ESCAPE-RELATED BEHAVIOUR OF ATLANTIC COD (GADUS MORHUA): MOTIVATION TO ESCAPE FROM SEA CAGES AND SPATIOTEMPORAL DISPERSAL POST-ESCAPE

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ESCAPE-RELATED BEHAVIOUR OF ATLANTIC COD (*GADUS MORHUA*): MOTIVATION TO ESCAPE FROM SEA CAGES AND SPATIOTEMPORAL DISPERSAL POST-ESCAPE

by

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A Thesis submitted to the

School of Graduate Studies

in partial fulfillment of the requirements for the degree of

Master of Science

Cognitive and Behavioural Ecology Program

Memorial University of Newfoundland

December 2012

St. John's Newfoundland

ABSTRACT

This study addresses the potential for interaction between escapee farmed and wild cod following escape from aquaculture sea cages. The first chapter introduces the topic of fish escapes from a behavioural perspective. The second chapter investigates the role of suboptimal conditions and individual temperament on net biting behaviour. The data suggest that appropriate feeding levels combined with cage enrichment, as well as good net maintenance, may lead to reduced net interactions and thus fewer holes, reducing the potential for fish to escape. In the third chapter, I used acoustic telemetry to determine the spatiotemporal distribution of local wild cod and escapee farmed cod following a simulated escape. Farmed cod dispersed from the cage site rapidly and mixed with local wild cod, suggesting a high potential for interactions and highlighting the importance of reducing escapes before they occur. These results can be applied to reduce the number of escapes, streamlining the development of the industry before mitigation becomes too difficult and costly to implement.

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my co-supervisors, Dr. Craig F. Purchase and Dr. Ian A. Fleming, for the opportunity to pursue my interests in marine science and for their endless guidance and advice. I would also like to thank committee member Dr. John Brattey for his advice and guidance during the field portion of my thesis, as well as the input of committee member Dr. Edward Trippel. I also thank Chris Canning and the staff at the Joe Brown Aquaculture Research Building (JBARB) and Andy Walsh and the staff of Sapphire Sea Farms, Bay Bulls, NL for their help with the farmed fish. Many thanks to Peter Williams for the use of his fishing boat and his expertise and local knowledge of Bay Bulls. Thanks to all members of the Purchase and Fleming labs, especially Corinne Conway, for always being available for help and assistance throughout the research project. I would like to thank Peter Westley, Shad Mahlum, and Paul Regular for advice during data analyses. I would also like to thank Amy-Lee Kouwenberg, Olivia Puckrin, and Margie Wilkes for all the impromptu thesis discussions, and of course my family for their continued support and encouragement.

This research was supported by funding from the National Sciences and Engineering Research Council of Canada by way of a Strategic Project grant to Ian A. Fleming and Craig F. Purchase. Student funding was provided by a School of Graduate Studies Fellowship, the Research Development Corporation of Newfoundland and Labrador, and the Dr. Wilfred Templeman Memorial Graduate Scholarship.

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1. Introduction and overview

Aquaculture has become a major supplier of fish in worldwide markets, representing 46% of the global food fish supply for human consumption, and it is growing more rapidly than any other food-producing sector (FAO 2010). The volume of farmed fish and shellfish nearly tripled between 1995 and 2007, driven by the decline of natural fisheries and increased consumer demand (Shelton and Rothbard 2006; Naylor et al. 2009). Environmental and economic problems have forced the aquaculture industry to improve the quality and rate of production. However, fish escapes remain a persistent problem for almost all cultured species (Jensen et al. 2010). Escapes are economically detrimental to the farmer and raise concerns about aquaculture's environmental sustainability (Hansen et al. 2009). The problem of fish escapes is still unresolved despite improvements by the industry to reduce the incidence and severity of such events.

Domestication is inherent in the process of plant and animal culture, due to human intervention during the culture of a species in an unnatural environment. Traditional agriculture is land-based, and cultures alien-invasive (nonnative) species, or species that are no longer similar to wild conspecifics due to their history of domestication, such as corn, wheat, poultry, and cattle (Vigouroux et al. 2011). Therefore, the risk of interaction with wild conspecifics is negligible; however there is a risk of establishing an invasive alien population, such as from escapes from zoological parks (IUCN 2002; Pimentel et al. 2005; DAISIE 2008; Huntingford et al. 2012). Unlike traditional agriculture, aquaculture often grows cultured species in the habitat of their native conspecifics (e.g. Naylor et al. 2005).

Interactions between escapees and wild populations can have detrimental effects both genetically and ecologically. Differences in morphology, physiology, and behaviour arise from differences in rearing environments and selective breeding, favoring desirable traits such as fast growth and delayed maturation, but such differences can also arise through the variable survival of individuals in culture systems (Einum and Fleming 2001; Huntingford 2004; Bekkevold et al. 2006; Diana 2009). These differences, including the lack of local adaptation and lower genetic variation due to small founder populations (Huntingford et al. 2012), can be maladaptive and result in a reduced ability for farmed fish to survive in the wild (Wilson 1992). When farmed fish interbreed with wild fish, the fitness of the wild population can therefore be lowered through hybridization events and outbreeding depression (Fleming et al. 2000; McGinnity et al. 2003; in cod see Uglem et al. 2008). Offspring of such crosses often have intermediate or poorer performance than the parental populations (Einum and Fleming 1997; reviewed in: Utter 1998; Bekkevold et al. 2006; Hindar et al. 2006). In addition to the genetic impacts of escapes, there can be negative ecological effects. Domestic strains are often more vulnerable to diseases than wild strains, and can potentially transfer novel pathogens or parasites into the local environment (Wilson 1992; reviewed in Naylor et al. 2005). Escapees can also compete for food, habitat resources, and mates once in the wild, or impact populations through direct predation such as on salmon smolts (Brooking et al. 2006; Naylor et al. 2005).

Fish escapes occur in large, relatively rare episodic events, such as extreme weather, as well as occurring at a low, constant level of leakage (Jensen et al. 2010). Fish can escape through holes in the net that are caused by mechanical abrasion, external predators, and by the fish themselves biting the net (Dempster et al. 2007). Some fish, such as sea bream (*Dicentrarchus labrax*) and Atlantic cod (*Gadus morhua*), are particularly prone to escape because of their behavioural tendencies to explore and bite the net walls of sea cages, rather than schooling like salmon (Dempster et al. 2007; Moe et al. 2007; Hansen et al. 2009; Rillahan et al. 2011). As a further impact to the environment, cod are able to spawn inside cages and release genetic material into the environment (Jorstad et al. 2008). Norway is currently the world's leader in farmed cod, and they report an escape rate of 1% per year, much higher than the rate of 0.2% for farmed salmon (Jensen et al. 2010). It has been suggested that suboptimal conditions such as feeding, biofouling, net damage, and over-crowding may further encourage net interactions (Hansen et al. 2009; Moe et al. 2007).

In the northern Atlantic the aquaculture industry is dominated by salmonids (Naylor et al. 2005), but the industry is diversifying to include other marine species such as Atlantic cod (*Gadus morhua*), Atlantic halibut (*Hippoglossus hippoglossus*), and haddock (*Melanogrammus aeglefinus*) (Rosenlund and Halldorsson 2007; Paisley et al. 2010). Atlantic cod helped to fuel the economy and culture of the northern Atlantic for hundreds of years (Kurlansky 1997). In addition, cod is one of the top predators of the marine food web (COSEWIC 2010). Following the decline of cod stocks in the northeast Atlantic and their collapse in the northwest Atlantic in the late 20th century, the slow recovery of wild stocks has led to an increased incentive to farm cod (Myers et al. 1997; Brown et al. 2003, DFO 2012). Although interest in farming cod has waned recently due to numerous factors including economics and a resurgence of wild cod stocks, upon increased demand for cod there is potential to further develop cod aquaculture (Bolton-Warberg and Fitzgerald 2012). However, the low abundance of coastal cod populations in addition to the localized genetic structure of these populations increases the risks of adverse impacts of escapes from cod aquaculture (Ruzzante et al. 2001; Hutchings and Baum 2005; Bekkevold et al. 2006; COSEWIC 2010). Wild coastal cod populations are therefore vulnerable to escapees from even low industry levels, and thus there may be considerable local impacts.

My thesis addresses the potential for interaction between escaped farmed and wild cod and aims to reduce the negative ecological and economic impacts of escape. The second chapter focuses on cod behaviour prior to escape, by investigating factors that motivate net biting based on four parameters: individual temperament, nutrition, cage enrichment, and net damage. The third chapter focuses on cod behaviour post-escape, by using acoustic telemetry to investigate dispersal behaviour of both escapee farmed and local wild cod following a simulated escape from a sea cage.

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Co-authorship Statement

The author of this thesis planned, designed and carried out the data collection in the lab and in the field, processed and analyzed all the data and wrote all the subsequent manuscripts. Dr. Craig F. Purchase and Dr. Ian A. Fleming contributed to experimental design and the evolution of data interpretation, as well as providing editorial reviews of all the chapters. Dr. John Brattey provided similar contributions for the third chapter.

Publication and submission status:

Chapter 2: (Zimmermann, Purchase, and Fleming) published in Applied Animal Behaviour Science 2012 **141**(1-2): 71-78.

Chapter 3: (Zimmermann, Purchase, Fleming, and Brattey) in press at Canadian Journal of Fisheries and Aquatic Sciences.

2. Reducing the incidence of net cage biting and the expression of escape-related behaviours in Atlantic cod (*Gadus morhua*) with feeding and cage enrichment

2.1 Abstract

The escape of fish from aquaculture is a persistent economic problem for farmers as well as an environmental problem that threatens wild fish populations as a consequence of potential negative ecological and genetic interactions. Farmed Atlantic cod (*Gadus morhua*) cause significant damage by biting the net and creating holes through which they escape. We determined the role of food, cage enrichment, net damage, and individual temperament on net biting behaviour. During four separate trials, net interactions by fish were observed in relation to combinations of the above treatments. Fish with no access to food and in plain (not enriched) cages interacted the most with the net wall, with 7.5 and 12.6 more interactions per hour, respectively, than fish with food that were in enriched cages (food $P = 0.01$; enrichment $P < 0.01$) . Of the stimulating objects used to enrich cages, 97% of interactions were with the tubes that provided refuge ($P < 0.01$). Cod were attracted to damaged areas of net, interacting 0.12 more times per hour than at undamaged areas ($P < 0.01$). Individuals showed consistent behaviour over time, but there was no relationship between temperament, measured as the willingness of cod to leave shelter, and net interactions ($P = 0.17$). The results indicate that appropriate feeding levels and cage enrichment may lead to reduced net interactions and thus fewer holes, reducing the potential for fish to escape.

Key words: Aquaculture; Fish farm escapes; Fish biting; Temperament; Boldness; Sea cage damage.

2.2 Introduction

Aquaculture is the fastest growing food producing sector in the world (Food and Agriculture Organization, FAO, 2010). Fish escaping from net pens is a persistent problem in the aquaculture industry, with escapes reported for almost all cultured species worldwide (Jensen et al., 2010). Despite numerous improvements by industry to reduce the incidence and severity of fish escapes, the problem of escapes is still unresolved. Fish can escape during large episodic events, such as extreme weather events, in addition to low-level leakage through holes in the net caused by mechanical abrasion, external predators, and by biting the net themselves (Dempster et al., 2007; Jensen et al., 2010).

Unlike traditional agriculture, aquaculture often grows cultured species in the habitat of their native conspecifics (e.g. Naylor et al., 2005). Differences in morphology, physiology, and behaviour arise from variations in rearing environments and selective breeding in captivity (Diana, 2009; Huntingford, 2004). These differences can have negative consequences if farmed individuals escape and interact with wild populations (Bekkevold et al., 2006; Einum and Fleming, 2001; Huntingford, 2004). Adult escapees can potentially interact with wild fish on spawning grounds, lowering the fitness of wild fish (Fleming et al., 2000; McGinnity et al., 2003; in cod see Uglem et al., 2008). Domesticated individuals often have less genetic variation than wild individuals, since stocks often come from small, non-native founder populations that lack local adaptations (Huntingford et al., 2012). Outbreeding depression, in which the offspring are often inferior and maladapted compared to the parents, and population hybridization events could therefore occur as a result of interbreeding (reviewed in: Bekkevold et al., 2006; Hindar et al., 2006; Utter, 1998). Other potential negative interactions with wild conspecifics include pathogen transfer and resource competition (Fleming et al., 2000; McGinnity et al., 2003; reviewed in Naylor et al., 2005). Other species can also be impacted through competition or direct predation (Brooking et al., 2006; Naylor et al., 2005).

Though aquaculture in the North Atlantic is dominated by salmonids (Naylor et al., 2005), other marine species such as Atlantic cod (*Gadus morhua*), Arctic char (*Salvelinus alpinus*), Atlantic halibut (*Hippoglossus hippoglossus*), turbot (*Scophthalmus maximus*), and haddock (*Melanogrammus aeglefinus*) are now being commercially farmed (Paisley et al., 2010; Rosenlund and Halldorsson, 2007). These species can differ markedly from salmonids in their behaviour and ecology. For example, cod are able to spawn inside cages and release genetic material into the environment (Jorstad et al., 2008). In addition, cod are 10-20 times more prone to escape than salmon due to their tendency to bite holes in nets and their willingness to escape (Esmark et al., 2005; Jensen et al., 2010; Moe et al., 2007). In Norway, the world's leader in cultured cod production, 1.05 million cod escaped from net cages between 2004 and 2009 (or 175,000 yr^{-1}), representing 1.02% of cod held in sea cages (compared with 0.19% escaped salmon) (Jensen et al., 2010). Escapes of up to 160,000 cod from a single farm have been recorded (Moe et al., 2007).

