PART I: ANALYSIS OF BIOMASS TRENDS

ESTIMATING FISH ABUNDANCE OF THE NORTH ATLANTIC, 1950 TO 1999

Villy Christensen[1], Sylvie Guénette, Johanna J. Heymans, Carl J. Walters, Reg Watson, Dirk Zeller and Daniel Pauly

[1] *Fisheries Centre, University of British Columbia, 2204 Main Mall, Vancouver, BC, Canada, V6T 1Z4*
e-mail: v.christensen@fisheries.ubc.ca

ABSTRACT
We estimate the biomass of high trophic-level fish in the North Atlantic at a spatial scale of ½ degree latitude by ½ degree longitude over the time period from 1950 to 1999, based on 23 spatialized, ecosystem models, each constructed to represent a given year or short period from 1880 to 1998. We extract over 7800 data points that describe the abundance of high trophic-level fishes as a function of year, primary production, depth, temperature, latitude, ice cover, and catch composition. We then use a multiple linear regression to predict the spatial abundance for all North Atlantic spatial cells for each year from 1950 to 1999. The results indicate that the biomass of high trophic-level fishes has declined by two-thirds during the fifty-year period. Catches increased from 2.4 to 4.7 million tonnes annually in the late 1960s, and subsequently declined to below 2 million tonnes annually in the late 1990s. The fishing intensity for high trophic-level fishes tripled during the first half of the time period, and remained high during the last half of the time period. We estimate that the high trophic-level species contributed 53% to the value of total fish landings in 1950, and that this declined to 29% by the end of the century. Comparing the fishing intensity to similar measures from 35 assessments of high trophic-level fish populations from the North Atlantic, we conclude that the trends in the two data series are similar. Our results raise serious concern for the future of the North Atlantic as a diverse, healthy ecosystem; we may soon be left with only low trophic-level species in the sea.

"*You see something and then you try everything you can think of to make it go away; you turn it upside down and inside out, and push on it from every possible angle. If it's still there, maybe you've got something*"

K.C. Cole (1998, p.96)

INTRODUCTION

How is the world doing today? We often tend to stick to *Terra firma* when reflecting on this question, but the oceans have a role to play as well. We know that global climate is closely linked to the oceans circulation patterns, and that the oceans serve as a major food source, two roles too important to jeopardize. In that connection, it has been comforting to hear, as we have for decades, that the food supply from the oceans keeps increasing, but that comfort is beginning to erode with reports that the global catches have been decreasing for the last decade (Watson and Pauly, 2001). We hear of a fisheries crisis in the North Sea, in Northeastern Canada, actually we have heard of fisheries crises about everywhere regularly for the last couple of decades. What *is* happening to the fish in the ocean?

We have to be concerned for several reasons, with food supply being a major factor. But, our concern goes beyond this: we have seen drastic changes in ecosystem structure in a number of marine systems, a notable example being the Black Sea (Daskalov, 2002), and there is fear that ecosystems may change to alternate stable states if severely disturbed. We have also seen repeatedly that once fish populations' collapse, it may take decades for them to rebuild, perhaps because depensatory effects may lead to such changes in ecosystem states (Walters and Kitchell, 2001).

To minimize the risk of adversely impacting the oceans, we should seek to maintain healthy ecosystems, a notion that is already widely incorporated in many countries' laws and policy directives, (e.g., Canada's Ocean Act, U.S.' Stevens-Magnussons Act, and the E.U. Common Fishery Policy), as well as in the UN Convention on the Law of the Sea, where nations have accepted a mutual obligation to consider the impact of their policies on marine ecosystems; to take all appropriate actions to preserve the marine environment; and to manage ecosystem resources based on the interdependence of the system components. An important part of this is to maintain sufficient stock sizes at all trophic levels as a safety margin, avoiding the process of fishing down the food web, where predatory species are gradually eliminated (Pauly *et al.*, 1998), since the hope that we may be able to replace the predators in the sea is unfounded (Christensen, 1996). Perhaps we should make comparisons to stock portfolio theory: a safe portfolio is diversified, hedging a bet on many different sectors. Our living marine resources should be managed in a similar way if we are to

see but short-term gain and long-term loss; mining is not a viable option for managing living resources.

How much fish is there then in the sea? This is a crucial question for management of individual stocks in individual areas, and in that context a question for which we have at hand a suite of approaches for addressing it. Our interest in the present study is, however, wider: we are asking the question with regard to all species in a large area: How much fish is there in the North Atlantic?

Even before embarking on an attempt to quantify the total fish biomass, we know that whatever answer we may produce will be fairly uncertain. However, just as is the case for stock assessments, the biomass of fish in itself is not of real importance; what is relevant is how the biomass of fish has changed over time. Recognizing this *a priori,* we refine the question: How has the biomass of fish in the North Atlantic changed over the last fifty years?

We will examine a time period stretching half a century – partly because we cannot expect to see any clear trends if the time period is too brief, and partly because the fifty year period will cover the period following the relative peace (for the fish) of the Second World War up through a period with strong industrialization and expansion of the North Atlantic fisheries, and onwards to the years of fisheries collapses that have characterized the end of the 20th Century across the North Atlantic.

Estimating basin-level abundance of fish is a novel idea, as fisheries science has so far always worked on smaller scales (Pauly and Pitcher, 2000), and we are not familiar with any previous attempts we could use for guidance. Fisheries science does not have much tradition of addressing questions at such level, at least not questions that go beyond the amount of catches that may be extracted from the oceans (Pauly, 1996). In recent years, however, we have seen more interest in reconstructing prior states of ecosystems (an early example of this is given in Christensen and Pauly, 1998), and find it important to look beyond our own time horizon when evaluating the state of the oceans (Pauly, 1995).

In seeking to estimate total fish abundance, we may take two different routes. One is a bottom-up approach, where we would attempt to estimate the abundance of the individual species and sum these abundances up to the North Atlantic level. Such an approach is, however, not likely to succeed; for one, we only have abundance estimates for a few populations of fish, and the chance of actually going out and measuring how much fish there is in the sea is a formidable task, beyond the capacity of any research group. Instead, we adopt a modeling approach, where we use a number of spatial ecosystem models to quantify how much life there is in the area and at the point in time characterized by each model. We then use the physical and biological properties of the ½ degree latitude by ½ degree longitude grid cells in the area covered by the individual models in a multiple linear regression to search for patterns that may predict how abundance is distributed over space and time.

In order to estimate the abundance of fishes in the North Atlantic, it is necessary to adopt a suitable level of aggregation, the species level being too detailed. One option is to summarize the abundance of fishes by trophic level. We know the average trophic level for each group from either diet composition studies, (e.g., through FishBase) or from ecosystem models, (e.g., Ecopath), and the models tell us how individual groups are distributed between trophic levels. Hence, it becomes feasible to estimate the abundance of fish at, e.g., trophic level 4. However, we do not have much knowledge about the fish abundances at the lower trophic levels, e.g., for the forage fishes. This reflects the fact that forage fishes have been of little interest historically, and that the sampling methods in general use are unable to sample small fishes reliably.

Indications about historic abundances of, e.g., menhaden in Chesapeake Bay, points to the sea being full of forage fish, while some studies indicate that the abundance of forage fishes may have increased in recent time, due to cascading effects caused by decreasing predator abundance as a result of human exploitation, e.g., for capelin in the Newfoundland area, (Carscadden *et al.*, 2001), and for small pelagics in the Black Sea, (Daskalov, 2002). However the evidence for cascading in marine ecosystems is inconclusive (Pace *et al.*, 1999; Pinnegar *et al.*, 2000), and while the jury is out, we avoid the controversy by not dealing here with the lower trophic levels.

Thus, in this study, we focus our attention on high trophic-level fishes, and emphasize that this focus reflects the understanding that these organisms serve as indicator species for the health status of marine ecosystems. The pattern emerging from studying human impact on a variety of system shows repeatedly that the top predators are the first to go when fishing turns intensive – be it

groupers on a coral reef, bluefin tuna in the Gulf of Maine, or Atlantic cod in the Barents Sea.

As tools of analysis for assessing the biomass of fish in the North Atlantic, we have constructed a series of ecosystem models of North Atlantic ecosystems as part of the *Sea Around Us* project (SAUP), and use these together with published models from various areas in the North Atlantic to obtain a wide spatial and temporal coverage. The models have varying levels of spatial coverage and details. This paper provides an outline for how such a strategy has been implemented to address basin-level questions, and presents results from the data extraction that has been conducted, based on these models.

METHODOLOGY

The methodology we have used to predict the biomass of fish in the North Atlantic relies on a combination of ecosystem modeling, information from hydrographic databases, statistical analysis, and GIS modeling. A flowchart for this approach is presented in Figure 1 to guide further reading.

Ecosystem models from the North Atlantic

The available information about biomasses at the ecosystem level is very incomplete, making it necessary to rely on modeling to obtain a coherent picture of the distribution and abundances of fish in the North Atlantic. We can base the modeling on the array of information that is available at the population level, mainly due to stock assessments made as part of the regulatory process. In addition, we have information from research surveys (which serve as a major information-provider for the assessments) as well as from biological oceanographic studies. A major part of the biological and ecological information required for construction of the ecosystem models is available from the FishBase database, available online at *www.fishbase.org*. The aim of the modeling efforts is to combine such information to derive a realistic picture of biomasses and their interaction in a series of ecosystems throughout the North Atlantic.

In the present study we rely on ecosystem models constructed using the widely distributed Ecopath with Ecosim (EwE) approach and software, for which Christensen and Walters (2000) and Pauly *et al.* (2000) give overviews in term of capacity and limitations. Ecopath models are intended to summarize the abundances and interactions of all major functional groups in an ecosystem, along with detailed descriptions of how we exploit such ecosystems through fishing activities. A typical Ecopath model (such as the bulk of those on which this study is based) may include 25 to 40 functional groups ranging from primary producers to marine mammals, and incorporating a number of fishing fleets for which catches, discards and bio-economical details are provided.

The present study is based on a total of 23 ecosystem models, all of which are available from the first author (see also *www.ecopath.org*). The models describe 15 geographic areas, and are all made to represent a given year or short time period between 1880 and 1998 (see Table 1). Many of the models incorporate time series information in addition to the year-specific information on which the model description is based (see references in Table 1 for further details). The time series information is used to assess how well the model can replicate trends over time in the ecosystem, as part of what may be considered a validation procedure. This, however, has limited implications for the present study, which does not incorporate the time-dynamic aspects usually considered when using the Ecosim routine of EwE (see Walters *et al.*, 1997; Christensen and Walters, 2000; Walters *et al.*, 2000) .

For nearly all models, the time periods have been chosen to best take advantage of available data sources. Notably, the start of biomass data from stock assessment has often dictated the period to be used for the models. The only models that break with this trend are the two historic models for the North Sea (1880s), and for the Newfoundland area (1900). We have included these models to provide extremes on the temporal scale, and fully realize that the biomass estimates used in these models are more uncertain than those in the more current models. Therefore we also investigate the impact that these (and other models) have on the overall results, as is described in more detail below.

