HISTORICAL ANALYSIS OF FISH IN COASTAL ECOSYSTEMS

by

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Submitted in partial fulfillment of the requirements
for the degree of Master of Science

at

Dalhousie University
Halifax, Nova Scotia
March 2016

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Abstract

Fisheries have contributed to human well-being for centuries. Coastal ecosystems function as fish nurseries, thus adding to fisheries productivity. This thesis examines historical change of commercially important fish in coastal ecosystems. Firstly, I examine the impacts of extreme overfishing on coastal ecosystems by comparing coastal fish communities before and after the dramatic collapse of Atlantic cod. I found an overall shift in the community likely due to decreased predation by adult cod and fewer juveniles in coastal regions. Secondly, I have quantitatively compared historical abundances of juvenile commercially harvested fish in coastal vegetated habitats using various case studies. This second chapter addresses fish habitat management in Canada with a uniquely historical lens, specifically examining potential shortcomings with respect to recovery prospects. In light of these results, I discuss the connection of coastal ecosystems with commercial fisheries.

List of Abbreviations and Symbols Used

ε	Model error term
$\varepsilon \sim N(0, \sigma^2)$	Errors are normally distributed around zero with some standard deviation (σ)
CRA	Commercial, Recreational, and Aboriginal
DFO	Fisheries and Oceans Canada
EBSA	Ecologically and Biologically Significant Area
EFH	Essential Fish Habitat
FA	Fisheries Act
FAO	Food and Agriculture Organization of the United Nations
GLM	Generalized Linear Model
GPS	Global Positioning System
H	Shannon diversity Index
HAPC	Habitat Area of Particular Concern
J	Pielou's Evenness Index
MPA	Marine Protected Area
MSFCMA	Magnuson-Stevens Fishery Conservation and Management Act
NAFO	Northwest Atlantic Fisheries Organization
NMDS	Non-Metric Multidimensional Scaling
NOAA	National Oceanic and Atmospheric Administration
SD	Standard Deviation
SE	Standard Error of the Mean
Sum-of-LR	Sum of Likelihood Ratios

Acknowledgements

I have many people to thank for helping me along the way. First and foremost, my supervisor Dr. Heike Lotze. She has provided me with an ideal environment to grow as a young scientist, and her door is always open. Not only has Heike taught me critical scientific thinking, but I have also learned important life skills and balance. I am extremely thankful for the experiences she has provided me with.

I also thank Dr. David Schneider for his time, effort, and excellent teachings on statistics and writing. Thank you to my committee members, Drs. Boris Worm and Melisa Wong, for their guidance both in the scientific and communication realms. To Dr. Bob Rangeley, thank you for your support and discussions regarding policy.

To the Lotze Lab members, you were all essential components of my multiple field work seasons, and had an enormous positive influence on my experience both inside and outside the lab environment. Thank you to John Lindley and Pat Fitzgerald for fieldwork support and guidance. Thank you to my loving family for enduring my scientific rants, and for endlessly providing support and advice. To my friends in graduate school, I would not have survived without you. You have made my experience so fun, and I'm so happy to have experienced this with you. I would like to thank the National Sciences and Engineering Research Council of Canada as well as the Sobey Fund for Oceans graduate scholarships for providing financial support.

Chapter 1 – Introduction

Humans have profoundly changed marine ecosystems for centuries (Jackson *et al.*, 2001; Lotze *et al.*, 2006). These changes are largely due to our dependence on oceans for food and other resources through exploitation, such as fisheries. For example, 4.3 billion people rely on fish as it makes up ~15% their animal protein intake (FAO, 2014). Even with dependence on fisheries for food security and various industries, effective management is still lacking in many countries (Murawski, 2010).

Habitat is an essential component of many fishes life history, however habitat management is not traditionally seen as an important component of fisheries management (Langton *et al.*, 1996; Caddy, 2014). Vegetated habitats and other biogenic structures introduce structural complexity and can therefore reduce predation risk. This is particularly important for juvenile fish, as they experience extremely high mortality during their early life history stages. Coastal ecosystems provide such complex habitats, including seagrass, rockweed, and kelp beds, and thus support many different commercially important fisheries as nurseries, primarily decreasing post-settlement mortality (Juanes, 2007; Seitz *et al.*, 2014; Bertocci *et al.*, 2015). However, quantifying the contribution coastal ecosystems provide for fish and fisheries is inherently difficult (Beck *et al.*, 2001; Dahlgren *et al.*, 2006; Sheaves *et al.*, 2014). Despite this, coastal fish habitat availability, recovery, and degradation have all been linked to changes in the abundance of fish stocks (Aburto-Oropeza *et al.*, 2007; Koenig *et al.*, 2011; Sundblad *et al.*, 2014; Jokinen *et al.*, 2015). Increasingly, coastal ecosystems and habitats are

recognized as an important component of fisheries and therefore should be managed (Seitz *et al.*, 2014).

Coastal ecosystems are ecologically and economically important for a variety of reasons. However, quantifying long-term impacts on coastal ecosystems is difficult, as these systems are subject to both long-term fishing impacts and direct coastal changes. Therefore, using a historical approach can yield significant advantages. Historical approaches have been particularly important for managing marine ecosystems, as they provide baselines and reference points to set management and conservation targets (e.g. McClenachan, 2009; McClenachan *et al.*, 2012; Engelhard *et al.*, 2015; Thurstan *et al.*, 2015). Historical approaches can also advance our fundamental understanding of species interactions and roles within coastal ecosystems. For example, Baden *et al.* (2012) used a historical approach to conclude that top-down trophic control of coastal predatory fish influences the susceptibility of coastal ecosystems to eutrophication and consequently seagrass loss. Here, I examine long-term changes of fish in coastal ecosystems and discuss how these changes may influence fish habitat management.

1.1. Thesis Structure

This thesis is structured into two distinct data chapters (Chapters 2 and 3). Both data chapters examine long-term changes in fish within coastal ecosystems in a historical context.

Chapter 2 uses a unique dataset to quantify coastal fish community change before and after the collapse of Atlantic cod in the Northwest Atlantic. I used a model-based approach to analyze changes in juvenile cod abundance and the fish community as a

whole. I also looked at regional differences and impacts of vegetation, particularly as they interact with changes between time periods. These results are interpreted within the context of marine fish population collapses and connectivity with coastal ecosystems.

In Chapter 3, I quantified long-term changes in juvenile fish abundance in coastal habitats across three case studies in three provinces in Atlantic Canada. Quantifying changes in juvenile fish abundance which coincide with changes in adult stocks supports the coupling of adult decline with juvenile decline. I discuss the implications of this connectivity for Canadian fisheries management and fish habitat management, and make suggestions for strengthening current policy frameworks.

In Chapter 4, I conclude the thesis with a discussion of the overall findings, as well as future research directions.

Chapter 2 – Long-term Shift in Coastal Fish Communities Before and After the Collapse of Atlantic Cod (*Gadus morhua*)*

2.1. Abstract

The collapse of the Northwest Atlantic cod (*Gadus morhua*) stocks in the early 1990s led to widespread ecological changes offshore. Changes in coastal fish communities are less known, largely due to the lack of historical records and long-term, standardized research surveys in coastal ecosystems. We aimed to overcome this with a unique dataset known as the Fleming survey. From 1959 to 1964, a systematic beach seine survey was conducted to examine juvenile cod abundance in 84 bays (42 of which were consistently sampled and therefore analyzed) along the east coast of Newfoundland. In addition to cod, all other fish collected in the seines were recorded. These surveys were repeated from 1992 to 1996 after the cod collapse, and document a substantial reduction in a dominant inshore species — juvenile Atlantic cod. We show that total fish abundance declined significantly with the decrease of cod, whereas Shannon diversity and species evenness significantly increased. Species richness increased in some regions but decreased in others. We also found significant changes in the composition of the fish community likely due to a combination of release from predation from fewer large cod feeding in inshore areas as well as a release from competition from fewer juvenile cod occupying the coastal habitat. Region and the presence of vegetated habitats

also significantly influenced the fish community. This study shows a strong

reorganization of coastal fish communities after a large-scale fisheries collapse with

implications for ecosystem-based and cross-ecosystem management.

2.2. Introduction

Fish stock collapses can result in pronounced changes to marine ecosystems.

Trophic cascades, regime shifts, and altered nutrient dynamics have all been

demonstrated after population collapse due to overfishing (Frank *et al.*, 2005, Daskalov *et

al.*, 2007; Layman *et al.*, 2011). On the Scotian Shelf, for example, the collapse of

Atlantic cod (*Gadus morhua*) led to trophic cascades and a restructuring of the entire

foodweb with strong increases in forage fish and invertebrates (Frank *et al.*, 2005, 2011).

In contrast to these documented effects on offshore ecosystems, the impacts of the North

Atlantic cod collapse on coastal ecosystems are largely unknown. Coastal ecosystems

serve as nurseries for a variety of commercially and ecologically important fish species

(Beck *et al.*, 2001; Heck *et al.*, 2003; Bertelli and Unsworth, 2014, Seitz *et al.*, 2014;

Sheaves *et al.*, 2014) and at the same time serve as seasonal foraging areas for migratory

fish stocks (Rose, 1993). Theoretically, an offshore fish population collapse could induce

ecological changes in coastal habitats through the reduction in juvenile recruitment to

coastal nursery areas as well as through reduced predation pressure on inshore species.

Baden *et al.* (2012) linked overfishing of Atlantic cod on the Swedish coast to a shift in

seagrass foodweb structure, showing some form of mesopredator release. Similarly,

Sobocinski *et al.* (2013) attributed some of the long-term fish community changes in

Chesapeake Bay to altered predator-prey relationships. Alongside long-term fishing

impacts, coastal ecosystems in general have undergone a multitude of other anthropogenic impacts (Lotze *et al.*, 2006), making it difficult to separate the various sources of change.

Another major reason coastal ecosystem changes are less known is due to a paucity of long-term, standardized research surveys in many inshore regions. Most available long-term studies of fish community change were enabled by consistent long-term research surveys by government agencies (*e.g.* Lotze and Milewski, 2004; Myers *et al.*, 2007, Frank *et al.*, 2011, Ferretti *et al.*, 2013) or standardized catch records (*e.g.* Britten *et al.*, 2014). Others have used historical records or qualitative research to trace long-term ecological changes (Rose, 2004; Lotze *et al.*, 2006). Here, we use a unique historical dataset, the "Fleming" (1960-1964) and "Resurrected Fleming" (1992-1996) surveys, which allowed quantitative analysis of coastal fish community structure before and after the 1992 cod collapse in Newfoundland.

The collapse of the Northwest Atlantic cod stocks in the late 20th century was among the most ecologically and socially devastating fish collapses in history (Hutchings and Myers, 1994; Hutchings and Rangeley, 2011). The industrialization of the fishing industry in the early 1960s marked the onset of unsustainable fishing for these Atlantic cod stocks, with a reduction of approximately 98.6% in spawner biomass from this onset until the eventual collapse in 1992 (Hutchings and Myers, 1994). This collapse caused dramatic long-term changes in the ecology of the Northwest Atlantic Ocean (*e.g.* Dwyer *et al.*, 2010; Frank *et al.*, 2005, 2011). Catches in inshore areas were higher than offshore areas before the industrialization of the fishing industry in the late 1950s (Hutchings and Myers, 1995). This resulted in long-term depletion of inshore cod populations; however,

the major collapse began with the onset of industrialized fishing fleets primarily offshore. Our dataset documents the structure of coastal fish communities at the beginning of rapid industrialization, compared with immediately after the collapse in the early 1990s.

Our principal objective was to quantify the change in juvenile cod abundance and the structure of the coastal fish community after the Atlantic cod collapse. Using a comparable set of beach seine surveys in the 1960s and 1990s along the east coast of Newfoundland, Canada, we tested whether the abundance, species composition, and diversity of the fish community changed between the two periods. A secondary objective was to determine if observed long-term changes varied regionally or with the presence of vegetated habitats (*e.g.* seagrass or macroalgae) in coastal areas. Because Atlantic cod settle in coastal areas, and larger cod move inshore to feed in summer (Dalley and Anderson, 1997) we expected a substantial change in the relative abundance of inshore species after the collapse of cod stocks in the early 1990s.

2.3. Methods

2.3.1. Beach Seine Surveys

Alistair Fleming and assistants from the Fisheries Research Board of Canada conducted a series of systematic beach seine surveys along the east coast of Newfoundland, Canada from 1959-1964 (Methven *et al.*, 1997; Schneider *et al.*, 1997a). They surveyed 84 different sites in coastal bays from mid-September to late October going north, aiming to examine juvenile Atlantic cod abundance. These sites cover ~3 degrees of latitude, with ~1500km of intervening coastline (Figure 1a). Of these 84 sites,

42 had sufficient data to allow year-to-year comparison. In 1960-1964, between 17 and 41 sites were sampled in any one year depending on weather and ocean conditions.

A 25m bottom seine was used, where one person holding one of the hauling ropes stands on land and a boat pays out a hauling line to a distance of 55m from the beach. The seine was then deployed parallel with the shore. When the net was completely in the water, the boat returned to shore letting out the second hauling line held by another person who lands 16m away from the first. The seine sweeps approximately 880m^2 (16m across at point of landing beginning 55m off shore). The seine fishes upward from bottom held weights to floats that stretch the net to about 2m above the bottom. For detailed seine specifications see Schneider *et al.* (1997b).

During the 1960s a variable number of sets were made at a site. In general, two sets were done consecutively when a site was first sampled. Therefore, comparison of the 1960s to 1990s data was restricted to the first two sets at any one site (Cull, 1997). During the 1990s three seining sets were completed at each site, two tows occurring over the same location (1-2 hours apart) with the third occurring adjacent to these. Fish were sorted live and returned to the water under license restrictions, a potential source of resampling in the second and third set. In this analysis we used the two sets that were in adjacent locations and summed the two sets. The seining method was found to have high catchability (Gotceitas *et al.,* 1997), with > 95% retention of all fish in the path of the net. The summed catch is a measure of density for species with high catchability and low mobility. For species that re-populate rapidly after disturbance, such as juvenile cod, the sum is an index of density contaminated by lateral recruitment from adjacent areas. All fish collected in the seine hauls were identified and counted. Juvenile cod were aged

based on their standard length, and binned into ages 0 (<97mm), 1 (97-192mm) or 2 (>192mm). These age bins were based on distinct and annually repeatable modes in the catch curve for juvenile Atlantic cod (Methven *et al.*, 1997). Due to time constraints lengths of other fish species were not recorded.

The "Resurrected Fleming Survey" (1992-1996) was initiated in response to the collapse of the Northwest Atlantic cod stocks. The seasonal timing of the surveys (mid-September to mid- or late-October) was the same between these two time periods. Photographs of the point of deployment at each location in the 1960s allowed the same sites to be revisited, using shoreline configuration ("fishermen's marks") to relocate seining locations within several tens of meters. The deployment protocol for the seine in the resurrected survey was confirmed by Tom Collier, who participated in the earlier survey and provided minor adjustments from memory during a visit to one of the sites. In the 1960s a rowed dory was deployed from a small inshore vessel near the beach. In the 1990s a motorized boat was used to deploy the seine. Catch rates from the motorized boat depended on speed (David Methven, pers. comm.), so low speeds were used to increase comparability. The location of sampling, gear specifications, gear deployment, sampling design, date of sampling at a location, and time of day of sampling were all given attention to ensure comparability between the two surveying periods (Cull, 1997; Methven *et al.*, 1997; Schneider *et al.*, 1997a). The data are potentially biased estimates of fish density, but they are comparable between the two periods based on matching the protocols as closely as possible.

The study sites were grouped into six different regions (Figure 1a) based on their location, mostly within distinct bays of eastern Newfoundland. Only sites that were

sampled in both time periods were included in our analysis, as seven sites were not sampled in the later period due to the building of wharfs. Bottom type, vegetation presence/absence, and notes on the tow were recorded for only 42 sites in field notes during the original Fleming survey – therefore only these 42 sites were used in our analysis. These site characteristics, specifically the presence or absence of vegetation (described as "kelp" or "eelgrass"), were retrieved from field notes and used for the analysis. Unfortunately, we do not have any indication of long-term changes in the presence/absence of vegetation of these sites. However, sites which had direct habitat degradation (*e.g.* through wharf building) were not sampled in the "Resurrected Fleming"; therefore, it is unlikely that the vegetation in sites we included in the analysis had changed dramatically. The entire dataset will be freely available through the data archive PANGAEA (www.pangaea.de/).

2.3.2. *Statistical Approach*

We used generalized linear models (Nelder and Wedderburn, 1972) to analyze differences in (i) juvenile cod abundance and (ii) total fish abundance, species richness, diversity, and evenness. We were primarily interested in differences between time periods (1960s vs 1990s), among regions, and between sites with and without vegetation. Therefore, the model structure looked similar throughout, including the following fixed categorical factors: time period, year nested within time period, region, and vegetation presence/absence, with every possible interaction. Year was included as a nested fixed factor within time period, as opposed to a random factor, as year was explicitly not a random sample within these time periods and the set of years encompasses the entire time

period. Using year as a fixed factor assumes negligible temporal autocorrelation, which we tested for using the following method. For every site in the data set sampled in consecutive years, the values (*e.g.* juvenile cod abundance, total fish abundance, diversity, richness, and evenness) from two consecutive years were matched. Site by site, we measured the correlation of the values, then plotted the Pearson's correlation coefficient and found a random scatter around zero for all community metrics in both time periods. This is expected due to the extremely high variability in counts of fish caught and consequently the community metrics as well. This method emphasizes evaluation of effect sizes (Nakagawa and Cuthill, 2007). We took year as a fixed factor free of temporal autocorrelation at a one year lag. Region was included as a fixed factor because we were inferring only to the six regions along a south to north gradient, not to a larger population of regions. Region was specifically included in the models to detect whether the effect of the cod collapse differed across a latitudinal gradient. Specifying "year" as a fixed effect in the models moves the site to site variation into the error term (Venables and Dichmont, 2004). We implicitly model the site as a random effect, as the site-to-site variability is encompassed by the error term (ε), where we assume $\varepsilon \sim N(0, \sigma^2)$. To test the impact of time period on various metrics in different regions (as shown in Figures 1 and 2), we took subsets of the data by region and tested the reduction in deviance. All statistical analyses were completed in R (R version 3.2.1; R Core Team, 2014). The criterion for statistical significance was set at a Type I error rate of 5%. Residual plots were used to check the assumptions of homogeneity and normality where Type I error was calculated from *t* or *F* distributions. Complete analysis of variance and deviance tables can be found in the Supplementary materials.

2.3.3. Juvenile Atlantic Cod Abundance

For age 0 Atlantic cod we used a negative binomial Generalized Linear Model (GLM) with a log link, which is appropriate for overdispersed count data. For zero-inflated counts of age 1 and 2 Atlantic cod, we used two-stage (zero-inflated) models. In these models, the presence or absence (zero) of a count is first modelled with a binomial GLM, then counts are modelled separately with a Poisson or negative binomial GLM. In our case, we used a negative binomial GLM for the counts with a log link. The "MASS" package in R was used for fitting a negative binomial GLM (Venables and Ripley, 2002). Due to unavoidable rank deficiency in the data, higher order interactions for the first stage (binomial GLM) of the two-stage models exhibited probabilities which are numerically 0 or 1. We used a sequential analysis of deviance table for age 0 Atlantic cod (negative binomial GLM) to test each explanatory variable for statistical significance. For all sequential analysis of deviance or variance tables used, model terms are added sequentially beginning with the null model, and the reductions in residual deviance or residual sum of squares were tested sequentially.