Although the majority of escapes are caused by structural, external or operational factors (e.g. storms, abrasion, predators; Jensen et al., 2010), significant net damage can occur due to net biting (e.g. one bite per cod per day, creating one hole per net cage per month) (Hansen et al., 2009; Moe et al., 2009). Unlike schooling salmon, cod spend a lot of time exploring the net wall, increasing the chances of finding a hole and escaping (Hansen et al., 2009; Rillahan et al., 2011). Cod have also been observed to bite at loose threads associated with small holes or repairs, thereby potentially enlarging existing holes in addition to creating new ones (Moe et al., 2007, 2009). Suboptimal conditions, such as the level of feeding, biofouling, or crowding, may further encourage net interactions (Hansen et al., 2009; Moe et al., 2007).

In addition, individual temperament may contribute to the tendency to bite the net wall. Temperament can be defined as the tendency of individual behavioural difference to repeat over time and, in behavioural syndromes, across situations (Réale et al., 2007; Sih et al., 2004b).

Behaviours such as net interactions may therefore be strongly influenced by variation amongst individuals, such as along the bold-shy continuum, where bold individuals are more prone to take risks and explore their environments (Fraser et al. 2001), such as the net wall of a cage (Hansen et al., 2009). Temperament may be particularly relevant as aquaculture may inadvertently select for bold, more easily captured fish (Bekkevold et al., 2006; Sundström et al., 2004). Shy individuals copying the behaviours (i.e., net biting, escape) of bold fish through social learning could increase the number of escapes (Hansen et al., 2009).

The collapse and slow recovery of wild cod populations in the northwest Atlantic (Committee on the Status of Endangered Wildlife in Canada, COSEWIC, 2010; Myers et al., 1997; Rose et al., 2000) has increased the economic incentive to farm cod. However, the industry has faced many challenges (Brown et al., 2003; Øiestad, 2005), and the problem of escapes has yet to be addressed. To reduce the negative ecological and economic impacts of escapes, we examined factors that may mitigate the motivation of cod to bite net cage walls. We tested the hypothesis that interactions with the net increase with suboptimal conditions, specifically that: (1) net interactions increase with food deprivation and net damage; (2) stimulating cage environments reduce net interactions; and (3) cod exhibiting 'bold' temperaments interact more with the net than those with 'shy' temperaments. The results aim to provide direction for reducing potential ecological effects and industry costs of escapes from aquaculture.

2.3 Materials and methods

2.3.1. Experimental fish

Farmed cod (F_2; ~1.5 years of age; mean ± sd, 320 ± 70 g; 31 ± 2 cm) were obtained from a semi-commercial scale hatchery at the Joe Brown Aquaculture Research Building of Memorial University's Ocean Sciences Centre (OSC; St. John's, Canada), where they had been fed 1% of their body weight daily. After transfer to an experimental facility at the OSC in winter 2011, the cod were kept in a holding tank in ambient seawater (1.0 ± 0.6 °C; 105 ± 5% O_2; ~31 practical salinity units, psu) for 2-21 days prior to experimentation (variable among trials).

2.3.2. Experimental design

The experiment was conducted in a large indoor flume tank (11 m x 2.5 m) that housed 20 circular net compartments (1 m diameter, 0.5 m deep) made from white knotless nylon netting (3.8 cm stretch mesh size). This mesh is commonly used in the commercial Newfoundland cod industry. Throughout the experiment, the flume tank was supplied with heated (3.7 ± 2.1 °C) and oxygenated (129 ± 10% O_2) seawater and was on an ambient day-night cycle (daylight, 39 ± 13 lux, measured at three locations along the flume tank). Cod were transferred from the holding tank to the experimental tank, where they were held for 1 (trials 2-4) to 4 (trial 1) days prior to filming. Experiments were run from March through May of 2011 (Table 1).

Four temporal trials were conducted, with four treatments distributed randomly among the 20 cages within each trial (Table 1). The four treatments (Fig. 1) were replicated twice in the first trial (initially limited by the number of video cameras) and five times in each of the subsequent trials (17 replicates total) and were: (1) plain, un-enriched cage deprived of food, (2) plain cage supplied with food, (3) enriched cage deprived of food, and (4) enriched cage supplied with food. Cod in the "food" cages were offered ~1% of their body weight in chopped frozen herring daily after filming ended at 13:00 h. Net cages were enriched with pipes (one 30.5 cm x 10.2 cm white PVC pipe near the center of each cage lying horizontally on the bottom, approximately twice the height of the cod) for cod to swim through and as a potential refuge, and with stimulating objects (one green, red, or blue tennis ball on a knotted rope because cod are attracted to fraying rope, and one orange or green knobby rubber ball toy (Pet Store, China, model 17-1700168 H4P 0A1) suspended near the cage bottom by fishing line). Within all net cages, a randomly chosen quarter of the net wall had frayed strings (extending 6 cm into the cage, same colour as mesh) tied to it to simulate net "damage"/repair and to determine whether this would attract more biting activity than "undamaged" netting.

Each net cage contained five cod (~one-quarter of the typical commercial stocking density of 15 kg cod m^{-3}). Within each trial, cod were size matched with no initial difference in weight between trials (generalized linear mixed model, GLMM, with trial as fixed and random factor, see equation 1 for more detail: $F_{3,318} = 1.88$, $P = 0.13$) or treatments (GLMM: $F_{3,318} = 0.92$, $P = 0.43$). Cod were tagged externally with t-bar tags for individual identification within each cage. During the first trial, cod were distributed sequentially through the cages (i.e., the first five cod from the holding tank were placed in the first net cage). For all following trials, cod were distributed randomly among the cages as they came from the holding tank.

2.3.3. Behavioural observations

All cages were filmed daily between 10:00 and 13:00 h for 9 days per trial using overhead cameras in real time at 25 frames s^{-1} at a resolution of 640 by 480 pixels (Axis 221 Day and Night Network Cameras, model no. 0221-01-04, Axis Communications, Lund, Sweden) placed 2.2 m above the water surface. We analyzed the behaviour of individual fish for a minimum of 30 min each day (two randomly selected 15 min segments) for 9 days (4.5 h total). Recordings were analyzed at 4x native speed and were scored for frequency of interactions with the net wall (touching the net with the snout and biting at the net; Hansen et al., 2009).

In addition to examining the effects of cage enrichment, food deprivation, and net "damage" on net biting behaviour, we also explored the role of individual temperament, measured as the willingness of cod to leave shelter; i.e. bold versus shy (exploration vs. avoidance according to Réale et al., 2007). To do this, each cod was placed in a closed box (50.8 cm x 63.5cm x 33 cm) for a 2 min settling period following the net cage trial. A mesh door (40.6 cm x 44.5 cm) was opened, and we measured the time for the cod to emerge fully from the box (see Brown et al., 2005; Brydges et al., 2008). Cod that had not emerged within 5 min were assigned a maximum time of 300 s. Cod were tested individually to decrease the possibility of social status or learning influencing behaviour (Fenderson et al., 1968). Quickly emerging cod were assumed to be bolder (see Toms et al., 2010). Temperament traits may correlate across contexts, suggesting that this test of temperament may correlate with exploration of the netting (Huntingford , 1976; Mas-Muñoz et al., 2011; Réale et al., 2007).

2.3.4. Ethical note

This study was approved by the Memorial University Animal Care Committee (protocol 10-15-IF), in accordance with the regulations of the Canadian Council on Animal Care for the treatment and welfare of animals.

2.3.5. Data analysis

All data were analyzed using R 2.12.2 (R Development Core Team, 2011) and the R package *lme4* (Bates and Maechler, 2009). Null hypotheses were rejected when $P < 0.05$. Residuals of all models were checked for normality and homogeneity. Test statistics and p-values are only approximations because regular distributions do not apply to the random effects structure of linear mixed effects models (Bates, 2006; Winter, 2011). Fish that died during the experiment (14 of 340, spread across all treatments) were removed from all analyses.

Food, enrichment, fish size, and temperament: To determine if food level and cage enrichment affected net interactions, a generalized linear mixed model (GLMM) with Poisson error distribution was run with the response variable of total net interactions per fish per day (9 observational days per individual cod).

$$\begin{gathered}\text{Net interactions} \sim \text{food*enrich} + \text{time*food} + \text{time*enrich} + \text{weight*food} + \\ \text{weight*enrich} + \text{weight} + \text{day} + (1|\text{trial/cage}) + (1 + \text{day}|\text{tag})\end{gathered} \qquad \textbf{(1)}$$

where * represents both an additive and multiplicative relation between the two terms (i.e., food*enrich = food + enrich + food*enrich) and | represents random effects. Fixed effects included food level, enrichment and time to emerge, with initial weight and day included as covariates. Random effects included trial (n = 4), cage nested within trial (n = 68), and individual fish (n = 326) allowing for a random variation in slope by day. Three-way and higher order interactions were considered biologically overly complex and not included in the initial model.

Specific enrichment: To further examine the influence of stimulating objects on net interactions, a subset of data including only enriched cages was used. The relationship between net interactions and interactions with stimulating objects was determined with a GLMM with Poisson error distribution and the response variable of total net interactions per fish summed over all days:

$$\text{Net interactions} \sim \text{object interactions} + \text{food} + (1|\text{trial/cage}) \qquad \mathbf{(2)}$$

The fixed effects were total interactions with stimulating objects and food level. The random effects were trial and cage nested within trial (n = 34). Furthermore, to determine if interactions with stimulating objects varied with object type, a subset of data with an average number of interactions per cage for each object type (i.e. maximum of three observations per cage) was used with a GLMM with Poisson error distribution:

$$\text{Object interactions} \sim \text{object type} + \text{food} + (1|\text{trial/cage}) \qquad \mathbf{(3)}$$

The response variable was total object interactions per cage, with fixed effects of object type and food level, and random effects of trial and cage nested within trial (n = 33).

Net damage: Total interactions at undamaged net were divided by three to standardize the net area with the damaged area (one-quarter of the net cage). To determine if mean interactions depended on net damage, a GLMM was run with mean interactions per cage as the response variable:

$$\text{Mean net interactions} \sim \text{treatment*net status} + (1|\text{trial}) \qquad \mathbf{(4)}$$

Treatment (combination of food level and enrichment) and net status (damaged or not) were fixed effects, and trial as a random effect.

Individual temperament: Using only data from cod in enriched cages, a GLMM was run to determine if time to emerge (i.e., temperament test) varied between fish that interacted with the tube and those that did not interact with the tube:

$$\text{Time to emerge} \sim \text{tube} + (1|\text{trial/cage}) \qquad \textbf{(5)}$$

Random effects included trial and cage nested within trial. A subset of data from cod that swam into the tubes was used for a second GLMM to see if time to emerge varied significantly with the number of interactions with the tube:

$$\text{Time to emerge} \sim \text{tube interactions} + (1|\text{trial/cage}) \qquad \textbf{(6)}$$

Random effects included trial and cage nested within trial.

2.4 Results

Two-way interaction terms associated with the GLMM model to examine effects of food, enrichment, fish size and temperament on net interactions were not significant ($P > 0.22$), and thus were removed from the final model. Both food level and enrichment had a significant effect on the rate at which cod interacted with the net wall in the final model (food $z = -2.46$, $P = 0.01$; enrichment $z = 6.47$, $P < 0.01$; Fig. 2). However, there was no significant relationship between time to emerge and net interactions ($z = -0.65$, $P = 0.17$, Fig. 3). For all treatments, the mean number of interactions increased over each 9 day trial by an average of 3.4 ± 4.1 interactions per fish per h ($z = 3.11$, $P < 0.01$).

2.4.1. Food deprivation and enrichment

Unfed (hungry) cod had on average 7.5 more interactions with the net wall per fish per h than fed cod (Fig. 2). Assuming similar interaction numbers per fish throughout a 12 h day (cod are more active during daytime; Rillahan et al. 2011), this equates to 90 more interactions with the net wall per day per fish than fed cod. In comparison, cod in plain cages had on average 12.6 more interactions with the net wall per fish per h than cod in enriched cages (Fig. 2). Using the same assumptions, this equates to 151 more interactions with the net wall per day per fish than cod in enriched cages.

Cod interacted with stimulating objects in enriched cages as well as with the net wall. There was a significant negative correlation between interactions with the net and the objects: cod that interacted more with stimulating objects had fewer interactions with the net ($z = -25.18$, $P < 0.01$). Interactions did depend on object type ($z = 18.60$, $P < 0.01$): 97% of all interactions with stimulating objects were with the tube (Fig. 4).

2.4.2. Damage

Cod interacted at damaged areas 0.12 more times per fish per h than at undamaged areas ($F_{1, 122} = 69.94$, $P < 0.01$). Extrapolated to a 12 h day, this equates to 1.4 more interactions at damaged areas per day per fish than at undamaged areas. However, there was no significant interaction between net status (damaged /undamaged) and treatment (four unique combinations of food level and enrichment; $F_{3, 122} = 0.16$, $P = 0.93$).