We have also sought to include models that are extreme with regard to other characteristics; a notable example is the Lancaster Sound model from Northeastern Canada. Reflecting the typical characteristics of such an arctic system, the model includes a variety of marine mammal groups, but only very limited amounts of high trophic-level fish; in addition a large part of the area is covered by ice for a good part of the year.
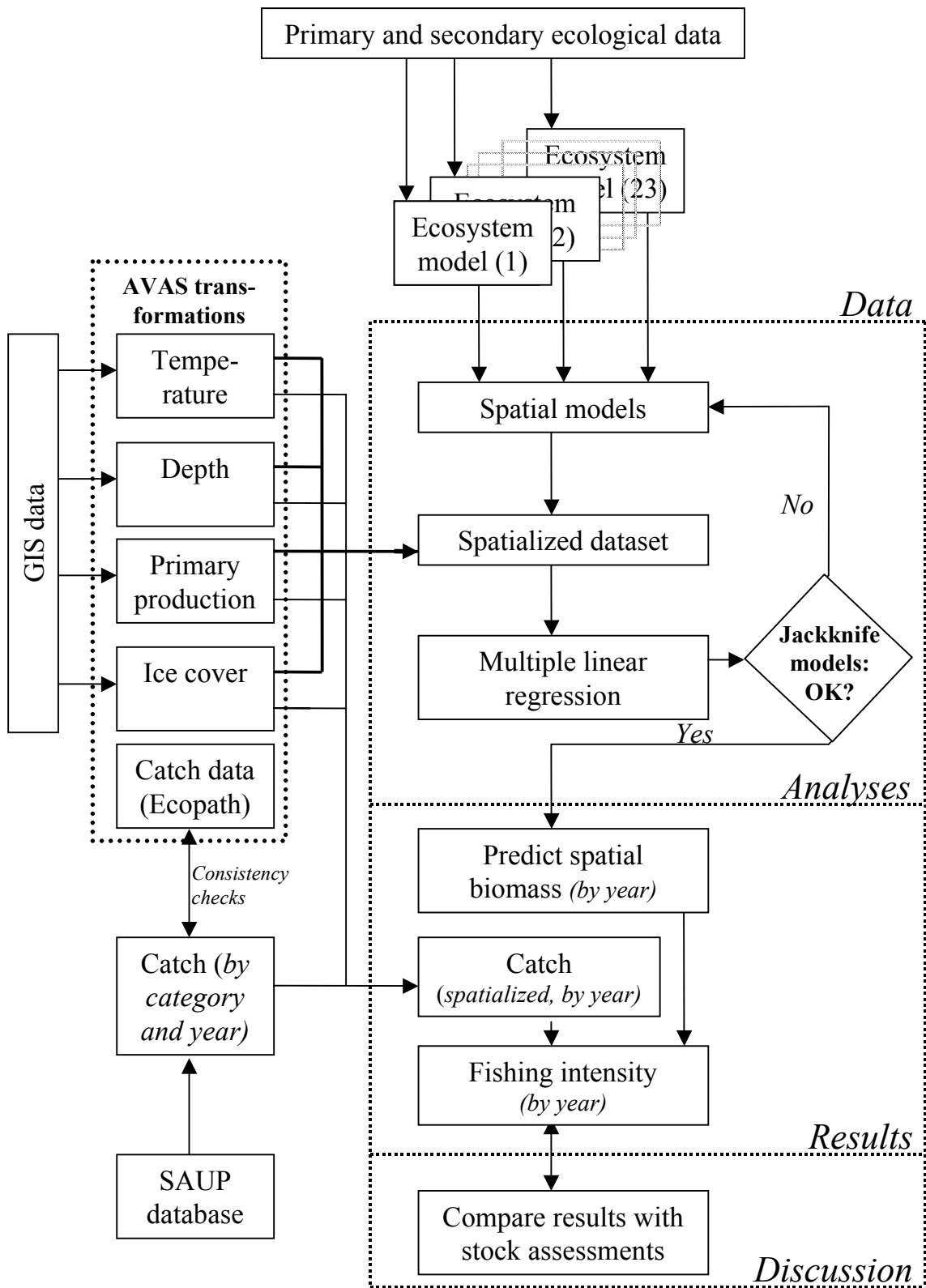
Figure 1. Schematic overview of the methodology used for predicting the biomass of high trophic-level fish in the North Atlantic.

Table 1. Overview of ecosystem models used for estimating abundance patterns of predatory fish in the North Atlantic. The third column indicates the number of half-degree spatial cells covered by each model. The lists of fish groups indicate the selection used for estimating abundance. Dem. is demersal, Grl. is Greenland, L is large, med is medium, pel. is pelagic, pisc. is piscivorous, pred. is predatory, S is small, TL is trophic level, trans. is transient. See the individual models for further information about the groups.

Area	Year	Cells	Fish groups with TL > 3.75	Reference
North Sea	1880	369	Bluefin tuna, Halibut and turbot, Saithe, Cod, Whiting, Sharks, Other pred. fish, Rays and skates, Sturgeon. Haddock, Horse mackerel, Salmon and seatrout, Gurnards, Mackerel, West mackerel, Brill, Other prey fish	Mackinson, this vol.
Newfoundland (2J3KLNO)	1900	563	Grl. halibut, Cod, L pel. Feeders, Skates, Pisc. SPF	Heymans *et al.*, in prep.a)
Faeroe Islands	1961, 1997	132	Grl. halibut, Cod, Saithe, Other deep water, Other dem. fish	Zeller and Reinert, this vol.
North Sea	1963, 1974	369	Saithe, Cod, Whiting, West mackerel, Haddock, O. predators, Raja, Mackerel, Gurnards, Horse mackerel, Herring,	Christensen *et al.*, in prep.
Gulf of Biscay	1970, 1998	51	Extra L pelagic, L sharks, Tuna-like fish, L deepwater, S Sharks	Ainsworth *et al.*, this vol.
Lancaster Sound	1980	169	Grl. Halibut	Mohammed, this vol.
North Sea	1981	369	Saithe, O.pred.fish, Whiting, Cod	Christensen, 1995
Scotian shelf	1982	160	Dem. piscivores, Trans. pel., Halibut, Dogfish, Cod, Silver hake, Pollock	Bundy in prep.
Gulf of Maine & Georges Bank	1982	77	Summer flounder, L pelagic feeders, Bluefin tuna, Bluefish, Cod, L. Demersal feeders, Pollock	Heymans, this vol.
Morocco	1984	99	L pelagic, L dem. sharks/rays, Very L dem. comm., L deepwater comm., L and med bathypelagic, Very L dem., Sm. dem. sharks/rays	Stanford *et al.*, this vol.
Chesapeake Bay	1985	4	Blue fish, Summer flounder, Weak fish, Striped bass	Baird and Ulanowicz., 1989
Gulf of St. Lawrence (4RS)	1986	58	Grl. halibut, L cod, Skates, L pelagics	Morisette, this vol.
Newfoundland (2J3KL)	1986	563	Grl. halibut, Cod, L pel. Feeders, Skates, Pisc. S pel. feeders	Bundy *et al.*, 2000
US South Atlantic States	1996	81	Billfishes, Sharks, Tuna, Mackerel, Snappers, Groupers, Jacks, Pel. pisc., Dem. pisc., Benthic pisc.	Okey and Pugliese, this vol
Norwegian-Barents Sea	1997	2307	Cod	Dommasnes *et al.,* this vol.
Newfoundland (2J3KLNO)	1997	563	Grl. Halibut, Dogfish, Pollock, Transient pelagics, Cod, Transient mackerel, L dem. pisc., Skates	Heymans, *et al.*, in prep. b)
Greenland, west coast	1997	218	Grl. Halibut, Cod	Pedersen and Zeller, this vol.
Iceland	1997	288	Grl. Halibut	Mendy and Buchary, this vol.
Azores	1997	240	Pelagic L pred., Deepwater L, Sharks L, Coastal L pred., Dem. L pred, Phycis phycis, Pagellus bogaraveo, Coastal M pred, Sharks M, Dem. M inv, Rays, Dem. M pred, Pel. M pred,	Guénette and Morato, this vol.
US Mid Atlantic Bight	1998	48	Billfishes, Tunas, Bluefish, Goosefish, Striped bass, Weakfish, Coastal sharks, Spiny dogfish, Jacks, Benthic piscivores, Snapper / grouper, Black seabass, Dem. piscivores, Cods and hakes, Redfish	Okey, this vol.

Our initial selection of available models included two that we later chose to exclude from the analysis. One of these described the Icelandic waters in 1950, but did not include any biomasses that were based on empirical data. The other, from the Cantabrian Sea, covered the narrow shelf area only, and our half by half degree spatial cells did not represent this area in a realistic fashion; hence we would attribute the biomasses to unrepresentative depths.

Because of the uncertainty about abundance of small fish in the North Atlantic in general, we find it premature to estimate their abundances from the models on which this study is based. Instead we focus on the larger, predatory fish for which much more information is available, notably through stock assessment and research surveys. We define predatory fishes as those fish groups for which the trophic level is estimated at 3.75 or above. This effectively means that we include all

fish groups that predominantly eat prey species that feed on fish, zooplankton and/or small benthic organisms, (i.e., we excluded all primarily planktivorous, herbivorous and detritivorous fishes).

A list of fish groups included in the high trophic-level fish category is presented in Table 1, which illustrates that the species included are those of main interest for human consumption. This is demonstrated by comparing the value of the landings of high trophic-level fish species to the total value of the landings in Figure 2. It may be noted from the figure that in 1950, the high trophic-level fish contributed more than 50% to the total landing value, and that this had declined to 29% by the end of the century. The figure also demonstrates the overall importance of the cods and their high trophic-level relatives (mainly haddock and saithe).
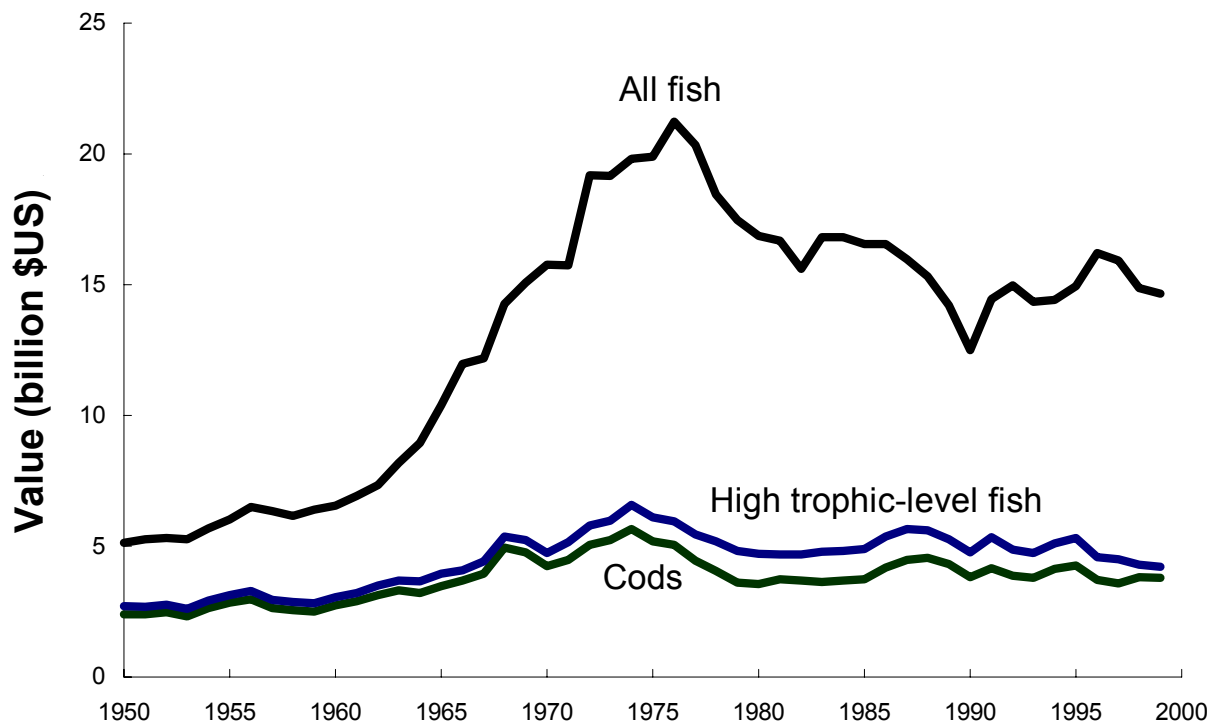

Figure 2. Value of total fish landings, of high trophic-level fish (TL ≥ 3.75) in the North Atlantic (as defined in Figure 3) during the second half of the 20th Century. The figure illustrates that the major contribution comes from cod and its close relatives. Overall, the value of high trophic-level fishes decreased from 53% of the total landing value of fish to 29% during the time period. Prices are year specific but converted to 2000-values using the U.S. consumer price index. See (Sumaila and Watson, 2002) for details about the value of landings.
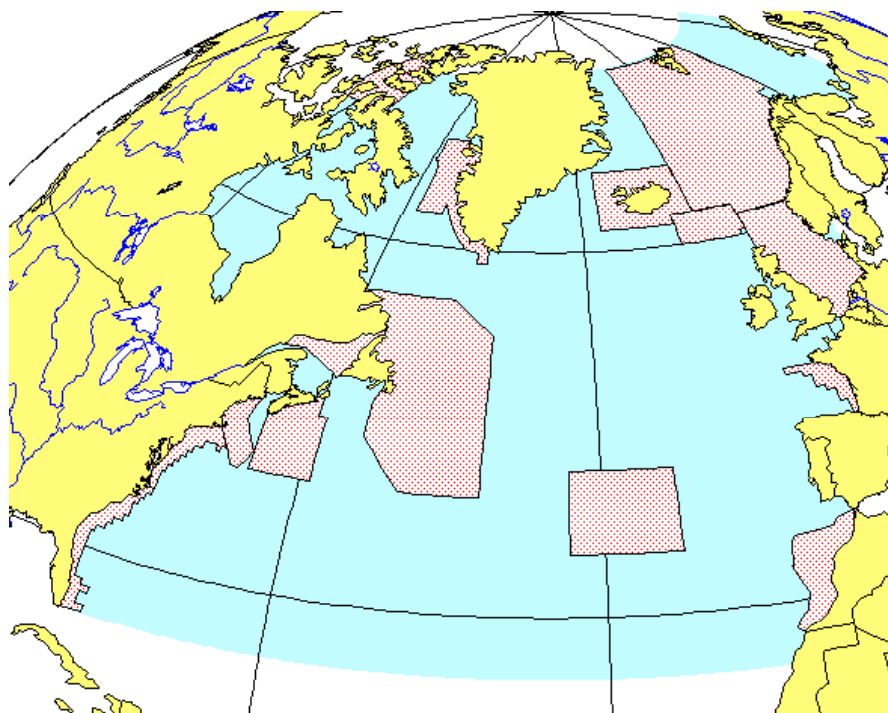
Figure 3. Map of the 15 geographic areas in the North Atlantic for which a total of 23 ecosystem models (shaded polygons, red in color) were used to obtain estimates for a total of approximately 18,000 half degree by half degree spatial cells (shaded background, light blue in color). The total water area included in the analysis is 28 million km². The models for the Newfoundland/Grand Banks area off Canada do no all cover the same area.

