

1                   **End-to-end food web control of fish production on Georges Bank**

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7  
8 Abstract

9  
10 The ecosystem approach to management requires the productivity of individual fish  
11 stocks to be considered in the context of the entire ecosystem. In this paper, we derive an  
12 annual end-to-end budget for the Georges Bank ecosystem, based on data from the  
13 GLOBEC program and fisheries surveys for the years 1993-2002. We use this budget as  
14 the basis to construct scenarios that describe the consequences of various alterations in  
15 the Georges Bank trophic web: reduced nutrient input, increased benthic production,  
16 removal of carnivorous plankton such as jellyfish, and changes in species dominance  
17 within fish guilds. We calculate potential yields of cod and haddock for the different  
18 scenarios, and compare the results with historic catches and estimates of maximum  
19 sustainable yield (*MSY*) from recent stock assessments. The *MSYs* of cod and haddock  
20 can be met if the fish community is restructured to make them the dominant species in  
21 their respective diet-defined guilds. A return to the balance of fish species present in the  
22 first half of the 20<sup>th</sup> century would depend on an increase in the fraction of primary  
23 production going to the benthos rather than to plankton. Estimates of energy flux through

24 the Georges Bank trophic web indicate that rebuilding the principal groundfish species to  
25 their *MSY* levels requires restructuring of the fish community and repartitioning of energy  
26 within the food web.

27

28 Keywords: community dynamics, ecosystem-based management, Georges Bank, marine  
29 fish , end-to-end.

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38 Introduction

39

40 The super-abundance of cod on the fishing grounds of the northwest Atlantic  
41 fueled the development of early settlements in North America (Kurlansky, 1997;  
42 Rosenberg *et al.*, 2005). The collapse of cod and other principal groundfish stocks was  
43 caused primarily by excessive fishing mortality, but the delayed recovery of some stocks  
44 has been attributed to several factors in addition to over-fishing. Climate change  
45 (Beaugrand *et al.*, 2003), regime shifts (Choi *et al.*, 2004), trophic cascades (Frank *et al.*,  
46 2005), and habitat disturbance (National Research Council, 2002) have all been invoked

47 as causes of ecosystem change, while proliferation of pelagic fish species (Frank *et al.*,  
48 2005), elasmobranchs (Myers *et al.*, 2007), jellyfish (Jackson *et al.*, 2001) and  
49 crustaceans (Worm and Myers, 2003) are described as consequences. These explanations  
50 are based predominantly on correlations between individual species or trophic groups and  
51 do not quantify the changes in energy fluxes within the overall food web.

52 Measures to halt over-fishing and to rebuild depleted ground-fish stocks (effort  
53 reduction, gear modification, and area closures) were implemented by the New England  
54 Fishery Management Council starting in 1993 and are continuing with subsequent  
55 amendments to the fishery management plans (Fogarty and Murawski, 1998). The US  
56 Sustainable Fisheries Act mandates rebuilding of over-fished stocks to levels capable of  
57 sustaining maximum sustainable yield (*MSY*) within 10 years (Safina *et al.*, 2005). *MSY*  
58 estimates are uncertain, not only because they require knowledge of the productivity and  
59 compensatory capacity of each stock, but also because they often imply rebuilding to  
60 levels beyond those observed in recent decades. Further, it is very difficult to derive  
61 quantitative estimates of the abundance of the pristine stocks, either from historical data  
62 (Rosenberg *et al.*, 2005) or by solving for the unfished biomass from population models  
63 (Myers *et al.*, 2001). As fish stocks begin to rebuild there is some doubt as to whether  
64 *MSY* levels of individual stocks can be attained collectively, given increases in non-  
65 commercial species (Link, 2007) and other changes in the marine ecosystem. Decreased  
66 growth rates, particularly in haddock (Northeast Fisheries Science Center, 2008), can be  
67 interpreted as density- dependent growth caused by limited food supply.

68 A new assessment of the Georges Bank ecosystem (Fig. 1) provides estimates of  
69 production at all trophic levels (Steele *et al.*, 2007). We use a unified version of this web

70 to calculate the effects on all trophic groups of a range of adjustments to the internal  
71 structure of the ecosystem. These different scenarios determine the consequent changes in  
72 production of the three fish guilds, planktivores, benthivores and piscivores (Fig. 1). We  
73 estimate the potential production of cod, a piscivore and haddock, a benthivore, under  
74 different food-web scenarios by using the maximum fraction that the individual species  
75 contribute to the trophic guilds. We compare these scenarios with observed patterns of  
76 yields of cod and haddock during the 20<sup>th</sup> century. Finally, we evaluate the extent to  
77 which rebuilding the cod and haddock stocks to *MSY* levels is constrained by the basic  
78 productivity of the ecosystem.

