QUANTITATIVE APPROACHES FOR THE ANALYSIS OF MORTALITY IN MARINE FISH POPULATIONS

by

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For my bicycle, in recognition of
its innate capacity to help clear
my head and to promote
problem solving

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Abstract

Fisheries science has historically focused on recruitment variability and fishery landings as key drivers of dynamics in populations exposed to fishing. However, comprehending the persistence of these populations and successfully managing fishing impacts on them depends on understanding the magnitude, dynamics and causes of mortality from all sources. In this thesis, I develop a series of approaches for the analysis or estimation of discard and natural mortality, two key sources of mortality that have often previously been overlooked. In chapters two and three I present methods for estimating indicators of discard mortality (DM). These approaches provide simple and cost-effective means to evaluate the influence of factors affecting DM and case-specific risks posed by DM, and to improve formal DM estimates in directed studies. In chapters four and five, I present a case study for the estimation of fishing mortality for principally discarded species, skates in the southern Gulf of St. Lawrence (sGSL; Atlantic Canada). Estimating fishing mortality for these species of conservation concern poses several challenges, including catch reporting that is not disaggregated to species and that is somewhat sparse. I derive and apply a method to disaggregate the catches and an integrated approach, based in part on the methods from chapter two, to estimating landed and discarded catch amounts and DM rates. In chapter six, I develop and validate a model for data from DM experiments that is generalizable to estimate different components of mortality, including jointly estimating discard and natural mortality. Finally in chapter 7, I develop a simulation model to evaluate whether predation by a top predator is a scientifically defensible explanation for elevated natural mortality in three fish species of conservation concern in the sGSL. This approach is presented as a means of evaluating the possible consequences of predation in the absence of reliable estimates of predator diets. Together, the methods developed in this thesis represent new tools for the estimation of mortality components and for the attribution of their likely drivers. In turn, these tools should help inform management actions aimed at mitigating mortality or sustainably managing populations and communities in light of existing mortality.

List of Abbreviations Used

ACF	Autocorrelation function
AF	Activity factor (bioenergetics modelling)
AIC	Aikaike's Information Criterion
BCLHR	Baseline-category logits harmonic regression
CFP	European Union Common Fisheries Policy
CH	Capture and release (of bycatch)
CHR	Capture, handling and release (of bycatch)
CV	Coefficient of variation
DMP	Dock-side catch monitoring program
dt	deck time
ED	Energy density (bioenergetics modelling)
GEI	Daily gross energy intake (bioenergetics modelling)
GL	Generalized logits model
GP	Growth premium (bioenergetics modelling)
ICES WKMEDS	ICES Workshop on Methods for Estimating Discard Mortality
kg	Kilograms
KM	Kaplan-Meier non-parametric survival model
M	Natural mortality
ME	Metabolizable energy (bioenergetics modelling)
MSRD	Mass-specific respiration demand
N	Abundance or number
PAT / PSAT	Pop-up archival satellite transmission tags
PO	Proportional odds model
RB	Relative bias
RE	Relative error
SE	Standard error
sGSL	southern Gulf of St. Lawrence
TM	Time-to-mortality
Z	Total mortality

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I thank my committee members, Dr. Sandra Walde and Dr. Joanna Mills-Flemming, for their questions and insightful comments concerning my thesis research, and Dr. Aaron MacNeil for stepping in as a late committee member.

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This thesis is based primarily on the analysis of existing research survey and fishery-dependent data, and I would like to sincerely thank all of the individuals involved in the collection of those data. I also wish to thank the following people who contributed to the collection of new data used in this thesis : the management team and at-sea observers of the BIOREX consulting firm, the captains and crew of the CCGS Opilio and CCGS Teleost, S. LeBlanc, C. Briggs, N. Alfonso, C. Archibald, L. Aucoin, T. Pickering,

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Chapter 1. Introduction

Fisheries science has historically focused on recruitment variability and fishing mortality as key drivers of population dynamics in populations that are exposed to fishing. Until recently, stock assessments have assumed that natural (non-fishing) mortality was time invariant and that reported landings represented the fishery removals from populations (Megrey 1989; Hilborn and Walters 1992; Cotter et al. 2004). Despite advances for some stocks, this is still largely true based on a current overview of world-wide stock assessments (RAM legacy database; Ricard et al. 2012). This situation reflects the technical difficulties in teasing apart the relative magnitudes of time-varying fishing and natural mortalities, and possible confounding with other factors such as temporal changes in selectivity and catchability. It also reflects difficulties in estimating the magnitude of more cryptic sources of fishing mortality such as the mortality associated with discarding and with fish escaping from fishing gear.

Understanding the magnitude and dynamics of mortality and the factors that contribute to it are fundamental to comprehending the persistence of populations subjected to fishing. While management actions can be undertaken to control or alter fishing mortality, natural mortality, which results from factors such as predation and disease, is less amenable to management action. Correctly accounting for fishing mortality from all sources is therefore an important contributor to achieving sustainable fisheries and the persistence of populations that are affected but not targeted by fisheries.

In this thesis, I develop a series of quantitative approaches for the analysis or estimation of discard and natural mortality. The approaches related to discard mortality have two principal aims. The first is to quantify the effects of factors that contribute to this mortality to, *inter alia*, identify measures to mitigate discard mortality and promote successful live release of incidentally captured organisms. The second is to estimate the magnitude of discard related losses in fish populations. This is of particular importance for species for which most or all of the fishing mortality is incidental (i.e., discarded bycatch). The approaches for natural mortality also have two aims. The first is to devise a method to jointly estimate discard and natural mortality from fish tracking data. The second is to evaluate the likelihood of predation as a contributing factor to natural mortality when predator diets are unavailable. The overarching goal is to provide enhanced understanding of the causes of natural mortality and to better inform management actions directed at top predators to control prey mortality rates.

1.1 Objectives

The main body of the thesis begins with studies aimed at quantifying the mortality of discarded fish and evaluating the role of factors affecting this mortality. This is followed by methods for quantifying and evaluating predation as an important contributor to natural mortality.

Field studies to directly estimate discard mortality are very expensive and logistically complex. Chapters two and three present methods for estimating indicators of discard mortality that are proposed as simpler means to evaluate the relative influence of factors associated with discard mortality and to improve discard mortality estimates from formal directed studies.

In chapters four and five, I present a case study for discard mortality estimation, using skates in the southern Gulf of St. Lawrence (sGSL; Atlantic Canada). This research was undertaken to support Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assessments of the status of smooth skate *Malacoraja senta* (Swain et al., 2012a) and of thorny skate *Amblyraja radiata* (Swain et al., 2012b), and a recovery potential assessment for the sGSL designatable unit of winter skate *Leucoraja ocellata* (Swain and Benoît, 2017). Specifically, chapter four proposes a method for estimating the species composition of mixed fishery catches. This work was required because incidental catches of skates are not reliably reported to species in the sGSL and neighboring areas. Chapter five integrates the methods proposed in chapters two and four to estimate discard-related losses for the three skate species from1991 to 2011.

In chapter six, I develop a model for longitudinal data from discard mortality experiments that is easily generalizable to estimate different components of mortality, including jointly estimating discard and natural mortality from electronic tagging data. Simulation testing of the model and a case study for the estimation of discard mortality and natural mortality for Gulf of Maine Atlantic cod *Gadus morhua* are presented.

Finally in chapter 7, I develop a simulation model to evaluate whether predation by grey seals represents a scientifically defensible explanation for elevated natural mortality in three marine fish species in the sGSL: Atlantic cod, white hake *Urophycis tenuis* and winter skate. These three depleted populations have been designated as Engangered by COSEWIC and high rates of natural mortality appear to be responsible for their lack of recovery and ongoing declines despite very low fishing mortality (Swain and Benoît, 2015). The simulation model is based on spatio-temporal overlap between the fish and seal predators and a bioenergetics model for prey consumption by seals.

1.2 Thesis overview

In chapter two, I present a semi-quantitative indicator of discard mortality for individual fish. This vitality or condition indicator comprises four ordinal classes based on fish responsiveness and degree of injury just prior to discarding, and is shown in this chapter and elsewhere (e.g., chapter 6) to be a good predictor of discard mortality. A mixed-effects proportional-odds model for multinomial data is proposed and applied to vitality data collected by at-sea fishery observers in the sGSL for 18 species-fishery combinations. A key feature of the model is the inclusion of a random effect term that can account for observer subjectivity when classifying individuals according to vitality. The model is used to evaluate the relative contributions of different biological (e.g, length, sex), environmental (e.g., depth, water temperature) and technical (e.g., fishing gear, handling time) factors affecting vitality and, by extension, discard mortality. This model is incorporated in the analyses presented in chapter 5 and has since also been applied to discard mortality analyses for plaice in the English Channel (Morfin et al. 2017a) and skates in New England fisheries (Knotek et al., in press).

In chapter three, I propose the time required to induce mortality in air-exposed fish (time to mortality; TM) as an indicator of discard mortality. Data for 48 marine fish species were collected during routine annual multispecies trawl surveys undertaken by DFO. First, I show that this indicator corresponds well with formal estimates of discard mortality in a cross-species comparison, as would be expected given a predominant role of asphyxia in the mortality of discarded fish. Then I use parametric survival analysis methods to consider the effects of environmental factors, biological traits and phylogenetic similarity on TM. Amongst other findings, these analyses identified an important intra- and inter-specific relationship between individual body size and TM, presumably resulting from allometric relationships for respiration and oxygen demand. While TM is not a substitute for formal discard mortality estimates, it appears to be a powerful proxy for which the data are easy to collect and which can be used in risk assessments related to sustainability of bycatch or to prioritize species for further work. Notably TM has recently been used to identify priority species for study following the new European Union landings obligation, which will ban discarding except in instances in which discard mortality is estimated to be low (Morfin et al. 2017b).

In chapter four, I present an empirical model to predict the species composition of mixed fishery catches. The approach is motivated by the unreliable identification of related and morphologically similar species by at-sea fisheries observers, the main source of data on discarded fish. The model is founded on the observation that water depth and season are strong predictors of fish assemblage composition. The model is a baseline-category logits model for multinomial data and was fitted to data from seasonal surveys in the sGSL for mixed catches of flatfish and of skates. The suitability of the model for flatfish was assessed by comparing catch compositions reported by observers to those predicted by the model, under the assumption that fisheries observers correctly identify flatfish (which are subject to commercial fisheries in the sGSL). The model performed reasonably well and was, therefore, presumed to be suitable for the estimation of species composition in mixed catches of skates.

In chapter five, I propose a model, incorporating empirical and parametric boostrapping, to estimate discard amounts and discard mortality rates, along with associated variability, for the three skate species in the sGSL. The approach incorporates the model from chapter four as part of the estimation of species-specific landing and discard amounts. Then it uses data and the model from chapter 2, and a special case of the model in chapter 6, to estimate species-specific discard mortality rates. The results for winter skate have recently been incorporated in a population model to estimate fishing and natural mortalities as part of a recovery potential assessment for this population (Swain and Benoît 2017).

In chapter six, I develop a model for longitudinal data from discard mortality experiments that can be used to estimate different components of mortality such as capture and handling mortality, post-release mortality and natural mortality. The model can be used to predict mortality for different vitality classes (see chapter 2), and a number of case studies are presented to demonstrate the strong association between discard mortality and vitality scores. This work supports one of the conclusions in chapter 2. A key case study and associated model simulations are presented to demonstrate the use of the model to correctly estimate discard mortality and natural mortality. The case study – cod discarded in the Gulf of Maine recreational fishery – was further elaborated in a subsequent publication (Capizzano et al. 2016).

In chapter seven, I present a simulation model to evaluate whether, and under which conditions, predation by grey seals can explain the elevated natural mortality in sGSL cod, white hake and winter skate. This work was undertaken as part of a large zonal DFO review on the impacts of grey seals on fish populations in Eastern Canada (DFO 2011a). Direct estimates of predation impacts were not possible because of the lack of spatially and temporally representative diet estimates for grey seals. Instead, the simulation model uses an inverse-modelling approach to determine whether there is sufficient opportunity, based on spatio-temporal overlap between the predator and prey, and scope, based on bioenergetic considerations, for predation explain large portions of the natural mortality rates estimated independently for the fish species. This work built on two other working papers that were prepared for the DFO review (Benoît et al. 2011a,b). Results from the simulations indicate that predation by grey seals can explain the elevated natural mortality for the three fish species under reasonable assumptions for the predator's diet.

1.3 Publications constituting this thesis

The research undertaken for this thesis was published prior to appearing here. The following journal articles constitute the chapters of this thesis. My contribution to each multi-authored paper is indicated in parentheses below each reference. Information concerning copyright permissions related to reproducing these published papers in this thesis is available in Appendix E.

Chapter 2: Benoît, H.P., Hurlbut, T., and Chassé, J. 2010. Assessing the factors influencing discard mortality of demersal fishes in four fisheries using a semi-quantitative indicator of survival potential. Fish. Res. 106: 436-447.

[I designed the study, managed the data collection and storage (prior to commencing my thesis), designed and undertook the analyses, and wrote the paper; the co-authors helped collect field data, provided temperature data, and reviewed the draft manuscript].

Chapter 3: Benoît, H.P., Plante, S., Kroiz, M., and Hurlbut, T. 2013. A comparative analysis of marine fish species susceptibilities to discard mortality: effects of environmental factors, individual traits, and phylogeny. ICES J. Mar. Sci. 70: 99-113.

[I designed the study, managed the data collection and storage, planned and undertook the analyses, and wrote the paper; the co-authors helped collect field data, helped to complete the species-specific biological information, and reviewed the draft manuscript].

Chapter 4: Benoît, H.P. 2013. An empirical model of seasonal depth-dependent fish assemblage structure to predict the species composition of mixed catches. Can. J. Fish. Aquat. Sci. 70: 220-232.

Chapter 5: Benoît, H.P. 2013. Twenty years of annual landed and discarded catches of three southern Gulf of St. Lawrence skate species estimated under multiple sources of uncertainty. ICES J. Mar. Sci. 70: 554-563.

Chapter 6. Benoît, H.P., Capizzano, C.W., Knotek, R.J., Rudders, R.B., Sulikowski, J.A., Dean, M.J., Hoffman, B., Zemeckis, D.R., and Mandelman, J.W. 2015. A generalized model for longitudinal short- and long-term mortality data for commercial fishery discards and recreational fishery catch-and-releases. ICES J Mar Sci 72:1834-1847.

[I designed the study, developed and implemented the modelling methodology, and wrote the paper; the co-authors provided unpublished data used for the case studies and reviewed the draft manuscript].

Chapter 7. Benoît, H.P., Swain, D.P., Bowen, W.D., Breed, G. A., Hammill, M.O., and Harvey, V. 2011. Evaluating the potential for grey seal predation to explain elevated natural mortality in three fish species in the southern Gulf of St. Lawrence. Mar. Ecol. Prog. Ser. 442:149-167.

[I designed the study, developed and implemented the modelling methodology, and wrote the paper; the co-authors provided data to parameterize the simulation, guidance on the bioenergetics modelling and reviewed the draft manuscript].

1.4 Additional publications resulting directly from this thesis

Research that led to the above articles has also been published elsewhere, notably in research documents prepared in support of Fisheries and Oceans Canada science advisory processes related to discards and discard survival, and the impacts of grey seal predation on groundfish populations:

Benoît, H. P., and Hurlbut, T. 2010. Incidental catch, discards and potential post-release survival of fish captured in fixed-gear groundfish fisheries in NAFO 4T (Estuary and southern Gulf of St. Lawrence). DFO Can. Sci. Advis. Sec. Res. Doc. 2010/031. iv+21 p.

Benoît, H. P., Swain, D.P., Niles, M. LeBlanc, S. and Davidson, L.-A. 2010. Incidental catch amounts and potential post-release survival of winter skate (*Leucoraja ocellata*) captured in the scallop dredge fishery in the southern Gulf of St. Lawrence (2006-2008). DFO Can. Sci. Advis. Sec. Res. Doc. 2010/043. iii + 20 p.

Benoît, H.P., Hammill, M.O, and Swain, D.P. 2011a. Estimated consumption of southern Gulf cod by grey seals: bias, uncertainty and two proposed approaches. DFO Can. Sci. Adv. Sec. Res. Doc. 2011/041. iv + 29 p.

Benoît, H.P., Swain, D.P., and Hammill, M.O. 2011b. Seasonal patterns in the spatial overlap of southern Gulf cod and grey seals, with a discussion of sources of error and possible bias. DFO Can. Sci. Adv. Sec. Res. Doc. 2011/018. iv + 16 p.

Swain, D.P. and Benoît, H.P. 2017. Recovery potential assessment of the Gulf of St. Lawrence Designatable Unit of Winter Skate (*Leucoraja ocellata* Mitchill), January 2016. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/119. xviii + 131 p.

Swain, D.P., Benoît, H.P., and Aubry, É. 2012. Smooth skate (*Malacoraja senta*) in the southern Gulf of St. Lawrence: life history, and trends from 1971-2010 in abundance, distribution and potential threats. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/033. iii + 34 p.

Swain, D.P., Benoît, H.P., Daigle, D., and Aubry, É. 2012. Thorny skate (*Amblyraja radiata*) in the southern Gulf of St. Lawrence: life history, and trends from 1971 to 2010 in abundance, distribution and potential threats. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/032. iii + 42 p.

Chapter 2. Assessing the Factors Influencing Discard Mortality of Demersal Fishes in Four Fisheries Using a Semi-Quantitative Indicator of Survival Potential

2.0 Abstract

Understanding the factors affecting the likelihood that discarded fish will die can contribute to better management of resources by enhancing the potential for successful live release and by improving the estimation of otherwise unaccounted fishing mortality. Semi-quantitative measures of individual fish vitality or physical condition, obtained by at-sea observers aboard commercial fishing vessels, are often used as an indicator of survival potential for discarded fish. The present study and previous ones have shown that these measures relate well to eventual survival. However, observer subjectivity in fish vitality scoring can affect the precision and accuracy of inferences drawn from an analysis of the observations. Here we propose the use of a mixed-effects multinomial proportional-odds model, which is appropriate for modelling the ordinal vitality data and is a useful approach for addressing observer scoring subjectivity. This model was used to analyse data collected for eleven fish taxa captured by four gear types. The effect of eight factors previously shown to affect discard survival was evaluated. The gear type used and amount of time that fish spent on deck prior to discarding most strongly and consistently affected the distribution of fish among vitality levels. Sea surface and air temperatures, and fish body size, were also important factors for a number of taxa, while other factors such as the depth fished, catch size and fishing activity duration were important only for certain taxa. A random effect in the model, used to account for observer subjectivity, was significant for most taxa and fisheries. Failure to account for this effect could affect both the precision and accuracy of inferences on the survival potential of discarded fish.

2.1 Introduction

Unwanted fish discarded by commercial harvesters can represent a high proportion of total catches (Alverson 1997; Harrington et al. 2005). Discarded fish that die as a result of capture and release are a wasted potential resource, may represent an unaccounted and difficult to quantify additional source of fishing mortality for population assessments, and may contribute to fishing-induced changes in ecosystem structure and functioning (Alverson et al. 1994; Hall et al. 2000). However, not all discarded fish die (Muoneke and Childress 1994; Davis 2002; Suuronen 2005; Broadhurst et al. 2006). Numerous factors determine the probability of survival following release, including characteristics of the species (e.g., presence of a closed swim bladder), the type of fishing gear employed, fishing practices (e.g., set durations), fish handling practices (e.g., amount of time fish are on the vessel's deck) and environmental factors (e.g., the depth fished, air temperature) (see reviews by Muoneke and Childress 1994; Davis 2002; Suuronen 2005; Broadhurst et al. 2006). Understanding how these factors affect survival can help determine appropriate mitigation measures to maximize the potential for successful live release (e.g., Richards et al. 1995; Trumble et al. 2002; Carruthers et al. 2009) when the capture of unwanted species or sizes of fish is too difficult or costly to avoid by other means (reviewed by Hall 1996; Hall and Mainprize 2005). Such an understanding might also contribute to the estimation of discard mortality rates, for inclusion in population assessments for commercially important species (e.g., Casey 1996; Punt et al. 2006) and incidentally-captured species of conservation concern (e.g., Benoît 2006a; Swain et al. 2009), and in understanding the ecosystem-level impacts of fishing (e.g., Hall 1999; Benoît and Swain 2008).

Experiments are commonly used to study the factors affecting the survival of discarded fishes. In these studies, fishing is simulated either in the laboratory (e.g., Olla et al. 1997; Davis and Olla 2001) or the field (Parker et al. 2003; St John and Syers 2005), and fish are subsequently held in tanks or pens to assess survival rates. Experimental manipulation facilitates the inferences made on the different factors believed to affect survival, particularly under controlled laboratory conditions. In other studies (termed here 'fish holding'), fish captured during commercial fishing operations are held to assess mortality rates, and a correlative approach is used to examine the impact of different factors contributing to that mortality (e.g., Jean 1963; Wassenberg and Hill 1989; Ross and Hokenson 1997). For both experimental and fish holding studies, limitations on the number of fish that can be held restricts the number of factors and factor-levels that can be tested experimentally or statistically. Furthermore, it is likely that study results will not reflect the variability of overall conditions experienced by fish discarded during commercial fishing operations and following release (e.g., predation). Exposure and susceptibility to disease may also differ between laboratory-held and discarded fish.

A complementary approach to studying the factors affecting discard survival is the use of semi-quantitative indices of individual fish condition or vitality recorded just prior to discarding. In these studies, observers on board commercial fishing vessels characterize fish according to binomial (alive or dead; e.g., Carruthers et al. 2009) or ordinal multi-category (e.g., Table 1; Richards et al. 1994; Laptikhovsky 2004) criteria. Ordinal scoring of individuals corresponds well with eventual survival in studies involving tagging and recapture (e.g., Hueter and Manire 1994; Richards et al. 1995; Kaimmer and Trumble 1998) or holding of fish (van Beek et al. 1990; this study). This result is consistent with the finding that degree of injury and reflex impairment, the two aspects of fish vitality qualified by ordinal scoring criteria (Table 2.1), are good predictors of eventual survival (Davis and Ottmar 2006; Humborstad et al. 2009; Davis 2010). Because the scoring is based on a rapid visual and tactile assessment by observers, a large number of individual fish from a variety of fishing sets can be sampled. To the extent that observers obtain samples that are representative of the activities of a fishery, the observed frequency distribution of fish among vitality levels will reflect the overall survival potential of discarded fish, integrating over all of the various factors contributing to that survival. Furthermore, these studies typically yield sufficient sample sizes and contrasts in the factors affecting survival to allow for correlative analyses over the relevant ranges of a number of those factors. The principal disadvantage of these studies is the somewhat subjective nature of the scoring criteria, which could lead to differences between observers in their vitality assessments. A second disadvantage is the need for additional studies to relate vitality scores to eventual survival.

In this paper, we present the results of a study of semi-quantitative vitality sampling by at-sea observers undertaken during four southern Gulf of St. Lawrence

(Canada) groundfish fisheries (Fig. 2.1). The study addresses the two disadvantages of vitality-score studies listed above. We propose the use of a mixed-effects multinomial linear model based on proportional-odds (e.g., Agresti 2002, pp. 513-515), which is appropriate for modelling the ordinal vitality data and is a useful approach for addressing observer scoring subjectivity. We use this model to evaluate the effect of relevant factors believed to influence the survival potential (e.g., gear type, fish size, set durations, handling times) for eleven fish taxa. We also present analyses of an experimental study aimed at relating vitality codes to eventual survival.

2.2 Methods

Data for this study of the potential post-release survival of discarded fish were collected during the 2005 and 2006 fishing seasons in the southern Gulf of St. Lawrence. The study comprised two parts, one based on data collected by at-sea observers and a second based on experiments. These are described in turn below. We then describe the approach used to model the data collected by the observers.

2.2.1 At-sea observer data

Groundfish in the southern Gulf of St. Lawrence are fished using four main gear types: gillnets, demersal (bottom-set) longlines, handlines (i.e., hook and line) and mobile gear (bottom trawls, Danish and Scottish Seines) (Fig. 2.1). All of the commercial groundfish fisheries in the area (defined by the target species and gear type) have some level of at-sea coverage by certified third-party observers, which at the time was paid by Fisheries and Oceans Canada and the fishing industry. Target coverage levels are set by fishery, typically at 5% or 10% (up to 25%) of fishing trips, though actual coverage varies (Benoît and Allard 2009). It is a condition of fishing license to carry an observer, should one be assigned to a given fishing trip (see Kulka and Waldron (1983) and Benoît and Allard (2009) for more details on the commercial fishery observer program). In addition to the commercial fisheries, there is also a scientific fishery, termed the Sentinel Survey, in which selected commercial harvesters fish demersal longlines on historical fishing grounds following a standardized protocol (Gillis 2002). Observers cover 100% of Sentinel Survey trips. Though soak times, numbers of hooks and general locations fished are standardized, fishing sets in the Sentinel Surveys provide a strong contrast in environmental conditions (e.g., depths and season) that is of interest in this study.

In addition to carrying out their regular duties, at-sea observers collected data on the condition of fish captured during the 2005 and 2006 commercial groundfish fisheries and the Sentinel Survey. Specifically, observers measured the length of individual fish and scored their ‘vitality’ on a four level ordinal scale (Table 2.1), based on a rapid (10 s.) evaluation for each individual fish. Observers attempted to solicit a response from immobile fish by depressing the fish’s eye with a finger and by repositioning the fish on the measuring board. Observers also noted the amount of time the fish spent on deck prior to being sampled (henceforth, deck time) and reported other relevant factors such as the depth fished (see section 2.2 below). Observers were provided training on vitality scoring prior to commencing the study, as well as a detailed protocol to follow.

Up to 25 individuals of a given fish taxon were sampled by the observer during a given fishing set, just prior to discarding. For those taxa that are not presently discarded in the fisheries, sampling occurred at around the time that the discarded portion of the catch was released. For several of the trips, observers obtained samples from more than one set. Data were collected for a variety of commercial and non-commercial taxa. For some of these taxa, discarding was permitted in the past but has been prohibited since 1993: American plaice (*Hippoglossoides platessoides*), Atlantic cod (*Gadus morhua*), white hake (*Urophycis tenuis*), and witch flounder (*Glyptocephalus cynoglossus*). For others, discarding below a certain size is either permitted (winter flounder, *Pseudopleuronectes americanus*) or required (Atlantic halibut, *Hippoglossus hippoglossus*) for conservation purposes. For yet another group, discarding is either permitted or the discard bans are not strictly respected: eelpouts (*Lycodes lavalaei*, *L. vahlii*, *Zoarces americanus*), Greenland cod (*Gadus ogac*), sculpins (*Myoxocephalus octodecemspinosus*, *M. scorpius*, and *Hemitripterus americanus*) and skates (*Amblyraja radiata*, *Malacoraja senta* and *Leucoraja ocellata)*. Taxonomic groups above the species level, as shown above, were used in certain cases in our study because observers did not consistently identify the fish to species.

2.2.2 Factors potentially affecting survival

The observers also collected information on a number of relevant factors related to the capture and handling of the fishes (described below). Each of these factors has previously been shown experimentally or correlatively (in the case of depth) to affect discard survival (Muoneke and Childress 1994; Davis 2002; Suuronen 2005; Broadhurst et al. 2006) and is therefore a sensible candidate for a broader analysis of multiple effects, as undertaken here.

Fish length and deck time were recorded for individual fish. For each fishing set, observers noted the geographic position, depth, set duration (soak time for gillnets and longlines, towing and haul-back time for mobile gear), total catch weight and time of day. Using the geographic position and time of day, we obtained an estimate of air temperature from measurements taken at the nearest of three meteorological stations (Fig. 2.1). We also estimated the sea surface temperatures for the date and location of each set from a spatially-explicit (6′ latitude x 6′ longitude grid) seasonal harmonic regression model following a method identical to Ouellet et al. (2003) but using in situ data instead of remotely sensed values. That model, which incorporates annual, semi- and tri-annual cycles in temperature, explains over 80 % of observed variation in temperature profiles collected throughout the southern Gulf and the annual cycle. Model estimates therefore reliably reflect the large temperature disparities that would have existed among the geographically and seasonally disparate fishing sets that occurred during the study.

Some of the variables listed above are not pertinent to particular fisheries. Soak time is negligible in handline fisheries because fish are brought to the surface soon after they are hooked. Deck time is pertinent only to the mobile gear fisheries, where the catch must first be dumped on deck and sorted, with important consequences for eventual survival (Neilson et al. 1989; Richards et al. 1994; Broadhurst et al. 2006). In the other fisheries, fish are handled as the gear is progressively retrieved from the water resulting in minimal deck time (exceptional cases with associated deck time >5 min were excluded from our analysis). Likewise, catch amount was considered pertinent only for fish captured by mobile gear, where it might reflect a possible effect of crushing.

Collinearity among variables was generally low (Pearson correlation coefficient, $r<0.35$ for most pairs of variables). Air and surface temperatures ($r=0.56$) were the only pair of collinear variables. Observed mean, minimum and maximum values of the variables (except length) are presented by gear type in Table 2.2. The range of body lengths captured varied among taxa and gear, as may be the case also for the conditions experienced during capture. Consequently, coefficients of variation for each potential explanatory variable specific to each taxon and gear type are presented in Table 2.3 as an indication of the amount of contrast observed during the study.

Some of the covariates listed above may also interact to influence survival. We initially chose to consider only what were felt to be the strongest potential interactions: air temperature-deck time (an exposure effect), length-deck time (a size-dependent exposure effect), and length-catch weight (size-dependent susceptibility to crushing). However, because the first two interactions were highly collinear with deck time ($r \geq 0.93$) and the third highly collinear with catch ($r=0.94$) we did not include them in the analyses and we used only the primary variables.

2.2.3 Post-capture survival experiments

Experiments were undertaken in 2005 and 2006 aboard the *CCGS Opilio* (an 18-m stern trawler), to relate 'pre-release' vitality codes (Table 2.1) to short-term survival in a number of fish taxa. Fish were captured using a bottom trawl commonly used by local commercial fish harvesters and following common commercial fishing tow speed (2.75 knots) and set duration (1-2 hr.). An electronic temperature sensor was attached to the trawl to measure near-bottom water temperatures. When fish were brought aboard the vessel, they were handled as they would have been during commercial fishing operations and sampled in the manner employed by the observers (section 2.1): measured for length, vitality assessed and deck time noted. Fish were then individually tagged (t-bar streamer tags) and placed in onboard holding tanks (each 1,200 litres) containing continuously exchanged refrigerated sea water. Tank temperatures were set to the bottom temperatures where the fish were captured. Fish were held for at least 48 hrs (though often >72 hrs) to assess short term survival and fish surviving the entire holding period were released alive.

The duration of the holding period was chosen based on preliminary results that suggested that most mortality occurred during the first 24 hrs of holding and that survival to 48 hrs predicted very well survival over a longer period of 5 days (H. Benoît, unpublished analyses). The 48 hr period therefore represented a good compromise between describing the mortality rate of individual fish and the number of fish that could be studied.

Here we merely present for each species the proportion of fish surviving the minimum 48-hr holding period, as a function of their pre-holding vitality code score. These results are presented to support the contention that there is a monotonic relationship between vitality score and survival. A more rigorous analysis of the post-capture survival experiments was published subsequent to this paper (Benoît et al., 2012).

2.2.4 Analysis

2.2.4.1 General model

The choice of model for analysis is motivated by our belief that the ordinal vitality scores used by observers represent an underlying continuous latent variable process (Anderson and Philips 1981; Agresti 2002, pp. 277-279). This unobserved, and realistically unmeasurable, variable integrates the many ways in which injury, trauma, suffocation and stress interact to determine whether a fish will survive following discarding (e.g., Wood et al. 1983; Davis 2002; Broadhurst et al. 2006). A model that describes how the probability of a fish belonging in a given vitality category changes due to a covariate would effectively therefore also describe the effect of that covariate on the latent variable, provided that the discrete scores are an adequate representation of the underlying process and that observers consistently apply the vitality scoring criteria (the latter is addressed below). The proportional-odds multinomial linear model based on cumulative logits is one such model:

$$(2.1)\qquad \text{logit}[P(Y_j \leq v \mid \mathbf{X_j})] = \log\left(\frac{P(Y_j \leq v \mid \mathbf{X_j})}{P(Y_j > v \mid \mathbf{X_j})}\right) = \alpha_v + \mathbf{X}_\mathbf{j}^{'}\boldsymbol{\beta}$$

where Y_j is the observed vitality score for fish j, v is the vitality score level, α_v is an intercept specific to v, $\mathbf{X_j}$ is the design matrix of covariates and $\boldsymbol{\beta}$ is a vector of fixed covariate parameter values (Agresti 2002, pp. 275-277). Because $P(Y_j \leq 4)$ must equal one, there are only three uniquely defined probabilities and therefore only 3 values of α_v to estimate. The intercepts, α_v, increase with v since $P(Y_j \leq v \mid \mathbf{X_j})$ increases in v for fixed values of $\mathbf{X_j}$. Estimates for $\boldsymbol{\beta}$ under this model are invariant to the number of categories used or how the categories 'divide-up' the latent variable (i.e., they need not be equally spaced along the latent variable's distribution) (Ananth and Kleinbaum 1997).

However, the model described by eqn. 2.1 may not be appropriate in this study because the application of scoring criteria used to assess vitality likely differed among observers and among fishing trips sampled by particular observers (henceforth, observer differences). For example, it would be unreasonable to assume that the 21 observers involved in this study could consistently agree on what constitutes 'weak' body movement or 'minor' injuries (Table 2.1). An observer may also be more apt to classify fish differently when all fish in a set are in similar condition compared to sets where there are fish that more broadly reflect the full range of injury severity and response impairment. The impact of observer differences on inferences drawn using eqn. 2.1 depends on the degree of inconsistency and how the observer differences are distributed among the sampled fish. If sampled fish were randomly distributed between observers and over time, observer differences would be reflected only in the standard errors of the estimated parameters $\hat{\boldsymbol{\beta}}$ in eqn. 2.1. Consequently, the estimates of those parameters would be unbiased, though the statistical power to detect significant covariate effects would vary inversely with the degree of scoring inconsistency. However, sampled fish were not randomly distributed among observers or fishing trips for nearly all fish species and fisheries (results not shown). Observer differences would therefore likely lead to biased parameter estimates using eqn. 2.1. Furthermore, the clustered nature of the sampling scheme used in this study (i.e., up to 25 individuals from a taxon sampled in a given set) also means that individual fish often did not constitute independent samples (i.e., intra-cluster correlation), with possible consequences on both the precision and accuracy of $\hat{\boldsymbol{\beta}}$.

It is now common practice to use random effects to account for within-cluster correlations among individual responses in linear models (e.g., Pinheiro and Bates 2000; Zuur et al. 2009). When random effects are incorporated in generalized linear models for ordinal outcomes, they can also be used to account for observer differences (e.g., Hartzel et al. 2001; Sheu 2002). Within-cluster and within-observer correlation can be introduced to eqn. 2.1 through a shared random effect in the linear predictor:

$$(2.2) \quad \text{logit}[P(Y_{ij} \leq v \mid \mathbf{X_{ij}}, u_i)] = \alpha_v + \mathbf{X}'_{\mathbf{ij}}\boldsymbol{\beta} + u_i, \qquad \text{where } u_i \sim N(0, \sigma^2)$$

Y_{ij} is now the observed vitality score for fish j captured in fishing set i, and u_i is the random effect specific to set i (e.g., Carrière and Bouyer 2006), drawn from a normal distribution with a mean of zero and a variance σ^2. Eqn. 2.2 is therefore a random-intercept mixed-effects model, where $P(Y_{ij} \leq v \mid \mathbf{X_{ij}}, u_i)$ is the probability that an individual observed vitality score is less than or equal to vitality level v, conditional on the covariates and the random effect. For this model, estimates of the fixed parameters $\hat{\boldsymbol{\beta}}$ are obtained conditionally on the random effect. The random intercepts effectively model unobserved differences among observers in their application of vitality scoring criteria, while addressing the within-cluster correlation of fishes captured in the same fishing set. The likelihood function of eqn. 2.2 has no closed form solution and was therefore approximated using numerical integration (adaptive Gauss-Hermite quadrature method, Pinheiro and Bates 1995; Hartzel et al. 2001). The standard Newton-Raphson method was then used to maximize the likelihood and obtain the parameter estimates. The analyses were implemented using the SAS (version 9.1. SAS Institute Inc., Cary, N.C.) NLMIXED procedure (Kuss and McLerran 2007). Parameter estimates from an exclusively fixed-effects analysis (i.e., eqn. 2.1) were used to provide relevant starting values for the parameters to be estimated by the NLMIXED procedure

2.2.4.2 Model construction and analysis

Analyses were undertaken separately by taxon because the monotonic relationship between vitality codes and survival probability cannot be assumed to be common among taxa. Two types of analysis were undertaken. In the first we tested exclusively for an effect of fishing gear for those taxa captured by two or more gear types. The results of this analysis will reflect not only the effect of the gear itself on vitality, but also the gear-specific handling practices used by harvesters and differences in the environments in which the gears are fished (e.g., depth, see Fig. 2.1 and Table 2.2). In the second set of analyses, we evaluated the effect of the potential explanatory variables on vitality. Those analyses were undertaken separately by taxon and gear type (the combination is henceforth termed 'case') because the covariate for set duration does not have the same meaning among gears and the covariates total-catch and deck time are germane only to fish captured by mobile gear.

Each analysis proceeded as follows. First, a saturated model including all relevant fixed and random effects (eqn. 2.2) was fitted. Significance of the random effect was determined by a one-tailed t-test (H_0: $\sigma^2=0$; H_A: $\sigma^2>0$), based on the ratio of $\hat{\sigma}$ (i.e. $\sqrt{\hat{\sigma}^2}$) and its standard error computed from the Hessian matrix, with approximate degrees of freedom computed as the number of fishing sets minus one (SAS Institute Inc. 2008). In the case of the analyses of the potential explanatory variables, the purpose of testing the significance of random effects in a saturated, beyond optimal, model is to ensure that the random component of the model does not contain any structure that would otherwise be explained by deliberately excluded fixed effects (Zuur et al. 2009, p. 121). For individual analyses in which the random effect was not statistically significant ($P>0.05$), we proceeded using the fixed-effects model of eqn. 2.1, whereas the mixed-effects model (eqn. 2.2) was used in the other cases.

Second, we aimed to find a parsimonious subset of covariates that best explained variation in observed vitality scores for each species-gear case. Beginning with an intercept-only model and incrementally increasing the number of covariates, we compared all possible candidate models using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). An additional variable to a candidate model was only considered important if it resulted in an AICc that was lower by 3. Different models composed of an equal number of variables were considered equally plausible if the difference in their AICc was ≤ 3. Only the final 'plausible' models are presented here.

For each selected covariate in a case, we calculated the probability of a fish being in vitality-level 4 (i.e., moribund) for values of the covariate equal to its mean plus and minus its standard deviation, holding other selected covariates at their mean. Taking the ratio of these two values (with the maximum of the two in the numerator), we calculated the 'relative risk', as a measure of the effect size associated with the covariate (i.e., its influence on vitality over the observed 'range' of the covariate).

In the proportional odds models (PO, eqns. 2.1 and 2.2), ordering of the predicted response depends exclusively on the ordering of the intercepts α_v, and a common slope determines the predicted probability that an observation will belong to a given vitality category as a function of a covariate. These models can be generalized to allow separate slopes (henceforth, generalized logits model, GL) for covariate effects at each vitality level (i.e., $\boldsymbol{\beta}\mathbf{v}$; e.g., Carrière and Bouyer 2006). In order to keep our analysis tractable, we considered the evidence for separate slopes only for those covariates contained in the plausible model(s) selected as described above. PO and GL models were compared again using AICc. A decrease >3 in AICc relative to the PO model was interpreted as strong evidence for the separate slopes of the GL model for a particular covariate. One undesirable property of GL models with different slopes is that there will be values of the covariate where the lines will cross, violating the hierarchy in response ordering. In practice, this generally occurs well outside the range of covariates used to estimate the model (e.g., Carrière and Bouyer 2006). We confirmed that this was true for cases where the GL model was considered plausible, by calculating the values of the covariate where the intersections occur (results not shown).

2.3 Results

At-sea observers collected vitality data on over 13, 000 fish. For most of the gear type-taxa cases, >100 individuals were sampled (Table 2.3). In each case, numerous sets were sampled, typically by a total of five or more observers.

Fish of all taxa tended to be in overall better condition (i.e., higher proportion of individuals with lower vitality code scores) in hook and line fisheries compared to mobile gear fisheries (Fig. 2.2a). For all taxa captured by more than one gear type, the difference between gear types was statistically significant, as was the random effect (Table 2.4). The model employed, which implies that the effect of gear type is a uniform shift in the intercepts of eqn. 2.2, appears to fit the observations reasonably well, though it tends to slightly overestimate the proportion of individuals in vitality code 1 in longline fisheries (compare Figs. 2.2a and 2.2b). The condition of cod was best in the handline fishery, where nearly all individuals were in excellent vitality, followed by the longline, gillnets and mobile gear fisheries (Fig. 2.2; Table 2.4).

A significant random effect was found in saturated covariate models for all but five taxa-gear cases (Table 2.5). The latter tended to be cases in which a relatively small average number of individual fish were sampled in a set (e.g., wolffish and eelpouts) or in which relatively few sets were sampled (e.g., halibut in mobile gear) (Table 2.3). For most cases, preferred models included one to three covariates. For four of the cases, an intercept-only model was preferred (eelpout and Greenland cod caught by longlines; cod caught by gillnets and handlines). For cod captured by handlines, this is because of a lack of contrast in observed vitality code (>97% individuals were code 1). Examples of predicted and observed proportions of individuals in each vitality code are presented for cases in which the preferred model(s) comprised one (Fig. 2.3) or two (Fig. 2.4) covariates. These plots suggest that the models fit the data reasonably well.

There was some commonality across taxa-gear cases in the covariates selected in the preferred PO models (Table 2.5). For all taxa caught by mobile gear, deck time was negatively associated with vitality (i.e., increasing proportion of fish in the low vitality and moribund categories as time increases). With the exception of skates captured by mobile gear, deck time was also consistently the covariate with the highest effect size (relative risk); on average fish were 33 times more likely to be scored in vitality-level 4 for high observed deck times relative to short ones. A negative effect of either air or surface temperature was also noted for a number of taxa caught by mobile gear, whereas a positive effect was found for two longline caught taxa: Atlantic halibut (one of two selected models) and skates. Recalling that neither air nor sea surface temperature was measured directly at the fishing location and that the two variables are correlated, these results should most appropriately both be interpreted as reflecting an effect of seasonal temperature near the air-water interface. Other factors associated with decreasing condition were depth (white hake, Atlantic cod and Atlantic halibut), longline soak times (i.e., duration; halibut and sculpins) and catch amounts (skates in mobile gear). In contrast, increasing fish length was associated with better condition for a number of taxa caught by both mobile and longline gear. On average, covariates other than deck time were associated with comparable effect sizes (relative risks).

There was support for the inclusion of separate vitality-level-specific slopes (i.e., GL model) for some of the covariates in certain analyses (see ΔAICc in Table 2.5). For American plaice, skates and witch flounder captured by mobile gear, the estimated slope for the effect of deck time generally decreased with the vitality level (Table 2.6). The result is that with increasing deck time, the predicted proportions of individuals in upper vitality levels (codes 3 and 4) will increase more rapidly than they would with the common slope of the PO model. There was also support for separate slopes for the effect of catch for the skates, relative to the PO model, though the support was not as strong as for the effect of deck time (Table 2.5). Furthermore, there was little support for a model that simultaneously included separate slopes for both the effects of deck time and catch for skates (ΔAICc with the PO model = +4.2). For cod captured by mobile gear (both selected models), the slope for the length effect increased with increasing vitality level, causing the predicted probabilities for upper vitality levels to decline more rapidly with increasing length in the GL model compared to the PO model (Table 2.6). For cod captured by longlines, the slope for the effect of depth increased with increasing vitality level, shifting to a positive slope for *v*=3. As a result, the predicted proportions of individuals in vitality-levels 1 and 4 decreased, while predicted probabilities for levels 2 and 3 increased, with increasing depth (Fig. 2.3a). Note however that across all depths, the predicted proportion of cod in vitality level 4 was very small (<0.02).

It is well known in linear regression analysis that even when one variable is known to depend on another, the range of values of the independent variable over which observations of the dependent variable are made can affect the chances of detecting the relationship because of error in the individual observations. This should be true in the present analyses as well. For most covariates however, the degree of observed variation in the covariates was not associated with increased chances of inclusion in the model for a taxon-gear case (Table 2.3, compare values that are and are not underlined). One possible exception was for depth, where the four taxon-gear models that retained that variable were generally instances where observations were made on fish captured over a relatively broad range of depths.

Results of the holding experiments confirm that there is a monotonic relationship between vitality code and short-term survival rate for all the taxa studied, though in some cases the number of individuals monitored was small (Table 2.7). For all species, some unresponsive individuals scored as moribund (vitality code 4) nonetheless survived at least 48 hrs. Short-term survival for trawl-caught winter flounder, skates and sculpins was relatively high for vitality codes 1 and 2. Survival was considerably lower for cod.

2.4 Discussion

There are two general applications of the results of discard mortality studies: the identification of potential mitigation measures to improve the likelihood of successful live release, and the estimation of otherwise unaccounted fishing mortality. The results of the present study are discussed in the context of these uses. Potential biases inherent in vitality-code sampling by observers are then discussed.

2.4.1 Success of live release

Reducing the fishing-induced mortality of organisms that are not utilized by humans, or for which capture is restricted for conservation reasons, is an important objective for fisheries worldwide. Technical (e.g., gear selectivity) and regulatory (e.g., bycatch quotas, time and area closures) measures, and social pressures (e.g., eco-certification) can result in decreased capture of unwanted fish (Hall 1996; Hall et al. 2000; Hall and Mainprize 2005). However, there can be important consequences associated with these measures. These can include financial implications, such as lost opportunity and gear modification costs, and ecological implications, such as a shift in the species that are incidentally captured (e.g., Hall and Mainprize 2005; Coggins et al. 2007). For certain taxa and situations, live release may represent a simple, cost-effective measure to achieve discard management objectives, in conjunction with other management measures (e.g., Trumble et al. 2002; Carruthers et al. 2009).

The results of this and past studies indicate that much of the success of live release depends on the circumstances surrounding a fish's capture and release. A number of the factors affecting mortality can be controlled, such as the type and configuration of gear used, the seasons and depths fished, and onboard handling practices. The relative impact of these factors on survival potential needs to the quantified to increase the likelihood of achieving the desired management objectives related to discard survival. There are two principal advantages to studying the factors affecting discard mortality using a semi-quantitative discard survival indicator collected by at-sea observers. First, the impacts of a given factor on fish vitality are studied under the actual range of conditions in the fishery, and quantification of the impacts incorporates the variability in vitality resulting from the various other conditions pertinent to actual fishing operations. In principle, this should result in a more realistic expectation of the benefits of a given management action aimed at improving the likelihood of discard survival. The second advantage is that a large amount of data can be collected across the range of fishery conditions, allowing for a simultaneous evaluation of the relative impact of a large number of potential explanatory factors that would not otherwise be possible experimentally.

Across all taxa included in this study, three factors most consistently appeared as potential candidates for mitigating discard mortality. Reducing deck time appears to be one of the strongest measures to promote post-release survival, consistent with the results of other studies (e.g., Neilson et al. 1989; Richards et al. 1994; Parker et al. 2003). Prioritizing the sorting of catches to rapidly return species of conservation concern to the water, and reducing catch sizes, via reduced net size or activity duration, which in turn reduces sorting times (e.g., Wassenberg and Hill 1989; Berghahn et al. 1992), are two possible approaches. The second potential mitigation measure would be restricting fishing to times of the year when water surface and air temperatures are lower or when waters are well mixed, since increased temperatures were associated with decreased condition in many taxa in this study and decreased survival in other studies (e.g., Jean 1963; Olla et al. 1998; Davis and Olla 2001, 2002). The third measure is the choice of fishing gear, with the ensuing circumstances surrounding how it is fished. Consistent with our results, others have found that discard mortality was higher in gillnet-captured vs. hook-captured fish (Murphy et al. 1995) and higher in trawl-caught vs. hook caught fish (Neilson et al. 1989; Davis et al. 2001). In the present case however, we cannot definitively conclude that significant differences in vitality scores reflect differences in eventual survival because fish-holding experiments aimed at relating vitality codes to survival have only been conducted for fish caught by trawls. However, to the extent that a fish's reflex impairment and degree of injury determine eventual survival, our inter-gear comparisons should provide at least a relative indication of differences in potential survival.

Other factors affecting survival may be more important for particular taxa. For example, depth may be most important for taxa possessing a physoclistous (closed) swim bladder, such as white hake and cod in this study (e.g., St. John and Syers 2005; Parker et al. 2006; Hannah et al. 2008). However, the effect of depth may not manifest itself only as barotrauma for fish, but also as an effect of thermal shock resulting from depth-dependent temperature gradients, such as those generally found in the southern Gulf of St. Lawrence (Koutitonsky and Bugden 1991) for the locations and dates at which most fishing took place in 2005-2006.

Failure to infer an effect of depth on vitality for other taxa in our study may also have reflected a lack of contrast in the depths over which they were captured during the study (Table 2.3). Although variability (contrast) in other potential explanatory variables did not appear related to whether the variables were selected in the preferred models, it may be that overall this variability was low across taxa-gear cases. For example, soak times were standardized in the Sentinel Survey and were regulated in the gillnet fishery. There may therefore have been little chance of detecting a significant effect of activity duration, even though this has been shown to be an important determinant of discard survival in other studies (e.g., Neilson et al. 1989; Bettoli and Scholten 2006). This lack of contrast is a limitation of this type of correlational study that may result in a failure to identify key mitigation measures. Experimental studies therefore have an important role to play in identifying factors potentially affecting discard survival that may not be possible in a study such as the present one.

2.4.2 Estimating discard mortality rates

Discard mortality can represent much of the fishing mortality experienced by some species and sizes of fish, and can therefore be an important element to include in assessments of populations (e.g., Casey 1996; Punt et al. 2006) or communities (e.g., Benoît and Swain 2008). Aside from the difficulties in estimating the amount of fish discarded (Rochet and Trenkel 2005; Cotter and Pilling 2007), estimating the fraction of those fish that eventually survive in cases where survival is non-negligible presents its own challenges. The goal is to estimate a long-term survival rate that is representative of the entire fishery and that reflects only the losses resulting from capture and release (i.e., excludes natural mortality). These losses may be a direct effect or an indirect one, such as death resulting from disease brought on by injury or stress related to the capture, or enhanced predation risk resulting from reflex impairment (Davis 2002).

The only feasible 'direct' manner of estimating a representative discard mortality rate is using data on the recapture of individuals tagged prior to discarding (e.g., Hoag 1975; Hueter and Manire 1994; Kaimmer and Trumble 1998). Here we use the term recapture to include two connotations, physical and virtual (i.e., using data from satellite pop-up archival transmission (PAT) tags). This approach requires that tagging be undertaken on a representative subset of fishing trips, and requires estimation of numerous rates: background natural and tagging-related mortalities, tagged fish disappearance, tag loss, and in the case of traditional tags, the recovery reporting rate (e.g., Hoag 1975; Pollock et al. 1995; Cadigan and Brattey 2006). With traditional tags, estimating discard mortality in this manner is therefore likely to be limited to species for which there are high levels of catch and strong incentives for tag reporting. Estimating the mortality of discarded species at risk of extinction would therefore rarely be possible, for example. Estimating mortality using satellite PAT tags circumvents many of the problems described above (e.g,. Campana et al. 2009), though present costs limit the number of discarded individuals that can be monitored. In general, the results of a tagging study would be relevant to the fishery conditions at the time; any changes in the fishery potentially resulting in a change in discard survival would necessitate further tagging or some sort of post hoc adjustment of mortality rates.

Combining the results of experimental or tagging studies with samples of a semi-quantitative survival indicator (i.e., vitality scores) obtained during commercial fishing operations may represent an alternate and complimentary indirect manner of estimating relevant discard mortality rates. The required inputs are an estimated rate of survival that is a function of pre-release vitality score (i.e., a conditional survival rate) and a representative frequency distribution of vitality scores. Jointly, these inputs should result in estimated survival that better reflects overall fishery conditions and which is adaptable to changes in those conditions occurring over time, as discussed below.

Conditional survival rates have been successfully estimated for Pacific halibut (*Hippoglossus stenolepis*; Hoag 1975; Trumble et al. 2000) and sharks (Hueter and Manire 1994), based on tagging. Preliminary analyses in the present study, suggest that this is possible for a broader suite of species, based on laboratory holding. In the proposed context, the objective of direct survival monitoring would not be to characterize survival as a function of the various factors in the fishery known to affect it (deck time, etc.) but rather as a function of pre-release vitality. This objective is more in line with the inferences that are possible given the modest number of animals that can be tracked.

A relevant frequency distribution of vitality scores for a given fishery can be obtained in two ways. It can be obtained directly, if at-sea observers are distributed amongst fishing trips in a representative manner. Because at-sea observers are already deployed in many fisheries world-wide, and collecting data on fish vitality represents a very small incremental effort, this can be done very cost effectively. The frequency distribution can also be estimated indirectly, using empirical relationships with parameters of the fishery (e.g., locations and times, activity durations, catch amounts to estimate deck time, etc.), as presented in this paper. In this manner, inter-annual changes in how the fishery is conducted can be incorporated in the predicted frequency distribution of vitality codes and therefore also in the estimated fishery-scale survival rate, without necessarily requiring additional tagging or holding studies (Benoît et al., 2012a; Chapter 4).

2.4.3 Potential biases in observer-collected vitality data

Subjectivity in vitality-code scoring was the main motivation for introducing a random effect to the multinomial model used here. We have argued in the Methods section why it makes sense to account for effects of subjectivity in the analysis and have proposed what we feel was a reasonable approach to do so. However, the approach has not been completely validated. For example, the appropriateness and sufficiency of the normally-distributed random-intercepts to account for scoring subjectivity should be evaluated. An analysis of scores obtained when two or more observers sample fish from common fishing sets could be used to that end.

The presence of observers may also have specifically influenced catch handling by harvesters. Many of the harvesters whose catches were sampled were aware of our study's objectives. It is therefore possible that they applied enhanced caution when handling their catch, even though they were asked to follow their normal handling procedures. Consequently, the vitality scores recorded by observers may provide a more optimistic picture of pre-discarding condition of fish compared to the condition of fish caught in fishing activities not covered by observers. This type of bias is again likely inherent to most studies of discard survival, including experimental studies, where scientists that are used to following animal care protocols may be more likely to handle their experimental subjects more gently than would normally occur in a fishery. In the analyses presented here, it is likely that gentler handling would manifest itself as a roughly uniform improvement of the vitality of all individuals in a fishing set relative to what would have occurred had that set not been observed. The consequence would be biased estimates of the intercepts of eqns. 2.1 or 2.2. The degree of bias would of course depend on the average degree of enhanced caution applied by harvesters when handling the fish. Differences among harvesters in the amount of extra caution would be incorporated in the random effect of eqn. 2.2. However, enhanced caution is unlikely to be reflected in the estimated slope of the covariate effects. There is no reason, for example, to expect that the degree of additional caution varies with the depth fished. Consequently, the degree to which the probabilities associated with each vitality code change with changes in a covariate should nonetheless be well estimated.

Table 2.1**.** Description of the codes used to score the vitality of captured fishes during commercial and Sentinel Survey fishing trips.

Vitality	Code	Description
Excellent	1	Vigorous body movement; no or minor[a] external injuries only
Good / Fair	2	Weak body movement; responds to touching/prodding; minor[a] external injuries
Poor	3	No body movement but fish can move operculum; minor[a] or major[b] external injuries;
Moribund	4	No body or opercular movements (no response to touching or prodding)

[a] Minor injuries were defined as ‘minor bleeding, or minor tear of mouthparts or operculum (≤10% of the diameter), or moderate loss of scales (i.e. bare patch)’.

[b] Major injuries were defined as ‘major bleeding, or major tearing of the mouthparts or operculum, or everted stomach, or bloated swim bladder’.

Table 2.2. The mean [minimum, maximum] values for each of six potential explanatory variables in each fishery (i.e., gear type). The means were calculated from set-specific observation or estimations (in the case of temperatures) for all variables except deck time, where an average over all observed individual fishes was used. A dash indicates that the variable is not relevant for fisheries using the particular gear type.

