



Contribution to the Symposium: 'Oceans Past V'

Original Article

Long-term shift in coastal fish communities before and after the collapse of Atlantic cod (*Gadus morhua*)

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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 analysed) 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.

Keywords: community change, connectivity, cross-ecosystem management, fisheries collapse, juvenile cod, predator release, vegetated habitat.

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 ~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.

Methods

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 to 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 ~1500 km 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 1 year depending on weather and ocean conditions.

A 25 m 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 55 m 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 16 m away from the first. The seine sweeps ~880 m² (16 m across at point of landing beginning 55 m off shore). The seine fishes upwards from bottom held weights to floats that stretch the net to ~2 m 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–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 h apart) with the third occurring next 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 (<97 mm), 1 (97–192 mm), or 2 (>192 mm). 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 periods. Photographs of the point of deployment at each location in the 1960s allowed the same sites to be revisited, using shoreline configuration (“fishers’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 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

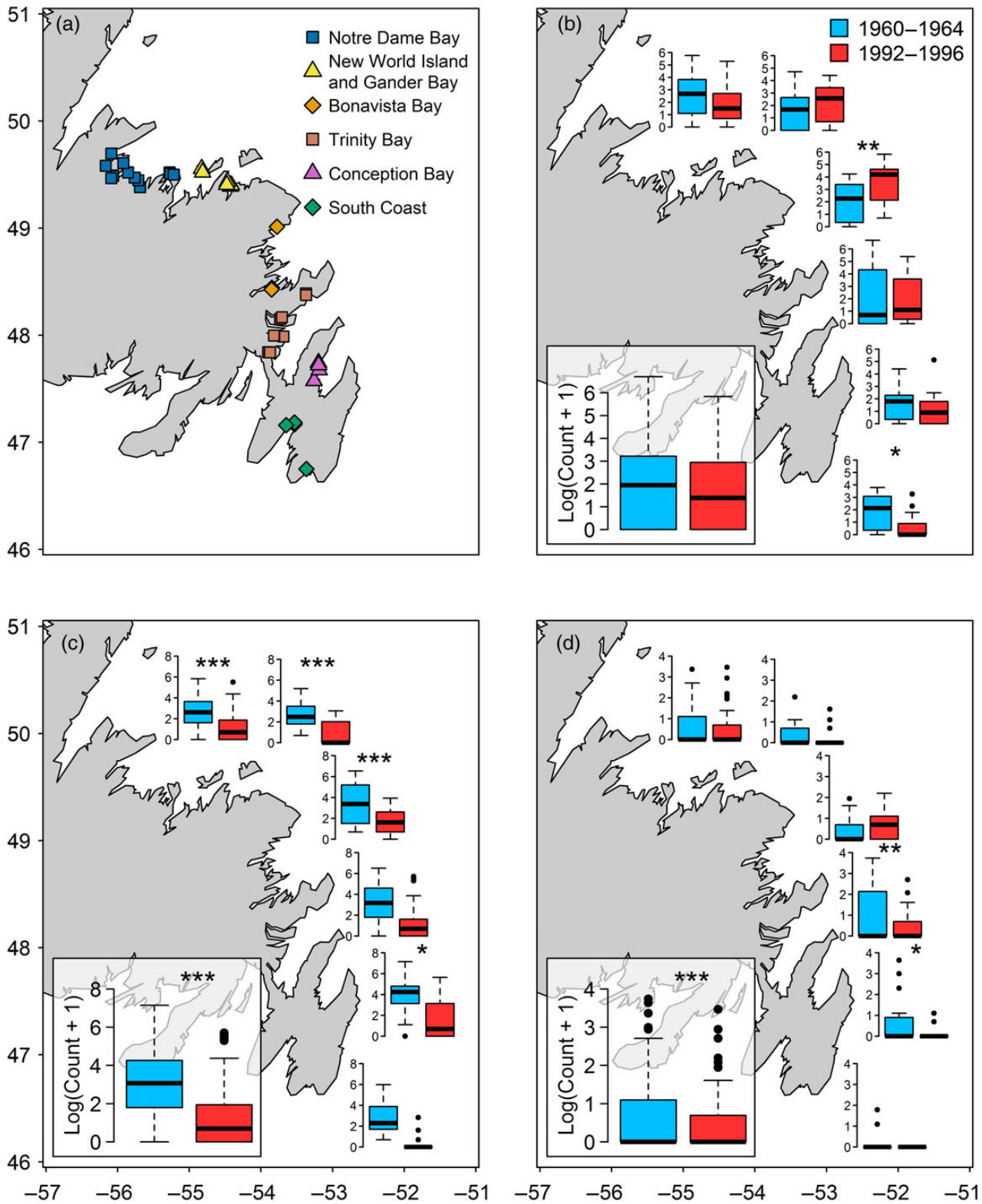


Figure 1. Map of all sites sampled (a) with points coloured by region and ordered from the northwest regions to the southeast regions in the legend. Maps (b–d) show raw data boxplots of natural log(count + 1) of ages 0, 1, and 2 Atlantic cod (*Gadus morhua*), respectively, in the 1960s and 1990s in each region. Inset boxplots display the overall differences between 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 period effect in every region alone are given in Supplementary materials. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

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/).

Statistical approach

We used generalized linear models (Nelder and Wedderburn, 1972) to analyse differences in (i) juvenile cod abundance and (ii) total fish abundance, species richness, diversity, and evenness. We were primarily interested in differences between 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: period, year nested within period, region, and vegetation presence/absence, with every possible interaction. Year was included as a nested fixed factor within period, as opposed to a random factor, as year was explicitly not a random sample within these periods and the set of years encompasses the entire 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 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 1-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 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 Supplementary material.

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 over-dispersed count data. For zero-inflated counts of ages 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.

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 analysed with a negative binomial GLM and a log-link function. Species richness was analysed 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 analyse 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.

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 before 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,b) 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

