EFFECT OF ENVIRONMENTAL CONDITIONS ON THE NATURAL ACTIVITY RHYTHMS AND BOTTOM TRAWL CATCHABILITY OF ATLANTIC COD (Gadus morhua)

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Effect of environmental conditions on the natural activity rhythms and bottom trawl catchability of Atlantic cod (*Gadus morhua*)

by

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Abstract

Environmental conditions such as water temperature and ambient light level are expected to exert a strong influence on the natural behaviour and bottom trawl catchability of marine groundfish species such as Atlantic cod (*Gadus morhua*). In this thesis, I use acoustic telemetry to investigate this prediction for cod inhabiting coastal inshore waters in the North Atlantic ocean.

Laboratory and field experiments were first conducted to examine two intragastric methods for attaching acoustic transmitters to cod. I found that cod which voluntarily swallowed transmitters wrapped in bait exhibited a delayed onset of initial regurgitation, longer periods of retention, higher food consumption, and lower mortality in comparison to fish tagged using the method of forced insertion into the gut. Under field conditions, cod in shallow coastal waters were successfully tagged by lowering a tagging frame near the seafloor containing baited acoustic transmitters. The technique did not appear to affect natural behaviour and was found to be ideal for short-term telemetry studies.

Temporal patterns in the natural activity level of acoustically tagged cod were investigated using a stationary positioning system. Time-of-day was found to have a significant affect on the activity level of cod inhabiting two study areas, the coastal waters of Norway and Newfoundland. High resolution tracking of juvenile cod revealed significant between-individual variation, suggesting that juvenile cod may make different trade-offs in balancing the demands of foraging and predator avoidance. Adult cod in Smith Sound on the northeast coast of Newfoundland exhibited seasonal variation in diel activity rhythm. During summer, cod were active throughout the diel cycle with a pronounced increase in activity during daylight hours. During winter, cod occupied deeper water and were significantly less active. Water temperature and ambient light intensity are thought to be the key proximate factors responsible for this seasonal difference in behaviour.

Finally, the behaviour of cod was examined in response to an approaching vessel and bottom trawl at different times of year. Using acoustic telemetry, the swimming speed of cod was estimated for the periods before, during, and after passage of a vessel travelling at different speeds as well as in response to this vessel towing a bottom trawl. The likelihood of reaction, reaction distance, and the duration of disturbance produced by the encounter were examined. The results showed that cod are capable of reacting to an approaching vessel from considerable distances and that the disturbance produced by the encounter can persist for periods up to 56 min.

In summary, the findings from this thesis indicate that variation in environmental conditions play an important role in modifying the behaviour of cod. Diel variation in ambient light intensity and seasonal variation in water temperature appear to be important proximate factors. Both are predicted to affect the availability and vulnerability of inshore cod populations to acoustic and bottom trawl sampling tools used in resource assessment surveys.

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I am indebted to many individuals for their support. Of greatest importance, I give special recognition to my loving wife, Jennifer. Without her faith, support, and encouragement, none of this could have been possible. I also thank my parents and extended family for their continuing support and encouragement over the years.

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And thank-you to Barry McCallum for teaching me a thing or two about gear technology, but perhaps most all, for giving me his laboratory! Also a tremendous thank-you to Anders Fernö and Svein Løkkeborg for inviting me to Bergen and providing me an opportunity to expand my mind.

Finally, I would like to say thank-you to several students and staff at Fisheries and Oceans Canada, most of whom I have chosen to mention at the end of each chapter.

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Chapter 1. Introduction and Overview

Commercial finfish stocks are commonly managed using two sources of information: 1) catch and effort statistics from commercial fisheries, and 2) data from scientific research surveys. Both may be used by assessment scientists to describe the current state of stocks and to forecast trends in abundance and size composition. However, given the inherent uncertainties of commercial catch data, research surveys have become increasingly important for stock assessment (see Fernö and Olsen 1994).

In Newfoundland waters, multi-species research surveys are primarily conducted using two types of sampling tools: bottom trawls (Doubelday and Rivard 1981; Walsh 1996) and acoustics (Rose 1995). Following the collapse of the "northern cod" (*Gadus morhua*) stocks in the early 1990s (see Lilly et al. 2001 for review), Fisheries and Oceans Canada funded several initiatives to study sources of bias in survey abundance indices, including the following study on the effects of environmental conditions on natural behaviour and bottom trawl catchability of cod. The major objectives were to examine the influence of seasonal changes in bottom temperature and diel changes in ambient light intensity on the activity rhythms of cod as well as their behaviour in response to an approaching vessel and bottom trawl.

This Chapter provides an overview of the current state-of-knowledge on the natural activity rhythms and vessel-trawl induced behaviour fundamental to understanding catchability of cod, as well as a brief outline of the work presented in this thesis.

1.1 Natural Activity Rhythms

Like other taxa, fish are constantly engaged in making important behavioural decisions based on ecological factors (Dill 1987). Over the lifetime of an individual, choices must be made such as when and where to feed, whether to avoid predators, and how much energy to allocate toward reproduction. Each time a fish chooses a certain behaviour over one or more alternatives, it is assumed that the individual has behaved so as to maximize benefits and minimize costs toward itself (Noakes 1992). Balancing these trade-offs is expected to affect spatial and temporal patterns of activity (Ali 1992) and be observable at the population level (Fréon and Misund 1999).

The natural activity of fish can present a serious bias for research surveys designed to assess population characteristics. Changes in fish distribution, migration, vertical movement, and activity level during a survey can all have a pronounced influence on the *availability* of fish (see MacLennan and Simmonds 1992; Aglen 1994; Godø 1994; Fréon and Misund 1999; Benoît and Swain 2003, for reviews). Availability is defined as the proportion of fish accessible to a sampling tool, e.g. the beam of an acoustic transducer or swept volume of a bottom trawl (Gunderson 1993). Assessment models that use indices derived from surveys assume that the *availability* of various age classes remains constant while the survey is being conducted and that it is consistent from year to year. If the availability of fish changes in a non-systematic (i.e. unpredictable) manner, then misrepresentation of true population abundance and size-composition may occur, raising sampling variability, and lowering the accuracy and reliability of a survey time-series.

Several studies have recently investigated the natural activity of adult Atlantic cod in the coastal inshore waters of Newfoundland. During the late 1980s and early 1990s, observations of overwintering cod in Trinity Bay on the northeast coast renewed interest in the ecology of these inshore populations (Wroblewski et al. 1994, 1995; Smedbol and Wroblewski 1997). Much of this work involved attaching acoustic transmitters to fish and tracking their movements over a period of time. Since then, several additional studies have also employed acoustic telemetry in a number of Newfoundland bays (Green and Wroblewski 2000; Robichaud and Rose 2001, 2002, 2003). Together, these studies have greatly advanced the knowledge of the ecology of inshore cod populations, particularly with respect to migration, spawning, and overwintering behaviour. However, information at even smaller temporal and spatial scales is necessary to understand the behavioural trade-offs (i.e. decisions) that cod make in response to fine-scale ecological conditions (e.g. Ydenberg and Dill 1986; Dill 1987; Lima and Dill 1990).

One approach to observing behaviour at fine temporal scales is to use a stationary positioning system for the continuous and automatic tracking of individual fish (see Fig. 1.1 for example). This provides real-time high resolution movements at the individual level. In Newfoundland waters, only juvenile cod have been studied in this manner (Clark and Green 1990; Cote et al. 1998, 2002, 2003). Complementary work on adult cod has been conducted in a Scottish sea loch (Hawkins et al. 1974) and in the coastal waters of Norway (Løkkeborg 1998; Løkkeborg and Fernö 1999; Kallayil et al. 2003). Together, these studies have shown that juvenile and adult cod exhibit significant variation in *in situ* swimming speeds over diel and seasonal time scales. Several

Figure 1.1: Illustration of a stationary positioning system. Three or more hydrophones triangulate the position of an acoustically tagged fish in real-time at rates < 20 s (image courtesy of the Institute of Marine Research, Bergen).

proximate factors have been identified, including water temperature (Clark and Green 1990), ambient light level (Løkkeborg 1998; Løkkeborg and Fernö 1999), and habitat complexity (Cote et al. 2002). These studies indicate that environmental conditions can have a strong influence on the natural activity rhythms of cod. However, what is still unknown is the extent to which environmental conditions affect the activity rhythms of adult cod in Newfoundland waters. This is the first major goal of this thesis.

1.2 Bottom Trawl Catchability

A bottom trawl is an active (or mobile) type of fishing gear that is towed along the seafloor (Fig. 1.2). The process of fish capture involves a complex sequence of fish behaviour in response to the fishing vessel and the various components of the trawl. These behaviour patterns generally occur in response to the visual and auditory stimuli produced by the vessel, doors, sand clouds, sweeps, footgear and trawl netting (see Wardle 1993; Engås 1994; Godø 1994 for reviews).

Research surveys using bottom trawls have been conducted in Newfoundland waters for a number of decades (Doubelday and Rivard 1981; Walsh 1996) using several gear types (McCallum and Walsh 1997). The average proportion of fish that are effectively captured per unit of fishing effort is defined as the *catchability* of a survey trawl (Gunderson 1993). Godø (1994) described three zones during the fish capture process in which fish behaviour can influence bottom trawl catchability (Fig. 1.3; see also Walsh 1996). The process begins ahead of the doors (*zone 1*) where vessel avoidance behaviour can first occur. Low frequency noise produced by the vessel has been shown to generate avoidance behaviour well before the vessel or trawl can be

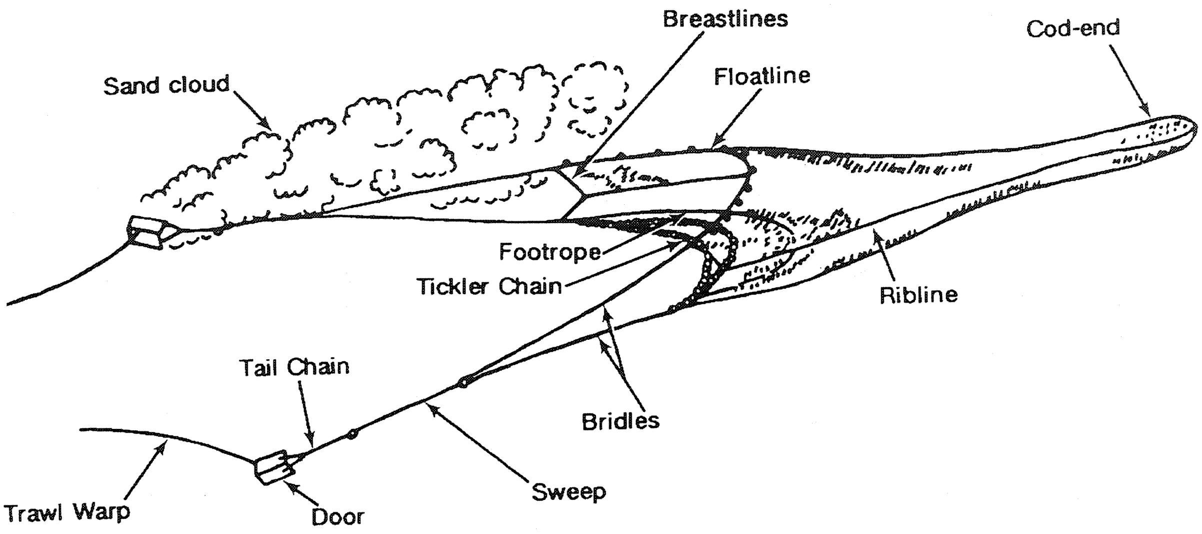

Figure 1.2: Schematic drawing of a bottom trawl (Adapted from Gunderson 1993).

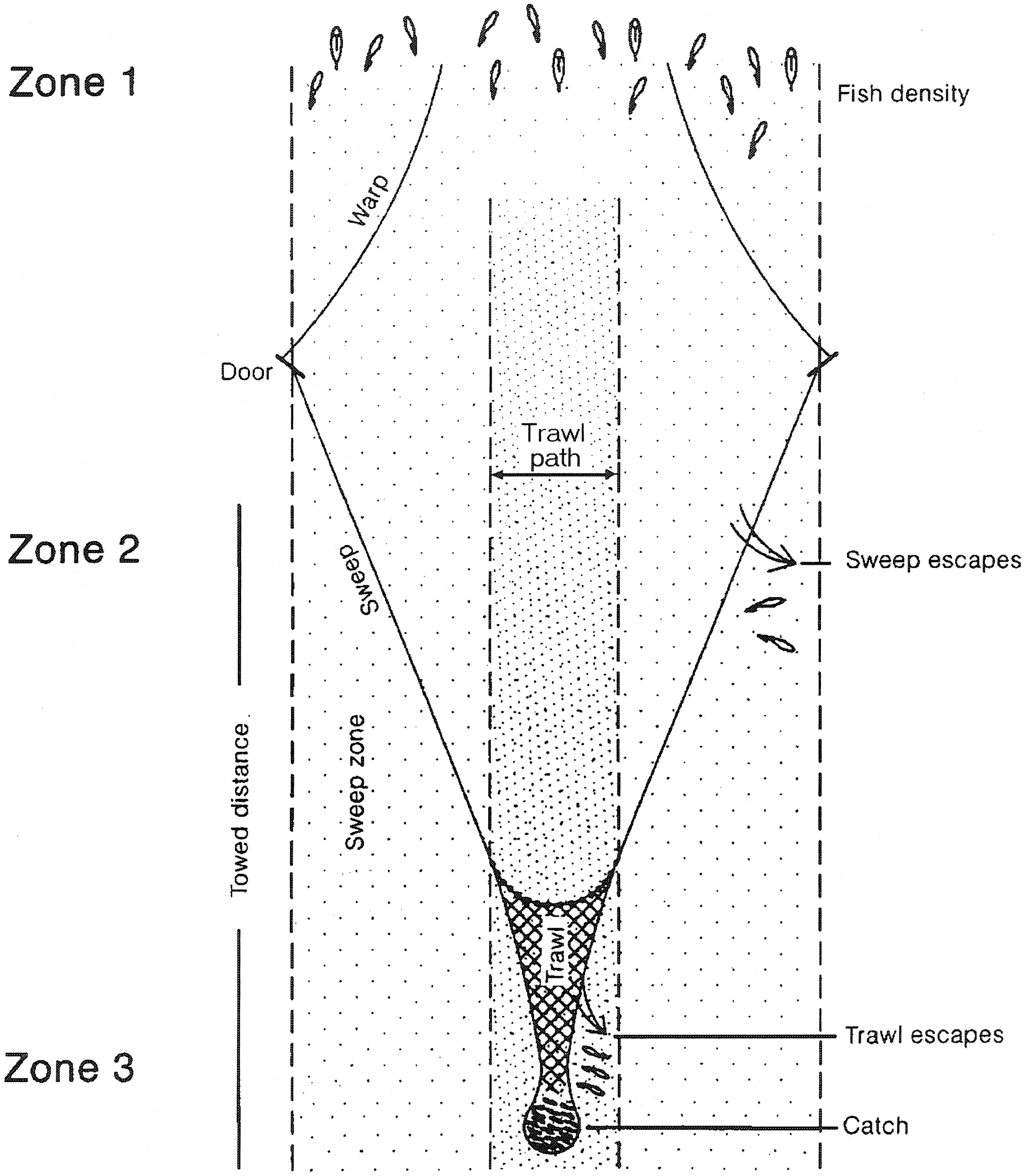

Figure 1.3: The three catching zones of influence in the fish capture process (Adapted from Godø 1994; Walsh 1996).

visually observed (e.g. Olsen 1971; Olsen et al. 1983; Misund et al. 1996). Species such as Atlantic cod have been shown to increase swimming speed (Olsen et al. 1983; Handegard et al. 2003) and dive toward the seafloor (Ona and Godø 1990; Hjellvik et al. 2003) in response to an approaching vessel. If avoidance behaviour (vertical or horizontal) is significant, then the volume of fish available to be captured by the approaching trawl will vary. Such variability could bias abundance indices in annual resource surveys which use bottom trawls.

As the trawl begins to move through an aggregation of fish, a proportion of these fish will enter between the doors (*zone 2*, Fig. 1.3). For roundfish such as cod, the general behaviour has been described as a 'fountain manoeuvre' (Wardle 1993). In general, fish appear to avoid an approaching door by swimming either to the left or right while maintaining at least one eye on the door at all times. Those fish which swim to the inside of the doors tend to immediately enter the trawl path and begin swimming toward the trawl mouth maintaining position equidistant between the sweeps. Fish which eventually arrive at the mouth of the trawl will tend to orient in the direction of the tow and keep station with the advancing trawl. This behaviour appears to be an optomotor reflex in response to the visual cues produced by the surrounding footgear and/or netting of the trawl wings (Wardle 1993; Walsh and Hickey 1993; Kim and Wardle 2003). As the fish begin to exhaust, the majority will turn and fall back into the trawl (*zone 3*, Fig. 1.3), but some escape over the headline (Main and Sangster 1981) or under the footgear (e.g. Engås and Godø 1989; Godø and Walsh 1992; Walsh 1992). Once inside the trawl, mesh selection can still occur depending on the design of the codend, mesh size, mesh shape, catch size and towing speed (see Glass 2000 for review).

Variation in bottom trawl catchability is known to be associated with spatial and temporal changes in environmental conditions. Ambient light intensity and water temperature are generally considered to be the two most influential factors governing fish capture behaviour. At light intensities below 10^{-4} lux, ordered patterns of reaction behaviour cease (Glass and Wardle 1989; Walsh and Hickey 1993) and the vulnerability to capture greatly increases. The role of water temperature, by comparison, is poorly understood. It is generally thought to influence trawl catchability in three ways: 1) by affecting spatial distribution and therefore the availability of fish to trawl capture (Smith and Page 1995; Swain and Kramer 1995), 2) by affecting the swimming capability and therefore the vulnerability of fish to trawl capture (He 1993; Winger et al. 2000), and 3) by affecting response threshold and therefore avoidance behaviour of fish ahead of the approaching vessel/trawl (no data). Yet despite advances in underwater technology (see Urquhart and Stewart 1993; Godø 1998; Graham et al. 2004 for reviews), direct empirical evidence of temperature-dependent catchability is still lacking (Winger and Walsh 2001). The influence of seasonal differences in bottom temperature and ambient light intensity on vessel- and trawl-induced behaviour have not been previously investigated and is the second major goal of this thesis.

1.3 Chapter Outlines

In Chapter 2, I examine two intragastric techniques for attaching acoustic transmitters to adult cod. A fundamental criterion for any tagging technique is the need to minimize adverse effects on the natural behaviour of the fish. If the presence of a transmitter affects a fish's posture, swimming capability, or foraging activity, then the resulting tracking data may be biased (see Bridger and Booth 2003 for review). Previous studies have examined the feasibility of intragastric tagging on cod under laboratory conditions (Lucas and Johnstone 1990; Armstrong et al. 1992), but employed different techniques, size ranges, and temperature regimes. In this chapter, I examine the effects of the two commonly used techniques, forced insertion and voluntary ingestion, in a comparative study. I test the null hypotheses that there are no differences in transmitter retention, food consumption or survival for cod tagged using these techniques. I also investigate the effect of transmitter size on the duration of retention. This chapter is an important prerequisite to carrying out field experiments using these techniques.

In Chapter 3, I examine the feasibility of tagging Atlantic cod in the field using the technique of voluntary ingestion. This is the least invasive tagging technique currently available to researchers working with piscivorous species and has been successfully applied to cod in the Northeast Atlantic (e.g. Engås et al. 1998; Løkkeborg and Fernö 1999). I evaluate a low cost device suitable for the tagging of cod in the inshore waters (< 40 m) of Smith Sound, Newfoundland. Video footage of cod interacting with baited transmitters near the seafloor is quantified to determine the efficiency and size-selectivity of the technique. In particular, I examine the frequency of several modal action patterns (Barlow 1968) similar to those exhibited by cod toward baited hooks (e.g. Løkkeborg et al. 1989). Tagged cod are subsequently tracked for up to two weeks to determine post-tagging behaviour and transmitter retention.

In Chapter 4, I examine the swimming speeds and diel activity rhythms of four Atlantic cod inhabiting the inshore waters of Ramfjord, northern Norway. I examine tracking data for individual acoustically tagged cod collected during the summer and develop a methodology for estimating swimming speed at fine temporal scales. Although several studies have previously reported *in situ* swimming speeds for cod (e.g. Clark and Green 1990; Løkkeborg 1998; Løkkeborg and Fernö 1999; Cote et al. 2002) using acoustic telemetry, few have reported high resolution tracking for individual fish in an effort to quantify within- or between-individual variation. This is the main goal of this chapter.

In Chapter 5, I examine seasonal variation in diel activity rhythms of 13 adult Atlantic cod inhabiting the inshore waters of Smith Sound, Newfoundland. Previous studies investigating activity rhythms have only been conducted for juvenile cod in Newfoundland waters (Clark and Green 1990; Cote et al. 2002). In this chapter, I use acoustic telemetry to track individual adult cod over a period of several weeks during the summer and winter seasons. Using the methodology developed in Chapter 4, I estimate swimming speeds from the tracking data to determine diel activity rhythms for the different seasons. Functional explanations for observed seasonal differences in activity rhythm are discussed.

In Chapter 6, I examine the behaviour of Atlantic cod to an approaching vessel and bottom trawl at different times of year. Previous studies examining this type of behaviour have indicated that demersal species may initiate avoidance responses at significant depths and distances ahead of an approaching vessel and/or trawl (Olsen et al. 1983; Engås et al. 1998; Handegard et al. 2003) and that the behaviour may be highly variable (Godø et al. 1999; Michalsen et al. 1999). However the role that environmental conditions play in avoidance behaviour is poorly understood. In this chapter, I examine the behaviour of cod during the summer and winter seasons. Using acoustic telemetry, I estimate the swimming speed of cod during the period before, during, and after an encounter with a vessel travelling at different speeds as well as in response to a vessel towing a bottom trawl. The likelihood of reaction, reaction distance, and the duration of disturbance produced by the encounter are examined. Functional explanations for observed seasonal differences in behaviour are discussed.

Finally, in Chapter 7 I provide an integrated account of the results and conclusions from each chapter. I discuss functional explanations for the behaviours observed, implications of the results for research surveys, limitations of the approach used, and future research challenges.

1.4 Co-Authorship Statement

I am the major intellectual contributor and principal author of all chapters presented in this thesis. This includes all practical aspects of the research, data analysis, interpretation, and manuscript preparation. The work could not have been undertaken without the collaborative contribution of several individuals. Their involvement is recognized here.

Chief collaborator for Chapter 2 was Stephen Walsh. Dr. Walsh assisted with the laboratory experiment and aided with the data interpretation and editing of the manuscript. This chapter was published in the ***Journal of Applied Ichthyology*** in 2001 (17:234-239). I am the primary author and Dr. Walsh is second author.

Chief collaborators for Chapter 3 were Barry McCallum, Stephen Walsh, and Joseph Brown. Mr. McCallum designed and built the tagging frame, participated with the field work, and aided with the data interpretation and editing of the manuscript. Dr.

Walsh participated with the field work, and aided with the data interpretation and editing of the manuscript. Dr. Brown aided with the data interpretation and editing of the manuscript. This chapter was published in the journal ***Hydrobiologia*** in 2002 (483:287-292). I am the primary author and Mr. McCallum, Dr. Walsh, and Dr. Brown are co-authors 2 through 4, respectively.

Chief collaborators for Chapter 4 were Anders Fernö, Svein Løkkeborg, and Terje Jørgensen. These individuals carried out the field work associated with this project. I was invited to Bergen in 2001 by Dr. Fernö as part of the Memorial University - University of Bergen Exchange Program to undertake an examination of the data with the purpose that it be included in this thesis. Drs. Fernö, Løkkeborg, and Jørgensen aided with the data interpretation and editing of the manuscript. This chapter has not been published.

Chief collaborator for Chapter 5 was Stephen Walsh. Dr. Walsh participated with the field work, and aided with the data interpretation and editing of the manuscript. This chapter has not been published.

Chief collaborators for Chapter 6 were Stephen Walsh, Barry McCallum, and Joseph Brown. Dr. Walsh and Mr. McCallum participated with the field work, and aided with the data interpretation and editing of the manuscript. Dr. Brown aided with the data interpretation and editing of the manuscript. This chapter has not been published.

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Chapter 2. Tagging of Atlantic cod (*Gadus morhua*) with intragastric transmitters: effects of forced insertion and voluntary ingestion on retention, food consumption and survival

2.1 Abstract

The effects of intragastric tagging on transmitter retention, food consumption and survival were investigated in Atlantic cod (*Gadus morhua*) under laboratory conditions. Cod (60 - 84 cm) were intragastrically tagged with two different sizes of dummy acoustic transmitters (16 x 45 and 16 x 80 mm) using the methods of forced insertion and voluntary ingestion. Cod that were tagged by forced insertion began to regurgitate transmitters the first day after tagging and continued to do so throughout the period of study (87 days). The percentage of fish retaining transmitters in this group dropped to 50% after 32 days. By comparison, cod that were tagged by voluntary ingestion exhibited a 44 day delay in the onset of initial regurgitation. This was followed by a rapid rate of regurgitation, with the percentage of fish retaining transmitters in this group dropping to 50% after 60 days. These retention times are prolonged in comparison to previous studies and have been attributed to the lower temperature regime used in this study. Transmitter size did not significantly affect the duration of retention. During the first 20 days following tagging, the average food consumption per fish was higher in the voluntary ingestion group compared with the forced insertion and sham groups. Mortality levels were 13%, 44% and 56% for the voluntary ingestion, forced insertion and sham groups respectively over the period of study. I associate low food consumption and high mortality rates in the first 20 days of the experiment with high levels of stress due to handling. The findings indicate that voluntary ingestion is a more viable technique

for the intragastric tagging of cod in field studies.

2.2 Introduction

A growing number of studies are using radio and acoustic telemetry to monitor the free-ranging movements of fish. Consequently, various techniques for attaching transmitters to fish have evolved over the past few decades. These can be broadly classified as either external attachment or internal implantation into the peritoneal cavity, oviduct, or stomach (Winter 1983). Each technique has its own unique advantages and disadvantages depending on the research objectives and species of interest. A fundamental criterion for any technique is the need to minimize adverse effects on the natural behaviour of the fish. If the presence of a transmitter affects a fish's posture, swimming capability, or foraging activity, then the resulting tracking data could be biased. This has increased the concern regarding the ethical considerations of tagging (Smolowitz and Wiley 1998) and has encouraged the use of less invasive tagging techniques where possible.

