Movement and environmental preferences of large marine predators by electronic tagging

by

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Dedication

I dedicate this dissertation to my father, James L. Stokesbury.

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Abstract

The understanding of movement, distribution and environmental preferences of large marine predators is necessary for their proper management and conservation. This information can be used by managers to make informed decisions on the vulnerability of species in directed and by-catch fisheries. Also, it can be used to form a baseline for ecological impact assessment as the climate changes and as anthropogenic exploitation of terrestrial and marine environments increases. In this thesis, I report on the results of electronic tagging studies of two large marine predators, Atlantic bluefin tuna (*Thunnus thynnus*) and Greenland sharks (*Somniosus microcephalus*). In addition, I propose a hypothesis of early life imprinting that may enable fishes to home to natal spawing grounds through relatively featureless environments. Through the tagging studies, new information has been gathered on the life histories of these enigmatic marine species. This information is crucial to the proper management and conservation of Atlantic bluefin tuna. Also, the study provides new information on the distribution, environmental preferences and behaviour of Greenland sharks of which little was previously known.

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Chapter 1: Introduction

1.1. Introduction

Electronic tags provide information on fish movement and environmental preferences (Block et al.1998a, Block et al. 2001, Itoh et al. 2003). This information may indicate fish distribution (Block et al. 2001, Stokesbury et al. 2004, Wilson et al. 2005), vertical (Nelson 1997, Weng and Block 2004, Stokesbury et al. submitted) and horizontal movement (Block et al. 2001, Boustany et al. 2001, Stokesbury et al. 2004, Stokesbury et In preperation), survival (Lacroix et al. 2005), spawning locations (Block et al. 2001, Stokesbury et al. 2004, Block et al.in press) and fidelity (Block et al. in press), and stock structure (Block et al.in press). Knowledge of these characteristics is crucial for understanding the evolution and ecology, as well as the proper management and conservation of highly migratory fishes (National Research Council 1994).

1.2. Objectives

The objective of this thesis is to increase the knowledge of how large marine predators use their environment by identifying their movement patterns and the physical characteristics that they target in the water column. These objectives were met through the electronic tagging of two species of large marine predators, one Osteichthyes and one Chondrichthyes, that appear to have very different life histories. The bony fish, Atlantic bluefin tuna (*Thunnus thynnus*), the largest member of the family Scombridae, is distributed in the Atlantic Ocean from sub-polar regions to the tropics (Block et al. 2001). The cartilaginous fish, the Greenland shark (*Somniosus microcephalus)*, the largest

member of the family Squalidae, has a known distribution in the northern hemisphere that includes the Arctic Ocean, and sub-Arctic regions of the North Atlantic Ocean (Scott and Scott 1988).

1.3. Thesis Overview

In the second chapter, I begin the examination of movement and environmental preferences of Atlantic bluefin tuna tagged with electronic tags in waters off New England. The largest commercial fishery for Atlantic bluefin tuna in North America is conducted in this area in late summer and autumn. However, little is known about the movement and stock structure of the bluefin tuna exploited in this fishery. Also, other important information on this aggregation is not known, including spawning locations and fidelity, and migration patterns. The third chapter also focuses on the movement of Atlantic bluefin tuna, however, in this study the bluefin tuna were tagged in the eastern Atlantic Ocean in waters off northwestern Ireland.

Movement and environmental preferences of Greenland sharks in the St. Lawrence Estuary, P.Q., Canada is the focus of the fourth chapter. Greenland sharks are large, mostly benthic sharks found in Arctic and sub-polar waters. There is virtually no behavioural information available for Greenland sharks. Regardless of this lack of knowledge, they are fished in waters off Iceland and Greenland (Scott and Scott 1988), and are a common by-catch in fisheries such as the Greenland halibut longline fishery.

The fifth chapter of this thesis consists of an essay that examines natal homing in marine fish. This section proposes a hypothetical framework of mechanisms and environmental stimuli that fishes may use to navigate and home to specific areas when

traveling in the blue ocean. The focus of this chapter was inspired by Cury's (1994) early life imprinting hypothesis. Also, I propose a hypothesis of early life imprinting in marine broadcast spawners and suggest how this hypothesis may be tested.

The major findings of these studies are summarized in chapter six, the last chapter of the thesis. This chapter integrates the results of my research, and complementary studies.

1.4. Summary of information on Atlantic bluefin tuna

Bluefin tuna are large, highly migratory marine pelagic fishes. There are three recognized species of bluefin tuna, Southern bluefin tuna (*Thunnus maccoyii*), Pacific bluefin tuna (*Thunnus orientalis*), and Atlantic bluefin tuna. Bluefin tuna are endothermic (Carey and Lawson 1973) as they retain metabolic heat by counter current heat exchangers. This allows them to spawn in tropical waters but feed in productive cool waters, and influences their highly migratory nature (Block et al. 2001).

Atlantic bluefin tuna have been fished in the eastern Atlantic Ocean and Mediterranean Sea since antiquity, with almost continuous fishery records available for trap fisheries in the Mediterranean Sea from the 1500's to the present (Ravier and Fromentin 2001, 2004). Since the 1950's the populations of bluefin tuna in the Atlantic Ocean have been devastated by industrial fishing (Myers and Worm 2003).

Bluefin tuna are managed by the International Commission of the Conservation of Atlantic Tunas (ICCAT). ICCAT recognizes two stocks in the Atlantic Ocean, one in the West Atlantic and one in the East Atlantic, and proposes a low level of mixing between

the two (<4% • year^{-1}). In the western Atlantic Ocean, bluefin tuna are fished commercially on the eastern seaboard of the US and in Canada by harpoon, purse seigne, hand-line, long-line and rod and reel, commercially in only Canada by trap net and recreationally in only the US by rod and reel. The population of bluefin tuna is the western Atlantic is estimated to have declined by 80% during the 1970's and 1980's (Magneson et al. 2001) and is predicted to be at approximately 10% of it's pre-industrial fishing level (Myers and Worm 2003).

1.5. Summary of information on Greenland sharks

Greenland sharks are the only non-laminid sharks known to forage in the Arctic Ocean (Stokesbury et al. submitted). They are one of three species in the genus *Somniosus*, the other two members of the genus being the Pacific sleeper shark (*Somniosus pacificus*) and the little sleeper shark (*Somniosus rostratus*). Neither of these two species is known from the North Atlantic Ocean (Scott and Scott 1988). Little is known of the life history of Greenland sharks including their stock structure, distribution, spawning location and fidelity, and growth.

Greenland sharks are fished in Iceland and Norway with the product being liver oil and protein for dog food. They are live bearers, proposed to grow and reproduce at very low rates and therefore may be susceptible to over fishing (Scott and Scott 1988).

1.6. Publications Related to this Thesis

Stokesbury, M.J.W., Cosgrove, R., Boustany, A., Teo, S.L.H., O'Dor, R.K., Block, B.A. In Preparation. Movement of Atlantic bluefin tuna from the eastern Atlantic Ocean to the western Atlantic Ocean as determined with pop-up satellite archival tags.

Stokesbury M.J.W, Harvey-Clark, C., Gallant, J., Block, B.A. and Myers, R.A. Submitted. Movement and environmental preferences of Greenland Sharks (*Somniosus microcephalus*) electronically tagged in the Saint Lawrence Estuary, Canada. Marine Biology.

Block, B. A., Teo, S. L. H., Walli, A., Boustany, A., Stokesbury, M. J. W., Farwell, C., Weng, K., Dewar, H., Williams, T. In Press. Electronic Tagging and Population Structure of Atlantic Bluefin Tuna (accepted, Nature, 17 February 2005).

Stokesbury, M.J.W., Teo, S.L.H., Seitz, A., O'Dor, R.K., and Block, B.A. 2004. Movement of Atlantic bluefin tuna (*Thunnus thynnus*) as determined by satellite tagging experiments initiated off New England. Canadian Journal of Fisheries and Aquatic Sciences. 61: 1976–1987

Chapter 2. Movement of Atlantic bluefin tuna (*Thunnus thynnus*) as determined by satellite tagging experiments initiated off New England

2.1 Introduction

Atlantic bluefin tuna (*Thunnus thynnus*) are large, highly-migratory pelagic fish that are distributed in the western Atlantic Ocean from tropical waters off Brazil (Mather et al. 1995) to polar waters off Newfoundland (Caddy et al. 1976) and south of Greenland (Mather et al. 1995). Bluefin tuna conserve metabolic heat and can tolerate ambient temperatures that range from 2.8 °C to 31.0 °C (Carey and Lawson 1973; Block et al. 2001), while maintaining a relatively constant body temperature (Carey and Teal 1969, Block et al. 2001, Blank et al. 2004). These fish forage in productive cool waters during the summer, and return to warm water masses to spawn (Block et al. 1993; Mather et al. 1995; Block et al. 2001). This gives bluefin tuna the broadest thermal niche of all species of the family Scombridae (Block et al. 1998a).

Atlantic bluefin tuna are currently managed as two stocks in the Atlantic Ocean and Mediterranean Sea (National Research Council 1994). It is hypothesized that the western Atlantic Ocean stock spawns in the Gulf of Mexico (Richards 1976) and the Straits of Florida (Rivas 1954) and the eastern Atlantic Ocean stock spawns in the Mediterranean Sea (Richards 1976). Larval tows support the hypothesis that these three areas are primary spawning grounds (Richards 1976; McGowan and Richards 1989). Abundance estimates indicate that the western Atlantic Ocean stock of mature Atlantic bluefin tuna has decreased markedly since the 1970's (Magnuson et al. 2001), in spite of

the recovery plan that was put in place by the International Commission for the Conservation of Atlantic Tunas (ICCAT) in the early 1980's. The current management plan assumes that mixing between the two stocks occurs at a low rate ($< 4\% \bullet year^{-1}$; National Research Council 1994). However, recent archival and conventional tagging data indicate that fish in the western Atlantic Ocean cross to the eastern Atlantic Ocean at a rate that ranges from 10-30 % (Block et al. 2001). Increased understanding of the movement patterns and the level of mixing between the two stocks are crucial to improving the management and conservation of bluefin tuna (National Research Council 1994; Sissenwine et al. 1998; Magnuson et al. 2001).

Historically, conventional tag returns from Atlantic bluefin tuna tagged in the northwestern Atlantic Ocean have linked these fish to several regions. Tagging of bluefin tuna with conventional tags in St. Margaret's Bay, Nova Scotia, produced returns from the waters off New England, southwestern Nova Scotia, and the Gulf of St. Lawrence (Burnett et al. 1977). Also, two fish conventionally tagged off Massachusetts were recaptured in the Gulf of Mexico (Mather et al. 1995). Mather et al. (1995) proposed that after spawning bluefin tuna migrate from the Gulf of Mexico through waters east of the Bahamas and off the southeastern USA. They then follow the eastern edge of the Florida Current to Cape Hatteras. Next, they follow the Gulf Stream northeastward, leaving at varying intervals to make their way north to various feeding grounds (Mather et al. 1995). It was also proposed that some bluefin tuna might follow the Gulf Stream into the northeast Atlantic Ocean to feeding grounds off Norway. The route of the southern return migration of adult bluefin tuna was less clear from the tagging results (National Research Council 1994).

Recently, investigators have used electronic tagging technology to examine the movements of Atlantic bluefin tuna (Block et al. 1998a, 2001; Lutcavage et al. 1999). Block et al. (1998a, 2001, 2002) reported results from a study using both archival data storage tags and pop-up satellite archival tags (PSAT) that investigated the migration and environmental preferences of electronically tagged fish released off the coasts of North Carolina, New England, and in the Gulf of Mexico. Block et al. (2001, 2002) determined that bluefin tuna tagged in the western Atlantic Ocean exhibited four migratory behaviors over one to three years after tagging: western Atlantic residency without visiting a recognized spawning ground; western Atlantic residency with visitation to a known western spawning ground; western residency for 1-3 years with visitation to the known eastern spawning ground, the Mediterranean Sea; and trans-Atlantic movement west to east and back. Western residency was the prevalent pattern for adolescent bluefin tuna, as they occupied offshore waters off North Carolina in the winter, the Gulf Stream in spring and New England waters in summer and autumn.

Atlantic bluefin tuna electronically tagged in the North Carolina winter fishery resided in waters offshore of North and South Carolina, and then arrived in summer and autumn in waters off New England. For fish tagged off of North Carolina, the most likely place to recover an archival-tagged fish was New England, strongly linking the two groups of fish and the associated fisheries (Block et al. 2001). Also, although many bluefin tuna in New England waters are from a larger more mature component of the population, there remains a large overlap in the adolescent and early breeding cohorts.

While the waters off New England were clearly important for many Atlantic bluefin tuna tagged in previous studies, some archival and pop-up satellite tagged fish

released off North Carolina, did not visit this area. Data from Block et al. (2001, 2002) provided strong evidence for a movement of fish from North Carolina waters to the Mediterranean Sea spawning grounds and to the area east of the Flemish Cap and south of Greenland. Fish moving from North Carolina to either the Mediterranean Sea or the Flemish Cap showed no association with waters off New England either on the way to the Flemish Cap or on their way to western or eastern known spawning grounds after residency in feeding areas (Block et al. 2001, 2002).

In another study, using externally placed pop-up satellite tags, Lutcavage et al. (1999) reported on the movements of Atlantic bluefin tuna tagged in the Great South Channel off Massachusetts, USA. Of 20 satellite tags deployed on fish in the Great South Channel, five reported from the mid-Atlantic east of 45 °W, the ICCAT stock management boundary line. Although most of the pop-up satellite tags surfaced on the western side of the stock boundary line, the major conclusion of the paper was that fish from New England travel toward the mid-Atlantic during the winter. The authors raised the possibility, based on these results, that bluefin tuna tagged off New England spawn in the mid-Atlantic.

In the current study we examine the movements of Atlantic bluefin tuna tagged and released off New England with two types of pop-up satellite tags of increasingly sophisticated software generations. The evolution of the tag software and hardware permitted increased data acquisition during the three-year period of this study. The results of this study have important implications for bluefin tuna management and conservation, and clarify previous data reported from this assemblage in the western Atlantic Ocean.

2.2 Materials and methods

Pop-up satellite tags were deployed on Atlantic bluefin tuna in three different years (1998, 2000, and 2001) off the coast of Massachusetts, USA. Tags were secured to the fish using two procedures of capture and release.

In autumn 1998, Atlantic bluefin tuna were captured using a purse seine by the fishing vessel, Sea Rover. For release, the net was opened enough to permit the release of one bluefin tuna at a time. As the fish swam out of the net one individual tagged it using a harpoon deployment procedure. A titanium dart anchor with the attached pop-up satellite tag was inserted close to the second dorsal fin. A pop-up satellite tag was secured to the titanium dart by a monofilament leader (136 kg) covered in shrink wrap to increase its stiffness (Block et al. 1998a). Two experienced purse seine vessel captains estimated the sizes of the fish. Of the nine tags deployed, five were first-generation single-point PAT 1.0 tags built by Wildlife Computers and four were single-point Microwave Telemetry PTT100 tags (Table 2.1). Both types of tags provided an end point location based on the Doppler shift of the tags radio transmission to the Argos satellites (root mean square errors for class 2 and class 3 readings were 350 m and 150 m respectively; Taillade 1992).

In 2000 and 2001 Atlantic bluefin tuna were captured by rod and reel, using 120 kg-line test and 9.0'-11.0' Gamagatsu baited circle hooks. Fish were boated, using a "lip hook", a short-handled gaff inserted into the lower jaw of the fish in order to pull it aboard the vessel. The fish were pulled through an opening in the transom of the vessel, onto a wet vinyl mat on the deck of the boat, using methods previously described by Block et al. (1998a, 1998b). The curved fork length (CFL) of the fish was measured (cm)

prior to tagging. Only fish larger than 172 cm CFL were tagged. A titanium dart was inserted into the dorsal musculature at the base of the second dorsal fin, so that the tag head was pushed though the pterygiophores, thus providing a solid point of attachment for the tag. The rubber shrink wrap covering the leader of the PSATs had an identification number and telephone contact that provided the opportunity for additional recapture information. A conventional dart tag was also attached on the opposite side of the second dorsal fin from the PSAT. The fish were then released by sliding them off the wet vinyl mat headfirst through the tuna door and into the water. This method was applied to fish as large as 287 cm CFL.

The three types of pop-up satellite tags acquired and transmitted data differently. PTT100 tags acquired ambient temperature data at 1 h intervals for the first 60 days of deployment and the day prior to the tag report. The tag then transmitted the daily mean temperature (calculated from the hourly readings) for the first 60 days and the day prior to tag report. Wildlife Computer PAT 1 tags acquired ambient temperature at 0.5 h intervals for the first 60 days of deployment and transmitted the entire data archive. PAT 2.0 tags acquired data in 60 s intervals for light, ambient temperature, and pressure, and archived data in 120 s intervals to memory. Data were summarized into 12 h or 24 h bins prior to transmission (Table 2.1). The summary data for each time period comprised percentage distributions of time-at-depth and time-at-temperature, and temperature vs depth profiles that were generated by dividing the maximum dive during the interval into eight equally distributed points, inclusive of the surface and maximum depth. A minimum and maximum temperature at each of these depths was stored and transmitted.

Table 2.1. Satellite tag hardware, software, and programming information.

Tag type	Tag no.	Tag hard-ware	Tag soft-ware	Data summary period	Prerelease program	Type of data				
						Ambient temp. (3600S)[a]	Ambient temp (1800S)[b]	Ambient temp (120S)	Light (120S)	Pressure (120S)
PAT1	381						X			
PAT1	382						X			
PAT1	383						X			
PAT1	384						X			
PAT1	385						X			
PTT100	25171					X				
PTT100	8971					X				
PTT100	9685					X				
PTT100	8836					X				
PAT2	590	.00	.03	12 h				X	X	X
PAT2	763	.00	.03	24 h				X	X	X
PAT2	764	.00	.03	24 h				X	X	X
PAT2	765	.00	.03	24 h				X	X	X
PAT2	770	.00	.03	24 h				X	X	X
PAT2	760	.00	.03	12 h				X	X	X
PAT2	761	.00	.03	24 h				X	X	X
PAT2	751	.00	.03	24 h				X	X	X
PAT2	753	.00	.03	24 h				X	X	X
PAT2	771	.00	.03	24 h				X	X	X
PAT2	752	.00	.03	24 h				X	X	X
PAT2	772	.00	.03	24 h				X	X	X
PAT2	750	.00	.03	24 h				X	X	X
PAT2	738	.00	.03	24 h				X	X	X
PAT2	1027	.00	2.06a	24 h	X			X	X	X
PAT2	1024	.00	2.06a	24 h	X			X	X	X
PAT2	1019	.00	2.06a	12 h	X			X	X	X
PAT2	1026	.00	2.06a	12 h	X			X	X	X
PAT2	1018	.00	2.06a	24 h	X			X	X	X

PAT2	953	.00	2.06a	24 h	X	X	X	X
PAT2	946	.00	2.06a	12 h	X	X	X	X
PAT2	1015	.00	2.06a	24 h	X	X	X	X
PAT2	949	.00	2.06a	12 h	X	X	X	X
PAT2	871	.00	2.06a	12 h	X	X	X	X
PAT2	859	.00	2.06a	12 h	X	X	X	X
PAT2	943	.00	2.06a	12 h	X	X	X	X

[a] The first 60 ambient temperature measurements are daily averages derived from hourly measurements from the previous 24 h period. The 61st ambient temperature measurement is the average for the 24 h period prior to the tags' programmed report date.

[b] Ambient water temperatures are recorded every 0.5 h and archived for the first 60 days of deployment.

In 2000 and 2001 PSATs (PAT 2.0) with two versions of software (2.03 and 2.06a respectively) were used. The PAT 2.0 (software version 2.06a) tags were equipped with a pre-release program and an auto depth correction in the 2001 deployments. Therefore, if the tag prematurely detached from the fish and floated to the surface it reported to the satellite 4 days after detachment. PAT 2.0 tags deployed in 2000 (software versions 2.03) did not have this program, and drifted from the date of detachment from the fish until the pre-programmed reporting date. However, the pressure sensor provided direct evidence of the date of tag pre-release from the fish. All PAT 2.0 tags deployed in 2000 and 2001 provided a full archival record at 120 s intervals if recaptured (Table 2.1).

Early-generation PAT tags had a tendency to release before the scheduled pop-up date (Gunn and Block 2001). Pre-release could be due to a variety of factors, including failure of the titanium dart to remain attached to the monofilament, failure of the stainless steel pin that is the point of attachment of the tag to the leader, and wearing through of the monofilament.

The first step in data analysis was to assess whether individual tags remained attached to the respective Atlantic bluefin tuna for the full duration of the deployment. This was not possible in the case of the Microwave Telemetry PTT100 tags. For Wildlife Computers PAT 1.0 tags, the complete archive of external temperature data at 0.5 h intervals allowed collection of an increased amount of data on external temperature to discern changes of water temperature in association with vertical and horizontal movements. Therefore, it was possible to estimate when the tag prematurely released for those tags that were on the fish for the period of time that the temperature data was

archived (60 days after release). The tags for which it was possible to verify whether they remained on the fish and, that produced end point positions, were divided into two groups, 1) tags that remained attached, as determined by the temperature and pressure records, or temperature alone, and 2) tags that were "drifters" for a period greater than four days prior to data transmission (the length of time pre-programmed into the tag to activate transmission if the tag came prematurely to the surface).

2.3 Geolocation

Information on daily movements of Atlantic bluefin tuna was obtained from light-based calculation of longitude using PAT Decoder 7.08.0005 of Wildlife Computers (Hill 1994; Hill and Braun 2001), combined with latitude estimates based on sea surface temperature (SST; Teo et al. 2004). The accuracy of these geolocation estimates was determined by comparing end point positions from pop-up satellite tags and GPS, with geolocation estimates based on light-level longitude and SST latitude (Teo et al. 2004). End point data based on radio transmissions at the surface from PAT 2.0s on 49 fish (including 12 from this study) had a root mean square error for geolocation estimates of 1.30° for light-based longitude and 1.89° for SST-based latitude (Teo et al. 2004). Therefore, this geolocation validation provides an ellipse of error estimate around each point.