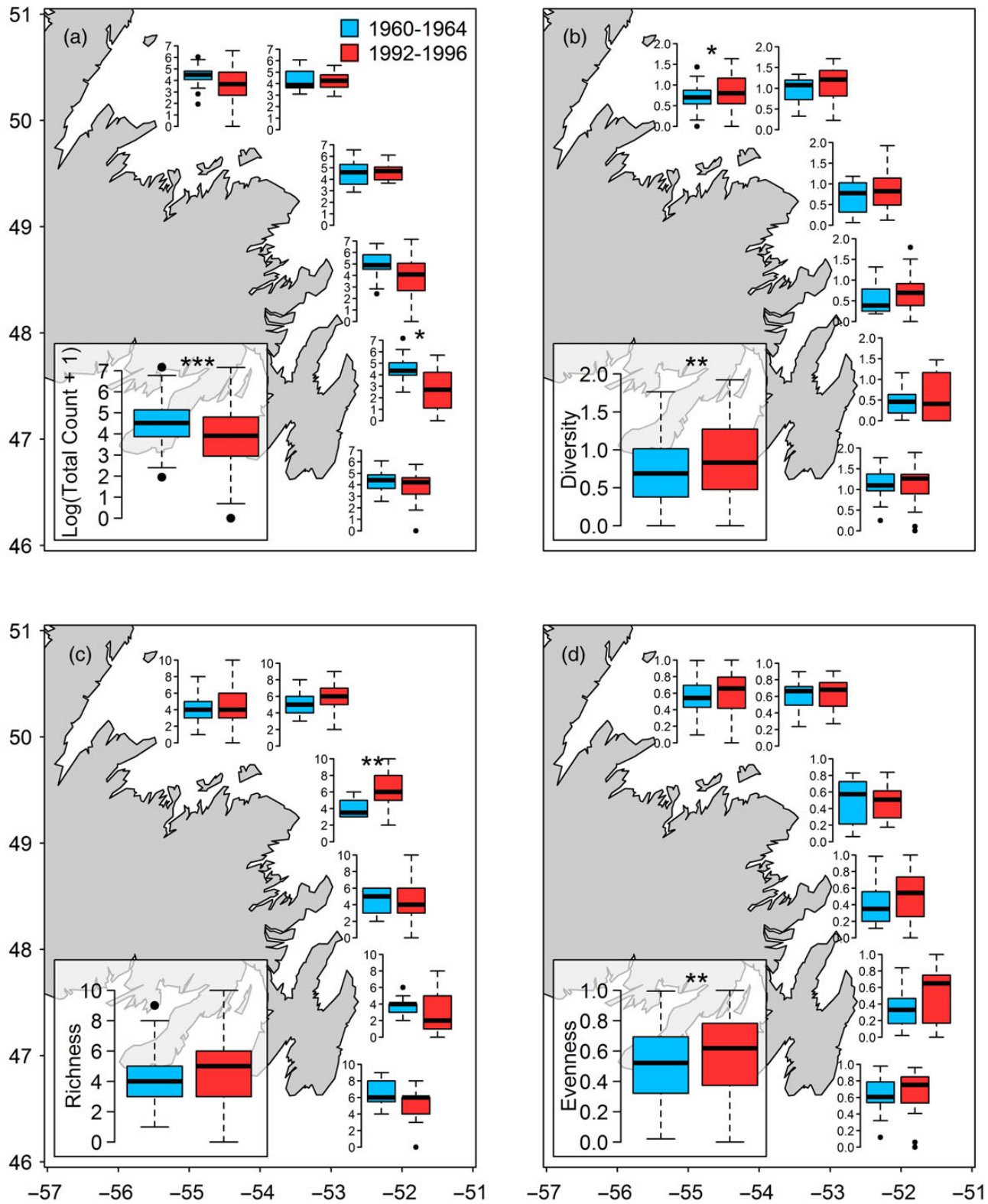


Figure 2. Boxplots of raw data for natural log(total fish count + 1) (a), Shannon diversity (b), species richness (c), and species evenness (d) in the 1960s and 1990s in each region. Inset boxplots display the overall difference between periods. Significant differences are represented by asterisks with p values from $0.05 - 0.01 = *$, $0.1 - 0.001 = **$, and $< 0.001 = ***$. p values for the period effect in every region alone are given in Supplementary materials. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

four-way fixed factor model structure (period, year nested within 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 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).

Results

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–d). The effect sizes (differences in means) were large for every age group (Table 1); however, only the declines in ages 1 and 2 cod were statistically significant (Table 2). Using a two-stage model, we found that the time-period effect was significant for both the presence/absence of ages 1 and 2 juvenile cod as well as for the counts (Table 2). Year nested within period was significant for every cod age group, indicating high variability among years within both periods.

Table 1. Species list and mean abundance in the 1960s and 1990s of all recorded individuals in the beach-seine surveys across 42 sites.

Common name	Scientific name	Mean abundance (SE)	
		1960–1964	1992–1996
American plaice	<i>Hippoglossoides platessoides</i>	0.008 (0.01)	0.000 (0)
Angler	<i>Lophius piscatorius</i>	0.008 (0.01)	0.000 (0)
Arctic shanny	<i>Stichaeus punctatus punctatus</i>	0.000 (0)	0.045 (0.02)
Atlantic Cod 0	<i>Gadus morhua</i>	32.992 (7.75)	25.450 (3.68)
Atlantic Cod 1	<i>Gadus morhua</i>	77.826 (14.12)	13.760 (3.29)
Atlantic Cod 2	<i>Gadus morhua</i>	2.470 (0.55)	0.995 (0.22)
Atlantic herring	<i>Clupea harengus</i>	0.136 (0.13)	0.225 (0.18)