2.3.4. Total Fish Abundance, Species Diversity, Richness, and Evenness

To investigate changes in the overall fish community, we examined changes in total fish abundance, Shannon diversity index (H), species richness, and Pielou's evenness index (J). We used species richness to refer to taxonomic richness, as two groups (sculpin and sticklebacks) were not resolved to the species level. Total fish abundance was analyzed with a negative binomial GLM and a log link function. Species richness was analyzed with a Poisson GLM with a log link function. Statistical significance for both total fish

abundance and species richness was tested in an analysis of deviance table. To analyze differences in diversity and evenness we used GLMs with categorical explanatory variables as above, an identity link function, and a normal error structure. Sequential analysis of variance tables were produced to test the statistical significance of each explanatory factor. Residuals were examined for every model to check the assumptions of normal and homogenous error.

2.3.5. Community Composition

To display changes in the species composition graphically we used non-metric multidimensional scaling (NMDS) plots. The data were square-root transformed and Wisconsin double-standardized prior to the calculation of the Bray-Curtis dissimilarity matrix (Bray and Curtis, 1957). The square-root transformation diminishes the influence of large counts. Wisconsin double-standardization scales each species to its maxima (each observation divided by species maxima), then these are standardized by observation (each set of species observations is given as a percentage of the total scaled observations in that observation row). This scales the variability of different species to each other. We took the mean value for each species by region and by year. This aggregation was used to decrease the stress value associated with the non-aggregated NMDS, due to the low tolerance of NMDS to zero-inflation. We recognize that the Bray-Curtis dissimilarity matrix (as well as other distance/dissimilarity-based analyses) implicitly assumes a mean-variance relationship of the data which may not always be met (Warton *et al.*, 2012), and therefore used it only as a means to visualize community change.

Two distinct approaches in assessing ecological communities have been advocated: a distance-based approach (Anderson, 2001a, 2001b) and a model-based approach (Warton *et al.*, 2014). Distance-based approaches confound location and dispersion effects (Warton *et al.*, 2012). The model-based approach (R package "mvabund", Wang *et al.* 2012) solves this problem using simultaneous generalized linear models (ManyGLM; Warton, 2011; Wang *et al.*, 2012) that specify the mean-variance relationship in the data instead of relying on the assumptions of a distance-based approach. Specifically, our count data had a quadratic mean-variance relationship; hence, we used a GLM with a negative binomial distribution and a log link function (O'Hara and Kotze, 2010). We used a 4-way fixed factor model structure (time period, year nested within time period, region and vegetation presence/absence with interactions) in the analysis of the ecological community. Examination of residual plots from ManyGLM showed little pattern indicating that the mean-variance relationship assumed with a negative binomial GLM was appropriate.

Using ManyGLM, a model is fit to each species and the likelihood ratios of each model are summed to create an overall *Sum-of-LR* that can be used as a test statistic via randomization. The routine resamples counts by site and time period to generate a null distribution from which Type I error is computed for rejecting the null (no overall relation) hypothesis. This procedure is analogous to a permutational multivariate analysis of variance using a Bray Curtis dissimilarity matrix as the dependent variable. It has the advantage that the test statistic is a likelihood ratio – a measure of evidence (Royall, 1997). To determine which species contributed most to the shift in community structure, the individual contribution to the *Sum-of-LR* was assessed, which is analogous to the

SIMPER procedure (Clarke, 1993). For example, if a specific species model contributes substantially to the *Sum-of-LR*, the percentage contribution of log-likelihood will be high. Unlike SIMPER, the *Sum-of-LR* contribution has more power and is able to detect between-group differences rather than detecting taxa with high variance (Warton *et al.*, 2012).

2.4. Results

2.4.1. *Juvenile Atlantic Cod Abundance*

Overall there was a decline of juvenile Atlantic cod abundance in all age groups (0, 1, and 2) from the 1960s to the 1990s (Figure 1b, c, d). The effect sizes (differences in means) were large for every age group (Table 1); however, only the declines in age 1 and 2 cod were statistically significant (Table 2a). Using a two-stage model, we found the time period effect was significant for both the presence/absence of age 1 and 2 juvenile cod as well as for the counts (Table 2a). Year nested within time period was significant for every cod age group, indicating high variability among years within both time periods.

There were significant regional differences in abundance for all age groups (Table 2a, Figure 1), with no clear latitudinal trend. The south coast region had the lowest mean abundance by site for every age group of cod (6.68, 19.84, and 0.22 for ages 0, 1, and 2 respectively), while Trinity Bay had the highest mean abundance by site of age 0 and age 2 cod (54.51 and 2.57, respectively) and Conception Bay had the highest mean abundance by site of age 1 cod (93.00). The time period by region interaction term was significant for age 0 cod, indicating that in some regions the magnitude or direction of

change between time periods differed (Figure 1b). This interactive effect was also

significant for the presence/absence of age 1 cod and the counts of age 2 cod (Table 2a,

Figure 1c-d). The interactive effect of region and year nested within time period was also

significant for age 0 Atlantic cod, as well as for the counts of ages 1 and 2. Incorporating

regional differences allowed for finer spatial resolution influencing temporal changes.

Vegetation was a significant explanatory variable for the presence/absence of age

1 cod, and the counts of age 2 cod (Table 2a). For example, there were on average 5.07

age 2 Atlantic cod in vegetated habitats compared to 3.85 in non-vegetated habitats.

There was a significant interaction between region and vegetation for the

presence/absence of age 2 cod (Table 2a). We also found a significant interaction

between vegetation and year nested within time period for age 0 cod (Table 2a). There

was also a significant interaction between time period, region and vegetation for age 0

cod (Table 2a). In each case, we found that vegetated habitats had higher abundances or

more presences than absences of juvenile cod.

2.4.2. Total Fish Abundance, Species Diversity, Richness, and Evenness

A total of 34 species of fish were caught in the beach seines from both time

periods (Table 1), of which 22 species were common to both periods. Sculpin and

stickleback species were both aggregated to a single taxonomic group in the field due to

similar morphologies within these two groups that are difficult to distinguish in the field.

Regarding the overall fish community, we found a significant decrease in total

fish abundance between the 1960 and 1990 time periods (Figure 2a; Table 2b).

Concomitantly, we found a significant increase in Shannon diversity index and evenness

between the 1960s and 1990s (Figure 2b; 2d; Table 2b). There was a significant region by time period interaction (Figure 2c; Table 2b). More southern regions along the coast exhibited a decline in species richness (South Coast and Conception Bay), while more northern regions (Bonavista Bay) exhibited an increase in species richness. For every community metric, there was a significant effect of year nested within the two time periods (Table 2b). This year to year variability depended on region for both total fish abundance and Shannon diversity (Table 2b). In vegetated sites, we found significantly higher total fish abundance (40% higher mean total abundance by site) and species richness (26% higher mean species richness by site) compared with non-vegetated sites, but no significant differences in diversity and evenness (Table 2b). There was also a significant interactive effect of region and vegetation on total fish abundance (Table 2b). Of note is the most northerly bay (Notre Dame Bay), where the total fish abundance in non-vegetated sites was lowest on average (53.7) compared with the vegetated sites (111.4).

2.4.3. *Community Composition*

Fish community structure, as visualized by NMDS, differed between time periods (Figure 3). Consistent with this interpretation we found significant changes in the community composition between time periods, using ManyGLM (Table 3). Rock gunnel, snakeblenny, Atlantic cod (age 1), Greenland cod, and lumpfish contributed most to the community shift between time periods as indicated by their contribution to the *Sum-of-LR* (Table 3, Figure 4). Within the two time periods Greenland cod, Atlantic cod, winter flounder, white hake, sculpin spp., and lumpfish contributed most to the year to year

variability in community composition. There was significant regional variation in community composition (Table 3). This was largely driven by winter flounder, cunner, and sculpin spp. (Table 3). Winter flounder was most abundant in hauls from Notre Dame Bay and least abundant in hauls from Conception Bay. Cunner and sculpin spp. were both most abundant in the New World Island and Gander Bay region as well as the South Coast, and both least abundant in Conception Bay. We examined each of the species driving the regional community differences (winter flounder, cunner, sculpin spp., Atlantic cod age 1, rainbow smelt, rock gunnel, and sea raven; Table 3). Along a latitudinal gradient (among bays) we found no trend for any taxonomic group, nor did any one region have consistently high abundances across all groups. Regional differences occurred between time periods, but with no species alone showing a significant effect. There was a significant effect of year by region, driven largely by Atlantic cod ages 0, 1, and 2 (Table 3). This again points to high year-to-year variability within regions along the Newfoundland coast. We found significant differences in community composition between vegetated and non-vegetated sites. These differences depended on region for winter flounder and cunner. Greenland cod and white hake were significantly more abundant in vegetated sites, while sand lance were significantly more abundant in non-vegetated sites.

2.5. Discussion

The dramatic collapse of Newfoundland Atlantic cod stocks coincided with significant changes in coastal fish communities. The decline in juvenile and adult Atlantic cod likely facilitated these community changes. We report the magnitude and

direction of change in a coastal ecosystem in the wake of the collapse of a species that ranges across the entire continental shelf. In addition to community changes, we have explored regional differences and vegetation impacts on coastal fish communities. We first describe the changes in juvenile vs. adult Atlantic cod from the 1960s to the 1990s and the associated coastal fish community changes. We then look at regional and vegetation influences on the fish community. Finally, we examine the influence of connectivity in this system.

Our analysis of comparable beach seine surveys along the east coast of Newfoundland in the 1960s and 1990s showed a strong decline in the abundance of juvenile Atlantic cod, which was statistically significant for ages 1 and 2. As with many marine fishes, Atlantic cod recruitment variability and thus variability in juvenile abundance is extremely high (Fromentin *et al.*, 2001) making it difficult to detect significant changes. We found strong year-to-year variability within each time period as well as differences among regions; still, mean abundance in age 0, 1, and 2 decreased by 22%, 82.4%, and 60%, respectively. In comparison with the decline in juveniles, the magnitude of declines in the adult stocks were much more dramatic, with a 98.6% reduction from an estimated 1.6 million tonnes of Atlantic cod spawner biomass in 1962 to only 22,000 tonnes in 1992 (Hutchings and Myers, 1994). This discrepancy in the magnitude of change in adult vs. coastal juvenile abundance has several possible explanations. First, the reduction in tonnage, as opposed to juvenile counts, reflects the loss of large fish from the population as the stock was fished down. Another consideration is the annual migration of offshore cod populations to inshore waters, following capelin and other forage fish. The less severe decline in juvenile cod could also

be due to decreased predation by adult cod in inshore waters, since cannibalism is a significant source of juvenile mortality in cod populations (Bogstad *et al.*, 1994; Yaragina *et al.*, 2009; Ottersen *et al.*, 2014). Thus, the supply of juveniles to coastal habitats would not be limiting their abundance, but rather the predation by older conspecifics. A third possible explanation is that juveniles were not subjected to fishing mortality in either time period, while adults were strongly reduced by fishing and thus enhancing the magnitude of decline. Overall, the decline in juvenile Atlantic cod is undoubtedly related to the cod stock collapse, with reduced recruitment from a reduced spawning stock, while the discrepancy in the magnitude of decline may be due to a variety of mechanisms.

We found no change in species richness after cod stock collapse, when compared with richness at the onset of industrialized fishing. In contrast to our findings, there was an overall decline in biodiversity of coastal ecosystems over a long period of overfishing in the Gulf of Maine (Steneck *et al.*, 2004; Bourque *et al.*, 2008). This difference is possibly due to the shorter time period we examined, as well as our restriction of looking at fish biodiversity alone, excluding invertebrates. We found an increase in Shannon diversity, which can be attributed in part to the reduction in abundance of a dominant coastal species, juvenile cod.

The decline in juvenile Atlantic cod may have resulted in a functional change in the fish community as top-down control by fish play a large role in coastal ecosystems (*e.g.* Moksnes *et al.*, 2008; Whalen *et al.*, 2013). Top-down control is largely imparted through predation, and juvenile Atlantic cod shift their diet from primarily pelagic to demersal prey as they age (Lomond *et al.*, 1998). Age 0 Atlantic cod are planktivorous, while in the water column, making a transition to benthic prey after settlement (Lomond

et al., 1998). The diet of age 1 Atlantic cod consists of primarily benthic crustaceans (~80%), such as krill, amphipods and shrimp (Dalpadado and Bogstad, 2004). These are also important prey for other coastal fish such as white hake, stickleback spp., Greenland cod, and lumpfish (Imrie and Daborn, 1981; Daborn and Gregory, 1983; Knickle and Rose, 2014); thus, the decline in juvenile cod may have increased the availability of these prey for other species. The diet of age 2 Atlantic cod shifts mainly to small fish (~50%) such as capelin, in addition to shrimp and zooplankton (Dalpadado and Bogstad, 2004). Consequently, such a dramatic reduction in the abundance of post-settlement juvenile Atlantic cod may have contributed to the community shift via reduced predation pressure on small fish by age 2 cod, and reduced pressure on benthic prey by younger (smaller) cod.

Concomitant with the decline in juvenile Atlantic cod was the decline in abundance of large adult Atlantic cod (ages 3 and above) in inshore waters, made up of adult cod which migrate from offshore to inshore areas following capelin as well as stationary (non-migratory) cod inhabiting inshore areas (Hutchings and Myers, 1994, 1995). The increase in stickleback species, which are prey of adult Atlantic cod (Hop *et al.*, 1992), is potentially attributable to the decline of their adult Atlantic cod predators. This decline occurred in conjunction with an increase in small bodied prey (such as Greenland cod and white hake, which are typically juveniles in coastal areas). Baden *et al.* (2012) also found an increase in small bodied prey (gobids and sticklebacks) after a significant decline in top predators (gadoids and trout) in eelgrass beds along the Swedish west coast. Hence the decline in large adult cod (ages 3 and above) in Newfoundland may have led to predator release effects.

There also appeared to be a complete shift in the abundance of two similar species, snakeblenny and rock gunnel. These fishes are both thin, eel-like benthic invertivores (Froese and Pauly, 2015). Rock gunnels were completely absent in the 1960s, while snakeblennies were completely absent in the 1990s. It is unclear why this shift occurred, since both species have similar ecology (Froese and Pauly, 2015), and better taxonomic discrimination in the 1990s cannot be discounted as an explanation.

Regional differences were evident in every community metric (total fish abundance, species richness, diversity, and evenness) as well as in the community composition. While region was included in the models to determine possible effects across a latitudinal gradient, there was no apparent trend besides species richness. In contrast, latitude has been shown to influence fish assemblages in estuaries along the Portuguese coast although this is along a larger latitudinal gradient (França *et al.*, 2009). Furthermore, fish species assemblages can show variability within spatially close estuaries with distinct abiotic characteristics (França *et al.*, 2011). For example, Selleslagh *et al.* (2009) found that salinity and sediment type are dominant abiotic components structuring fish communities in the estuaries of the Eastern English Channel. Thus, the regional differences in species abundances were likely due to different oceanographic, biogeochemical, or ecological conditions unique to each region. Regional differences in species abundances can guide more fine-scale regional management for those species which are commercially harvested along the Newfoundland coast.

Vegetation plays an important role in determining fish abundance and community composition (Schein *et al.*, 2012; Lazzari, 2013). Providing three-dimensional habitat, vegetation is used by fish primarily for predator avoidance and higher food availability

(Juanes, 2007; Renkawitz *et al.*, 2011). We found significantly higher species richness, total fish abundance, and different community composition in vegetated sites. The significantly higher abundance of Greenland cod and white hake in vegetated habitats was expected for these gadoid species (Renkawitz *et al.*, 2011). In contrast, sand lance, also driving differences in the vegetation term, was significantly higher in non-vegetated sites. Our results are consistent with those of Scott (1982) who found that sand lance select sand and gravel habitats. The influence of vegetation on fish community structure differed among regions, with no clear latitudinal trend. Vegetation impacts on fish community structure may depend on overall fish abundance and density. Therefore, in regions with higher overall abundances, the impact of vegetation could differ from regions with lower abundances. Habitat-mediated density-dependence is exhibited by juvenile Atlantic cod in eelgrass habitats, and therefore may also be related to other fish species (Laurel *et al.*, 2004).

Connectivity through the transportation and settlement of offshore spawned fish to coastal nurseries is poorly understood. However, connectivity driven by adult migrations has been demonstrated across the Atlantic (*e.g.* the Northwest Atlantic (Rose, 1993), the Northern Gulf of St. Lawrence (Le Bris *et al.*, 2013), in Icelandic cod populations (Grabowski *et al.*, 2011; Sólmundsson *et al.*, 2015) and the Northeast Atlantic (Nordeide *et al.*, 2011)). Mechanisms that connect inshore and offshore regions include transport of larval fish toward shore and expansion by demersal stages 1 and 2 (Dalley and Anderson, 1997). Juvenile fish in this instance are a spatial subsidy from offshore ecosystems to coastal areas, consequently moving back offshore (Polis *et al.*, 1997). Recognizing and quantifying connectivity among different marine ecosystems will

contribute to stronger cross-ecosystem fisheries management (*e.g.* coastal habitat protection may positively influence fisheries). Our results suggest that the collapse of Atlantic cod influenced coastal ecosystems through two forms of connectivity: adult migration and juvenile transport.

