nedreaas 2000) waters in northern latitudes (>45° N) in the Arctic, Atlantic and Pacific Oceans (Bowering 1984; Dyck et al. 2007). Older fish usually move to greater depths, where they spawn (Bristow 1992; Gundersen et al. 2010). Greenland halibut feed on a variety of species (Bowering and Lilly 1992; Pedersen and Riget 1993) and their diet changes with fish size, water depth and latitude of occurrence (Orr and Bowering 1997). Despite being a flatfish, it has been suggested that Greenland halibut
may feed on fast swimming pelagic organisms, such as capelin (*Mallotus villosus*) (Dennard *et al.* 2009b) and cephalopods (Pedersen and Riget 1993; Dawe *et al.* 1998). Greenland halibut are also an important prey item for key predators in Arctic food webs, including whales and Greenland shark (*Somniosus microcephalus*) (Crawford 1992; Fisk *et al.* 2002; Laidre 2004). Among flatfish species, Greenland halibut are considered to be exceptional swimmers (de Groot 1970; Anonymous 1993) and are thought to be highly migratory; a recaptured T-bar anchor-tagged Greenland halibut travelled a straight line distance of 2500 km over two years (Boje 2002).

Cumberland Sound is a large inlet located on the south-eastern side of Baffin Island, Canada with bottom topography of shallow margins surrounding a deep central basin that descends to ~1500 m (Dennard *et al.* 2009a). Typically, seasonal land fast ice forms in the Sound, dividing the year into two major periods: ice covered (winter), when the Sound is predominantly covered with land fast or drifting pack ice, and ice free (summer). These two periods have dictated two fishing seasons for Greenland halibut, a traditional winter fishery through the sea ice and the newly developed summer vessel-based fishery that operates in open water. The winter fishery is dependent on land fast sea ice forming a stable platform on which to base fishing camps (DFO 2008b). Nearshore areas of Cumberland Sound that are typically covered by land fast sea ice are characterized by having uneven bottom habitats with shallow areas (<300 m) that are interspersed with medium deep areas (350-700 m) (DFO 2008b). Greenland halibut seem to be most abundant in a few of these medium deep areas (Pike 1994). Efforts to locate commercial concentrations of Greenland halibut in shallow locations (350-500 m) on the winter fishing grounds during the summer open water period have not been successful.
However, fishing has been good in the summer in deeper areas (>700 m) within the central portion of Cumberland Sound (Young 2010). These observations have led to speculation that the distribution of Greenland halibut within the Sound may vary across seasons.

I hypothesize that Greenland halibut move from the deep water area into shallower habitats with the onset of colder temperatures and sea ice formation. Given evidence of pelagic feeding (Dennard et al. 2009b), it was also hypothesized that Greenland halibut would show rapid and regular vertical movements into the water column following the normal diel vertical migration of zooplankton and potential pelagic prey species such as capelin (Bailey et al. 1977; Davoren et al. 2006). To quantify the vertical movement patterns and temperature preferences of Greenland halibut in Cumberland Sound, Baffin Island, nine large fish were tagged with pop-off archival transmitting (PAT) tags (MiniPAT, Wildlife Computers Inc., Redmont, WA) in August 2010. The distribution of archival tag pop-off locations, the bathymetry of Cumberland Sound, and the timing of ice cover were used to identify seasonal horizontal movement patterns and site fidelity of this species. Finally, the performance of MiniPAT tags attached to Greenland halibut and exposed to unique depths (up to 1400 m) and extreme environmental conditions was summarized.

2.2 MATERIALS AND METHODS

Study sites and tag attachment

Tagging of fish was carried out on the 17th of August 2010 within the deepwater region in central Cumberland Sound, Baffin Island, Canada (65° 39’ 32” N, 065° 51’ 04” W; Fig. 2.1). All fish were captured using bottom long lines set at ~900-1100 m water
depth. Each long line was ~1900 m in length, with 1500-2000 gangions (1 m with Mustad’s Duratin Tuna Circle (O. Mustad & Son (USA) Inc., Auburn, NY) hooks sizes 15 and 16), baited with frozen squid and soaked for ~12 hours. Long lines were pulled to the surface and fish were gently unhooked and fork length (FL) recorded. In order to successfully retain the tag with minimal effect on the fish’s behaviour, the largest individuals (over 80 cm FL) that had no apparent injuries were chosen for tagging. Each tagging procedure took ~3-4 minutes, following which each tagged fish was kept onboard in a sea water holding tank for 15 minutes to verify that the tagging was successful and that the animal was healthy prior to release. Tags were attached externally to the eye-side of Greenland halibut using a titanium dart and a 15 cm tether (300 lb. test monofilament with stainless steel Nicopress sleeves), following the methods of Loher and Seitz (2006) and Loher (2008). The wire and sleeves were covered with polyolefin shrink to minimize the irritation and abrasion of tissue. The dart was inserted below the dorsal set of pterygiophores, within the deepest section of muscle tissue (Tim Loher, International Pacific Halibut Commission, Seattle, WA, personal communication).

Tag model and set up

Wildlife Computers pop-off archival transmitting (MiniPAT) tags were preset to record both depth and ambient temperature at time intervals of 150, 300 and 600 seconds and were deployed for 70 (August 2010 to October 2010), 100 (August 2010 to November 2010), and 300 days (August 2010 to June 2011), respectively; deployment times and data collection reflected the memory capacity of the tags. Short deployment periods provided the highest resolution data on depth and temperature profiles to provide insight into detailed vertical behavioural patterns, whereas longer deployments provided
data on longer-term behavioural patterns and movements. A total of nine MiniPAT tags were placed on Greenland halibut (mean fork length ± SD: 88.8 ± 4.4 cm; Table 2.1); three tags were designated for each of the deployment periods. Premature release of the tag at constant depth was disabled because of the benthic nature of Greenland halibut and the expectation that periods of potentially minimal movement would occur.

Data analysis

All analyses were performed on time-series depth and temperature data sets that were transmitted by the tags via satellites. To summarize depth and temperature preferences all data were pooled (i.e., data from all 70, 100, and 300 day deployments) into bins of 100 m (300–1500 m) for depth and by 0.5°C (0.0–6.0°C) for temperature to depict the main depth/temperature trends over the course of the tag deployment (Fig. 2.2). The relationship between the raw depth data, i.e. time series depth data for each fish, and three major covariates were analyzed using linear mixed-effect models fit using restricted maximum likelihood in the \textit{lme4} package in R (R Core Development Team 2012; Bates and Maechler 2010). The three covariates were: day/night, representing the light/dark period of the day (derived from Nautical almanac, 66 ° N lat, NavSoft), modelled as a fixed-effect; month (August -November, ~ duration of the fishing season) and; individual fish (n = 5, i.e., individuals within the deployment period August -November), modelled as a crossed random effect. An examination of the probability plots of residuals from the model relating depth to day/night indicated adequate model fit and quantile–quantile plots showed data to be generally described by normally distributed errors.

To estimate a downward swimming speed for Greenland halibut in the pelagic water column, data for the change in depth (as an approximation of distance) over time
(the initial ten minute descent of the fish after it was tagged) were extracted. The initial
descent was used because it was a guaranteed movement in the pelagic water column,
thus an approximate estimate for the baseline swimming speed that a Greenland halibut
can achieve in the pelagic water column. Swimming speeds for upward and downward
movements within the natural depth range of Greenland halibut were estimated from
randomly selected ten minute periods (30 periods/ movement) during which an individual
made clear ascent/descent movement with apparent change in depth between each two
consecutive observations. These speeds were then compared to the swimming speed of
the initial descent in the pelagic water column. Swimming speeds calculated here
captured distance as a two dimensional movement based on change in depth, and did not
account for horizontal movements, e.g., when fish swam above a flat plain or moved
sideways at the same depth level. Swimming was assumed to be continuous if two
consecutive depth observations showed changes in depth (i.e., it was assumed the fish did
not rest for any portion of the sampling interval between two consecutive depth
observations). Given that the above two described inaccuracies are embedded in these
estimates, the calculated swimming speeds are considered a method of evaluating pelagic
behaviour and do not represent actual swimming speeds.

2.3 RESULTS

*Functionality of the tags*

All of the tags deployed on Greenland halibut reported to Argos satellites within
days (mean ± SD: 3.6 ± 4.6 days after, min = 1, max = 12 days after) of the programmed
pop-off dates (Table 2.1). None of the tags were physically retrieved. Two of the tags
(tags 03, 07) reported constant depths for 70/70 days and 278/300 days (constant depth
after Sep 19, 2010) (Fig. 2.3), respectively, prior to the pre-programmed pop-off date. Consequently, only a portion of the archival data record provided by tag 07 was analysed (from August 17- September 19, 2010), and the record by tag 03 was omitted from our analyses. All nine tags transmitted between 8.9-72.8 % (mean ± SD: 57.3 ± 21.4 %) of their depth and 8.5-73.4 % (mean ± SD: 56.0 ± 21.2 %) of their temperature records yielding a total of 749 and 731 days of depth and temperature data, respectively (Table 2.1). Tags did not provide any light level data, which was consistent with the depths occupied by Greenland halibut.

*Pop off positions*

All of the tags popped off in Cumberland Sound (Fig. 2.1) between 3.2 and 27.4 km (mean ± SD: 10 ± 8.7 km) from the tagging location (Fig. 2.1). All fish (except for tag 06, which moved south of the tagging location) moved North, West or Northwest from the tagging location (Fig. 2.1). Fish that were tagged in the same deployment period did not show any clear trends in direction of movement. Two fish that spent 100 days at liberty (DAL) (tags 05, 06) moved the farthest distance from the tagging location, 27.4 and 15.7 km, respectively. All three 300 DAL fish tags (tags 07, 08, 09) popped of within a 16 km radius of the tagging location (Fig. 2.1). Tag 07 reported constant depths after September 19, 2010 and did not provide data for the ice cover season. Depth profiles recorded by tag 09 showed that this fish occupied shallower waters (<600 m) during the winter (Fig. 2.4). If the fish moved to winter fishery areas (assuming that these movements were tied to the bathymetry of Cumberland Sound and were not a result of the fish swimming in the pelagic water column) this would mean the fish travelled at least 50 km during its time at
liberty. However, we cannot exclude the possibility the fish moved to the shallower waters surrounding this area.

**Depth and temperature preferences**

Greenland halibut (n = 7) ranged between ~400-1400 m depth, but spent 89% of the days at liberty below 900 m (Fig. 2.2). Depth preferences changed over the course of the year; Greenland halibut occupied deeper waters from August to December (mean ± SD: 1047 ± 112 m; n = 7) and then moved to shallower waters between January and June (mean ± SD: 823 ± 121 m; Fig. 2.5), although data for January to June included only two fish. Results of the model used to describe the relationship between depth and day/night, was not significant (t < -2; Table 2.2). The negligible difference from the overall intercept (mean level of depth was 1076 m, Table 2.2) associated with the day/night variable (-1.287; Table 2.2), and the weak correlation between the two variables (-0.008; Table 2.2) indicated there was no relationship between depth and day/night (Fig. 2.6), i.e., diel cycles were not important variables explaining depth preferences. The variance attributed to individual fish was lower than the variance attributed to month (Table 2.2), indicating that month had a greater effect on depth preference. Residual variability was higher than both individual fish and month (Table 2.2), indicating greater within individual/month variation. Five of seven fish showed an overall trend towards inhabiting deeper waters from August to November, being at the deepest depth in November (Fig. 2.6). One fish that was tagged for 300 days (tag 09) moved into shallower depths (ranging up to 361 m) in January, returning to deeper waters in May (Table 2.3; Fig. 2.7A). A second fish that was tagged for 300 days (tag 08), remained at greater depths throughout the tag deployment period except for a single excursion up to 457 m in January (Fig. 2.7B).
Although fish 08 did not inhabit the same depths as fish 09 over the 300 day period, it did occupy shallower depths on average between January and June (mean ± SD: 881 ± 41 m) compared to the August to December period (mean ± SD: 1102 ± 108 m; Fig. 2.4B, 2.7B).

Greenland halibut (n = 7) experienced temperatures between 1.3-2.7°C, but spent >85% of their days at 2.0-2.5°C (Table 2.3, Fig. 2.2). The temperature profiles from the tags varied over the course of the year. Between September and November fish occupied waters >2.3°C, whereas between February to April the mean temperature was 1.8-1.9°C.

