The role of a dominant predator in shaping biodiversity over space and time in a marine ecosystem

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Summary

1. Exploitation of living marine resources has resulted in major changes to populations of targeted species and functional groups of large-bodied species in the ocean. However, the effects of overfishing and collapse of large top predators on the broad-scale biodiversity of oceanic ecosystems remain largely unexplored.

2. Populations of the Atlantic cod (*Gadus morhua*) were overfished and several collapsed in the early 1990s across Atlantic Canada, providing a unique opportunity to study potential ecosystem-level effects of the reduction of a dominant predator on fish biodiversity, and to identify how such effects might interact with other environmental factors, such as changes in climate, over time.

3. We combined causal modelling with model selection and multimodel inference to analyse 41 years of fishery-independent survey data (1970–2010) and quantify ecosystem-level effects of overfishing and climate variation on the biodiversity of fishes across a broad area (172 000 km^2) of the Scotian Shelf.

4. We found that alpha and beta diversity increased with decreases in cod occurrence; fish communities were less homogeneous and more variable in systems where cod no longer dominated. These effects were most pronounced in the colder north-eastern parts of the Scotian Shelf.

5. Our results provide strong evidence that intensive harvesting (and collapse) of marine apex predators can have large impacts on biodiversity, with far-reaching consequences for ecological stability across an entire ecosystem.

Key-words: beta diversity, causal model, collapse of cod, human impact, marine fish, path analysis, relative abundance, species composition, top predator, trophic cascade

Introduction

Populations of many apex predators in natural systems have collapsed, due to overexploitation by humans (reviewed in Estes *et al.* 2011). Top-down ecological effects of predator removal on specific taxa or food webs *via* trophic cascades have been well documented (Pinnegar *et al.* 2000; Frank *et al.* 2005; Baum & Worm 2009), including the release of mesopredators (e.g. see Crooks &

Soulé 1999). Potential impacts on overall ecosystem-level biodiversity, however, remain poorly understood, especially in marine systems (Ritchie & Johnson 2009). Furthermore, the removal of apex consumers may act synergistically with other anthropogenic impacts, such as climate change, to affect ecosystem functioning (Estes *et al.* 2011). Critical assessments of biodiversity should ideally evaluate multiple potential sources of impact simultaneously at broad spatial and temporal scales.

In the north-west Atlantic, several populations of a large generalist predator, Atlantic cod (*Gadus morhua*), known to have a strong structuring role in North Atlantic

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ecosystems (Jackson 2001; Link *et al.* 2009; Steneck 2012), were overfished and collapsed in the early 1990s across Atlantic Canada (Hutchings 1996). On the Scotian Shelf, two spatially discrete, reproductively isolated stocks of cod exist, with one residing on the eastern half of the shelf and the other on the western side. Only the eastern stock collapsed during the early 1990s and the fishery was closed there (Frank *et al.* 2005). The western-region cod stock, despite being severely depleted, was never closed to fishing and has persisted in a depleted state (Shackell *et al.* 2010). Cod on the eastern Scotian Shelf unexpectedly failed to recover (Frank *et al.* 2005), although after 20 years, limited recovery was evident (Frank *et al.* 2011). Slow recovery has been linked to fundamental changes in ecosystem structure from excessive rates of exploitation (Frank *et al.* 2006, 2011; Frank, Petrie & Shackell 2007). It has also been linked to predation by grey seals (Trzcinski, Mohn & Bowen 2006) and/or the lack of reproductive success through predator–prey reversals, where forage fish such as herring or capelin consume the eggs, larvae or young-of-the-year cod (Bundy & Fanning 2005; Steneck 2012). While several other commercially exploited groundfish species have also declined in this region (Frank *et al.* 2005), primary prey of the benthic fish community, including small benthic and pelagic fishes and benthic crustaceans (e.g. snow crab and northern shrimp), have increased (Zwanenburg 2000; Worm & Myers 2003; Choi *et al.* 2004; Frank *et al.* 2005). Similar ecosystem responses to declining groundfish abundances have also been observed on the western half of the Scotian Shelf, but only minor changes in benthic crustaceans were evident (Shackell *et al.* 2010).

Composition and abundances of commercial and non-commercial fishes on the Scotian Shelf have been monitored by fishery-independent bottom trawl surveys conducted annually by the Canadian Department of Fisheries and Oceans (DFO) using a spatially extensive design over a 41-year period, from 1970 to 2010. These surveys span the period over which the reduction of cod occurred, ranging from collapsed in the east to severely depleted in the west. These data therefore provide a unique opportunity to study the potential community-wide effects of the reduction of a dominant predator on patterns of fish biodiversity, while concurrently examining the potential effects of variation in climate.

We expect that, in the past, when cod were prevalent, spatial variation in the composition of fish communities (beta diversity) would have been lower than in more recent years. A decrease in the spatial scale of similarity through time for communities of twenty commercially exploited species on Georges Bank and the eastern Scotian Shelf (Shackell *et al.* 2012) suggests widespread changes in beta diversity of fishes have occurred. In addition, the occurrence of organisms, including their probability of detection, is directly linked to their abundance (Brown 1984; Smith, Anderson & Millar 2012). Reductions in predators such as cod should lead to increased abundances and hence increased occurrences of prey species, yielding higher values of alpha diversity. Thus, we expect that alpha diversity of fishes in this system has increased over time, due to changing predation pressure, competitive release (Frank *et al.* 2005) or increases in temperature (Fisher *et al.* 2008). Here, we explore the combined roles of cod and climate in shaping the biodiversity of the entire fish community over this transitional period, including species not targeted by fisheries (*c.* 150 spp. in total).