Variable	Mobile gear	Longlines	Handlines	Gillnets
catch (kg)	432.4 [12, 7789]	-	-	-
Deck time (min)	22.1 [1, 120]	-	-	-
depth (m)	104.8 [29,265]	59.7 [19, 201]	37.2 [30, 55]	50.7 [30, 65]
duration (hr)	1.6 [0.5, 5.1]	19.6 [2, 233]	-	13.8 [2.2, 36.2]
temperature (°C):				
air	16.3 [5.5, 24.8]	16.3 [5.1, 24.1]	15.4 [-7, 21.8]	19.7 [15.8, 22.1]
surface	13.3 [3.9, 18.7]	15.1 [4.7, 18.9]	13.7 [0.4, 15.5]	14.7 [13.8, 16.4]

Table 2.3. The total numbers of individual fish sampled for vitality, numbers of sampled sets and numbers of observers (Obs.) involved in the sampling for each case, defined by gear type and fish taxon. Also presented are the coefficients of variation (CV, in %) for each of the seven covariates considered in the analysis. Underlined values of CV indicate cases where the covariate was retained in the multinomial analysis (Table 2.5). Values of CV are not indicated for cases where a covariate was not considered relevant for a particular gear type.

Gear type				Covariate						
Taxon	Fish	Sets	Obs.	Catch	Deck time	Depth	Activity duration	Air temp.	Surface Temp.	Body length
Trawls and seines										
American plaice	1550	66	10	185	71	50	44	28	22	19
Atlantic cod	1186	54	11	250	84	44	30	29	21	15
Atlantic halibut	72	11	4	109	191	50	19	29	37	18
Sculpins	86	27	2	194	56	57	40	32	26	17
Skates	497	43	6	84	124	26	26	30	22	29
White hake	105	13	5	103	86	56	20	24	23	12
Winter flounder	282	16	6	202	54	34	19	21	18	15
Witch flounder	748	37	6	86	79	23	23	25	21	12
Longlines										
Atlantic cod	3867	219	14			79	138	23	14	14
Atl. halibut	962	101	18			84	55	18	12	25

Gear type				Covariate						
Taxon	Fish	Sets	Obs.	Catch	Deck time	Depth	Activity duration	Air temp.	Surface Temp.	Body length
Eelpouts	146	49	7			14	42	20	9	12
Greenland cod	360	29	6			11	30	19	7	15
Sculpins	868	101	10			55	44	22	12	18
Skates	181	26	4			41	63	24	11	13
White hake	1164	98	11			83	49	24	13	16
Wolffishes	65	46	10			74	74	26	19	21
Handlines										
Atlantic cod	450	21	11			15		41	23	17
Gillnets										
Atlantic cod	519	26	8			13	69	10	4	12

Table 2.4. Results of a mixed-effects analysis of the influence of gear type on vitality code scores for the five fish taxa captured by two or more gear types. The parameter estimates, their standard error and statistical significance of the effect of a gear type relative to the effect of mobile gear, and the estimate and significance of $\hat{\sigma}$ are presented.

Species	*Parameter*	*Estimate*	*S.E.*	*P*
Atlantic cod	Gillnets	1.737	0.452	0.0001
	Handlines	6.979	0.652	<0.0001
	Longlines	4.649	0.309	<0.0001
	$\hat{\sigma}$	1.801	0.110	<0.0001
Atlantic halibut	Longlines	4.161	0.772	<0.0001
	$\hat{\sigma}$	1.506	0.340	<0.0001
Sculpins	Longlines	4.797	0.858	<0.0001
	$\hat{\sigma}$	3.014	0.452	<0.0001
Skates	Longlines	1.917	0.692	0.0071
	$\hat{\sigma}$	2.208	0.287	<0.0001
White hake	Longlines	3.437	0.577	<0.0001
	$\hat{\sigma}$	1.561	0.180	<0.0001

Table 2.5. Results of multinomial proportional-odds model analyses conducted by gear type and fish taxon. The estimate of the random effect in a saturated model ($\hat{\sigma}$), its standard error (S.E.) and the associated p-value based on a one-tailed t-test are presented first. Results for each covariate from the selected plausible models (numbered in instances where more than one model was retained for a given gear type-taxon case) are then presented: parameter estimates, standard error, p-value and relative risk. The rightmost column (ΔAICc) presents the difference in AICc between the selected proportional odds model and generalized logits model for the covariate in question. Values of ΔAICc≤-3 were interpreted as indicating support for the generalized logits model (Table 2.6). No results are shown for Atlantic cod captured by handlines because there was too little contrast in observed vitality codes to properly estimate the random effect or characterize the effects of covariates.

Gear type *Taxon*	*Model #*	*Param.*	*Estimate*	*S.E.*	*P*	*Rel. risk*	*ΔAICc*
Trawls and seines							
American plaice		$\hat{\sigma}$	1.399	0.173	<0.0001		
		airT	-0.187	0.054	0.0009	1.4	-2.8
		length	0.091	0.014	<0.0001	1.2	-1.2
		surfaceT	-0.280	0.082	0.0011	1.3	-1.1
		time	-0.158	0.011	<0.0001	6.7	-11.0
Atlantic cod		$\hat{\sigma}$	2.210	0.285	<0.0001		
	1	surfaceT	-0.447	0.123	0.0006	2.6	-2.7
		length	0.036	0.011	0.0022	1.2	-10.1
		time	-0.222	0.016	<0.0001	24.4	+1.1
	2	airT	-0.220	0.079	0.0071	2.2	+6.1
		length	0.036	0.011	0.0024	1.3	-7.1
		time	-0.219	0.016	<0.0001	24.6	+5.2
Atlantic halibut		$\hat{\sigma}$	0.000	0.285	0.5017		
		time	-0.211	0.059	0.0004	21.4	-2.4
Sculpins		$\hat{\sigma}$	1.990	0.560	0.0007		
		time	-0.254	0.055	<0.0001	55.6	+3.7
Skates		$\hat{\sigma}$	2.155	0.348	<0.0001		
		catch	-0.008	0.002	0.0092	1.6	-5.0
		surfaceT	-0.554	0.172	0.0021	1.6	+0.8

Gear type *Taxon*	*Model #*	*Param.*	*Estimate*	*S.E.*	*P*	*Rel. risk*	*ΔAICc*
		time	-0.099	0.013	<0.0001	1.6	-8.4
White hake [1]		airT	-0.461	0.154	0.0035	3.3	+1.1
		depth	-0.037	0.008	<0.0001	4.1	+4.3
		time	-0.198	0.070	0.0055	65.2	+3.0
Winter flounder		$\hat{\sigma}$	1.082	0.318	0.0021		
		time	-0.286	0.033	<0.0001	66.3	+1.2
Witch flounder		$\hat{\sigma}$	1.787	0.337	<0.0001		
		length	0.091	0.028	0.0023	1.2	+2.4
		time	-0.324	0.044	<0.0001	25.6	-7.6
Longlines							
Atlantic cod		$\hat{\sigma}$	1.301	0.108	<0.0001		
		depth	-0.007	0.002	0.0006	2.0	-29.7
Atlantic halibut		$\hat{\sigma}$	0.777	1.131	0.2486		
	1	depth	-0.017	0.004	0.0002	2.9	+3.1
		duration	-0.045	0.014	0.0017	3.2	+1.9
	2	duration	-0.042	0.014	0.0035	3.0	+2.6
		surfaceT	0.220	0.062	0.0004	2.2	+2.1
Eelpouts [2]		$\hat{\sigma}$	3.010	1.35	0.0611		
Greenland cod [2]		$\hat{\sigma}$	0.644	0.175	0.0004		
Sculpins		$\hat{\sigma}$	3.425	0.684	<0.0001		
		duration	-0.184	0.075	0.0154	13.6	-0.3
		length	0.086	0.040	0.0329	2.9	+0.5
Skates		$\hat{\sigma}$	0.534	0.272	0.0607		
		airT	0.222	0.067	0.0010	4.6	+3.0
White hake		$\hat{\sigma}$	1.221	0.157	<0.0001		
		depth	-0.010	0.003	0.0013	3.0	+0.1
Wolffishes		$\hat{\sigma}$	0.000	0.522	0.9999		
		length	0.100	0.042	0.0205	8.7	+3.5
Gillnets							

Gear type *Taxon*	*Model #*	*Param.*	*Estimate*	*S.E.*	*P*	*Rel. risk*	*ΔAICc*
Atlantic cod [2]		$\hat{\sigma}$	1.466	0.237	<0.0001		

[1] Could not estimate random effects for white hake captured in bottom trawls due to strong confounding between observer differences and the fixed effect of other covariates.

[2] There were no significant covariates for this taxon captured by this gear-type

Table 2.6. Parameter estimates (S.E.) for the covariates for taxon and gear-type cases for which there was support for separate vitality-level slopes (*v*) in a generalized logits model.

Gear type *Taxon*	*Model #*	*Effect*	*v=1*	*v=2*	*v=3*
Trawls and seines					
American plaice	-	time	-0.134 (0.012)	-0.148 (0.011)	-0.164 (0.011)
Atlantic cod	1	length	0.011 (0.016)	0.036 (0.013)	0.067 (0.013)
	2	length	0.010 (0.016)	0.035 (0.013)	0.067 (0.013)
Skates	-	catch	-0.006 (0.002)	-0.004 (0.002)	-0.006 (0.002)
		time	-0.080 (0.016)	-0.122 (0.015)	-0.104 (0.014)
Witch flounder	-	time	-0.235 (0.053)	-0.327 (0.051)	-0.354 (0.049)
Longlines					
Atlantic cod	-	depth	-0.008 (0.002)	-0.004 (0.002)	0.001 (0.003)

Table 2.7. Results of the fish holding experiments: percentage (numbers, in brackets) of fish surviving at least 48 hours post capture, as a function of the vitality code attributed to individual fish prior to putting them in the holding tanks. A dash indicates that no fish scored at that vitality code level were included in the experiments.

	Vitality code			
Species	1	2	3	4
American plaice	88.1 (109)	64.8 (71)	53.8 (52)	3.9 (642)
Atlantic cod	65.1 (43)	39.4 (66)	14.8 (54)	1.9 (483)
Atlantic halibut	100 (3)	-	50.0 (5)	-
Skates	100 (56)	100 (31)	62.5 (24)	42.1 (38)
Sculpins	100 (19)	100 (20)	83.3 (12)	55.6 (9)
White hake	100 (2)	66.7 (3)	50.0 (4)	-
Winter flounder	100 (19)	92.0 (25)	63.2 (19)	19.1 (47)
Witch flounder	-	75.0 (8)	50.0 (14)	-

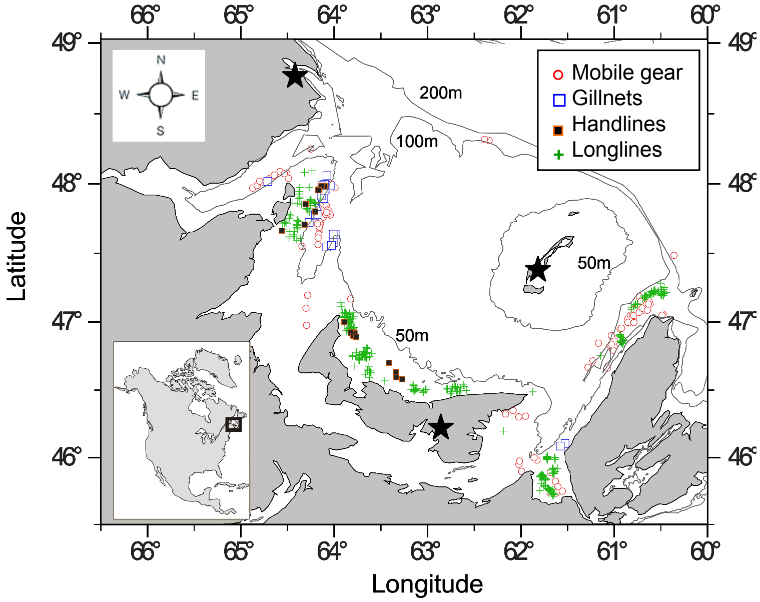

Figure 2.1. Location of fishing trips in the southern Gulf of St. Lawrence sampled by at-sea observers in mobile gear (trawls and seines), gillnet, handline and longline fisheries. The 50-m, 100-m and 200-m isobaths are indicated by the short-dashed, long-dashed and solid lines, respectively. The locations of the three meteorological stations from which air temperature data were obtained are indicated by black stars. The inset shows the location on the east coast of Canada.

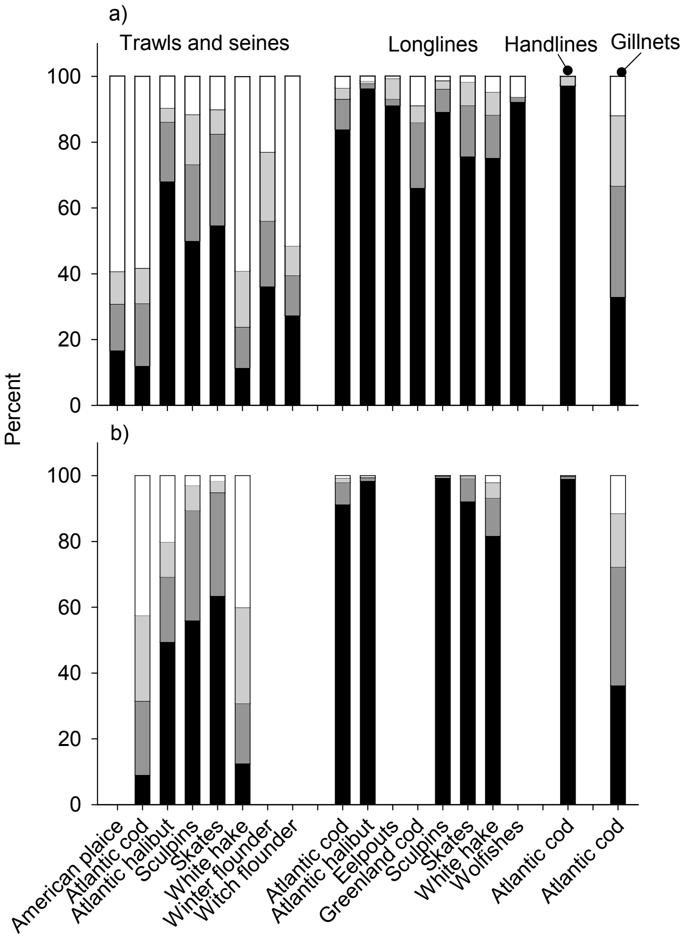

Figure 2.2. The proportion of fish of in each vitality code category (code 1=black, 2=dark grey, 3=light grey, 4=white) by species and gear class a) as observed in the fisheries and b) as predicted by eqn.2 with a factor for 'gear-type'. No prediction is presented for species not included in the analysis of the gear-type effect

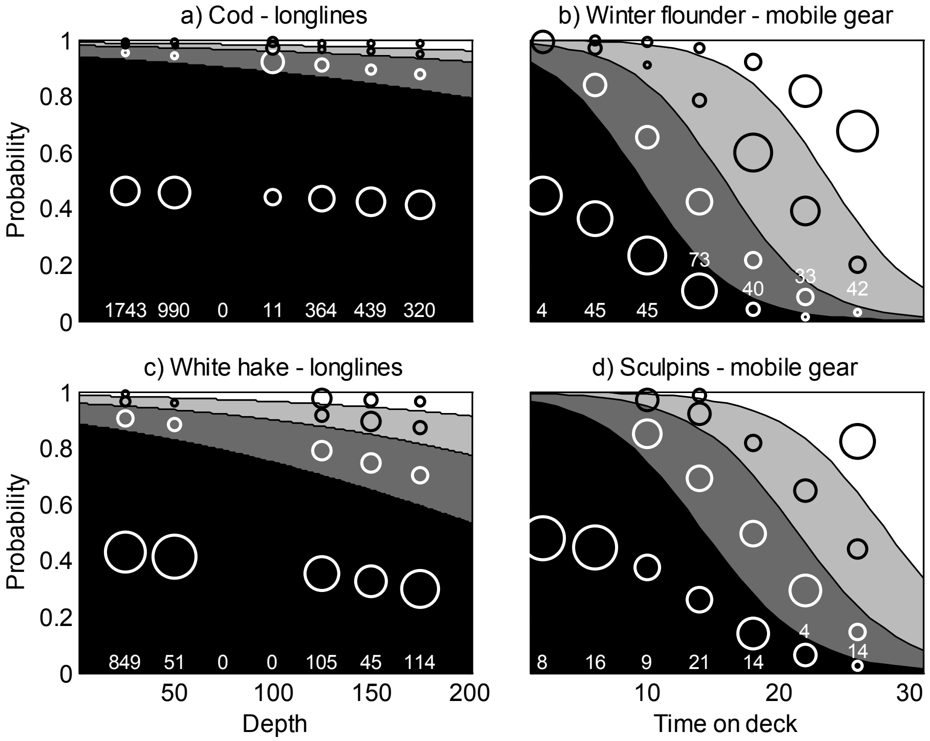

Figure 2.3 Examples of the predicted probability of a fish occurring in each vitality code category (shaded area) as a function of depth in longline fisheries (panels: a – cod, c – white hake) or deck time in mobile gear fisheries (panels: b – winter flounder, d - sculpins). Predicted probabilities for cod are from the generalized logits model with separate slopes for the vitality levels, whereas a proportional odds model was used for the other species. Shading of vitality codes is: code 1=black, 2=dark grey, 3=light grey, 4=white. Superimposed in each plot are expanding circles showing the relative proportion of individuals of the species observed in each vitality code category in a given bin for the covariate. The total number of fish observed for each covariate bin is indicated near the bottom of each plot.

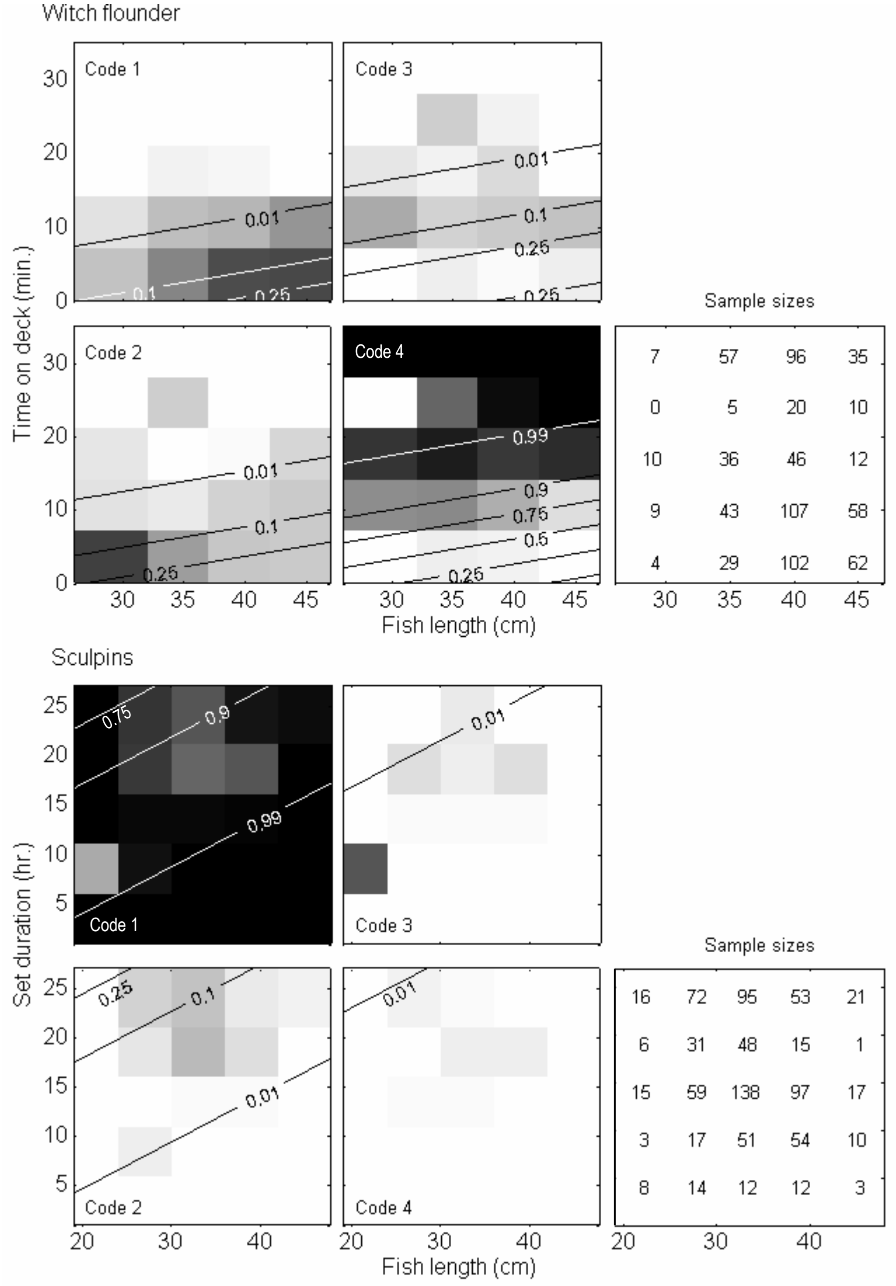

Figure 2.4. The predicted probability (contours) and observed proportion of individuals (shading) in each vitality code category (panels) as a function of the two covariates selected in the favored models for witch flounder caught in mobile gear (top 5 panels) and sculpins caught by longlines (bottom 5 panels). The relative distribution of observations among vitality code categories, within bins of the two covariates, is presented using shading which increases from light to dark as the percentage of observations increases from 0% to 100%. The rightmost panels show the number of individual witch flounder (top panel) and sculpins (bottom) observed in each covariate bin.

Chapter 3. A Comparative Analysis of Marine Fish Species Susceptibilities to Discard Mortality: Effects of Environmental Factors, Individual Traits, and Phylogeny.

3.0 Abstract

Determining the sustainability of fishing mortality for discards requires information on discard amounts as well as capture and release mortality rates. Formal estimates of these rates are costly and only available for a limited number of species and fisheries. In their absence, proxies for discard mortality could inform risk assessments of fishing mortality sustainability for discarded species. Here, time-to-mortality (TM) was assessed for 48 marine fish species exposed to air following capture during an annual multi-species bottom-trawl survey. Species-specific estimates of TM were related qualitatively to more formal estimates of discard mortality from commercial fisheries, confirming the use of TM as a proxy. The effects on TM of species and individual traits, phylogenetic similarity (proxy for traits not explicitly included in the analysis) and environmental factors related to capture were also assessed. Much of the observed individual variability was explained by intra- and inter-specific positive relationships between body size and TM. Sedentary species and those lacking a gas bladder or deciduous scales had greater TM. Effects of phylogeny and capture depth and temperature were also found. This study demonstrates how reliable proxies of discard mortality rate can be readily obtained in the field or estimated from relevant covariates.

3.1 Introduction

Determining the sustainability of fishing mortality for organisms targeted and incidentally captured in commercial fisheries is a key aspect in adopting an ecosystem approach to fisheries, as codified in the Food and Agriculture Organisation's Code of Conduct for Responsible Fisheries (FAO, 1995) and the Aichi Biodiversity Target #6 of the Convention on Biological Diversity (http://www.cbd.int/sp/targets/). For discarded organisms, determining sustainability requires information on capture and release mortality rates. However, formal estimates of discard mortality are costly and technically difficult to obtain (e.g., Broadhurst et al. 2006; Neilson et al. 2012), and are therefore only available for a limited number of species and fisheries. For example, there are unlikely to be sufficient resources to estimate the discard mortality of many non-commercial species, and ethical concerns for species at elevated risk of extinction may further preclude undertaking such studies.

While reliable formal estimates of discard mortality are desirable, they may not be required in many instances to assess the risk that fishing mortality is not within safe biological limits for a stock or species. Instead, reliable proxies of discard mortality rate that provide a relative magnitude of expected mortality may be sufficient. For example, easily obtained semi-quantitative indicators of individual fish responsiveness and degree of injury, observed just prior to discarding, have been found to relate well to eventual mortality (Hueter and Manire 1994; Richards et al. 1995; Benoît et al. 2012; Chapter 2), as have some biochemical indicators in certain instances (e.g., Beamish 1966; but see Davis and Schreck 2005; Davies et al. 2009). Because semi-quantitative proxies can be obtained easily and broadly throughout a fishery, it is also possible to explore their relationship with various factors believed to affect discard mortality, in turn highlighting opportunities where management actions might increase the chances of successful live release (e.g., Richards et al. 1994; Chapter 2).

In this paper, we argue for the utility of another proxy of discard mortality, the time-to-mortality (TM) of fish captured and exposed to air during an annual scientific multi-species bottom-trawl survey. Previous studies have shown that air exposure is one of the greatest contributors to discard mortality rates within and across species (e.g., Davis 2002; Broadhurst et al. 2006; Chapter 2), making TM a potentially good candidate for a discard mortality proxy. We took advantage of the fact that these surveys typically capture a large number and diversity of species, comprising individuals that are very likely to die during survey operations, in order to monitor the fate of over 3,300 individuals across 48 temperate marine fish species.

The study had two main objectives. The first was to establish that TM is indeed a suitable proxy for mortality estimates obtained from a more detailed and intensive study of discard mortality in local commercial fisheries (Benoît et al., 2012). The second was to explore the relative roles of biological (species and individual traits, phylogenetic relationships) and environmental (depth and temperature of capture) factors in shaping an individual's TM. On one hand, this permitted an analysis of the environmental (extrinsic) factors in a standardized framework that is presently unavailable in any existing study to our knowledge, in turn providing an unbiased indication of the possible discard mortality consequences associated with factors that are under management control (e.g., location fished). On the other hand, this approach also permitted examination of the biological factors that may confer different discard mortality susceptibilities to individuals and species, either explicitly by considering the traits themselves or implicitly by considering the effect of phylogeny (assuming greater trait similarity between closely related species). This, in turn, might allow for the estimation of discard mortality potential for unstudied species. Though the factors that result in different bycatch mortality rates for individuals and species have been reviewed by comparing studies involving one or a few species (Davis 2002; Suuronen 2005; Broadhurst et al. 2006), this is to our knowledge the first study to address the question in a more systematic and standardized manner.

3.2 Methods

3.2.1 Fish mortality following capture and air exposure

The analyses were based on sampling that was undertaken during the multi-species bottom-trawl survey of the southern Gulf of St. Lawrence (sGSL), Canada. This survey follows standardized protocols and is undertaken each September by Fisheries and Oceans Canada (details in Chadwick et al., 2007). The target fishing procedure for each haul is a 30 min tow at 3.5 knots. The trawl used is an Atlantic Western IIA survey trawl, with a 19 mm liner in the codend to retain small specimens. The survey area generally ranges in depth from 20-350 m. Once a haul is completed, the net is brought back and its contents are dumped below deck where they are sorted into component species, which are then weighed and subjected to detailed sampling of individual fish for various demographic parameters.

This study is based on additional parameters obtained from a subset of individual fish captured during the regular survey. The analysis used data from two types of sampling aimed at quantifying the TM resulting from capture and air exposure: cross-sectional sampling focused on skates (Order Rajiformes) and longitudinal sampling covering the diversity of fish species captured in the survey (see Appendix Table A1 for the scientific names). With cross-sectional sampling, mortality rates are determined by examining whether individuals are alive at a particular instance in time, whereas with longitudinal sampling, mortality rates are determined by following the fate of individuals to determine their 'exact' time of mortality.

The cross-sectional sampling was undertaken in 2005 to obtain a rough estimate of the discard mortality rate for recovery planning for winter skate (Benoît 2006), a species designated as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2005). As part of that sampling, data were collected for each of the three skate species that inhabit the sGSL: winter, smooth and thorny skates. During that specimen sampling, survey operations proceeded as usual, except for when it came time to measure individual skates, they were also briefly monitored for 10 s. to establish whether they were still alive. The main signs of life that were assessed were movements of the body and attempts at ventilation indicated by movement of the spiracles. The amount of time an individual spent out of water (i.e., the time of observation minus the time at which the trawl codend left the water) was also recorded. Skates still alive after sampling were released to the sea. Data were obtained for all skates captured during the 2005 survey.

The longitudinal sampling took place during the 2006 and 2007 surveys, and targeted all marine fish species captured. As soon as the catch from a haul was brought below deck, a dedicated sampler randomly selected up to 10 individuals (depending on availability) for further mortality monitoring, from each of three to six species caught in the haul. Immediately after all of the specimens were selected for this purpose, they were monitored for 10 sec approximately every 1-5 min for signs of life (as above for skates), until they were required by samplers conducting the routine survey sampling or until they were released in preparation for a subsequent haul (note that monitoring frequency was greater when individuals were first selected to accurately characterize TM for rapidly dying species). Attempts were made to solicit a response from immobile fish by manipulating them or depressing one of their eyes with a finger or small blunt instrument in the case of smaller fish. Unresponsive individuals were placed in seawater to determine if ventilation would resume. Fish that failed to ventilate were considered dead, and the duration of their period of air exposure (i.e., their time-to-mortality, TM) was recorded, as was their fork length (cm). Fish that resumed ventilation (<5% of cases) were kept out of water for further monitoring.

For the longitudinal sampling, fish that were dead when first observed at time T were retained in the analysis and were treated as left-censored observations in that their actual time of mortality, t, was smaller than T (details below). Fish that were still alive when mortality monitoring ceased were considered as right-censored observations in that $t>T$. The remaining individuals (i.e., those that died during TM monitoring) were considered as uncensored observations given that $t \approx T$. Divided in this manner, the skates from the 2005 cross-sectional sampling fell into only two censoring categories: left (dead when observed) and right (alive when observed). The combined numbers of observations in each censoring category and for each species are indicated in Appendix Table A1.

Unlike the cross-sectional study that was restricted to the three skate species, the individuals of each species in the longitudinal sampling represent a subset of those captured in the survey. In selecting these individuals, attempts were made to obtain samples that were representative of the habitats (temperature and depth) occupied, and body sizes normally observed for each species. Observations were made on individuals identified at the species level in all cases except for redfish, for which *Sebastes mentella* and *S. fasciatus* were not distinguished during the survey, and hookear sculpins, *Artediellus atlanticus* and *A. uncinatus*, which were grouped at the genus level for analysis to increase sample size.

3.2.2 Relevant covariates, species traits and phylogeny

The analyses presented in this paper consider the effects of environmental factors, species traits and phylogenetic relationships on fish TM following capture and air exposure. The two environmental covariates, temperature and depth, and one quantitative species trait, body length, have been shown to affect discard mortality both within and between species (Davis, 2002; Broadhurst et al., 2006). For these variables, specimen-specific observations made as part of this study were used in the analyses (Appendix Table A1). For the other traits, species-specific values were obtained from general references (Scott and Scott, 1988; Collette and Klein-MacPhee, 2002), except where indicated below. Only those traits for which information was available for all of the species included in this study, and which were considered relevant to discard mortality susceptibility *a priori*, were included: presence of deciduous scales, presence and type of gas bladder, high mucus production, sedentariness and body softness. Species-specific values of the various covariates used in the analyses are shown in Appendix Table A1.

The nature of the covariates used in our analysis and justification for their inclusion is presented below. We deliberately include explanations for why covariates were believed to be relevant here, rather than in the Discussion, to give the reader the required context up front.

3.2.2.1 Temperature

In the analyses, the effect of temperature was modeled as the difference between the mean air temperature in the ship-board laboratory (18^oC) and the bottom water temperature measured during the haul in which a specimen was captured (note that nearly all of the fish in our study were captured from waters $\leq 18\ ^oC$). It was modeled this way to reflect an anticipated inverse relationship between thermal stress (based on the temperature differential) and TM (Davis, 2002; Cicia et al., 2012). Furthermore, because the fish considered here are all ectotherms, an increase in core temperature generally involves an increase in the rates of oxygen uptake and biochemical reactions (Fry, 1971; Jobling 1993), hastening asphyxiation when exposed to air and enhancing the buildup of metabolic byproducts that contribute to a decline in physiological condition.

3.2.2.2 Depth

The anticipated effect of depth, taken here to be an effect of barometric pressure, was difficult to predict a priori for at least a couple of reasons. First, its effect is somewhat confounded with that of temperature. During the summer and into September, the sGSL is characterized by three water layers: a shallow mixed layer and thermocline (surface to approximately 40 m; 20°C to 2°C), a cold intermediate layer (50-110 m; 0-1.5°C) and a deeper, warmer and saltier layer (200-350 m; ~5°C). Second, depth and mortality rate are likely to covary for species with organs that retain gas (e.g., gas bladder) and that may expand or rupture as a result of decompression when the fish is brought to the surface. However, this relationship may not be linear, for example, if there are threshold effects whereby the organs rupture as a result of a given pressure change and additional pressure changes do not inflict greater damage. In contrast, species lacking these organs may not be as sensitive. Third, the effect of depth is confounded with haul-back duration (and therefore total haul duration) in our study, and factors affecting a species' susceptibility to barotraumas may not be the same as those affecting susceptibility to compaction in the net. Depth was measured using the ship's sonar.

3.2.2.3 Body size (mass-specific respiration demand, MSRD)

Smaller fish generally appear to be more vulnerable to discard mortality (Davis, 2002; Suuronen, 2005). This may in part be related to a greater susceptibility to injury due to crushing during the haul or to changes in barometric pressure when the trawl is brought to the surface, or greater fatigue from swimming to try to escape the trawl. However, an effect that is likely to be more important, especially in the present context, is that smaller fish are likely more susceptible to hypoxia due to their higher mass-specific metabolic rate (Peters, 1983; Jobbling, 1993) and an often higher energy cost for breathing (e.g., Kalinin et al., 1993). To model this anticipated effect, the individual lengths measured during this study were used to estimate body masses using species-specific length-mass relationships developed from recent regular survey observations (H. Benoît, unpublished analyses). These masses were then transformed into an index of mass-specific respiration demand (MSRD) for the subsequent analyses (Peters, 1983):

$$(3.1)\quad MSRD = mass^{-0.25}$$

3.2.2.4 Deciduous scales

Scale loss and skin injury contribute to mortality in fish that escape from fishing gear, and also likely in discarded fish. Such mortality appears to be greater in fish with deciduous scales, compared to fish without them (Suuronen et al., 1996a,b). Though scale loss and skin injury are mainly expected to contribute to mortality in the medium to long term due to increased risk of infection, the stress resulting from the injury and an increased susceptibility to desiccation constitute an acute effect pertinent to this study.

3.2.2.5 Physoclistous and physostomous gas bladders

The gas bladder of fish is derived from an out-pocket of the esophagus, and in some groups a connection to the gut is maintained via the pneumatic duct (the physostomous condition), while in others there is no pneumatic duct, resulting in a closed gas bladder (the physoclistous condition). Depressurization as fish are brought to the surface can contribute significantly to mortality in species possessing a closed gas bladder through the creation of emboli, the rupture of the gas bladder itself, and the extrusion of internal organs (reviewed in Broadhurst et al., 2006). Physoclistous fish are therefore most susceptible to the effects of barotraumas, though these effects are not necessarily permanent (e.g., Nichol and Chilton, 2006; Midling et al., 2012). While physostomous fish can more readily regulate the amount of gas in their gas bladders by venting it via their esophagus, we hypothesized that they may nonetheless be more vulnerable to barotraumatic effects compared to fish lacking a gas bladder entirely. The presence and type of gas bladder for individual species was obtained from McCune and Carlson (2004) and general texts.

3.2.2.6 Mucus production

Certain fish taxa exude relatively large amounts of mucus when stressed. We hypothesized that this might protect against abrasion and skin injury during the fishing haul and as the catch is sorted on deck, and against the effects of desiccation during exposure to air. Species were categorized as producing above average quantities of mucus based on reports of the density of mucus pits reported in general texts, and based on the experience of the authors in handling these fish.

3.2.2.7 Activity level – Sedentariness

A fish species' average activity level can have a major impact on their overall resistance to stress. The hormonal stress responses of many sedentary marine species with low metabolic activity differ from those of more active fishes, presumably as an adaptation to prevent excess energy mobilization (e.g., Vijayan and Moon, 1994; MacCormack and Driedzic, 2004). Furthermore, fish capable of metabolic depression and activating anaerobic metabolism have an enhanced hypoxia tolerance (e.g., shorthorn sculpin, hagfish) (MacCormack and Driedzic, 2004, 2007; Corkum and Gamperl, 2009; Cox et al. 2011). In "active" fish such as salmon, *Salmo salar*, physical disturbances typically elevate blood lactate concentrations, whereas subtle and even non-existent lactate responses are observed in flatfish exposed to similar physical disturbances. Since most flatfish are sedentary, with a lower aerobic capacity, they retain lactate for further metabolism within the muscle instead of releasing it into the circulation (Turner et al., 1983). In the absence of detailed cross-species information on the various traits associated with sedentariness that contribute to resistance to stress and hypoxia, we merely classified species as to whether they were generally sedentary, as indexed by a benthic distribution, actual reports of their activity levels or based on the above studies of stress and/or hypoxia resistance.

3.2.2.8 Body softness

Individuals and species differ in the softness of their tissues, possibly resulting in a differential risk of internal organ damage due to crushing in the net. We measured the softness of tissues prior to the onset of rigor mortis on the belly and dorsal surface of between 5-40 individual fish of each species using a 2.25 kg gauge durometer (Pacific Transducer Corp.©, California, U.S.A.), with a scale ranging from 0 to 100 units. There was a strong correlation between belly and dorsal tissue softness overall ($r = 0.86$) and within species (average correlation, $\bar{r} = 0.49$), so only the dorsal softness variable was retained for analysis. There was also a significant positive linear relationship between softness and length for seven fish species: Atlantic and Greenland cod, Greenland halibut, gaspereau, mackerel, shorthorn sculpin and lumpfish. In these cases, species-specific linear regressions were used to estimate softness as a function of the length of the individuals in the mortality study. The apparent absence of a relationship for the other species, for which a species-average softness value was used for the analyses (Appendix Table A1), may reflect a failure to sample softness over a broad range of lengths.

3.2.2.9 Phylogeny

There are likely numerous traits that confer resistance to the traumas and stresses imposed by trawl capture, manipulation and exposure to air that could not be elucidated for inclusion in our analyses. It is reasonable to assume that similarity in these traits is likely to be highest amongst the most closely related species. In the absence of actual measurements, we used taxonomic Order as a proxy for species relatedness and included it as a factor in our analyses (see below). This taxonomic level was chosen as it balances having a high number of taxonomic categories and avoids having too many that are represented by a single species. Nonetheless, species were sorted taxonomically from class to species when plotting analysis results, so that possible covariance between TM and phylogeny might be evident.

3.2.3 Analysis

3.2.3.1 The model

The TM data were analyzed using survival analysis (e.g., Cox and Oakes, 1984; Ibrahim et al., 2001), which models the survival probability as a function of time, and which accommodates both uncensored and censored observations. We used a Weibull-type survival function, chosen for its ability to mimic common survival functions encountered in ecology (e.g., Deevey's (1947) Type I, II and III survival functions) and its use in other discard survival studies (Neilson et al., 1989; Campana et al., 2009; Benoît et al., 2012). It is defined as:

$$(3.2) \qquad S(t) = \exp[-(\alpha \cdot t)^{\gamma}]$$

where $S(t)$ is a vector of the survival probability of individual fish to time t, and α and γ are respectively the scale and shape parameters of the underlying Weibull distribution. The effect of covariates on survival are commonly included via α, such that

$$(3.3) \qquad S(t \mid \mathbf{X}) = \exp[-(\exp(\mathbf{X'}\boldsymbol{\beta}) \cdot t)^{\gamma}]$$

where $S(t \mid \mathbf{X})$ is a vector of the survival probability, conditional on the matrix of covariate observations $\mathbf{X}$, and $\boldsymbol{\beta}$ is a vector of parameters for the effect of the covariates. Holding other covariates constant, $100 \cdot (\exp\beta_j - 1)$ gives the percent change in expected survival time for an explanatory variable j. For a quantitative variable, the percent change is relative to a one-unit change in the variable. For binary variables (e.g., presence of a physoclistous gas bladder), the percent difference is relative to the baseline condition.

The survival model was fit using the maximum-likelihood method implemented in the SAS LIFEREG procedure (SAS Institute Inc., Cary, NC, USA), which properly accommodates both right and left-censored data, simultaneously modeling data from both the cross-sectional and longitudinal studies. Suitability of the survival model was assessed using a non-parametric estimate of the survival function based on a modified Kaplan-Meier method that adjusts for covariates, plotted as a function of log-time (probplot option in the LIFEREG procedure) (details in Ch. 4 of Allison, 2010).

The model in eqn. 3.3 assumes that mortality occurs only once the codend leaves the water (i.e., considered t=0). Strictly speaking, this is incorrect in that some proportion of individuals, λ, will have died during the haul and net retrieval. These individuals would form part, but not all, of the left-censored observations. A modified version of eqn. 3.3 was fit to the data to try to account for within-net mortality:

$$(3.4) \qquad S(t \mid \mathbf{X}) = (1 - \lambda)\exp[-(\exp(\mathbf{X'}\boldsymbol{\beta}) \cdot t)^{\gamma}]$$

While this model provided a modest improvement in fit relative to eqn. 3.3 for certain species with a number of left-censored observations (e.g., herring, American plaice, and Atlantic poacher), the model was difficult to fit for others and likely wasn't justified for cross-species analysis given inter-species differences in λ. Consequently, it was not pursued further. Estimated mortality times are therefore slightly biased high for species with a high proportion of left-censored observations (i.e., rapidly dying species).

3.2.3.2 Specific analyses

Six separate classes of analyses were undertaken using the TM data. The first analysis (termed species-specific effect of covariates) aimed to assess the relative roles of temperature, depth and MSRD on within-species TM using eqn. 3.3 and an information theoretic approach based on Aikaike's information criterion (AIC; Burnham and Anderson, 2002). For each species, the seven possible candidate models of the single and joint effects of the three covariates were fit to the data. For a given model k, a delta-AIC value Δ_k was calculated as:

$$(3.5) \quad \Delta_k = \mathrm{AIC}_k - \mathrm{AIC}_{\mathrm{min}}$$

where $\mathrm{AIC}_{\mathrm{min}}$ is the value for the model with the lowest AIC. Models with $\Delta_k \leq 3$ were considered to have equivalent support the model associated with $\mathrm{AIC}_{\mathrm{min}}$. Akaike weights ($w_k$) were also calculated for each model:

$$(3.6) \quad w_k = \exp(-0.5\Delta_k) \Big/ \sum\nolimits_{r=1}^{7} \exp(-0.5\Delta_r)$$

and the relative importance of each of the three covariates (termed evidence weight, ranging from 0-1) was then measured as the sum of these Akaike weights for the models in which a given covariate was present.

The second analysis (termed global effect of covariates) aimed to assess the relative roles of temperature, depth and MSRD on TM across individuals and species using eqn. 3.3. The data for all species were pooled and analyzed jointly. Multi-model comparisons were made as in the first analysis.

The third analysis (termed baseline species survival function estimation) sought to obtain an estimated survival function for each species sample for comparison with the results of subsequent cross-species models. Eqn. 3.2 (i.e., no covariates) was fit independently to the data for each species and the predicted time to 50% mortality (T_{50}) was calculated as the basis for further comparison. There was concern that the assumption of a fixed Weibull shape parameter γ might be too restrictive in subsequent cross-species analyses. To assess suitability of a fixed γ assumption, eqn. 3.3 with temperature, depth and MSRD effects, and a factor for species, was fit to the species aggregated mortality data. The predicted T_{50} for each individual was calculated using the estimated parameter values, and an average was calculated for each species sample. These averages were then compared to the estimates from the baseline species survival functions. Close correspondence between these two sets of estimates was taken as support for the fixed γ assumption.

The fourth analysis (termed global effect of traits) aimed to assess the relative roles of the biological traits on TM in a cross-species analysis using eqn. 3.3 and controlling for the effects of temperature, depth and MSRD. Most traits were treated as factors, except MSRD and softness, which were treated as quantitative variables. Given the number of traits to analyse, a forward stepwise selection approach based on AICc was used to determine the best and most parsimonious combination(s) of traits to explain mortality. An additional variable to a candidate model was only considered important if it resulted in an AICc that was lower by 3. Different models composed of an equal number of variables were considered equally plausible if the difference in their AICc was ≤ 3. Overall, correlation among traits was generally low (Appendix Table A2), lessening concerns about the effects of multicolinearity when interpreting the analysis results.

The fifth analysis (termed global effect of phylogeny) aimed to assess the role of taxonomic Order (treated as a factor), independent of the effects of temperature, depth and MSRD. Orders represented by a single species were excluded from the analysis. The sixth analysis (termed global effect of relevant traits and phylogeny) considered the joint effects of phylogeny and the traits retained in the fourth analysis.

Variants of a couple of the above analyses were run as part of two validation approaches. First, a sort of cross-validation for analyses four and five was undertaken by sequentially removing the data for a given species and predicting it's T_{50} based on parameter estimates obtained using the remaining data and the covariate values for the species in question. The second validation approach was motivated by concerns about the possible effect of unequal sample sizes between species (Appendix Table A1). A random subset of 20 individuals was drawn for each species (note that only 12% of taxa had sample sizes less than this), and the analyses were repeated. Note that this was done for a single random draw to illustrate the possible effect. The subsampling resulted in an overall sample size of 928 observations, from a total of 3,363.

3.3 Results

3.3.1 Species-specific effect of covariates

For most species, there was generally strongest evidence for an effect of MSRD on mortality rate, though on average, moderate evidence for the effects of temperature and depth was also found (Table 3.1). The effect of MSRD was uniformly negative across species. The sign for the effects of depth and temperature was not consistent across species.

Models could not be reliably fit for capelin and barracudina because all of the observations were left-censored (Table 3.1). Estimates of mortality time in subsequent analyses were therefore positively biased.

3.3.2 Global effect of covariates

MSRD, temperature and depth, acting singly or in combination, contributed significantly to lowering AIC (Table 3.2). Consistent with the species-specific results, MSRD contributed most to lowering AIC. The sign of the linear effects of the covariates was consistent across models: negative for MSRD and temperature, positive for depth.

3.3.3 Baseline species survival function

Considerable variation in estimated T_{50} was found across species, with rainbow smelt having the lowest average value at 1.3 min, and Atlantic hagfish having the highest at 169 min (Fig. 3.1, grey symbols). Estimates of T_{50} relate qualitatively to Benoît et al.'s (2012) estimates of trawl-fishery discard mortality rates for four taxa: Atlantic cod, American plaice, winter flounder and skates (which were analyzed jointly at the Order level in their paper) (Fig. 3.1). This relationship is also consistent for large sculpins (longhorn and shorthorn sculpin, and sea raven), for which a survival rate at least as high as that of skates is predicted based on the results in Table 7 of Benoît et al. (2010; Table 2.7 this thesis). (Note that a survival rate for these species could not be reliably estimated by Benoît et al. (2012) because too few dead individuals were observed). However, it is not clear whether this relationship also holds for witch flounder, which had 100% mortality in the experiments of Benoît et al. (2012), a result that may be accurate or may have reflected an experimental effect related to holding such a deep-water species in surface tanks.

A model based on eqn. 3.3 and including the effects of temperature, MSRD and depth, and a factor for species fit the TM data very well, resulting in similar predictions to the single species models (Fig. 3.1, open symbols; Table 3.2). This confirmed the validity of using a constant Weibull shape parameter in the cross-species analyses.

3.3.4 Global effect of the biological traits

Relative to a model including only the effects of temperature, MSRD and depth (AIC=7570), each trait individually resulted in an improved model for TM (Table 3.2). While the improvement was relatively modest for the mucus and body softness traits, it was large for the other traits, especially sedentariness. The sign of the effect was consistent with a priori predictions for all traits except softness, for which a positive sign was observed when it was modeled singly and a negative sign was observed when it was analyzed jointly with certain other traits. The combined effect of possessing a physoclistous or physostomous gas bladder, and deciduous scales, and of sendentariness, hereafter termed the relevant traits, provided the best fitting and most parsimonious model to explain TM. A delta-AIC value of over 22 was estimated for the next best parsimonious model. The signs of the effects of these variables remained consistent with the signs in single variable models (Table 3.2).

Possessing a physoclistous gas bladder resulted in an estimated 42.3% decrease in TM, compared to fish lacking a bladder, all else being equal (Table 3.3). The survival cost of possessing a physostomous gas bladder was considerably less than this (27.4%), consistent with our predictions. Estimated survival advantage was greatest for sedentary species with an 82.2% higher TM than ‘active’ species. The survival cost of possessing deciduous scales was comparable to that of possessing a physostomous gas bladder.

Though this model clearly led to improvement in fit based on AIC, its ability to predict T_{50} varied among species (Fig. 3.2). The model predicted reasonably well the low T_{50} of Clupeiforms, Osmeriforms and certain Perciforms and Scorpaeniforms, but generally overestimated the T_{50} values of Pleuronectiforms and greatly underestimated the values for the longest surviving species (winter skate, shorthorn and longhorn sculpin, sea raven and hagfish). Overall, the correlation between single species mean estimates of T_{50} and estimates from this model was 0.60. The correlation between predictions for individual fish from both approaches was 0.69.

Very consistent results were obtained when species T_{50} values were estimated using all available data (Fig. 3.2, open symbols) and when cross validation was employed (Fig. 3.2, crosses), demonstrating a lack of sensitivity of results to the data of particular species. Likewise, when data were subsampled to equalize sample sizes among species, very similar parameter estimates were obtained (Table 3.3, columns Est2 and SE2).

3.3.5 Global effect of phylogeny

A model including the effects of temperature, MSRD, depth and a factor for taxonomic order resulted in an AIC value (5840) that was considerably lower than that obtained from the model based on the relevant traits (Table 3.2). Predicted T_{50} values from this model corresponded well to those from single species models (section 3.3) for Clupeiforms, Gadiforms, Osmeriforms, Rajiforms and most Pleuronectiforms (Fig. 3.3). Among Perciforms, the model fails substantially to predict the T_{50} for mackerel and soft pout. Among Scorpeaniforms, the model greatly underestimated the values for the longest surviving species and overestimated the values for some of the shortest surviving species (moustache sculpin, variegated snailfish and redfish). The model clearly fails to include one or more factors that affect mortality rate following capture and air exposure. Overall the correlation between single species estimates of T_{50} and estimates from this model was 0.69. The correlation between predictions for individual fish from both approaches was 0.77.

The effect size of individual taxonomic Orders was assessed relative to that for the Scorpaeniformes. The Clupeiformes, Gadiformes and Osmeriformes had an average estimated relative survival rate that was at least 70% lower than Scorpaeniformes, while only the skates had a higher rate (Table 3.4). Both the cross-validation (Fig. 3.3, crosses) and sub-sampling (Table 3.4, columns Est2 and SE2) analyses revealed that the model results were not overly sensitive to data from particular species.

3.3.6 Global effect of relevant traits and phylogeny

Inclusion of the relevant traits in the model with taxonomic Order resulted in yet another improvement in model fit, by 330 AIC units (Table 3.2). Overall, the correlation between single species mean estimates of T_{50} and estimates from this model with 15 degrees of freedom was 0.88 (r=0.81 for the correlation for individual fish), suggesting a reasonable ability to explain and predict interspecies differences (Fig. 3.4). The model nonetheless did not predict the relatively high survival of cunner or certain Scorpaeniforms, for example (Fig. 3.5). The estimated parameters for this model (columns Est3 and SE3 in Table 3.4) are very comparable to those from the previous models of the effect of phylogeny (columns Est and SE in Table 3.4) and the effect of relevant traits (Table 3.3). The estimates of the effect for many Orders are attenuated relative to a model excluding the traits. This is not surprising given the confounding between phylogeny and biological traits.

3.4 Discussion

This study makes at least three new general contributions to our understanding of discard mortality. Each is discussed briefly, followed by a discussion of the key uncertainties and opportunities resulting from the study.

First, the approach used here appears to produce estimates of a reliable discard mortality rate proxy that can be obtained rapidly and inexpensively during existing surveys, and which relates reasonably well to more formal and difficult to obtain estimates of discard mortality from fisheries (e.g., Benoît et al., 2012). This result makes sense in that the present study effectively considers the effect of capture and air exposure on mortality, with exposure to air typically being one of the largest contributors to discard mortality (e.g., Neilson et al., 1989; Richards et al., 1994; Parker et al., 2003; Benoît et al., 2010). Our study was undertaken for a moderate number of taxa, under very controlled conditions (e.g., with little exposure to the drying effect of the sun and to rough handling) and with short haul durations (30 min) compared to commercial fisheries (several hrs). There is therefore a need to determine the extent to which TM values reflect survival differences for a broader suite of species and fishing conditions. However, in the interim it at least appears reasonable that estimates of T_{50} could be used as an indicator of discard mortality potential in a risk analysis of bycatch sustainability or in the formulation of more effective mandatory live release policies.

The second contribution of this study is an enhanced and more unified understanding of the relative effects of body size (treated here as the MSRD variable), temperature and depth on discard mortality. The effect of body size was prevalent and prominent both intra- and inter specifically, confirming the general result of previous studies (reviews in Davis, 2002; Broadhust et al., 2006). Smaller fish, with a higher mass-specific respiration cost and susceptibility to crushing in the net, have a higher rate of discard mortality. While the effect of temperature varied among species, perhaps in part due to the limited ranges available (Appendix Table A1), the global effect of temperature was as expected. The effect of depth was also variable among species, perhaps for the same reason as temperature. For most fish from the sGSL, the effect of depth would be considerably smaller than that of temperature change. For example, given the parameters in Table 3.3 and a typical depth of 100 m and temperature of 1°C in the sGSL ecosystem, the expected contributions of depth and temperature to a difference in TM between a fish captured at depth and another captured at the surface are 20% and 66% respectively.

The third contribution of this study is a greater understanding of the broader biological factors (size, traits and phylogeny) that determine an individual's susceptibility to mortality as a result of capture and discarding. While there were no real surprises concerning the role of a small number of relevant traits, it is nonetheless interesting to see the extent to which these traits can explain variability in mortality rate among individual fish. The species covered by this study are broadly representative of those found in other boreal and temperate NW Atlantic ecosystems (Scott and Scott, 1988; Collette and Klein-MacPhee, 2002). This suggests that the results of this study could be extended to other ecosystems for validation and practical application.

Of the traits considered, sedentariness most affected TM. Treated here as a binomial trait, it encompasses a number of physical and physiological adaptations that differ among species and that likely result in a spectrum of stress and hypoxia resistance. At one extreme, there are hagfishes which are well known for having the lowest routine metabolic rate among fishes (Brauner and Berenbrink 2007; Forster 1990) as an adaptation to inhabiting hypoxic sediments or the bodies of dead animals on which they feed (Martini 1998). Other resistant fish include sea raven and shorthorn sculpins, which are coastal ambush predators, adapted on one had to an energy conserving foraging strategy and, on the other, to potentially important rapid short-term shifts in water properties (e.g., Mandic et al. 2009). Along with skates, these species clearly stood out with considerably greater TM relative to other sedentary fish. At the other end of the spectrum are fast swimming species such as mackerel which appear to be adapted to avoiding rather than tolerating hypoxic waters (e.g., Silkin and Silkina, 2004, and references therein), likely making them more vulnerable to forced hypoxia when exposed to air. We expect that had we been able to reliably characterize this spectrum of resistance for the suite of species considered here, we would have been able to better explain variation in TM. For example, a comparative analysis of the physiological traits that determine a fish's stress response and lethal oxygen threshold (e.g., Plante et al., 1998) could prove useful, though this would be challenging for such a wide diversity of species, given the need for measurements in both unstressed (baseline) and stressed conditions (e.g., Plante et al. 2003).

Our analyses also raise a number of additional key challenges. There is clearly a need to elucidate which traits implicit in phylogenetic similarities are responsible for explaining TM variation. There is also a need to identify the traits other than those related to sendentariness that might explain the observed discrepancies. Traits requiring further consideration include the form and function of the respiratory organs (e.g., gill morphology, relative lamellar area, spiracles in skates), susceptibility to the formation of emboli, and better estimates of body robustness to crushing. We hope that the observed patterns and discrepancies will stimulate experts in fish physiology and comparative anatomy to propose possible explanations.

A second challenge is in determining the generality of the estimated effect of taxonomic Order in determining mortality rate. Though the species considered here are broadly representative of the most common members of the Orders in this study, inclusion of data for the same and additional species from other ecosystems would help confirm the generality of the estimated effect sizes.

Most studies of discard mortality, including this one, cannot reasonably incorporate all of the factors that eventually contribute to mortality potential in fish discarded in commercial fisheries. Key factors that have been difficult to study include the additive effects of enhanced predation susceptibility resulting from reflex impairment (e.g., Ryer 2004) and of release of discards into different environmental conditions compared to where they were caught. A comparative approach such as used here holds some promise in incorporating such effects in assessments and decision making. Species' relative susceptibilities to behavioural impairment and predation, and their environmental tolerances, could inform an analysis of their vulnerability.

