

Community size spectra provide indicators of ecosystem recovery on the Newfoundland and Labrador shelf

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ABSTRACT: Species- and size-selective overexploitation often have ecosystem-wide impacts that are evident in community size spectra. To both derive potential ecosystem targets for community rebuilding and assess contemporary indicators relative to these targets, we constructed theoretical size spectra to predict pristine biomass densities using a combination of species- and size-specific nitrogen stable isotope signatures and a range of trophic efficiencies and primary productivity estimates within and among 3 sub-regions of the Newfoundland and Labrador shelf. Theoretical size spectra were compared to empirically derived size spectra using trawl survey data. The descending slopes of the empirically determined size spectra were between 1.25 and 2.42 times steeper than the theoretical slopes. The percentage of the theoretical distribution represented by the empirical size structure ranged between 1.1 and 29.4%, with the closest and furthest estimates associated with the smallest- and largest-sized fishes, respectively, and strongly influenced by estimates of trophic efficiency and primary productivity. Regional variation was also observed, with southern regions reaching 1.3–32.3% of the theoretical biomass density and the northernmost region reaching only 0–8.3%. Importantly, the descending slopes varied depending on fish size, with biomass density of larger sizes decreasing faster than that of smaller sizes. Variations among sub-regions and fish guilds were also observed. These analyses provide a means to derive potential ecosystem targets and indicators through which recovery of fish communities can be monitored and assessed.

KEY WORDS: Size spectra · Biomass density · Predator:prey mass ratio · Northwest Atlantic · Nitrogen stable isotope

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1. INTRODUCTION

Both biomass densities and the abundances of organisms have been observed to decrease with increasing body size (White et al. 2007), a relationship that is the foundation for size spectra modeling (Sheldon et al. 1972). These models treat organisms solely on the basis of size, thereby concealing taxonomic identity (Petchey & Belgrano 2010), and have been used extensively to model size-structured marine ecosystems (Blanchard et al. 2017). Since growth is

dependent on food intake, size-structured models are considered a subset of physiologically structured models (De Roos & Persson 2001). The expanding field of size-structured models helps explain community organization (Shin et al. 2005, Hartvig et al. 2011, Blanchard et al. 2017) and community responses to anthropogenic influences, including climate change, species invasions, and exploitation (Jennings & Blanchard 2004, Andersen & Rice 2010, Petchey & Belgrano 2010, Woodward et al. 2010, Engelhard et al. 2014, Jacobsen et al. 2014). As management of

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marine fisheries moves towards community and ecosystem approaches (Mangel & Levin 2005), it is necessary to evaluate community and ecosystem indicators relative to new or established conservation targets (Shin et al. 2005, Jennings & Dulvy 2005).

Fishing pressure and climate change represent 2 of the greatest anthropogenic pressures facing marine communities (Jackson et al. 2001, Tremblay-Boyer et al. 2011). Larger individuals and species are often selectively captured by commercial fishing, reducing predation pressure and leaving remaining individuals to exhibit increases in biomass to fill the opened ecological niches (Andersen & Rice 2010). This can result in observed decreases in the species-specific maximum length (Hixon et al. 2014), mean length in a community (Fisher et al. 2010, Shin et al. 2010), and a steeper descending slope of community size spectra (Pimm & Hyman 1987, Jennings & Blanchard 2004, Daan et al. 2005, Shin et al. 2005). Quantifying such changes within ecosystems having a long history of exploitation from a size-spectrum perspective requires both quantifying the current state and identifying a baseline reference state (Jennings & Blanchard 2004).

In the 1980s and early 1990s, demersal fisheries in the Newfoundland and Labrador (Canada) region experienced high levels of exploitation during poor environmental conditions, leading to stock collapses and subsequent declaration of fisheries moratoria on Atlantic cod *Gadus morhua* and other, co-occurring species (Lilly et al. 2008). The loss of this top predator was associated with ecosystem-wide changes (Lilly et al. 2000, Rice 2002, Frank et al. 2006, Pedersen et al. 2017), including the size structure of shelf communities (Haedrich & Barnes 1997, Fisher et al. 2010). This marine ecosystem is presently recovering from overexploitation (Pedersen et al. 2017, DFO 2018), a process that from a size-structure perspective may take decades (Fung et al. 2013). The earliest recorded accounts of exploitation of this ecosystem date to the late 15th century (Cell 1982, Rose 2007). Therefore, establishing a baseline to assess contemporary recovery based on historical data is challenging and has been attempted only for Atlantic cod populations in this system (Myers et al. 2001, Rose 2004). Here we conducted analyses that provide complementary community-level baselines and contemporary indicators of ecosystem recovery focusing on a broad base of size classes and species.

Using methods first proposed by Jennings & Blanchard (2004), we compiled data from 3 sub-regions within the Newfoundland and Labrador Shelf ecosystem to quantify the current status of the marine

fish communities in the context of ecosystem 'recovery' and its variation among sub-regions and body size classes. Jennings & Blanchard (2004) integrated predator:prey mass ratio (PPMR) data, estimates of primary productivity, and a range of ecologically reasonable trophic efficiency estimates, defined as the proportion of consumed energy that consumers convert to biomass in one trophic level, to provide theoretically expected biomass densities across a wide range of fish sizes within North Sea fish communities. However, Jennings & Blanchard (2004) also noted that it was uncertain whether the cessation of fishing would allow recovery to an unexploited community size structure and that question was beyond their North Sea analyses. Therefore, we sought to quantify the extent of community reversion towards a theoretical unexploited state over 25 yr after the initial groundfish fisheries moratoria were established in Newfoundland. By similarly deriving theoretical biomass densities for the Newfoundland and Labrador Shelf communities, our study addresses the questions: How far is the current biomass of fish communities from a theoretical unexploited biomass? Furthermore, do empirical community-level signatures of prior overexploitation remain evident over 2 decades later? Separate analyses were conducted among the 3 regions and within 3 size categories of fishes to further partition the community-wide impacts of past exploitation. The 3 sub-regions are known to differ in prey species richness and trophic overlap (Krumsick & Fisher 2019).