Our primary objective was to quantify the effects and relative importance of the occurrence of cod, bottom temperature, depth, and the North Atlantic Oscillation (NAO) on alpha and beta diversity of the fish communities of the Scotian Shelf using causal modelling (Pearl 2000; Shipley 2009) coupled with model selection and multimodel inference (Burnham & Anderson 2002). We quantified beta diversity using several different measures, allowing us to tease out the effects of variation in numbers of species from models of variation in species identities or relative abundances through time (Anderson *et al.* 2011). From correlations in observational data alone, it is not strictly possible to infer that any changes in biodiversity over time are attributable to removal of cod by fishing, despite the clear temptation to do so in the context of a so-called natural experiment (e.g. see Underwood 1990). The main weakness of observational data is confounding, and causal modelling (also called path analysis), although not a panacea, provides one way to account for possible (measured) confounding variables (Shipley 2009; Paul & Anderson 2013). Causal models are limited by the variables that are available, as well as being contingent on the structural form of model relationships and errors. Nevertheless, by combining this approach with the tools of model selection and multimodel inference, one may develop and choose among competing hypotheses (Burnham & Anderson 2002). The blending of multimodel inference and causal modelling across a suite of biodiversity measures provided novel insights into the potential effects of predators on long-term, large-scale trends in marine ecosystem biodiversity.

Materials and methods

DESCRIPTION OF THE DATA

Data consisted of all commercial and non-commercial fish species sampled by the DFO annual summer (July) research bottom trawl surveys of the Scotian Shelf, north-west Atlantic, over a period of 41 years (1970–2010). Annual surveys use methods that were adopted and approved by the International Commission of Northwest Atlantic Fisheries (ICNAF) and later by the Northwest Atlantic Fisheries Organization (NAFO). These surveys use a stratified random design and are intended to provide unbiased, fishery-independent indices of groundfish abundance and recruitment for the Scotian Shelf/Bay of Fundy region.

There have been changes to the vessel and gear over the span of the time series. In 1982, the side trawler *A. T. Cameron* was replaced by a stern trawler, and at the same time, the Yankee 41

trawl was replaced by the Western IIA box trawl. The *Lady Hammond* was used in 1982, but the *Alfred Needler* has been the primary survey vessel since 1983. Comparative studies were conducted to determine conversion factors for these gear and vessel changes. Conversion factors were derived for cod and haddock and adjustments have been made to the data to account for the gear changes, accordingly.

A standard trawl set is 30 min long at a speed of 3·5 knots, timed from when all warp is out to the start of the haul-back. Tows of <20 min or >40 min are not considered to be valid sets. The trawl is equipped with a 19-mm codend liner, and this configuration has never been changed since the initiation of the surveys. There were small differences in the area swept by each tow; hence, counts of abundances of individual species were standardized to the nearest whole number for an area of 0·0404 km^2 (Shackell & Frank 2003). A total of 7330 trawl sets were completed at depths ranging from 11 to 282 m. The data primarily consist of benthic fish species, although other species, including small pelagic fishes, are also routinely captured. All fish caught were identified to the species level with the exception of redfish, which were all classed as 'unspecified redfish' due to uncertainties in their taxonomy. Whenever identification was not achieved at sea, unidentified specimens were frozen and brought ashore for positive identification by individuals having relevant ichthyological taxonomic expertise. For each fish species, the total number, total weight, and length-frequency data were collected in every year. The data were extracted from the Ocean Biogeographic Information System (OBIS) data base (IOC 2012).

The Scotian Shelf spans latitudes 42–47°N and was divided into an eastern region (sub-areas 1–3) and a western region (sub-areas 4–5, including the Bay of Fundy), corresponding to the NAFO Divisions 4VW and 4X, with a total area of 172 000 km^2 (Fig. 1). For this study, the total area was divided into five sub-areas (Fig. 1) in accordance with the original division into strata by DFO (based on bathymetry, Shackell & Frank 2003), enabling spatial comparisons of alpha and beta diversity among different portions of the shelf.

The number of trawl sets varied per sub-area and year, ranging from 16 to 68, with a maximum of 109 and 101 trawl sets in

Fig. 1. Study area and delineation of five sub-areas on the Scotian Shelf off Nova Scotia, Canada.

2005 in sub-areas 2 and 4, respectively. Variation in effort and the spatial extent of sampling can affect diversity, due to the species–area relationship (Crist & Veech 2006). Spatial extent was therefore quantified as the area of the spatial convex hull (based on latitude and longitude in a round-earth model) of the group of trawl sets within each sub-area in each year and included in all models.

MEASURES OF BIODIVERSITY

All diversity measures were calculated after excluding cod. The number of fish species in a single trawl set was used as a measure of alpha (local) diversity (sensu Whittaker 1972). Alpha diversity was measured as the annual mean number of species of all trawl sets within each sub-area. The choice of which measure to use for analysing beta diversity has important consequences on the nature of the results and their interpretation (reviewed in Anderson, Ellingsen & McArdle 2006; Anderson *et al.* 2011). We used a variety of different measures to emphasize different known aspects of variation in community structure for multispecies data sets. Specifically, beta diversity was measured as the average distance-to-centroid (Anderson, Ellingsen & McArdle 2006) among all trawl sets within each sub-area in each year on the basis of three different dissimilarity measures, each having a somewhat different meaning and interpretation (Anderson *et al.* 2011): (i) Jaccard (variation in species identities), (ii) modified Gower, log base 10 (variation in relative log-abundances, Anderson, Ellingsen & McArdle 2006), and (iii) Raup–Crick (variation in species identities that omits effects of variation in the number of species, Raup & Crick 1979).

MODELS AND STATISTICAL ANALYSES

Our purpose was to model changes in fish biodiversity vs. changes in environmental variables through time, and to determine whether the reductions in cod abundance resulting from overfishing had, in turn, detectable causal effects on fish biodiversity. The environmental variables included here were as follows: mean depth (average of the maximum and minimum depth recorded for each tow), mean bottom temperature (per tow, measured *in situ*) and a broad-scale measure of climatic variation (the PC-based wintertime December/January/February NAO index, Hurrell 2003).