Intragastric tagging entails placing a transmitter into the stomach cavity of a fish. This technique has been widely used in both marine (e.g. Priede and Smith 1986; Sarno et al. 1994; Godø et al. 1997; Løkkeborg et al. 2000; Wroblewski et al. 2000) and freshwater species (e.g. Kynard and Warner 1987; Gerlier and Roche 1998; Matinelli et al. 1998). Comparative studies conducted under laboratory conditions have indicated that this is one of the most viable techniques for short-term tagging studies (Mellas and Haynes 1985; Peake et al. 1997a). Transmitters placed in the stomachs of fish will lie near their centre of gravity, will not snag or cause increased drag while swimming, do not cause tissue abrasion and are eventually regurgitated. Inserting the transmitters can be accomplished using either one of two methods: forced insertion or voluntary ingestion. The method of forced insertion has been widely used, particularly for its reduced handling time and quick recovery of the fish. Often taking less than 30 s to complete, the basic technique involves inserting a transmitter into the stomach cavity via the oesophagus (Hawkins and Urquhart 1983; Winter 1983). The method of voluntary ingestion, by comparison, relies on the 'trickery' of placing transmitters in baited packages and allowing fish to voluntarily ingest the contents *in situ* (e.g. Priede and Smith 1986; Bagley and Priede 1997; Godø et al. 1997; Løkkeborg 1998; Løkkeborg and Fernö 1999; Løkkeborg et al. 2000). The advantage of this method of intragastric tagging is that it is entirely non-invasive. This eliminates the stress associated with capture, including possible hydrostatic changes in the swimbladder, anaesthetization, and handling. By removing these stressors, it has been hypothesized that the natural behaviour of the fish would be less affected, survival would be improved, and the retention of transmitters would be prolonged (Armstrong et al. 1992a, 1992b).

The purpose of this study was to compare the two methods of intragastric tagging in Atlantic cod (*Gadus morhua*) under laboratory conditions. I test the null hypotheses that there are no differences in transmitter retention, food consumption or survival for cod tagged using either the method of forced insertion or voluntary ingestion. I also investigate the effect of transmitter size on the duration of retention. The temperature regime used in this study is typical for Newfoundland waters and is lower than previously examined in intragastric studies using cod.

2.3 Materials and Methods

Dummy transmitters were manufactured to meet the size and weight specifications of two sizes of acoustic transmitters commonly used in the field: 16 x 45 mm (diameter x length) with a mean weight of 25.14 g (s.d. = 0.30) in air, and 16 x 82 mm with a mean weight of 39.48 g (s.d. = 0.30) in air. The transmitters were cylindrical in shape and were constructed of an epoxy-resin compound. Each transmitter was individually marked with an identification number for recognition.

Atlantic cod were captured by longline in the inshore waters of Trinity Bay, Newfoundland in March 1997. The fish were transported to St. John's where they were held in flow-through tanks with a continuous supply of ambient temperature seawater and fed a diet of chopped Atlantic herring (*Clupea harengus*) once a day to satiation. The tank adaptation period was approximately nine weeks. The experiment commenced in mid-May using a total of 40 cod (60 - 84 cm) in late-spawning or post-spawning condition. The fish were starved for eight days immediately prior to tagging to ensure the stomachs were sufficiently empty. They were then randomly distributed into five experimental treatments: 1) forced insertion with small transmitters, 2) forced insertion with large transmitters, 3) voluntary ingestion with small transmitters, 4) voluntary ingestion with large transmitters, and 5) sham forced insertion.

The forced insertion treatments each contained eight fish and were kept together in a round fiberglass tank with dimensions 1.7 x 1.5 m (diameter x depth). These fish were anaesthetized (2-Phenoxyethanol, 1ml:8L seawater) for the purpose of tagging and length measurement. Transmitters were carefully inserted into the stomach cavity via the oesophagus (Winter 1983). The cod implanted with small transmitters had a mean length of 68.4 cm (s.d. = 5.6) while the cod with large transmitters had a mean length of 71.1 cm (s.d. = 8.2).

The voluntary ingestion treatments each contained four fish and were kept together in a rectangular tank with dimensions 3.2 x 2.3 x 1.1 m (length x width x depth). For the purpose of tagging the fish, a small arena was established at one end of the tank using a temporary partition. Each fish was individually placed into the tagging arena and presented with a baited package for voluntary ingestion without the feeding competition of the other fish. The baited package consisted of a transmitter wrapped in a fillet of herring enclosed in a piece of cheesecloth. The most effective method for encouraging ingestion was to suspend the baited package in the water using a line of thread (similar to Løkkeborg 1998; Løkkeborg and Fernö 1999). The cod typically took either immediate interest in the baited package, tearing it off the suspension thread with little hesitation, or returned later to take the bait. Once the baited package was consumed, the partition was lifted and the fish was permitted to swim into the remaining area of the tank, i.e. unhandled, joining those fish already tagged. The cod which ingested small transmitters had a mean length of 73.3 cm (s.d. = 5.0) while the cod with large transmitters had a mean length of 69.3 cm (s.d. = 7.4).

The sham treatment was established to test for the artifacts of the anaesthetic and handling on food consumption and survival. These cod (n = 16) were not tagged but underwent the anaesthetization and handling procedure similar to the forced insertion treatments. The cod in this treatment had a mean length of 69.7 cm (s.d. = 7.5) and were kept together in a separate tank with dimensions 1.7 x 1.5 m (diameter x depth).

Daily feedings of chopped Atlantic herring were resumed the day after tagging for all experimental treatments. The fish were fed to satiation by slowly throwing the feed into the tanks and allowing all fish to actively compete for the food. Feeding was terminated for each tank after three successive pieces of herring sank to the bottom and were not eaten after a duration of 20 s. The total weight of feed consumed by each tank was then recorded and each fish was assumed to have eaten an average share.

All tanks were inspected twice daily for regurgitated transmitters, mortality and water temperature. If transmitters were discovered, they were retrieved immediately and the date, time and transmitter identification number were recorded. If dead fish were found, they were immediately retrieved and dissected to determine their stomach contents and sex.

2.4 Results

Analyses of variance showed no significant effect of either transmitter size ($F_{.05\,[1,19]} = 0.360$, $p = 0.556$) or fish length ($F_{.05\,[1,19]} = 3.290$, $p = 0.086$) on the duration of transmitter retention. Hence, the data were pooled across the treatments for transmitter size within each tagging technique for further analysis.

The duration of transmitter retention varied between the two tagging techniques (Fig. 2.1). Cod in the forced insertion group began to regurgitate transmitters the first day after tagging and continued to do so throughout the period of study. The percentage of fish retaining transmitters dropped to 50% after 32 days. The longest period a transmitter was retained in this group was 87 days by both a 61 and 66 cm fish. By comparison, cod in the voluntary ingestion group exhibited a delayed onset of regurgitation, with the first occurrence recorded 44 days after tagging. This was followed by a rapid rate of regurgitation, with the percentage of fish retaining transmitters dropping to 50% after 60 days. The longest period a transmitter was retained in this group was 77 days by a 63 cm fish.

Survival varied considerably among the experimental groups (Fig. 2.2). Mortality rates during the first 20 days were highest in both the forced insertion and sham groups. Overall, the mortality levels were 13%, 44% and 56% for the voluntary ingestion, forced insertion, and sham groups respectively. Cod which were tagged using voluntary ingestion exhibited the lowest mortality (1 of 8), with only one fish dying on day 47. Dissection revealed that it had not regurgitated its transmitter prior to death and that it was a female in post-spawning condition. In contrast, cod which were tagged by forced insertion suffered a 44% mortality (7 of 16), with three fish dying by day seven, six by day 25, and the seventh on day 84. Dissection revealed that all were female and were either in late- or post-spawning condition. All but one fish had regurgitated their transmitters and they were all devoid of feed in the stomach at the time of death. In the sham group, 9 out of 16 fish (56%) died over the period of study, two by day seven and the remainder by day 21. Dissection revealed that all were female and were either in late- or post-spawning condition. All were devoid of feed in the stomach at the time of death.

Average daily consumption per fish was found to vary within and between experimental groups over the period of study. The data were pooled for each five day interval and are presented in Figure 2.3a along with 95% confidence intervals. Most of the significant variation in feeding took place during the first 20 days following tagging. Average consumption levels in the sham and forced insertion groups initially decreased

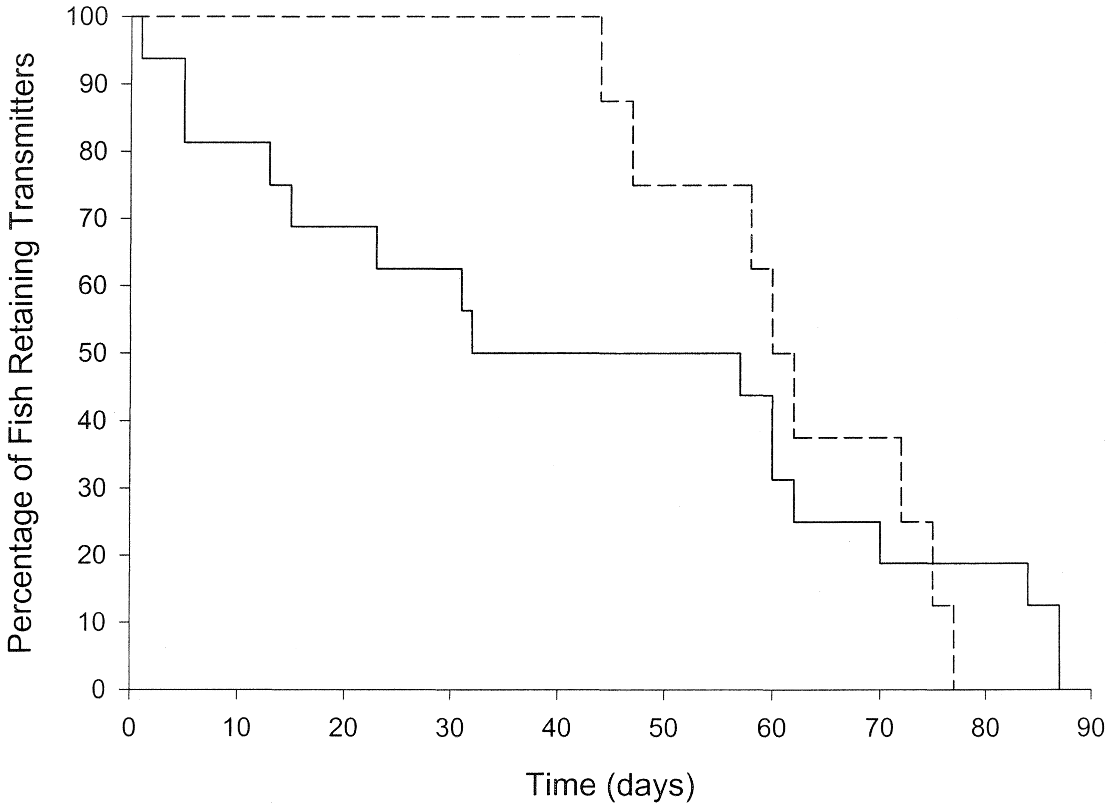

Figure 2.1: Percentage of fish retaining intragastric transmitters over the period of study for each of the tagging methods tested: forced insertion (solid line, n = 16) and voluntary ingestion (dashed line, n = 8).

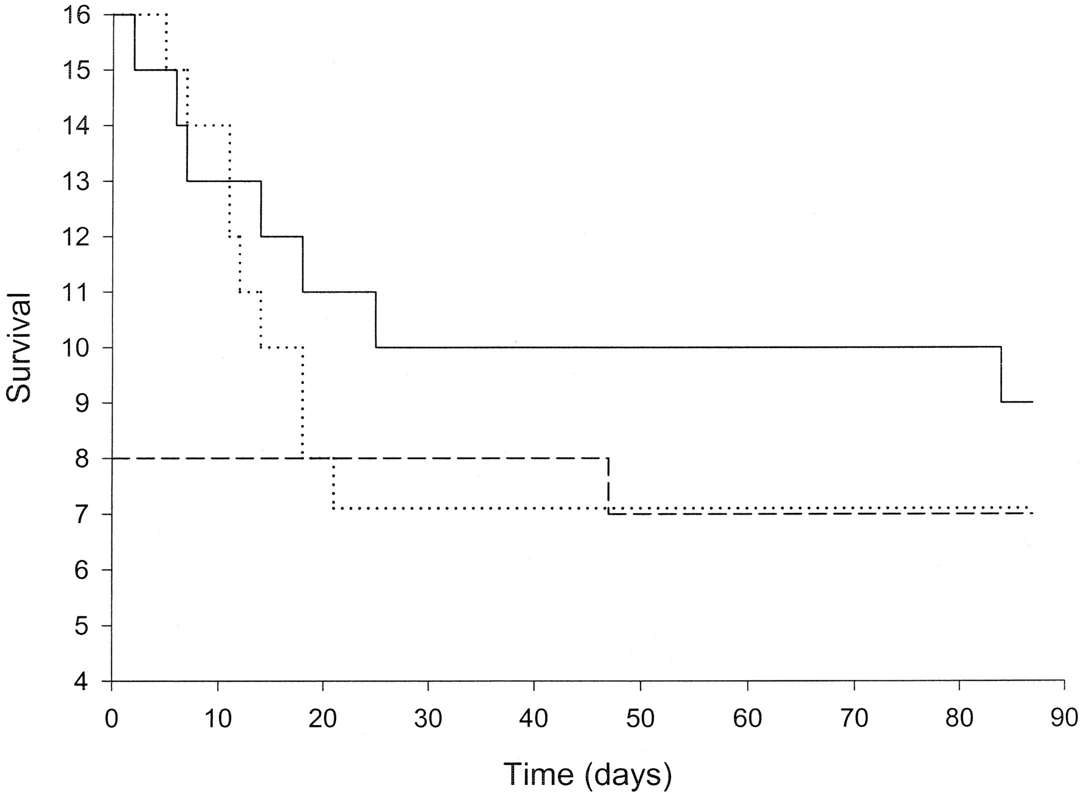

Figure 2.2: Number of fish surviving over the period of study in the forced insertion (solid line), voluntary ingestion (dashed line), and sham (dotted line) groups.

from day 6 to day 15 before beginning to increase. Average consumption levels in the voluntary ingestion group were noticeably higher during this period. By day 20, there was little difference in consumption levels between the three groups. From day 20 to day 55, the average consumption was slightly higher in the sham group and beyond day 55, all groups experienced a gradual increase in feeding.

Given the high mortality observed in the sham and forced insertion groups during the first 25 days, it is questionable whether all of the fish actually began feeding following the handling/tagging procedure. To determine whether my calculation of consumption levels may have been biased, I re-weighted the consumption data for the first 25 days, removing the data from those fish that eventually died during this period (Fig. 2.3b). Except for an increase in consumption by the forced insertion group during the first five days, the results are otherwise similar to Figure 2.3a, indicating that my estimates of average consumption per fish were not biased due to the onset of mortality in some fish. The effect of transmitter size on food consumption could not be assessed since these treatments were not isolated within separate tanks.

Ambient temperature of the incoming seawater supply to all tanks increased over the period of study (Fig. 2.4). Water temperatures ranged from 2.07 to 13.49 °C and were not significantly different between the experimental groups (ANCOVA, $F_{.05\,[2,231]} = 0.043$, p = 0.958).

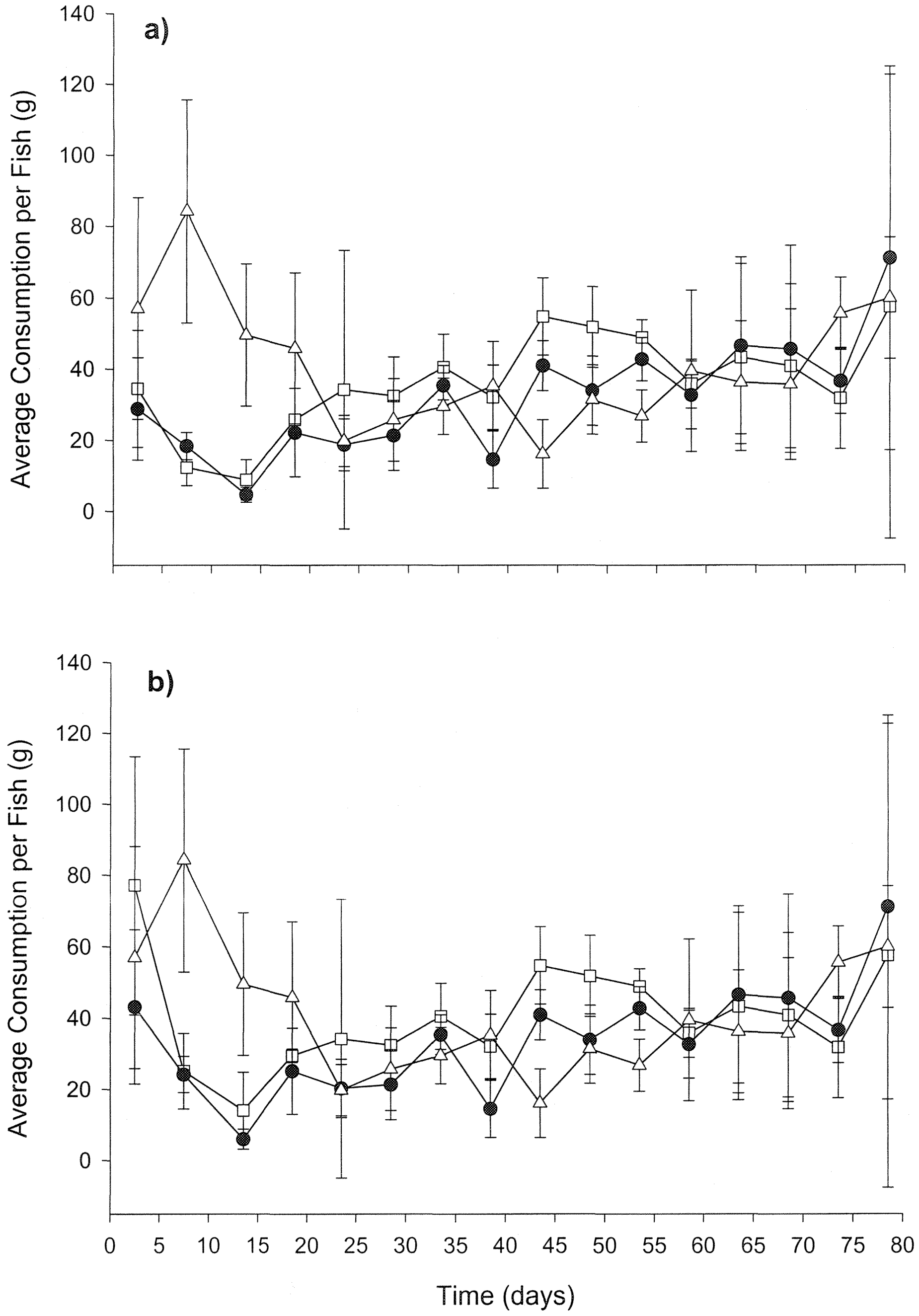

Figure 2.3: Average consumption (g) per fish over the period of study for a) the total number of fish in each tank, and b) re-weighted for the number of fish potentially not feeding due to the onset of mortality. Values shown are the means (95% CI) for five day intervals: forced insertion (●), voluntary ingestion (Δ), and sham (□).

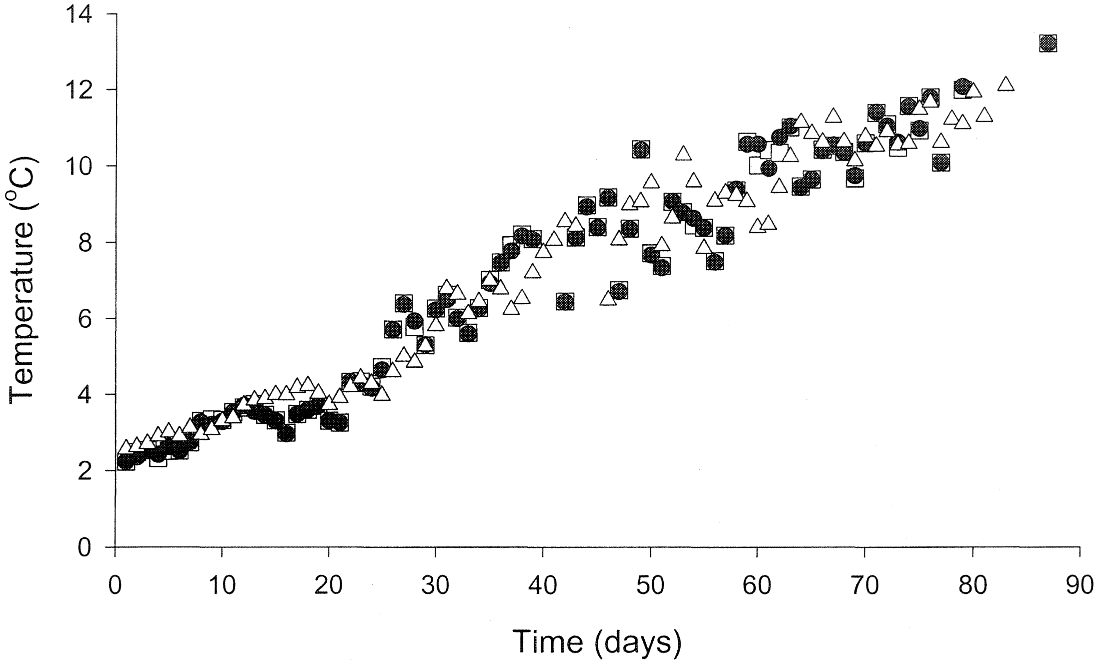

Figure 2.4: Ambient seawater temperatures observed over the period of study in the forced insertion (●), voluntary ingestion (Δ), and sham (□) groups.

2.5 Discussion

The duration of transmitter retention by cod which were tagged using forced insertion is prolonged in comparison to previous laboratory work by Lucas and Johnstone (1990), who reported a 50% retention time of only five days for North Sea cod (mean individual weight = 984.6 g) at 10 °C using transmitters of the size 16 x 56 mm. This is remarkably less than the 50% retention time of 32 days found in the current study. Lucas and Johnstone (1990) reported that the rate of regurgitation in their study decreased over time, with only one fish retaining its transmitter after 35 days. These authors also reported a higher regurgitation of transmitters within the first day following tagging (30%), compared to only 6% in the current study. Field studies using the forced insertion method have reported that cod are capable of retaining transmitters for reasonable periods of time with good success (e.g. Hawkins et al. 1974, 1980; Clark and Green 1990; Wroblewski et al. 1995, 2000). The longest retention time reported was 21 days by Clark and Green (1990) for cod (29 – 33 cm) in Newfoundland waters using transmitters of the size 17 x 57 mm. Among other gadoid species, retention times in the field have been reported as high as 19 days for *Pollachius pollachius* L. (43 - 44 cm) and 28 days for *Pollachius virens* L. (35 - 38 cm) using transmitters of the size 16 x 51 mm (Sarno et al. 1994).

The duration of transmitter retention by cod which were tagged using voluntary ingestion is also prolonged in comparison to previous laboratory work (Armstrong et al. 1992b). These authors showed that North Sea cod (67 - 92 cm), which voluntarily consumed transmitters (16 x 56 mm) wrapped in squid and held at 12 °C, had a 50% retention time of eight days. Again, this is much less than the 50% retention time of 60 days observed in the current study. Both experiments, however, did note a delayed onset of initial regurgitation. In the Armstrong et al. (1992b) experiment, cod began regurgitating transmitters six days after tagging. Similar to the current study, they then exhibited a rapid rate of regurgitation with only one fish retaining its transmitter after 21 days. Field studies using the voluntary ingestion method have reported the occurrence of transmitter regurgitation by cod (40 - 55 cm) after seven to eight days using transmitters similar in size to the current study: 16 x 48 mm and 16 x 80 mm (Løkkeborg 1998; Løkkeborg and Fernö 1999). Maximum retention times in the field are unknown, but have been reported as high as 68 days (Engås et al. 1996).

Water temperature has been hypothesized as a potential factor affecting the duration of transmitter retention (Armstrong et al. 1992a). These authors suggested that at low temperatures, transmitters might be retained longer due to a slowed digestive process; the results of the current study support this hypothesis. Low water temperatures observed during the beginning of this study may have been responsible for the prolonged periods of transmitter retention by cod in both tagging groups. In Newfoundland waters, cod are known to occupy temperatures ranging from -1.5 °C (Wroblewski et al. 1994) up to 12.0 °C (Clark and Green 1990) depending on the region and season. In Trinity Bay, Newfoundland, intragastrically tagged cod have been tracked at temperatures well below 2 °C for periods up to five days (Wroblewski et al. 1995). If temperature has an effect on transmitter retention, then field studies conducted during low water temperatures should potentially benefit from an increased number of tracking days.

Hart and Summerfelt (1975) suggested that the presence of a transmitter in a fish's stomach might affect its appetite. Evidence to support this hypothesis has been reported in juvenile Atlantic salmon (*Salmo salar*, Armstrong and Rawlings 1993) and chinook salmon (*Oncorhynchus tshawytscha*, Martinelli et al. 1998). However, laboratory and field studies have indicated that this is not the case for adult cod (Lucas and Johnstone 1990; Armstrong et al. 1992b; Løkkeborg 1998; Løkkeborg and Fernö 1999). Løkkeborg (1998) demonstrated that the natural foraging behaviour of cod in the ocean is not altered by the presence of a transmitter in the stomach. The results from the current study (Fig. 2.3a) support this finding. The similarity in consumption levels between my sham and forced insertion groups suggests that the presence of the transmitter in the latter group was not the reason for a decrease in feeding. I interpret the diminished appetites of cod in the sham and forced insertion groups during the first 20 days to be the result of the stress of the handling and the anaesthetic. A similar reduction in feeding may be expected to occur under field conditions, which could bias tracking data.