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted as part of acoustic-trawl surveys conducted by the Centre for Fisheries Ecosystems Research (CFER) aboard the RV 'Celtic Explorer' in May 2013 and 2015 on the offshore shelves from southern Labrador and eastern Newfoundland, in Northwest Atlantic Fishery Organization (NAFO) subdivisions 2J, 3K, and 3L (Rose & Rowe 2018; Fig. 1). Combined, these subdivisions represent the management unit for the 'Northern cod' stock of Atlantic cod (Templeman 1979, Rose et al. 2000, Smedbol & Wroblewski 2002). Three major trenches or corridors within these regions had previously been identified as important onshore-offshore cod migration pathways: Hawke Channel (HC), Notre Dame Channel (NDC), and the Bonavista Corridor (BC) (Rose 1993). Given their potential importance,

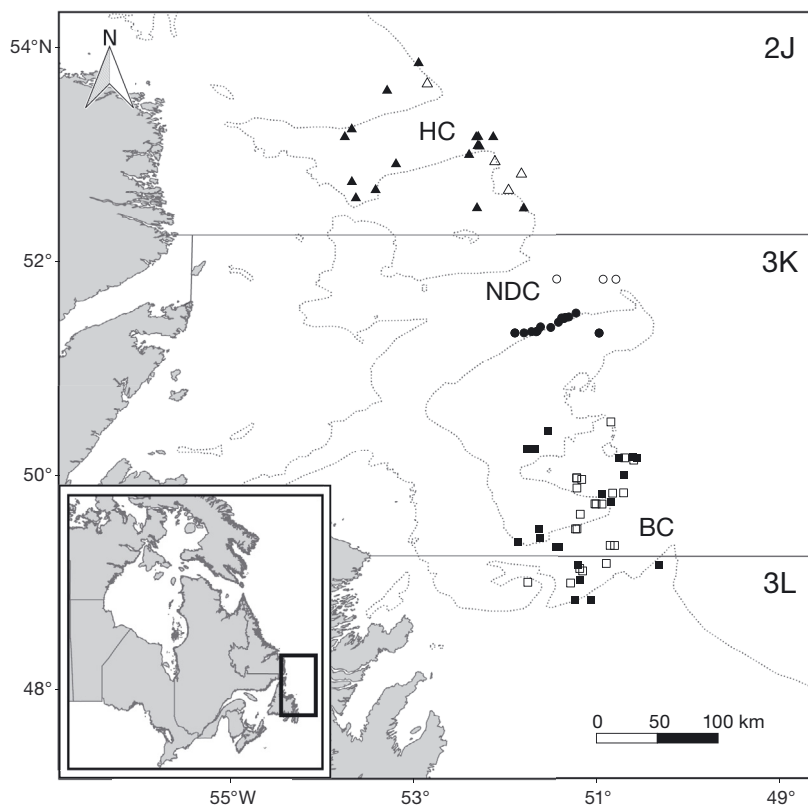


Fig. 1. Newfoundland and southern Labrador, with sampling locations indicated for the 2013 (open symbols) and 2015 (closed symbols) locations within the Hawke Channel (HC, triangles), Notre Dame Channel (NDC, circles), and Bonavista Corridor (BC, squares). The inset outlines the study domain in eastern Canada. The relevant NAFO subdivisions 2J, 3K, and 3L boundaries are also indicated. Dashed lines represent 300 m depth contours. The bathymetry map is reproduced with permission from GEBCO world map 2014 (www.gebco.net), and NAFO subdivisions are reproduced from NAFO (www.nafo.int)

these trenches served as the focal regions for sampling. Set locations were chosen based on information obtained from acoustic signals for cod and other species. Sets in the absence of cod acoustic signals were also undertaken to complement these targeted sets. Sets averaged 11–13 fish species per set (Krumnick & Fisher 2019) with no significant differences in the number of fish species per set between cod targeted sets and other sets (1-way ANOVA: HC, $p = 0.760$; NDC, $p = 0.760$; BC, $p = 0.371$). The following analyses were conducted for each region separately and then pooled for the entire region in order to both assess spatial variation in size spectra and to define trends for the entire region. Data for the fish species relative biomass composition and numbers were collected in May 2013 using a Campelen 1800 trawl (Walsh & McCallum 1997). Samples for nitrogen isotope analysis were collected during May 2015, using a combination of Campelen 1800 and mid-water trawl

(Table S1 in the Supplement, www.int-res.com/articles/suppl/m635p123_supp.pdf).

2.2. Sample collection and preparation

During both years, all fish caught were sorted by species, and standard lengths were recorded. The total biomass of each species was also determined. In cases where a species was particularly abundant, we subsampled 100 randomly selected individuals. In 2015, tissue samples were taken from all fish species, with equal representation from the observed size ranges for each species. From most fish, a transverse sample of dorsal muscle tissue directly posterior to the head was collected at sea, placed in a 1.5 ml centrifuge vial and frozen at -20°C . Frozen stomach samples were also collected from these fish at sea. Remaining fish with small, difficult to sample stomachs were individually labelled and bagged, frozen whole at sea, and later dissected in the laboratory for their muscle tissue and stomachs.

Muscle tissue samples were oven-dried at 75°C for 48 h and homogenized using an amalgamator. The dry, homogenized samples were shipped

to the Cornell University Stable Isotope Laboratory (Ithaca, New York, USA) for weighing and analysis. Approximately 1 mg of the powdered sample was placed into 7×7 mm tin capsules. These samples were flash combusted using a Carlo-Erba NC2500 elemental analyzer coupled online to a Finnigan MAT Delta Plus mass spectrometer for analyses of the nitrogen gases.

2.3. Empirical size spectra

Analyses for this study were conducted in R version 3.5.3 (R Core Team 2019). A visual representation of the analytical methods and inputs is presented in Fig. S1. Fish length data from the 2013 samples were converted to mass of individual fish mostly through species-specific length–weight relationships (Table S2). For the 2248 measured weights, there was

~1:1 correspondence with species-specific length-weight relationships (Fig. S2). However, when the weight of an individual fish was recorded, empirical weights (g) were used. Species-specific biomasses were also adjusted by dividing by the catchability, assumed to be 0.25 (Jennings et al. 2002), unless published species- and size-specific estimates were available (available for 53 % of species sampled; Table S2). To generate the size spectra, we followed recommendations provided by Edwards et al. (2017), although the prescribed maximum likelihood estimate approach departed from the empirical data (Fig. S3). Fish masses were binned into \log_2 mass categories (M). The total observed biomass at M was converted to density (g m^{-2}) by dividing by the swept area of the trawl (distance trawled \times wing spread). Data collected from each set were treated in this manner, and the mean binned biomass density obtained among sets was used to account for varying set durations. These biomass densities were divided by the width of the \log_2 mass category to create a mean binned normalized biomass density (B). Size spectra were then plotted as $\log_{10} B$ as a function of $\log_{10} M$, starting at 64 g, to determine the scaling coefficient between the 2 variables. Separate

analyses were conducted across each sub-region as well as for all 3 sub-regions pooled.

We further assessed variation in size-spectra slopes among size categories and fish guilds. As per Daan et al. (2005), empirical size spectra were analyzed as described above but for 3 separate size groups: small ($M < 4$ kg), medium ($M = 4\text{--}8$ kg), and large ($M > 8$ kg). Five separate size spectra were created for guilds of fish (flatfishes, pelagics, gadoids, elasmobranchs, and demersal mesopredators; Table 1) to assess whether the size spectra slopes observed in guilds differed systematically from the community slope. Guild-specific size spectra were calculated within the size categories identified above, but pooled across regions.