Causal modelling (Pearl 2000; Shipley 2009) was used to model each diversity measure separately as a function of two fixed exogenous factors: year (Y, temporal position as a linear covariate) and sub-area (A, spatial position, with five levels), and five potential endogenous variables: bottom temperature (T), depth (D), NAO index (N), sampling extent (E) and cod (C, the proportion of trawls within each sub-area × year containing cod). We also considered using the mean abundance of cod per sub-area per year as a predictor variable; however, the average log-abundance and proportional occurrence of cod were highly correlated (Pearson correlations ranged from $r = 0.78$ to 0.90 across the five sub-areas), so only occurrence was used in analyses. NAO was modelled as a function of year only (as it did not differ across sub-areas), while all other endogenous variables were modelled as a function of year and sub-area. Furthermore, bottom temperature was also considered to be potentially dependent on depth and NAO, while cod was also considered to be potentially dependent on depth, NAO and bottom temperature. Although spatial extent is merely a consequence of
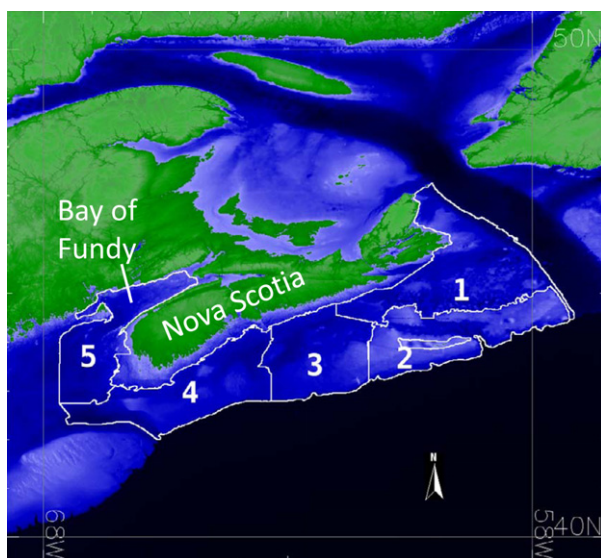
the sampling design, it was appropriate to model its potential variation across sub-areas and years.

Based on the above, the initial structural equations for the full causal diagram were as follows:

$$A = \varepsilon_A$$

$$Y = \varepsilon_Y$$

$$N = f_N(Y, \varepsilon_N)$$

$$D = f_D(A, Y, \varepsilon_D)$$

$$E = f_E(A, Y, \varepsilon_E)$$

$$T = f_T(A, Y, D, N, \varepsilon_T)$$

$$C = f_C(A, Y, D, N, T, \varepsilon_C)$$

$$R = f_R(A, E, D, N, T, C, \varepsilon_R)$$

where R indicates a specific biodiversity response variable (there were four of these, each modelled separately, namely alpha diversity *or* beta diversity based on Jaccard, *or* modified Gower *or* Raup–Crick, respectively), $f_i(\cdot)$ indicates a functional relationship between the variables listed within the brackets (predictors) and variable i (response), and ε_i indicates an unmeasured error variable associated with variable i. All ε_i are assumed to be mutually independent. Also, although A (spatial position) and Y (temporal position) are represented as random variables, in this study A was fixed with five levels (sampled every year) and Y was a systematic annual sample, so can be expressed simply as an integer from 1970–2010. The above structural equations yield a causal diagram with no reciprocal directed paths, bidirectional arrows or feedback loops; hence, predictors are independent of errors in each equation, and estimation can proceed using a sequence of ordinary least-squares regressions (Fox 2002).

First, we performed model selection on the basis of Akaike's information criterion, corrected for small samples (AICc, Hurvich & Tsai 1989) for each of the following variables: N, D, E, T and C, starting with the above full models, and including all potential interactions between each of the quantitative variables and the factor of sub-area. Wherever possible, we simplified the causal model structure further, removing links associated with non-significant terms ($P > 0.70$). We fit linear regression models in all cases and used diagnostic plots of residuals to check model assumptions.

Next, an overall goodness-of-fit test (Shipley 2009) was used to assess the full causal hypothesis represented by the directed acyclic graph corresponding to the causal model structure proposed for each response variable. Specifically, we applied directional separation (d-separation) rules to identify all conditional independence claims among variables in the basis set implicit in each causal diagram (Pearl 2000; Shipley 2009). For each diagram, the $j = 1, \ldots, k$ probabilities p_j generated by the individual tests of conditional independence were combined to form the test statistic $C = -2 \sum_{j=1}^{k} \log(p_j)$, which was then compared with a chi-square distribution having $2k$ degrees of freedom (Shipley 2009). These tests included the test for no direct link between year and each of the diversity (response) variables (R) in our proposed causal diagram; that is, we tested explicitly the hypothesis that the effect of time (year) on diversity was sufficiently accounted for by temporal changes in cod, bottom temperature, depth, spatial extent and the NAO index.

Finally, we performed multimodel inference (Burnham & Anderson 2002) to generate coefficients for a final causal diagram separately for each of the four response variables (i.e. letting R = alpha diversity *or* beta diversity based on Jaccard, *or* modified Gower *or* Raup–Crick, respectively). A confidence set of models for which the evidence ratios (Akaike weights) relative to the best model were greater than a cut-off value of 1/8 (Burnham & Anderson 2002) was obtained using the MuMIn library (Bartoń 2012) in R (R Core Team 2014). The relative importance of each predictor variable in the confidence set was quantified as the sum of Akaike weights over all models in which the variable of interest appeared (Burnham & Anderson 2002). Variables were standardized so that the full model-averaged coefficients (with shrinkage) were equivalent to standardized partial correlations (r_p), allowing direct comparison of their relative importance for display in the causal diagram. There was no single r_p value for the factor of 'sub-areas', because this is an ANOVA term having 4 d.f. Hence, to provide a suitable value that would show its relative importance in the causal diagram, we calculated the square root of the partial adjusted R^2 associated with the removal of sub-areas from the model. This would be equivalent to r_p if calculated directly on any of the other quantitative (1 d.f.) variables (such as depth or temperature), so was deemed appropriate to enable direct comparisons for display in the final causal diagram. Partial residual plots were used to visualize the effects of cod on response variables within each model.