79

80

81 Food-web Analysis [main heading]

82

83 A general equation for a prey-predator food web (Steele, 2009) is

84

85 
$$\frac{dB_i}{dt} = e_i \left( \sum_j Q_{ij} + G_i \right) - \sum_i Q_{ij} - L_i \quad (1)$$

86

87 where  $B_i$  = the biomass of “trophic component”  $i$ ,  $Q_{ij}$  = rate at which  $B_j$  is consumed by  
88  $B_i$ ,  $G_i$  = gains from external sources,  $L_i$  = losses from the system, and  $G_i, L_i > 0$ . The  
89 transfer efficiency,  $e_i = \text{Production } (P_i) / \text{Consumption } (C_i)$ , is assumed constant for each  
90 component  $i$ .

91 The units of biomass can be energy, live weight, particulate organic carbon or a  
92 nutrient such as nitrogen. In the last case, “consumption” can include nutrients recycled

93 from heterotrophs to autotrophs. This is the most general formulation, with the  $Q_{ij}$  as  
94 variables. Because there are typically many more  $Q_{ij}$  than equations, the usual practice is  
95 to associate a single variable with each compartment – biomass, production or  
96 consumption rate – and to linearize the system, permitting matrix solutions for the steady  
97 state. There are two options:

98

99 (A)  $Q_{ij} = a_{ij} P_j \quad a_{ij} \geq 0$  (bottom-up)

100 and

101 (B)  $Q_{ij} = b_{ji} C_i \quad b_{ji} \geq 0$  (top-down).

102

103 Option (A) follows the expected direction of energy flux, with production by prey  
104 determining intake by predators (e.g. Steele, 1974; Sissenwine *et al.*, 1984). Whereas for  
105 (B) consumption by the predator determines output from the prey (Christensen and Pauly,  
106 1993). Thus (A) describes “bottom-up” and (B) describes “top-down” control.

107

108 Application to Georges Bank [subheading]

109 Recently, the desire to construct end-to-end budgets that encompass external  
110 forcing from both climatic change and fishing, has led to combinations of the two  
111 approaches (Aydin *et al.*, 2005; Field *et al.*, 2006; Plaganyi, 2007) with bottom-up  
112 depictions forced by nutrient fluxes into the system (e.g. NEMURO; Fuji *et al.*, 2002)  
113 and top-down treatments starting from fisheries yields (e.g. ECOPATH; Christensen and  
114 Pauly, 1993). Steele *et al.* (2007) followed this general approach, dividing the ecosystem  
115 components into a lower and upper trophic webs because of their disparate space/time

116 scales and different relation to physical processes (Steele and Collie, 2005). The lower  
117 food web is driven by nutrient recycling, and by physical influx of NO<sub>3</sub>-rich deeper water  
118 with concomitant export off Georges Bank of near-surface water and associated plankton.  
119 To encompass the spatial and temporal variability Steele *et al.* (2007) constructed nine  
120 budgets for three seasons in three distinct hydrographic regimes on Georges Bank. The  
121 output from the nine budgets was used to estimate the annual average fluxes from the  
122 lower to the upper components of the web. The data on NO<sub>3</sub> fluxes to drive this part of  
123 the system, and the data on plankton and benthos to constrain the output were derived  
124 largely from GLOBEC surveys from 1995 to 1999 (Wiebe *et al.*, 2001). The output is  
125 expressed as annual average production (gC m<sup>-2</sup> yr<sup>-1</sup>) of mesozooplankton, suspension-  
126 feeding macrobenthos, and deposit-feeding macrobenthos (Fig.1).

127 Fish biomass data from trawl surveys on Georges Bank from 1963 to 2002  
128 (Smith, 2004; Steele *et al.*, 2007) were partitioned as piscivores, planktivores and  
129 benthivores (Table 1) based on fish diets (Garrison and Link, 2000). For the budget  
130 calculations we used the decade 1993-2002, which is coincident with the period of the  
131 Georges Bank GLOBEC field program. Further, we assumed (1) the fish eaten by other  
132 fish are juvenile pre-recruits (Overholtz, 2000) that eat predominantly zooplankton, and  
133 (2) this piscivory is the dominant source of mortality for the pre-recruits. These data and  
134 assumptions permitted us to make top-down estimates of the food requirements of the  
135 fish communities on Georges Bank in terms of two functional, rather than species,  
136 groups—total plankton and total benthos (Fig. 1). The top-down and bottom-up fluxes  
137 were matched for the decade 1993-2002 by estimating the required fluxes through the  
138 invertebrate carnivore components of the plankton and benthos (Fig. 1) and comparing

139 these fluxes with the available observations (Steele *et al.*, 2007). Flux estimates for these  
140 components of the food web generally have relatively large uncertainties, and so are often  
141 used to reconcile web budgets (Mackinson and Daskalov, 2007; Link *et al.*, 2008).

142

143 Main findings of previous work [subheading]

144 Three patterns of variability in the Georges Bank ecosystem, which are influenced  
145 by some combination of climatic change and fishing pressure, are relevant to this  
146 analysis.