2.4.3. Individual temperament

Time to emerge into a novel environment ranged from 0.85 to 300 s (the maximum time) (Fig. 3). Furthermore, there was no significant difference in time to emerge between cod that interacted with the tube and those that did not interact with the tube ($t = 0.29$, $P = 0.82$). There was also no significant relationship between time to emerge and number of interactions with the tube ($t = 1.59$, $P = 0.36$). Net biting behaviour was consistent within individuals: the most active cod (i.e. having the most net interactions on average for each trial) within each cage interacted the most with the net on 60 ± 21% of the days over the 9 day trial.

2.5 Discussion

Fish that escape from aquaculture operations not only represent a direct economic loss for the farmer but are also of significant environmental concern. Although the potential impacts of these losses are widely documented for salmonids, Atlantic cod may escape at much higher rates.

Escapes could become a serious problem and to avoid this occurrence, further mitigation measures are required. Here we found that Atlantic cod escape-related behaviours can be reduced with cage enrichment, food availability, and net maintenance.

Cage enrichment resulted in the greatest reduction in net interactions. Cod housed in net cages enriched with stimulating objects interacted less with the net wall than cod housed in plain cages. This is an exciting result because cage enrichment would presumably be relatively easy and inexpensive to achieve on commercial farms. Numerous studies have investigated the use of housing enrichment on rodents and other species for medical research (e.g. Olsson and Dahlborn, 2002) and when rearing animals to be released for stock enhancement programs (in cod see Moberg et al., 2011; Salvanes and Braithwaite, 2006). Apart from studies on maintaining animals in zoos (Shyne, 2006) and organic animal husbandry (Spoolder, 2007), few studies have investigated the use of enrichment in a purely captive situation, such as for aquaculture, where the aim is not for better survival in the wild but easier management of captive fish (but see Brydges and Braithwaite, 2009).

Our results suggest that the stimulating objects (especially the tubes) distracted cod from investigating and interacting with the net wall. The enrichment may also provide a complex habitat such as those preferred by cod in the wild (Cote et al., 2002). The use of enrichment in aquaculture cages may therefore help reduce the amount of damage caused by net biting incidents and may also reduce the incidence of escapes through holes created by storm damage by reducing the net inspection behaviour of cod. We tested a limited variety of stimulating objects in this study; by using other enrichment objects a bigger impact may also be observed. There was a clear preference for the tubes over the other enrichment objects, suggesting that the tubes may act as a preferred refuge for the cod. In our study, up to three fish could fit inside a tube at one time, however some individuals never approached the tube. To scale up to a commercial sized cage, an array of multiple tubes could be added to the cage, either adding large tubes to accommodate full grown fish, or changing the sizes of the tubes as the fish grow. A stationary tube array would possibly be more conducive as a shelter or refuge, however resting on the bottom of a cage may lead to net fraying and damage. Further studies need to be implemented to determine the efficacy of tubes as a stimulating object and refuge for farmed cod in a sea cage.

Food availability also led to a reduction in the number of interactions with the net, with hungry cod interacting more with the net wall than cod with access to food. Hansen et al. (2009) found that cod starved for 9 days were more prone to escape, but they observed no correlation in net exploration and net biting. However, behavioural differences between stocks have been observed, especially between migratory and resident populations (Brown et al., 2003; Hansen et al., 2009). We conclude that well fed cod have less motivation to escape, resulting in fewer interactions with the cage wall. Furthermore, we suggest that hungry cod may investigate the net in search of additional food, as suggested by Moe et al. (2007). We observed 11.2 ± 14 interactions on average with the net per h, which is similar to the interaction rate of 13.8 interactions per h observed by Hansen et al. (2009). Our study used fish that were 219 g lighter and stocked at a density of 3.92 kg m^{-3} greater than that of Hansen et al. (2009). Moreover, the entire wall area of our cages consisted of mesh compared to only 34% in Hansen et al. (2009). Hungry cod interacted with the net 90 times more in a 12 h day than fed cod; when extrapolated to a commercial scale of 200,000-400,000 fish per cage (Jensen et al., 2010) this equates to 18-36 million more interactions per cage per day, representing a significant potential source of damage. This indicates that maintaining an appropriate feeding level in aquaculture cages is a key factor in reducing the number of escapes through holes cause by net biting. In addition, the effects of enrichment and food appear to be additive, resulting in the least amount of net interactions of all the treatments. This suggests that combining enrichment with appropriate feeding levels may further reduce net interactions.

Interactions with both the net and the stimulating objects increased across days during each experimental trial. This rate of increase did not vary significantly between treatments, indicating that the increase was not due to food availability or cage enrichment. As time elapsed, the novelty of the net cages and stimulating objects would have decreased, potentially encouraging the cod to try to escape from the cages. This may suggest an increase in exploratory behaviour with habituation to the cage environment. Compared to the length of time cod would be housed in commercial net cages, the duration of our experiment (each trial = 9 days) was very short. Within the constraints of the current experiment, we could not test the potential response of cod to objects over longer time scales that are more applicable to commercial operations, suggesting a direction for future studies.

Cod were more likely to interact with damaged net areas than undamaged areas. These results correspond with previous studies, which have observed increased attraction to damaged areas (Moe et al., 2007, 2009). However, these other studies used a pre-damaged net panel that was suspended in the aquaculture cages. Cod may have been attracted to these net panels as novel objects (similar to the stimulating objects used in this experiment), rather than due to the actual net damage. Furthermore, cod have been observed to be attracted to repairs made with string of contrasting colour to the mesh (Moe et al., 2007). In our study, we used string of the same colour as the mesh, potentially resulting in lower visibility of the strings and thus fewer interactions. These results suggest the importance of regular net maintenance to avoid frayed or damaged strings that may attract the attention of cod, resulting in investigatory biting which could develop into larger holes.

Individual behaviour varied widely, as seen in other studies (i.e. see Sverdrup et al., 2011). There was no effect of fish size on behaviour within the narrow size range we examined. We observed inter-individual variation but intra-individual consistency over time (within the tested context of net biting, there were consistent net-interactors over the course of the trials), suggesting that cod showed stable behavioural types (Conrad et al., 2011). Many studies have suggested that temperament traits correlate across contexts (i.e. domain-general), indicating the presence of behavioural syndromes (Sih et al., 2004b). For example, different genotypes may exhibit varying behaviour along the "shyness-boldness" continuum, with bold fish more willing to take risks, explore the net cage environment, and escape for possible resource gains (Fraser et al., 2001; Hansen et al., 2009). This suggests that behaviour in net cages may be strongly influenced by individual variation.

Our results, however, indicate that performance in our temperament test (emergence into a novel environment) is not a good predictor of interactions with the net. In contrast to domain-general temperament traits, other studies have found that behaviours are context specific (for review see Conrad et al., 2011). Depending on the circumstances (i.e. predator absence/presence), behavioural flexibility is important and it is optimal to have context-specific behaviour (Conrad et al., 2011; Komers, 1997; Sih et al., 2004a; Toms et al., 2010; Wilson, 1998). Therefore, it is not necessarily surprising that inter-individual variation was not explained by cod size, or exploration behaviour (as in Hansen et al., 2009). In addition, our experiment did not control for the role of social interactions experienced prior to the temperament test. Despotic interactions in the net cages may have caused subordinate fish to remain less mobile when tested for temperament (Øverli et al., 1998). It is generally accepted that animals have consistent behavioural types, as observed in our study, however the mechanisms controlling these types are not well understood and merit further study (see Conrad et al., 2011). In addition, we assessed temperament with only one test, the propensity to leave shelter. Due to logistical limitations, we were unable to conduct further temperament tests on the same individuals. Caution must therefore be used in drawing conclusions from the temperament portion of this study.

In summary, appropriate feeding levels, cage enrichment, and net maintenance may lead to reduced net interactions by farmed cod. Hansen et al. (2009) found that cod could rapidly discover new openings from several meters away, emphasizing the need to avoid net damage and maintain constant screening. In addition, we found consistent inter-individual variation in behaviour, suggesting the presence of stable behavioural types (within but not across contexts). More studies are needed to further understand the mechanisms driving this variation and the linkages between behaviours. In comparison with commercial aquaculture, this study was of short duration (9 days) with a low stocking density (~one-quarter of typical stocking density), which may have affected the rate of net interactions observed. Further studies should be conducted to better relate these experimental findings to conditions typically encountered in commercial aquaculture environments. The results of this study can be used by aquaculture managers to avoid conditions which result in increased interactions between Atlantic cod and the net walls, decreasing damage to the net and reducing the number of escapes. These results may also be applied to other farmed pelagic marine fishes that bite at the net, such as sea bream (Dempster et al., 2007). Cage enrichment and appropriate feeding may also enhance the welfare of the captive fish, for example by reducing stereotypies such as repeated circular swimming, and even net biting, and encouraging natural behaviours in a complex habitat (Ashley, 2007; Cote et al., 2002).

2.6 Conclusion

This study indicates that cage enrichment and appropriate feeding, coupled with net maintenance may lead to reduced interactions with the net by cod. Proactively addressing the conditions that encourage net biting may prove to be a cost efficient and complementary means, along with that of improving net materials, to reduce escapes.

2.7 Acknowledgements

We thank C. Canning at Memorial University of Newfoundland for his help maintaining the cod, as well as assistance from the staff of JBARB. We also thank C. Conway and P.A.H. Westley for their help during the experiment, B. Damsgård and C. Noble for helpful comments, and G.H. Bolstad for statistical guidance. This work was supported by funding from the National Sciences and Engineering Research Council of Canada by way of a Strategic Project grant to I.A.F. and C.F.P. and graduate funding to E.W.Z. from the Research and Development Corporation of Newfoundland and Memorial University of Newfoundland. The funding sources had no role in study design, data analysis, or writing.

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Table 2.1. Initial mean weight (g) of experimental fish by temporal trial.

There were no significant differences in fish weight between trials or treatments.

Temporal trial	Plain		Enriched	
	Fed	Deprived	Fed	Deprived
Trial 1[a]	n/a	290 ± 50	n/a	290 ± 80
7 – 15 March				
Trial 2	320 ± 60	300 ± 60	320 ± 70	320 ± 70
18 – 26 March				
Trial 3	340 ± 80	350 ± 70	320 ± 70	310 ± 80
31 March – 8 April				
Trial 4	350 ± 70	350 ± 100	320 ± 60	340 ± 60
27 April – 8 May[b]				

a. Fish did not eat during the first trial, so only one food level (no food) was tested.

b. Data were not recorded 30 April – 2 May due to condensation problems with the cameras. Thus, trial 4 ran for 12 days to provide 9 days of video data.

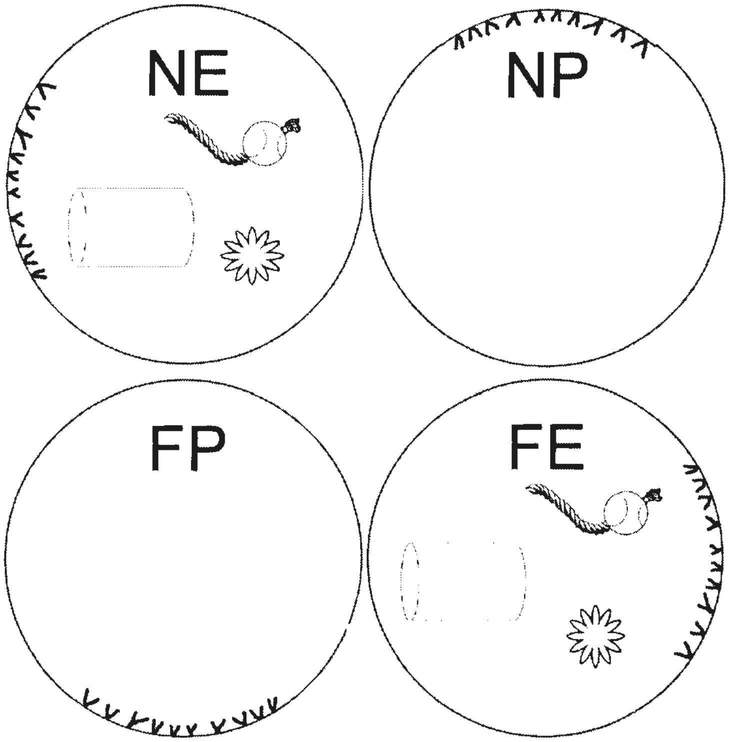

Figure 2.1. Schematic representation of experimental setup.

Four circular net compartments (1 m diameter x 0.5 m deep), depicting the four unique treatment combinations: food (F), no food (N), enrichment (E), plain (P). One randomly selected quarter of each net cage was tied with frayed string. Treatments were randomly distributed within the 20 cages per trial. Five cod were distributed randomly into each cage.