Experimental estimates of tagging related mortality are variable. Mortalities as high as 13% (Cote et al. 2000) and 75% (Mellas and Haynes 1985) have been reported for surgical implantation, 50% (Mellas and Haynes 1985) and 93% (Ross and McCormick 1981) for external attachment, and 33% for oviduct insertion (Peake et al. 1997b). Studies using intragastric methods, by comparison, have generally reported lower mortalities. The method of voluntary ingestion yielded 13% mortality for cod in the current study and 0% in the Armstrong et al. (1992b) study. Studies using the method of forced insertion have also reported relatively low mortalities: 0% in Atlantic cod (Lucas and Johnstone 1990), chinook salmon (Adams et al 1998), and rockfish (*Sebastes* sp., Starr et al. 2000), 13% in Atlantic salmon (*Salmo salar*, Armstrong and Rawlings

1993) and 17% in white perch (*Morone americana*, Mellas and Haynes 1985). In the current study, mortality in the sham and the forced insertion groups occurred rapidly and simultaneously over the first 20 days before leveling off as evident in Figure 2.2. I explore arguments why this may have happened.

The tanks used for the sham and forced insertion groups were smaller in size and shape than that used for the voluntary ingestion group. This is similar to field situations where cod are generally held in small tanks on the deck of a vessel prior to intragastric tagging and are often returned to those tanks for an observation period prior to release (e.g. Wroblewski et al. 1995, 2000). Fish tagged using voluntary ingestion are not restricted spatially since they are tagged *in situ*. By giving my voluntary ingestion group a larger tank, I attempted to replicate natural field conditions. As a result, the estimated stocking densities for the sham and forced insertion groups (14.7 kg/m^3) were higher than the voluntary ingestion group (3.3 kg/m^3). Although I cannot completely rule out a tank effect on mortality, my stocking densities were well within the recommended range for rearing cod in aquaculture (e.g. Kvenseth 1993; Lambert and Dutil 2001). Aggressive behaviour among cod may also occur during the spawning season (Brawn 1961), but none was observed in this study. Rather, when compared with the voluntary ingestion group with only 13% mortality, I believe that the handling/tagging process itself contributed to the reduced survival in the sham and forced insertion groups. Both groups experienced being captured, physically handled, and anaesthetization. Cod in the voluntary ingestion group did not experience this treatment. Finally, it is interesting to note that all of the mortalities observed in this study were female. Although the sex distribution was not known for the study group as a whole, the finding might indicate that females are differentially susceptible to handling stress. Future research could address this issue.

The findings from this study demonstrate the advantages of using the method of voluntary ingestion for the intragastric tagging of cod. I found that cod which voluntarily ingested transmitters exhibited a delayed onset of initial regurgitation, longer periods of retention, higher food consumption and lower mortality in comparison to fish tagged using the method of forced insertion. Voluntary ingestion techniques should reduce the cost of tracking studies due to premature transmitter loss and minimize potential biases in natural behaviour such as feeding.

2.6 Acknowledgements

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Chapter 3. Taking the bait: *in situ* voluntary ingestion of acoustic transmitters by Atlantic cod (*Gadus morhua*)

3.1 Abstract

Voluntary ingestion of acoustic transmitters by Atlantic cod (*Gadus morhua*) was investigated under field conditions in the shallow inshore waters off Newfoundland. A surface-controlled tagging frame was used to suspend and monitor baited transmitters (16 x 45 mm up to 16 x 108 mm) near the seafloor at depths ranging from 12.5 to 39.0 m. The behaviour of cod toward the transmitters was quantified using an underwater video camera. Cod ranging in size from 11 to 92 cm approached and touched the transmitters. Both biting and ingestion were size-dependent. Eight successful taggings were completed with cod ranging in size from 34 to 92 cm. Transmitters deployed in the morning were consumed faster (mean soak time = 3.3 hr) than transmitters deployed in the afternoon (mean soak time = 9.1 hr). Tracking revealed that cod were active immediately following tagging, suggesting no effect of the tagging procedure. Individual fish were tracked for periods ranging from 5.6 to 18.8 d, with none of the fish regurgitating transmitters during the period for which they were tracked.

3.2 Introduction

The scientific community has recently been challenged to adopt ethical tagging techniques (Smolowitz and Wiley 1998). This is in response to a growing use of electronic tracking devices such as transmitters, transponders, and data storage tags used to monitor movements of aquatic animals. The large number of studies devoted to examining tagging-related effects on fish (see reviews by Holm et al. 1999; Lucas and

Baras 2000, Bridger and Booth 2003; Jepsen et al. 2002) are evidence that researchers are concerned about the bias that such devices may have on the behaviour and survival of the animals under investigation. Among the tagging techniques now available, there is a growing number of *in situ* field techniques designed to minimize invasive tagging procedures. These techniques are executed underwater and involve either surgical implantation (Starr et al. 2000), forced intragastric insertion (Parrish and Moffitt 1993), or voluntary ingestion (e.g. Priede et al. 1991) of electronic devices.

In situ voluntary ingestion is the least invasive tagging technique currently available to researchers working with piscivorous species. Tracking devices are placed inside bait and deployed underwater where they are ingested voluntarily by fish. This form of intragastric tagging is advantageous because it eliminates stress associated with capture, anaesthetization, attachment, and handling. Several abyssal species have been successfully tagged using voluntary ingestion, including grenadier *Coryphaenoides* sp. (e.g. Armstrong et al. 1991), Portuguese dogfish *Centroscymnus coelolepis* (Bagley et al. 1994), and blue antimora *Antimora rostrata* (Bagley et al. 1994). However, the pursuit of less invasive tagging techniques by telemetry researchers has also lead to the recent application of this technique to shallow water studies. To date, several groundfish species have been tagged in inshore waters (< 250 m), including whiting *Merlangius merlangus* (Engås et al. 1996), wolffish *Anarhichas* sp. (Godø et al. 1997), ling *Molva molva* (Løkkeborg et al. 2000), and Atlantic cod *Gadus morhua* (e.g. Engås et al. 1998).

Atlantic cod is a suitable species for voluntary ingestion since adult fish readily ingest baited transmitter packages. Cod tagged in this manner have been shown to exhibit improved transmitter retention, food consumption, and survival in comparison to other intragastric tagging techniques (Chapter 2). The purpose of this study was to evaluate a low cost tagging frame suitable for the *in situ* tagging of cod in shallow water (< 40 m). I also examined the behaviour of cod toward baited acoustic transmitters and track tagged fish to determine post-tagging behaviour and transmitter retention.

3.3 Materials and Methods

Study Site

The study was conducted on the northeast coast of Newfoundland in the inshore waters of Smith Sound, Trinity Bay (48°12.2' N, 53°53.2' W) during the month of July in 1996 and 1997. Deployment of the tagging frame and subsequent tracking of fish were conducted using the research vessel *CCGS Shamook*. Deployment sites were located within a 0.2 nautical mile radius of each other and were selected on the basis of known fish abundance and suitable anchorage for the vessel. Sunrise and sunset occurred at approximately 0430 and 1955 Newfoundland Standard Time (NST) respectively and civil twilight extended from 0350 to 2030 NST.

Tagging Frame

The tagging frame consisted of upper and lower sections connected by four ropes and had a total height of approximately 3.9 m (Fig. 3.1). The upper section (0.75 x 0.75 m) served as a mounting platform for a pan and tilt unit, underwater camera, and light. The lower section (1.0 x 1.5 m) was heavily weighted and designed to rest on the seafloor to provide stability against tides or currents. A calibrated pole was attached to two ropes located mid-way between the camera and the base of the frame. Baited transmitters were

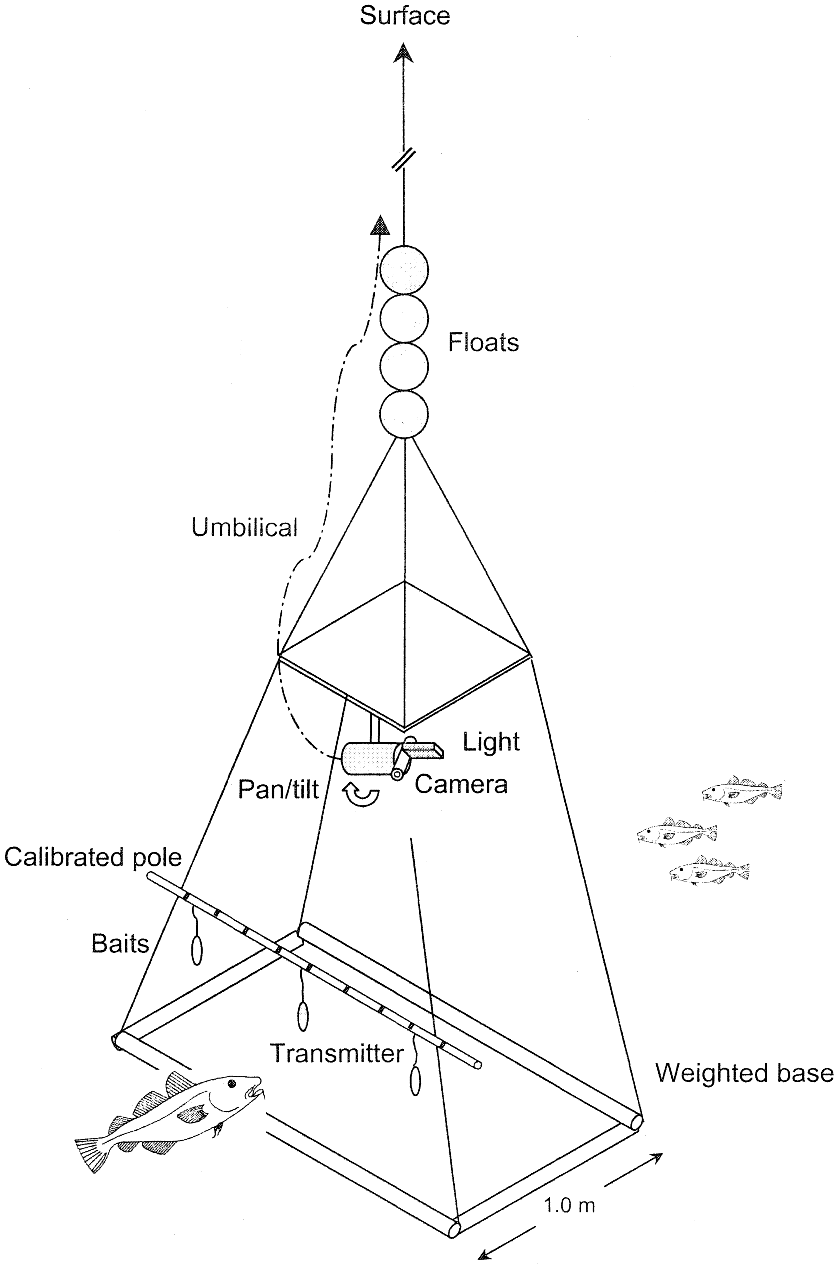

Figure 3.1: Tagging frame used for *in situ* voluntary ingestion of baited acoustic transmitters by Atlantic cod.

suspended from the pole using lines of thread and were positioned within the field of view of the camera. A high definition colour camera (Simrad/Osprey, OE1365) was used during the daytime deployments without the need for artificial lighting. At night, an Intensifier Silicon-Intensifier Target Tube (ISIT) monochrome camera (Simrad/Osprey, OE1325) was used under low light conditions (capable to 5×10^{-6} lux) in conjunction with a 150 watt halogen light. Either camera could be mounted to the pan and tilt unit (Simrad/Osprey, OE1147B) which was capable of rotating $\pm 170^{\circ}$ in the horizontal and vertical planes. The pan and tilt unit, camera, and light were connected to the research vessel by an umbilical cable and operated using a surface control unit (Simrad/Osprey, OE1236A). This arrangement permitted continuous monitoring of the baited transmitters and allowed for immediate retrieval of the tagging frame once they were consumed.

During the study, the tagging frame was baited with one or two transmitters and two or three additional mackerel baits to increase the odour plume. Transmitters were 16 mm in diameter and varied in length from 45 to 108 mm (Vemco Ltd., Lotek Wireless Inc). Weight of the transmitters ranged from 25.1 to 41.0 g in air and 12.0 to 19.3 g in water. Individual transmitters were wrapped in a thin fillet of mackerel and enclosed in a hand-sewn mesh sac made either from nylon hosiery or cheesecloth.

Behaviour Toward Baited Transmitters

Fish behaviour toward the baited transmitters was observed onboard the research vessel in real time and was recorded on 8 mm videocassette. A total of 9.3 hr of video footage was collected for the purpose of behavioural analysis and estimation of fish sizes. Cod behaviour toward the transmitters was quantified by recording the frequency of several modal action patterns (Table 3.1; Barlow 1968) similar to those exhibited by cod toward baited hooks (e.g. Fernö and Huse 1983; Løkkeborg et al. 1989). A behavioural response was recorded if a fish demonstrated any sequence of one or more of these action patterns. Each sequence began with an approach and terminated when the fish turned away from the transmitter. Individual fish were monitored for as long as possible and their total length estimated (to the nearest cm) using image analysis software. If a fish left the field of view of the camera for more than 1 min, the next arrival was considered to be a new fish (as in Løkkeborg et al. 1989).

Tracking

Cod which voluntarily ingested baited transmitters were tracked to determine post-tagging behaviour and transmitter retention. Automated tracking was conducted using a VR20 radio acoustic positioning (RAP) system (Vemco Ltd.) as described in detail by Voegeli et al. (2001). I used an array of four radio-linked hydrophone buoys anchored to the seafloor in the shape of a diamond with distances between adjacent buoys ranging from 400 to 800 m. The position of individual cod within the array could be determined at a rate up to once every 15 to 20 s and was transmitted by VHF radio to the research vessel (see Section 7.5 for a discussion on the limitations of this system). Swimming speeds were then calculated as a function of the elapsed time and distance between successive positions. If cod left the array, manual tracking was conducted using a VR60 ultrasonic receiver with a hand-held V10 directional hydrophone (Vemco Ltd.). Cod were tracked routinely for as long as possible until either they migrated out of the study site or the study was terminated.

Table 3.1: Definition of the five modal action patterns displayed by Atlantic cod toward baited acoustic transmitters.

Modal Action Pattern	**Description**
Approach	Swimming toward the baited transmitter in a directed manner.
Touch	Contact with the baited transmitter by the lips or barbel.
Incomplete Bite	Biting the baited transmitter, without fully engulfing into the mouth.
Complete Bite	Fully engulfing the baited transmitter into the mouth.
Ingestion	Successful removal of the baited transmitter from the tagging frame by breaking the attachment thread.

3.4 Results

Seven deployments of the tagging frame were conducted during the two field seasons, two in 1996 and five in 1997. Each deployment to the seafloor was performed during daylight hours between 0600 and 1815 NST. The period of time spent on the seafloor ranged from 0.6 to 14.0 hr (mean = 5.6 hr, s.d. = 5.6) with overnight deployments on two occasions. The combined period for all deployments was 39.0 hr, consisting of 22.0 hr during the day and 17.0 hr during the night. Deployment sites ranged in depth from 12.5 to 39.0 m and bottom temperature from 1.1 to 6.9 ^{o}C.

A total of 150 cod demonstrated a behavioural response toward the baited transmitters during the period for which video footage was collected. The number of modal action patterns performed by individual fish ranged from 1 to 25 (mean = 3.1, s.d. = 3.8), with 468 behavioural sequences recorded in total (Table 3.2). Cod of all sizes (11 to 92 cm) approached and touched the baited transmitters. Approach rates were approximately once every 0.5, 1.0, and 2.8 min during the morning, afternoon, and night, respectively. Of the 468 approaches recorded, 294 (62.8%) were followed by a touch. Biting and successful ingestion of the transmitters was size-dependent. Incomplete bites were observed on 37 (7.9%) occasions by cod $\geq$ 21 cm and complete bites were observed on seven (1.5%) occasions by cod $\geq$ 34 cm (Note: eight successful taggings were completed, however only seven were observed by camera). All cod which demonstrated a complete bite were successful at ingesting and removing the transmitter.

The range of fish sizes observed in the vicinity of the tagging frame in 1996 (11 to 92 cm, mean = 28.8, s.d. = 11.4) was similar to 1997 (11 to 89 cm, mean = 26.0, s.d. = 12.9). However, smaller fish ($\leq$ 20 cm) contributed less to the proportion of behavioural

Table 3.2: Number of observations, their relative proportion, and fish lengths for each modal action pattern displayed by Atlantic cod toward the baited acoustic transmitters.

Modal Action Pattern	Observations	Proportion	Fish length (cm)		
			Min.	Max.	Mean (s.d.)
Approach	468	1.000	11	92	26.7 (8.8)
Touch	294	0.628	11	92	28.0 (9.1)
Incomplete Bite	37	0.079	21	92	35.3 (17.4)
Complete Bite	7	0.015	34	92	61.9 (25.9)
Ingestion	7	0.015	34	92	61.9 (25.9)

sequences observed in 1996 (2.1%) compared to 1997 (21.4%). Bottom type at the 1996 deployment sites was characterized as flat and sandy, whereas the 1997 sites consisted of boulders and macro-algal patches. Shoals of small fish were observed seeking shelter among the latter, accounting for their increased encounter rate with the tagging frame in 1997. Smaller cod were quickly displaced from the vicinity if larger cod were present and interspecific competition was low as cod appeared to be the dominant predator in the area.

Eight successful taggings were completed during the study, three in 1996 and five in 1997 (Table 3.3). These cod ranged in length from 34 to 92 cm (mean = 64.8 cm, s.d. = 25.4) and ingested transmitters that were 5.3 to 27.1% (mean = 14.8%, s.d. = 6.8) their body length. The period of time elapsed between the initial touch and successful removal of the transmitter, or handling time, ranged from 5.2 to 31.7 s (mean = 15.6 s, s.d. = 8.8) and increased with relative transmitter size ($r^2 = 0.535$, $p = 0.062$). All transmitters were consumed during daylight hours. The period of time elapsed until transmitters were consumed ranged from 0.6 to 14.0 hr and was dependent on the timing of deployment. Transmitters deployed prior to 1200 hr were consumed the fastest and had a mean soak time of 3.3 hr (s.d. = 2.1). Transmitters deployed in the afternoon and evening had a mean soak time of 9.1 hr (s.d. = 7.4), with two of the three not consumed until the following morning. Video footage was collected for seven of the eight taggings. The single unobserved ingestion occurred on 23 July 1997. During this deployment, the transmitter (16 x 108 mm) broke free from the tagging frame and was lost from sight of the camera for reasons unknown. Acoustic tracking of the transmitter revealed that it

Table 3.3: Details of individual Atlantic cod tagged *in situ* by allowing them to voluntarily ingest baited acoustic transmitters.

				Tagged		End of Track		
Fish	**Transmitter size (mm)**	**Length (cm)**	**Handling time (s)**	**Date**	**Time (NST†)**	**Date**	**Time (NST†)**	**Days Tracked**
1	16 x 108	92	9.2	12-Jul-96	0600	25-Jul-96	0630	13.0
2	16 x 92	34	31.7	12-Jul-96	1235	25-Jul-96	0945	12.9
3	16 x 108	55	9.3	12-Jul-96	1404	22-Jul-96	1300	10.0
4	16 x 45	37	17.0	12-Jul-97	1450	31-Jul-97	1016	18.8
5	16 x 80	41	18.5	13-Jul-97	0550	31-Jul-97	0835	18.1
6	16 x 45	85	5.2	13-Jul-97	0700	26-Jul-97	1622	13.4
6*	16 x 108	85	---	23-Jul-97	1850	29-Jul-97	0950	5.6
7	16 x 92	89	18.3	24-Jul-97	1045	31-Jul-97	1150	7.1

†Newfoundland Standard Time (GMT - 3.5 hr)

*Not observed by camera

was ingested at 1850, approximately 0.6 hr following deployment. Further tracking revealed that it had been ingested by Fish No. 6, which was tagged 10 d previously on 13 July 1997 and now contained two transmitters for the remainder of the study.

Tracking of Fish No. 6 and 7 immediately following tagging suggested no detrimental effect of the tagging procedure. Fish No. 6 had a mean swimming speed of 0.24 m/s (s.d. = 0.12) and swam a cumulative distance of 1085 m over a period of 1.25 hr. Fish No. 7 had a mean swimming speed of 0.41 m/s (s.d. = 0.14) and swam a cumulative distance of 637 m over a period of 0.6 hr. Both cod swam actively and restricted their movement to the vicinity where the tagging frame had been deployed during the periods monitored.

Tracking over several days revealed wide ranging geographic movements characteristic of adult cod. Manual tracking was often necessary as cod frequently moved out of range of the positioning system. Regurgitation of transmitters was not observed. All cod were continuously moving up to the point at which either they migrated out of the study site or the study was terminated. The number of days individuals were tracked ranged from 5.6 to 18.8 (Table 3.3).

3.5 Discussion

Instrumental to any tracking study are decisions regarding when and where to conduct tagging activities. With *in situ* voluntary ingestion, this means choosing an effective strategy for deployment of the tagging frame. If information is known about the activity rhythms and habitat preferences of the size and species targeted, then informed decisions can be made regarding the timing and location of deployment. In the current study, the timing of deployment affected tagging efficiency. I found that baited transmitters deployed earlier in the day were consumed on average nearly three times faster than those deployed later in the afternoon. This change in tagging efficiency may have been related to a diel change in the activity rhythm of cod. Feeding behaviour and activity levels of adult cod have been shown to vary diurnally (Løkkeborg et al. 1989; Løkkeborg and Fernö 1999), with a pronounced increase in activity during daylight hours. These findings support this observation, given that cod approached the baited transmitters with greater frequency during the day compared to the night and all transmitters were ingested during the day despite overnight deployments.

Choice of deployment location is important as different species and size-classes may not be distributed homogeneously within a study area. If other piscivorous species are present, then interspecific competition for the food source may occur (e.g. Godø et al. 1997). In the current study, interspecific competition was not observed, although differences in the size-distribution of cod were evident between the 1996 and 1997 sites. This was probably attributed to differences in water depth and bottom type. Coastal juvenile cod are known to preferentially select habitats consisting of algal beds and boulders (Gregory and Anderson 1997) as well as adjust their use of space diurnally (Cote et al. 1998) in order to reduce predation risk. By comparison, adult cod do not experience high predation risk (Pálsson 1994) and tend to forage over a wider geographic range (Løkkeborg 1998), explaining their presence in the open sandy areas (1996 sites).

To achieve successful taggings, baited transmitters must provide 1) sufficient visual or gustatory incentive to stimulate fish to bite, 2) suitable shape and size for physical ingestion, and 3) suitable taste and texture to initiate an irreversible swallowing reflex (see Sutterlin et al. 1982). In the current study, I found that the length of the baited package appeared to be a limiting factor in determining successful ingestion. Research on the size-selectivity of longline fishing gears has demonstrated that the size, shape, and type of bait can all influence the size-distribution of fish caught (e.g. Huse and Soldal 2000). In addition, the texture of the material used to enclose a transmitter and bait may be important. Løkkeborg (1991) reported an increase in the mean length of cod caught by longline when using bait placed in nylon sacs compared to bait alone. In the current study, I found that both nylon hosiery and cheesecloth material worked well in constructing baited packages, however I did not investigate their comparative tagging effectiveness.

Cod in the current study retained intragastric transmitters for periods up to 18.8 d without regurgitation. Previous field studies using voluntary ingestion have reported various retention times for cod. Løkkeborg and Fernö (1999) reported initial regurgitation as early as seven to eight days for cod (40 - 50 cm) tagged with transmitters 16 x 48 and 16 x 80 mm. Estimation of the maximum retention time under field conditions has been difficult to determine as adult cod tend to migrate out of tracking range. The longest retention observed to date has been 68 days (Engås et al. 1996). This is comparable to the maximum retention of 77 days observed under laboratory conditions (Chapter 2).

In summary, I found that the tagging frame worked successfully and that voluntary ingestion of baited transmitters was an effective method for the intragastric tagging of cod under field conditions. Variation in tagging efficiency observed in this study indicates that additional research is needed to improve deployment and baiting strategies. The tagging procedure did not appear to adversely affect natural behaviour and transmitter retention was sufficient for short-term tracking studies.

3.6 Acknowledgements

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Chapter 4. Temporal use of swimming speeds by individual Atlantic cod (*Gadus morhua*) determined using acoustic telemetry

4.1 Abstract

Although several studies have previously reported *in situ* swimming speeds for Atlantic cod (*Gadus morhua*) using acoustic telemetry, few have reported high resolution tracking for individual fish in an effort to quantify within- or between-individual variation. In this study, the movements of acoustically tagged Atlantic cod were recorded throughout the diel cycle during the summer in a fjord in northern Norway. Using a stationary positioning system, high resolution tracking produced more than 29,000 estimates of *in situ* swimming speed. The frequency distribution and temporal use of swimming speeds are presented for individual juvenile and adult cod (~30 to 60 cm). Swimming speeds below 1.0 bl/s were most common (>70%), with all fish swimming on average within the aerobic scope for this species. Swimming speeds exceeding 2.0 bl/s were observed on occasion, with the indication that juvenile cod exhibited a wider range of speeds compared to larger conspecifics. Individual variation in swimming speed and diel activity rhythm was observed among juvenile and adult cod. Functional explanations for this variation may be related to individual differences in balancing the conflicting demands of foraging and predator avoidance.

4.2 Introduction

Juvenile and adult Atlantic cod (*Gadus morhua*) exhibit significant variation in *in situ* swimming speeds over diel and seasonal time scales. Using acoustic telemetry, several proximate factors have been identified, including water temperature (Clark and Green 1990), ambient light level (Løkkeborg 1998; Løkkeborg and Fernö 1999), and habitat complexity (Cote et al. 2002). Functional explanations for the different behavioural patterns have been associated with maximizing foraging and growth, minimizing energy expenditure, and predator avoidance. In many cases, these patterns have been reported on the basis of pooling telemetry data for multiple fish. While this could provide the best picture of species-specific behaviour, it effectively conceals information about individual fish and their use of swimming speed. Pooling also obscures variation among individual fish, given that factors intrinsic to an individual's state such as hunger, condition, motivation, and experience can have significant effects on the decisions it makes (Krebs and Kacelnik 1993).