2.6. Conclusion

Coastal ecosystems have been altered by humans for centuries, highlighting the need for historical perspectives to understand the magnitude of long-term change (Jackson *et al.*, 2001; Lotze *et al.*, 2006). Alongside various coastal human impacts, ecosystem-level changes due to extreme fish population depletion have been documented on the Scotian Shelf and in the Northwest Atlantic (Dwyer *et al.*, 2010; Frank *et al.*, 2005, 2011). In this system, coastal human impacts are restricted to local fishing, as eastern Newfoundland is relatively sparsely populated. We investigated the intersection of offshore and coastal changes, demonstrating a significant shift in the coastal fish community after the collapse of the formerly dominant offshore Atlantic cod. Fishery induced changes to coastal ecosystems are not unique to our study however, and have also been documented in tropical/subtropical ecosystems (Jackson *et al.*, 2001; Shepherd and Myers, 2005). Our results stress the importance of understanding long-term ecosystem changes and connectivity between offshore oceanic systems and inshore ecosystems. Moreover, they highlight the necessity for ecosystem-based and cross-ecosystem management for effectively managing wide-ranging species and inter-connected marine ecosystems (Beger *et al.*, 2010; Eriksson *et al.*, 2011).
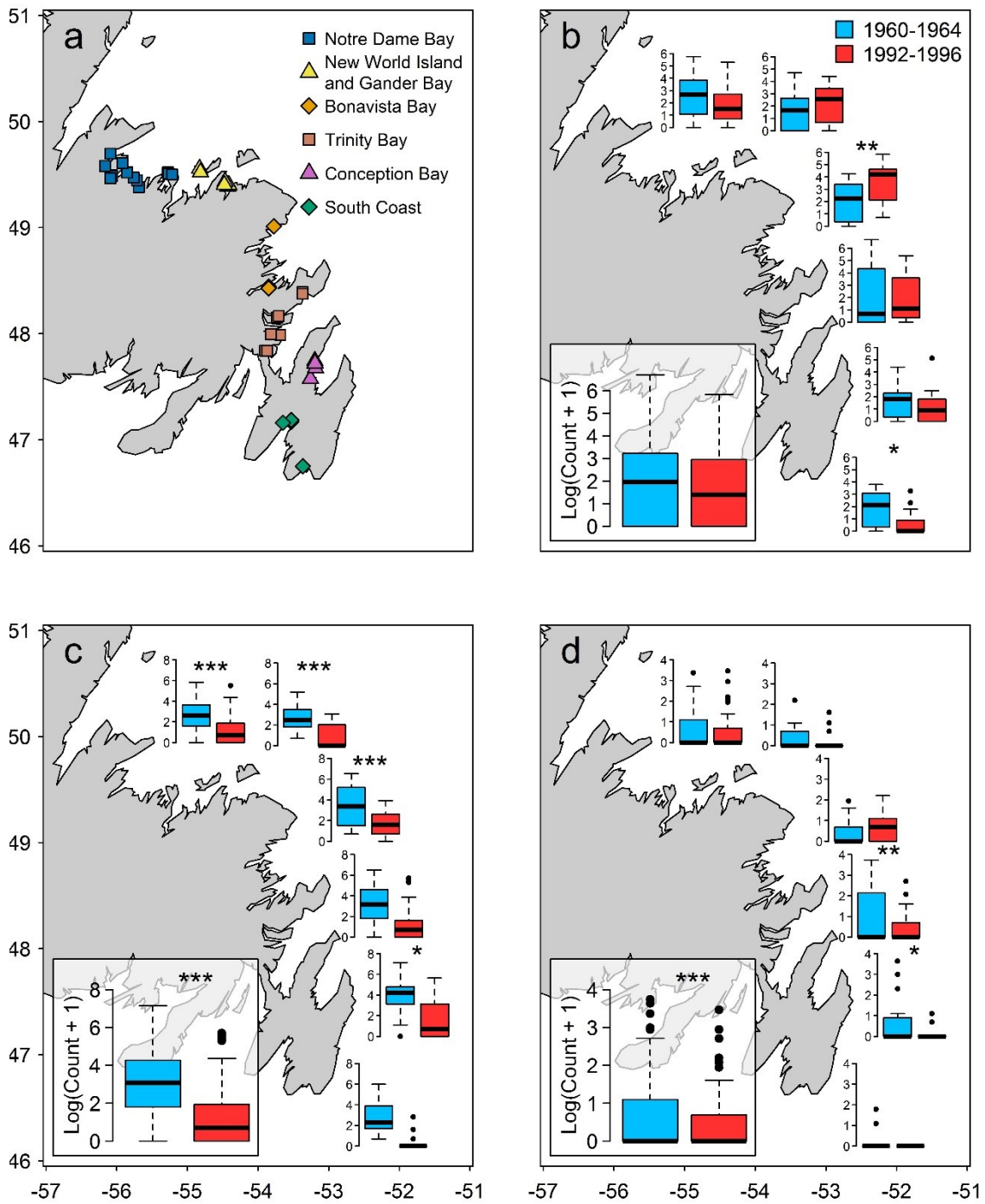
Figure 1. Map of all sites sampled (a), with points coloured by region and ordered from the northwest regions to the southeast regions in the legend. Maps (b)-(d) show raw data boxplots of natural log(count + 1) of age 0, 1 and 2 Atlantic cod (*Gadus morhua*), respectively in the 1960s and 1990s in each region. Inset boxplots display the overall differences between time periods. Significant differences are represented by asterisks with p values from 0.05-0.01 = *, 0.1-0.001 = **, and <0.001 = ***. Since two-stage models were used, these significance asterisks represent those of the count models only. P values for the time period effect in every region alone are given in the supplementary materials.
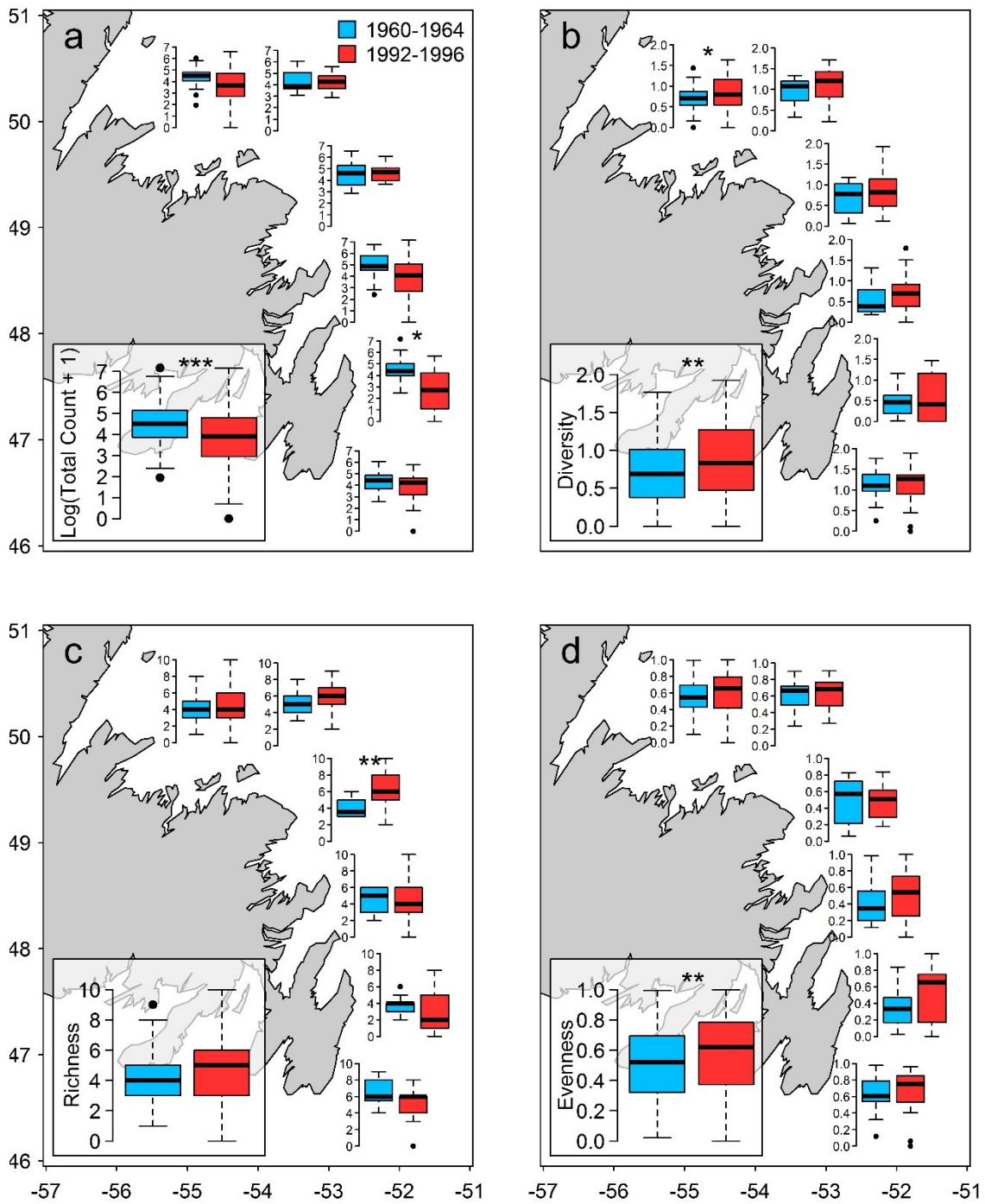
Figure 2. Boxplots of raw data for natural log(total fish count + 1) (a), Shannon diversity (b), species richness (c) and species evenness (d) in the 1960s and 1990s in each region. Inset boxplots display the overall difference between time periods. Significant differences are represented by asterisks with *p* values from 0.05-0.01 = *, 0.1-0.001 = **, and <0.001 = ***. *P* values for the time period effect in every region alone are given in the supplementary materials.
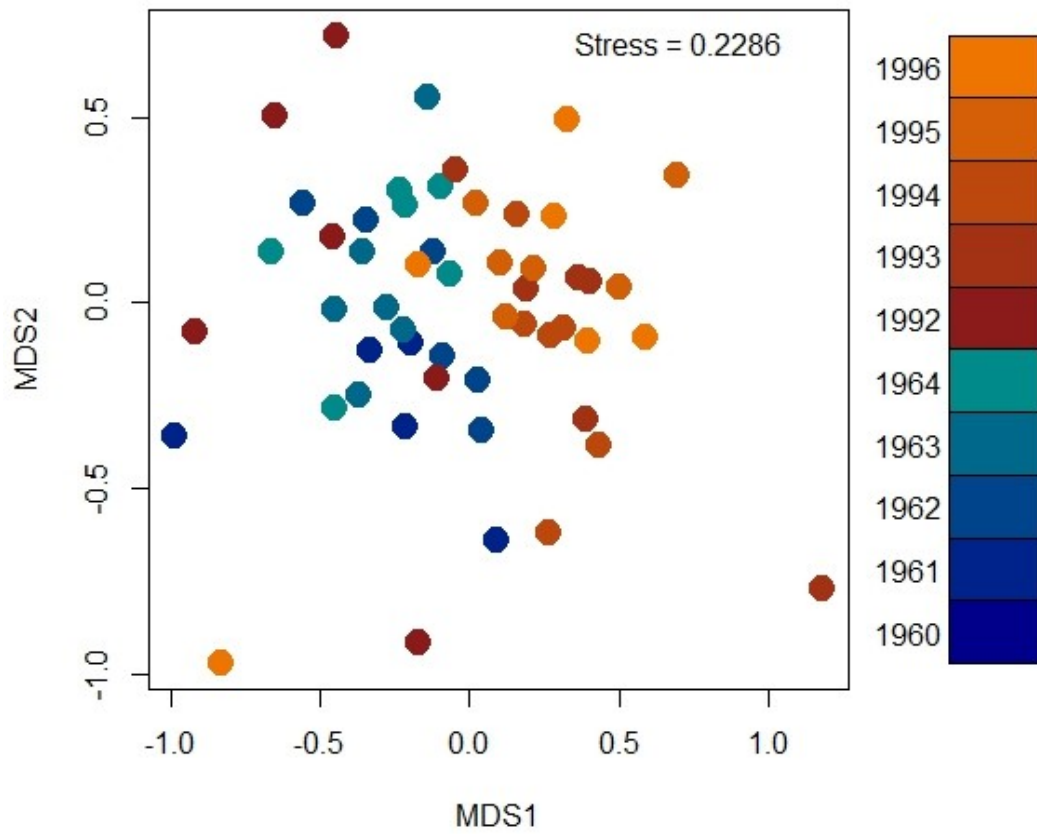
Figure 3. Non-metric multidimensional scaling plot of fish communities summarized by Bray-Curtis dissimilarity, aggregated by regions within each year. Years and time periods are coloured accordingly.
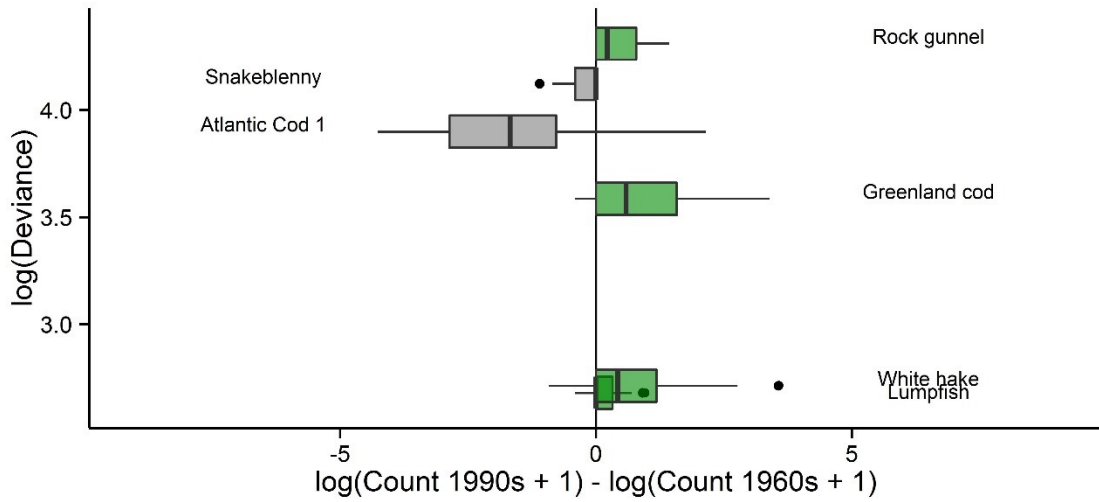
Figure 4. Species with the strongest contribution to the community changes (deviance) plotted by their mean change in abundance (natural logarithm) between the two time periods. Boxplots are filled according to their mean change – either above or below zero. The plot shows the community level changes with respect to the "Time Period" term, with higher deviance values indicating higher contribution to community change.

Table 1. Species list and mean abundance in the 1960s and 1990s of all recorded individuals in the beach seine surveys across 42 sites. Abundances are the sum of counts from two seine sets per site, averaged within each time period.

Common Name	Scientific Name	Mean Abundance (SE)			
		1960-1964		1992-1996	
American plaice	*Hippoglossoides platessoides*	0.008	(0.01)	0.000	(0)
Angler	*Lophius piscatorius*	0.008	(0.01)	0.000	(0)
Arctic shanny	*Stichaeus punctatus punctatus*	0.000	(0)	0.045	(0.02)
Atlantic Cod 0	*Gadus morhua*	32.992	(7.75)	25.450	(3.68)
Atlantic Cod 1	*Gadus morhua*	77.826	(14.12)	13.760	(3.29)
Atlantic Cod 2	*Gadus morhua*	2.470	(0.55)	0.995	(0.22)
Atlantic herring	*Clupea harengus*	0.136	(0.13)	0.225	(0.18)
Atlantic mackerel	*Scomber scombrus*	0.000	(0)	0.030	(0.03)
Atlantic salmon	*Salmo salar*	0.015	(0.01)	0.045	(0.04)
Banded gunnel (Tansy)	*Pholis fasciata*	0.008	(0.01)	0.000	(0)
Brook trout	*Salvelinus fontinalis*	0.008	(0.01)	0.005	(0.01)
Butterfish	*Peprilus triacanthus*	0.000	(0)	0.005	(0.01)
Capelin	*Mallotus villosus*	0.008	(0.01)	0.025	(0.02)
Cunner	*Tautogolabrus adspersus*	11.129	(3.2)	4.380	(1.19)
Daubed shanny	*Leptoclinus maculatus*	0.000	(0)	0.020	(0.02)
Eel	*Anguilla rostrata*	0.030	(0.02)	0.005	(0.01)
Flying gurnard	*Dactylopterus volitans*	0.000	(0)	0.005	(0.01)
Greenland cod	*Gadus ogac*	0.121	(0.06)	4.750	(1.14)
Haddock	*Melanogrammus aeglefinus*	0.008	(0.01)	0.000	(0)
Lumpfish	*Cyclopterus lumpus*	0.053	(0.02)	0.290	(0.06)
Ocean pout	*Zoarces americanus*	0.106	(0.05)	0.045	(0.02)
Radiated shanny	*Ulvaria subbifurcata*	0.061	(0.02)	0.080	(0.02)
Rainbow smelt	*Osmerus mordax mordax*	1.970	(0.9)	2.460	(0.63)
Rock gunnel	*Pholis gunnellus*	0.000	(0)	0.690	(0.10)
Sand lance	*Ammodytes* spp.	2.432	(1.70)	2.835	(1.66)
Sculpin spp.	*Myoxocephalus scorpius, M. aenaeus, M. octodecemspinosus, Gymnocanthus tricuspis*	1.977	(0.29)	2.630	(0.47)
Sea raven	*Hemitripterus americanus*	0.129	(0.04)	0.015	(0.01)
Skate (unidentified)		0.015	(0.01)	0.000	(0)
Snakeblenny	*Lumpenus lumpretaeformis*	0.364	(0.07)	0.000	(0)
Spotted skate	*Raja straeleni*	0.008	(0.01)	0.000	(0)
Stickleback spp.	*Gasterosterus aculeatus, G. wheatlandi*	0.970	(0.60)	22.745	(7.27)
Stout eelblenny	*Anisarchus medius*	0.008	(0.01)	0.055	(0.05)
Thorny skate	*Amblyraja radiata*	0.008	(0.01)	0.035	(0.02)
White hake	*Urophycis tenuis*	1.462	(0.50)	5.425	(0.96)
Winter flounder	*Pseudopleuronectes americanus*	15.644	(2.32)	13.495	(1.60)
Yellowtail flounder	*Limanda ferruginea*	0.144	(0.04)	0.275	(0.09)

Table 2. Analysis of deviance tables for juvenile Atlantic cod abundance (A; age 0, 1, and 2) and all community metrics (B; total fish abundance, Shannon diversity, species richness, and species evenness). For age 0 cod, a negative binomial GLM was used, while for ages 1 and 2 a two stage model (binomial for presence/absence and negative binomial for counts) was used. Total fish abundance and species richness had negative binomial and Poisson error structure, and Shannon diversity and species evenness had normal error structure. The tables contain test statistics and associated p values comparing the reduction in deviance for the row to the residuals. Chi-squared tests for models with known dispersion are used, the raw deviance is reported (synonymous with the Chi-square value), and F tests for models with estimated dispersion. All main effects and interactions (':') are shown, and year is nested in time period ('/'). Significant results ($p < 0.05$) are bolded. Full analysis of variance and deviance tables are given in the supplementary material.

A)

Variable	Age 0 Count Deviance	Age 0 Count P Value	Age 0 Presence/Absence Deviance	Age 0 Presence/Absence P Value	Age 1 Count Deviance	Age 1 Count P Value	Age 1 Presence/Absence Deviance	Age 1 Presence/Absence P Value	Age 2 Count Deviance	Age 2 Count P Value
Time Period	2.002	0.1571	**71.394**	**<0.0001**	**65.316**	**<0.0001**	**4.281**	**0.0386**	**18.179**	**<0.0001**
Region	**60.070**	**<0.0001**	**15.187**	**0.0096**	**81.448**	**<0.0001**	**26.385**	**0.0001**	**19.889**	**0.0013**
Vegetation	2.111	0.1463	**4.631**	**0.0314**	2.507	0.1133	0.002	0.9687	**4.245**	**0.0394**
(Time Period/Year)	**24.809**	**0.0017**	**21.709**	**0.0055**	**101.674**	**<0.0001**	**17.108**	**0.029**	**19.447**	**0.0126**
Time Period:Region	**19.622**	**0.0015**	**12.783**	**0.0255**	8.270	0.142	6.040	0.3024	**20.021**	**0.0005**
Time Period:Vegetation	0.070	0.791	1.556	0.2123	0.662	0.4158	0.000	0.9832	2.040	0.1533
Region:Vegetation	0.006	0.9972	0.931	0.628	0.557	0.7571	**6.673**	**0.0356**	0.180	0.9142
(Time Period/Year):Region	**116.081**	**<0.0001**	0.000	1	**129.625**	**<0.0001**	0.000	1	**45.095**	**0.0026**
(Time Period/Year):Vegetation	**22.607**	**0.0039**	0.000	1	14.727	0.0647	0.000	1	4.022	0.7773
Time Period:Region:Vegetation	**8.555**	**0.0139**	865.048	**0**	0.327	0.849	**6649.551**	**0**	0.068	0.7945
(Time Period/Year):Region:Vegetation	20.877	0.0754	0.000	1	10.501	0.1619	0.000	1	0.182	0.9961

B)

Variable	Total Fish Abundance Deviance	Total Fish Abundance P Value	Shannon Diversity F	Shannon Diversity P Value	Species Richness Deviance	Species Richness P Value	Species Evenness F	Species Evenness P Value
Time Period	**18.238**	**<0.0001**	**9.970**	**0.0018**	2.056	0.1516	**8.331**	**0.0043**
Region	**24.707**	**0.0002**	**14.338**	**<0.0001**	**37.912**	**<0.0001**	**5.583**	**0.0001**
Vegetation	**14.046**	**0.0002**	2.461	0.1181	**9.369**	**0.0022**	2.478	0.1168
(Time Period/Year)	**41.741**	**<0.0001**	**4.096**	**0.0001**	**24.380**	**0.0020**	**2.411**	**0.0162**
Time Period:Region	5.519	0.3559	0.307	0.9086	**13.055**	**0.0229**	0.711	0.6160
Time Period:Vegetation	3.091	0.0787	0.563	0.4536	0.308	0.5790	0.010	0.9217
Region:Vegetation	**6.504**	**0.0387**	2.118	0.1226	5.613	0.0604	0.118	0.8892
(Time Period/Year):Region	**82.785**	**0.0001**	**1.558**	**0.0246**	31.175	0.8096	1.232	0.1768
(Time Period/Year):Vegetation	9.627	0.2922	0.383	0.9289	5.523	0.7005	0.309	0.9620
Time Period:Region:Vegetation	5.654	0.0592	0.287	0.7509	2.354	0.3082	0.121	0.8858
(Time Period/Year):Region:Vegetation	18.150	0.1519	0.542	0.8969	3.771	0.9934	0.755	0.7067

Table 3. Community composition changes with all predictor variables using the ManyGLM approach. A significance value for each predictor is given and those species with significant ($p < 0.05$) parameter terms are listed. For each species the contribution (%) to the parameter deviance is provided in brackets. NA = no species had a significant contribution.