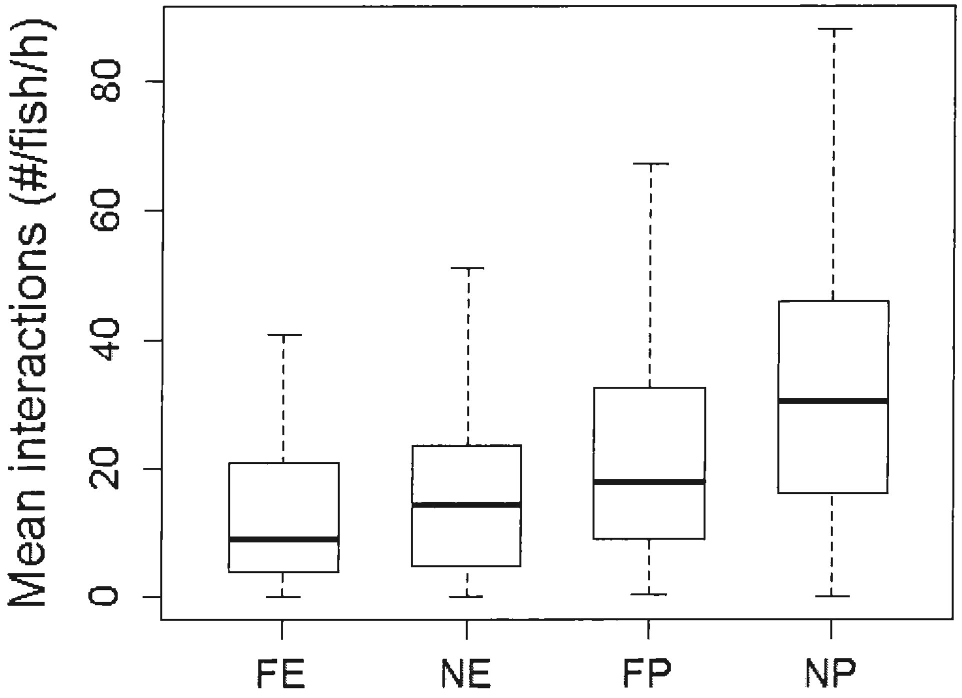

Figure 2.2. Mean net interactions per fish per hour by treatment.

Treatments include food (F), no food (N), enriched (E), and plain (P). Each box represents the 50% quartile, the dark line the median, and the whiskers 1.5 times the inner quartile range.

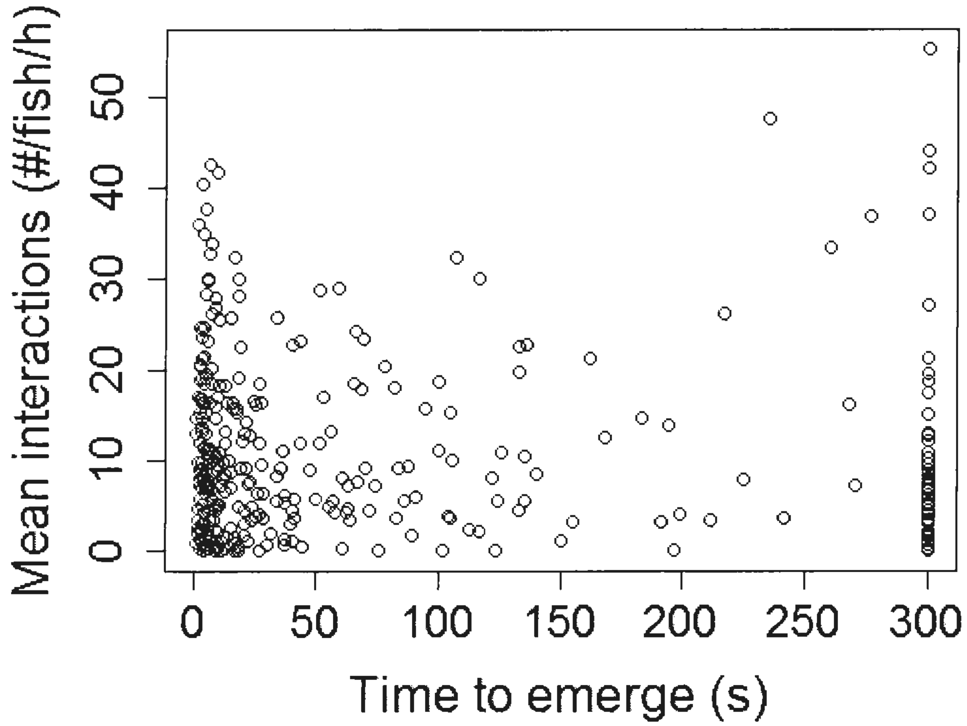

Figure 2.3. Relationship between time to emerge and mean net interactions.

Each point represents data from an individual fish, comparing the mean net interactions per hour with the time to emerge from the shelter for each fish.

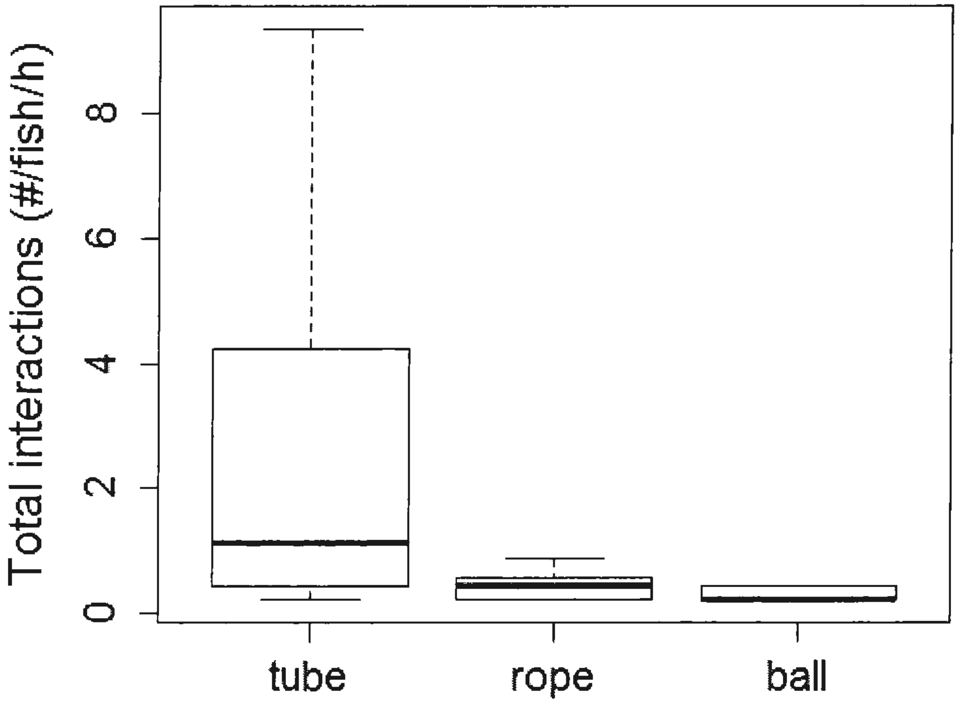

Figure 2.4. Total number of interactions per fish per hour with stimulating objects.

Stimulating objects in the cages included a length of PVC pipe, a tennis ball on a rope, and a knobby rubber ball. Each box represents the 50% quartile, the dark line the median, and the whiskers 1.5 times the inner quartile range.

3. Dispersal of wild and escapee farmed Atlantic cod (*Gadus morhua*) in Newfoundland

3.1 Abstract

Differences in morphology, physiology, and behavior that arise through selective domestication could be maladaptive in nature and lead to negative ecological consequences when non-native individuals escape, such as from aquaculture sea cages, and interact with wild populations. To determine the potential for interactions between farmed escapees and wild populations, we used acoustic telemetry to map the spatiotemporal distribution of local wild (n = 29) and "escapee" farmed cod (n = 52) through experimental releases off eastern Newfoundland. Dispersal from the cage (>600 m) was rapid (50% dispersal: 12 h for farmed; 5 h for wild) and non-random. Most cod (85% farmed, 55% wild) moved northward, remaining close to shore. Although recaptures of escapees during small-scale recreational and commercial fisheries was high (11% farmed; 10% wild), our results suggest that directed efforts to recapture escapees would be logistically challenging. Cod migrated a considerable distance (max. of 256 km for wild; 157 km for farmed), and some returned to the bay the following year. The similarity of the distribution of "escapee" farmed and wild cod suggest the strong potential for interactions between farmed and wild fish, highlighting the importance of minimizing escapes.

3.2 Introduction

Local adaptation plays a key role in maintaining ecosystem productivity and the genetic diversity of wild populations (Kawecki and Ebert 2004). Selective domestication combined with captive rearing environments lead to differences in morphology, physiology, and behaviour between farmed and wild conspecifics (Einum and Fleming 2001; Huntingford 2004). These potentially non-adaptive differences could lead to negative ecological consequences if escapees interact and ultimately breed with wild populations (Fleming et al. 2000; Huntingford et al. 2004; Bekkevold et al. 2006). Interbreeding with wild fish could potentially reduce the fitness of native populations through outbreeding depression (McGinnity et al. 2003; Hindar et al. 2006). Non-native farmed fish may lack local adaptations and have reduced genetic variation due to small founder populations (Ferguson et al. 2007) and crosses with wild fish could result in hybrid offspring with intermediate or poorer performance than the parental populations (Einum and Fleming 1997; McGinnity et al. 2003; Fraser et al. 2010). Knowledge is based on the developed salmon industry, as little work has been done on the potential genetic impacts of farmed cod on local wild cod (Bekkevold et al. 2006).

Fish escaping from net pens is a persistent problem (Jensen et al. 2010) that occurs almost everywhere net pen aquaculture is practiced (Naylor et al. 2005). In addition to interbreeding, other potentially negative impacts of escapes include disease transmission and resource competition (reviewed in Naylor et al. 2005; Diana 2009). Most knowledge of the effects of escapees comes from studies on salmon, however some recent work has been done on escapee cod (*Gadus morhua*; Moe et al. 2007; Uglem et al.

2008, 2010; Meager et al. 2009). In the north Atlantic, the slow recovery of wild cod stocks following their decline (northeast Atlantic) and collapse (northwest Atlantic) in the late 20th century has led to increased farming incentive (Myers et al. 1997; Brown et al. 2003, DFO 2012). However, due to net biting, cod are particularly prone to escape from sea cages, with escape rates of 1.02%, much higher than the rates of 0.19% for salmon (Moe et al. 2007; Hansen et al. 2009; Jensen et al. 2010; Damsgård et al. 2012; Zimmermann et al. 2012). Interbreeding is likely as escapees have been found at wild spawning areas in Norway (Uglem et al. 2008; Meager et al. 2009). Wild cod in the Northwest Atlantic may be particularly susceptible to hybridization with escapees due to the low abundance and localized genetic structure of coastal populations (Ruzzante et al. 2001; Bekkevold et al. 2006; COSEWIC 2010), especially when escapees originate from non-native populations (Diana 2009).

The susceptibility of wild cod to interactions with escapees depends on the migratory patterns of the two groups; however, little is known about the migration patterns of wild cod in the northwest Atlantic. The stock structure of Newfoundland cod is complex with some discrete groups (Ruzzante et al. 1996) spawning in specific habitats (offshore, Lear 1984; inshore off headlands, Templeman 1966; or in bays Hutchings et al.1993; Smedbol and Wroblewski 1997; Brattey et al. 2008), as well as some mixing of individuals between groups (Taggart 1997). In eastern Newfoundland, cod stocks may be a mix of summer feeding groups from the northeast and south coasts (Lawson and Rose 2000; Robichaud and Rose 2004).

The degree of interactions between escapee and wild cod may depend on the movement patterns of the escapees relative to wild individuals. Previous studies have observed escapee farmed cod remaining in the local area in Norwegian fjords; however, population differences in dispersal and migration may occur between the east and west North Atlantic, as well as between bay systems (Uglem et al. 2008, 2010). For example, wild juvenile cod reared in a farm setting in Newfoundland for three years prior to release traveled up to 170 km from the release site (Wroblewski and Hiscock, 2002), overlapping in the movements of local wild cod. The movements of escapee hatchery-reared cod in the Northwest Atlantic have to our knowledge not been studied previously.

The risk of negative impacts due to escaping fish has been demonstrated in salmon, however few studies have focused on escaping cod (see Moe et al. 2007; Uglem et al. 2008; Meager et al. 2009). To determine the potential for interaction between escapee farmed cod and local wild cod, we quantified the spatiotemporal distribution of both farmed and wild cod following simulated escape events. We tested the hypotheses that: (1) escapee farmed cod remain near the cage for some time following escape, facilitating recapture (based on Bridger et al. 2001; Wroblewski and Hiscock 2002; and Arechavala-Lopez et al. 2011, 2012); (2) the local-scale dispersal pattern of escapee farmed cod overlaps with that of local wild cod, facilitating interactions near the release site; (3) farmed cod dispersal outside the release site bay is localized relative to wild cod; and (4) based on dispersal patterns, wild cod in Bay Bulls are a mix of migrants from southern (i.e. NAFO SubDiv. 3Ps) and northern (NAFO Divs. 2J3KL) cod stocks.