In summary, while it is desirable to have formal estimates of discard mortality for evaluating the sustainability of bycatch and discards, this will often not be feasible. Simple to obtain proxies of discard mortality, such as those measured during routine fishery-independent monitoring (this paper) or during commercial fisheries (e.g., Richards et al. 1994; Benoît et al. 2010) can help fill this void. These proxies can provide information on the relative magnitude of discard mortality for sustainability risk assessments, as well as a large enough sample size to explore the possible effect of technical, environmental and biological factors that affect mortality. This in turn will contribute to a better understanding of the ecosystem effects of fishing and an enhanced ability to manage discards sustainably.

Table 3.1. Results of individual species multi-model analyses of TM as a function of the covariates mass-specific respiration demand (M), depth (D) and temperature (T), and their various combinations (e.g., MD: model including mass-specific respiration demand and depth). Shown are the evidence weights for each covariate for species for which the best models (those with a ΔAICc≤3) included one or more of the covariates. The sign of the effect of covariates that were both contained in the best models and displayed a consistent sign across models is also shown. Species for which an intercept-only model was the best are not included in the table below: Alewife, Alligatorfish, Arctic Staghorn Sculpin, Cunner, Daubed Shanny, Longfin Hake, Longhorn Sculpin, Marlin-Spike Grenadier, Shorthorn Sculpin, Snakeblenny, Threespine Stickleback, Vahl's Eelpout, Witch Flounder and Windowpane. A model with covariates could not be fit for Capelin and White Barracudina because all observed fish were left censored.

	Evidence weights				Effect sign		
Name	M	D	T	Best model(s)	M	D	T
American Plaice	1	0.81	0.46	MD,MDT	-	+	+
Arctic Alligatorfish	0.99	0.21	0.18	M	-		
Atl. Spiny Lumpsucker	0.67	0.61	0.8	T,MT,MDT	-	+	+
Atlantic Cod	1	1	0.96	MDT	-	+	-
Atlantic Hagfish	0.26	1	1	DT		-	-
Atlantic Halibut	1	0.85	0.46	MD,MDT	-	+	+
Atlantic Herring	1	0.97	0.34	MD,MDT	-	+	+
Atlantic Mackerel	0.98	0.25	0.34	M,MT	-		+
Atlantic Poacher	0.28	0.99	0.62	D,DT		+	-
Atlantic Soft Pout	0.99	0.98	0.17	MD	-	+	
Fourbeard Rockling	0.17	1	0.14	D		+	
Fourline Snakeblenny	0.98	0.56	0.37	M,MD,MT,MDT	-	-	-
Greenland Cod	0.88	0.66	1	MT,MDT	-	+	-
Greenland Halibut	1	0.35	0.33	M,MD,MT	-	+	-
Hookear Sculpin	0.25	0.36	0.97	T,MT,DT	-	-	-
Lumpfish	1	0.74	0.31	MD,MDT	-	+	+
Moustache Sculpin	1	0.37	0.32	M,MD,MT	-	+	+
Newfoundland Eelpout	1	0.64	0.38	M,MD,MDT	-	+	-
Northern Sand Lance	0.96	0.1	0.11	M	-		
Ocean Pout	0.68	0.26	0.25	M	-		

	Evidence weights				Effect sign		
Name	M	D	T	Best model(s)	M	D	T
Rainbow Smelt	0.35	0.47	1	T,MT,DT	-	-	
Redfish unspecified	1	0.29	0.78	MT	-		-
Sea Raven	1	0.23	0.23	M	-		
Smooth Skate	1	0.26	0.55	M,MT	-		-
Spatulate Sculpin	0.22	0.98	0.17	D		+	
Stout Eelblenny	1	0.27	0.96	MT	-		+
Thorny Skate	1	0.55	0.48	M,MD,MDT	-	+	+
Varigated Snailfish	1	0.3	0.35	M,MT	-		+
White Hake	0.99	0.4	0.6	M,MD,MT,MDT	-	+	+
Winter Flounder	1	1	1	MDT	-	-	+
Winter Skate	1	0.96	0.96	MDT	-	-	+
Yellowtail Flounder	0.39	0.95	0.56	D,MD,DT,MDT	-	-	

Table 3.2. Comparison of models fit to the combined species TM data based on AIC: intercept only, effect of global covariate affecting individuals and species, effect of individual species traits and results for the best model incorporating species traits and effect of taxonomy at the species and order levels. The signs of the linear relationships for each global and trait covariate are also shown. Note that these signs remained consistent across different model formulations, except for the effect of softness in the analysis of traits.

Model	*AIC*	*Sign(s)*
Intercept only	8102	
Global covariates		
Mass-specific respiration demand (M)	7686	-
Depth (D)	8028	+
Temperature (T)	8029	-
MD	7611	- +
MT	7642	- -
DT	7921	+ -
MDT	7570	- + -
Effect of species traits (with MDT)		
1. mucus	7541	+
2. physoclistous bladder	7015	-
3. physostomous bladder	7195	-
4. sedentariness	6514	+
5. softness	7538	+/-
6. deciduous scales	7054	-
Relevant traits (2,3,4,6)	6185	- - + -
Effect of taxonomy		
species	4808	
species (with MDT)	4304	
Orders	6618	
Orders (with MDT)	5840	
Orders (with MDT and relevant traits)	5510	

Table 3.3. Estimated parameter values, standard errors (SE), effect size and P-values (based on Wald's χ^2 statistic) for the best model including species traits. For the quantitative variables (MSRD, temperature, depth), the effect size is the percent change in expected mean survival time for each one-unit increase in the variable. For the binary variables, the effect size is the percentage difference in expected mean survival time for species possessing the trait relative to species that do not. Also shown are parameter estimates (Est2) and standard errors (SE2) for the same model but limiting each species to ≤20 observations.

Parameter	*Est.*	*SE*	*Effect*	*P*	*Est2*	*SE2*
Intercept	4.11	0.06		<0.0001	3.98	0.10
MSRD	-0.31	0.01	-26.6	<0.0001	-0.26	0.02
depth	0.0020	0.0002	0.2	<0.0001	0.0020	0.0003
temperature	-0.03	0.01	-3.0	<0.0001	-0.03	0.01
physoclistous	-0.55	0.04	-42.3	<0.0001	-0.58	0.06
physostomous	-0.32	0.05	-27.4	<0.0001	-0.33	0.09
sedentariness	0.60	0.03	82.2	<0.0001	0.80	0.06
deciduous scales	-0.40	0.06	-33.0	<0.0001	-0.41	0.11
γ	1.51	0.03			1.46	0.05

Table 3.4. Estimated parameter values, standard errors (SE), effect sizes and P-values for the model of the effect of taxonomic Order. Parameter estimates, SE, effect size (percent difference in mean survival time) and P-values for the effects of Orders, are relative to the effect for the Order Scorpaeniformes. Also shown are parameter estimates and standard errors for the same model but limiting each species to ≤20 observations (Est2 and SE2) and for a model fit to all available data which also included the effect of the traits from the best fitting model in Table 3.2 (Est3 and SE3).

Parameter	*Est.*	*SE*	*Effect*	*P*	*Est2*	*SE2*	*Est3*	*SE3*
Intercept	5.04	0.05		<0.001	4.91	0.10	4.60	0.07
MSRD	-0.36	0.01	-30.4	<0.001	-0.37	0.03	-0.36	0.01
depth	$3.0e^{-4}$	$2.0e^{-4}$	0.03	0.065	$1.1e^{-3}$	$3.0e^{-4}$	$1.5e^{-3}$	$2.0e^{-4}$
temperature	-0.03	0.003	-3.3	<0.001	-0.04	0.005	-0.03	0.003
Order								
Clupeiformes	-1.31	0.05	-73.1	<0.001	-1.14	0.12	-0.56	0.09
Gadiformes	-1.22	0.05	-70.4	<0.001	-1.36	0.10	-0.24	0.06
Gasterosteiformes	0.01	0.15	0.67	0.965	0.13	0.18	0.40	0.15
Osmeriformes	-1.81	0.07	-83.6	<0.001	-1.96	0.15	-0.71	0.08
Perciformes	-0.34	0.04	-28.6	<0.001	-0.31	0.07	-0.27	0.05
Pleuronectiformes	-0.69	0.04	-50.0	<0.001	-0.62	0.09	-0.84	0.04
Rajiformes	0.35	0.05	41.5	<0.001	0.39	0.15	0.03	0.05
γ	1.62	0.03			1.46	0.05	1.72	0.03
physoclistous							-0.65	0.05
physostomous							-0.36	0.06
sedentary							0.62	0.04
deciduous[1]							-	-

[1] The effect of possessing deciduous scales could not be included in the model because this trait is completely confounded with the effect of taxonomic Order.

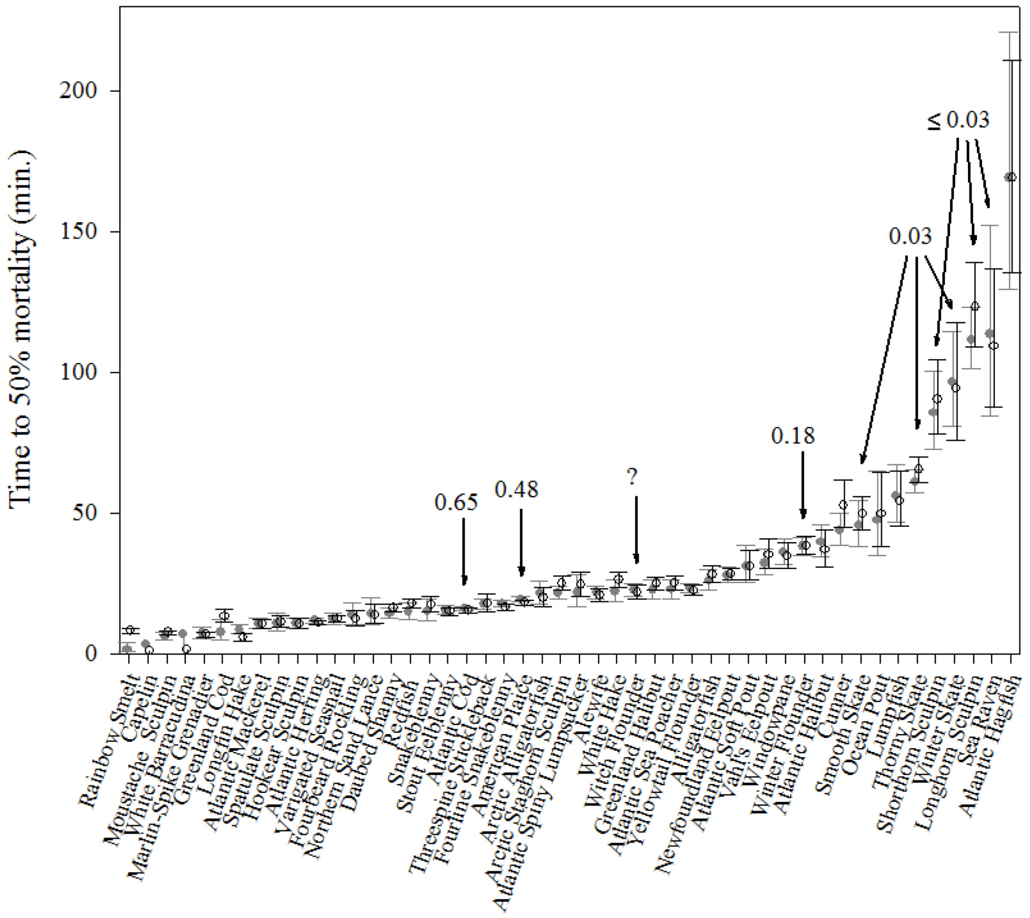

Figure 3.1. Estimated time to 50% mortality (with 95% confidence interval) as a result of capture and air exposure for 48 southern Gulf of St. Lawrence marine fish species captured in a bottom-trawl survey. Estimates are based on individual species models excluding covariates (grey symbols) and on a single model incorporating the effects of respiration, depth of capture, temperature and a factor for species (open symbols). The numbers included in the plot are published discard mortality rates for certain species (see text for details).

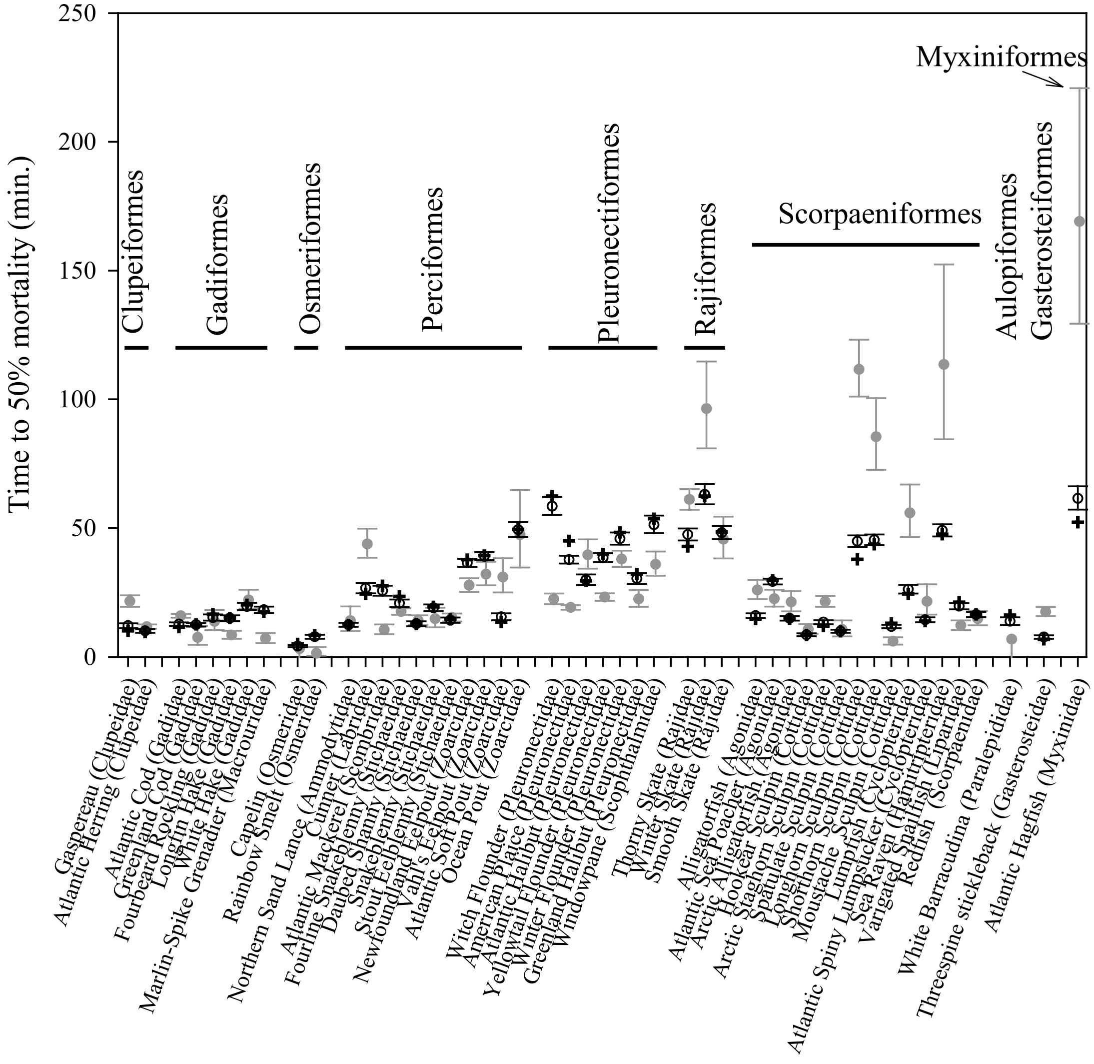

Figure 3.2. Estimated time to 50% mortality (with 95% confidence interval) as a result of capture and air exposure for 48 southern Gulf of St. Lawrence marine fish species captured in a bottom-trawl survey. Estimates are based on individual species models excluding covariates (grey symbols) and on a single model incorporating the effects of respiration, depth of capture, temperature and relevant species traits, using all available data (open symbols) and as part of the cross-validation exercise (crosses). Species are sorted alphabetically along the abscissa based on their taxonomy: Order (indicated in the plot), family (indicated in the abscissa labels), genus and species.

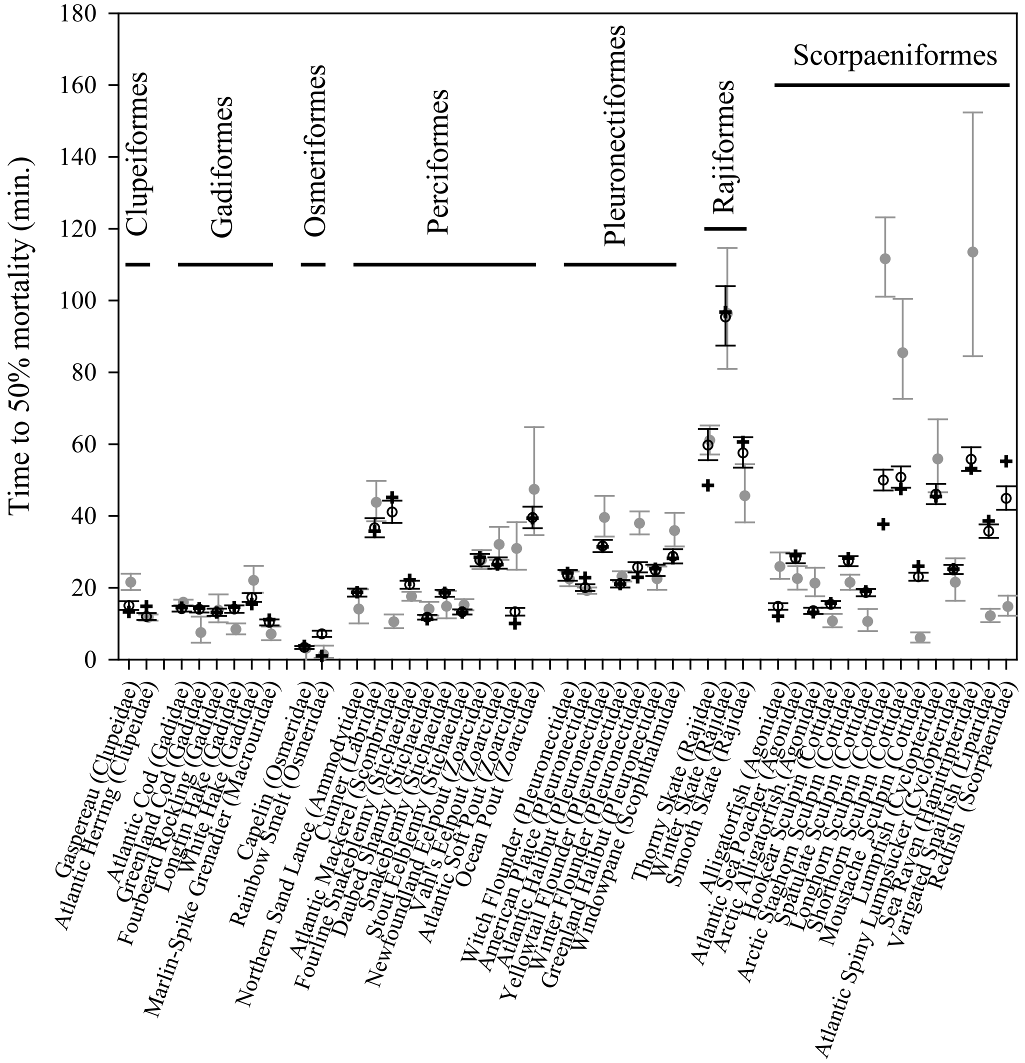

Figure 3.3. Estimated time to 50% mortality (with 95% confidence interval) as a result of capture and air exposure for 45 southern Gulf of St. Lawrence marine fish species captured in a bottom-trawl survey. Estimates are based on individual species models excluding covariates (grey symbols) and on a single model incorporating the effects of respiration, depth of capture, temperature and a factor for taxonomic Order, using all available data (open symbols) and as part of a cross-validation exercise (crosses). Species are sorted along the abscissa in the same manner as Fig. 3.2.

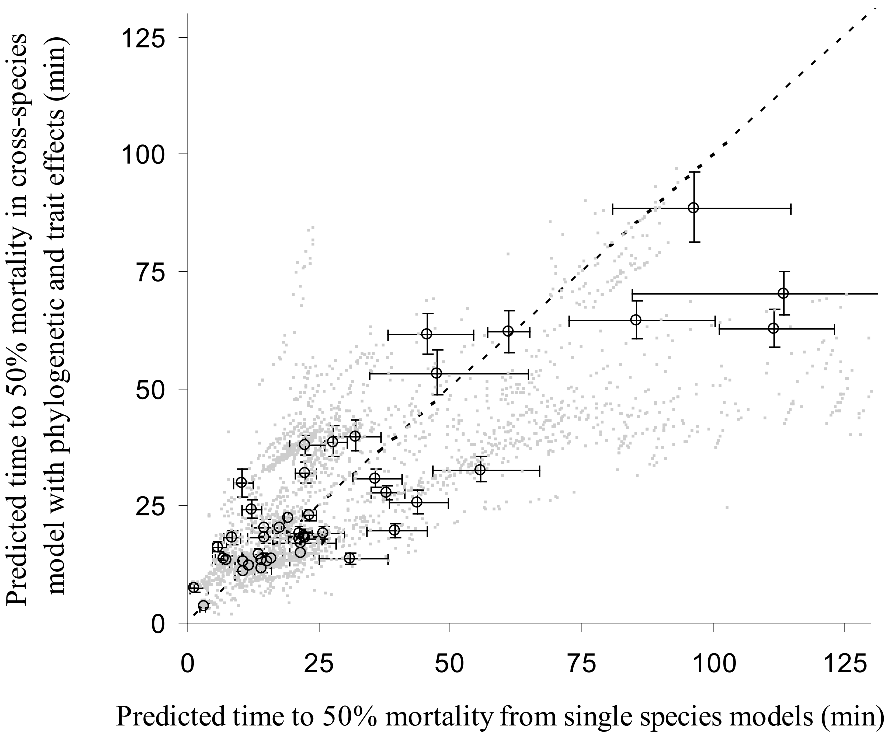

Figure 3.4. Predicted time to 50% mortality from single species models versus predictions for a model including the effects of phylogeny (indexed by taxonomic Order), relevant species traits and three covariates (temperature, depth and respiration). Open circles are individual species mean estimates (with 95% confidence intervals), while grey dots represent estimates for individual fish.

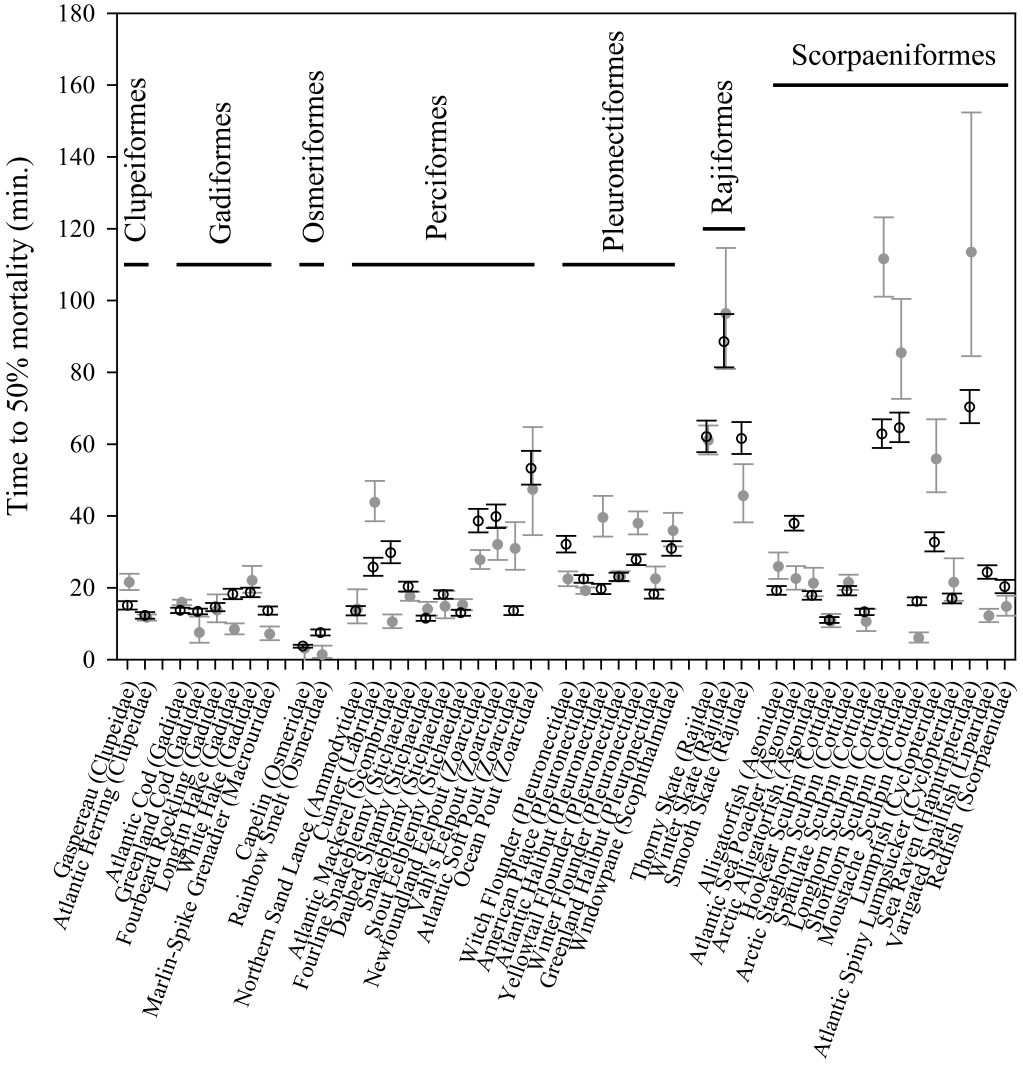

Figure 3.5. Estimated time to 50% mortality (with 95% confidence interval) as a result of capture and air exposure for 45 southern Gulf of St. Lawrence marine fish species captured in a bottom-trawl survey. Estimates are based on individual species models excluding covariates (grey symbols) and on a single model incorporating the effects of respiration, depth of capture, temperature, taxonomic Order and relevant species traits, using all available data (open symbols). Species are sorted along the abscissa in the same manner as Fig. 3.2.

Chapter 4. An Empirical Model of Seasonal Depth-Dependent Fish Assemblage Structure to Predict the Species Composition of Mixed Catches.

4.0 Abstract

Reliable catch statistics are essential for assessing fishing impacts on individual stocks. However, fisheries that capture a mixture of stocks or species for which catch statistics are not disaggregated pose a challenge. Nonetheless, catch composition can be inferred given information on fishing date and location, and a prevalent role of season and habitat in structuring fish assemblage composition. Here, a harmonic regression model for multinomial data, intended to predict the species composition of catches based on season and depth, is developed using bottom-trawl survey data. Model development was motivated by the need to quantify catches of individual skate (Rajidae) species in fisheries for which landing and discard data are only reliable at the Family level. The model was validated by applying it to flatfishes (Pleuronectidae), whose catches are generally reliably and consistently disaggregated by species. The predicted species composition of flatfish matched the composition observed in fishery catches well. The present approach should be applicable to other well-surveyed ecosystems where assemblage composition is structured by one or more key environmental variables of known spatial distribution.

4.1 Introduction

Fisheries commonly produce catches that are a mixture of species or distinct stocks of a single species. In many instances, distinguishing the catches (retained and/or discarded) of morphologically similar species or stocks has been too expensive and impractical, or those monitoring the catches have lacked the expertise or direction to do so consistently and reliably. This severely limits our ability to quantify fishing mortality at the population or species level, in turn compromising efforts towards establishing sustainable harvests on commercially important species and reductions in the adverse impacts of fisheries on incidentally-captured species (e.g., Hilborn 1985).

The issue of mixed catches has received considerable attention for commercially-important stocks, and techniques have been developed for disaggregating catches based on characteristics (meristic, morphometric and genetic) obtained from samples or based on tagging (e.g., Millar 1990; Michielsens et al. 2006; Shelton et al. 2012). Addressing mixed catches in the absence of such information, as occurs for stocks with less or no commercial importance (i.e., principally discarded species), remains a difficult problem. Nonetheless, catch composition can be inferred given information on fishing date and location, and a prevalent role of season and habitat in structuring fish assemblage composition.

This paper presents a harmonic regression model for multinomial data that is fit to data from multi-species bottom-trawl surveys and that predicts the relative species composition of fish assemblages for a given date and location (based on habitat). Given that bottom depth accounts for much of the spatial variation in the species composition of demersal fish communities (e.g,. Bianchi 1992; Francis et al. 2002; Tolimieri and Levin 2006), it was used as the predictor habitat variable. Furthermore, depth is often the only habitat variable recorded during commercial fishing. Consequently, depth and date are often the only covariates available to estimate the species composition of a particular catch, unless detailed maps of other environmental variables (e.g., sediment type and temperature) are available for spatial matching post hoc. Furthermore, predicting composition based on geographic location using latitude and longitude as covariates is unlikely to be feasible in most instances as this would require spatially and seasonally representative data to fit the model.

Model development was motivated by the need to quantify catches of individual skate (family Rajidae) species for which landing and discard data are only reliable at the Family level in commercial fisheries of the southern Gulf of St. Lawrence (sGSL), Canada (Fig. 4.1). Of the three skate species of the sGSL, winter skate (*Leucoraja ocellata*) has been designated as endangered (COSEWIC 2005), and both thorny skate (*Amblyraja radiata*) and smooth skate (*Malacoraja senta*) have experienced large declines in adult abundance (Swain et al. 2012). Understanding the impact of fisheries is a key element in uncovering the causes of population declines and in recovery planning for these species (e.g., Swain et al. 2009). The model was also applied to sGSL flatfishes (Pleuronectidae) to validate the approach and demonstrate its applicability to other assemblages. Validation, by comparing predicted and observed species composition in fishery catches, was possible because flatfish catches are generally reliably and consistently disaggregated to species by fisheries observers in the sGSL. Robustness of the approach to important long-term interannual changes in abundance and distribution of both sGSL skates and flatfishes was also examined.

4.2 Methods

4.2.1 Study area

The sGSL consists of a large shallow shelf area with depths mostly <100 m, the Magdalen Shallows, bordered by a 450-m trench, the Laurentian Channel (Fig. 4.1). A pronounced seasonal cycle in the oceanographic conditions of the sGSL results in important seasonal movements of resident fish species (Clay 1991). In summer and early autumn, the ecosystem is generally composed of three water layers: a warm relatively fresh surface layer, a cold intermediate layer that extends from about 50 to 150 m with temperatures ranging from <0°C–2°C, and a warmer (4°C–6°C) saltier layer covering areas deeper than 200 m (Koutitonsky and Bugden 1991). In winter, the sGSL is typically ice covered, with water temperatures near the freezing point from the surface to the bottom, except where the warm deep-water layer covers the bottom in the Laurentian channel.

4.2.2 Background – Trends in abundance and distribution

A standardized bottom-trawl survey conducted each September since 1971 (henceforth, the September survey) is the main source of information on the status of marine fish populations in the sGSL (Hurlbut and Clay 1990; Benoît et al. 2009). Results from that survey indicate that the abundance and summer distribution of most sGSL skate and flatfish species have changed dramatically since 1971 (Fig. 4.2). These trends and possible causes are discussed in more detail elsewhere (e.g., Swain et al. 2005; Swain and Benoît 2006; Benoît and Swain 2008), and briefly summarized here for context.

Total abundance of thorny skate has declined by around 60% since 1971 in the sGSL (Fig. 4.2b), with mature individuals declining by 95% (Swain et al. 2012). The summer distribution of this formerly broadly-distributed species contracted during the 1990s and 2000s, and is now restricted to deeper waters along the edge of the Laurentian channel and to the west of Cape Breton Island (Fig. 4.2a) (Swain and Benoît 2006). Winter skate abundance has declined by over 98% (Fig. 4.2b), largely due to declines in adult abundance (Swain et al. 2009). Their summer distribution has contracted since 1990, and is now restricted largely to an area in the western portion of the Northumberland Strait (Fig. 4.2a) (Swain et al. 2006). In contrast, the distribution of smooth skate has changed little and total abundance has varied without trend (Fig. 4.2), though abundance of adults has declined by over 65% since 1971 (Swain et al. 2012). The declines in abundance of all three species appear to have largely resulted from elevated rates of adult mortality (Swain et al. 2009; Swain et al. 2012). Fishing appears to have been an important component of this mortality until the early 1990s, though natural mortality, possibly due to predation by grey seals (*Halichoerus grypus*), appears to have been the most important component since then (Benoît and Swain 2008; Swain et al. 2009; Benoît et al. 2011a). The causes of the distribution shifts have yet to be established, though they likely include density-dependent changes (e.g., Swain and Benoît 2006).

There are five principal flatfish (family Pleuronectidae) species that are commonly captured in the September survey and in sGSL fisheries. American plaice (*Hippoglossoides platessoides*), the most abundant and broadly distributed large demersal fish in the sGSL, has declined by over 75% since 1971 (Fig. 4.2b), initially as a result of fishing mortality, but more recently due to elevated adult natural mortality (Morin et al. 2008; DFO 2011b). Since 1990, densities have declined most sharply in the southwestern Gulf for unknown reasons (Fig. 4.2a). Winter flounder (*Pseudopleuronectes americanus*), a coastal species during summer, has declined in abundance by around 20% (Fig. 4.2b), also as a result of high adult natural mortality (DFO 2012a), though its distribution and that of another coastal species, yellowtail flounder (*Limanda ferruginea*), has changed little (Fig. 4.2a) (Benoît et al. 2003). Since 1980, total abundance of the deeper water witch flounder (*Glyptocephalus cynoglossus*) has increased in the sGSL, largely due to increases in small individuals, and their distribution has contracted and shifted eastward, for unknown reasons (Swain and Morin 2006). Finally, Greenland halibut (*Reinhardtius hippoglossoides*), also a deeper water species, has increased several-fold in abundance in the sGSL since 1970 (Fig. 4.2b), and its distribution has progressively spread from the northwest corner of the survey area (Fig. 4.2a).

4.2.3 Survey data

The basic data for the analyses come from a number of different fishery-independent surveys conducted in the sGSL since the mid-1980s (Appendix B, Table B1). The surveys were all based on either a random or stratified-random sampling design and each employed standardized fishing procedures, though those procedures differed between certain surveys (Appendix B, Table B1). Only two of the surveys provided synoptic coverage of the entire area, the annual September survey, and the Sentinel survey conducted each August since 2003 (Figs. 4.2 and 4.3). Note that only the September survey data collected since 1985 were used to be consistent with the period for which data from other surveys were available. Other surveys covered only portions of the sGSL, often for a limited number of years (Appendix B, Table B1; Fig. 4.3). There has been sampling in all months other than February and March, when the sGSL is typically ice-covered.

During each survey tow, catch was sorted to species and the number captured was recorded (other catch characteristics such length frequencies were not recorded in all surveys and are not used here). Catch sampling was undertaken by trained scientific staff from the department of Fisheries and Oceans Canada (DFO) during all surveys except the Sentinel survey. Species identification by DFO staff is considered accurate. Sampling during the Sentinel survey was undertaken by fishery observers though the only data retained for the present analyses were those collected by one observer who has participated in numerous DFO surveys and for which the accuracy of taxonomic identification has been validated.

4.2.4 Model descriptions

Two generalized linear models based on baseline-category logits (Agresti 2002, p. 267-274) were fit to the survey data in separate analyses for each taxonomic Family, skates and flatfish. These are models of the probability that a fish is of a given species *j* in a taxonomic family under study, given that the fish is a member of the Family. The application of the models hinges on the ability of fisheries observers to correctly separate members of the various taxonomic Families that are captured; an assumption that has been verified for sGSL observers (H. Benoît, unpublished observations).

The first model was used to characterize possible inter-annual changes in summer depth-dependent species composition based on observations from the September survey, the only source of information on inter-annual change. Let $\pi_j(d) = P(Y = j \mid d)$ be the response probability, i.e., the probability that an observed fish Y is of species j, given that it was caught at depth d, in meters. Now define the linear model:

$$(4.1) \qquad \log\frac{\pi_j(d)}{\pi_J(d)} = \beta_{0,j} + \beta_{1,j}\cdot d + \beta_{2,j}\cdot d^2, \qquad j=1,\ldots,J\text{-}1$$

where J is the number of species in the taxonomic family (i.e., J=3 for skates and J=5 for flatfish) and $\beta_{0,j}$, $\beta_{1,j}$, and $\beta_{2,j}$ are parameters to be estimated. Note that $\sum_{j=1}^{J}\pi_j(d) = 1$. The left-hand part of eqn. 4.1 is the logit for the response of species *j* relative to a chosen baseline species *J*. The choice of baseline species is arbitrary, as the *J*-1 equations defined by eqn. 4.1 determine the parameters required to define the logit of any pair of the *J* species (Agresti 2002, p. 268). A quadratic effect of depth was included in eqn. 4.1 based on preliminary analyses that suggested that the resulting added flexibility provided a better fit to data. A comparison of fits of different subsets of eqn. 4.1 is nonetheless presented in the Results. The model in eqn. 4.1 was fit to the September survey data in semi-decadal blocks of years to look for long-term changes: 1985-1989, 1990-1994, 1995-1999, 2000-2004, and 2005-2010. Years were grouped in this manner to increase sample size and the precision of predictions, while still providing sufficient resolution to reflect long term change in summer distribution.

The second model was used to characterize seasonal changes in the relative bathymetric distribution of the species in the sGSL. The model included both time-invariant and time-varying components of depth distribution. Seasonal movements of sGSL fish are at least partly related directly or indirectly to changes in ocean temperatures (Clay 1991). Seasonal changes in surface and bottom waters of the sGSL are well modeled empirically using a harmonic analysis that includes annual, semi-annual and tri-annual frequencies (e.g., Ouellet et al. 2003). The seasonal distribution of fish was therefore modelled likewise:

$$\text{(4.2)} \quad \log \frac{\pi_j(d,t)}{\pi_J(d,t)} = \beta_{0,j} + \beta_{1,j} \cdot d + \beta_{2,j} \cdot d^2 + d \cdot \sum_{p=1}^{3} \alpha_{p,j} \cdot \sin(p\omega t - \varphi_{p,j}),$$

j=1,..., J-1

where $\pi_j(d,t)$ is the response probability as a function of depth and day of the year, t, $\omega = 2\pi/365$ is the fundamental annual frequency, p defines the cycle frequency (annual, p=1; semi-annual, p=2; tri-annual, p=3) and $\beta_{0,j}$, $\beta_{1,j}$, $\beta_{2,j}$, $\alpha_{p,j}$ (signal amplitude) and $\varphi_{p,j}$ (signal phase) are parameters to be estimated. The model was fit to the data from all of the surveys in Table B1 (Appendix B). The seasonal effect was modeled as an interaction with depth to reflect the intention of modeling seasonal changes in relative depth distribution. It is generally ill-advised in linear modelling to omit a ‘main’ effect for a predictor that also occurs in an interaction term because it can lead to incorrect significance tests for the interaction and biased parameter estimates (e.g., Nelder 1977). Eqn.4. 2 was used nonetheless because the interest was in overall model predictions, rather than the interpretation of parameters and because a model with both main and interaction effects of season was judged less reliable (see Appendix B supplemental text and Figs. B1 and B2).

The baseline-category logits harmonic regression (BCLHR) model described in eqn. 4.2 has at least two advantages in the current application compared to multivariate approaches that directly model relationships in the abundance of the different species (e.g., Canonical Correspondence Analysis). First, because abundance is not being modeled, there is no need to assume that the catchability of each species is the same across different surveys and in the commercial fishery. Instead, there is a less restrictive assumption of constant relative catchability among species. In taxonomically-related, morphologically-similar species that utilize their habitat in similar ways, such as the ones considered here, violations of this assumption might be sufficiently small for the approach to remain generally valid. This was assessed in validation analyses (see below). The second advantage is that it is possible to combine survey data from different years despite changes in overall abundance, provided that the relative patterns in seasonal bathymetric distribution of species don't change. This assumption was examined using the analyses by semi-decadal block for eqn. 4.1 described above. Ideally, a BCLHR model that accounted for possible interannual distribution change would have been used; however this was not possible because the availability of multi-annual survey data was limited to September. As a next best alternative, the BCLHR model was fit in semi-decadal blocks to accommodate for interannual changes based on the September survey data, however this approach performed no better than the simpler single BCLHR model and was therefore not pursued (see Appendix B supplemental text and Tables B2 and B3).

4.2.5 Model fitting

The maximum-likelihood method was used to fit eq.1 and eq.2 (Agresti 2002, p. 272-274) to unstandardized catches of individual fish captured in the various fishery-independent surveys (i.e., nominal data, with each fish indicating the presence of its species). The fits of a small number of models that are comprised of subsets of explanatory covariates from eqn. 4.1 and from eqn. 4.2 were compared using delta-values of Akaike's Information Criterion (ΔAIC; Burnham and Anderson 2002) to evaluate whether a more parsimonious model might be more appropriate. To assess model fitting abilities, response probabilities predicted by the selected model were compared to survey observations, expressed as the proportion of each species in bins of 25 m, and in the case of the BCLHR model, also in bins of approximately 1-2 months duration (depending on data availability). Predicted response probabilities were obtained using the logit-transformation of eqs. 1 and 2:

$$(4.3) \qquad \hat{\pi}_j = \frac{\exp(\boldsymbol{\beta}'_j \mathbf{X})}{\sum_{h=1}^{J} \exp(\boldsymbol{\beta}'_h \mathbf{X})}, \qquad \text{with } \boldsymbol{\beta}_J = 0 \text{ and for } j=1,\dots, J$$

where $j=J$ is the baseline species and $\boldsymbol{\beta}$ and $\mathbf{X}$ are shorthand for the vector of parameters and the matrix of explanatory variables, respectively.

Confidence intervals for the response probabilities in eqn. 4.3 were estimated using percentiles from an empirical bootstrap (Efron and Tibshirani 1993). Survey sets were sampled with replacement from within individual surveys (and years, for multi-year surveys) and within survey strata. Strata in the sGSL are defined largely by depth (e.g., Hurlbut and Clay 1990), and stratifying the bootstrap in this way ensured that re-sampling was representative of the original temporal and depth-distribution of sets and that broad-scale spatial and temporal correlation structures in the data were preserved.

4.2.6 Model validation

Given that the five sGSL flatfish species are likely generally correctly identified by at-sea observers, the BCLHR model in its intended application could be validated by comparing model predictions with observations in individual commercial fishing sets. Recall that data from the commercial fisheries were not used in model fitting and are ultimately the target for the application of the technique proposed here. Consequently this validation is different from traditional validation which would involve testing the model's ability to correctly predict survey data not used in the fitting, and constitutes a greater challenge to the model.

Observers have covered an average target of around 10% of trips in the numerous groundfish-directed fisheries and in the shrimp fishery of the sGSL (Benoît and Allard 2009). To fully challenge the model in its potentially broad applicability, observer records covering both fixed-gear (gillnets and longlines) and mobile-gear (bottom trawls, Danish and Scottish Seines) groundfish fisheries and the GSL shrimp trawl fishery were included in the validation. Sets in which the harvesters were targeting one or more of the flatfish species were excluded to conform with the assumption of constant relative catchabilty of the BCLHR model and to be consistent with its intended application to species that are only incidentally captured, such as skates. The number of observed commercial fishing sets used in the validation analysis, as a function of depth, day of the year and fishery, is shown in Fig. 4.4.

Three validation methods were used, each involving the expected number of individuals in flatfish species, *j*, in commercial fishing set, *k*, calculated as:

$$(4.4) \qquad \mathrm{E}(n_{j,k} \mid N_k) = N_k \hat{\pi}_{j,k}, \qquad \text{with } N_k = \sum_{j=1}^{J} n_{j,k}$$

where $\hat{\pi}_{j,k}$ is the response probability for species *j* in set *k*, as predicted by eqn. 4.3. Because observers report the weight of fish caught rather than the number, an average individual fish weight of 0.333 kg was assumed to obtain the $n_{j,k}$ values. This assumption is not critical and is really only used to have a more correct scale for generating random multinomial variates (see below).

First, the expected values were compared to the observed numbers of individuals, $n_{j,k}$, using correlation analysis. Second, the bias of the estimates was calculated as:

$$(4.5) \qquad bias_j = \sum_{k=1}^{K} \left[\mathrm{E}(n_{j,k} \mid N_k) - n_{j,k} \right] \Big/ K$$

where *K* is the total number of observed fishing sets not targeting flatfish.

Third, the coverage probability of the confidence intervals for $\mathrm{E}(n_{j,k} \mid N_k)$ was calculated. The coverage probability, also known as the confidence coefficient, is the proportion of the time that the confidence interval contains the true value of interest (Kalbfleisch 1985, sections 11.2-11.4), in this case $n_{j,k}$. If all assumptions used in deriving a confidence interval are met, the actual or true coverage probability will equal the nominal coverage probability, set here at 0.95.

For each observed fishing set *k*, a confidence interval for each of the J=5 flatfish species was constructed using a Monte Carlo simulation. For each iteration, *l*, of the simulation, parameters of eqn. 4.2 were obtained by fitting the model to empirically bootstrapped data, as described above. A vector of species response probabilities $\hat{\boldsymbol{\pi}}_{k,l} = (\hat{\pi}_{1,k,l},...,\hat{\pi}_{J,k,l})$ was predicted using the fitted model and the reported fishing depth and day-of-year for set *k* (eqn. 4.3). A vector of the predicted number of fish from each species, $\hat{\mathbf{n}}_{k,l} = (\hat{n}_{1,k,l},...,\hat{n}_{J,k,l})$, was then obtained by drawing random multinomial variates:

$$(4.6) \qquad \hat{\mathbf{n}}_{k,l} \sim multinomial(N_k, \hat{\boldsymbol{\pi}}_{k,l})$$

Five-thousand iterations of the Monte Carlo simulation were undertaken to obtain the frequency distribution of $\hat{n}_{j,k}$ for each species *j* and set *k*. The 2.5th and 97.5th percentiles of each of those distributions were taken as defining the respective 95% confidence intervals, $[\hat{n}^{*0.025}, \hat{n}^{*0.975}]_{j,k}$. The marginal coverage probability for species *j*, CP(n_j), was then calculated as the proportion:

$$(4.7) \qquad \text{CP}(n_j) = K^{-1}\sum_{k=1}^{K} I_{j,k}\text{, where } I_{j,k} = \begin{cases} 1 & \text{if } (\hat{n}_{j,k}^{*0.025} \le n_{j,k} \le \hat{n}_{j,k}^{*0.975}) \\ 0 & \text{otherwise} \end{cases}$$

In addition to the marginal species-specific coverage probabilities, a pseudo joint-coverage probability for the five flatfish species was also calculated. The proportion of fishing sets for which a number *S* of the J=5 species-specific confidence intervals contained the observed abundances, CP(S), was calculated as:

$$(4.8) \quad \text{CP}(S) = K^{-1}\sum_{k=1}^{K} G_k \qquad \text{for } S=0,\ldots,J$$

and where $G_k = \begin{cases} 1 & \text{if } \sum_{j=1}^{J} I_{j,k} = S \\ 0 & \text{otherwise} \end{cases}$, and $I_{j,k}$ is as defined above.

Note that CP(*S*) is not a true measure of the joint coverage probability in that it does not account for the multivariate nature of the confidence intervals for each fishing set, which is a statistical problem that is beyond the scope of this paper.

4.3 Results

The full model in eqn. 4.1 provided a better fit to data compared to a model excluding the quadratic effect of depth, based on AIC (ΔAIC values ranged from 707-3685 for skates and 539-2417 for flatfish, depending on the semi-decadal block in question). Despite considerable changes in the abundance and distribution of sGSL skate and flatfish (see Methods: Background; Fig. 4.2), modelled patterns in their depth-dependent assemblage composition in September have not varied dramatically since 1985, though some systematic changes over time are apparent (Fig. 4.5). For example, the thorny skate have become more prevalent over time at depths ranging from around 150-350 m, at the expense of smooth skate (Fig. 4.5a). Likewise, Greenland halibut have become more prominent in deeper waters, largely at the expense of witch flounder (Fig. 4.5b,c). The largest departure from the overall patterns was for the 1985-1989 block for both families. Confidence intervals for the predictions in the various semi-decadal blocks nonetheless largely overlapped (e.g. in Fig. 4.5).

Of the BCLHR models considered (i.e., eqn. 4.2 and subsets thereof), there was the most support in the data for the complete model for both skates and flatfish, based on ΔAIC (Table 4.1). This model provided a good fit to the available survey data across the seasons for all species in both the skate (Figs. 4.6 and Appendix B1) and flatfish (Figs. 4.7 and Appendix B2) assemblages. For skates, the model describes the summer near-shore, mid-water and deep-water distributions of winter skate, thorny skate and smooth skate, respectively. It also captured the offshore movements of winter skate (onto the Magdalen Shallows) and thorny skate (into the Laurentian channel) for the winter (Fig. 4.2a), and then back again in spring (Fig. 4.6). For flatfish, the model helped to highlight the distributional separation of the five species along the depth axis (Fig. 4.7). During the summer, modes in the relative composition occurred at <15 m for winter flounder, around 35 m for yellowtail flounder, between 55-120 m for American plaice, around 200 m for witch flounder, and >300 m for Greenland halibut. The model also captured slight offshore movements of yellowtail flounder onto parts of the Magdalen shallows and movement of American plaice and witch flounder into deeper water for the winter (Fig. 4.2a). For both skates and flatfish, the magnitude of seasonal changes in depth-dependent species composition (Figs. 4.6 and 4.7) were considerably greater than the estimated long-term changes in summer distribution (Fig. 4.5).

Uncertainty in predictions from the BCLHR model varied inversely with the availability of samples for a given depth and date and was greatest in the absence of samples (Fig. 4.8). For the dates and depths for which samples were available, the predictions and associated confidence intervals for the various species were reasonably well separated, particularly for the more data rich flatfish assemblage (Figs. 4.6 and 4.7).

The BCLHR model stood up reasonably well to the validation using catch records from at-sea observers. For most flatfish species caught in most fisheries, correlations between observed and predicted catch amounts were generally intermediate to high (Table 4.2a; Fig. 4.9). A low correlation was observed for yellowtail flounder in the fixed gear fishery, though this is because predicted and observed catches were low to nil. Likewise, no correlation was calculated for this species and winter flounder in the shrimp fishery because nearly all observed catches were nil and predictions were essentially nil.

The bias of the predictions tended to be low to intermediate (≤3.1 kg) resulting in an average bias of 29% of the mean catch for a given species and fishery (Table 4.2b). This relative bias was greatest for very low predicted/observed occurrences (yellowtail and winter flounder in the shrimp fishery) and was lowest for the three most abundant flatfish species caught incidentally in the mobile-gear fishery. For all species, there was a slight tendency in certain fishing sets to predict catches when none were observed (Fig. 4.9). The reverse occurred much less frequently.

The marginal coverage probability of estimated confidence intervals around the predictions was high (≥0.70) in all cases and close to (≥0.90) or above the nominal value of 0.95 in over half of the cases (Table 4.2c). The pseudo joint-coverage probability was also relatively high, with a 67% chance that the estimated confidence intervals of all five species would overlap the actual values in shrimp and fixed-gear fisheries, and a 58% chance for mobile gear (Table 4.3). Depending on the fishery, there was a 90-98% chance of overlap for at least three of the five species (i.e., $S \geq 3$ in Table 4.3).

4.4 Discussion

The approach presented in this paper addresses the difficult problem of estimating the species composition of fishery catches in the absence of concurrent sampling in or outside (e.g., fishery-independent surveys) the fishery. The model is fairly simple and is founded on the well-established dominant roles of depth and seasonality in structuring marine fish assemblages worldwide (e.g., Hyndes et al. 1999; Demestre et al. 2000; Mueter and Norcross 2002). Though more accurate and precise models of distribution could likely be constructed using additional environmental variables (e.g., Martin et al. 2012), the present results show that it is possible to construct a reasonable predictive model using the covariates associated with individual commercial fishing hauls that are generally available to fishery scientists.

For the sGSL, where seasonal fish movements are species-specific and can be pronounced, fitting the model required survey data that were collected through much or all of the year and covering a broad range of depths. The approach can therefore be fairly data intensive. However, these data need not come from synoptic, contemporary, ecosystem-scale seasonal surveys. Two features of the approach allow for the integration of data from a number of different surveys carried out at different times and in different portions of the ecosystem of interest. First, because the BCLHR (eqn. 4.2) models the conditional relative species composition of the assemblage, there is no need to model or otherwise account for absolute abundance. Furthermore, because patterns in depth-dependent relative species composition appear fairly robust to very large changes in species abundance and distribution, at least in summer, input data need not be contemporary or collected in the same or adjoining years. This robustness stemmed in large part because the dramatic changes in abundance and distribution experienced by a number of the species in this study (e.g., winter skate, thorny skate, American plaice) occurred in areas where there was less overlap with other species in their assemblage, resulting in little change in conditional relative abundance. Second, the BCLHR model in its intended application to fisheries does not assume a fixed catchability of species across surveys and fishery sectors, but rather a less restrictive assumption of constant relative catchability of species within an assemblage. However the relative catchability assumption does limit the applicability of the model to species with similar shapes, sizes, behaviours and other factors known to affect selectivity by fishing gear. Fortunately, these are often the species groups for which catch disaggregation in the fishery is most problematic and for which the present approach is needed most. Future predictive models with even less restrictive catchability assumptions would represent an important step forward in facilitating the estimation of catch composition for broader species assemblages.

Though the model fit survey data well for skates and flatfish, the validation suggests that the model may not be fully adequate for reliably predicting the species composition of flatfish catches in fisheries. For example, the model tended to predict some non-negligible catches of particular species when none were observed and coverage probability confidence intervals on predictions was less than the nominal coverage probability in more than half the cases (species and fishery) examined. The possible reasons for these discrepancies are numerous, though they fall roughly into two categories which are discussed in turn: model inadequacy and issues with the data used for validation.

The model may be mispecified or inadequate for at least five reasons. First, the heuristic treatment of depth and seasonal effects may not properly reflect their actual biological and ecological effects (Austin 2002; Guisan et al. 2006). Correspondence between model predictions and survey data suggest that this effect may be small for well sampled dates and depths, though it might be important when and where survey sampling is sparse or absent. Second, there may have been long-term changes in the relative depth distribution of the species in months other than September that were not reflected in the available survey data and the resulting models. Validation with contemporary reliable catch composition data across the seasons could help resolve uncertainty concerning these first two possible sources of model inadequacy.

Third, the estimated depth and seasonal effects may be biased as a result of the spatially unrepresentative sampling inherent in the available survey data for certain months. The bias may be most prevalent when sampling of the fish community is unrepresentative or nonrandom with respect to an unaccounted environmental variable that contributes to assemblage structure. Fortunately, the data for model estimation used here generally also covered the seasons and depths of commercial fishing, lessening such possible biases in the intended model application.

Fourth, eqs. 4.1 and 4.2 assume that individual fish are captured independently. This assumption is unlikely to be true given that demersal fish aggregate across a range of spatial scales, thereby introducing a dependency in the probability of capture (i.e., overdispersion). Failure to address such lack of sample independence is known to lead to overestimated model precision (e.g., Hansen et al. 1953). This may partly explain the tendency for the coverage of the estimated confidence intervals to be less than the nominal level in the validation. This problem might be addressed by introducing a random effect for survey hauls in the linear predictor of eqn. 4.2 (Hartzel et al. 2001), or by allowing for extra binomial variation via a beta-binomial model structure (Agresti 2002, p. 553-556). Both presented a computational challenge that was beyond the scope of the present paper.

Fifth, violations of the assumption of constant relative catchability between species may be severe enough to affect the reliability of predictions for commercial fishery catches, where fishing gears and practices are likely to enhance selectivity for certain species. Though this effect may have been present for the flatfish assemblage, which is targetted by some fishery sectors, it is likely to be less pronounced for assemblages that are not of commercial interest such as skates in the sGSL.

The model validation results may also reflect problems with the observer data used to challenge the model. First, catch amounts are usually estimated visually by observers in sGSL fisheries, contributing unaccounted observation error to the validation. Second, the observers rely on the ship's crew to sort catches. Inadequate or incorrect sorting would also result in errors in the reported relative species composition. Species that are relatively less common in the catch may be most vulnerable to underrepresentation resulting from inadequate sampling, potentially explaining some or many of the cases with no observed catches despite predictions of non-negligible catches. Third, species misidentification is likely to have occurred for flatfishes in some of the catches due to variation in observer experience and attention to detail.