2.4 Results

A total of 35 Atlantic bluefin tuna were tagged with pop-up satellite tags in three seasons of autumn tagging (1998, 2000, 2001; Table 2) off New England. The tagged fish ranged from 173 to 287 cm CFL. Radio end point locations indicating the last position of the fish prior to tag release were obtained from 14 tags that transmitted within 4 days of tag release. A single tag-recapture position of a bluefin tuna recaptured with a pop-up satellite tag attached was provided by the fishers' global positioning system (Figure 2.1). The radio end point locations and GPS position indicate the region in which the fish were present at tag detachment, recapture, or, in the case of the engagement of the premature release program, the position of the tag 4 days after detachment. These radio transmission end points indicate that most of the tagged fish moved due south from the initial tagging location off Massachusetts. Three tags (381, 382, 1026) reported end points close to the tagging site after short deployments of 10, 12, and 4 days, respectively. Tags 381 and 382 remained attached to the fish for the intended term of deployment. Tag 1026 was attached to a fish that died shortly after tagging and, due to the pre-release program reported 4 days after the death of the fish. One tag (1027) reported an end point close to the tagging site after 236 days at liberty. A single tag (859) also reported an end point from an area off shelf south of Halifax, Nova Scotia, after 105 days at liberty. A single tag (383) reported an end point off New Jersey. Seven tags (590, 949, 946, 1018, 1019, 1024, 943) reported end point positions from continental shelf and slope waters off the Carolinas (Figure 2.1). One tag (1015) reported an end point position in the eastern slope waters of the Gulf of Mexico on 3 February 2002

(Figure 2.1). Commercial fishers and beachcombers recovered two tags. Tag 770 was returned when a commercial longline vessel captured the fish off the coast of New Jersey, and the fisher provided a GPS position for the recapture point. Tag 763 was found detached from the fish on a beach in the Bahamas. A single tag leader (871) was recovered after tag release by an American purse seiner, providing an end point for the tagged fish (Figure 2.1).

Two mature Atlantic bluefin tuna (1015 and 1027) that were tagged off New England, moved into the Gulf of Mexico spawning area. Bluefin tuna 1015 moved south from New England along the continental shelf of the Mid-Atlantic Bight and into North Carolina waters by late November. This bluefin tuna remained in on shelf waters off North Carolina in the winter months and slowly moved into slope waters, then south along the Blake Plateau. This fish traveled south across the Bahama Banks (25°00'N, 75°36'W) into off shelf waters in December and into the Gulf of Mexico in mid-December. It remained in the Gulf of Mexico until the PSAT reported in early February from slope waters off of Florida (Figure 2.2a). The estimated geolocation track of 1015 is consistent with the water column structure and maximum depth data obtained from the temperature-depth profiles from the PSAT (Figure 2.2b). The data indicate that this fish was bathymetrically restricted in diving activity while in the shelf waters off New England and North Carolina, and then began a period of deeper dives in off shelf waters. During the portion of the track that the fish was off New England and in the waters of the Mid-Atlantic Bight, the temperatures were cool (16 °C to 20 °C). Ambient temperatures increased as the fish moved south along the US continental shelf, corroborating geolocation estimates of southward movement. After a period of residency in winter off

North Carolina the fish moved off the Carolina shelf. It moved into the Straits of Florida and then into the Gulf of Mexico in December. A warm surface water mass and deep thermocline are characteristic of the Straits of Florida and Gulf of Mexico waters. The pop-up end point position places the fish in the eastern Gulf of Mexico.

Atlantic bluefin tuna 1027 had a pop-up end point position located 171.15 km from the initial deployment location off New England, after 8 months at liberty. This indicates that this fish showed fidelity, returning to the region where it was tagged. This is consistent with conventional tagging records from this area. Geolocation estimates indicate that a complex migration occurred between tag deployment and pop-up. Bluefin tuna 1027 displayed a pattern of movement from New England south along the continental shelf in the period from October to March (Figure 2.2c). A geolocation estimate indicates that the fish moved to the west into a region consistent with the Gulf of Mexico in March. Due to the bluefin tuna's deep diving behavior, and a lack of transmissions, the reported data did not provide many daily light level positions for estimating geolocation. This is consistent with implantable archival tag data from bluefin tuna that entered the Gulf of Mexico and pop-up satellite tag data from the Gulf of Mexico. These data indicated extensive deep diving during the period that the fish enter the Gulf of Mexico (Block et al. 2001, 2002). For 18 days before and 17 days after the single geolocation (9 March 2002) in the Gulf of Mexico no light level data were reported. The temperature-depth profiles from this tag, that were also limited in number, indicate a period of on shelf bathymetrically limited diving at the beginning of the track and movement from a cooler water mass through the Gulf Stream and, into a warmer water mass consistent with the Gulf of Mexico during March (Figure 2.2d). This water

mass had a 25 °C to 26 °C maximum surface water temperature and a 50 m themocline depth, which are consistent with that observed for this period on fish tagged in the western Gulf of Mexico (Block and Teo, unpublished data). After the fish was in the Gulf of Mexico, it had a period of deep diving and entered water masses cooler than the Gulf of Mexico. This corroborates geolocation estimates that indicate that the fish moved to the north. Geolocation estimates indicate that this fish was in the region of the Charleston Bump (29°54'N, 76°18'W), and then moved to waters off the Georgia-Carolina shelf before returning to New England (Figure 2.2a). One geolocation position (26 March 2002; 32°65'N, 78°66'W) as the fish moved north to the Carolina Shelf was 19.49 km from a geolocation position (11 February 2002; 32°74'N, 78°48'W) recorded during the fish's movement south, suggesting fidelity to this location. The fish moved from Carolina waters into the Gulf Stream and spring geolocation estimates place the fish on a cold (9 °C) frontal edge. The tags end point position was 171.15 km from its point of release.

The seasonal movements from New England of potentially mature (>198 cm CFL) and adolescent (<198 cm CFL) Atlantic bluefin tuna are shown (Figure 2.3). In the autumn (Figure 2.3a) and winter (Figure 2.3b) seasons, based on the autumnal equinox and winter solstice, both adolescent and mature bluefin tuna generally remain aggregated along the North American continental shelf and slope waters between New England and North Carolina. However, in the winter months bluefin tuna, which are assumed by length measurements to be adolescent, aggregate in the Carolinas. Mature fish also pass through the Carolina shelf waters and move south to Blake's Plateau and to the waters of the Bahamas and the Gulf of Mexico in the winter months.

Table 2.2. Results of pop-up satellite archival tagging of 35 Atlantic bluefin tuna off Nantucket Island, Massachusetts, during the autumn of 1998, 2000, and 2001.

		Tag deployment date and location			Tag report date and location				Track length (days)	Dist. travel (km)	Min. speed
Tag no.	Curved fork length (cm)	Date	Lat. (N)	Lon. (W)	Date	Lat. (N)	Lon. (W)	Days off fish at time of report			(km•d^{-1})
381	229[a]	17 Sept. 1998	41.270	-69.141	29 Sept. 1998	42.008	-69.450	0	12	85.6	7.31
382	272[a]	14 Sept. 1998	41.267	-69.320	24 Sept. 1998	41.668	-69.726	0	10	58.1	6.57
383	245[a]	14 Sept. 1998	41.267	-69.320	17 Nov. 1998	39.416	-73.475	0	64	408.3	6.30
384	252[a]	14 Sept. 1998	41.267	-69.320	13 Dec. 1998	38.191	-71.408	?[f]	90	386.1	4.23
385	238[a]	17 Sept. 1998	41.270	-69.141	29 Jan. 1999	32.524	-77.483	?[f]	134	1221.8	9.05
25171	238[a]	17 Sept. 1998	41.270	-69.141	4 March 1999	36.087	-50.396	?[f]	175	1720.0	9.75
8971	217[a]	17 Sept. 1998	41.270	-69.141	11 March 1999	33.315	-56.560	?[f]	178	1416.8	7.96
9685	Unk.[e]	17 Sept. 1998	41.270	-69.141	Tag did not report						
8836	245[a]	17 Sept. 1998	41.270	-69.141	11 Sept. 1999	34.96	-44.034	?[f]	371	2295.5	6.19
590	173	4 Oct. 2000	41.260	-69.178	15 Dec. 2000	35.22	-75.03	0	72	843.7	11.72
763	221	29 Sept. 2000	41.249	-69.194	15 April 2001	29.49	-67.46	145	198	1316.8	6.65
764	206	30 Sept. 2000	41.258	-69.195	15 May 2001	32.42	-74.10	175	227	1073.5	6.13
765	252	27 Sept. 2000	41.252	-69.175	1 June 2001	39.74	-42.25	195	247	2272.7	9.20
770[b]	191	27 Sept. 2000	41.243	-69.192	15 Oct. 2000	40.00[c]	-70.28[c]	0	18	465.3	25.9
760	287	12 Oct. 2000	41.183	-69.147	Tag did not report						

761	> 287	13 Oct. 2000	41.322	-69.076	Tag did not report						
751	218	13 Oct. 2000	41.335	-69.056	1 July 2001	40.18	-33.15	190	261	3002.8	11.5
753	246	12 Oct. 2000	41.261	-69.132	15 June 2001	34.96	-52.85	197	246	1581.6	6.4
771	213	12 Oct. 2000	41.157	-69.157	1 Aug. 2001	40.15	-56.34	123	293	1083.4	3.70
752	279	13 Oct. 2000	41.165	-69.142	1 Aug. 2001	27.59	-55.19	130	292	1974.3	6.76
772	218	12 Oct. 2000	41.157	-69.157	1 Sept. 2001	33.534	-60.368	319	324	1085.2	3.3
750	279	13 Oct. 2000	41.328	-69.059	1 Sept. 2001	40.80	-44.47	296	323	2054.9	6.4
738	218	14 Oct. 2000	41.331	-69.075	1 Sept. 2001	35.20	-53.78	289	322	1495.8	4.6
1027	226	27 Sept. 2001	41.118	-69.025	20 May 2002	40.258	-67.902	0	236	134.3	0.6
1024	237	3 Oct. 2001	41.120	-69.038	21 Jan. 2002	33.84	-76.78	4	110	1058.3	9.6
1019	232	3 Oct. 2001	41.120	-69.038	24 Jan. 2002	36.27	-73.82	4	115	679.9	5.9
1026[d]	231	3 Oct. 2001	41.144	-69.048	7 Oct. 2001	41.14	-69.050	4	4	9.0	2.25
1018	241	15 Oct. 2001	41.168	-69.125	21 Jan. 2002	34.41	-76.76	4	99	1005.1	10.2
953	262	19 Oct. 2001	41.307	-68.927	25 Feb. 2002	Unknown		4	130	Unknown	
946	189	20 Oct. 2001	41.277	-68.962	1 Jan. 2002	35.67	-75.16	4	74	824.4	11.1
1015	267	31 Oct. 2001	41.259	-68.919	3 Feb. 2002	25.16	-83.97	4	95	2263.9	23.8
949	196	31 Oct. 2001	41.291	-68.893	21 Feb. 2002	34.32	-76.11	4	114	999.6	8.8
871	242	31 Oct. 2001	41.277	-68.887	12 Nov. 2001	Unknown		4	12	Unknown	
859	186	29 Oct. 2001	41.211	-68.922	10 Feb. 2002	40.47	-63.67	4	105	449.1	4.3

943	232	1 Nov. 2001	41.293	-68.890	30 Jan. 2002	32.81	-78.53	4	91	1271.5	14.0

[a] Fish were tagged over the side of the tagging vessel, therefore round weight was estimated and curved fork lengths were calculated. [b] Fish recaptured by American longliner. [c] Estimate of position reported by recapture vessel. [d] Mortality at tagging event. [e] Fish curved fork length was not estimated. [f] For PTT100 tags or PAT 1 tags that were at liberty for a duration longer than their temperature archive (60 days) it was not possible to discern at what time the tag released from the fish.

Figure 2.1. Position data from pop-up satellite tags deployed on Atlantic bluefin tuna (*Thunnus thynnus*) off Massachusetts (green triangle = release location) in 1998, 2000, and 2001 obtained from radio transmission end points to the Argos satellite system (yellow squares; N = 14), tag recapture (yellow square with x; N = 1) and leader recapture (red square with x; N = 1) positions and geolocation estimates based on light level longitude and sea surface temperature latitude estimates (white circles; N = 645). The end point location for tag 1026 is obscured by the symbol representing the release location.

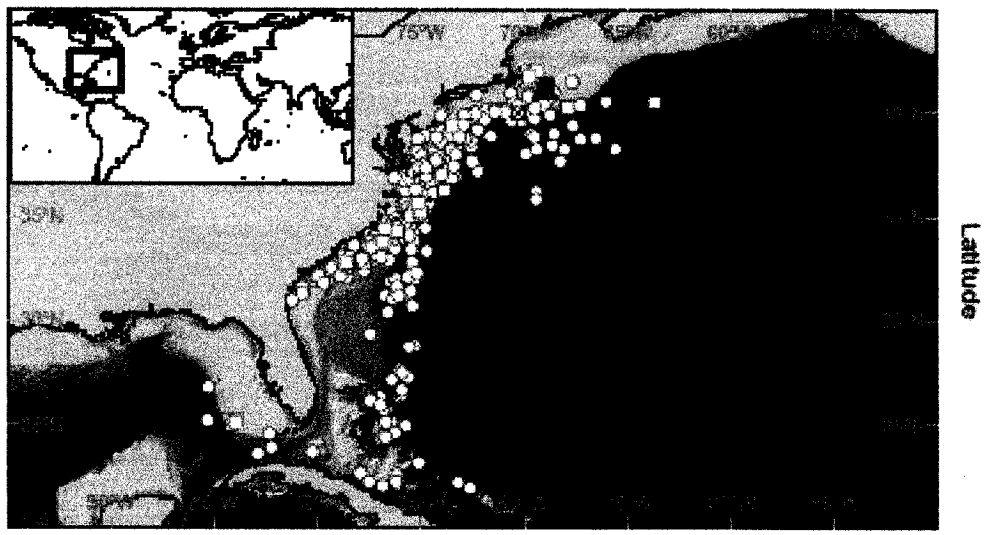


Figure 2.2. (a) Geolocation track for an Atlantic bluefin tuna (*Thunnus thynnus*; 1015) tagged with a pop-up satellite archival tag off New England (tag model is PAT 2.0) in autumn 2001 (green triangle = release location; yellow circles = geolocation estimates based on light level longitude and sea surface temperature latitude; red square = tag radio end point location). (b) Maximum depth, and ambient temperature profiles of the water column (°C) for bluefin tuna 1015. (c) Geolocation track for one bluefin tuna (1027) tagged with a pop-up satellite archival tag (PAT 2.0) off New England in autumn 2001 (green triangle = release location; yellow circles = geolocation estimates based on light level longitude and sea surface temperature latitude; red square = tag radio end point location). The broken portion of the yellow line represents a period of 18 days before and 17 days after the estimated geolocation position in the Gulf of Mexico for which there were no geolocation estimates available due to insufficient light data. However the geolocation position is accompanied by three additional depth temperature profiles in the March period of Gulf of Mexico visitation that show a water column structure consistent with the Gulf of Mexico (see 3d). (d) Maximum depth, and ambient temperature profiles of the water column (°C) for bluefin tuna 1027.

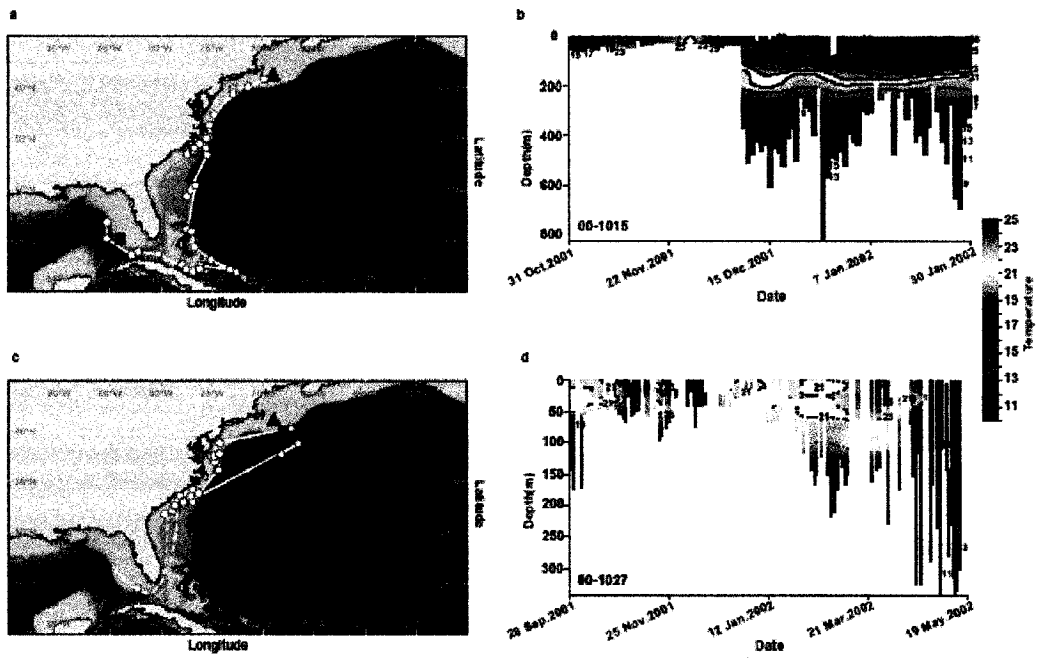
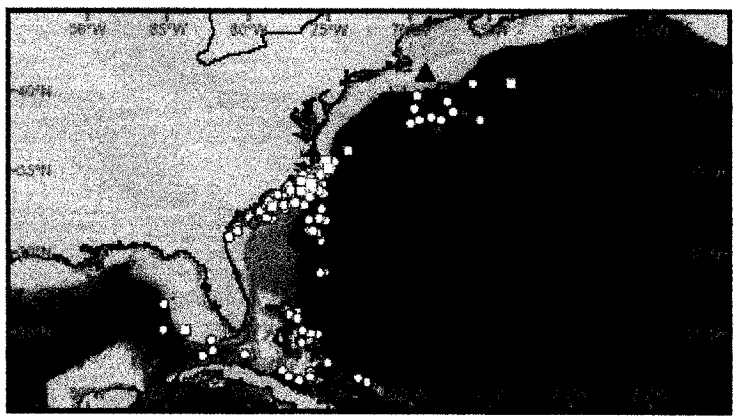


Figure 2.3 Seasonal movements in autumn (a) and winter and spring (b) of Atlantic bluefin tuna (*Thunnus thynnus*) tagged off New England. Autumn (a) is defined as the period between the autumnal equinox and the winter solstice; winter (b) is the period between the winter solstice and the spring equinox; spring (b) is the period between the spring equinox and the summer solstice. Maturity was assigned based on curved fork length, (white circles = adolescent bluefin tuna and are defined as < 198 cm CFL; yellow circles = potentially mature bluefin tuna and are define as > 198 cm CFL; green triangle = release location; yellow square with x = tag recapture; red square with x = leader recapture; orange = spring locations for one mature bluefin tuna 1027 ; squares = Argos radio end point locations; circles = geolocation estimates based on light level longitude and sea surface temperature latitude).

a

b



Atlantic bluefin tuna showed seasonal differences in their ambient temperature preferences (Figure 2.4). Ambient water temperature recorded by the PAT 2.0 tags indicate that the bluefin tuna occupied similar water temperatures during autumn and winter with slightly broader temperatures experienced in autumn. In autumn, bluefin tuna spent 95% of the time in ambient water temperatures from 14 °C to 26 °C (Figure 2.4). In winter, the bluefin tuna had narrower preferences in ambient temperatures spending 93.5% of the time in water from 18 °C to 24 °C (Figure 2.4).

Archival data logged in the memory of two PAT 2.0 tags were recovered from Atlantic bluefin tuna, one upon recapture (770) and one upon recovery of the tag off a beach (763). Bluefin tuna 770 provided 14 days of high resolution data on diel diving patterns. This fish occupied deeper depths during the night (31.54 ± 35.82 m; mean ± SD) than during the day (20.88 ± 21.44 m; mean ± SD). Tag 763 was not analyzed due to a non-linear depth drift.

Ten PAT 2.0s (software version 2.03), which were deployed prior to the development of the pre-release software program, detached from the Atlantic bluefin tuna prematurely (more than 4 days prior to the pre-programmed release date) and drifted for from 123 to 319 days after release (Table 2.2). These tags were not included in the location analysis above. These tags were attached to fish for one to 23 weeks prior to detachment. The end points of these drifting tags provide information on movement of tags that detach early from bluefin tuna. The tags all exhibited a general drift off the continental shelf to the east and northeast, following the general path of the Gulf Stream. Several of the tags reported end point positions in the mid-Atlantic region (Figure 2.5).

Figure 2.4. Time at temperature distribution of Atlantic bluefin tuna (*Thunnus thynnus*) tagged with pop-up satellite tags (PAT 2.) in 2000 and 2001. Twelve bluefin tuna were tagged and released and provided transmissions that were used to construct the graph. The tags reported ambient temperature data for a total of 293 days (N = 12; mean = 24.42; SD = 16.91) during the autumn (black bars) (autumn equinox [22 September] to winter solstice [21 December]) of the years 2000 and 2001. Four bluefin tuna were at large, retained their tags and reported data from a total of 85 days (N = 4; mean = 21.33; SD = 14.57) during winter (white patterned bars) (winter solstice [21 December] to spring equinox [20 March]) 2001 and 2002.

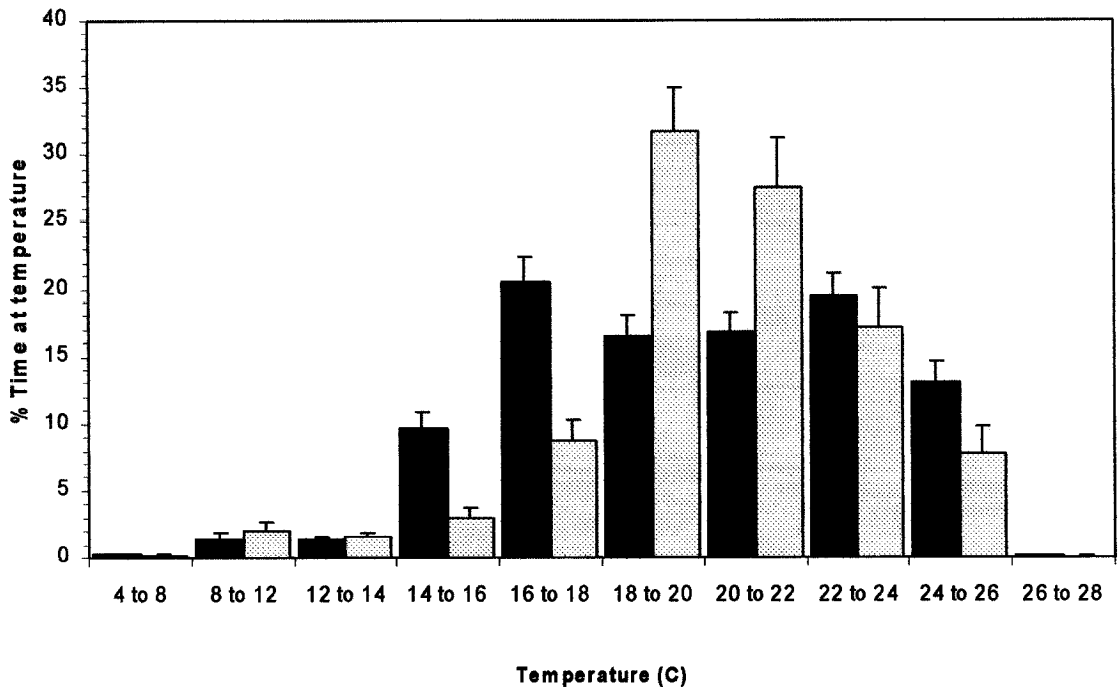


Figure 2.5. Argos radio end point locations for ten (PAT 2.0) tags that were confirmed by pressure data (2000 and 2001 releases), to have prematurely released from Atlantic bluefin tuna (*Thunnus thynnus*) and drifted for from 123 to 319 days prior to reporting (white triangle = release location; white squares = Argos end points for drifting tags).