In summary, our modelling approach had three steps: (i) model selection was used for each endogenous predictor variable in order to simplify (reduce the numbers of arrows) in the final causal diagram; then, for each response variable in turn, (ii) an overall test (Shipley 2009) was done to test the validity of the final causal diagram; and (iii) multimodel inference was used to obtain coefficients to label the arrows in the final causal diagram. Note that this approach differs somewhat from that described by Shipley (2013), in which no multimodel inference was employed and an AIC criterion was used instead to choose among multiple potential causal diagrams. All analyses were done using R (R Core Team 2014).

Results

ANALYSIS OF ENDOGENOUS PREDICTOR VARIABLES

The proportion of trawl sets with cod was highly variable, but decreased significantly across all sub-areas over the 41-year period (Fig. 2a, Table 1c). In sub-area 5 (southwest), the proportional occurrences of cod were generally the highest and, although there was no clear change over time for the first 30 years, a marked decrease (from c. 0·90 to 0·55) was apparent over the last decade. Sub-area 3 had generally the lowest proportional occurrences of cod. Despite significant decreases over the entire period, increases have been observed in sub-areas 1–4 since about 2002, particularly in sub-area 3 (from c. 0·20 to 0·60).

The average bottom temperature did not change significantly over time, nor was it significantly related to the
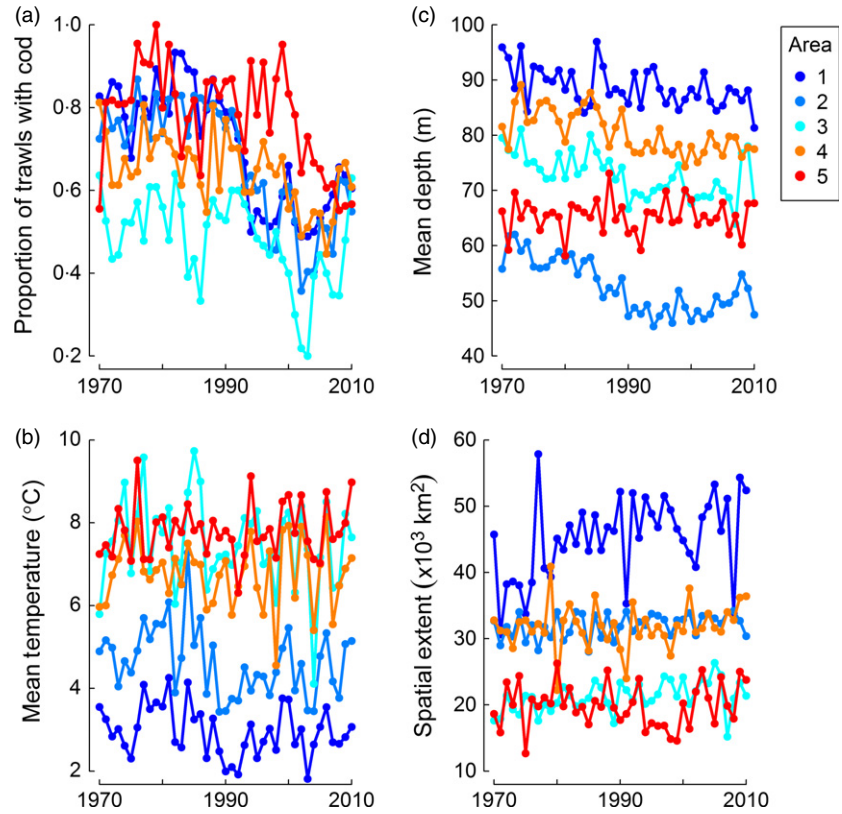
Fig. 2. Annual values from 1970 to 2010 within each of five sub-areas across the Scotian Shelf (see legend) for each of four variables: (a) the proportion of trawls containing cod; (b) mean bottom temperature (°C); (c) mean depth (*m*) per trawl set; and (d) spatial extent of sampling within each sub-area and year.

Table 1. Analyses of variance of the most parsimonious models on the basis of AIC_c for each of four variables: (a) depth, (b) spatial extent, (c) cod and (d) bottom temperature and subsequently omitting non-significant terms ($P > 0.7$). For cod, the variables removed from the AIC_c model were depth ($P = 0.73$), temperature ($P = 0.76$) and North Atlantic Oscillation (NAO) ($P = 0.93$). For bottom temperature, the variables removed from the AIC_c model were NAO ($P = 0.78$) and year ($P = 0.89$)

		(a) Depth			(b) Spatial extent			(c) Cod			(d) Temperature				
Source	d.f.	MS	F	P	MS	F	P	MS	F	P	Source	d.f.	MS	F	P
Area (A)	4	7914·5	821·0	<0·001	$4·30 \times 10^9$	357·1	<0·001	0·505	57·4	<0·001	Area	4	175·73	277·0	<0·001
Year (Y)	1	863·4	89·6	<0·001	$2·11 \times 10^8$	17·5	<0·001	1·133	128·6	<0·001	Depth	1	5·38	8·5	<0·005
A × Y	4	74·4	7·7	<0·001	$4·37 \times 10^7$	3·6	<0·008	0·042	4·8	<0·002					
Residual	195	9·6			$1·21 \times 10^7$			0·009			Residual	199	0·63		

NAO index, but was cooler at deeper depths and differed significantly among the five sub-areas, with sub-areas 1 and 2 towards the north-east being the coolest (Fig. 2b, Table 1d). In addition, there was no significant linear relationship between the NAO index and year ($F_{1,39} = 0.106$, $P = 0.746$). There were significant effects of sub-area, year and their interaction on the depth and spatial extent of the sampling (Table 1a,b). The average depth of the trawls decreased over time. Sub-area 1 had the deepest trawl sets, followed by sub-area 4, sub-area 3 and sub-area 5, with sub-area 2 having the shallowest trawl sets (Fig. 2c). Concomitantly, the spatial extent of the sampling tended to increase over time, with the greatest average areal extent being sampled from sub-area 1, followed by sub-areas 2 and 4, and smaller extents from sub-areas 3 and 5 (Fig. 2d).