It is presently impossible to know the relative contributions of model inadequacy and problems with the validation dataset to the lack of full validation for the BCLHR model. Additional research on the above issues would help to ensure the reliability of the model. In the interim, there appears to be sufficient evidence from the model's fitting abilities and from the validation to suggest that the model is useful, especially in the absence of an equally well-supported alternative.

The present approach should be broadly applicable to other well-surveyed ecosystems where assemblage composition is structured by one or a few key environmental variable(s) of known spatial distribution. Of course, due to local environmental conditions and how fish are adapted to them, parameters of the BCLHR model are likely to be ecosystem specific. For ecosystems that have not been as broadly surveyed as the sGSL, the data required to fit a model such as the BCLHR model could be obtained in whole or in part from the fishery itself by enhancing the taxonomic resolution of data collection during a subset of trips sampled by fishery observers.

The applications of the present approach need not be limited to predicting the species composition of fishery catches, but can be used more generally to parsimoniously describe seasonal and spatial patterns in distribution and seasonal resource partitioning (e.g., Ferrier and Guisan 2006; Planque et al. 2011). Furthermore, the BCLHR model is not limited to modelling species and stock composition, but could be used to model patterns in demographic composition within a population. For example, the well-known relationship between fish size and bathymetry for most marine fish species (Macpherson and Duarte 1991) could readily be modelled. The resulting predictions of seasonal depth-dependent distribution of fish size classes could, among other things, inform management decisions on where and when fisheries are least likely to unnecessarily capture undersized individuals.

Table 4.1. Values of ΔAIC for five competing models based on eqn. 4.2 for seasonal depth-dependent catches of sGSL skates and flatfish communities. Models are indicated by the subset of parameters that were included in the estimation; the remaining parameters of eqn. 4.2 were set to zero. These competing models were chosen as they consider the consequences of including a quadratic effect of depth and of including different periodicities for the seasonal effect.

Model	Skates	Flatfish
$\beta_0, \beta_1, \beta_2$	6664	37550
$\beta_0, \beta_1, \beta_2, \alpha_1/\varphi_1$	1369	10642
$\beta_0, \beta_1, \beta_2, \alpha_1/\varphi_1, \alpha_2/\varphi_2$	91	6884
$\beta_0, \beta_1, \beta_2, \alpha_1/\varphi_1, \alpha_2/\varphi_2, \alpha_3/\varphi_3$	0	0
$\beta_0, \beta_1, \alpha_1/\varphi_1, \alpha_2/\varphi_2, \alpha_3/\varphi_3$	2133	15201

Table 4.2. Species-specific results of the validation exercise comparing observed catches of flatfish to those predicted by the BCLHR model: (a) Pearson correlation, (b) estimation bias (eqn. 4.5), and (c) marginal coverage probability of estimated confidence intervals (eqn. 4.7). Values in parentheses in (b) are the mean catches for the species and provide a scale against which to assess bias. Results are presented for three fishery groupings: shrimp trawl-fishery, and mobile-gear and fixed-gear groundfish fisheries.

		Fishery	
Species	Shrimp	Mobile	Fixed
(*a*) Correlation			
Greenland halibut	0.77	0.88	0.91
American plaice	0.70	0.94	0.75
Witch flounder	0.50	0.45	0.46
Yellowtail flounder	-	0.58	0.05
Winter flounder	-	0.74	0.73
(*b*) Bias (kg)			
Greenland halibut	-2.08 (6.20)	0.48 (7.75)	-3.11 (6.80)
American plaice	0.86 (2.95)	-2.06 (67.19)	1.03 (3.88)
Witch flounder	1.19 (1.86)	0.05 (6.51)	1.58 (1.94)
Yellowtail flounder	0.001 (0.001)	0.78 (2.10)	0.50 (1.02)
Winter flounder	0.001 (0.001)	0.76 (2.45)	0.01 (0.94)
(*c*) Coverage			
Greenland halibut	0.70	0.88	0.84
American plaice	0.93	0.73	0.85
Witch flounder	0.90	0.73	0.88
Yellowtail flounder	0.99	0.93	0.96
Winter flounder	0.99	0.95	0.93

Table 4.3. Estimated pseudo joint-coverage probability (eqn. 4.8) for a given number, *S*, of the five flatfish species in the validation exercise comparing observed catches to those predicted by eqn. 4.2. Results are presented for three fishery groupings: shrimp trawl-fishery, and mobile-gear and fixed-gear groundfish fisheries.

		Fishery	
No. species (*S*)	Shrimp	Mobile	Fixed
0	0.00	0.00	0.00
1	0.00	<0.01	0.00
2	0.02	0.10	0.07
3	0.13	0.24	0.13
4	0.17	0.08	0.14
5	0.67	0.58	0.67

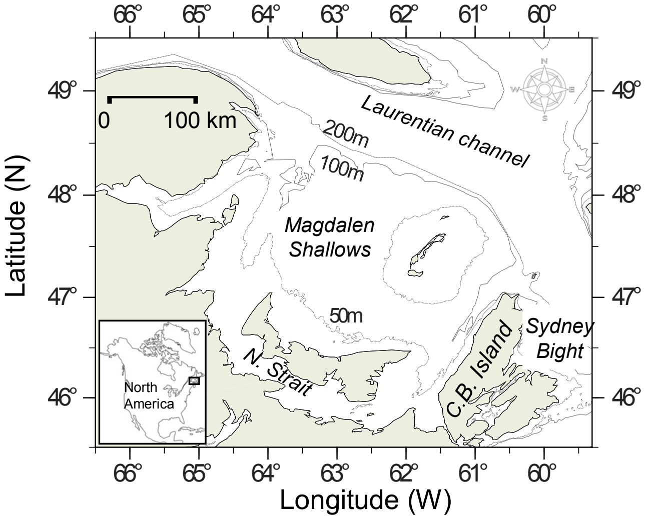

Figure 4.1. Map of the southern Gulf of St. Lawrence (sGSL) including the 50m, 100m and 200m isobaths and location names mentioned in the text (N. Strait is the Northumberland Strait and C.B. Island is Cape Breton Island). The inset shows the location of the sGSL with respect to the North American continent.

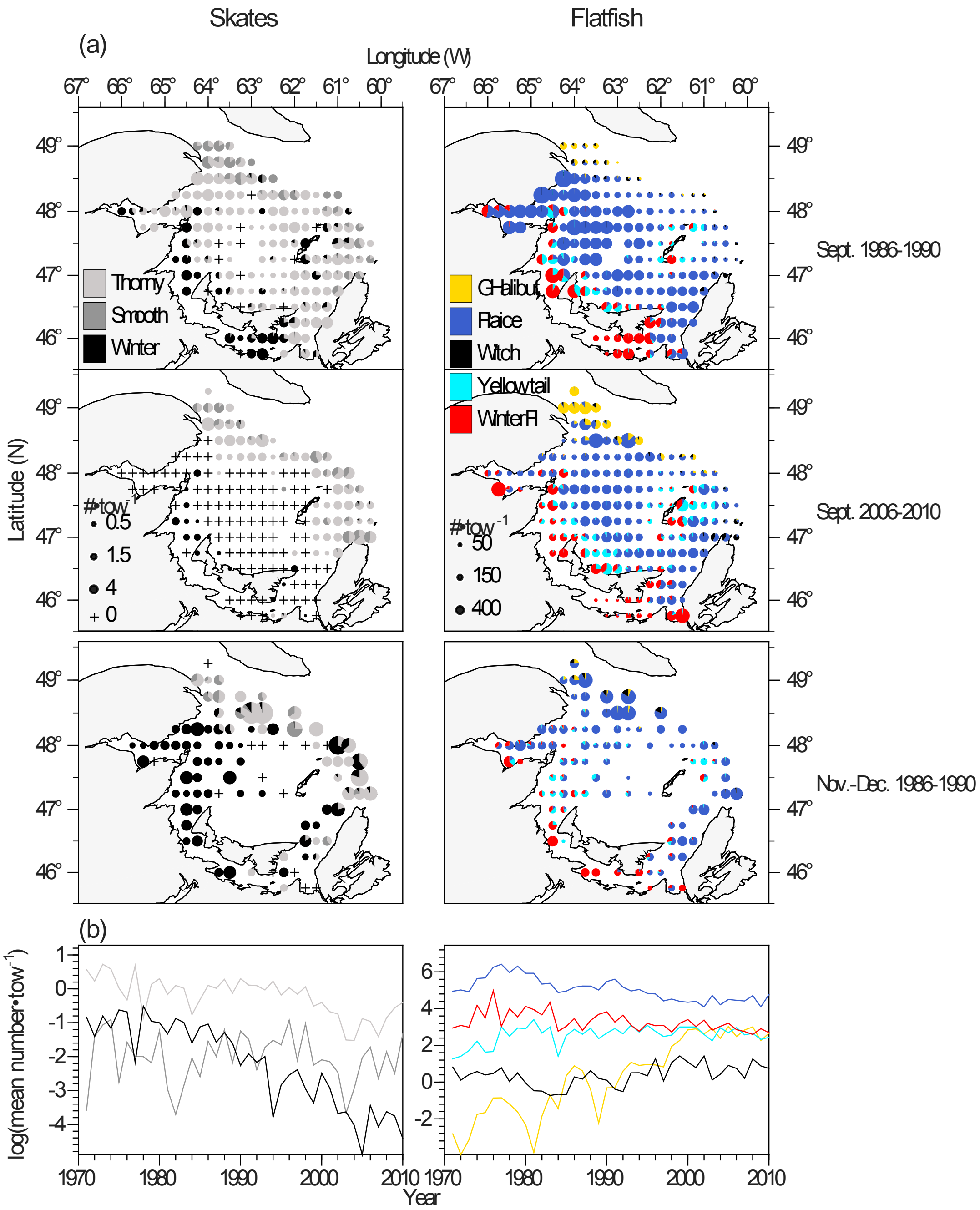

Figure 4.2. a) Distribution of sGSL skate (left column) and flatfish (right column) species in September 1986-1990 and 2006-2010, and in November-December 1986 and 1990. Distribution is summarized as pie charts of the mean numbers per tow in 15 by 15 minute blocks of latitude and longitude, with circle size proportional to group abundance and relative abundance of species indicated by the relative sizes of coloured areas in each pie. Note that small crosses indicate blocks in which no individuals of the group were captured and absence of a symbol indicates absence of sampling. b) Relative abundance trends on the log-scale for southern Gulf skate (left column) and flatfish (right column) species based on the September survey, 1971-2010.

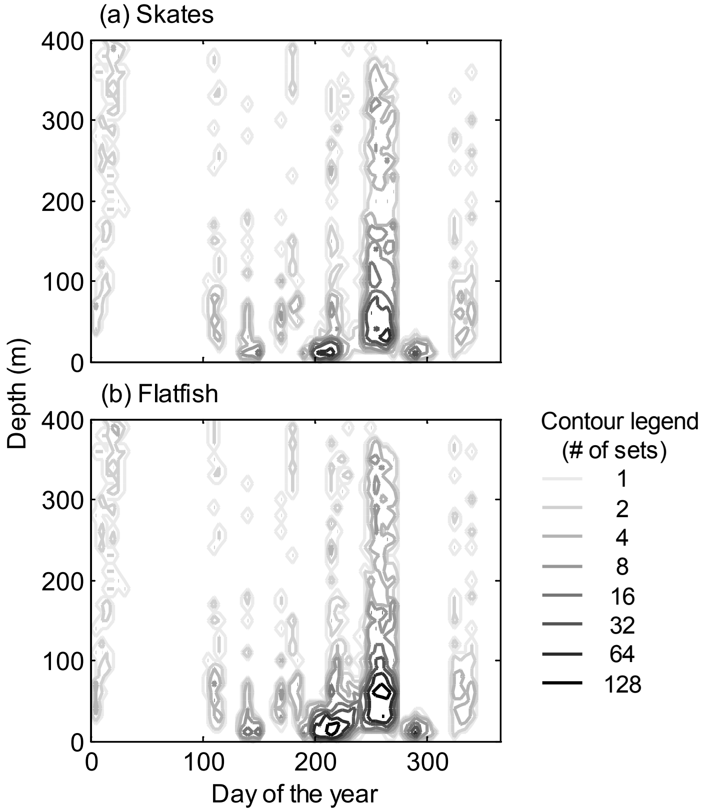

Figure 4.3. Contour plots of the number of survey bottom-trawl sets, as a function of day of the year and depth, (a) that caught skates and (b) that caught flatfish. The number of sets was summarized in cells spanning 10 m of depth and 5 days. Contour lines are drawn for exponentially increasing numbers of sets using incrementally increasing line darkness, as per the legend.

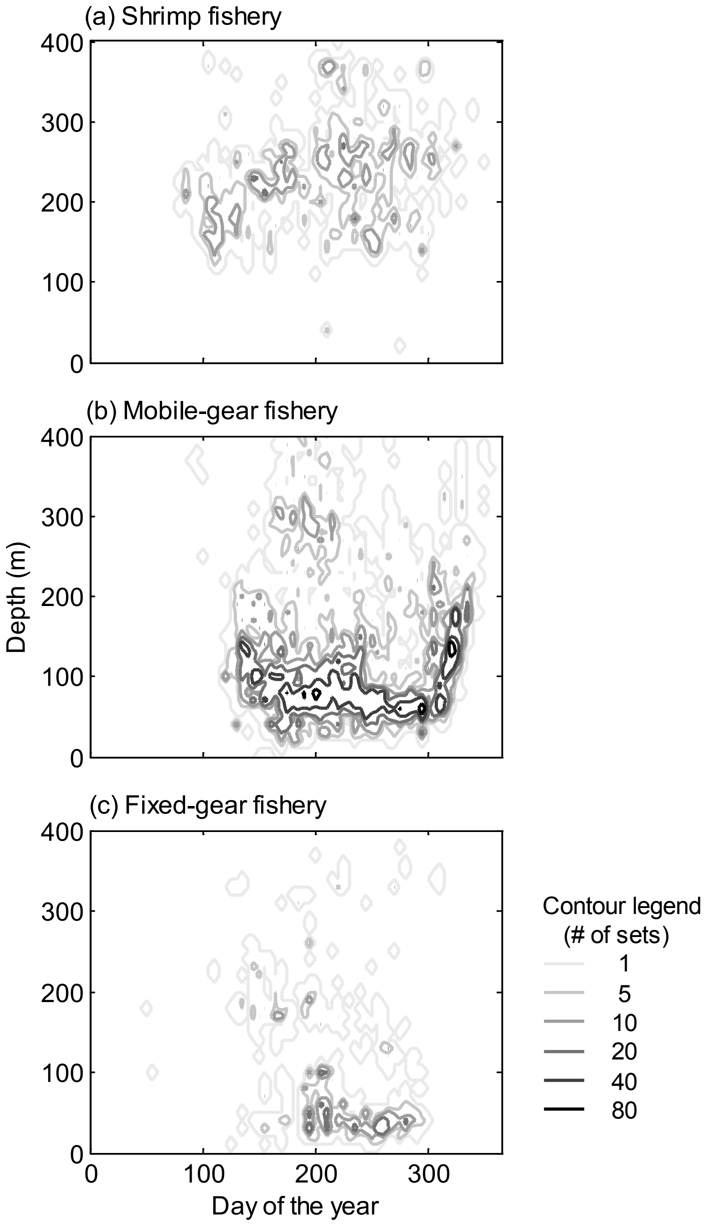

Figure 4.4. Contour plots of the number of commercial fishing sets observed by fisheries observers, 1990-2010, as a function of day of the year and depth, in (a) the shrimp fishery, (b) mobile-gear fisheries and (c) fixed-gear fisheries. In all cases, only fishing sets that did not target the species of interest in this study were retained for analysis and are plotted. The number of sets was summarized in cells spanning 10 m of depth and 5 days. Contour lines are drawn for geometrically increasing numbers of sets using incrementally increasing line darkness, as per the legend.

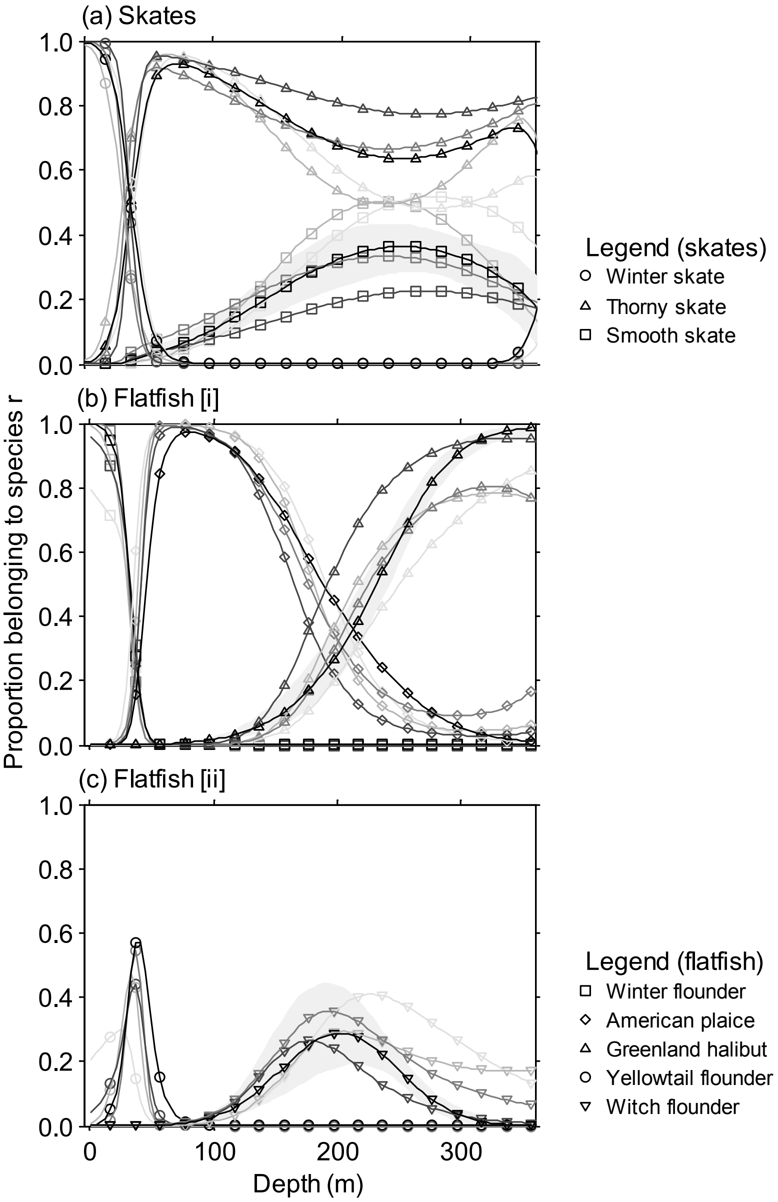

Figure 4.5. Predicted relative bathymetric distribution in September from eqn. 4.1 for five distinct semi-decadal blocks for: (a) skates (winter skate, thorny skate and smooth skate); (b) winter flounder, American plaice and Greenland halibut, and; (c) yellowtail flounder and witch flounder. Note that predictions for flatfish were separated into two figure panels, b and c, to enhance clarity. The predicted distribution functions for each semi-decadal block are distinguished using increasing darkness, beginning with 1985-1989 (light grey) and ending with 2005-2010 (black). In each panel, the 95% confidence interval for the predicted function for the 2005-2010 block for one of the species is plotted to illustrate the approximate magnitude of prediction uncertainty. The model predictions are based on fits to the September survey data only.

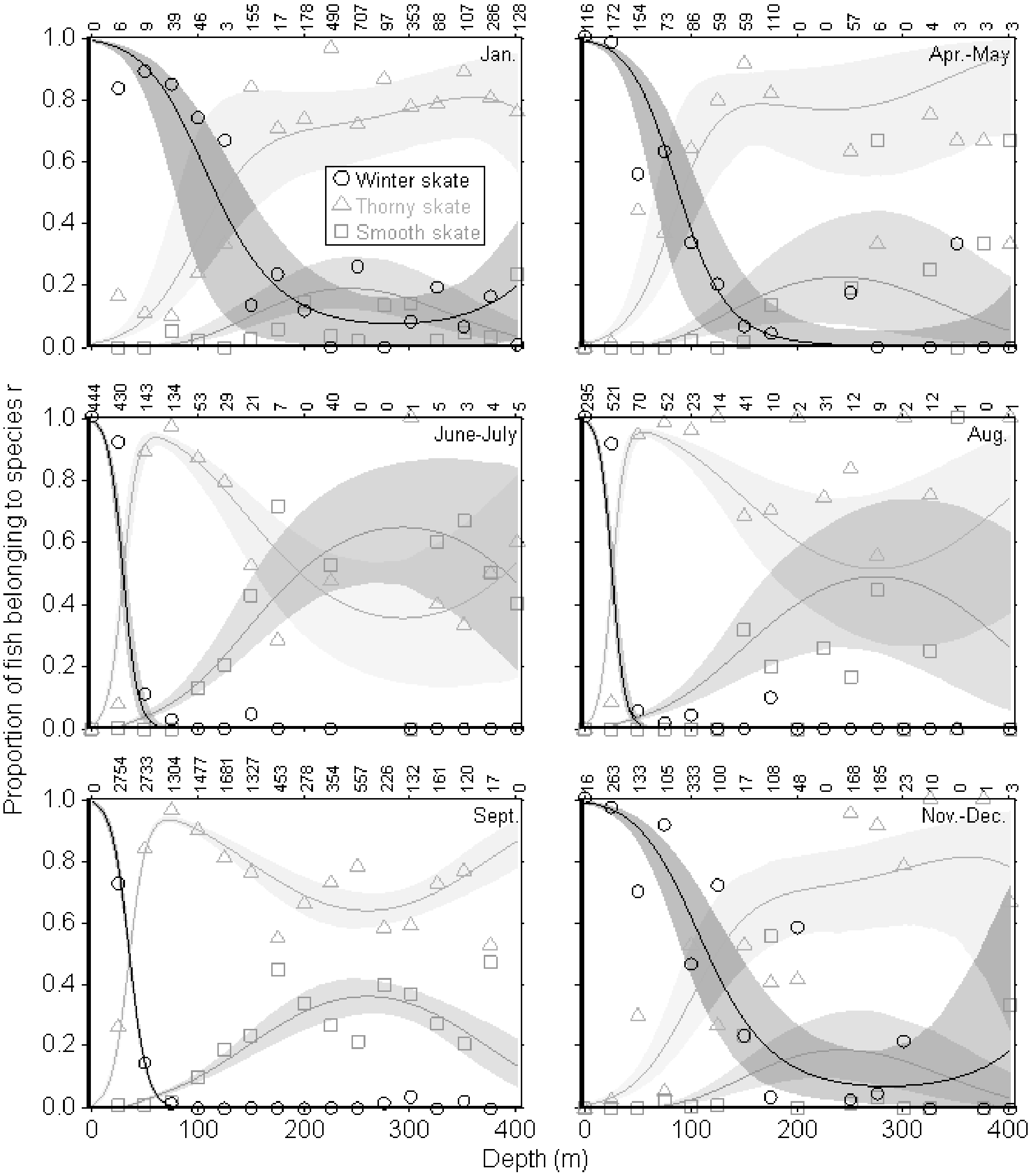

Figure 4.6. Observed (symbols) and predicted (lines, with the 95% confidence band denoted by shading) relative proportions of the three skate species (thorny skate, light grey; smooth skate, medium grey; winter skate, dark grey) as a function of depth (x-axes) and months (panels). Survey catches were summarized in depth bins of 25 m for plotting, and the displayed months are those for which there were sufficient survey data. The displayed model predictions are based on the midpoint date of the survey data plotted for a given panel. The numbers above each panel indicate the number of individual skate from a particular depth and time bin that were used to fit the BCLHR model (eqn. 4.2), based on the data from all of the surveys in Table B1 (Appendix B).

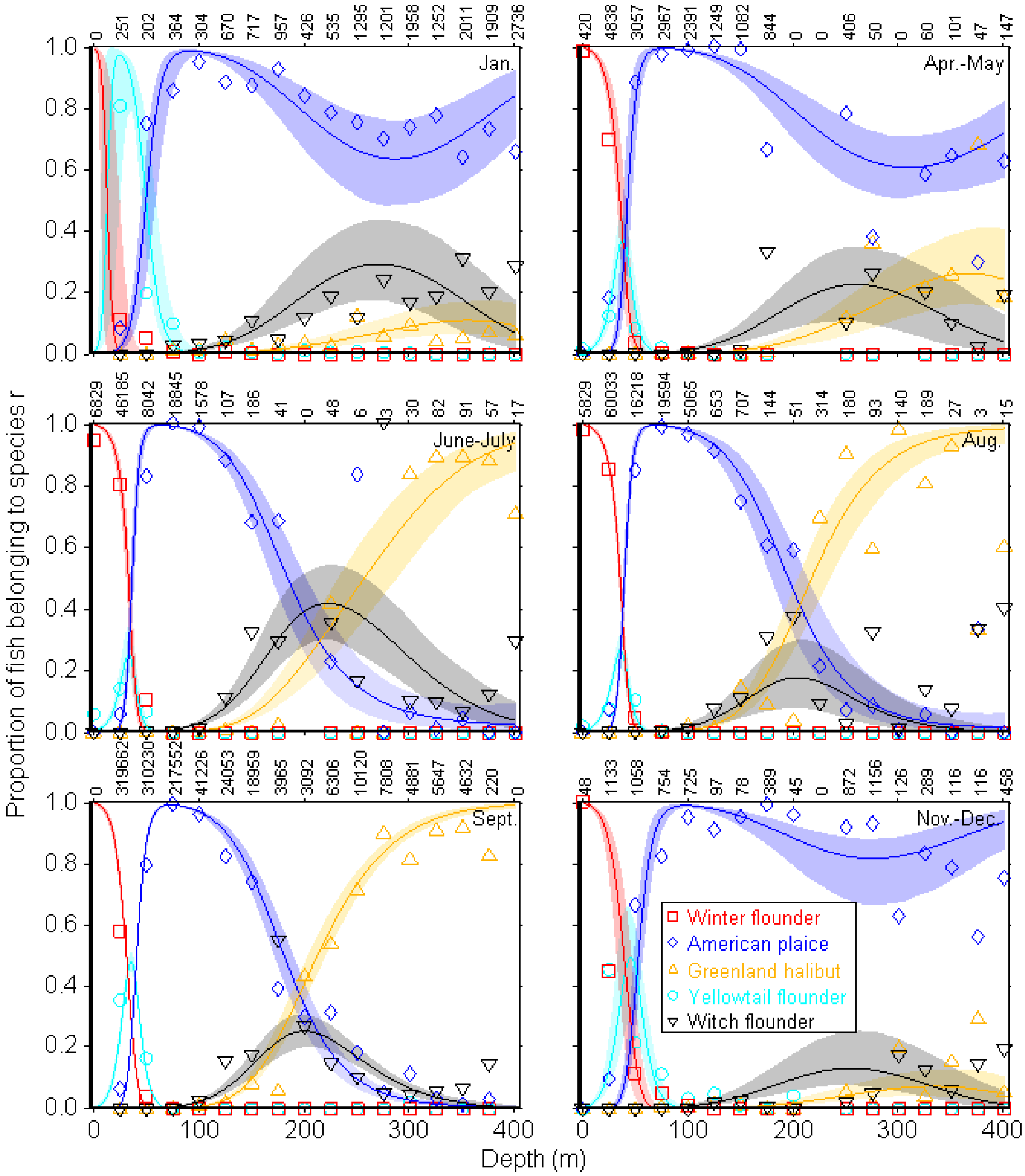

Figure 4.7. Observed (symbols) and predicted (lines, with the 95% confidence band denoted by shading) relative proportions of the five flatfish species as a function of depth (x-axes) and months (panels). Survey catches were summarized in depth bins of 25 m for plotting, and the displayed months are those for which there were sufficient survey data. The displayed model predictions are based on the midpoint date of the survey data plotted for a given panel. The numbers above each panel indicate the number of individual flatfish from a particular depth and time bin that were used to fit the BCLHR model (eqn. 4.2), based on the data from all of the surveys in Table B1 (Appendix B).

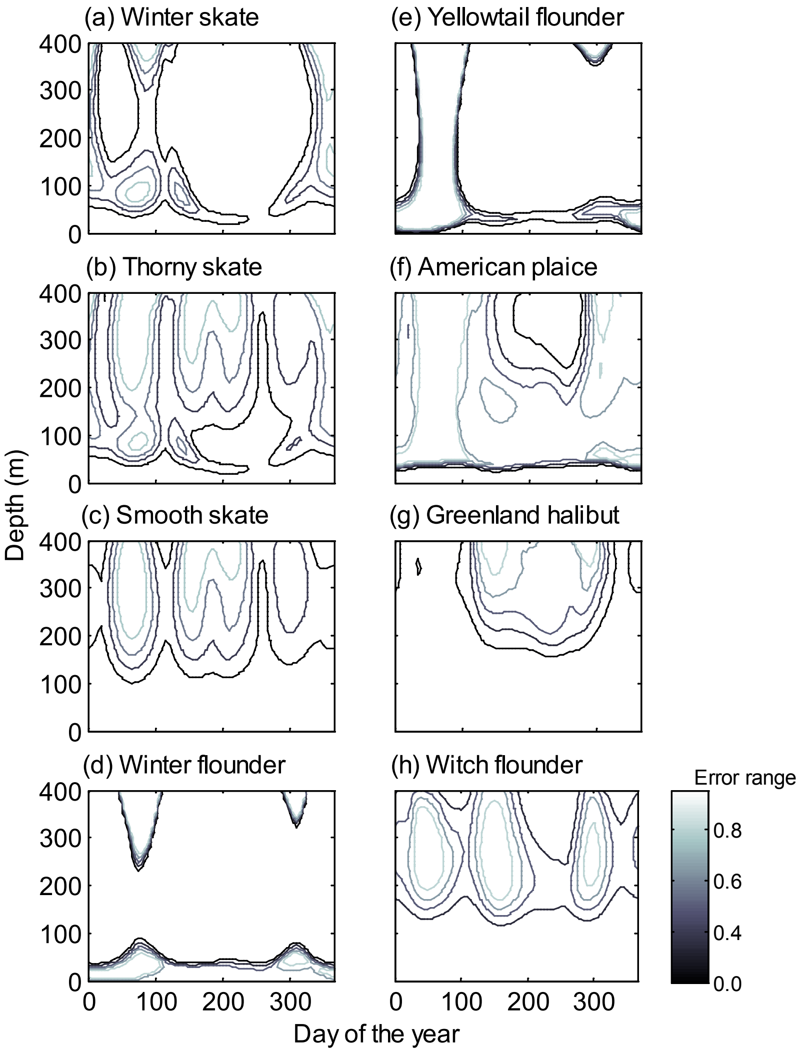

Figure 4.8. Contour plots of the prediction error range (difference between the upper and lower 95% confidence intervals) for the BCLHR model, as a function of day of the year and depth for each species in this study. Contour levels are indicated by shading according to the legend in the lower right of the figure.

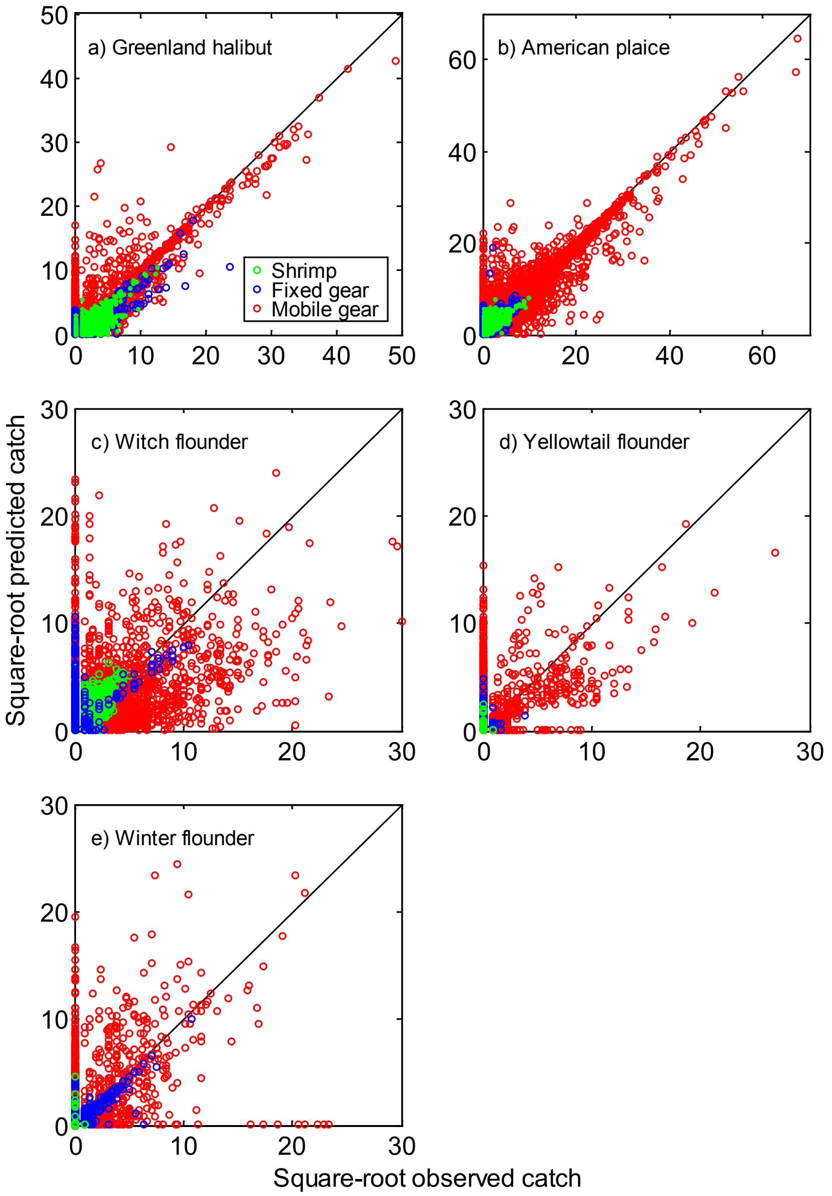

Figure 4.9. Comparison of observed and predicted non-directed commercial fishery catches (kg) for the five flatfish species, by fishery. Note the square-root transformation for the catches for both axes.

Chapter 5. Twenty Years of Annual Landed and Discarded Catches of Three Southern Gulf of St. Lawrence Skate Species Estimated Under Multiple Sources of Uncertainty.

5.0 Abstract

Estimating fishery impacts on commercially unimportant species is often hindered by limited and possibly biased data for landed and discarded catch and poor information on discard mortality. The three skate (family Rajidae) species occurring in southern Gulf of St. Lawrence (Canada) exemplify this problem. Assessing the contribution of fishing to important declines in their adult abundance has been complicated by catch data that are not disaggregated by species, concerns about the reliability of discard amounts estimated from fisheries observer surveys, and unknown discard mortality rates. An approach is presented for producing annual estimates of landed and discarded catch, as well discard mortality rates, for the three species for the period 1991-2011. The approach used data from landing statistics and from observer surveys, and models for disaggregating mixed fishery catches into their constituent species and for estimating minimum discard mortalities. Bootstrapping was used to propagate errors associated with different components of the estimation process. The estimation was partly validated by comparing recorded landings and landings estimated from fisheries observer surveys. This paper demonstrates how multiple sources of uncertainty in discard loss estimation can be addressed by dividing the estimation process into linked components that can be individually addressed and, ideally, validated.

5.1 Introduction

Understanding the impacts of fishing on commercially unimportant species remains a key challenge in the study and implementation of an ecosystem approach to fisheries. Historically, research has focussed on commercially important species, resulting in considerably less knowledge of the biology, and especially the catch history, of species that are generally discarded. Techniques based on life-histories and, in some cases, spatio-temporal overlap between species and fisheries, have been developed to assess the risk of adverse fishing impacts for non-target species in the absence of catch data (e.g., Pope et al. 2000; Zhou and Griffiths 2008; Le Quesne and Jennings 2012). However, the utility of these techniques is limited when species' life histories (e.g., natural mortality) change or when actual estimates of exploitation rates are required for recovery potential assessments for depleted species.

Assessments for non-target, and especially non-commercial, species that require exploitation rate estimates are often hindered by limited and possibly biased data for landed and discarded catch and poor information on discard mortality (e.g., Broadhurst et al. 2006; Cotter and Pilling 2007; Dickie-Collas et al. 2007). This is exemplified in the case of the three skate (family Rajidae) species occurring in the southern Gulf of St. Lawrence (sGSL; NW Atlantic, Canada). All three species have undergone important declines in adult abundance since 1971: 65% decline for Smooth Skate (*Malacoraja senta*), 95% for Thorny Skate (*Amblyraja radiata*), and 98% for Winter Skate (*Leucoraja ocellata*) (Swain et al. 2012). Over that same period, all three species experienced important changes in mortality rates, with decreases for small juveniles and increases for large juveniles and adults (Swain et al. 2012). While there are no directed fisheries for skates in the sGSL, skates are incidentally captured in a number of fisheries (e.g., Benoît 2006, 2011; Benoît and Hurlbut 2010), most of which allow harvesters the discretion of retaining or discarding skates.

Assessing the contribution of fishing to declines in sGSL skate abundance has been complicated by three main factors. First, skates are not identified to species in the landings data, and are not consistently or reliably identified to species by fisheries observers (Benoît 2006), the only source of information on skate discard amounts. Second, discard mortality rates were unknown. Third, whether the data from fisheries observer surveys are reliable for producing accurate estimates of skate discards has yet to be established. There are concerns that the data may not be reliable for target species in the sGSL due to non-random deployment of observers and changes in harvester behaviour when an observer was present (observer effects) (Benoît and Allard 2009). However the data for principally-discarded species such as the skates may be less affected by these potential sources of bias if, for example, their distribution is approximately random with respect to the location of observed fishing hauls and the observer effects reflect changes in fishing practices that do not affect their catch rates (e.g., changes in fishing effort or changes in discarding practices restricted to the commercial species in the catch). These three limiting factors are certainly not unique to the sGSL, and assessments for skates in other areas with similar data limitations have necessitated using assumptions for catch history to which assessment models were quite sensitive (e.g., Gertseva 2009).

Here, an approach is presented for producing species-specific annual estimates of landed and discarded catch, as well discard mortality rates, for the three skate species for the period 1991-2011. The approach uses data from landing statistics and from observer surveys, and models for disaggregating mixed fishery catches into their constituent species and for estimating minimum discard mortalities. Boostrapping is used to propagate errors associated with different components of the estimation process (e.g., Blukacz et al., 2005). Furthermore validation of the estimation for key components is presented either in this paper (catch estimation) or in a recent paper (species disaggregation; Benoît 2013 [Chapter 4]). Estimated catches are also presented as a ratio of estimated trawlable biomass from a fishery-independent bottom-trawl survey to show trends in relative fishing mortality for each species over the past two decades. Ultimately, this paper aims to demonstrate how multiple sources of uncertainty in the estimation of losses due to fishing can be addressed by dividing the estimation process into linked components that can be individually addressed and validated.

5.2 Methods

5.2.1 Data

The data for this study come from three sources: recorded landings, fisheries observer surveys for thirteen fisheries targeting eleven commercially important species (Table 5.1), and an annual fishery-independent bottom-trawl survey. Except for some Winter Skate caught in an inshore scallop fishery (Benoît 2011), the commercial fisheries likely account for almost all skate captures in the sGSL for the study period. The availability of sufficient observer survey data limited the analysis to 1991 to 2011.

Beginning prior to 1991, a complete census of landings in the Cod and Redfish mobile gear fisheries has been provided by a mandatory dockside catch monitoring program (DMP). A similar program was put in place in different years in the remaining fisheries of the sGSL in this study (Table 5.1). For the years between 1991 and the implementation of a full DMP program, 25% of fishing trips were randomly sampled for dockside catch monitoring. Selection of trips was facilitated by a mandatory requirement for harvesters to hail-in several hours before their intended arrival in port. Landings for the unsampled trips were based on fish sales slips which were validated against the monitored landings. Given the quality of catch monitoring, landings since at least 1991 for the thirteen sGSL fisheries are considered to be generally accurate in the respective stock assessments (e.g., Morin and LeBlanc 2012; Swain et al. 2009b). Furthermore, skate landings are assumed to be accurate because there are no obvious incentives for their misreporting, such as restrictive quotas.

Fisheries observer surveys are the only reliable source of information on skate discards in the sGSL. Target observer coverage levels are fishery-specific and generally vary between 5-15% of fishing trips, though actual coverage levels have often been lower (Benoît and Allard 2009). The main sampling unit for the surveys are individual fishing trips and deployments are effected on a fishery-specific basis. Observers provide reports for individual fishing hauls that include information on the geographic position, depth, date, time, duration and catch composition. The masses of both retained and discarded catches are recorded for each captured taxon. Catches of commercially-important species are generally recorded at the species level, whereas catches of other species tend to be recorded at coarser taxonomic levels.

A bottom-trawl survey of the sGSL, based on a stratified-random design, has been conducted each September since 1971 (Chadwick et al. 2007). Estimates of trawlable biomass from this survey for each skate species were used in this study (details below).

5.2.2 *Estimating total annual skate landings and discards*

Fisheries observer records of retained (and therefore landed) catch amounts allow for the estimation of landings, which can then be compared with official landing statistics which are assumed to be generally accurate. This provides an opportunity to validate the catch and discard estimation process.

Annual total catches of skates in sGSL fisheries were estimated using the ratio of skate and commercial species catches in observed fishing hauls, and reported landings for the commercial species. This approach was used instead of the preferred design-based estimation (Rochet and Trenkel 2005; Cotter and Pilling 2007) because the deployment of fisheries observers to fishing trips in the various fisheries followed an undocumented deployment scheme (details in Benoît and Allard 2009).

Let $\hat{b}_{c,t}$ be the estimated total biomass of captured skate for the sGSL in catch category *c* and year *t*. There are two catch categories, retained (*c*=*r*) and discarded (*c*=*d*) catch. The value of $\hat{b}_{c,t}$ was estimated as:

$$(5.1) \quad \hat{b}_{c,t} = \sum_{f} \left[\left(\frac{\sum_{k} B_{c,k,f,t}}{\sum_{k} \sum_{s} C_{s,k,f,t}} \right) \cdot \sum_{s} L_{s,f,t} \right]$$

where $B_{c,k,f,t}$ is the mass of skates in catch category *c* of observed fishing haul *k* in fishery *f* and year *t*, $C_{s,k,f,t}$ is the retained catch of commercial fish species *s* reported by observers for haul *k*, and $L_{s,f,t}$ is the landed amount of species *s* in fishery *f* and year *t* taken from the official landings records. The estimates were stratified by fishery because this is the level at which decisions on fishery observer allocations are made (Benoît and Allard 2009). This stratification also accounts for differences in bycatch rate between fisheries.

The annual total numbers fishing trips, observed fishing trips, and observed trips that reported skates in each catch category are summarized in Table 5.2. A limited number of fisheries observer records for certain fisheries and years meant that observed trips from the fishery in adjoining years were sometimes used to calculate $\hat{b}_{c,t}$ (details in Table 5.1). With the exception of the 1991 cod fixed-gear fishery, sparse observer records generally corresponded to fisheries and years in which there was relatively little fishing effort and few landings.

5.2.3 *Estimating species-specific annual landings and discards*

Skate catches reported by fisheries observers were disaggregated into the constituent species using an empirical model that uses capture depth and date to predict the species composition of mixed groundfish catches (Benoît 2013 [Chapter 4]). Given that a skate has been observed in haul *k*, let $\pi_{j,k} = P(Y = j \mid d_k, t_k)$ be the probability that skate *Y* is of species *j*, given that it was caught at depth *d* (in meters) and at time *t* (day-of-year). Now define the linear model:

$$(5.2) \qquad \log\frac{\pi_{j,k}}{\pi_{J,k}} = \beta_{0,j} + \beta_{1,j}\cdot d_k + \beta_{2,j}\cdot d_k^2 + d_k \cdot \sum_{p=1}^{3}(\eta_{p,j}\cdot \sin(p\omega t_k - \delta_{p,j})),$$

$j=1,\ldots,J-1$

where $\omega = 2\pi/365$ is the fundamental annual frequency, *p* defines the cycle frequency (annual, $p=1$; semi-annual, $p=2$; tri-annual, $p=3$), $J=3$ is the number of skate species in the sGSL and $\beta_{0,j}$, $\beta_{1,j}$, $\beta_{2,j}$, $\eta_{p,j}$ and $\delta_{p,j}$ are parameters. The left-hand part of eqn. 5.2 is the logit for the response probability of species *j* relative to that of a chosen baseline species *J*, making this a baseline-category logits model (Agresti, 2002, p. 267-274). The choice of baseline species is arbitrary, given $\sum_{j=1}^{J}\pi_j(d,t)=1$; the J-1 equations defined by eqn 5.2 therefore determine the parameters required to define the logits of any pair of skate species. Justification for the model structure, including the use of three seasonal cycle frequencies, and details on how the parameters were estimated, how prediction uncertainty was estimated and how the model was validated are available in Benoît (2013 [Chapter 4]).

Predicted response probabilities $\hat{\pi}_{j,k,f,t}$ for observed fishing haul *k* in fishery *f* and year *t* were obtained using the logit-transformation of eqn 5.2:

$$(5.3) \quad \hat{\pi}_{j,k,f,t} = \frac{\exp(\boldsymbol{\beta}_j^{'} \mathbf{X}_{\mathbf{k,f,t}})}{\sum_{h=1}^{J} \exp(\boldsymbol{\beta}_h^{'} \mathbf{X}_{\mathbf{k,f,t}})}, \quad \text{for } j=1,\ldots,J \text{ with } \boldsymbol{\beta}_J = 0,$$

where $\boldsymbol{\beta}_{\mathbf{j}}$ and $\mathbf{X}_{\mathbf{k,f,t}}$ are shorthand for the vector of estimated parameters for species *j* and the matrix of explanatory variables for set *k*, respectively. From eqns. 5.1 and 5.3, the total annual biomass of skate species *j* for the catch category *c* was estimated as:

$$(5.4) \quad \hat{b}_{j,c,t} = \sum_f \left[\left(\frac{\sum_k B_{c,k,f,t} \cdot \hat{\pi}_{j,k,f,t}}{\sum_k \sum_s C_{s,k,f,t}} \right) \cdot \sum_s L_{s,f,t} \right]$$

A procedure for estimating the uncertainty in $\hat{b}_{j,c,t}$ that incorporates uncertainty related to the estimation of total annual catch as well as the estimation of species composition is described in a later subsection. However, I note here that when estimating species-specific landings, we are only interested in composition estimation uncertainty. This is because the official landings records are intended to provide a complete census of landings (i.e., they are assumed to be known without error). Consequently, annual species-specific landings were estimated as:

$$(5.5) \quad \hat{L}_{j,t} = L_{skate,t} \frac{\hat{b}_{j,c=r,t}}{\sum_{j=1}^{3} \hat{b}_{j,c=r,t}}$$

where $\hat{L}_{j,t}$ is the estimated amount of the official skate landings, $L_{skate,t}$, that is comprised of skate species *j*, in year *t*.

5.2.4 Estimation of annual mobile-gear discard survival rates

Benoît et al. (2012a) describe an approach for estimating fishery-scale rates of discard survival. Their approach was applied here to estimate the annual mobile-gear discard survival rates for each of the sGSL skate species. Information on survival rates for fixed-gear fishery discards in the sGSL is incomplete, preventing calculation of annual rates, though relative magnitudes are noted in the Discussion.

The estimation is based on the classification of fish vitality, a measure of the degree of injury, reflex impairment and liveliness of individual fish obtained by fishery observers just prior to discarding (details in Benoît et al. 2010). Vitality, v, is scored on an ordinal four-level scale ranging from v=1 (lively and uninjured) to v=4 (moribund) (Table 5.3). Ordinal schemes such as this have been shown to be good predictors of discard mortality in fish in general (reviewed briefly in Benoît et al. 2010) and skates specifically (Enever et al. 2009; Benoît et al. 2012a).

The estimation uses three conditionally-linked probabilities for individual fish which depend on characteristic of the fishing hauls in which the skates were captured. The first is the probability of belonging to each vitality level, conditional on factors related to capture (Benoît et al., 2010). This can be calculated directly when observer records of vitality are available for a fishery, or can be estimated using an empirical model as is done here (details below). The second is the probability of surviving capture and catch handling (i.e., probability of being alive when discarded), conditional on vitality and the amount of time spent on the ship's deck (Benoît et al. 2012a). The third is the probability of surviving after being discarded, conditional on vitality and on having survived capture and handling. Each of these probabilities is calculated using parameters that were estimated in the original studies (see Benoît et al. 2010, 2012a).

The conditional probability of belonging to a given vitality level was estimated using a multinomial regression model based on cumulative logits (Benoît et al. 2010):

$$(5.6) \quad P(v_k = r \mid \mathbf{z_k}, u_k) = \begin{cases} 1/(1+\exp(-\mu_r - \mathbf{z}_\mathbf{k}^{'}\boldsymbol{\varphi} \ - u_k)) & \text{for} \quad r = 1 \\ 1/(1+\exp(-\mu_r - \mathbf{z}_\mathbf{k}^{'}\boldsymbol{\varphi} \ - u_k))\ldots & \\ \quad -1/(1+\exp(-\mu_{r-1} - \mathbf{z}_\mathbf{k}^{'}\boldsymbol{\varphi} \ - u_k)) & \text{for} \quad r \in (2,3) \\ 1 - 1/(1+\exp(-\mu_{r-1} - \mathbf{z}_\mathbf{k}^{'}\boldsymbol{\varphi} \ - u_k)) & \text{for} \quad r = 4 \end{cases}$$

where $P(v_k = r \mid \mathbf{z_k}, u_k)$ is the probability of vitality level *v*=*r* in haul *k* (dropping the subscripts *f* and *t* for simplicity), for $r \in \{1,..,4\}$, conditional on the vector of relevant covariates found to affect skate vitality, $\mathbf{z_k}$, and a haul-specific random effect, u_k, $\mu_\bullet$ is a vitality level specific intercept and $\boldsymbol{\varphi}$ is a vector of parameter values. Predictions of vitality scores for haul *k* in the sGSL fisheries were made using covariates found to be relevant for skates: haul-specific total catch (kg), sea surface temperature (SST, ^{o}C) and deck time, (*dt*, minutes spent out of water) (Benoît et al. 2010). The value for catch was taken directly from the observer record for haul *k* and SST was calculated as the mean temperature from satellite-derived measurements for a 49 km^2 area and 9 day window, centered on haul *k* in space and time respectively. Values for *dt* were obtained using a relationship with catch amounts (Appendix C).

The capture and handling survival probability, $\rho(v, dt)$, depends on vitality and on *dt*, and was predicted using a logistic-regression:

$$(5.7) \quad \rho(v = r, dt = dt_k) = \begin{cases} 1 & \text{for} \quad r \in (1,2,3) \\ [1+\exp(-\psi_0 - \psi_1\, dt_k)]^{-1} & \text{for} \quad r = 4 \end{cases}$$

where ψ_0 and ψ_1 are estimated parameters for sGSL skates (Benoît et al. 2012a). Note that by definition all fish in vitality categories 1-3 have survived capture and handling.

The discard survival probability was predicted using the following mixture model:

$$(5.8) \quad S(v=r)=\begin{cases} 1 & \text{for} \quad r \in (1,2) \\ \tau \cdot \exp[-(72 \cdot \alpha)^{\gamma}]+(1-\tau) & \text{for} \quad r \in (3,4) \end{cases}$$

where α, γ and τ are parameters (details in Benoît et al., 2012a). Eqn 5.8 predicts survival to 72 hrs following release, which Benoît et al. (2012a) show is likely to also reflect long-term survival from discarding for captive held skates, and is likely to represent a maximum survival rate for skates in the wild (see Discussion). Though eqns. 5.6-5.8 were developed for sGSL skates in aggregate, the results are likely valid for the individual species since they appear to have comparable survival rates after accounting for the effects of body size, and temperature and depth of capture (Benoît et al. 2013 [Chapter 3]).

Combining eqns. 5.6, 5.7 and 5.8, the estimated survival rate of skates following capture, handling and release (i.e., the overall discard survival rate) from haul *k*, R_k, is given by:

$$(5.9) \quad R_k = \sum\nolimits_{r=1}^{4} P(v_k = r \mid \mathbf{z_k}) \cdot \rho(v=r, dt=dt_k) \cdot S(v=r)$$

Combining eqns.5. 4 and 5.9, the average annual overall discard survival rate for skate species *j* discarded in mobile-gear fisheries in year *t*, $\overline{R}_{j,t}$, is estimated as:

$$(5.10) \quad \overline{R}_{j,t} = \frac{\sum\limits_{f}\left(\sum\limits_{s} L_{s,f,t} \cdot \left(\sum\limits_{s}\sum\limits_{k} C_{s,k,f,t}\right)^{-1} \cdot \left(\sum\limits_{k} \hat{\pi}_{j,k,f,t} \cdot B_{c=d,k,f,t} \cdot R_k\right)\right)}{\sum\limits_{f}\left(\sum\limits_{s} L_{s,f,t} \cdot \left(\sum\limits_{s}\sum\limits_{k} C_{s,k,f,t}\right)^{-1} \cdot \left(\sum\limits_{k} \hat{\pi}_{j,k,f,t} \cdot B_{c=d,k,f,t}\right)\right)}$$

5.2.5 Error estimation and propagation

Uncertainty in the estimated bycatch amount and mortality was estimated using empirical boostrapping for three key estimated quantities, as part of a Monte Carlo simulation (Efron and Tibshirani 1993). Uncertainty in annual catch estimates (eqn. 5.1) related to catch sampling by the observer survey was simulated by randomly selecting, with replacement, observed fishing trips within fisheries, *f*, and years, *t*. Uncertainty in the response probabilities in eqn. 5.3 was simulated by re-sampling the data used to fit eqn. 5.2 and obtaining a new model fit for each Monte Carlo iteration (details in Benoît 2013 [Chapter 4]). Uncertainty for the discard survival rate $\overline{R}_{j,t}$ (eqn 5.10) was simulated using the bootstrapping procedure described in Benoît et al. (2012a, their Appendix B), with the exception that the simulation of deck times proceeded as described in Appendix C (this thesis). One thousand iterations were found to be sufficient to provide stable estimates of uncertainty for species specific discards and landings and discard mortality.

5.2.6 Relative fishery catches

Trends in the ratio of fishery removals and estimated trawlable biomass from a fishery-independent bottom-trawl survey generally reflect trends in fishing mortality (e.g., Sinclair 1998). Here, trends in relative fishery catches were broken down into four categories based on the estimates derived from the fishery observer data: landings, dead and live mobile-gear fishery discards, and fixed-gear fishery discards. The ratio with trawlable biomass of landings plus dead mobile-gear fishery discards provides a minimum estimate of relative fishing mortality, knowing that a portion of the estimated live mobile-gear fishery discards and fixed-gear fishery discards very likely also died as a result of capture and release. Note that the ratio can exceed a value of 1 as a result of lower catchability and/or availability to the survey compared to the fishery.

5.3 Results

Total official skate landings in the sGSL have varied considerably over time, from a high of around 130 tonnes per year in the mid-1970s, to a low of 0 to 3 tonnes per year during much of the 1980s and into the early 1990s (Fig. 5.1). After a peak of 56 tonnes in 1994, landings have generally declined to 2 to 5 tonnes per year in the late 2000s.

Estimates based on retained skate catches reported by observers predict landings well (Fig. 5.1). As one would expect from a reliable predictor, predicted landings exceed observed landings in approximately half of the years (13 of 21) (Fig. 5.1), and there was no significant autocorrelation in residual values (observed-predicted landings; Appendix

Fig. C1). Confidence intervals for the estimates were large, a reflection of the small number of trips covered by observers that reported retained skate catches: on average 4.8% of observed trips and 0.22% of all fishing trips (Table 5.2). Confidence intervals for predicted landings overlapped with observed values in 17 of 21 years, which is smaller than the expected coverage of around 20 of 21 years. This result may partly reflect stochasticity. Assuming that the estimation approach is the correct one, the probability of having a coverage of 17 or fewer intervals (i.e., of the approach doing this 'badly' or worse) is 0.019, based on the binomial cumulative distribution function with 21 trials and a probability of 'success' of 0.95. Though this indicates a less than ideal coverage, the result is not entirely implausible either. Another possible explanation is that the estimation approach is not entirely correct, which is discussed in the Discussion.