3.3 Materials and Methods

3.3.1. Study site and cod farm characteristics

This study was focused in Bay Bulls (47° 18'N, 52° 48'W) in eastern Newfoundland (NL), Canada (Fig. 1). Bay Bulls is 4.5 km long with an average width of 1.1 km, an area of 5.5 km^2 and a maximum depth of 90 m. The cod farm in the harbour of Bay Bulls, run by Sapphire Sea Farms, had 8 pens (average water depth 15 m), three of which each contained 5,000 Atlantic cod (*Gadus morhua*) 39-54 cm long. These adult fish (3+ years of age) came from 26 families that originated from the Cod Genome Project (CGP; Trippel et al. 2011). The CGP was designed to develop a breeding program and genomics tools to supply the developing Atlantic cod aquaculture industry in Canada with improved broodstock. Under the auspices of CGP, wild broodstock from Smith Sound, NL (NAFO Division 3L) were brought to Memorial University's Ocean Sciences Centre (OSC; St. John's, NL) in July 2007. The offspring used in the present study were spawned in Sept.-Oct. 2008, hatched Oct.-Nov. 2008 and were placed in the cages in July 2009.

For comparison with the farmed cod, adult wild cod were caught in baited cod pots (poly netting on a metal frame, 1.83 x 1.83 x 1.04 m) within Bay Bulls a maximum of 24 h prior to tagging and by hand line at the southern headland of Bay Bulls (47°17'14"N, 52°45'49"W), approximately 4 km from the farm, 6 h prior to tagging, with care taken to minimize damage to the fish during retrieval of the gear. These wild cod, believed to be a mix of migrants from northern (NAFO divisions 2J3KL) and southern (NAFO subdivision 3Ps) cod stocks, come to the Bay Bulls area in the summer to feed, before migrating elsewhere to spawn in late winter and spring. The farmed cod are from a wild Newfoundland source, so it is likely they would spawn at the same time as the wild cod. Time of spawning was therefore not expected to affect the dispersal patterns of the two groups of cod.

3.3.2. Acoustic tagging

To determine possible influences of season, two releases of acoustically tagged farmed and wild cod were performed at the same site in Bay Bulls in 20 m of water. The first occurred on 9 August 2011 when 21 farmed and 14 wild cod were tagged and released simultaneously (Table 1). The second occurred on 10 October 2011 when 17 farmed cod were tagged and released, followed an hour later by a release of 14 farmed and 15 wild tagged cod (Table 1). The delayed release was undertaken to determine whether farmed cod followed the wild cod post-release. Wild and farmed cod were size-matched by length as closely as possible, however wild cod were on average 13% longer than farmed cod in the first release (GLM: $F_{1,33} = 5.47$, $p = 0.02$), but not in the second (GLM: $F_{1,27} = 0.61$, $p = 0.44$).

$$\text{Length} \sim \text{release*cod type} \tag{7}$$

where * represents both an additive and multiplicative relation between the two terms. There were no significant differences in length between releases (GLM: $F_{2,76} = 0.09$, $p = 0.92$), nor an interaction between release and cod type (GLM: $F_{1,76} = 1.01$, $p = 0.31$). Farmed cod had greater girth than wild cod as well as other key morphometric differences such as neck curvature, as has been previously observed (see Uglem et al. 2011).

To tag the cod, individuals were placed on a V-shaped surgical table, ventral side up to induce tonic immobility. The eyes were covered with a wet dark cloth, and seawater was continuously poured over the gills. Each fish was surgically implanted with an individually coded transmitter (VEMCO, Halifax, Nova Scotia, Canada) and externally tagged with a T-bar tag (Floy Tag manufacturing, Seattle, WA, USA) following the methods of Uglem et al. (2008). Cod less than 60 cm were tagged with model V13-1H transmitters (13x45mm, weight in water 6 g, frequency 69 kHz, 120 ± 60 s ping rate), while cod longer than 60cm were tagged with model V16-5H transmitters (16x93mm, weight in water 16 g, frequency 69 kHz, 120 ± 60 s ping rate). Tagged fish were allowed to recover for up to 60 min post-surgery (resumption of normal, upright swimming behavior at the bottom of the tank) prior to release. Transmitter function was checked with a mobile receiver (VEMCO VR100) prior to release. Cod were then released by lowering them into the water with dip nets adjacent to the cage site. Cod were tracked for the battery life of the tags (up to one year). All handling and tagging were conducted according to the Canadian Council on Animal Care regulations for the treatment and welfare of animals and was approved by the Memorial University Animal Care Committee (protocols 11-17-IF and 12-17-IF).

3.3.3. Acoustic array

The movements and distribution of the tagged cod were recorded using nine individual receivers (VEMCO model VR2W) deployed on anchored ropes throughout Bay Bulls (Fig. 1; for mooring apparatus details see Brattey et al. 2008). All receivers recorded the transmitter identification code, date, and time of detection when a tagged cod was within the receiver range. Receivers were retrieved as in Brattey et al. (2008). The detection range of the transmitters was determined by carrying out a series of range tests in which a transmitter was towed slowly away from the receiver (as in Uglem et al. 2008). The average detection range of the receivers was a radius of 500-600 m.

In addition, detection rate of stationary reference transmitters moored near the farm (VEMCO model V16 4-H, 16x68mm, weight in air 24 g, frequency 68 kHz, 700 ± 60 s ping rate) was compared with weather conditions (air temperature, water temperature at 10m, wind direction, and wind speed). During June and July, data were binned in four hour blocks. Average weather conditions when the detection rate was poor ($< 50\%$) were air temperature of 8.5 ± 2.3°C (mean ± sd), water temperature of 5.5 ± 1.1°C, wind direction of 155 ± 79° (SSE), and wind speed of 16.2 ± 11.7 kph. In comparison, when the detection rate was good ($> 50\%$), the air temperature was significantly higher (12.5 ± 4.8°C; $F_{1,331} = 7.57$, $p < 0.01$), however water temperature (5.6 ± 2.1°C; $F_{1,331} = 0.01$, $p = 0.97$), wind direction (193 ± 83° SSW; $F_{1,331} = 2.26$, $p = 0.13$) and wind speed (19.1 ± 9.2 kph; $F_{1,331} = 1.00$, $p = 0.32$) were similar to periods of poor detection. It is unclear how air temperature would impact detection rates, however we concluded that weather was not hindering the detection rates of the transmitters and therefore any differences in weather conditions between the releases of tagged fish would not impact our results. There is therefore likely no receiver failure dependent on air temperature.

Within the bay, a portable VR100 hydrophone was used to listen for five minutes at a grid of stations located 500 m apart to determine the general location and transmitter serial number of tagged cod on 22 Aug., 2 Sept., 13 Sept., and 16 Nov., 2011. Data acquired with the VR100 were pooled with detections from the VR2W arrays. An extensive inshore network of receivers deployed by Fisheries and Oceans Canada, comprising 30 arrays of two to ten receivers (VEMCO VR2W receivers) across 250km of the northeast coast of Newfoundland, including known cod spawning areas, was used to detect the cod after leaving Bay Bulls (Brattey et al. 2008). In addition, temperature was recorded by data loggers (Onset Hobo U22 Water Temp Pro v2, Bourne, MA, USA) co-moored with each hydrophone and by CTD (Seabird Electronics SeaCAT Profiler 19, Bellevue, WA, USA) casts in the middle of Bay Bulls.

In case of recapture by local fisherman, a monetary reward was offered upon receipt of the tags of \$10 for T-bar tags and \$25 for acoustic tags, to encourage reporting of capture location, gear type, and fish size.

3.3.4. Data analysis

Fish that did not survive post-release (i.e., lack of movement post-release over a period of several months) were excluded from the analyses (n = 1 farmed, 1 wild cod; 97.5% survival rate, as in Brattey et al. 2008). Data were pooled into three receiver arrays (C, H1-H2 and H3-H5) within Bay Bulls (Fig. 1). Detection of a fish on at least one of the receivers within the array was defined as presence within that array's detection area. Acoustic noise and signal collisions caused some false signals, so single ping detections separated by more than 1 h were considered to be erroneous, unless validated by detection at one of the nearby receivers. Fish were defined as departed from the cage when there were no detections for 3 h. Proportion of time within Bay Bulls spent within the various receiver arrays was determined by the number of hours during which individual cod were detected at the array relative to the total number of hours each individual was detected within the bay.

All data were analyzed using R 2.15.1 (R Core Team 2012). Null hypotheses were rejected when $p < 0.05$. Residuals of all models were checked for normality and homogeneity. Data were analyzed with a generalized linear model (GLM) with Poisson error distribution and log link, unless stated otherwise. To determine the role of release date and fish type on departure time from the release site as well as arrival time at receiver array detection zones, we used a GLM with a response variable of departure time and fixed effects of release dates (n = 3), type of fish (n = 2), and the interaction between the two:

$$\text{Departure/Arrival time} \sim \text{release*fish type} \tag{8}$$

where * represents both an additive and multiplicative relation between the two terms. Subsets of data including only farmed cod were used to determine differences in departure time of farmed cod between releases. To determine the proportion of time spent at the receiver arrays within Bay Bulls, we used a GLM with a response variable of percent time detected at each array (out of the total detections within the bay for each individual) and fixed effects of fish type (n = 2), receiver array (n = 3), and release (n = 3) and all interactions:

$$\text{Time} \sim \text{fish type*receiver array*release} \tag{9}$$

To determine the role of detection location on swimming speed of cod (calculated from the minimum straight line distance and assuming that fish are at the receiver location when the signal was received), we used a GLM with response variable of swimming speed and a fixed effect of receiver array location:

$$\text{Swimming speed} \sim \text{receiver array} \tag{10}$$

3.4 Results

3.4.1. Distribution and dispersal within the bay

Farmed cod remained near the cage longer (Fig. 2; $F_{1,74} = 114.2$, $p < 0.01$), and reached the inner fence later than wild cod ($F_{1,76} = 51.89$, $p < 0.01$). Fish from the second release dispersed away from the cage quicker than those from the first release (Fig. 2; $F_{2,74} = 78.38$ $p < 0.01$) and reached the inner fence sooner ($F_{2,76} = 75.33$, $p < 0.01$). Within 3-8 h (among the three releases) post release, 50% of the wild cod had dispersed > 600 m from the cage; for farmed cod this took 5-21 h. Time to 90% dispersal from the cage was 7-15 h for wild cod, and 20-42 h for farmed cod. There was no significant interaction between release and fish type at the cage ($F_{1,74} = 0.17$, $p = 0.68$) or the inner fence ($F_{1,76} = 0.85$, $p = 0.36$). Farmed cod released independently (Release 2.1) dispersed more slowly from the cage ($F_{1,28} = 15.89$, $p < 0.01$) and arrived at the inner fence more slowly ($F_{1,29} = 47.71$, $p < 0.01$) than those released simultaneously with wild cod (Release 2.2). All the tagged cod were detected at the inner fence, and the southern receiver (H1) detected more pings than the northern receiver (H2; Table 2).

Wild cod arrived at the outer fence on average 16 h before farmed cod ($F_{1,73} = 77.14$, $p < 0.01$). In addition, cod from the October releases took an average 22 h longer to reach the outer fence than cod released in August ($F_{2,73} = 117.96$, $p < 0.01$). There was a significant interaction between release and fish type ($F_{1,73} = 79.53$, $p < 0.01$), with farmed cod released independently in Release 2.1 taking the longest (57 h) to arrive at the outer fence. However, there was no significant difference in arrival time between farmed cod from Release 2.1 and 2.2 ($F_{1,27} = 3.35$, $p = 0.07$). All but three of the tagged cod (all from Release 2) were detected within the outer fence array; however, the northernmost receiver (H5) had not been retrieved since Sept. 2011 (i.e. before Release 2). The three cod that left the bay undetected by the rest of the outer fence array may have been detected by H5. Each receiver in the outer fence array detected between 80-88.6% (Release 1) and 78.3-94% (Release 2) of the cod. The southernmost receiver (H3) detected the most total pings, but more cod (particularly of farmed origin) were detected by the middle receiver (H4) (Table 2).

The proportion of time spent by cod within Bay Bulls in range of various receiver arrays differed ($F_{2,231} = 55.55$, $p < 0.01$), with cod spending 38.8 ± 32.1% of their time at the outer fence, compared with 31.7 ± 26.3% near the cage and 29.6 ± 22.7% at the inner fence. There was a significant interaction between cod type and receiver array (Fig. 3, $F_{1,231} = 528.04$, $p < 0.01$) and release and receiver array ($F_{1,231} = 104.79$, $p < 0.01$): cod from Releases 1 and 2.2 spent the most time at the outer fence (45.8 ± 31.3% and 42.4 ± 35.2% respectively), while farmed fish from Release 2.1 (released independently) spent the most time at the cage (54.3 ± 19.8%). Overall, the median time spent in the bay was relatively short, with farmed cod spending 14 days (range of 9 h to 29 days) and wild cod 20 days (range of 5 h to 40 days) within the bay. The receiver array at the feeding grounds off of the mouth of Bay Bulls (M1 and M2) was deployed just prior to Release 2, so no comparison can be made between Release 1 and 2 at this location. Cod spent a significant proportion of time at this array, with cod from Release 2 spending ~ one-quarter of their time within and near Bay Bulls (27.0 ± 37.0%) at the feeding grounds. Wild cod spent significantly more time at the feeding grounds than farmed cod ($F_{1,44} = 5.76$, $p = 0.02$), spending on average 30% of their time in Bay Bulls at the feeding grounds, compared with only 26% for the farmed cod.