Atlantic mackerel	<i>Scomber scombrus</i>	0.000 (0)	0.030 (0.03)
Atlantic salmon	<i>Salmo salar</i>	0.015 (0.01)	0.045 (0.04)
Banded gunnel (Tansy)	<i>Pholis fasciata</i>	0.008 (0.01)	0.000 (0)
Brook trout	<i>Salvelinus fontinalis</i>	0.008 (0.01)	0.005 (0.01)
Butterfish	<i>Peprilus triacanthus</i>	0.000 (0)	0.005 (0.01)
Capelin	<i>Mallotus villosus</i>	0.008 (0.01)	0.025 (0.02)
Cunner	<i>Tautoglabrus adspersus</i>	11.129 (3.2)	4.380 (1.19)
Daubed shanny	<i>Leptoclinus maculatus</i>	0.000 (0)	0.020 (0.02)
Eel	<i>Anguilla rostrata</i>	0.030 (0.02)	0.005 (0.01)
Flying gurnard	<i>Dactylopterus volitans</i>	0.000 (0)	0.005 (0.01)
Greenland cod	<i>Gadus ogac</i>	0.121 (0.06)	4.750 (1.14)
Haddock	<i>Melanogrammus aeglefinus</i>	0.008 (0.01)	0.000 (0)
Lumpfish	<i>Cyclopterus lumpus</i>	0.053 (0.02)	0.290 (0.06)
Ocean pout	<i>Zoarces americanus</i>	0.106 (0.05)	0.045 (0.02)
Radiated shanny	<i>Ulvaria subbifurcata</i>	0.061 (0.02)	0.080 (0.02)
Rainbow smelt	<i>Osmerus mordax mordax</i>	1.970 (0.9)	2.460 (0.63)
Rock gunnel	<i>Pholis gunnellus</i>	0.000 (0)	0.690 (0.1)
Sand lance	<i>Ammodytes</i> spp.	2.432 (1.7)	2.835 (1.66)
Sculpin spp.	<i>Myoxocephalus scorpius</i> , <i>M. aeneus</i> , <i>M. octodecemspinosus</i> , <i>Gymnocanthus tricuspis</i>	1.977 (0.29)	2.630 (0.47)
Sea raven	<i>Hemitripteris americanus</i>	0.129 (0.04)	0.015 (0.01)
Skate (unidentified)		0.015 (0.01)	0.000 (0)
Snakeblenny	<i>Lumpenus lumpretaeformis</i>	0.364 (0.07)	0.000 (0)
Spotted skate	<i>Raja straeleni</i>	0.008 (0.01)	0.000 (0)
Stickleback spp.	<i>Gasterosteus aculeatus</i> , <i>G. wheatlandi</i>	0.970 (0.6)	22.745 (7.27)
Stout eelblenny	<i>Anisarchus medius</i>	0.008 (0.01)	0.055 (0.05)
Thorny skate	<i>Amblyraja radiata</i>	0.008 (0.01)	0.035 (0.02)
White hake	<i>Urophycis tenuis</i>	1.462 (0.5)	5.425 (0.96)
Winter flounder	<i>Pseudopleuronectes americanus</i>	15.644 (2.32)	13.495 (1.6)
Yellowtail flounder	<i>Limanda ferruginea</i>	0.144 (0.04)	0.275 (0.09)