2.4. Quantification of unexploited size spectra

The nitrogen ratios from analyzed fish tissue samples were expressed in delta (δ) notation, representing the parts per thousand deviation from the standard material (i.e. atmospheric nitrogen). The calculation for delta is as follows:

Table 1. Fish species categorized within 5 guilds with percentage of sampled biomass during the 2013 survey presented next to each species. Numbers of individuals in each size category for each guild are also displayed

Guild	Species included (% subgroup biomass)	Size (kg)	Number
Flatfishes	Greenland halibut <i>Reinhardtius hippoglossoides</i> (81.7), American plaice <i>Hippoglossoides platessoides</i> (14.4), witch flounder <i>Glyptocephalus cynoglossus</i> (4.0)	<4	1512
		4–8	0
		>8	0
Pelagics	White barracudina <i>Arctozenus risso</i> (36.0), myctophiids (<i>Notoscopelus</i> sp. and <i>Benthosema glaciale</i> ; 34.5), Atlantic herring <i>Clupea harengus harengus</i> (18.2), capelin <i>Mallotus villosus</i> (9.2), stout sawpalate <i>Serrivomer beanii</i> (1.8), viperfish <i>Chauliodus sloani</i> (0.1), Atlantic argentine <i>Argentina silus</i> (<0.1), anglerfish <i>Oneirodes macrosteus</i> (<0.1), lightless loosejaw <i>Malacosteus niger</i> (<0.1)	<4	478
		4–8	0
		>8	0
Gadoids	Atlantic cod <i>Gadus morhua</i> (99.9), white hake <i>Urophycis tenuis</i> (0.1), Arctic cod <i>Boreogadus saida</i> (<0.1), longfin hake <i>U. chesteri</i> (<0.1), threebeard rockling <i>Gaidropsarus ensis</i> (<0.1)	<4	2728
		4–8	393
		>8	28
Elasmobranchs	Thorny skate <i>Amblyraja radiata</i> (99.9), smooth skate <i>Malacoraja senta</i> (0.1)	<4	91
		4–8	12
		>8	2
Demersal mesopredators	Redfish (<i>Sebastes</i> sp.; 91.1), checker eelpout <i>Lycodes vahlii</i> (3.2), Atlantic wolffish <i>Anarhichas lupus</i> (2.0), Atlantic hookear sculpin <i>Artediellus atlanticus</i> (0.8), marlin-spike <i>Nezumia bairdii</i> (0.7), northern wolffish <i>Anarhichas denticulatus</i> (0.6), Atlantic lumpfish <i>Cyclopterus lumpus</i> (0.3), moustache sculpin <i>Triglops murrayi</i> (0.2), bigeye sculpin <i>Triglops nybelini</i> (0.1), spotted wolffish <i>Anarhichas minor</i> (0.1), alligatorfish <i>Aspidophoroides monopterygius</i> (<0.1), Atlantic poacher <i>Leptagonus decagonus</i> (<0.1), daubed shanny <i>Lumpenus maculatus</i> (<0.1), fourline snakeblenny <i>Eumesogrammus praecisus</i> (<0.1), sea tadpole <i>Careproctus reinhardti</i> (<0.1), shorthorn sculpin <i>Myoxocephalus scorpius</i> (<0.1), snakeblenny <i>Lumpenus lumpretaeformis</i> (<0.1), wolf eelpout <i>Lycenchelys verrilli</i> (0.1), wrymouth <i>Cryptacanthodes maculatus</i> (<0.1)	<4	2292
		4 – 8 kg	2
		> 8 kg	0

$$\delta^{15}\text{N} = \left(\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right) \times 1000 \quad (1)$$

$$R = {}^{15}\text{N}/{}^{14}\text{N} \quad (2)$$

The $\delta^{15}\text{N}$ estimates were then converted to trophic level (TL) estimates using the equation:

$$\text{TL} = \left(\frac{(\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{ref}})}{3.4} \right) + 2 \quad (3)$$

The previous equation assumes a fractionation coefficient of 3.4 (Post 2002). The $\delta^{15}\text{N}_{\text{ref}}$ represents the nitrogen signature of a species close to the base of the food chain, in our case the herbivorous copepod *Calanus finmarchicus* (Dakin 1908, Marshall & Orr 1955, Nejstgaard et al. 1997). A linear relationship was determined between the TL and the logged mass of the fish (M). PPMR was determined from this linear relation by the relation $\text{PPMR} = 10^{1/b}$, where b is the slope of the regression line fitted between the TL and logged mass (Jennings & Blanchard 2004).

The intercept of the theoretical unexploited size spectrum was estimated using primary productivity estimates obtained from the literature (Table S3). A value of $336 \text{ gC m}^{-2} \text{ yr}^{-1}$ (midway between extremes among the estimates shown in Table S3) was used to define the theoretical size structure with error bars derived from the highest ($540 \text{ gC m}^{-2} \text{ yr}^{-1}$) and lowest ($132 \text{ gC m}^{-2} \text{ yr}^{-1}$) published estimates. The primary production does not influence the magnitude of the descending slope but rather the intercept of the theoretical distribution. Primary productivity estimates were converted to annual wet weight (grams) produced per square meter following Greenstreet et al. (1997). The relationship between TL and \log_2 mass category (M) was derived from the PPMR relationship determined previously where $\text{TL} = a + b \log(M)$. The production (P) at each TL that the ecosystem could sustain given this primary production (PP) was calculated as $P_{\text{TL}} = \text{PP} \times \text{TE}^{(\text{TL} - 1)}$, analyzed for 3 values of trophic efficiency ($\text{TE} = 0.1, 0.125, \text{ and } 0.15$), consistent with marine ecosystems in other parts of the world (Ware 2000, Jennings & Blanchard 2004). The production (P) at a given TL was converted to biomass (B) at that TL through the relationship $P:B = 2M^{-0.25}$ (Banse & Mosher 1980). In order to compare to the empirical size distribution, the theoretical distribution was normalized by dividing the biomass estimates by the width of the same \log_2 size categories. The descending slope of the theoretical size distribution was calculated from the linear relationship of the normalized theoretical biomass density (B) and \log_2 body mass category (M). These analyses were conducted at a community level and for each of the 3 sub-regions.

2.5. Statistical analyses

Differences in the slope of both the empirical and theoretical biomass density (B) against body mass (M) between regions was determined using an ANCOVA, with body mass and region as explanatory variables. To test for linearity between the empirical biomass density and body mass, Ramsey's RESET test for functional form was implemented (Ramsey 1969). Differences in the slope of the regression between TL and logged body mass and region were also assessed with an ANCOVA. Furthermore, an ANCOVA was used to determine whether the slope between size categories differed in the regression of TL and logged body mass. The mean TL for fish within the same size range was compared among regions using an ANCOVA predicting TL from region and fish mass.

3. RESULTS

3.1. Species composition

A total of 38 species were recorded during the 2013 survey (Table 1). HC was dominated by redfish (50% by biomass; 50% by numbers) and Atlantic cod (29%; 8%). Similarly, NDC was dominated by Atlantic cod (60%; 34%) and redfish (28%; 41%), while biomass in BC was nearly exclusively composed of Atlantic cod (82%; 29%) with redfish (7%; 37%) making a minor contribution. For the entire study area, the contributions of cod were 78% by biomass and 31% by numbers and those of redfish were 15 and 36%, respectively, with other notable species being Greenland halibut (4%; 7%) and American plaice (1%; 9%). In both 2013 and 2015, BC was more extensively surveyed, resulting in larger sample sizes (Table 1, Table S4). In 2013, no fish larger than 8 kg were collected in HC or NDC, although 1 was caught in HC in 2015. The 2 species whose observed body sizes exceed 8 kg were Atlantic cod and thorny skate.