2.5 Discussion

The pop-up satellite tag positional data sets from three sources (radio end points, recovery location, and light-level longitude and SST latitude estimations of geolocation), provided a total of 661 days of position data on the assemblage of Atlantic bluefin tuna found off New England. For the Argos radio position data the quality of the end point location was calculated by the Argos system. The restriction of end point locations to accuracy classes of 2 or 3 ensured that the end point locations were likely to have an accuracy better than 350 m. If the tag drifted for one to 4 days it was possible that the tag had moved up to 1.5 degrees from the actual fish location, based on drift rates calculated from transmitting tags. The estimated geolocation positions have a reported error estimate that is less than two degrees around the geolocation based on comparisons of satellite end points, GPS points and estimated geolocations (Teo et al. 2004). The data sets demonstrate that bluefin tuna from this region, if tagged and tracked for less than a year, are most likely to be found in the western Atlantic Ocean on the North American continental shelf, the North American slope waters or in the Gulf of Mexico. These results are consistent with previously reported implantable archival tag data (Block et al. 2001) but differ in several significant respects to a prior pop-up satellite tag study on this same assemblage of fish (Lutcavage et al. 1999).

The satellite tags placed on Atlantic bluefin tuna in this study remained attached primarily for the autumn and winter seasons (less than 6 months) and on a single fish into the spring season (~8 months). The position data collectively show a pattern of migration by season where the bluefin tuna leave New England, move southward along the North American continental shelf and reside in the vicinity of the North Carolina shelf. Data

indicate that some fish move into the South Atlantic Bight, and that two of the fish entered the Gulf of Mexico. Bluefin tuna 1015 represents the first record of a bluefin tuna being electronically tagged in New England and confirmed by radio end point position to visit the Gulf of Mexico breeding ground. Geolocation estimates for this fish (1015) indicate that it entered the Gulf of Mexico in December and was in the eastern slope waters of the Florida shelf when the tag popped off on 2 February 2002. Bluefin tuna 1027 entered the Gulf of Mexico in March. Bluefin tunas 1015 and 1027 recorded maximum depth and ambient temperature data consistent with their movements into the Gulf of Mexico. The data was similar to an implantable archival tagged bluefin tuna (98-512) previously reported (Block et al. 2001). This fish was tagged off Hatteras, North Carolina and in one year moved to the north of the Gulf Stream in spring, then south along the continental shelf into the Gulf of Mexico and back to the waters of the Mid-Atlantic Bight. In this study, bluefin tuna (1027) moved to the Gulf of Mexico in March and then returned to waters off New England, indicating fidelity to the New England feeding aggregation after migration into the Gulf of Mexico. The tag detached from this fish on 20 May 2002 the pre-programmed date of release, 236 days after tag and release. A portion of this 236 day track overlaps the track of a bluefin tuna that was tagged with a pop-up satellite tag in the Gulf of Mexico (Block et al. unpublished data) and moved into the North Atlantic. Consistent with these tracks is a propensity for deep diving that prevents obtaining light data and estimates of longitude. The release and recapture 334 days later of bluefin tuna 871 (leader recapture), indicates that this fish also showed fidelity to the New England feeding aggregation.

Geolocation estimates provide some distinctions between the movements of adolescent and mature Atlantic bluefin tuna. Movements of tagged adolescent bluefin tuna were recorded for durations of 18 to 114 days post release show a general distribution to the south of New England waters. In all but one case these tuna migrated to the region along the North American continental shelf and remained in shelf waters north of North Carolina, USA. Maximum depth records (28-40m) from these tags indicated that the dives of the bluefin tuna were depth-limited, indicating that they remained in on shelf waters. A single tagged adolescent bluefin tuna (tag 859, 186 cm CFL) moved to off shelf waters south of Halifax, Nova Scotia, Canada in February. This is similar to an off-shelf movement pattern for adolescent bluefin tuna observed by Mather et al. (1995) and Block et al. (2001).

In the first weeks of their autumnal southern migration mature Atlantic bluefin tuna display similar movement patterns to adolescent bluefin tuna moving along the continental shelf and Mid-Atlantic Bight and into Carolina shelf waters. During winter months, however, mature bluefin tuna moved to positions further south than adolescent bluefin tuna, including the Blake Plateau, Bahamas and the Gulf of Mexico. The passage of fish through the Carolina region is consistent with previous studies showing that fish tagged in the Carolina region moved to the south or occasionally into western breeding regions (Block et al. 2001, 2002).

The movements of Atlantic bluefin tuna were seasonal. All fish, whose tags remained on long enough to record a movement to the south, indicated migration along the shelf and toward Carolina after a period of autumn residency in the waters off New England. Bluefin tuna with implantable archival tags displayed similar movements south

after SSTs cooled to 11 °C to12 °C (Block et al. 2001, supplemental data). Winter geolocation estimates and pop-up satellite tag end point positions indicate a winter distribution of bluefin tuna from waters off the Carolinas to the Blake Plateau and Gulf of Mexico.

Atlantic bluefin tuna showed a preference for waters from 14 °C to 26 °C during the autumn. During the winter, bluefin tuna appeared to reside in a narrower temperature range centered on 18 °C to 24 °C. In winter off North Carolina the water column is generally within this temperature range (Block et al. 2001, Boustany et al. 2001). Pop-up satellite tags of earlier generations that detached prematurely from tagged Atlantic bluefin tuna and were not equipped with pre-release software drifted toward the mid-Atlantic prior to reporting. Four of the 12 free drifting tags (30 %) reported from the eastern Atlantic Ocean ICCAT management zone (east of 45° W). This is in contrast to the pop-up satellite tags that remained attached to the bluefin tuna that showed no movement into the eastern management zone and indicated a western residency period after release. Importantly, this study only covered the eight month period after tagging and is consistent with Carolina pop-up satellite tagging studies that suggested western residency for most fish in the first eight months after release. However, implantable archival tags have shown that after one to three years after release bluefin tuna may move into the eastern Atlantic or Mediterranean. While short-term studies indicate western residency of bluefin tuna tagged in the autumn assemblage, it remains possible that bluefin tuna tagged for longer durations will move to the eastern Atlantic Ocean.

The results of this study differ from that of Lutcavage et al. (1999) who used an early generation of pop-up satellite tags that lacked pressure sensors and premature

release software. The major contrast between the two studies is that in the current study, tags that remained attached to fish showed positions that were distributed primarily on the North American continental shelf and slope waters due south of New England, and importantly, recorded movements into known western breeding grounds in the Gulf of Mexico and the Florida Straits. Only drifting tags from the current study show agreement with the results of Lutcavage et al. (1999). Several studies have pointed out the challenges of interpreting the results of the earlier generations of pop-up satellite tags that lacked pressure sensors or temperature sensors that recorded significant archival data (Gunn and Block 2001). The lack of archival data makes the determination of when and where the tag releases from the bluefin tuna highly challenging to discern (Gunn and Block 2001). Block et al. (2002) reported that results from studies that used single point pop-up satellite tag technology to track bluefin tuna (i.e. Block et al. 1998a; Lutcavage et al. 1999) must be viewed with extreme caution if tags are interpreted beyond the period of data archive. Clarifying what the New England assemblage of fish do, and how much mixing occurs between this assemblage and fish from the eastern Atlantic Ocean is of critical importance. It is up to the electronic tagging community to carefully present the results from electronic tagging studies and qualify any uncertainty in positions.

This tagging study was initiated in the autumn, and selected for Atlantic bluefin tuna moving from New England waters toward winter feeding and breeding grounds. These results indicate that fish tagged in the autumn feeding aggregation off New England feed in summer and early autumn in New England waters and in winter in Carolina waters, consistent with archival tagging results reported by Block et al. (2001).

Also, our results are consistent with prior archival tagging results that tightly link the commercial and recreational fisheries off New England and Carolina (Block et al. 2001).

The results of this study only represent a short duration of activity for a long-lived pelagic species. Each Atlantic bluefin tuna is at a distinct period in its life cycle and their behavior might be different if studied for longer durations. Deployment of implantable archival tags that log multiple years of behavior are crucial for understanding the longer term biology and behavior of bluefin tuna (Block et al. 2001, 2002). Tagging data indicate that bluefin tuna movements are complex. Tag pre-release is an ongoing problem for external implantation of pop-up satellite tags. In addition, data compression and uplinking to the satellite are influenced by the state of the antenna that is often damaged after long durations of attachment. Long duration tracks spanning multiple years may best be obtained by tagging with implantable archival tags. However, efforts to reduce the size of pop-up satellite tags and improved attachment techniques may help to lengthen their duration of attachment. Efforts to continue electronically tagging bluefin tuna off New England with tags that remain in place for multiple years are necessary to discern the relationship of these fish to eastern assemblages over durations longer than 12 months.

Chapter 3. Movement of Atlantic bluefin tuna from the eastern Atlantic Ocean to the western Atlantic Ocean as determined with pop-up satellite archival tags

3.1 Introduction

The study of fish migration and stock identification are closely related (Mather et al. 1995). Recently, tagging studies initiated in the western Atlantic Ocean and using Pop-up Satellite Archival Tags (PSATs) and implantable archival tags have investigated the movement patterns of Atlantic bluefin tuna (*Thunnus thynnus*; Block et al.2001, Teo et al. 2004, Stokesbury et al. 2004). Bluefin tuna are commercially important, highly migratory members of the scombridae. Their migration patterns and stock structure are complex (Mather 1995, Block et al. 2001) and understanding their movement patterns is crucial for their proper management and conservation (National Research Council 1994).

Fisheries for Atlantic bluefin tuna are managed by the International Commission for the Conservation of Atlantic Tunas (ICCAT) under a two stock hypothesis (National Research Council 1994). One eastern Atlantic Ocean and Mediterranean Sea stock that spawns in the Mediterranean Sea (Richards 1976) and a western Atlantic Ocean stock that spawns in the Gulf of Mexico (McGowan and Richards 1989) and the Florida Straits (Rivas 1954). The stock boundary line used by ICCAT to divide the stocks is at 45 °W Longitude. Bluefin tuna are managed as if there is a low mixing rate (<4% • year $^{-1}$ National Research Council 1994) between the two stocks. However, recent electronic and conventional tagging studies indicate movement of bluefin tuna from the western Atlantic Ocean to the eastern Atlantic Ocean of 10 – 30 % (Block et al. 2001).

In 2000, a small sport fishery for Atlantic bluefin tuna began in Donegal Bay and more recently one has also begun off Mayo, on the mid-west coast of Ireland. Little is known about the life history of the large giant bluefin tuna exploited in these fisheries. Possibly, bluefin tuna that enter Norwegian waters may travel through the waters off the northwest coast of Ireland (Mather et al. 1995). Also, fish may pass western Ireland on route to the spawning grounds in the Mediterranean Sea (Mather et al. 1995). Interestingly, bluefin tuna present off Norway in the autumn have also been linked to the Western Atlantic Ocean as nine large bluefin tuna tagged in the Bahamas were captured off Norway (Mason et al. 1977). Also, recent electronic tagging experiments indicated that bluefin tuna tagged off North Carolina moved to the Eastern Atlantic Ocean (Block et al.2001).

The migration pattern and stock of origin of the Atlantic bluefin tuna now being exploited off the west coast of Ireland is unknown. In this study we employed the PSAT tagging procedure used in the western Atlantic Ocean, to tag giant bluefin tuna captured in the eastern Atlantic Ocean. The study enabled the examination of movements and environmental preferences of bluefin tuna released off the west coast of Ireland.

3.2 Materials and methods

Atlantic bluefin tuna were fished in two different locations off the west coast of Ireland. Fish were captured by trolling squid spreader bars with rod and reel off Donegal and Mayo. The fish were boated, measured, and tagged with PSATs using procedures described by Stokesbury et al. (2004). The PSATs (hardware PAT4, software 4.01e) provided an end point location based on the Doppler shift of the tags radio transmission

to the Argos satellites (root mean square error of < 350 m; Taillade 1992). PSATs also measured and archived to memory, light, ambient temperature, and pressure at 60 s intervals. Depth and temperature data were summarized into 12 h bins prior to transmission. Also, temperature vs. depth profiles were generated with minimum and maximum temperature at each of the 8 equally spaced depths. The tags were equipped with a pre-release program and an auto-depth correction. So, if the tag prematurely detached from the fish and floated to the surface it reported to the satellite 4 days after detachment.

The daily movements of Atlantic bluefin tuna were estimated from light-based calculation of longitude using Wildlife Computers PAT Decoder 7.08.0005 (Hill and Braun 2001), and latitude estimates based on satellite derived sea surface temperatures (SST) compared with SST's recorded by the tag (Teo et al. 2004). Geolocation estimates for PSATs deployed on Atlantic bluefin tuna had a root mean square error of 1.30° for light-based longitude and 1.89° for SST-based latitude (Teo et al. 2004).

3.3 Results

Three Atlantic bluefin tuna were tagged and released with second generation PSATs off the west coast of Ireland in 2003. Two fish were tagged off Donegal on 20 September. The two bluefin tuna were hooked by the same boat at the same time. The bluefin tuna were 221 and 225 cm curved fork length (CFL). Both fish were tagged with a single PSATs (# 267 and 191, respectively) and a conventional tag, and were released within 15 minutes of each other. The third fish was tagged off Mayo on 15 October 2003. This bluefin tuna was 264 cm CFL and was tagged with PSAT # 275. The tags

deployed on the two fish released in Donegal Bay at 55°22'N, 7°31'W, reported 224 (PSAT #267) and 236 (PSAT #191) days later from different sides of the Atlantic Ocean. Tag # 275 failed to report.

Tag 267 reported on 1 May 2004 from the Bahamas at 25°40'N, 67°23'W, a straight line distance of 5805 km from the tagging site (Figure 3.1). Geolocation positions indicate that this fish resided in water over the Irish shelf from tagging until 26 October. It then moved to off shelf waters for a period of 24 days, corroborated by multiple dives to depths deeper than 400 m (Figure 3.2a). The fish then returned to waters over the Irish shelf for from 19 November until 18 December then again moved off shelf. The fish stayed in off shelf waters until the tag reported from the Bahamas in May 2004 (Figure 3.1).

Atlantic bluefin tuna 267 spent 79.92 % of it's time in the top 100 m of the water column including 42.76 % in the top 5 m (Figure 3.2b). The fish spent 55.51 % of its time in water with temperatures between 12 and 16 °C (Figure 3.2b). Ambient SST's from 12 to 26 °C were recorded by the tag while the fish crossed the mid-Atlantic and entered the waters of the Bahamas (Figure 3.2c).

The tag on bluefin tuna #191 reported on 15 May 2004 from waters off southwest Portugal, at 38°10'N, 1320'°W, a straight line distance of 1962 km from the tagging site (Figure 3.1). Geolocation positions indicate that this fish resided in waters over the Irish shelf from tagging until 21 October, and then moved off shelf as indicated by geolocation positions (Figure 3.1) and it's maximum depth profile (Figure 3.2d). The fish occupied waters off the west coast of Ireland from 20 September to 21 October. It then moved off shelf to waters over the mid-Atlantic Ridge and back to the Eastern Atlantic Ocean.

Finally the fish resided in shelf waters, southwest of Portugal until the tag reported (Figure 3.1).

Atlantic bluefin tuna 191 spent 84.25% of it's time in the top 100 m of the water column (Figure 3.2e). Also, the fish spent 93.84 % it's time in water with temperatures between 12 and 18 °C (Figure 3.2e). The temperature depth profile indicated that during the period on the Irish shelf the water column was mixed and cool. However when the fish moved to the mid-Atlantic Ocean the water column became more stratified and the thermocline was deep. Finally, off Portugal the water column again became mixed and cool (Figure 3.2f).

Figure 3.1. Location data from pop-up satellite tags deployed on 2 Atlantic bluefin tuna (yellow circles = fish 267, white circles = fish 191) off Ireland (circle with dot = release location; N = 1) in autumn 2003 obtained from radio transmission end points to the Argos satellite system (red circles; N = 2), and geolocation estimates based on light level longitude and sea surface temperature latitude estimates (yellow and white circles; N = 184).

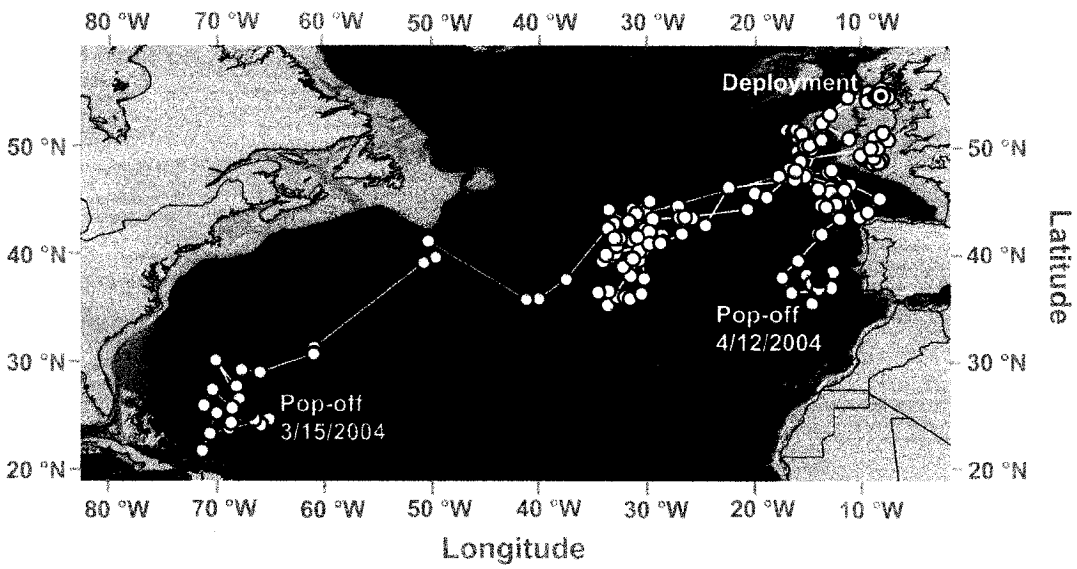
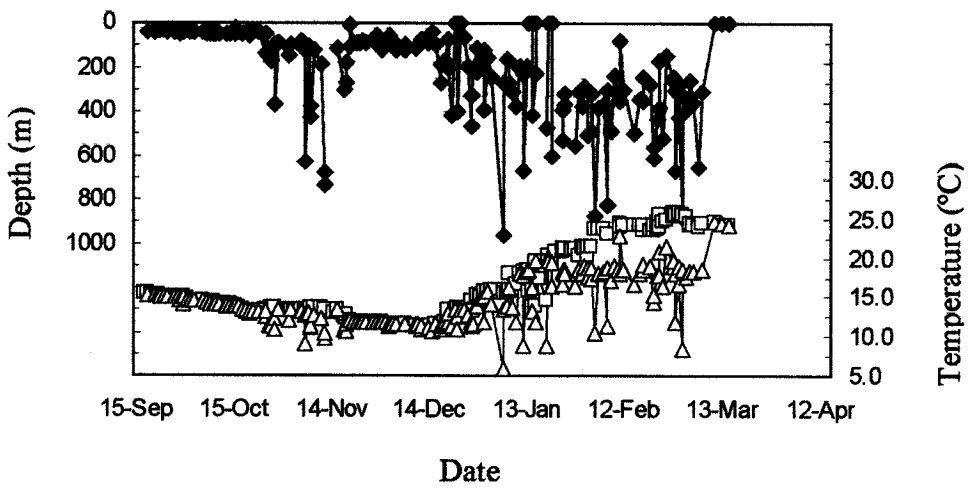
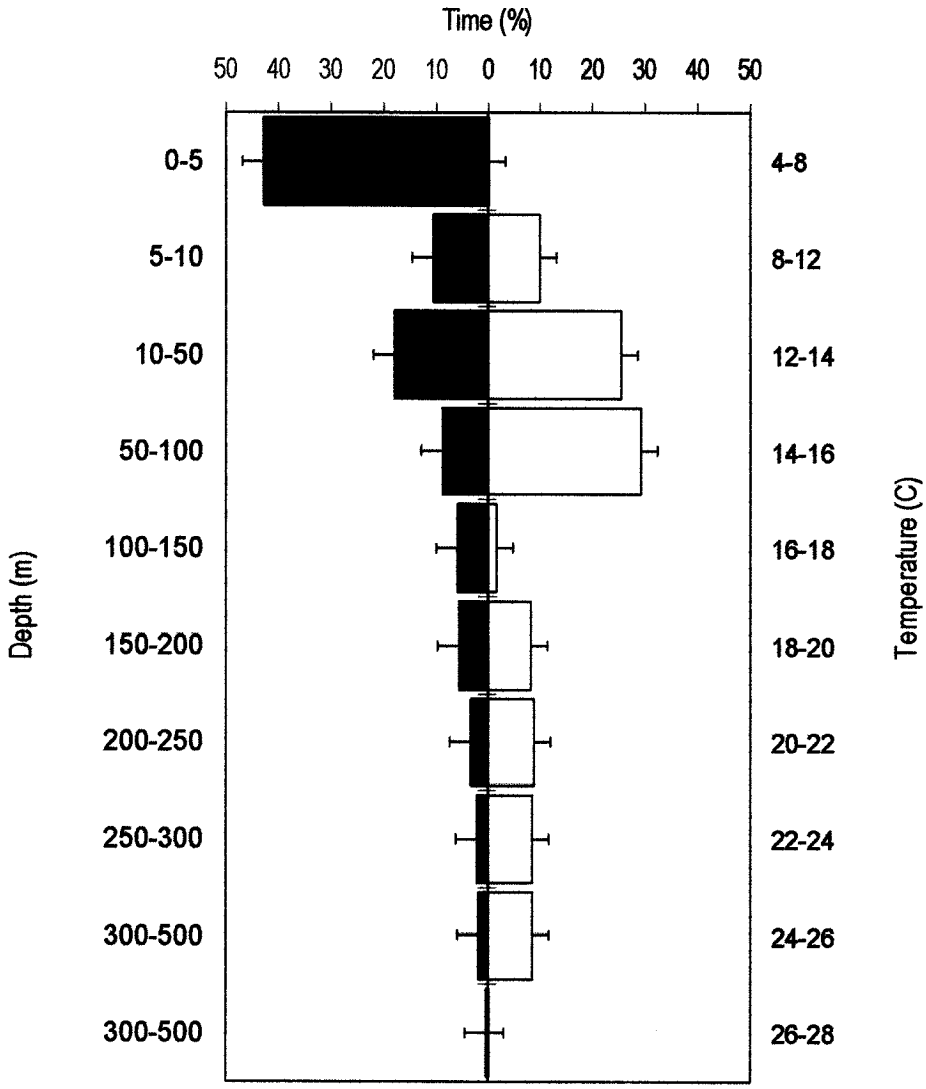