147 (1) The 40 years of data for fish populations revealed great inter-annual and inter-  
148 decadal variation in species composition (Steele *et al.*, 2007; Gifford *et al.*, 2009) and in  
149 the three feeding guilds (Fig. 2a). Over time the species composition shifted from  
150 benthivores in the first decade, to piscivores in the third decade, and planktivores in the  
151 second and last decades (Fig. 2a). The species in each trophic guild actually feed to  
152 different degrees on all three prey categories (Table 1). Benthivores (e.g., haddock and  
153 ocean pout) and planktivores (e.g., herring and mackerel) are more restricted in their  
154 diets, but piscivores (e.g., cod and winter skate) have an average intake spread fairly  
155 evenly among plankton, benthos and juvenile fish. The piscivores should in fact be  
156 termed omnivores, but we retain the conventional nomenclature to emphasize predation  
157 on fish in the food web. Partitioning of consumption among guilds will be altered by  
158 changes in the lower trophic web.

159 (2) Fish consumption of plankton plus benthos (Fig. 2b) showed a marked  
160 increase in total food intake by fish after the first decade of the time series. Steele *et al.*  
161 (2007) attributed the markedly lower consumption during 1963-1972 to lower primary

162 production resulting from a significantly decreased concentration of NO<sub>3</sub> (Petrie and  
163 Yeats, 2000) in an intrusion of the cold Labrador Current (Pershing *et al.*, 2001) at the  
164 shelf edge. Because the food web model assumes linear responses, reductions in primary  
165 production are distributed proportionally among the three trophic groups.

166 (3) There was a marked decrease in benthos as a fraction of total food  
167 consumption by fish (Fig. 2c). Steele et al (2007) attributed this to a decrease in the  
168 epifaunal suspension feeders that compete for phytoplankton (Fig. 1), possibly due to  
169 habitat destruction (National Research Council, 2002; Hermsen *et al.*, 2003).

170

171

172 Bottom-up representation of the end-to-end food web [main heading]

173 In this study, we have converted the top-down and bottom-up components to a  
174 single bottom-up representation of the annual average production by each element of the  
175 total food web in carbon units. For the fish components, we took averages for the decade  
176 1993-2002, which corresponds most closely to the GLOBEC years used for the lower  
177 web calculations. For the lower web, we took weighted averages over the spatial  
178 domains and seasons.

179 From equation (1) the resultant expression for a bottom-up food web at steady  
180 state is:

181

$$182 \quad e_i \left( \sum_j a_{ij} P_j + G_i \right) - \sum_i a_{ij} P_i - f_i P_i = 0. \quad (2)$$

183 Since  $\sum_i a_{ij} = 1$ , then

184 
$$P_i = e_i \left( \sum_j a_{ij} P_j + G_i \right) - f_i P_i \quad (3)$$

185

186 The matrix  $[a_{ij}]$  is given in Table 2, and the vectors for  $e_i$  and  $f_i$  in Table 3. Upper closure  
187 is obtained by total removal of fish guilds by fishing and top predators. Marine mammals  
188 and sea birds are implicit as top predators in this budget. Estimates of their consumption  
189 of fish (Yodzis, 2001) are approximately 4% and 1% respectively. The coupled set of  
190 equations (3) was solved by matrix inversion to obtain the annual production of each  
191 trophic component (Table 3). These results were used as a baseline (Scenario 0) for  
192 comparing production in other scenarios.

193

194 Food-web scenarios [subheading]

195 Our goal is to examine the consequences of alterations in particular ecosystem  
196 processes on the yields of the benthivore, haddock (*Melanogrammus aeglefinus*) and the  
197 piscivore, Atlantic cod (*Gadus morhua*). To do this, we first estimate changes in the fish  
198 feeding guilds produced by changes in internal food web processes. To translate from  
199 guilds to species requires estimates of the maximum, or expected, fraction contributed by  
200 member species to the total biomass of each guild. Using Steele *et al.*'s (2007) fish  
201 biomass data, we calculated the maximum fractional abundance of each guild member for  
202 each year and then found the 40-year maximum and mean, as percentages, for the three  
203 guilds (Table 4).

204 A variety of explanations have been invoked to explain the major changes in the  
205 fish communities on Georges Bank and other fishing grounds in the western North

206 Atlantic (Beaugrand *et al.*, 2003; Choi *et al.*, 2004; Frank *et al.*, 2005; Myers *et al.*, 2007;  
207 Jackson *et al.*, 2001; Worm and Myers, 2003). We consider a set of scenarios that  
208 simulate such changes in the trophic groups resulting from adaptations in internal food-  
209 web processes. These scenarios are produced by altering the relative magnitudes of fluxes  
210 in the food web from the baseline 1993-2002 production values (Table 3). Technically,  
211 this is done by changing values in the production matrix (Table 2; see Appendix for  
212 changes). The results are expressed as percent changes from the baseline values in the  
213 production of plankton, benthos, and juvenile fish as prey (Fig. 3a) and in the production  
214 of planktivores, benthivores, and piscivores as consumers (Fig. 3b).