**Vertical activity and swimming speeds**

Detailed depth profiles revealed that Greenland halibut displayed a continuum of activity levels (from zero to moderate to high activity) that varied without any clear cyclic or temporal patterns (Fig. 2.3, 2.4). The two ends of the activity continuum yielded two distinct behaviours, which were common to most of the tagged fish. The first behavioural type was characterised by long periods (>1 hour) of zero or minimal change in depth, i.e. minimal activity. This behaviour was observed for all fish except one (tag 07, Fig. 2.3E) and was randomly scattered throughout the time series depth records. The other end of the spectrum was defined by gradual upward and downward vertical movements, with typical short breaks (~5-30 minutes) of no change in depth, and an overall change in depth of ~100-300 m hr⁻¹. This behaviour was considered high activity behaviour and was observed over the steepest depth changes throughout the time series depth profiles. This behaviour was typical for fish 07 (Fig. 2.3E) and was observed throughout the duration of the time series record (30 days). For the remaining fish the duration of this behaviour was between one hour (e.g. tags 02, 08, Fig. 2.3B, 2.4B
respectively) and several days (e.g., tag 09, Fig. 2.4A), but occurred less frequently. The majority of the time series depth records of all fish consisted of up and down vertical movements with amplitudes ranging randomly between ~10-100 m hr\(^{-1}\) with frequent short breaks (~5-30 minutes).

Swimming speeds calculated for the randomly selected upward/downward movements ranged between 0.02-0.18 m s\(^{-1}\) for upward and 0.02-0.15 m s\(^{-1}\) for downward swimming (mean ± SD: 0.08 ± 0.01 and 0.07 ± 0.01 m s\(^{-1}\) for upward and downward swimming, respectively) (Table 2.3). The maximum swimming speed (~pelagic swimming speed) obtained by Greenland halibut during their initial decent after tagging was 0.40 m s\(^{-1}\) (mean ± SD: 0.29 ± 0.08 m s\(^{-1}\), n = 6, Table 2.3); however, it should be noted that these speeds might not reflect normal behaviour due to effects of the tagging process and that Greenland halibut do not normally swim in a strictly vertical manner (Albert et al. 2011). Swimming speeds estimated for the high activity periods were typically lower than that of the initial descent, suggesting that rapid movements into the pelagic water column were scarce. Alternatively, Greenland halibut could enter the pelagic water column at lower swimming speeds than that of the initial descent.

### 2.4 DISCUSSION

Pop-off archival transmitting tag data found that Greenland halibut from Cumberland Sound showed a preference for deep (>900 m) and cold (~2.3°C) waters, but there was an indication of movement from the deep waters that were occupied during the ice free season to shallower (and relatively colder) waters during the ice covered season. Tagged Greenland halibut showed strong site fidelity for deepwater areas within the central part of the Sound from August to November, when most of the tags were
programmed to pop off. This site fidelity in the deepwater area correlated with the preferred location of the summer commercial Greenland halibut fishery. Depth data from two fish that were at liberty for 300 days including the ice cover season indicated that Greenland halibut were moving within the Sound during ice covered periods and inhabited shallower depths. Although previous evidence has suggested that Greenland halibut feed on pelagic prey (Dennard et al. 2009b), tagged Greenland halibut did not show any diel differences in depths and rapid vertical movements into the water column were scarce.

*Tag performance*

All of the MiniPAT tags performed well in the extreme environmental conditions experiencing temperatures as low as -1.7°C and depths of 1400 m. All nine tags reported back (100% report rate), a report rate that is 17% higher than the overall pop-off satellite archival transmitting (PSAT) report rate registered by the tag manufacturer, Wildlife Computers (Musyl et al. 2011). Seven tags remained attached until the programmed pop-off date (77.8%) and returned 68% of the data on average. We found no difference in the rate of data return among tags that were logging different numbers of total messages. Tags that were deployed for the longest periods (i.e., 300 days) transmitted the largest portion of their total record, despite the higher total record size (3150 vs. 1680 vs. 2058 total messages for 300 vs. 100 vs. 70 days). These data return rates may suggest that Arctic weather plays an important role in transmission success, with more favourable transmission conditions in late spring compared to early winter.

Two tags (03, 07) reported a constant depth prior to release, but because these tags released at the pre-programmed date, this constant depth was likely not caused by tag
malfunction. Rather, the tags recorded constant depth because the fish either died remaining on the bottom or the combined weight of the anchoring device including the dart and leader wire, coupled with the dense, deep Arctic waters might have held the tag at depth until the link corroded (Heather Baer, Wildlife Computers Inc., Redmont, WA, personal communication). Given the high rate of scavenging in the Arctic, for example by the amphipod *Anonyx nugax* (Klages *et al.* 2002; Fisk *et al.* 2003), it seems unlikely that a fish would not be consumed, therefore the latter explanation is more likely. The two tags returned 23.2% of data on average. A potential explanation for low transmission rates of the prematurely detached tags may be worsened weather conditions or decreased battery life, considering these tags popped off with a delay compared to the rest of the tags.

*Depth preference*

Pop-off archival transmitting data indicated that large (>80 cm) Greenland halibut occupied any area of the Sound where depths were greater than 375 m; the greatest depth experienced by a Greenland halibut (~1400 m) matched the deepest depth known for Cumberland Sound. However, all of the fish preferred depths that were below 900 m, which was expected, as Greenland halibut are known to move to deeper waters as they mature (Atkinson and Bowering 1987), preferring deepwater channels running between shallower banks (Bowering and Nedreaas 2000). Multi-species fish surveys in Davis Strait found that larger Greenland halibut occurred at greater depths and population densities were highest between 750 and 1250 m (Treble and Jørgensen 2002; Treble 2011). Although the sample size in this study was small (i.e., n = 2 from January to June), the linear mixed-effect model found that depth preference varied between August and
November, and further variation in depth preference was coincidental with the development of land fast ice (December to June), with fish moving into shallower waters as the ice formed.

Detailed depth records showed that Greenland halibut exhibited two distinct types of vertical behavioural movement patterns. The two behavioural types were randomly interspersed in a continuum of moderate activity levels and, vertical movements varied in amplitude, frequency and slope, similarly to the behaviour observed in Pacific halibut (Hippoglossus stenolepis) (Seitz et al. 2003). The first behaviour was defined as zero or minimal change in depth lasting from one hour to greater than a day, which likely indicated resting. A second behaviour, high activity, was defined by a vertical displacement of 100-300 m hr\(^{-1}\). These longer ascents and descents were often interspersed with periods (5-30 minute) of no change in depth. This lack of change in depth could have resulted from resting on the bottom, gliding mid water, or via the inaccuracy of the tag pressure sensor. The former explanation would appear to be the most plausible considering the diverse bottom topography of Cumberland Sound. Observed changes in depth (for the vast majority of cases) were therefore likely a result of the fish following the uneven topography of the bottom of the Sound. However, other movement behaviours cannot be ruled out and more complex biologging tags, for example, accelerometer tags, would be required to resolve this point.

The vertical movement by Greenland halibut was not related to diel cycles, which is consistent with the results of stratified random bottom and pelagic surveys (Jørgensen 1997a). The estimated swimming speeds (steep ascents and descents) throughout the depth record were largely not indicative of rapid vertical movements into the pelagic
water column potentially to feed, as has been reported for Greenland halibut in the Northeast Atlantic (Vollen and Albert 2007; Albert et al. 2011). Studies have reported fast swimming prey in Greenland halibut diets, including demersal fishes, particularly redfish (*Sebastes* sp.), and capelin, which was identified as a major diet component in Cumberland Sound based on stable isotopes (Dennard et al. 2009b). The occurrence of pelagic fishes in the diet of Greenland halibut might be explained by Greenland halibut feeding on pelagic fishes and invertebrates when they occupy shallower water (i.e., during the ice covered period) and habitats overlap (Allen and Smith 1988). Flatfish often use an ambush foraging strategy to capture prey (Gibson 2005), for example, Kawabe et al. (2004) observed rapid ambush movements into the pelagic water column by Japanese flounder (*Paralichthys olivaceus*) of ~40 seconds to catch prey. Greenland halibut may employ a similar strategy as Japanese flounder, however, given the shortest sampling period interval of pop-off archival transmitting tags in this study was 150 seconds, such rapid foraging movements would likely not be identified by these tags. Alternatively, Greenland halibut could scavenge pelagic fishes, such as capelin (also proposed in Bjelland et al. 2000), when mass die-offs occur following spawning events (Vilhjálmsson 2002), assuming that the dead biomass becomes available at depths occupied by Greenland halibut.

**Temperature preference**

Greenland halibut occupied a narrow range of temperatures, between 1.3 to 2.7°C, and spent the majority of time in water temperatures of 2.0 to 2.5°C. This temperature range was in agreement with that where Greenland halibut are most abundant in offshore waters (0 to 6°C) (Bowering and Nedreaas 2000; Treble and Jørgensen 2002).
Considering peak spawning temperatures in Davis Strait were estimated at 3.0 to 3.5°C (Jørgensen 1997b), the slightly cooler temperatures experienced by Greenland halibut in Cumberland Sound (the warmest bottom temperature measured by a satellite tag there was 2.7°C, CTD (conductivity, temperature, depth) casts measured temperatures just above 0°C at 850 m (Simonsen and Treble 2003)) suggest the region is less suitable for spawning.

Although Greenland halibut have been shown to occupy waters below 2°C (Treble and Jørgensen 2002; Treble 2011), only one of the fish (tag 09) spent continual periods of time (30%; especially during the winter) at temperatures ≤2°C. Low temperatures are thought to affect the metabolic and growth rates of adult Greenland halibut (Fonds et al. 1992; Patnaik et al. 1994), thus movements to shallower waters during the winter might represent a strategy to reduce metabolic rates when ice is present and primary productivity decreases.

**Seasonal movements**

The vertical displacement of one fish (tag 09) to shallower water potentially indicates that some Greenland halibut undertake seasonal movements out of the deep waters in Cumberland Sound. This movement could be driven by an ice cover-associated factor, as the fish moved to shallower water after ice had formed in January and moved back to the deeper water area when it started to recede/break-up in May. Considering that the second fish (tag 08) that was tagged for 300 days did not undertake such a prominent movement to shallower water, this type of seasonal movement may be either a rare event or suggest that not all the Greenland halibut move to the shallower water for the ice
covered period. Because of the limited sample size it is difficult to draw conclusions about how typical this behaviour is.

The summer fishery is currently concentrated in the deep water area in the center of the Sound and efforts to catch Greenland halibut in the shallow areas of the winter fishing grounds were unsuccessful during the summer (Young 2010). The fact that one of the 300 DAL Greenland halibut remained in deep water during the ice covered period is also consistent with historic catches of these fish in deeper areas of the winter fishing grounds (DFO 2008b). It would therefore appear that Greenland halibut might use a variety of residency-movement strategies with season. This potential variation in season-related movement tactics warrants further study as data will be critical for developing effective management plans for Cumberland Sound.

Why would Greenland halibut remain in deeper waters during the ice free season and then move to shallower waters during the ice cover season? One possibility could be to avoid predation by whales, in particular beluga whale (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*), which are both thought to feed on Greenland halibut (Laidre and Heide-Jørgensen 2005; Bluhm and Gradinger 2008). Reports from Greenlandic waters have noted that the periodic disappearance of Greenland halibut often coincided with increased sightings of beluga (Anonymous 1993). A recent stable isotope study suggested that beluga did not feed on Greenland halibut during the spring and summer (Marcoux *et al.* 2012). This fits with our current understanding of the distributions of beluga and Greenland halibut within the Sound; they occupy separate areas during spring and summer (May to October), as Greenland halibut stay in deep water pockets in the central part of Cumberland Sound and beluga are mainly
concentrated in Clearwater fiord within the Cumberland Sound management zone and along the west side of Cumberland Sound. However, their distribution may overlap during fall and winter when belugas gather over deeper areas around the margins of the growing land fast ice, where Greenland halibut may be present (DFO 2008c; Kilabuk 1998).

Other studies have suggested that observed seasonal movements by Greenland halibut and other flatfishes are related to spawning and feeding (Jørgensen 1997b; Loher 2008; Loher and Blood 2009). Although spawning by Greenland halibut typically occurs in water temperatures >3°C (Jørgensen 1997b), occasional spawning has been observed in the fiords of northwestern Greenland, despite the low bottom temperatures in the fiords that likely inhibit the maturation process (Templeman 1973). No evidence of spawning by Greenland halibut in Cumberland Sound has been reported (e.g., no ripe or spent males or females were found between 1990-1992) (Pike 1994); however, the size of individuals suggested that adult females were present (Fadeev 1971; Pike 1994; Morgan et al. 2003). A final explanation could relate to seasonal movements of prey. Although data are not available for Cumberland Sound, prey abundance due to seasonal changes in primary production is expected to vary (Rysgaard et al. 1999) and may affect the movement patterns of predatory fishes.