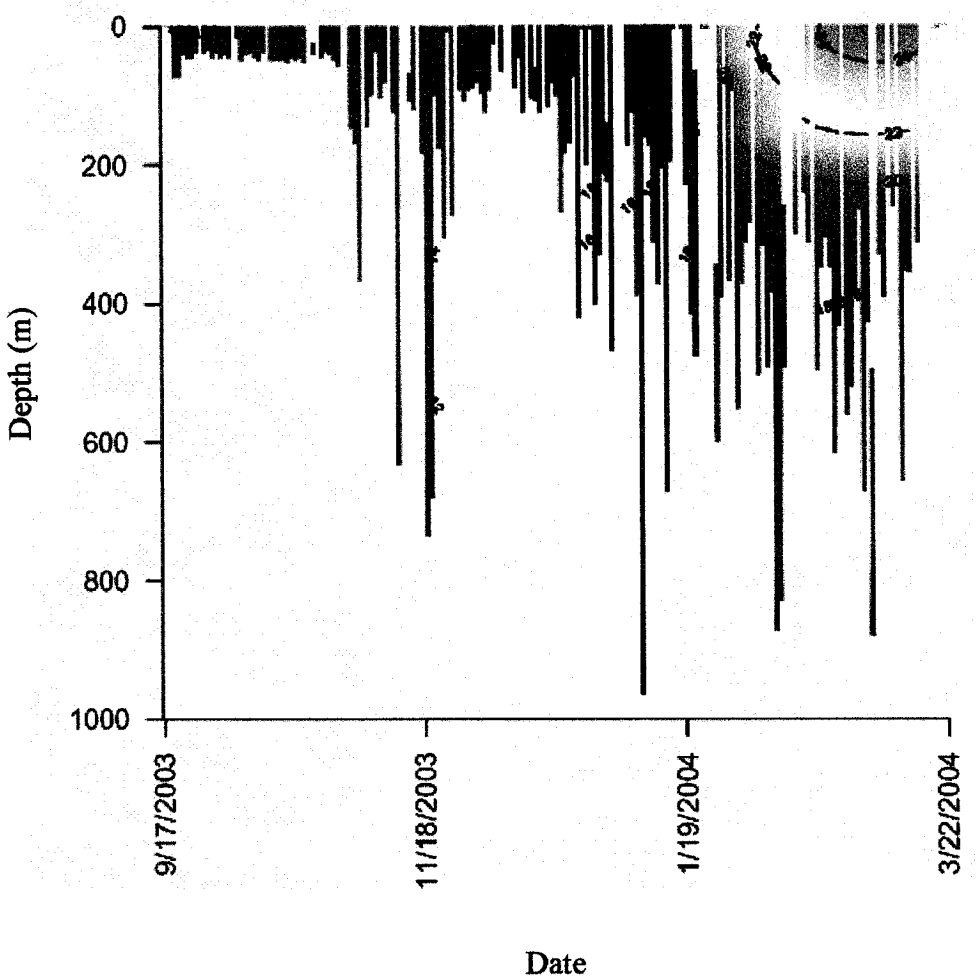
Figure 3.2. a) Maximum depth (black ◊), maximum (red □) and minimum (blue Δ) temperatures reported a PSAT deployed on Atlantic bluefin tuna 267 off the west coast of Ireland in autumn 2003. b) Bluefin tuna 267's time at depth distribution (black bars) and time at temperature distribution (white bars). c) Water column temperature profile generated by tag 267. d) Maximum depth (black ◊), maximum (red □) and minimum (blue Δ) temperatures reported a PSAT deployed on Atlantic bluefin tuna 191 off the west coast of Ireland in autumn 2003. e) Atlantic bluefin tuna 191's time at depth distribution (black bars) and time at temperature distribution (white bars). f) Water column temperature profile generated by tag 191.



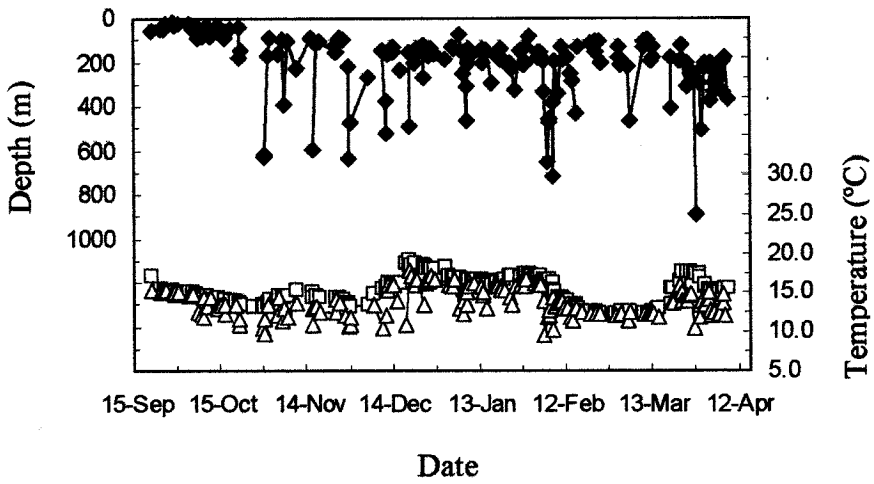
b)


Time (%)
50 40 30 20 10 0 10 20 30 40 50
Depth (m)
0-5
5-10
10-50
50-100
100-150
150-200
200-250
250-300
300-500
300-500
4-8
8-12
12-14
14-16
16-18
18-20
20-22
22-24
24-26
26-28
Temperature (C)

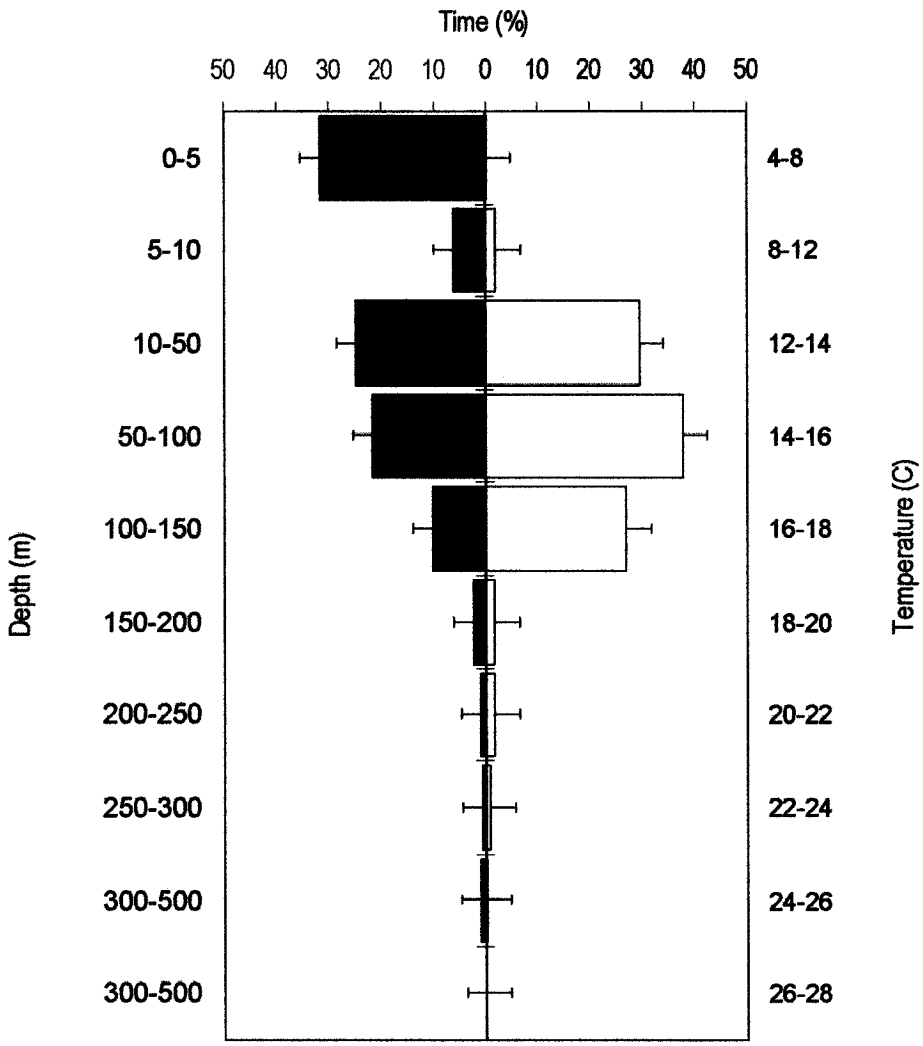
c)


0
200
400
600
800
1000
Depth (m)
9/17/2003
11/18/2003
1/19/2004
3/22/2004
Date

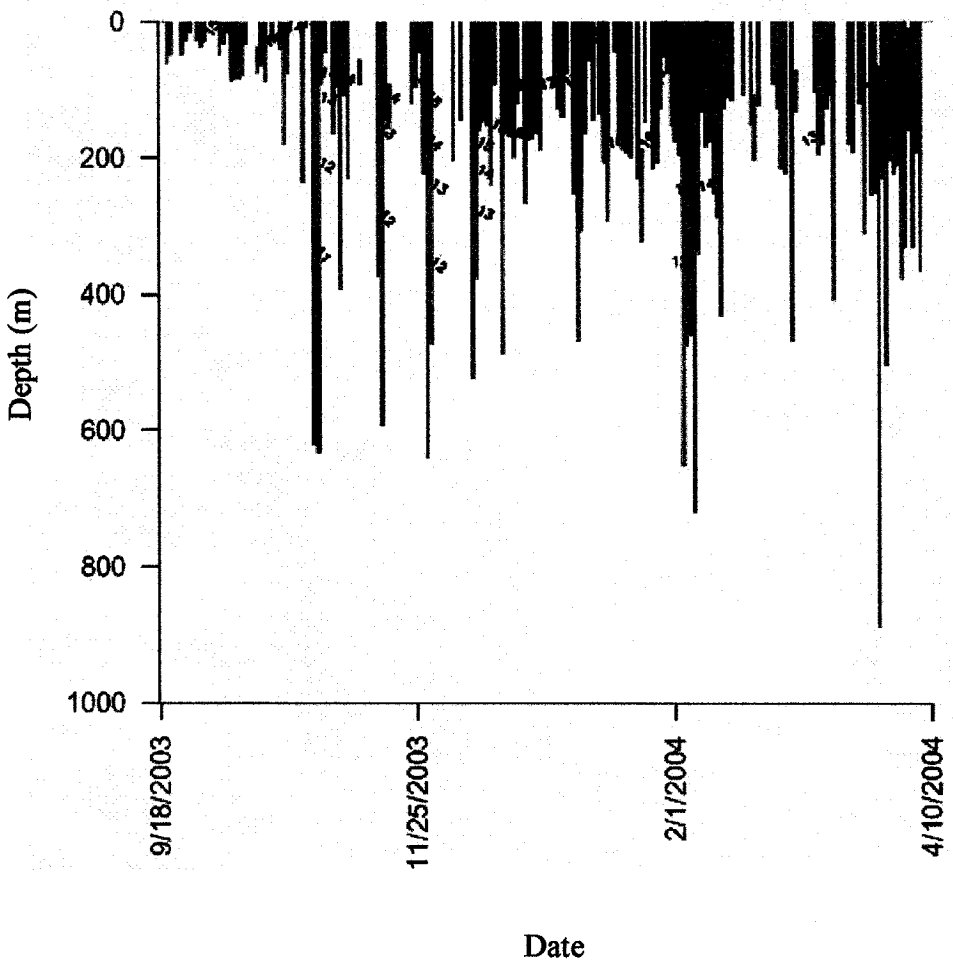
d)


0
200
400
600
800
1000
Depth (m)
30.0
25.0
20.0
15.0
10.0
5.0
Temperature (°C)
15-Sep
15-Oct
14-Nov
14-Dec
13-Jan
12-Feb
13-Mar
12-Apr
Date

e)


Time (%)
50 40 30 20 10 0 10 20 30 40 50
Depth (m)
0-5
5-10
10-50
50-100
100-150
150-200
200-250
250-300
300-500
300-500
4-8
8-12
12-14
14-16
16-18
18-20
20-22
22-24
24-26
26-28
Temperature (C)

f)


0
200
400
600
800
1000
Depth (m)
9/18/2003
11/25/2003
2/1/2004
4/10/2004
Date

3.4 Discussion

Atlantic bluefin tuna caught simultaneously and tagged at approximately the same time in September 2003 off the west coast of Ireland, moved to opposite sides of the Atlantic Ocean by May 2004. Bluefin tuna 267 traveled to the waters of the Bahamas, close to the Florida Straits, a proposed spawning ground for bluefin tuna in the northwest Atlantic Ocean (Rivas 1954). The water in this area was warm enough for a bluefin tuna to spawn (> 24 °C; Block et al. 2001). Electronically tagged bluefin tuna have moved to this region in winter and spring and encountered ambient water temperatures indicative of spawning (Block et al. 2001). This fish was tagged 2342 km east of the ICCAT stock boundary line, and moved to a recognized Western Atlantic Ocean bluefin tuna spawning location, during the spawning season. Importantly, prior electronic tag data indicates that bluefin tuna from the western Atlantic Ocean move to the eastern Atlantic Ocean to feed and back to western spawning grounds (Block et al. submitted).

Fish 191, traveled to waters off south western Portugal near the Ibero-Moroccan Bay. However, the water temperatures at the time the tag reported were well below the accepted temperatures in which bluefin tuna are hypothesized to spawn. The tag reported approximately 755 km from the Straights of Gibraltar.

Both Atlantic bluefin tuna spent a large portion of their time in the top 5 m of the water column. Also, both fish migrated great distances during the study. This supports the proposition that bluefin tuna migrate in the top of the water column (Mather et al. 1995). Also, the tuna spent the majority of their time in a fairly narrow temperature range. However, the two temperature ranges differed with fish 267 and 191 experiencing warmer and cooler time-at-temperature profiles, respectively. This was likely caused by

bluefin tuna 267 moving into the warmer waters of the Bahamas while bluefin tuna 191 occupied the cooler waters of the mid and eastern Atlantic Ocean.

The results of this study support a potential link between Atlantic bluefin tuna on the feeding grounds in the eastern Atlantic Ocean and putative spawning grounds in the western Atlantic Ocean. This may indicate, consistent with the results of Block et al. (2001), that bluefin tuna from independent breeding stocks are mixing on feeding grounds and then sorting to breeding grounds. It is important to increase the tagging effort in the eastern Atlantic Ocean to gain further knowledge of the movement patterns and stock structure of the autumn aggregation of bluefin tuna that is present off the west coast of Ireland.

Chapter 4. Movement and environmental preferences of Greenland sharks (*Somniosus microcephalus*) electronically tagged in the Saint Lawrence Estuary, Canada

4.1 Introduction

Greenland sharks (*Somniosus microcephalus*) are the only non-lamnid sharks known to live in polar waters. They can reach a total length of 7 m (Compagno 1984) and a mass of over 1000 kg (Bigelow and Schroeder 1948). Length at maturity is not known, however, adolescent sharks have been recorded as large as 311 cm total length (Beck and Mansfield 1969). They are present in the Northern hemisphere in the Atlantic Ocean, Arctic Ocean and range into southern latitudes, occupying deep waters as far south as off Georgia, United States (Herdendorf and Berra 1995).

Greenland sharks are primarily considered a benthic species, however incidental catches and sightings indicate they occupy a broad depth niche (Beck and Mansfield 1984, Herdendorf and Berra 1995). They have been taken by harpoon at the surface (Beck and Mansfield 1969), captured in the pelagic zone (Kondyurin and Myagkov 1982) and recorded by a submersible at 2,200 m (Herdendorf and Berra 1995). These sharks also display a cold thermal tolerance not evident in many sharks, as they have been tracked in ambient water temperatures below -1.5 °C (Skomal and Benz 2004). Greenland sharks are present under land fast ice in the Canadian Arctic where they have been previously tracked using acoustic tags (Skomal and Benz 2004). In the earlier study, six sharks were tracked using tags with pressure sensors for up to 42.8 h. Although no significant depth or temperature preferences were reported, the authors did note that the

sharks appeared to remain at deeper depths during the morning than in the afternoon and evening (Skomal and Benz 2004).

Studies of stomach contents (Beck and Mansfield 1969) and anthropogenic contaminants and stable isotopes (Fisk et al. 2002) of Greenland sharks, indicate that they feed on a wide variety of prey. In the Canadian Arctic, they feed upon pelagic and benthic fishes and invertebrates, and marine mammals (Beck and Mansfield 1969; Fisk et al. 2002). Fisk et al. (2002) proposed that Greenland sharks feed in the pelagic zone at the same trophic level as turbot (*Reinhardtius hippoglossoides*) and ringed seals (*Phoca groenlandics*), and at a higher trophic level than harp seals (*Phoca groenlandica*).

Although several studies have identified their prey, the movements, environmental preferences and general life history of Greenland sharks are largely unknown. In this study we electronically tagged three Greenland sharks, using two types of electronic tagging technology. From these data, we report the movement and environmental preferences of Greenland sharks from the St. Lawrence Estuary, Canada.

4.2 Materials and methods

Greenland sharks were tagged in Baie St. Pancrace (49°17' N, 68°03' W), Province du Quebec, Canada. This small bay (approximately 250 m wide and 500 m long) is located on the north shore of the St. Lawrence Estuary. It has steep walls that drop to a maximum bottom depth of 67 m. In this region the St. Lawrence Estuary is approximately 40 km wide, and has a maximum depth of approximately 350 m.
All three tags were attached to the Greenland sharks by divers using SCUBA. An acoustic telemetry tag (Vemco Ltd. V16 pressure, temperature tag) was applied using a

sling type spear with a stainless steel barb on the end. Attached to the barb was a 10 cm long piece of stainless steel monofilament, 90.9 kg test, looped and crimped at the other end. This cable was attached to a reinforced loop of nylon connected to the transmitter. The tag transmitted pressure and depth data alternately, at 69 kHz, approximately every 30 seconds. A receiver (Vemco Ltd. VR 60) with an omni-directional hydrophone was used to initially locate the tagged shark. When the shark was located, a receiver (Vemco Ltd. VR 2) was suspended on a mooring 10 m above the bottom of the bay in which the shark was present. A 605 m maximum detection radius was determined for the VR2 receiver. Data from the VR 2 receiver were downloaded to a laptop computer using a Vemco Ltd. VR 1 PC interface.

Pop-up satellite archival tags (PSATs) were applied using a stainless steel spear tipped with a titanium barb. A 10 cm length of 136.4 kg test monofilament, covered in shrink wrap was attached to the barb using a crimp. Attached to the monofilament was a Wildlife Computers PSAT (hardware PAT4, software 4.01e). The tags provided an end point location based on the Doppler shift of the tags' radio transmission to the Argos satellites (root mean square error of < 350 m; Taillade 1992). PSATs measured and archived, light level, ambient temperature and pressure at 60 s intervals. Also, depth and temperature data were summarized into 12 h bins prior to transmission approximating a day-night cycle. PSATs were programmed to release at 0800 Eastern Standard Time, on 1 November 2004.

Daily mean time-at-depth profiles for satellite tagged sharks were generated by multiplying the percentage time-at-depth by the middle value of the depth bin. Then by taking the mean for that daytime or nighttime period. Modal time-at-depth and

temperature values were calculated by taking the mid-value of the modal temperature or depth bin.

4.3 Results

Three Greenland sharks were electronically tagged in the St. Lawrence Estuary. One female shark was tagged with an acoustic telemetry tag and two sharks, one male and one female, were tagged each with one PSAT. In total, the tags provided 179 days of data on Greenland shark movement and environmental preferences.

One Greenland shark was tagged with acoustic telemetry tag number 32 (Table 4.1) in Baie St. Pancrace, PQ, Canada, on 23 July 2004 (Figure 4.1). Collection of data from this tag began on 27 July 2004 when a VR2 receiver was moored in Baie St. Pancrace. The tag reported data on ambient temperature and pressure for 47 days. Data indicate that shark 32 occupied waters close to the bottom of the bay during the daylight hours, and moved throughout the water column at night (Figure 4.2a). This is corroborated by ambient water temperature data as the shark experienced a very narrow range of colder temperatures during the day and a broader range of temperatures during the night (Figure 4.2c). For the first 4 weeks of the tags deployment, the shark spent the majority of its time at depths below 30 m (Figure 4.3a). During this time the deeper water temperatures remained consistently at or below 1 °C. However, in the fourth and fifth weeks (Figure 4.3b) the shark spent more of its time in mid-water and less time near the bottom. By this time the upper water column had warmed and the shark was experiencing water temperatures of 2 to 3 °C in the middle of the water column (Figure 4.4). The daily depth and temperature profile for this shark indicated multiple vertical

movements throughout the bottom and middle portions of the water column (Figure 4.5). Interestingly, the shark did not spend much time at the shallower depths, but reached a shallow point and immediately reversed and started its descent, as indicated by the sharp peaks on the depth distribution (Figure 4.5).

There were 176 instances (Mean = 1:21h; SD = 0.12; Max = 20:05h) when Greenland shark 32 was not recorded by a receiver for more than 30 minutes, between 28 July and 8 September 2004 (Figure 4.6). These periods likely represent departures from the bay, although other explanations are possible. Then the shark left the bay on 8 September 2004 at 22:38 h only to return for approximately 10 minutes on 26 September 2004. The shark was not detected from this time until removal of the receiver from Baie St. Pancrace on 1 November 2004.

Two Greenland sharks were each tagged with a PSAT, in Baie St. Pancrace, on 27 August 2004 (Table 4.1). Tag number 166 was attached to a female shark and tag number 581 was attached to a male shark (Table 4.2). The two tags each reported on the preprogrammed day, 66 days later on 1 November 2004. Tag 166 reported from Baie St. Pancrace (Figure 4.1). Therefore this female shark resided in the bay for the duration of data collection. Tag number 581 reported from 48°30' N 69°05' W, a position in the main channel of the St. Lawrence Estuary, 114.9 km to the south west (upstream) of the tagging location (Figure 4.1). Shark 581 departed Baie St. Pancrace the same day it was tagged.