We also exclude marine mammals and birds as well as high trophic-level invertebrates from our analysis. Marine mammals are better dealt with in a separate study using a different methodology (see Kaschner *et al.*, 2002), while for marine birds and invertebrates, it is a consequence of their representation being fairly superficial in the ecosystem models we have at hand. We also note that the biomasses involved for these groups are negligible in any case.

The definition of the trophic level cut-off point chosen here is somewhat arbitrary, and indeed a few models groups are included which we would not normally consider predatory, while in a few other cases some groups one would expect to see included have been excluded. The reason for this may well be that the trophic level estimation depends on how well the diets (from which the trophic levels were estimated) have been defined; this is something we have not been able to standardize completely between models. However, the general patterns emerging from the selections are very much in accordance with expectations, e.g., few species (but fairly high biomasses on continental shelves) in the colder, northern areas as compared to the more species-rich, warmer, southern areas. We believe the sheer mass of information will outweigh the few

cases where the trophic level estimates were problematic.

Assigning models to strata

The ecosystem model coverage of the North Atlantic is incomplete, precluding simple scaling of flows and rates from the individual ecosystem to the basin level, and calling for a stratification scheme. The scheme we have chosen builds on the structure that is applied for catches and other data in the SAUP databases: ½ by ½ degree spatial cells (Watson *et al.*, 2002).

Each of the ecosystem models covers a distinct geographic area consisting of a variable number of the half-degree spatial units (see Figure 3). As part of the present study, we have constructed a spatial model for each ecosystem using the Ecospace model incorporated in the EwE software (Walters *et al.*, 1999). Ecospace, in essence, incorporates an Ecosim model in each spatial, non-land cell – of which there are for instance 369 in the North Sea model represented in the right panel of Figure 4. In total, the models covered 24% of the area of the North Atlantic, with the coverage reaching 40% in the depth strata where most concentrations of high trophic levels occur (Table 2).
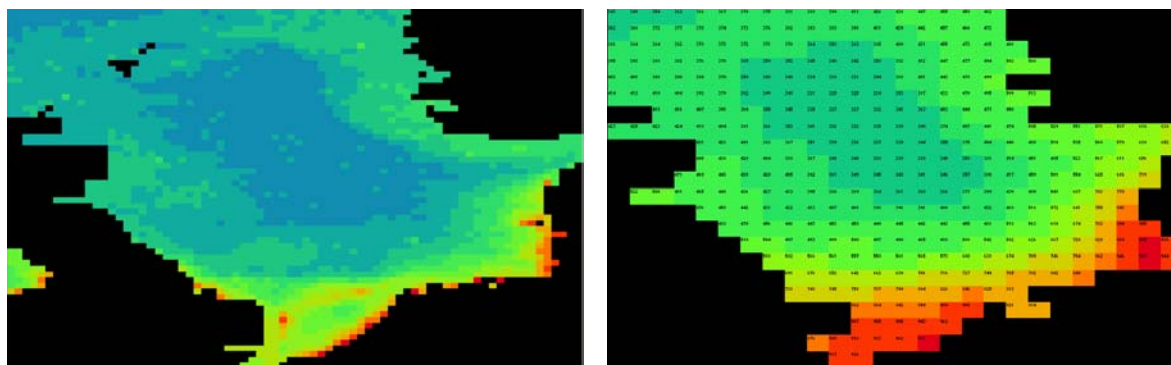
Figure 4. Patterns of annual primary production in the North Sea at two different resolutions scaling from high at the coasts in southeast to low in the central parts of the area. The left panel shows estimated productivity at a one-sixth degree scale based on SeaWIFS data, as made available by the EU Joint Research Centre. The right panel shows how this information is averaged, scaled to the original mean, and represented using ½ by ½ degree cells in the Ecospace models of the North Sea. The demise of the Shetland Islands is unintentional, reflects a consequence of using a coarse map, and does not represent any actual event.

Table 2. Area covered by Ecopath models from the North Atlantic, total area and proportion of total area covered by Ecopath models. All areas are in 10^3 km².

Depth (m)	Sampled stratum	Total area	Proportion sampled
0-10	73	200	0.37
11-50	472	1150	0.41
50-100	576	1408	0.41
100-200	754	2177	0.35
200-1000	1413	3507	0.40
>1000	3567	19683	0.18
Total	6855	28124	0.24

Exchange between spatial cells is modeled for each time step (typically monthly), while accounting for food availability, predation and fishing patterns. The Ecospace models were constructed based on general information about habitat and depth preferences for the functional groups of the ecosystems. Primary production was distributed spatially based on SeaWIFS data as described below, while fishing effort was distributed spatially based on distance to coast, depth zone preferences of fleets, and fish abundance.

For each of the spatial model the cells were distributed between habitats based on depth only. The following depth strata were used for all models: (1) <10 m; (2) 11-50 m; (3) 51-100 m, (4) 101-200 m; (5) 201-1000 m, (6): >1000 m, see Table 2. Depth information at the ½ by ½ degree scale was obtained from the ETOPO5 dataset available on the U.S. National Geophysical Data Center's Global Relief Data CD (*www.ngdc.noaa.gov/products/ngdc_products. html*) as implemented in the *Sea Around Us* project database (*www.fisheries.ubc.ca/projects/saup*), and obtained by linking Ecospace to a GIS system, see Figure 5.A.

The predicted distributions in Ecospace models show marked sensitivity to primary productivity patterns, and these have in general not been well described in previous Ecospace models. To improve on this, we cooperated with the Institute for Environment and Sustainability of the European Commission's Joint Research Centre in Ispra, Italy, to make global primary productivity maps based on SeaWIFS data available to ecosystem modelers. The primary productivity maps are based on a model that incorporates the SeaWIFS estimated chlorophyll, photosynthetically active radiation, and sea surface temperature patterns (Hoepffner *et al.,* MS), based on the model of Behrenfeld and Falkowski (1997). The maps are available on a monthly and quarterly basis from October 1997 onwards (*www.me.sai.jrc.it*), but for the present study, a one-year production average representing 1999 was used, as this was the only yearly average available (Figure 5.B).
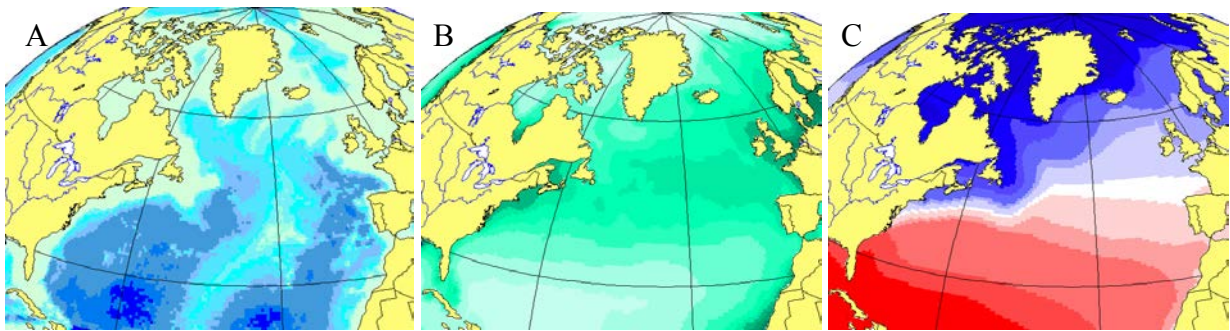
Figure 5 (A) Depth, (B) primary production and (C) temperatures (at 10 m depth) in the North Atlantic. Data sources are the same as mentioned above for the respective variables. The depths scale from light being low depth to dark being deep, with the lightest intensity representing the zone down to around 400 meters, i.e., the zone where most of the fishing for demersal species takes place. Primary Production (B) scales from light being low productivity to dark representing high productivity. The temperatures are coldest (blue) in the arctic region, and the color scale is linear.

The primary productivity maps have a spatial resolution of approximately $1/6$ degree, while the database used for the present study operates with ½ degree latitude by ½ degree longitude cells, i.e., with a resolution of one ninth of the SeaWIFS resolution. Therefore, a facility was included in Ecospace that aggregates the finer resolution maps, averaging, while maintaining the overall mean, and prepares the basemap for the Ecospace modeling (for details, see the EwE User's Guide, available at *www.ecopath.org)*.

Temperatures at 10 meters depth were obtained from climatology based on the NOAA World Ocean Atlas 1998 (*www.nodc.noaa.gov/OC5/ wod98v2.html*), as implemented in the *Sea Around Us* project database (see Figure 5.C). Ice cover information was obtained from the U.S. National Snow and Ice Data Centre, Boulder, Colorado (*www.nsidc.org/index.html*), in form of monthly limits of sea ice coverage.

Fisheries catches

There is a relationship, but not a simple one, between fish biomasses and how much fish one can catch. If catches are high, there at least must have been some high biomasses present to support these catches. However, high biomasses may also be associated with low catches, if the reason is low fishing effort. We do not, however, have reliable data on development of fishing effort over time for the North Atlantic as a whole, nor for any major parts of the basin; hence it is not straightforward to derive overall biomass levels from total catches. We expect, however, that the catch composition will change as a function of the biomass level of the preferred fishing target: i.e., of the high trophic-level species. It is by now well established that fisheries expansions go hand in hand with the process of

'fishing down the food web' (Pauly *et al.*, 1998), and we can therefore use the catch composition by spatial unit to draw inferences about the overall biomass of high trophic-level fish species, (see below).

The catches entering the regression analyses come from the ecosystem models, which in turn have utilized numerous sources (see model references in Table 1). For this purpose a routine has been added to the Ecopath software that allows allocation of catches of ecosystem groupings to the catch categories used in the SAUP database, as described further below. In order to carry out this allocation, we extracted catch distributions by ISSCAAP categories (see *www.fao.org* for details of this classification) for the years and areas covered by the individual models, and used this to guide the distribution for the groups where the allocation was not obvious.

The catches in the SAUP database are used for predictive purposes based on the biomass regression. The main source for the catches is the FAO catch database (*www.fao.org*), with information added from the Statlant database maintained by ICES (*www.ices.dk*), as well as from ICES assessment working group reports. Spatial distribution of the catches was undertaken using an elaborate, rule-based procedure implemented and described by Watson and Pauly (2001) and Watson *et al.* (2002). For this, the statistics were progressively disaggregated based on known distributions for the taxa, hydrographic conditions, and on where reporting countries were permitted access through fisheries agreements in the individual years.

The catches are distributed in twelve categories: (1) anchovies, (2) herrings, (3) perches, (4) tunas and billfishes, (5) cods, (6) salmoniformes, incl.

smelts and capelin, (7) flatfishes, (8) scorpionfishes, incl. redfish, (9) sharks and rays, (10) crustaceans, (11) molluscs, and (12) 'other' groups.

For the regression analysis in the present study, we merged herrings and the salmoniformes (the latter being totally dominated by capelin). There are indications, both from the catches and ecological studies, that capelin replaced herring during the 1970s-1980s when herring abundance in the northern Atlantic was low. Also, the two species serve as important forage species for the high trophic-level species considered in this study. We chose to combine the two invertebrate groups, (10) and (11), in the regression analysis based on the expectation that high invertebrate catches are associated with low biomass levels of high trophic-level catches (an effect of 'fishing down the food web'), and noting that it did not have any observable effect on the regressions; hence, one less variable is to be preferred.

Finally, when examining the regression it was clear that the overall catches of tuna and billfishes shows very little trend over the fifty year period under study (linear slope 0.1% of intercept, r^2 = 0.01, std = 12% of mean). This is in accordance with expectations as the catch composition of tuna have changed over the fifty year period; indeed we now have evidence for declining trophic levels of catches within the tunas (Pauly and Palomares, MS). Illustrative of this is that bluefin tuna catches were estimated to 38,000 tonnes in 1960 and 100 tonnes in 1999, while the decrease was compensated for by increased catches of smaller, lower trophic-level tunas, so as to maintain (within 1%) the total tuna catch. Thus, the tuna and billfish category turned out not be a significant predictor of the biomass of high trophic-level fishes, and the category was omitted as a predictive variable from the regression analysis.