ANALYSIS OF BIODIVERSITY RESPONSE VARIABLES

There were 152 fish species (excluding cod) recorded from the trawl sets sampled across the Scotian Shelf from 1970 to 2010. The mean number of species per trawl set (alpha diversity) was highest in sub-area 5 and increased significantly in all sub-areas, with the exception of sub-area 2, which showed no clear temporal trend (Fig. 3a).

Beta diversity increased through time in sub-areas 1, 2 and 4 (based on Raup–Crick, Jaccard or modified Gower), although for sub-area 2 there was first a decrease and then an increase from the mid-1970s (Fig. 3b–d). Thus, there was greater variability among the trawl sets towards the end of the time series than at the beginning, when samples were more homogeneous. In sub-area 5, beta diversity based on Raup–Crick also increased over
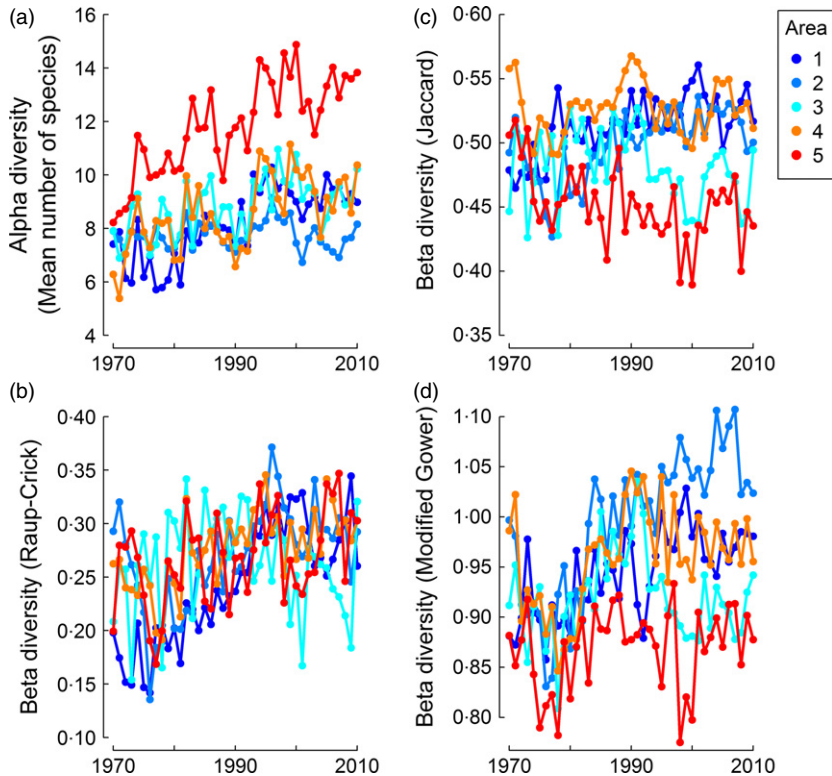
Fig. 3. Annual values from 1970 to 2010 within each of five sub-areas across the Scotian Shelf (see legend) for each of four biodiversity variables calculated from all fishes caught in trawl sets, excluding cod: (a) alpha diversity (mean number of species); mean distance-to-centroid (beta diversity) based on (b) Raup–Crick; (c) Jaccard; or (d) modified Gower dissimilarity measures.

the 41 years (Fig. 3b), but showed no clear temporal trend when based on either Jaccard or modified Gower (Fig. 3c,d). In contrast, sub-area 3 showed no clear trends in beta diversity over time for any of these measures (Fig. 3b–d).

Beta diversity was lowest in sub-area 5 compared to the other sub-areas from the mid-1970s onwards based on the Jaccard or modified Gower measures (Fig. 3c,d), but this was not the case when Raup–Crick was used, for which all sub-areas showed similar temporal patterns of variation (Fig. 3b). The levels of beta diversity across the different sub-areas of the shelf diverged over time when using either Jaccard or modified Gower (Fig. 3c,d). However, this divergence was not apparent using Raup–Crick (Fig. 3b).

To what extent are the observed temporal trends and patterns in biodiversity caused by changes in cod populations in concert with the measured environmental variables over time? Causal modelling revealed that the proportional occurrence of cod resulted in important negative effects on all biodiversity measures (Fig. 4). Alpha diversity was most strongly affected by sub-area ($r_p = 0.623$), followed by the (negative) effects of cod ($r_p = -0.480$), bottom temperature ($r_p = -0.211$) and depth ($r_p = -0.147$), with only minor effects of spatial extent ($r_p = -0.093$) and no apparent effect of NAO ($r_p = 0.0001$) (Fig. 4). For all of the measures of beta diversity, the most important causal variables were consistently sub-area, cod and depth, and the relative importance of cod was highest for the Raup–Crick measure ($r_p = -0.832$) (Fig. 4). Spatial extent had a positive effect on beta diversity (range of $r_p = 0.114$–0.193), but

temperature and NAO had no strong effects ($r_p < 0.08$). The coefficients for cod and for depth were negative in all of the models of all biodiversity response variables (Fig. 4); hence, deeper samples and samples with greater proportions of cod show decreased numbers of species and greater homogeneity of assemblage structure, in terms of identities of species and also their relative abundances.

The relative importance of sub-area, cod, sub-area × cod and depth all feature especially strongly in the confidence sets of all measures of beta diversity. Plots of partial residuals revealed significant negative effects of cod on alpha diversity for sub-areas 1, 4 and 5 (Fig. 5). The negative effect of cod on beta diversity, that is that the trawl sets were more heterogeneous when the occurrence of cod was lower, was evident in sub-areas 1 and 2 (in the colder north-eastern part) and sub-area 4 for Raup–Crick, and in sub-areas 1 and 2 for either the Jaccard or modified Gower measures (Fig. 5). In contrast, in sub-area 3, which had the lowest overall proportions of cod, the relationship between beta diversity based on Raup–Crick and cod was positive (Fig. 5). Further detailed results of model averaging, including a summary of the models making up the multimodel confidence set for each response variable (Table S1, Supporting Information) and the relative importance of each term within each confidence set (Table S2), are provided in Supporting Information.