Parameter	Residual DF	DF	Deviance	P value	Individual Species with Significant Effect
Time Period	**323**	**1**	**337.5**	**0.001**	Rock gunnel (22.1%), Snakeblenny (18.3%), Atlantic Cod 1 (14.6%), Greenland cod (10.7%), White hake (4.5%), Lumpfish (4.3%)
Region	**318**	**5**	**661.71**	**0.001**	Winter flounder (13.5%), Cunner (10.5%), Sculpin spp (10.1%), Atlantic Cod 1 (6.0%), Rainbow smelt (5.8%), Atlantic Cod 0 (5.3%), Rock gunnel (4.8%), Sea raven (3.8%), Radiated shanny (3.7%)
Vegetation	**317**	**1**	**87.09**	**0.001**	Greenland cod (17.9%), Sand lance (15.5%), White hake (12.2%)
(Time Period/Year)	**307**	**10**	**542.96**	**0.001**	Greenland cod (11.7%), Atlantic Cod 1 (10.0%), Winter flounder (9.7%), White hake (7.1%), Sculpin spp (5.5%), Lumpfish (5.3%)
Time Period:Region	**302**	**5**	**182.31**	**0.001**	NA
Time Period:Vegetation	301	1	19.95	0.251	
Region:Vegetation	**299**	**2**	**91.98**	**0.004**	Cunner (21.7%), Winter flounder (20.9%)
(Time Period/Year):Region	**254**	**45**	**860.93**	**0.001**	Atlantic Cod 1 (12.5%), Atlantic Cod 0 (10.6%), Atlantic Cod 2 (10.2%)
(Time Period/Year):Vegetation	245	9	117.27	0.192	
Time Period:Region:Vegetation	243	2	22.49	0.227	
(Time Period/Year):Region:Vegetation	239	17	96.49	0.244	

Chapter 3 – Historical Abundance of Juvenile Commercial Fish in Coastal Habitats: Implications for Fish Habitat Management in Canada

3.1. Abstract

An important component of science-based fisheries policy is the provision of habitat adequate for population renewal. In Canada, the Fisheries Act pays little attention to managing fish habitat, and was further weakened by changes enacted in 2012. Specifically, determining the role of fish habitat in stock recovery is challenging when many stocks, such as Atlantic cod and pollock, have severely declined or collapsed and no longer occupy former habitats. To evaluate this issue, we compared the abundance of juvenile commercial fish in coastal vegetated habitats before and after collapse or decline of major groundfish stocks. We compiled past studies that surveyed juvenile Atlantic cod and pollock in vegetated habitats across three provinces in Atlantic Canada. We repeated two of the studies and report one that had already been repeated post-collapse in order to quantify changes in juvenile fish abundance in these habitats. In all three cases we found that juvenile fish abundance was strongly reduced coinciding with strong declines in adult stocks. However, juvenile fish still occur in coastal habitats and could thus aid in adult stock recovery. The Fisheries Act of Canada, as of 2013, requires the presence of an ongoing fishery to trigger habitat protection. This change is particularly problematic; fewer fish due to population reduction leads to lowered habitat protection and potentially habitat degradation, with less or lesser-quality habitat for fish in the future. To address this gap, we recommend repealing the 2012 changes to enable directed management of fish habitat. Furthermore, we recommend enhancing current legislation to strengthen fish habitat management in Canada. We also stress using a precautionary approach for coastal fish habitat management, particularly in valuing the

potential impact for fish stocks. Lastly, we recommend mechanistic in place of purely correlative approaches to identifying essential fish habitat with depleted fish stocks.

3.2. Introduction

Fisheries have shaped global economies and vastly influenced marine ecosystems for centuries. Fisheries are also vital for food security, as fish provides more than 2.9 billion people with ~20% of their average per capita intake of animal-based protein, with the majority coming from marine capture fisheries (FAO, 2014). Furthermore, rebuilding overfished stocks could increase capture fisheries production and associated annual value by US$32 billion (Ye *et al.*, 2013). Effective fisheries management is therefore imperative. Habitat management is not traditionally seen as an important component of fisheries management, despite habitat playing an essential role in various stages of fish life history (Langton *et al.*, 1996; Naiman and Latterell, 2005). Specifically, complex habitats mediate mortality of juvenile fish, and therefore play a critical role in supporting fisheries (Beck *et al.*, 2001; Juanes, 2007; Aburto-Oropeza *et al.*, 2008; Verweij *et al.*, 2008; Bertelli and Unsworth, 2014; Lilley and Unsworth, 2014; Seitz *et al.*, 2014). The protection and management of coastal ecosystems and complex habitats is an integral component of ecosystem-based fisheries management (Pikitch *et al.*, 2004).

At a time when many commercially important fish stocks have been depleted (Worm *et al.*, 2009), protection and restoration of juvenile habitats may be contributing factors for recovery. For example, population recovery of goliath grouper (*Epinephelus itajara*) in the southeastern United States, stemmed directly from their nursery habitat – mangroves (Koenig *et al.*, 2011). Mangroves functioning as nursery habitat have also been shown to increase local

fishery yield in the Gulf of California (Aburto-Oropeza *et al.*, 2008). Nursery and juvenile

habitat conservation can even far outweigh the effects of no-take reserves in coral reef

fisheries (Nagelkerken *et al.*, 2012). Moreover, nursery habitat availability may limit the adult

stock size and recruitment for some fish species (Collins *et al.*, 2000; Aburto-Oropeza *et al.*,

2007; Sundblad *et al.*, 2014), and nursery habitat degradation has been related to population

decline of flounder (*Platichthys flesus)* in the northern Baltic Sea (Jokinen *et al.*, 2015). While

there is a wealth of evidence supporting nursery habitat function, directly quantifying the

contribution of juveniles to an adult population continues to be challenging (Sheaves *et al.*,

2014). Furthermore, measuring the value of a nursery habitat solely by contribution to adult

fish stocks has recently been criticized as an oversimplification (Sheaves *et al.*, 2006, 2014).

Due to the challenges associated with directly quantifying contributions of nursery habitats to

fisheries, the value of coastal nurseries in Canada for sustaining fish populations, as well as

aiding recovery, is largely unknown.

In Atlantic Canada, there have been strong declines of major groundfish stocks,

namely Atlantic cod and pollock (Hutchings and Myers, 1994, 1995; DFO, 2015a). Due to the

substantial depletion of adult stocks, juvenile abundance may also be low, such that the

current value of coastal habitat as important juvenile habitat may be underestimated. To

overcome this issue, we used a historical approach, which is increasingly important for setting

baselines of healthy ecosystems and fisheries for marine management (McClenachan, 2009;

McClenachan *et al.*, 2012; Engelhard *et al.*, 2015). The principal objective of this study was to

quantify change of juvenile fish abundance in coastal vegetated habitats, specifically

corresponding to time periods of stock decline. To do so, we identified three historical surveys

of juvenile commercial fish abundance in vegetated habitats across three provinces in Atlantic

Canada. We then either repeated these surveys using the same methodology, or analyzed already available data from post-collapse surveys. The results are discussed in relation to concomitant declines in adult fish stocks and the effectiveness of Canadian fisheries management to protect fish habitat. We then compare Canadian fish habitat management with best practices for managing coastal nursery habitats in the United States and recommend how to strengthen management of coastal zones and fish habitat in Canada.

3.3. Methods

We identified published studies that quantified juvenile fish abundance of commercially important species in vegetated habitats in Atlantic Canada before the major collapse of groundfish stocks in the early 1990s. Because our goal was to compare juvenile abundances between time periods in which stock collapse or declines occurred, we either needed published data on both periods or needed to repeat available past studies. To achieve the latter, we needed detailed descriptions of the methods and results (i.e. raw abundance, or mean and standard variation). We identified three possible studies: firstly, a highly resolved data set from beach seine surveys of juvenile cod in coastal habitats along the east coast of Newfoundland in the 1959-1964 and again 1992-1996 (Methven *et al.*, 1997). We then found two suitable dive survey studies, one quantifying juvenile pollock (*Pollachius virens*) in Brandy Cove, New Brunswick in 1989-1990 (Rangeley and Kramer, 1995a), and a second measuring juvenile Atlantic cod (*Gadus morhua*) in vegetated habitats in St. Margaret's Bay, Nova Scotia in 1992 (Tupper and Boutilier, 1995). In the following, we present details of each of the three case studies as well as the statistical analyses required for comparing past and

contemporary abundances. We used a Type I error rate of 5% as the criterion for statistical significance.

3.3.1. *Case Study 1: Eastern Newfoundland – Atlantic Cod*

A systematic series of beach-seine surveys was done along the east coast of Newfoundland from 1959-1964, and repeated after the collapse of Atlantic cod from 1992-1996 (Methven *et al.*, 1997). 84 different sites were surveyed from mid-September to late-October examining juvenile Atlantic cod abundance in coastal bays in the first series, known as the "Fleming survey". Of the 84 sites sampled, 42 were sufficiently sampled to allow year to year comparisons (this eliminated the first year of the data series, 1959), and in any one year between 17 and 41 sites were sampled depending on weather and ocean conditions. For the purpose of this study, we only analyzed sites with vegetation (described as "kelp" or "eelgrass" in the field notes), which totalled 35 sites.

A 25m bottom seine was used, where one person on land stands holding one hauling rope while the seine is let out 55m from shore. Then, the seine is let out parallel to shore, and then the other hauling rope is towed into shore. This second hauling rope is received by another person on shore, with 16m between individuals, and the ropes are simultaneously pulled in. The seine thus censused of $880m^2$ from the shore and the water column up to ~2m above the bottom. Full specifications are described in Schneider *et al.* (1997b).

In the 1960s, the number of sets at each site varied; therefore, the data were reduced to 42 sites where there were consecutive sets in many years, removing those years at sites where there were not two consecutive sets. We thus restricted our comparison of juvenile cod abundance to the first two sets of beach seines performed at each site. Abundances of cod in

the two sets were summed, which represents an index of density, only contaminated by lateral movement from adjacent areas. This seining method has high catchability (Gotceitas *et al.*, 1997), with higher than 95% retention of all fish in the path of the net. Once hauled in, all fish were counted and identified. Here, we only use the densities of juvenile cod, classified into three age bins: Age 0 (<97mm), Age 1 (97-192mm) or Age 2 (>192mm), based on annually repeatable modes in the catch curves (Methven *et al.*, 1997).

The "Resurrected Fleming Survey" (1992-1996) was initiated after the collapse of the Northwest Atlantic cod stocks. The seasonal timing, location of sampling, gear specifications, gear deployment, sampling design, and time of day sampled were all given attention to ensure comparability between the two periods (Cull, 1997; Methven *et al.*, 1997; Schneider *et al.*, 1997a). Any sampling bias is constant between time periods based on close matching of the sampling protocols. Sites which had direct habitat degradation due to development (e.g. wharf building) were not sampled in the "Resurrected Fleming Survey", so it is unlikely that vegetation and habitat within the sites used in this analysis had changed dramatically due to anthropogenic causes.

To analyze changes in juvenile cod abundance, we used generalized linear models (GLMs; Nelder and Wedderburn, 1972). Every GLM used had a common set of categorical explanatory variables: time period (1960-1964 and 1992-1996), and year nested within time period. We used year as a categorical variable, as temporal autocorrelation of cod abundance counts between years was negligible. Every age group of cod had overdispersed counts, with ages 1 and 2 also exhibiting zero inflated counts. Thus, for Age 0 cod, we used a GLM with negative binomial error structure and a log link function. For Age 1 and Age 2 cod, we used a two-stage model, with the first stage examining presence and absence of a count (a binomial

error structure with a logit link function) and the second stage examining the counts themselves, a GLM with negative binomial error structure and a log link function. We used sequential analysis of deviance tables, testing the reduction in residual deviance from the null model to assess significance of the observed contrasts among means.

3.3.2. Case Study 2: Brandy Cove, Passamaquoddy Bay, New Brunswick – Pollock

Rangeley and Kramer (1995a) examined tidal impacts on habitat selection in juvenile pollock. They used seven fixed 140m dive transects which were set at random intervals perpendicular to shore along 200m of coastline in Brandy Cove, Passamaquoddy Bay, New Brunswick (Figure 1). Transects reached a depth of 4-6m, and the habitat consisted mainly of rocky macroalgal reef, mostly rockweed (*Ascophyllum nodosum*) with interspersed mud flats. At different tidal stages (low rising, low falling, high rising, and high falling), two divers counted juvenile pollock along 1m wide transects from late May to the end of August in 1989 and 1990. They then reported the mean, standard error and sample size (number of transects) of juvenile pollock density (m^{-2}) for each tidal stage and for spring (May-June) and summer (July-August) separately (Table 2 within Rangeley and Kramer, 1995a), however raw data were no longer available. We explored simulating historical datasets and consequently comparing raw data, however the assumptions required for these simulations were not met and so we chose a simpler approach (see Appendix C). A related study found no significant site differences in juvenile pollock density between Brandy Cove and three other sites in Passamaquoddy Bay (Rangeley and Kramer, 1995b), allowing us to generalize pollock abundance in the region.

In 2015, we returned to Brandy Cove to repeat the dive surveys described above (Rangeley and Kramer, 1995a). We chose to compare densities in the spring period, from the

end of May until the end of June, and at the low rising and low falling tide because these had the highest densities reported (Rangeley and Kramer, 1995a). Instead of using transect lines, we swam along a compass bearing perpendicular to shore, diving to a maximum depth of 5m, and measured the dive transect length retroactively using a surface-towed Global Positioning System (GPS). As in the original study, two divers counted juvenile pollock and other organisms within a 1m wide transect, which we then converted to pollock density. We completed a total of 142 transects, 72 for the low rising and 70 for the low falling tidal stage. Eight transects were completed for each sampling day, with a total of 9 sampling days. To compare mean densities, we used an unpooled two-sample t-test comparing independent means. Degrees of freedom were calculated assuming unpooled independent means with different standard deviations.

3.3.3. Case Study 3: St. Margaret's Bay, Nova Scotia – Atlantic Cod

Tupper and Boutilier (1995) used visual dive surveys to examine the effect of habitat on settlement, growth and survival of juvenile Atlantic cod. Specifically, they completed four, 15m long transects in four different habitat types (rocky reef with macroalgae, small cobble bottom, eelgrass *Zostera marina* beds, and sandy bottom), within three separate study sites in St. Margaret's Bay, Nova Scotia (Birchy Head, Back Cove, and Mill Cove). They counted juvenile Atlantic cod (age 0) within 1m of each side the transect line, with a total planar area of 30m^2, sampling every 10 days from May 1st until July 1st in 1992. They report the mean density of cod m^{-2} and the SD for each sampling time (Figure 2 within Rangeley and Kramer, 1995a); the raw data were not available anymore.

We returned to the same three study sites in 2014 to repeat the same survey methods. We anchored floats at 15m intervals within two of the habitats (rocky reef with macroalgae and eelgrass beds), which had the highest survivability of juvenile cod reported in 1992, and similarly used dive transects to count juvenile Atlantic cod (age 0). One diver completed all surveys to ensure comparable estimates. Counts were restricted to within 1m of each side of the transect to also ensure the same sampling intensity, again with a total planar area of 30m^2. We similarly sampled from May 6th to July 7th, on average every 8 days (varying due to weather constraints) with a total of 9 sets, with four transects in each habitat at each site.

In order to statistically compare abundances between 1992 and 2014, we extracted the time series of mean number of individuals per transect and standard deviations from (Tupper and Boutilier, 1995). Since the goal of our study was to compare overall abundances, we chose to only statistically compare the maximum reported abundance. This was due to the variable timing of highest juvenile abundance. Similar to the previous case study, we used an unpooled two-sample t-test comparing independent means, calculating the standard error from the extracted standard deviation and sample size ($n = 4$). In addition, we visually compared the entire time series from May-July in 1992 and 2014, emphasizing effect sizes rather than significance levels (Nakagawa and Cuthill, 2007).

3.4. Results

We found decreased juvenile fish abundances in the latter time periods in each of the three case studies. Within vegetated habitats across Newfoundland, we found strongly reduced abundance of juvenile Atlantic cod in different age groups and high within-time period variability (Fig. 2a). For Age 0 cod, the high variability within time period was evident with a significant year nested within time period effect (Table 1). However, there was no statistically

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significant change in overall Age 0 cod abundance between the two time periods. For both ages 1 and 2 cod, we found statistically significant declines in the log-odds ratios for the presence/absence of a count (fewer sites occupied), as well as in the abundances from the 1960s to the 1990s, with an overall 5.38-fold decline in mean abundance of Age 1 and 2.37-fold in Age 2. There was also significant variability within time periods for Age 1 cod, but not for Age 2 cod (Table 1).

In the rockweed beds in Brandy Cove, New Brunswick, we found significantly lower juvenile pollock density in 2015 compared with 1989-90. Mean pollock density declined more than one order of magnitude from 0.376 to 0.018 individuals m^{-2} ($p < 0.001$) at the low-rising tide, and from 0.531 to 0.009 individuals m^{-2} ($p = 0.035$) at the low-falling tide (Fig. 2b).

In St. Margaret's Bay, Nova Scotia, we found reduced overall abundance of juvenile cod in both rocky reefs with macroalgae and eelgrass beds at all three study sites (Fig. 2c). However, statistically significant lower abundance maxima were only detected in two of the six surveys, namely in rocky reefs at Back Cove and Mill Cove ($p << 0.001$ and $p = 0.002$, respectively; Fig. 2c). Yet we also observed much higher variability in peak abundance in 2014 compared with 1992, evident in the larger standard deviations (Fig. 2c). In addition, across both habitats at all three sites, the pulse of juvenile cod was much shorter, only evident in one week in 2014 compared to six weeks in 1992. In all other weeks, the abundance of juvenile cod in 2014 was near zero.

3.5. Discussion

Our three case studies confirm the expected reduction in abundance of juvenile cod and pollock in coastal vegetated habitats in Atlantic Canada over periods of severe adult stock

decline. During these periods, we found a corresponding reduced juvenile density and less sites occupied compared to surveys done before stock declines. We did still find juvenile fish of commercially important species in coastal habitats, despite collapsed or depleted adult stocks. This finding highlights the continued importance of coastal vegetation as juvenile fish habitat with the potential to supply adult stocks and aid in stock recovery. Our findings have important implications for the protection of coastal fish habitats and for enabling policy and regulatory improvements in Canadian federal and provincial coastal and habitat management.