In summary, Greenland halibut in Cumberland Sound appeared to be a deep dwelling species that spent the majority of their time near the sea bottom at depths greater than 900 m during the ice free period. Detailed depth records found that individuals did not undertake diel movements into the upper water column or rapid vertical movements, expected behaviours if fish were feeding on pelagic prey. One Greenland halibut moved
to shallower water following the occurrence of seasonal land fast ice, returning to deep water for the ice free period, while one individual remained in deep water throughout the same period. This indicated that Greenland halibut undertook different movement strategies across seasons within Cumberland Sound. This is an important consideration given that Cumberland Sound is currently divided into two management areas that manage Greenland halibut as two separate stocks. The mechanisms driving movement/residency of Greenland halibut are unknown but may be related to feeding and predator avoidance.

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Division
Table 2-1 Biological and pop-off archival transmitting (MiniPAT) tag data for Greenland halibut (*Reinhardtius hippoglossoides*) tagged in Cumberland Sound (65.659° N and 65.851° W) on Aug 17, 2010.

<table>
<thead>
<tr>
<th>Tag ID</th>
<th>Fork Length (cm)</th>
<th>Programmed pop-off date</th>
<th>Actual pop-off date</th>
<th>Sampling interval (sec)</th>
<th>Days at liberty</th>
<th>Days of depth Data</th>
<th>Days of temperature data</th>
<th>% Depth data reported(^1)</th>
<th>% Temperature data reported(^1)</th>
<th>Pop-off position (lat/long)(^2)</th>
<th>Distance travelled (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>01</td>
<td>84</td>
<td>26-Oct-10</td>
<td>29-Oct-10</td>
<td>150</td>
<td>70</td>
<td>45.1</td>
<td>44.7</td>
<td>64.0</td>
<td>63.4</td>
<td>65.708/-65.935</td>
<td>6.7</td>
</tr>
<tr>
<td>02</td>
<td>85</td>
<td>26-Oct-10</td>
<td>27-Oct-10</td>
<td>150</td>
<td>70</td>
<td>50.1</td>
<td>48.4</td>
<td>71.1</td>
<td>68.8</td>
<td>65.658/-66.003</td>
<td>3.4</td>
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<tr>
<td>03(^3)</td>
<td>85</td>
<td>26-Oct-10</td>
<td>7-Nov-10</td>
<td>150</td>
<td>84</td>
<td>0</td>
<td>0</td>
<td>37.5</td>
<td>37.7</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>04</td>
<td>95</td>
<td>25-Nov-10</td>
<td>26-Nov-10</td>
<td>300</td>
<td>101</td>
<td>59.5</td>
<td>58.3</td>
<td>58.8</td>
<td>57.6</td>
<td>65.691/-65.899</td>
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<td>05</td>
<td>90</td>
<td>25-Nov-10</td>
<td>26-Nov-10</td>
<td>300</td>
<td>101</td>
<td>58.0</td>
<td>52.7</td>
<td>57.6</td>
<td>52.3</td>
<td>65.859/-66.197</td>
<td>27.4</td>
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<td>06</td>
<td>88</td>
<td>25-Nov-10</td>
<td>26-Nov-10</td>
<td>300</td>
<td>101</td>
<td>73.4</td>
<td>74.1</td>
<td>72.7</td>
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<td>65.521/-65.894</td>
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<td>07(^4)</td>
<td>93</td>
<td>13-Jun-11</td>
<td>24-Jun-11</td>
<td>600</td>
<td>310</td>
<td>27.7</td>
<td>26.3</td>
<td>8.9</td>
<td>8.5</td>
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<td>08</td>
<td>83</td>
<td>13-Jun-11</td>
<td>14-Jun-11</td>
<td>600</td>
<td>300</td>
<td>219.0</td>
<td>217.6</td>
<td>72.8</td>
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<td>65.658/-66.151</td>
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<td>14-Jun-11</td>
<td>600</td>
<td>300</td>
<td>216.2</td>
<td>208.9</td>
<td>71.9</td>
<td>69.4</td>
<td>65.715/-65.843</td>
<td>6.3</td>
</tr>
</tbody>
</table>

\(^1\)Actual count of readings/max count of readings (within the deployment period), mean (± SD); \(^2\) decimal degrees, \(^3\) tag reported constant depths starting 18-Aug-10 and the record was not included in analyses. \(^4\) tag reported constant depth after 19-Sep-10, data recorded between 17-Aug-10 to 19-Sep-10, were analyzed.
Table 2-2 Results of the mixed-effect model with crossed random effects (‘individual fish’ and ‘month’ were treated as random variables, ‘day/night’ was included as a fixed covariate).

<table>
<thead>
<tr>
<th>Random effects</th>
<th>Variance</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Individual fish (intercept)</td>
<td>3115.4</td>
<td>55.816</td>
</tr>
<tr>
<td>Month (intercept)</td>
<td>5194.6</td>
<td>72.073</td>
</tr>
<tr>
<td>Residual</td>
<td>7902.4</td>
<td>88.895</td>
</tr>
</tbody>
</table>

Number of observations: 78869, groups: Individual fish 5, Month 4

<table>
<thead>
<tr>
<th>Fixed effects</th>
<th>Estimate</th>
<th>SE</th>
<th>t-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>1076.6243</td>
<td>43.8395</td>
<td>24.558</td>
</tr>
<tr>
<td>Day/night</td>
<td>-1.2868</td>
<td>0.6589</td>
<td>-1.953</td>
</tr>
</tbody>
</table>

Correlation of fixed effects: -0.008
Table 2-3 Mean (± SD) and minimum and maximum depth (m) and temperature (°C) data for Greenland halibut (*Reinhardtius hippoglossoides*) monitored using pop-off archival transmitting (MiniPAT) tags in Cumberland Sound in 2010.

<table>
<thead>
<tr>
<th>Tag ID</th>
<th>Months deployed</th>
<th>Mean Depth</th>
<th>Min Depth</th>
<th>Max Depth</th>
<th>Mean Temp</th>
<th>Min Temp</th>
<th>Max Temp</th>
<th>Swimming Speed(^1)</th>
<th>Upward Speed(^2)</th>
<th>Downward Speed(^3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>01</td>
<td>Aug-Oct</td>
<td>1007 (37)</td>
<td>743.0</td>
<td>1132.5</td>
<td>2.37 (0.07)</td>
<td>1.8</td>
<td>2.5</td>
<td>0.25</td>
<td>0.07(0.01)</td>
<td>0.04(0.01)</td>
</tr>
<tr>
<td>02</td>
<td>Aug-Oct</td>
<td>1033 (99)</td>
<td>727.0</td>
<td>1389.0</td>
<td>2.38 (0.11)</td>
<td>1.6</td>
<td>2.6</td>
<td>0.40</td>
<td>0.12(0.04)</td>
<td>0.10(0.04)</td>
</tr>
<tr>
<td>03</td>
<td>Aug-Oct</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>04</td>
<td>Aug-Nov</td>
<td>985 (77)</td>
<td>693.0</td>
<td>1131.5</td>
<td>2.30 (0.21)</td>
<td>1.6</td>
<td>2.5</td>
<td>0.33</td>
<td>0.05(0.02)</td>
<td>0.06(0.02)</td>
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<tr>
<td>05</td>
<td>Aug-Nov</td>
<td>1090 (92)</td>
<td>759.0</td>
<td>1380.0</td>
<td>2.41 (0.17)</td>
<td>1.8</td>
<td>2.7</td>
<td>-</td>
<td>0.08(0.03)</td>
<td>0.06(0.03)</td>
</tr>
<tr>
<td>06</td>
<td>Aug-Nov</td>
<td>1131 (118)</td>
<td>789.5</td>
<td>1386.0</td>
<td>2.40 (0.08)</td>
<td>2.0</td>
<td>2.6</td>
<td>0.36</td>
<td>0.08(0.02)</td>
<td>0.10(0.04)</td>
</tr>
<tr>
<td>07</td>
<td>Aug-Sep</td>
<td>4821 (137)</td>
<td>274.0</td>
<td>1106.5</td>
<td>2.14 (0.18)</td>
<td>1.4</td>
<td>2.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>08</td>
<td>Aug-Jun</td>
<td>998 (163)</td>
<td>457.0</td>
<td>1383.5</td>
<td>2.21 (0.19)</td>
<td>1.3</td>
<td>2.6</td>
<td>0.18</td>
<td>0.07(0.02)</td>
<td>0.05(0.01)</td>
</tr>
<tr>
<td>09</td>
<td>Aug-Jun</td>
<td>942 (242)</td>
<td>361.0</td>
<td>1370.5</td>
<td>2.19 (0.36)</td>
<td>1.3</td>
<td>2.7</td>
<td>0.24</td>
<td>0.07(0.02)</td>
<td>0.06(0.02)</td>
</tr>
</tbody>
</table>

\(^1\) Downward pelagic swimming (return to naturally occupied depths after being tagged) (m s\(^{-1}\)), \(^2\) mean peak swimming speed upward (m s\(^{-1}\)), \(^3\) mean peak swimming speed downward (m s\(^{-1}\)), \(^4\) data recorded between 17-Aug-10 to 19-Sep-10, were analyzed.
**Figure 2.1** Tagging location and pop-off locations for 70, 100 and 300 days at liberty (DAL) deployments for Greenland halibut (*Reinhardtius hippoglossoides*) (total n = 7) tagged in Aug 2010 in Cumberland Sound, Baffin Island. Winter fishing grounds (hatched area); deep water area ~ summer fishery grounds (1000 m contour); Cumberland Sound and Division 0B management areas (separated by a dashed line). Pop off positions labelled with (Tags 01-09), contour lines (500, 1000 m) were sketched based on bathymetrical records.
Figure 2.2 Depth and temperature preferences for Greenland halibut (*Reinhardtius hippoglossoides*) (n = 8), combined over all 70, 100 and 300 days at liberty deployments.
Figure 2.3 Individual depth (black dots) and temperature (grey dots) profiles (n = 6) for 70 and 100 day deployments for Greenland halibut (*Reinhardtius hippoglossoides*). Tag 07 reported a constant depth after 19/9/2010 possibly due to premature detachment from the fish or due to death of the tagged fish: the tag stayed at the same depth until the end of the preset deployment period.
Figure 2.4 Individual Greenland halibut (*Reinhardtius hippoglossoides*) depth (black dots) and temperature (grey dots) profiles (n = 2) for 300 day tag deployments.
Figure 2.5 Monthly depth (bars) and temperature (bullets) (mean + SE) preferences of Greenland halibut (*Reinhardtius hippoglossoides*). Aug – Oct 2010 (n = 7), Nov 2010 (n = 5), Dec 2010 - Jun 2011 (n = 2), shaded area = ice covered season.
Figure 2.6 Mean depth ± SD for individual Greenland halibut (*Reinhardtius hippoglossoides*) during day and night for individual months (Aug –Nov).
Figure 2.7 Monthly mean (± SD) and minimum and maximum depth (m) and temperature (°C) profiles for Greenland halibut (*Reinhardtius hippoglossoides*) (Tags 08 and 09). Depth profile for Tag 09 indicated a seasonal movement, the fish stayed in the deep water pocket during the ice free period and moved to shallower waters for the ice covered season. The second fish (Tag 08) showed a less pronounced change in depth occupied with season, but still inhabited deeper waters during the ice free period. Shaded area = months with complete ice cover (Environment Canada archive; [http://ice-glaces.ec.gc.ca](http://ice-glaces.ec.gc.ca)).
3 MOVEMENT AND DEPTH AND TEMPERATURE PREFERENCES OF ARCTIC SKATE (*Amblyraja hyperborea*) IN CUMBERLAND SOUND, BAFFIN ISLAND, CANADIAN ARCTIC

3.1 INTRODUCTION

Sea ice has protected much of the marine faunal resources present in seasonally ice covered, marine Arctic ecosystems from the unprecedented commercial exploitation that is occurring in most of the world’s oceans. Over the past 30 years the extent and thickness of winter and especially summer sea ice has rapidly declined in the Arctic ocean (e.g., Stroeve *et al.* 2008; Kwok *et al.* 2009), which is of particular concern given that many Arctic species are dependent on spatial and temporal ice dynamics. As commercial fisheries are expected to grow in temporally ice covered parts of the Arctic (Schrank 2007), Arctic marine fauna will be exposed to new threats from humans. Thus, it is of critical importance to better understand aspects of the ecology of Arctic marine fish, such as the connection between environmental parameters and species dispersal, abundance and movement patterns, to enable effective management and conservation practices to be developed (Schick *et al.* 2008). At present, the limited number of commercial fisheries and the remoteness and harshness of the Arctic environment make the study of Arctic marine fish extremely difficult. The use of pop-off archival transmitting (PAT) tags provides a novel means to quantify environmental conditions and behavioural movement patterns of Arctic fish, linking both together without the requirement for direct observation and extended periods of fieldwork.