The goodness-of-fit tests for the overall causal hypothesis (d.f. = 20 in each case, see Table S3 for further details) were statistically significant for alpha diversity ($C = 88.14$,
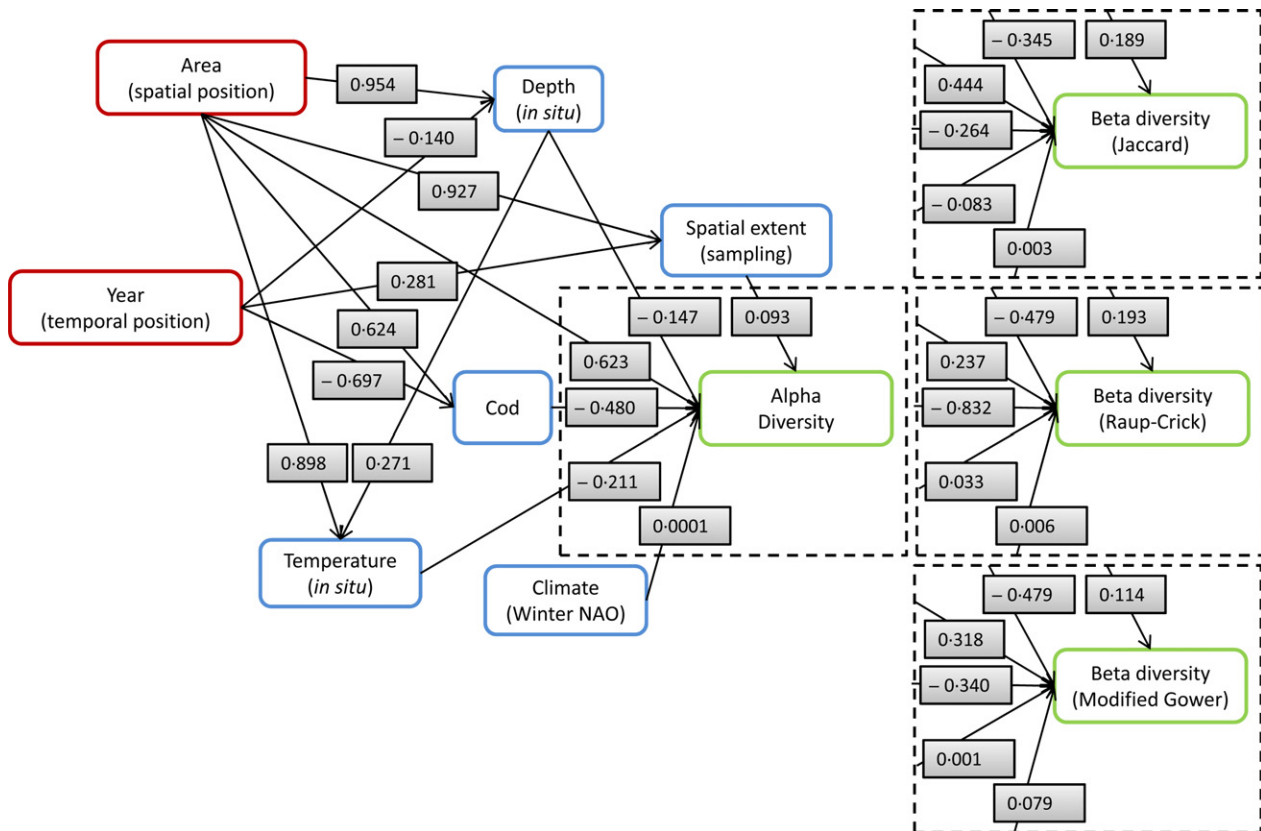
Fig. 4. Causal diagram including two fixed exogenous factors (red) and five potential endogenous variables (blue) for each of four biodiversity response variables (green), calculated from all fishes caught in trawl sets excluding cod: alpha diversity (mean number of species), and beta diversity (mean distance-to-centroid) based on Raup–Crick, Jaccard or modified Gower dissimilarity measures. Numbers on arrows are standardized partial correlations (or, for 'Areas', the square root of the adjusted R^2) from multimodel inference. Relationships among exogenous and endogenous predictor variables are equivalent for all of the causal models, but their relationships with each of the four individual biodiversity response variables differ for each causal model and are specified separately (enclosed by dotted lines).

$P < 0.0001$) and for Jaccard ($C = 35.35$, $P = 0.0183$), but not for Raup–Crick ($C = 30.02$, $P = 0.0695$) or modified Gower ($C = 27.69$, $P = 0.1169$). Thus, the effects of cod and environmental variables (that were included) on alpha diversity and Jaccard beta diversity, given in the causal diagrams (Fig. 4), are to be viewed with some caution and an awareness that other latent temporally structured causal variables may be missing here.

Discussion

Despite growing recognition of the importance of ecosystem-based management of fisheries (Pikitch *et al.* 2004), there exists very little scientific evidence regarding the actual effects of fishing on overall biodiversity for broad-scale oceanic ecosystems. This is likely due to the infeasibility of controlled experimental manipulations in such systems and the lack of appropriate time-series or spatial replication even to allow 'pseudo-experimental' approaches (Baum & Worm 2009). We have combined causal modelling with model selection and multimodel inference to provide a detailed study and quantification of the potential role and relative importance of cod and several key environmental variables to shape the biodiversity

of fishes along the Scotian Shelf from trawl data gathered over a period of 41 years that include the collapse of cod populations due to overfishing.