Sampling frequency can be a critical factor when investigating fish behaviour at small spatial and temporal scales. If tracking resolution is too low, loss of accuracy may occur (Baras 1998). For single-channel positioning systems, the interval between successive position fixes is largely determined by the number of fish tracked. Choosing the optimal balance between position-fixing interval and the number of fish tracked can be a difficult decision. Recent studies have shown that increasing the interval can quickly introduce bias into the estimation of the distance travelled, swimming speed, activity rhythm, and movement pattern (Lagardère et al. 1990; Løkkeborg et al. 2002). Achieving the highest possible tracking resolution is therefore important in order to accurately assess activity level and spatial dynamics.

In this study, I examined the individual movements of acoustically tagged Atlantic cod using a stationary positioning system. Emphasis was placed on tracking only a few fish in order to reduce the position-fixing interval and achieve high tracking resolution. *In situ* swimming speeds are presented for individual cod tracked throughout the diel cycle during summer in the inshore waters of northern Norway.

4.3 Materials and Methods

Study Site and Tracking

The experiment was carried out in August-September 2000 in the inshore waters of Ramfjord, northern Norway (69°33'N, 19°07'E). Water depth ranged from 50 to 70 m and water temperature at the seabed was 5-6 °C. Sunrise and sunset occurred at approximately 0450 and 2030 hours respectively and civil twilight extended from approximately 0330 to 2155 hours.

Eight cod were tagged *in situ* by allowing them to voluntarily ingest a transmitter (V16-3H, Vemco Ltd., 16mm in diameter and 58 mm in length) wrapped in mackerel bait. An underwater camera mounted on a tagging frame was used to identify the species and size of fish that ingested the transmitters, similar to that described by Engås et al. (1996). Once tagged, the cod were tracked by means of a stationary positioning system (VRAP, Vemco Ltd.). The system consisted of an array of three hydrophone buoys anchored to the seafloor in a triangular configuration with radio transmission to a base station on board a research vessel. The transmitters emitted acoustic pulses and based on the delay times of the pulses at the hydrophones, the base station was able to calculate the position of the fish. A number of pulse-times were received over a 10 s period and an average position was calculated and logged to disk. Adding time for data transmission between the buoys and base station, the minimum time between position fixes was 17 s.

The system was capable of tracking several fish tagged with transmitters operating on different frequencies, but monitored only one frequency at a time. Thus the time elapsed between successive positions for each fish varied with the number of fish being tracked. Only a few fish (usually ≤ 3) were tracked at any given time in order to reduce the position-fixing interval and achieve high tracking resolution. See Section 7.5 for a full discussion on the limitations of this system.

Data Analysis

The movements of four cod, two juveniles and two adults, were selected for detailed analysis on the basis of their data quality (Table 4.1). As erroneous positions can occur with stationary positioning systems (Smith et al. 1998), the fish tracks were first visually inspected and any invalid positions were discarded. Swimming speeds were then calculated as a function of the elapsed time and distance between successive positions for intervals ≤ 120 s. The distance swum between positions was assumed to be in a straight-line and therefore swimming speeds are expected to represent minimum estimates. When several fish were tracked simultaneously, swimming speed was assumed to be underestimated due to bias associated with increasing the position-fixing interval (single-channel positioning systems). This bias was corrected using the relationship previously reported for cod in this study area (Løkkeborg et al. 2002), allowing the estimation of swimming speed over an interval of 17 s. Finally, swimming speeds were removed if they were considered biologically impossible. The criteria for this decision was based on whether the elapsed time between two positions exceeded the endurance capable of cod for a given speed. These were identified using the logarithmic

Table 4.1: Individual Atlantic cod tracked in Ramfjord, Norway, during August-September 2000.

Fish No.	**Length (cm)**[*]	**Start of Track**		**End of Track**		**Days Tracked**
		Date	**Time**	**Date**	**Time**	
1	30	23-Aug-00	0946	05-Sep-00	1203	13.1
2	30	24-Aug-00	1029	05-Sep-00	1155	12.1
3	42.5	29-Aug-00	1942	04-Sep-00	1921	6.0
4	55-60	26-Aug-00	1833	05-Sep-00	1158	9.7

[*] Fish length was estimated from video observations using reference marks on the tagging frame, except for fish 3 which was caught and measured.

relationship for cod endurance;

$$\log E = 4.87 - 2.27U$$

where E is swimming endurance in s and U is swimming speed in m/s (Winger et al. 2000). Using each of the criteria mentioned above, approximately 2% of the original dataset was discarded.

Statistical comparison of individual cod was conducted using a Kruskal-Wallis one-way ANOVA. Multiple comparisons between fish were performed according to Siegel and Castellan (1988) using an error rate of $\alpha = 0.05$. To determine whether cod exhibited different swimming speeds at different times of day, I divided the 24 hr cycle into 3 hr periods for each fish and compared the swimming speeds during these related periods using a Friedman ANOVA.

4.4 Results

Cod were tracked for periods ranging from 6.0 to 13.1 d (Table 4.1), producing a total of 29,040 estimates of swimming speed. The distribution of swimming speeds for each cod was skewed to the right, with fewer observations at increasing speeds (Fig. 4.1 and 4.2). In each case, the distribution was roughly unimodal with the modes ranging from 0.1 to 0.4 bl/s. Instantaneous swimming speeds ranged from 0.0 to 164.1 cm/s (0.0 to 5.1 bl/s) and mean hourly speeds ranged from 23.1 to 38.9 cm/s (0.7 to 0.9 bl/s) over the observation period (Table 4.2). A comparison of the cod revealed a significant difference in both absolute swimming speed ($\chi^2 = 1935.78$, df = 3, $p < 0.0001$) and length-specific swimming speed ($\chi^2 = 231.84$, df = 3, $p < 0.0001$). Pairwise comparisons subsequently revealed that each cod was significantly different from each of its

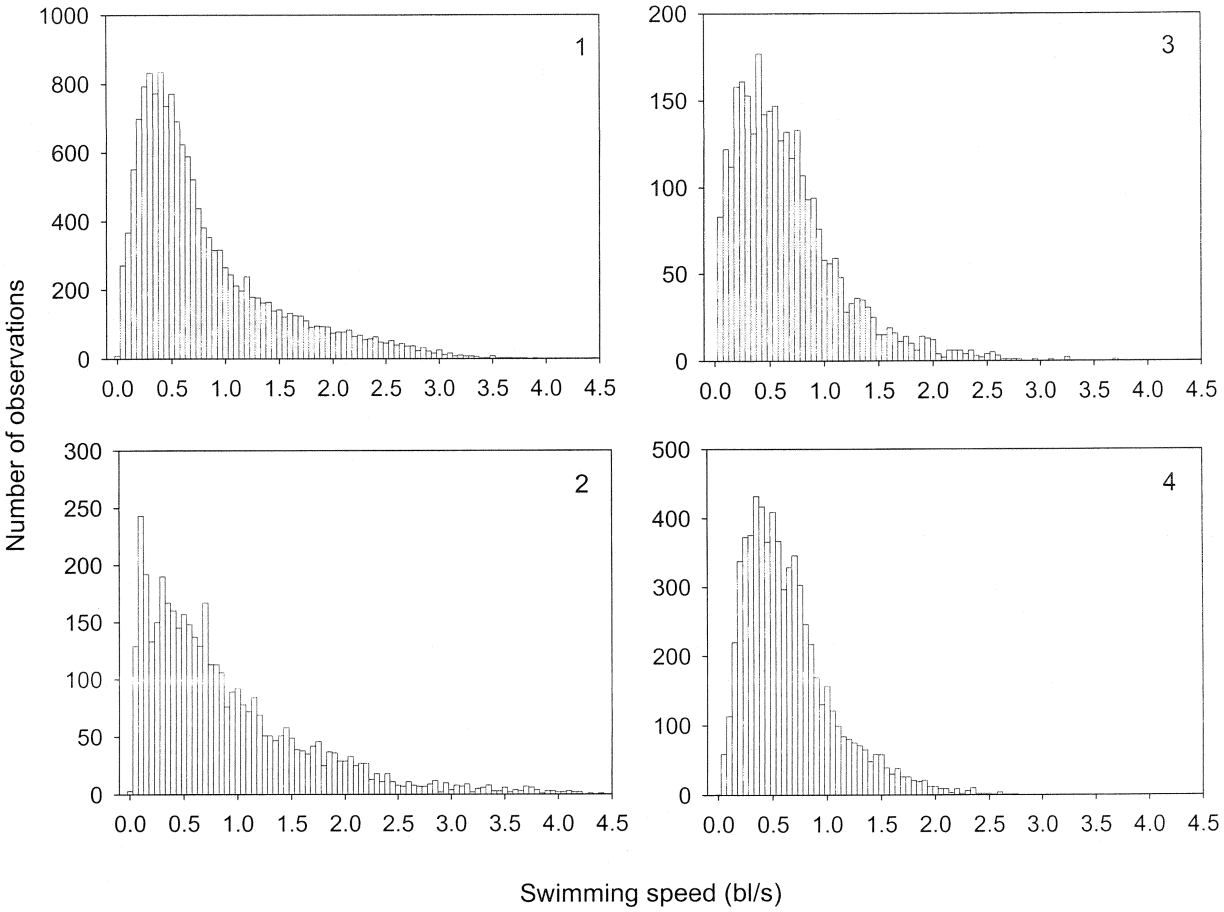

Figure 4.1: Frequency distribution of swimming speed (bl/s) for individual Atlantic cod in Ramfjord, Norway during August-September 2000. Numbers located in the top corner of each panel refer to the individual fish.

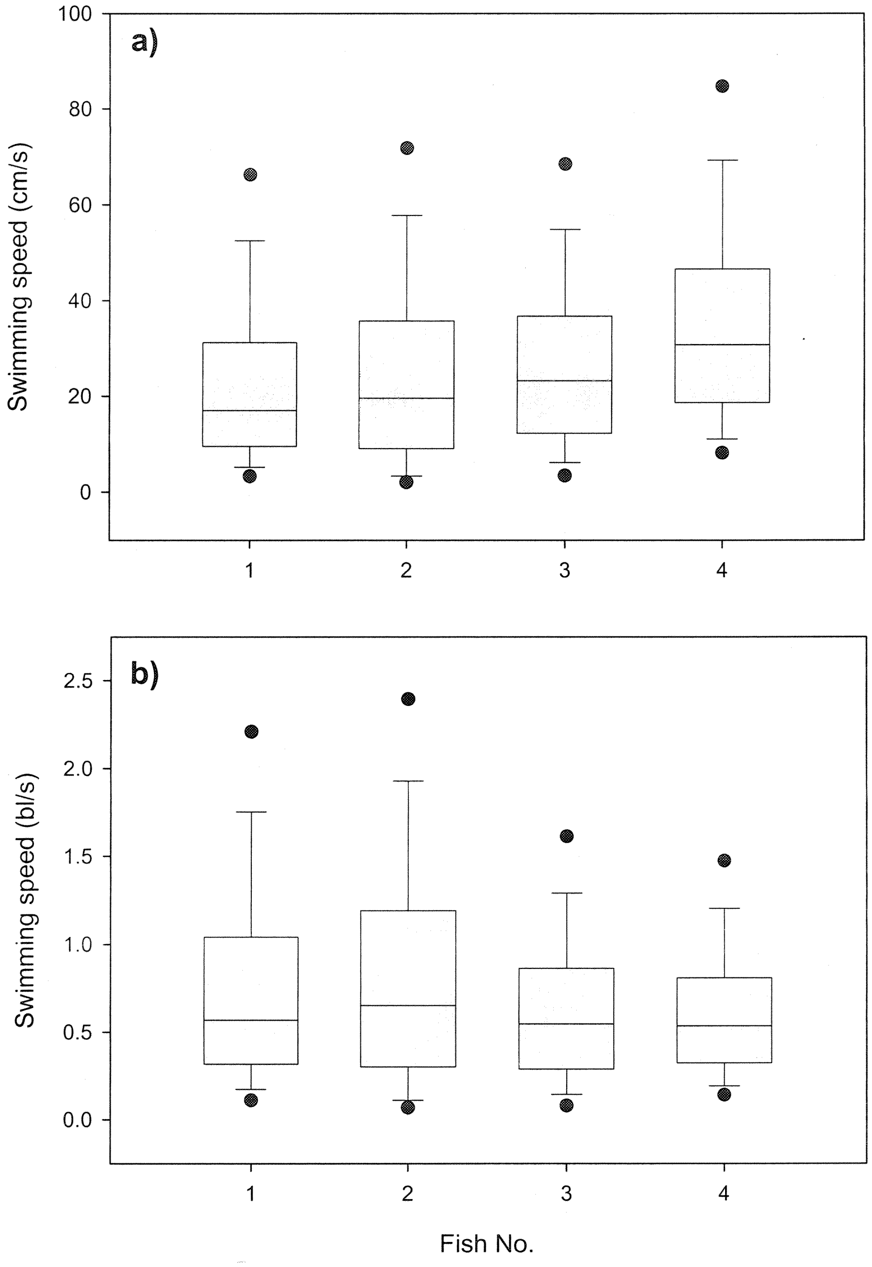

Figure 4.2: Boxplots of a) absolute swimming speed, and b) length-specific swimming speed for individual Atlantic cod (1-4) in Ramfjord, Norway during August-September 2000. Bars represent 10th and 90th percentiles, while black circles represent 5th and 95th percentiles.

Table 4.2: Summary statistics for the swimming speeds of individual Atlantic cod tracked in Ramfjord, Norway, during August-September 2000. Speeds presented are based on 60 min observation periods.

	Speed (cm/s)			Speed (bl/s)		
Fish No.	**Mean**	**Min**	**Max**	**Mean**	**Min**	**Max**
1	23.08	2.62	52.86	0.77	0.09	1.76
2	27.14	7.20	62.79	0.90	0.24	2.09
3	28.67	13.24	58.29	0.67	0.31	1.37
4	38.93	18.34	62.22	0.68	0.32	1.08

conspecifics in both absolute and length-specific swimming speed ($p < 0.05$).

The frequency of use of higher swimming speeds, i.e. greater than 2.0 bl/s, was size-dependent (Fig. 4.3). Swimming speeds greater than 2.0 bl/s constituted 7.1 and 9.0% of all swimming speeds for juvenile fish 1 and 2, compared to only 2.0 and 0.7% for adult fish 3 and 4, respectively. Speeds in the range of 3.0 to 4.0 bl/s were observed for all but the largest cod (no. 4) and speeds exceeding 4.0 bl/s were only observed among the juvenile cod.

Variation between individual cod was also attributed in part to different activity rhythms (Fig. 4.4). Although each fish remained active throughout its diel cycle, time of day had a significant effect on the swimming speeds employed by each cod (Friedman ANOVA, $p < 0.0001$). Among the juveniles, fish 1 exhibited increased activity near dawn and fish 2 exhibited a pronounced suppression in activity during the midday, followed by a marked increase in activity during the late afternoon and evening. Fish 3, the smallest adult fish, showed a minor increase in activity at both dawn and dusk. These three fish thus had a tendency to suppress activity around noon. The largest adult (fish 4) exhibited a weak diurnal rhythm with a slight increase in activity during the daylight hours.

4.5 Discussion

The cod in this study were continuously active, swimming on average within the aerobic scope for this species (Tang et al. 1994; Reidy et al. 2000). The majority of speeds were within the sustained swimming speed range, with only a fraction potentially anaerobic. The maximum sustained swimming speed (U_{ms}) for cod has been estimated

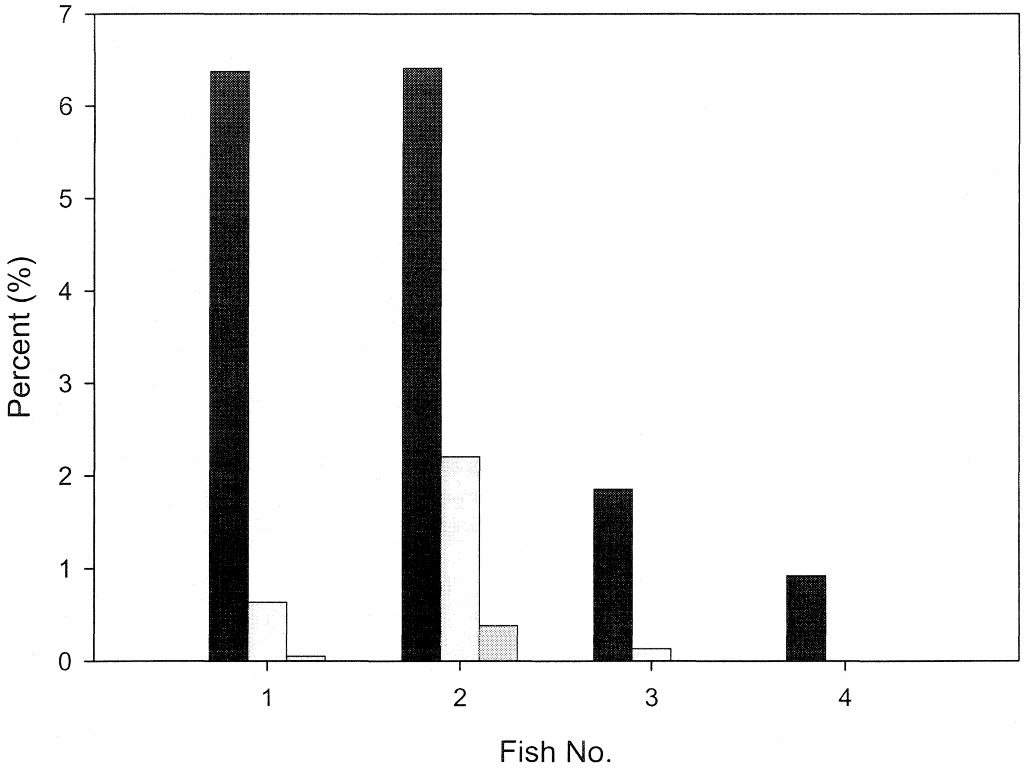

Figure 4.3: Percent use of higher swimming speeds by individual cod in Ramfjord, Norway during August-September 2000. Black (2-3 bl/s), grey (3-4 bl/s), and dark grey (> 4 bl/s).

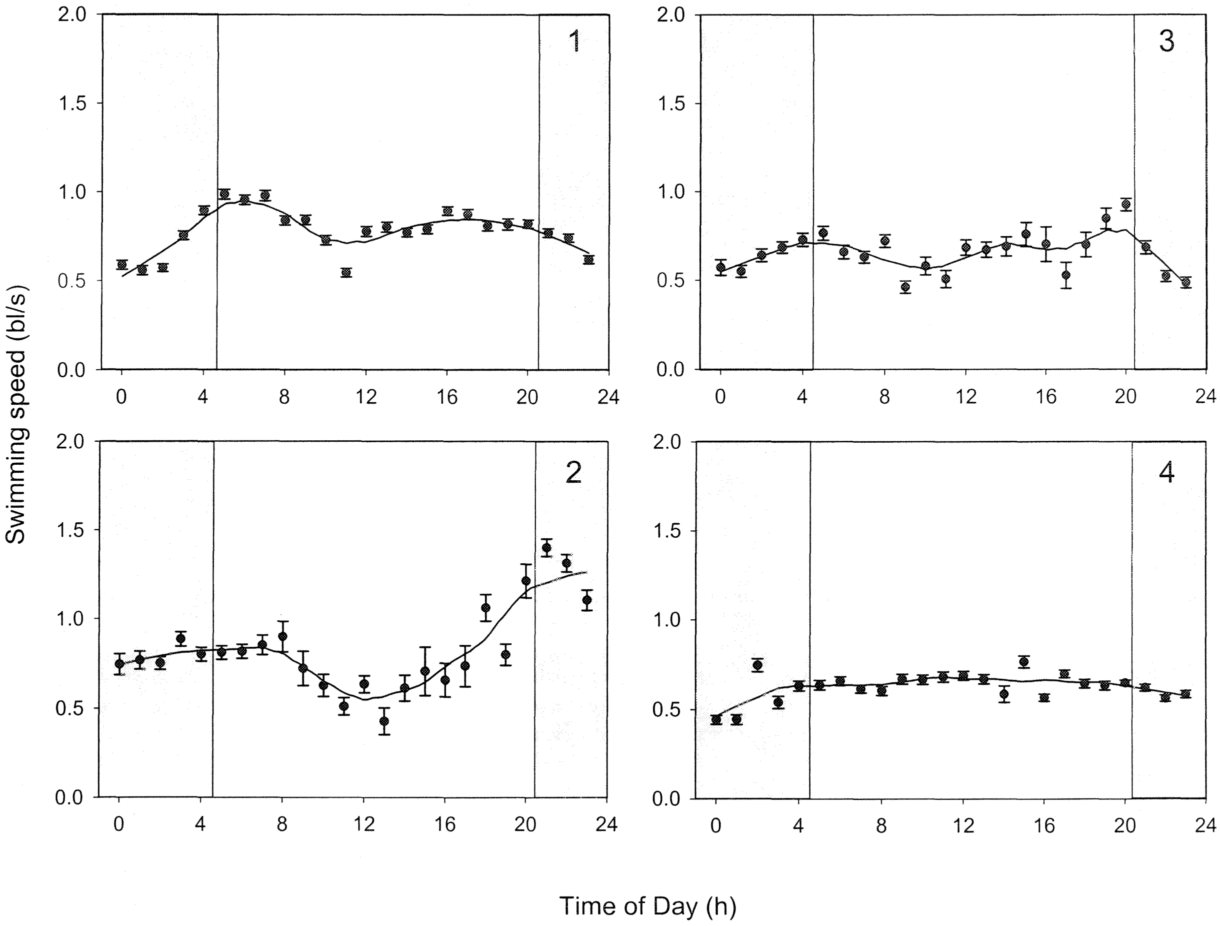

Figure 4.4: Daily activity rhythms (bl/s) for individual Atlantic cod in Ramfjord, Norway during Aug-Sept 2000. Swimming speeds are binned by the hour for all days. Error bars denote standard error of the mean. Shaded areas represent dark hours and delineate both sunrise and sunset. Solid line is fitted using a Loess smoother.

under laboratory conditions to be between 42.0 - 90.0 cm/s (He 1991; Winger et al. 2000), depending on the population, fish size, and water temperature. According to these benchmarks, approximately 4 - 7% of the swimming speeds observed in this study could have been anaerobically fuelled. The unimodal frequency distributions provide no indication of distinct behavioural patterns separated on the basis of swimming speed. Rather, it appears the activities of juvenile and adult cod require a blend of swimming speeds. As foraging is the predominant activity at this time of year, this blend of speeds may reflect searching, with and without environmental cues, for a wide range of prey organisms using both chemical and visual senses with variations related to the diel cycle (Løkkeborg 1998; Løkkeborg and Fernö 1999).

Juvenile cod are expected to regulate their activity in order to maximize foraging and growth while minimizing the risk of predation. The three smallest cod in this study exhibited a suppression of activity during the highest light levels (noon) as well as an increased activity during the dawn and/or dusk periods. The occurrence of crepuscular and nocturnal activity may reflect 1) opportunistic foraging on planktonic prey that change in availability over the diel cycle, or 2) predator avoidance behaviour (Lima and Dill 1990). Both types of activity rhythm have been previously reported for juvenile cod of this size at this time of year (Clark and Green 1990; Cote et al. 2002). However, previous studies have never observed both activity rhythms among conspecifics at the same time and within the same habitat. These results suggest that juvenile cod may be capable of making different trade-offs in balancing the conflicting demands of foraging and predator avoidance. These trade-offs may change within an individual over time, for example in response to the level of satiation.

Adult cod, by comparison, do not experience a high risk of predation (Pálsson 1994) and as such their activity rhythm is expected to reflect an opportunistic foraging strategy. Both stomach content analysis (Adlerstein and Welleman 2000) and acoustic tracking (Løkkeborg and Fernö 1999) have shown that adult cod are effective foragers throughout the diel cycle. The weak diurnal rhythm exhibited by fish 4 suggests that this individual was capable of foraging throughout the diel cycle with near equal efficiency. This behaviour is similar to activity rhythms reported for adult cod during the spring (Løkkeborg 1998), but does not clearly exhibit the expected decline in nighttime activity for cod at this time of year as reported by Løkkeborg and Fernö (1999).

Average swimming speeds in this study were approximately 2.0-3.0 times higher than the mean speeds previously reported for coastal (Løkkeborg 1998; Løkkeborg and Fernö 1999; Cote et al. 2002) and migratory cod (Rose et al. 1995; Wroblewski et al. 2000) of similar sizes. I attribute this difference to the reduced position-fixing interval, i.e. high tracking resolution, and swimming speed correction (see Data Analysis) applied in this study. Lagardère et al. (1990) and Løkkeborg et al. (2002) have previously demonstrated that reducing the time interval between positions can lead to a substantial increase in the estimation of swimming speed. This suggests that the mean speeds presented in earlier studies on cod may be underestimated. The results from this study indicate that when stationary positioning systems are operated at high resolution, they are capable of recording prolonged swimming speeds (i.e. > U_{ms}) that exceed the aerobic capacity of cod (Winger et al. 2000). Careful examination of the tracks has lead me to believe that this behaviour is not an artifact of erroneous positioning (Smith et al. 1998) or false movement (Cote et al. 2002).

Differences in the proportion of higher length-specific swimming speeds among the cod could be related to both size-specific energy budgets and differences in behavioural expression. As aerobic capacity typically increases with decreasing fish size (Goolish 1991), juvenile cod are expected to use proportionally more aerobic metabolism to fuel activity and have relatively less oxygen debt to repay during recovery, compared to their larger conspecifics (see Tang et al. 1994). This may explain, in part, the relatively large proportion of high length-specific swimming speeds observed for the juvenile cod in this study. Interestingly, juvenile cod seem to use both high and low swimming speeds in relation to their size more frequently than adult cod. Restricted movements may be related to antipredator behaviour in the same way as decreased activity at noon. High swimming speeds, on the other hand, may reflect escape from predators or reactions to prey. A possible explanation for the similar absolute speeds of small and large cod is that these represent the speeds required to catch mobile prey, irrespective of the size of the predator.

In summary, individual variation in *in situ* swimming speeds and diel activity rhythms was observed among juvenile and adult cod in northern Norway during the summer season. These results are based on over 29,000 estimates of swimming speed for four fish. Tracking of additional fish and detailed spatial analyses will be necessary in order to define the extent to which variation exists within and between individual cod and to determine functional explanations for the different behaviour patterns.