215 Scenario I: Piscivores are the dominant fish guild. We transferred 70% of the  
216 production of planktivores and benthivores to the piscivores, while retaining the  
217 proportions of juvenile fish, plankton and benthos in the piscivore diet. This change gave  
218 the piscivore guild 66% of total production, matching the maximum in Fig. 2a. The result  
219 was a 200% increase in piscivore production (Fig.3b). Total fish production is reduced  
220 because more food goes through the juvenile fish.

221 Scenario II: Benthivores are the dominant guild. The benthivore diet consists  
222 predominantly of benthos, so relatively little food can be reallocated from the other fish  
223 guilds, especially planktivores. Switching some benthos production from piscivores to  
224 benthivores increases benthivore production by only 111% (Fig.3b).

225 Scenario III: Carnivorous zooplankton are eliminated. There are numerous  
226 suggestions in the recent literature (Pauly *et al.*, 1998; Mills, 2001; Jackson *et al.*, 2001;  
227 Lyman *et al.*, 2006) that over-fishing has produced a marked increase in gelatinous  
228 zooplankton. On Georges Bank the invertebrate predators on the mesozooplankton

229 include ctenophores, chaetognaths, hydroids and carnivorous copepods. As an extreme  
230 case, we have removed them from the food web so that mesozooplankton production  
231 goes directly to fish. This removal increases piscivore production by only 51% (Fig. 3b).  
232 Understandably planktivore production also increases, but the benthivore increase is  
233 negligible.

234 Scenario IV: Carnivorous benthos is eliminated. Increases in shrimp, crabs and  
235 lobster in the North Atlantic (Worms and Myers, 2003) and the North Sea (Heath, 2005)  
236 have been attributed to over-fishing of cod and other demersal species. An increase in  
237 crustaceans has not been reported on Georges Bank, but as an extreme case we  
238 eliminated all benthic invertebrate carnivores. Elimination of this link results in an  
239 increase of only 32% in piscivore production, but 60% in benthivore production (Fig. 3b).

240 Scenario V: Production of suspension feeding benthos is increased. In the  
241 analysis of food consumption by fish over the four decades, consumption of benthos as a  
242 percentage of the total fish intake decreased from > 60% at the beginning of the time  
243 series to ~30% in later decades (Fig. 2a) (Steele *et al.*, 2007). We simulated this process  
244 by redirecting the fluxes of phytoplankton from mesozooplankton to suspension feeding  
245 benthos. This reallocation changed the percent of benthos in the aggregate fish diet from  
246 31% to 65%, close to the observed change. The switch from plankton to benthos also  
247 increases the total (plankton plus benthos) food available because the benthos, unlike the  
248 plankton, is not subject to fractional loss by physical export off the Bank. This change  
249 resulted in a large increase in benthivore production and a much smaller increase in  
250 piscivores (Fig. 3b).

251           Scenario VI: The role of microzooplankton is reduced. It is not evident that  
252 changes in fish stocks will restructure the lower trophic web, but this type of trophic  
253 cascade has been said to occur in other ecosystems (Frank *et al.*, 2005; Oguz and Gilbert,  
254 2007). To illustrate changes within the lower web, we reduced consumption of  
255 phytoplankton by microzooplankton by 1/3 and redirected it to the suspension feeding  
256 benthos. As expected, this scenario produced a large increase in benthivore production  
257 (219%) and smaller gains in piscivores (88%) (Fig. 3b).

258           Scenario VII: Direct input of phytoplankton to detritus is eliminated. Bacterial  
259 decomposition of detritus in recycling nutrients is a critical process, but its magnitude in  
260 any system is uncertain. In calculating energy budgets for Georges Bank Steele *et al.*  
261 (2007) took the fraction of detritus recycled to NH<sub>4</sub> as an unknown and used it to match  
262 the calculated and observed rates of recycling. To illustrate the possible effects of  
263 decreased recycling, we eliminated the direct input of phytoplankton to detritus. Again,  
264 the benthivores gained more than the piscivores (Fig 3b).

265           The general conclusion from these scenarios (Fig. 3b) is that, for piscivores,  
266 including cod, the main factors increasing production occur at the higher trophic levels by  
267 redistributing fish food (Scenario I) or removing pelagic invertebrate predators (Scenario  
268 III). For benthivores, including haddock, the primary increases occur at lower trophic  
269 levels and depend predominantly on the switch from mesozooplankton to suspension  
270 feeding benthos (Scenarios V, VI). The changes produced by Scenario IV are relatively  
271 small and, because there is no evidence of increased carnivore populations in the benthos  
272 on Georges Bank, we do not consider this scenario further. Similarly there is no evidence

273 for changes in the lowest trophic levels, so Scenarios VI and VII are not considered  
274 further, although they could potentially enhance the switch to benthivores.