3.2. Body size and TL relation

The derived TL at which fish fed increased nearly linearly with \log body mass ($p < 0.001$; Fig. 2). For the entire area, the increase in TL with size was described by the linear function $\text{TL} = 0.37 \log(M) + 3.07$. The slope of this relationship represented a species-averaged PPMR of 521:1. When divided by regions, the PPMR was 64:1 within NDC, lower than either BC (966:1) or HC (2110:1) ($p = 0.003$), indicating that

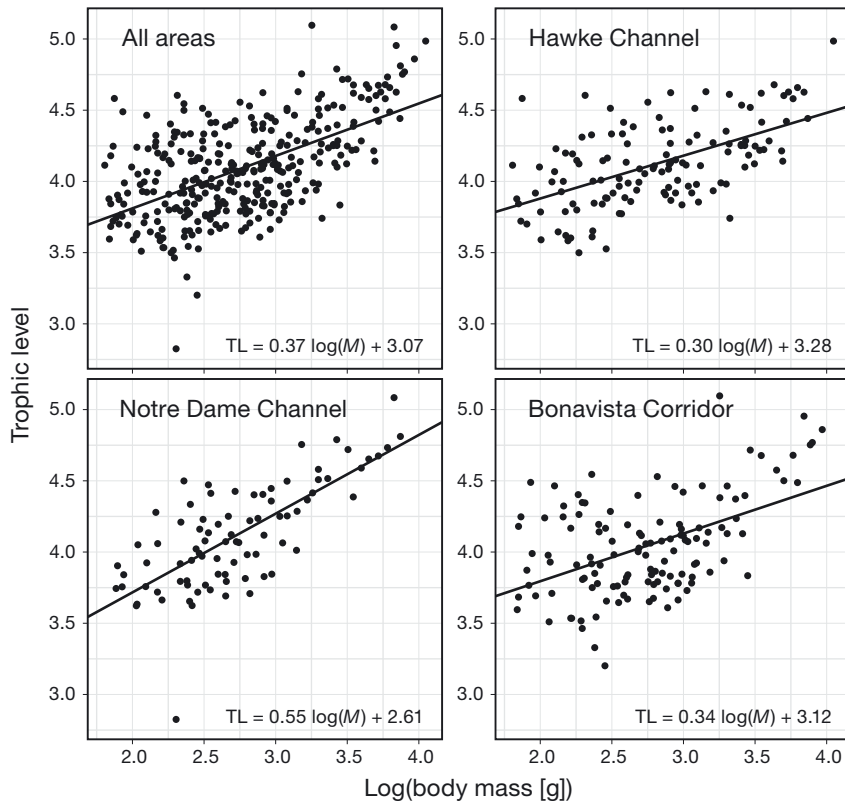


Fig. 2. Regression analysis of the increase in trophic level (TL) with logged body mass (M) to determine predator:prey mass ratios (PPMR) for each region

fish in HC appear to be feeding on smaller prey. There is insufficient evidence to say that the slope of the linear regression between TL and logged body mass varied among small, medium, and large body size categories ($p = 0.27$).

3.3. Theoretical size structure

The slopes of the theoretical size spectra ranged from -0.43 to -0.74 , with lower TE yielding steeper slopes (Fig. 3, Table 2). The descending slopes of HC and BC were comparable, while NDC showed a steeper decline in biomass with increasing body size due to lower PPMR ($p < 0.001$; Table 2).

3.4. Empirical size spectra

As expected, the biomass of fishes declined with increasing body mass ($p < 0.001$; Fig. 3). In the empirical community, and assuming a linear relationship, biomass for the entire pooled regions was observed to scale as $M^{-0.69}$ (Table 3). Slopes within sub-regions (pooled sizes) ranged from -0.69 to -1.04 , although these slopes did not differ significantly ($p = 0.603$; Table 3). In most cases, the relationships were not linear (testing for non-linearity yielded $p = 0.01$ for BC and $p = 0.04$ for NDC) as residuals were not randomly distributed; HC was the exception ($p = 0.50$). The steepest empirical slopes were observed in HC and NDC, and the shallowest slopes in BC (Table 3).

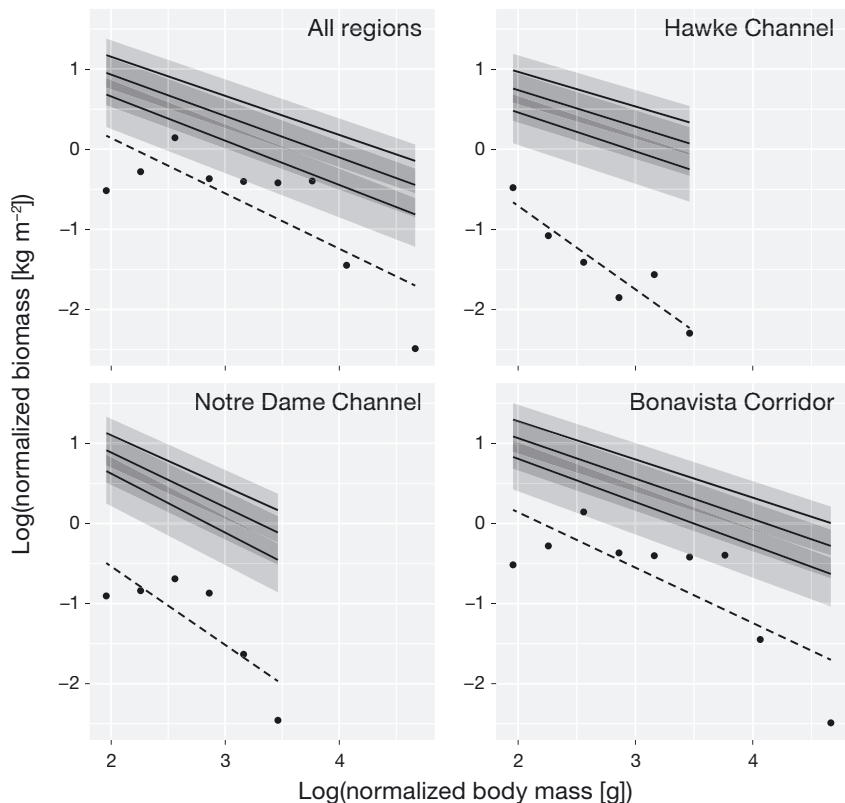


Fig. 3. Comparison of theoretical size structure (solid lines) at 3 levels of trophic efficiency and the empirical size structure regression (dashed line). Points represent the values from the empirical size spectra. The top theoretical line represents the highest trophic efficiency and the bottom the lowest trophic efficiency. The gray bars represent the range of annual primary productivity measured for this area for each theoretical line