Regression analysis

All regression analyses were performed using multiple linear regression using the S-Plus 6 software (Anon., 2001b). Prior to performing the regression analyses, we used an additive and variance stabilizing transformation (AVAS), as implemented in S-Plus, to study how individual variables are best transformed to obtain linearity (Figure 6). AVAS seeks for transformations, $\Theta(y)$

$= \phi_1(x_1) + \phi_2(x_2) + \ldots + \phi_p(x_p) + \varepsilon$, which provides a good additive model approximation for the data, $y_i, x_{i1}, \ldots, x_{ip}$, for $i = 1, 2, \ldots, n$ observations, while seeking to achieve variance stabilization. Based on the AVAS analyses, we concluded that logarithmic transformations were suitable for primary production and biomass, while no transformations were required for year and latitude. For depth, indications pointed to the use of a quadratic transformation (truncated at 5000 meter to avoid extrapolation). Ice cover was treated as a categorical variable (no ice cover, ice cover part of the year, and ice cover year-round) and hence required no transformation. The various catch categories, as defined above, were transformed using logarithmic transformations (catch in $kg \cdot km^2 \cdot year^{-1}$, with $1\ kg \cdot km^2 \cdot year^{-1}$ added to enable log-transformation of catches of zero).

As data material for the regression analysis, we extracted 7811 records based on the ½ by ½ degree spatial cells of the 23 ecosystem models. Each of the records included estimates of biomass and catch of high (≥ 3.75) tropic level, depth, distance from coast, water temperature at 10 meters depth, ice cover category, number of seamounts and reefs, primary production, upwelling index, catch by each of the catch categories defined above, latitude, and year of the model. The upwelling index we used was based on latitude and basin-specific temperature anomalies (V. Christensen, unpublished data).

We were not able to use the following as predictive variables: distance from coast (it appears that the North Atlantic is so accessible that any fishing ground will be exploited; fishing was indeed the reason Europeans started crossing the Atlantic regularly); number of seamounts and reefs (both are negligible), and the upwelling index (there are no significant upwelling cells in the study area, hence, no effect can be expected). Further, we could not demonstrate any effect of temperature, probably because of the inclusion of the latitude and ice cover terms.

To prevent the records extracted from models covering large areas from swamping those from other models, the records were included in the regression analysis using a weighting factor, the inverse of the square root of the number of non-land cells in the models to which the given record belongs.
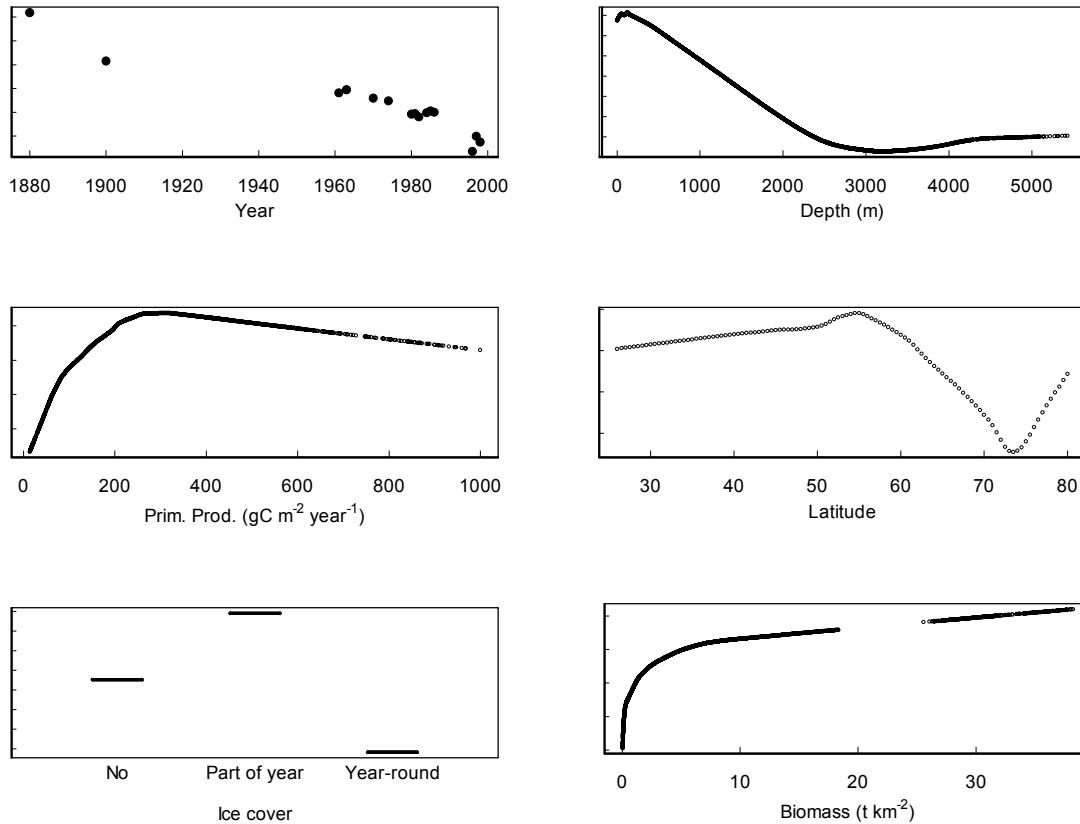
Figure 6. AVAS transformations indicating how parameters (X-axis) may be transformed (Y-axis indicate biomass, linear scale) to linearize the individual parameters while considering their joint effects. Results indicate that no transformations are required for year and latitude, while a quadratic transformation is acceptable for depth, and log-transformations for primary production and biomass. Ice cover is treated as a categorical variable.

The multiple linear regression takes the following form,

$$\log(\text{Biomass}) = a + b_1 \cdot \text{year} + b_2 \cdot \log(\text{PP}) + b_3 \cdot \text{Depth} + b_4 \cdot \text{Depth}^2 + b_5 \cdot \text{Latitude} + b_6 \cdot \text{ICE}_{\text{PartOfYear}} + b_7 \cdot \text{ICE}_{\text{YearRound}} + b_8 \cdot \log(\text{Catch anchovies}) + b_9 \cdot \log(\text{Catch herring and smelts}) + b_{10} \cdot \log(\text{Catch perciformes}) + b_{11} \cdot \log(\text{Catch cods}) + b_{12} \cdot \log(\text{Catch flatfishes}) + b_{13} \cdot \log(\text{Catch scorpionfishes}) + b_{14} \cdot \log(\text{Catch invertebrates})$$

where,

a is the regression intercept, and b_1 to b_{14} the slopes to be estimated by the regression;

Biomass is the predicted biomass of predatory fishes (g·m⁻²);

PP is the average primary production (gC·m⁻²·year⁻¹);

Depth is the average depth (m);

Latitude is the latitude of the observation;

$\text{ICE}_{\text{PartOfYear}}$ and $\text{ICE}_{\text{YearRound}}$ are categorical parameters that takes the value 1 if the cell is ice-covered part of the year or year-round, respectively, and the value 0 if not; and

Catch variables are in kg·km⁻²·year⁻¹ with 1 kg·km⁻²·year⁻¹ being added to accommodate log-transformations for zero catches.
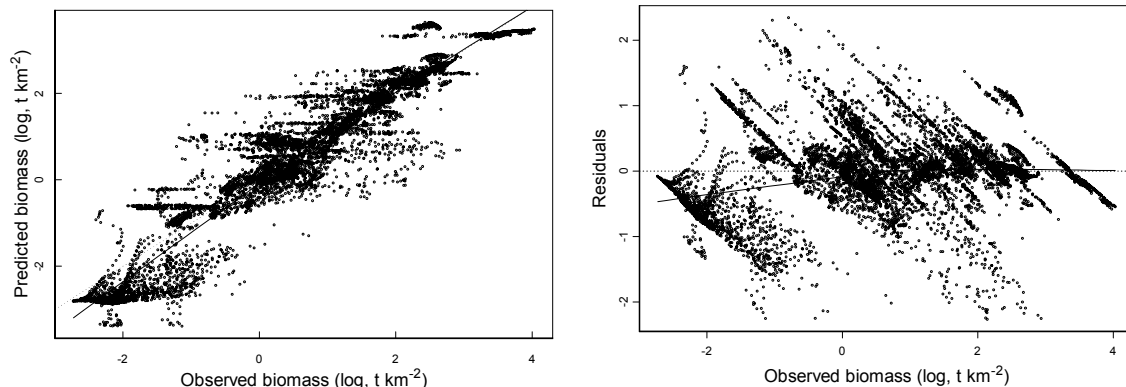
Figure 7. *Left*. Observed versus predicted biomass (log-scales, t·km⁻²) for predatory fish in the North Atlantic during the second half of the 20th Century. *Right*. Plot of residuals (predicted - observed biomass, log-scale) versus predicted biomass (log-scale, t·km⁻²) for predatory fish in the North Atlantic during the second half of the 20th Century.

Table 3. Parameters estimates and associated test statistics for a multiple linear regression predicting the biomass (log, g·m⁻²) of predatory fishes (TL>3.75) in the North Atlantic during the second half of the 20th Century. The primary production (PP) is in log, gC·m⁻²·year⁻¹, while catches are in log, kg·km⁻²·year⁻¹. Depth is included with a linear and a quadratic term. The variable are arranged after t-value (value relative to standard error, given) corresponding to adjusted partial slopes (Blalock, 1972).

Variable	Value	Std. error	t-value	Pr(>|t|)
Year	-0.017415	0.000255	-68.3	0.0000000
(Intercept)	35.873360	0.541	66.3	0.0000000
Latitude	-0.0458485	0.000858	-53.4	0.0000000
Depth	-0.0009162	0.0000194	-47.2	0.0000000
Catch, anchovies	-0.2390645	0.00731	-32.7	0.0000000
Catch, herring and capelin	0.1216986	0.00387	31.5	0.0000000
Catch, scorpionfishes	0.116684	0.00382	30.5	0.0000000
Catch, perches	-0.1420623	0.00472	-30.1	0.0000000
Catch, cods	0.1119097	0.00495	22.6	0.0000000
Depth²	0.000000089	0.000000005	19.5	0.0000000
Catch, flatfish	0.0520826	0.00350	14.9	0.0000000
Ice cover, year-round	-0.2849061	0.0224	-12.7	0.0000000
Catch, invertebrates	-0.0269938	0.00290	-9.3	0.0000000
Primary production	0.1646445	0.0195	8.4	0.0000000
Ice cover, part of year	0.0381208	0.0115	3.3	0.0008919

The multiple R^2 of the regression is 0.859 with 7796 degrees of freedom. The F-statistic is 3389 on 14 and 7796 degrees of freedom, with a p-value of 0. [Given spatial autocorrelation, we do not really believe our cells to provide true degrees of freedom; yet the results indicate that the regression is fairly robust]. The Residual standard error is 0.1280 on 7796 degrees of freedom. All parameters are highly significant (P < 0.001).

Summing up the regression results, we conclude that the predictive variables are able to explain the major part of the variance in the dataset (R^2 = 0.86), and the slopes have the right sign for the variables where we had expectations about their impact. The t-values give indications for the internal 'ranking' of the parameters, i.e., which ones matter most (or where the probability of exceeding the t-value by chance is smallest). Due to co-variation between variables, we acknowledge that any interpretation of the 'rankings' should be treated with extreme caution. We find that the highest t-value is associated with the year parameter, followed by the intercept, latitude and depth.

Primary production has a surprisingly low t-value, partly reflecting that depth and primary production show covariance, and partly that we do not have models covering the Gulf Stream region across the North Atlantic where primary production and depth are both fairly high (see Figure 5).

As with any other multiple regression or statistical model, results depend on the input data, and we need to consider what we included in the analysis, both with regard to outliers and to predictive variables. To study this further, we have conducted a series of analyses where we sampled the original datasets. This is described in more detail in the following sections.

Effect of individual models on the regression analyses

The regressions we obtain will depend on what observations (here: ecosystem models) we include. To study the robustness of the regressions we have analyzed the data using a jackknife approach (Sokal and Rohlf, 1995), omitting one model at the time from the regression. Subsequently, we used the jackknifed models to provide estimates of biomass over time (see Figure 1). The results from the jackknife analyses are presented in Table 4, while Figure 8 shows the biomass trends resulting from the jackknifing. The jackknife approach can be used in a formal context for estimating confidence intervals of biomasses, but because of the small

number of observation groupings (models) and the use of a logarithmic scale, the confidence intervals that could be derived here are too wide to be meaningful. We do not find that the standard method for estimating confidence intervals based on jackknifing is applicable to the analyses in the present study, and hence, we are for the time being not able to associate confidence intervals with the results.