Abundances are the sum of counts from two seine sets per site, averaged within each period.

Table 2. Analysis of deviance tables for juvenile Atlantic cod abundance (ages 0, 1, and 2).

Variable	Age 0		Age 1				Age 2			
	Count		Presence/absence		Count		Presence/absence		Count	
	Deviance	p-value	Deviance	p-value	Deviance	p-value	Deviance	p-value	Deviance	p-value
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
(Period/year)	24.809	0.0017	21.709	0.0055	101.674	<0.0001	17.108	0.029	19.447	0.0126
Period:region	19.622	0.0015	12.783	0.0255	8.270	0.142	6.040	0.3024	20.021	0.0005
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
(Period/year):region	116.081	<0.0001	0.000	1	129.625	<0.0001	0.000	1	45.095	0.0026
(Period/year):vegetation	22.607	0.0039	0.000	1	14.727	0.0647	0.000	1	4.022	0.7773
Period:region:vegetation	8.555	0.0139	865.048	0	0.327	0.849	6649.551	0	0.068	0.7945
(Period/year):region:vegetation	20.877	0.0754	0.000	1	10.501	0.1619	0.000	1	0.182	0.9961

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 tables contain 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). All main effects and interactions (":") are shown, and year is nested in period ("/"). Significant results (*p* < 0.05) are bolded. Full analysis of variance and deviance tables are given in Supplementary material.

There were significant regional differences in abundance for all age groups (Table 2, 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 ages 0 and 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 period by region interaction term was significant for age 0 cod, indicating that in some regions the magnitude or direction of change between 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 2, Figure 1c and d). The interactive effect of region and year nested within 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 2). For example, there were on average 5.07 age 2 Atlantic cod in vegetated habitats compared with 3.85 in non-vegetated habitats. There was a significant interaction between region and vegetation for the presence/absence of age 2 cod (Table 2). We also found a significant interaction between vegetation and year nested within period for age 0 cod (Table 2). There was also a significant interaction between period, region, and vegetation for age 0 cod (Table 2). In each case, we found that vegetated habitats had higher abundances or more presences than absences of juvenile cod.

Total fish abundance, species diversity, richness, and evenness

A total of 34 species of fish were caught in the beach-seines from both 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 periods (Figure 2a; Table 3). Concomitantly, we found a significant increase in Shannon diversity index and evenness between the 1960s and

1990s (Figure 2b and d, Table 3). There was a significant region by period interaction (Figure 2c, Table 3). 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 periods (Table 3). This year-to-year variability depended on region for both total fish abundance and Shannon diversity (Table 3). 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 3). There was also a significant interactive effect of region and vegetation on total fish abundance (Table 3). 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).