4.6 Acknowledgements

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Chapter 5. Seasonal variation in the diel activity rhythms of adult Atlantic cod in Smith Sound, Newfoundland

5.1 Abstract

Monitoring the activities of fish can provide insights into the ecological decisions fish make. These decisions are expected to affect the spatial and temporal patterns of activity over diel and seasonal time scales. Using a stationary positioning system, diel activity rhythms of acoustically tagged adult Atlantic cod (*Gadus morhua*) inhabiting the inshore waters of Smith Sound, Newfoundland were investigated during summer (July) and winter (January-March) seasons over a two year period. During summer, cod were active throughout the diel cycle with a pronounced increase in activity during daylight hours. Individual mean speeds ranged from 10.6 to 25.0 cm/s and between individual variation was high. During winter, cod occupied deeper water and were significantly less active. Individual mean speeds ranged from 2.9 to 10.7 cm/s and between individual variation was low. Several proximate factors responsible for this seasonal variation in activity level are discussed.

5.2 Introduction

Like other taxa, fish are constantly engaged in making important behavioural decisions based on ecological factors (Dill 1987). Over the lifetime of an individual, choices must be made such as when and where to feed, whether to avoid predators, and how much energy to allocate toward reproduction. Each time a fish chooses a certain behaviour over one or more alternatives, it is assumed that the individual has behaved so as to maximize benefits and minimize costs toward itself (Noakes 1992). Biological and environmental conditions can exert a strong influence on how fish balance these trade-offs. The outcome is expected to affect the spatial and temporal patterns of activity (Ali 1992) and be observable at the population level (Fréon and Misund 1999). Recent studies investigating the activity rhythms of Atlantic cod (*Gadus morhua*) inhabiting coastal areas have revealed variation in activity level at both diel and seasonal time scales. For juvenile cod, explanations for this variation have mainly been attributed to changes in ambient light intensity, predation risk, and habitat complexity (e.g. Clark and Green 1990; Grant and Brown 1998; Cote et al. 2002). For adult cod, studies during the late spring through autumn periods have shown that foraging is the primary activity, with diel and seasonal differences in activity levels associated with changes in foraging tactic and seasonal day length (Løkkeborg 1998; Løkkeborg and Fernö 1999; Kallayil et al. 2003). High resolution tracking of individual cod has indicated that between individual differences in activity rhythm may be significant (Chapter 4). Studies investigating cod in the offshore using archival data storage tags have also shown seasonal and diel changes in activity levels linked to migration, spawning, and feeding (e.g. Godø and Michalsen 2000; Righton and Metcalfe 2002).

In Newfoundland waters, cod have traditionally moved into offshore regions during the winter months to avoid cooling seawater temperatures in the inshore region (see Lilly et al. 2001 for review). During the late 1980s and early 1990s, observations of overwintering cod in Trinity Bay on the northeast coast of Newfoundland renewed interest in the ecology of inshore cod populations (e.g. Wroblewski et al. 1994, 1995; Brattey 1997; Brattey and Porter 1997; Porter et al. 1997; Smedbol and Wroblewski 1997). Since then, several studies have investigated the movements of adult cod in a number of Newfoundland bays (Green and Wroblewski 2000; Robichaud and Rose 2001, 2002, 2003). However studies investigating fine-scale activity rhythms have only been conducted for juvenile cod (Clark and Green 1990; Cote et al. 2002).

The purpose of this study was to investigate seasonal variation in the diel activity rhythm of adult cod in coastal Newfoundland. The study was conducted in Smith Sound, Trinity Bay, a region known to support a very large and dense winter aggregation estimated at times to be as large as 25,000 t (Lilly et al. 2001; Rose 2003). The study was conducted over a two year period in which acoustically tagged cod were tracked for periods up to three weeks during both winter and summer seasons.

5.3 Materials and Methods

Study Area:

The study was conducted during the summer and winter seasons of 1996-98 in the inshore waters of Smith Sound on the northeast coast of Newfoundland, Canada (Fig. 5.1). Smith Sound is one of the three fjord-like arms on the western side of Trinity Bay. It is approximately 1 nm wide and 25 nm long, opened on both ends, shallow (less than 10 m) at its western point and moderately deep at its eastern entry into Trinity Bay. In addition to historically supporting a summer inshore cod fishery, the region is also known to support an overwintering population (Wroblewski et al. 1994, 1995; Lilly et al. 2001) which in recent years has formed into a very large and dense winter aggregation estimated to be as large as 25,000 t at times (Lilly et al. 2001; Rose 2003). This aggregation is often located in a deep narrow trench approximately 5 nm long with depths ranging from 200-220 m.

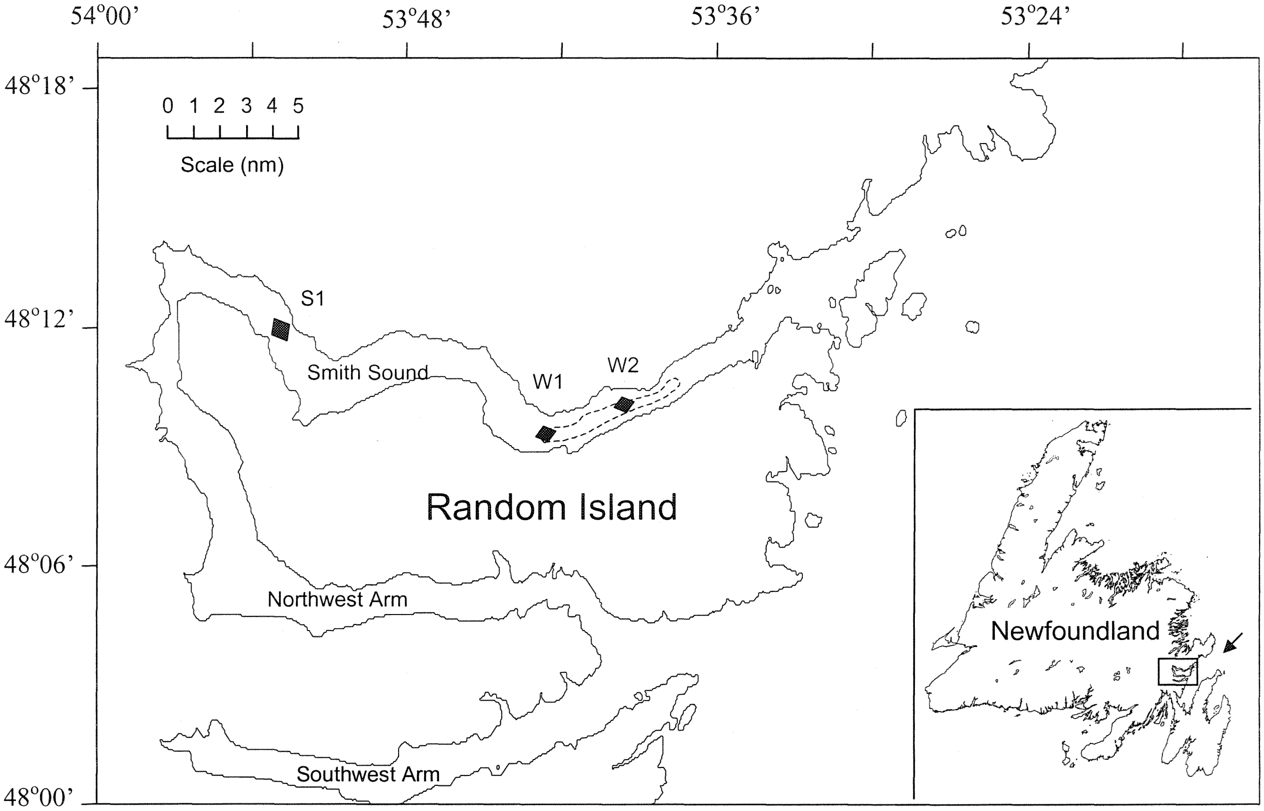

Figure 5.1: Map of the study area, located in Smith Sound, Newfoundland. The acoustic positioning system was deployed during the summer seasons at site S1 and during the winter seasons at sites W1 and W2. Dashed line represents the 200 m depth contour of the trench.

Summer field seasons were conducted during July in 1996 and 1997 near the western end of the Sound (48° 12.2′ N, 53° 53.2′ W; Fig. 5.1). Water depth at this site (S1) ranged from 10 to 40 m. Steep temperature gradients were observed in both years, with surface water temperatures of 15.5 and 11.7 °C and bottom temperatures of 6.0 and 6.9 °C for 1996 and 1997 respectively (Fig. 5.2). Bottom type was observed by underwater camera and was characterized as flat and sandy with several large boulders and large macro-algal patches (Chapter 3). Sunrise and sunset occurred at approximately 04:30 and 19:55 Newfoundland Standard Time (NST) respectively.

Winter field seasons were conducted during March in 1997 and January-February in 1998 at two sites near the middle of the Sound (48° 09.6′ N, 53° 40.8′ W; Fig. 5.1). I was unable to use the summer site during the winter due to an absence of fish, and instead focused on the large aggregation of cod present in the 200 m trench. The westerly site (W1), with a water depth of 100–210 m, spanned a section of the edge and bottom of the trench and was used in both years. The easterly site (W2), with a depth of 200–220 m, was located near the middle of the trench and was used only in 1998. Temperature gradients were absent in both years (Fig. 5.2), with surface temperatures (-1.1 to -0.8 °C) similar to bottom temperatures (-0.2 to 0.2 °C) for each year and site. Detailed knowledge of the bottom habitat at these locations is limited, but navigation charts indicate the presence of mud and gravel (Canadian Hydrographic Service 1996) and underwater video has confirmed the presence of mud nearby (G. Lilly, Fisheries and Oceans Canada, Newfoundland Region, pers. com.). Sunrise and sunset were approximately 06:15 and 18:15 NST in 1997, and 07:20 and 17:25 NST in 1998, respectively.

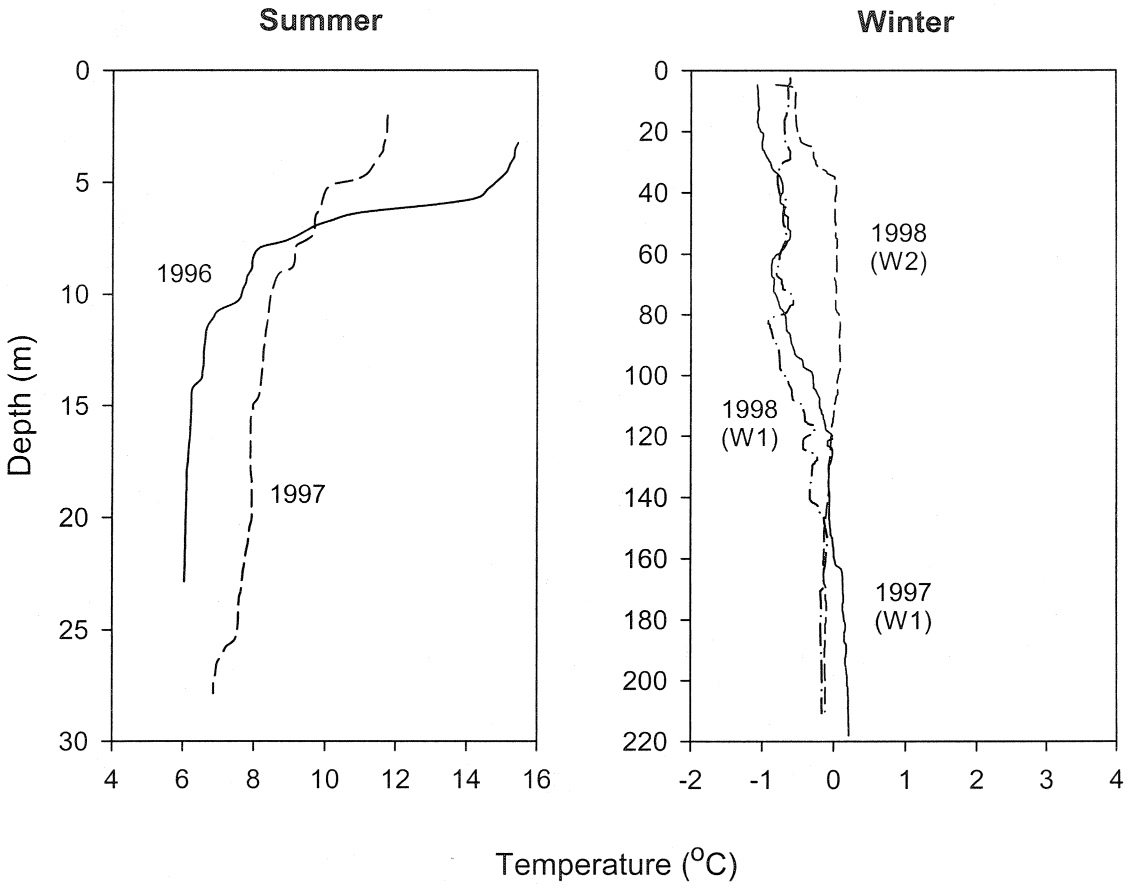

Figure 5.2: Vertical temperature profiles recorded at each of the tracking sites in summer (site S1) and winter (sites W1 and W2).

The study was conducted using the vessel "CCGS Shamook". The vessel was equipped with an echosounder (Simrad EQ100), CTD, longlines, and bottom trawl for the collection of biological and environmental information. A limited number of fishing sets were conducted near the study sites to gather biological information on community structure as well as the length, sex, maturity, and stomach contents of cod.

Tagging:

Cod were tagged using one of three methods, including one *in situ* technique and two requiring capture and handling. The *in situ* technique was performed underwater and was the least invasive of the three methods. Using a surface-controlled tagging frame, individual transmitters were wrapped in mackerel bait and lowered to the seafloor where they were voluntarily swallowed by cod (see Chapter 3 for details). Due to the limited depth capability of the tagging frame, it was only used during summer to tag a total of 7 cod ranging in length from 34 to 92 cm (mean = 64.8 cm, s.d. = 25.4).

The remaining cod were tagged onboard the research vessel. These fish were captured by handline, longline, or bottom trawl and were brought to the surface as slowly as possible to reduce the effects of barotrauma. The fish were held in subsurface holding cages or in onboard tanks for an average of 1.9 d prior to tagging. Following this, care was taken to only select cod that appeared in good physical condition and that were able to maintain proper buoyancy and equilibrium. Twenty cod (total length 53-90 cm, mean = 69.0 cm, s.d. = 10.2) were tagged externally by attaching a transmitter below the first dorsal fin. Stainless steel wires 0.5 mm in diameter were passed horizontally through the upper dorsal musculature in the manner described by Bridger and Booth (2003) and were anchored on the opposite side of the fish using Petersen discs. The remaining cod ($n = 3$, 52–60 cm, mean = 55.7 cm, s.d. = 4.0) were tagged intragastrically by pushing a transmitter slowly past the oesophagus and into the stomach cavity in the manner described in Chapter 2. The majority of fish were tagged without anaesthetic as cod in this region, especially in winter, are lethargic and easily handled without apparent stress to the animal (Wroblewski et al. 1994; Robichaud and Rose 2002). If cod were overly active, they were gently anaesthetized using 2-phenoxyethanol (dosage: 1 ml : 8 L seawater). Once tagged, the fish were held onboard for an average of 2.7 h for post-tagging observation and then released into the study area. Given that cod were initially retrieved from deeper water (> 150 m) in some cases, I cannot rule out the probability that some individuals may have experienced a ruptured swimbladder (Harden Jones and Scholes 1985; Arnold and Greer Walker 1992). If this were the case, healing is expected to have been quick, with cod acquiring a functional swimbladder within a few days (Godø and Michalsen 2000).

Transmitters used in this study were 16 mm in diameter and varied in length from 45 to 108 mm (Vemco Ltd., Lotek Wireless Inc), depending on the size of the fish. Weight of the transmitters ranged from 25.1 to 41.0 g in air and 12.0 to 19.3 g in water. Similar size transmitters have been used on adult cod (e.g. Godø 1995; Løkkeborg and Fernö 1999; Robichaud and Rose 2002) without any report of adverse affects on behaviour or swimming capability.

Tracking:

Automated tracking was conducted using a VR20 radio acoustic positioning

(RAP) system (Vemco Ltd.) as described in detail by Voegeli et al. (2001). This consisted of four radio-linked hydrophone buoys anchored to the seafloor in the shape of a diamond with distances between adjacent buoys ranging from 400 to 800 m. The position of individual cod within the array was determined at a rate up to once every 15 to 20 s and was transmitted by VHF radio to the research vessel (see Section 7.5 for a discussion on the limitations of this system). If cod left the array, manual tracking was conducted using a VR60 ultrasonic receiver with a hand-held V10 directional hydrophone (Vemco Ltd.). Cod were tracked routinely for as long as possible during each field season until they either migrated out of the study site or the study was terminated.

Analysis:

The movements of cod recorded during each of the four field seasons (i.e. two summer and two winter) were examined for variation in diel activity rhythm. Positions recorded within the first 24 h of release were deleted to reduce any bias in behaviour associated with stress due to capture and tagging. However, given that most of the fish had been released for several days (mean = 3.6 d) before the RAP system was deployed and tracking commenced, it is assumed that any short-term bias was minimized. As erroneous positions can occur with stationary positioning systems (Smith et al. 1998), the fish tracks were visually inspected and any invalid positions were discarded. Swimming speeds were calculated as a function of the elapsed time and distance between successive positions for intervals ≤ 300 s. Swimming speeds were removed if they were considered biologically impossible. The criteria for this decision was based on whether the elapsed time between two positions exceeded the endurance capable of cod for a given speed. These were identified using the logarithmic relationship for cod endurance;

$$\log E = 4.87 - 2.27U$$

where E is swimming endurance in s and U is swimming speed in m/s (Winger et al. 2000). All statistical analyses were conducted using SYSTAT 10.2. A general linear model for repeated measures was used to examine the effects of year, season, and fish length on diel activity rhythm.

5.4 Results

Biological Information:

The length composition of cod sampled was different between the summer and winter seasons but consistent within each season across years (Fig. 5.3). During summer, cod ranged from 11 to 143 cm with a pronounced modal peak observed near 30 cm. During winter, cod ranged from 9 to 104 cm with two modal peaks observed near 35cm and 55 cm.

During the summer of 1996, 43% of individuals were sexually immature and 57% were near spawning condition or had already spawned. Fewer fish (15%) were immature during the summer of 1997, with 85% of the cod in the pre-spawning, spawning, or spent stage. In contrast, during both winters the gonads were either sexually immature (24% in 1997 and 20% in 1998) or in the early stages of maturation for the current spawning season.

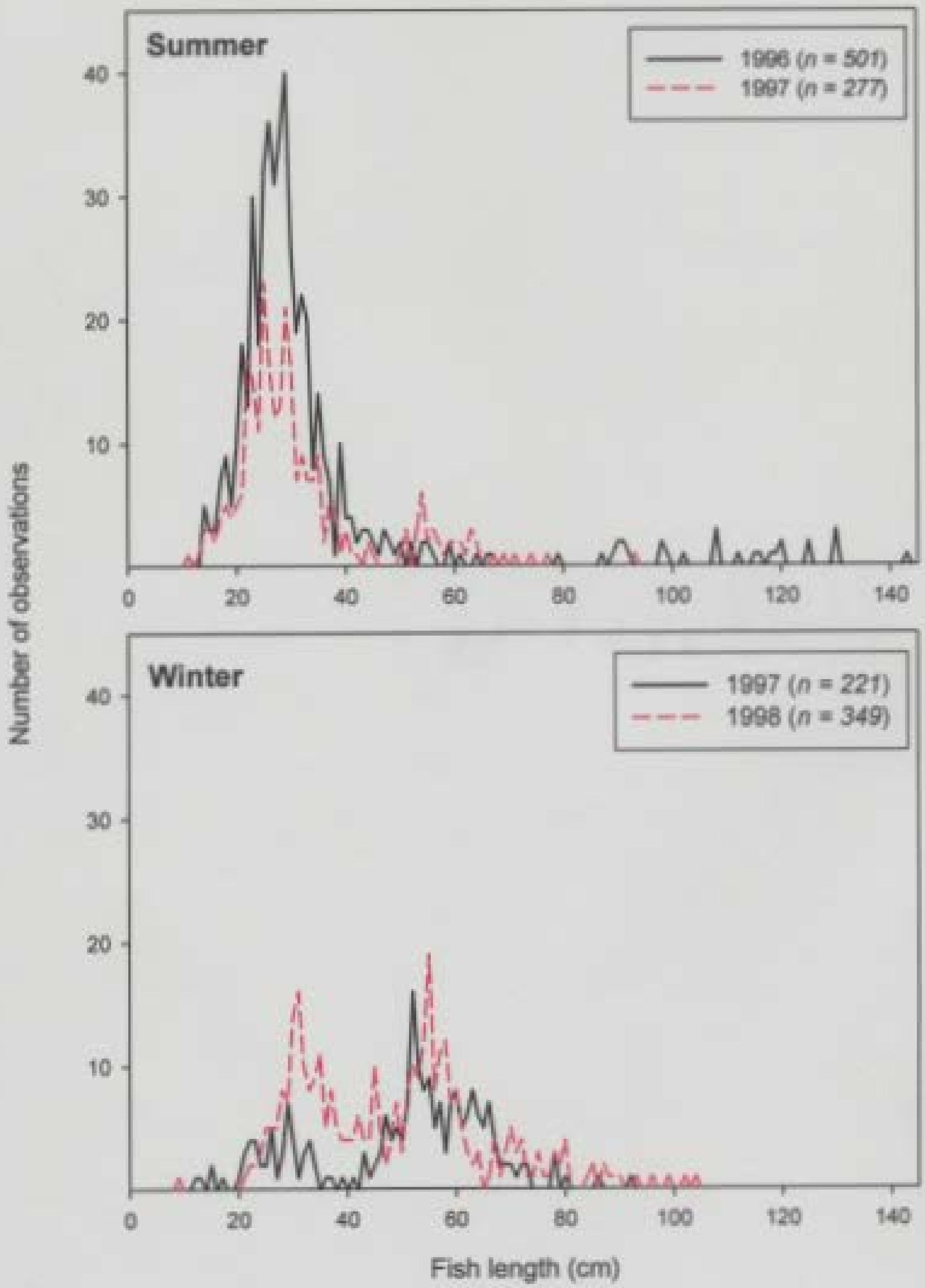

Figure 5.3: Length (cm) frequency of cod from catches near the Smith Sound study areas, 1996-1998.

Stomach samples revealed an obvious difference in the feeding level of cod between summer and winter. During the summer of 1996 and 1997, an average of 73% (n = 50) and 85% (n = 41) of cod respectively, had food items dominated by finfish and shellfish in their stomachs. Feeding was reduced during winter, with an average of only 7% (n = 6) in 1997 and 24% (n = 10) in 1998 of cod with food, dominated by finfish and echinoderms in their stomachs.

Catches of finfish and shellfish in the summer fishing sets revealed 8 species of finfish (dominated by cod and American plaice *Hippoglossoides platessoides*) and two crab species, some of which were identified in the stomach contents of cod. During winter, catches in the trench contained mostly cod with small catches of three flatfish species and crab (1997 only), while fishing sets less than 200m contained a wide variety of finfish species (n = 8 in 1997 and n = 15 in 1998) and three species of crab.

Echograms recorded during each of the field seasons revealed a seasonal difference in the density and distribution of cod at the study sites (Fig. 5.4). During summer, the density of cod was low and the distribution widespread. During winter, densities were substantially higher, corresponding with the increase in biomass that has recently been documented at this time of year (Brattey 1997; Rose 2003). The distribution in 1997 was characterized as patchy and off bottom while in 1998 it was aggregated and close to the seafloor.

Activity Rhythms:

A total of 30 cod were tagged and released in Smith Sound during the four field seasons. Of these, 14 left the study area soon after release, two exhibited reduced activity

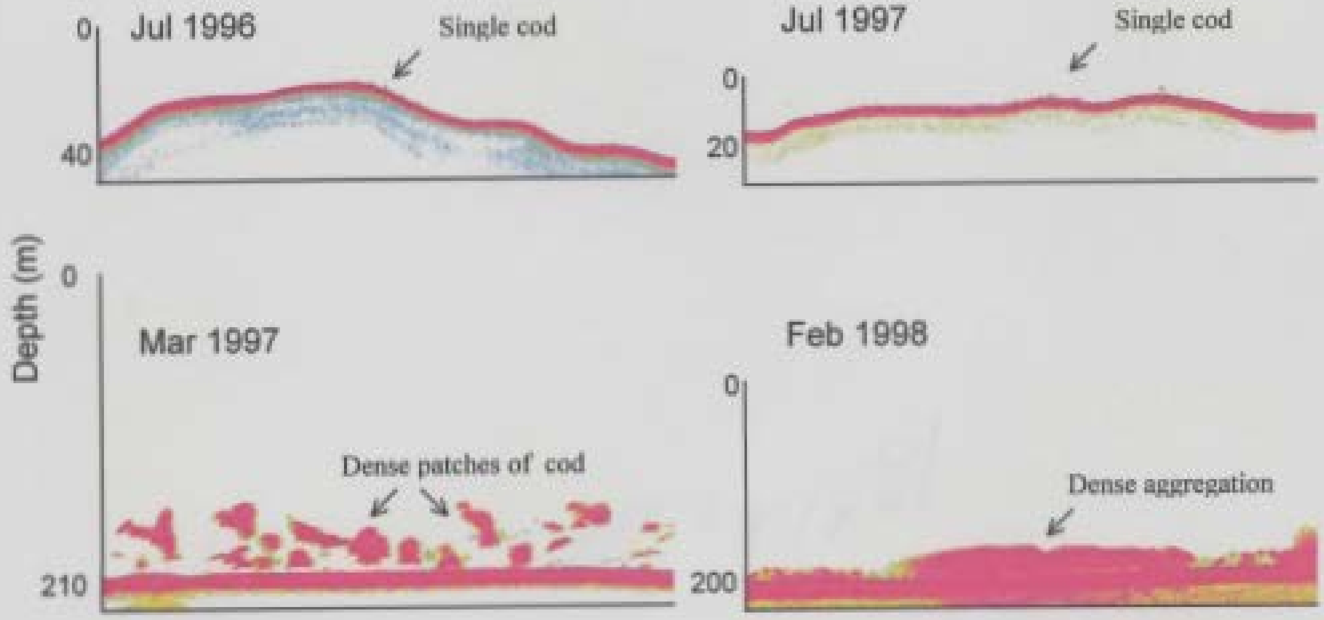

Figure 5.4: Echograms produced by the vessel's echosounder (Simrad EQ100) during each of the four field seasons. Transects range from 0.3 to 0.4 nm and were each recorded during midday at the tracking sites. In summer, the density of cod was low and the distribution widespread. In winter, densities were higher with a patchy off bottom distribution observed in 1997 and an aggregated mass close to the seafloor observed in 1998. The seabed is delineated by the solid black line.