275

276 Relation to fishery yields [subheading]

277 As a prelude to considering future changes, we can evaluate how well food-web  
278 Scenarios I-VII explain past fishery yields. Several authors (Pauly, 1995; Kurlansky,  
279 1997; Myers *et al.*, 2007) have pointed out the problems of “shifting baselines” and  
280 emphasized the difficulty of reconstructing the pristine structure of ecosystems such as  
281 Georges Bank that have been exploited for centuries (Hennemuth and Rockwell, 1987;  
282 Steele and Schumacher, 1999). Quantitative data for landings of cod and haddock extend  
283 back to the beginnings of the 20<sup>th</sup> century (Fig. 4). The early dominance of cod landings  
284 is attributed to the fact that haddock did not salt well (Hennemuth and Rockwell, 1987).  
285 From 1921 to 1950 the stocks were not considered to be over-fished (Hennemuth and  
286 Rockwell, 1987), providing one set of reference values (Fig. 5). After the combined  
287 period of low basic productivity and excessive fishing effort in the 1960s and early 1970s  
288 (Gifford *et al.*, 2009), the relative magnitude of cod and haddock catches was reversed for  
289 the two decades 1971-1990 (Fig. 5). Lastly, for the decade used to construct the food-web  
290 budget, 1993-2002, both fisheries were at a low level (Fig. 5). These observations  
291 provide a baseline for comparison with the food-web scenarios (Fig. 3).

292 The values for *MSY* of cod and haddock in Fig. 5 are taken from the most recent  
293 available estimates (NEFSC, 2008). To relate haddock and cod production to the  
294 scenarios for their respective guilds, we take 71% and 74% as the maximum percentage  
295 production for a single species in the respective guilds (Table 4). We use the following

296 formula to convert the food-web production rates,  $P$  ( $\text{gC m}^{-2} \text{ yr}^{-1}$ ), to fishery yields,  $Y$  ( $\text{t}$   
297  $\text{yr}^{-1}$ ) for the whole of Georges Bank

298

$$299 \quad Y = \frac{F}{C/B} \times \frac{P \cdot A}{P/B} \times \frac{MSY}{B_{MSY}}$$

300

301 where,  $F$  is the fraction of guild production allocated to cod or haddock (Table 4),  $A$  is  
302 the area of Georges Bank ( $43,000 \text{ km}^2$ ),  $C/B$  is the ratio of carbon to biomass (0.114) and  
303  $P/B$  is the production-biomass ratio of piscivores (0.41) or benthivores (0.39) (Steele *et*  
304 *al.*, 2007). We used the most recent estimates of  $MSY$  and biomass at  $MSY$  ( $B_{MSY}$ )  
305 (NEFSC, 2008) to calculate the exploitation rate ( $U_{MSY}$ ) and hence the fraction of  
306 production required to support the fishery at  $MSY$  (Table 5).

307 In Fig. 5, Scenario 0 represents the maximum potential yields of cod and haddock  
308 assuming no change from the 1993-2002 food-web configuration in terms of fish diets  
309 (Table 1), other than realizing maximum dominance of these species within their  
310 respective guilds. The yields are intermediate between the earlier (1921-1950) and middle  
311 (1971-1990) periods, and can almost achieve the  $MSY$  levels for haddock and cod if both  
312 species are at their maximum achievable abundances within their respective guilds (Table  
313 4). If cod and haddock abundances are closer to the recent 40-year average dominance  
314 (Table 4), yields would be well below estimated  $MSY$ . Thus it is necessary to consider the  
315 consequences of changes within the food web.

316 Scenario I switches the available food toward cod (Fig. 5), but this switch does  
317 not benefit haddock and requires a massive reduction in pelagic fish (Fig. 3b). Another  
318 possibility is to reduce significantly the role of invertebrate pelagic predators (Scenario

319 III, Fig. 5). This scenario increases the abundance of all fish guilds and, in particular,  
320 corresponds to the relative abundance of cod and haddock in the period 1971-1990.  
321 Although there is increasing speculation about such ecosystem alterations (Mills, 2001;  
322 Jackson *et al.*, 2001; Lyman *et al.*, 2006), there is no direct evidence of such a change in  
323 the Georges Bank food web.