For more than two decades, satellite telemetry, particularly PAT tags, has evolved into an important tool to study the vertical and horizontal movements and behavioural
patterns in relation to environmental conditions of a wide range of marine species (e.g., Sims et al. 2003; Hunter et al. 2004a; Block et al. 2005; Loher and Seitz 2006; Wearmouth and Sims 2009; Queiroz et al. 2010). PAT tags typically collect light level data that provide geolocation estimates, high resolution time series depth data to describe vertical movements, water column use and behavioural patterns, and environmental data such as depth-temperature profiles to quantify the range of preferred environmental conditions (e.g., Seitz et al. 2003; Sims et al. 2003; Loher 2008; Viswanathan 2010).

Externally attached to an animal, PAT tag collects data until its release at a pre-programmed date. At that point the tag detaches from the animal, floats to the surface and transmits the accumulated data record to overhead satellites. Due to the relative simplicity of the tag software and attachment method, its ability to perform in harsh conditions and without the requirement for animal recapture, PAT tags are particularly useful in seasonally ice covered, hard-to-access environments such as the Arctic. Nevertheless, only a few studies have used PAT tags in polar ecosystems to date (Fisk et al. 2012; Peklova et al. 2012).

Cumberland Sound is a large (250 km long and 80 km wide), bathymetrically diverse inlet of uneven bottom, shallow margins and central deep areas reaching depths up to ~1500 m (DFO 2008; Dennard et al. 2009). The Sound stretches from the south eastern side of Baffin Island to the Labrador Sea and has two major seasons, ice free (summer) and ice covered (winter). Land fast ice forms in December and dominates most of the inner parts and coastal areas of the inlet until May or June, when the ice starts to recede. Fisheries for the commercially important species Greenland halibut (Reinhardtius hippoglossoides) within Cumberland Sound are associated with these two major seasons.
The newly opened, summer, vessel operated fishery takes place during the ice free period (August – November) in relatively small part of the central deep water region (roughly delineated by 1000 m depth contour; Fig. 3.1). This highly localised, developing commercial fishery is more efficient than the traditional Inuit winter fishery (February – May) that is dependent on land fast ice and is generally confined to shallower areas where suitable ice develops to enable fishing operations (DFO 2008). Cumberland Sound is divided into two fisheries management zones as there were separate stocks of fish, in particular Greenland halibut (Fig 3.1). However, historical catches have suggested that both the commercially important Greenland halibut and a primary bycatch species Arctic skate (*Amblyraja hyperborea*) may seasonally migrate between these two zones. However, in terms of Arctic skate very little is known regarding vertical depth and temperature preference or the extent and timing of localised movements in Cumberland Sound and/or large-scale migrations.

Arctic skate is a largely unstudied Rajidae that is common to higher latitudes (Last and Stevens 1994) and typically inhabits depths from 140-2500 meters (RAS 2000; Dolgov *et al.* 2005a). The distribution of this benthic elasmobranch is thought to be tied to cold temperatures, exclusively below 4°C (Bigelow and Schroeder 1953). Arctic skate is considered mid-size amongst skates, with maximum total length (TL) around 86 cm for male and 91 cm for female (Bjelland *et al.* 2000; Dolgov *et al.* 2005b). No relationship between skate size and depth has been reported, however skates generally appear to be more abundant on the lower continental slope in depths below 650 m (Dolgov *et al.* 2005b; Kulka *et al.* 2007). Last and Stevens (1994) suggested that Arctic skate feed on a variety of benthic prey, whereas Bjelland *et al.* (2000) reported stomach contents
dominated by fish remains (e.g., herring (*Clupea harengus*), blue whiting (*Micromesistius poutassou*) and zoarcids). The ventral position of the mouth of Rajidae suggests that they are likely to take prey from above, instead from a frontal attack (McKone and LeGrow 1983). Additionally, it is thought that the position of the mouth in Rajidae is an adaptation to extract the prey from bottom substrates using bite and suction feeding behaviour (Wilga et al. 2007). Thus, it was proposed that pelagic diet items might reflect scavenging (Bjelland et al. 2000). Euphasids and other pelagic crustaceans such as hyperid amphipods have also been found in Arctic skate stomachs (Bjelland et al. 2000). To date, detailed studies of Arctic skate feeding habitats and specific foraging strategies are lacking.

An extremely flattened body is an adaptation that allows Rajidae to lie camouflaged on the sea bottom. This evolutionary adaptation is considered a trade off for a decreased locomotor ability. These traits in turn are thought to result in lower activity and longer resting periods for these species (Wearmouth and Sims 2009). Nonetheless, Wearmouth and Sims (2009) showed that common skates (*Dipturus batis*) were very active, especially during the night, travelling up to 100 meters daily within the water column, likely to find prey. In fact, this study suggested that the activity levels of some flattened fish may equal those with a fusiform body shape, when prey distribution is sparse and the density of available prey is low.

Whereas the economic value of some skate species is recognised in commercial fisheries (e.g., spotted ray (*Raja montagui*), thornback ray (*Raja clavata*), blonde ray (*Raja brachyura*) and common skate) (Bonfil 1994; Holden 1997; Walker and Hislop 1998), others are considered as an unwanted bycatch. Arctic skate have been reported as
one of six skate bycatch species in deep water trawl and longline fisheries for demersal fish including cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), blue catfish (*Anarhichas denticulatus*) in Barents Sea and Greenland halibut (*Reinhardtius hippoglossoides*) and shrimp (*Pandalus spp.*) in the Davis Strait (Dolgov *et al.* 2005a; Kulka *et al.* 2007). More recently, Arctic skate have been reported as a common bycatch species in the developing Greenland halibut summer fishery in Cumberland Sound, Baffin Island (Kevin Hedges, *personal observation*) in addition to bycatch in the traditional Inuit winter fishery. Most of the skate bycatch in Cumberland Sound is taken in the summer, as the vessel operated fishery targets deep central areas (~ 1000 m), where both Arctic skate and Greenland halibut are abundant. Some Arctic skates are also caught during the winter, ice covered period, however, the overall bycatch through the ice fishery is generally much smaller due to significantly lower fishing effort in recent years (Young 2010).

At present, the IUCN Red List of Threatened Species recognizes Arctic skate as a species of least interest, due to its wide distribution around both poles which is outside the range of most current fishing activities (Kulka *et al.* 2007). Nonetheless, a cautionary approach is required because the majority of elasmobranch species have low fecundity and a slow growth and maturation rate, which makes them particularly vulnerable to fishing pressure (Bonfil 1994; Dulvy and Reynolds 2002; Sims 2008). This level of vulnerability may be more significant for Arctic skate because of the extremely cold environment it inhabits.

The objective of this study was twofold: (i) to describe depth and temperature preferences of Arctic skate, and (ii) to determine coarse scale horizontal movement
patterns of this species. This is of particular importance given the potential growth of Arctic fisheries and future increased levels of exploitation of this species. As well, I hypothesise that Arctic skate will spend long periods of time resting on the sea bed due to its distinct morphological adaptation and assumed sedentary lifestyle (Wearmouth and Sims 2009). In addition, I predict the species will be largely independent of diel cycles because it is assumed to preferentially feed on benthic prey or scavenge on the offal located at the sea bottom rather than feeding in the pelagic water column (Last and Stevens 1994; Bjelland et al. 2000).

3.2 MATERIALS AND METHODS

Study sites

Tagging of fish was undertaken during two consecutives summers (17th August 2010 and from 9-13th August 2011) in Cumberland Sound, Baffin Island, Canada (Fig. 3.1; Table 3.1). All skates selected for tagging were caught in the central deep portion of the Sound (from depths ~800-1100 m, Fig. 3.1). Skates were caught off a commercial fishing boat (in 2010) and research vessel (in 2011) using bottom long lines. In both years, long lines were ~700/2000 m long with ~ 400/1000 gangions (0.3 m in length; hook sizes 15 and 16 (Mustad’s Duratin Tuna Circle (O. Mustad & Son (USA) Inc., Auburn, NY)) with squid used as bait. Soak times of lines were approximately 12 hours. Once removed from the hooks, skates were examined for injuries and larger individuals (> total length: 62 cm) were chosen for tagging. All tagged skates were adults based on presence of calcified claspers in males and large eggs present in dissected females, indicating skates were in mating condition.

Tag attachment and set up
The tagging procedure took approximately five minutes and skates were released immediately after tagging. Assembled MiniPAT tags (diameter x length: 11.5 x 4 cm, mass: 53 g, Wildlife Computer Inc., Redmont, WA) consisted of 15 cm leader wire covered in polyolefin shrink that was crimped to the tag on one end and to steel leader wire on the other. Following the methods of Wearmouth and Sims (2009) the tag was fixed to the mid-section of the wing of the skate (Fig. 3.2) using the steel leader wire and two circular plastic discs. The tag was attached to the animal by feeding the steel leader wire through the mid section of the wing and securing it in position with two disc plates (positioned on the dorsal and the ventral side of the wing). The wire was then twisted to lock the plate (2010 tagged skates) or crimped behind the plate on the ventral side of the skate’s body (2011 tagged skates).

A total of nine MiniPAT tags were deployed on both male and female Arctic skate (Table 3.1). Utilizing the most of the memory capacity of the tags, three tags were preset for three deployment periods. In 2010, three tags were deployed for 70 days (August to October) with 150 second sampling period interval. In 2011, three tags were deployed for 40 days (August to September; 75 second interval) and three for 100 days (August to November; 300 second interval; Table 3.1). Premature release of the tags was disabled, due to the assumed benthic nature of Arctic skate that might include long periods of resting.

**Data analysis**

All analyses were performed on time-series depth and temperature data sets that were reported via satellites by tags that were successfully retained by the fish (n = 5). Data from all deployment periods were pooled together into bins of 100 m (range: 300–
1500 m) for depth and of 0.5°C (range: 0.0–6.0°C) for temperature to describe the main depth/temperature trends over the course of the tag deployment periods (Fig. 3.2).

The absolute mean change in depth, a measure of the relative amount of vertical movement within ten minute interval periods, was estimated from raw time series depth data by calculating the difference between two consecutive depth measurements over ten minute interval periods. Differences in depths, i.e., changes in depth over ten minute intervals were then averaged for each day and also for dark/light period of each day. To statistically test if movement patterns of skates were related to diel cycles, the relationship between the time series depth data for each fish (n = 5, tags 01, 03, 04, 05, 06) and three covariates (day/night, individual fish and week) were analyzed by linear mixed-effect models fit using restricted maximum likelihood in the lme4 package in R (R Core Development Team 2012; Bates and Maechler 2010). Similarly, the absolute mean change in depth data for each fish (n = 5, tags 01, 03, 04, 05, 06) and three covariates (day/night, individual fish, depth) were analyzed using the same package in R. The day/night covariate was derived from the nautical almanac (66 ° N lat, NavSoft) to represent diel cycles across the changing day and night schedule in the Arctic. Each time, for which measurement of depth was taken by the tag, was assigned either a ‘day’ or ‘night’ label. The ‘day/night’ covariate was modelled as a fixed-effect, the ‘individual fish’, the ‘week’ and the ‘depth’ (i.e. the time series depth data) covariates were considered as random effects. The probability plots of residuals from the model relating depth to day/night covariate showed that the model fit adequately and quantile–quantile plot confirmed that data were generally described by normally distributed errors. The
absolute change in depth data were log transformed \((X' = \log(X + 1))\) and zeros (no change in depth) were filtered out to ensure normal distribution of the data.

We used change in depth as an approximation of distance over time to estimate swimming speeds of Arctic skate. First, the initial descent (change in depth over ten minute interval periods), after the skate was tagged was used to estimate swimming speed in the pelagic water column (Table 3.2). At the point when the skate had returned to the sea bottom and was assumed to be exhibiting normal behaviour, the maximum swimming speeds for up/down vertical movement (change in depth over ten minute interval periods) was estimated and compared to the initial descent speed. This enabled a coarse level determination if the skate re-entered the pelagic water column. These swimming speed estimates do not represent actual swimming speeds as inaccuracies were inherent to the calculations, e.g., fish were assumed not to rest between two consecutive depth measurements; movement along horizontal axis was not accounted for, i.e., fish was assumed to swim straight up or down.