Estimated landings of Winter Skate were highest in 1995 at 7.63 tonnes, declining to 0.04 tonnes in 2007 (Fig. 5.2a). They then rose steadily to 1.5 tonnes in 2010 before declining to low values in 2011. Estimated landings of Thorny Skate and Smooth Skate peaked in 1994 at around 38 tonnes and 16 tonnes respectively, with a smaller peak in 2004, followed by low values of around 1.0-2.7 tonnes and 0.5-1.5 tonnes (Fig. 5.2b,c).

Estimated discard amounts for each of the three skate species exceeded estimated landings by an order of magnitude or more in most years (Fig. 5.2). A notable exception is that approximately 25% and 34% of estimated Winter Skate captures were predicted to have been landed in 2009 and 2010 respectively. Estimated discards for each skate species have declined since the early 1990s (Fig. 5.2). In 1991-1992, Thorny Skate was the most commonly discarded skate (490 tonnes/year on average), followed by Winter Skate (210 tonnes/year) and Smooth Skate (100 tonnes/year). Following a large decline in estimated Winter Skate discards in 1993, skate discards were dominated by Thorny Skate, followed by Smooth and Winter Skates. Average estimated annual discard amounts in the 2006-2011 period were 53.7, 28.0 and 6.2 tonnes for Thorny, Smooth and Winter Skates respectively.

The proportion of the total uncertainty in species-specific discards that was caused by uncertainty in the estimation of discarded amounts varied by species: 0.97 for Winter

Skate, 0.90 for Smooth Skate and 0.93 for Thorny Skate. The remaining uncertainty was due to uncertainty in disaggregating catches into the constituent species.

The majority of estimated Winter Skate discards came from mobile-gear fisheries, principally those targeting the coastal flatfish, Winter and Yellowtail Flounder (Fig. 5.3a). The proportion of estimated Winter Skate discards coming from fixed-gear fisheries, principally targeting Winter Flounder and Cod using gillnets, declined from a peak of around 0.4 in 1999 to an average of 0.05 in the late 2000s. During most of the 1990s, estimated discards of both Smooth and Thorny Skates came mostly from mobile-gear fisheries, principally those targeting the offshore flatfish, American Plaice and Witch Flounder (Fig. 5.3b,c). Beginning in 1998 and through to the mid-2000s, an increasing proportion of the estimated discards came from a gillnet fishery for Greenland Halibut. The proportion coming from mobile-gear fisheries peaked again slightly during 2006-2008, but fell back to below 0.4 and 0.5 in 2009-2011 for Smooth and Thorny Skates respectively.

Estimated survival rates for discarded skates were generally elevated, especially for Winter Skate. The estimated survival rate for Winter Skate discarded in mobile-gear fisheries was lowest in 1991 at around 0.6, varied around 0.9 from 1992 to 2006, and was around or above 0.95 for 2007 to 2011 (Fig. 5.4a). The estimated survival rates of Smooth and Thorny Skates followed similar trends to one another (Fig. 5.4b,c). Rates were low in the early 1990s (around 0.5), rising to values between 0.8 and 0.9 through to 2001, followed by an oscillation of low, high and low values. Estimates for 2010-2011 were the lowest (and most uncertain) in the series at around 0.35 and 0.39 for Thorny and Smooth Skates, respectively. For all three species, trends in estimated survival rates corresponded to trends in the relative contribution of different fisheries to the capture of skates (Fig. 5.3).

The relative fishery catches of all three skate species have generally declined since 1991, especially for Smooth Skate and Thorny Skates (Fig. 5.5). Whether relative fishing mortality for Smooth and Thorny Skates actually decreased or remained generally stable depends on the survival rate for skates discarded in the fixed-gear Greenland halibut fishery and the degree to which mobile-gear discard survival rates were overestimated. For example, if the fixed-gear survival rate was high, then overall fishing mortality is likely to have declined. However, if the fixed-gear survival rate was low and there was only a slight over estimation of the mobile-gear survival rate, then fishing mortality may have largely have varied without trend.

5.4 Discussion

The maintenance of sustainable fishery removals and of biodiversity are key objectives of an ecosystem approach to fisheries (e.g., Pikitch et al. 2004; Worm et al. 2009). Ensuring that incidentally-captured non-commercial species are not adversely affected by fisheries requires estimates of their losses to fisheries, as exemplified by the sGSL skates. This study demonstrates why this estimation may often not be straightforward for species that are mainly discarded, while providing an example of how it may nonetheless proceed, despite numerous sources of uncertainty. The key to the approach is dividing the estimation process into tractable linked steps that can be individually assessed and (ideally) validated, and then assembled to provide overall estimates with associated uncertainty estimated via Monte Carlo simulation.

A key result of this study was finding that skate landings could reliably be predicted from reports of retained catch in fisheries observer surveys with modest coverage levels. This result is noteworthy because it validates the catch estimation process for landings and suggests that discard amounts are also well estimated. In doing so, it suggests that deployment and observer effects identified for sGSL fisheries do not result in biased sampling of skate catches, contrary to the general predictions of Benoît and Allard (2009) for commercially-important species. The result bolsters the validity of using the model in eqn 5.2 to predict the species composition of catches by suggesting that skate catches sampled by fisheries observers are representative of catches in the fisheries as a whole. Given the apparent general reliability of that model based on a validation exercise (see Benoît 2013 [Chapter 4]), it appears that species-specific landings and discards of sGSL skates can be estimated with some confidence.

Despite finding that catch amounts are likely to be reasonably well estimated, at least two key uncertainties remain. The first key uncertainty concerns the non-random deployment of observers in many sGSL fisheries, which may have resulted in an overestimation of the precision of estimated catch amounts (Benoît and Allard 2009). Benoît and Allard (2009) used a simulation, based on index-fishery data with 100% observer coverage, to estimate the degree to which precision could be overestimated for discards in general. Applying their approach to skates suggests that the 'true' uncertainty in skate catch might be 1.5-2.0 times greater, or more, than the uncertainty estimated here when assuming that skate catches sampled by observers were independently and identically distributed (details available in Appendix C). This may explain the less than ideal coverage of confidence intervals for estimated skate landings. The second key uncertainty concerns the empirical model used to disaggregate bulk skate catches into species-specific catches (eqns. 5.2 and 5.3). Though this model fit survey data for skates well, validation of its ability to provide unbiased predictions of the species composition of fishery catches has only been undertaken for sGSL flatfish (Benoît, 2013 [Chapter 4]). It is not presently possible to directly validate the model for skates and its validity must therefore be inferred based on the results for flatfish. Furthermore, the confidence intervals for the predictions of species composition from that model may also be too narrow (see Benoît 2013 [Chapter 4]). Though further research may help reduce these uncertainties for retrospective estimations, modifications to the observer programs to enhance the randomness of deployment and decrease the possibility of observer effects (discussed in Benoît and Allard, 2009), and to improve the identification of captured species, could reduce or eliminate future such uncertainties at the source.

Declining trends in the catches of Thorny and Winter Skates are consistent with declining trends in their abundance (Benoît and Swain, 2008; Swain et al., 2012). Additionally, catches of all three skate species declined to some degree as a result of long-term decreases in the relative fishing rate (catches per unit of trawlable biomass). Based on population modelling that used previous estimates of catch and discards, fishing mortality for Winter Skate has been low since the early 1990s (Swain et al. 2009a). Meanwhile, natural mortality of adult Winter Skate has increased such that it places them at a very elevated risk of extirpation (COSEWIC 2005; Swain et al. 2009a). Current population models for Thorny and Smooth skates do not separate the contributions of fishing and natural mortality (Swain et al. 2012). However, the trends in relative fishing rate presented here imply that fishing mortality for these species since 1991 has been either stable or declining, depending on the degree to which discard mortality rates were underestimated in mobile-gear fisheries and the magnitude of these rates in fixed gear fisheries. The implied trends in fishing mortality run counter to an estimated increase in total mortality for large juvenile Thorny and Smooth skates (individuals 33-50 and 33-47 cm respectively), but may explain a slight decline in otherwise high rates of adult mortality in the 2000s compared to the 1990s (Swain et al. 2012).

The estimated survival of skates discarded in mobile-gear fisheries varied between species, and over time for Thorny and Smooth Skates, as a result of the observed conditions and expected deck time experienced by fish during capture and handling. These estimates, which ideally should be validated by an independent study of discard survival using fish tagging, likely represent a maximum estimate of survival because they do not include factors such as the effect of enhanced predation risk resulting from the temporary impairment of reflexes due to capture, handling and release in the fishery (e.g., Ryer 2004; see discussion in Benoît et al. 2012a). The estimates nonetheless help establish a general scale for possible discard-related losses and can serve to highlight how conditions in the fisheries catching skates may be influencing these losses. A key missing element is a survival rate estimate for skates discarded in the sGSL Greenland halibut gillnet fishery, which has produced the majority of estimated Thorny and especially Smooth Skate discards since the late 1990s. Gillnet soak times for this fishery are unusually long, with a median of 3 days, resulting in an average within-net mortally rate of at least 63% for the target species (personal communication, S. Ménégat, Université du Québec à Rimouski, Canada). The sensitivity of skates to such long soak times is not known, and studies of skate mortality in gillnet fisheries would be beneficial.

The estimated discard survival rates suggest a high potential for successful live release of incidentally caught individuals, particularly for Winter Skate. Though exploitation rates for sGSL Winter Skate captured in groundfish, shrimp and scallop fisheries are estimated to be low and far exceeded by elevated rates of natural mortality (Swain et al. 2009a; Benoît 2011), the introduction to the fisheries of rules for mandatory discarding of skates in a manner that minimizes harm could reduce fishing mortality to negligible levels. This can only be beneficial, given the recent increases in landings of the endangered sGSL Winter Skate (COSEWIC 2005). Likewise, mandatory discarding rules would also benefit sGSL Thorny and Smooth Skates given their reasonable prospects for discard survival. The costs to the fishing industry of mandatory skate discarding is likely to be relatively minor given the small magnitude of skate catches and their low landed value (CAN$0.29/kg), relative to other species: cod ($1.28/kg), Atlantic halibut ($6.98/kg), Greenland halibut ($1.99/kg) and other flatfish ($1.05/kg-$1.20/kg) (values based on 2005-2010 averages from official landing statistics).

This study presents the elements required to estimate annual losses of skates due to fishing in the sGSL since 1991. An important next step will be to incorporate these estimates in population models for sGSL Thorny and Smooth Skates, populations which have experienced substantial increases in adult mortality leading to large declines in adult abundance and for which such modelling has yet to be undertaken (Swain et al. 2012). Establishing the relative roles of fishing and natural mortality is an important step in understanding the causes of the declines (Benoît and Swain 2008; Swain et al. 2009a; Benoît et al. 2011a). As was the case for sGSL Winter Skate (Benoît 2006), a key challenge will be estimating discards and species-specific landings for the years prior to 1991, when fishing effort in the sGSL was considerably greater (Benoît et al. 2012b) and observer coverage in all fisheries was considerably smaller or absent.

Table 5.1. Commercial fisheries (identified by number) included in the estimation of skate bycatch. Fisheries are defined by target species and gear class, fixed gear (F) and mobile gear (M). Also provided is the year in which a 100% dockside monitoring program (DMP) was introduced to each fishery, and a summary of the observer data pooling used in the analysis for the fisheries and years with inadequate observations. No pooling across years was employed for a given fishery for years not listed here.

	Target species	Gear class	DMP	Years requiring pooled data	Pooled years
1.	Atlantic Cod (*Gadus morhua*)	F	1994	1991	1991-1993
				1993-1997	1991-1999
2.	Atlantic Cod	M	<1991	-	-
3.	Redfish (*Sebastes* spp.)	M	<1991	1998,1999	1991-1999
				2000-2008; 2010	2000-2011
4.	Atlantic Halibut (*Hippoglossus hippoglossus*)	F	1997	1991-1993, 1996, 1997	1991-1999
5.	Greenland Halibut (*Reinhardtius hippoglossoides*)	F	1997	1992	1991-1994
6.	White Hake (*Urophycis tenuis*)	F&M	1995[1]	1991-1995	1991-1995
7.	American Plaice (*Hippoglossoides platessoides*)	F	2003	1991-1993, 1998-2007	1991-2010
8.	A. Plaice and Witch Flounder (*Glyptocephalus cynoglossus*)	M	1994	-	-
9.	Winter Flounder (*Pseudopleuronectes americanus*)	F	2003	1991-2011	1991-2011
10.	Winter Flounder	M	1998	2006-2011	2000-2011
11.	Yellowtail Flounder (*Limanda ferruginea*)	M	2002	1991-1998	1995-1998
				1999-2002	2000-2005

	Target species	Gear class	DMP	Years requiring pooled data	Pooled years
12.	Spiny Dogfish (*Squalus acanthias*)	F	1994	1991, 1992	1993-1995
				2000-2006	1998-2006
13.	Northern Shrimp (*Pandalus borealis*)	M	1991	-	-

[1] The directed White Hake fishery has been under moratorium since 1995

Table 5.2. Annual summary for the sGSL of the total number of fishing trips and summary of trips covered by fishery observers (total, reporting discarded skates, and reporting retained skates).

		Observed trips		
Year	Total fishing trips	Total	Reporting discarded skates	Reporting retained skates
1991	19689	416	249	8
1992	16929	324	242	3
1993	12041	207	180	19
1994	9056	307	211	17
1995	5539	259	172	29
1996	4544	213	129	14
1997	5766	174	128	14
1998	4975	238	180	12
1999	7835	238	145	10
2000	7668	377	213	16
2001	6214	330	145	6
2002	5427	306	161	12
2003	3353	249	168	24
2004	4775	390	183	24
2005	4679	336	158	12
2006	4044	267	141	6
2007	2928	160	90	9
2008	2803	148	89	2
2009	2646	125	89	3
2010	3829	125	74	4
2011	3324	109	62	5

Table 5.3. Description of the codes used by onboard observers to score the pre-discarding vitality of individual fish (from Benoît et al., 2010).

Vitality	Code	Description
Excellent	1	Vigorous body movement; no or minor[a] external injuries only.
Good / Fair	2	Weak body movement; responds to touching/prodding; minor[a] external injuries.
Poor	3	No body movement, but fish can move operculum; minor[a] or major[b] external injuries.
Moribund	4	No body or opercular movements (no response to touching or prodding).

[a] Minor injuries were defined as ‘minor bleeding, or minor tear of mouthparts or operculum (≤10% of the diameter), or moderate loss of scales (i.e. bare patch)’.

[b] Major injuries were defined as ‘major bleeding, or major tearing of the mouthparts or operculum, or everted stomach, or bloated swim bladder’.

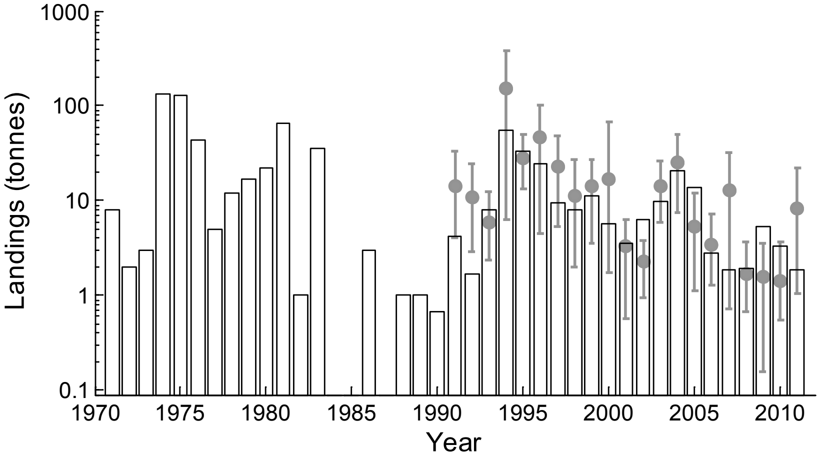

Figure 5.1. Reported landings of skates in the sGSL, 1971-2011 (bars) and estimated landings based on fisheries observer reports of retained skate catches, 1991-2011 (mean and 95% confidence interval; grey symbol and error bars). Note the log-scale for landings (tonnes).

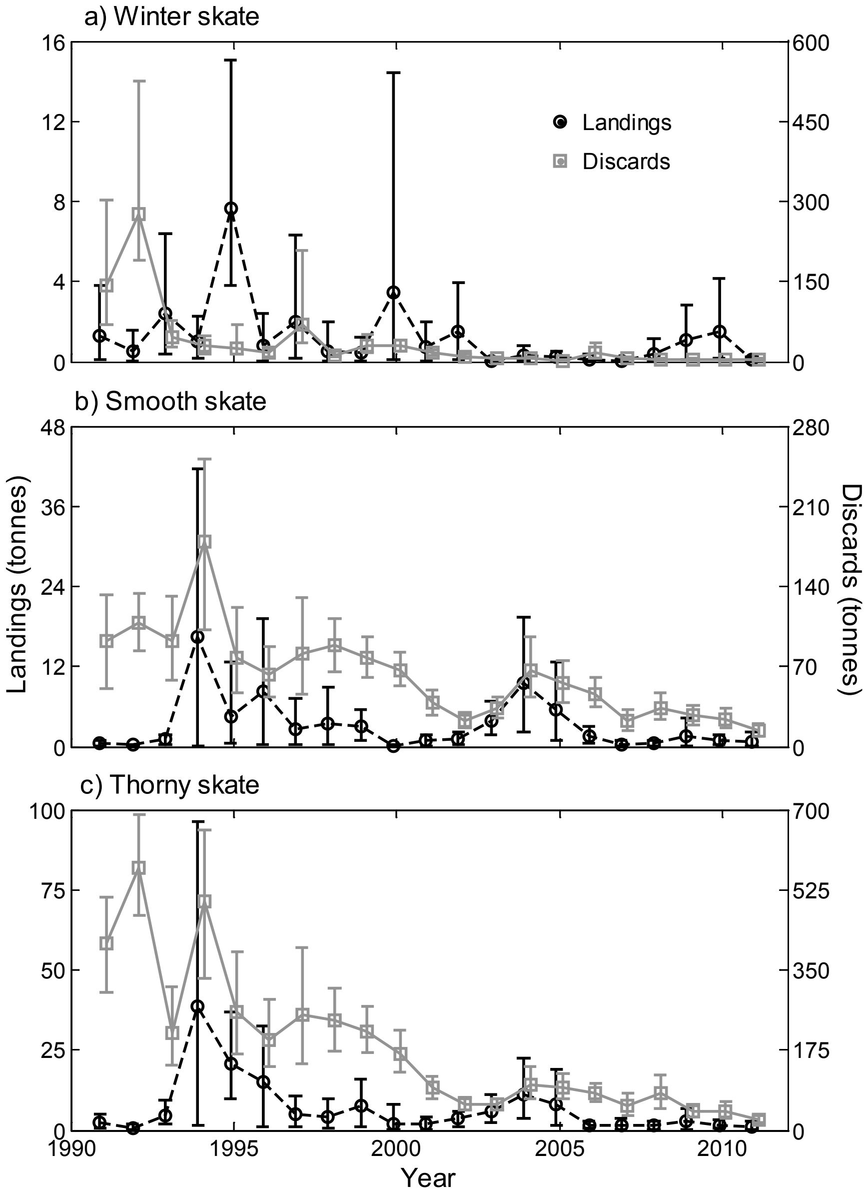

Figure 5.2. Estimated landings (black circles) and discards (grey squares) for each of the three sGSL skate species, 1991-2011. The error bars are estimated 95% confidence intervals. The annual values have been slightly horizontally offset to make the differences between the two series clearer.

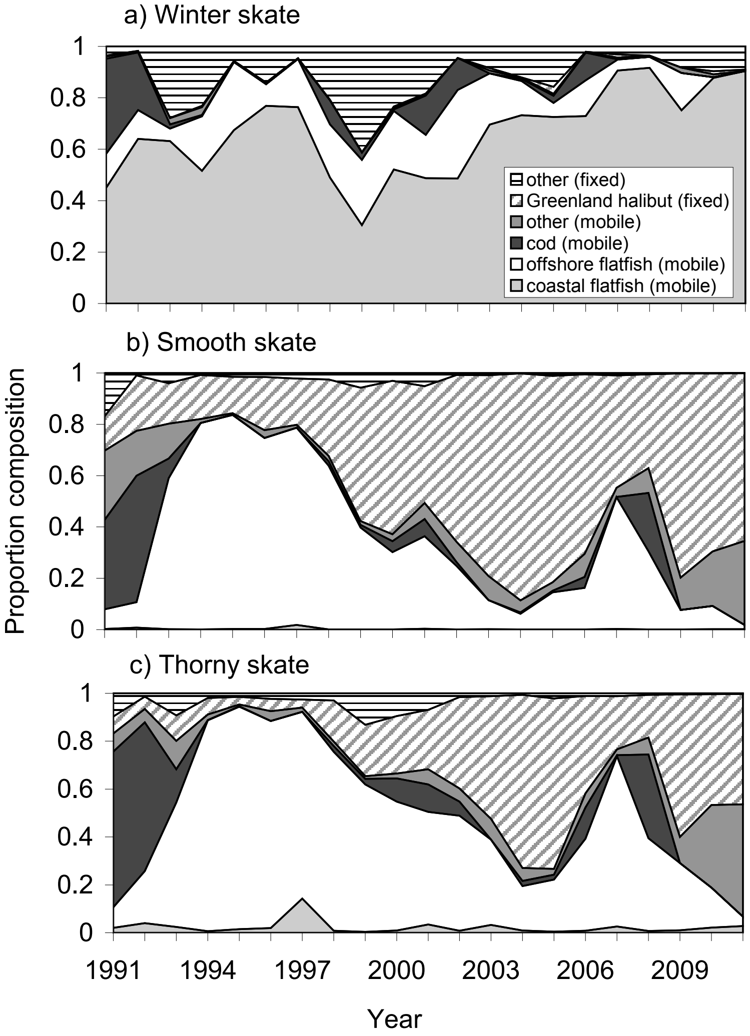

Figure 5.3. Annual estimates of the contribution of the various fisheries to the discards of each sGSL skate species. The graph areas for mobile-gear fisheries are presented in solid shading whereas the areas for fixed-gear fisheries are presented using a striped fill. Coastal flatfish mobile-gear fisheries are those that target Winter and Yellowtail Flounder, whereas the offshore flatfish mobile-gear fisheries are those that target Witch Flounder and American Plaice.

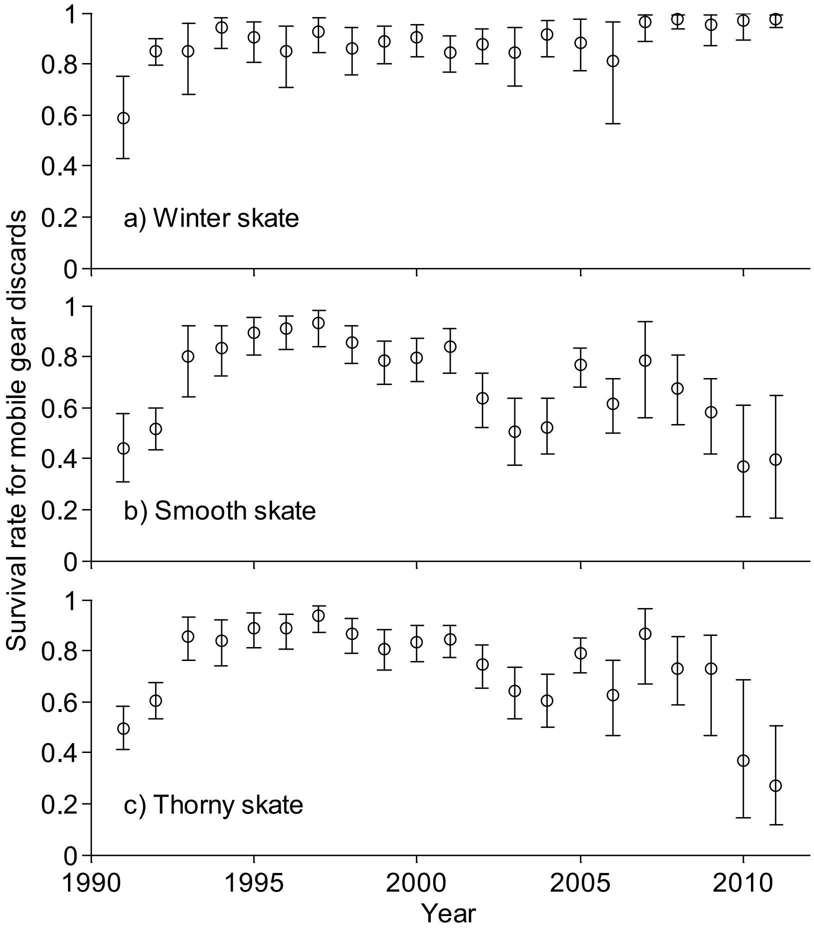

Figure 5.4. Species-specific annual estimates (mean and 95% confidence interval) of the survival rate of Winter, Smooth and Thorny skates discarded in mobile-gear fisheries, 1991-2011.

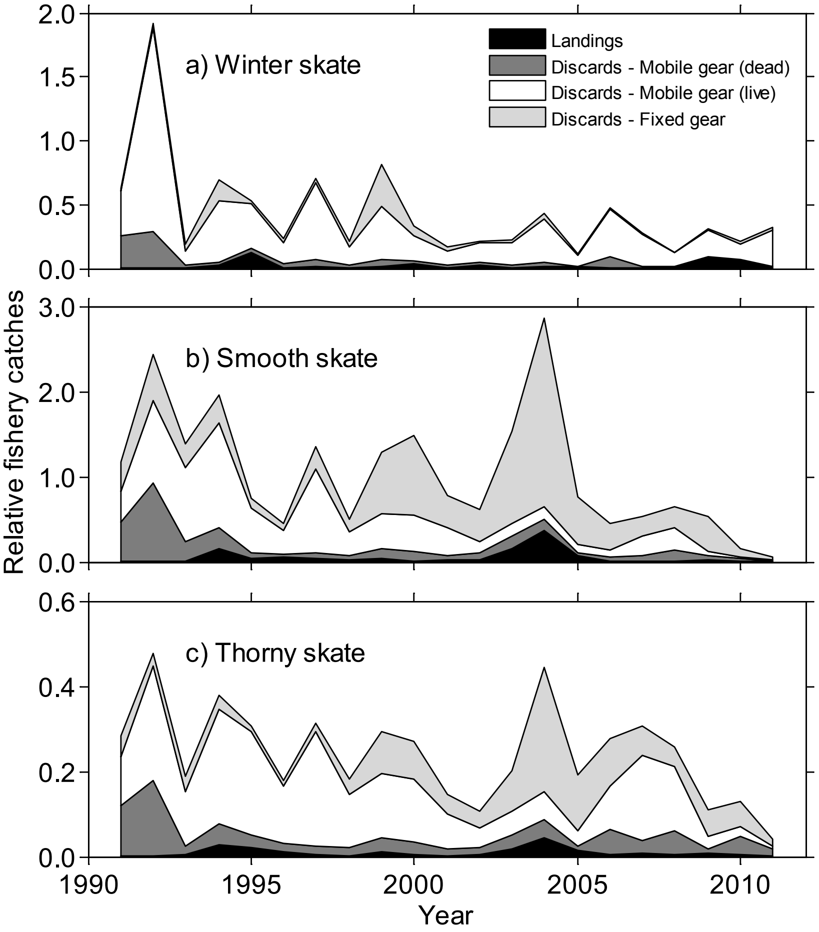

Figure 5.5. Relative fishery catches (catch/survey trawlable biomass) for Winter, Smooth and Thorny skate, 1991-2011. Catches are separated into landings, dead and live mobile-gear fishery discards, and fixed-gear fishery discards, based on the estimates derived from the fishery observer data. The separation of mobile-gear discards is based on the estimated species-specific annual rates of discard survival.

Chapter 6. A Generalized Model for Longitudinal Short- and Long-Term Mortality Data for Commercial Fishery Discards and Recreational Fishery Catch-and-Releases.

6.0 Abstract

Conservation concerns and new management policies such as the implementation of ecosystem-based approaches to fisheries management are motivating an increasing need for estimates of mortality associated with commercial fishery discards and released fish from recreational fisheries. Traditional containment studies and emerging techniques using electronic tags on fish released to the wild are producing longitudinal mortality-time data from which discard or release mortalities can be estimated, but where there may also be a need to account analytically for other sources of mortality. In this study, we present theoretical and empirical arguments for a parametric mixture-distribution model for discard mortality data. We show analytically and using case studies for Atlantic cod (*Gadus morhua*), American plaice (*Hippoglossoides platessoides*) and winter skate (*Leucoraja ocellata*) how this model can easily be generalized to incorporate different characteristics of discard mortality data such as distinct capture, post-release and natural mortalities, and delayed mortality onset. In simulations over a range of conditions, the model provided reliable parameter estimates for cases involving both discard and natural mortality. These results support this modelling approach, indicating that it is well suited for data from studies in which fish are released to their natural environment. The model was found to be less reliable in simulations when there was a delay in discard mortality onset, though such an effect appears only in a minority of existing discard mortality studies. Overall, the model provides a flexible framework in which to analyse discard mortality data and to produce reliable scientific advice on discard mortality rates and possibilities for mitigation.

6.1 Introduction

A large proportion of worldwide commercial fishery catches are discarded for economic or regulatory reasons, with rates varying by region, species, and gear-type (Alverson 1997; Harrington et al. 2005). Discarding is typically a wasteful practice that may have far reaching consequences on populations and ecosystems (e.g. Kappel 2005; Bellido et al. 2011). Meanwhile, catch-and-release in recreational marine and freshwater fisheries is becoming a more common practice given an increasing conservation ethic among anglers and the implementation of management measures that require such behaviour; however, mortality rates and thus the resulting conservation benefits from such practices can vary greatly by region and species (e.g. Cooke and Schramm 2007; Cowx et al. 2010).

Many fisheries management agencies are trying to limit discarding by improving gear selectivity to reduce incidental catch, or by instituting regulations that minimize discarding. In some instances, the amount of bycatch in a fishery has been capped either overall or as a percentage of directed species catch. Additionally, some fisheries management bodies have instituted mandatory landing of fish that would otherwise be discarded, as will occur under the revised European Union Common Fisheries Policy (CFP; European Union 2013). Such landing obligations provide a strong incentive for harvesters to reduce incidental catch; however, they can also have the unintended consequence of increasing fishing mortality if the survival rate of otherwise discarded fish is high. In recognition of this, the CFP has provisions that allow for discarding in instances where there is a demonstrated high likelihood of survival. Consequently, additional studies on discard mortality will be required to this end. The need for such studies is also being motivated elsewhere by the desire to establish management measures that can improve the likelihood of successful live release, such as for protected or depleted species (e.g., Grant and Hiscock 2014) or in recreational fisheries (e.g., Cooke and Schramm 2007), as well as the need to account for discard-related losses of incidentally captured fish in population assessments (e.g., Benoît 2013).

Many experimental approaches have been used to estimate discard or post-release mortality rates. These methods typically involve fish that are obtained on-board commercial or recreational fishing vessels, during scientific research trips that are designed to approximate typical fishing operations, or from simulated fishing activities in the laboratory (Pollock and Pine 2007; Gilman et al. 2013; ICES 2014). The fate of these fish is then observed by keeping them in captivity (aquaria or sea cages; e.g. Mandelman et al. 2013), inferred via recaptures of conventionally-tagged fish (e.g. Wilson and Burns 1996; Kaimmer and Trumble 1998), or from the inferred activity of fish tagged with acoustic transmitters (e.g. Yergey et al. 2012; Baktoft et al. 2013) or pop-up satellite archival tags (PSATs; e.g. Campana et al. 2009). While varied in their experimental design, all approaches generate one of the two types of mortality data. "Cross sectional" data take the form of the numbers of dead and live animals at one or more fixed points in time. In contrast, "longitudinal" mortality data are made up of the times at which individuals died or at which they were last observed alive. Ongoing tracking of the fate of individuals is required to obtain these event times. Individuals that were alive when last observed at time *t* provide right-censored observations in that their time of death is only known to occur after *t*. In fact, cross sectional data are merely a special case of longitudinal data, in that individuals that are alive at time *t* are right-censored observations, while dead ones are left-censored observations, that is, observations for which the time of death is only known to have occurred before *t* (e.g. see application in Benoît et al. 2013 [Chapter 3]). Compared with cross-sectional data, longitudinal data have the advantage that they describe survivorship over time (the survivor function), providing information on the mechanisms affecting mortality and potentially helping to distinguish different sources of mortality. Furthermore, some form of longitudinal data is required to ensure full accounting of discard mortality (Davis 2002).

Traditionally used methods for the analysis of longitudinal data generally fall under the class of survival or event analysis. They model survival as a function of time using non-parametric [e.g. Kaplan-Meier method (KM)], semi-parametric (e.g. Cox proportional-hazards regression), or parametric forms (Cox and Oakes 1984). Non-parametric models have the advantage of making very few assumptions about the survivor function, but cannot make predictions beyond the range of the data and inferences on the mechanisms underlying the shape of the survivor function are necessarily subjective. In contrast, parametric models allow predictions beyond the range of the observations and models can be built based on assumed forms of survivorship, including forms with mechanistic interpretations for survival patterns over time. Models making different assumptions about mechanisms can then be compared objectively using data. This is a particularly useful feature for the analysis of discard mortality data, where researchers are often ultimately interested, for example, in parsing out the effects of discard and background (or natural) mortality, in distinguishing capture and post-release mortality, and in objectively determining how long after release fish in a sample will continue to die as a direct result of capture and release events.

In this study, we elaborate on a parametric survival analysis model that appears particularly well-suited for the analysis of discard and release mortality data (hereafter termed discard mortality data). This model, which comprises a latent mixture of survivor functions, was first applied to this field of study by Benoît et al. (2012). We begin by briefly describing this basic mixture model and by presenting supporting arguments and examples. We then show, analytically and by three brief case studies, how this model can be generalized to incorporate different characteristics of discard mortality data such as distinct capture, post-release and natural mortalities, and delayed mortality onset. We also use simulations to evaluate whether and under what conditions the model can reliably estimate the parameters for two challenging cases: separating fishing-related and natural mortalities and survival functions that include a delay in the onset of mortality.

6.2 The Model

6.2.1 Basic structure

The cornerstone for the generalized model is a basic parametric survivor function. Here we have chosen the commonly used Weibull-type survival function (Cox and Oakes 1984, their chapter 2):

$$(6.1) \qquad S(t) = \exp[-(\alpha \cdot t)^{\gamma}]$$

where $S(t)$ is the survival probability to time t, and α and γ are, respectively, the scale and shape parameters of the underlying Weibull distribution. This simple function is particularly attractive due to its flexibility, whereby different values of α and γ can produce a range of survival function shapes commonly encountered in ecological data such as Deevey's (1947) Type I, II and III survival functions (Fig. 6.1). Notably, exponential mortality, typically assumed in stock assessments, is a special case of eqn. 6.1 for $\gamma=1$. The Weibull model has been successfully applied to discard survival data in many studies (e.g., Neilson et al. 1989; Campana et al. 2009; Depestele et al. 2014).

A basic assumption of eqn. 6.1 and of other basic parametric survivor functions is that they represent a mortality process that begins at time $t=0$ and for which $S(t)$ is continuously decreasing as a function of t. To the extent that discard mortality data conform to a basic parametric survivor function and that the mortality is believed to result solely from the capture, handling and release (CHR) process, the analyst must conclude that discard-related mortality is complete and survival is nil. While this may be the case in some instances, it is not the norm [see review presented in Fig. 4 of Benoît et al. (2012)]. Instead, many longitudinal discard mortality studies have revealed a pattern of initial loss of individuals during the first hours or days of the study, followed by little or no losses of the remaining survivors.

To account for these patterns, Benoît et al. (2012) relaxed the assumption that $S(t)$ is the same for all individuals in a sample of discarded animals, instead assuming that the sample was composed of a latent mixture of two groups of individuals; those that were adversely affected by the CHR process and which will die as a result, and those that were unaffected (i.e., immune individuals). Mathematically, this can be written as:

$$(6.2)\quad S(t) = \pi \cdot S_A(t) + (1 - \pi)\cdot S_I(t)$$

where $S(t)$ is the overall survival function for the sample, π is the probability that an individual is adversely affected, and $S_A(t)$ and $S_I(t)$ are the survival functions for the affected and immune groups, respectively. Benoît et al. (2012) were interested in the short-term (scale of days) mortality of fish held for observation in captivity following capture and handling under commercial fishery-like conditions. At such a short time-scale relative to natural longevity, and given the exclusion of predators, the authors assumed $S_I(t)=1$; that is that the likelihood of death during the experiment for individuals that were not adversely affected by CHR was essentially nil. This assumption enhances model identifiability when fitting to data. Clearly the validity of this assumption declines if experimental subjects are exposed to predators and as the duration of the observation period increases, thereby increasing the likelihood of mortality from natural causes during the span of the experiment. Below we show how this assumption can be relaxed.

Using eqn. 6.2, modelling $S_A(t)$ using the Weibull survival function as in eqn. 6.1 and setting $S_I(t)=1$, we obtain

$$(6.3) \quad S(t) = \pi \cdot \exp[-(\alpha \cdot t)^{\gamma}] + (1-\pi)$$

from which it is easy to see that as $t \rightarrow \infty$, $S(t) \rightarrow 1-\pi$, where π is the discard mortality rate. When $\pi=1$, all individuals are said to be adversely affected by the fishing event, such that $S(t)= S_A(t)$ and the ultimate CHR survival rate is 0. With eqn. 6.3, there is no need to arbitrarily define a time at which to evaluate $S(t)$ such as to provide an estimate of discard mortality (e.g. Neilson et al. 1989). In fact, eqn. 6.3 can be re-arranged to solve for t and therefore provide an estimate of the time when essentially all (e.g. 99.9%) of the CHR-related mortality has occurred:

$$(6.4) \quad t_{S(t)\approx 1-\pi} = (\alpha)^{-1}(-\log(0.001))^{1/\gamma}$$

The influence of covariates believed to influence discard mortality can be incorporated in $S_A(t)$, typically by including them in the α term, in π, or both (Benoît et al., 2012a; Depestele et al., 2014). An exponential function is typically used for covariate effects on α, $\alpha = \exp(\mathbf{X}_1'\boldsymbol{\beta}_1)$, whereas a logistic function is used for π, $\pi = [1+\exp(-\mathbf{X}_2'\boldsymbol{\beta}_2)]^{-1}$, where $\mathbf{X}_1$ and $\mathbf{X}_2$ are design matrices for the covariates and $\boldsymbol{\beta}_1$ and $\boldsymbol{\beta}_2$ are vectors of parameters for the effect of the covariates. The same set of covariates need not be used for the effects on α and on π, as indicated by the different subscripts for the two generic design matrices above.

Researchers are increasingly modelling discard mortality as a function of semi-quantitative status indicators that summarize the degree of injury of individuals just before release, the degree of impairment of movement and response to stimuli, or a combination of the two which is often termed vitality or condition (e.g. Richards et al. 1995; Campana et al. 2009; Benoît et al. 2012; Depestele et al. 2014). These measures (hereafter, status indicators) are known to be good predictors of eventual mortality (Davis and Ottmar 2006; Humborstad et al. 2009; Davis 2010), and are particularly useful in scaling up the results of small-scale CHR experiments to the fishery-wide level (Richards et al. 1995; Benoît et al. 2012; ICES 2014).

Benoît et al. (2012) found strong support for the model in eqn. 6.3, with status indicator effects on π for four of the five species they studied (e.g,. Fig. 6.2c, d), which included Atlantic cod (*Gadus morhua*), two flatfish species and skates (*Rajiidae* spp.). Similarly, Depestele et al. (2014) also found support for four species captured in a North Sea commercial fishery (cod, skates and two flatfish). Further support for this model is also evident in the data for discarded blue sharks (*Prionace glauca*), whose fate was inferred using data from PSATs (Fig. 6.2a; Campana et al. 2009), and in recent data for scallops (*Placopecten magellanicus*) captured in a commercial dredge fishery and held for observation in ship-board refrigerated seawater tanks (Fig. 6.2b; R. Knotek, University of New England, pers. comm.). In all of these cases, patterns in survivorship are characterized by initial loss of individuals during the first few hours or days after release to the water, followed by the absence of mortality thereafter (Fig. 6.2). Furthermore, in each case the level at which survivorship reaches an asymptote, $1-\pi$ (the discard survival rate), is inversely related to an individual's semi-quantitative pre-release status.

6.2.2 Generalization of the basic model

While the mixture distribution model in eqn. 6.3 appears appropriate for discard mortality data across a diversity of taxa, the contexts to which it applies are limited to cases where all individuals are alive at time t=0, some individuals begin dying soon after

t=0 and there is no additional mortality [i.e., $S_I(t)$=1]. However, simple modifications to the model can be made to relax these assumptions.

First, a parameter τ can be added to account for mortality occurring prior to release:

$$(6.5) \qquad S(t) = \tau \cdot \left(\pi \cdot \exp[-(\alpha \cdot t)^{\gamma}] + (1-\pi)\right)$$

where 1-$\boldsymbol{\tau}$ is the probability that an individual died during capture or handling. While this mortality could be estimated separately, with the post-release mortality estimated using eqn. 6.3 only for those individuals that were alive at release (e.g. Benoît et al., 2012), joint estimation of τ with the other parameters provides an estimate of covariance among all parameters. Under this formulation, $1-\tau+\tau\pi$ is the total CHR (discard) mortality probability.

Second, a delay in the onset of the post-release mortality can be incorporated by subtracting the time delay, t_0, from t in eqn. 6.5:

$$(6.6) \qquad S(t) = \tau \cdot \left(\pi \cdot \exp[-(\alpha \cdot (t-t_0))^{\gamma}] + (1-\pi)\right)$$

This delay reflects the time interval following discarding before any mortality occurs, and is not the part of the among-individual variability in times of death that occurs normally due to attrition. Such a delay may occur, for example, if initial capture-induced metabolic perturbations progress and/or are not resolved (Wood et al., 1983), or, if captivity represents an additive stressor that eventually induces mortality in the sample (e.g. Mandelman et al., 2007).

Third, it may be important to model not only discard-related mortality but also natural or background mortality, for instance if individuals are released back into their natural environment which contains predators, pathogens, and other sources that might lead to mortality in the absence of CHR. Assuming an exponential function for the natural mortality, M, as is common in stock assessments and population modelling, we obtain:

$$(6.7) \qquad S(t) = \tau \cdot \left(\pi \cdot \exp[-(\alpha \cdot (t - t_0))^{\gamma}] + (1 - \pi)\right) \cdot \exp(-M \cdot t)$$

The influence of the natural mortality function differs from that of τ with respect to its time dependence. In this formulation, M is assumed to act equally on both the affected and unaffected components and is therefore an independent additional mortality source. Any increase in predation risk that results from being affected by the CHR process, a component of discard mortality, is subsumed in the mortality modelled by the Weibull function.

As with other parameters of the model, it is possible to model these additional parameters as a function of status indicators or other covariates. The parameters t_0 or M can be written as a linear function of the covariates with a log-link to ensure that these parameters take on strictly positive values. For the τ parameter, a linear predictor with a logit link could be used to ensure that the parameter is bounded in the interval [0,1]. Of course, it is unlikely that all three of these additional parameters t_0, M or τ will be pertinent for a given study. They are shown together in eqn. 6.7 to illustrate the basic flexibility of the model, which of course could be modified in other ways to accommodate the particularities of a study, species or context.

6.3 Methods and Materials

Special cases of eqn. 6.7 were fit to three case studies to illustrate the use and relevance of the model. The goal is illustration and not to draw specific conclusions about the results of each study in the context in which they were conducted. Consequently, the methods for each study are presented with only enough detail for the reader to understand the application of the model. The first case study uses data from published research and further details on the study and its conclusions can be found in Benoît et al. (2012). The other two case studies are from yet to be published experiments. Further methodological details and more fulsome analysis will be available in forthcoming papers.

Model fitting via maximum-likelihood and simulations were all undertaken using the R statistical computing software (R Core Team, 2014). Optimization of the log-likelihood functions for the models (Appendix D) was undertaken using the R *optim* function.

6.3.1 Case study I: Distinguishing capture and handling mortality from post-release mortality

Benoît et al. (2012) examined the mortality of American plaice, *Hippoglossoides platessoides*, caught using a bottom-trawl in the southern Gulf of St. Lawrence (Canada, NW Atlantic) under conditions similar to those in the local commercial fisheries. Fish were caught in hauls lasting 1-2 hrs, dumped on deck and handled in a manner comparable to that used by harvesters. They were then individually measured, scored with respect to vitality class, tagged using streamer tags and placed in on-board refrigerated seawater tanks. The vitality classes used by the authors were: 1-excellent (lively fish with minor injuries only), 2-good (injured and with weak body movements), 3-poor (injured and unresponsive but ventilating) and 4-moribund (unresponsive and apparently not ventilating). Tanks were monitored regularly and dead animals were removed from the tanks and their time of mortality was recorded. Fish were held for holding periods of up to 110 hrs, and the holding times for individuals that were still alive at the end of a given holding period were treated as right-censored observations. All event times were in hours.

The authors undertook the analysis of their data in two parts. First, capture and handling mortality was modelled using a binomial model. Individuals that were dead when the tanks were first monitored after an initial 30 to 60 min holding period were assumed to have been dead before being placed in the tanks. These were all fish that had been classified as moribund. Second, the authors modelled the conditional in-tank mortality of individuals considered to have been alive when they were placed in tanks (i.e., post-release survival) using eqn. 6.3, with vitality scores as covariates.

Here we modelled the data for American plaice using a variant of eqn. 6.7 that includes capture and handling mortality and a vitality effect on π:

$$(6.8) \qquad S(t) = \tau \cdot \left(\pi \cdot \exp[-(\alpha \cdot t)^{\gamma}] + (1-\pi)\right) \text{ with } \pi = [1+\exp(-\mathbf{X}'\boldsymbol{\beta})]^{-1} \text{ and}$$

$$\tau = \begin{pmatrix} 1, & vitality \in (1,2,3) \\ \tau_0, & vitality = 4 \end{pmatrix}$$

where **X** is a design matrix for the injury scores, τ_0 is a parameter to estimate and the other parameters are as defined above. Capture and handling mortality applies only to moribund individuals (vitality=4) by definition. Furthermore, natural mortality was not included in the model because the fish were held in tanks sheltered from predators and the duration of the study was too short for other mortality risks to be of importance. To fit the model, individuals that were dead when first monitored in the tanks were treated as left-censored observations, consistent with the fact that their time of mortality is only known to have occurred before the first observation period. This approach remains closer to the true nature of the data, compared with Benoît et al.'s (2012) assumption that the fish were necessarily dead before release to the tanks. For all other individuals, the mortality or censoring times used by Benoît et al. (2012) were used.

6.3.2 Case study II: Distinguishing discard mortality from natural mortality

In 2013, Capizzano et al. (C. Capizzano, University of New England, pers. comm.) studied the post-release mortality of Atlantic cod captured in the recreational rod-and-reel fishery that occurs on Jeffreys Ledge in the Gulf of Maine (USA, NW Atlantic). One hundred and thirty captured fish were brought to the surface, measured, tagged with an external acoustic transmitter with a depth-sensor (Vemco© V9P-1H), assessed for their degree of injury on an ordinal four-level scale (none, minor, moderate and severe) and released alive. The release area was monitored by an array of 31 acoustic receivers (Vemco VR2W) that were spaced approximately 1.1 km apart, covering ca. 35 km^2. Acoustic transmitters emitted a unique, coded signal and depth measurement every 2 min for the first 7 d, every 5 min for the next 23 d, and then every 15 min until transmissions terminated at 365 d. Fish that exhibited minor vertical and horizontal movements, such as those observed for known dead fish that were tagged as a reference, were considered dead. The time of onset of those limited movement patterns was taken as the time of death. The other fish were monitored until they left the array, at which point they were considered right-censored observations. In a few instances, fish were detected by receivers in the surrounding area or were captured in fisheries. The times of these later observations were considered as the censoring times. All event times were in days.

Here we modelled these data using:

$$(6.9) \quad S(t) = \left(\pi \cdot \exp[-(\alpha \cdot t)^{\gamma}] + (1-\pi)\right) \cdot \exp(-M \cdot t / 365) \quad \text{with}$$

$$\pi = [1 + \exp(-\mathbf{X}'\boldsymbol{\beta})]^{-1}$$

where **X** is a design matrix for the injury scores.

Delayed mortality onset was not included in the model because there was no evidence for this effect in the Kaplan-Meier (KM) survivor functions for these data. Furthermore, the KM survival functions for fish classified as being uninjured or having minor injuries only before release were statistically indistinguishable (log-rank test: $\chi^2_{df=1}$ =0.01, p=0.859) and therefore those two categories were combined. The natural mortality rate M was scaled by 365 in eqn. 6.9 to estimate an annual instantaneous rate that could then be compared with values used in stock assessments or predicted from meta-analyses, as a means of validating the model estimates.

6.3.3 Case study III: Delayed onset of discard mortality

Knotek et al. (R. Knotek, University of New England, pers. comm.) undertook a study similar to that of Benoît et al. (2012). The discard mortality rate for three skate species captured in scallop dredge fisheries on Georges Bank (USA, NW Atlantic) was assessed by placing individuals in on-board refrigerated seawater tanks. Here we consider only the results for winter skate (*Leucoraja ocellata*). Individuals were captured and handled under conditions typical of the fishery, with dredge hauls that varied in duration between 10 and 90 min. Individuals were measured, tagged and attributed a semi-quantitative physical injury score (none/minor, moderate and severe) before being placed in the tanks for a target holding period of 72 hrs. Event times were in hours.

Preliminary analyses using the non-parametric KM method revealed a delay in the onset of mortality. The magnitude of this delay appeared to be inversely related to the severity of injury. Skates were placed in the tanks alive (i.e., no capture and handling mortality) and, given the experimental conditions, it appeared reasonable to assume $M=0$. Therefore, the post-release survival of winter skate from the experiment was modelled as:

$$(6.10)\quad S(t) = \pi \cdot \exp[-(\alpha \cdot (t - t_0))^{\gamma}] + (1 - \pi) \text{ with } \pi = [1 + \exp(-\mathbf{X}'\boldsymbol{\beta}_1)]^{-1} \text{ and }$$
$$t_0 = \exp(\mathbf{X}'\boldsymbol{\beta}_2)$$

where the notation $\boldsymbol{\beta}_1$ and $\boldsymbol{\beta}_2$ is used to distinguish two distinct vectors of parameters, and **X** is the design matrix for the injury scores.

To ensure that all calculations remained defined in light of logarithms used during the fitting process, we removed five right-censored observations that were made before the first mortality observations. Assuming there truly is a delay in mortality onset, fish removed from the experiment before any mortality is observed contribute no information to define the shape of the survivor function.

6.3.4 Simulations

Simulations were undertaken to evaluate whether and under what conditions it is possible to reliably estimate the parameters for a model involving discard mortality and natural mortality (eqn. 6.9), or for a model with delayed mortality onset (eqn. 6.10). These two special cases of eqn. 6.7 present the greatest potential model fitting challenges given possible confounding among the parameters that determine discard mortality and parameters for either natural mortality or mortality delay. Limiting the simulations to these two special cases kept the number of simulations tractable. The model fitting associated with the simulations was always done assuming the correct model structure. The goal was to establish whether correct parameter estimates could be recovered. Exploring the extent to which the model is robust to misspecification is a separate issue and is beyond the scope of this paper.

Two sets of simulations were undertaken; one aimed at replicating the conditions for case studies II and III, and a second generic set to consider the effects for a diversity of conditions. For the first set of simulations, injury-group specific sample sizes and study durations were matched to those of the case studies, and the parameter estimates obtained from the analyses of the case studies were used as the ‘true’ parameter values for the simulation.

For the generic simulations, three status-classes of fish were simulated, each defined by a discard mortality rate that was common across the simulations: π_1=0.75, π_2=0.50, or π_3=0.25. Three groups of generic simulations were undertaken. In the first, discard mortality with additional natural mortality was modelled using eqn. 6.9. In the second, discard and natural mortalities were also modelled, but with status-class dependent natural mortalities [i.e., assuming $M = \exp(\mathbf{X}'\boldsymbol{\beta})$ in eqn. 6.9]. This was done to evaluate model robustness for cases where the assumption of a common natural mortality for affected and immune individuals is not met (refer to “Generalization of the basic model”). This would occur if there are long-term survivorship differences between status-classes that are not subsumed in the rapidly depleting survivor function for affected individuals. For these two groups of generic simulations, we looked at the effect on estimation robustness of differences in sample size, study duration, and the relative magnitude of discard and natural mortality (cases 1-17 in Table 6.1 and Figs. 6.3a and 6.3b). In the third group of generic simulations, discard mortality with delayed onset was modelled using eqn. 6.10, assuming an inverse relationship between class-dependent discard mortality and delay. For this third group of simulations we looked at the effect on estimation robustness of differences in study duration, the shape of the discard mortality function and the magnitude of delays (cases 18-22 in Table 6.1 and Fig. 6.3c).

A modification of the method of Bender et al. (2005) was used for the simulations. For each simulated individual, i, a value of $S(t)_i$ was drawn from a uniform distribution:

$$S(t)_i \sim U(0,1)$$

The associated survival time t_i was then obtained by solving the simulated survival function equation using the Newton-Raphson algorithm. For each individual, a censoring time was also simulated, and the lesser of the survival and censoring times was used as the simulated observation for that individual. For simulations of case study II and for all the generic simulations, censoring times were drawn from a modified Beta distribution (α=0.7, β=1.4 and with support rescaled to 185 days), chosen to broadly reflect the observed distribution of censoring times in case study II (Fig. 6.4, black line). We used this single distribution to keep the number of simulations tractable and because the preliminary results obtained using other reasonable censoring functions produced very comparable results. A separate case-specific modified Beta distribution (α=1.8, β=0.2 and with support rescaled to 75 hrs) was used to simulate censoring times for the simulations of case study III (Fig. 6.4, grey lines).

Once the observations for all individuals were simulated, the relevant survival model was fit to the data to estimate parameter values. Each simulation comprised 1000 iterations, from which the mean, median, 2.5th and 97.5th percentiles of estimated parameter values were calculated. For the case-study specific simulations, relative bias (RB) for each parameter was also calculated as:

$$\mathrm{RB} = \frac{100}{n}\sum_{i=1}^{n}\frac{\hat{\theta}_i - \theta_{true}}{\theta_{true}}$$

where n is the number of iterations, $\hat{\theta}_i$ is the estimate of the parameter for iteration i and θ_{true} is the simulated 'true' value for the parameter. Relative bias was not calculated for the results of the generic simulations because those results were summarized only in graphical form and bias can be inferred from those graphs.

6.4 Results

6.4.1 Case study I: Distinguishing capture and handling mortality from post-release mortality

The model in eqn. 6.8 fit the estimated Kaplan-Meier (KM) survivor functions for the American plaice data very well (Fig. 6.5a), suggesting that the model provides an adequate description of those data. Relatively large samples sizes in each vitality class resulted in narrow confidence intervals for the KM estimates and the parameters of the parametric model. Discard mortality was lowest for fish with excellent vitality, increasing with worsening vitality across classes (Table 6.2). The total mortality probability for moribund plaice was very high at 0.962. Most of the observed mortality in this vitality class occurred during the capture and handling process.

6.4.2 Case study II: Distinguishing discard mortality from natural mortality

The mixture-distribution model that included M [eqn. 6.9] provided a substantially better fit to the cod data compared to the model that excluded M [eqn. 6.3], with a reduction in the value of the Akaike Information Criterion corrected for small sample size, ΔAICc, of 18.9. The favoured model fit the estimated KM survivor functions well (Fig. 6.5b), suggesting that the model provides an adequate description of the data. The estimates of CHR mortality increased with the severity of injury among classes (Table 6.3). The precision of the estimates was low for the moderate and severely injured classes, as a result of low sample sizes. The estimate of M from the favoured model was similar to the values assumed in a recent assessment of Gulf of Maine cod (0.2 or 0.4; NEFSC, 2013), as well as with the values predicted from empirical life history approaches: assuming von Bertalanffy parameters for cod of k=0.15 and L_∞=110 (Froese and Pauly, 2014), M = 0.30 using Jensen's (1996) estimator and M = 0.46 using Gislason et al.'s (2010) estimator for a mean length of 47 cm.