Table 5.1: Summary statistics for individual Atlantic cod tracked in Smith Sound, Newfoundland, during the summer and winter seasons of 1996-98.

Fish No.	Length (cm)	Tagging Method	RAP Site	Released Date	Released Time	End of Track Date	End of Track Time	Days Tracked	No. of Speeds	Speed (cm/s) Mean	Speed (cm/s) CV
Summer											
1	72	external	S1	23 Jul 96	1815	30 Jul 96	1431	6.8	395	14.92	0.86
2	61	external	S1	24 Jul 96	1645	29 Jul 96	1921	5.1	180	24.44	0.69
3	37	voluntary	S1	12 Jul 97	1450	31 Jul 97	1016	18.8	1624	18.10	0.69
4	41	voluntary	S1	13 Jul 97	0550	31 Jul 97	0835	18.1	806	10.62	0.97
5	85	voluntary	S1	13 Jul 97	0700	29 Jul 97	0950	16.1	924	25.03	0.55
6	89	voluntary	S1	24 Jul 97	1045	31 Jul 97	1150	7.1	1761	16.05	0.49
Winter											
7	63	external	W1	9 Mar 97	1630	25 Mar 97	1334	15.9	1501	10.73	0.92
8	67	external	W1	13 Mar 97	1500	24 Mar 97	1024	10.8	1094	7.67	1.28
9	69	external	W1	13 Mar 97	1500	25 Mar 97	1317	11.9	893	8.91	1.32
10	64	external	W1,W2	31 Jan 98	1800	8 Feb 98	1532	7.9	5203	2.16	1.65
11	74	external	W1,W2	31 Jan 98	1800	23 Feb 98	1220	22.8	1427	2.86	1.90
12	74	external	W1	6 Feb 98	0753	19 Feb 98	1059	13.1	1393	2.06	1.59
13	53	external	W1	6 Feb 98	1835	18 Feb 98	0952	11.6	525	4.60	1.28

suspected to be associated with tagging by intragastric insertion (see Chapter 2) and were removed from the analysis, and one was suspected to have died. The remaining 13 cod stayed within tracking range for periods up to 22.8 d and produced a total of more than 17,400 estimates of swimming speed (Table 5.1).

During summer, cod were very active and exhibited wide geographic movements. Swimming speed was highly variable with individual mean speeds ranging from 10.6 to 25.0 cm/s. Cod were active throughout the diel cycle (Fig. 5.5), with a significant increase in activity recorded during daylight hours ($F = 2.57, p < 0.01$). Fish length did not explain any of the observed variation in activity ($F = 0.02, p = 0.90$) and no significant difference was observed between years ($F = 0.06, p = 0.80$).

During winter, cod tended to be less active although wide geographic movements were exhibited by certain individuals. Swimming speeds were less variable and significantly reduced compared to summer ($F = 15.01, p < 0.01$), with individual mean speeds ranging from 2.2 to 10.7 cm/s. In 1998, several cod released near site W1 moved east approximately 2 nm over a period of 3-5 d to site W2 located in the 200 m trench (e.g. cod 10 and 11). Activity levels were significantly higher in the winter of 1997 compared to 1998 (Fig. 5.5, $F = 176.89, p < 0.001$). A change in activity level over the diel cycle could not be detected in either year ($F = 0.65, p = 0.85$, and $F = 1.61, p = 0.08$, respectively) and fish length did not explain any of the observed variation in activity ($F = 0.13, p = 0.75$).

Four cod equipped with depth telemetering transmitters remained in the study area and provided information on depth-use. During summer, these cod (no. 2, 4, 5) occupied depths ranging from 7 to 35 m (mean = 14.4, S.E. = 0.9). Cod no. 5 showed

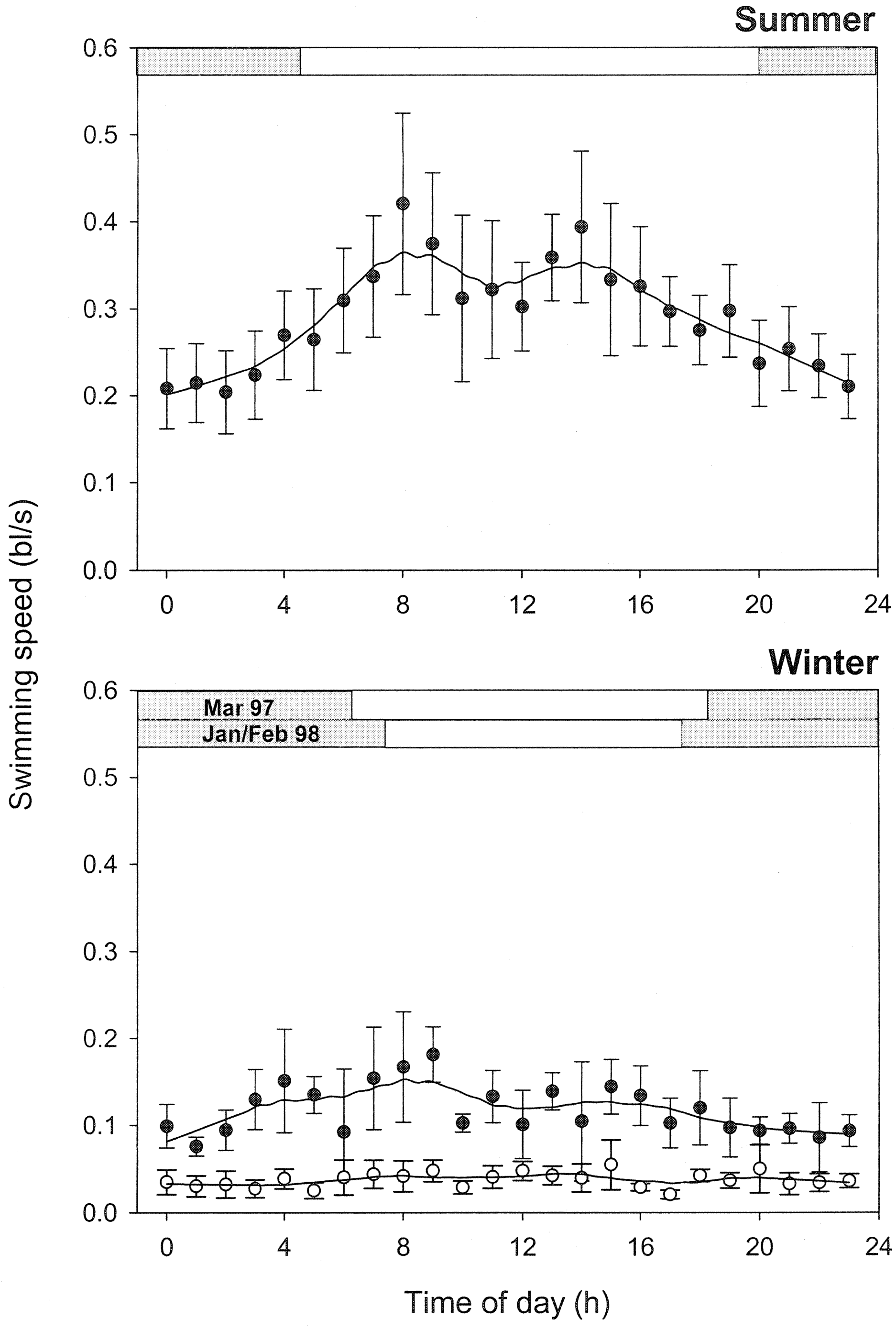

Figure 5.5: Daily activity rhythms (hourly mean ± S.E.) for Atlantic cod in Smith Sound during the a) summers of 1996 and 1997 combined and b) winters of 1997 (closed circles) and 1998 (open circles). Shaded areas represent dark hours and delineate both sunrise and sunset. Solid line is fitted using a Loess smoother.

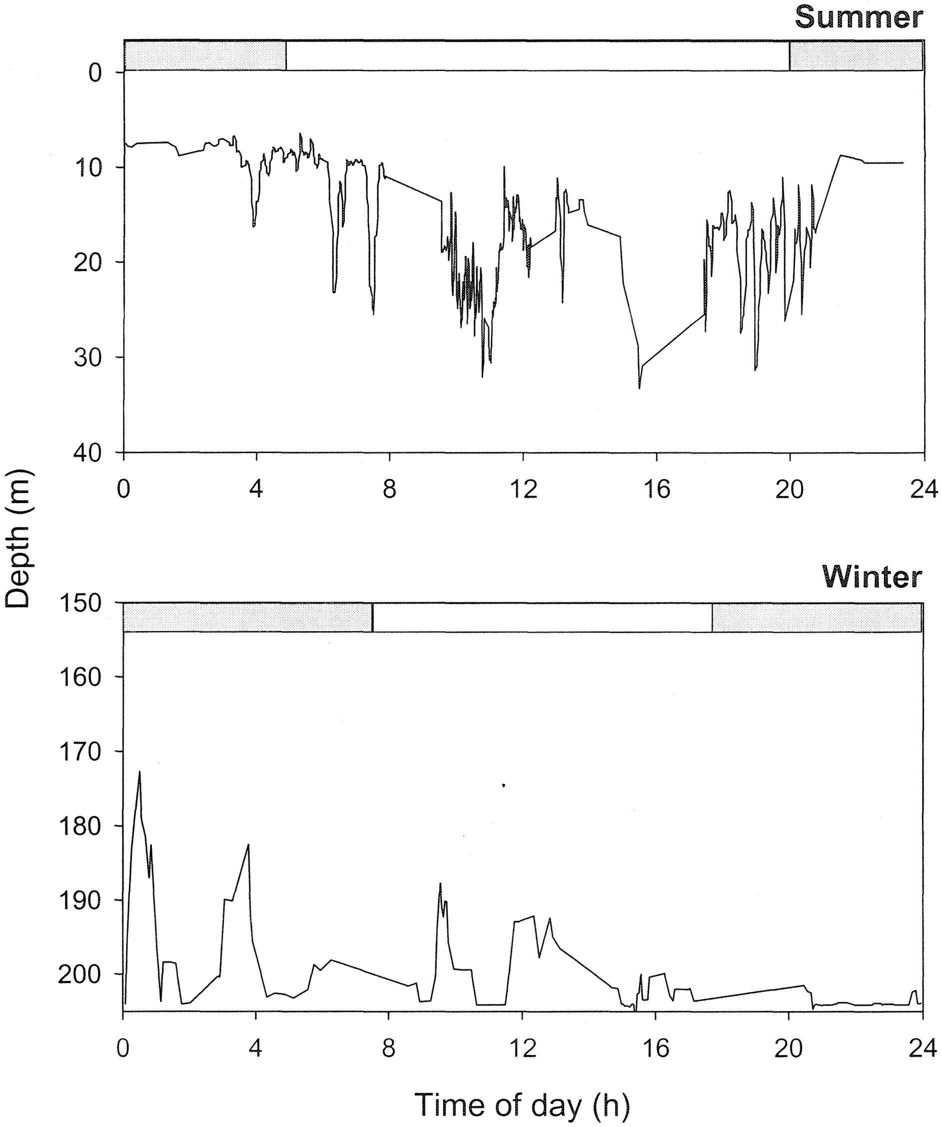

Figure 5.6: Examples of depth use by Atlantic cod in Smith Sound during a) the summer of 1997 by fish no. 5, and b) the winter of 1998 by fish no. 13. Shaded areas represent dark hours and delineate both sunrise and sunset.

systematic changes in depth on 28 Jul 1997 (Fig. 5.6a). The behaviour was closely associated with shifts between shallow and deep water habitat rather than migration into the pelagic zone. This fish inhabited the area near a large boulder in 6 m of water at night and again near noon, with periods in deeper water during mid morning and afternoon. Only one cod (no. 13) provided depth information during the winter. This fish occupied the 200 m trench and had an average water depth of 200.3 m. It exhibited frequent changes in depth throughout the diel period on 18 Feb 1998 (Fig. 5.6b) which did not appear to be associated with shifts in bottom habitat, but rather vertical movements off bottom within the large aggregation in the trench (Fig. 5.4).

5.5 Discussion

During summer, cod were active throughout the diel cycle with a pronounced increase in activity during daylight hours. This is consistent with the diurnal pattern of activity previously reported for adult cod inhabiting the inshore waters of Norway during the late spring (Løkkeborg 1998) and autumn seasons (Løkkeborg and Fernö 1999). Two functional explanations may account for this pattern of behaviour. First, adult cod in Smith Sound are expected to regulate their activity level in order to maximize foraging and growth, with changes in activity rhythm reflecting changes in foraging tactic. The reduction but not cessation of activity at night suggests that cod may have switched to chemically-mediated search patterns with the reduction in visual cues (see Løkkeborg 1998 for review). Second, cod in Smith Sound at this time of year may have been engaged in spawning activity. Catches from the experimental fishing revealed that adult cod in Smith Sound were in either pre-spawning, spawning, and post-spawning condition during the time of the study. This evidence of cod spawning inshore is consistent with a number of reports in the literature (e.g. Hutchings et al. 1993; Wroblewski et al. 1995, 1996) including Smedbol and Wroblewski (1997) who observed a peak in spawning from mid-June to mid-July for cod in this region. Laboratory studies have shown that cod are capable of spawning throughout the diel cycle (Kjesbu 1989) and that the courtship and mate selection behaviours entail active movements involving visual inspection, vocalization, and physical contact (Brawn 1961; Hutchings et al. 1999). Hence, it is probable that the tagged cod in this study may have been balancing the demands of both foraging and spawning activity. Differentiating between these behaviours was not within the scope of this study and would require further analysis of spatial and temporal patterns of movement.

During the winter, cod exhibited reduced swimming speeds and limited variation in activity over the diel cycle. Low water temperature is thought to be the key proximate factor responsible for this seasonal difference in behaviour. Previous tagging studies have reported cod in sub-zero temperatures in Smith Sound (Wroblewski et al. 1994; Brattey 1997) and recent underwater observations using a remote-operated-vehicle (ROV) have confirmed that these cod are lethargic and exhibit low vigilance toward approaching threats (G. Lilly, Fisheries and Oceans Canada, Newfoundland Region, pers. comm.). Cod at this time of year are also expected to begin allocating energy reserves toward sexual maturation in preparation for spring spawning (Hutchings and Myers 1994). Catches from the experimental fishing indicated that 76% of cod in 1997 and 80% in 1998 were beginning maturation for the coming year. This increase in reproductive effort may have also contributed to the reduced activity observed during this season. Finally, reduced activity may have been partly related to a lack of prey availability. Stomach samples indicated that the majority of cod in the trench had not been feeding. As cod is an opportunistic feeder and will apparently feed at this time of year (Walsh, unpublished data for Northwest Arm, Trinity Bay), increased activity might have been observed if more prey were available in Smith Sound. Alternatively, the lack of feeding might have been a function of shoal density given that feeding has been shown to drop when cod are densely aggregated (Lilly 1994).

My results indicated that the activity rhythm of cod was significantly higher in winter of 1997 compared to 1998. This difference in activity level combined with the systematic difference in distribution observed near the seafloor (Fig. 5.4), suggests that cod were engaged in different behaviours between the two observation periods. The echogram for March 1997 looks a lot like pre-spawning behaviour while the February 1998 echogram is more typical of over-wintering behaviour (G. Rose, Memorial University, pers. com.). Pre-spawning behaviour is known to be associated with off-bottom migration (e.g. Rose 1993) and may be a functional explanation for this difference in behaviour.

In summary, adult cod inhabiting the inshore waters of Newfoundland demonstrated seasonal variation in diel activity rhythm. During summer, cod were active throughout the diel cycle with a pronounced increase in swimming speed during daylight hours. In contrast, activity levels were significantly reduced during the winter with little variation in swimming speed observed over the diel cycle. Diel and seasonal variation in ambient light intensity and water temperature, respectively, as well as differences in spawning behaviour are thought to be the key proximate factors responsible for these observed changes in behaviour.

5.6 Acknowledgements

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Chapter 6. Vessel- and trawl-induced behaviour in Atlantic cod at different times of year

6.1 Abstract

Environmental conditions are generally considered to influence the behaviour of fish in response to vessels and mobile fishing gears. In this chapter, the behaviour of Atlantic cod (*Gadus morhua*) is examined in response to an approaching vessel and bottom trawl at different times of year. Using acoustic telemetry, the swimming speed of individual cod was estimated for the periods before, during, and after an encounter with a vessel travelling at 3.0, 4.5, and 10.0 knots as well as in response to a vessel towing a bottom trawl at 3.0 knots. Reaction distances ranged from 206 to 1512 m and were generally shorter during the winter compared to the summer. The duration of disturbance produced by the vessel lasted for an average of 20 min and was independent of vessel speed and season. When the vessel was towing a trawl, it produced elevated swimming speeds for periods up to 56 min. The results indicate that cod are capable of reacting to an approaching vessel from considerable distances and that the disturbance produced by the encounter can persist for a period of time after the vessel has left the area. These findings could have implications for acoustic and bottom trawl surveys conducted in fjord environments.

6.2 Introduction

Most species of fish are capable of detecting sounds over considerable distances. However, it is not until the level of sound significantly exceeds the hearing threshold of fish, that an avoidance reaction may be initiated (see Anon 1995 for review). Vessels and mobile fishing gears both produce high levels of low-frequency sound within the hearing range of fish that are capable of producing an avoidance reaction (see Fréon and Misund 1999 and Popper 2003 for reviews). Several studies have examined the avoidance behaviour of demersal fish to an approaching vessel and bottom trawl (e.g. Harden Jones et al. 1977; Olsen et al. 1983a; Ona and Godø 1990; Engås et al. 1998; Godø et al. 1999a; Michalsen et al. 1999; Handegard et al. 2003) as well as the behaviour immediately following trawl passage (Morgan et al. 1997). These studies have indicated that avoidance behaviour, although highly variable, can occur at significant depths and distances ahead of the vessel.

Abundance estimation of Atlantic cod (*Gadus morhua*) in Newfoundland waters is conducted using both bottom trawl (Walsh 1996; McCallum and Walsh 1997) and acoustic surveys (Rose 1995). If avoidance behaviour (vertical or horizontal) occurs in the area ahead of the vessel, i.e. pre-vessel zone, then the volume of cod available to the acoustic transducer or bottom trawl may be biased. If this bias is consistent over time, then it will have little effect on estimates of abundance indices. However, if the bias changes over time, then the reliability of the indices may be in question (see Aglen 1994; Godø 1994 for reviews). Major factors which contribute to vessel and trawl radiated noise include vessel speed, engine load, propeller pitch, vessel age, and vibration of the trawl warps. Yet, correlating such factors with specific avoidance behaviours has proven difficult (Mitson 1993). Certain environmental and social factors have been shown to influence avoidance behaviour and therefore the availability and vulnerability of fish to trawl capture. These include ambient light intensity, fish depth, and fish density, (e.g. Ona and Godø 1990; Walsh and Hickey 1993; Godø et al. 1999b). Other factors such as bottom temperature are expected to influence avoidance behaviour and therefore catchability, but still lack direct empirical evidence (Winger and Walsh 2001).

The purpose of this study was to investigate the behaviour of Atlantic cod in response to an approaching vessel and bottom trawl under different environmental conditions, i.e. water temperatures, at different times of the year. Using acoustic telemetry, the swimming speed of individual cod was estimated for the periods before, during, and after an encounter with a vessel travelling at 3.0, 4.5, and 10.0 knots as well as in response to a vessel towing a bottom trawl at 3.0 knots.

6.3 Materials and Methods

Study Area:

The study was conducted during the summer and winter seasons of 1996-98 in Smith Sound, an inshore fjord on the northeast coast of Newfoundland (Fig. 6.1). For a detailed description of the study area, see Chapter 5. In brief, the Sound is approximately 25 nm long, open on both ends, shallow (less than 10 m) at its western point and moderately deep (~150 m) at its eastern entry into Trinity Bay. It is characterized by a deep narrow trench approximately 5 nm long with depths ranging from 200-220 m.

Summer field seasons were conducted during July in 1996 and 1997 near the western end of the Sound (48° 12.2′ N, 53° 53.2′ W; Fig. 6.1). Water depth at this site (S1) ranged from 10 to 40 m. Steep temperature gradients were observed in both years, with surface water temperatures of 15.5 and 11.7 °C and bottom temperatures of 6.0 and 6.9 °C for 1996 and 1997 respectively.

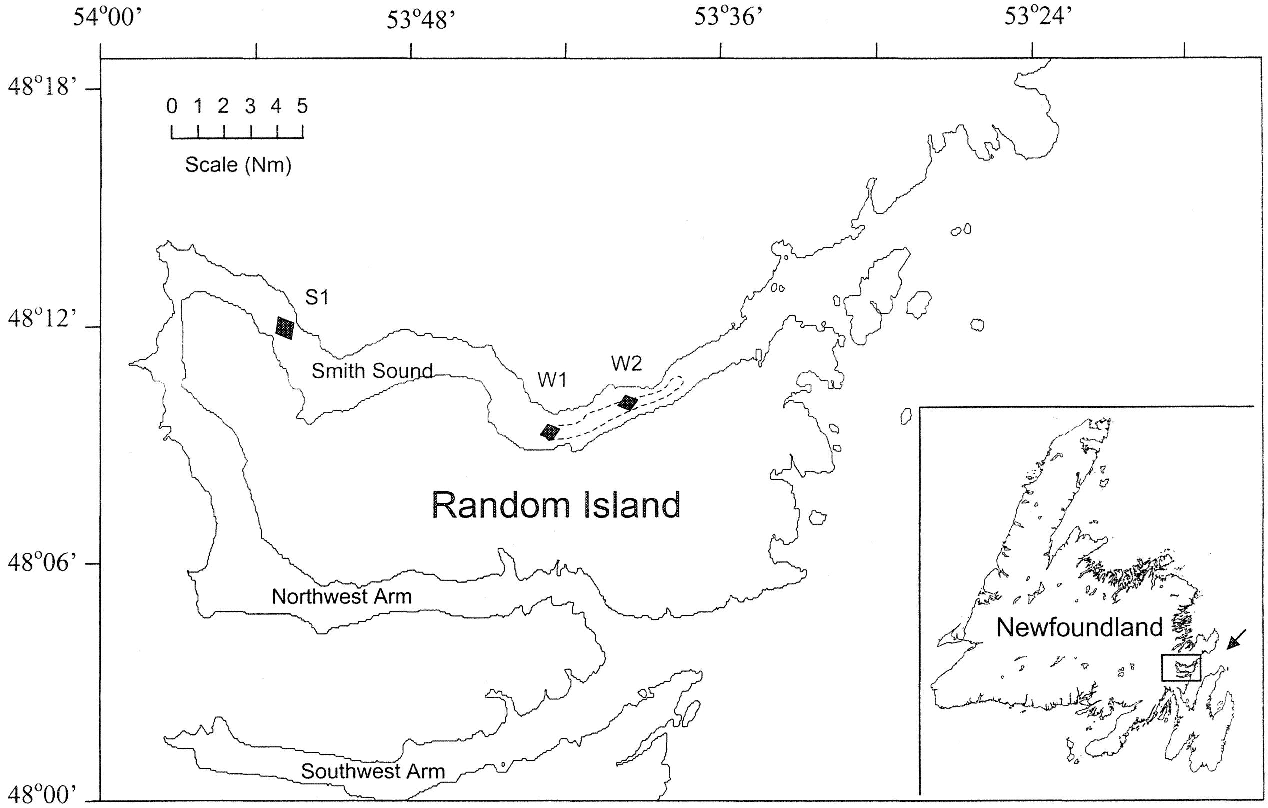

Figure 6.1: Map of the study area, located in Smith Sound, Newfoundland. The acoustic positioning system was deployed during the summer seasons at site S1 and during the winter seasons at sites W1 and W2. Dashed line represents the 200 m depth contour of the trench.

Winter field seasons were conducted during March in 1997 and February in 1998. Due to an absence of fish at the summer site at this time of year, I was forced to explore alternative study sites where fish were more abundant. Using acoustics and several bottom trawl tows, cod were found in sufficient numbers near the middle of the Sound (48° 09.6′ N, 53° 40.8′ W; Fig. 6.1). The westerly site (W1) had a water depth of 100–210 m and spanned a section of the edge and bottom of the trench while the easterly site (W2) had a depth of 200–220 m and was located near the middle of the trench. Temperature gradients were absent in both years, with surface temperatures (-1.1 to -0.8 °C) similar to bottom temperatures (-0.2 to 0.2 °C) for each year and site.

Tagging and Tracking:

Cod were tagged with acoustic transmitters either by *in situ* voluntary ingestion or by external attachment during the summer experiments, and by external attachment only during the winter experiments (Table 6.1). For a detailed description of these tagging techniques, see Chapter 3 and Chapter 5. In brief, the *in situ* technique was performed underwater using a surface-controlled tagging frame (Chapter 3). Individual transmitters were wrapped in mackerel bait and lowered close to the seafloor where they were voluntarily swallowed by cod. Due to water depths beyond the capability of the tagging frame, external attachment of transmitters was conducted during the winter onboard the research vessel using cod captured by handline, longline, or bottom trawl. Care was taken to only select cod that appeared in good physical condition and that were able to maintain proper buoyancy and equilibrium. Transmitters were attached below the first dorsal fin by passing stainless steel wires 0.5 mm in diameter through the upper dorsal

Table 6.1: Summary statistics for individual acoustically tagged Atlantic cod tracked in Smith Sound, Newfoundland, during the summer and winter seasons of 1996-98.