We found that fish communities were less homogeneous, with greater variation in species' identities and relative abundances, in systems where cod no longer dominated. We show that the reduction of cod has affected the biodiversity of the entire fish community. Our results correspond with observations that apex predators (such as cod) are generally larger, live longer, have larger home ranges, occur in lower densities and have lower reproductive rates than most mesopredator species, which tend to have more variable short-term population dynamics, occurring more sporadically and in higher densities (Ritchie & Johnson 2009). Increased heterogeneity can result in lower resistance, lower resilience and higher reactivity for ecological communities (Britten *et al.* 2014). The key implication of our results is that overexploitation has yielded ecosystems that are fundamentally more variable, in which management efforts, even if consistently applied, are nevertheless likely to have inconsistent outcomes, and where predictive models are apt to be less reliable and fisheries catches less stable.
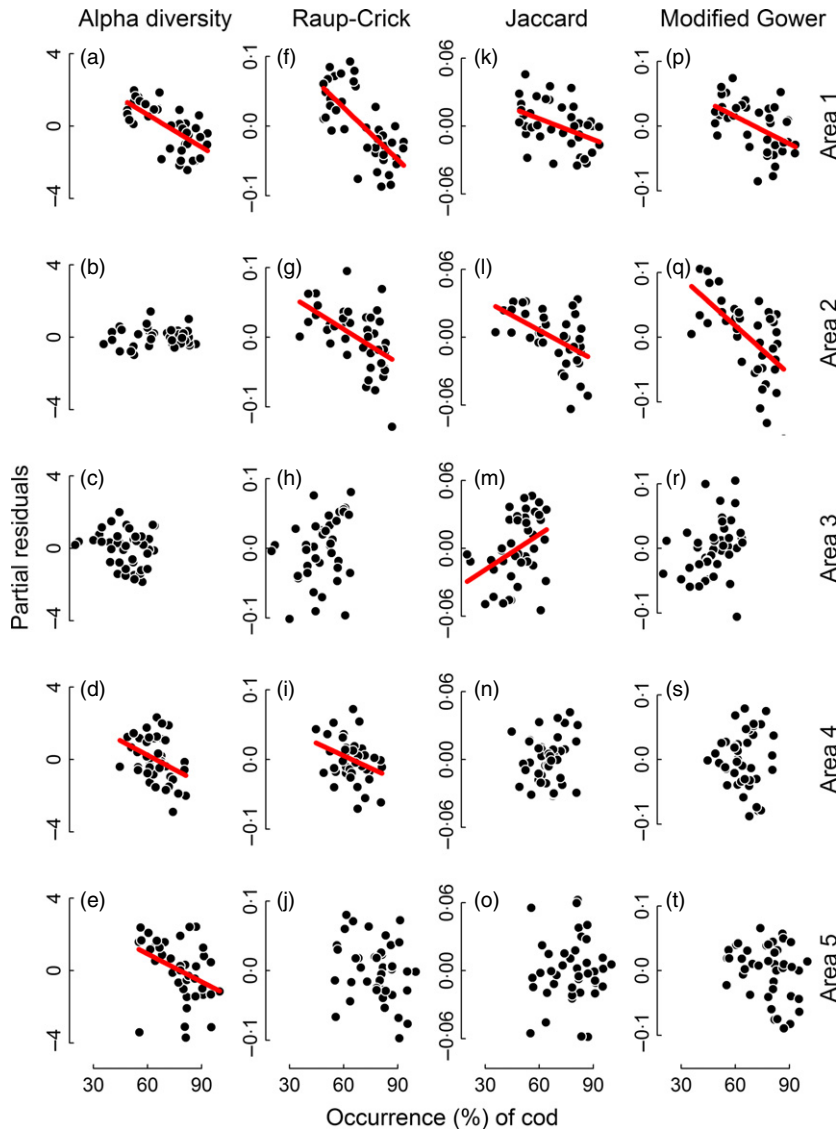
Fig. 5. Partial residual plots from multimodel inference for alpha diversity (mean number of species) (a–e) and beta diversity (mean distance-to-centroid) based on Raup–Crick (f–j), Jaccard (k–o) or the modified Gower measure (p–t) vs. the proportional occurrence of cod in each of five sub-areas. Solid lines indicate statistically significant linear trends.

Further complexity accrues in this system through significant spatial variation in the effects of cod (and other drivers) on alpha and beta diversity across different sub-areas, supporting the idea that smaller spatial scales (i.e. the sub-areas) can host important and variable ecosystem dynamics. For example, in the central part of the Scotian Shelf (sub-area 3), we found no trend in beta diversity over time in contrast to the other sub-areas, although there was high interannual variability; simultaneously, the occurrence of cod was clearly lowest in this sub-area. Furthermore, we found that average bottom temperature varied considerably among the different sub-areas, and in particular between the two colder north-eastern sub-areas (1 and 2) and the rest of the shelf. Interestingly, these two north-eastern sub-areas had the most pronounced effects of cod on beta diversity (Fig. 5). Frank *et al.* (2006) have also documented spatial variation in the measured relative strength of top-down vs. bottom-up effects in this system. Regional specificity of the effects of cod may be due to the mosaic nature and fragmentation of recovering cod populations, with local individual stocks being uniquely identifiable genetically and having separate estimated birth, growth and death rates (Stenseth *et al.* 1999; Steneck & Wilson 2010), hence varying at local scales in their ability to recover through time. Other factors driving sub-area-level variation might include habitat-specific effects of predators or spatial variation in the guilds of available mesopredators (Ritchie & Johnson 2009).

By focusing on both alpha and beta diversity, and using different dissimilarity measures in our analyses of beta diversity, we were able to more fully decipher the changes in fish assemblage structure that occurred on the Scotian Shelf. Beta diversity based purely on presence/absence information (i.e. the proportion of unshared species measured by the Jaccard dissimilarity measure) increased in response to declines in the prevalence of cod; this pattern was mirrored by the Raup–Crick measure, which takes into account variation in the number of species among sample units (Chase *et al.* 2011). Moreover, a similar pattern was revealed when beta diversity was measured using

the modified Gower measure, which emphasizes variation in relative log-abundances of fish species. Hence, increased heterogeneity in fish assemblages was not just a matter of increased variation in alpha diversity within particular sub-areas. Importantly, these beta diversity measures also captured changes in fish assemblages before the reported collapse of the cod population, indicating that they may serve as effective early-warning signals for ecosystem-level changes.