Table 4.1. Period of deployment and data collection for electronic tags attached to Greenland sharks in Baie St. Pancrace, Quebec, in summer 2004.

Tag #	Date of deployment	Start of data collection	End of data collection	Days of data collection
32	23/7/2004	27/7/2004	9/9/2004[a]	47
166	27/8/2004	27/8/2004	1/11/2004	66
581	27/8/2004	27/8/2004	1/11/2004	66

[a] The last date that data from tag 32 was recorded by a receiver was 26 September 2004. It is not known at what time the tag ceased to transmit.

Figure 4.1. Map of the St. Lawrence River, tag release site showing Baie St. Pancrace, Quebec, where the acoustic tag data was collected, and the shark with PSAT tag 166 resided (PSAT pop off = grey triangle, offset from the bay for clarity) for the duration of the study. Also, the pop-off position for PSAT tag 581 (grey triangle with dot) in the main channel of the St. Lawrence Estuary.

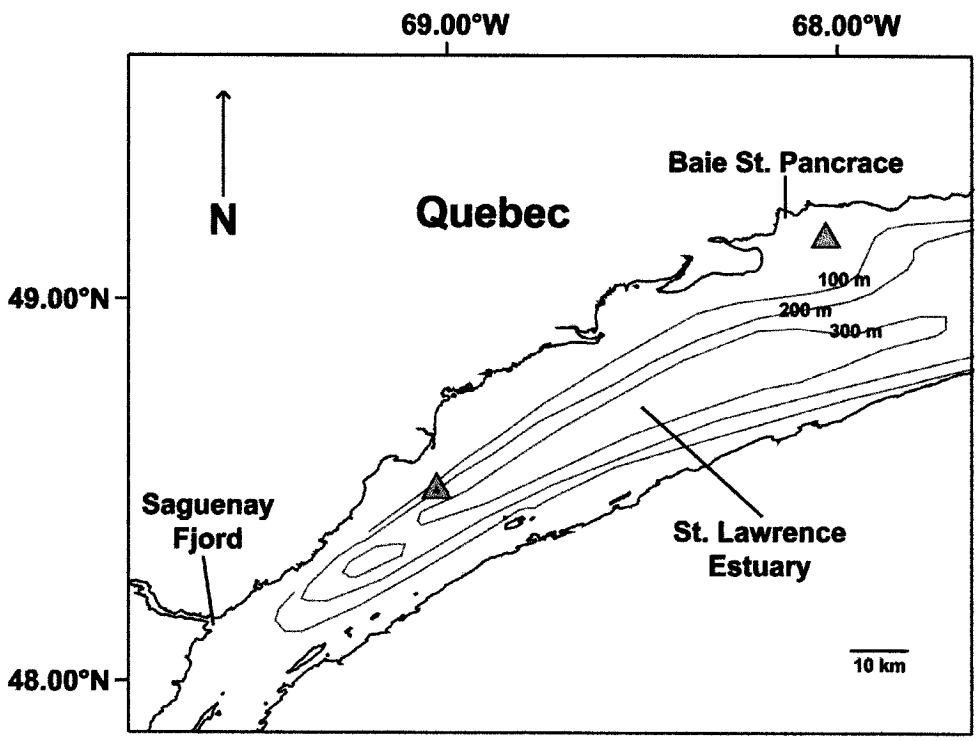
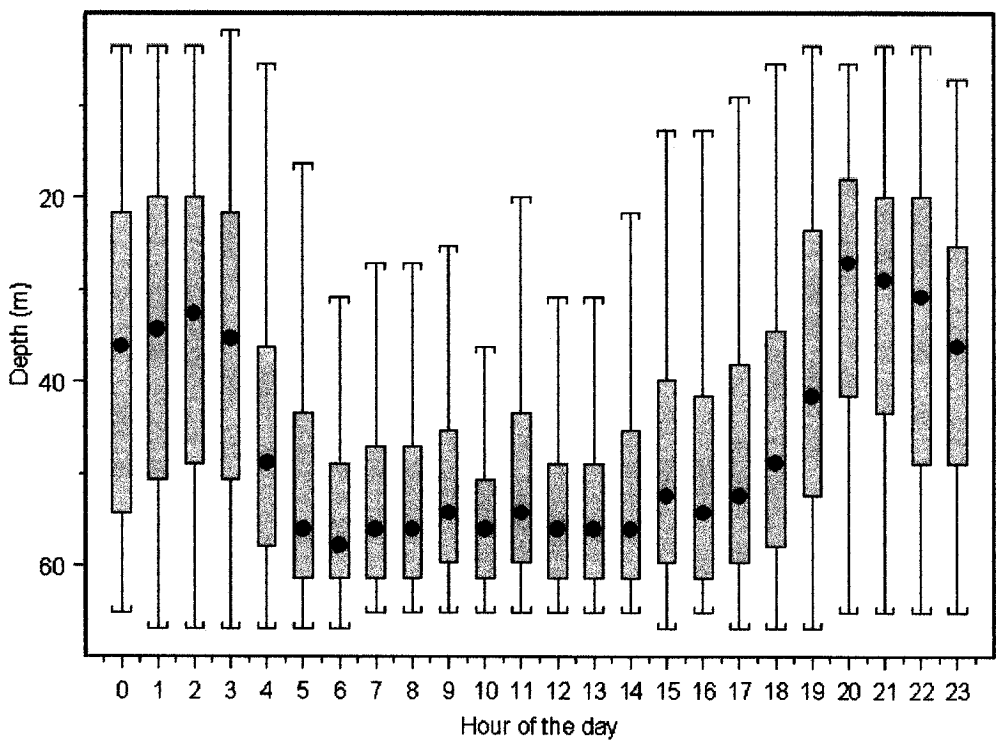


Figure 4.2. Record of a) depth (N = 20799) and b) ambient temperature (N = 20691) experienced by an acoustically tagged female Greenland shark while it resided in Baie St. Pancrace, Quebec, from 27 July to 9 September 2004. Data are binned hourly and standardized for sunrise at 04:59 and sunset at 20:17, the conditions on the first day of tracking, 28 July 2004 (circles = median, box = 1st to 3rd quartiles, whiskers = 1.5 * inter-quartile range; because of large numbers 57 outliers were removed from a., and 196 outliers were removed from b.).



b)

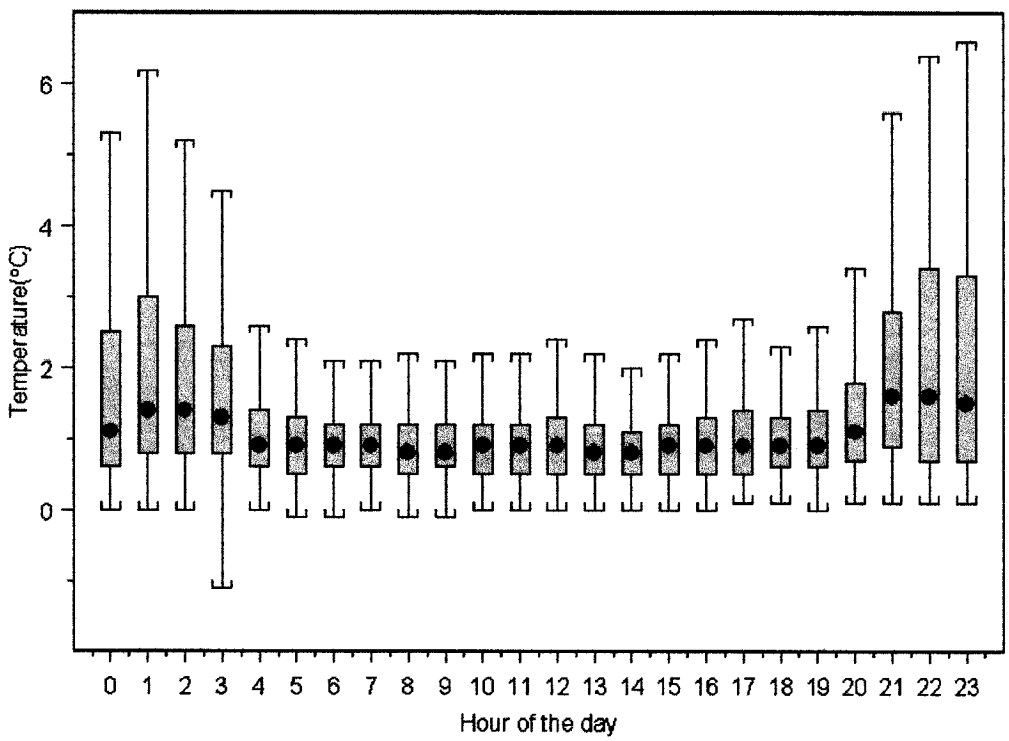
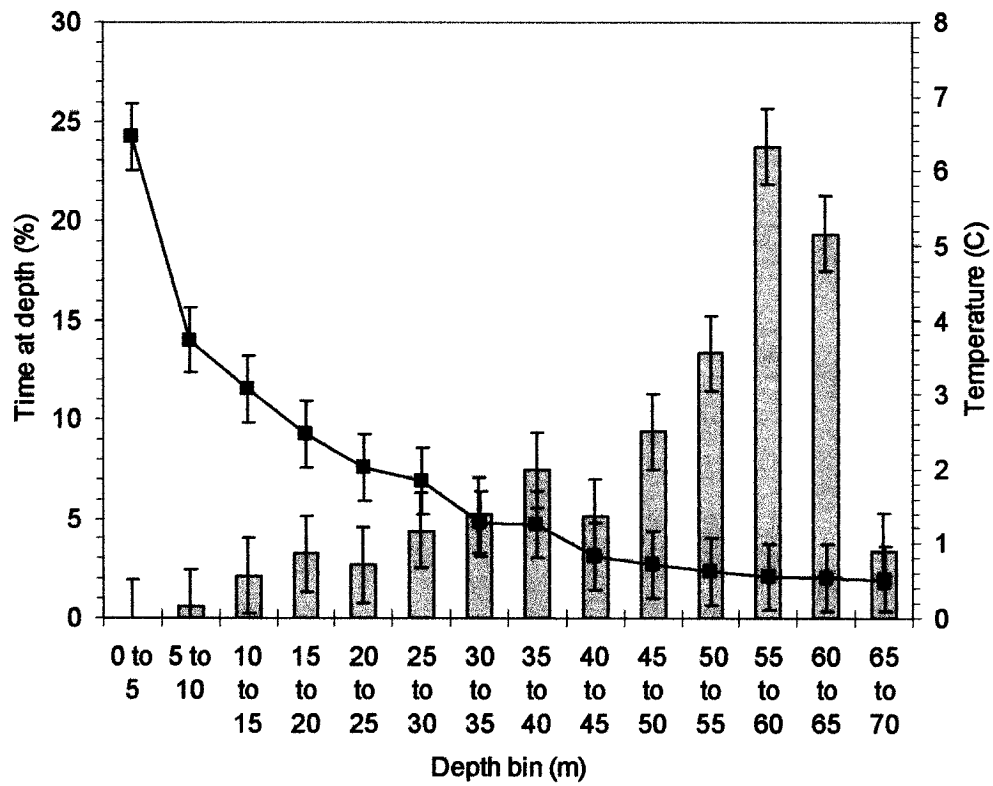

Temperature(°C)
6
4
2
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Hour of the day

Figure 4.3. Percentage time-at depth (bars) and water column temperature profile (line; square = mean; error bars ± one standard deviation) and for an acoustically tagged female Greenland shark while it resided in Baie St. Pancrace, Quebec, from a) 28 July to 1 September 2004 and b) 2 September to 8 September 2004.



b)

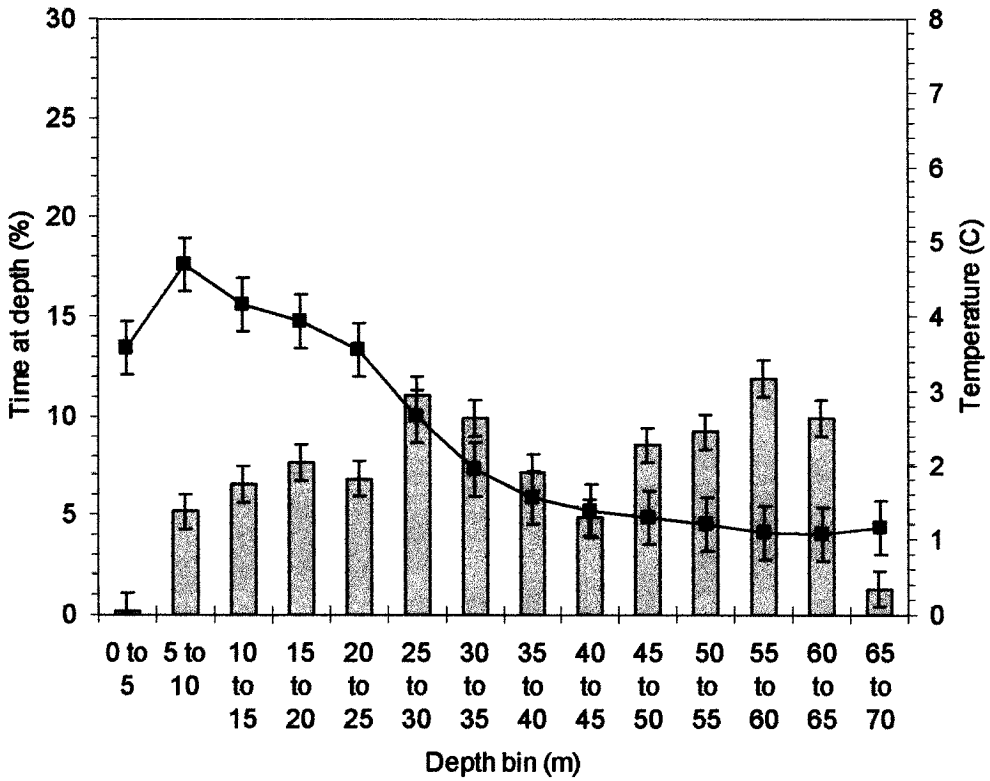

Time at depth (%)
Temperature (C)
Depth bin (m)
0 to 5
5 to 10
10 to 15
15 to 20
20 to 25
25 to 30
30 to 35
35 to 40
40 to 45
45 to 50
50 to 55
55 to 60
60 to 65
65 to 70

Figure 4.4. Thermal profile of the water column in Baie St. Pancrace, Quebec, means calculated from temperature data measured by an acoustic tag attached to a female Greenland shark in summer 2004 for the weeks of 28 July to 3 August (grey diamond); 4 to 10 August (grey square); 11 to 17 August (grey circle); 18 to 24 August (black diamond); 25 to 31 August (black square) and 1 to 8 September (black circle).

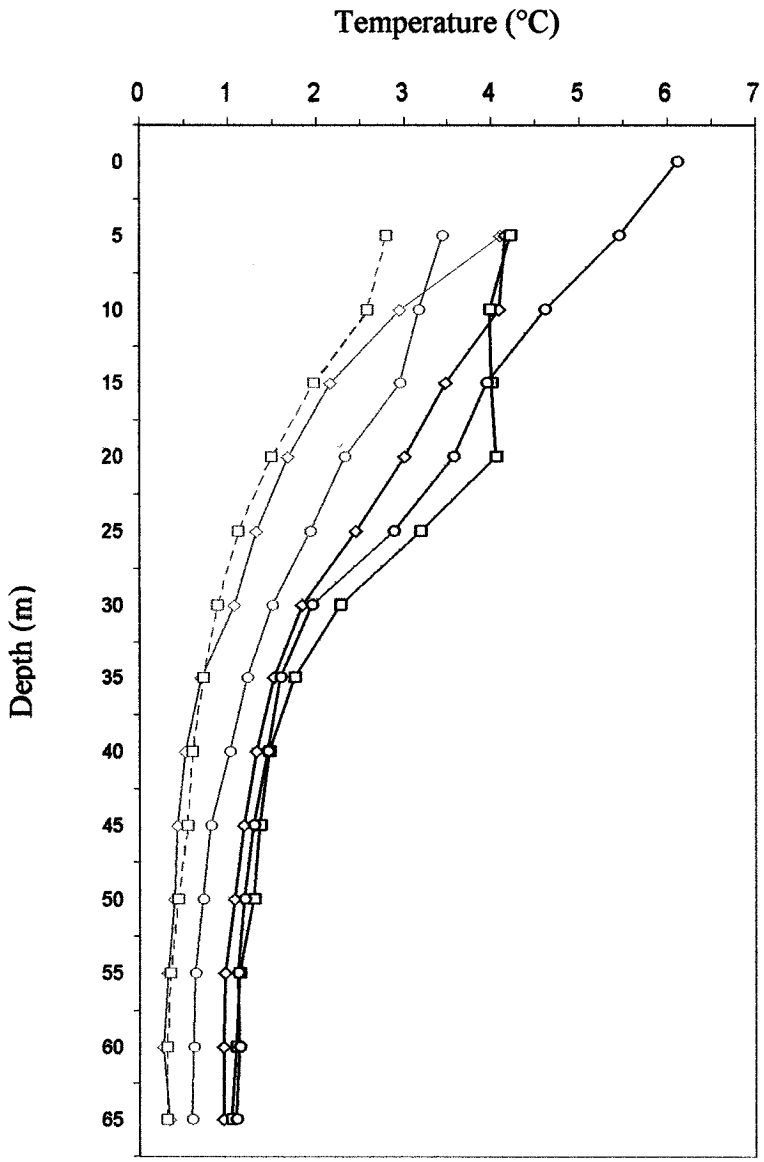


Figure 4.5. Depth recorded by an acoustically tagged Greenland shark over a 24 hour period on 2 August 2004.

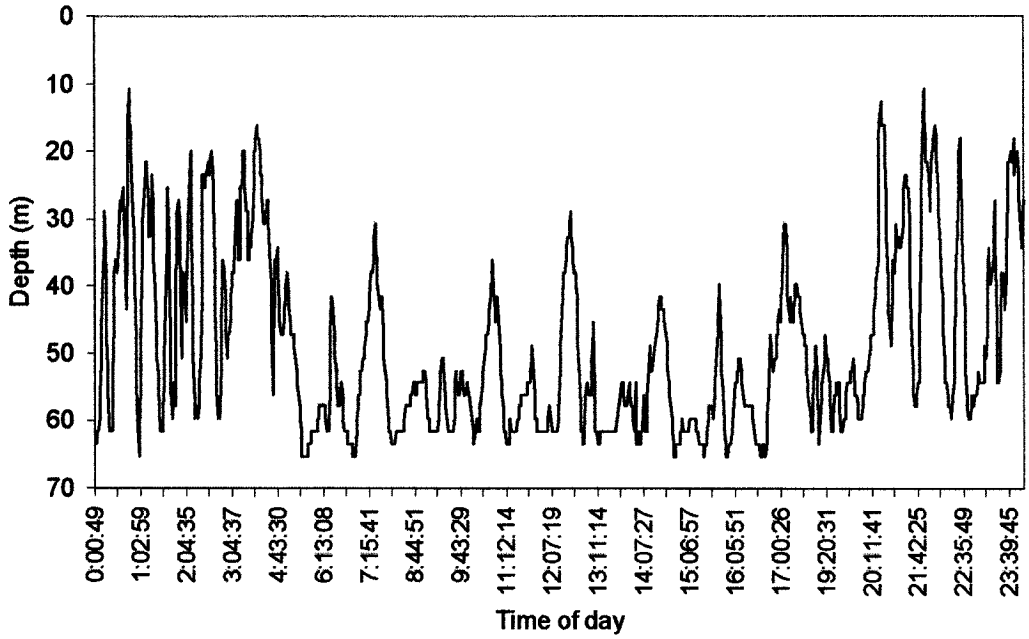
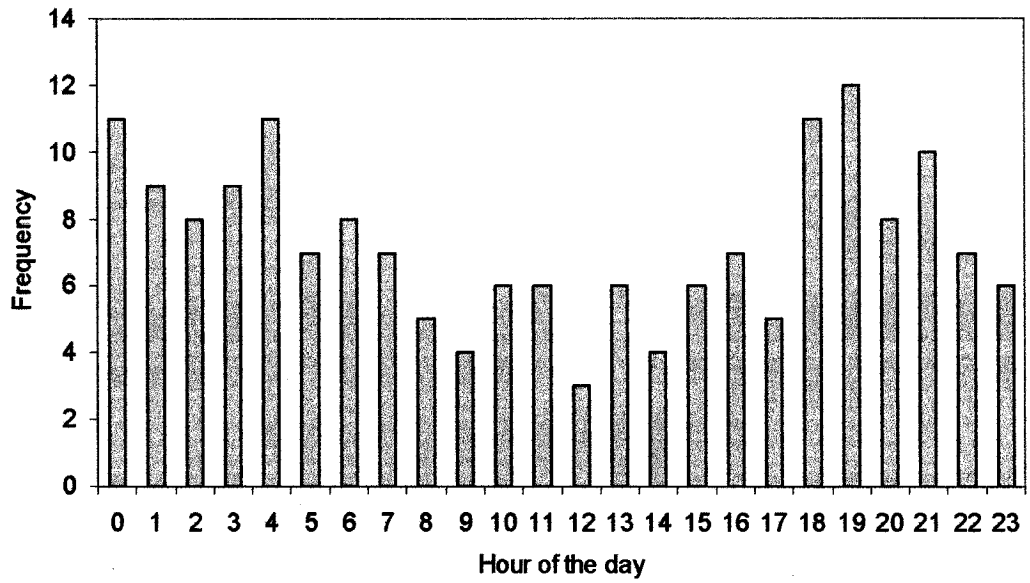


Figure 4.6. Frequency of 30 minute or longer departures from Baie St. Pancrace, Quebec, by an acoustically tagged Greenland shark between 28 July and 8 September 2004. Data are binned hourly and standardized for sunrise at 04:59 and sunset at 20:17, the conditions on the first day of tracking, 28 July 2004.