Table 2. Descending slopes of theoretical unexploited size spectra for 3 levels of trophic efficiency across the whole sampled region ('total area') and within sub-regions (see Fig. 1)

Area	Trophic efficiency		
	0.1	0.125	0.15
Total area	-0.55	-0.52	-0.49
Hawke Channel	-0.48	-0.46	-0.43
Notre Dame Channel	-0.74	-0.68	-0.64
Bonavista Corridor	-0.54	-0.50	-0.48

Table 3. Descending slopes of empirical size spectra in partitioned regions (see Fig. 1) and fish guilds (see Table 1). Values in parentheses represent the r^2 of empirical size spectra

Subset	Descending slope
Total area	-0.69 (0.59)
Hawke Channel	-1.04 (0.87)
Notre Dame Channel	-0.98 (0.65)
Bonavista Corridor	-0.69 (0.59)
Pelagics	-2.52 (0.83)
Gadoids	-1.02 (0.55)
Flatfishes	-0.75 (0.61)
Elasmobranchs	-0.34 (0.15)
Demersal mesopredators	-1.47 (0.83)

3.5. Variation among guilds

Variation among guilds underlies the overall community size structure. Based purely on biomass, the gadoids (predominantly Atlantic cod) are the dominant guild in this community, representing 77.7% of the fish biomass (pelagics represented 0.2%, flatfish 6.2%, elasmobranchs 0.8%, and demersal mesopredators 15.1%). As such, gadoids were an important group in defining the community trends. Within this group, Atlantic cod has received the most attention in this region. In BC, Atlantic cod represented 78.6% of the fish biomass and 39.6% by numbers in the trawl. These numbers decreased to 75.8% (biomass) and 16.1% (numbers) in NDC and 28% (biomass) and 4.6% (numbers) in HC. The steepest slope was observed among the pelagics, which consisted primarily of barracudina *Notolepis rissoi* and myctophids (*Notoscopelus* sp. and *Benthosema glaciale*) (Table 3). The shallowest slopes were observed in elasmobranchs, primarily thorny skate *Amblyraja radiata*, which likely results from a relative deficit of data from small sample sizes. Flatfish, primarily American plaice *Hippoglossoides platessoides* and Greenland halibut *Rheinhardtius hippoglossoides*, demersal mesopredators, primarily checkered eel-

pout *Lycodes vahli* and redbfish (*Sebastes* sp.), and gadoids also exhibited slopes steeper than that for the whole community (Fig. S4).

3.6. Theoretical vs. empirical comparison

For all regions, TE, and pooled size categories, the empirical biomass density was typically a fraction of an unexploited ecosystem biomass density (Table 4, Fig. 4). For example, in the scenario of TE = 0.1, the combined size classes and regions within the empirical size spectrum represented only 27% (range 16.8–68.7%) of the theoretical biomass (Fig. 4A). The only scenario where the empirical biomass fell within the range of the theoretical biomass was for BC when the lowest TE and primary productivity were used (Fig. 4D). Consistently across regions with increasing body masses the percentage of the theoretical biomass represented by the 2013 empirical biomass distribution decreased, such that at the largest size category the empirical distribution was between 0% (NDC and HC, where no large fish were sampled) and 14.4% (BC, assuming TE = 0.1 and low primary productivity) of the theoretical distribution (Table 4, Fig. 4). The mean TL at approximately 4.04 was not found to vary with region ($p = 0.18$) and did not differ significantly between the empirical and the theoretical analyses ($p = 0.29$).

4. DISCUSSION

Quantifying the magnitude and timelines of marine fish community recoveries is challenged by appropriate characterization of baseline community conditions within long-exploited systems and changing ocean conditions (Pauly 1995). Frequently, however, researchers establish biomass baselines using historical biomass estimates or data from nearby unexploited environments (e.g. Friedlander & DeMartini 2002, Sandin et al. 2008). Yet such baselines may still contain the remnants of anthropogenic effects such as human-induced climate change, pollution, etc. Indicators at the community level of organization are reliable and robust to sampling variability and ecosystem differences, yet sensitive to ecosystem changes and are therefore useful for management (Fulton et al. 2005). The empirical descending slopes and the biomass densities relative to a theoretical pristine size structure may function as ecological indicators (Jennings & Blanchard 2004, Shin et al. 2005). We therefore sought to approximate a theoret-

Table 4. Comparison of theoretical biomass density estimates across 3 trophic efficiencies (TE) with the biomass density estimate from the 2013 survey. The '±' values represent the range of primary productivity estimates investigated. Percent columns indicate the percent of the theoretical biomass densities at 3 TE values represented by the 2013 empirical biomass densities (presented in the final column)

Region	Body mass class (kg)	TE = 0.1		TE = 0.125		TE = 0.15		2013 Biomass density (g m ⁻²)
		Biomass density (g m ⁻²)	%	Biomass density (g m ⁻²)	%	Biomass density (g m ⁻²)	%	
All regions	All sizes	77.2 ± 47.0	28.2	164.9 ± 100.1	13.2	306.8 ± 186.2	7.1	21.8
	<4	28.8 ± 17.6	60.3	59.2 ± 36.0	29.4	106.7 ± 64.7	16.3	17.4
	4–8	25.6 ± 15.5	13.2	55.3 ± 33.6	6.4	104.0 ± 63.1	3.6	3.8
	>8	22.8 ± 13.9	2.6	50.4 ± 30.6	1.1	96.1 ± 58.4	0.6	0.6
Hawke Channel	All sizes	84.5 ± 51.3	6.2	179.21 ± 108.8	2.9	331.5 ± 201.3	1.6	5.2
	<4	29.3 ± 17.8	17.4	61.4 ± 37.8	8.3	114.3 ± 71.7	4.5	5.1
	4–8	28.7 ± 17.4	0.3	60.2 ± 36.1	0.2	108.8 ± 63.9	0	0.1
	>8	26.5 ± 16.1	0	57.7 ± 35.0	0	108.4 ± 65.6	0	0
Notre Dame Channel	All sizes	50.0 ± 30.4	9.6	110.2 ± 66.9	4.4	210.9 ± 128.1	2.3	4.8
	<4	22.8 ± 13.8	20.6	47.5 ± 28.8	9.9	86.7 ± 52.7	5.4	4.7
	4–8	15.0 ± 9.1	0.4	34.2 ± 20.8	0.2	67.0 ± 40.7	0.1	0.1
	>8	12.2 ± 7.4	0	28.5 ± 17.3	0	57.2 ± 34.7	0	0
Bonavista Corridor	All sizes	90.5 ± 54.9	30.1	190.5 ± 115.7	14.3	350.2 ± 212.6	7.8	27.2
	<4	32.6 ± 19.8	65.7	66.2 ± 40.2	32.3	118.1 ± 71.7	18.1	21.4
	4–8	30.3 ± 18.4	17.8	64.6 ± 39.2	8.8	116.7 ± 69.7	4.3	5.8
	>8	27.6 ± 16.8	2.9	59.7 ± 36.2	1.3	112.3 ± 68.2	0.7	0.8