Fish	Length (cm)	Capture Method	Tagging Method	Released Date	Released Time	Days previously at Liberty
Summer						
1	72	handline	external	23-Jul-96	18:15	6.1
2	61	handline	external	24-Jul-96	16:45	3.6
3	37	---	voluntary	12-Jul-97	14:50	10.0
4	85	---	voluntary	13-Jul-97	7:00	10.2
5	89	---	voluntary	24-Jul-97	10:45	6.0
Winter						
6	63	trawl	external	9-Mar-97	16:30	7.0
7	67	longline	external	13-Mar-97	15:00	3.0
8	64	trawl	external	31-Jan-98	18:00	21.7
9	74	trawl	external	31-Jan-98	18:00	20.0
10	74	trawl	external	6-Feb-98	7:53	11.1

musculature in the manner described by Bridger and Booth (2003). Once tagged, the fish were held onboard for an average of 5.0 h for post-tagging observation and then released into the study area. The cod were at liberty for periods up to 22 d (mean = 9.9 d, s.d. = 6.5) prior to the start of their first avoidance trial (Table 6.1). Transmitters used in this study were 16 mm in diameter and varied in length from 45 to 108 mm (Vemco Ltd., Lotek Wireless Inc), depending on the size of the fish. Weight of the transmitters ranged from 25.1 to 41.0 g in air and 12.0 to 19.3 g in water. Each transmitter had a different frequency to enable the distinction of individuals.

Automated tracking was conducted using a VR20 radio acoustic positioning (RAP) system (Vemco Ltd.) as described in detail by Voegeli et al. (2001). This consisted of four radio-linked hydrophone buoys anchored to the seafloor in the shape of a diamond with distances between adjacent buoys ranging from 400 to 800 m. Acoustic pulses emitted from the tagged fish were received by the hydrophones, and based on delays in the time of arrival, positions of fish within the array were calculated. Normally, several pulses recorded by each buoy are averaged to calculate each position, but in this study, the software was optimized such that a position was recorded with each pulse (time lag 1-5 s). This was then transmitted by VHF radio to the research vessel and logged to disk. See Section 7.5 for a discussion on the limitations of this system.

Experimental Procedures:

Experimental trials were conducted over a period of 4-10 days during each of the four field seasons. Separate trials were undertaken to assess the behaviour of cod in response to an approaching vessel and vessel/trawl combination. All trials were conducted using the research vessel "CCGS Shamook", a 24.9 m trawler (560 hp, 117 gross tonnes). During general operation of this vessel, low frequency noise (within the hearing range of fish) is mainly produced by an 8 cyl. diesel CAT engine, 40 kw service generator, hydraulic pump, gearbox, and controllable pitch propeller (C. Stevens, Fisheries and Oceans Canada, Newfoundland Region, pers. com.). Trials involving only the vessel (without trawl) were conducted at speeds of 3.0, 4.5, and 10.0 knots. These are comparable to the speeds used during trawling, inshore and offshore acoustic surveys, respectively. Trawling was conducted using a Yankee 36 bottom trawl rigged with 54 m sweeps (bridles and ground warps), 36 cm rockhopper groundgear, and Brompton-type wooden doors. Towing speed of the trawl was 3.0 knots and the codend was left open. Acoustic trawl instrumentation (SCANMAR) and occasionally an underwater camera were used to monitor trawl geometry and bottom contact. Trawl geometry was known to vary with the depth of fishing. Towing in shoal water (< 50 m) during the summer produced average door and wing spreads of approximately 20.9 and 6.9 m respectively and a headline opening of 2.2 m. Towing in deeper water during the winter (> 150 m) produced comparatively larger door and wing spreads of 56.9 and 12.8 m respectively and a slightly lower headline opening of 1.9 m. The position of the trawl in relation to the array and tagged fish was monitored by attaching an acoustic transmitter to either the headline or trawl door. The trawl was estimated to pass through the centre of the array approximately 0.6 and 3.5 min behind the vessel during the summer and winter tows, respectively (note: the trawl lagged the vessel by a greater distance during winter due to increased warp paid out).

Experimental trials began by tuning the positioning system's software to listen for

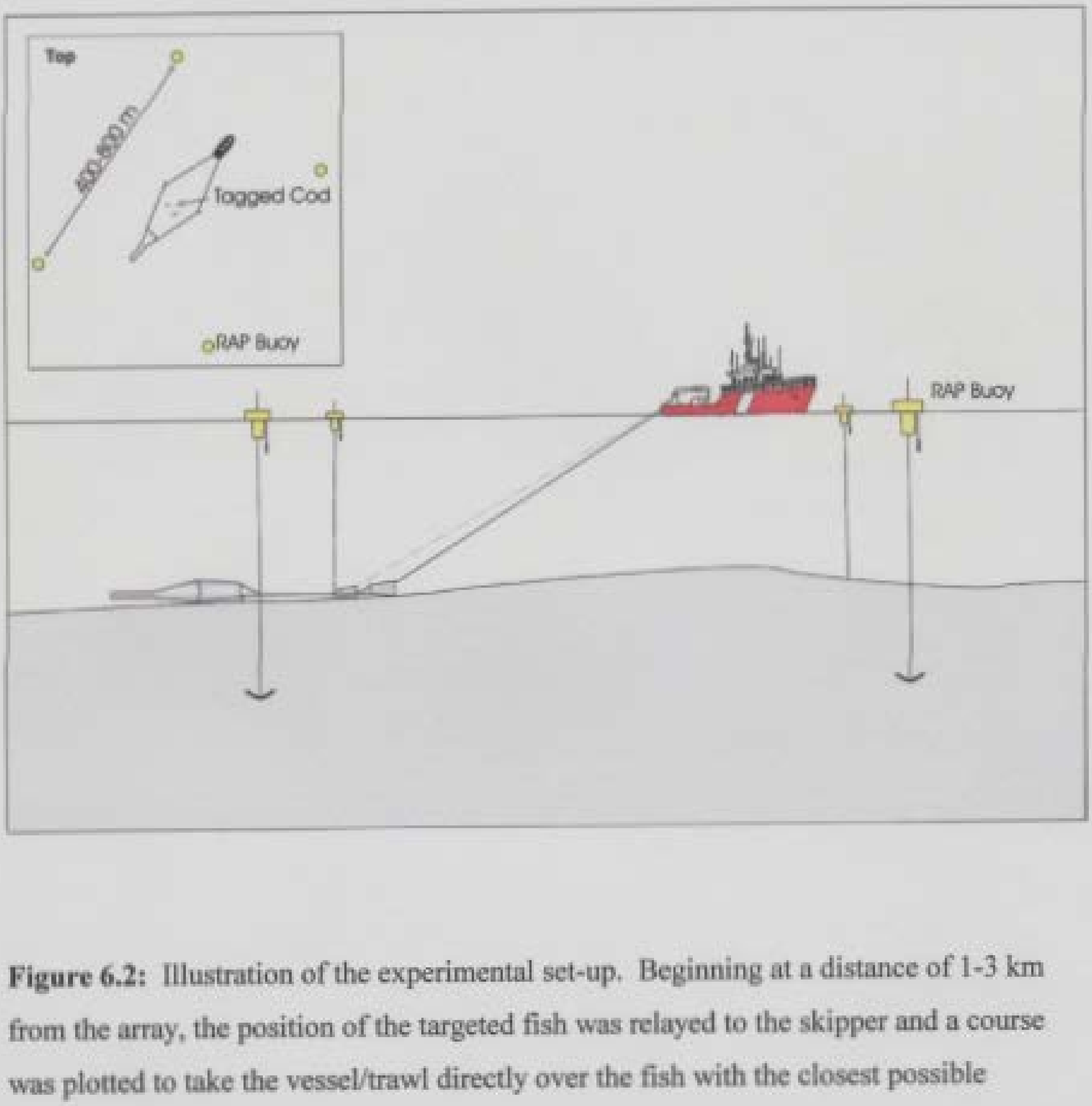

Figure 6.2: Illustration of the experimental set-up. Beginning at a distance of 1-3 km from the array, the position of the targeted fish was relayed to the skipper and a course was plotted to take the vessel/trawl directly over the fish with the closest possible precision. The vessel/trawl then exited the opposite end of the array and took up position at a distance of 1-3 km.

a single randomly selected fish. Beginning at a distance of 1-3 km from the array, the position of the targeted fish was relayed to the skipper and a course was plotted to take the vessel/trawl directly over the fish with the closest possible precision (Fig. 6.2). The vessel/trawl then exited the opposite end of the array and took up position at a distance of 1-3 km. The position of the vessel was determined using a differential global positioning system (DGPS) and was logged to computer throughout each trial. The duration of the trials ranged from 8-70 min depending on the approach distance, termination distance, vessel speed, and whether or not the trawl was used. All trials were conducted during daylight hours and cod were assumed to be near the seafloor in an undisturbed state prior to the start of each trial.

Analysis:

The behaviour of cod was analyzed relative to the Cartesian coordinate system generated by the positioning system. Using the DGPS position of the buoys as known reference points, the latitude and longitude of the vessel's position was converted into xy coordinates (already shared by the fish and trawl). As erroneous positions can occur with stationary positioning systems (Smith et al. 1998), the fish and trawl tracks were visually inspected and any invalid positions were discarded (< 5%). Using linear interpolation, the position of the vessel and trawl were then estimated for each timestamp of the fish, permitting temporal comparison of all three components (fish, vessel, and trawl).

Swimming speeds of cod were calculated as a function of the elapsed time and distance between successive positions. Swimming speeds were estimated for the periods before, during, and after each experimental trial. In most cases, before- and after-trial observation periods of up to one hour were available. A behavioural reaction to the approaching vessel and/or trawl was considered to have occurred if a change in swimming speed was observed. The distance between the vessel and the fish at the time of the reaction was considered to represent the *reaction distance.* In trials where a reaction was observed, the time elapsed between the initial reaction and resumption of the pre-trial activity level was estimated. This was considered to represent the *duration of disturbance* generated by exposure to the vessel and/or trawl.

A total of 49 avoidance trials were conducted. Of these, 10 were excluded from the analysis on the basis of a) interference of the positioning system by vessel/trawl noise, b) poor precision of the vessel/trawl, or c) mechanical difficulties.

6.4 Results

Vessel Only:

The approach of the vessel toward cod produced either an increase, decrease, or no change in swimming speed. The proportion of trials in which cod demonstrated a change in swimming speed, varied with both vessel speed and season (Table 6.2). The majority of these reactions (87%) were characterized by an increase in swimming speed, while the remainder (13%) were characterized by a decrease in swimming speed (see Fig. 6.3 for examples). Cod were more likely to react at the lower vessel speeds of 3.0 and 4.5 knots compared to 10.0 knots and were more likely to exhibit a reaction during the summer compared to winter. No avoidance reactions were observed at 10.0 knots during the winter, but this may have been due in part to small sample size.

Reaction distances to the approaching vessel ranged from a minimum of 206 m to

Table 6.2: Number of trials conducted for each treatment and the percentage in which a change in swimming speed was observed.

	Speed (knots)	**Summer**		**Winter**	
		n	**% Reaction**	**n**	**% Reaction**
Vessel Only	3.0	10	70	5	60
	4.5	4	75	3	33
	10.0	3	33	2	0
Vessel and Trawl	3.0	8	63	4	75

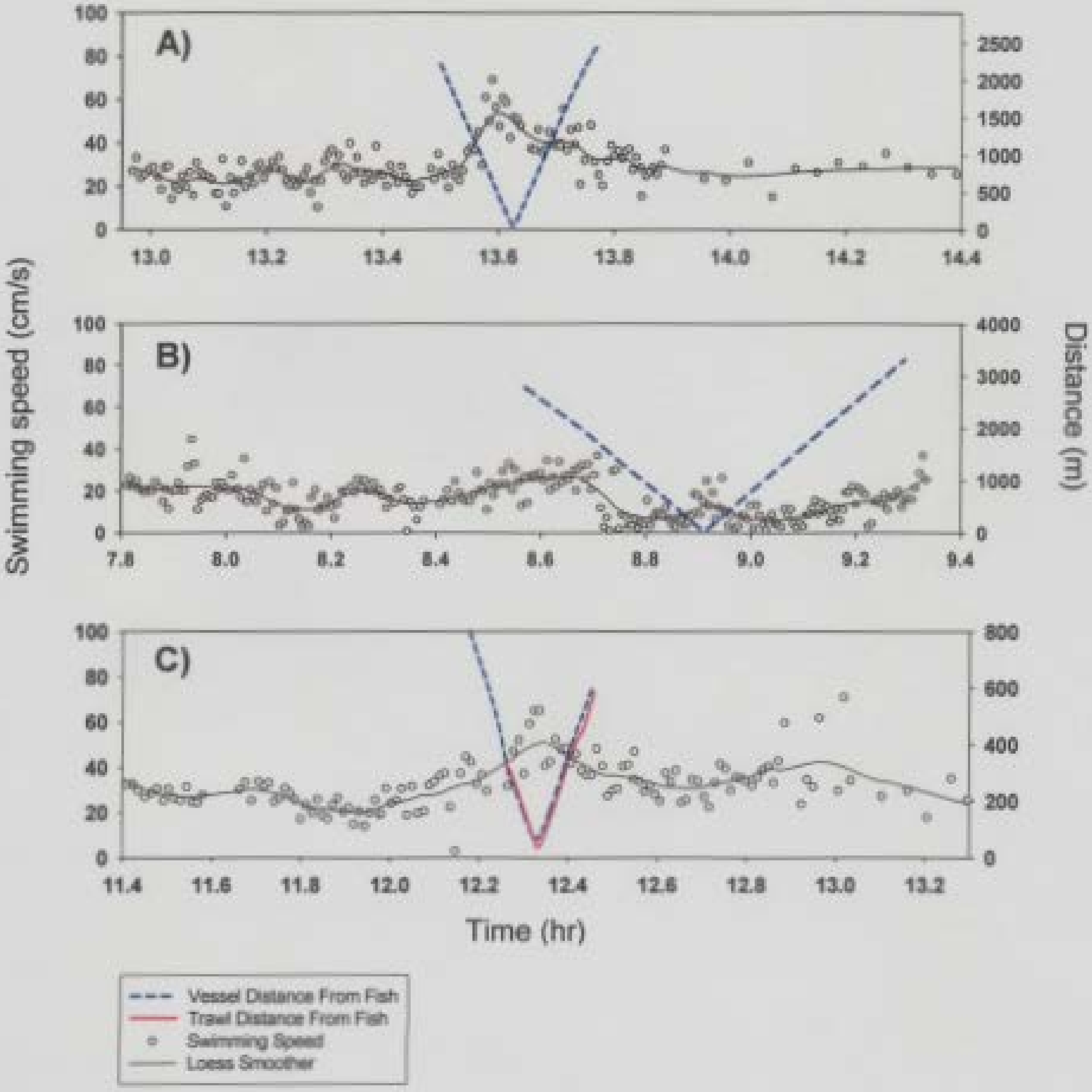

Figure 6.3: Examples of Atlantic cod behaviour in response to an approaching vessel (Panels A & B) and vessel plus trawl (Panel C). Panel A shows an increase in swimming speed by Fish no. 4 in response to the vessel approaching at 10.0 knots. Panel B shows a decrease in swimming speed by Fish no. 5 in response to the vessel approaching at 4.5 knots. Panel C shows an increase in swimming speed by Fish no. 4 in response to the vessel and trawl approaching at 3.0 knots.

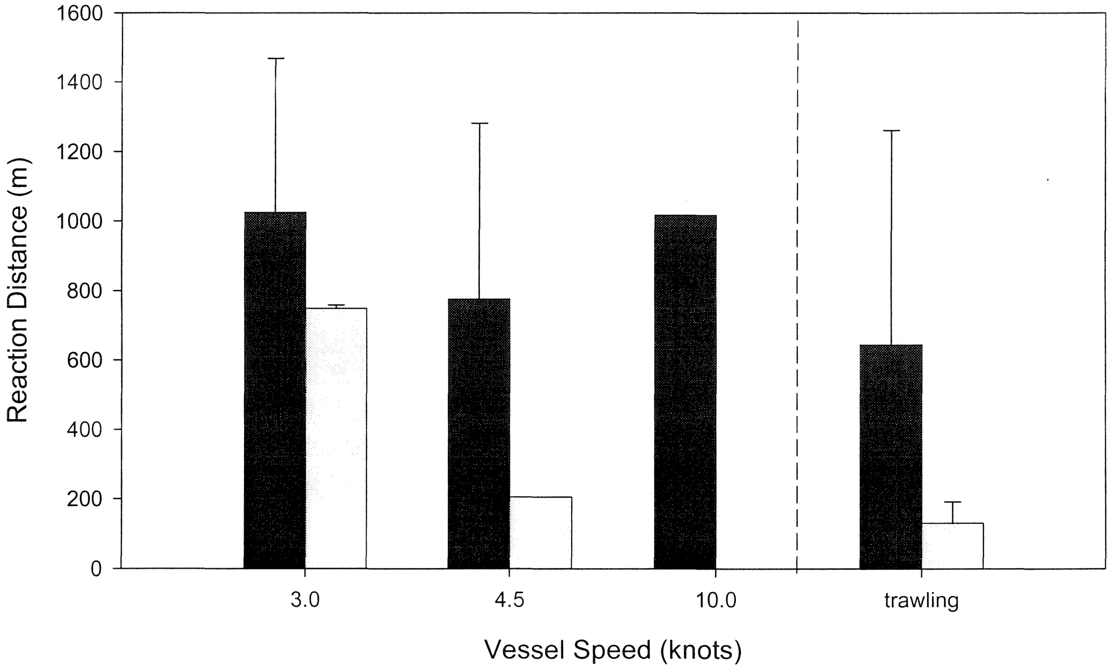

Figure 6.4: Average reaction distances (± SD) of cod to an approaching vessel (three speeds) and bottom trawl during the summer (black bars) and winter (grey bars).

a maximum of 1512 m. Average reaction distances were lower during the winter compared to summer at vessel speeds of 3.0 and 4.5 knots (Fig. 6.4), although no significant effect could be detected ($p > 0.05$). Reaction distance was independent of vessel speed during the summer but was significantly lower at 4.5 knots compared to 3.0 knots during the winter ($p < 0.001$).

The duration of disturbance was similar whether cod increased or decreased their swimming speed in response to the approaching vessel. These ranged from 9.7 and 32.4 min (mean = 19.7 min; s.d. = 6.6) and were independent of vessel speed during both seasons ($p > 0.05$; Fig. 6.5).

Vessel and Trawl:

The approach of the vessel and trawl toward cod produced either an increase in swimming speed (Fig. 6.3) or no change in swimming speed. In none of the trials was a decrease in swimming speed observed. The proportion of trials in which cod demonstrated a reaction varied slightly with season and was comparable to that observed during vessel only trials at 3.0 and 4.5 knots (Table 6.2).

Reaction distance was more variable during summer compared to winter (Fig. 6.4). Average reaction distance was 644 m during summer, dropping to 131 m during winter, however no significant seasonal difference could be detected ($p > 0.05$).

The duration of disturbance produced in response to trawling was significantly longer during summer compared to winter ($p = 0.001$; Fig. 6.5). Elevated swimming speeds persisted for an average of 56.1 min during summer and only 12.4 min during winter.

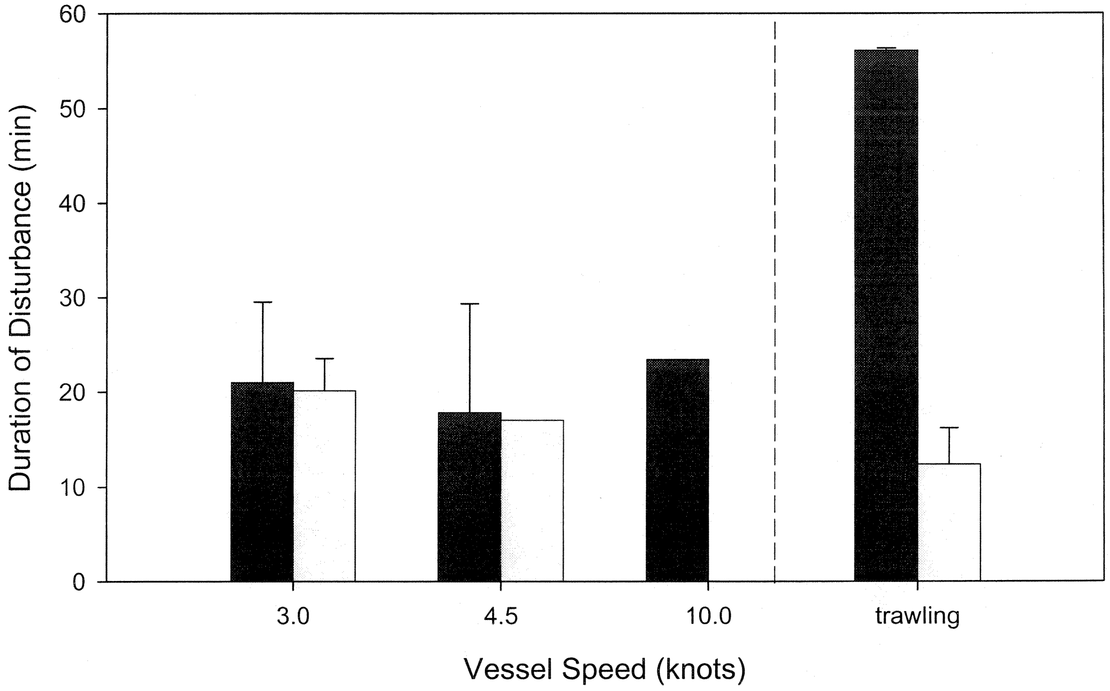

Figure 6.5: Average duration of disturbance (± SD) produced by an approaching vessel (three speeds) and bottom trawl during summer (black bars) and winter (grey bars).

6.5 Discussion

Type of Response:

Behavioural responses described in this chapter are based on an examination of changes in swimming speed and do not consider changes in spatial movement or orientation of the fish. Using this approach, cod in this study exhibited one of three behaviours in response to the approaching vessel/trawl. They either increased, decreased, or showed no change in swimming speed. All of these are considered to have adaptive value from a predator-evasion point of view (Lima and Dill 1990). An increase in swimming speed was the most common response, occurring at all vessel speeds and during trawling. This is consistent with the general pattern of avoidance previously reported for cod (Olsen et al. 1983a; Handegard et al. 2003; McQuinn and Winger 2003).

A decrease in swimming speed was less frequent and only occurred twice during vessel avoidance trials. This type of response has not been widely reported in the literature. The only case is Engås et al. (1998) who observed a single acoustically tagged cod reduce its swimming speed by half in response to a vessel/trawl approaching from a distance 1290 m. Functional explanations for this type of response are unclear but could be related to seeking a refuge.

Experimental trials in which no change in swimming speed was observed may have two explanations. Either the stimulus did not exceed the threshold for reaction and these cod simply continued their current activities, or a behavioural response did occur that was not characterized by a change in swimming speed. Olsen et al. (1983b) predicted that fish should first begin with a change in horizontal or vertical swimming direction in response to an approaching vessel, and only at a later point if necessary, adjust their swimming speed. If this occurred in the current study, an early change in swimming direction by cod away from the path of the vessel/trawl would have lead to a reduction in the perceived threat and reduced the need for a change in swimming speed. This type of behaviour (i.e. a change in direction without change in speed) has been previously documented for cod (Engås et al. 1998), indicating that a spatial analysis of the cod behaviour in this study should be pursued. Finally, the lack of a change in swimming speed in response to a vessel/trawl has been previously reported for other species such as herring (Misund et al. 1996) and saithe (Godø et al. 1999a).

Reaction Distance:

Compared to other species, cod are known to have sensitive hearing (Mitson 1993), capable of both long-range detection (Buerkle 1977; Sand and Karlsen 1986) and directional hearing (Olsen 1969; Schuijf 1975). However, the difference between their detection threshold and reaction threshold is likely to be considerable. Buerkle (1977) estimated that cod could detect trawling noise from a minimum distance of 3.2 km during summer, but was reduced to 2.5 km during winter due to increased ambient noise in the sea at that time of year. In this study, I found that cod reacted at distances well within these limits, with a maximum reaction distance of 1512 m during summer and 759 m during winter. Using the same approach, Engås et al. (1998) found that cod initiated an avoidance response to an approaching trawler at distances ranging from 470 to 1470 m. That study was conducted during autumn using a slightly smaller vessel (400 hp) over depths of 60-80 m. Together, these studies indicate that cod are capable of detecting and reacting to an approaching trawler from considerable distances and that reaction distance can be somewhat variable.

Several factors may have influenced the reaction distance of cod in this study. These include water temperature, fish depth, fish density, and ambient light level near the seafloor. All of these factors are of critical importance in determining avoidance behaviour of fish to mobile gears (e.g. Suuronen 1988; Ona and Godø 1990; Walsh and Hickey 1993; Engås et al. 1998; Godø et al. 1999b; Winger and Walsh 2001; Vabø et al. 2002). Low water temperature and low ambient light intensity in particular, are known to be strong environmental constraints and are expected to be important proximate factors responsible for reducing the sensitivity (i.e. raising the response threshold) of cod during winter in this study. Underwater observations using a remote-operated-vehicle (ROV) of a dense cod aggregation in Smith Sound in April 2003 at a depth of 205 m and bottom temperature of –1.7°C revealed that cod did not show any avoidance reaction to the sounds and lights of the ROV (G. Lilly, Fisheries and Oceans Canada, Newfoundland Region, pers. comm.). Although water temperature does not typically drop this low, the finding would suggest that over-wintering cod in dense inshore aggregations may exhibit reduced vigilance toward potential threats. In the current study, the winter sites in both years were characterized by dense aggregations of cod found mainly at depths between 200 and 220 m at temperatures between –0.2 and 0.2°C. Acoustic estimates of the biomass at the time of this study are unknown, but was reported to be approximately 15,000 t one year after the present study (Rose 2003). An investigation of the natural behaviour of cod inhabiting these dense winter aggregations revealed that the cod were not feeding and exhibited very low levels of activity (Chapter 5). Together, these observations support the findings in this study of reduced likelihood of cod to react as well as reduced reaction distance to an approaching vessel and/or trawl during winter.