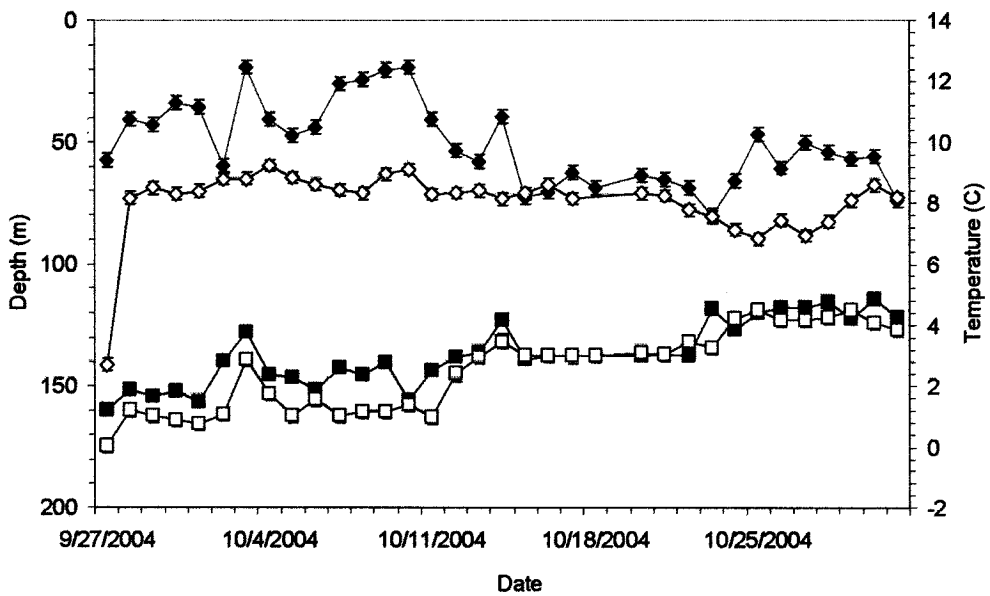


Shark 166 spent the daylight hours at significantly deeper depths than the nighttime hours (paired *t*-test, $p = < 0.01$) (Figure 4.7a). Also, ambient temperatures experienced by the shark were significantly cooler during the day than during the night (paired *t*-test, $p = 0.04$). The shark experienced cold bottom temperatures from 27 August 2004 until 11 October 2004 when the minimum ambient water temperatures began to increase (Figure 4.7a). There is a slight trend for the shark to move deeper as the water worms, possibly suggesting a preference for colder water (Figure 4.7a). Shark 166 spent the majority of its time between 10 and 50 m, and at 2 to 4 °C, however, it did spend more time higher in the water column at night than during the day (Figure 4.7b).

Overall, Greenland shark 581 exhibited no significant difference between daytime and nighttime mean depth (paired *t*-test, $p = 0.29$) or mean temperature (paired *t*-test, $p = 0.25$) (Figure 4.8a), although there is evidence for individual excursions into the water column at night. The maximum depth recorded by this tag was 352 m (Table 4.2). The minimum depth recorded by the tag was 132 m, which occurred on two occasions, and the modal depth was 326 m. The minimum depth recorded corresponds with the coldest temperatures that the tag recorded, 1 °C. This shark spent the majority of its time at depths deeper than 250 m and at temperatures between 4 and 6 °C, with very little difference in night and day, depth distribution (Figure 4.8b).

Temperature and salinity profiles for the water column in the St. Lawrence Estuary taken by CTD casts between 48°35' N, 68°29' W and 48°50' N, 68°45' W on 8 June 2004 by the Department of Fisheries and Oceans, Canada, are shown in Figure 5.9. Corroborating the depth and temperature data from tag 581, this profile indicates that the shark resided in a highly saline deep water layer, with temperatures between 4 and 6 °C.

Figure 4.7a. Daytime (empty symbols) and nighttime (filled symbols) depth (diamonds) and temperatures (squares) for PSAT tagged female Greenland shark 166 that resided in Baie St. Pancrace, Quebec, from 27 August to 1 November 2004 (means ± standard error). b. Daytime (white) and nighttime (grey), time at depth for PSAT tagged female Greenland shark 166 that resided in Baie St. Pancrace PQ from 27 August to 1 November 2004 (means ± standard error).



b)

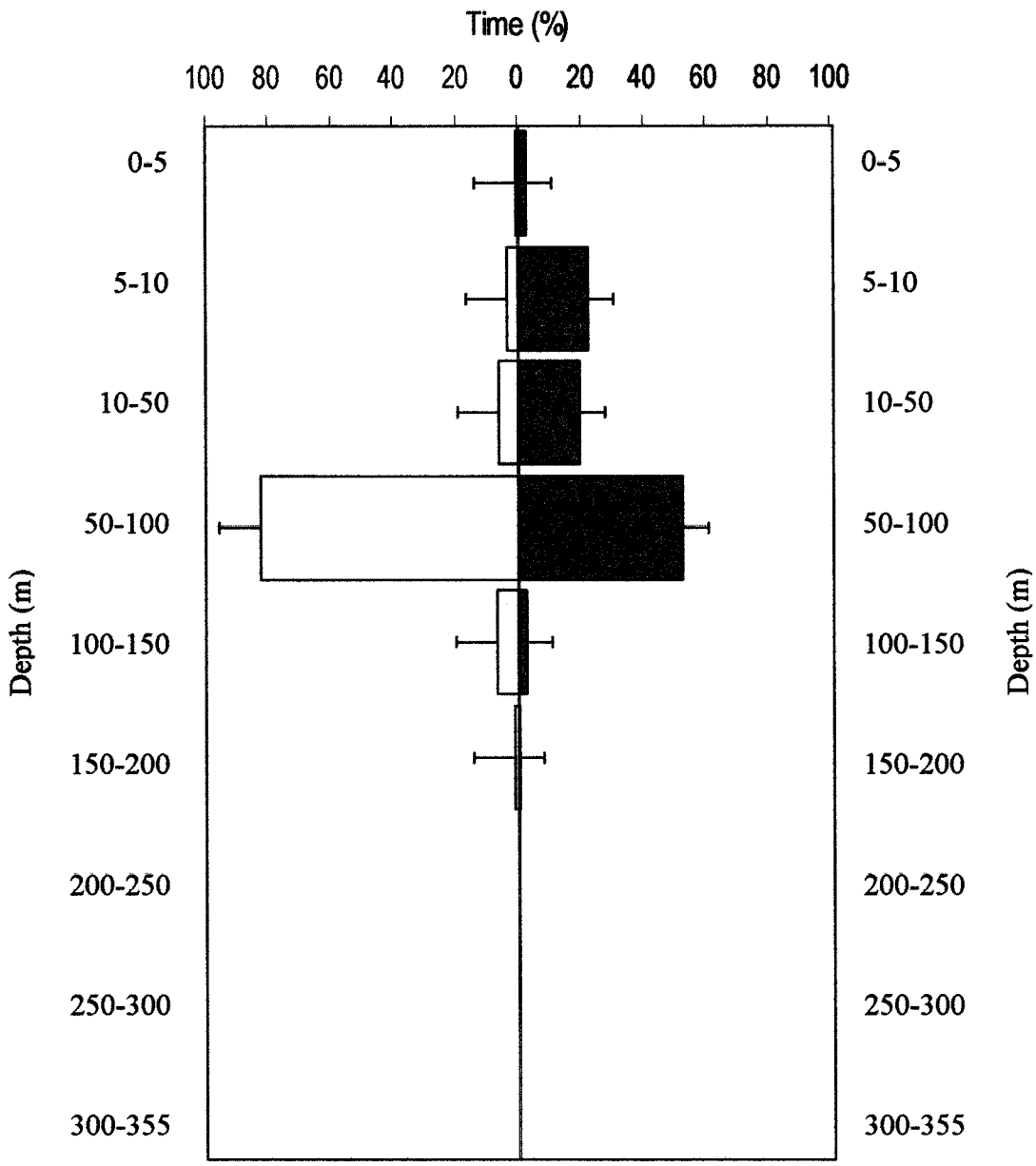
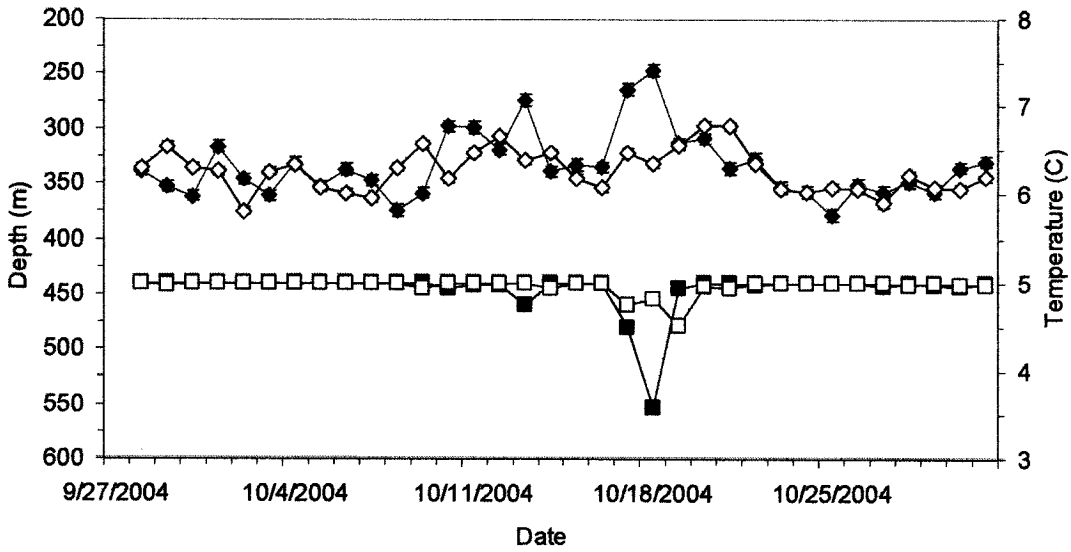

Time (%)
100 80 60 40 20 0 20 40 60 80 100
0-5
5-10
10-50
50-100
100-150
150-200
200-250
250-300
300-355
Depth (m)
Depth (m)

Table 4.2. Results of electronic tagging of three Greenland sharks in Baie St. Pancrace, Quebec, during summer 2004.

Tag #	Tag type	Estimated total length (cm)	Sex	Location of data collection	Min. depth (m)	Max. depth (m)	Modal depth (m)	Min. temp. (C)	Max. temp. (C)	Modal temp. (C)
32	V 16	235	F	Bay	1.8	67	61.5	-1.1	8.6	0.6
166	PSAT	270	F	Bay	0	72	30	0.8	7.4	3.0
581	PSAT	270	M	Channel	132	352	326	1.0	5.4	5.0

Figure 4.8a. Daytime (empty symbols) and nighttime (filled symbols) depth (diamonds) and temperatures (squares) for PSAT tagged male Greenland shark 581 that resided in the open channel of the St. Lawrence Estuary from 27 August to 1 November 2004 (means ± standard error). b. Daytime (white) and nighttime (grey) time-at-depth record for PSAT tagged male Greenland shark 581 that resided in the open channel of the St. Lawrence Estuary from 27 August to 1 November 2004 (means ± standard error).



b)

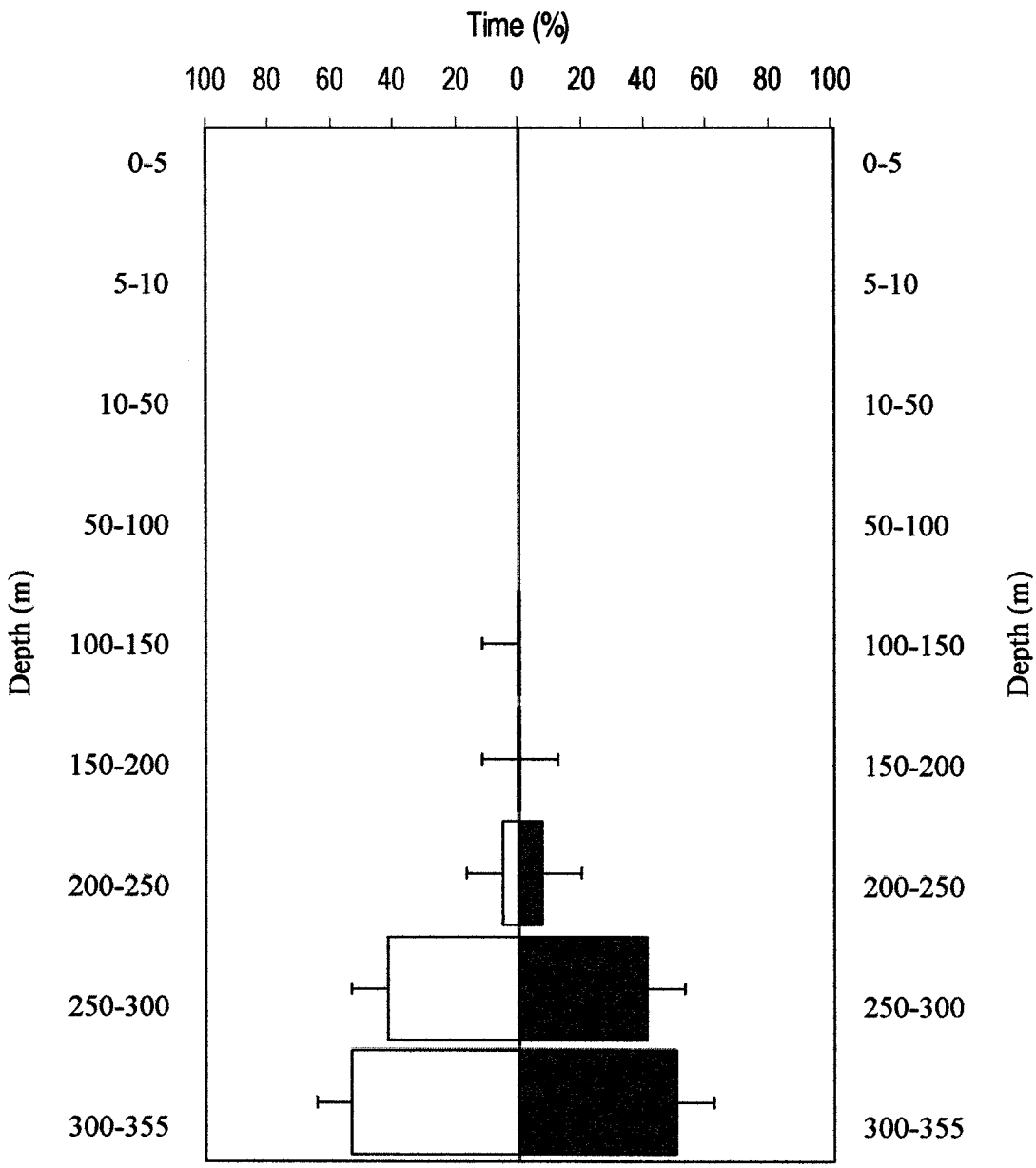
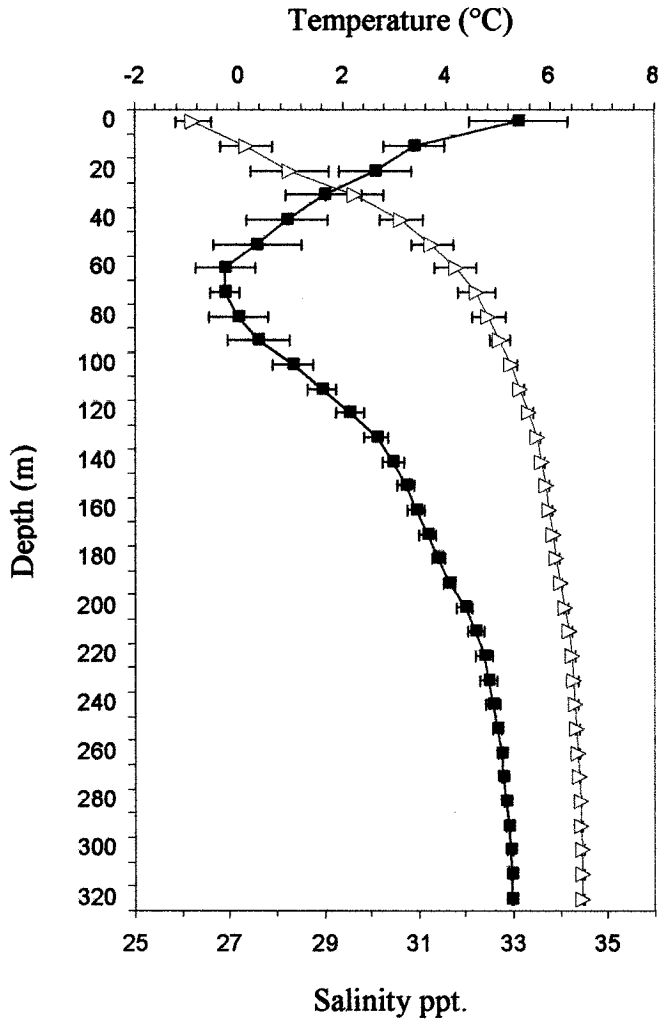

Time (%)
100 80 60 40 20 0 20 40 60 80 100
Depth (m)
0-5
5-10
10-50
50-100
100-150
150-200
200-250
250-300
300-355
Depth (m)
0-5
5-10
10-50
50-100
100-150
150-200
200-250
250-300
300-355

Figure 4.9. Water column profile of temperature (squares; mean ± SD) and salinity (triangles; mean ± SD) from the main channel of the St. Lawrence Estuary between 48°35' N, 68°29' W and 48°50' N, 68°45' W on 8 June 2004.



4.4 Discussion

This study provides 179 days of behaviour and environmental data on a sub-polar species of shark of which there is little known. While in Baie St. Pancrace, tagged female Greenland sharks displayed diel depth differences. The sharks occupied mostly demersal waters during the day, and moved throughout the water column at night. Similar diel patterns were observed in a megamouth shark (*Megachasma pelagious*; Nelson et al. 1997), bigeye thresher sharks (*Alopias superciliosus*; Weng and Block 2004, Ward and Myers in Press) and school sharks (*Galeorhinus galeus*; West and Stevens 2001). Diel patterns were not found in sixgill (*Hexanchus griseus*), blue (*Prionace glauca*), crocodile (*Psuedocarcharhinus kamoharai*), oceanic whitetip (*Carcharhinus longimanus*), shortfin mako (*Isurus oxyrinchus*) and silky sharks (*Carcharhinus falciformis*) (Ward and Myers in Press) or Greenland sharks tracked under land fast ice (Skomal and Benz 2004).

However, the tracks of the sharks under land fast ice were short (5-48h), and, although no significant depth preferences were reported, the observed shift from deep depths in the morning to shallower depths in the afternoon and evening (Skomal and Benz 2004) are consistent with our findings. No diel depth pattern was demonstrated by the male shark that moved into the main channel of the St. Lawrence Estuary. This is likely a result of the shark residing below the photic zone (depth > 300m). As Greenland sharks demonstrated diel depth differences in the shallow bay, but did not at greater depth in the main channel of the St. Lawrence Estuary, they may be demonstrating an aversion to light as has been proposed for sixgill sharks (Bigelow and Schroeder 1948; Compagno 1984).

The cold thermal tolerance displayed by the Greenland sharks in this study (< 1 °C) and under land fast ice (< -1 °C; Skomal and Benz 2004) is not a common trait in shark species, even inside of Squalidae. For example, other bottom dwelling squaloid sharks such as the spiny dogfish (*Squalus acanthias*; 6.62 to 9.19 °C; Shepherd et al. 2002) are not known to frequent the arctic temperatures occupied by Greenland sharks. There are two other known Arctic sharks beside the Greenland shark, they are the porbeagle shark (*Lamna nasus*) and the salmon shark (*Lamna ditropis*). Both of these are endothermic laminid sharks. The porbeagle shark is generally caught at temperatures between 5 and 10 °C (Campana and Joyce 2004) and the salmon shark frequents temperatures only as low as 2 °C (Weng et al. 2003). Therefore, the cold thermal tolerance of Greenland sharks likely allows them to forage in areas where there is no competition from other shark species.

On 176 occasions between 28 July and 8 September 2004, no signals were received from Greenland shark 32 for over 30 minutes. This likely represented instances when the shark left the bay and was out of receiver range. It is possible that there are locations in the bay where a signal to the receiver might be blocked. However, it is unlikely that if a structure did exist the shark would stay under or behind it for periods of time as long as 20 hours. It seems more likely that in these instances, the shark left the bay to hunt. The sharks peak departure time corresponds to sunrise and just before sunset. These are times that many large pelagic predators are most active and likely hunting prey (Nakano et al. 2003). Therefore, if the sharks leave the bay to feed, they likely reside in the bay for reasons other than the abundance of prey.

Of the three sharks that were tagged, one left the bay on 27 August 2004, one left the bay on 8 September 2004 and one was still in the bay on 1 November 2004. The shark that left the bay on 27 August had moved 114.9 km upstream to the south west, by the time the tag reported on 1 November 2004. Greenland sharks have been taken in winter in the ice fishery in the Saguenay Fjord. It is possible that the sharks present in Baie St. Pancrace are a component of this population. If so, this may have been the destination of the male shark that was moving up the St. Lawrence Estuary toward the Saguenay Fjord. More long-term tagging is needed to determine the relationship of the sharks found in these two areas.

The Greenland shark that moved into the main channel of the St. Lawrence Estuary resided in the middle of the main channel, as this is the only place where the water is in excess of 300 m deep. This shark did not move through the entire water column as did the sharks that were located in the bay. The waters of the St. Lawrence Estuary east of the Saguenay Fjord are composed of three layers in summer and two in winter. In summer there is a warm surface layer, an intermediate cold layer and a deep warm layer (Lauzier and Bailey 1957). In winter there is a sub-zero mixed layer overlaying the deep warm layer (Lauzier and Bailey 1957). The deep layer retains its characteristics through the seasons (Lauzier and Trites 1958). The shark that moved into the main channel remained mostly in the deep warm (4 – 6 °C) layer. This shark made vertical migrations, however, the two shallowest depths reached were both 132m. This may indicate that a characteristic of the water structure created a barrier to the upward migration of the shark. It is unlikely that any barrier would be temperature related. In both instances that the shark moved to 132 m, the lowest temperature that it experienced

was 1 °C. The sharks that resided in the bay regularly experienced temperatures < 1 °C, and Greenland sharks are known to inhabit waters with temperatures as low as -1.7 °C (Skomal and Benz 2004). The middle layer of the St. Lawrence flows downstream, as does the surface layer. However, the bottom layer flows into the St. Lawrence Estuary terminating at the Saguenay Fjord, where it is part of the production of the Gaspe Current (Lauzier and Trites 1958). Possibly the Greenland shark remained in the bottom water layer to conserve energy as it moved toward the Saguenay Fjord.

This is the first report of Greenland sharks residing in shallow near shore bays, in summer and autumn. Large numbers of sharks were observed in Baie St. Pancrace in summer 2004. For example, 11 different sharks were recorded on video on one shallow dive in low visibility. The sharks were all individually identified by different scarring patterns. No shark was recorded more than once. Therefore, the sharks in the bay appear to be seasonally plentiful (C. Harvey-Clark unpublished data). Also, the male to female ratio of sharks identified to sex was 0.36:1 (C. Harvey-Clark unpublished data), suggesting that there may be behavioural difference between sexes that are further supported by the limited evidence from tagging.

Although more research will be required to be certain of the significance of this unique behaviour and location, it is useful to lay out some of the possibilities to better design future studies. Is the bay a source of prey? Is it a haven from predators? Is it a temperature refugium? Is it a refuge from strong currents? Is it a breeding site or a nursery?