### 3.3 RESULTS

**Functionality of the tags**

Seven of nine of the MiniPAT tags deployed on Arctic skate (mean total length and width ± SD: 68.7 ± 4.3 cm and 50.9 ± 2.4 cm, respectively) in 2010 and 2011 uplinked to Argos satellites within days (mean ± SD: 2 ± 3 days after, min = 0, max = 8 days after) of the programmed pop-off dates (Table 3.1). These tags transmitted between 4.8-76.4 % (mean ± SD: 35.7 ± 27.0 %) of the depth and 5.1-77.0 % (mean ± SD: 36.8 ± 27.3 %) of the temperature time series data to provide a total of 112 and 116 full days of depth and temperature data, respectively (Table 3.1). None of the tags was physically recovered. As
expected, tags did not record any light levels throughout the deployment periods to reconstruct fine-scale horizontal movements, as Arctic skate did not occupy waters with sufficient light levels. Depth profiles showed that four of the tags (tags 03, 04, 07, 09) had been afloat for various periods of time (9/40, 97/100, 93/100, 49/70 days, respectively), prior to corrosion of the safety pin (i.e., prior to the release of the tag from the anchoring mechanism) (Table 3.1). These tags usually stayed at a constant depth (e.g., tag 03, Fig. 3.4B) for the rest of the deployment period, likely being held down by a combination of the weight of the anchoring mechanism and dense Arctic water. Data from these tags (except for tag 03, which reported 21 days before it detached) were not included in further behavioural and environmental data analyses.

*Pop-off positions*

Three out of seven tags (01, 05 and 06) that reported back to satellites, released directly from fish at the pre-programmed date after 70, 40 and 40 days respectively. These tags surfaced in Cumberland Sound (Table 3.1), 30, 37 and 10 km straight line distance away from the respective tagging locations (Fig. 3.1). The three skates did not show any trends in the direction of movement between tagging and pop-off locations. One fish (tag 05) stayed within the deep water region in central Cumberland Sound for the entire deployment (40 days), except for two excursions to ~700 m depth water (Fig. 3.1). The two other fish moved between shallow and deep water areas. Four tags that detached prematurely (tags 03, 04, 07 and 09) popped off in Cumberland Sound and the Labrador Sea but the pop-off location could not be used to assess coarse scale movements as the tags were carried by currents in the meantime (Table 3.1).

*Depth and temperature preferences*
During their time at liberty between August and September/October (40-70 days), skates (n = 5) occupied (mean ± SD) depth of 944 ± 154 m and ranged between ~300 and 1350 m in depth, where they spent 98.0 % of time (Fig. 3.3, Table 3.2). Skates did not display any clear temporal pattern in occupied depths (Fig. 3.4). Closer investigation of the time series depth data of the two female skates (tags 01, 05) showed that they revisited similar depths (~480-520 m four times, ~720-770 three times, respectively) at the very upper limit of their depth ranges every 9-14 days (Fig. 3.4A and 3.4D).

Noticeably, each skate occupied different depth ranges (usually spanning over ~400-500 m), where they spent 86.5-96.0 % of the time at liberty. The first mixed effect model found that the relationship between the time series depth data and day/night was significant (t > 2; Table 3.3) and the difference between the overall intercept (mean depth: 855.482 m) and the day/night variable was estimated at -12.026. Altogether, the two random variables (‘week’ and ‘individual fish’) explained more than two thirds of the variance in the data set. The residual, reflecting differences within individual data sets, accounted for the remaining variance in the data (Table 3.3). As a visual representation of these results, the time series depth data were sorted by day/night time (D/N), months and individual fish into two graphs (Fig 3.5). The graphs depicted the variable relationship between the time series depth data and the diel cycle (Fig. 3.5A) and showed the variability in the time series depth data when sorted by a month and the individual fish (Fig. 3.5B). The second mixed effect model showed that the absolute mean change in depth was not significantly related to the day/night variable (t < 2, Table 3.4). The ‘individual fish’ covariate explained most, whereas ‘depth’ accounted for the least amount of variability in the absolute mean change in depth data set. A large residual
showed that significant variability in the data set was not explained by any of the covariates. Arctic skate spent 85% of the time at liberty in temperatures from 2.0-2.9°C. Skates spent the remaining 15% of the time at liberty in waters between 0.0-2.0°C.

*Vertical activity and swimming speeds*

Detailed depth profiles recorded by the 75 and 150 sec sampling period intervals (tags 01, 04, 05 and 06) showed variability in activity levels within and between individual fish (e.g., Fig. 3.4 and 3.6). Periods of zero or minimal change in depth were displayed as straight horizontal lines in the time series data and most likely indicated low activity levels (Fig. 3.6D, 3.6E, 3.6F). These periods lasted from ~1 to ~48 hours and were observed throughout time series data of two fish (tags 05, 06). Vertical movements ranging over ~200-300 m per 0.5-1 hour time period, which were displayed as steep peaks in the time series data, were used as indicators of relatively high activity levels. Such vertically high activity behaviour was typically randomly distributed throughout the time series data, interspersed with periods of low and moderate activity levels (e.g., Fig. 3.4A, 3.4D and 3.4E). One fish (tag 04) displayed high activity levels during the entire time at liberty (30 days) and did not show signs of moderate or minimal activity (Fig. 3.4C and 3.6A). Depth profiles for the remaining fish were largely dominated by constant movement but instead of spanning a large vertical distance at once, fish moved within a narrower range of depths, indicating moderate activity levels (Fig. 3.4A, 3.4D, 3.4E, 3.6D and 3.6E).

To further distinguish between high and moderate activity levels, depth profiles were compared to graphs depicting the absolute mean change in depth estimated for each day, a second measure to quantify activity levels (Fig. 3.7). For example, resting (no
change in depth) will result in virtually zero absolute mean change in depth, i.e. low activity levels. The absolute mean change in depth was large for vertical movement over a wide range of depths (100s m per hour) and confirmed that such vertical movement indicates high activity behaviour (Fig 3.7). Alternatively, relatively high values of the absolute mean change in depth were associated with periods in time series data when fish did not make large vertical changes in depth, but showed continual, short, upward and downward movements (e.g., 9/10/2010, Fig. 3.7A). The large absolute mean change in depth during these periods shows that highly active behaviour was also associated with movement within a narrow range of depths. The absolute mean change in depth during the day time and night time did not show consistent pattern confirming the results of the second mixed effect model which showed that activity levels were not related to diel cycles (Fig. 3.8).

The activity levels were also compared to the lunar cycle (Fig. 3.7) and the combination of diel and lunar cycle (Fig. 3.8) by overlaying the absolute mean change in depth with a graph depicting the trajectory of the moon, with the spring tides shown as the highest points and neap tides as the lowest points of the sinusoidal curve. The absolute change in depth did not appear to be related to the lunar cycles or the combination of the lunar and diel cycles based on observation of the data.

To determine if skates swam into the pelagic water column, swimming speeds were estimated from upwards and downwards movements and compared to the speed of the initial descent of the fish following tagging. The initial descent speeds reported by two of the tags were 0.38 and 0.24 m s\(^{-1}\). Maximum swimming speeds attained by skates throughout the rest of the deployment periods were 0.21 m s\(^{-1}\) for upward and 0.22 m s\(^{-1}\).
for downward movement (mean ± SD: 0.12 ± 0.07 m.s\(^{-1}\), 0.16 ± 0.05 m.s\(^{-1}\) for upward, downward movement respectively, n = 4, Table 3.3), indicating that skates potentially swim into the pelagic water column.

3.4 DISCUSSION

Although the Arctic skate did not range into the upper water column (above 400 m), they occupied a wide range of depths, reaching close to the maximum depths (~1400 m) of Cumberland Sound. The Arctic skate studied were not confined to deep water areas in the central part of the Sound during the ice free period of the year, but ranged into shallower coastal margins. This contrasts the behaviour of Greenland halibut within this system, which typically occupied deeper waters (> 900 m) during the ice free period (Chapter 2). This finding demonstrates that the depth ranges of Arctic skate and Greenland halibut overlap, but not entirely. Nonetheless, some of the tagged skates spent significant amount of time in depths targeted by the fishery for Greenland halibut, confirming the issue of Arctic skates as a major bycatch species (Dolgov et al. 2005; Young 2010). Arctic skate experienced a narrow range of temperatures, which is likely related to known stable temperature regimes below 800 m and overall low variability in water temperatures in Cumberland Sound. Similarly to another species, the common skate, Arctic skates did not show much evidence of a presumed sedentary lifestyle (Wearmouth and Sims 2009), but rather appeared mostly active. High activity levels were observed for two distinct behaviours, which may potentially be a result of intraspecific differences in foraging. The Arctic skate occupied shallower waters during the dark period of the day; however, activity levels were not tied to diel cycles. The estimates of swimming speeds potentially indicate that skate swim into the pelagic water column.
Tag performance

Despite the relatively high recovery rate of MiniPAT tags in this study (seven out of nine), three of the seven tags that uplinked to satellites did not provide valuable data. These tags reported constant or unrealistic depths (> three days, e.g., Fig 3.4 B) until the link corroded and the tag popped off. This suggested that the animals had either died during the deployment period or the tag had detached from the animal, likely by tearing through the thin muscles of the wing. The tags remained at depth because of the dense Arctic waters and the weight of the anchoring mechanism (Heather Baer, Wildlife Computers Inc., Redmont, WA, personal communication). Given the high rate of prematurely detached tags, a different method for attaching satellite tags to this species, and other smaller batoids, should be considered (e.g., attachment method according to Le Port et al. 2008). Variability in the rate of transmission (4.8-77.0 %) likely reflected weather conditions, however tags that detached prematurely were generally the least successful in transmitting the archival records (Table 3.1).

Depth preference

Both female and male adult Arctic skates ranged between 300-1350 m in depth and spent 97 % of time in depths > 500 m. The observed range is consistent with the overall depth range of 140-2500 m reported for Arctic skates (RAS 2000; Dolgov et al. 2005a), and the depth ranges below 650 m in the Barents Sea, where Arctic skate were most abundant (Dolgov et al. 2005b; Kulka et al. 2007). Two fish (tags 01 and 06) occupied shallower waters with month (August – September/October), but the other two fish (tags 04 and 05) moved to deeper waters over time. Inconsistent trends in depth occupied may indicate that there was no temporal trend in the preferred depth of Arctic skate, contrary
to a tendency of Greenland halibut to move to deeper water during the open water period within the same system. However, it is difficult to draw conclusions given the limited sample size and the relatively short deployment period during the ice free period only.

Alternatively, other behaviours such as spawning (considering that tagged individuals were mature and in mating condition) may be potentially associated with this depth preference. Little information is known about spawning and reproduction of Arctic skate. To date, the only nursery grounds of Arctic skate were reported from depths of \(~780\) m in the Barents Sea (Arve Lynghammar, University of Tromsø, Tromsø, Norway, \textit{personal communication}). Considering the deep topography and stable temperatures between \(1-3^\circ\)C year round (within range of preference), Cumberland Sound may provide a suitable nursery area for this species. Some Rajidae such as longnose skate and thornback rays were shown to display strong site fidelity during spawning. In such cases, female skates make multiple visits to the same nursery area throughout the spawning season to lay eggs (Hunter \textit{et al.} 2005; Love \textit{et al.} 2008). Multiple trips to the nursery grounds might occur also in Arctic skate. A batch of egg capsules, all at different stages (i.e., recently deposited eggs, ready to hatch and freshly hatched eggs) were collected at one time from the nursery area in the Barents Sea (Arve Lynghammar, \textit{personal communication}).

Considering that spawning site fidelity may be a common feature across Rajidae, spawning events might become evident from the time series depth data of females skates as multiple visits of a similar depth (i.e., the preferred spawning location). The two tagged females of Arctic skate (tags 01, 05) ranged between deeper and shallower waters, repeatedly returning to a similar depth at the shallow end of their vertical range.
However, accepting the small sample size, and unknown details about spawning of Arctic skate, it is difficult to draw conclusions about the presumably repetitive movement of females to the same depth and if these patterns were truly related to spawning.

Considering that female Arctic skate that were ready to spawn were caught in shallower waters (~500 m) during the ice covered season (April) (Aaron Fisk and Nigel Hussey, *personal observation*), this question would require year-round deployment of PAT tags and warrants further study.