3.5.1. *Juvenile Fish Decline Coupled with Adult Stock Decline*

The decline in juvenile Atlantic cod in Newfoundland shown in the first case study, specifically ages 1 and 2, is the expected outcome of the substantial reduction of the Northwest Atlantic cod stocks which reduced adult stocks to <1-3% of former abundance (Hutchings and Myers, 1994, 1995). High inter-annual variability may explain why the observed decrease in age 0 juvenile cod was not statistically significant despite the magnitude of adult decline (Fromentin *et al.*, 2001). Another potential explanation is community changes and altered predator dynamics (McCain *et al.*, 2015). Specifically, reduction in juvenile numbers may have been offset by reduced cannibalism, which is a substantial source of juvenile mortality (Bogstad *et al.*, 1994; Yaragina *et al.*, 2009; Ottersen *et al.*, 2014). Reduced cannibalism may also explain why observed declines in juveniles ages 1 and 2 are less severe than those reported for adult stocks. The large spatial scale and long temporal coverage of the Newfoundland surveys allow us to infer the relationship between stock status and juvenile fish abundance (Ings *et al.*, 1997).

Our second and third case studies were much smaller scale, but also confirm the expected decrease in juvenile abundance after stock decline. The decreased juvenile pollock abundance coincided with a 6-fold decline in pollock biomass index (3-year geometric mean) from over 60 kg/tow in 1989 to under 10 kg/tow in 2015 in the management area adjacent to Passamaquoddy Bay, New Brunswick (NAFO Areas 4XOPQRS5; DFO, 2015a). Thus, lowered juvenile pollock abundance in our surveys was anticipated, as pollock juveniles recruit to coastal habitats and have not been found in deeper waters (Clay *et al.*, 1989). Similarly, the Atlantic cod biomass index in the adjacent management area to St. Margaret's Bay, Nova Scotia (NAFO Area 4X5Yb) declined 6.5-fold from 1992 to 2014 (DFO, 2015b), which may explain the lower juvenile cod abundance we found in coastal vegetated habitats. Unfortunately, we were unable to measure changes in habitat for the case studies we presented. However due to the relatively low development of coastal zones near these sites and the exclusion of developed sites in the "Resurrected Fleming" surveys, we are confident our results are not confounded by changes in habitat. To improve the second and third case studies, sampling over multiple years would have contributed to quantifying better estimates of coastal juvenile abundance, given high juvenile recruitment variability in marine fishes (Fromentin *et al.*, 2001).

Overall, results from these last two case studies support our conclusion from the Newfoundland case study about the connection between stock status and juvenile fish abundance. Such declines in adult stocks and consequently juvenile fish abundance in coastal ecosystems has also been observed in the Skagerrak (Svedäng and Svenson, 2006; Baden *et al.*, 2012). These concomitant declines in adult and juvenile abundance highlight the connectivity between coastal habitats and offshore fish stocks (Eriksson *et al.*, 2011). While

concomitant declines may reflect connectivity, it is important to note that the presence of fish alone does not indicate their importance for contributing to fish populations. In order to test the contribution of these habitats to fish populations, further research aimed at quantifying the proportion of fish which use coastal ecosystems in a population is required. Despite this research gap, there is extensive evidence that commercially important fish use coastal ecosystems in Atlantic Canada (Clay *et al.*, 1989; Rangeley and Kramer, 1995b; Gotceitas *et al.*, 1997; Ings *et al.*, 1997, 2008; Robichaud and Rose, 2006; Coll *et al.*, 2011; Schmidt *et al.*, 2011; Lawrence *et al.*, 2013), warranting the use of coastal habitat management as a tool for fisheries management in Canada.

3.5.2. *Fish Habitat Management in Canada*

Management of coastal fish habitat encompasses three different legislative avenues in Canada: fish habitat management through the Fisheries Act (FA) (DFO, 1986), coastal zone management through the Oceans Act (Ricketts and Hildebrand, 2011), and biodiversity conservation through international and national commitments (e.g. the Aichi Biodiversity Targets, the Species At Risk Act of Canada; Hutchings *et al.*, 2012; VanderZwaag *et al.*, 2012). Each of these avenues requires significant improvements, and some of their weaknesses have been previously addressed (Ricketts and Hildebrand, 2011; Favaro *et al.*, 2012; Hutchings *et al.*, 2012; VanderZwaag *et al.*, 2012; Hutchings and Post, 2013; Gantner, 2014; McDevitt-Irwin *et al.*, 2015; Bailey *et al.*, 2016). Here, we focus on the management of coastal fish habitat in light of our case studies' results.

Canadian fish habitat management began with the guiding principle of "no net loss of productive capacity" of fish habitat, where productive capacity is defined as "the maximum

natural capability of habitats to produce healthy fish" (DFO, 1986). Fish habitat management significantly shifted with changes made to the FA of Canada with Bill C-38, in particular the re-naming of Section 34, formerly "Fish Habitat Protection and Pollution Prevention" into "Fisheries Protection and Pollution Prevention". Prior to 2012, Section 35(1) stated that: "No person shall carry on any work or undertaking that results in the harmful alteration, disruption or destruction of fish habitat." The changes made in 2012 then mandated that: "No person shall carry on any work, undertaking or activity that results in serious harm to fish that are part of a commercial, recreational or Aboriginal fishery, or to fish that support such a fishery." In essence, the FA as it stands in 2012 no longer protects fish habitat per se but instead focuses on the protection of fish that are part of a fishery, or fish that support such a fishery. It also protects habitats of commercial, recreational, or aboriginal (CRA) fisheries, as the definition of "serious harm to fish" includes both the "death of fish" or "any permanent alteration to, or destruction of, fish habitat". Furthermore, the FA as of 2012 allows for alteration and disruption of fish habitat, but does not allow for permanent destruction. The changes outlined above were scrutinized due to the potential negative impacts on freshwater fish species and aquatic conservation (Hutchings and Post, 2013), as well as the reasoning for implementing these changes (de Kerckhove *et al.*, 2013). A repeal would re-establish and enable the need for habitat-based research and management. Repealing these changes would be enabling but not sufficient to protect fish habitat as there has been a long-standing deficiency of systematic research and management action.

Under current legislation, evaluation of fish habitat by different CRA fishery species can only be done when there is an active fishery. Specifically, the 2012 FA changes were justified by "shift[ing] the focus of protection from habitat per se to the sustainability and

ongoing productivity of CRA fisheries" (Rice *et al.*, 2015). At a time when many fish

populations have been severely depleted and are no longer experiencing "ongoing

productivity", such as those focused on in our case studies, this potentially results in a self-

reinforcing downward trend for fish habitat protection. That is, fewer fish due to population

reduction leads to lowered habitat protection and potentially degradation, with less or lesser-

quality habitat for fish in the future. However, habitat protection is particularly important

because of the connection between commercial fish populations and coastal ecosystems,

discussed above. Accordingly, there have been calls that these habitats should be protected to

maintain their function and services, as habitat may aid in the potential recovery of adult

stocks (Murawski, 2010; Schmidt *et al.*, 2011; Seeley and Schlesinger, 2012; Caddy, 2014). In

Atlantic Canada, the importance of eelgrass beds has been recognized by listing eelgrass as an

ecologically significant species in 2009 by Fisheries and Oceans Canada (formerly the

Department of Fisheries and Oceans; DFO) (DFO, 2009). However, there is no legal

protection associated with this listing. In contrast, despite also being recognized as important

coastal habitat to juvenile fish and other species (Rangeley and Kramer, 1995b; Schmidt *et al.*,

2011; Seeley and Schlesinger, 2012), rockweed beds are commercially harvested with

currently increasing harvest pressure and under provincial jurisdiction (DFO, 2013).

Underestimation of the value of coastal ecosystems as juvenile fish habitat could be a critical

gap in Canadian fisheries management due to poor protective legislation. This gap brings with

it an opportunity for significant improvement in the legislation to increase conservation-

oriented habitat management (Hutchings and Post, 2013).

3.5.3. *Comparison of Canadian and American Fish Habitat Management*

In contrast to Canada, effective protection of all life history stages of commercially important species as well as ecologically and biologically significant coastal zone habitats is required under the Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA) in the United States ('Magnuson-Stevens Fishery Conservation and Management Act, Subpart J — Essential Fish Habitat', 2003). This Act recognizes areas and habitats that are important for fisheries productivity and recovery. The National Oceanic and Atmospheric Administration (NOAA) in the United States manages fish habitat by assessing what constitutes "Essential Fish Habitat" (EFH) for every managed species. For example, eelgrass meadows in our case studies would very likely be considered EFH for Atlantic cod. Via the MSFCMA, NOAA then works with regional fishery management councils to identify EFH and habitat areas of particular concern (HAPCs), and to assess the largest threats to EFH. For example, the New England Fishery Management Council designated a large inshore area an HAPC for juvenile Atlantic cod, specifically from 0-20m depth in the Gulf of Maine and southern New England in order to "focus attention on coastal and nearshore development activities" (Fisheries Leadership and Sustainability Forum for the Mid-Atlantic Fishery Management Council, 2015). Importantly, American federal agencies (e.g. U.S. Army Corps of Engineers) are required to consult with NOAA if they carry out any activities which may adversely affect EFH ('Magnuson-Stevens Fishery Conservation and Management Act, Subpart J — Essential Fish Habitat', 2003). EFH and particularly HAPCs are therefore protected to some degree. The MSFCMA is fundamentally different from its Canadian counterpart in that it explicitly mandates fish habitat management.

Another important difference is that the MSFCMA also requires that management councils adhere to binding scientific advice, thereby effectively eliminating the discretionary decision-making authority of the American equivalent to the Fisheries Minister in Canada (Hutchings *et al.*, 2012). Strengthening accountability and the links between policy and science in fisheries management would go a long way to ensuring coastal fish habitats get the protection that they require (Hutchings *et al.*, 2012).

3.5.4. *Moving Habitat Management Forward in Canada*

Marine conservation, coastal zone management, and fish habitat management are all connected, so moving management forward can be done through any combination of these three avenues. The critical missing tool for fishery managers in Canada is one that enables directed, specific management actions that safeguard areas of high-quality juvenile habitat – those areas which maximize growth and reduce predation risk for juveniles. Ecologically and Biologically Significant Area (EBSA) designation is a potential tool which could be enhanced for this purpose, however it currently provides no legal protection once implemented (DFO, 2004). In that way they are similar to HAPCs in the United States, as they are used as a tool for increasing risk adverse management (DFO, 2004). An important difference is that EFH in the United States is legally protected under the MSFCMA, and HAPCs are used to concentrate management effort. Whether it be through EBSA designation or another avenue, Canadian fisheries managers require an effective tool for protecting fish habitat, which potentially enables recovery.

Improvements in habitat management have been made in recent years by the DFO, including formalizing "offsetting policies" that theoretically compensate habitat destruction

with habitat creation (Clarke and Bradford, 2014). Furthermore, the DFO has begun analyzing habitat in terms of "adult equivalents", which attempts to quantify how many adults may be produced by a habitat (DFO, 2015c). Both of these are steps in the right direction towards adequate fish habitat assessments, although implementation of habitat offsets ("compensation" prior to 2012) is largely deficient in Canada and in general (Quigley and Harper, 2006; Levrel *et al.*, 2012) and estimation of adult equivalents is still challenging in practice for any nursery habitat (Sheaves *et al.*, 2014). The key missing component is protection of fish habitat in a proactive manner, potentially contributing to fisheries recovery.

Uncertainty around the value of fish habitat remains because direct quantification of fish habitat impacts for fish stocks is challenging (Beck *et al.*, 2001; Dahlgren *et al.*, 2006; Sheaves *et al.*, 2014). Despite this challenge, recent work in Australian seagrass meadows estimated that commercial juvenile fish were enhanced via reduced predation and increased growth, thus valuing seagrass beds ~$A230,000 ha^{-1} year^{-1} (Blandon and zu Ermgassen, 2014). This estimate demonstrates the potentially high value of coastal fish habitat in Canada. Estimates of fish habitat contributions to fisheries may be more challenging in Canadian temperate waters where many juvenile fish use coastal ecosystems opportunistically, while others settle into complex habitat offshore (Lough, 2010). Alongside the challenges of quantifying habitat contributions, human impacts are persistent throughout many coastal ecosystems (Lotze *et al.*, 2006) and continued threats are sometimes even concentrated in important fish habitats (e.g. reproduction areas; Sundblad and Bergström, 2014). For example, aquaculture development was identified as one of three main threats to Canadian marine biodiversity (Hutchings *et al.*, 2012). It is also extremely difficult to restore degraded or destroyed habitats in coastal marine ecosystems (Orth *et al.*, 2002; Elliott *et al.*, 2007; Tanner

et al., 2010), which highlights using a precautionary approach for habitat management. A precautionary approach for valuing coastal fish habitat is important, and protection of fish habitat should not wait until adequate quantification of fish habitat contribution to fish stocks (Hutchings *et al.*, 2012).

Evaluating essential fish habitat for fish populations that have collapsed or declined is a critical challenge. Coastal ecosystems differ fundamentally in larval supply, which is a key determinant of the value of a nursery habitat (Beck *et al.*, 2001). For some species (e.g. Atlantic cod), oceanographic circulation models would be an ideal tool for modelling larval supply to nurseries (e.g. Stanley *et al.*, 2013). Alongside identifying areas of high larval supply, looking at factors of juvenile success (e.g. survival and growth) as a function of habitat variables (e.g. Werner *et al.*, 1983) is critical to determine differential habitat quality. Examining habitat influences on survival and growth of juveniles would mechanistically describe the relationship fishes have with their habitats.

Given the weaknesses addressed above concerning Canadian fish habitat management, we recommend the following:

1) Canada should use directed coastal management (e.g. coastal MPAs, EBSAs, or restricted development zones) to safeguard areas of high quality juvenile habitat. To do this, Canadian fishery managers therefore require a tool for protecting fish habitat, which could be through EBSA designation if it were enhanced with legal authority. We are recommending the development of a management tool with an intermediate level of protection, below that of a Marine Protected Area (MPA) but above no-management.

2) Canada should broadly approach fish habitat management with a precautionary approach.

3) Canada should focus research efforts to describe mechanistically the relationship between harvested fish species and their habitats.

3.6. Conclusion

Evaluation of fish habitat use is challenging when many fish populations are severely depleted. We have partially overcome some of these difficulties by using a historical approach. By quantifying change in juvenile fish abundance with historical reference points, our results suggest that coastal vegetated habitats have been heavily used by commercially important fish in the past and are still used today, albeit in much reduced numbers. Therefore, these coastal vegetated habitats should be managed. We stress the use of precautionary approaches for managing fish habitat, as restoring destroyed eelgrass meadows or other biogenic structures is extremely difficult. Strengthening fish habitat management will move Canada towards ecosystem-based fisheries management. Moreover, managing habitats is an integral component of rebuilding depleted fish stocks (Murawski, 2010), and should be used as a tool contributing to Canadian fisheries recovery strategies.
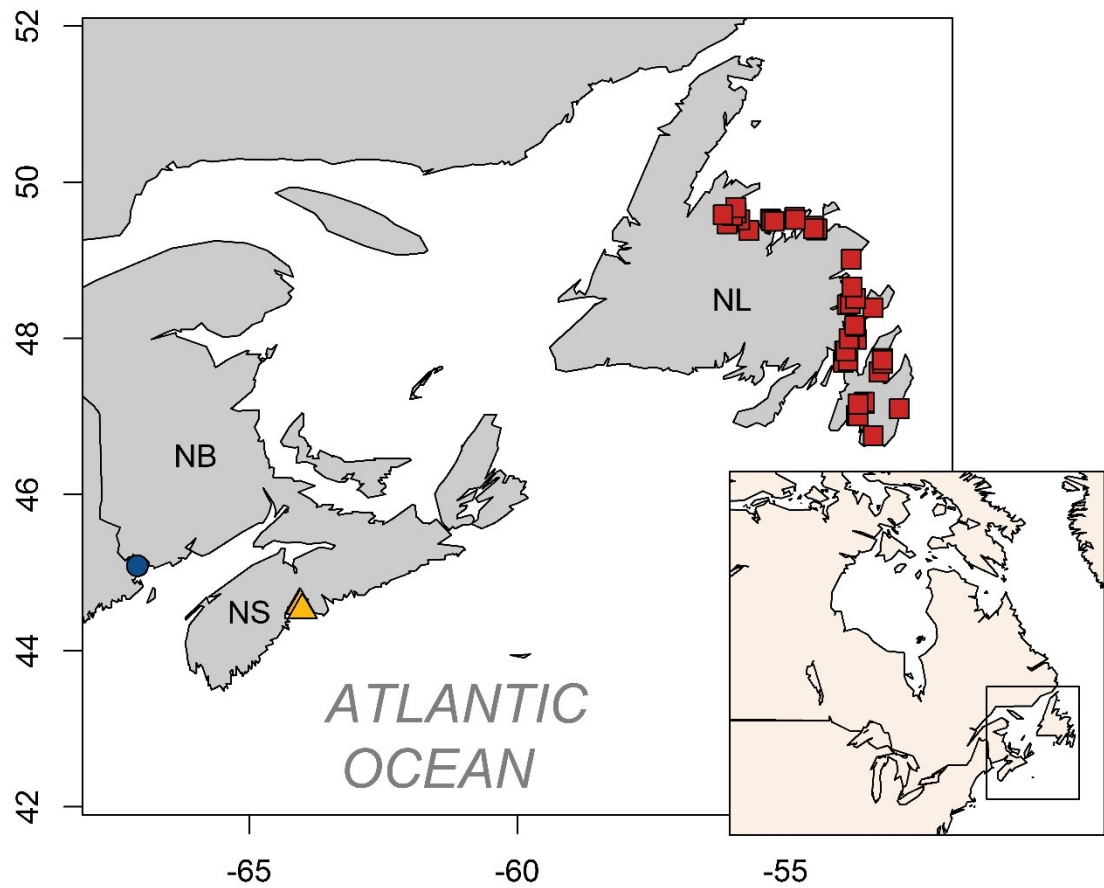
Figure 1. Map of the study sites for all case studies in Atlantic Canada: (1) juvenile cod along the east coast of Newfoundland (NL; squares), (2) juvenile pollock in Brandy Cove, New Brunswick (NB; circle), (3) juvenile cod in St. Margaret's Bay, Nova Scotia (NS; triangles).
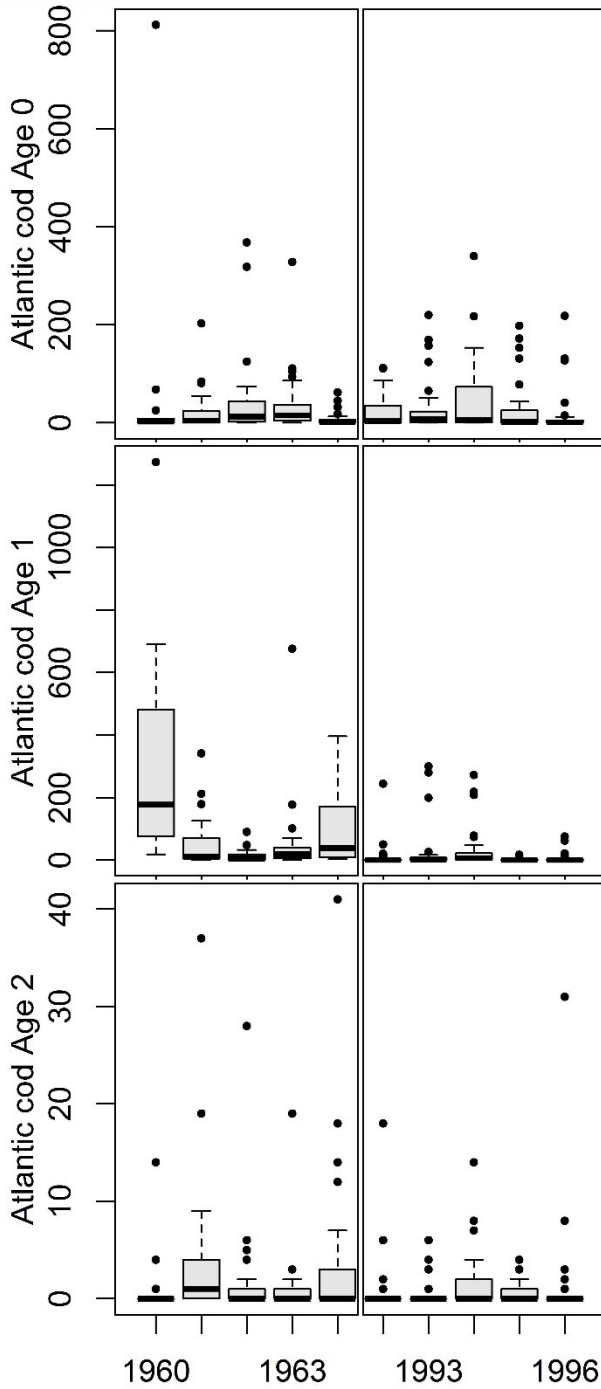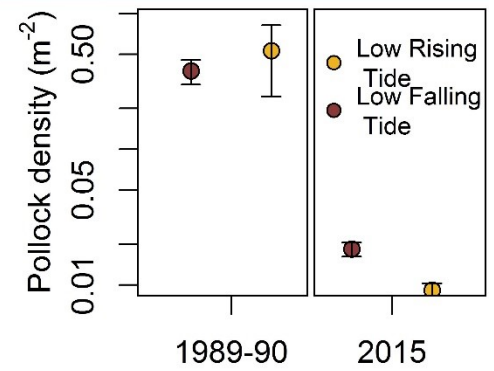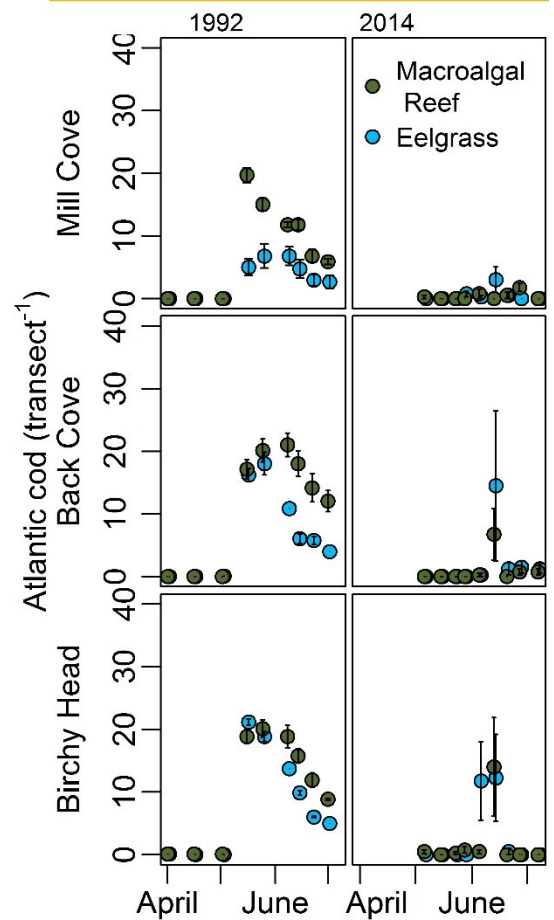
Figure 2. Summary of case study results: (a) Juvenile Atlantic cod abundance for Age 0, 1 and 2 in vegetated habitats across 35 study sites in eastern Newfoundland. Abundances are an index of density given as a sum of counts in two consecutive beach seines per site (described in Methods). Boxplots indicate the median, the first and third quartiles, and outliers (points) are 1.5x above the interquartile range. (b) Changes in juvenile pollock density (mean ± SE, n = 277, 311, 70, and 72 from left to right)