It is hard to imagine that such a limited area could provide prey for such a large number of predators, therefore, the departures from the bay are likely for hunting. There

is little information on what might prey on Greenland sharks other than humans (Scott and Scott 1988) and sea lamprey (Gallant et al. Submitted). Sperm whales have been observed in the St. Lawrence Estuary (Silvan Sirios personal communication) and are known to be predators of large deep sea animals, perhaps the site provides protection from these or some other form of predators.

Some animals (e.g. lobsters) seek elevated temperatures to accelerate egg development and control the time their young enter the ecosystem (Aiken and Waddy 1989). In this case the bay is colder than the adjacent bottom waters in the Estuary, so it seems unlikely. Alernatively, the McLaren Hypothesis proposes that vertically migrating plankton lower metabolic rates and conserve energy at depth in the day and elevate rates in warmer, near surface waters at night when they hunt (Mclaren 1963). A similar mechanism could be happening in the bay. There is some evidence that one of the tagged females actively sought lower temperature at depth as the temperature in the bay increased. There were, in fact, much lower temperatures at similar depths in the Estuary, but the sharks would have to elevate their metabolic rates to swim against the currents there or drift out to sea.

The large number of females and the apparently distinctive behaviour of the tagged male could be consistent with a lek site. There was also evidence of complex vertical behaviours that had no other identifiable function. Such behaviour is often associate with mating in other fish (Hutchings et al. 1999, Block et al. 2001). The possibility that the area functions as a nursery would require direct observations of juveniles that might be a target of later studies. More information is needed to address

any of these questions, but it is clear that the sort of detailed information additional tagging studies could provide would help to resolve them.

In this study, I demonstrate that when in the photic zone Greenland sharks showed diel differences in depth distribution. They occupied both very cold temperatures, and warmer temperatures than have been previously reported. Greenland sharks are seasonally plentiful in near shore, shallow bays, for long periods of time. Also, the sharks in Baie St. Pancrace may be linked to the over wintering population in the Saguenay Fjord. The two hypotheses about the occupation of the bay that seem most likely and testable are that it is a temperature refugium and perhaps associated with reproductive activity.

Chapter 5. Can fishes in early life imprint on the magnetic field of the Earth and sunlight to facilitate natal homing as adults?

5.1. Introduction

Homing is movement undertaken to reach a spatially restricted area that is known to an animal (Papi 1992). Homing has been demonstrated in several marine fish species including the bluehead wrasse (*Thalassoma bifasciatum*; Warner 1995), cardinal fish (*Apogon doerlerlini, Cheilodipterus artus, Cheilodipterus quinquilineatus*; Marnane 2000), Atlantic cod (*Gadus morhus*; Robichaud and Rose 2001, Robichaud and Rose 2002), greasy grouper (*Epinephelus tauina*; Kaunda-Arara and Rose 2004) and plaice (*Pleuronectes platessa*; Burrows et al. 2004). Some marine animals are known to undergo long-distance homing migrations in relatively featureless environments (Lohmann and Lohmann 1996, Block et al. in press). To do this, they must determine their position relative to their home and set a course for home (Kramer 1953). Therefore, animals must be able to compare the characteristics of environmental stimuli at their current location with characteristics at the home location (Walker et al.2003). In the simplest case the animal may use a bi-coordinate system (Quinn 1982) of two environmental stimuli to form a grid map (Quinn 1982, Phillips 1996, Benhamou 2003) to guide their homing movement.

Walker et al.(2003) proposed four conditions that must be met for an environmental stimulus to be used for large-scale movements. The stimulus must: 1) be able to be used to determine position within the environment used by the species; 2) vary

systematically such that locations on the Earth can be uniquely identified; 3) be stable over time or follow a similar annual cycle; and 4) be able to be used by the animal at sufficient resolution to meet the animals needs. I add a fifth condition that is relevant to fishes that may be transported by currents as egg-stage embryos from their natal spawning grounds: the fish must have knowledge of the value of the stimulus at its home location.

Although the mechanisms have not been proven, it has been proposed that amphibians (Phillips 1995), birds (Wiltschko and Wiltschko 2003, Cochran 2004), and crustaceans (Boles and Lohmann 2003) can determine geographical position from the Earth's magnetic field. Therefore, the animals have to be able to derive position from scalar values such as the total field intensity (Walker et al. 2002). For the compass portion of navigation they can use vector values, such as inclination (Walker at el 2002). Also, they may employ some directional correcting input such as sunlight (Cochran et al. 2004).

Knowledge of geographical position at a fish's natal spawning ground may occur by imprinting (Lorenz 1937). Salmonids imprint on environmental stimuli that occur at early life stages (Dittman and Quinn 1996). Also, imprinting has been proposed as a tool used for homing in marine turtles (Bowen et al. 1992) and aquatic vertebrates in general (Cury 1994).

Egg-stage embryonic imprinting is of particular interest when examining homing in fishes. Many fishes spawn eggs into the pelagic environment where they incubate for long periods of time. During this incubation period the eggs may be transported long distances by currents away from the spawning site before hatching. How do these

individuals know to return to their natal spawning ground and identify it when they get there? Perhaps egg-stage embryonic fishes imprint on characteristics of the Earth's magnetic field and polarized sunlight at their natal spawning ground to facilitate natal homing as adults.

In this essay I describe how peaks in the plasma concentration of a hormone previously correlated with imprinting events in fishes, may indicate that fishes experience an imprinting event while in the egg-stage. I discuss environmental stimuli, polarized sunlight and the magnetic field of the Earth that, if imprinted upon at the egg-stage, may provide a reference of the position of the natal spawning ground for the homing adult. Next, homing using two environmental stimuli as a bi-coordinate navigation system is briefly touched upon. The seasonal reference needed for the use of the bi-coordinate navigation system may be provided by endogenous factors such as spawning condition or melatonin production in the pineal gland. Finally, I summarize the main points of the essay, and offer a hypothesis to be tested.

5.2. Geographic position and compass orientation

Animals can derive their geographical positional presumably from characteristics of the Earth's magnetic field (Phillips 1995, Boles and Lohmann 2003, Wiltschko and Wiltschko 2003, Cochran et al. 2004). The mechanisms that are used to do this are not readily understood (Lohmann et al. 2004). By deriving their geographic position, animals may display true navigation, which requires a map and a compass component (Kramer 1953), the map being the positional component (Able 2001). True navigation was first

demonstrated in homing pigeons (Walcott and Schmidt-Koenig 1973). Since then it has been demonstrated by displacement experiments that deprive animals of orientation cues in alligators (Rodda 1984ab), western newts, *Taricha rivularis* (Phillips et al. 1995), spiny lobsters, *Panulirus argus* (Boles and Lohmann 2003) and green sea turtles (*Chelonia mydas,* Lohmann et al. 2004). Sharks have been shown to sence changes in the geomagnetic field (Meyer et al. in press). Also, in birds, the magnetic orientation of thrushes, *Catharus*, was experimentally shifted while they were stationary in their cages. This indicated that they do not have to be moving to sense position by the Earth's magnetic field (Cochran et al.2004). Further, it was demonstrated in this experiment that the thrushes recalibrate their magnetic compass from twilight cues from polarized sunlight. Therefore, they demonstrated true navigation through the use of cues from sunlight at sunset, and the magnetic field of the Earth. If an animal imprinted on these characteristics while at their natal spawning ground, they could provide the cues needed to home to this location as adults.

5.3. Egg-stage imprinting indicated by peaks in thyroxine concentration

Do fish imprint as egg-stage embryos? Studies that investigated embryonic imprinting in fishes strongly indicated that it did occur (Arvedlund et al. 1999, 2000). This was demonstrated experimentally as anemone fishes (*Amphiprion melanopus*) imprinted on the olfactory cue of host anemones while in the embryo stage (Arvedlund et al. 1999). Also, in the wild, embryonic imprinting dictated their spawning site preferences (Arvedlund et al. 2000). This is reasonable, as fish eggs are permeable to

most molecules so odor may pass through the egg membrane and be perceived by the embryo (Courtenay et al. 2001).

In salmonids there is a link between imprinting and plasma levels of the hormone thyroxine (Morin et al. 1989, 1994; Dittman and Quinn 1996). Salmonids imprint during developmentally regulated periods at which times peaks in thyroxine occur (Dittman and Quinn 1996). However, it has not been proven that thyroxine has a causal relationship with imprinting (Dittman and Quinn 1996).

Is thyroxine present in the egg-stage embryo? At the first stages of embryonic development the thyroid gland has not yet differentiated (Power et al. 2001). However, maternally produced (Power et al. 2001) thyroxine levels in egg-stage embryos were high in several salmonids (Leatherland et al. 1989, Kobuke et al. 1987, Tagawa and Hirano 1987, 1989) and other diadramous, marine and freshwater fishes (Table 5.1). In each case thyroxine levels were high immediately after fertilization then decreased and remained low until the differentiation of the thyroid gland and production of thyroxine by the embryo. Peak levels of maternally deposited thyroxine could signal embryonic imprinting on environmental stimuli at the natal spawning ground.

Table 5.1. Studies that reported levels of maternal thyroxine present in fertilized fish eggs.

Species	Study
Coho salmon (*Onchorynchus kisutch)*	Kobuke et al. 1987
Chum salmon (*Onchorynchus keta)*	Tagawa and Hirano 1987
	Tagawa and Hirano 1989
Sockeye salmon (*Oncorhynchus nerka)*	Leatherland et al. 1989
Pink salmon (*Oncorhynchus gorbuscha)*	Leatherland et al. 1989
Chinook salmon (*Oncorhynchus gorbuscha)*	Leatherland et al. 1989
Striped bass (*Morone saxatilis)*	Brown et al. 1987
Rabbitfish (*Siganus guttatus)*	Ayson and Lam 1993
Conger eel (*Conger myriaster)*	Yamano et al. 1991
Tilapia (*Oreochromis mossambicus)*	Weber et al. 1992
	Reddy and Lam 1992

5.4 Environmental stimuli theoretically used for navigation

Polarized sunlight and fish navigation

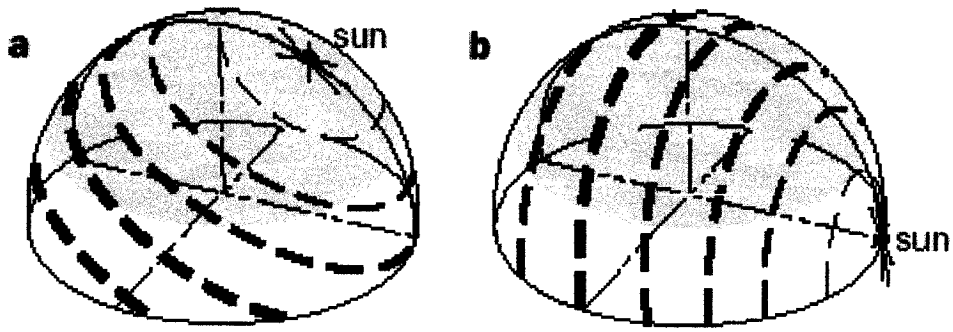
The polarization of sunlight in the water column provides an external stimulus that could be used for fish navigation (Horvath and Varju 1995) as it demonstrates an object's latitudinal location (Cronin and Shashar 2001). Migratory songbirds have been shown to orient to compass information from the sun and its polarized light (Kramer 1953, Helbig 1990, Able and Able 1993). Also, migratory *Catharus* thrushes have been shown to recalibrate their magnetic compass daily using the twilight cues of the suns azimuth and polarized light (Cochran et al. 2003).

Physical properties

How is polarized sunlight used as a navigational tool? The e-vector of scattered rays of light exhibits a predominant direction perpendicular to their plane of deflection (Brines and Gould 1982, Cronin and Sashar 2001). E-vector angles are mixed during the day, however, they are predominantly of one direction at sunrise and sunset (Dacke et al. 1999; Figure 5.1). This results in a symmetrical e-vector pattern that is fixed in respect to the solar and anti-solar meridians (Freake 1999).

Is polarized sunlight in the water column visible in cloudy conditions? Polarization of sunlight in water is less than in air during clear skies and greater than in air during cloudy conditions, so it is relatively insensitive to sky state except under heavily overcast conditions (Cronin and Shashar 2001).

Figure 5.1. (From Dacke et al. 1999) Sky polarization pattern showing E-vector position and strength for solar positions high above the horizon (a) and at the horizon (b).



Physiological

Can fish see polarized sunlight? The light wavelength of maximum sensitivity for salmon is 451 nm (Soni et al.1998) and is within the range of wavelengths of polarized sunlight in water (360 to 550 nm; Cronin and Shashar 2001). Sunlight is 40% polarized in the water column during the day and 67% polarized at crepuscular periods (Novales Flamarique and Hawryshyn 1997). Rainbow trout (*Oncorhynchus mykiss*) detected sunlight that was between 63 and 72% polarized, so they could use polarized light vision only at crepuscular periods (Novales Flamarique and Hawryshyn 1997). Further, it has been demonstrated experimentally that sockeye salmon (Groot 1965, Dill 1971), steelhead trout (*Oncorhynchus mykiss*), brook char (*Salmo trutta*; Parkyn et al. 2003) and other fishes (Forward et al. 1972, Waterman and Forward 1972, Forward and Waterman 1973) can perform compass orientation relative to plane-polarized light. Also, all three of the salmonids can discriminate between different e-vector orientations of polarized light (Coughlin and Hawryshyn 1995, Parkyn and Hawryshyn 2000). Interestingly, as was demonstrated in birds (Cochran et al. 2004), it appears that sunrise and sunset may be crucial times for fish to orient by sunlight.

At what stage of development are fish able to see polarized sunlight? During vertebrate embryogenesis the two layers of the optic cup evaginate, the inner layer becomes the neural retina composed of rods and cones (photoreceptors) and the outer layer becomes the retinal pigment epithelium (Kunz and Callaghan 1989). The embryonic fissures contain discs perpendicular to the long axis of the outer segment, and when light passes transversely across the outer segment the fissures may become polarization sensitive (Kunz and Callaghan 1989). Embryonic fissures were present in 8-day-old

Mozambique tilapia (*Tilapia mossambica*) and one-month-old brown trout (*Salmo trutta*) embryos. The time that the fissures actually developed was not known.

In many species the pineal gland forms earlier during development than the retina of the eye (Forsell et al.1998). The pineal glad is crucial in the detection of the light dark cycle (Cahill 1996). Whether fish in the embryo stage can determine the polarization of sunlight through the use of the pineal gland is not known.

Behavioural

Do fish employ behavioural adaptations to allow them to use polarized sunlight as a navigation tool at crepuscular periods? Most fishes live in the photic zone. However, there are fish that are migratory and live at depth. Through electronic tagging several deep water migratory species have demonstrated vertical migration into and out of the photic zone in response to dawn and dusk changes in light. Several large, deep water, migratory fish that have been electronically tagged, swordfish (*Xiphias gladius*; Carey and Robinson 1981), megamouth sharks (*Megachasma pelagios*; Nelson et al. 1997), and bigeye thresher sharks (*Alopias superciliosus*; Nakano et al. 2003, Weng and Block 2004) have been demonstrated to be present in the photic zone at sunrise and sunset. These species all spend the daytime at depth, then move into shallower water at sunset, and move deeper at sunrise. It has been proposed that this vertical migration plays a part in feeding on the vertically migrating sound scattering layer (Nakano et al. 2003), or is to do with adjusting depth to light in the water column (Nakano et al. 2003). It also affords the fish the opportunity to use polarized sunlight in the water column for orientation (Klimely et al. 2002), or correction of a magnetic compass based of the Earth's magnetic field (Cochran et al. 2004).

5.5 Magnetic field of the Earth

Loggerhead turtles are known to orient to the magnetic field of the earth, both in the longitudinal and latitudinal plane (Lohmann and Lohmann 1996). In the longitudinal plane, a turtle senses the change in polarity as it transects the north-south isolines of the magnetic field, also it can detect the changes in the inclination of the magnetic field as it moves in the north-south direction (Lohmann and Lohmann 1994, Lohmann and Lohmann 1996). It has been demonstrated that sandbar sharks (*Carcharhinus plumbeus*) and scalloped hammerhead sharks (*Sphyrna lewini*) detect changes in the geomagnetic field (Meyer et al. in press). Interestingly, at least in some instances, animals may not have to be moving to sense the values of the polarity and inclination of the magnetic field of the Earth (Cochran et al. 2004).

Physical atributes

The Magnetic field of the Earth is a three dimensional vector in space, derived from sources in the Earth's core and crust (Walker et al. 2002) and it's two sets of isolines form a grid map (Figure 5.2) that animals could use for global positioning (Lohmann and Lohmann 1996) . The main field is produced by convection and eddy currents in the Earth's molten core (Figure 5.3). Local fields result from magnetized rocks in the Earth's crust. The dipole in the Earth's core dominates the magnetic field and causes the vector to vary systematically between the magnetic equator and the magnetic poles (Figure 5.3). Its intensity varies from 25 to 65 micro-Tesla (Walker et al. 2002).

Figure 5.2 (From Lohmann and Lohmann 1996) Isoclines (broken lines) and isodynamics (solid lines) in the North Atlantic, that form a bi-cordinate map that animals may use to determine geographic position.

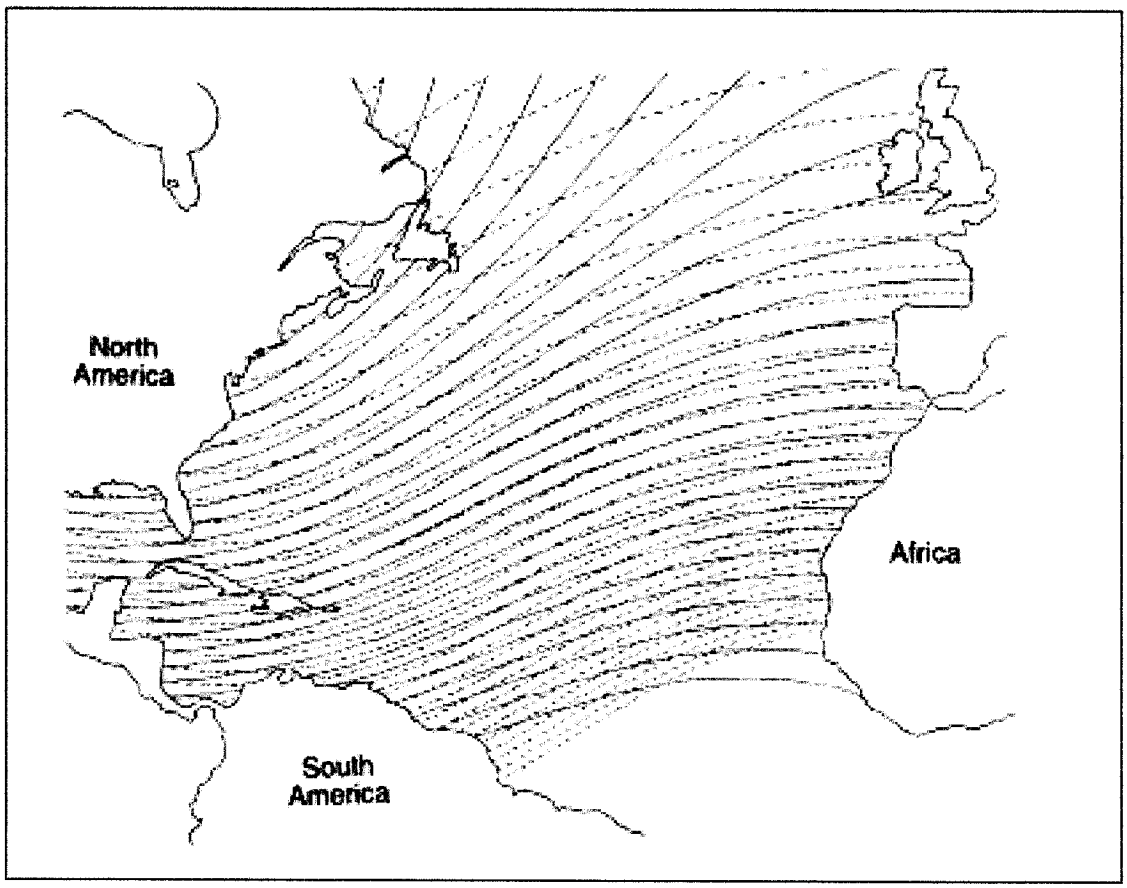
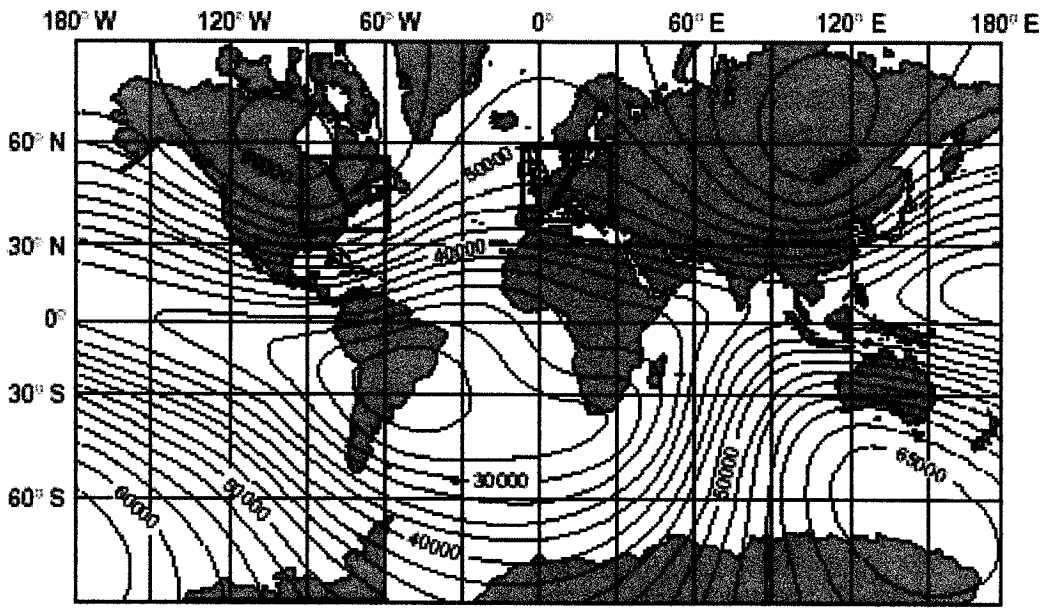


Figure 5.3 (From Walker et al. 2002) The intensity of the main magnetic field of the Earth. Contours show the change in strength from the magnetic equator to the magnetic poles.