We found a (negative) effect of bottom temperature on alpha diversity, in accordance with Fisher *et al.* (2008) and Fisher, Frank & Leggett (2010), but our results showed that cod clearly explained patterns in fish biodiversity better at the relatively smaller spatial scale used in our study. Given that there was no trend in broad-scale climate (NAO index) and that climatic effects on diversity may have long time-lags, the lack of any significant effects of broad-scale climate on these biodiversity variables may not be that surprising, even though the NAO index is considered to be a major driving force for many ecological processes (Ottersen *et al.* 2001), especially bottom-up oceanic processes (e.g. Pitois *et al.* 2012). Although water depth *per se* does not change over time, depth was more important than local temperature or NAO in predicting the beta diversity of these fish assemblages (see also Anderson, Tolimieri & Millar 2013, and their study on fish beta diversity vs. depth). However, our finding that the effects of cod on beta diversity were most pronounced in the coldest sub-areas to the north-east suggests that there might be some interactions with temperature at broader scales.

If cod and other benthic predatory fish species drive patterns in fish biodiversity, then it can be expected that decreases in alpha and beta diversity will occur if the system returns to dominance by cod and/or other groundfish (see Frank *et al.* 2011), although such a pattern may take considerable time to develop. For some of the sub-areas on the Scotian Shelf, lower beta diversity occurred towards the end of this time period (Fig. 3) along with increases in the prevalence of cod (Fig. 2); however, ongoing monitoring is clearly required to test hypotheses regarding the anticipated recovery of cod and associated changes in fish diversity into the future. Interestingly, in the south-east Bering Sea and the Gulf of Alaska, there was a transition in the late 1970s from a community dominated by small pelagic fish and crustaceans to a community dominated by groundfish, that is in the opposite direction to the situation with the Scotian Shelf ecosystem (Litzow, Urban & Laurel 2008). This transition coincided with the 1976–1977 climate regime shift associated with the Pacific Decadal Oscillation (e.g. see Litzow, Urban & Laurel 2008), but overfishing of crustaceans may also have contributed to this community transition (Orensanz *et al.* 1998; Litzow, Mueter & Hobday 2014). In another large marine ecosystem, the Barents Sea, cod has increased in both numbers and distribution over large spatial scales (ICES 2011); this cod population is currently

the largest in the world (Johannesen *et al.* 2012). Based on the results from the Scotian Shelf, our expectation would be a more homogenous fish community as cod increases. Future research is needed to elucidate ecosystem-level effects of cod recovery on the biodiversity of fishes across multiple systems globally.

Our results show that the fish biodiversity on the Scotian Shelf today is quite different to what it was when cod were more prevalent in the ecosystem (Figs 4 and 5). Although our study found increased heterogeneity (increased beta diversity) in the system with fewer predators, several other studies have suggested that declines in predation have led to decreased diversity (Paine 1966; Crooks & Soulé 1999; Schmitz 2003; Estes *et al.* 2011). The main take-home message is that the reduction of dominant predators on land and in the ocean has led to considerable changes to biodiversity globally; hence, a suite of management actions may be required for broad-scale recovery of ecosystems.

Our causal models would clearly be enhanced by incorporating other potentially important broad-scale predictor variables, such as nutrients, phytoplankton or zooplankton, or local-scale features such as habitat complexity, enabling more refined discrimination among a larger number of competing hypotheses and the quantification of the effects of these additional processes to drive patterns. Our causal diagrams and models would also be enhanced by the explicit inclusion of fishing itself (i.e. actual catch data) within each sub-area and year, so the relative strength of fishing effects on cod could also be quantified and compared. Although estimates of fishing mortality for cod are available at the broader scale of whole management units (NAFO Divisions 4VW and 4X), we did not include this in our models as the effects of cod on biodiversity clearly varied at smaller spatial scales, among individual sub-areas. An experimental approach (e.g. with predator exclusion treatments, Schmitz 2003) to demonstrate specific trophic cascades is not feasible for open marine systems with wide-ranging species at large geographical scales. Causal models do not, however, equate with experimental demonstrations of causation, as they naturally depend on many choices, such as the potentially confounding variables to include, the mathematical form of the relationships posited among variables, their individual error distributions and other model assumptions, such as the independence of errors. For example, nonlinear relationships of cod populations vs. time, given what is known about the fishery and subsequent closures, might also be considered here (e.g. see fig. 9 in Paul & Anderson 2013). Another augmentation would be to include individual effects of fishing on other large-bodied fishes alongside cod, explicitly quantifying relationships (and time-lags) among predators, mesopredators and lower trophic levels within a more complex biological food web (e.g. Frank *et al.* 2011; Shackell *et al.* 2012). While others have focused on mesopredator release following the removal of top predators (e.g. Crooks & Soulé 1999; Prugh *et al.*

2009; Strong & Frank 2010), our main focus was to explain the overall patterns of fish biodiversity. However, these two issues are probably linked, and our work raises the question of whether mesopredators may play a role to generate observed increases in heterogeneity. Future development of more refined causal models for these and other ecosystems will enable a greater understanding of large-scale and long-term impacts of human interventions on the biodiversity and stability of global ecosystems. Hilborn & Hilborn (2012) stated that there remains great confusion about the actual amount of overfishing and its ecological impact. It is therefore important to understand the effects of overfishing on biodiversity at ecosystem levels. Our work indicates that intensive harvesting (and collapse) of marine apex predators can have large impacts on ecosystem biodiversity.

Acknowledgements

Data accessibility

Data are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.76sv3 (Ellingsen *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Multimodel inference in analyses of alpha and beta diversity.

Table S2. Relative importance of variables in the confidence set of models used for multimodel inference in Table S1.

Table S3. Goodness-of-fit tests of the causal model diagrams in Fig. 4.