from 1989-90 to 2015, at the low-rising and low-falling tide. (c) Time series of juvenile Atlantic cod abundance at three sites in St. Margaret's Bay, Nova Scotia, comparing abundances (±SE, n = 4 for every point) in 1992 and 2014. Data are jittered to visualize error bars.

Table 1. Analysis of deviance tables for juvenile Atlantic cod (ages 0, 1, and 2). For Age 0 cod, a negative binomial GLM was used, while for ages 1 and 2 a two-stage model (binomial for the presence/absence and negative binomial for counts) was used. The table contains test statistics and associated p-values comparing the reduction in deviance for the row to the residuals. χ^2 tests for models with known dispersion are used, the raw deviance is reported (synonymous with the χ^2 value). Period and year nested in period ("/") are the explanatory variables. Significant results (p < 0.05) are bolded.

Response	Variable	DF	Deviance	Residual DF	Residual Deviance	*p* value
Cod 0	Null			276	338.0085	
	Period	1	1.6776	275	336.3308	0.1952
	Period/Year	**8**	**19.1662**	**267**	**317.1646**	**0.0140**
Cod 1 Presence/Absence	Null			276	334.7840	
	Period	**1**	**55.4307**	**275**	**279.3533**	**<0.0001**
	Period/Year	**8**	**21.2964**	**267**	**258.0569**	**0.0064**
Cod 1 Counts	Null			195	324.8323	
	Period	**1**	**33.6390**	**194**	**291.1934**	**<0.0001**
	Period/Year	**8**	**58.6867**	**186**	**232.5066**	**<0.0001**
Cod 2 Presence/Absence	Null			276	343.1895	
	Period	**1**	**4.6980**	**275**	**338.4915**	**0.0302**
	Period/Year	**8**	**21.3814**	**267**	**317.1101**	**0.0062**
Cod 2 Counts	Null			85	100.2846	
	Period	**1**	**4.6884**	**84**	**95.5962**	**0.0304**
	Period/Year	8	11.5308	76	84.0654	0.1734

Chapter 4 – Conclusion

Quantifying long-term changes is increasingly important for marine management and conservation (McClenachan *et al.*, 2012). This is particularly true for coastal ecosystems, which have been impacted by human activities for centuries (Lotze *et al.*, 2006) and are at the interface of both land- and ocean-based impacts – such as coastal development and fishing. By delving into the ecological history of coastal ecosystems, we gain reference points which can inform the basic ecology of the system (e.g. Collie *et al.*, 2008), the magnitude and range of past changes, and how these have altered coastal ecosystem structure and function (Lotze and McClenachan, 2014). Historical ecology can also inform management goals, conservation targets, and policy (McClenachan, 2009; McClenachan *et al.*, 2012; Engelhard *et al.*, 2015; Thurstan *et al.*, 2015).

In this thesis, I have examined long-term changes in the abundance and composition of fish in coastal ecosystems in Atlantic Canada. In Chapter 2, I used a set of beach-seine surveys completed along the east coast of Newfoundland, Canada, to quantify fish community change between two time periods, before and after the collapse of the Northwest Atlantic cod stocks. The results showed significant changes in the composition of coastal fish communities. These changes were likely due to reduced abundance of Atlantic cod juveniles and increases in other fish species. Moreover, fewer adult cod predators in inshore regions consequently lowered predation pressure, thus influencing the fish community.

In Chapter 3, I used three case studies in vegetated coastal ecosystems across Atlantic Canada to quantify long-term changes in juvenile abundance and density of commercially important fish species. By repeating or re-analyzing available studies on juvenile fish, I was able to quantify the magnitude of historical change in juvenile abundance. Such a quantitative

assessment was critical to compare changes within coastal fish habitat to corresponding adult

stock declines further offshore. I discussed these results in light of a lack of specific

management of nursery habitat and fish habitat in general in Canada. The results of this thesis

inform both our understanding of the impacts of fish population collapse on coastal

ecosystems, as well as how we could improve our management of coastal fish habitat.

4.1. Future Research Directions

Extending from this thesis, future research should focus on the relationship between

coastal ecosystems and commercial fisheries. Important questions about this relationship are:

1) What proportion of an adult fish stock directly uses coastal ecosystems as juvenile
   or nursery habitats?

2) What is the contribution of coastal ecosystems to adult fish stocks?

3) Which nursery habitats are most important?

Quantifying the purported importance of coastal ecosystems for fisheries is a critical

next step. This has been done with some success in other regions, such as the Gulf of

California and the Baltic Sea (Aburto-Oropeza *et al.*, 2008; Sundblad *et al.*, 2014; Jokinen *et

al.*, 2015). There are a variety of reasons why habitat-fisheries relationships are enigmatic in

certain fisheries, perhaps due to different fish life history characteristics. Some fish species

have obligate relationships with certain habitats. For example, juvenile yellow snapper

(*Lutjanus argentiventris*) have a near-obligate relationship with mangrove habitats in the Gulf

of California (Aburto-Oropeza *et al.*, 2009). Similarly, mangroves are essential nursery habitat

for goliath grouper (Koenig *et al.*, 2007). Quantifying the contribution of these habitats to

fisheries was enabled by the specificity that these species have for mangroves. For other

species, such as Atlantic cod, there is no obligate relationship with a specific habitat. Some Atlantic cod settle from the water column in coastal eelgrass meadows (e.g. Gotceitas *et al.*, 1997), while others remain in deeper waters and settle in cobble habitats (e.g. Lough, 2010). Structural complexity is common to both of these habitats and they are therefore both important juvenile habitats.

The relationship some fishes have with a mixture of habitats makes it difficult to discern the impact specific habitats have on a fishery. However, natural tags can disentangle contributions of fish from a mixture of nursery habitats (Dahlgren *et al.*, 2006). Otoliths are an example of a useful natural tag, as their chemical composition reflects the water masses that a fish inhabits. Otolith chemical composition can therefore be used to determine if an individual was in a certain habitat. Despite this idea being over 20 years old (e.g. Gillanders and Kingsford, 1996), the application for identifying important nursery habitats and informing management is lacking. There are also a multitude of technical and analytical challenges associated with using otolith microchemistry, primarily due to the high temporal variability (Mercier *et al.*, 2011; Tournois *et al.*, 2013). However recent work in Western Patagonia has used carbon and oxygen isotope ratios within otoliths to distinguish between coastal and continental shelf Patagonian grenadier *Macruronus magellanicus* (Niklitschek *et al.*, 2014). Other recent research has also used otolith and fin microchemistry to determine nursery habitat use, homing in on contributions of specific nursery habitats to an adult stock (Vasconcelos *et al.*, 2010; Dierking *et al.*, 2012; Bailey *et al.*, 2015). The use of natural tags for identifying nursery habitat specific contributions is an important tool which has yet to realize its potential to contribute to fisheries management, particularly in Canada.

If the contribution of a specific nursery habitat to an adult stock is high, then protecting or managing that nursery habitat is important. But which nursery areas are most important for the population? Tools for determining this are essential for directed management action. One component of valuing a nursery habitat is larval supply (Beck *et al.*, 2001). For some species in Atlantic Canada, ocean circulation models could be used to identify potentially high value nurseries. Specifically, ocean circulation models coupled with known fish spawning areas could be used to predict and designate coastal areas with the highest likelihood of being important fish nursery habitats. In Canada, this could be used to identify coastal areas which should be safeguarded. Specifically implementing management actions, for example an EBSA designation enhanced with legal authority, would be appropriate once high-larval supply areas are identified.

Quantifying the contribution of coastal ecosystems to commercial fisheries is challenging for a variety of reasons. However, this quantification is critical in order to evaluate the importance of coastal habitats for fisheries management. It is also important to recognize that viewing nursery habitats solely by their contribution to adult fish stocks is over-simplistic (Sheaves *et al.*, 2014), although it is a good starting point. Assessing the value of coastal ecosystems and fish habitat for fisheries will only progress with increased research on the basic mechanisms of fish life history and fisheries ecology.

Bibliography

Aburto-Oropeza, O., Dominguez-Guerrero, I., Cota-Nieto, J., and Plomozo-Lugo, T. 2009. Recruitment and ontogenetic habitat shifts of the yellow snapper (*Lutjanus argentiventris*) in the Gulf of California. Marine Biology, 156: 2461–2472.

Aburto-Oropeza, O., Ezcurra, E., Danemann, G., Valdez, V., Murray, J., and Sala, E. 2008. Mangroves in the Gulf of California increase fishery yields. Proceedings of the National Academy of Sciences of the United States of America, 105: 10456–9.

Aburto-Oropeza, O., Sala, E., Paredes, G., Abraham, M., and Ballesteros, E. 2007. Predictability of reef fish recruitment in a highly variable nursery habitat. Ecology, 88: 2220–2228.

Anderson, M. J. 2001a. Permutation tests for univariate or multivariate analysis of variance and regression. Canadian Journal of Fisheries and Aquatic Sciences, 58: 626–639.

Anderson, M. J. 2001b. A new method for non-parametric multivariate analysis of variance. Austral Ecology, 26: 32–46.

Baden, S., Emanuelsson, A., Pihl, L., Svensson, C., and Åberg, P. 2012. Shift in seagrass food web structure over decades is linked to overfishing. Marine Ecology Progress Series, 451: 61–73.

Bailey, D. S., Fairchild, E. A., and Kalnejais, L. H. 2015. Microchemical Signatures in Juvenile Winter Flounder Otoliths Provide Identification of Natal Nurseries. Transactions of the American Fisheries Society, 144: 173–183.

Bailey, M., Favaro, B., Otto, S. P., Charles, A., Devillers, R., Metaxas, A., Tyedmers, P., *et al.* 2016. Canada at a crossroad: The imperative for realigning ocean policy with ocean science. Marine Policy: 1–8. Elsevier. http://dx.doi.org/10.1016/j.marpol.2015.10.002.

Beck, M. W., Heck Jr, K. L., Able, K. W., Daniel, L., Eggleston, D. B., Gillanders, B. M., Halpern, B., *et al.* 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. BioScience, 51: 633–641.

Beger, M., Grantham, H. S., Pressey, R. L., Wilson, K. A., Peterson, E. L., Dorfman, D., Mumby, P. J., *et al.* 2010. Conservation planning for connectivity across marine, freshwater, and terrestrial realms. Biological Conservation, 143: 565–575.

Bertelli, C. M., and Unsworth, R. K. F. 2014. Protecting the hand that feeds us: Seagrass (*Zostera marina*) serves as commercial juvenile fish habitat. Marine Pollution Bulletin, 83: 425–429.

Bertocci, I., Araujo, R., Oliveira, P., and Sousa-Pinto, I. 2015. Potential effects of kelp species on local fisheries. Journal of Applied Ecology, 52: 1216–1226.

Blandon, A., and zu Ermgassen, P. S. E. 2014. Quantitative estimate of commercial fish enhancement by seagrass habitat in southern Australia. Estuarine, Coastal and Shelf Science, 141: 1–8. Elsevier Ltd. http://linkinghub.elsevier.com/retrieve/pii/S0272771414000213.

Bogstad, B., Lilly, G. R., Mehl, S., Pálsson, Ó., and Stefánsson, G. 1994. Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland, and eastern Newfoundland). ICES Marine Science Symposia, 198:

576–599.

Bourque, B. J., Johnson, B. J., and Steneck, R. S. 2008. Possible prehistoric fishing effects on coastal marine food webs in the Gulf of Maine. *In* Human Impacts on Ancient Marine Ecosystems, pp. 165–185. Ed. by E. J and T. Rick. University of California Press, Berkeley, CA.

Bray, J. R., and Curtis, J. T. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs, 27: 325–349.

Britten, G. L., Dowd, M., Minto, C., Ferretti, F., Boero, F., and Lotze, H. K. 2014. Predator decline leads to decreased stability in a coastal fish community. Ecology letters, 17: 1518–1525.

Caddy, J. F. 2014. Why do assessments of demersal stocks largely ignore habitat? ICES Journal of Marine Science, 71: 2114–2126.

Clarke, K. D., and Bradford, M. J. 2014. A review of equivalency in offsetting policies. DFO Can. Sci. Advis. Sec. Sci. Resp. 2014/109. v + 18p.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology, 18: 117–143.

Clay, D., Stobo, W. T., Beck, B., and Hurley, P. C. F. 1989. Growth of juvenile pollock (*Pollachius virens* L.) along the Atlantic coast of Canada with inferences of inshore-offshore movements. Journal of Northwest Atlantic Fishery Science, 9: 37–43. http://journal.nafo.int/J09/clay.pdf.

Coll, M., Schmidt, A., Romanuk, T., and Lotze, H. K. 2011. Food-web structure of seagrass communities across different spatial scales and human impacts. PloS one, 6: e22591.

Collie, J. S., Wood, A. D., and Jeffries, H. P. 2008. Long-term shifts in the species composition of a coastal fish community. Canadian Journal of Fisheries and Aquatic Sciences, 65: 1352–1365.

Collins, M. R., Rogers, S. G., Smith, T. I. J., and Moser, M. L. 2000. Primary factors affecting sturgeon populations in the Southeastern United States: Fishing mortality and degradation of essential habitats. Bulletin of Marine Science, 66: 917–928.

Cull, D. J. 1997. Interannual and decadal variation in abundance of coastal marine fishes of eastern Newfoundland. Honours Thesis. Memorial University of Newfoundland.

Daborn, G. R., and Gregory, R. S. 1983. Occurrence, distribution, and feeding habits of juvenile lumpfish, *Cyclopterus lumpus* L. in the Bay of Fundy. Canadian Journal of Zoology, 61: 797–801.

Dahlgren, C. P., Kellison, G. T., Adams, A. J., Gillanders, B. M., Kendall, M. S., Layman, C. A., Ley, J. A., *et al.* 2006. Marine nurseries and effective juvenile habitats: Concepts and applications. Marine Ecology Progress Series, 312: 291–295.

Dalley, E. L., and Anderson, J. T. 1997. Age-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in inshore/offshore northeast Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences, 54: 168–176.

Dalpadado, P., and Bogstad, B. 2004. Diet of juvenile cod (age 0-2) in the Barents Sea in relation to food availability and cod growth. Polar Biology, 27: 140–154.

Daskalov, G. M., Grishin, A. N., Rodionov, S., and Mihneva, V. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. Proceedings of the National Academy of Sciences of the United States of America, 104: 10518–10523.

de Kerckhove, D. T., Minns, C. K., and Shuter, B. J. 2013. The length of environmental review in Canada under the Fisheries Act. Canadian Journal of Fisheries and Aquatic Sciences, 70: 517–521. http://www.nrcresearchpress.com/doi/abs/10.1139/cjfas-2012-0411.

DFO. 1986. Policy for the Management of Fish Habitat, 1.

DFO. 2004. Identification of Ecologically and Biologically Significant Areas. DFO Can. Sci. Advis. Sec. Ecosystem Status Rep., 006.

DFO. 2009. Does eelgrass (Zostera marina) meet the criteria as an ecologically significant species? Canadian Science Advisory Secretariat: 1–11.

DFO. 2013. Assessment of information on Irish Moss, Rockweed and Kelp harvests in Nova Scotia. DFO Canadian Science Advisory Secretariat: 17.

DFO. 2015a. Western component (4XOPQRS5) pollock harvest control rule update report. DFO Can. Sci. Advis. Sec. Sci. Resp. 2015/003.

DFO. 2015b. 2014 4X5Yb Atlantic cod stock status update. DFO Can. Sci. Advis. Sec. Sci. Resp. 2015/010.: 1–9.

DFO. 2015c. Science guidance for fisheries protection policy: Advice on equivalent adult calculation. DFO Can. Sci. Advis. Sec. Sci. Resp. 2015/011.

Dierking, J., Morat, F., Letourneur, Y., and Harmelin-Vivien, M. 2012. Fingerprints of lagoonal life: Migration of the marine flatfish *Solea solea* assessed by stable isotopes and otolith microchemistry. Estuarine, Coastal and Shelf Science, 104-105: 23–32. Elsevier Ltd. http://dx.doi.org/10.1016/j.ecss.2011.03.018.

Dwyer, K. S., Buren, A., and Koen-Alonso, M. 2010. Greenland halibut diet in the Northwest Atlantic from 1978 to 2003 as an indicator of ecosystem change. Journal of Sea Research, 64: 436–445.