Figure 8 shows that omitting the Lancaster Sound model would lead to nearly twice as high biomass estimates for the North Atlantic basin, and illustrates the importance of including extremes (here a temperature extreme with low fish biomasses) in the multiple linear regressions. The model, which if omitted, would result in the second highest biomasses, is the one for the Norwegian Sea and the Barents Sea, for which the same can be said.

The most noteworthy finding from the jackknife analyses is that while the absolute estimates of abundance is sensitive to in- or exclusion of individual models; the overall trends over time show remarkably little sensitivity to model deletion. Hence, the overall conclusions from the present study are not very sensitive to the selection of models. Rather, they are emergent properties based on many models.

Table 4 mainly serves to illustrate the degree to which the intercepts and slopes change as a result of the jackknife exercise.
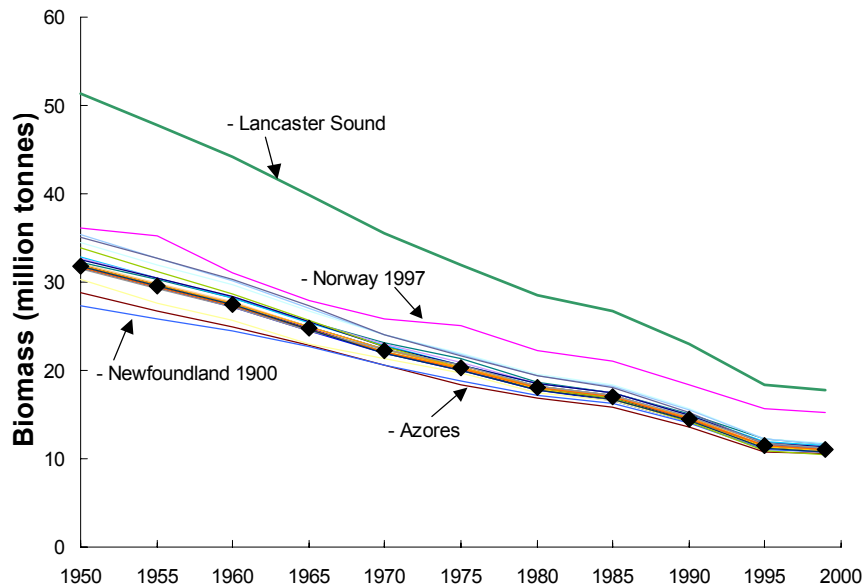

Figure 8. Illustrates the effect of excluding individual models from the regression analysis in a jackknife fashion (excluding one model at a time and repeating the regression analysis and predictions over time). The thick line with diamond markers indicates the regression with all models included. Jackknifed models are indicated only for the few cases generating strong deviations from the mean trend.

Table 4. Effect on the parameters of the regressions for estimating biomass of high trophic-level fishes in the North Atlantic based on jackknifing of the models included in the analysis.

	Including all models	Azores 97	Biscay 70	Biscay 98	Chesa-peake Bay 85	Faroe Islands 61	Faroe Islands 97	Gulf of St. Lawrence 86
(Intercept)	35.873	31.999	35.879	35.879	35.880	36.718	35.629	35.828
year	-0.017	-0.016	-0.017	-0.017	-0.018	-0.018	-0.017	-0.017
Prim. prod.	0.165	0.334	0.165	0.165	0.183	0.151	0.152	0.214
Depth (10^3)	-0.916	-1.039	-0.916	-0.916	-0.923	-0.917	-0.933	-0.932
Depth^2 (10^7)	0.890	1.190	0.890	0.890	0.920	0.880	0.950	0.920
Latitude	-0.046	-0.031	-0.046	-0.046	-0.044	-0.046	-0.047	-0.047
Ice, part	0.038	0.054	0.038	0.038	0.041	0.025	0.069	0.078
Ice, all	-0.285	-0.225	-0.285	-0.285	-0.279	-0.296	-0.293	-0.259
Anchovies	-0.239	-0.251	-0.239	-0.239	-0.178	-0.237	-0.232	-0.246
Herring, capelin	0.122	0.174	0.122	0.122	0.121	0.117	0.140	0.116
Perches	-0.142	-0.196	-0.142	-0.142	-0.119	-0.140	-0.152	-0.139
Cods	0.112	0.094	0.112	0.112	0.086	0.114	0.106	0.114
Flatfish	0.052	0.090	0.052	0.052	0.058	0.053	0.055	0.046
Scorpionfishes	0.117	0.099	0.117	0.117	0.118	0.122	0.108	0.125
Invertebrates	-0.027	-0.018	-0.027	-0.027	-0.021	-0.029	-0.039	-0.023

Table 4, continued.

	Greenland west coast 97	G. of Maine / Georges Bank 82	Iceland 97	Lancaster Sound	Morocco 84	Newfound land 1900	Newfound land 85-87	Newfound land 95-00
(Intercept)	35.507	35.892	37.340	39.363	36.406	29.193	34.817	35.674
year	-0.017	-0.017	-0.018	-0.018	-0.018	-0.014	-0.017	-0.017
Prim. prod.	0.166	0.179	0.194	-0.232	0.140	0.189	0.162	0.168
Depth (10^3)	-0.906	-0.918	-0.974	-1.036	-0.848	-0.893	-0.918	-0.910
Depth^2 (10^7)	0.860	0.900	1.040	1.080	0.680	0.840	0.940	0.860
Latitude	-0.047	-0.045	-0.049	-0.048	-0.050	-0.043	-0.047	-0.046
Ice, part	0.025	0.041	0.080	-0.032	0.039	0.024	0.035	0.042
Ice, all	-0.277	-0.279	-0.276	0.119	-0.265	-0.247	-0.286	-0.284
Anchovies	-0.234	-0.323	-0.221	-0.198	-0.249	-0.222	-0.233	-0.241
Herring, capelin	0.130	0.125	0.102	0.121	0.128	0.096	0.130	0.124
Perches	-0.150	-0.124	-0.134	-0.146	-0.141	-0.146	-0.160	-0.144
Cods	0.117	0.087	0.128	0.107	0.111	0.145	0.115	0.109
Flatfish	0.047	0.057	0.040	0.065	0.049	0.070	0.059	0.052
Scorpionfishees	0.114	0.120	0.107	0.108	0.123	0.107	0.118	0.119
Invertebrates	-0.033	-0.023	-0.037	-0.050	-0.026	-0.029	-0.039	-0.028

Table 4, continued.

	North Sea 1880	North Sea 81	North Sea 63	North Sea 74	Norwegian-Barents Sea 97	Scotian shelf 80-85	US South Atlantic States	US Mid Atlantic Bight
(Intercept)	39.655	36.757	35.656	35.488	24.918	37.694	36.174	36.235
year	-0.019	-0.018	-0.017	-0.017	-0.013	-0.018	-0.017	-0.018
Prim. prod.	0.187	0.160	0.173	0.169	0.414	0.180	0.118	0.153
Depth (10^3)	-0.916	-0.934	-0.926	-0.912	-0.679	-0.981	-0.941	-0.911
Depth^2 (10^7)	0.880	0.920	0.910	0.890	0.650	1.070	0.930	0.880
Latitude	-0.044	-0.046	-0.046	-0.045	-0.020	-0.048	-0.049	-0.046
Ice, part	0.026	0.034	0.039	0.039	0.081	0.017	0.029	0.039
Ice, all	-0.275	-0.281	-0.282	-0.283	-0.426	-0.260	-0.294	-0.297
Anchovies	-0.239	-0.242	-0.239	-0.239	-0.185	-0.237	-0.259	-0.229
Herring, capelin	0.115	0.120	0.120	0.121	0.168	0.075	0.123	0.124
Perches	-0.151	-0.136	-0.145	-0.148	-0.111	-0.142	-0.124	-0.147
Cods	0.129	0.101	0.116	0.115	0.180	0.155	0.100	0.112
Flatfish	0.056	0.045	0.051	0.052	-0.128	0.039	0.052	0.050
Scorpionfishes	0.107	0.135	0.114	0.109	0.087	0.124	0.115	0.123
Invertebrates	-0.020	-0.022	-0.025	-0.019	0.003	-0.008	-0.020	-0.033

Effect of catch composition on the regression analyses

In an exercise analogous to the jackknifing for quantifying the effect of excluding individual models from the regression analyses, we have investigated the effect of excluding each of the nine individual catch categories from the regressions. Omitting individual catch categories was found to have negligible impact on the estimated biomasses of high trophic-level fish in the North Atlantic, as can be seen from Figure 9. Nearly all the predicted biomasses fall close to the original regression (which is marked with diamonds in the figure).

The effect that omitting catch categories has on the intercepts and slopes of the biomass regressions is shown in Table 5. As might be seen, the intercepts and slopes of the regressions omitting individual catch categories are fairly stable across the analyses.
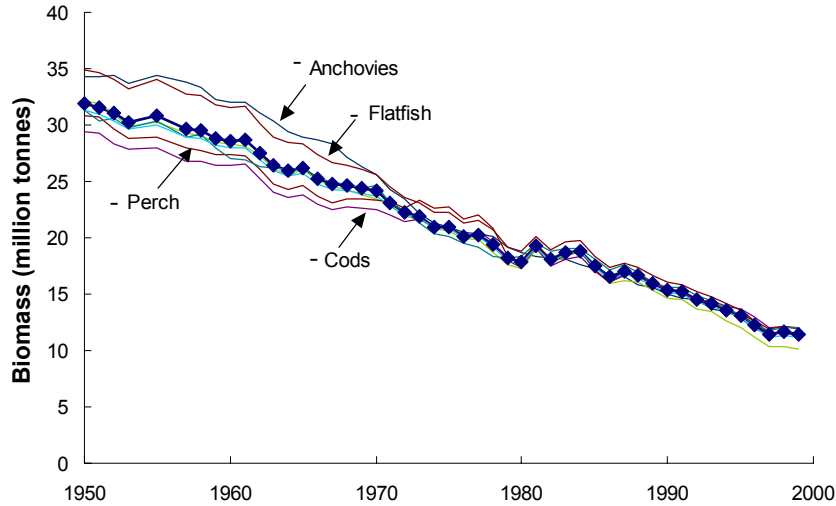
Figure 9. Effect on the estimated biomass of high trophic-level fish in the North Atlantic of omitting individual catch groupings from the regression analysis. The thicker line with diamond markers is based on the original regression including all catch categories (the data marked 'None' in Table 5). Groups that when omitted have any noticeable impact on the results are indicated.

Table 5. Effects on parameters (intercept, slope and correlation coefficient) of multiple linear regression of omitting individual catch categories from the regressions. The column headings indicate the catch category that was omitted from each of the 10 regressions made. The catch categories are the same as discussed earlier.

Variable	None	Anchovy	Herring	Perches	Cods	Flatfish	Scorpion	Invert.
(Intercept)	35.873	36.756	40.308	42.314	35.596	37.111	31.426	36.680
year	-0.017	-0.018	-0.020	-0.021	-0.017	-0.018	-0.015	-0.018
Prim. Prod.	0.165	0.052	0.246	0.104	0.214	0.167	0.155	0.188
Depth (10^3)	-0.916	-0.901	-0.945	-0.951	-0.933	-1.006	-0.811	-0.924
Depth^2 (10^7)	0.890	0.860	0.940	1.030	0.950	1.060	0.720	0.910
Latitude	-0.046	-0.047	-0.040	-0.047	-0.041	-0.050	-0.043	-0.044
Ice, part	0.038	0.036	0.002	0.056	0.041	0.034	0.048	0.019
Ice, all	-0.285	-0.372	-0.281	-0.262	-0.278	-0.280	-0.318	-0.259
Anchovies	-0.239		-0.234	-0.294	-0.294	-0.225	-0.218	-0.258
Herring, capelin	0.122	0.119		0.085	0.142	0.122	0.128	0.106
Perches	-0.142	-0.181	-0.096		-0.083	-0.139	-0.198	-0.128
Cods	0.112	0.165	0.148	0.029		0.132	0.183	0.111
Flatfish	0.052	0.038	0.053	0.047	0.074		0.088	0.051
Scorpionfish	0.117	0.105	0.123	0.161	0.157	0.136		0.117
Invertebrates	-0.027	-0.053	0.012	0.000	-0.026	-0.026	-0.027	
r^2-Squared:	0.859	0.859	0.841	0.842	0.850	0.855	0.842	0.857

The overall conclusion from the two series of regression analyses that omitted parts of the data is that the results are robust with regards to the slope of the resulting biomass trends, whereas the absolute values of the predicted biomasses are more uncertain. This is in line with the general expectation for this form for multiple regression, i.e., we expect to be able to distinguish change better than we can predict absolute values.