3.4.2. Dispersal outside the bay

Once the cod left Bay Bulls, we could only detect them along the coast, where receiver arrays were located. Of the cod detected outside Bay Bulls (n = 67, 82.7%), most were detected on arrays to the north, including Petty Harbour (73.2%), approximately

21.3 km along the coast north of Bay Bulls. Cod from Release 1 (August) took the longest to arrive at Petty Harbour (40.1 ± 29.3 d; $F_{2,57} = 59.5$, $p < 0.01$; Fig. 4). Overall, farmed cod arrived more quickly (28.1 ±22.7 d) than wild cod (41.9 ± 27.6 d; $F_{1,57} = 37.6$, $p < 0.01$), and specifically farmed cod from Release 2.1 arrived more quickly (21.4 ± 7.3 d) than those from Release 2.2 (28.9 ± 24.1 d; $F_{1,34} = 19.99$, $p < 0.01$). However there was no significant interaction between the release and cod type ($F_{1,57} = 0.42$, $p = 0.52$). A greater percentage of the farmed than wild cod were detected at Petty Harbour (Fisher's Exact Test $p < 0.01$). As of the end of January 2012 (when detections ceased for the winter), 44 of the 52 tagged farmed cod (84.6%) had been detected at Petty Harbour, compared with only 16 of 29 tagged wild cod (55.2%). Arrival in Petty Harbour was highly variable, and took from 4 d (0.13 body lengths, BL s^{-1}) to 117 d (0.005 BL s^{-1}) with cod traveling on average 1.1 ± 0.9 km d^{-1} (0.03 ± 0.02 BL s^{-1}). Seventy-one percent (34 farmed, 10 wild) of the tagged cod spent one day or less in Petty Harbour. Based on the average travel speed, these fish simply passed by the array, while 27% (12 farmed, 6 wild) remained in the area for 2-23 d (mean: 2.8 ± 4.3 d). The four cod that passed Cape Broyle, 27.8 km along the coast south of Bay Bulls, traveled the same speed as those that went north, traveling on average 1.5 ± 2.1 km d^{-1} (0.04 ± 0.06 BL s^{-1}; $F_{1,64} = 0.03$, $p = 0.86$).

Further afield, 16 cod (12 farmed, 4 wild) were detected in Conception Bay through December 2011, approximately 80 km along the coast north from the release site (Fig. 5). Total detections decreased after December, with no detections from January to April, when water temperatures were significantly colder (-0.28 ± 0.95°C) than when fish were present (1.82 ± 2.40°C; $F_{1,7548} = 2034$, $p < 0.01$). Cod were not detected again until

April 2012 (see following section). None of the cod released herein were detected on the DFO arrays beyond Bellevue in southern Trinity Bay (256 km along the coast from Bay Bulls) north to Twillingate (see Brattey et al. 2008 for array locations) or on an additional array located at Triton, Notre Dame Bay.

3.4.3. Post-January acoustic detections

As of mid-September 2012, ten cod had been detected since January 2012. From Release 1, two farmed cod were detected at the mouth of Bay Bulls (one in September, and one in April which was also in Petty Harbour in July), one farmed cod was detected in Bauline (76 km north and west along the coast from Bay Bulls), and one wild cod was detected at Grates Cove between Conception and Trinity Bays (160 km away). Another wild cod was detected heading north past Cape Broyle in May, then past the mouth of Bay Bulls and Petty Harbour, into Conception Bay and Trinity Bay as far as Bellevue by June 27, having covered a minimum distance of 256 km in 36 days, traveling 0.2 body lengths per second (BL s^{-1}), before returning to Conception Bay in July. One farmed cod from Release 2.1 was detected in Conception Bay in May. From Release 2.2, one farmed cod was detected in Petty Harbour and the mouth of Bay Bulls in May, as well as one wild cod in Petty Harbour in June, one wild cod in Conception Bay in July, and one wild cod in Conception Bay in August. Based on detections and recaptures, at least 80.2% (48 farmed and 17 wild) of the cod went north for the winter. Of these, only 22.2% (13 farmed and 5 wild) were detected beyond Petty Harbour. In addition, 12.3% (4 farmed, 6 wild) oscillated north and south between Petty Harbour, Bay Bulls, and Cape Broyle. In contrast, 2.5% were detected only south of Bay Bulls (2 wild, one detected on an array, one recaptured).

3.4.4. Recaptures of tagged fish

Within one year of release, a total of nine (six farmed, three wild) of the 81 tagged cod were recaptured by fishermen. Most of these were caught by local fishermen (one farmed cod in Bay Bulls, one wild and four farmed cod in Petty Harbour) with hand lines (recreational) or gillnet (small commercial fishery). Five of these from Release 1 (four farmed, one wild cod) were recaptured between 31 Aug. and 10 Sept. 2011, and one farmed cod from Release 2.2 was recaptured 3 Dec. 2011. Recaptures in 2012 involved one wild cod from Release 1 recaptured on 7 June 2012 in Placentia Bay (~260 km south along the coast from the release site) in an adjacent stock management area (NAFO Subdiv. 3Ps, Fig. 5), as well as one wild cod from Release 2.2 and one farmed cod from Release 1 captured during August 2012 in Conception Bay near Brigus and Gull Island, respectively. The recapture rate for escaped farmed cod was 11.5% and for wild cod was 10.3%, but this was not significantly different between groups ($X^2 = 0.05$, df = 1, p = 0.83).

3.5 Discussion

Escapes of farmed fish can be both economically and ecologically detrimental, especially if farmed fish are from a non-native population. This study showed that escaped farmed cod dispersed away from the farm site quickly and broadly, and overlapped with the range of local wild cod, indicating the considerable potential for interactions. In the worst case scenario, such interactions could adversely affect the recovering wild populations of cod (through interbreeding, competition, and pathogen transfer).

Intentionally released farmed cod dispersed away from the farm more slowly than wild cod, as has been seen in previous studies in Newfoundland using juvenile wild cod reared in captivity for three years prior to release (Wroblewski and Hiscock 2002), as well as in other species that show a high degree of site fidelity to sea cages, including sea bream (*Dicentrarchus labrax*; Arechavala-Lopez et al. 2011), sea bass (*Sparus aurata*; Arechavala-Lopez et al. 2012), and steelhead trout (Bridger et al. 2001). We observed post-release dispersal rates (i.e. moving > 600 m from the farm) for farmed cod of 12 h for 50% dispersal and 38 h for 90% dispersal, which are similar to the dispersal rates (i.e. moving > 1.3 km from the release site) of 10 h (50%) and 41 h (100%) observed by Wroblewski and Hiscock (2002). For wild cod, we observed dispersal rates of 5 h for 50% dispersal and 12 h for 90% dispersal, which are longer than the dispersal rate of 3 h for 100% observed by Wroblewski and Hiscock (2002), even though their measure of distance to dispersal (1.3 km) was more than twice that in our study (600 m). Farmed cod may have remained near the cage site due to familiarity of the environment, as a known food source, while wild cod may have returned straight to the location of capture, at their feeding grounds.

We also observed a seasonal difference, with cod from later releases (October) departing from the cage more quickly than those released earlier (August). Wroblewski and Hiscock (2002) released their cod (wild juveniles that had been reared in captivity for three years prior to release) in late April and early May. This may suggest a seasonal difference in dispersal rates of wild cod, possibly due to seasonal activities such as migration and feeding. We observed no clear differences in the geographic dispersal of cod between releases; however, environmental conditions (i.e. water temperature) were similar between the releases due to the short separation in time (2 months). We detected few fish from December until April when the water was colder, suggesting that the cod were avoiding the cold shallow coastal waters where our receivers were located. Adult cod are known to be present in Conception Bay from May until September, after which the shallow thermocline disappears, supporting our observations (Aggett et al. 1987; Lawson and Rose 2000).

Dispersal rates observed in this study differ from previous studies conducted in Norway that have shown that farmed cod initially disperse more quickly than wild cod (Svasand et al. 2000; Uglem et al. 2008). These conflicting results may be due to original capture location of wild cod: wild cod used in the present study were captured around 2 km away from the cage site at the local feeding grounds, whereas wild cod used by Uglem et al. (2008) were caught < 200 m from the cage site. It is known that fish farms can attract wild fish aggregations (Dempster et al. 2010), which may slow the dispersal away from the farm area. Differing results may also be due to heritable difference in migratory behaviour. The farmed cod used by Uglem et al (2008) came from a non-local stock that was more migratory and pelagic in behaviour than the local wild cod stocks. In the northwest Atlantic, groups of cod inhabit a more variable environment and tend to disperse along the coast, in contrast with groups of cod in the more stable environment of the northeast Atlantic that tend to be accurate homers and sedentary (Robichaud and Rose 2004). In addition, some bays and fjords are home to a resident population of cod (Wroblewski et al. 1996; Wroblewski and Hiscock 2002). Our results suggest that the farmed cod had migratory tendencies similar to that of the local wild cod.

Dispersal within the release bay varied between farmed and wild cod, keeping in mind that time spent within the bay was of relatively short duration (around two weeks, with 50% of farmed cod and 24% of wild cod gone within 48 h). Many of the wild cod quickly returned to the area at the mouth of the bay where they had been captured before tagging, staying close to the south shore of the bay, and some remained in the area for several months. In contrast, more farmed cod were detected along the northern shore of the bay. The wild cod had previous experience of the local environment and location of feeding areas at the mouth; however, the farmed cod may have been exploring the bay due to their lack of knowledge of the environment, and possibly their inability to evaluate habitat qualities (Uglem et al. 2008; Dempster et al. 2010). In addition, farmed cod released together with wild cod dispersed more rapidly (~ 5 h) than farmed cod released independently of wild cod, suggesting that farmed cod may have been using cues from the wild cod to disperse quickly to the feeding grounds. The high variability in arrival time at Petty Harbour indicates that, although many wild and farmed cod moved in the same direction (i.e. northward), individual fish were not in close proximity. This suggests that farmed cod may have been attracted to aggregations of wild cod through some unknown sensory mechanism beyond vision. Farming cod near areas of local wild cod aggregations may increase the likelihood of interactions between escaped farmed and wild fish, as the farmed fish may be attracted to local aggregations of wild fish. In addition, the attraction of escapee farmed fish to local wild cod makes targeted fisheries for recovery more difficult because they may result in high incidental catches of wild fish.

We observed a wide geographic dispersal of both wild and farmed cod from Bay Bulls north to Trinity Bay and south to Placentia Bay. Following dispersal from Bay

Bulls, the majority of farmed cod (85%) were detected at Petty Harbour, arriving faster than wild cod (of which only 55% were detected there). In addition, most cod did not linger in Petty Harbour for more than a day, suggesting they were passing through on their way north. Previous studies have shown that wild cod are able to migrate along the same route, returning to the same site several years in succession, creating different 'stocks' of cod (Rose 1993; Robichaud and Rose 2001). For example, data from return migrations have suggested the existence of a Placentia Bay coastal cod stock (Lawson and Rose 2000).

The average travel speed of 0.03 BL s^{-1} reported here matched that observed by Comeau et al (2002) for summer migrants. Rose et al. (1995) reported a mean swimming speed of 0.23 BL s^{-1} during the spring migration. Our study was conducted primarily during the summer, when cod come inshore to feed, possibly resulting in slower migrations along the coast, as seen by Comeau et al. (2002). Furthermore, basal swimming speed in fishes is a function of body length, with larger individuals tending to show greater swimming speeds (Santos 2011). Comparisons are therefore influenced by many factors, including the size composition of the cod being studied.

Few studies have tracked the dispersal of escapee farmed cod, and these studies have frequently been limited to tracking within fjord systems up to 15 km, however Uglem et al. (2008) recaptured farmed cod 40 km away from the release site. Courtesy of the DFO acoustic receiver arrays dispersed around the island of Newfoundland, we detected farmed cod up to 114 km away from the release site. Similar results were observed in an earlier study, with wild juvenile cod (raised in a farm situation for three years prior to release) detected up to 170 km away from a release site in Trinity Bay, Newfoundland (Wroblewski and Hiscock 2002). Our results indicate that farmed cod are able to disperse great distances, and overlap with the range of wild cod.

Migrations observed in this study from Bay Bulls north to Trinity Bay and south to Placentia Bay are consistent with historical descriptions of the 'Avalon stock complex' (Templeman 1962, 1979). Lear (1984) found that cod that overwinter on the eastern and southeastern slopes of Funk Island Bank as well as the Northern Grand Bank migrate to eastern Newfoundland from Trinity to St. Mary's Bay for the summer, further supporting the wide dispersal observed in this study and illustrating the wide overlap of cod from different management divisions. Furthermore, the size and age of cod tagged in this study are consistent with the ontogenetic threshold of cod migration, with long migrations occurring by age 4 or 5 (Rose 1993; Lawson and Rose 2000). Our results agree with previous studies indicating that the eastern Avalon is a summer feeding area for cod that may be a mix of migrants from the south and northeast coasts of Newfoundland (Lawson and Rose 2000; Robichaud and Rose 2004).