6.4.3 Case study III: Delayed onset of discard mortality

Fitting the model with injury-specific mortality delays to data was a little less straightforward than for the other case studies. Achieving model convergence and obtaining an invertible Hessian required that initial parameter values for the mortality delay parameters be close to the first observed mortality times and that a range of values be examined. There were strong correlations (r≥0.93) among the estimates of the Weibull shape parameter ($\hat{\gamma}$) and the three parameters that define the t_0's, as well as among the three parameters that define the π's. The former set of correlations can be explained by the fact that delays are constrained to occur before the first observed mortalities. Estimates of the delay are therefore derived from a backwards projection of the shape of the subsequent survivor function, leading to a strong confounding between the magnitude of delay and the parameters that shape the post-delay survivorship function.

The model fit the KM estimates of the survivor function well (Fig. 6.5c). The estimated magnitude of the delay was inversely related to the severity of injury, though the estimates did not differ statistically (Table 6.4). A lack of mortality observations soon after the initial onset of mortality may largely explain the wide confidence intervals for the estimates of t_0. As with the other examples presented here, estimates of discard mortality varied inversely with the severity of injury (Table 6.4). Confidence intervals on those estimates were wide given that mortality had yet to level off over the time span in which the data were collected.

6.4.4 Simulations

The simulated survival functions for the cod case study (Fig. 6.6a) produced patterns comparable to the original observations (Fig. 6.5b). The means and medians of parameters obtained from the simulations were essentially identical to the simulated values with very little estimation bias (Table 6.3). Furthermore, the 2.5th and 97.5th quantiles for the estimated parameters from the simulations were comparable to estimated 95% confidence intervals for the original parameter estimates. Taken together, this suggests that the properties of the empirical dataset for case study II were simulated reasonably well and that the model could reliably estimate the parameters.

The simulated survival functions for the winter skate case study (Fig. 6.6b) produced patterns that also were comparable to the original observations (Fig. 6.5c), again suggesting that the simulations were reasonably accurate. The simulations indicated that there were estimation biases particularly for the delay parameters for all three injury classes and the discard mortality parameter for the moderately injured class ($\pi_{Moderate}$) (Table 6.4). Among the simulations, there were high densities of estimated delay parameters with values near zero (Supplementary Fig. D1, Appendix D). Likewise, there were high densities of extreme values for the CHR parameters for the uninjured and severely injured classes ($\pi_{None/Minor}$ and π_{Severe}). These results occurred even when initial parameter values were set in a manner similar to what was done in the analysis of the winter skate case study. However, while careful attention was paid to model fitting for the case study (e.g., visual assessment of the fits and examination of a range of initial values), this degree of rigour was not replicated in the simulation study. Had this degree of rigour been implemented, it is likely that estimation problems would have been flagged for most simulation iterations for which the delay parameter estimates were close to zero (indicative of poor fits to the data).

In the generic simulations that included natural mortality, the discard mortality parameters were estimated accurately in almost all cases examined and even when the estimates were biased, the magnitude of RB was no more than 20% (Fig. 6.7). The estimates were slightly biased when the study duration (T_{max}) was less than the time it took for the survival functions to level off (cases 5, 6, 8, 9). A moderate bias was present when the rates of loss for discard and natural mortality were of similar magnitude (cases 10 and 11), or when there were large absolute differences in natural mortality rates between status classes and sample sizes were small (case 17). Reductions in sample size resulted in predictable increases in the dispersion of simulated estimates (e.g. compare cases 1, 2 and 3). Simulated estimates of the natural mortality parameter were also generally accurate and always had a skewed distribution. Bias in parameter estimates was greater when the simulated discard and natural mortality rates were of similar magnitude (cases 10 and 11). Parameter estimates were also biased when there were large differences in class-specific natural mortality rates (cases 16 and 17), particularly when sample sizes were smaller (case 17).

In the generic simulations that included a delay in discard mortality onset, the discard mortality parameters were accurately estimated when the study duration included the asymptote of the survival functions and when there was moderate variation among classes in the magnitude of the delay (cases 18 and 19; Fig. 6.8). Estimates were biased when variation in the delay was greater (cases 21-23), especially when T_{max} occurred before the survival functions reached their asymptote (case 23). Biases were of similar magnitude whether the simulated Weibull function for affected individuals followed a Deevey type II curve (e.g., case 18) or a Deevey type I curve (e.g., case 19). Estimates of the delay terms were highly biased in all simulated cases (Fig. 6.7). These problematic results are like those obtained in the simulations mimicking the winter skate case study (Table 6.4), probably also as a reflection of poor data fits in many iterations, likely resulting from sensitivity to initial parameter values.

6.5 Discussion

In this paper, we present theoretical arguments and empirical support for parametric mixture-distribution models for the analysis of longitudinal discard mortality data. A common feature of these data is an eventual asymptote in mortality in the absence of other mortality sources. We are aware of few current alternative modelling approaches that can satisfactorily deal with this property in light of the need to provide scientific advice on discard mortality. While non-parametric and semi-parametric (e.g. Cox proportional hazards) models can adequately fit the data, these models cannot be used to parse out different mortality sources (capture/handling, post-release and *M*), nor do they provide mechanistic interpretation for the shape of the survival function. Multi-phase or change-point models, in which survivorship is modelled with different survival functions (and therefore different underlying mechanisms) over time (e.g., Arani et al. 2001), are a possible alternative; however, the underlying assumption of these models seems unlikely for post-release mortality. Rather, the impacts of CHR should be manifested continuously, and not involve distinct interventions over time unless there are plausible external or physiological reasons to expect them. Of course, our model with a mortality onset delay is a type of multi-phase model; however, reasonable biological explanations are possible for the two phases as noted earlier in this study.

We have also shown how the mixture model can be generalized to accommodate key aspects common to survival data, as illustrated by the case studies. Using simulations, we demonstrated that special cases of the generalized model can provide robust estimates of discard mortality rates with little or no bias when there is additional low to moderate natural mortality. Moderate estimation bias occurred when the natural mortality rate was large (M>1.5), with values representative of short-lived species, not of the species considered in our case studies. Furthermore, under many conditions M was also reliably estimated, with biases occurring mainly when M was large, in which case some natural mortality was incorrectly attributed to discard mortality. Surprisingly, discard mortality and M parameters were reasonably well estimated even when observations were terminated before the survival functions showed signs of levelling-off. The model presented here is therefore likely to be highly useful given the move towards greater a ecological realism in discard and post-release mortality studies (Raby et al. 2014).

The model that incorporated a delay in mortality presented some challenges. Fitting the model required attention to starting parameter values, in contrast to the model with M, which was largely insensitive to starting values. The simulations for the ‘delay model’ indicated that the discard mortality rates were only accurately estimated when mortality delays were at most moderate. However, the delay parameters were generally underestimated, as the estimation procedure tended towards delays close to nil for many simulation iterations. In effect, the estimations tended towards implied very low probability of mortalities during the early part of the experiments, rather than consistently estimating a nil probability of mortality as was simulated. Unfortunately, there will be very little information in the data during the initial part of an experiment to distinguish between these two possibilities unless sample sizes are large and the experiments well replicated. However, using information from past studies or knowledge of physiological processes to derive informative priors for the delay parameters would certainly improve estimation for models fit under the Bayesian paradigm. More generally, our results suggest that diligence is required when fitting models with mortality delays, and we recommend the use of case-specific simulations to explore the robustness of the model for the situation at hand. Despite the preceding, it must be noted that delays in mortality onset appear rare in the available literature on discard mortality, with no cases identified in the review of longitudinal studies undertaken by Benoît et al (2012). The above considerations may therefore only apply to a limited number of cases.

Here, we paid little attention to multi-model comparison; that is, comparing the evidence for a suite of models based on the data. Multi-model comparisons can guide the selection of the most probable model(s) to have generated the observed data, in light of data variability, and are considered good practice (Hilborn and Mangel 1997; Burnham and Anderson 2002). We have reserved this type of analysis for the detailed examinations of the case studies (Benoît et al. 2012; C. Capizzano *in prep*; R. Knotek *in prep*). Additionally, we did not consider the consequences of model misspecification. A logical next step for longitudinal discard mortality modelling research would be to use simulations to study the consequences for discard mortality estimates of assuming an incorrect model. Identifying the most robust models would help ensure that scientific advice on discard mortality is as reliable as possible.

Though the generalized model presented here can provide estimates of natural mortality, given appropriate data, these estimates may not accurately reflect actual rates. For example, in the case of acoustic transmitters, if a predator consumes a tagged fish and carries the tag outside of the array, the individual will be assumed to provide a censored observation and predation mortality (part of the discard mortality for ‘affected’ individuals or part of *M* for ‘immune’ individuals) will be underestimated. Such an effect, combined with the estimation variability, means that the present approach may not be suitable for providing reliable independent estimates of *M* for stock assessments. However, the approach does appear to provide an estimate that is of the correct scale. It is also worth noting that if tags are shed before fish die or become censored observations, mortality (discard or natural) is likely to be overestimated, and scientists may need to account for such effects in their study design or perhaps during analysis to ensure accurate estimation of mortality terms.

In summary, we have provided theoretical arguments, and empirical support via simulations and case studies, for the generalized mixture model to estimate discard mortality from longitudinal data. This model appears particularly well suited for this field of study and performed well for the cases most-likely to be encountered: CHR-mortality only, CHR-mortality with additional natural mortality, and distinct CH and post-release mortalities. As the case studies illustrate, this modelling approach – assuming satisfaction of assumptions – is conducive to both shorter term enclosure studies or more temporally extended electronic tagging and telemetry studies where animals are at liberty. Because this model is founded on a basic parametric survival function, it can easily be adapted to include other effects not modelled here, and can be fit using maximum-likelihood or Bayesian methodologies. Furthermore, model fitting can readily incorporate both left- and right-censored data thereby allowing data from cross sectional studies to be readily combined with longitudinal data to improve estimation of key parameters (e.g. Benoît et al. 2013 [Chapter 3]). We believe that these properties, taken together, result in a powerful framework in which to analyse discard mortality data and to produce reliable scientific advice on discard mortality rates and possibilities for mitigation.

Table 6.1. Parameters used for each generic simulation (case). In each case, three status-classes of fish were simulated, each containing N_{sim} fish and each defined by a discard mortality rate that was common to all simulations π_1=0.75, π_2=0.50, and π_3=0.25. The duration of the study period (T_{max}) was varied between cases, as were the parameters of the Weibull survival function for the affected fish (α and γ). Cases 1-11 are simulations with additional natural mortality common to all status-classes (M_{All}), cases 12-17 are simulations with status-dependent natural mortality (M_1, M_2 and M_3), and cases 18-23 are simulations with status-dependent delays in mortality onset ($T_{0,1}$, $T_{0,2}$ and $T_{0,3}$).

Case	N_{sim}	T_{max}	α	γ	M_{All}	M_1	M_2	M_3	$T_{0,1}$	$T_{0,2}$	$T_{0,3}$
1	100	200	0.10	1.99	0.25	-	-	-	-	-	-
2	30	200	0.10	1.99	0.25	-	-	-	-	-	-
3	10	200	0.10	1.99	0.25	-	-	-	-	-	-
4	100	25	0.10	1.99	0.25	-	-	-	-	-	-
5	100	18	0.10	1.99	0.25	-	-	-	-	-	-
6	100	12	0.10	1.99	0.25	-	-	-	-	-	-
7	30	25	0.10	1.99	0.25	-	-	-	-	-	-
8	30	18	0.10	1.99	0.25	-	-	-	-	-	-
9	30	12	0.10	1.99	0.25	-	-	-	-	-	-
10	100	200	0.03	1.99	0.82	-	-	-	-	-	-
11	100	200	0.03	1.99	2.71	-	-	-	-	-	-
12	100	200	0.10	1.99	-	0.25	0.15	0.09	-	-	-
13	30	200	0.10	1.99	-	0.25	0.15	0.09	-	-	-
14	100	200	0.10	1.99	-	0.61	0.37	0.08	-	-	-
15	30	200	0.10	1.99	-	0.61	0.37	0.08	-	-	-
16	100	200	0.10	1.99	-	2.71	1.65	0.05	-	-	-
17	30	200	0.10	1.99	-	2.71	1.65	0.05	-	-	-
18	100	200	0.03	1.99	-	-	-	-	1	8	15
19	100	200	0.02	7.39	-	-	-	-	1	8	15
20	100	60	0.03	1.99	-	-	-	-	1	8	15
21	100	200	0.03	1.99	-	-	-	-	1	25	50
22	100	200	0.02	7.39	-	-	-	-	1	25	50
23	100	60	0.03	1.99	-	-	-	-	1	25	50

Table 6.2**.** Parameter estimates and associated confidence intervals for Case Study I, American plaice captured using a bottom-trawl. Results are presented for the vitality-class-specific discard mortality probability estimates (π's for excellent, good and poor vitality classes; $\mathrm{CHR}_{Moribund} = 1 - \tau + \tau\pi_{Moribund}$ for the moribund vitality class), the capture and handling mortality rate for moribund individuals ($\mathrm{CH}_{Moribund}$) and the number of fish in each injury class (N).

Parameter	*N*	*Estimate*	*95% C.I.*
$\pi_{Excellent}$	129	0.113	0.067-0.177
π_{Good}	86	0.315	0.232-0.413
π_{Poor}	59	0.532	0.405-0.649
$\mathrm{CH}_{Moribund}$	664	0.851	0.819-0.877
$\mathrm{CHR}_{Moribund}$		0.962	0.945-0.975

Table 6.3. Parameter estimates and associated confidence intervals for Case Study II, cod released from a recreational rod-and-reel fishery, and a summary of results from a simulation based on those estimated parameter values (mean, median, 2.5th and 97.5th percentiles [95% interval], and relative bias [RB]). The injury-class-specific discard mortality parameters (π's) and the natural mortality parameter (*M*) are presented, along with the number of fish in each injury class (N).

		Study results		Simulation results			
Parameter	N	Estim	95% C.I.	Mean	Med.	95% Int	RB
$\pi_{None/Minor}$	101	0.071	0.031-0.150	0.070	0.070	0.031-0.150	-0.83
$\pi_{Moderate}$	17	0.329	0.144-0.597	0.325	0.311	0.086-0.617	1.91
π_{Severe}	10	0.699	0.293-0.938	0.696	0.700	0.257-0.999	1.61
M		0.173	0.056-0.564	0.197	0.171	0.001-0.616	-1.80

Table 6.4. Parameter estimates and associated confidence intervals for Case Study III, winter skate captured in a scallop dredge, and a summary of results from a simulation based on those estimated parameter values (mean, median, 2.5th and 97.5th percentiles [95% interval], and relative bias [RB]). The injury-class-specific discard mortality parameters (π's) and mortality onset delay parameters (t_0's) are presented, along with the number of fish in each injury class (N).

		Study results		Simulation results			
Parameter	N	Estim	95% C.I.	Mean	Med.	95% Int	RB
$\pi_{None/Minor}$	26	0.341	0.042-0.870	0.362	0.250	0.011-0.999	19.2
$\pi_{Moderate}$	39	0.500	0.169-0.831	0.393	0.303	0.105-0.952	-31.4
π_{Severe}	46	0.998	0.048-1.000	0.924	0.998	0.586-0.999	-5.5
$t_{0,None/Minor}$		39.4	12.8-115.6	20.9	7.0	0.0-63.0	-48.3
$t_{0,Moderate}$		28.6	11.7-69.9	8.6	$2.6e^{-4}$	0.0-46.2	-71.3
$t_{0,Severe}$		2.7	0.0-51.7	1.8	$1.3e^{-2}$	0.0-11.2	-48.8

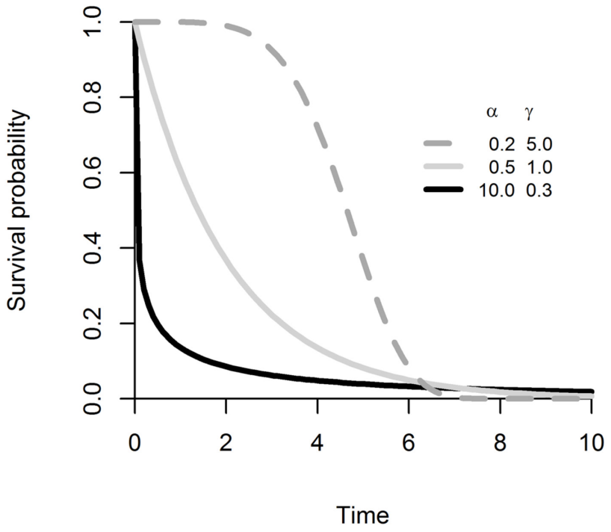

Figure 6.1. Examples of the form of the Weibull survival function as a function of its rate (α) and shape (γ) parameters, illustrating patterns comparable to Deevey's (1947) Type I (dashed grey line), Type II (solid grey) and Type III (black) survivorship curves.

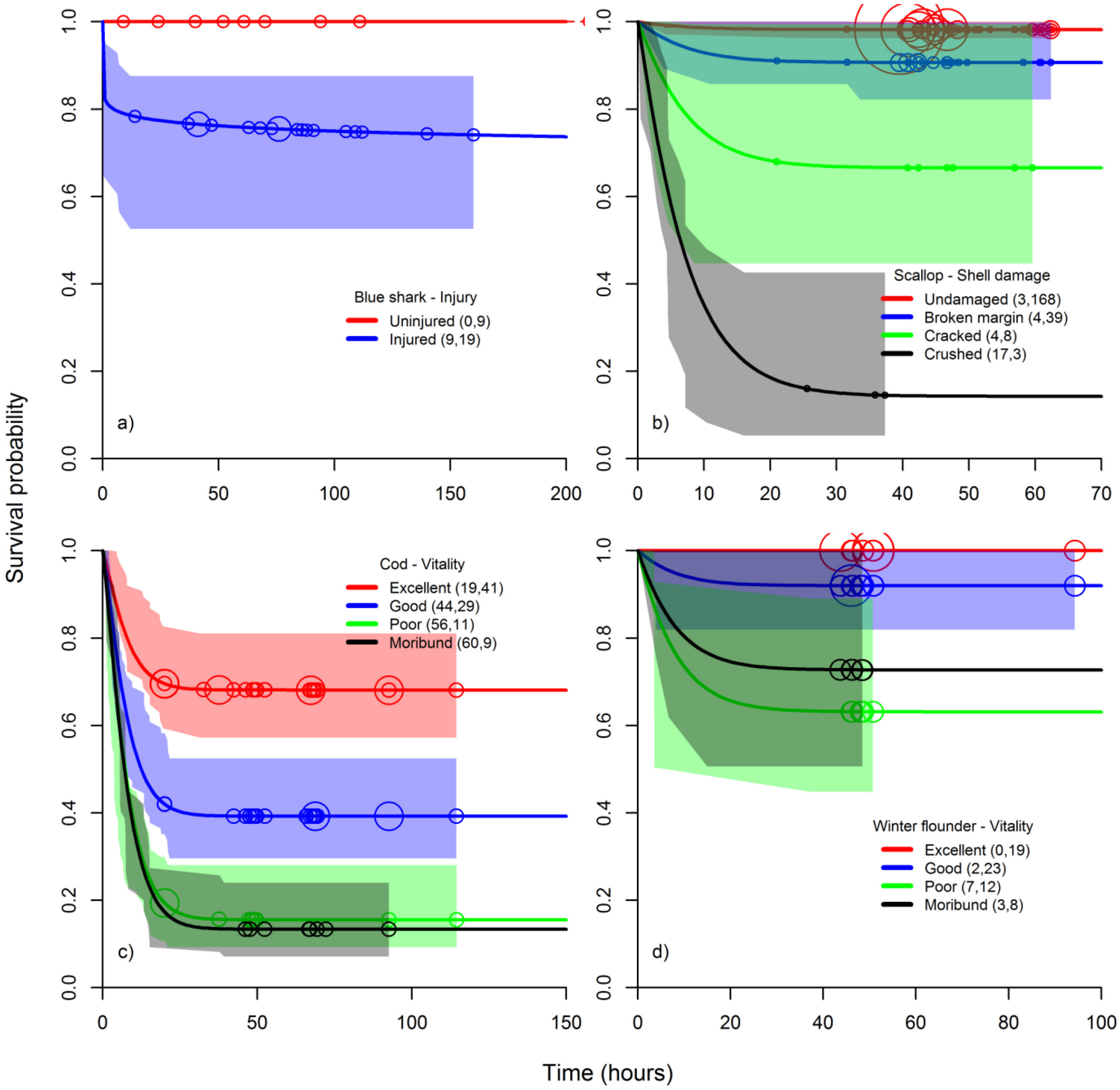

Figure 6.2. Examples of longitudinal discard survival functions for a diversity of taxa, as a function of the degree of injury, shell damage or pre-release vitality: (a) blue sharks released from commercial longlines and tagged with pop-up satellite archival tags [redrawn from Campana et al. (2009)], (b) scallops captured in a commercial dredge fishery and released into on-board refrigerated seawater tanks for monitoring (Knotek et al., unpublished results), and (c) Atlantic cod and (d) winter flounder captured in bottom-trawls and held for monitoring [redrawn from Benoît et al. (2012)]. In each plot, the shaded areas are the 95% confidence band for estimated injury/vitality-specific non-parametric Kaplan-Meier (KM) survivor functions, the solid lines are estimates from the survival mixture model [eqn. 6.3], and the circles indicate the occurrence and relative frequency (circle size) of censored observations (plotted along

the estimated survival curves for ease of presentation). The KM estimates are presented as a means of demonstrating model fit, given that the KM estimates are non-parametric representations of the patterns in the data. The horizontal span of the KM bands indicates the span of the data. The numbers in parentheses in the legend indicate the number of (dead, censored) observations for each injury or vitality class.

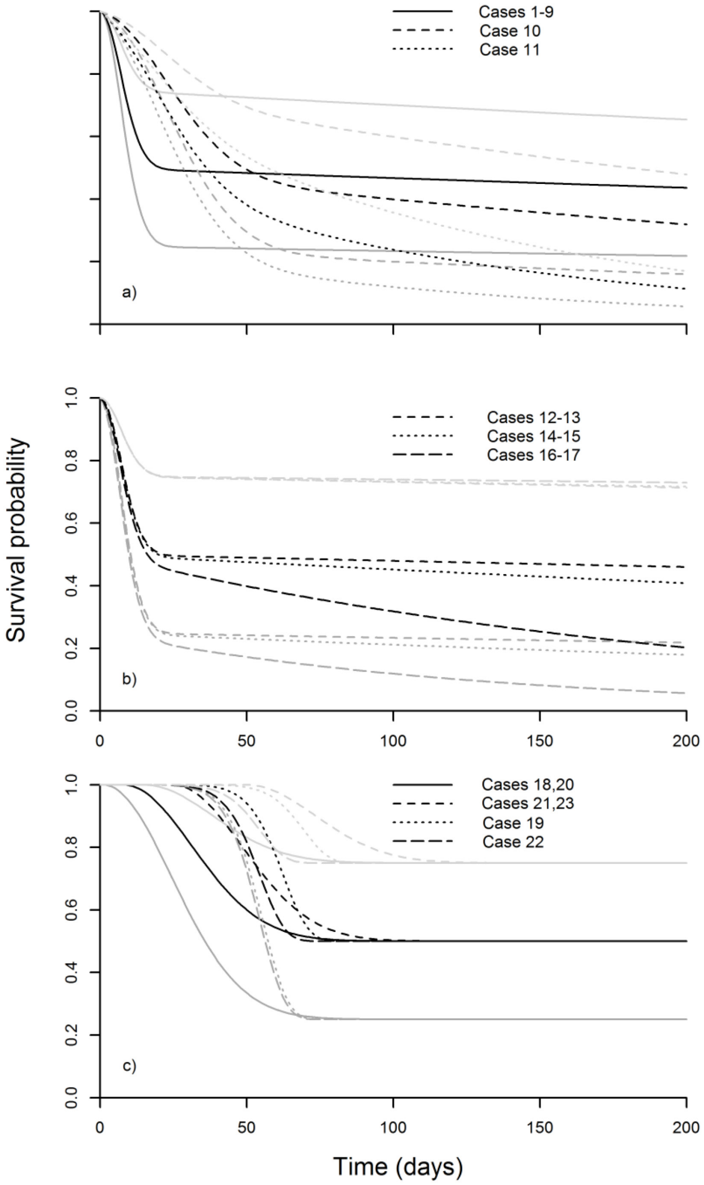

Figure 6.3. Survival functions used in the generic simulations, as defined by the parameters in Table 1. Status-specific functions are distinguished by shading for all simulated cases with discard mortality and a) a single overall natural mortality, b) status-specific natural mortalities or c) delays in discard mortality onset.

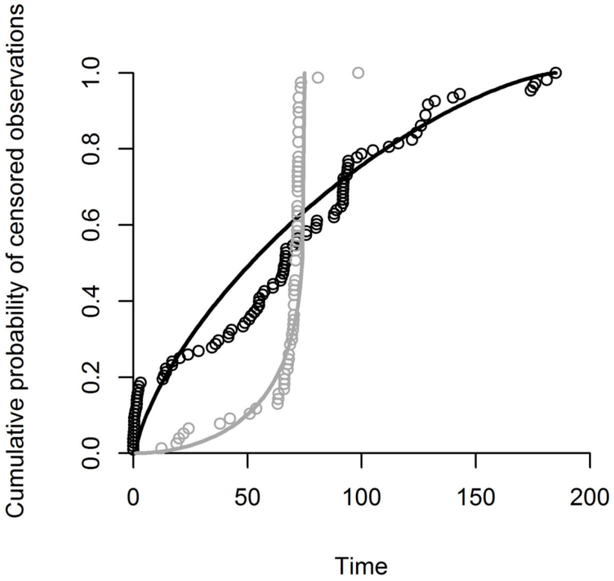

Figure 6.4. Cumulative distributions of observed censoring times in the cod case study (time in days; black circles) and the winter skate case study (time in hours; grey circles), and the modified Beta distributions used to generate censoring times in the simulations for each (solid black and grey lines respectively). The distribution described by the black line was used for the generic simulations.

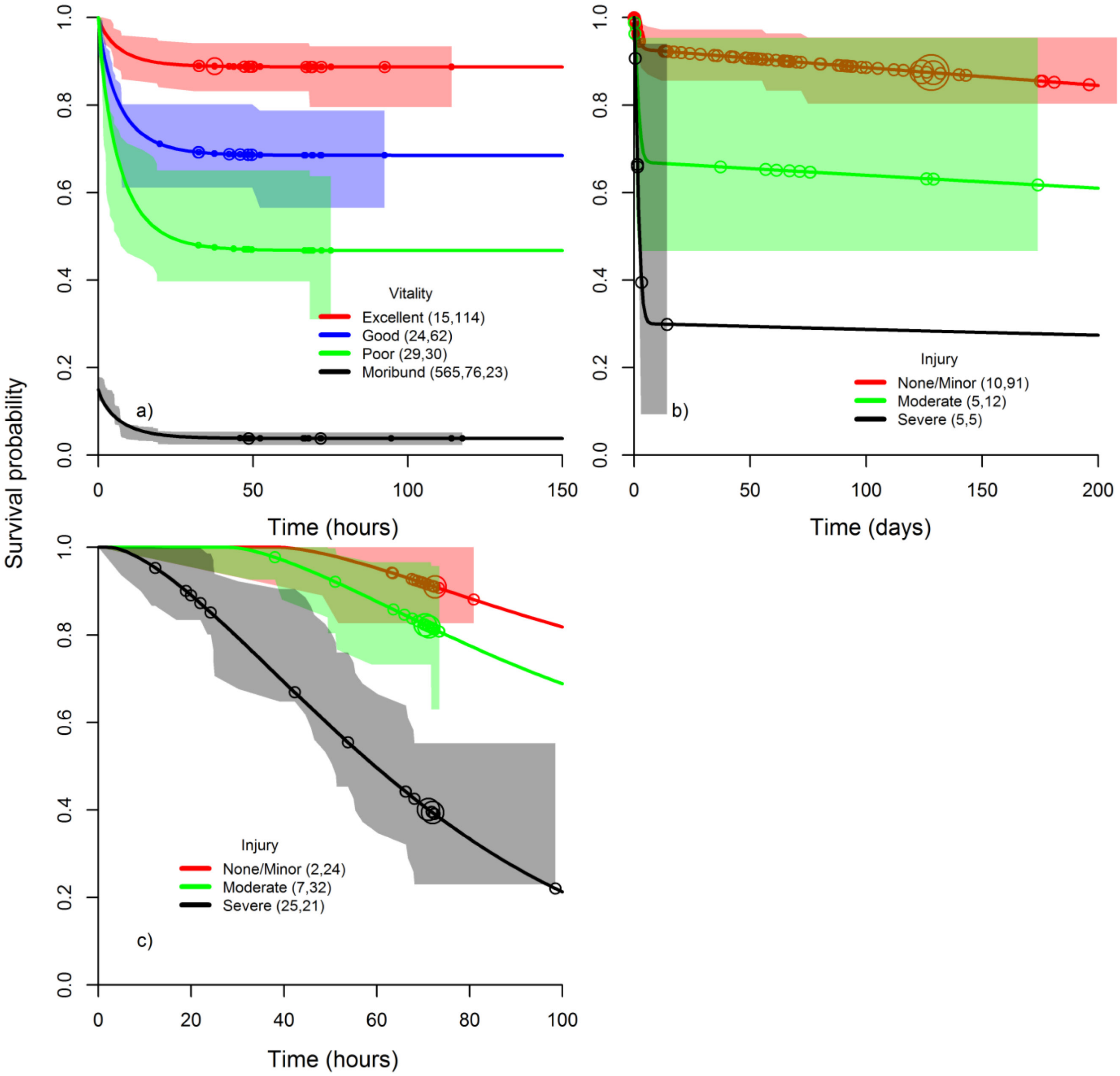

Figure 6.5. Non-parametric (KM; shaded areas) and estimated parametric survival functions for the three case studies: a) American plaice captured by bottom-trawls and monitored in refrigerated seawater tanks (model with distinct capture/handling mortality and post-release mortality; Benoît et al. 2012), b) Atlantic cod captured in a recreational fishery and released with acoustic tags (model with distinct discard and natural mortalities; Capizzano et al., pers. comm.), and c) winter skate captured in a commercial scallop dredge fishery and held for monitoring (model with delayed mortality onset; Knotek et al., pers. comm.). The interpretation of the contents of the plots is described in the caption for Figure 6.2.

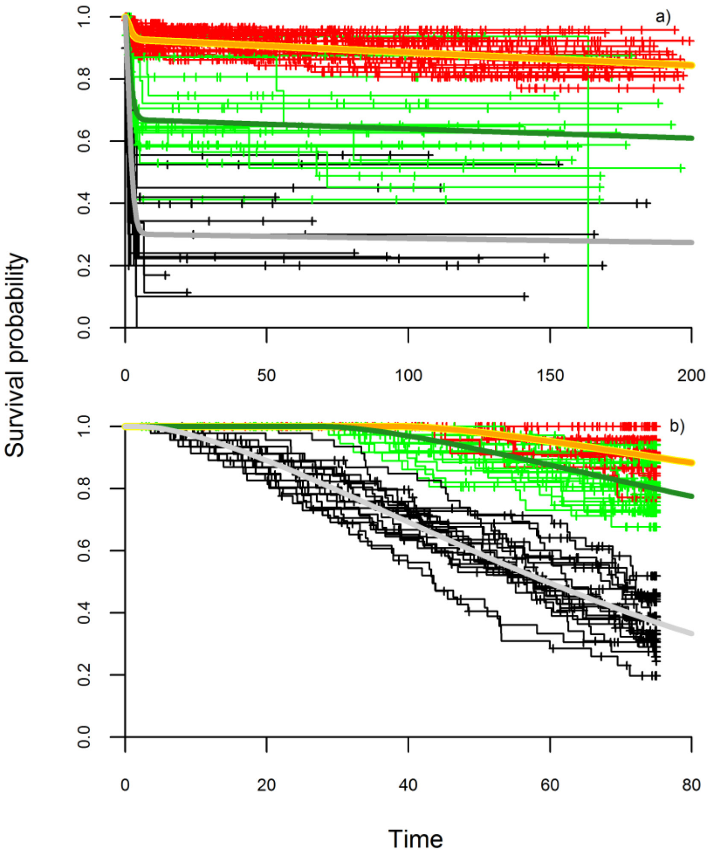

Figure 6.6. Injury-class-specific underlying survival functions (thick lines) and examples of Kaplan Meier (KM) estimates for 20 simulation iterations (thin lines with crosses to indicate censored observations) for a) the cod case study and b) the winter skate case study. Injury classes are distinguished using colours: red/orange = none/minor, green = moderate, and black/grey = severe. Note how the variability among KM curves scales with sample size, for example by comparing the results for the simulated none/minor (N=101) and severely injured (N=10) classes in (a).

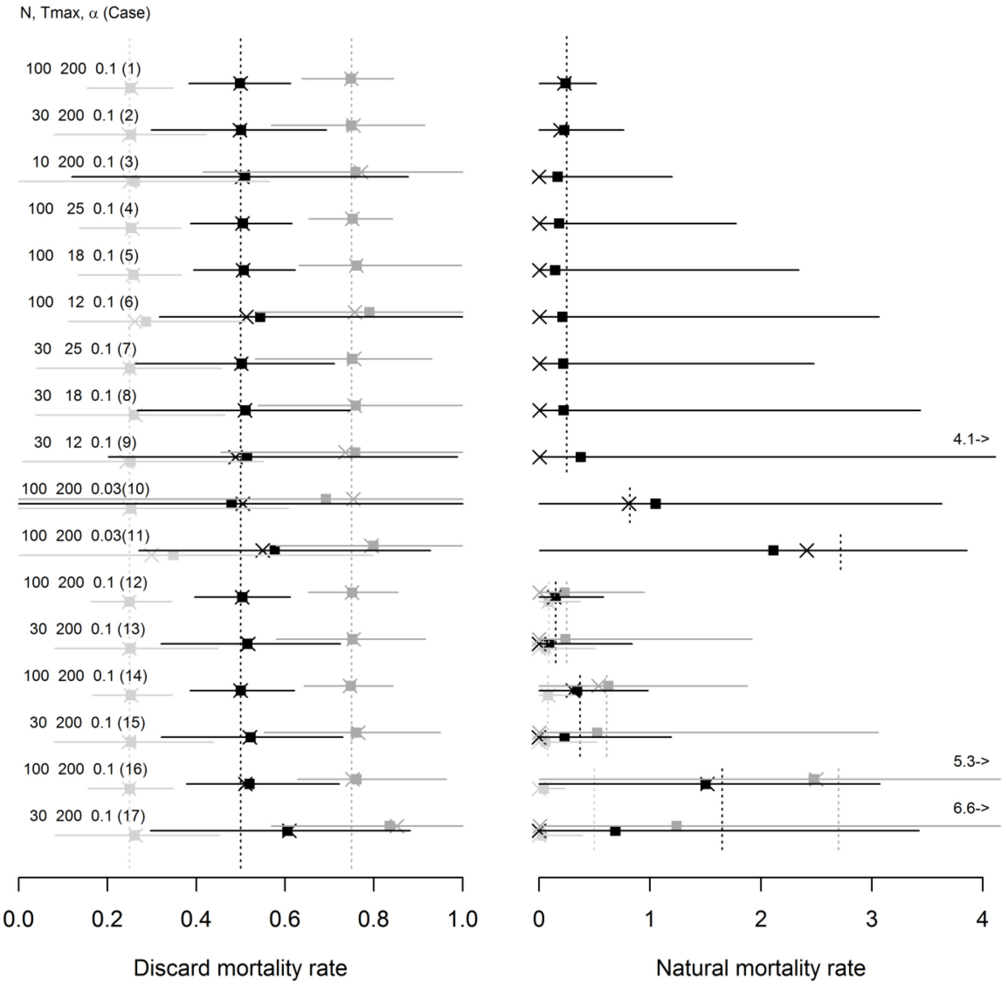

Figure 6.7. Summary of the results of the generic simulations with discard and natural mortalities [based on eqn. 6.9]. Results for the different simulated cases are presented along the y-axis. The mean (square), median (x) and 95 percentile interval (horizontal line) are presented for the estimated discard mortality rate parameter for each of the three status classes (distinguished by shading) in the left panel and for the global (cases 1-11) or class-specific (cases 12-17) natural mortality rates (*M*) in the right panel. In each panel, the vertical dashed lines indicate the simulated value of the parameter. The numbers on the left indicate the value of the simulated parameters other than *M* that were varied among cases. Details on the parameters used in the simulations can be found in Table6. 1 and the shapes of the simulated survival functions that generated these results are in Figure 6.3a and 6.3b.

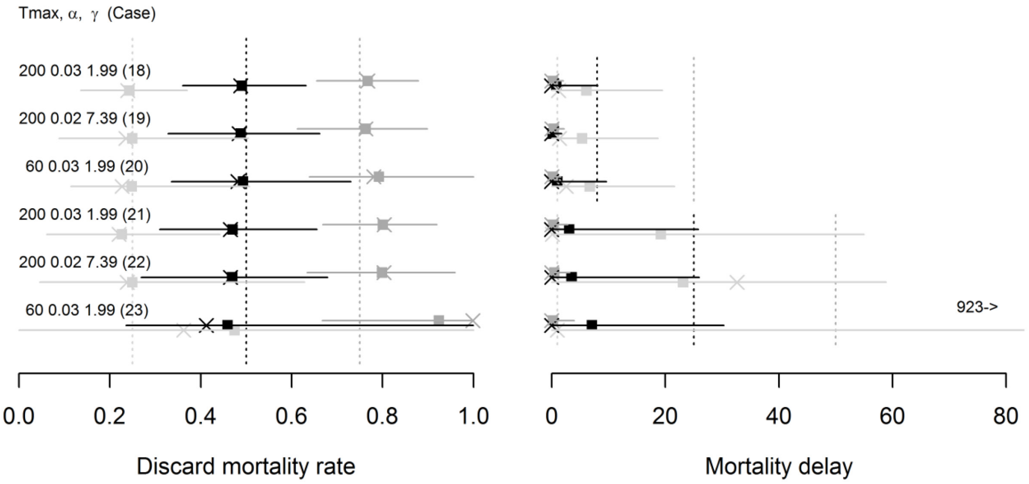

Figure 6.8. Summary of the results of the generic simulations with discard mortality and status-dependent mortality delays [based on eqn. 6.10]. Results for the different simulated cases are presented along the y-axis. The mean (square), median (x) and 95 percentile interval (horizontal line) are presented for the estimated discard mortality rate parameter for each of the three status classes (distinguished by shading) in the left panel and for the class-specific delay parameters in the right panel. In each panel, the vertical dashed lines indicate the simulated value of the parameter and the numbers on the left indicate the value of the simulated parameters other than the delay parameters that were varied among cases. Details on the parameters used in the simulations can be found in Table 6.1 and the shapes of the simulated survival functions that generated these results are in Figure 6.3c.

Chapter 7. Evaluating the Potential for Grey Seal Predation to Explain Elevated Natural Mortality in Three Fish Species in the Southern Gulf of St. Lawrence

7.0 Abstract

Despite two decades of very low fishing, numerous Northwest Atlantic demersal fish stocks have failed to recover from collapsed states or are presently collapsing. In the southern Gulf of St. Lawrence, adult natural mortality (*M*) appears to be the demographic rate that most limits population productivity in at least three species: Atlantic cod (*Gadus morhua*), white hake (*Urophycis tenuis*) and winter skate (*Leucoraja ocellata*). The causes of elevated *M* are not well understood, though there is indirect evidence consistent with an effect of predation by grey seals (*Halichoerus grypus*). However, direct evidence is lacking due to uncertainty in the seal diet. Consequently, Monte Carlo simulations were undertaken using data on the spatial overlap between the seals and the fishes, and a seal food-consumption model, to estimate the plausibility that different seal diet compositions could explain observed *M* levels. Under the simulation assumptions, we find that predation could explain up to 20-50% of *M* in adult white hake and cod even if these species comprise a small percentage of grey seal diets (<25%). If seals consume some of these fish only partially, by selectively feeding on soft tissues, a predation effect becomes more plausible. Predation can also plausibly explain the observed elevated *M* in adult winter skate, even if they comprise a negligible (<0.1%) percentage of the grey seal diet. Though the simulations deal with the factors that shape the potential for predation, a greater understanding of prey selection is required to conclude whether grey seals are actually adversely impacting these fish populations.

7.1 Introduction

The failure of Northwest (NW) Atlantic groundfish stocks to recover from population collapses that occurred in the early 1990s, despite severely curtailed fishing, has generated numerous hypotheses but few conclusions regarding its cause (DFO 2003; Shelton et al. 2006). Potential contributing causes include unreported fishery catches (e.g., Bousquet et al. 2010), fisheries-induced life history change (e.g., Rochet 1998;

Hutchings 2005; Hutchings and Baum 2005; but see Swain 2011), impaired recruitment at low stock size (e.g., Myers, et al. 1999; Frank and Brickman 2000), adverse environmental effects (e.g., Dutil and Lambert 2000) and food-web interactions (e.g., Swain and Sinclair 2000; Savenkoff et al. 2007). One such interaction, predation by pinnipeds, has received considerable attention (Mohn and Bowen 1996; Fu et al. 2001; Chouinard et al. 2005; Trzcinski et al. 2006; Chassot et al. 2009). The reason for this is likely twofold. First, the link is direct and easy to visualize: abundant seal species such as harp (*Phoca groenlandica*) and grey seals (*Halichoerus grypus*) eat commercially important fish species, though the degree to which this occurs is uncertain. Second, the populations of both harp and grey seals grew rapidly in the latter half of the 20th century, recently reaching the highest levels on record (Hammill 2005; DFO 2009). Harvesters increasingly encounter these species around their fishing gear and have long viewed them as direct competitors.

Establishing the role of seal predation in the dynamics of NW Atlantic fish populations has been hindered by difficulties in obtaining unbiased estimates of prey composition in the predator’s diet. These diets have traditionally been inferred using hard parts (mainly otoliths) recovered from seal digestive tracts or in faeces (e.g., Murie and Lavigne 1985; Hammill et al. 2007). There are numerous potential sources of bias inherent in this method, such as the differential digestibility of different species and sizes of prey (e.g., Bowen 2000; Grellier and Hammond 2006). Also, the heads (and otoliths) and other hard parts of some fish, principally larger ones, may selectively not be ingested (e.g., Moore 2003; Gudmundson et al. 2006; Hauser et al. 2008), leaving little or no specific evidence of the predation event. Furthermore, diets inferred from seal stomach contents reflect feeding that occurred 5-8 hours prior to sampling, while those from intestines and scats typically reflect feeding in the preceding 2-3 days (Grellier and Hammond 2006). Because these samples are only collected in accessible areas, on or near land, diet estimates do not properly reflect offshore feeding (e.g., Fig. 7.1). Likewise, weather conditions may hinder sampling during certain months, potentially leading to a seasonal bias in the inferred diet. Seal diets have been estimated also using quantitative fatty acid signature analysis, which, in principle should provide a better integration of spatio-temporal variability in prey consumption (Iverson et al. 2004; Iverson 2009). However, like the more traditional methods, experimental feeding experiments and field studies have identified problems with this technique (e.g., Nordstrom et al. 2008; Grahl-Nielsen et al. 2011).

In the absence of a representative diet for seals, traditional trophic modeling approaches aimed at understanding the predator's influence on fish populations, such as mass balance models (e.g., Savenkoff et al. 2007), extended single species assessment models (e.g., Fu et al. 2001), and minimum realistic models (e.g., Punt and Butterworth 1995), are likely to provide misleading results. Furthermore, because the direction and magnitude of some of the biases in seal diets are poorly characterized, formulating a tractable set of reasonable alternate diet scenarios for simulation is difficult. However, inferences on seal-fish interactions can still be made in the absence of reliable diet information. An alternative approach, that does not include diet as an input, uses the factors that constrain annual consumption of particular prey by the predator to consider the potential for a predation effect (e.g., Williams et al. 2004; Matthiopoulos et al. 2008). These constraints include the bioenergetic demand of the predator, itself a function of the abundance and sizes of individuals, spatio-temporal overlap with the prey, prey abundance and prey quality (size and energy content). Because the mean and error of many of these constraints can be quantified, it is possible to establish whether and under which conditions (i.e., seal diet composition) predation could plausibly explain an important component of mortality in fish species of interest.

We applied this constraints-based inverse modelling approach to a study of predation by grey seals on three marine fish species with endemic populations in the southern Gulf of St. Lawrence (sGSL; Fig. 7.1): Atlantic cod, *Gadus morhua*, winter skate, *Leucoraja ocellata*, and white hake, *Urophycis tenuis*. These fish species were selected because all three share the common characteristic of an adult natural (non-fishing) mortality rate (*M*) that has risen over the past three decades (Fig. 7.2), reaching levels that render the populations at risk of extirpation given current productivity conditions (Swain and Chouinard 2008; Swain et al. 2009a; Benoît et al. 2011b). Grey seals are the focal marine mammal predator for the study because they are the principal seal species feeding in the area (Hammill and Stenson 2000), and because the abundance of the grey seal populations that feed to some extent in the sGSL has increased in tandem with changes in fish natural mortality (Fig. 7.3; Bowen et al. 2003, 2007; Hammill 2005). Furthermore, grey seals are known predators of the three fish species of interest, with cod and white hake jointly comprising approximately 30% of the energy in diet samples obtained in the sGSL (Beck et al. 2007; Hammill et al. 2007). We constructed a simulation that includes a published bioenergetics model for grey seals (e.g., Mohn and Bowen 1996; Hammill and Stenson 2000), and fish-seal spatio-temporal overlap, quantified using satellite-telemetry results (seals) and bottom-trawl surveys (fish). We then estimated the relative likelihood that different fractions of the fishes'natural mortality could be explained by seal predation given different assumptions for the composition of seal diets.

7.2 Methods

Our goal was not to model interannual patterns in consumption of fish by grey seals, but rather to establish whether seal predation could be an important component of recent elevated natural mortality in the three fish species. The focal year for the study was 2005, since this is the most recent year for which there are estimates of many model input parameters (e.g., abundance, mortality). Abundance and size composition of both grey seals and fish in that year are representative of recent trends (i.e., there is no evidence that 2005 was an outlier).

The simulation model used is comprised of three main parts which are described in more detail below: a consumption model for grey seals (a function of abundance, demography and estimated bioenergetic demands), parameters describing the abundance, demography and energy content of the three fish species, and estimates of seal-fish spatial and temporal overlap. Monte Carlo sampling from the assumed error distributions of the various parameters that describe the predation process was used to generate a set of simulation realizations that characterize the uncertainty in the process. The simulation is based on a monthly time step.

7.2.1 Simulation components

7.2.1.1 Seal abundance

NW Atlantic grey seals occur year-round in the sGSL. For management purposes, the population is divided into three herds or colonies that feed to some extent in the sGSL, and each is defined by their breeding area: the Gulf herd that breeds on small islands or pack ice in the sGSL, the Sable Island herd, and a Coastal Nova Scotia herd that breeds on small islands along the eastern and southwestern shores of Nova Scotia (Fig. 7.1). Abundance in all three herds has increased substantially since the mid-1960s, particularly at Sable Island (Fig. 7.3; Bowen et al. 2003, 2007; Hammill 2005). Based on traditional tagging and satellite telemetry of Gulf and Sable Island individuals, these herds use the sGSL to different degrees (Fig. 7.4; Stobo et al. 1990; Goulet et al. 2001; Breed et al. 2006).

Grey seal abundance, N_{seal}, in each herd in 2005 and associated estimation error were obtained from an updated fit of the deterministic age-structured model of Mohn and Bowen (1996) (see Hammill et al. 1998; Hammill 2005; Bowen et al. 2007). For each iteration of our simulation, the beginning of the year abundance of grey seals in each herd was drawn from a normal distribution (Table 7.1) and divided among ages (0-39 years) using the average age structure from the population model. Within-year natural mortality of seals (instantaneous annual rate, M_{stage}) was incorporated as a deterministic effect: $M_{\text{Sable\&Coastal pups}} = 0.103$, $M_{\text{Gulf pups}} = 0.146$, and $M_{\text{ages1+}} = 0.051$ (Trzcinski et al. 2006). The number of seals alive in month number m is $N_{\text{seal,age}} \cdot \exp(-M_{\text{stage}} \cdot m/12)$.

7.2.1.2 Seal energetics

The basic model of grey seal consumption used in the simulations is identical in structure and in the value of most parameters to the model used in other recent studies (e.g., Mohn and Bowen 1996; Hammill and Stenson 2000; Trzcinski et al. 2006). This model is considered accurate to the extent that the various experiments and observations used to construct and parameterize it accurately reflect seal bioenergetics in the wild.

The daily gross energy intake (GEI; in kilojoules/day) of an individual grey seal was estimated as:

$$(7.1) \quad \mathrm{GEI}_{s,a\,m} = \alpha \mathrm{W}^{\beta}_{s,a,m} \cdot \mathrm{AF} \cdot \mathrm{GP}_{a} \cdot \mathrm{ME}^{-1}$$

where *s*, *a* and *m* index sex, age and month respectively, $\alpha \mathrm{W}^{\beta}_{s,a,m}$ is the Kleiber equation (Kleiber 1975) describing the allometric relationship between seal body mass (W) and metabolism, where α is the intercept and β is the scaling exponent for the Kleiber equation, GP is a growth premium that accounts for the additional energy required by rapidly growing young seals, AF is the 'activity factor' that accounts for increased metabolism due to activity in the field, and ME is the metabolizable energy (i.e., assimilation efficiency or the proportion of GEI available to the seal for maintenance and growth) (Table 7.1).

Summer sex-specific seal mass-at-age $\mathrm{W}_{s,a}$ (in kg) was estimated using a Gompertz growth model (Mohn and Bowen 1996) fit to individual seal masses collected in the Gulf:

$$(7.2) \quad \mathrm{W}_{s,a} = \gamma_{1s} \cdot \exp(-\gamma_{2s} \cdot \exp(-\gamma_{3s} \cdot a))$$

where γ_1, γ_2, and γ_3 are model parameters (Table 7.1). Variability in $\mathrm{W}_{s,a}$ was introduced by sampling from probability distributions for each of the parameters of eqn. 2 (Table 7.1). The $\mathrm{W}_{s,a}$ were adjusted for seasonal changes in mass due to growth, lactation and reduced feeding during moulting and breeding following Beck et al. (2003) to produce values of mass as a function of age in years and months, $\mathrm{W}_{s,a,m}$ (Fig. 7.5). Uncertainty in basal metabolism estimates was simulated by drawing values of the Kleiber equation parameters from a multivariate normal distribution with an assumed coefficient of variation (CV) of 25% for each parameter and a negative correlation between the parameters, typical of linear regression (Table 7.1).

Average daily energy requirements of free-living and captive seals vary between 1.7 and 3 times the basal metabolic rate, with most studies estimating a value around 2 (Innes et al. 1987; Worthy 1987a,b, 1990; Castellini et al. 1992; Sparling and Fedak 2004). To account for this uncertainty, values for AF were sampled from a pert distribution; a modified beta distribution that acts like a smoothed triangular distribution (e.g., Overholtz and Link 2007), here with a range of 1.7 to 3.0, and a mode at 2.0.

The growth premium adjusts the GEI for the elevated metabolic rate of juveniles relative to adults (Lavigne et al. 1986; Innes et al. 1987). In the simulation, age-specific values of GP were drawn from uniform distributions with ranges based on results from published studies (Table 7.1). Simulated values for metabolizable energy were based on results of experiments (Ronald et al. 1984) (Table 7.1). The simulations included periods of fasting as observed for wild grey seals: 21 days during lactation/breeding for females ages 5+ (occurring between late December and February), 24 days for adult males (ages 9+) during breeding, and two weeks during moulting (May for females, June for males).

7.2.1.3 Fish abundance, natural mortality and body size

A standardized annual bottom-trawl survey conducted each September since 1971 in the sGSL provides information on the abundance and demographic structure (size and, for some species, age) of a large number of marine fish species (Hurlbut and Clay 1990; Benoît 2006b; Benoît and Swain 2008). These data were used to estimate the abundance and natural mortality of cod, white hake and winter skate, though the manner in which this was done differed somewhat between species.

The principal assessment model for sGSL cod is a sequential population analysis (SPA). SPA reconstructs total abundance-at-age using fishery landings-at-age and assumptions concerning natural mortality (M), and is calibrated to survey catches-at-age. We define M as the instantaneous rate of natural mortality whereby exp(-M) is the proportion of fish surviving the year in the absence of fishing. By fixing values of M for the years prior to 1980, Swain et al. (2009b) estimated M in 7- or 8-year blocks for the period 1980-2008. For the 2001-2008 period, values of *M* were estimated for three cod age groups: ages 2 to 4, 5 to 10, and 11+ years.

Trends in survival of cod to age 2 (not shown here) are uncorrelated with seal population growth, rather being strongly related to spawning stock biomass and an inferred impact of predation by pelagic fishes (Swain and Sinclair 2000; Swain et al. 2000; Swain et al. 2009b). Likewise, trends in *M* of cod aged 2-4 years are also inconsistent with a predominant seal effect, peaking in about 1990 and declining since then (Fig. 7.2a). In contrast, trends in *M* for ages 5-10 and 11+ cod have generally been increasing, particularly for the latter age group. As a result, cod ages 5 years and older were included in the simulations. Because estimates of cod abundance-at-age $N_{cod,a}$ and *M* from the SPA are correlated within age groups, a multivariate normal distribution was used to generate values during the simulations (Table 7.1).

Estimates of relative abundance of sGSL white hake from the survey were converted to absolute abundances using a length-dependent relationship for survey efficiency (i.e., catchability) derived for demersal roundfish (Harley and Myers 2001). These abundance values were assumed to follow a normal distribution (Table 7.1). Benoît and Swain (2011) estimated trends in the total mortality ($Z = M$ + fishing mortality) of white hake ages 5-7 using a modified catch-curve analysis (Sinclair 2001). Trends in *M* were obtained given assumptions for catchability and observed fishery catches (Benoît et al. 2011b), indicating that *M* has risen to a very high level of around 1.9 in recent years (Fig. 7.2c). For the simulations, the values of *M* estimated for 2005 were assumed to apply to white hake ages 3-7 years (Table 7.1). In contrast, survival of juveniles (up to age 3) appears to have increased (Fig. 7.2c), consistent with the reduction in predation mortality caused by the reduction in the abundance of large sized piscivorous fish (Benoît and Swain 2008). This reduction appears to exceed the potential effects of predation by expanding grey seal populations. Consumption of juvenile white hake was therefore not included in the simulations.

Swain et al. (2009a) used a Bayesian stage-structured model to estimate trends in *M* for juvenile (individuals <42 cm) and adult southern Gulf winter skate in approximately decadal blocks. Inputs to their model included catchabilty-adjusted abundance and estimates of fishery catches. Estimated juvenile winter skate M decreased dramatically from the 1970s to the period covering the 1980s to mid-2000s (Fig. 7.2b), a trend that is inconsistent with a strong effect of seal predation. Juveniles were therefore not included in the simulations. In contrast, adult M increased over the series (Fig. 7.2b), consistent with a hypothesized impact of seal predation. The posterior distribution of adult winter skate M estimated for the period 1990-2006 (Swain et al. 2009a) and the 2005 catchability-adjusted survey abundance was used in our simulations (Table 7.1).

Numbers-at-age of cod and white hake were converted to numbers-at-length (cm) and vice versa in the simulations using survey derived age-length matrices. For winter skate, the 2005 survey length-frequency distribution was used. The length-specific biomass of each species was calculated using survey-derived length-mass relationships. Cod and white hake have a pronounced seasonal cycle in mass-at-length (Schwalme and Chouinard 1999; H. Benoît, unpublished results). The relationships were therefore estimated by yearly quarter using data from multispecies seasonal surveys conducted from 1986-1991 (Clay 1991) and cod-directed sampling during the 1990s and 2000s (e.g., Schwalme and Chouinard 1999), with values adjusted to 2005 values based on observations from the September surveys. The seasonal cycle in winter skate mass-at-length is less pronounced therefore a single length-mass relationship was used (H. Benoît, unpublished results). Variability in length-mass relationships was incorporated in the simulation using a bootstrap of observed values.

7.2.1.4 Partial consumption of fish prey

Seals do not always consume their prey whole. Belly-biting, whereby seals consume only the viscera of their prey, has been reported by fish harvesters and has been documented for harp seals feeding on free-swimming large cod in Newfoundland, Canada (Lilly and Murphy 2004). Others have documented seals consuming all but the heads of fishes (e.g., Roffe and Mate 1984; Moore 2003; Hauser et al. 2008). For large prey, these behaviours are consistent with optimal foraging theory, whereby seals may maximize their net rate of energy acquisition by differentially feeding on the most energy rich or easiest to process portions of individual prey items, leaving a prey partially consumed when it is more profitable to search for another intact prey item (e.g., Sih 1980; Gende et al. 2001).