Predicting biomass of predatory fishes

We have derived a linear regression to predict the abundance of high trophic-level fishes in the North Atlantic based on information from a number of ecosystem models dispersed over the region and in time from the late 19th Century through to the end of the 20th Century. The regression is based on a total of 18,024 spatial units of ½ by ½ degree, and uses year, depth, primary production, temperature, ice cover, and catch quantity and composition to predict the biomass.

For predictive purposes we then established a spatialized database including the same information for all spatial units globally and for all years from 1950 through 1999. For the present analysis, however, we use the database only to predict biomasses in the North Atlantic region to avoid extrapolation beyond the area covered by the ecosystem models in Table 1.

Based on the biomass regression analysis applied to the North Atlantic in 1950, 1975 and 1999 the maps in Figure 10 can be derived. These maps, prepared using ArcView GIS 3.2, indicate how biomasses were predicted to be distributed in the three years represented, and are intended to describe general patterns only. They will obviously miss out on specific events, such as the emergence of a big year-class of a major population for obvious reasons, however, they will capture the big picture. The maps indicate a strong decline in biomass over the fifty-year period studied; we will return to this theme below.
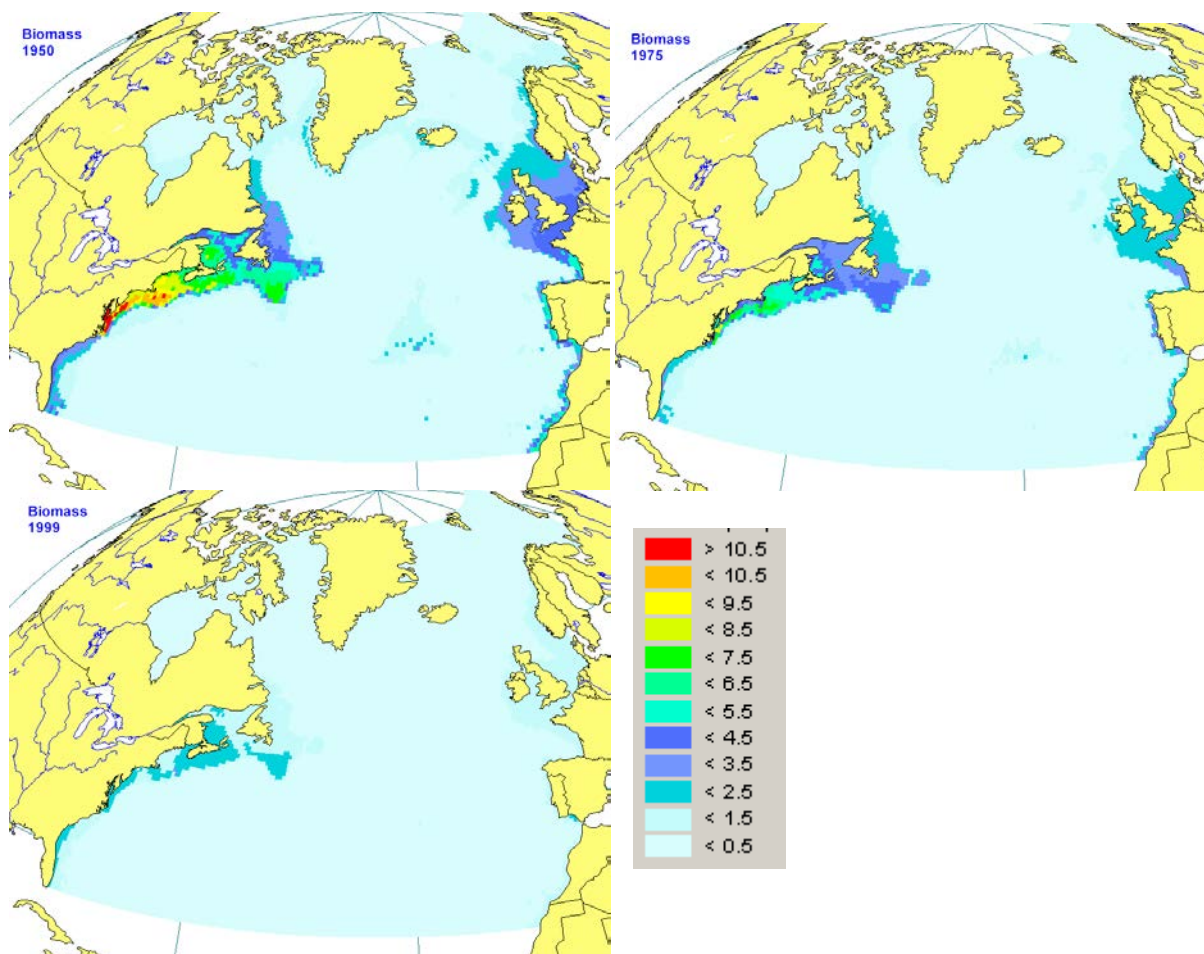

Figure 10. Biomass distributions for high trophic-level fish in the North Atlantic in 1950, 1975 and 1999. The distributions are predicted from linear regressions based on primary production, depth, temperature, year, ice cover, latitude, and catch composition. Units for the legend are t·km^{-2}.

Catches

The catches of high trophic-level species, i.e., of the main species of interest for human consumption, as demonstrated in Figure 2, increased steadily from 1950 through to the end of the 1960s, and have declined as steadily ever since (Figure 11). The catch level in the late 1990s was thus lower than in 1950, in spite of major development in catch capacity and technological progress, along with geographic expansion across the North Atlantic region.

The estimated spatial distributions of the high trophic-level catches are mapped in Figure 12. They are based on the rule-based method for distribution of catches described by (Watson and Pauly, 2001) and (Watson *et al.*, 2002), but applied only to fish species with a trophic level of 3.75 or more.

Fishing mortalities

The catch figure and catch maps (Figure 11 and Figure 12) by themselves paint a dire picture of what has happened in the North Atlantic area over the past fifty years, but they do not directly address a major question: "Do we catch less because there are less fish, or is it due to catch restrictions imposed to limit catches?" In order to address this question, we need to derive measure of how fishing effort has developed over time. Ideally we would have a direct measure of the fishing effort, but such information is pathologically poor, even in this well-studied and highly regulated region. *In lieu* of a direct measure, we will revert to a classic estimation. Beverton and Holt (1957) describe the ratio of catch to biomass for a population as a direct measure of fishing intensity, and the catch/biomass ratio, commonly described as 'fishing mortality', is indeed the method of choice in fisheries assessment for regulating fishing effort. We emphasize that the measure of fishing mortality we have derived here is not directly comparable to the mortality rates commonly reported, as the absolute level of the biomasses estimated here is associated with considerable uncertainty. Therefore, we prefer to interpret the measure as a relative index of 'fishing intensity' only, especially since Beverton and Holt proposed this term for use in spatial applications.
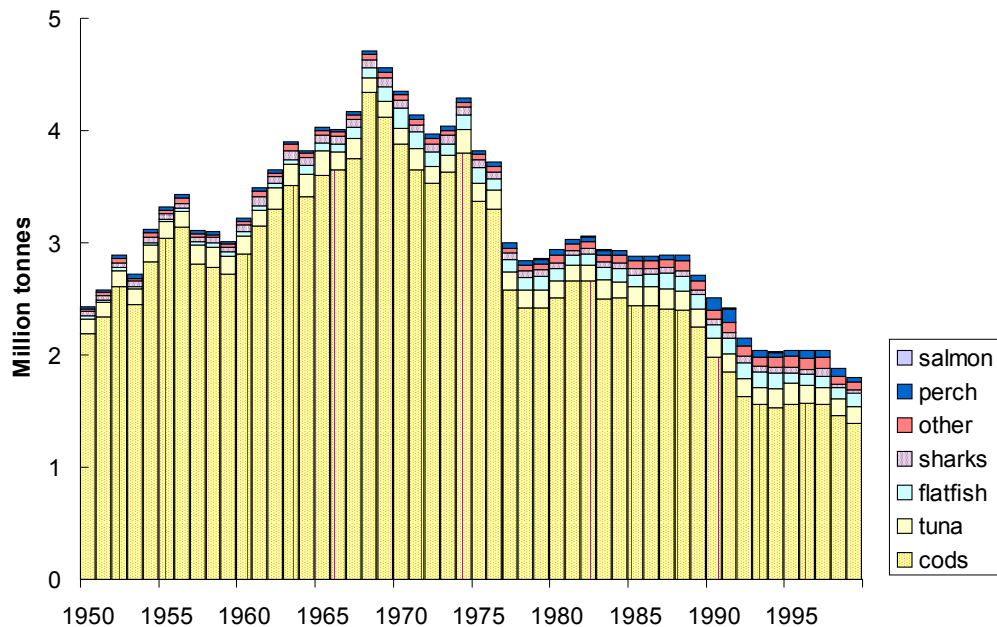

Figure 11. Annual catches of high trophic-level fish in the North Atlantic during 1950 to 1999. Primarily based on catch data from FAO (see Watson et al., 2001, for details). The catches include only fish species with a trophic level of 3.75 or more. The trophic levels are mainly based on diet compositions, and are extracted from FishBase.
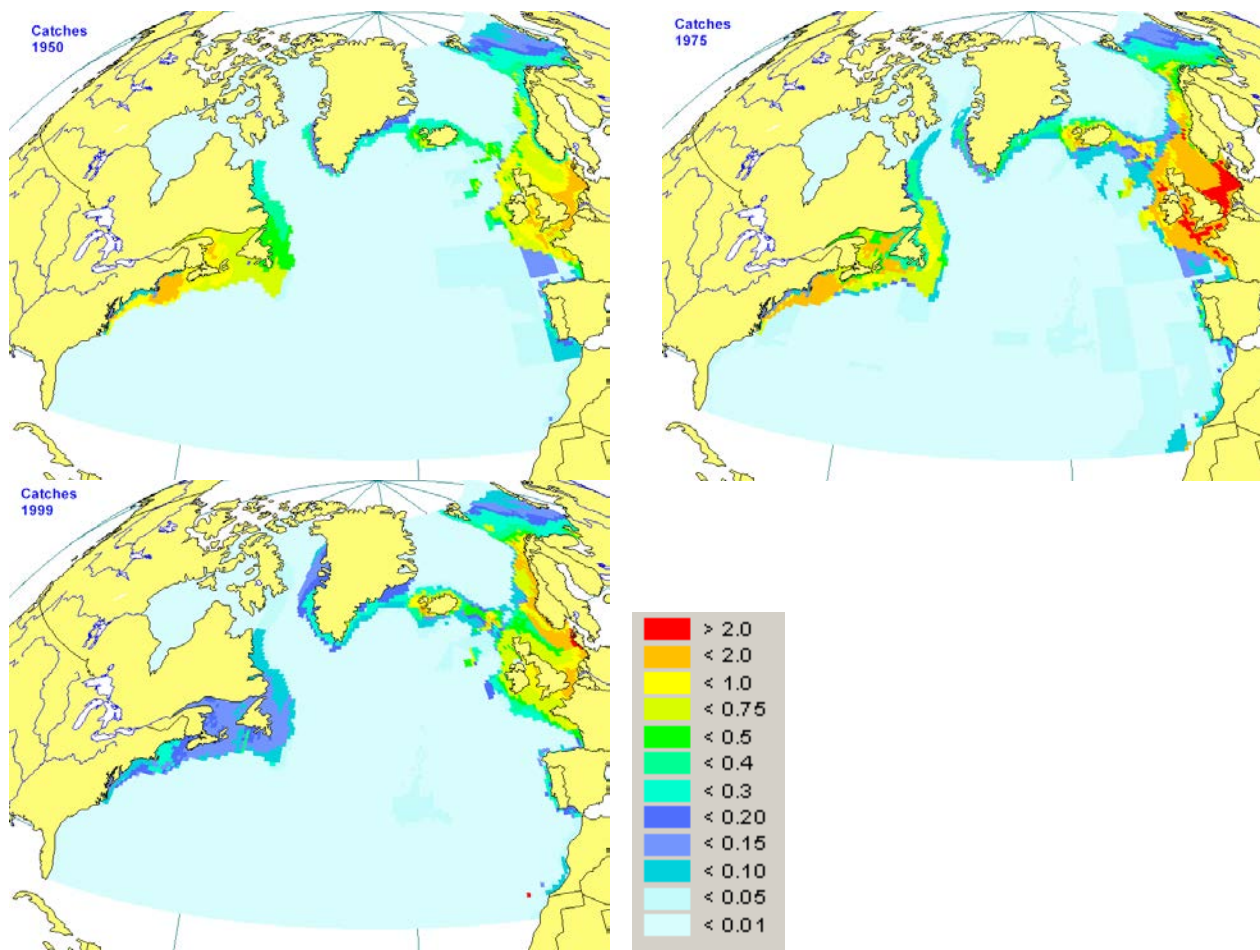
Figure 12. Predicted catch distributions of high trophic-level fishes in the North Atlantic in 1950, 1975 and 1999. The catches are based on FAO catch data information supplemented with other sources using a rule-based system for spatial allocation (Watson et al. 2001), and are here extracted for fish with trophic level $\geq$ 3.75 (based on trophic levels in FishBase). Units for the legend are $t \cdot km^{-2} \cdot year^{-1}$

Combining information about catch and biomass levels over time, we obtain the results shown in the maps in Figure 13 and in the plot in Figure 14. The figure neatly summarizes trends over the last fifty years for high trophic-level fishes in the North Atlantic. Biomasses are found to have been declining steadily over the period at a rate that was slightly lower in the first twenty years than in the last thirty years. The catches peaked in the late 1960s, and have declined steadily since to the extent that the level in 1999 was lower than in 1950. The resulting measure of fishing intensity, estimated as the ratio between catch and biomass, provides part of the explanation. Fishing intensity increased with catches, and has remained nearly constant since the late 1960s, while both catches and biomasses declined steadily (Figure 14).