Movement of tagged cod south from Petty Harbour was consistent with results of a tagging study by Brattey et al. (2008). Previous studies found that 10-30% of the tagged Placentia Bay cod migrated east and north along the Avalon Peninsula, traveling as far as Trinity Bay (Lawson and Rose, 2000; Robichaud and Rose 2001). Of all the tagged wild cod released in this study, only 55% (80% of all wild cod detected beyond Bay Bulls) were detected at Petty Harbour (i.e. north of Bay Bulls), suggesting that some wild cod may have originated from either Placentia Bay or the offshore banks. The single wild cod recaptured in Placentia Bay in June 2012 further suggests that cod groups along the eastern Avalon Peninsula may contain migrants from Placentia Bay that move along the south and eastern Avalon during the summer (Brattey 2000; Brattey et al., 2008). However, due to the small sample size we cannot draw further conclusions on the origins of the wild cod. In addition, four tagged cod were detected near Bay Bulls in the spring of 2012 as well as one in September, indicating a return migration to the site of tagging, as well as over-winter survival (six others were also detected or recaptured elsewhere after winter).

All tagged cod were detected within Bay Bulls; however, 14.8% were never detected along the coast beyond Bay Bulls. It is not possible to distinguish between natural mortality, unreported fishing mortality, emigration, or transmitter failure. Transmitters are reliable and were tested prior to release. Some undetected cod may have been caught in lost fishing gear (e.g. "ghost-fishing"), or the fisher did not claim the reward (maximum of $35 per fish); however, tagging is well advertised and it is believed that most recaptures are reported (Brattey et al. 2008). It is therefore more likely that undetected cod moved to an area beyond the range of the receiver arrays, offshore to deeper water. If feasible, future studies should extend the coverage of the receivers to include more deep water habitat, in addition to expanding the receiver array along the southern coast of the Avalon Peninsula.

Although escapee farmed cod left the farm area more slowly than wild cod, most of the escapees had dispersed within 24 hours, much quicker than found in previous studies (Uglem et al. 2008, 2010), indicating that any attempt at a recapture fishery would need to be undertaken immediately after an escape incident. Few studies have quantified the recapture rate of escaped farmed cod, however results from an acoustic telemetry study in Norway as well as from stock enhancement studies suggest that the incidental recapture rates may be high (30-44%) with even a modest fishing effort (Svåsand et al. 2000; Uglem et al. 2008). In comparison, recapture rates from targeted recapture fisheries for escaped salmon have been found to be much lower, at around 1-7% (Skilbrei et al. 2006; Skilbrei and Jørgensen 2010), though incidental catches over several weeks can be considerably higher, at 40% or more (Skilbrei and Jørgensen 2010). Although there was no dedicated recapture fishery, 11% of the farmed cod were recaptured over 10-12 months. This recapture rate was higher than the 7% observed by Wroblewski and Hiscock (2002). Several factors, such as differences in fish size at release and local fishing effort, however make direct comparisons difficult. Wild cod in our study had a recapture rate of 10%, similar to that seen by Brattey et al. (2008). Overall, we saw no significant difference in the recapture rates of escapee farmed and wild cod, in contrast to previous studies (Wroblewski and Hiscock, 2002; Uglem et al. 2008).

The timing and recapture locations in this study reflect the pattern of seasonal, summer small-scale fisheries (recreational, sentinel and commercial) at the mouth of Bay Bulls and off Petty Harbour. In addition, detections and recaptures at Petty Harbour indicate cod remained in a narrow corridor close to shore as they migrated northward. This suggests that a higher proportion of escapees could be recaptured within and near Bay Bulls than if they dispersed randomly. Differences among stock origins and the geography near cod farms preclude the ability to make predictions on the success of recapture attempts in other areas. However, quantitative measures of recapture rates of escaped farmed cod require information on the fishery effort, size of the wild stock, and the number of escapees (Uglem et al. 2008). Knowledge of the dispersal patterns of escapees will increase the efficiency of a recapture fishery, for example targeting areas where local wild cod aggregate as shown by the recaptured tags in this study as well as previous studies (Uglem et al. 2008). However, given the broad spatial overlap of farmed escapees with wild cod and the similarity in percentages of each group recaptured (11% farmed versus 10% wild), it is likely that any targeted fishery for escapee recapture is likely to result in significant incidental catch of wild cod.

In conclusion, escapee farmed cod dispersed from the release site more slowly than wild cod. However, dispersal of both groups was rapid (within 24 h), making recapture of escapees logistically challenging. Following the initial dispersal period, most cod moved northward, staying close to the shore. This non-random dispersal and narrow migration corridor may facilitate an efficient recapture fishery, but also a high incidental catch of wild cod. Furthermore, the spatiotemporal distributions of escapee farmed cod and wild cod were very similar, suggesting the potential for negative interactions between the domesticated and often non-local farmed cod and the local wild cod. Further studies are therefore needed to minimize the number of escapes from farms, to investigate the potential for an effective recapture strategy and to consider means of preventing interactions, such as interbreeding, with wild fish. These steps will help with the development of environmentally sound aquaculture not only for cod, but other marine finfish raised in net pens.

3.6 Acknowledgments

We thank D. Porter for his help with the receiver arrays and P. Williams for the use of his fishing boat. We also thank Sapphire Sea Farms for their help with the farmed fish. This work was supported by funding from grants awarded to I.A.F. and C.F.P. from the National Sciences and Engineering Research Council of Canada by way of a Strategic Project grant and the Canada Foundation for Innovation. In addition, we received funding from the Fish, Food and Allied Workers Union to J.B. through the Fisheries Science Collaborative Program, and graduate funding to E.Z. from the Research and Development Corporation of Newfoundland and Labrador and Memorial University.

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Table 3.1. Mean length and number of acoustically tagged farmed and wild cod. Released in three simulated escape events in 2011 in Bay Bulls, Newfoundland (N47 18.663 W52 48.259).

Release	Fish type	Release Date	No. of fish	Mean length (cm ± sd)
1	Farmed	9-Aug-11	21	46.3 ± 2.4
	Wild		14	51.9 ± 10.5
2.1	Farmed	10-Oct-11	17	48.8 ± 2.8
2.2	Farmed	10-Oct-11	14	46.9 ± 3.3
	Wild		15	48.9 ± 3.2

Table 3.2. Details of acoustic receiver deployments along the Avalon Peninsula.

Indicates location, deployment date, depth deployed, and amount of time deployed during the study (9 Aug. 2011 to 19 Sept. 2012). Total number of pings and the number of individual farmed and wild cod detected at each array are summarized. See Figures 1 and 5 for locations.

Receiver array ID	Location of array	Distance to next array (km)	Deployment Date	Last Retrieval Date	Receivers (#)	Depth (m)	Deployment time (%)	No. of pings (#farm, #wild)
C	Cage	0	6-Jun-11	12-Sept-12	1	20	84	43 643 (51f, 28w)
H1	Inner fence	1.5	10-Jun-11	19-Sept-12	1	40	100	24 635 (51f, 29w)
H2	Inner fence		10-Jun-11	19-Sept-12	1	40	100	22 750 (52f, 29w)

Receiver array ID	Location of array	Distance to next array (km)	Deployment Date	Last Retrieval Date	Receivers (#)	Depth (m)	Deployment time (%)	No. of pings (#farm, #wild)
H3	Outer fence	1.9	10-Jun-11	19-Sept-12	1	50	100	32 330 (38f, 27w)
H4	Outer fence		10-Jun-11	19-Sept-12	1	70	100	14 402 (47f, 27w)
H5	Outer fence		10-Jun-11	1-Sept-11*	1	70	100†	4 692 (18f, 10w)
M1	Mouth	2.1	4-Oct-11	19-Sept-12	1	40	86	22 092 (15f, 16w)
M2	Mouth		4-Oct-11	12-Aug-12	1	40	76	50 015 (18f, 13w)
CB	Cape Broyle	25.7	9-Jun-11	12-Jun-12	3	100-163	100	552 (1f, 3w)

Receiver array ID	Location of array	Distance to next array (km)	Deployment Date	Last Retrieval Date	Receivers (#)	Depth (m)	Deployment time (%)	No. of pings (#farm, #wild)
PH	Petty Harbour	20.2[†]	29-Jun-11	18-Jun-12	2	91-115	100	34 325 (46f, 18w)
CSF	Cape St. Francis	45.7	29-Jun-11	18-Jun-12	4	50-210	100	7 309 (12f, 2w)
BL	Bauline	10.2	12-Jul-11	19-Sept-12	3	30	100	1923 (6f, 3w)
BI	Bell Island	10.7	27-Jun-11	18-Jun-12	4	136-163	100	633 (6f, 1w)
SC	Salmon Cove	22.4	29-Jun-11	18-Jun-12	3	43-92	100	69 (3f, 1w)

Receiver array ID	Location of array	Distance to next array (km)	Deployment Date	Last Retrieval Date	Receivers (#)	Depth (m)	Deployment time (%)	No. of pings (#farm, #wild)
BC	Baccalieu	43.7	30-Jun-11	27-Aug-12	3	105-120	100	227 (4f, 3w)
GC	Grates Cove	11.2	30-Jun-11	28-Jun-12	2	65-324	100	17 (0f, 2w)
HH	Hants Harbour	35.9	1-Jul-11	28-Jun-12	2	66-286	100	1 (0f, 1w)
BV	Bellevue	39.3	1-Jul-11	28-Jun-12	4	74-146	100	39 (0f, 1w)

Note: Minimum distances to next array were calculated using straight line approximations. See Figures 1 and 2 for locations of receivers. Deployment time was calculated from 9 Aug. 2011 to 19 Sept. 2012.

*Receiver has not been retrieved since the second release of cod.

†Data was only recovered from 9 Aug. 2011 to 1 Sept. 2011 (5% of the study duration).

'Distance measured from mouth of Bay Bulls

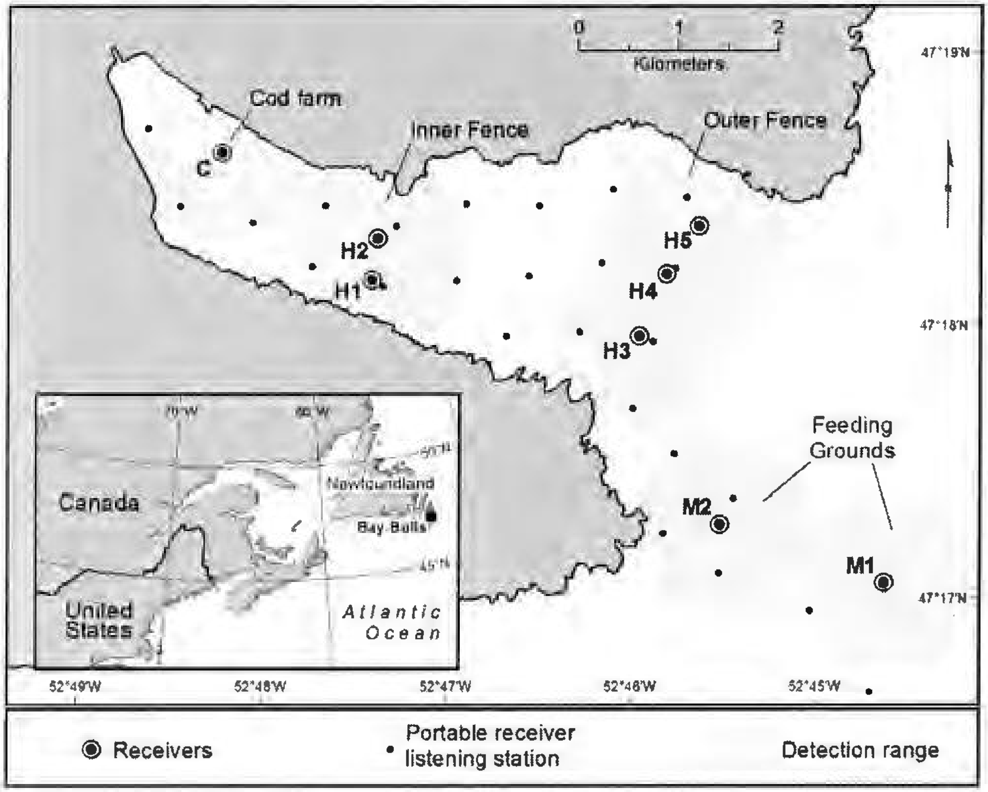

Figure 3.1. Location of the study area in eastern Canada, with Bay Bulls in detail. Light grey areas represent the detection range of the receivers (500-600 m). C, H1-H5, and M1-M2 refer to the receivers (see Table 2 for details).