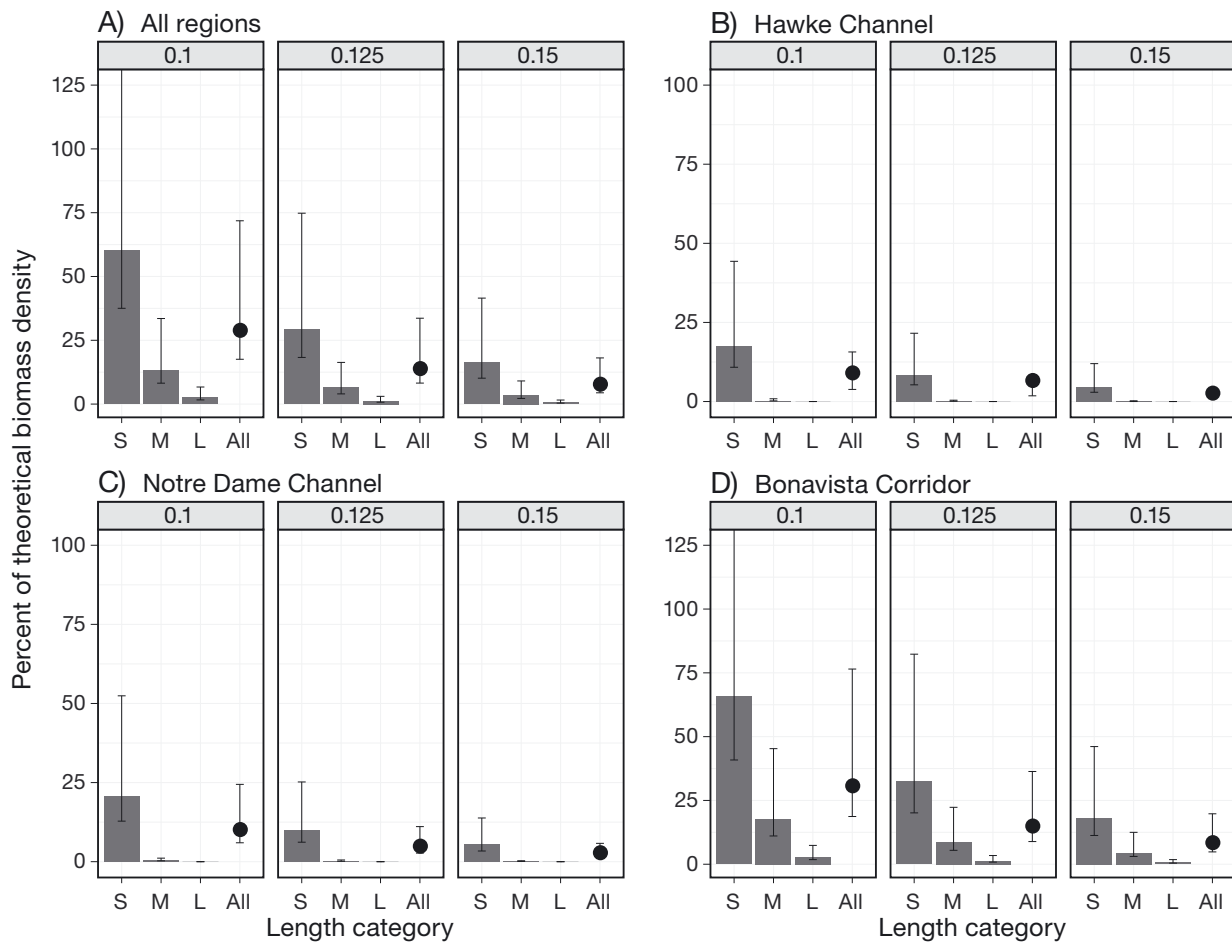


Fig. 4. Measured average biomass density as a percentage of the theoretical pristine biomass density by size class (S: small, M: medium, L: large) and among pooled size classes ('all') calculated for 3 levels of trophic efficiency (0.1, 0.125, and 0.15) within (A) the pooled regions, (B) Hawke Channel, (C) Notre Dame Channel, and (D) Bonavista Corridor. Error bars represent the range of primary productivity estimates for this region

ical pristine ecosystem size structure and respective biomasses based on ecological principles in order to provide an indicator of ecosystem recovery. We acknowledge that our study represents only one year of data with no seasonality in the interest of avoiding potential temporal confounding variables. Though inspired by Jennings & Blanchard (2004), our work expands to include modern recommended approaches towards size spectra analysis as prescribed by Edwards et al. (2017), enhanced data on catchabilities, uncertainties around input parameter values (including primary productivity), and consideration of different fish guilds and size groupings to analyze a recovering ecosystem.

Among our most striking findings are the apparent distances between the contemporary biomass densities of small, medium, large, or pooled size classes and the theoretical biomass densities within and among regions of the Newfoundland and Labrador continental shelf (Figs. 3 & 4). The only cases where the empirical spectrum was within range of the theoretical size spectra was for small fish in the situation where primary productivity and TE were both assumed to be low. Since the moratoria on groundfish fishing (some of which were first initiated in 1992), this region represents a recovering ecosystem following overexploitation, providing a system in which to address the unresolved question of whether and when cessation of fishing allows a community to recover towards the unexploited abundance–body mass structure (Jennings & Blanchard 2004, Fung et al. 2013).

Important regional variations were also observed across both the empirical and theoretical size spectra. BC, the southern-most and most biodiverse of the regions analyzed (Krumsick & Fisher 2019), was characterized by empirical spectra closest to the theoretical spectra. This result aligns with observed recovery rates of Atlantic cod in these regions. It has been observed that the recovery rates in BC have proceeded faster than the recovery rates in either NDC or HC (Lilly et al. 2008, Rose & Rowe 2015, DFO 2018). HC had the highest PPMR of all the regions studied, resulting in the shallowest descending slopes of the theoretical spectra. Such higher PPMRs are associated with shorter food chains such as one might expect from a predominantly invertebrate diet with relatively reduced food chain length (Jennings & Warr 2003). Although a wide range of PPMRs is observed, they lie within the range of biologically feasible values (Nakazawa et al. 2011, Tsai et al. 2016). While the study area is treated as a single management unit for Atlantic cod (DFO 2018, 2019), a great deal of community heterogeneity is evident in this region. This

regional heterogeneity in PPMR is consistent with complementary studies investigating stomach contents, trophic interactions, and isotopic niches (Krumsick & Rose 2012, Krumsick & Fisher 2019, K. Krumsick & J. Fisher unpubl. data). In light of the observed differences among the 3 focal regions, they are treated in this study as 3 separate ecosystems. These regions are not isolated from each other, and migration, to a small extent, between these regions has been documented for Atlantic cod (Templeman 1979, Smedbol & Wroblewski 2002) and Greenland halibut (Bowering 1984). However, despite this assumption, clear differences are observed among communities within sub-regions and as such they should not be considered functionally identical.