How long can this continue? There are no indications in the results of a slowing down in the declining biomass trend. Indeed, the decline was lower during the period up to the peak in catches in 1968, and higher since. The results thus predict that high trophic-level fishes will be all but gone from the North Atlantic region within a few decades if the current trend continues.
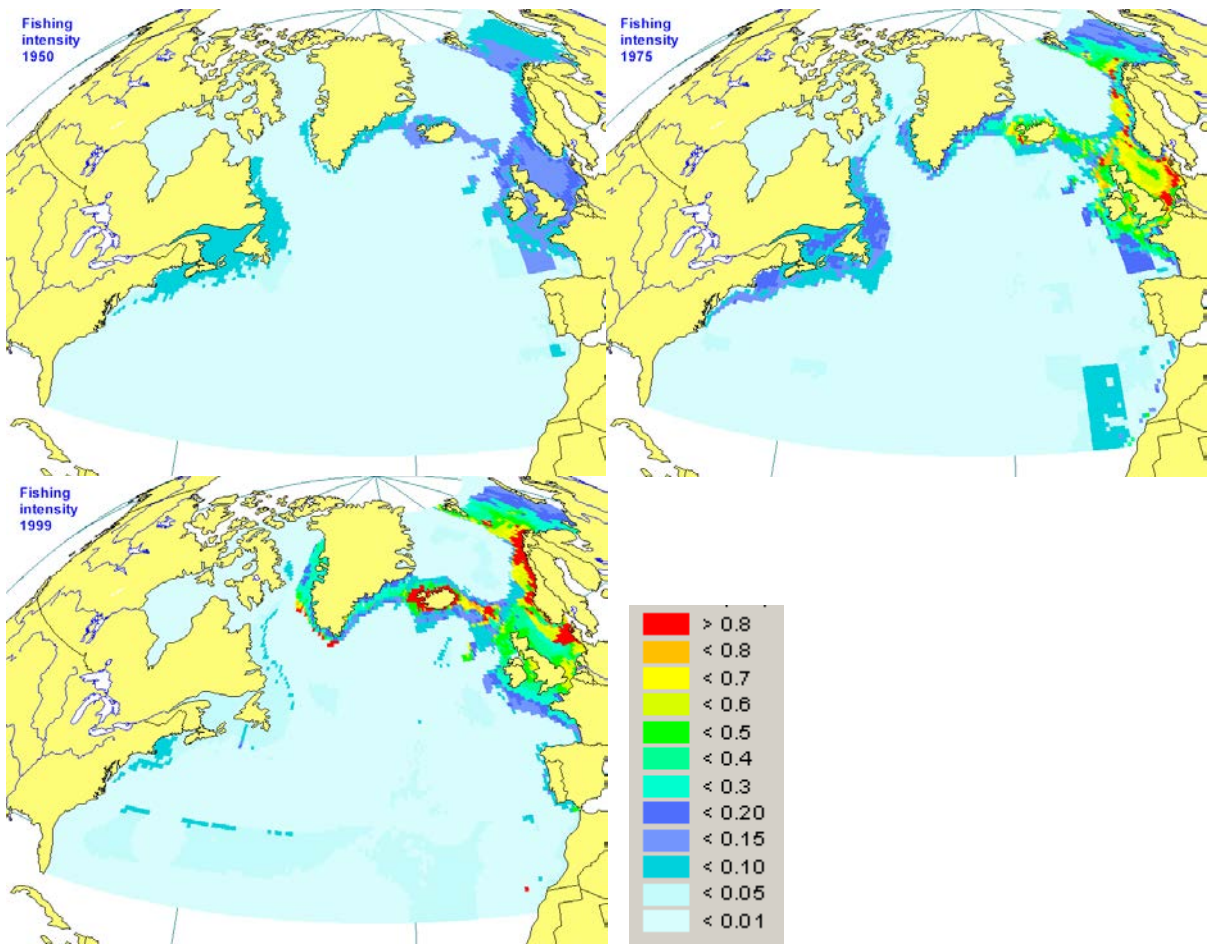
Figure 13. Estimated fishing intensity for high trophic-level fishes (TL≥3.75) in the North Atlantic region in 1950, 1975 and 1999. The fishing effort is derived from spatial estimates of biomasses (Figure 10) and catches (Figure 12). Units for the legend are year^{-1}, but the measure should be seen as a relative measure only.
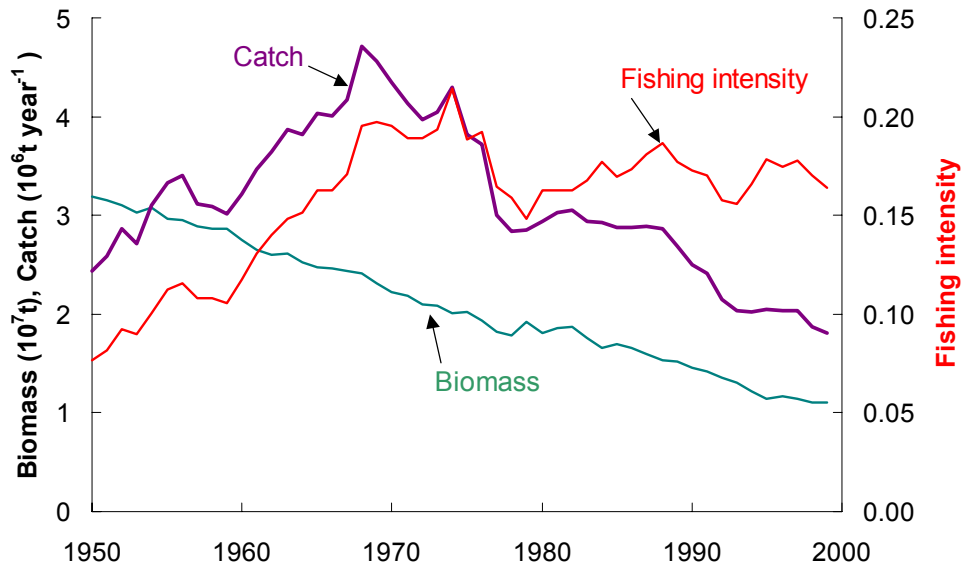

Figure 14. Estimated catch (10^6 tonnes·year^{-1}) and biomass (10^7 tonnes) of high trophic-level fishes in the North Atlantic during 1950-1999. The ratio between catch and biomass is an expression of fishing intensity (Beverton and Holt, 1957).

DISCUSSION

Overall we estimate that the biomass of high trophic-level fish species in the North Atlantic declined by two-thirds during the second half of the 20th century. We should ask then, how reliable is this estimate? We note that the finding seems to be fairly robust to the extent that it did not matter much if we omitted part of the data material on which the estimate is built. However, despite the jackknifing that led to Figure 8, we are at present unable to assign a formal confidence interval to the estimate. It is also a fairly difficult task to find supportive evidence in the form of bottom-up approaches summing up the biomasses of all major fish populations in the North Atlantic. This is reflective of the varying time periods for which assessments have been made for the many populations in the area. Thus, some form of modeling is needed to fill in the blanks, i.e., to provide estimates for the years where none have been made. Also, far from all stocks are being assessed, making a bottom-up estimate likely to be an underestimate.

While waiting for a bottom-up approach, we can examine some trends from various stock assessments in the North Atlantic (Figure 15).

Assembling the plots in Figure 15 was done by going through the majority of the recent stock assessments made for the North Atlantic, and extracting biomass time series for high trophic-level fishes. The most difficult task in doing this was to decide which populations to include here – virtually all showed the same patterns, be it target or non-target species: massive decline during the period for which assessments were made, and a present critical state of the stocks (see Table 6 for an overview of the state of affairs for the majority of the high trophic-level species under ICES auspices). In contrast, there were very few populations that did not show a clear decline (such as, e.g., cod at the Faroe Islands, see Figure 15). Some groups show increases due to what may be replacement or cascading, but these were mainly intermediate trophic-level species; very few high trophic-level species show increase – exceptions may be some small sharks and rays, but for these, it is fairly uncertain whether the mechanism involved is predator removal or simply that more food has been made available, notably in form of the massive discarding that appears to go hand in hand with stock depletions and the subsequent collapses.

Table 6. Status of high trophic-level fish stocks in the Northeastern Atlantic according to the ICES Advisory Committee for Fisheries Management (ACFM, 2001). Only two smaller stocks (of saithe) are considered within safe biological limits (SBL).