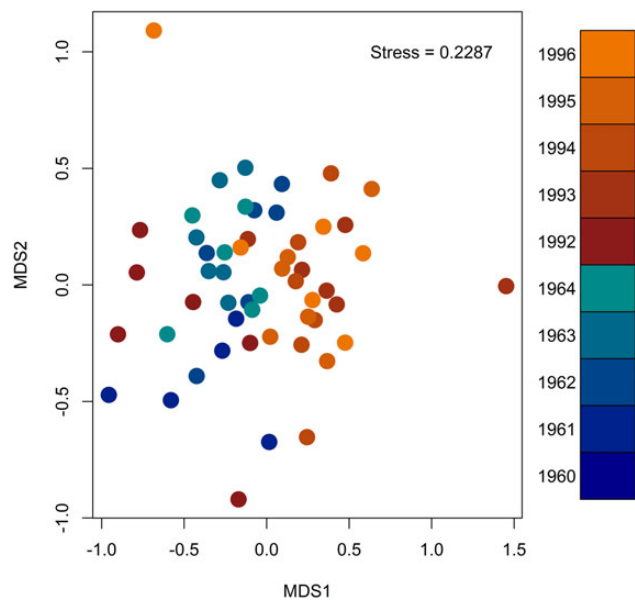
Community composition

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

Table 3. Analysis of deviance and variance tables for all community metrics (total fish abundance, Shannon diversity, species richness, and species evenness).

Variable	Total fish abundance		Shannon diversity		Species richness		Species evenness	
	Deviance	<i>p</i> -value	<i>F</i>	<i>p</i> -value	Deviance	<i>p</i> -value	<i>F</i>	<i>p</i> -value
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
(Period/year)	41.741	<0.0001	4.096	0.0001	24.380	0.0020	2.411	0.0162
Period:region	5.519	0.3559	0.307	0.9086	13.055	0.0229	0.711	0.6160
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
(Period/year):region	82.785	0.0001	1.558	0.0246	31.175	0.8096	1.232	0.1768
(Period/year):vegetation	9.627	0.2922	0.383	0.9289	5.523	0.7005	0.309	0.9620
Period:region:vegetation	5.654	0.0592	0.287	0.7509	2.354	0.3082	0.121	0.8858
(Period/year):region:vegetation	18.150	0.1519	0.542	0.8969	3.771	0.9934	0.755	0.7067

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. χ^2 tests for models with known dispersion are used, the raw deviance is reported (synonymous with the χ^2 value), and *F* tests for models with estimated dispersion. All main effects and interactions (":") are shown, and year is nested in period ("/"). Significant results (*p* < 0.05) are bolded. Full analysis of variance and deviance tables are given in Supplementary material.

**Figure 3.** Non-metric multidimensional scaling plot of fish communities summarized by Bray–Curtis dissimilarity, aggregated by regions within each year. Years and periods are coloured accordingly.

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 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 4). 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 unvegetated 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.

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 period as well as differences among regions; still, mean abundance in ages 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

Table 4. Community composition changes with all explanatory variables using the ManyGLM approach.

Parameter	Residuals DF	DF	Deviance	p-value	Individual species with significant effect
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 (Period/year)	317	1	87.09	0.001	Greenland cod (17.9%), Sand lance (15.5%), White hake (12.2%)
	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%)
Period:region	302	5	182.31	0.001	NA
Period:vegetation	301	1	19.95	0.251	
Region:vegetation	299	2	91.98	0.004	Cunner (21.7%), Winter flounder (20.9%)
(Period/year):region	254	45	860.93	0.001	Atlantic Cod 1 (12.5%), Atlantic Cod 0 (10.6%), Atlantic Cod 2 (10.2%)
(Period/year):vegetation	245	9	117.27	0.192	
Period:region:vegetation	243	2	22.49	0.227	
(Period/year):region:vegetation	239	17	96.49	0.244	

A significance value for each explanatory variable 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.

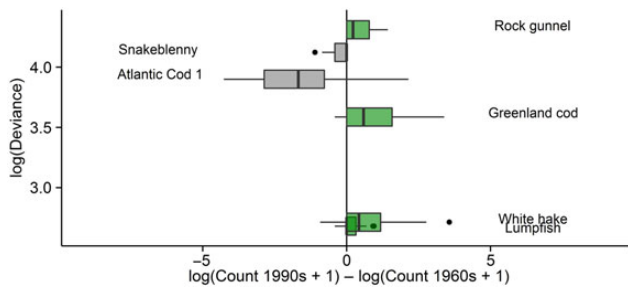


Figure 4. Species with the strongest contribution to the community changes (deviance) plotted by their mean change in abundance (natural logarithm) between the two periods. Boxplots are filled according to their mean change—either above or below zero. The plot shows the community level changes with respect to the “Period” term, with higher deviance values indicating higher contribution to community change. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

possible explanation is that juveniles were not subjected to fishing mortality in either 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 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 lesser 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.

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).

Supplementary data

Supplementary material is available at *ICEJMS* online version of the manuscript.

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