Vessel speed did not have a consistent effect on reaction distance in this study. This is inconsistent with the general prediction for vessel avoidance (Olsen et al. 1983b) as well as previous observations for cod (Olsen et al. 1983a). While a significant speed effect was detected during winter, high variation in reaction distance during summer may have confounded the detection of any underlying effect at that time of year. Alternatively, because propeller cavitation often decreases slightly with increasing speed for vessels with controllable pitch propellers (Mitson 1993), this may have reduced the overall noise level produced within the hearing range of cod with increasing speed. The similarity in reaction distance between the vessel and trawl avoidance trials suggests that the vessel itself was the major determinant of the avoidance behaviour. This is consistent with the fact that vessel noise is believed to mask trawl noise over most of the noise frequency spectrum (Chapman and Hawkins 1969; Buerkle 1977; Anon 1995).

Duration of Disturbance:

This study revealed that cod were disturbed before and after the immediate passage of the vessel and trawl. From the initial time of reaction, average disturbances during vessel avoidance trials lasted about 20 min, were independent of vessel speed or season, and were characterized by either an increase or decrease in swimming speed. However if the vessel was towing the trawl, it produced elevated swimming speeds lasting for an average of 12 min during winter and 56 min during summer. While these observations do not indicate a graded response to increasing vessel speed, they do suggest that trawling produced a significant element of stimulation, beyond the vessel itself, especially during summer when cod were active and engaged in foraging/spawning activities (Chapter 5). Previous observations of an offshore spawning aggregation of cod found that bottom trawling produced a large-scale change in shoal structure in the form of a 300 m wide hole that persisted for a least 77 min following trawl passage (Morgan et al. 1997). Together these studies indicate that trawling on spawning aggregations may have a significant effect on the spatial movement and physiological expenditure of spawning cod. Recent work by Handegard et al. (2003) also reported that the swimming speed of cod remained elevated following an encounter with a bottom trawl, but the duration of the disturbance could not be estimated.

Other Influences:

Several covariate factors were recorded throughout the study, to which no apparent relationships with reaction distance or the duration of disturbance were found. These included repeated exposure, fish length, and time of day. Each of these factors is likely to affect avoidance behaviour, but due to the limited number of trials and tagged fish in this study, their role could not be determined. A prolonged discussion has focused on the effect of repeated vessel and trawl exposure on avoidance behaviour (e.g. Olsen 1971; Pyanov, 1993; Fréon and Misund 1999; Vabø et al. 2002). While it was not within the scope of this study, the approach used here and previously by Engås et al. (1998) is well suited for this type of investigation. The tracking of individual fish over extended periods cannot be achieved with other technologies.

Summary:

This chapter examined behaviour of cod in response to a vessel and bottom trawl at different times of year. The likelihood of reaction and reaction distance were both generally lower during winter compared to summer. The duration of disturbance appeared to be independent of vessel speed and season, but became significantly higher during summer trawling operations. These observations are based on a small sample of acoustically tagged fish in an inshore fjord and may not be representative of open sea environments. They do however indicate that seasonal differences in environmental conditions and habitat selection can affect avoidance behaviour of cod to a vessel and bottom trawl. This should be taken into account when conducting acoustic and bottom trawl surveys in fjord environments. Finally, these results are specific to the research vessel *CCGS Shamook* and may not be applicable to all vessels.

6.6 Acknowledgements

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Chapter 7. Summary and Synthesis

In this thesis, I examined the effect of environmental conditions on the natural activity rhythms and bottom trawl catchability of Atlantic cod using acoustic telemetry. I began with an investigation of different techniques for tagging cod intragastrically with acoustic transmitters (Chapters 2 and 3). I then described the natural activity of cod at high resolution (Chapter 4) and during different seasons (Chapter 5). Finally, I examined the behaviour of cod in response to an approaching vessel and bottom trawl (Chapter 6). The following sections are an integrated account of the results and conclusions from these chapters. I also include a discussion on possible implications for resource assessment surveys and limitations of the approach used.

7.1 Intragastric Tagging of Cod

The findings from Chapters 2 and 3 demonstrate the advantages of using the method of voluntary ingestion for the intragastric tagging of cod. I found that cod which voluntarily ingested transmitters exhibited a delayed onset of initial regurgitation, longer periods of retention, higher food consumption and lower mortality in comparison to fish tagged using the method of forced insertion. The tagging frame proved to be an effective method for applying the technique in shallow inshore field conditions, eliminating the need for capture and handling. The technique could be easily modified for deeper applications (e.g. Godø et al. 1997), however in very deep water a deployable video-recorder would be more appropriate than an umbilical to the surface. This tagging procedure did not appear to affect natural fish behaviour or transmitter retention.

I recommend that short-term tracking studies use voluntary ingestion as the preferred method of intragastric tagging in cod. I predict that studies which employ this technique will benefit from an increased number of tracking days due to reduced transmitter loss. I also speculate that studies conducted under conditions of low water temperature will benefit from an increased number of tracking days as a result of longer retention due to a slowed digestive process. However variation in the tagging efficiency observed in Chapter 3 indicates that additional work is needed to improve deployment and baiting strategies. In particular, deployment strategies should take into consideration the feeding and activity levels of cod (e.g. Løkkeborg 1998; Løkkeborg and Fernö 1999) as well as the influence of bait texture on size-selectivity and tagging efficiency (e.g. Løkkeborg 1991).

7.2 Diel Activity Rhythms in Cod

The findings from Chapters 4 and 5 showed that time-of-day had a significant effect on the *in situ* swimming speeds employed by cod. Juvenile cod tracked in Ramfjord during late summer (Chapter 4) exhibited suppressed activity during the highest light levels (noon) as well as increased activity during the dawn/dusk periods. I hypothesize that the underlying mechanism for this behaviour was predator avoidance (see Lima and Dill 1990 for review). By limiting activity during ‘risky’ periods of the day, the fish traded-off the benefits associated with foraging in order to reduce the costs associated with injury or death (i.e. predation).

Adult cod by comparison, do not usually experience a high risk of predation (Pálsson 1994). I hypothesize that the behaviour of adult cod tracked in Ramfjord (Chapter 4) reflected an opportunistic foraging strategy, hunting mainly by vision during the day and switching to chemically-mediated search at night (see Løkkeborg 1998 for review). In Smith Sound (Chapter 5), diel activity rhythms were shown to vary seasonally for adult cod. During summer, these adult cod were active throughout the diel cycle with a pronounced increase in activity during daylight hours. Similar to the Ramfjord cod, these fish were likely exhibiting an opportunistic foraging strategy, but were also clearly engaged in spawning activity and were therefore balancing the demands of both activities. During winter, cod in Smith Sound were significantly less active with little change in activity over the diel cycle. Low water temperature and low ambient light intensity near the seafloor were probably responsible for this behaviour. Because these variables were correlated, it is difficult to conclude the specific mechanism modifying activity rhythms at the seasonal scale. Of the two, I would suspect that low water temperature was the key proximate factor driving behaviour during winter. In fact, it is probable that the timing of arrival, habitat selection, shoal structure, and degree of activity and feeding of these cod were all linked directly or indirectly to the low water temperature experienced at this time of year (Wroblewski et al. 1994; Smith and Page 1995; Swain and Kramer 1995; Cadigan and Shelton 1997; Colbourne et al. 1997; Godø and Michalsen 2000).

Finally, when emphasis was placed on high resolution tracking of individual fish in Ramfjord (Chapter 4), variation at the individual level was observed. Although both crepuscular and nocturnal activity rhythms in juvenile cod have previously been reported for fish of this size during summer (e.g. Clark and Green 1990; Cote et al. 2002), they have not been observed among conspecifics at the same time and within the same habitat, as was found in Chapter 4. Functional explanations for this variation may be related to individual differences in balancing the demands of foraging and predator avoidance, suggesting that optimal behaviour may not be the same for all individuals (Magurran 1993). Tracking of additional fish, detailed spatial analyses of movement patterns, and biological information on the feeding, sexual maturity, population density, and population size-structure will be necessary in order to test this prediction.

7.3 Vessel- and Trawl-Induced Behaviour in Cod

Chapter 6 revealed seasonal variation in the behaviour of cod toward an approaching vessel and bottom trawl. In particular, I found that the likelihood of reaction and reaction distance were both lower and less variable during winter compared to summer. These findings are novel and to my knowledge have not been previously reported.

It has been predicted (Fernö and Huse, unpublished) that the timing of reaction by cod to an approaching vessel and trawl should follow similar economics to prey fleeing from predators (Ydenberg and Dill 1986). If this is true, then it is possible to apply basic principles from established predator-prey theory (see Godin 1997 for review). In general, when a fish detects a threat, usually an attacking predator, it must sequentially decide 1) whether and when to flee, 2) in which direction to flee, 3) how fast to flee, and 4) how far to flee. For ambush predators, step one of this sequence typically lasts less than 1 s before the prey reacts, whereas stalking or pursuit predators offer their prey more time to decide. For the sake of this discussion, I will focus on the latter scenario as it relates most closely to the nature of Chapter 6. In Ydenberg and Dill's (1986) economic (cost-benefit) model, a fish under threat of a predator continually chooses between two behavioural options, staying where it is (and perhaps continuing with an ongoing activity) or fleeing, as the distance between it and the predator shrinks. The distance at which the fish flees (i.e. reaction distance) is determined by a balance between the costs of these two options (Fig. 7.1). The costs of fleeing (F) are assumed to increase linearly and the costs of remaining (R) to decrease proportionately, with increasing distance to the predator. Timing is critical as fleeing too early may result in lost opportunities and remaining too long may result in injury or death. A fish under threat is assumed to choose at every distance between itself and the threat, the behavioural option (fleeing or remaining) with the lowest cost, and should opt for fleeing when $R > F$. The optimal reaction distance (D^*) is defined as the intersection of the two curves. The model predicts that the optimal reaction distance should increase with increasing cost of remaining ($D_2^* \rightarrow D_3^*$) and decrease with increasing cost of fleeing ($D_2^* \rightarrow D_1^*$).

As a vessel and trawl approach cod in the wild, fish in the pre-vessel zone (i.e. *zone* 1, see Chapter 1) are faced with the important decision of whether and when to react. The optimal reaction distance (D^*) should be determined by a balance between the costs of fleeing (F) and remaining (R). Factors which define the R cost curve will be both vessel-related (e.g. type, age, speed, engine load, and propeller pitch) and trawl-related (e.g. type, rigging, performance, and operation). The F cost curve will be defined by lost opportunities (e.g. foraging and spawning) and energy expenditure. At the proximate level, environmental and social conditions are expected to exert a strong influence on the *response threshold* and therefore the reaction distance of cod (Godin 1997). In this study, summer and winter trials varied in water temperature, fish depth, ambient light level near the seafloor, and fish density. In my opinion, each of these

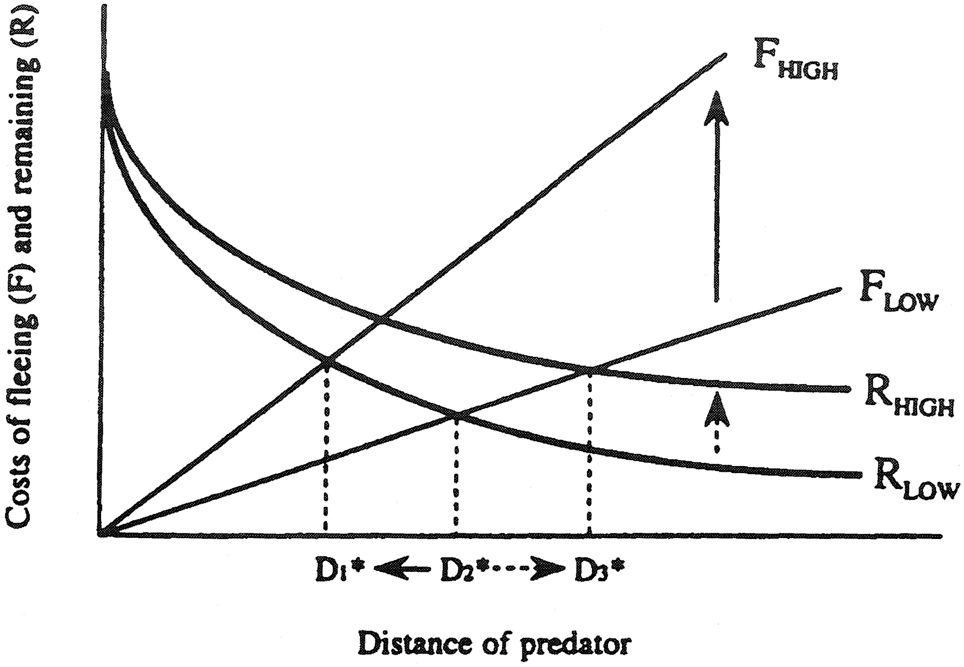

Figure 7.1: Ydenberg and Dill's (1986) economic model of reaction distance (D) for fish under the threat of a predator. See text for details. (Adopted from Godin 1997).

variables was likely to reduce the sensitivity (i.e. raise the response threshold) of cod during winter, particularly low water temperature and low ambient light intensity. Because these variables were correlated, it is difficult to conclude the specific mechanism modifying the behaviour, however I would suspect that low water temperature was the key proximate factor. No other variable was likely to have produced the same constraint on response threshold. That said, avoidance behaviour appears to be highly variable and it is not likely to be driven by any one factor. In addition, some degree of variation in behavioural expression will always be related to individual differences in how cod balance the demands of their ongoing activities and initiating an avoidance response. This follows from the fundamental assumption that individual cod behave so as to maximize benefits and minimize costs specific to their own situation (Noakes 1992), implying that the optimal avoidance behaviour may not be the same for all individuals (Magurran 1993).

7.4 Implications for Research Surveys

Presented in this thesis are observations on the natural behaviour and vessel/trawl induced behaviour of cod inhabiting Smith Sound at different times of year under different environmental conditions. These observations provide a number of insights for resource assessment surveys conducted in fjords.

Natural Behaviour – Availability:

Substantial seasonal differences were observed in the distribution, abundance, size composition, swimming speed, and diel activity rhythm of Atlantic cod in Smith

Sound. During summer, cod were widely distributed, low in density, limited in size distribution, and highly active. In contrast, during winter cod were aggregated, high in density, absent from shallow areas, present in a wide range of sizes, and exhibited limited horizontal and vertical movement, as well as limited activity levels. Taken together, these observations suggest that winter would be an ideal time to carry-out a research survey in this region as cod are predicted to exhibit only limited changes in availability to sampling tools (see Chapter 1). Rose (2003) confirmed this hypothesis by conducting a systematic survey of Smith Sound at various times of the year between 1995 and 2002. The author found that acoustic surveys conducted during June-October revealed large variation in cod distribution and produced highly variable estimates of population biomass. Surveys conducted in January, by comparison, revealed dense, semi-pelagic, mono-specific aggregations of cod that were easily detectable by an echosounder. Hence, data at the individual level (this thesis) and the shoal level (Rose 2003) are in agreement as to the recommended timing of research surveys in Smith Sound.

Surveys conducted during the winter will, however, encounter certain limitations. For acoustic surveys, variation in the horizontal distribution of cod as well as variation in their detectability over the diel cycle have been identified as major sources of uncertainty (Rose et al. 2000). For bottom trawls, the most serious limitation is the inability to adequately sample such a massive aggregation. Standard tow durations used in the Newfoundland region (~15 min) would be impractical given the enormous catch rates that would be experienced, the difficulty bringing the catch onboard, and the lengthy sampling time required once the catch is on deck. Depending on the degree of spatial sampling, bottom trawling may also prove ineffective at resolving differences in size-structure within the aggregation (Rose 2003). Other limitations of a winter survey in Smith Sound would be year-to-year differences in a) the arrival time of the aggregation and b) the vertical distribution of cod, both of which were documented in this thesis. Both will bias the proportion of cod present in the dead-zone of an acoustic transducer as well as the swept area of a bottom trawl. If these changes in availability occur in a non-systematic manner, they would be predicted to lower the accuracy and reliability of a survey time-series (Engås and Godø 1986; Godø 1994; Fréon and Misund 1999).

Vessel/Trawl Induced Behaviour – Availability and Catchability:

The findings from Chapter 6 indicate that cod are capable of a) reacting to an approaching vessel from considerable distances, b) that the likelihood of reaction and reaction distance can vary with season, and c) that the disturbance produced by the encounter can persist for a period of time after the vessel/trawl has left the area. These findings could influence estimates of population abundance and size-composition in several ways:

1) If significant vertical or horizontal movement is associated with the avoidance behaviour observed, then acoustic and bottom trawl indices may not be representative of true fish densities near the seafloor and in the pelagic zones, respectively (Godø 1994; Fréon and Misund 1999). Detailed studies of the spatial and temporal patterns of fish movement will be necessary to test this hypothesis.
2) A reduction in both the likelihood of reaction and the reaction distance during winter indicates that a drop in *response threshold* may be occurring at this time of year, most likely in response to low water temperature and ambient light intensity. This suggests

that reduced vertical and horizontal dispersion of cod may occur in winter compared to summer, producing a seasonal bias in the proportion of cod available to an acoustic transducer and bottom trawl. Avoidance studies conducted at the same site in both seasons would be needed to adequately test this hypothesis and remove confounding influences such as those encountered in this study.

3) If an increase in response threshold (i.e. drop in sensitivity) during winter occurs in the near-field of the trawl (not investigated), than a reduction in herding efficiency would be predicted for cod located in the sweep zone (Fig. 1.3). This should lead to a smaller proportion of cod effectively herded into the trawl path and the potential to underestimate population abundance relative to the summer (Engås 1994; Winger et al. 1999).
4) An increase in response threshold (i.e. drop in sensitivity) during winter would also be expected to increase the vulnerability of cod located directly in the trawl path (Fig. 1.3). Combined with a reduction in swimming capability (Winger et al. 2000; Winger and Walsh 2001), this should lead to an increase in the turn-over rate of cod in the trawl mouth and the potential to overestimate population abundance relative to the summer.
5) The independence of vessel speed on reaction distance during summer (Fig. 6.4) suggests that the shallow regions of fjords may become saturated with vessel noise – effectively 'deafening' cod at all vessel speeds (C. Stevens, Fisheries and Oceans Canada, Newfoundland Region, pers. com.). While this is expected to be vessel-specific, it indicates that mobile sampling tools (e.g. acoustic surveys and bottom trawls) may not be effective in shallow environments (< 40 m) unless vessel-radiated

noise can be dramatically reduced. Static or even multiple gear types (e.g. longlines, gillnets, or cod traps) may be more appropriate for sampling this portion of the population distribution. While the use of multiple fishing gears is generally avoided during surveys (Godø 1994), it can on occasion be necessary if the information from just one or two tools could produce a misleading measure of abundance (e.g. Godø et al. 1989).

6) Disturbance produced by an encounter with a vessel and/or bottom trawl may influence the availability of cod to subsequent acoustic transects or trawl hauls. Sampling that is repeated in close proximity (time and space) before cod have time to resume natural behaviour may bias availability and possibly lead to habituation or even avoidance learning (Kieffer and Colgan 1992). Survey designs that identify optimal temporal/spatial observation windows could limit these effects.

7.5 Limitations of Acoustic Telemetry

Radio-acoustic-positioning (RAP) systems such as the one used in this thesis have been commercially available since the early 1990s and are now being used worldwide in a number of diverse disciplines (O'Dor et al. 1998).

Limitations of the system fall mainly in the area of position estimation. As acoustic energy travels through the water, it is subject to the influence of absorption, refraction, and reflection. Signal detection is further influenced by factors such as habitat type, sea state, ambient noise in the sea, and vessel traffic (see Voegeli and Pincock 1996 for review). These factors can exert a strong influence on the successful estimation of a fish's position. Several studies have quantified the error associated with positioning systems (e.g. Juell and Westerberg 1993; Smith et al. 1998; Ehrenberg and Steig 2002, 2003). However, erroneous positions will still occur despite best efforts in experimental setup and absolutely calm sea conditions. Visual inspection of the time series is therefore an established practice for removing outliers (e.g. Løkkeborg and Fernö 1999). While this is somewhat subjective, if information on the swimming capability is available for the species under investigation, then informed objective decisions can be made regarding removal of biologically meaningless datapoints (see Chapter 4 and 5).

Sampling frequency can be a critical factor when investigating fish behaviour at small spatial and temporal scales (Baras 1998). In Chapter 6, sampling frequency was identified as a limiting factor in the examination of vessel and trawl avoidance behaviour. For this reason, the behaviour of cod as they directly interacted with the vessel and bottom trawl (i.e. nearfield) could not be investigated. My analysis was therefore limited to an examination of swimming speed over time, without any attempt to associate specific movements of the fish in relation to different components of the vessel or trawl. This limitation is common to telemetry studies, whether it is examining fish behaviour in relation to fishing gear (e.g. Engås et al. 1998; Kallayil et al. 2003), hydroelectric plants (e.g. Scruton et al. 2002), underwater reefs (e.g. Glass et al. 1992; Sarno et al. 1994), aquaculture facilities (e.g. Bjordal and Johnstone 1993; Juell and Westerberg 1993; Bégout Anras et al. 2000), or seismic air guns (e.g. Wardle et al. 2001). Recent improvements in technology now permits multiple fish to transmit on a single frequency at high sampling rates (e.g. Cote et al. 1998; Niezgoda et al. 2002). This technology was not commercially available at the time of this study, but should permit the investigation of fish behaviour at even finer spatial and temporal scales.

Another limitation relates to position fixing interval. Single channel positioning systems such as the one used in this thesis identify individual fish based on the unique acoustic frequencies emitted by their transmitters. The system operates in a manner whereby it cycles between the various frequencies, adding increasing delay with each fish released into the water. This increase in position fixing interval has been shown to significantly bias the interpretation of fish behaviour (Løkkeborg et al. 2002). If sufficient high resolution data are available for individual fish (e.g. Chapter 4), than the bias has the potential to be corrected. Without such data, this type of bias cannot be corrected (e.g. Chapter 5). For this reason, the fine scale examination of swimming speed was omitted in Chapter 5. The recent improvement in technology which permits multiple fish to transmit on a single frequency (e.g. Cote et al. 1998; Niezgoda et al. 2002) should overcome this limitation.

The final limitation of acoustic telemetry is that it only provides information on a small portion of the population. While data quality is often quite excellent, sample size is generally low due to the high cost of equipment and the limited number of fish that can be effectively tracked (see Lucas and Baras 2000 for review). Only when large numbers of fish are monitored (e.g. Righton and Metcalfe 2002) can behaviour at the individual level be accurately scaled to the population level (Sumpter and Broomhead 2001). In this thesis, I present data on the natural behaviour of 17 cod (4 in Ramfjord, 13 in Smith Sound). These behavioural observations represent those individuals that remained within range of the positioning system (i.e. nearly half left upon their release in Smith Sound and were never located again) and therefore probably reflect individuals with limited home ranges. I also present observations of avoidance behaviour during 39 vessel/trawl passes. With the exception of Harden-Jones et al. (1977), few tracking studies have matched this effort. However, given the number of treatments investigated, the number of replicates was sometimes low (see Table 6.2), making direct comparisons difficult. What is certain from Chapter 6, is that avoidance behaviour can be significant and that it is highly variable. Discerning the full repertoire of behaviour is an important first step toward identifying the proximate factors that influence behaviour (i.e. response threshold) and determining functional explanations for the behaviours observed.

7.6 Future Directions

As part of this thesis, several obstacles and gaps in existing knowledge were identified. I offer the following key challenges for future research initiatives:

Tagging:

1) Increasing use of electronic tracking devices has lead to greater scrutiny on the ethics of tagging procedures (Smolowitz and Wiley 1998). Tagging fish with the least invasive methods possible should be aggressively pursued within the limitations of each study.

Natural Behaviour:

2) Crepuscular and nocturnal activity rhythms were both observed (at the same time) among juvenile cod in Ramfjord, Norway (Chapter 4). Additional studies are needed to investigate the extent to which between-individual variation in diel activity rhythm exists and to determine how these trade-offs may affect individual fitness.
3) Important questions remain unanswered regarding the ecology of the cod population in Smith Sound, including; a) the degree to which summer and winter aggregations

are distinct, b) the timing of arrival and departure of the winter aggregation, c) factors influencing density distribution during winter, d) factors determining habitat selection, and e) influences of spawning and feeding behaviour on activity level.

4) Acoustic tagging techniques are both time consuming and expensive. While the data can be exceptional, they generally produce only short-term observations of fish behaviour. Future studies could combine acoustic transmitter and data storage tag technology to provide longer term (seasonal/yearly) observations.

Avoidance Behaviour:

5) Observing and measuring avoidance behaviour continues to be the key research necessity at this time. Most of the research to date has produced what can only be considered to be a 'collection of scattered observations'. Gaps in knowledge still exist in our understanding of a) the biological basis of stimulus detection and reaction, b) proximate factors determining reaction distance, c) costs and benefits of different avoidance behaviours, and d) the degree to which species differ in sensory capacity, swimming capability, and risk willingness.
6) The influence of repeated exposure to vessel/trawl radiated noise has not been explored and is a potential area for new behavioural studies. Acoustic positioning systems such as the one used in this study are well suited for investigating the role of learning (e.g. habituation or avoidance) in fish behaviour. The tracking of individual fish over extended periods cannot be achieved with other technologies.
7) Researchers investigating vessel and trawl avoidance behaviour often experience small datasets due to the large cost and labour associated with this field of study.

Collaboration of data among institutes and the formation of an international database on avoidance behaviour is a potential means of overcoming the paralysis of small datasets.

8) Empirical evidence is still lacking for temperature-dependent catchability of cod in the nearfield of a bottom trawl. A growing list of new technologies for quantifying fish behaviour during fish capture (see Godø 1998; Graham et al. 2004 for review) are now available and must be acquired and dedicated to this task.
9) Vessel noise was shown to significantly influence the natural behaviour of cod in a fjord environment. Researchers should have the noise signature of the platform they are using documented in order that the validity of their observations can be assessed. As existing vessels age and need replacement, only vessels meeting the ICES recommendations for maximum noise levels (Mitson 1995) should be considered.
10) Finally, the biggest challenge for this field remains the inability to accurately correct indices of abundance derived from acoustic and bottom trawl surveys for avoidance behaviour. Current models are too general and cannot be applied in all contexts. While growing concern over avoidance behaviour does exist, sufficient variation between surveys must be shown before any correction could be justified. Significant strides in this area can not be achieved without accomplishing item 5.

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