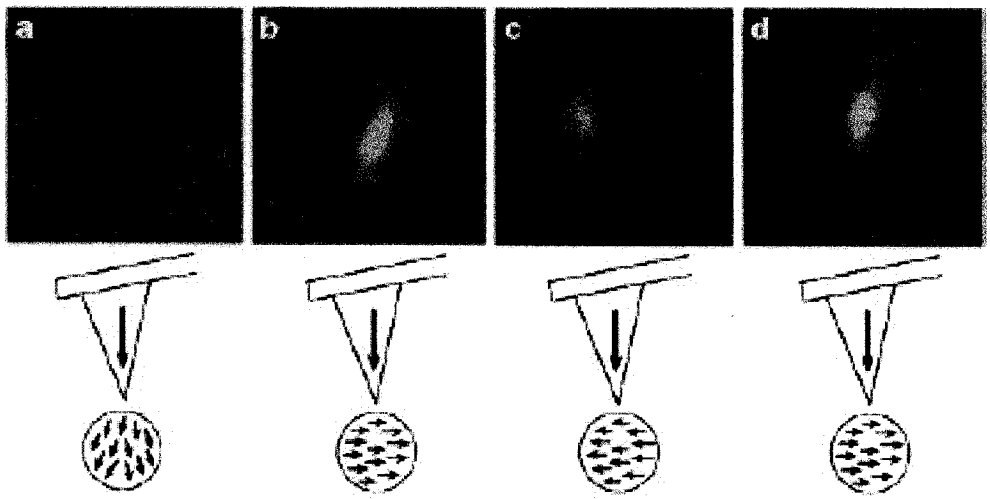
Physiological

Can fish detect the magnetic field of the Earth? Several species of fish including the American eel (*Anquilla rostrata*; Rommel and McCleave 1973), sandbar and hammerhead sharks (Meyer et al. in press) and Pacific salmon (Quinn 1980) have been proposed to detect the magnetic field of the Earth. For example, salmonids orient to the magnetic field of the Earth (Quinn 1980; Quinn and Brannon 1982) at least as early as the fry stage (Quinn 1980). To do this salmon likely utilize magnetite crystals (Walker at el. 1988, Ogura et al. 1992, Diebel et al. 2000) that detect magnetic intensity (Diebel et al. 2000; Figure 5.4) and are probably a family wide trait (Friedland et al. 2001). The crystals are produced throughout the fish's life with sufficient amounts for detection of changes in the Earth's magnetic field being present at least as early as the fry stage (Walker et al. 1988).

5.6 Homing using a bi-coordinate navigational system

The change in potential of the Earth's magnetic field has been demonstrated to be detected in the east-west plane by fishes (Moyle and Cech 1996) and in both the east-west and north-south planes by songbirds (Cochran et al. 2004). Also, the polarity of sunlight in the water column is used mostly in the north-south plane. When using a combination of these stimuli as a bi-coordinate system, as has been proposed for Pacific salmon (Quinn 1982), navigation error would be at its least when the stimuli are orthogonal (Phillips 1996, Benhamou 2003). If the stimuli were not orthogonal it is much more complex for an animal to calculate the correct vectors to guide it home (see Benhamou 2003).

Figure 5.4. (From Diebel et al. 2000) The response of a single magnetite crystal in a rainbow trout, to the presence of an applied magnetic field.



5.7 The pineal gland and the release of melatonin in the early egg-stage

The pineal gland is part of a system that is responsible for correct timing of daily and seasonal physiological rhythms (Ekstrom and Meissl 1997) that differentiates during the embryonic period (Cahill 1996). It is located dorsal to the forebrain beneath the roof of the skull and is attached to the diencephalons (Forsell et al. 2001). It contains photoreceptor cells (Roberts et al. 2003) and detects light-dark information through the bones of the fish's skull. This stimulus is transduced into a rhythmic endocrine signal in the form of melatonin. Melatonin is secreted into the blood and or brain fluid and reaches target tissues including other parts of the brain (Roberts et al. 2003). The pineal photoreceptors maintain the same amplitude for the duration of illumination, therefore they are not affected by the intensity of light such as might be caused by cloudy conditions (Kusmic et al. 1992).

The pineal gland has the capacity to perceive photic information while fish are in the embryo stage (Forsell et al. 1997, Roberts et al. 2003; Table 5.2). In Atlantic halibut (*Hippoglossus hippoglossus*) the first imunoreactive transduction molecules are opsins that are expressed at 70% of the embryonic period, approximately 11 days post fertilization (Forsell et al. 1997). At this stage the pineal organ has neural connections to the brain, suggesting signaling pathways between the two structures (Forsell et al. 2001). Opsins are present in the pineal gland in Atlantic herring (*Clupea harengus*) by 30% of the embryonic period and in Atlantic cod by 70% (Forsell et al. 2001). Melatonin is produced by the pineal gland at 5 days post fertilization in the mummichog (*Fundulus heteroclitus*; Roberts et al. 2003). Other fishes that have been demonstrated to have functioning pineal glands at the embryo stage are zebrafish (*Danio rerio*; Cahill 1996)

and Atlantic salmon (Ostholm, et al.1987). Also, the time to hatching of halibut (Forsell et al.1997) and haddock (*Melanogrammus aeglefinus*; Downing and Litvak 2002) embryos was affected by changing diel light cycles indicating a mechanism for the embryo to track cycles of light and dark.

Table 5.2. Embryonic functioning of the pineal gland or retina.

Species	Study	Percent of the embryonic period at which retinal or pineal photoreception occurs (%).
Mummichog (*Fundulus heteroclitus*)	Roberts et al.2003	36
Zebrafish (*Danio rerio*)	Cahill 1996	66
Rainbow trout (*Oncorhychus mykiss*)	Yamada et al. 2002	66
Atlantic halibut (*Hippoglossus hippoglossus*)	Forsell et al. 1998	65
Atlantic herring (*Clupea harengus*)	Forsell et al. 1998	30
Atlantic cod (*Gadus morhua*)	Forsell et al. 1998	70
Atlantic salmon (*Salmo salar*)	Ostholm et al. 1987	80

5.8 Summary and conclusions

In this Chapter I propose that fish may imprint on environmental stimuli at early life stages, to facilitate natal homing as adults. Peaks in plasma levels of the hormone thyroxine may indicate egg-stage imprinting events. Early life imprinting on the characteristics of polarized sunlight and/or the Earth's magnetic field at the natal spawning ground would provide a reference for natal homing by the returning adult. The seasonal reference for the migration may be provided by the pineal gland. At the egg-stage the embryonic pineal gland is producing melatonin during the dark part of the daily light cycle. Through the amount of melatonin produced, a seasonal reference for the homing migration is provided. Therefore, I hypothesis that through imprinting on a combination of these three spatial and one temporal environmental stimuli a fish may home by true navigation, to a location that it was transported from in early life.

Is this a testable hypothesis? Studies indicate that marine fishes may share feeding grounds, however, they generally sort to breeding grounds (Robichaud and Rose 2001, Block et al. in press). This has been demonstrated on cod populations in Placentia Bay Newfoundland (Robichaud and Rose 2001) and on Atlantic bluefin tuna tagged in the Northwestern Atlantic Ocean (Block et al. in press). For example, Atlantic bluefin tuna, tagged on the feeding grounds off North Carolina have frequented every major known feeding ground in the Atlantic Ocean, however, no tagged tuna visited more than one of the two major known spawning areas (Block et al, in press).

Studies have tested hypothesis of homing in marine fishes through displacement experiments conducted in the wild (Warner 1995, Marnane 2000, Robichaud and Rose 2001, Robichaud and Rose 2002, Kaunda-Arara and Rose 2004, Burrows et al. 2004).

Therefore, it has been difficult for researchers to control for the stimuli that fishes use to home. In studying the homing of Atlantic cod it was proposed that there was no support for contra-natant spawning migrations, or tracked water-borne chemical-olfactory signals, and that they did not stay together in a group (Robichaud and Rose 2002). In the study it was suggested that cod moved toward an omnidirectional "attractor" that may dissipate with distance. It has also been demonstrated that juvenile plaice home by showing site fidelity to location of capture, although the homing mechanism used in unknown (Burrows et al. 2004). Juvenile plaice offer an attractive species with which to test the hypothesis that fishes use the magnetic field of the Earth and/or sunlight clues for true navigation.

I propose a two step experimental design to test if juvenile plaice use the magnetic field of the Earth, and/or sunlight clues in the water column to home to their area of capture. 1) In step 1 of this experiment we will test if juvenile plaice navigate by the magnetic field of the Earth (based on experiments of Lohmann and Lohmann 1994). 2) If step 1 demonstrates that juvenile plaice do navigate by the magnetic field of the Earth we will then test if the direction of sunlight has an effect on their perception of the magnetic field of the Earth (based on experiments of Cochran et al. 2004).

Step 1.

Juvenile plaice could be captured on Tralee Beach, Scotland, by beach trawl as in Burrows et al. (2004). The fish would then be transported to a shore based facility and placed in tanks in a circular water filled tank (as described by Lohmann and Lohmann 1994) with a sand filled bottom, in a light tight room. The plaice would be dorsally tethered using a nylon-lycra filament that does not impede swimming. This would be

attached on the other end to a 360 ° rheostat positioned in the center of the circular tank. The arm must be free swinging to track the direction of the juvenile plaice. This is done through the differential resistance of a circuit through the arm that allows computation of the swimming direction of the fish (as in Lohmann and Lohmann 1994). A Rubens cube coil would be used to control the direction of the magnetic field around the circular tank. When connected the coil would generate a magnetic field twice the strength of the Earth's with a reversed magnetic north (Lohmann and Lohmann 1994). Therefore when the coil is on, the swimming direction of the tethered plaice should reverse if they are orienting by the magnetic field.

Step 2

If the plaice were found to be using the magnetic field of the Earth for navigation, we need to test to see if sunlight plays a role in this navigation. This part of the experiment will be based on experiments by Cochran et al. (2004). The plaice will be split into two groups. The experiments will be moved to outside tanks so that sunlight may be present. Again the tanks will be surrounds by a Rubens cube coil so that the magnetic field may be manipulated. Group A. This group will represent the control, the coils will not be used allowing the fish to orient to the magnetic field of the Earth, through a full daily cycle including sunrise and sunset. Group B. The coil will be turned on, adjusting the magnetic field by 180 degrees through a full daily cycle including sunrise and sunset.

Each plaice will then have a Vemco V8 acoustic transmitter attached to their dorsal side to allow tracking of the movements post release. The fish will then be taken to areas along the beach and released. Control fish should home to their site of capture. Fish

that use sunrise cues to move to their site of capture should initially move away from their site of capture, until a sunrise corrects their magnetic compass, then they may move toward their site of capture. Also, fish that use sunset cues to correct their magnetic field, should move away from their site of capture until a sunset at which time they should begin to move toward their site of capture.

These experiments, if successful should indicate if: 1) Plaice use the magnetic filed of the Earth for homing, and 2) Whether sunrise and/or sunset play a role in their navigation. It would also indicate that plaice in their first year have "imprinted" on regional characteristics of the Earth's magnetic field to use to home, and to recognize a specific location known to the fish.

Chapter 6. Conclusions

The objective of this thesis was to increase the knowledge of how large marine predators use their environment by identifying their movement patterns and the physical characteristics that they favor in the water column. I have achieved this objective by identifying the migration patterns, seasonal distribution, and spawning site preference of Atlantic bluefin tuna tagged in waters off New England USA, and northwestern Ireland. This information is critical to the management and conservation of Atlantic bluefin tuna and, in the case of New England, clarifies results of a previous study.

I describe movement patterns and environmental preferences for Greenland sharks in the St. Lawrence Estuary. This is the longest monitoring study executed on Greenland sharks to date. It is the first report of Greenland sharks demonstrating significant diel differences in depth and temperature preferences, when in the photic zone. Also, it is the first report of Greenland sharks from this location, and that they are seasonally plentiful in a small near-shore bay. This inspires questions for future research such as why are the sharks residing in such a small bay that is unlikely to provide the amount of food that a large group of sharks would require? Possibly the bay is a refuge from predators, a temperature refugia, or a spawning or puping site.

Finally, I propose a hypothesis of early life imprinting that may allow migratory marine fishes to home to their natal spawning grounds. Through early life imprinting on external stimuli such as the geomagnetic field of the Earth, and polarized sunlight, marine fishes may be able to home to their natal spawning ground. This chapter is theoretical, and based on literature that has been produced to investigate animal migration and navigation in relatively featureless environments.

6.1 Summary of research chapters

My work on Atlantic bluefin tuna was part of an on-going project named Tag-A-Giant (TAG) led by Dr. Barbara Block of Stanford University, California, USA. Therefore, the tagging studies that I executed in waters off New England and northwestern Ireland, are part of an evolution of knowledge of bluefin tuna behaviour. In this conclusion, I will explain the progress of knowledge in Atlantic bluefin tuna biology due to electronic tagging. I will highlight the contributions that my third and fourth chapters make to this progression, and touch on ongoing collaborative work.

The fourth chapter reports the results of the acoustic and satellite tagging study on Greenland sharks, executed in the St. Lawrence Estuary. This chapter is proof of the concept that full understanding of even enigmatic, deep, cold water species is possible with recent electronic tagging technology. Greenland sharks provided an interesting species to focus an electronic tagging study on as they are so different from most species that have been studied with electronic tagging technology. For example, in comparing the life history of Greenland sharks with that of Atlantic bluefin tuna they differ as Greenland sharks live in a cold, deep water environment, they are cold blooded, live bearers and are ancient fishes, while bluefin tuna generally live in warmer temperatures, spend the majority of their time at shallow depths, are ectothermic, broadcast spawners and are modern fishes. In my Greenland shark study, I not only report much of their behaviour for the first time, I also demonstrate that electronic tagging can be used to define the life history of deep water enigmatic species.

6.2 Electronic tagging of Atlantic bluefin tuna

Atlantic bluefin tuna in the Atlantic Ocean and Mediterranean Sea are managed by the International Commission for the Conservation of Atlantic Tunas (ICCAT) under a two stock hypothesis (Mather et al. 1995). It is hypothesized that the western Atlantic Ocean stock spawns in the Gulf of Mexico (Richards 1976) and the Straits of Florida (Rivas 1954) and the eastern Atlantic Ocean stock in the Mediterranean Sea (Richards 1976). The current management plan assumes that mixing between the two stocks occurs at a low rate ($< 4\% \bullet year^{-1}$; National Research Council 1994). However, recent archival and conventional tagging data indicate that fish in the western Atlantic Ocean cross to the eastern Atlantic Ocean at a rate that ranges from 10-30 % (Block et al. 2001). Increased understanding of the movement patterns and the level of mixing between the two stocks are crucial to improving the management and conservation of bluefin tuna (National Research Council 1994; Sissenwine et al. 1998; Magnuson et al. 2001).

Even in light of the strict quota system enforced on the countries that execute fisheries for Atlantic bluefin tuna in the western Atlantic management zone, the estimated size of the western stock has greatly declined (Magnusson et al. 2001, Myers and Worm 2003)

The depletion of the western Atlantic bluefin tuna stock inspired researchers to focus on determining the migratory patterns, spawning grounds and stock structure of western Atlantic bluefin tuna. In 1996, researchers from the Tag-A-Giant (TAG) program of Stanford University and the Monterey Bay Aquarium, began tagging bluefin tuna with first generation satellite tags in the winter catch and release sport fishery off

North Carolina (Block et al.1998ab). In 1997 a group from the New England Aquarium began tagging bluefin tuna with first generation satellite tags in the commercial fishery off Massachusetts (Lutcavage et al. 1999). The results of the New England Aquarium study indicated that bluefin tuna tagged off New England may migrate to the mid-Atlantic. The authors proposed, based on these results, that there may be a mid-Atlantic spawning ground for Atlantic bluefin tuna (Lutcavage et al. 1999). Importantly, the tags used in these studies did not have depth sensors and archived only daily mean temperatures for the first 60 days of their deployment and the day of tag release (Lutcavage et al. 1999). It was later proposed that tags of this generation, when the results were determined after the period of temperature archive (60 days), should be viewed with extreme caution, as it is hard to determine if the tag released prior to the preprogrammed tag report date (Gunn and Block 2001).

Block et al.(2001) reported results from internal archival and PSAT tagging of Atlantic bluefin tuna from North Carolina, New England, and the Gulf of Mexico. They reported on the first five years of the TAG project (1996-2001). From these data, Block et al.(2001) proposed four migratory behaviours for Atlantic bluefin tuna tagged in the western Atlantic Ocean: 1) western Atlantic residency without visiting a recognized spawning ground; 2) western Atlantic residency with visitation to a known western spawning ground; 3) western residency for 1-3 years with visitation to the known eastern spawning ground, the Mediterranean Sea; 4) trans-Atlantic movement west to east and back. Western residency was the prevalent pattern for adolescent bluefin tuna, as they occupied offshore waters off North Carolina in the winter, the Gulf Stream in spring and New England waters in summer and autumn.

In the second chapter of this thesis, I reported on the results of the pop-up satellite tagging of 35 Atlantic bluefin tuna off Nantucket Island, Massachusetts in 1998, 2000 and 2001. The data indicated that that the large bluefin tuna that aggregate off Massachusetts in the autumn were linked to known western Atlantic bluefin tuna spawning grounds in the Gulf of Mexico. Bluefin tuna, up to 9 months post tagging, generally followed the continental shelf of the USA eastern seaboard. Bluefin tuna moved from waters off New England in autumn to the aggregation off North Carolina in winter, and then to spawning grounds in the Gulf of Mexico in winter and spring. Also, from 11 tags that prereleased and drifted for from 132 to 300 days, I reported end-point locations in the mid-Atlantic. These endpoints were similar both in proximity and pattern to the tag end point locations reported in Lutcavage et al.(1999). As their tags did not contain depth sensors, the logical conclusion is that their tags prereleased from the fishes and drifted to the mid-Atlantic. Therefore, there is no evidence of a mid-Atlantic spawning ground for Atlantic bluefin tuna. A paper published after Stokesbury et al. (2004) also reported that tagged tuna from New England did not move to the mid-Atlantic, but stayed mostly in slope and shelf waters along the USA eastern seaboard (Wilson et al. 2005).

Although Atlantic bluefin tuna tagged off New England did not move to the mid-Atlantic it was demonstrated that many fish tagged in North Carolina did move to feeding areas in the eastern Atlantic (Block et al. 2001, Block et al.2002). Also, from the fourth chapter of this thesis, I report the results of a tagging program conducted off the west coast of Ireland that indicated that bluefin tuna tagged in the eastern Atlantic are linked to the West Atlantic spawning grounds (Stokesbury et al. submitted). Therefore, tagged

bluefin not only moved from west to east (Mather 1995, Block et al. 2001) but also from east to west (Stokesbury et al.submitted).

A recent paper by Block et al. (in press) reports on the cumulative results of the TAG program. In this paper it is demonstrated through the use of electronic tags that there are two populations of bluefin tuna in the Atlantic Ocean. Also, that bluefin tuna tagged in the western Atlantic Ocean are linked to major feeding grounds in the central and eastern Atlantic Ocean. Therefore, based on their results, they propose that bluefin tuna from the West Atlantic stock may be subject to high rates of fishing when feeding in aggregations in the eastern Atlantic Ocean. Thus, high fishing quotas in the eastern Atlantic Ocean management unit are likely to have a detrimental effect on the western Atlantic stock.

The TAG program, including my research inside its framework, demonstrates how electronic tagging of fishes can define their life history characteristic. This information can be used by management to help make informed decisions that may improve conservation of migratory marine species.

Geopositioning electronic tags provide data for which interesting behavioural and ecological questions can be investigated. For example, the east to west movement of the tuna tagged in the western Atlantic and the west to east movement of the bluefin tagged in the eastern Atlantic, suggest some interesting questions regarding their migration patterns. For example, the two bluefin tuna tagged off Ireland, whose tags successfully reported, moved to a mid-Atlantic feeding ground prior to one moving to the West Atlantic and the other moving back to the East Atlantic. It appears that these fish may have been moving toward their natal spawning grounds to reproduce. Also, as they

moved in different directions when they left the mid-Atlantic it is unlikely that they were following currents or navigating by bathymetric landmarks, noise or smell. Perhaps, as the bluefin tuna were migrating in the blue ocean over thousands of kilometers, they may have been navigating using an omnidirectional "attractor" as suggested for Atlantic cod (Robichaud and Rose 2002) or the magnetic field of the Earth as suggested for a variety of large pelagics (Klimely et al. 2002). More tagging is needed to address these questions. When dealing with a large, highly migratory species such as bluefin tuna only electronic tagging over long periods of time can define their life history characteristics and give us insight into the mechanisms that they use for migration in the blue ocean.

6.3 Electronic tagging of Greenland sharks

In the fourth chapter of this thesis, results from acoustic and PSAT electronic tags reveal novel insights into the life histories of Greenland sharks. This information is of great importance. For example, as the global climate warms, the way animals use their environments will change. To identify and predict changes in animal life histories, we must first have a baseline of knowledge from which to compare. Therefore, the Greenland shark study demonstrates another ecologically important aspect of the versatile applications of electronic tags.

More electronic tagging is needed to determine the navigational mechanisms that are used by Greenland sharks. Sharks that were resident in Baie St. Pancrace were active in the water column at sunrise and sunset. However, the shark that moved into the main channel of the St. Lawrence Estuary, and that was most likely to be migrating, did not show the patterns of vertical migration at sunrise and sunset. Sharks can detect changes

in the geomagnetic field of the earth (Meyer et al. in press) and it has been proposed that sharks that swim at one depth may be orienting to the Earth's main (core) magnetic field, while sharks that swim up and down through the water column are orienting to local (crust) magnetic topography (Klimley 1993, Klimley et al. 2002, Collin and Whitehead 2004). Therefore, the behaviour of the electronically tagged Greenland sharks may have been related to their use of the geomagnetic field for navigation. For example, the shark that moved into the main channel of the estuary may have been navigating by the Earth's main magnetic field for longer distance migration. The sharks that remained in the bay may have been moving in response to a local anomaly of the local magnetic topography for smaller scale movements (Klimley et al. 2002). Future electronic tagging research is needed to test this hypothesis.

As global warming changes the environment occupied by these sharks what effect will that have on the population? If Baie St. Pancrace is a breeding area, nursery or thermal refugium, and its characteristics are altered through environmental change caused by global warming, that may have a large effect on this population. For example, as stated in the McLaren Hypothesis (1963), some animals may feed in warm temperatures in the water column, and then occupy deeper colder depths where their metabolism slows. Perhaps this is the case for the Greenland sharks in Baie St. Pancrace? The bottom of this bay is cold, so when the shark is at depth its metabolism would slow. Also, there is virtually no current, so holding position or moving slowly would have a very low metabolic cost. Likely, the bottom of Baie St. Pancrace is a very low energy environment. That the sharks leave the bay to actively hunt, then rest in the bay to conserve energy for growth and/or reproduction seems likely. Perhaps future research

will determine the importance of the bay to the sharks, and enable predictions of the effect of environmental change on this population.

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