324 Scenario V involves the redistribution of primary production from  
325 mesozooplankton to benthos, particularly epifaunal suspension feeders (Fig. 5). This  
326 change produces relative abundances of cod and haddock similar to the earlier 1921-1950  
327 period. The overall increase in production of all fish guilds (Fig. 3) arises from the  
328 decrease in washout of plankton from Georges Bank when the benthos is dominant.  
329 Washout of plankton from this relatively small off-shore fishing ground is more  
330 significant than for larger coastal ecosystems (Klein, 1987). This scenario explains the  
331 relative abundance of benthic feeding fish in the decades before 1970, compared with  
332 areas such as the North Sea (Cohen and Grosslein, 1987) and compared with the present  
333 Georges Bank ecosystem. Steele *et al.* (2007) showed that the fraction of benthic food in  
334 the aggregate fish diet declined from ~0.6 in the early 1960s to ~0.3 after 1980 (Fig. 2c).  
335 This shift can be linked to the greatly increased habitat disturbance occasioned by  
336 modern trawling methods (Hermsen *et al.*, 2003) and/or to environmental changes (Collie  
337 *et al.*, 2008).

338

339

340 Discussion

341

342           The use of scenarios in this analysis depends on the acceptance of a linear steady-  
343 state description of the Georges Bank trophic web. The natural system is unlikely to be  
344 linear and certainly is not at steady state, even as an annual average. But non-linear  
345 dynamic simulation models with large numbers of state variables are unlikely to be more  
346 realistic and they have less heuristic value (Oreskes *et al.*, 1994; Ginsberg and Jensen,  
347 2004). Because linear bottom-up simulations of food webs are generally donor  
348 controlled (Steele, 2009) and therefore stable, these scenarios represent asymptotic  
349 solutions in dynamic simulations (Steele, 2009). We have not performed specific  
350 sensitivity analyses, but the scenarios approximate the sensitivity of the system to  
351 changes in the parameters (Appendix). Given these caveats, four inferences may be  
352 drawn from these calculations and from Steele et al (2007), beginning with physical  
353 processes at the base of the trophic web.

354           (1) Physical forcing, demonstrated by the changes occurring in 1963-1972, can  
355 decrease production by a factor of two compared with the later decades and must be  
356 considered a “natural” process influencing fish production. Our linear budget model  
357 implies that any change in nutrient flux affects the fish guilds equally. Large changes in  
358 nutrient supply could affect the partitioning of energy in the lower trophic web, but we  
359 have no evidence for a non-linear assumption in continental-shelf ecosystems. It seems  
360 unlikely that top-down cascades would alter nitrogen recycling within the microbial web  
361 significantly. Possible connections to climatic change (Pershing *et al.*, 2001) suggest a  
362 link to periods of negative NAO index. Because the years 1955-1972 experienced the  
363 most sustained negative NAO index during the last century (Wisbeck *et al.*, 2001), the  
364 total productivity in earlier and later decades may be comparable.

365 (2) Within this overall productivity, a long-term switch from benthic to pelagic  
366 production occurring in the 1970s is indicated by a 50% reduction in the fraction of  
367 benthos in the aggregate fish diet (Steele *et al.*, 2007). This switch can be attributed to  
368 habitat destruction by mobile fishing gear (Hermsen *et al.*, 2003). If nutrient fluxes were  
369 comparable for the interwar period and the decade 1993-2002, then the yields of haddock  
370 and cod during 1921-1950 would be achieved with 56% and 40% presence in their  
371 respective guilds. This is significantly less than the maximum observed value of 72%  
372 required with the *status quo*, and is closer to the long-term averages (Table 4).

373 (3) In the various scenarios, the largest changes in cod and haddock stocks arise  
374 from major restructuring of the fish community that changes the pattern of species  
375 dominance within the fish diet guilds. The marked decline of cod after the 1980s was  
376 | balanced by an outburst of another piscivore, winter skate (*Leucoraja ocellata*), a  
377 | predator of sand lance (*Ammodytes americanus*) (Gifford *et al.*, 2009). The subsequent  
378 decline in winter skate corresponded to an increase in other piscivorous species,  
379 principally spiny dogfish (*Squalus acanthias*). The decline in haddock corresponds to a  
380 reduction in the proportion of benthic food in the aggregate fish diet (Steele *et al.*, 2007)  
381 and also with some increase in another benthivore, ocean pout (*Macrozoarces*  
382 *americanus*).

383 (4) Possible increases in pelagic and benthic invertebrate predators are frequently  
384 proposed as factors that could result in significant diversion of food energy from  
385 vertebrates (Jackson *et al.*, 2001; Worm and Myers, 2003). There is no evidence of an  
386 empty fish niche on Georges Bank, nor should we expect such evidence. Significant  
387 increases in one fish guild require decreases in others, or major changes within the food

388 web. An increase in cod, within the piscivore guild would require decreases in other  
389 piscivores—such as the elasmobranches, winter skate or spiny dogfish—or changes in  
390 other guild species such as haddock, herring or mackerel, which maintain the overall  
391 balance in the diet of plankton, benthos and juvenile fish.