Although there are no data on the importance of partial consumption by seals in the wild, the fact that it is has been reported elsewhere suggested that it might be an important mode of feeding. Therefore, we simulated two independent selective feeding scenarios, belly-biting and head-rejection, for cod and white hake. Because seals obtain less energy when prey are only partially consumed, a greater number of prey must be eaten to meet metabolic demands. Selective feeding of winter skate was not simulated because there have been no reports of incomplete consumption of skates by seals and because we find that there is a high probability that seal predation could explain skate *M* even is consumption is complete (see Results: Probability of explaining *M* as a function of seal diet composition). Estimates of viscera mass and headless-body mass as a function of fish body length were required for cod and white hake to simulate partial consumption. The data required to estimate seasonal relationships between cod body length and viscera mass have been collected since 1991 (Schwalme and Chouinard 1999; Fisheries and Oceans Canada, unpublished data). Similar data for white hake were unavailable so we used the relationships for cod, adjusted proportionately for differences in the mean mass-at-length between the two species. Intra-season variability in the relationships was again estimated using bootstrapping of the observed values. To account for the consumption of the flesh surrounding the viscera, the estimated mass was multiplied somewhat arbitrarily by 1.3. Data on the mass of southern Gulf cod and white hake heads were unavailable. We used Gildberg's (2004) estimate for cod heads: 21 ± 2 (S.E.) percent of total body mass.

7.2.1.5 Fish energy content

Species-specific values for fish energy density (ED; kilojoules per gram body mass) were obtained from the literature (Table 7.1). A value for little skate (*Leucoraja erinacea*) was used for winter skate. Values for all three species, when consumed whole, were assumed to follow normal distributions with coefficients of variation of 15% (based on results for cod in Lawson et al. 1998). ED values for cod viscera were derived using the seasonal relationships between viscera and total mass (section 7.2.1.4) and assuming that the rejected portion had the ED values of cod fillets (Ingenbleek 2006). Because the relationship between viscera and total mass is allometric, the resulting viscera ED values were lognormally distributed (Table 7.1). In the absence of specific data, these values were also used for belly-bitten white hake. ED values for headless cod and white hake were assumed to be 5% higher than whole fish to account for the fact that the rejected fraction (the head) is less energy dense. Seasonal variation in fish ED was not incorporated in the simulation because the magnitude of change is relatively small (≤3%) (Beck et al. 2007).

7.2.1.6 Spatio-temporal overlap among all species

Bottom-trawl surveys of the sGSL and neighboring areas have been conducted in most months and were used to characterize the monthly spatial distribution of the three fish species. (Note that these additional surveys were used to assess distribution and were not used in the estimation of demographic parameters in section 7.2.1.3). These surveys include seasonal surveys undertaken in 1986-1987 (southeastern Gulf of St. Lawrence) and 1989-1992 (southwestern Gulf), January surveys conducted annually from 1994-1997 in the Cabot Strait, annual summer surveys of the Northumberland Strait from 2004-2006, and recent data (2004-2006) from surveys of the entire sGSL conducted in August and in September (Clay 1991; Darbyson and Benoît 2003; Swain et al. 2006; Hurlbut et al. 2010; Savoie and Surette 2010).

The spatial distribution of each species was summarized using survey strata as the spatial unit of interest (Fig. 7.6). These strata are based on bathymetry, which also largely defines fish distribution. Individual strata comprise on average ~4% of the study area, which is probably the finest reasonable scale (1000s km^2) at which to characterize distribution in our study. For each of the months from November to June, fish distribution was characterized as occupancy (i.e., equal density of fish among occupied strata) because there were no recent surveys in those months to inform a more refined depiction of distribution (Fig. 7.6). Strata in which no less than 10% of survey tows caught a given species were considered occupied by that species. The distribution of the fish species observed in August and September surveys in 2004-2006 was used to characterize the distribution among strata for July-August and September-October respectively. Because detailed recent information on distribution was available for those months, fish distribution was characterized based on observed densities in each stratum. Furthermore, bootstrapping of survey sets within strata was used to simulate the observation error associated with fish distribution during the summer and early autumn.

The seasonal distribution of the fishes can be summarized as follows (Fig. 7.6; for more details see Clay (1991) and Darbyson and Benoît (2003)). sGSL cod overwinter in the deeper waters of Sydney Bight and along the southeastern slope of the Laurentian channel (Fig. 7.1). In about April, cod migrate into the sGSL following the northwestern coast of Cape Breton Island as well as along the slope of the channel. They historically distributed themselves broadly throughout the sGSL from the late spring to mid-autumn, though concentrations in the centre of the Magdalen shallows have decreased substantially since the mid-1990s. The return migration to overwintering grounds now occurs in November (Comeau et al. 2002). White hake overlap substantially with cod during the winter. Spring migration occurs later in May, with some hake moving to coastal areas in the southernmost portion of the sGSL and others remaining in the Laurentian channel (Clay 1991). The fall migration to overwintering grounds appears to occur in late November and early December. Finally, winter skate appear to be broadly distributed over the Magdalen shallows during the winter (Darbyson and Benoît 2003). In late May and early June they migrate to the shallow areas of the sGSL, with important concentrations in the coastal waters of Prince Edward Island and New Brunswick (Swain et al. 2006). The fall migration is nearly complete by mid-November.

Satellite tags deployed between 1993-2010 on 131 grey seals from the Sable Island herd (mainly young of the year and individuals 8+ years old) and 56 from the Gulf herd (including 27 juveniles) provide information on seasonal distribution and movements (Goulet et al. 2001; Breed et al. 2006; Harvey et al. 2008). The average seal was tracked for about 7 months, and for any given month there were data for 7-107 tagged Sable herd seals and 5-44 tagged Gulf herd individuals. A state-space model described by Jonsen et al. (2005) was used to handle observation errors in raw Argos satellite-derived positions and to normalize the number of positions reported per day per seal to three (Breed et al. 2006; Harvey et al. 2008).

The seasonal distribution of grey seals can be briefly described as follows (Fig. 7.4). Grey seals are on their breeding grounds during December-February, after which they disperse to feed. During moulting animals spend more time ashore, dispersing once moulting is complete. Gulf animals may disperse to the Scotian Shelf, or other areas in the Gulf and estuary of the St. Lawrence, and Sable animals may disperse throughout the Scotian Shelf or move into the Gulf (Stobo et al. 1990; Lavigueur and Hammill 1993; Goulet et al. 2001; Austin et al. 2006; Breed et al. 2006; Harvey et al 2008).

Previous analyses of the tracking data have revealed sex- and stage-dependent differences in grey seal movements (Breed et al. 2006; Harvey et al. 2008). The respective monthly distribution of juvenile, adult male and adult female grey seals from each of the Sable and Gulf herds (henceforth, seal groups) was summarized as the proportion of normalized positions occurring each month in each bottom-trawl survey stratum. These monthly distributions were assumed to be representative of the populations of each seal group for 2005. In creating these summaries, data for a particular seal in a given month were only retained if that seal was tracked for at least ten days. Because there were few tagged seals in the spring, data from the months adjoining a month of interest were pooled. Variability in seal distributions was estimated by bootstrapping the satellite tracking data, treating individual seals within seal groups as sampling units.

There has been no satellite tracking of Coastal Nova Scotia grey seals, though some of them likely spend some time foraging where sGSL fish occur. We assumed that the movement patterns of these seals likely reflect those observed in the other two herds, though they are perhaps more like Sable Island seals. A portion, $P_{Coastal}$, of the Coastal Nova Scotia herd was assumed to have a monthly distribution identical to Sable Island grey seals, while the remainder, 1- $P_{Coastal}$, adopted the distribution of Gulf seals. $P_{Coastal}$

was somewhat arbitrarily defined to vary uniformly over the interval [0.3, 1.0] (Table 7.1).

7.2.1.7 Predation given seal-fish overlap

Within a stratum occupied by seals, we assumed that consumption of each fish species was proportional to their respective biomasses in that stratum. Though we acknowledge the multitude of possible multi-species functional responses relating prey availability to seal consumption (e.g., Koen-Alonso 2007), this was the simplest assumption to make in the absence of strong data on grey seal prey preference, the abundance of other prey in each cell, and possible prey switching. However, while this functional response results in proportional consumption at the local stratum scale, differential patterns in the spatial distribution of all animals considered in the simulation and bioenergetic limits on seal consumption, mean that the functional response is non-linear at the population scale. It is ultimately at this population scale that assumptions about functional responses are important for population dynamics modeling and where the assumption of a Type I multi-species functional response may be most tenuous (e.g., Mackinson et al. 2003; Koen-Alonso and Yodzis 2005; Matthiopoulos et al. 2008).

Fish of different sizes were also consumed proportional to availability in the simulations. This was assumed because current estimates of prey size composition in grey seal diets in the sGSL are considered unreliable. Diet samples collected during the summer and the fall reflect feeding mainly in shallow waters (Fig. 7.1), where the smaller individuals of the species of interest are most prevalent and larger individuals are rarer or absent (Macpherson and Duarte 1991; Swain 1993). This could explain the high proportion of smaller individuals in sampled seal diets (Fig. 7.7; Hammill et al. 2007). In contrast, winter sampling in an area where both small and large cod congregate (Fig. 7.1, location denoted by a star) suggests that seals may select larger fish (Fig. 7.7).

For simplicity, the biomass of each fish species remaining at the end of each month following seal consumption was distributed proportionately among the strata those fish occupy in the following month.

7.2.2 Simulation scenarios and output metrics

Separate scenarios were simulated to account for the possible partial consumption of cod and white hake, either by belly-biting or head-rejection. In each case, we simulated different proportions of fish eaten partially, ranging from [0, 1] and incremented by 0.1 between simulations. Though some, but not all, consumed cod and hake are eaten partially in nature, the true proportions are not known, so we simulated proportions over the full range for illustration purposes.

Each scenario comprised 5000 iterations of the simulation. From the resulting set of model realizations, we calculate three properties of interest. The first is the average monthly potential consumption of each fish species by seals (i.e., mean consumption in the absence of alternate prey). This is a measure of the scope for a predation effect based solely on the constraints of grey seal energy demands, fish energy content and overlap between seals and individual fish species. The second property of interest is the probability that seal predation can explain certain fractions of fish natural mortality given different assumptions for seal diets, conditional on the various assumptions of the simulation structure and parameters. For a given fish species, this was calculated as the proportion of realizations in which the simulated consumption resulted in a mortality that was equal to or exceeded a given proportion of the randomly drawn M for that species. Separate probabilities were calculated for the two age groups of cod because they had different M values. The third property of interest was the mean seal diet composition (%) implied by different proportions of fish species M, at different levels of partial consumption of fish. This was calculated specifically for those seals that overlap with a given fish species, and also at the seal herd level. The estimated diet of overlapping seals in the simulation provides an indication of the degree to which total consumption is constrained by spatial overlap.

7.3 Results

7.3.1 Total potential consumption

For the three fish species, the highest potential consumption occurred during the summer months (Fig. 7.8). This result may in part be because we allowed fish density to vary among occupied strata in those months based on the results of summer bottom-trawl surveys, and if seal densities were greatest in strata where fish densities were high. In 2005, an average of around 2 600 tonnes per month (31 044 per year) of whole age 5+ cod could potentially have been eaten by seals, based on the estimated overlap in the spatial distributions of seals and fish. In comparison, the point estimate of cod loss due to *M* that year was about 28 126 t (Table 7.2). In all but the summer months, cod overlapped overwhelmingly with grey seals from the Gulf herd (Fig. 7.8). Potential consumption of adult white hake by seals was estimated to average 2 350 t per month in 2005 (~28 300 t for the year) (Fig. 7.8), while estimated losses due to *M* for the year were 3 471 t (Table 7.2). For winter skate, Gulf herd seals contribute almost exclusively to an average potential consumption of 6 100 tonnes per month, which is more than an order of magnitude larger than the estimated annual loss to *M*.

A global sensitivity analysis of the contribution of input parameter variability to total variability in seal consumption was undertaken using a general linear model (Saltelli et al., 2000). Approximately 28% of variability in consumption was due to variability in seal abundance and overlap with fish, 40% due to variability in the bioenergetics model, with the remainder due to variability in the various other inputs.

7.3.2 Probability of explaining fish M as a function of seal diet composition

Even in the absence of partial consumption by seals there was a 0.5 probability of explaining approximately 70% of *M* in cod aged 5-10 years and a very high probability (≥0.95) of explaining around 20% of *M* (Fig. 7.9a). To explain 70% of *M* required that the diet of grey seals that overlapped spatially with these cod be dominated by them (~60% in the diet) (Fig. 7.10). This however translates to about 15% of sGSL cod ages 5-10 in the average diet of Gulf seals (Fig. 7.10) and 3% in the diet of Sable Island seals (not shown).

A predation effect was slightly more likely for cod aged 11+ years in the absence of partial consumption, with probabilities of 0.5 and 0.95 of explaining around 80% and 50% of *M*, respectively (Fig. 7.9c). To explain 80% of their *M*, 11+ cod must comprise approximately 3.3% of the diet of overlapping grey seals, and <0.8% of the mean diet of the Gulf herd (Fig. 7.10).

Consumption of whole age 3+ white hake by grey seals could explain approximately 40% and 15% of *M* with respective probabilities of 0.5 and 0.95. The 0.5 probability would be achieved if white hake comprise around 8% of the diet of overlapping seals and 2.5% and <0.5% of the respective mean diets of the Gulf and Sable Island herds (Fig. 7.10; results not shown for the Sable Island herd diet). Predation of white hake is heavily constrained by considerable spatial overlap with adult cod and our assumption of a proportional functional response, as is evident from the large potential consumption of hake noted previously (Fig. 7.8). White hake consumed whole would need to comprise about 12% and 4% of the diets of overlapping and Gulf herd grey seals respectively (Fig. 7.10), to explain all of the natural mortality in excess of the level estimated for years prior to 1985 (Fig. 7.2c).

For white hake and both cod age groups (5-10 and 11+), the probability that grey seal predation explains *M* increases as the seals include more partially-consumed fish in their diet (Fig. 7.9). The increases are most pronounced when partial consumption takes the form of belly-biting, because fewer kJ are obtained from each killed fish. The probability that a given proportion of *M* is explained by grey seals increases by 50% if 10-25% of white hake, and 25-50% of cod are consumed by belly-biting. At these levels, these fish also comprise 15-30% less of the total energy required by grey seals, compared to the scenario where seals always consume whole fish (Fig. 7.10). Increasing the proportion of fish that are consumed partially by head-rejection has considerably less impact on the probability of explaining *M* (Fig. 7.9). Compared to a situation where fish are all consumed whole, if seals consume 50% of cod and white hake by head-rejection, the proportion of *M* that can be explained at a given probability level increases by approximately 10%.

Given the very high potential for consumption of adult winter skate by grey seals (Fig. 7.8), all of winter skate *M* was explained by predation in every simulation undertaken (results not shown). To explain all of their *M*, adult winter skate must comprise no more than 0.6% of the diet of the grey seals that overlap spatially with them, and no more than 0.2% and <0.05% of the respective mean diets of the Gulf and Sable Island herds (Fig. 7.11).

7.2 Discussion

To date, modeling studies of the effect of seals on NW Atlantic cod populations (e.g., Trzcinski et al. 2006; Chassot et al. 2009) or the ecosystems in which they reside (e.g., Bundy and Fanning 2005; Savenkoff et al. 2007) have been parameterized using the species and size composition of fish observed in the available seal diet samples. While these studies have concluded that seals (harp or grey seals, depending on the ecosystem) have impeded the recovery of collapsed populations to a degree, the extent of this effect is estimated to be small and for many stocks a substantial proportion of the natural mortality of large fish remains unexplained. However, these results are largely driven by the estimated seal diets, which we suggest may underestimate the consumption of larger fish. Nevertheless indirect evidence points to an effect of grey seals on sGSL marine fish stocks. Changes in the species composition of the sGSL marine fish community are consistent with an effect of grey seal predation and basic consumption modeling suggests that removals of fish by grey seals may have replaced the extraction formerly imposed by fisheries, which are now closed or severely scaled back compared to the 1970s and 1980s (Benoît and Swain 2008; Savenkoff et al. 2008). Although numerous other hypotheses have been proposed to explain elevated *M* of adult cod, predation by grey seals remains the hypothesis with the greatest support (Bowen et al. 2009; Swain 2011; Swain et al. 2011). Finally, unusually high adult *M* is a common feature among all Canadian cod stocks located to the south of the Laurentian Channel, the area with the greatest overlap with NW Atlantic grey seals. Conversely, *M* does not appear to currently be as elevated, north of the Channel, where grey seals are less abundant.

Our approach shows that the conditions exist for grey seal predation to comprise a significant component of *M* among large cod, hake and skate, given the assumptions of our model. We find that while the consumption of cod aged 5-10 years in the simulation was particularly constrained by spatial overlap and seal bioenergetics, an important portion of their *M* (around 20%) could be explained with high certainty (0.95 probability) even in the absence of belly-biting. Furthermore this result was obtained even if these cod formed only 5% of the average diet of Gulf seals. In the simulation, there was also strong potential for seal predation to explain the elevated *M* of white hake, provided grey seals had some preference for them relative to ages 5-10 cod. In contrast, there was abundant scope for grey seals to consume winter skate in the simulations, regardless of the abundance of other species. Jointly, the results of our modelling suggest that, to the extent that the simulation assumptions are correct, predation by grey seals can account for the elevated adult mortality of the three fish species concerned. Jointly the sGSL populations of these three fish species need comprise only about 20% of Gulf and 3.5% of Sable Island grey seal diets to explain most of their *M*.

Attributing a large component of fish *M* to seal predation becomes more likely if seals consume some of their prey only partially, particularly if seals only consume the viscera of fish. Partial consumption of fish, particularly belly-biting, is believed by fish harvesters to be common, though quantitatively documenting its frequency has been difficult except for seals that forage near shore (e.g., Lilly and Murphy 2004; Hauser et al. 2008), in and around fishing gear (e.g., Moore 2003) or in captivity (e.g., Phillips and Harvey 2009). Animal-borne cameras (e.g., Marshall 1998; Bowen et al. 2002) might provide new insights into the size frequency and the prevalence of incomplete consumption of large demersal fishes eaten by grey seals, but the key will be in obtaining a representative sample. Further captive feeding trials with choices of live prey might also be beneficial.

There are specific conditions under which partial consumption of prey is an optimal predation strategy (e.g., Cook and Cockrell 1978; Sih 1980; Penry 1993). A predator consuming an individual prey item must be able to selectively feed on portions of differing net energetic value (i.e., energy gained relative to processing cost). There must also be a net energetic benefit of leaving an unfinished prey item to find and capture a subsequent prey. An optimal foraging model of partial consumption predicts that as prey density decreases, increasing the costs of prey acquisition, predators should consume increasing proportions of individual prey items (Sih 1980). The model predictions and the conditions under which partial consumption is an optimal strategy were borne out in a study of bears feeding on salmon (Gende et al. 2001). The conditions for partial consumption may also exist for cod and white hake in the southern Gulf. First, energy density is not uniform within their bodies: depending on the season, the viscera of adult cod comprise on average between 11-16% of total body mass but between 30-43% of total body energy content. Second, positive abundance-occupancy relationships mean that local fish density can remain high even as abundance decreases (e.g., Swain and Sinclair 1994). It may therefore still be profitable for seals that target aggregations to only partially consume individual prey despite declining fish abundance. Larger fish may be more likely to be partially eaten because their energy dense parts should be easier to target and their bones more costly to process in terms of handling time, compared to smaller fish. Nevertheless, the presence of alternative and potentially more profitable prey in areas occupied by cod could negate such expectations.

If predation by grey seals contributes significantly to adult cod and white hake *M*, our simulations suggest that the contribution of these species to average diet will be relatively small and highly clustered in the small proportion of seals that overlap spatially with them. Individual diet specialization has been observed in many other species (reviewed by Bolnick et al. 2003) and may also occur in grey seals (Beck et al. 2007; Tucker et al. 2007). Estimating a reliable average diet in the face of diet specialization and a diverse prey set requires a large sample that is spatially and seasonally representative. For species such as winter skate, which would occur only at trace levels in the diet and are unlikely to be detected by traditional hard-parts analyses, predation is likely to go undetected (but see results based on chemical analyses in Beck et al. 2007).

Though our simulations aimed to capture a number of sources of uncertainty related to consumption by seals and to fish losses, potential biases related to the monthly geographic distributions of all species likely remained. For the fishes, monthly distributions other than in summer and early autumn were inferred from past surveys conducted during periods of higher abundance and therefore may differ from present distributional patterns. Furthermore, by assuming that distribution is uniform over the occupied area in non-summer months, consumption may have been underestimated if grey seals concentrate in high density areas or overestimated if they aggregate in low density areas. For grey seals, transmitters were deployed in locations where they could be captured and not necessarily where animals were distributed. It is therefore unclear to what degree distributional patterns inferred from the few tagged individuals are representative of the respective herds.

Two important components of predator behaviour that determine prey consumption are decisions related to which foraging areas to occupy and decisions concerning prey selection in the chosen foraging areas. The simulations only dealt with the former component, which shapes the potential for predation. However the predator's functional response, when confronted with a choice of sizes and species of prey, can largely influence the resulting diet. This is an information gap that can be filled by simultaneous sampling of seal diets and the prey field (e.g., Smout and Lindstrøm 2007). At present, the simulations therefore cannot verify the hypothesis that grey seal predation is an important contributor to large fish natural mortality. Rather, they can only establish the degree to which the hypothesis is plausible, given constraints on food ingestion by seals, overlap between species and species abundances. The simulations are therefore another approach to increase our understanding of the ecosystem-level impacts of population increases in this generalist upper-trophic level predator. However, the largest challenge ahead will be in better understanding the diverse indirect interactions in the food webs (e.g., Punt and Butterworth 1995; Walters and Kitchell 2001; Wirsing et al. 2008) of which grey seals are an important component. It is these interactions in particular that make predicting the outcome of possible management actions very difficult (Bax 1998; Yodzis 1998, 2001). Quantifying these interactions means obtaining representative diets of all interacting species, highlighting again the need for more accurate estimates of grey seal prey composition at the population scale.

Table 7.1. Summary of the probability distribution functions for the parameters of the simulations of seal consumption and fish mortality. The notation ~ indicates ‘distributed according to’. Five theoretical distributions were used: normal [~*N*(mean, standard deviation)], lognormal [~*logN*(mean, standard deviation)], multivariate normal [$\sim N(\mu,\Sigma)$, where μ is a vector of means and Σ is the covariance matrix], uniform [~unif(minimum, maximum)] and pert. To simplify the presentation, rather than show the covariance matrix Σ for cod abundance and natural mortality, we present the correlation between these two variables ($\rho_{\mathrm{Na-Ma}}$) and their respective variances (σ^2_{Na} and σ^2_{Ma}).

Parameter name	*Symbol*	*Probability distribution function*	*References*
Gross Daily Energy intake	**GEI**		
Kleiber equation parameters	α, β	$\sim N(\mu,\Sigma)$ where $\mu=\begin{bmatrix}\alpha = 293.75 \\ \beta = 0.75\end{bmatrix}$ $\Sigma=\begin{bmatrix}5393.1 & -12.393 \\ -12.393 & 0.035\end{bmatrix}$	Kleiber 1975; Hammill and Stenson 2000
Gompertz parameters, eqn. 2 (seal mass-at-age, by sex)	γ_{1s}	$\gamma_{1m} \sim N(230.60, 6.93)$, $\gamma_{1f} \sim N(183.70, 3.57)$	M.O. Hammill unpublished analysis
	γ_{2s}	$\gamma_{2m} \sim N(1.521, 0.074)$, $\gamma_{2f} \sim N(1.242, 0.048)$	
	γ_{3s}	$\gamma_{3m} \sim N(0.250, 0.022)$, $\gamma_{3f} \sim N(0.190, 0.014)$	
Activity Factor	AF	~pert with median=2.0 and range=[1.7, 3.0]	Innes et al. 1987; Worthy 1987a,b, 1990; Castellini et al. 1992; Sparling and Fedak 2004
Growth premium (at age)	GP_a	GP_0~unif (1.80, 2.00), GP_1~unif (1.50, 1.70)	Ronald et al. 1984; Worthy

Parameter name	*Symbol*	*Probability distribution function*	*References*
		GP_2~unif (1.25, 1.45), GP_3~unif (1.10, 1.30) GP_4~unif (1.05, 1.20), GP_5~unif (1.03, 1.13), GP_{6+}=1.00	1987a,b; Olesiuk 1993; Mohn and Bowen 1996
Metabolizable energy	ME	$\sim N(0.830,0.048)$	Ronald et al. 1984
Seal and fish abundance, fish *M*			
Grey seal abundance	$N_{\text{seal, pop.}}$	$N_{\text{seal,Gulf}} \sim N(51\,311, 2\,696)$, $N_{\text{seal,Sable}} \sim N(244\,787, 6\,462)$, $N_{\text{seal, Coastal NS}} \sim N(12\,172, 568)$	updated fit of Hammill (2005) and Bowen et al. (2007)
Cod numbers (thousands) and *M* at ages 5-15+	$N_{\text{cod, a}}$, $M_{\text{cod, a}}$	$\sim N(\mu,\Sigma)$, where :	Swain et al. 2009b

Parameter name	*Symbol*	*Probability distribution function*	*References*
		$\begin{bmatrix} \text{ages(a)} & \mu_{Ma} & \sigma^2_{Ma} \\ 5-10 & 0.625 & 0.032 \\ 11+ & 1.113 & 0.046 \end{bmatrix} \begin{bmatrix} a & \mu_{Na} & \sigma^2_{Na} & \rho_{Na-Ma} \\ 5 & 33851.1 & 8846.9 & 0.35 \\ 6 & 15139.0 & 3199.4 & 0.29 \\ 7 & 7268.8 & 1314.7 & 0.17 \\ 8 & 5447.8 & 930.5 & 0.02 \\ 9 & 3019.8 & 504.1 & -0.12 \\ 10 & 1728.9 & 294.7 & -0.27 \\ 11 & 1111.9 & 193.8 & 0.38 \\ 12 & 249.6 & 40.07 & 0.17 \\ 13 & 127.5 & 23.60 & -0.01 \\ 14 & 40.96 & 7.81 & -0.25 \\ 15+ & 17.30 & 4.08 & -0.42 \end{bmatrix}$	
White hake numbers at ages 3-7 (thousands)	$N_{whk,a}$	$\sim N(\mu_a,\sigma^2_a)$, where: $\begin{bmatrix} \text{age(a)} & \mu_a & \sigma^2_a \\ 3 & 2041.1 & 636.74 \\ 4 & 2359.1 & 573.65 \\ 5 & 549.56 & 133.28 \\ 6 & 53.36 & 20.16 \\ 7 & 26.96 & 18.51 \end{bmatrix}$	This study

Parameter name	*Symbol*	*Probability distribution function*	*References*
White hake *M* (ages 3-7)	M_{whk}	$\sim N(1.905, 0.395)$	Benoît et al. 2011
Winter skate adult numbers (proportion at length from survey; assumed fixed)	N_{ws}	$\sim N(830\ 281, 207\ 800)$	Swain et al. 2009a
Winter skate adult *M*	M_{ws}	$\sim N(0.601, 0.118)$	Swain et al. 2009a
Fish energy content, prey size structure and spatial overlap with seals			
Energy density by fish species (cod, whk–white hake, ws–winter skate) and portion consumed (wh-whole, bb-bellybiten, hl-headless)	$\mathrm{ED}_{\mathrm{sp,\ p}}$	$\mathrm{ED}_{\mathrm{cod,\ wh}} \sim N(4.20, 0.60)$, $\mathrm{ED}_{\mathrm{whk,\ wh}} \sim N(6.30, 0.95)$ $\mathrm{ED}_{\mathrm{ws,\ wh}} \sim N(3.2, 0.48)$ $\mathrm{ED}_{\mathrm{cod,\ hl}} \sim N(4.41, 0.63)$, $\mathrm{ED}_{\mathrm{cod,\ bb}} \sim logN(2.39, 0.23)$ $\mathrm{ED}_{\mathrm{whk,\ hl}} \sim N(6.62, 1.00)$, $\mathrm{ED}_{\mathrm{whk,bb}} \sim logN(2.39, 0.23)$	Steimle and Terranova 1985; Lawson et al. 1998 Derived from Ingenbleek 2006
Body mass-at-length	$\mathrm{W(L)}_{\mathrm{sp}}$	Bootstrap samples of survey data: annual for winter skate, seasonal for cod and white hake.	H. Benoît, unpublished results
Gut mass-at-length	$\mathrm{G(L)}_{\mathrm{sp}}$	Bootstrap samples of seasonal cod data.	Schwalme and Chouinard 1999. This study.

Parameter name	*Symbol*	*Probability distribution function*	*References*
Head as a proportion of total body mass	H_{sp}	$H_{sp} \sim N(0.21, 0.02)$	Gildberg 2004
Monthly spatial distribution of fish and seals (proportion of the population found in each stratum)	$O_{sp,\,m}$	Seals: bootstrap samples of distribution (see text for details). Fish: bootstrap samples of distribution for summer months (see text for details) and deterministic distribution in other months.	Seals: Breed et al. 2006; Harvey et al. 2008. Fish: Hurlbut et al. 2010, Savoie and Surette 2010
Proportion of Coastal NS herd attributed to the Sable Herd	$P_{Coastal}$	$\sim$unif (0.3, 1.00)	This study

Table 7.2. Average 2005 beginning of the year fish biomass and total biomass loss implied by the estimated (empirically-derived) natural mortality.

Species	*Biomass (tones)*	*Biomass loss (tonnes)*
Atlantic cod, ages 5+	53 883	28 126
White hake, ages 5-7	4 078	3471
Winter skate adults	816	369

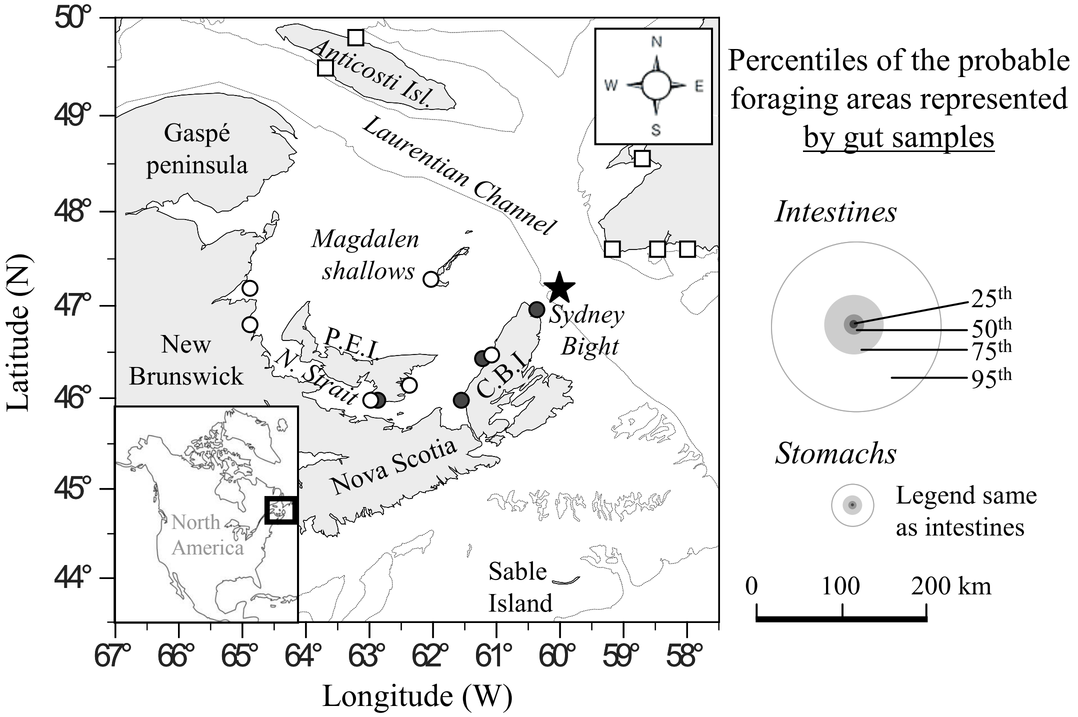

Figure 7.1. Map of the southern Gulf of St. Lawrence and neighboring eastern Scotian Shelf. Areas mentioned in the text are indicated on the map; C.B.I. – Cape Breton Island (Nova Scotia), N. Strait – Northumberland Strait, P.E.I. – Prince Edward Island. The dashed line is the 200m isobath. Also shown are the locations where grey seal stomach (squares) and intestine (circles) content samples have been taken either during spring and summer (white symbols) or during late autumn and winter (black) since 1994 (Hammill et al. 2007; Hammill et al. 2014). The location of the sample mentioned in the text (stomach, winter 2008 sample) is denoted by a black star. The legend to the right of the map shows the probable foraging area represented by each gut-content sample. The concentric circles reflect percentiles of net potential distance travelled by seals during the period represented by a diet sample, based on an analysis of movements from satellite tagged seals and gut-residency times for prey (H. Benoît, manuscript in prep.).

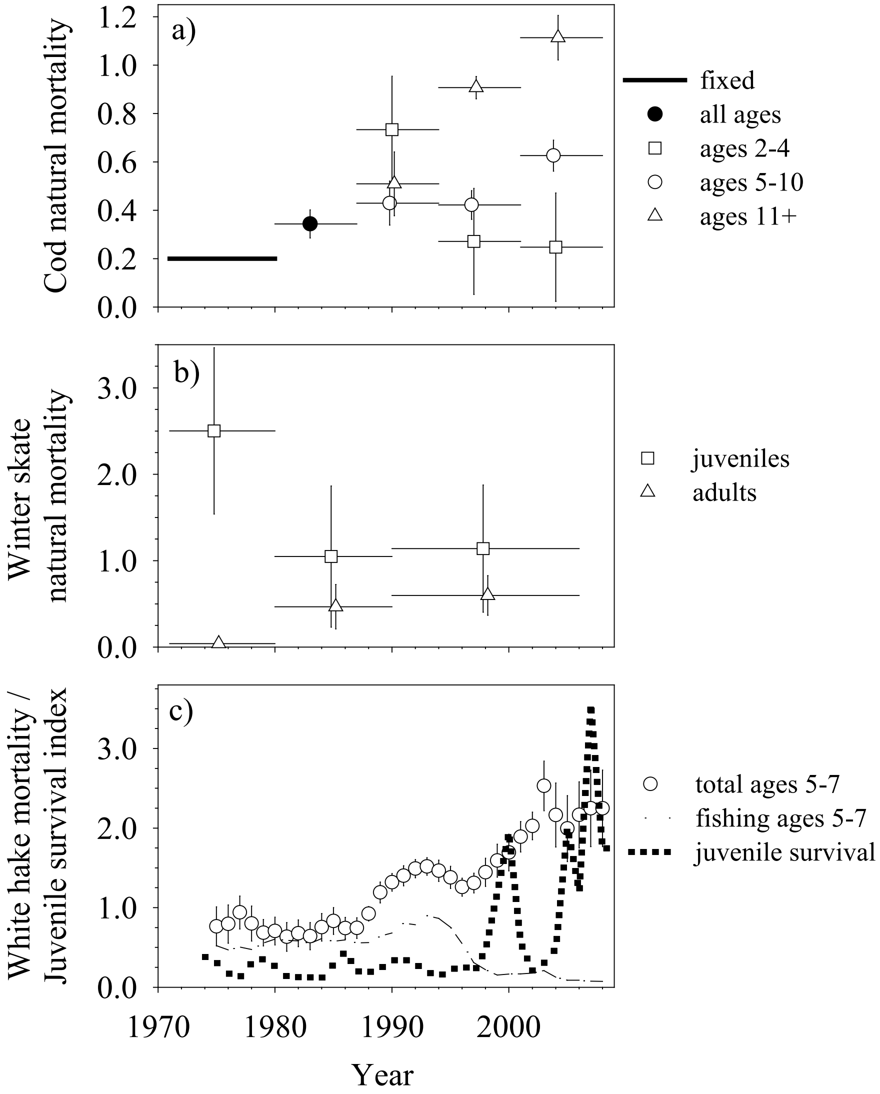

Figure 7.2. Age or stage dependent trends in mortality for three southern Gulf of St. Lawrence marine fishes. a) Age-dependent trends in cod natural mortality (mean ± 2 SE; redrawn from Swain et al. 2009b). Natural mortality was estimated via Sequential Population Analysis for blocks of years (denoted by the horizontal lines), assuming a fixed rate from 1971-1979 and estimating a common rate across ages for 1980-1986 (see Swain et al. 2009b for details). b) Stage-dependent estimates of winter skate natural mortality (mean ± 95 percentile range) in approximately decadal blocks of years (horizontal lines) from a Bayesian state-space model (Swain et al. 2009a). c) Index of juvenile survival (dotted line: numbers at age 3 in year *t* divided by the spawning stock biomass in year *t*-3), and age 5-7 total mortality (circles: mean ± 2SE) and fishing mortality (dashed line) for white hake estimated in this study (see text for details).

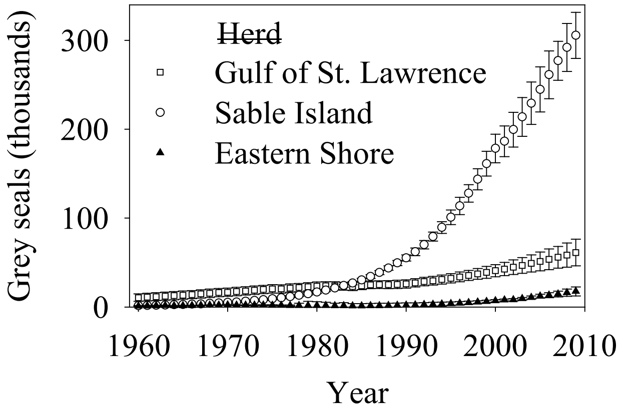

Figure 7.3. Abundance of grey seals (mean ± 2 SE) in the three NW Atlantic herds: Gulf of St. Lawrence, Sable Island and Coastal Nova Scotia (Eastern Shore).

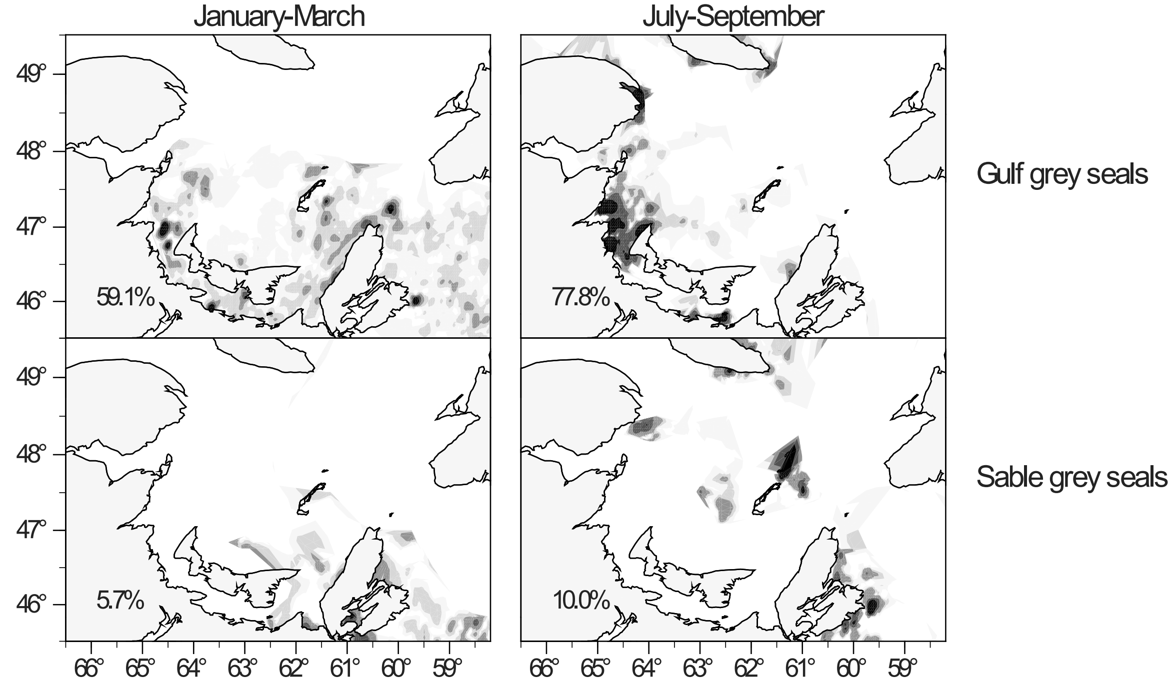

Figure 7.4. Summary of the geographic distribution grey seals in the southern Gulf of St. Lawrence and neighboring areas, by herd (rows) and for two example seasons, winter and summer (columns). The incrementing grey shading represents increasing grey seal density based on the 10th (lightest grey), 25th, 50th, 75th and 90th (black) percentiles for non-zero density in each panel. The percentage of transmitting tagged seals that occurred in the represented geographic area in the season in question is written in the left corner of each panel.

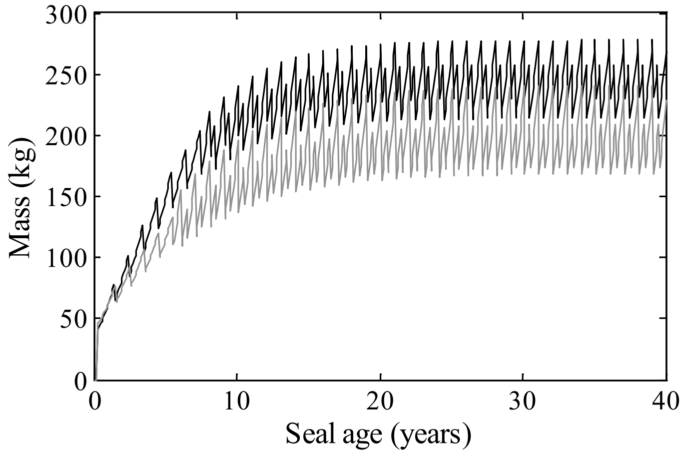

Figure 7.5. Seasonal and interannual patterns in female (grey line) and male (black) grey seal mass (kg) used in the simulation model.

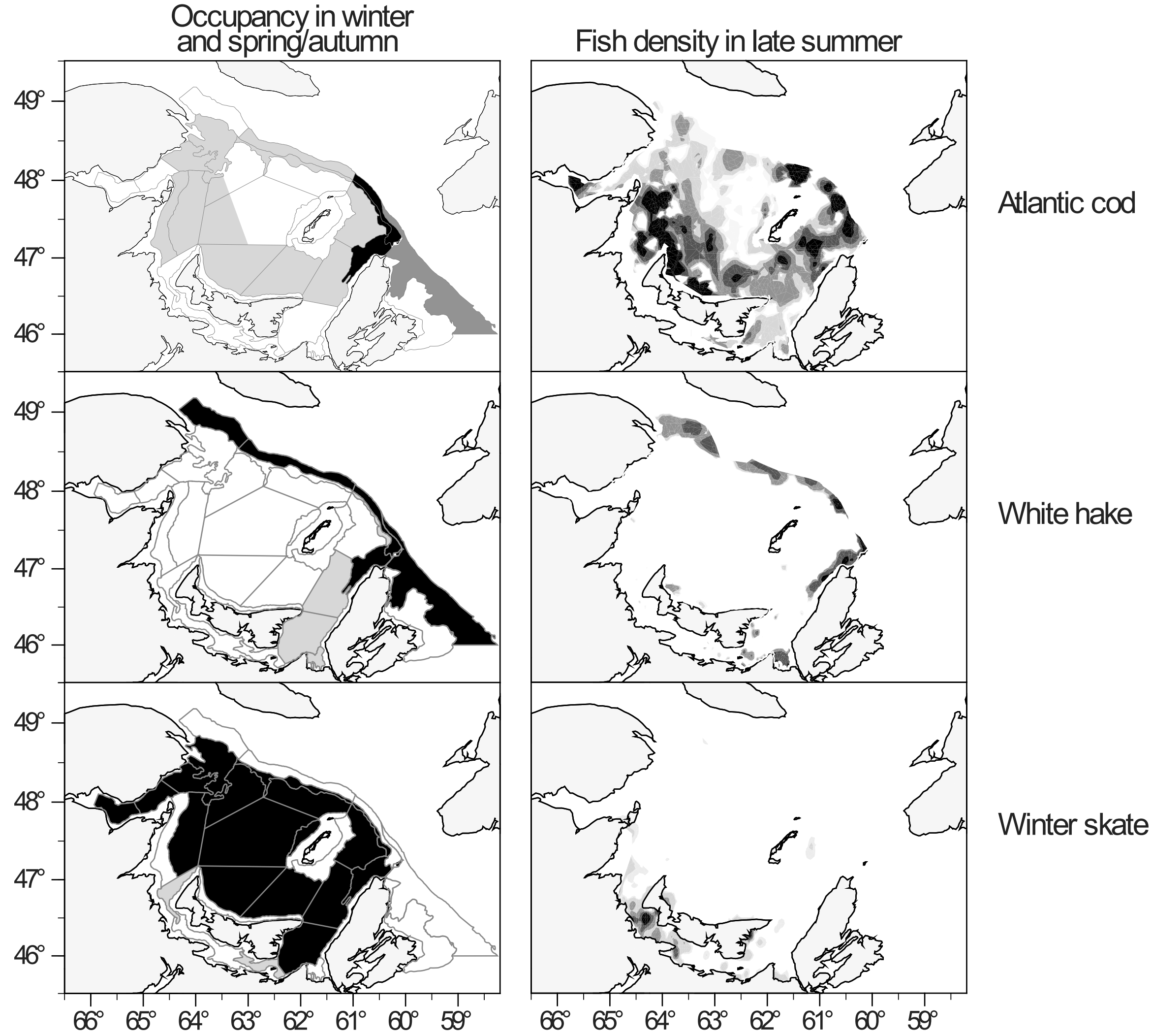

Figure 7.6. Summary of the geographic distribution of the three fish species (rows; cod, white hake and winter skate), as used in the simulation. The panels in the left-hand column present the occupancy of each fish species at the stratum scale during the winter (dark grey shading) and the spring and autumn (light grey shading). Strata occupied from autumn to spring are shaded black. The panels in the right-hand column show the distribution of density for each fish species based on summer bottom-trawl surveys. The incrementing grey shading represents increasing density based on the 10th (lightest grey), 25th, 50th, 75th and 90th (black) percentiles for non-zero density for each species.

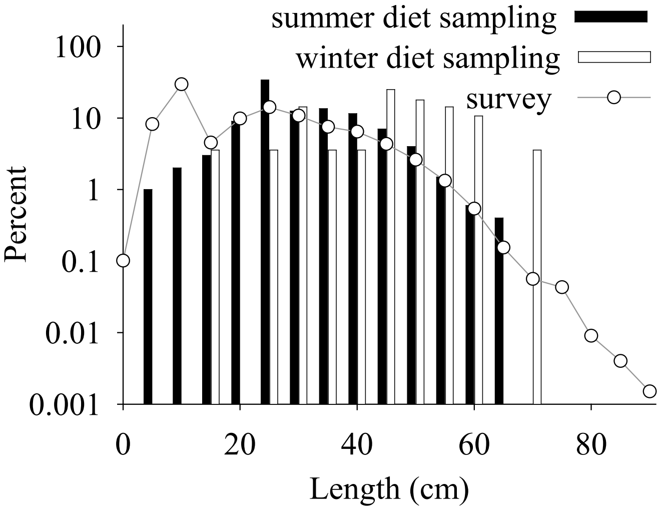

Figure 7.7. The frequency distribution of southern Gulf of St. Lawrence cod lengths in the 2005 population, and in grey seal diet samples collected during spring-summer and in the winter of 2008 (location denoted by a star in Fig. 7.1). The population frequency distribution is based on catchability-adjusted estimates from the annual September survey. Note that the percentage axis is on the log-scale.

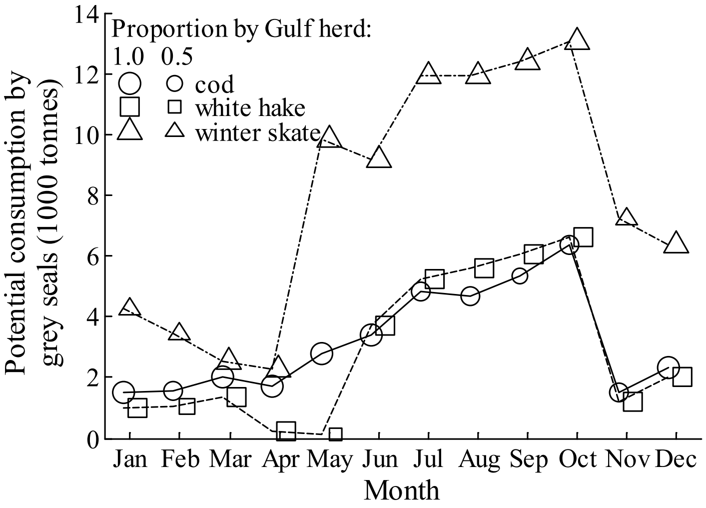

Figure 7.8. Average monthly potential consumption of sGSL cod, white hake and winter skate by grey seals. Symbol size indicates the relative contribution of the Sable Island and Gulf herds to potential consumption, as indicated in the legend. Note that symbols have been slightly offset horizontally for clarity.

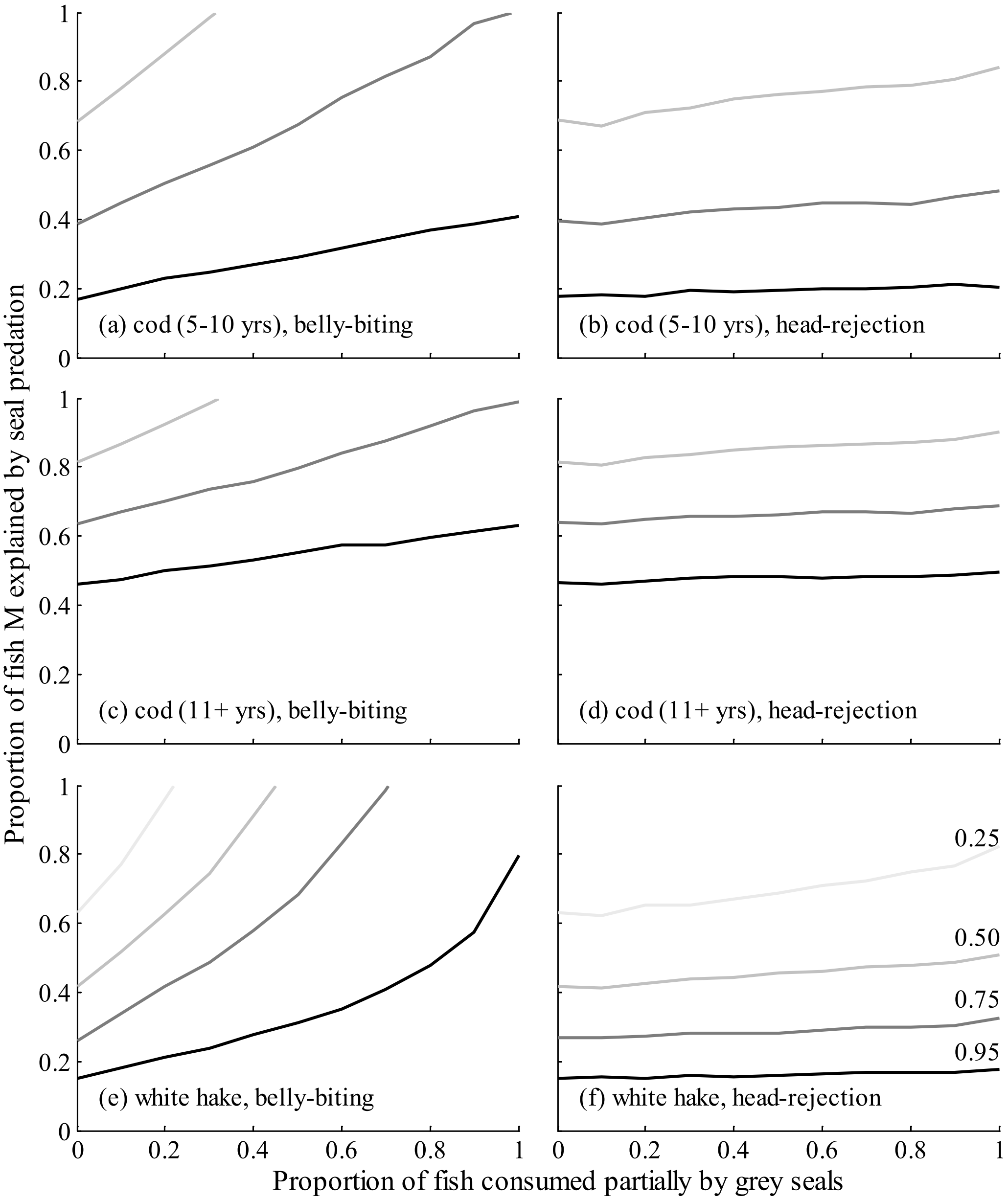

Figure 7.9. Contours of the probability from the simulation that grey seal predation can explain different proportions of fish *M* (ordinate) as a function of different proportions of fish consumed only partially (abscissa), for age 5-10 yr cod, age 11-15 yr cod or white hake (rows), consumed partially by either belly-biting (left column; panels a, c and e) or head-rejection (right column; panels b, d, f). The isoprobability contours are drawn using incrementing grey shading as indicated in panel f, e.g., probability=0.05 (lightest grey) and probability=0.95 (black).

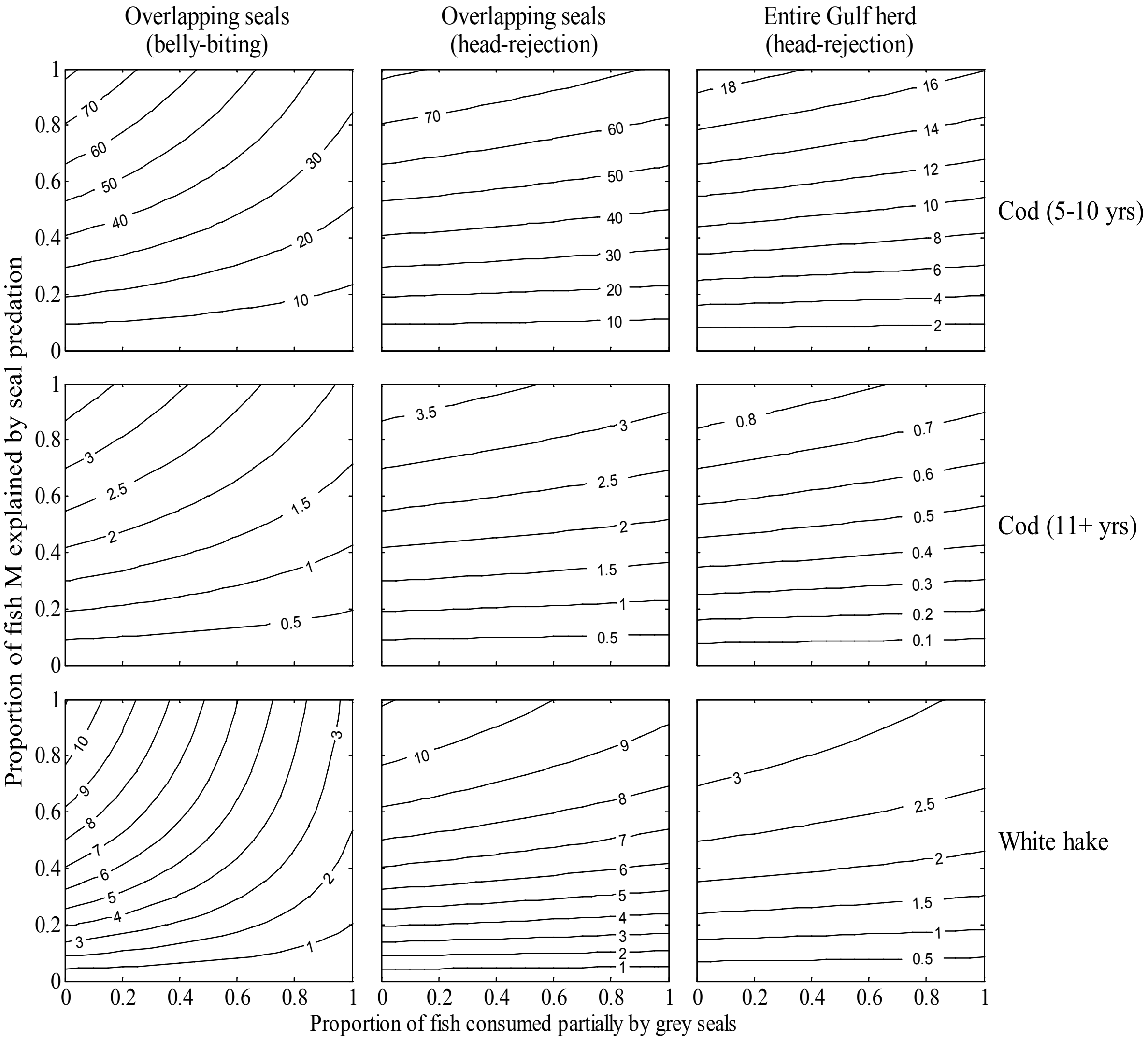

Figure 7.10. Contours of the grey seal diet composition (% of total diet) required to explain different proportions of fish *M* (ordinate) as a function of different proportions of fish consumed only partially (abscissa), for age 5-10 yr cod, age 11-15 yr cod or white hake (rows). The composition of the diet of seals overlapping with the fish species/age group in question is shown for the scenarios involving belly-biting (left column) and head-rejection (centre column) of prey. The composition of the average diet of a Gulf grey seal in the head-rejection scenario is shown in the right column.