Elliott, M., Burdon, D., Hemingway, K. L., and Apitz, S. E. 2007. Estuarine, coastal and marine ecosystem restoration: Confusing management and science - A revision of concepts. Estuarine, Coastal and Shelf Science, 74: 349–366.

Engelhard, G. H., Thurstan, R. H., MacKenzie, B. R., Alleway, H. K., Bannister, R. C. A., Cardinale, M., Clarke, M. W., *et al.* 2015. ICES meets marine historical ecology: placing the history of fish and fisheries in current policy context. ICES Journal of Marine Science: Journal du Conseil: fsv219. http://icesjms.oxfordjournals.org/lookup/doi/10.1093/icesjms/fsv219.

Eriksson, B. K., Sieben, K., Eklf, J., Ljunggren, L., Olsson, J., Casini, M., and Bergstrom, U. 2011. Effects of altered offshore food webs on coastal ecosystems emphasize the need for cross-ecosystem management. Ambio, 40: 786–797.

FAO. 2014. The State of World Fisheries and Aquaculture.

Favaro, B., Reynolds, J. D., and Côté, I. M. 2012. Canada's Weakening Aquatic Protection.

Science, 337: 154.

Ferretti, F., Osio, G. C., Jenkins, C. J., Rosenberg, A. A., and Lotze, H. K. 2013. Long-term change in a meso-predator community in response to prolonged and heterogeneous human impact. Scientific Reports, 3: 1057.

Fisheries Leadership and Sustainability Forum for the Mid-Atlantic Fishery Management Council. 2015. Regional Use of the Habitat Area of Particular Concern (HAPC) Designation.

França, S., Costa, M. J., and Cabral, H. N. 2009. Assessing habitat specific fish assemblages in estuaries along the Portuguese coast. Estuarine, Coastal and Shelf Science, 83: 1–12.

França, S., Costa, M. J., and Cabral, H. N. 2011. Inter- and intra-estuarine fish assemblage variability patterns along the Portuguese coast. Estuarine, Coastal and Shelf Science, 91: 262–271.

Frank, K. T., Petrie, B., Choi, J. S., and Leggett, W. C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science, 308: 1621–1623.

Frank, K. T., Petrie, B., Fisher, J. A. D., and Leggett, W. C. 2011. Transient dynamics of an altered large marine ecosystem. Nature, 477: 86–89.

Froese, R., and Pauly, D. 2015. FishBase. www.FishBase.org.

Fromentin, J.-M., Myers, R., Bjornstad, O. N., Stenseth, N., Gjosaeter, J., and Christie, H. 2001. Effects of density-dependent and stochastic processes on the regulation of cod populations. Ecology, 82: 567–579.

Gantner, N. 2014. Does Canada's new Fisheries Act leave some Arctic fish or habitats behind? Arctic, 67: 3–5.

Gillanders, B. M., and Kingsford, M. J. 1996. Elements in otoliths may elucidate the contribution of estuarine recruitment to sustaining coastal reef populations of a temperate reef fish. Marine Ecology Progress Series, 141: 13–20.

Gotceitas, V., Fraser, S., and Brown, J. A. 1997. Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 54: 1306–1319.

Grabowski, T. B., Thorsteinsson, V., McAdam, B. J., and Marteinsdóttir, G. 2011. Evidence of segregated spawning in a single marine fish stock: Sympatric divergence of ecotypes in Icelandic cod? PLoS ONE, 6.

Heck, J. K. L., Hays, G., and Orth, R. J. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Marine Ecology Progress Series, 253: 123–136.

Hop, H., Gjosaeter, J., and Danielssen, D. S. 1992. Seasonal feeding ecology of cod (*Gadus morhua* L.) on the Norwegian Skagerrak coast. ICES Journal of Marine Science, 49: 453–461.

Hutchings, J. A., Côté, I. M., Dodson, J. J., Fleming, I. A., Jennings, S., Mantua, N. J., Peterman, R. M., *et al.* 2012. Is Canada fulfilling its obligations to sustain marine biodiversity? A summary review, conclusions, and recommendations. Environmental Reviews, 20: 353–361.

Hutchings, J. A., and Myers, R. A. 1994. What can be learned from the collapse of a

renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Canadian Journal of Fisheries and Aquatic Sciences, 51: 2126–2146.

Hutchings, J. A., and Myers, R. A. 1995. The biological collapse of Atlantic cod off Newfoundland and Labrador: an exploration of historical changes in exploitation, harvesting technology, and management. *In* Arnason and L.F. Felt [eds], The North Atlantic Fishery: Strengths, Weaknesses, and Challenges, pp. 37–93. Institute of Island Studies, University of Prince Edward Island, Charlottetown, PEI.

Hutchings, J. A., and Post, J. R. 2013. Gutting Canada's Fisheries Act: No Fishery, No Fish Habitat Protection. Fisheries, 38: 497–501.

Hutchings, J. A., and Rangeley, R. W. 2011. Correlates of recovery for Canadian Atlantic cod. Canadian Journal of Zoology, 89: 386–400.

Imrie, D., and Daborn, G. 1981. Food of some immature fish of Minas Basin, Bay of Fundy. Proceedings of the Nova Scotia Institute of Science, 31: 149–153.

Ings, D., Schneider, D., and Methven, D. 1997. Detection of a recruitment signal in juvenile Atlantic cod (Gadus morhua) in coastal nursery areas. Canadian Journal of Fisheries and Aquatic Sciences, 54: 25–29.

Ings, D. W., Gregory, R. S., and Schneider, D. C. 2008. Episodic downwelling predicts recruitment of Atlantic cod, Greenland cod and white hake to Newfoundland coastal waters. Journal of Marine Research, 66: 529–561.

Jackson, J. B., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., *et al.* 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science, 293: 629–637.

Jokinen, H., Wennhage, H., Ollus, V., Aro, E., and Norkko, A. 2015. Juvenile flatfish in the northern Baltic Sea — long-term decline and potential links to habitat characteristics. Journal of Sea Research, in press: 67–75. Elsevier B.V.

Juanes, F. 2007. Role of habitat in mediating mortality during the post-settlement transition phase of temperate marine fishes. Journal of Fish Biology, 70: 661–677.

Knickle, D. C., and Rose, G. A. 2014. Dietary niche partitioning in sympatric gadid species in coastal Newfoundland: Evidence from stomachs and C-N isotopes. Environmental Biology of Fishes, 97: 343–355.

Koenig, C. C., Coleman, F. C., Eklund, A. M., Schull, J., and Ueland, J. 2007. Mangroves as essential nursery habitat for goliath grouper (*Epinephelus itajara*). Bulletin of Marine Science, 80: 567–586.

Koenig, C., Coleman, F., and Kingon, K. 2011. Pattern of recovery of the goliath grouper *Epinephelus itajara* population in the southeastern US. Bulletin of Marine Science, 87: 891–911.

Langton, R. W., Steneck, R. S., Gotceitas, V., Juanes, F., and Lawton, P. 1996. The interface between fisheries research and habitat management. North American Journal of Fisheries Management, 16: 1–7.

Laurel, B. J., Gregory, R. S., Brown, J. A., Hancock, J. K., and Schneider, D. C. 2004. Behavioural consequences of density-dependent habitat use in juvenile cod *Gadus*

morhua and *G. ogac*: the role of movement and aggregation. Marine Ecology Progress Series, 272: 257–270.

Lawrence, S., Ouellet, P., Olga, A., Bui, V., Lavoie, D., Chassé, J., Lambert, N., *et al.* 2013. Seasonal distribution, abundance, and growth of larval capelin (*Mallotus villosus*) and the role of the Lower Estuary (Gulf of St. Lawrence, Canada) as a nursery area. Canadian Journal of Fisheries and Aquatic Sciences, 70: 1508–1530.

Layman, C. A., Allgeier, J. E., Rosemond, A. D., Dahlgren, C. P., and Yeager, L. A. 2011. Marine fisheries declines viewed upside down: Human impacts on consumer-driven nutrient recycling. Ecological Applications, 21: 343–349.

Lazzari, M. A. 2013. Use of submerged aquatic vegetation by young-of-the-year gadoid fishes in Maine estuaries. Journal of Applied Ichthyology, 29: 404–409.

Le Bris, A., Frechet, A., Galbraith, P., and Wroblewski, J. S. 2013. Evidence for alternative migratory behaviours in the northern Gulf of St. Lawrence population of Atlantic cod (*Gadus morhua* L.). ICES Journal of Marine Science, 70: 793–804.

Levrel, H., Pioch, S., and Spieler, R. 2012. Compensatory mitigation in marine ecosystems: Which indicators for assessing the 'no net loss' goal of ecosystem services and ecological functions? Marine Policy, 36: 1202–1210. Elsevier.

Lilley, R. J., and Unsworth, R. K. F. 2014. Atlantic Cod (*Gadus morhua*) benefits from the availability of seagrass (Zostera marina) nursery habitat. Global Ecology and Conservation, 2: 367–377. Elsevier B.V.

Lomond, T., Schneider, D., and Methven, D. 1998. Transition from pelagic to benthic prey for age group 0-1 Atlantic cod, *Gadus morhua*. Fishery Bulletin, 96: 908–911.

Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., Kidwell, S. M., *et al.* 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science, 312: 1806–1809.

Lotze, H. K., and McClenachan, L. 2014. Marine historical ecology: informing the future by learning from the past. *In* Marine Community Ecology and Conservation, pp. 165–200. Ed. by M. Bertness, B. Silliman, J. Bruno, and J. Stachowicz. Sinauer.

Lotze, H., and Milewski, I. 2004. Two centuries of multiple human impacts and successive changes in a North Atlantic food web. Ecological Applications, 14: 1428–1447.

Lough, R. G. 2010. Juvenile cod (*Gadus morhua*) mortality and the importance of bottom sediment type to recruitment on Georges Bank. Fisheries Oceanography, 19: 159–181.

Magnuson-Stevens Fishery Conservation and Management Act, Subpart J — Essential Fish Habitat. 2003. . http://www.habitat.noaa.gov/pdf/efhregulatoryguidelines.pdf.

McCain, J. S. P., Cull, D. J., Schneider, D. C., and Lotze, H. K. 2015. Long-term shift in coastal fish communities before and after the collapse of Atlantic cod (*Gadus morhua*). ICES Journal of Marine Science.

McClenachan, L. 2009. Historical declines of goliath grouper populations in South Florida, USA. Endangered Species Research, 7: 175–181.

McClenachan, L., Ferretti, F., and Baum, J. K. 2012. From archives to conservation: why historical data are needed to set baselines for marine animals and ecosystems.

Conservation Letters, 5: 349–359. http://doi.wiley.com/10.1111/j.1755-263X.2012.00253.x.

McDevitt-Irwin, J. M., Fuller, S. D., Grant, C., and Baum, J. K. 2015. Missing the safety net: evidence for inconsistent and insufficient management of at-risk marine fishes in Canada, 1608: 1596–1608.

Mercier, L., Darnaude, A. M., Bruguier, O., Vasconcelos, R. P., Cabral, H. N., Costa, M. J., Lara, M., *et al.* 2011. Selecting statistical models and variable combinations for optimal classification using otolith microchemistry. Ecological Applications, 21: 1352–1364.

Methven, D. A., Schneider, D. C., Ings, D. W., Budgell, W., Bouzane, G., Butler, E., Caravan, W., *et al.* 1997. Fleming Survey of demersal cod in the coastal zone of eastern Newfoundland, 1959-1996: protocols and results. Report to Department of Fisheries and Oceans, St. John's, Newfoundland, Canada. 22 pp.

Moksnes, P., Gullstro, M., Tryman, K., and Baden, S. 2008. Trophic cascades in a temperate seagrass community. Oikos, 117: 763–777.

Murawski, S. A. 2010. Rebuilding depleted fish stocks: the good, the bad, and, mostly, the ugly. ICES Journal of Marine Science, 67: 1830–1840.

Myers, R. A., Baum, J. K., Shepherd, T., Powers, S., and Peterson, C. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science, 315: 1846–1850.

Nagelkerken, I., Grol, M. G. G., and Mumby, P. J. 2012. Effects of marine reserves versus nursery habitat availability on structure of reef fish communities. PloS one, 7: e36906.

Naiman, R. J., and Latterell, J. J. 2005. Principles for linking fish habitat to fisheries management and conservation. Journal of Fish Biology, 67: 166–185.

Nakagawa, S., and Cuthill, I. C. 2007. Effect size, confidence interval and statistical significance: A practical guide for biologists. Biological Reviews, 82: 591–605.

Nelder, A. J. A., and Wedderburn, R. W. M. 1972. Generalized linear models. Journal of the Royal Statistical Society, Series A (General), 135: 370–384.

Niklitschek, E. J., Secor, D. H., Toledo, P., Valenzuela, X., Cubillos, L. A., and Zuleta, A. 2014. Nursery systems for Patagonian grenadier off Western Patagonia: large inner sea or narrow continental shelf? ICES Journal of Marine Science, 71: 374–390.

Nordeide, J. T., Johansen, S. D., Jørgensen, T. E., Karlsen, B. O., and Moum, T. 2011. Population connectivity among migratory and stationary cod *Gadus morhua* in the Northeast Atlantic-A review of 80 years of study. Marine Ecology Progress Series, 435: 269–283.

O'Hara, R. B., and Kotze, D. J. 2010. Do not log-transform count data. Methods in Ecology and Evolution, 1: 118–122.

Orth, R. J., Batiuk, R. A., Bergstrom, P. W., and Moore, K. A. 2002. A perspective on two decades of policies and regulations influencing the protection and restoration of subnmrged aquatic vegetation in Chesapeake Bay, USA. Bulletin of Marine Science, 71: 1391–1403.

Ottersen, G., Bogstad, B., Yaragina, N., Stige, L. C., Vikebo, F., and Dalpadado, P. 2014. A review of early life history dynamics of Barents Sea cod (*Gadus morhua*). ICES Journal

of Marine Science, 71: 2064–2087.

Pikitch, E., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., *et al.* 2004. Ecosystem-based fishery management. Science, 305: 346–347.

Polis, G. A., Anderson, W. B., and Holt, R. D. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics, 28: 289–316.

Quigley, J., and Harper, D. 2006. Effectiveness of fish habitat compensation in Canada in achieving no net loss. Environmental Management, 37: 351–366.

R Core Team. 2014. . R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org/.

Rangeley, R. W., and Kramer, D. L. 1995a. Tidal effects on habitat selection and aggregation by juvenile pollock *Pollachius virens* in the rocky intertidal zone. Marine Ecology Progress Series, 126: 19–29.

Rangeley, R. W., and Kramer, D. L. 1995b. Use of rocky intertidal habitats by juvenile pollock *Pollachius virens*. Marine Ecology Progress Series, 126: 9–17.

Renkawitz, M. D., Gregory, R. S., and Schneider, D. C. 2011. Habitat dependant growth of three species of bottom settling fish in a coastal fjord. Journal of Experimental Marine Biology and Ecology, 409: 79–88.

Rice, J., Bradford, M. J., Clarke, K. D., Koops, M. A., Randall, R. G., and Wysocki, R. 2015. The Science Framework for Implementing the Fisheries Protection Provisions of Canada's Fisheries Act. Fisheries, 40: 268–275.

Ricketts, P. J., and Hildebrand, L. 2011. Coastal and Ocean Management in Canada: Progress or Paralysis? Coastal Management, 39: 4–19.

Robichaud, D., and Rose, G. 2006. Density-dependent distribution of demersal juvenile Atlantic cod (Gadus morhua) in Placentia Bay, Newfoundland. ICES Journal of Marine Science, 63: 766–774. http://icesjms.oxfordjournals.org/cgi/doi/10.1016/j.icesjms.2005.12.002.

Rose, G. A. 1993. Cod spawning on a migration highway in the north-west Atlantic. Nature, 363: 458–461.

Rose, G. A. 2004. Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years. Canadian Journal of Fisheries and Aquatic Sciences, 61: 1553–1557.

Royall, R. 1997. Statistical Evidence: A Likelihood Paradigm. Chapman & Hall, London.

Schein, A., Courtenay, S. C., Crane, C. S., Teather, K. L., and Heuvel, M. R. 2012. The role of submerged aquatic vegetation in structuring the nearshore fish community within an estuary of the Southern Gulf of St. Lawrence. Estuaries and Coasts, 35: 799–810.

Schmidt, A. L., Coll, M., Romanuk, T., and Lotze, H. K. 2011. Ecosystem structure and services in eelgrass Zostera marina and rockweed Ascophyllum nodosum habitats. Marine Ecology Progress Series, 437: 51–68. http://www.int-res.com/abstracts/meps/v437/p51-68/.

Schneider, D. C., Hennebury, P., Methven, D., Ings, D., and Pinsent, D. 1997a. Fleming

survey of demersal juvenile cod in coastal areas of eastern Newfoundland. NAFO Scientific Council Studies, 29: 13–21.

Schneider, D. C., Methven, D. A., and Dalley, E. L. 1997b. Geographic contraction in juvenile fish: a test with northern cod (*Gadus morhua*) at low abundances. Canadian Journal of Fisheries and Aquatic Sciences, 54: 187–199.

Scott, J. S. 1982. Selection of bottom type by groundfishes of the Scotian Shelf. Canadian Journal of Fisheries and Aquatic Sciences, 39: 943–947.

Seeley, R. H., and Schlesinger, W. H. 2012. Sustainable seaweed cutting? The rockweed (*Ascophyllum nodosum*) industry of Maine and the Maritime Provinces. Annals of the New York Academy of Sciences, 1249: 84–103.

Seitz, R. D., Wennhage, H., Bergstrom, U., Lipcius, R., and Ysebaert, T. 2014. Ecological value of coastal habitats for commercially and ecologically important species. ICES Journal of Marine Science, 71: 648–665.

Selleslagh, J., Amara, R., Laffargue, P., Lesourd, S., Lepage, M., and Girardin, M. 2009. Fish composition and assemblage structure in three Eastern English Channel macrotidal estuaries: A comparison with other French estuaries. Estuarine, Coastal and Shelf Science, 81: 149–159. http://dx.doi.org/10.1016/j.ecss.2008.10.008.

Sheaves, M., Baker, R., and Johnston, R. 2006. Marine nurseries and effective juvenile habitats: an alternative view. Marine Ecology Progress Series, 318: 303–306.

Sheaves, M., Baker, R., Nagelkerken, I., and Connolly, R. M. 2014. True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. Estuaries and Coasts, 38: 401–414.

Shepherd, T. D., and Myers, R. A. 2005. Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. Ecology Letters, 8: 1095–1104.

Sobocinski, K. L., Orth, R. J., Fabrizio, M. C., and Latour, R. J. 2013. Historical comparison of fish community structure in lower Chesapeake Bay seagrass habitats. Estuaries and Coasts, 36: 775–794.

Sólmundsson, J., Jónsdóttir, I., Björnsson, B., Ragnarsson, S., Tómasson, G., and Thorsteinsson, V. 2015. Home ranges and spatial segregation of cod *Gadus morhua* spawning components. Marine Ecology Progress Series, 520: 217–233.

Stanley, R. R. E., DeYoung, B., Snelgrove, P. V. R., and Gregory, R. S. 2013. Factors regulating early life history dispersal of Atlantic cod (Gadus morhua) from coastal Newfoundland. PloS one, 8: e75889.

Steneck, R. S., Vavrinec, J., and Leland, A. V. 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the Western North Atlantic. Ecosystems, 7: 323–332.

Sundblad, G., and Bergström, U. 2014. Shoreline development and degradation of coastal fish reproduction habitats. Ambio, 43: 1020–8. http://www.ncbi.nlm.nih.gov/pubmed/24943864.

Sundblad, G., Bergstrom, U., Sandstrom, A., and Eklov, P. 2014. Nursery habitat availability limits adult stock sizes of predatory coastal fish. ICES Journal of Marine Science, 71: 672–680.