There are some potential limitations to the choice of samples and analyses. We used major Atlantic cod migration routes as a means of dividing the region based on biological characteristics, but this is by no means the only way these areas could be characterized. However, the sampled sub-regions are representative of the broader stock distributions for dominant species, as these species are known to aggregate along and within these offshore channels to spawn and escape cold, shallow shelf waters in spring (Fitzpatrick & Miller 1979). The spatio-temporal and taxonomic breadth of sampling may be seen as another potential limitation. The sampling extent assumes that the surveyed region is representative of the wider area. Further, this study represents only 1 year of fish size data, with no characterization of potential seasonality in isotopic signatures, fish lengths, or species composition. A multi-year study of how these size spectra have changed with time (e.g. Daan et al. 2005) could provide further understanding of this ecosystem but was beyond the scope of this study. Furthermore, future analyses could assess whether these trends persist across seasons. Such consideration of temporal variability would help compare spatial vs. temporal variability within ecosystems with the potential for changes in prey dominance throughout the year.

As with Jennings & Blanchard (2004), invertebrates were not included in our study. Although invertebrates are an essential part of the ecosystem, the only species that we had reliable body mass data for were *Pandalus* shrimp and snow crabs. However, all caught invertebrate species were smaller than the 64 g cutoff point presented (with the exception of jellies, sea anemones, and large snow crabs). Despite our attempts to account for the lack of representation of smaller body sizes through the use of catchability estimates, our data of these smaller sizes were under-

represented and as such excluded from the analysis to avoid a potential bias. We also assumed a linear relationship between logged body mass and TL, and as such, a constant PPMR across sizes. Other studies, however, have indicated that PPMR would decrease with increased body mass (Barnes et al. 2010). We investigated this potential by fitting a number of potential functions to the plot and found that the fit was not improved over a simple linear function. As the PPMR was could not be proven to be non-linear, we therefore also assumed a constant TE through the relationship $TE = PPMR^{\beta + 0.75}$, where β is the descending slope of the size spectrum (Barnes et al. 2010). The size spectra presented in this study also do not take into account asymptotic size of the species nor other species-specific factors which could influence size spectra, such as variable assimilation efficiencies, daily intake, and search volume (Andersen & Beyer 2006, Persson & de Roos 2007). Finally, our analyses assume that size is the primary determinant of TL (Cohen et al. 1993, Romanuk et al. 2011), productivity (Banse & Mosher 1980, Schwinghamer et al. 1986, Andersen et al. 2009), and biomass within the ecosystem (Kerr 1974, Blanchard et al. 2017, Edwards et al. 2017).

Our analyses also highlight the influence of TEs and primary productivity estimates on theoretical size spectra. TE, combined with the observed regional variation in PPMR, determined the rate of decline of theoretical size spectra. These descending slopes are vital to understanding anthropogenic influences on community size spectra, as steeper slopes indicate a heavier impact on communities (Shin et al. 2005, Blanchard et al. 2017). This parameter alone is difficult to estimate, being influenced by season (Gaedke & Straile 1994), water visibility (Irigoiien et al. 2014), water temperature (Calbet et al. 2014), habitat complexity (Grabowski & Powers 2004), biodiversity (Ganfheldt et al. 2005), and predator and prey size diversity (Barnes et al. 2010, García-Comas et al. 2016). A range of TEs was presented to account for this uncertainty. The primary productivity determined the intercept of the theoretical size spectra. A range of estimates is provided, corresponding with estimated annual primary production for these regions to control for potential seasonal variability. In addition to uncertainty in the measurement of this parameter, it is expected to vary from year to year as it is influenced by nutrient availability (Howarth 1988), water temperature (Taucher & Oschlies 2011), and vertical mixing (Neale et al. 1998). The range of primary productivities used may not represent a pristine historical environment but rather a modern esti-

mate of primary production by which we can assess the impacts of long-term exploitation on fish communities. We therefore assume that the primary production of the exploited ecosystem would not vary substantially from that of a theoretical unexploited one. The model also makes the assumption that fish production is related to primary production, a relationship first proposed by Hrbáček (1969). From this relationship, we obtained estimates of potential fish production to obtain our biomass estimates. This approach is naturally a simplification of reality, as it does assume a high ecotrophic efficiency, a value which we do not presently have accurate estimations for, although previous work has assumed a value of 0.95 for most species (Bundy et al. 2000).

Most size-based studies assume a single rate of decline of B with M for the entire community (Macpherson et al. 2002, Jennings & Blanchard 2004, Fock & Czudaj 2019), although there are exceptions (e.g. Daan et al. 2005). Newfoundland and Labrador size spectra, however, appear to exhibit different rates of decline for different sized fishes. The rate is lower and even comparable at smaller sizes, reaching a turning point and increasing rapidly between 1.4 and 5.5 kg. With this trend, the proportion of the theoretical biomass represented by the empirical distribution decreased with increasing size, consistent with other studies (Jennings & Blanchard 2004, Petchey & Belgrano 2010). Several factors contribute to the observed departure. Given that Atlantic cod is the main contributing species for these larger size categories (96% by mass and 97% by numbers sampled in categories >3.5 kg), this turning point occurs between the ages of 8 and 10 yr (Cadigan 2016). The cod at the observed turning point would therefore have been from a mid-2000s year class. A time delay is expected for communities to recover (Frank et al. 2011, Fung et al. 2013), and therefore this point may represent signs of recovery of fish populations. Furthermore, with fewer larger predators to consume the mid-sized fish, their biomass might be expected to be relatively higher due to a release from predation (Andersen & Rice 2010). The rapid decline in larger individuals and the small percentage of the theoretical biomass represented by the observed biomass density is problematic, as not all biomass can be considered equal in regards to recovery. The larger, older individuals are essential to rebuilding the over-exploited fish stocks due to substantial contribution of large females to stock productivity (Longhurst 1998, Hixon et al. 2014), yet the size classes that could contribute most to recruitment and the recovery of fish stocks are the ones that are furthest away

from the theoretical pristine distributions (Xu et al. 2013).

Among fish guilds, all (except the elasmobranchs) exhibit steeper slopes than the theoretical size spectra (Tables 2 & 3). The gadoids, dominated by Atlantic cod (99% of gadoid biomass), were found to be primary drivers of the observed patterns of the community size structure, as they contributed the greatest proportion of sampled fish abundances and a wide range of sizes. Recent stock assessments for the spawning stock biomass of northern cod found the stocks to be at approximately 37% of the limit reference point (DFO 2018). The steepest slope observed was that of the pelagics, driven by their high biomass in the smallest size class, then serving as forage fish prey for upper trophic predators. Flatfish and demersal mesopredator fish exhibited slopes of intermediate magnitude. The vast majority of the demersal mesopredators were relatively small species (87.6% of the demersal mesopredator fish from the 2013 survey being less than 0.5 kg), with wolffish, redfish, and grenadiers rarely reaching larger sizes in this region (Templeman 1986, Power & Orr 2001, González-Costas 2010). The observed drop may therefore represent fewer species and fewer larger individuals. Similar to Atlantic cod, flatfishes have shown declines in abundance, being a fraction of their historical levels (Healey et al. 2010, Morgan et al. 2013, DFO 2019). The observed size spectra are associated with reduced size structure and spawning stock biomass compared to historical flatfish populations as well as size structures in other regions, potentially arising from poor recruitment and high bycatch mortality (Morgan et al. 2013, DFO 2019). The only other guild that showed representation in various size categories were the skates as part of the elasmobranch guild. These fish were not as plentiful in numbers, resulting in fairly scattered empirical size distributions with a flat slope.