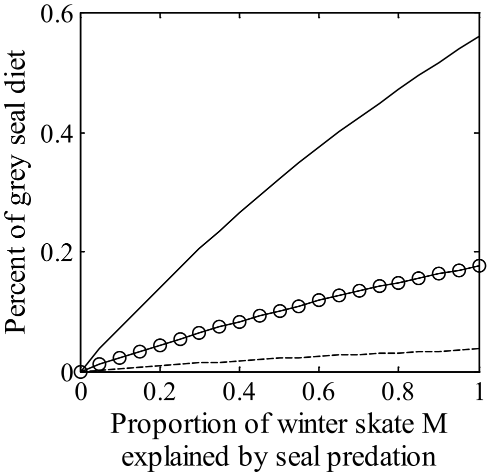

Figure 7.11. Percentage of winter skate in the grey seal diet required to explain different proportions of winter skate *M*. Shown is the required diet composition for the average Sable Island (dashed line) or Gulf (circles) grey seal, and for Gulf grey seals overlapping spatially and seasonally with winter skate (solid line).

Chapter 8. Conclusions

The general objectives of this thesis were to develop a series of quantitative approaches for the analysis or estimation of discard and natural mortality, two key, and often time-varying, sources of mortality that have often been overlooked in marine population assessments. Quantifying the magnitude of losses caused by these sources of mortality and establishing their causes is needed to achieve more accurate population assessments and hopefully more effective management actions.

The objectives for the thesis were met using a diversity of quantitative approaches. Empirical generalized linear models for multinomial data were adapted and used for the analysis of vitality data in chapter 2 and catch composition data in chapter 4. Notably, the inclusion of random effects in the model for semi-quantitative vitality data addressed an important criticism of this type of data, namely the potential consequences of observer subjectivity during data collection. Classical models for event (survival) data were used in chapters 3 and 6. In chapter 3, they were applied to derive an indicator for discard mortality and to evaluate, in a standardized and structured manner, the contribution to discard mortality of a large number of biological and environmental factors. In chapter 6, these models formed the basis of a mechanistic framework for the statistical estimation of different mortality components related to discarding and natural mortality. Finally, Monte Carlo simulations provided an important means of propagating errors to characterize variability in landings and discard loss estimates in chapter 5, and to evaluate the likelihood of hypotheses concerning predation impacts in chapter 7. This thesis highlights the importance of having a diverse toolbox of quantitative methods to address the diversity of applied research question in population ecology. I hope that that the applications that I have proposed in this thesis illustrate useful and novel applications for these tools and may, in certain instances, constitute new, though more specialized, tools.

In Section 8.1, I summarize the key findings presented in this thesis. In Section 8.2, I discuss key issues and perspectives for future research resulting from these findings and for the related fields of research more generally.

8.1 Summary

There has been a near exponential growth in the past two decades in research aimed at quantifying and understanding the mortality of discarded fish. This growth can be explained by an increased appreciation of the magnitude of discarding, its role in the depletion of populations that are targeted or not by fisheries, and the implementation of management measures aimed at controlling discard loss and achieving a more fulsome accounting of fishing mortality. The approaches developed in chapters 2 to 6 are general and applicable to fisheries worldwide. In addition to the methodological contribution made by this research, the approaches have also allowed for broad inference about the factors contributing to discard mortality and case-specific estimations for Atlantic Canadian species of conservation concern.

There are two principal contributions from the study of vitality data for discarded fish presented in chapter 2. The first is methodological. The chosen multinomial approach was demonstrated to be appropriate for these data both conceptually and in practice. The use of random effects to address observer subjectivity is conceptually an effective manner of addressing this important source of error and potential bias, while also accounting for other unexplained sources of variation among fishing trips. The prevalence of significant random effects among the studied cases confirmed that this extra variability could be important.

The second contribution of the study in chapter 2 concerns the use of vitality data to understanding the roles of various factors affecting discard mortality. Chapters 2 and 6, as well as other studies (e.g., Benoît et al. 2012; Depestele et al. 2014), have confirmed that vitality scores are reliable predictors of discard mortality. Vitality data are therefore an easily collected and relatively affordable means of evaluating the role of a suite of factors that is much broader than could be achieved using experimental manipulation or inferred in a field-based discard mortality study. In chapter 2, I was able to demonstrate that the gear type used, the amount of time that fish spent on deck prior to discarding and fish body size strongly and consistently affected vitality, and by inference mortality. Other environmental factors (temperatures, depth) were found to have a less consistent effect. Evaluating a broad suite of factors for a large number of species and fisheries arguably allowed for a more equitable and general evaluation of contributing factors compared to studies directly focussed on discard mortality.

Chapter 3 also made two principal contributions. First, it established the time-to-mortality metric as an indicator of discard mortality in trawl fisheries that can easily be obtained at low cost in existing surveys or derived using the empirical model presented in the chapter. This metric can help in prioritizing research, such as under the new European Union landing obligation (Morfin et al. 2017b), and will likely to be useful in risk-based approaches for evaluating the impact of fisheries on non-target species (e.g., Zhou and Griffiths 2008; DFO 2012b). The second contribution, similar to that of chapter 2, was the standardized evaluation of a broad suite of environmental factors and biological traits affecting time to mortality and, by inference, discard mortality. This allowed me to draw coherent inferences concerning these covariates within and across species, which was not previously possible in this field of research. Notably, this resulted in an enhanced understanding of the role of hypoxia in the mortality of discarded fish, via contributions from size- and “life-style” specific respiratory demands. I believe that that result and others concerning species traits constitute a large step towards a more mechanistic understanding of the causes of variability in discard mortality susceptibility within and among species.

Chapters 4 and 5 propose methodologies for the quantitative estimation of fishery losses for species that are killed, but not targeted by fisheries. Catch data for these types of species are often much sparser, less detailed and potentially less accurate compared to data for commercially important species. For skates in the southern Gulf of St. Lawrence, catch estimation required disaggregating catches by species in the absence of ancillary samples to do so. The approach in chapter 4 drew on simple important seasonal environmental associations to model assemblage composition using research survey data. This allowed for the estimation of species-specific discard amounts, as well as landings. The use of a nominal model, in which composition, rather than abundance, was modelled and predicted, was key to the relative success of the approach. That choice resulted in considerably less restrictive assumptions concerning differences in catchability over time (seasons, years) and between fishing events (vessels, gear, etc.), which otherwise would have precluded the use of the survey data. I am not aware of other papers having similarly tackled the common problem of mixed catches using such an empirical approach. Validation of the approach using survey and catch records for flatfish was important in establishing its dependability and uncertainties. Similarly, validation of the discard estimation process in chapter 5, by comparing observed and estimated landings, was important in establishing the dependability of the estimates and validity of the approach, particularly in light of relatively sparse bycatch observations.

Chapter 5 made two main contributions. The first is applied. It provided species-specific estimates of landings, discards and discard mortality for the three southern Gulf skate species. All three are of conservation concern, and in particular, winter skate is at imminent risk of extirpation (Swain and Benoît 2017). Mortality has risen to very high levels in these species (Swain et al. 2012; Swain and Benoît 2015) and determining how much of that mortality resulted from fishing was necessary for understanding the causes of ongoing declines and the planning of possible management action (e.g., Swain et al. 2009a). The results from chapter 5 have led to the determination that fishing mortality may have contributed to declines in earlier decades but is now trivial compared to natural mortality (Swain and Benoît 2017).

The second contribution of chapter 5 is methodological. The approach is a fundamentally integrated one. It relies on information from a number of sources (landings and observer catch statistics, research surveys, oceanographic information) and different methodologies, including those developed in chapters 2 and 6 for discard mortality estimation. The approach ensures that sampling error in the data and errors in the component empirical models is reflected as best possible in the uncertainty of the resulting estimates. While fairly basic in its application, the approach is consistent with the philosophy of modern fully integrated stock assessments (e.g., Cadigan 2016).

The modelling framework developed in chapter 6 is perhaps the contribution in this thesis of which I am most pleased. First, it addresses the longstanding and previously unresolved problem of distinguishing discard mortality from natural mortality for marine fish. Based on simulation results, the model appears able to estimate the two components of mortality with little to no bias under a range of conditions. Second, the model can estimate different components of discard mortality, such as mortality during capture, handling or post-release, allowing for a better targeting of management actions aimed at mitigating discard mortality. Third, the basic model was demonstrated to be easily generalizable. It can therefore serve as the basis for future, more complex models aimed at answering different questions related to discard and in situ mortality.

Finally, chapter 7 also makes both applied and methodological contributions. This research was important in establishing predation by grey seals as a plausible and reasonable explanation for very high adult mortality in three species at risk of extirpation in the southern Gulf of St. Lawrence. In the absence of reliable estimates of predator diets that would have allowed for a more direct evaluation of the hypothesis, this inverse approach contributed strongly to the weight of evidence for a predation effect (see the Discussion in Swain and Benoît 2015). The simulations in chapter 7 also represent a fundamentally integrated approach, drawing together information from a multitude of sources (e.g., surveys, animal tracking, and bioenergetics), and ensuring an accounting of the uncertainty associated with each input and component model.

8.2 Perspectives

Building on the developments presented in this thesis and which have arisen during its conception, I discuss below what I believe to be important challenges for future research in fisheries science on discard mortality and on natural mortality.

8.2.1 Discard mortality

The somewhat arcane field of discard mortality research is one which I believe to still lack a certain maturity. While there are many published studies, these are generally very case specific, are often unreplicated and often employ experimental and analytical methods in which discard mortality is confounded with other potential causes. Partly as a result, existing reviews of the literature have been informative but not very conclusive in my view (e.g., Davis 2000; Broadhurst et al. 2006). The field still lacks a strong mechanistic understanding of the determinants of discard mortality and an ability to accurately predict mortality rates. Given the vast number of fisheries and species requiring scientific advice on discard mortality for the management of populations affected by fishing, it is clear that the field needs to move away from a reliance on expensive, yet often inadequate, case-specific experiments. I see promising directions for this field in the near future.

First, there is a need to adopt of a suite of best practices for the design and analysis of discard mortality studies to best ensure that mortality estimates correctly reflect those experienced by fish in the field. Such best practices have been developed by the ICES Workshop on Methods for Estimating Discard Mortality (ICES WKMEDS; ICES, 2014, 2015). Whiles these have largely been adopted in European studies leading up to the implementation of the landings obligation (e.g., Morfin et al. 2017a), it is too early to determine whether there will be broader adoption. New technologies, particularly electronic tagging, hold considerable promise for the estimation of discard mortality *in situ*, where conditions represent those experienced by fish discarded in fisheries. This was demonstrated with the examples and a case study presented in Chapter 6. Notably, the combined use of traditional tag returns and telemetry has particular potential for the estimation of various components of fishing mortality (including retained catch) and natural mortality (Kerns et al 2016).

Second, the field will benefit from structured systematic critical reviews, including properly standardized meta-analyses from which to establish general principals. Systematic review methodology ensures that only those studies which meet pre-established quality requirements are used to draw inferences (Higgins and Green 2011; Collaboration for Environmental Evidence 2013). The goal is to disregard or down-weight those studies in which effects of interest may be confounded with other effects, or which may present unreliable estimates as a result of poor replication. A literature review or meta-analysis conducted using the suite of resulting filtered set of studies is more likely to draw more accurate conclusions. In recognition of the value of critical reviews, particularly in light of the weaknesses of many discard mortality studies, the ICES WKMEDS has established systematic review criteria and has been undertaking a structured review (ICES 2016). The next step will be to use those results more quantitatively in a formal meta-analysis. This is likely to be fruitful, as evidenced in a related field of study. The use of systematic review methodology, combined with meta-analysis, has led to a reasonably well-developed mechanistic understanding and predictive framework for the impacts of bottom-trawling impacts seabed ecosystems (e.g., Hiddink et al. 2017). Like research on discard mortality, this field of research had long been associated with expensive case-specific studies that were often unreplicated and in which impacts are confounded with other sources of variability.

Third, there is a need for the further development of methods for evaluating or estimating discard loss in the absence of situation-specific information. The methods presented in chapters 2 and 3 partly fill this niche, but predictions made using these methods remain relative rather than absolute. Studies aimed at determining how the fishing mortality of discarded species relates to that experienced by the population targeted by a fishery may be particularly useful. Inasmuch as fishing mortality for both the discarded and targeted species scales with fishing effort, stock assessments for commercial species can help inform on the mortality of discarded fish (e.g., Swain and Benoît 2017). In effect, this approach takes advantage of the more numerous and better data that tend to be available for assessing the status of commercial species, compared to non-commercial species. Of course, factors such as changes in the relative distributions of fisheries and the incidentally captured species will affect this proportionality. Research directed at understanding the effect of these factors could lead to general principles that would allow for the broad use of directed fishing mortality as a predictor of discard fishing mortality.

8.2.1 Natural mortality

The treatment of the natural mortality rate parameter (M) in stock assessment models has evolved considerably since the 1980s, and particularly during the last decade. State-space methodology now allows for the estimation of time-varying M for different age classes within a model (e.g., Jiao et al. 2012; Cadigan 2016) and researchers are beginning to explicitly model the causes of these changes within the models (e.g., Cook and Trijoulet 2016). Furthermore, these assessment models have been expanded to multispecies versions in order to better account for trophic interactions (e.g., Van Kirk et al. 2010; Curti et al. 2013). In a number of instances these developments have resulted in more reliable stock assessments by explicitly addressing time-varying productivity components that when left unaddressed result in poor model fit and large retrospective problems (e.g., Rossi et al., in press).

The acknowledgement that *M* can vary over time raises a number of challenges. First, short-term tactical and long-term strategic management planning requires projecting population dynamics into the future to evaluate the possible outcomes of different management options. This requires projecting or assuming future trends in natural mortality, which is a non-trivial task. Research aimed at understanding the causes of changes in *M*, their functional relationship, and in predicting future dynamics of those agents is likely to result in the most accurate projections. Furthermore, this research would support the simulation of different scenarios for the management of the agents of *M*. In the absence of such information, basic research aimed at finding the most appropriate statistical methodology for projection, such as using autoregressive techniques, would be valuable.

Second, because *M* is a key demographic rate that determines population productivity, non-stationary patterns (e.g., long-term trends) in *M* should motivate a revision of reference points used to promote the sustainable management of harvested populations (e.g., Trijoulet et al. 2017). However, it is still not clear how fishing mortality reference points should be modified, particularly if stock-recruitment relationships are uncertain (Legault and Palmer 2015). In cases where *M* has increased to levels that are high with respect to the life-history of the species, and have not been accompanied by compensatory increases in recruitment, it is clear that fishing mortality reference points need to be decreased. However, the amount of decrease required to promote rebuilding while not foregoing too much yield is not clear and is worthy of further investigation.

Finally, there is increasing recognition that changes in top predator abundances have resulted in important increases in *M* in their prey, notably with respect to seal top predators (e.g., Cook et al. 2015; Sinclair et al. 2015; Swain and Benoît 2015; Marshall et al. 2016). With increased conservation efforts, many populations of seals worldwide have increased in abundance, in some cases considerably (Magera et al. 2013). There is now evidence for increases in *M* related to seal-predation in the North Atlantic, Northwest Pacific, the Baltic Sea and elsewhere (e.g., Gårdmark et al. 2012; Mäntyniemi et al. 2012; Ward et al. 2012; Swain and Benoît 2015). In many instances, the increased abundance of seal predators coincided with periods of increased fishing mortality and eventual stock collapse of their fish prey. The combination of reduced prey abundance and high predator abundance can often result in a predator pit, in which *M* increases rapidly and prey populations struggle to rebuild (Gascoigne and Lipcius 2004; Bakun 2006; Pavlovà and Berek 2012). These strong depensatory dynamics are in effect an ‘emergent’ predator-related Allee effect (Hutchings 2013). Given the difficulty in overcoming an Allee effect once a population has been reduced to low levels, precautionary abundance thresholds (Allee effect reference points) have been proposed (Keith and Hutchings 2012). While these appear appropriate for internal-population Allee effects, such as those related to recruitment, analogous thresholds for predator-driven Allee effects will require consideration of both predator and prey demographics and understanding of predator functional response. In light of a dominant conservation ethic favoring marine mammals in many countries, there is an urgent need to develop predator-driven Allee-effect reference points to ensure resilience in harvested fish stocks.

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APPENDIX A. Supplemental information for Chapter 3.

Table A1. Scientific and common names, sample size with respect to censoring, and trait values for each of the southern Gulf of St. Lawrence marine fish species included in the study. The number of individual fish in each of three censoring categories is presented: uncensored (“none”), left censored (dead before first observed) and right censored (still alive when last observed). Ranges of values are presented for the quantitative species characteristics temperature, length and depth, whereas a value of 1 indicates the presence of a particular trait in a species for the qualitative characteristics and a species average is presented for the softness characteristic.

		Censoring			Covariate ranges								
Common name	Scientific name	none	left	right	Temper. (^{o}C)	Length (cm)	Depth (m)	deciduous	physoclistous	physostomous	mucus	sedentary	softness
Alewife	*Alosa pseudoharengus*	46	7	0	4.7-18.2	17-25	16-38	1	0	1	0	0	11.6
Alligatorfish	*Aspidophoroides monopterygius*	44	5	1	0.6-5.4	7-15	40-86	0	0	0	0	1	17.5
American Plaice	*Hippoglossoides platessoides*	242	19	1	0.2-4.4	19-36	30-82	0	0	0	0	1	13.2
Arctic Alligatorfish	*Uleina olrikii*	15	5	1	0.3-1.4	5-12	55-96	0	0	0	0	1	17.9
Arctic Staghorn Sculpin	*Gymnocanthus tricuspis*	52	10	4	0.1-1.5	6-19	34-72	0	0	0	0	1	4.2
Atlantic Cod	*Gadus morhua*	226	25	13	0.1-6.9	24-55	30-101	0	1	0	0	0	12.7
Atlantic Hagfish	*Myxine glutinosa*	11	0	37	4.8-5.6	31-42	171-358	0	0	0	1	1	4.2
Atlantic Halibut	*Hippoglossus hippoglossus*	18	0	6	1.7-13.1	31-76	26-298	0	0	0	0	0	19.9
Atlantic Herring	*Clupea harengus*	111	35	2	0.8-16.8	13-32	20-86	1	0	1	0	0	9.2
Atlantic Mackerel	*Scomber scombrus*	21	9	0	2.1-17.4	17-27	22-62	0	0	0	0	0	11.9

Common name	Scientific name	Censoring			Covariate ranges								
		none	left	right	Temper. (°C)	Length (cm)	Depth (m)	deciduous	physoclistous	physostomous	mucus	sedentary	softness
Atlantic Poacher	*Leptagonus decagonus*	46	13	3	0.4-1.7	14-22	60-121	0	0	0	0	1	10.8
Atlantic Soft Pout	*Melanostigma atlanticum*	18	2	1	5.4-5.4	9-12	280-358	0	0	0	1	0	2.1
Atlantic Spiny Lumpsucker	*Eumicrotremus spinosus*	15	3	3	0-0.9	3-9	47-68	0	1	0	0	1	2.8
Capelin	*Mallotus villosus*	0	93	0	0.4-4.4	8-15	47-102	1	1	0	0	0	4.1
Cunner	*Tautogolabrus adspersus*	21	2	5	10.3-17.9	8-29	22-33	0	1	0	0	1	11.1
Daubed Shanny	*Leptoclinus maculatus*	52	36	1	0.3-4.9	9-14	45-101	0	0	1	1	1	7.6
Fourbeard Rockling	*Enchelyopus cimbrius*	9	5	0	0.8-17.1	17-30	22-352	0	1	0	0	1	4
Fourline Snakeblenny	*Eumesogrammus praecisus*	81	4	0	0.1-2.2	10-20	45-99	0	0	1	1	1	2.9
Greenland Cod	*Gadus ogac*	9	12	0	0.5-14	20-41	27-60	0	1	0	0	0	4.7
Greenland Halibut	*Reinhardtius hippoglossoides*	55	9	12	1.1-5.6	16-50	64-352	0	0	0	1	0	15.4
Hookear Sculpin	*Artediellus sp.*	11	8	0	0.1-5.1	5-8	42-174	0	0	0	0	1	2.1
Longfin Hake	*Phycis chesteri*	2	12	0	5.3-5.6	20-32	214-346	0	1	0	0	0	4.3
Longhorn Sculpin	*Myoxocephalus octodecemspinosus*	40	0	72	1.5-17.9	16-28	22-45	0	0	0	0	1	11.7
Lumpfish	*Cyclopterus lumpus*	16	1	9	0.3-12.2	6-33	27-161	0	1	0	0	0	15.2
Marlin-Spike Grenadier	*Nezumia bairdii*	8	24	0	5.3-5.7	10-30	276-358	0	1	0	0	0	11.1
Moustache Sculpin	*Triglops murrayi*	23	63	0	0.4-2.3	8-15	40-89	0	0	0	0	1	9.1
Newfoundland Eelpout	*Lycodes lavalaei*	92	3	20	0.2-1.8	12-58	44-82	0	0	0	1	1	5.2
North. Sand Lance	*Ammodytes dubius*	8	4	0	0.7-8.3	5-24	25-54	0	0	0	0	0	5.2

Common name	Scientific name	Censoring			Covariate ranges								
		none	left	right	Temper. (^{o}C)	Length (cm)	Depth (m)	deciduous	physoclistous	physostomous	mucus	sedentary	softness
Ocean Pout	*Zoarces americanus*	8	0	3	1.7-17.9	20-66	23-44	0	0	0	1	1	5.5
Rainbow Smelt	*Osmerus mordax mordax*	10	45	0	3.9-16.8	13-19	20-33	1	1	0	0	0	6.6
Redfish	*Sebastes sp.*	55	28	11	2.1-5.7	12-43	99-346	0	1	0	0	0	12.6
Sea Raven	*Hemitripterus americanus*	10	1	29	1.8-16.8	16-38	23-60	0	0	0	0	1	7.8
Shorthorn Sculpin	*Myoxocephalus scorpius*	26	1	29	0.4-14.8	20-42	25-75	0	0	0	0	1	6.2
Smooth Skate	*Malacoraja senta*	11	52	38	1.2-5.5	10-53	93-311	0	0	0	0	1	6.2
Snake blenny	*Lumpenus lumpretaeformis*	14	10	1	0.5-4.9	13-34	41-153	0	0	1	1	1	6
Spatulate Sculpin	*Icelus spatula*	9	9	1	0.1-0.9	5-13	57-96	0	0	0	0	1	9.3
Stout Eelblenny	*Anisarchus. medius*	49	17	5	0-5.1	9-31	40-92	0	0	1	1	1	5
Thorny Skate	*Amblyraja radiata*	39	151	214	1-5.5	12-55	49-300	0	0	0	0	1	11.7
Threespine Stickleback	*Gasterosteus aculeatus*	16	2	2	0.5-15.9	4-7.5	20-79	0	0	0	0	0	4.8
Vahl's Eelpout	*Lycodes vahlii*	26	5	11	0.8-4.4	12-50	50-153	0	0	0	1	1	5.6
Varigated Snailfish	*Liparis gibbus*	32	25	1	0-4.4	5-30	42-99	0	1	0	0	1	1.1
White Barracudina	*Arctozenus risso*	0	31	0	0.9-5.7	19-25	72-353	1	0	0	0	0	4.6
White Hake	*Urophycis tenuis*	48	16	12	3.4-17.9	20-49	23-345	0	1	0	1	0	3.9
Windowpane	*Scophthalmus aquosus*	32	0	1	11.5-18.4	11-22	16-31	0	0	0	0	1	15
Winter Flounder	*Pseudopleuronectes americanus*	84	6	62	2.3-17.5	12-34	19-39	0	0	0	0	1	12.2
Winter Skate	*Leucoraja ocellata*	0	17	17	5-19.9	25-64	22-55	0	0	0	0	1	11.6

		Censoring			Covariate ranges								
Common name	Scientific name	none	left	right	Temper. (^{o}C)	Length (cm)	Depth (m)	deciduous	physoclistous	physostomous	mucus	sedentary	softness
Witch Flounder	*Glyptocephalus cynoglossus*	48	0	3	1.2-5.6	21-40	94-352	0	0	0	1	1	14.1
Yellowtail Flounder	*Limanda ferruginea*	82	2	14	0.7-16.8	18-30	23-54	0	0	0	0	1	15.7

Table A2. Spearman rank correlation matrix for the species traits used in the comparative analysis. Species averages were used to calculate the correlation coefficients for the continuous traits depth, temperature and softness. Correlation coefficients associated with a P-value of *P*<0.05 are indicated in bold.

Traits	1	2	3	4	5	6	7	8
1. MSRD								
2. depth	-0.02							
3. temperature	**0.35**	0.17						
4. mucus	0.01	**0.30**	0.14					
5. physoclistous	-0.19	0.17	-0.04	-0.22				
6. physostomous	0.15	-0.18	0.09	0.24	-0.23			
7. sedentary	-0.13	-0.20	0.11	0.20	-0.28	0.09		
8. softness	-0.24	-0.19	-0.27	-0.27	-0.17	-0.12	0.18	
9. deciduous scales	0.03	-0.06	-0.19	-0.19	0.10	0.28	**-0.37**	-0.10

APPENDIX B. Supplemental information for Chapter 4.

Table B1. The timing, location (see Fig. 4.1), and survey specifications (area surveyed, trawl type, dates, vessel, tow speed and target duration) for the fishery-independent bottom-trawl surveys of the Gulf of St. Lawrence (GSL) used in the seasonal depth-dependent distribution analysis. In the Area column, the abbreviations S., S.E., and S.W. indicate respectively, southern, south-eastern and south-western, and N. Strait is the Northumberland Strait.

Survey	Area	Trawl	Month	Year(s)	Vessel	Speed (kn)	Dur. (min)	Reference
Annual multi-species	S. GSL	Western IIA	9	85-91 92-05 04-10	*L. Hammond* *CCGS A. Needler* *CCGS Teleost*	3.5	30	Hurlbut and Clay (1990); Chadwick et al. (2007)
Northern GSL	Laurentian Channel	Engels	1	88-94	*MV Gadus Atlantica*	3.5	30	Pitt et al. (1981)
Seasonal multi-species surveys	S.E. GSL	Western IIA	1,5,6,12	86-87	*L. Hammond*	3.5	30	Clay (1991);
	S.W. GSL	Western IIA	4,6,7,8, 11,12	89-92	*L. Hammond;* *CCGS A. Needler*	3.5	30	Darbyson and Benoît (2003)
Overwintering fish survey	Sydney Bight	Western IIA	1	94-95	*CCGS A. Needler*	3.5	30	Chouinard and Hulbut (2011)
		Campellen	1	96-97	*CCGS Templeman*	3.0	15	

Survey	Area	Trawl	Month	Year(s)	Vessel	Speed (kn)	Dur. (min)	Reference
Sentinel survey	S. GSL	Star Balloon	8	03-10	Commercial vessel	2.5	30	Savoie and Surette (2010)
Inshore multi-species	N. Strait	286 Rockhopper	7,8,9,10	01-06	*CCGS Opilio*	2.5	15	Bosman et al. (2010)

References for Table B1

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Variations of the baseline-category logits harmonic regression model

i) Consequences of including both main and interaction effects for the day-of-the-year predictor variable

The fits to data and predictions of the baseline-category logits harmonic regression (BCLHR) model used in the paper (eqn. 4.2), which includes the quadratic effects of depth and the effects of the interaction between depth and time (day-of-the-year), were compared to fits and predictions of a BCLHR model that also included "main" effects of time. These models were defined respectively by eqn. 4.2, reprinted here as eqn. B.1, and by eqn. B.2:

$$\text{(B.1)} \quad \log\frac{\pi_j(d,t)}{\pi_J(d,t)} = \beta_{0,j} + \beta_{1,j}\cdot d + \beta_{2,j}\cdot d^2 + d\cdot\sum_{p=1}^{3}\alpha_{p,j}\cdot\sin(p\omega t - \varphi_{p,j})$$

(B.2)

$$\log\frac{\pi_j(d,t)}{\pi_J(d,t)} = \beta_{0,j} + \beta_{1,j}\cdot d + \beta_{2,j}\cdot d^2 + d\cdot\sum_{p=1}^{3}\alpha_{p,j}\cdot\sin(p\omega t - \varphi_{p,j}) + \sum_{p=1}^{3}\lambda_{p,j}\cdot\sin(p\omega t - \eta_{p,j})$$

with j=1,..., J-1 in both cases, and where $\pi_j(d,t)$ is the response probability for species j, J is the number of species in the taxonomic family, $\omega = {}^{2\pi}\!/_{365}$ is the fundamental annual frequency, p defines the cycle frequency (annual, p=1; semi-annual, p=2; tri-annual, p=3), and $\beta_{0,j}$, $\beta_{1,j}$, $\beta_{2,j}$, $\alpha_{p,j}$, $\varphi_{p,j}$, $\lambda_{p,j}$ and $\eta_{p,j}$ are parameters to be estimated. The parameters $\alpha_{p,j}$ and $\varphi_{p,j}$ are the signal amplitudes and phases, respectively, for the interaction effect of time and depth. The parameters $\lambda_{p,j}$ and $\eta_{p,j}$ are the signal amplitudes and phases, respectively, for the "main" effect of time.

The model in eqn. B.2 provided a better fit to the survey data compared to the model in eqn. B.1 based on AIC for both skates (ΔAIC=123) and flatfish (ΔAIC=1214).

However these improvements in overall fit resulting from the increased flexibility of eqn. B.2 over eqn. B.1 were accompanied by two costs.

The first cost is a poorer model fit for at least smooth skate and winter flounder during the winter months, when survey sampling, though sparse, indicates relative abundances that are not predicted by the model (Figs. B1 and B2). The result appears to have occurred because most of the data used in fitting were from September, thereby dominating the likelihood calculations such that small improvements in fit for that month at the expense of lesser fit for winter data nonetheless translated to improved fit overall.

The second cost associated with the more flexible eqn. B.2 is in generating fine temporal scale variability in predicted distribution that is appears to be beyond what is ecologically plausible (Figs. B1 and B2). For example, eqn. B.2 predicts that smooth skate, winter flounder, American plaice and witch flounder essentially vacate the ecosystem during the winter (particularly days 50-100), while yellowtail flounder come to dominate at all depths. Though there has been no survey sampling during that period, results from samples taken in early January and early April are not consistent with this result. For American plaice and yellowtail flounder, the dramatic shift in predicted distribution occurs over the course of a few days (Fig. B2), a movement speed that is simply not plausible for largely sedentary medium sized fish. Another example is the predicted rapid shifts in relative distribution for thorny and smooth skates at intermediate depths (50-150) during the summer, which again are difficult to explain ecologically (Fig. B1).

These two costs appear to be sufficiently greater than any benefit gained by improved model fit for September and the summer months. Analyses using eqn. B.2 were therefore not pursued further.

ii) Consequences of fitting the model in semi-decadal blocks for the September survey data

The BCLHR model defined by eqn. B.1 was fit separately for flatfish for each of four semi-decadal blocks spanning 1990-2010, and was validated by comparing the predictions to observations of flatfish catch composition made by fisheries observers in the relevant years. The objective was to see if accounting for interannual changes in relative distribution observed in the annual September survey resulted in better predictions of fishery catch composition. The blocks were defined as 1990-1994, 1995-1999, 2000-2004 and 2005-2010. In each case, the model was fit using the survey data from September for the relevant years for a given block, while the remaining data from other months were all included regardless of the year in which they were obtained. This was the only approach possible given the availability of data in those other months. Nonetheless, because most of the survey data used in the model fitting were for September, interannual changes reflected in those data could influence the predicted fish distributions overall, particularly for the summer when much commercial fishing takes place. The validations using the fishery observer data were then undertaken as described in the main text.

Separate BCLHR models for the different semi-decadal blocks did not result in improved predictions of flatfish catch composition in commercial fisheries (Tables B2 and B3), compared to predictions based on a single model fit to data for all years (Tables 4.2 and 4.3). In fact predictions appear slightly worse based on slightly weaker correlations for Greenland halibut, American plaice and witch flounder caught in fixed gear, slightly greater estimated biases for American plaice, yellowtail flounder and winter flounder caught in mobile gear and lower confidence interval coverage levels for American plaice in all fishery groups. Given this result, only results for the BCLHR model fit to all available data at the same time are presented in the main text.

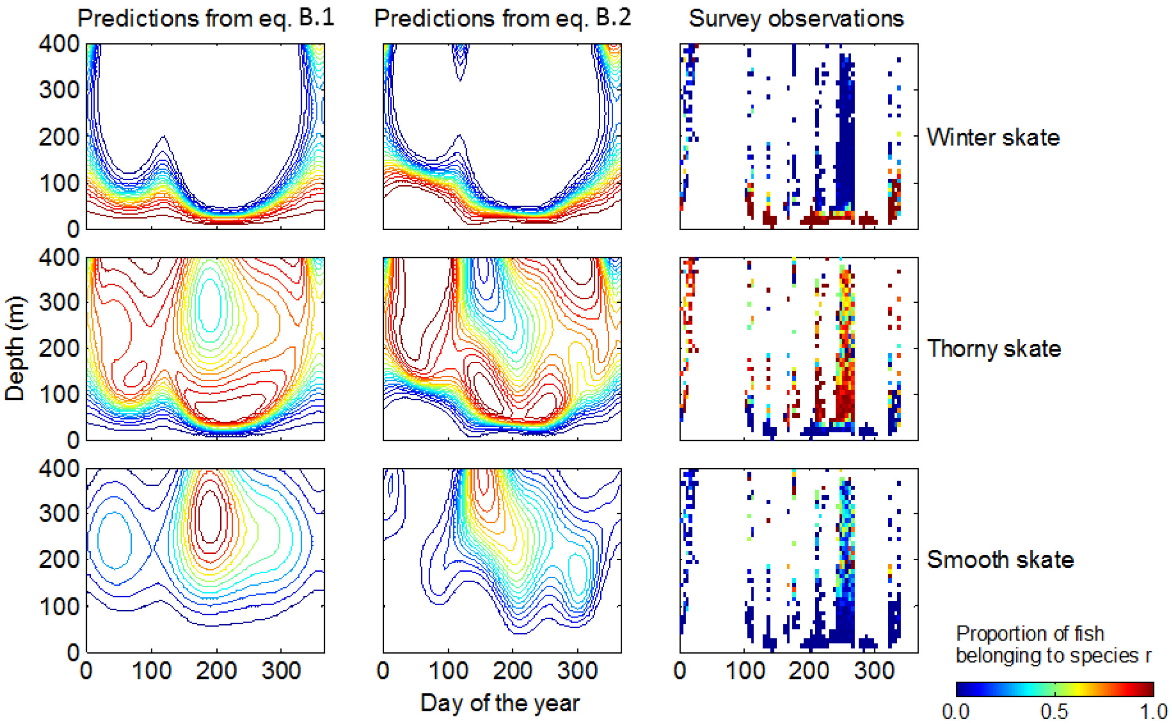

Figure B1. Contour plots of the predicted proportion of captured skate that belong to each skate species (left and center columns for predictions from eqn. B.1 and eqn. B.2 respectively) and summary of the observed proportions (right column), as a function of the day of the year and depth. Each row contains plots of the predictions and observations for one species. The species proportion level for the contours and for the summary of survey observations are indicated by colour as defined in the colour bar in the lower right-hand portion of the figure, with absence indicated by dark blue and exclusive occupation by a given species indicated by dark red. White cells in the plots summarizing observations (right column) indicate absence of survey sets that caught skates.

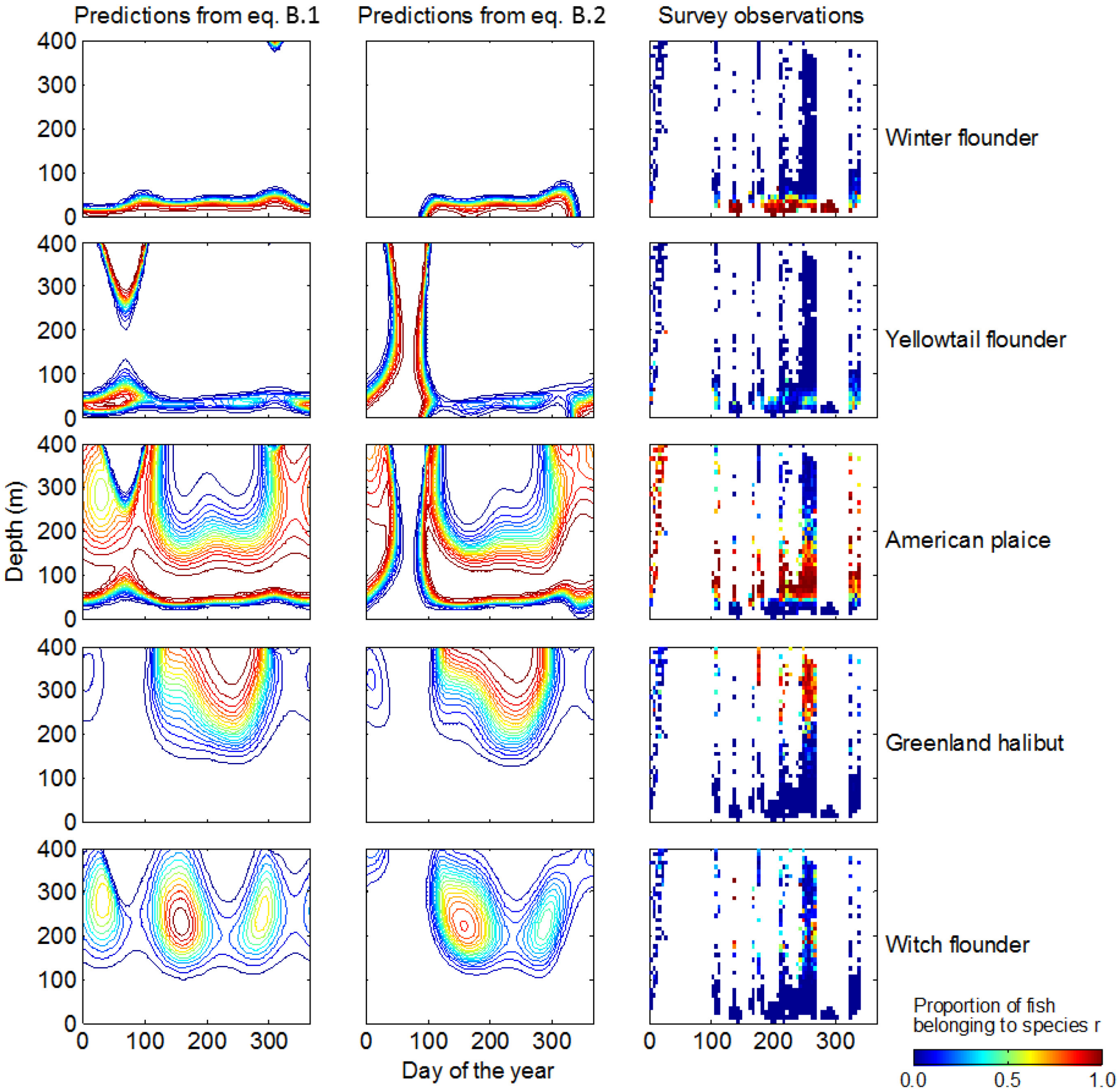

Figure B2. Contour plots of the predicted proportion of captured flatfish that belong to each flatfish species (left and center columns for predictions from eqn. B.1 and eqn. B.2 respectively) and summary of the observed proportions (right column), as a function of the day of the year and depth. Each row contains plots of the predictions and observations for one species. The species proportion level for the contours and for the summary of survey observations are indicated by colour as defined in the colour bar in the lower right-hand portion of the figure, with absence indicated by dark blue and exclusive occupation by a given species indicated by dark red. White cells in the plots summarizing observations (right column) indicate absence of survey sets that caught flatfish.

Table B2. Species-specific results of the validation exercise comparing observed catches of flatfish to those predicted by eqn. B.1 using parameters specific to the semi-decadal block in which the catches were observed: (a) Pearson correlation, (b) estimation bias, and (c) marginal coverage probability of estimated confidence intervals. Values in parentheses in (b) are the mean catches for the species and provide a scale against which to assess bias. Results are presented for three fishery groupings: shrimp trawl-fishery, and mobile-gear and fixed-gear groundfish fisheries.

		Fishery	
Species	Shrimp	Mobile	Fixed
(*a*) Correlation			
Greenland halibut	0.74	0.88	0.86
American plaice	0.70	0.93	0.59
Witch flounder	0.48	0.44	0.40
Yellowtail flounder	-	0.54	0.05
Winter flounder	-	0.75	0.72
(*b*) Bias (kg)			
Greenland halibut	-2.10 (6.20)	0.39 (7.75)	-3.21 (6.80)
American plaice	0.86 (2.95)	-2.40 (67.19)	1.03 (3.88)
Witch flounder	1.22 (1.86)	-0.05 (6.51)	1.60 (1.94)
Yellowtail flounder	0.001 (0.001)	1.03 (2.10)	0.52 (1.02)
Winter flounder	0.002 (0.001)	1.06 (2.45)	0.01 (0.94)
(*c*) Coverage			
Greenland halibut	0.68	0.88	0.83
American plaice	0.86	0.67	0.80
Witch flounder	0.89	0.73	0.89
Yellowtail flounder	0.98	0.93	0.97
Winter flounder	0.99	0.95	0.93

Table B3. Estimated pseudo joint-coverage probability for a given number, *S*, of the five flatfish species in the validation exercise comparing observed catches to those predicted by eqn. B.1 using parameters specific to the semi-decadal block in which the catches were observed. Results are presented for three fishery groupings: shrimp trawl-fishery, and mobile-gear and fixed-gear groundfish fisheries.

	Fishery		
No. species (*S*)	Shrimp	Mobile	Fixed
0	0.00	0.00	0.00
1	0.00	<0.01	0.00
2	0.02	0.10	0.07
3	0.13	0.24	0.13
4	0.17	0.08	0.14
5	0.67	0.58	0.67

APPENDIX C. Supplemental information for Chapter 5

C.1 Predicting deck time from the size of catch in a haul

The amount of time that a fish spends on a vessel's deck before being discarded (deck time, *dt*) is related to the time required to sort and process the contents of the fishing haul, which, in turn, is related to the size and compositional diversity of the catch (e.g., Wassenberg and Hill, 1989; Berghahn et al., 1992). Values for *dt* for this study were therefore obtained from a relationship relating it to catch amounts.

The information available to define such a relationship were observations on the joint distribution of *dt* and catch for 2005-2006 (from Benoît et al., 2010) and observations on the marginal distributions for the two variables for the late 1980s (from Figure 2 of Neilson et al., 1987), a period when catches were greater than in the 2000s but comparable to the early 1990s. In preliminary analyses, *dt* values for the early period were poorly predicted by contemporary observations for catch and the 2005-2006 relationship between the two variables, possibly as a result of an overall non-linear relationship between the variables. An approach involving between and within year correlations for *dt* and catch was therefore developed.

To estimate the between year relationship, data from the late 1980s and 2005-2006 were used to fit linear regressions relating the mean and the variance of log-*dt* to the mean of log-catch:

C.1) $\text{mean}(\text{log-}dt) = -20.93 + 3.88 \cdot \text{mean}(\text{log-catch})$

C.2) $\text{var}(\text{log-}dt) = 7.16 - 1.02 \cdot \text{mean}(\text{log-catch})$

The within-year correlation between log-*dt* and log-catch was then calculated using the 2005-2006 data (Pearson correlation=0.28).

A bivariate normal distribution was then parameterized separately for each fishery f and year t. The calculated $\text{mean}(\text{log-catch})_{f,t}$ and predicted $\text{mean}(\text{log-}dt)_{f,t}$ (eqn. C.1) were used to parameterize the vector of mean values for the bivariate distribution. The calculated var(log-catch)$_{f,t}$, predicted var(log-*dt*)$_{f,t}$ (eqn. C.2) and the within year correlation, were used to parameterize the covariance matrix. For a given observation of catch for haul *k*, a corresponding value of log-*dt* was then drawn from the bivariate distribution for the fishery and year in which haul *k* was made.

The reliability of this approach was verified by predicting *dt* values for the early 1990s and for 2005-2006 using catch observations only and comparing the predictions to the observations of *dt*.

C.2 Autocorrelation function for skate landings residuals

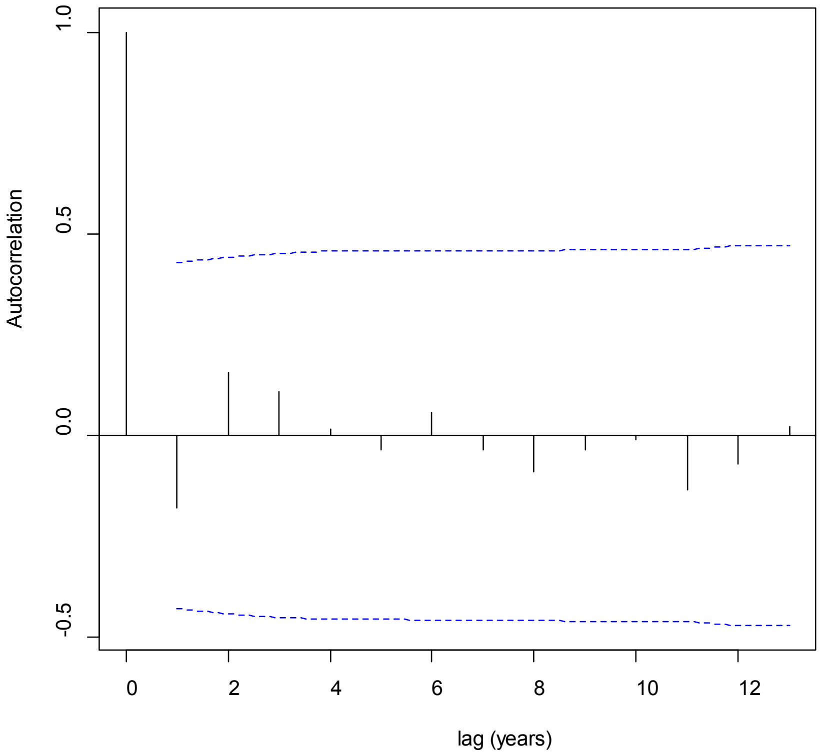

Figure C1. Autocorrelation function (ACF) for skate landings residuals (observed-predicted landings). The dashed blue line indicates the approximate 95% confidence interval for the ACF in which the standard error at lag *k* is based on a null hypothesis that the time series was generated by a pure moving-average Gaussian process of order *k*–1.

C.3 Estimation of the degree to which precision of skate discards might be overestimated

C.3.1 Background and methods

Benoît and Allard (2009) found that the deployment of observers to trips in many southern Gulf of St. Lawrence (sGSL) fisheries followed an undocumented non-random sampling scheme, particularly prior to the introduction in the early 2000s of mandatory pre-departure hail-outs by harvesters. This non-random sampling was manifested in certain vessels having a disproportionately large number of trips covered by fisheries observers, while others were sampled little if at all. These were effectively unplanned cluster sampling schemes, which are known to generally result in overestimated precision if there is no accounting for the clustering (e.g., Lumley, 2004).

While Benoît and Allard (2009) were unable to devise a method to satisfactorily adjust for this post hoc during data analysis, they attempted to estimate the general magnitude of precision overestimation using data from sGSL index fisheries with complete (100%) observer coverage of trips. This was achieved by simulating observer surveys with incomplete coverage using those data, and relating the estimated catches from the simulated surveys, $\hat{b}_A$, to the known catches based on complete sampling, *A*. One of the metrics they calculated was the mean relative error, *RE*, defined as:

$$\text{(C.3)} \qquad RE = \frac{1}{N}\sum_{n=1}^{N}\left|\hat{b}_A - A\right| \cdot A^{-1}$$

where *N* is the number of iterations used in their simulation. By comparing *RE* values for simulated surveys based on simple random sampling of trips to *RE* values based on surveys with cluster sampling, the possible magnitude of precision overestimation was obtained. For the present study, this approach was applied to skate catches. Observer surveys with mean coverage levels comparable to the commercial fisheries were simulated: 8% coverage for fixed-gear and 14% for mobile-gear. Cluster sampling was simulated using vessel-specific sampling probabilities estimated from the commercial fisheries (details in Benoît and Allard, 2009).

C.3.2 Results

Simulated surveys based on simple random sampling resulted in *RE* values of 0.354 and 0.305 for fixed and mobile-gear fisheries respectively. In contrast, simulated cluster sampling resulted in *RE* values that were respectively 1.53 and 2.04 times larger. These results illustrate the general magnitude of precision overestimation due to cluster sampling, though Benoît and Allard (2009) argue that these simulations may nonetheless underestimate the actual magnitude because of the standardized nature of the index fishery. Because the reliability of the *RE* estimates is not presently known, the results were not incorporated into the estimated error for skate catches.

References

Benoît, H.P., and Allard, J. 2009. Can the data from at-sea observer surveys be used to make general inferences about catch composition and discards? Can. J. Fish. Aquat. Sci., 66:2025-2039.

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APPENDIX D. Supplemental information for Chapter 6

Description of the likelihood function used to fit the model

The log-likelihood function for the generalized mixture model comprises three functions: the survival distribution function, the probability density function, and the mixture weight function [for the derivation see Ibrahim et al., (2001)]. The survival distribution function, *S*(*t*), is defined as the probability that an individual *i* survives to a time $T_i > t$. For the model in eqn.6.7, the survival distribution functions for affected and immune individuals are respectively given by:

(D.1) $$S_A(t) = \tau \exp\left(-Mt - [\alpha \cdot (t - t_0)]^{\gamma}\right)$$

(D.2) $$S_I(t) = \tau \exp(-Mt)$$

where *t* is the survival time, τ models capture and handling mortality and α and γ are respectively the scale and shape parameters of the Weibull distribution.

The probability density function, *f*(*t*), is the probability of dying at *t* and is the first-derivative of 1-*S*(*t*). For affected and immune individuals, the density functions are respectively given by:

(D.3) $$f_A(t) = \left(\alpha \cdot \gamma(\alpha \cdot (t - t_0))^{\gamma - 1} + M\right) \cdot S_A(t)$$

(D.4) $$f_I(t) = M \cdot S_I(t)$$

The mixture density, *m*(*t*), for uncensored observations is then given by:

(D.5) $$m(t) = \pi \cdot f_A(t) + (1 - \pi) \cdot f_I(t)$$

where π is the probability that an individual is adversely affected.

The mixture probability for right-censored observations is:

(D.6) $m_R(t) = \pi \cdot S_A(t) + (1-\pi) \cdot S_I(t)$

and the mixture probability for left-censored observations is:

(D.7) $m_L(t) = \pi \cdot \left(1 - S_A(t)\right) + (1-\pi) \cdot \left(1 - S_I(t)\right)$

Now, let **θ** denote the vector of unknown parameters, *y* denote the set of *b* independent observed event times (mortality or censorship, as the case may be) indexed by *i*, *d* is the vector for a binary variable that denotes whether observations are left-censored (d_i=1) or not (d_i=0), and let *e* be a vector for a binary variable denoting whether observations are right-censored. The resulting full log-likelihood function to be minimized is then given by:

(D.8)

$$\log L(\boldsymbol{\theta} \mid y, d, e) = \sum_{i=1}^{b} -(1-d_i) \cdot (1-e_i) \cdot \log\left(m(t)_i\right) - e_i \log\left(m_R(t)_i\right) - d_i \log\left(m_L(t)_i\right)$$

Supplementary Figure

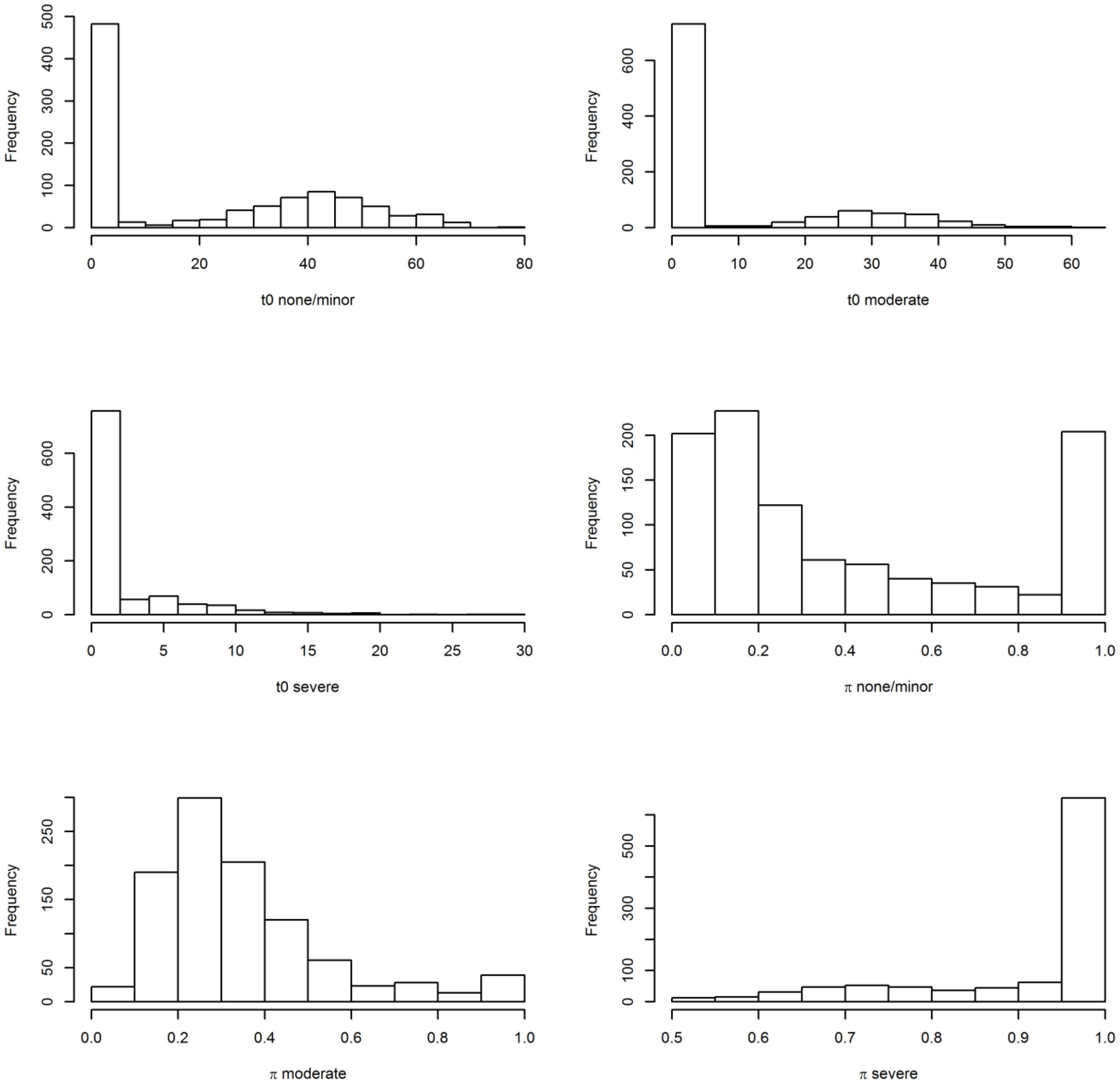

Figure D1. Histograms of the estimated parameter values for the injury-class specific mortality onset delays (t_0) and discard mortalities (π) from the simulations based on the winter skate case study.

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