*Temperature preference*

Arctic skate experienced a narrow range of temperatures, between 1.2 to 2.9°C (over the two tagging seasons), which was well within the estimated margins of their temperature tolerance (Bigelow and Schroeder 1953). Overall, Arctic skate spent 95% of their time within 2.0-2.9°C, which seems to be a suitable temperature range for sexual maturation and potential spawning given that successful incubation of eggs occurs at temperatures up to 0°C (Bigelow and Schroeder 1953). The water temperature at depths below 120 m in Cumberland Sound does not exceed the preferred thermal limits of skates over the course of a year (Jeannette Bedard, University of Victoria, Victoria, BC, *personal communication*). Thus, as long as skates continue to inhabit this fairly uniform thermal environment, it is not expected for temperature to be necessarily either a limitation or a driver of any movement patterns observed in Arctic skates.

*Activity levels and vertical movement*

Three skates (tags 04, 05 and 06) that were monitored at a sampling interval rate of 75 seconds provided the most useful data to investigate various activity levels related to depth change. Activity levels of Arctic skate ranged in a continuum from low to relatively
high. Overall, some of the skates appeared to be highly active, shown by constantly changing depth movements, which is surprising considering the general notion that flattened fish are less active and spend long periods of time resting on the sea bottom (Hunter et al. 2004a).

A closer investigation into the activity levels indicated three distinct behavioural types. The occurrence of these behavioural types varied within and among individual fish. The first behavioural type was indicated by long (> 30 minute) periods of minimal activity when fish remained at the same depth. This behaviour likely indicated resting at the sea bottom and has been previously described for other undulatory batoids monitored by electronic tags; common skate and thornback ray (Hunter et al. 2005; Wearmouth and Sims 2009). The resting behaviour was common throughout the depths profiles of two fish, a female and a male (tags 05 and 06) and was typically interspersed with periods of moderate to high vertical activity. Another behavioural type, exhibited by one male (tag 04), involved high activity levels with vertical displacement of 100-300 m hr$^{-1}$ resembling the oscillatory behaviour of pelagic fish species such as yellowfin tuna (Thunnus albacores), shortfin mako sharks (Isurus oxyrinchus) and basking sharks (Ceterohinus maximus), Sims et al. (2003); Shepard et al. (2006); Schaefer et al. (2007)) but at a much slower rate. The third distinct behavioural type displayed by Arctic skate was high activity movements within a narrow range of depth previously documented in the common skate (Wearmouth and Sims 2009). In accordance with observations of Arctic skate, common skate exhibited similar ranges of vertically active behaviour (Wearmouth and Sims 2009). In this study it was suggested that despite having a flattened body, skates may display comparable activity levels to teleost fishes at times. Additionally, the two
different types of prolonged high activity behaviour observed for both species, Arctic and common skates (i.e., high activity over a wide and narrow range of depths) was proposed to reflect distinct modes of foraging in common skate. High activity movement within a narrow range of depths could represent benthic foraging, where the movement of skate following the steep bottom topography would result in subtle changes in depths records. Alternatively, high activity over a wide range of depths may represent foraging in the pelagic water column or optimized searching for prey within a patchy resource environment as previously reported for large marine predatory fish such as sharks, tuna and ocean sunfish (Schaefer et al. 2007; Sims et al. 2008; Humphries et al. 2010; Vishwanathan 2010).

Swimming speeds estimated for upward and downward movements showed that skate moved at a comparable rate to the initial descent throughout the water column, possibly indicating pelagic movement. Considering the bentho-pelagic diet of Arctic skate (Last and Stevens 1994; Bjelland et al. 2000) potential intraspecific differences in modes of foraging are to be expected and require further study.

Diel vertical migration was examined as a factor driving movement patterns of Arctic skate, despite the fact that DVM is generally more common to species occupying pelagic habitats, such as fish (Reebs 2002) and pelagic elasmobranchs (Casterlin and Reynolds 1979; Carey and Scharold 1990; Shepard et al. 2006). Recently, DVM has been observed in benthic species such as lesser spotted dogfish (Scyliorhinus canicula); bat rays (Myliobatis californica), and the common skate (Matern et al. 2000; Sims et al. 2006; Wearmouth and Sims 2009).
The results of the mixed effect model suggested a significant relationship between the depth occupied by the Arctic skate and the diel cycle, with skates occupying shallower waters during the night time. However, the interpretation of the results is not simple. For example, some of the skates occupied the same depths during the day and night periods (Fig. 3.5B). These inconsistencies and the relatively large variability in the dataset may be explained by the physical variability in the bottom topography of Cumberland Sound. Considering that Arctic skate is a species that likely spend significant periods of time close to the sea bottom as oppose to free swimming in the open water, to some extent the bottom topography may have a randomizing effect on the depth occupied by the skates. Thus, preferred depth has to be investigated with caution. For example, it is likely relevant to look for temporal trends in occupied depths across long periods of time, such as seasons (e.g., differences between depths occupied during the ice free and the ice covered period, Chapter 2). However, it may not be appropriate to investigate the actual depth occupied by fish to infer if there is a relationship to the diel cycle.

As opposed to actual depth, which may be an improper indicator of diel movement, the change in depth may be better suited to investigate a potential relationship between the activity levels and the diel cycle. Assuming the fish follows DVM in order to feed, the activity levels should be higher during the night. The results of mixed effect model suggested that the activity levels did not vary with diel cycles, consequently, DVM may not be a common behaviour of Arctic skate or may be less pronounced than DVM observed in pelagic species. The actual depth did explain some of the variability in the absolute mean change in depth indicating that the skates were more active at certain layers of their vertical range. Activity levels may thus be related to a vertical distribution
of prey. Alternatively, DVM may only be adopted by some individuals (Fig. 3.6C). Such inter-individual variability has been previously reported in the short tailed stingray (*Dasyatis brevicaudata*) and the common skate (*Le Port et al. 2008; Wearmouth and Sims 2009*).

Arctic skate showed inter- and intra-individual variability in preferred depth range and relative amount of time spent resting to the time spent actively moving. These patterns may reflect differences between sexes (Skjæraasen and Bergstad 2000). Despite the fact that the mixed effect models indicated that activity levels in the tagged skates were not significantly different between males and females, these differences may arise with a larger sample size and longer deployment periods. Due to the fact that all tagged individuals were of a similar size (Table 3.1), the inter- and intra-individual variability were likely not affected by ontogenetic changes in swimming speed, behaviour or preferred prey as observed for thorny (*Amblyraja radiata*) and common skates (Skjæraasen and Bergstad 2000; Wearmouth and Sims 2009). Alternatively, the short tag deployment periods in this study might not provide a full representation of the normal movement behaviours of Arctic skates, as behaviour may also vary seasonally as a response to cyclical changes in the abiotic environment. For example, the movement of acoustically monitored freshwater whiprays (*Himantura dalyensis*) was driven by the diel cycle during the wet season, whereas movement was dictated by lunar and tidal cycles during the dry season (Hamish *et al.* 2012).

The lunar cycles were considered as a factor potentially driving movement of Arctic skate; however, a preliminary comparison of the depth records did not yield any clear correlation between the occupied depth/ the absolute mean change in depth and the
lunar cycles. A complete analysis was not considered due to the short deployment periods of the tags (40 and 70 days), but this type of analysis should be considered especially for longer tag deployment periods in future. Some flattened fish such as plaice (*Pleuronectes platessa*) have been shown to use selective tidal stream transport during seasonal movement to maximize their use of energy (Metcalfe *et al.* 1990) and Arctic skate may use similar mechanisms. Due to a low sample size, it was difficult to narrow down the possible factors contributing to the inter- and intra-individual variability in depth records.

*Horizontal movement*

Arctic skate travelled relatively short horizontal distance between tagging and pop-off locations; however, the reported straight line distance was likely an underestimation of the distance travelled during the time at liberty. It was determined that plaice (a bottom dwelling flatfish) moved approximately ten times further than the direct distance estimated between release and recapture positions (Metcalfe 1997; Hunter *et al.* 2004b). Based on pop-off locations and the long periods of time skates spent in shallow waters, Arctic skates were not confined to the deep water regions but dispersed into shallower areas. In contrast to this observation, Greenland halibut (another bottom dwelling flatfish) spent most of their time at liberty below 900 m during the ice free period, potentially to avoid predators such as beluga whales (Chapter 2). Considering that Arctic skate were monitored for a relatively short deployment period, further study should clarify long term movement patterns and potential seasonal migrations.

In summary, Arctic skate occupied a range of depths from ~300 m down to some of the deepest parts of Cumberland Sound, and a narrow range of temperatures between 1.2-2.9°C. Detailed depth records, activity levels and estimated swimming speeds suggested
that Arctic skate is an active forager that potentially exploits prey in both the pelagic water column and in benthic habitats. This is an unexpected finding considering their morphological adaptation for a slow paced, bottom dwelling lifestyle, typically presumed for many skate species. Acknowledging the small sample size, such findings indicate that further tagging is required. The depth profiles of female Arctic skates showed repetitive excursions to specific depths, which may be indicative of spawning events. However, considering insufficient knowledge of the spawning behaviour of Arctic skate, a year-round PAT tag deployment is required to support this hypothesis. The movement of Arctic skate may be linked to DVM but activity levels during day/night were not consistent for all individuals. Acknowledging the low sample size and that for related skate species only some individuals displayed movement patterns related to DVM, this question warrants further study.

The depth range occupied by Arctic skate largely overlapped with that occupied by Greenland halibut in Cumberland Sound. Overlapping vertical habitats are common for skates and flatfish and usually result in skate bycatch in fisheries for groundfish (Dolgov et al. 2005a; Ormseth et al. 2009; Stevenson and Lewis 2010). This is also the case for Arctic skate in Cumberland Sound with Greenland halibut. Due to the unknown life history traits of Arctic skate, with potentially low reproduction and slow growth rates typical for skates (Stevens et al. 2000), caution for management of this bycatch species is required. A simple mitigation measure to decrease the mortality of skates due to bycatch would be to handle skates with care. As shown in this study, when handled gently, the majority of the skates that were tagged survived.
3.5 REFERENCES

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Table 3-1 Biological and MiniPAT (pop-off archival transmitting) tag data for Arctic skate (*Amblyraja hyperborea*) tagged in Cumberland Sound (65.65° N and 65.85° W) in August 2010, 2011.

<table>
<thead>
<tr>
<th>Fish ID</th>
<th>TL/DW(^1) (cm)</th>
<th>Sex</th>
<th>Deployment date</th>
<th>Actual pop-off date</th>
<th>Premature detachment</th>
<th>DAL/DOD</th>
<th>Sampling interval (sec)</th>
<th>% Depth data reported(^2)</th>
<th>% Temp Data reported(^2)</th>
<th>Tagging location lat/long</th>
<th>Pop-off location lat/long</th>
<th>Distance travelled (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>01</td>
<td>62/50</td>
<td>F</td>
<td>17-Aug 2010</td>
<td>27-Oct 2010</td>
<td>no</td>
<td>70/70</td>
<td>150</td>
<td>42.9</td>
<td>44.3</td>
<td>65.659/-65.851</td>
<td>65.651/-66.504</td>
<td>30.06 W</td>
</tr>
<tr>
<td>02</td>
<td>72/51</td>
<td>M</td>
<td>17-Aug 2010</td>
<td>-</td>
<td>-</td>
<td>70/0</td>
<td>150</td>
<td>-</td>
<td>-</td>
<td>65.659/-65.851</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>04</td>
<td>66/47</td>
<td>M</td>
<td>10-Aug 2011</td>
<td>27-Sep 2011</td>
<td>10-Sep 2011</td>
<td>40/31</td>
<td>75</td>
<td>34.9</td>
<td>37.2</td>
<td>65.645/-65.862</td>
<td>65.645/-65.862</td>
<td>DP NA</td>
</tr>
<tr>
<td>05</td>
<td>72/52</td>
<td>F</td>
<td>13-Aug 2011</td>
<td>22-Sep 2011</td>
<td>no</td>
<td>40/40</td>
<td>75</td>
<td>63.4</td>
<td>65.2</td>
<td>65.810/-66.115</td>
<td>65.531/-66.689</td>
<td>36.76 SE</td>
</tr>
<tr>
<td>06</td>
<td>69/51</td>
<td>M</td>
<td>10-Aug 2011</td>
<td>19-Sep 2011</td>
<td>no</td>
<td>40/40</td>
<td>75</td>
<td>76.4</td>
<td>77.0</td>
<td>65.645/-65.868</td>
<td>65.580/-65.720</td>
<td>9.95 SE</td>
</tr>
<tr>
<td>08</td>
<td>73/55</td>
<td>M</td>
<td>10-Aug 2011</td>
<td>-</td>
<td>-</td>
<td>100/0</td>
<td>300</td>
<td>-</td>
<td>-</td>
<td>65.645/-65.852</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