392         The present challenge is to rebuild the principal demersal species, including cod  
393 and haddock, in an ecosystem with an altered fish species composition. Thanks to the  
394 very large 2003 year class, Georges Bank haddock is now considered to be in the process  
395 of rebuilding (Northeast Fisheries Science Center, 2008), but recent low growth rates  
396 suggest that production of benthic food may limit recovery. The yields of other species  
397 in the fish community must also be considered. For example, the combined *MSY* of the  
398 benthivores haddock, yellowtail (*Limanda ferruginea*), and winter flounder  
399 (*Pseudopleuronectes americanus*) totals 45.6 kt (Table 5). Under Scenario 0, the entire  
400 production of the benthivore guild would be required to support this combined yield.  
401 Scenarios III, IV or V would be required to allow production of the other 11 species in  
402 the benthivore guild (Steele *et al.*, 2007). There are several migratory species for which  
403 it is difficult to assign a yield to Georges Bank. Of these, Atlantic herring (*Clupea*  
404 *harengus*) and Atlantic mackerel (*Scomber scombrus*) are at historically high abundance  
405 levels (Steele *et al.*, 2007), a situation that exacerbates the challenge of recovering  
406 demersal fish stocks in a pelagic-dominated ecosystem.

407         In summary, we cannot specify whether past or future mechanisms of change,  
408 such as regime shifts (Collie *et al.*, 2004), are responsible for the decline of cod and  
409 haddock stocks, or are required for their recovery. Our approach cannot define the cause  
410 of transitions from one state to another, nor the modifications required to rebuild the

411 demersal fish stocks on Georges Bank. The observed trends in the patterns of dominance  
412 within the fish community implicate over-fishing as a primary cause of past changes on  
413 Georges Bank, and any future increase in commercial stocks will require significant  
414 redistribution within the fish community. A return to the balance of species present  
415 during the first half of the 20<sup>th</sup> century will depend on an increase in the fraction of  
416 primary production going to the benthos and may require changes in benthic habitats.

417

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423 |

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560

561 Table 1. Percentage diets of the three fish guilds. Average and range for the four decades  
562 1963-2002 (after Garrison and Link 2000).

563		Benthos	Plankton	Fish
564				
565		<hr/>		
566				
567	Benthivores	85 (82-88)	11 ( 8-14)	4 ( 0-10)
568				
569	Planktivores	14 ( 3-25)	82 (74-91)	4 ( 0-10)
570				
571	Piscivores	42 (37-45)	24 (18-29)	34 (28-37)
572		<hr/>		
573				

574

575 Table 2. The production matrix,  $AP = [a_{ij}]$  for an end-to-end Georges Bank food web,  
 576 expressed as the percentage of nitrogen or carbon transferred from food web component  $j$   
 577 (columns) to component  $i$  (rows) including recycling in the lower web. (Note that in the  
 578 actual calculations (Eq. 3) the  $a_{ij}$  are proportions.)

579

580	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13	B14	B15	B16	B17	
581	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	B1 Inorganic N
582	100	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	B2 Phytoplankton
583	0	60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	B3 Microzooplankton
584	0	26	21	0	0	0	0	0	0	0	14	0	0	0	0	0	0	B4 Mesozooplanton
585	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	B5 Inv. Carn. Plankton
586	0	6	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	B6 Susp.Feed Benthos
587	0	0	0	4	0	4	0	0	0	0	0	0	0	0	0	0	0	B7 Meiobenthos
588	0	0	0	16	0	16	100	0	0	0	0	0	0	0	0	0	0	B8 Dep. Feed Benthos
589	0	0	0	0	0	10	0	54	0	0	0	0	0	0	0	0	0	B9 Inv. Carn. Benthos
590	0	0	53	56	0	60	0	0	0	0	83	0	0	0	0	0	0	B10 Bact. Recycling
591	0	8	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	B11 Detritus
592	0	0	0	9	100	0	0	0	0	0	0	0	0	0	0	0	0	B12 Plankton for Fish
593	0	0	0	0	0	10	0	46	100	0	0	0	0	0	0	0	0	B13 Benthos for Fish
594	0	0	0	0	0	0	0	0	0	0	0	39	29	0	0	0	0	B14 Juvenile fish
595	0	0	0	0	0	0	0	0	0	0	0	54	26	47	0	0	0	B15 Planktivores
596	0	0	0	0	0	0	0	0	0	0	0	1	28	10	0	0	0	B16 Benthivores
597	0	0	0	0	0	0	0	0	0	0	0	6	17	43	0	0	0	B17 Piscivores

598

599

600 Table 3. Annual values of nutrient input ( $G$ ), transfer efficiency ( $e$ ) fractional physical loss ( $f$ ) for  
 601 equation (3) and the resultant rate of annual production  $P$ .  $G$  and  $P$  are in units of  $\text{gC m}^{-2} \text{yr}^{-1}$