Our consistent finding of low percentages of the theoretical biomass represented by the empirical spectra and low representation by the largest size classes is not unique to the Newfoundland and Labrador fish communities. Jennings & Blanchard (2004) found their North Sea empirical slopes to be 7 to 15 times greater than the theoretical slopes, whereas we found the slopes to be only 2 to 9 times greater. Their unexploited biomass densities, being between 0.8 and 9.2% of the theoretical biomass density (for TE of 0.125), were typically lower than those observed in our study. Other studies around the world found similarly small proportions of empirical biomass in exploited ecosystems compared to their

own unimpacted biomass estimates, despite methodological differences (e.g. 1.5%, Friedlander & DeMartini 2002; 10%, Christensen et al. 2003; 5.3–21.5%, Myers & Worm 2003; 5%, Tang et al. 2003; 0.8–33.3%, McClanahan et al. 2007; 25%, Sandin et al. 2008). Although the definition of un-impacted biomass varies among these studies, as differing baseline determination methods were used, the overarching results of exploitation on fish communities are consistent. Our community analyses further illustrate that these differences between the observed state of community size spectra and a pristine state can persist even following decades of fisheries moratoria. The combination of empirical and theoretical size spectra provides a basis from which we can establish indicators for this ecosystem. Many studies have attempted to measure ecosystem recovery based on a previous ecological state, despite the fact that this state may already have been heavily impacted by human activity (e.g. Neubauer et al. 2013, Pedersen et al. 2017). Theoretical size spectra, such as those presented in this study, seek to represent an ecosystem prior to anthropogenic interference (Hunter 1996), thereby providing a range of community reference points with which to direct and evaluate community rebuilding goals (Jennings & Dulvy 2005, Shin et al. 2005). Furthermore, these benchmarks may be used to set target biomass densities for recovering communities. Aiming for desired biomass densities targets at a set proportion of these theoretical densities may be helpful towards facilitating ecosystem recovery. The present study is not prescriptive in defining such targets, as they require contributions from society, but these results illustrate the wide range of potential targets. Upon setting these targets, analyses of the present empirical size spectra slopes and biomass density estimates provide an indication of the distance to the desired target state from which managers can assess the effectiveness of population and ecosystem based management decisions.

Given the variables present within the model, factors that would promote recovery and increased observed biomass densities include:

- (1) Increasing primary productivity to increase the intercept of the size spectra. This would also require that the extra production was consumed and depends on the nature of the links between members of the food web.

- (2) Decreasing PPMR to decrease the descending slope of the size spectra. In order to achieve this, diversity and size of prey would need to be increased to account for a range of sizes and availability of higher-quality prey.

(3) Increasing TE, thereby decreasing the descending slope. This stage could be facilitated through, for example, increases in lipid-rich prey and/or prey that is more effectively digested. The recent 'capelin hypothesis' limiting Atlantic cod recovery is more or less based on altering (2) and (3) (Rose & O'Driscoll 2002, Buren et al. 2014, Mullowney & Rose 2014).

(4) Modifying future fishing practices such that larger fish are not preferentially removed. This removal steepens the descending slope via the larger, more productive individuals which are essential for population recovery (Birkeland & Dayton 2005, Hixon et al. 2014).

Of these factors, the only one which we could feasibly alter and manage would be the modification of future fishing practices in order to increase the descending slopes of the size spectra.

The Newfoundland and Labrador fish communities are presently in a state recovering from overfishing in combination with changing ocean conditions which occurred in the late 1980s and early 1990s (Rice 2002, Pedersen et al. 2017). The removal of large fishes and subsequent expansion of lower TL populations led to ecosystem changes (Frank et al. 2006) and the addition of new invertebrate fisheries (Schrank 2005, Mather 2013). Contrary to recent portrayals of this ecosystem as one undergoing 'incipient recovery' relative to data collected in 1981 (Pedersen et al. 2017), our study shows that some sub-areas and size components have exhibited little recovery at the community level. While a single species may recover relatively quickly, our results support that a damaged community may take decades to recover community- and size-based characteristics (Frank et al. 2011, Fung et al. 2013). Conventional targeted fishing methods have resulted in selective removal of specific components of the ecosystem that have community-wide impacts (Pauly et al. 1998, Garcia et al. 2012). These impacts are exacerbated through the common practice of serial addition of low TL fisheries (Essington et al. 2006). Instead of heavily removing top predators, balanced harvesting has been proposed such that moderate removal of fish will take place across body sizes within the community and thereby ideally reduce damage to fish communities and allow for greater sustainable biomass yields (Garcia et al. 2012, Law et al. 2012, Rochet & Benoît 2012). Such balanced harvesting reduces the impacts of fishing mortalities, such that productivities approach more natural levels, and improves ecosystem resistance to disturbances (Law et al. 2012). Although this approach to ecosystem based management has been criticized as unrealistic in its simplification of reality

and the expected amount of micromanagement required for perfect implementation (Andersen et al. 2016, Froese et al. 2016, Reid et al. 2016), others argue it is still a viable solution if implemented properly (Borges et al. 2016, Howell et al. 2016, Reid et al. 2016, Plank et al. 2017). Discard bans have been proposed as a means to implement balanced harvesting, based on the idea that species with higher productivity will be more likely to be caught (Garcia et al. 2011, Borges et al. 2016), although this approach could have negative impacts for species with conservation concerns (Heath et al. 2014). As a moderate alternative, it has been recommended to gradually reduce fisheries discards to a level that would facilitate ecosystem stability (Fondo et al. 2015). In regards to first steps forwards towards a balanced harvesting approach, diversifying the catch, not only by species but also by sizes caught, would distribute the impact of fishing. In order to facilitate this shift, the implementation of a flexibly métier-based approach shows potential (Reid et al. 2016). This extra catch, however, has at present no market value. To facilitate cooperation of fishing fleets, either a market would need to be made for the unwanted bycatch or a strong incentive would need to be provided to comply. By increasing the combinations of vessels and gear configurations to increase diversity of overall catches in addition to adequate reporting of catches, cooperation of fishing fleets, at least partial retention of discard, and an adaptive approach to reduce stress on species of concern (such as wolffish, which are protected by the Canadian Species at Risk Act), we may approach a theoretical pristine ecosystem state and thereby limit damaging anthropogenic influences.

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