*All* 35.7(27.0) 36.8(27.3)

\(^1\)Total Length/Disk Width, \(^2\)Actual number of readings/max number of readings within deployment period, DAL=days at liberty, DOD= days of data, DP= detached prematurely, NA= not applicable
**Table 3-2** Depth (m) and temperature (°C) data (mean ± SD) for Arctic skate (*Amblyraja hyperborea*) that were monitored using MiniPAT tags in Cumberland Sound in 2010, 2011

<table>
<thead>
<tr>
<th>Tag ID</th>
<th>Months Deployed</th>
<th>Mean Depth (m)</th>
<th>Max Depth</th>
<th>Min Depth</th>
<th>Mean Temp (°C)</th>
<th>Max Temp</th>
<th>Min Temp</th>
<th>Swimming Speed(^1) (m s(^{-1}))</th>
<th>Upward Speed(^2)</th>
<th>Downward Speed(^3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>01</td>
<td>Aug-Oct</td>
<td>879 (242)</td>
<td>1355</td>
<td>399</td>
<td>2.12 (0.00)</td>
<td>2.8</td>
<td>1.2</td>
<td>-</td>
<td>0.13</td>
<td>0.22</td>
</tr>
<tr>
<td>03</td>
<td>Aug-Sep</td>
<td>1061 (95)</td>
<td>1278</td>
<td>836</td>
<td>2.42 (0.00)</td>
<td>2.6</td>
<td>2.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>04</td>
<td>Aug-Sep</td>
<td>761 (135)</td>
<td>1349</td>
<td>317</td>
<td>2.46 (0.12)</td>
<td>2.8</td>
<td>2.1</td>
<td>-</td>
<td>0.21</td>
<td>0.17</td>
</tr>
<tr>
<td>05</td>
<td>Aug-Sep</td>
<td>1130 (151)</td>
<td>1329</td>
<td>671</td>
<td>2.74 (0.20)</td>
<td>2.9</td>
<td>2.3</td>
<td>0.38</td>
<td>0.08</td>
<td>0.14</td>
</tr>
<tr>
<td>06</td>
<td>Aug-Sep</td>
<td>891 (142)</td>
<td>1115</td>
<td>420</td>
<td>2.53 (0.16)</td>
<td>2.8</td>
<td>1.8</td>
<td>0.24</td>
<td>0.06</td>
<td>0.10</td>
</tr>
<tr>
<td><strong>All</strong></td>
<td></td>
<td>944 (154)</td>
<td></td>
<td></td>
<td>2.45 (0.11)</td>
<td></td>
<td></td>
<td>0.12 (0.07)</td>
<td>0.16 (0.05)</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\)Downward pelagic swimming (return to naturally occupied depths after being tagged), \(^2\)Max peak swimming speed upward, \(^3\)Max peak swimming speed downward
Table 3-3 Results of the mixed effect model (Depth was a dependent variable, ‘Individual fish’ and ‘Week’ were treated as random variables; ‘Day/Night’ was included as a fixed covariate).

<table>
<thead>
<tr>
<th>Random effects</th>
<th>Variance</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Individual fish (intercept)</td>
<td>25164</td>
<td>158.63</td>
</tr>
<tr>
<td>Week (intercept)</td>
<td>32838</td>
<td>181.21</td>
</tr>
<tr>
<td>Residual (intercept)</td>
<td>20595</td>
<td>143.51</td>
</tr>
</tbody>
</table>

Number of observations: 90214, groups: Individual fish 5, Week 6

<table>
<thead>
<tr>
<th>Fixed effects</th>
<th>Estimate</th>
<th>SE</th>
<th>t-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>867.9089</td>
<td>102.3111</td>
<td>8.483</td>
</tr>
<tr>
<td>Day/Night</td>
<td>-12.0267</td>
<td>0.9893</td>
<td>-12.157</td>
</tr>
</tbody>
</table>

Correlation of Fixed effects

<table>
<thead>
<tr>
<th>(Intr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DN</td>
</tr>
</tbody>
</table>

-0.003
Table 3-4 Results of the mixed effect model (Absolute mean change in depth was a dependent variable, ‘Individual fish’, ‘Depth’ were treated as random variables; ‘Day/Night’ was included as a fixed covariate).

<table>
<thead>
<tr>
<th>Random effects</th>
<th>Variance</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Individual fish (Intercept)</td>
<td>0.034742</td>
<td>0.18639</td>
</tr>
<tr>
<td>Depth (Intercept)</td>
<td>0.028025</td>
<td>0.16741</td>
</tr>
<tr>
<td>Residual</td>
<td>0.068305</td>
<td>0.26250</td>
</tr>
</tbody>
</table>

Number of observations: 59842, groups: Individual fish 5, Depth 1616

<table>
<thead>
<tr>
<th>Fixed effects</th>
<th>Estimate</th>
<th>SE</th>
<th>t-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>1.079579</td>
<td>0.083507</td>
<td>12.928</td>
</tr>
<tr>
<td>Day/Night</td>
<td>-0.001677</td>
<td>0.002358</td>
<td>-0.711</td>
</tr>
</tbody>
</table>

Correlation of Fixed effects

<table>
<thead>
<tr>
<th></th>
<th>(Intr)</th>
<th>DN</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>-0.012</td>
</tr>
</tbody>
</table>


Figure 3.1 Tagging and pop-off locations of MiniPAT tags deployed on Arctic skate (*Amblyraja hyperborea*) (n = 3) tagged in Cumberland Sound, Baffin Island. Winter fishing grounds (hatched area); deep water area ~ summer fishery grounds (1000 m contour); Cumberland Sound and Division 0B management areas (separated by a dashed line). Pop off positions labelled with tag IDs, contour lines (500, 1000 m) were approximated based on bathymetrical records.
Figure 3.2 Position of the MiniPAT tag on Arctic skate (*Amblyraja hyperborea*) on the dorsal side (midsection of the wing). Photo courtesy ca.wikipedia.org
Figure 3.3 Depth and temperature preferences of Arctic skate (*Amblyraja hyperborea*) (n = 5), combined over 40 and 70 day liberty periods.
Figure 3.4 Individual depth (black dots) and temperature (grey dots) profiles (n = 5) for 40 and 70 day tag deployments on Arctic skate (*Amblyraja hyperborea*). Tags 03 and 04 reported constant depths after 7/9/2010 and 10/9/2011, respectively possibly due to premature detachment from the fish or due to death of the tagged fish: the tag stayed in the same depth until the end of the preset deployment period.
Figure 3.5 (A) Individual mean depths (± SD) for Arctic skate (*Amblyraja hyperborea*) (n = 5) during day and night, (B) Individual mean depths during day and night for separate months (Aug- Oct).
Figure 3.6 Detailed depth profiles of MiniPAT tags (75 second sampling period interval) for Arctic skate (*Amblyraja hyperborea*) (*n* = 3) showing different types of behaviour compared to the light and dark period of the day (black bars). (A) high activity, wide vertical ranging; (B) high activity interspersed with low and moderate activity; (C) Low activity during light period of the day, high activity during the dark period of the day; (D) high activity, narrow vertical ranging; (E) moderate activity; (F) seabed resting. Gaps in the depth profiles denote incomplete transmission of archival records via satellites.
**Figure 3.7** A line graph of mean depth per day (± SD, dotted lines) and a line graph of the absolute mean change in depth per day (± SD, dotted line) (derived from the time series depth data) as indicators of activity levels for one individual (Tag 01) of the Arctic skate (*Amblyraja hyperborea*). High activity levels are associated with a large vertical movement, but also with periods of active movement within a narrow range of depths. Black bullets depict moon, dotted trajectory shows the lunar cycle with high (spring tide), low (neap tide) moon.
Figure 3.8 The diurnal and nocturnal absolute mean changes in depth per day (+ SD, dotted lines) for the Arctic skate (*Amblyraja hyperborea*) (Tags 01, 04+05+06) shown as two solid lines. Black bullets depict moon, dotted trajectory shows the lunar cycle with high (spring tide), low (neap tide) moon.
4 GENERAL DISCUSSION

4.1. SUMMARY

Arctic ecosystems are cold, harsh and difficult to access environments. These characteristics have likely contributed to the lack of studies and limited knowledge regarding the ecology of Arctic marine fish. Given the global decline in marine fish stocks and the reduction in the extent and duration of sea ice associated with a warming climate in the Polar Regions (Schrank 2007), a growing number of commercial fisheries have shifted their focus towards Arctic marine fish species (Botsford 1997; Hilborn et al. 2003; Schrank 2007). As an example, an open water commercial fishery for Greenland halibut (Reinhardtius hippoglossoides) was recently developed in Cumberland Sound, a seasonally ice covered inlet in the Arctic. Given the changing environment and increasing levels of exploitation, it has become critical to understand the ecology of marine fish in order to allow for proper management and conservation of Arctic fish stocks.

The main objective of my thesis research was to increase our current knowledge of the movement and behaviour of Greenland halibut and Arctic skate, a major bycatch species in the Greenland halibut fishery in Cumberland Sound. Cumberland Sound is a large inlet of Baffin Island, the Canadian Arctic; an example of a profusion of biological, environmental and physiographical diversity, where the diverse bottom topography and two seasonal ice regimes support a plethora of deep dwelling fish species, forage fish, marine mammals, shark and birds (DFO 2008; Dennard et al. 2009; Marcoux et al. 2012). To address this objective, I deployed pop-off archival transmitting tags to quantify and compare the depth and temperature preferences, activity levels and seasonal movement patterns of halibut, a commercially exploited species, and skate, a bycatch
species. Given the rapidly developing Greenland halibut fishery in Cumberland Sound, the results of this research are very important and timely for developing an effective management and conservation plan.

In the following text, I will compare and contrast the results of Chapter 2 and Chapter 3. First, I will comment on the similarities and differences between depth and temperature regimes of both species from Cumberland Sound, reflecting the realized niches of these species. Next, I will discuss the most important findings about the vertical movement patterns of the two species and differences in activity levels assuming those were reflected in changes in depth. Lastly, I will elaborate on seasonal trends in depth preference and the site fidelity of the two species.

**Depth preference**

Both Greenland halibut and Arctic skate moved into some of the deepest areas of Cumberland Sound and stayed well within the depth ranges previously suggested for these species by other studies (Bowering and Nedreaas 2000; RAS 2000; Dolgov et al. 2005; Chapter 2; Chapter 3). The depth range of the Arctic skate spanned into slightly shallower waters (up to 300 m; Chapter 3), but for the most part, the depth ranges of both fish species overlapped. When data were pooled in to 100 m depth bins, frequencies of depth occupancy showed that Greenland halibut spent 90 % of their time below 900 m compared to 70 % in Arctic skate (Chapter 2; Chapter 3).

Longer tag deployment periods for Greenland halibut identified depth trends in movement across seasons, more specifically during the periods of open water and ice cover. The results of a mixed effect model showed most halibut stayed in deeper waters from August to November, but occupied shallower depths corresponding with presence
of the ice cover (difference in orders of 100s of m) from February to April (Chapter 2). Shorter tag deployment periods for Arctic skate designed to collect detailed behavioural data did not indicate such trends in the movement and depth occupancy for Arctic skate. For example, three skates spent increasingly more time in shallower waters from August to September/October whereas two other individuals moved in to deeper waters (Chapter 3). Such inconsistency might arise from a small sample size and short deployment periods. If present, year-round deployment periods would be expected to reveal the temporal trends in depth preference of Arctic skate.

*Diurnal vertical migration*

As a species known to be a vigorous swimmer and to feed on pelagic, fast swimming prey (Bowering and Lilly 1992; Anonymous 1993; Dennard et al. 2009), Greenland halibut were hypothesized to swim into the pelagic water column, while following prey and potentially show diel vertical migration. However, Greenland halibut movements did not relate to diel cycles and depth profiles and swimming speeds did not provide strong evidence for extended periods of time swimming in the pelagic water column. In contrast, Arctic skate showed a preference for shallower waters during the night time. Detailed analysis of activity levels did not reveal that skates were more active during this time and consequently why skates move to shallower waters is likely not related to feeding. Further work is required to determine why Arctic skate undertake this movement during darkness.