602

603

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604	Food-web component	$G$	$e$	$f$	$P$
605	B1 $\text{NO}_3$	127.0	1.00	0	127.0
606	B2 Phytoplankton	0	1.00	0.0493	344.0
607	B3 Microzooplankton	0	1.00	0.0346	201.4
608	B4 Mesozooplanton	0	1.00	0.1849	118.6
609	B5 Inv. Carn. Plankton	0	0.20	0	3.33
610	B6 Susp.Feeding Benthos	0	1.00	0	26.21
611	B7 Meiobenthos	0	0.20	0	1.17
612	B8 Dep. Feeding Benthos	0	0.20	0	4.88
613	B9 Inv. Carn. Benthos	0	0.20	0	1.07
614	B10 Bact. Recycling	0	1.00	0.0426	233.9
615	B11 Detritus	0	1.00	0.1567	63.69
616	B12 Plankton for Fish	0	1.00	0	13.59
617	B13 Benthos for Fish	0	1.00	0	5.857
618	B14 Juvenile fish	0	0.30	0	2.110
619	B15 Planktivores	0	0.10	0	0.988
620	B16 Benthivores	0	0.10	0	0.200
621	B17 Piscivores	0	0.10	0	0.264

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622

623

624

625

626 Table 4. Maximum and mean fractions of biomass contributed by the annual dominant  
 627 species within each of the three fish guilds over the 40 years, 1963-2002.

628

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629

	Piscivores	Benthivores	Planktivores
632			
633	0.71	0.74	0.92
634			
635	0.41	0.43	0.59
636			

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637

638

639

640

641

642 Table 5. Maximum sustainable yield (MSY), biomass at MSY ( $B_{MSY}$ ) and exploitation  
 643 rate at MSY ( $U_{MSY}$ ) for four Georges Bank fish stocks (from NEFSC, 2008).

644

Species	MSY (kt)	$B_{MSY}$ (kt)	$U_{MSY}$
Cod	31.159	148.084	0.210
Haddock	32.746	158.873	0.206
Yellowtail flounder	9.400	43.200	0.218
Winter flounder	3.500	16.000	0.219

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645

646

647 Figure legends

648

649 Figure 1. Georges Bank food web. Solid arrows represent predator-prey links. The input,  
650  $\text{NO}_3$ , drives the microbial food web including recycling of nitrogen as  $\text{NH}_4$  (dashed  
651 lines). Dotted lines are physical losses. The ovals for Total Plankton and Total Benthos  
652 indicate the food available for the fish guilds. See Table 3 for the flux values.

653

654 Figure 2. Time series of (a) percentage biomass in the three fish guilds, (b) consumption  
655 of benthos and plankton by the fish community, and (c) fraction of benthos in the total  
656 food intake—plankton plus benthos.

657

658 Figure 3. Effects of individual food web scenarios, I-VII, on (a) percentage changes in  
659 production of total plankton and benthos available as food for fish and of juvenile fish  
660 that form part of the diet of piscivores, and (b) the production of the three feeding guilds.

661

662 Figure 4. Landings of cod and haddock from Georges Bank ( $\text{kt yr}^{-1}$ ) (from NOAA web  
663 site [www.nefsc.noaa.gov/nefsc/publications/](http://www.nefsc.noaa.gov/nefsc/publications/))

664

665 Figure 5. Average biomass yields of haddock and cod for three periods on Georges Bank  
666 compared with maximum sustainable yields (MSY) and with yields estimated from  
667 various food-web scenarios assuming that cod and haddock yields are 71% and 74% of  
668 their respective guilds (see text).

669

670

671 Appendix. Changes to the percentages in matrix  $AP = [a_{ij}]$  (Table 2) required for the  
 672 seven Scenarios.

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673			
674	Scenario I	Scenario II	
675	AP(14,12)=55;	AP(14,12)=25;	
676	AP(14,13)=42;	AP(14,13)=18;	
677	AP(15,12)=18;	AP(15,12)=63;	
678	AP(15,13)=5;	AP(15,13)=17;	
679	AP(15,14)=4;	AP(15,14)=30;	
680	AP(16,12)=1;	AP(16,12)=5;	
681	AP(16,13)=19;	AP(16,13)=57;	
682	AP(16,14)=2;	AP(16,14)=13;	
683	AP(17,12)=25;	AP(17,12)=7;	
684	AP(17,13)=33;	AP(17,13)=9;	
685	AP(17,14)=94;	AP(17,14)=57;	
686			
687	Scenario III	Scenario IV	
688	AP(5,4)=0.1;	AP(9,6)=0.1;	
689	AP(12,4)=22.9;	AP(13,6)=19.9;	
690		AP(9,8)=0.1;	
691		AP(13,8)=99.9;	
692			
693	Scenario V	Scenario VI	Scenario VII
694	AP(4,2)=6;	AP(3,2)=40;	AP(6,3)=25;
695	AP(6,2)=26;	AP(4,2)=6;	AP(11,3)=1;
696		AP(6,2)=46;	AP(6,2)=14;
697			AP(11,2)=0;

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