Svedäng, H., and Svenson, A. 2006. Cod *Gadus morhua* L. populations as behavioural units: Inference from time series on juvenile abundance in the eastern Skagerrak. Journal of Fish Biology, 69: 151–164.

Tanner, C., Hunter, S., Reel, J., Parham, T., Naylor, M., Karrh, L., Busch, K., *et al.* 2010. Evaluating a large-scale eelgrass restoration project in the Chesapeake Bay. Restoration Ecology, 18: 538–548.

Thurstan, R. H., McClenachan, L., Crowder, L. B., Drew, J. A., Kittinger, J. N., Levin, P. S., Roberts, C. M., *et al.* 2015. Filling historical data gaps to foster solutions in marine conservation. Ocean & Coastal Management, 115: 31–40.

Tournois, J., Ferraton, F., Velez, L., McKenzie, D. J., Aliaume, C., Mercier, L., and Darnaude, A. M. 2013. Temporal stability of otolith elemental fingerprints discriminates among lagoon nursery habitats. Estuarine, Coastal and Shelf Science, 131: 182–193. Elsevier Ltd. http://dx.doi.org/10.1016/j.ecss.2013.07.006.

Tupper, M., and Boutilier, R. G. 1995. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 52: 1834–1841.

VanderZwaag, D., Hutchings, J., Jennings, S., and Peterman, R. M. 2012. Canada's international and national commitments to sustain marine biodiversity. Environmental Reviews, 20: 312–352. http://www.nrcresearchpress.com/doi/abs/10.1139/a2012-011.

Vasconcelos, R. P., Reis-Santos, P., Maia, A., Fonseca, V., Fran??a, S., Wouters, N., Costa, M. J., *et al.* 2010. Nursery use patterns of commercially important marine fish species in estuarine systems along the Portuguese coast. Estuarine, Coastal and Shelf Science, 86: 613–624.

Venables, W. N., and Dichmont, C. M. 2004. GLMs, GAMs and GLMMs: An overview of theory for applications in fisheries research. Fisheries Research, 70: 319–337.

Venables, W., and Ripley, B. 2002. Modern applied statistics with S. Springer, New York.

Verweij, M. C., Nagelkerken, I., Hans, I., Ruseler, S. M., Mason, R. D., and Mason, P. R. D. 2008. Seagrass nurseries contribute to coral reef fish populations. Limnology and Oceanography, 53: 1540–1547.

Wang, Y., Naumann, U., Wright, S. T., and Warton, D. I. 2012. mvabund - an R package for model-based analysis of multivariate abundance data. Methods in Ecology and Evolution, 3: 471–474.

Warton, D. I. 2011. Regularized sandwich estimators for analysis of high-dimensional data using generalized estimating equations. Biometrics, 67: 116–23.

Warton, D. I., Foster, S. D., De'ath, G., Stoklosa, J., and Dunstan, P. K. 2014. Model-based thinking for community ecology. Plant Ecology: 1:14.

Warton, D. I., Wright, S. T., and Wang, Y. 2012. Distance-based multivariate analyses confound location and dispersion effects. Methods in Ecology and Evolution, 3: 89–101.

Werner, E. E., Gilliam, J. F., Hall, D. J., and Mittelbach, G. G. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology, 64: 1540–1548. http://www.jstor.org/stable/1937508.

Whalen, M. A., Duffy, J. E., and Grace, J. B. 2013. Temporal shifts in top-down vs. bottom-up control of epiphytic algae in a seagrass ecosystem. Ecology, 94: 510–20.

Wilson, R. W., Millero, F. J., Taylor, J. R., Walsh, P. J., Christensen, V., Jennings, S., and Grosell, M. 2009. Contribution of fish to the marine inorganic carbon cycle. Science, 323: 359–362.

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., *et al.* 2009. Rebuilding Global Fisheries. Science, 578.

Yaragina, N. A., Bogstad, B., and Kovalev, Y. A. 2009. Variability in cannibalism in Northeast Arctic cod (*Gadus morhua*) during the period 1947-2006. Marine Biology Research, 5: 75–85.

Ye, Y., Cochrane, K., Bianchi, G., Willmann, R., Majkowski, J., Tandstad, M., and Carocci, F. 2013. Rebuilding global fisheries: The World Summit Goal, costs and benefits. Fish and Fisheries, 14: 174–185.

Appendix A – Supplementary Materials for Chapter 2

       The following tables are full analysis of variance and analysis of deviance tables testing the reduction in deviance for sequentially added variables. The third table includes details from region-specific analyses of the time period effect.

Table 1. Analysis of deviance tables for juvenile Atlantic cod abundance (age 0, 1, and 2). For age 0 juvenile Atlantic cod, a negative binomial GLM was used. For age 1 and age 2, a two stage GLM was used, with the first stage a binomial GLM and the second stage a negative binomial GLM. Binomial and negative binomial GLMs are abbreviated to B and NB within the table. Significant factors are indicated in bold, "/" indicates a nested factor (e.g. year nested in time period) and":" indicates and interaction between factors.

Response	Variable	DF	Deviance	Residual DF	Residual Deviance	P value
Age 0 NB						
	Null			324	620.8295	
	Time Period	1	2.0019	323	618.8277	0.1571
	Region	**5**	**60.0699**	**318**	**558.7578**	**<0.0001**
	Vegetation	1	2.1105	317	556.6473	0.1463
	(Time Period/Year)	**8**	**24.8087**	**309**	**531.8386**	**0.0017**
	Time Period:Region	**5**	**19.6215**	**304**	**512.217**	**0.0015**
	Time Period:Vegetation	1	0.0702	303	512.1468	0.791
	Region:Vegetation	2	0.0056	301	512.1412	0.9972
	(Time Period/Year):Region	**39**	**116.0809**	**262**	**396.0603**	**<0.0001**
	(Time Period/Year):Vegetation	**8**	**22.6072**	**254**	**373.4531**	**0.0039**
	Time Period:Region:Vegetation	**2**	**8.5552**	**252**	**364.8979**	**0.0139**
	(Time Period/Year):Region:Vegetation	13	20.8771	239	344.0208	0.0754
Age 1 B						
	Null			324	401.2072	
	Time Period	**1**	**71.3938**	**323**	**329.8133**	**<0.0001**
	Region	**5**	**15.187**	**318**	**314.6263**	**0.0096**
	Vegetation	**1**	**4.631**	**317**	**309.9954**	**0.0314**
	(Time Period/Year)	**8**	**21.7089**	**309**	**288.2864**	**0.0055**
	Time Period:Region	**5**	**12.7832**	**304**	**275.5032**	**0.0255**
	Time Period:Vegetation	1	1.5556	303	273.9476	0.2123
	Region:Vegetation	2	0.9306	301	273.017	0.628
	(Time Period/Year):Region	39	0	262	5766.9845	1
	(Time Period/Year):Vegetation	8	0	254	5766.9845	1
	Time Period:Region:Vegetation	**2**	**865.0477**	**252**	**4901.937**	**0**
	(Time Period/Year):Region:Vegetation	13	0	239	5478.6353	1
Age 1 NB						
	Null			224	656.4022	
	Time Period	**1**	**65.3163**	**223**	**591.0859**	**<0.0001**
	Region	**5**	**81.4477**	**218**	**509.6383**	**<0.0001**
	Vegetation	1	2.5072	217	507.1311	0.1133
	(Time Period/Year)	**8**	**101.6744**	**209**	**405.4567**	**<0.0001**
	Time Period:Region	5	8.2703	204	397.1864	0.142
	Time Period:Vegetation	1	0.6621	203	396.5243	0.4158

Table 1 (continued)

Response	Variable	DF	Deviance	Residual DF	Residual Deviance	*P* Value
	Region:Vegetation	2	0.5565	201	395.9678	0.7571
	(Time Period/Year):Region	**34**	**129.6249**	**167**	**266.3429**	**<0.0001**
	(Time Period/Year):Vegetation	8	14.727	159	251.6159	0.0647
	Time Period:Region:Vegetation	2	0.3273	157	251.2886	0.849
	(Time Period/Year):Region:Vegetation	7	10.5005	150	240.788	0.1619
Age 2 B						
	Null			324	410.4239	
	Time Period	**1**	**4.2806**	**323**	**406.1433**	**0.0386**
	Region	**5**	**26.3854**	**318**	**379.7579**	**0.0001**
	Vegetation	1	0.0015	317	379.7563	0.9687
	(Time Period/Year)	**8**	**17.1081**	**309**	**362.6482**	**0.029**
	Time Period:Region	5	6.0395	304	356.6088	0.3024
	Time Period:Vegetation	1	0.0004	303	356.6083	0.9832
	Region:Vegetation	**2**	**6.6733**	**301**	**349.935**	**0.0356**
	(Time Period/Year):Region	39	0	262	6559.9449	1
	(Time Period/Year):Vegetation	8	0	254	6920.3815	1
	Time Period:Region:Vegetation	**2**	**6649.551**	**252**	**270.8301**	**0**
	(Time Period/Year):Region:Vegetation	13	0	239	6920.3815	1
Age 2 NB						
	Null			105	217.5667	
	Time Period	**1**	**18.1793**	**104**	**199.3874**	**<0.0001**
	Region	**5**	**19.8893**	**99**	**179.4981**	**0.0013**
	Vegetation	**1**	**4.245**	**98**	**175.2531**	**0.0394**
	(Time Period/Year)	**8**	**19.4472**	**90**	**155.8059**	**0.0126**
	Time Period:Region	**4**	**20.0208**	**86**	**135.7851**	**0.0005**
	Time Period:Vegetation	1	2.0396	85	133.7455	0.1533
	Region:Vegetation	2	0.1795	83	133.5661	0.9142
	(Time Period/Year):Region	**22**	**45.0946**	**61**	**88.4715**	**0.0026**
	(Time Period/Year):Vegetation	7	4.0219	54	84.4496	0.7773
	Time Period:Region:Vegetation	1	0.0678	53	84.3818	0.7945
	(Time Period/Year):Region:Vegetation	4	0.1823	49	84.1994	0.9961

Table 2. Analysis of deviances tables for total fish abundance (negative binomial error), Shannon diversity (normal error), species richness (Poisson error), and species evenness (normal error). The table contains test statistics and associated p values comparing the reduction in deviance for the row to the residuals. Chi-squared tests for models with known dispersion (in this case both species richness and total fish abundance) are used, and F tests for models with estimated dispersion (Shannon's diversity and species evenness). Significant results are indicated in bold.

Response	Variable	DF	Deviance	Residual DF	Residual Deviance	F	*P* value
Total Fish Abundance	Null			324	600.0529		
	Time Period	**1**	**18.2379**	**323**	**581.8150**	—	**<0.0001**
	Region	**5**	**24.7068**	**318**	**557.1082**	—	**0.0002**
	Vegetation	**1**	**14.0459**	**317**	**543.0623**	—	**0.0002**
	(Time Period/Year)	**8**	**41.7413**	**309**	**501.3210**	—	**<0.0001**
	Time Period:Region	5	5.5190	304	495.8020	—	0.3559
	Time Period:Vegetation	1	3.0912	303	492.7109	—	0.0787
	Region:Vegetation	**2**	**6.5037**	**301**	**486.2071**	—	**0.0387**
	(Time Period/Year):Region	**39**	**82.7854**	**262**	**403.4217**	—	**0.0001**
	(Time Period/Year):Vegetation	8	9.6273	254	393.7945	—	0.2922
	Time Period:Region:Vegetation	2	5.6541	252	388.1404	—	0.0592
	(Time Period/Year):Region:Vegetation	13	18.1498	239	369.9906	—	0.1519
Shannon Diversity	Null			324	66.0282		
	Time Period	**1**	**1.5180**	**323**	**64.5102**	**9.970**	**0.0018**
	Region	**5**	**10.9150**	**318**	**53.5952**	**14.338**	**<0.0001**
	Vegetation	1	0.3746	317	53.2205	2.461	0.1181
	(Time Period/Year)	**8**	**4.9897**	**309**	**48.2309**	**4.096**	**0.0001**
	Time Period:Region	5	0.2335	304	47.9973	0.307	0.9086
	Time Period:Vegetation	1	0.0858	303	47.9115	0.563	0.4536
	Region:Vegetation	2	0.6448	301	47.2667	2.118	0.1226
	(Time Period/Year):Region	**39**	**9.2511**	**262**	**38.0155**	**1.558**	**0.0246**
	(Time Period/Year):Vegetation	8	0.4669	254	37.5486	0.383	0.9289
	Time Period:Region:Vegetation	2	0.0873	252	37.4613	0.287	0.7509
	(Time Period/Year):Region:Vegetation	13	1.0723	239	36.3890	0.542	0.8969
Species Richness	Null			324	319.7327		
	Time Period	1	2.0563	323	317.6764	—	0.1516
	Region	**5**	**37.9123**	**318**	**279.7641**	—	**<0.0001**
	Vegetation	**1**	**9.3687**	**317**	**270.3955**	—	**0.0022**
	(Time Period/Year)	**8**	**24.3800**	**309**	**246.0154**	—	**0.0020**

Table 2 (continued)

Response	Variable	DF	Deviance	Residual DF	Residual Deviance	F	*P* value
	Time Period:Region	**5**	**13.0551**	**304**	**232.9603**	**—**	**0.0229**
	Time Period:Vegetation	1	0.3079	303	232.6524	—	0.5790
	Region:Vegetation	2	5.6132	301	227.0391	—	0.0604
	(Time Period/Year):Region	39	31.1749	262	195.8643	—	0.8096
	(Time Period/Year):Vegetation	8	5.5227	254	190.3416	—	0.7005
	Time Period:Region:Vegetation	2	2.3542	252	187.9874	—	0.3082
	(Time Period/Year):Region:Vegetation	13	3.7710	239	184.2163	—	0.9934
Species Evenness	Null			315*	20.0156		
	Time Period	**1**	**0.4732**	**314**	**19.5424**	**8.331**	**0.0043**
	Region	**5**	**1.5855**	**309**	**17.9569**	**5.583**	**0.0001**
	Vegetation	1	0.1408	308	17.8161	2.478	0.1168
	(Time Period/Year)	**8**	**1.0957**	**300**	**16.7205**	**2.411**	**0.0162**
	Time Period:Region	5	0.2018	295	16.5186	0.711	0.6160
	Time Period:Vegetation	1	0.0005	294	16.5181	0.010	0.9217
	Region:Vegetation	2	0.0134	292	16.5047	0.118	0.8892
	(Time Period/Year):Region	39	2.7284	253	13.7763	1.232	0.1768
	(Time Period/Year):Vegetation	8	0.1406	245	13.6358	0.309	0.9620
	Time Period:Region:Vegetation	2	0.0138	243	13.6220	0.121	0.8858
	(Time Period/Year):Region:Vegetation	13	0.5577	230	13.0642	0.755	0.7067

Table 3. Region specific p-values for the "Time Period" model term for every community metric and Atlantic cod counts, as displayed in Figures 1 and 2.

Response Variable	Region	P Value
Species Richness	South Coast	0.1233
	Conception Bay	0.1710
	Trinity Bay	0.7959
	Bonavista Bay	**0.0066**
	New World Island and Gander Bay	0.1675
	Notre Dame Bay	0.2085
Evenness	South Coast	0.5817
	Conception Bay	0.0635
	Trinity Bay	0.0859
	Bonavista Bay	0.8674
	New World Island and Gander Bay	0.9369
	Notre Dame Bay	0.1590
Shannon Diversity	South Coast	0.8857
	Conception Bay	0.4839
	Trinity Bay	0.1346
	Bonavista Bay	0.2154
	New World Island and Gander Bay	0.2217
	Notre Dame Bay	**0.0474**
Total fish abundance	South Coast	0.4615
	Conception Bay	**0.0090**
	Trinity Bay	0.1186
	Bonavista Bay	0.2516
	New World Island and Gander Bay	0.3430
	Notre Dame Bay	0.1727
Cod Age 0	**South Coast**	**0.0438**
	Conception Bay	0.7985
	Trinity Bay	0.1353
	Bonavista Bay	**0.0092**
	New World Island and Gander Bay	0.4768
	Notre Dame Bay	0.3622
Cod Age 1 Presence/Absence	**South Coast**	**<0.0001**
	Conception Bay	**0.0109**
	Trinity Bay	**0.0044**
	Bonavista Bay	0.0505
	New World Island and Gander Bay	**<0.0001**
	Notre Dame Bay	**<0.0001**
Cod Age 1 Counts	South Coast	0.0754

Table 3 (continued)

Response Variable	Region	*P* Value
	Conception Bay	**0.0253**
	Trinity Bay	0.1361
	Bonavista Bay	**<0.0001**
	New World Island and Gander Bay	0.0007
	Notre Dame Bay	**0.0004**
Cod Age 2 Presence/Absence	**South Coast**	**0.0417**
	Conception Bay	0.1646
	Trinity Bay	0.2849
	Bonavista Bay	0.5460
	New World Island and Gander Bay	0.1466
	Notre Dame Bay	0.3906
Cod Age 2 Counts	South Coast	NA
	Conception Bay	**0.0162**
	Trinity Bay	**0.0002**
	Bonavista Bay	0.7530
	New World Island and Gander Bay	0.8456
	Notre Dame Bay	0.7611

*NA = No counts were observed in the 1990s on the South Coast.

Appendix B – Copyright Agreement for Chapter 2

Chapter 2 is a pre-copyedited, author-produced document of an article accepted for publication in ICES Journal of Marine Science following peer review. The version of record "McCain et al. (2015) Long-term shift in coastal fish communities before and after the collapse of Atlantic cod (*Gadus morhua*). doi: 10.1093/icesjms/fsv216." is available online at: http://icesjms.oxfordjournals.org/content/early/2015/12/07/icesjms.fsv216.abstract.

Appendix C – Simulation of Historical Data Sets

Raw data were not available for the second and third case studies in Chapter 3. We therefore began by simulating raw data sets given the extracted means, standard deviations, and sample sizes. This appendix details these simulations and why we chose to compare means using an independent means two-sample t-test instead of using these simulations.

For the second case study, Rangeley and Kramer (1995a) compared juvenile pollock densities using an analysis of variance (ANOVA). Prior to the ANOVA, they log-transformed their data. An assumption of the ANOVA is normally distributed errors, so we assumed that the underlying distribution of their data were log-normal. In order to simulate log-normal data, given the mean and standard deviation of the non-logged distribution, we calculated the simulation input values (μ and σ) based on the following:

$$\text{Mean} = exp\left(\mu + \frac{\sigma^2}{2}\right)$$

$$\text{Variance} = (exp(\sigma^2) - 1)exp(2\mu + \sigma^2)$$

$$\mu = \ln\left(\frac{m}{\sqrt{1 + \frac{v}{m^2}}}\right)$$

$$\sigma = \sqrt{\ln(1 + \frac{v}{m^2})}$$

I developed a simple acceptance-rejection algorithm to filter simulations. Simulated historical datasets with mean and standard deviation equal to the population mean and standard deviation were chosen. With over a billion simulations and rounding of mean and standard deviations to 3 decimal places, we were unable to recreate a sample mean and standard deviation equal to the population mean and standard deviation. We concluded that the log-transformation of the data were likely used to decrease influence of very large

observations, but the underlying distribution of the data was not in fact log-normal. We therefore chose to simply compare mean abundances between time periods.

For the third case study, Tupper and Boutilier (1995), we had a similar challenge. Simulating the data points relied on the assumption that the underlying distribution were Poisson distributed. We could not verify this assumption. We chose to only compare abundance maxima for this case study, as the date of maximum abundance differed between time periods.

We decided to use a simple method of analysis for these case studies, however throughout the chapter we emphasized examining the raw data itself. This was done specifically to highlight effect sizes as opposed to statistical significance (Nakagawa and Cuthill, 2007).