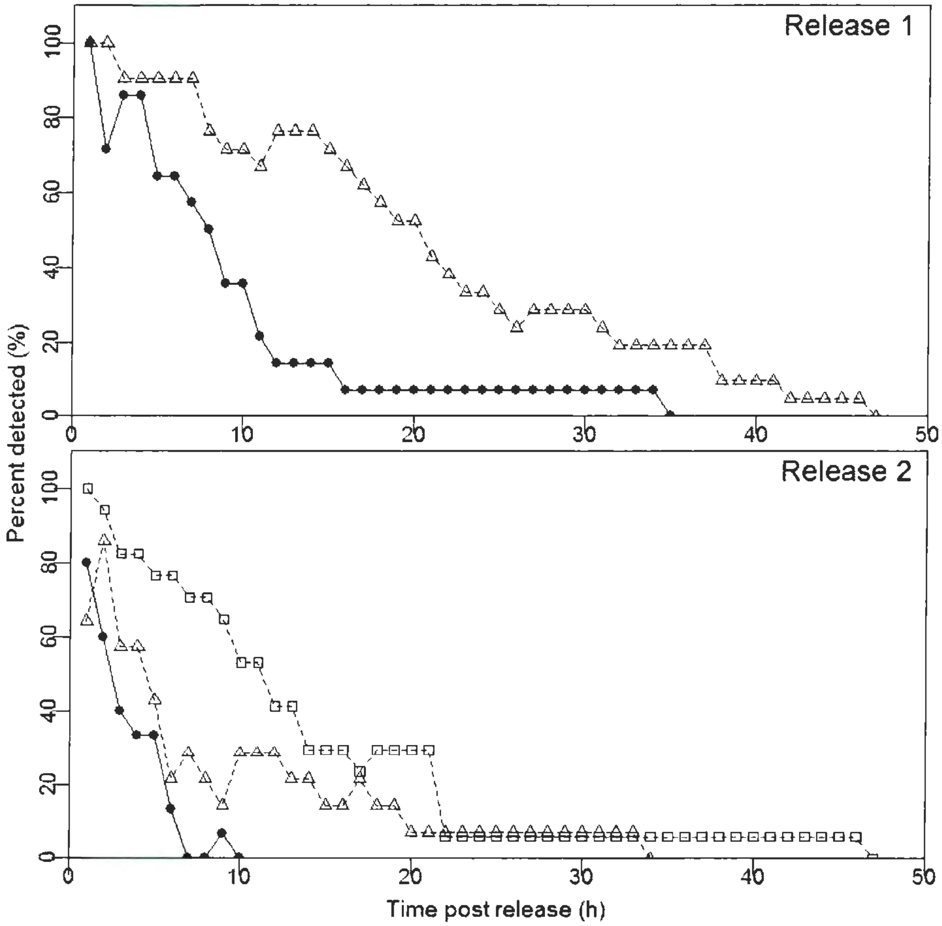

Figure 3.2. Dispersal of tagged cod away from the cage release site.

As measured by the percent of fish detected following release at the cage site hydrophone, for Release 1 and Release 2. Farmed (Δ) and wild (●) cod released simultaneously, as well as the farmed cod released independently (an hour earlier) during the second release (□) are shown.

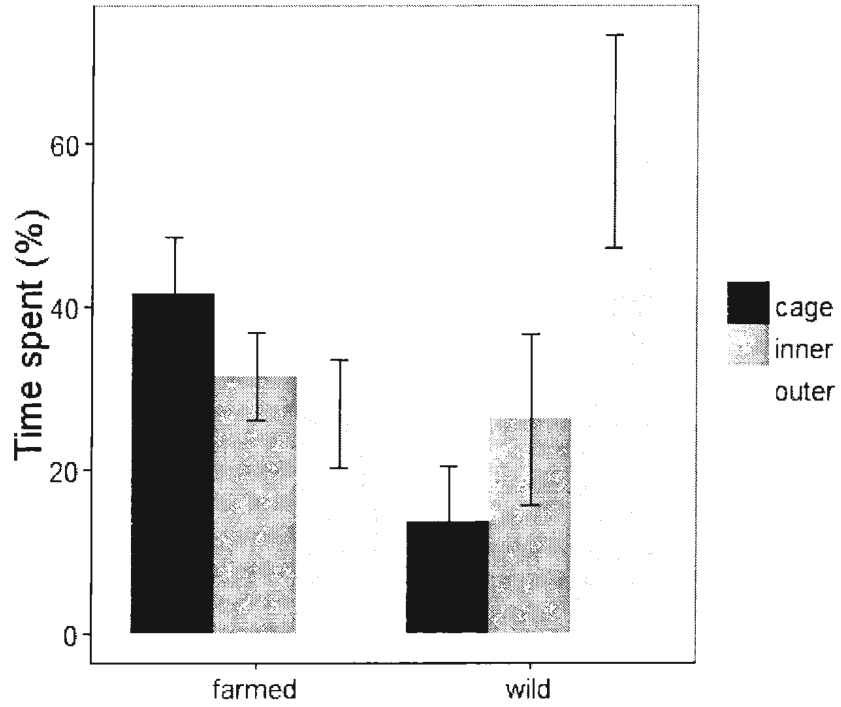

Figure 3.3. Proportion of time within Bay Bulls spent by tagged cod within range of each of three receiver arrays: the cage site, the inner fence, and the outer fence.

Data based on total detections within the bay. Error bars show standard deviation among individual cod.

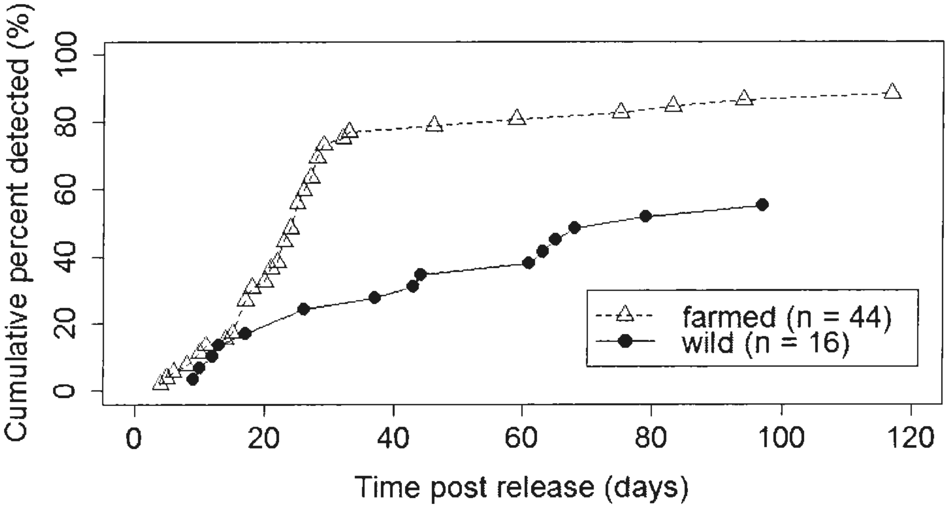

Figure 3.4. Cumulative arrival of tagged cod at Petty Harbour.

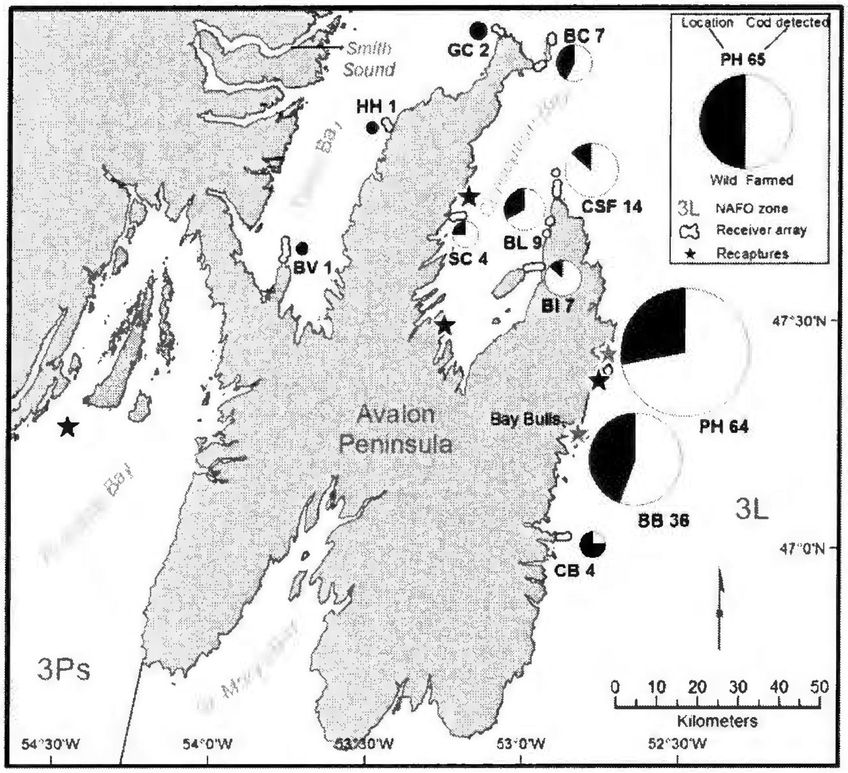

Figure 3.5. Number of cod detected on DFO receiver arrays moored in coastal waters along the northeast coast of Newfoundland.

In total, 81 cod were released with acoustic transmitters from Bay Bulls. Bold letters refer to receiver arrays (for details see Table 2). Black stars represent wild cod recaptured by fishermen, while grey stars represent a mix of wild and farmed cod recaptured. Overall size (diameter) of pie charts are scaled to the total number of cod detected at each array, noted by bold number (i.e., maximum detections at Petty Harbour (PH), 64; minimum detections at Bellevue Beach (BV), 1).

4. Summary and conclusions

This thesis examined the potential for interaction between escaped farmed and wild cod. Fish escapes represent both a direct economic loss for the farmer as well as an environmental concern with regard to local wild populations. The impact of escapee salmonids on local ecosystems has been well studied (reviewed by Naylor et al. 2005; Bekkevold et al. 2006), however with the diversification of marine aquaculture to include other species such as Atlantic cod (*Gadus morhua*) comes the need to understand the environmental impacts of escapes. Fish that bite at nets such as sea bream and cod are particularly prone to escape (Dempster et al. 2007; Jensen et al. 2010). This study found that escape-related behaviours can be reduced with cage enrichment, food availability, and net maintenance, and that it is important to reduce escapes as the potential to recapture escapees is low.

To reduce interactions with the net wall, I tested the hypothesis that suboptimal conditions encourage net biting. The data supported this hypothesis, and indicated that adding stimulating objects to the cage resulted in the largest reduction in interactions. There was a clear preference for stationary benthic tubes which may have provided refuge for the cod. Cage enrichment could be a relatively easy and inexpensive method to reduce net biting. Future studies should be conducted to determine the feasibility of adding structures to increase the complexity of the cage habitat at commercial farms, as well as to determine the optimal structure or object type to achieve reduced net biting. Appropriate feeding levels, while important for production and welfare, are also an important method for reducing net biting, especially when combined with cage enrichment. In addition, regular net maintenance to avoid frayed or damaged strings can also help reduce net interactions. Combining these three factors may be part of an effective strategy to reduce the number of cod escapes from aquaculture sea cages. Future studies at commercial farms will gain further insight into the efficiency of this strategy when applied at relevant temporal and spatial scales.

To gain a better understanding of the behaviours underlying the tendency to bite nets, I tested the hypothesis that individual temperament affects net interactions. The hypothesis was not supported; however individual behaviour toward the net was consistent for the duration of the experiment. Combined with the wide range of behaviours between individuals, this suggests the presence of behavioural syndromes, such as along the "shy-bold" continuum (Fraser et al. 2001; Sih et al. 2004). Individual behaviour may explain some of the variation in activity among farmed cod and merits further study to understand the mechanisms driving behavioural variation among individuals and the linkages between behaviours.

Although escapes can be reduced, it is unlikely that escapes will be eliminated completely. It is therefore essential to understand the spatiotemporal distribution of escapees in order to assess the potential for interactions with wild populations. Following a simulated escape event, escapee farmed cod remained near the cage longer than local wild cod, however most dispersed within a day. Recapturing escapees with a dedicated fishery would be challenging, as the fishery would have to be implemented as soon as possible following an escape incident. The feasibility of a successful recapture fishery would be highly dependent on the local environment near the cage, as well as the local fishery effort, size of the wild stock, and number of escapees (Svåsand et al. 2000; Skilbrei et al. 2006; Uglem et al. 2008).

Efficiency of recaptures could be increased with knowledge of the dispersal patterns of escapees. Although dispersal out of the bay varied between escapee farmed and wild cod, the geographic dispersal was similar between the two groups. Rather than dispersing randomly, most cod migrated northward and remained close to shore. This may facilitate higher proportions of recaptures of escapees. The similarity in dispersal between wild and farmed cod suggest that the escapees were attracted to aggregations of wild cod at favorable sites (i.e., feeding, spawning, or overwintering areas) by some unknown sensory mechanism, or both were drawn to the same cue.

This study also gave insight to the dispersal of local wild Newfoundland cod, which dispersed both north and south along the coast. The dispersal pattern matches historical data that suggest the cod of the eastern Avalon are a mix of migrants from northern and southern stocks (Templeman 1962, 1979; Lear 1984; Brattey et al. 2008). Future studies are needed to determine the quantity of exchange between these stocks. In addition, 19% of the cod were never detected again once leaving the study bay. It is possible that these fish moved to deeper offshore waters, however future studies are needed to confirm this theory.

In conclusion, this thesis has given further insight into the stock structure and movements of Newfoundland cod. This knowledge may lead to more efficient management of wild stocks. In addition, this thesis demonstrates there is a high potential for negative interactions between escapee farmed and local wild cod. Recapture of escapees will be logistically challenging, so it is therefore crucial to reduce the number of escapees. Proactively addressing the conditions that encourage net biting may prove to be a cost efficient and complementary means, along with that of improving net materials, to reduce escapes. In addition to an effective recapture fishery, these steps will help to develop environmentally sound aquaculture of marine species such as cod.

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