*Temperature occupancy*

Both species stayed within a narrow range of temperatures, which may indicate a strong temperature preference. However, given the fish resided within their known
temperature range, the observed narrow range is likely a result of the low variability in temperature regimes in deeper waters beyond the mixing zone (Jeannette Bedard, University of Victoria, Victoria, BC, *personal communication*). Consequently, it can be concluded that temperature regimes were not driving or limiting Arctic skate movements during the short time at liberty as the species is known to tolerate waters below 4°C (Bigelow and Schroeder 1953). Greenland halibut, a slightly more temperature sensitive species, is known to spawn in waters above ~3.5°C (Jørgensen 1997). Due to the fact that temperatures in Cumberland Sound are lower than this, Greenland halibut are unlikely to spawn in Cumberland Sound; no historical evidence of spawning in the Sound has been documented (Pike 1994). However, Greenland halibut showed a trend towards occupying slightly cooler (-0.5°C difference) waters during the winter, ice covered season. Such a trend may indicate a preference; given that temperature is a controlling factor that affects rate of growth and metabolism of fish (Brett and Grooves 1979; Macpherson and Duarte 1991). The occupancy of cooler temperatures would result in decreased metabolic rates and energy demands and thus may be an adaptation to balance the energy needs of the fish during the ice covered, least productive part of the year. Alternatively, the seasonal change in occupied temperature may be a result of movement in response to other environmental or ecological drivers such as predator avoidance or feeding (see section seasonal movement).

*Vertical movement and activity levels*

Both species expressed a continuum of activity levels from low to relatively high activity. As expected, low activity behaviour was common to both species and likely indicated resting; however, Greenland halibut rested for longer and more often than
Arctic skate (Chapter 2; Chapter 3) indicating skates were the more active of the two species. The high activity behaviour of Greenland halibut was typical of gradual ascents or descents with typical short ‘breaks’ of no change in depth (Chapter 2). These behaviour patterns were not observed in the high activity behaviour of the skates. This is important, as it may indicate that Greenland halibut were largely constrained to benthic habitats and potentially rested or camouflaged in between movements as oppose to Arctic skate, which moved continuously. The continuous, active movement of Arctic skate suggested potential movement into the pelagic water column, which was also supported by relatively fast swimming speeds. On the contrary, Greenland halibut did not show evidence for extended pelagic movement (see the section Diel vertical migration), but rather displayed sedentary behaviour with occasional high activity periods. During these short high activity periods, Greenland halibut may potentially move into the pelagic water column, for example to ambush their prey; however, PAT tags are not capable of recording such vertical behaviour, due to the required sampling interval duration (Kawabe et al. 2004). These differences in vertical movement and activity between these two flattened species may either be a result of differences in predator avoidance behaviour or differences in diet and associated foraging strategies (see section Seasonal movement and site fidelity). Additionally, both species showed inter- and intra-individual differences, which may be related to sex (Skjaeraasen and Bergstad 2000; Wearmouth and Sims 2009) but given low sample sizes, further tags would be required to address this question.

*Seasonal movement and site fidelity*
Greenland halibut exhibited high site fidelity to the deep central areas of Cumberland Sound (> 900 m) for the ice free period of the year. With the onset of the ice cover period, two fish started to move into shallower waters, but moved back to deeper waters in the summer (Chapter 2). Such movement is in agreement with historical catches of Greenland halibut, with fish being caught in shallower waters (~500-600 m) during the winter, but not in the summer (Dennard et al. 2009; Fisk et al. 2012). These results are potentially important for the management of the local commercial fishery, showing that halibut resided in highly localized areas in summer before they dispersed into shallower areas during winter.

In contrast, Arctic skate which were monitored only during the ice free period of the year, showed larger horizontal mobility, with tags popping off as far as 37 km direct distance from the tagging location after 40 days at liberty (Chapter 3). Pop off locations within and outside of the deep water pockets, where both fish were tagged, suggested that both species overlapped in the habitats they use, but unlike halibut, skates were not confined to the deep water areas during the summer. Such evidence of overlapping habitat use is an important consideration for management considering Arctic skate is a common bycatch in fisheries for Greenland halibut and groundfish in general.

Why did the two flattened, deep dwelling species show differences in preferred depth and site fidelity? One possible explanation is that the two species were displaying different predator avoidance tactics. Greenland halibut is a common prey item of whales such as beluga (Delphinapterus leucas) and narwhal (Monodon monoceros), whereas Arctic skate is likely not (Laidre and Heide-Jørgensen 2005; Bluhm and Gradinger 2008; Marianne Marcoux, Institute of Biological and Environmental Sciences, University of
Aberdeen, UK, *personal communication*). Historically, periodic disappearance of Greenland halibut from Greenland fiords was observed to correspond with increased sightings of beluga (Anonymous 1993). A further explanation may relate to spawning. Whereas Greenland halibut have not been documented to spawn in Cumberland Sound likely due to suboptimal temperatures (Jørgensen 1997), Arctic skates appeared to be in mating condition during tagging in August 2010 and 2011. Thus, spawning may play a role in driving the movement patterns of Arctic skate. Given that little is known about Arctic skate spawning and mating behaviour and that the tags were only deployed for a short period of time, it is difficult to draw definitive conclusions about the effect of spawning on the movement of Arctic skate.

A final explanation for differences in skate and Greenland halibut movements may be related to differences in preferred prey and movement of the prey. Previous studies from the Arctic and North Atlantic Oceans have documented a wide range of prey species including demersal and pelagic fishes and benthic organisms in the diet of both species but also noted opportunistic feeding on the most abundant prey (Bowering and Lilly 1992; Last and Stevens 1994; Orr and Bowering 1997). Given the unknown diet of Arctic skate from Cumberland Sound, it is difficult to evaluate the potential influence of different prey items on the depth patterns during the ice free period.

*Pop-off archival (PAT) tags*

Few studies conducted in the Arctic environment have used PAT tags. To evaluate the relative success of the PAT tags deployed in Cumberland Sound, I compared the report rate and transmission rate for PAT tags for both species to the tags deployed in tropical and temperate parts of the world. Most of the tags reported back, yielding 100 %
report rate for Greenland halibut and 78 % for Arctic skate (Chapter 2; Chapter 3). These values were close to and even exceeded the overall report rate (83 %) registered by the tag manufacturer, Wildlife Computers Inc. (Redmont, WA) (Musyl et al. 2011), despite the potential issues with the tags being deployed in areas seasonally covered with ice. Seven of nine and three of nine tags for Greenland halibut and Arctic skate, respectively, remained attached to the fish until the programmed pop-off date. The low percentage of tags that remained attached to Arctic skate for the full deployment period may indicate that the anchoring mechanism used for Arctic skate was not ideal. In future, alternative anchoring mechanisms should be considered, for example, an attachment with the tag holding-monofilament sutured through the base of the tail, following the method of Le Port et al. (2008). Tags attached to Greenland halibut and Arctic skate returned (mean ± SD) 56.6 ± 20.7 % and 36.3 ± 26.1 % of the data, respectively (Chapter 2; Chapter 3). Generally, tags that detached before their programmed pop-off date had two common features; first, the tags had a delayed pop-off by approximately a week, compared to the tags that remained on the fish. Secondly, they had a much lower transmission rate, but reasons for that are yet unknown. The various numbers of messages logged by the tag did not affect the success of transmission rate (Chapter 2), even though the tags were preset to log more than the number of messages recommended by Wildlife Computers. Additionally, weather likely plays role in successful transmission rate of the data to overhead satellites.

4.2. IMPLICATIONS AND FUTURE DIRECTIONS

Ecological implications
1) I have quantified the depth preference of adult/large bodied Greenland halibut and Arctic skate and provided tangible results of the temperature range they occupied.

2) I have provided evidence for a seasonal movement of Greenland halibut, which is in agreement with historic fishery observations.

3) I have examined the relationship between depth and diel cycles for Arctic skate and Greenland halibut.

4) I have described the activity levels of Greenland halibut and Arctic skate and suggested potential explanations for the difference observed in the two species.

**Technical implications**

1) I have gathered data from PAT tags deployed on fish that inhabit harsh and extremely deep environments, testing PAT tags successful in such environments.

2) I have evaluated the performance of PAT tags in the Arctic environment from the rate of return of data that were collected.

3) I have confirmed the suitability of the attachment method for Greenland halibut and suggested the use of an alternative attachment method for Arctic skate.

**Potential management implications**

1) I showed that Greenland halibut exhibited high site fidelity to the deep water area in the central part of Cumberland Sound during the ice free period of the year. This is an important consideration for fishery managers given the
boundary between the two fishery management areas runs through this deep water area.

2) I provided supporting evidence for the seasonal movement of Greenland halibut in Cumberland Sound, although only two fish reported data for 300 days. Halibut are likely more dispersed during the winter (ice covered period) than the summer.

3) I confirmed that both species overlapped large portions of their habitats, thus management measures addressing the issue of Arctic skate bycatch need to be developed, especially considering that the number of groundfish fisheries in the Arctic may increase in the future.

Potential responses to climate change and implications for fishery management

1) I showed that the distribution of Greenland halibut throughout Cumberland Sound may fluctuate over the course of a year with a wider distribution throughout shallower waters when ice is present to the stock being concentrated in deep water regions during the ice free season. Thus, changes in the sea ice cycles may have an effect on the distribution patterns of Greenland halibut. For example, a prolonged ice free season may result in longer occupancy of deep water regions by halibut and also longer availability to the open water fishery efforts. Considering that the stock may be confined to relatively limited areas during this period, the local fishery management should consider separate quotas for summer and winter fisheries to secure sustainable harvest.
2) If the water temperature in Cumberland Sound increased as a response to global warming, this might result in Cumberland Sound becoming a potentially suitable region for Greenland halibut to spawn. If spawning in the Sound, the halibut population may become less dependent on immigrants from Davis Strait and other areas in order to maintain a stable population. However, considering that halibut larvae are usually pelagic that may drift vast distances before settling down and relatively unknown rate of homing of Greenland halibut, it is not clear what effect spawning will have on the stability of the local population.

3) Additionally, changes in climate may bring new species into the area and further disrupt the current dynamics of the current food web, for example by decoupling of food resources. Generalist feeders such as Greenland halibut and Arctic skate that are flexible to feed on a variety of species may be better equipped to face such changes.

Future directions

In conclusion, this study was one of the first to use pop-off archival transmitting tags to successfully monitor the movements of deep water fish species in the Arctic marine environment. Thus, this study showed the practical use of this technology in distant and extremely harsh environments. Furthermore, we increased the current body of knowledge regarding the movement and behavioural patterns of two species that are directly affected by commercial fisheries. This will enable better, more knowledgeable decision making in the future management and conservation practices regarding these species.
So what would be the next step? This study represents a good starting point for better understanding the environmental preferences, movement and behaviour of two deep dwelling fish species, Greenland halibut and Arctic skate. However, the pop-off archival transmitting technology has limitations that leave certain aspects of our research objectives unanswered. First, the data from the tags cannot be used to quantify fine-scale horizontal movement when species occupy waters beyond the level of light penetration, which is the case for both Greenland halibut and Arctic skate. Secondly, if not recovered, the tags only transmit a certain fraction of the collected data set, which makes the data management challenging and unsuitable for some of the standardized analyses of time series data (e.g., Fourier analysis). Thirdly, the cost of the tags is generally a limitation to an ideal sample size. Lastly, the memory capacity of the tag constrains the data collection to a period of a year or shorter. In terms of the life span of these species, this time period is still rather short and may not represent the full set of movement and behavioural patterns. Thus, despite the information provided by PAT tags being powerful and applicable, future work should consider a number of additional techniques such as acoustic telemetry and stable isotopes to better define the movement of Greenland halibut and Arctic skate. These methods would enable future research to tackle the remaining research objectives and draw firmer conclusions.

First, the results reported in this study should be compared to data that is currently being collected by acoustic equipment deployed in Cumberland Sound since 2010. These data should help elucidate the extent and timing of the horizontal movement of the two species. Next, to determine if predation is driving the movement of Greenland halibut or Arctic skate, these results should be compared to the movement of the top predators in
the Cumberland Sound system, (i) Greenland shark that were tagged with both PAT and acoustic tags concurrently with the tagging of the two study species (Fisk et al. 2012) and, (ii) beluga whale and its known seasonal movements within Cumberland Sound (Kilabuk 1998). Secondly, results from the stable isotopes analyses of tissues collected in August 2010-11 for both species should be compared to other stable isotope studies conducted in Cumberland Sound on, capelin (Mallotus villosus), shrimp (Lebbeus polaris) (Dennard et al. 2009), beluga whale (Marcoux et al. 2012), Greenland shark (McMeans et al. 2010), and ring seal (Pusa hispida) (Dave Yurkowski, University of Windsor, Windsor, ON, personal communication). Comparison of all these results will determine trophic relationships, pinpoint foraging strategies and provide insights into movement and habitat use of Greenland halibut and Arctic skate in the Cumberland Sound ecosystem.

4.3. REFERENCES

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