| Species	Area	State of stock/exploitation
Cod	NE Arctic (I, II)	Stock is outside of SBL
Cod	Norwegian coastal	Spawning stock is at a historical low
Saithe	NE Arctic (I, II)	Stock within SBL following good year classes
Redfish	NE Arctic (I, II)	Stock considered outside SBL
Greenland halibut	NE Arctic (I, II)	Stock considered outside SBL
Cod	Greenland (XIV, NAFO 1)	Stock is outside SBL
Cod	Icelandic waters (Va)	Stock near historic low
Greenland halibut	Greenland (V, XIV)	Stock harvested outside SBL
Saithe	Icelandic waters (Va)	Stock considered outside SBL
Cod	Faroe Plateau (Vb1)	Stock harvested outside SBL
Haddock	Faroe (Vb)	Stock outside SBL
Saithe	Faroe (Vb)	Stock harvested outside SBL
Cod	West of Scotland (VIa)	Stock remains outside SBL
Haddock	West of Scotland (VIa)	Stock harvested outside SBL
Haddock	Rockall (VIa)	Stock remains outside SBL
Cod	North Sea (IV, VIId, IIIa)	Stock outside SBL
Haddock	North Sea (IV, IIIa)	Stock being harvested outside SBL
Saithe	North Sea (IV, IIIa, VI)	Stock is within SBL
Anglerfish	North Sea (IV, VI)	Stock is harvest outside of SBL
Cod	Kattegat (IIIa)	Stock considered outside SBL
Cod	Kattegat (IIIa)	Stock considered outside SBL
Cod	Irish Sea (VIIa)	Stock remains outside of SBL
Haddock	Irish Sea (VIIa)	Stock harvested outside of SBL
Whiting	Irish Sea (VIIa)	Stock remains outside of SBL
Cod	VIIe-k	Stock outside of SBL
Hake	Southern (VIIx, IXa)	Stock outside SBL
Hake	Northern (IIIa, IV, VI, VIII, VIIIa,b,d)	Stock is outside SBL
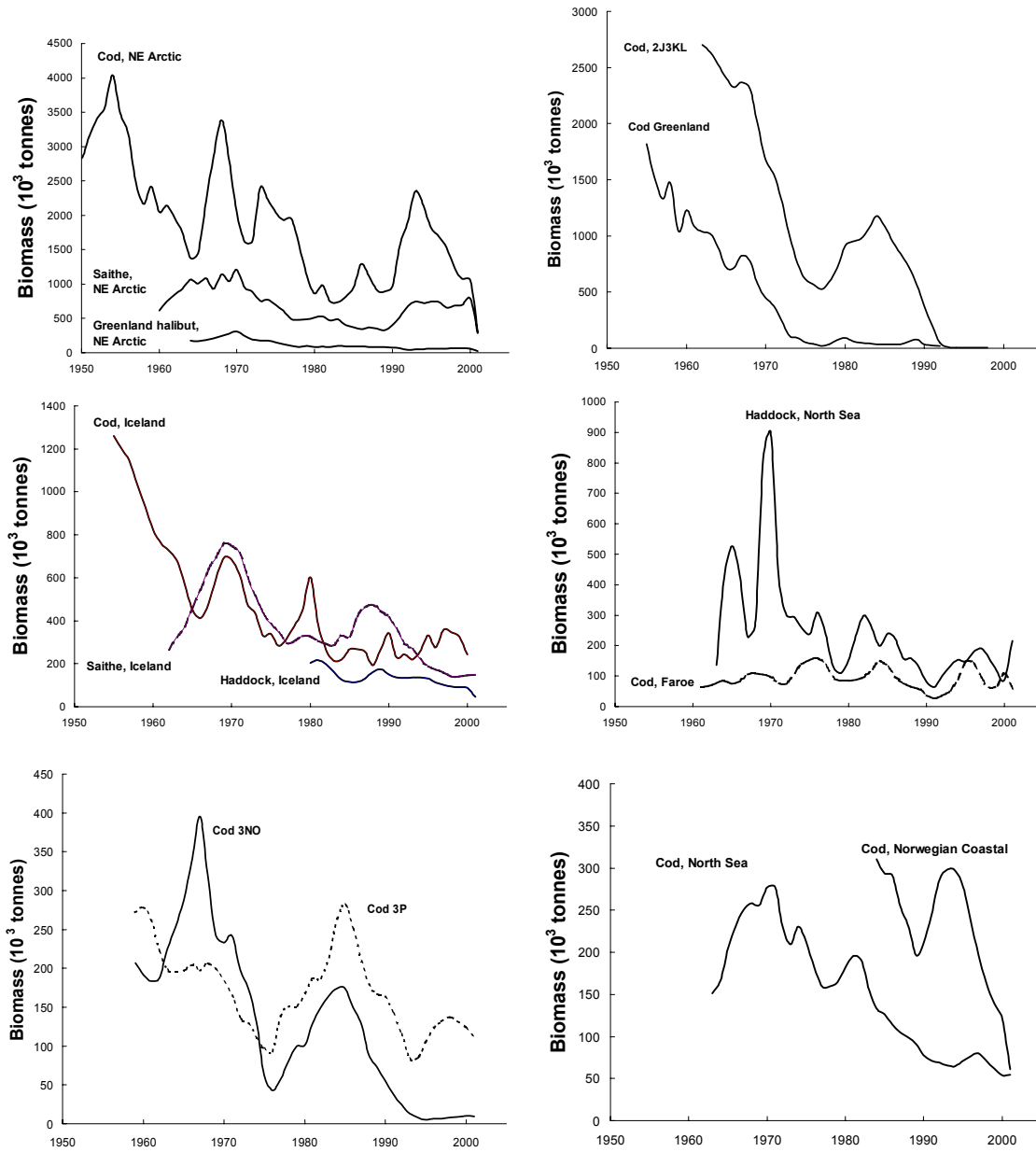
Figure 15. Trend over time (1950-2001) in biomass (thousand tonnes) of a variety of high trophic-level fish stocks in the North Atlantic. Based on ACFM (2001), Lilly *et al.* (1998), Lilly *et al.* (2001), NAFO (2000), Anon. (2001a), Brattey *et al.* (2000), O'Brien and Munroe (2001) and ICCAT (2001).
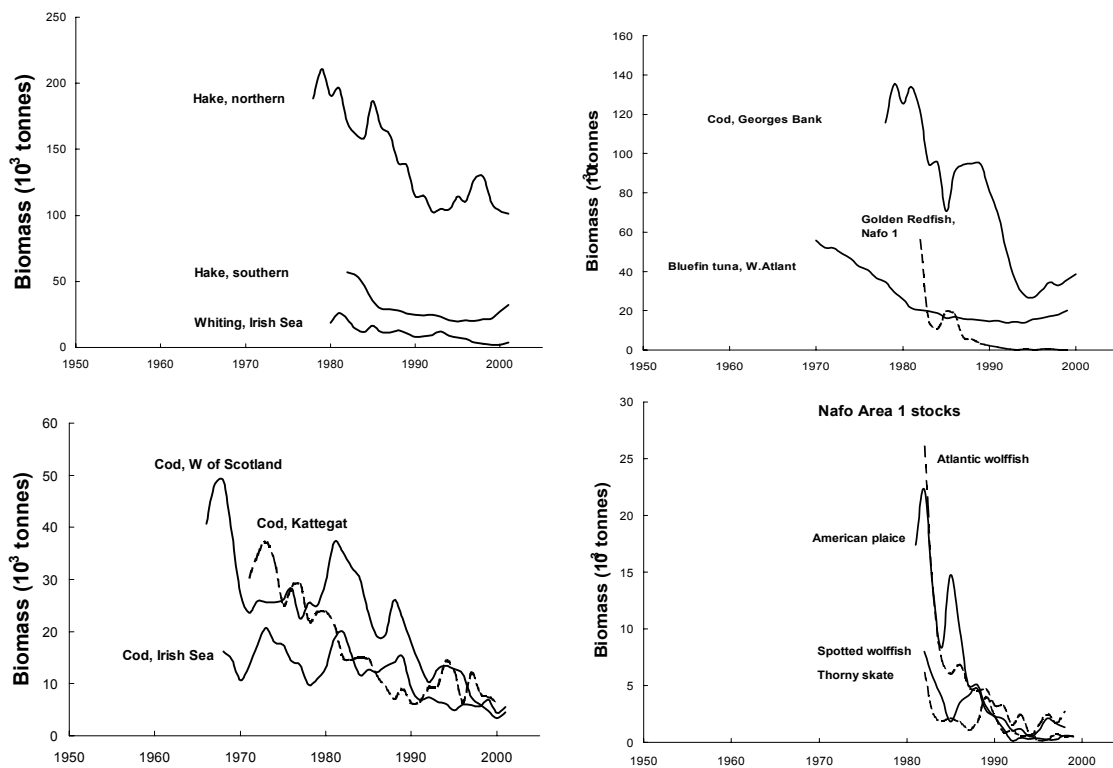
Figure 15. Cont.

The pattern that seems to emerge when examining biomass trends for a variety of North Atlantic fish populations is one of massive decline, indicating that the decline over time we estimated in this study is at least a feasible scenario. This is also the conclusion reached when examining the trends for the high trophic-level species included in the stock-recruitment database assembled by R. Myers (available at *http://fish.dal.ca/~myers/welcome.html*), as indicated in Figure 16, which gives a summary of the trends for a large number of populations from the database.

Our study indicates that fishing intensity in the North Atlantic increased through the 1950s and 1960s, and has remained at what appears to be an unsustainably high level ever since. For comparison, the trend for fishing mortality in 35 populations in the North Atlantic based on stock assessments is compared to the fishing intensity from our study (Figure 14) in Figure 17. We conclude from the graph that the two sets of fishing intensity, (i.e., mortality) bear much similarity.

Several observations require mentioning when examining Figure 17; one is the different scaling of the two Y-axes. Fishing intensity is calculated as the annual catch over the biomass, and while our study indicates a ratio approaching 0.20

year^{-1}, the indications of fishing mortalities from the assessments are three times higher. This indicates that the biomasses we estimate are considerably higher than those originating from averaging over the assessed stocks. This apparent difference may have several causes, of which two bare mentioning. First is that only some populations are subject to stock assessment, and these tend to be the ones with highest exploitation rates. Secondly, biomass estimates based on regressions with log-transformations are quite uncertain, and indeed, we trust the trend in biomass more than the face value of the estimates. We do not know, at present, which of the two explanations contribute most toward an explanation, but we do expect both factors to be contributing.

We are aware that the mean fishing intensity of assessed stocks presented in Figure 17 should not be interpreted as the mean fishing intensity for high trophic-level fish in the North Atlantic. For this, the fishing intensities should have been weighted according to population sizes. However, our intention is rather to discover something about the average population – since the measure of fishing intensity is calculated as catch over biomass, it is a measure of exploitation rate and, as such, an ecologically more representative measure.
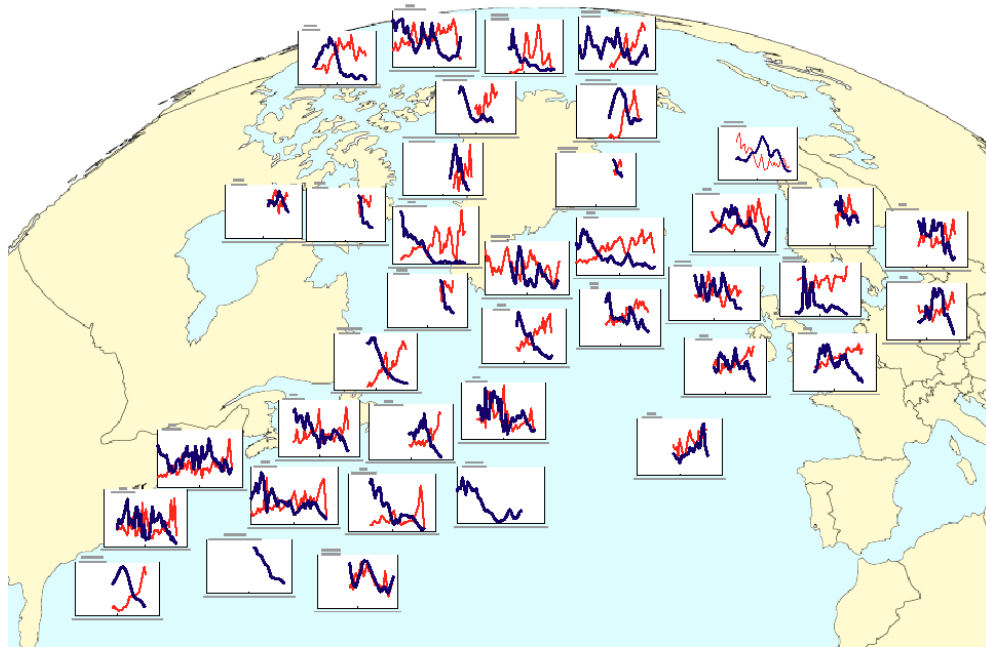
Figure 16. Trend over time in biomass (thick, dark lines) and fishing effort (thin lines) from assessments of major resource species in the North Atlantic, including many of the commercially important, high trophic-level species that are the focus of this study. The horizontal axes span the second half of the 20th Century. The general trend of decreasing biomasses and increasing fishing effort is in line wit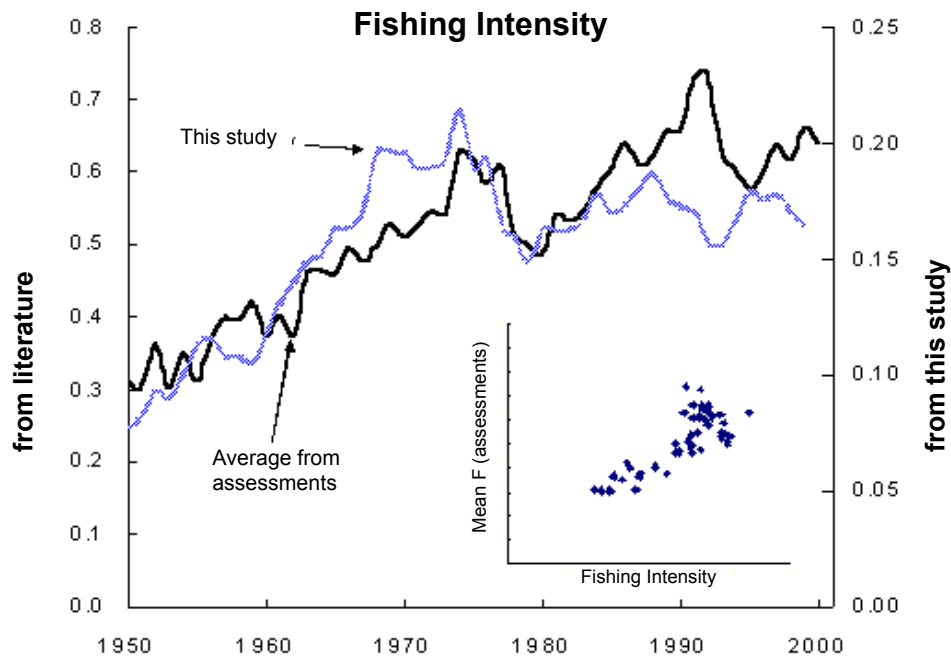h the findings reported here. Based on data from the database assembled by R. Myers *(http://fish.dal.ca/~myers/welcome.html)*.

Figure 17. Trend in fishing intensity (mortality) for assessments of 35 populations of high trophic-level fish species from the North Atlantic, (solid line, primary Y-axis, year^{-1}). These fishing intensity rates are from the same sources as the biomasses in Figure 15. The lighter thick line (secondary Y-axis, year^{-1}) indicates the fishing intensity from the present study (Figure 14). The insert shows the series of fishing intensity plotted versus each other, with the values from this study on the X-axis.

The maps and figures presented here indicate that fishing intensity and catch levels have been higher in the Northeastern Atlantic than in the Northwestern Atlantic. Yet, the decline in biomass of high trophic-level fish has been most severe in the northwestern part of the basin. This may seem inconsistent, but may well result from the waters of the northwest being colder, deeper, and less productive than in the northeast, i.e., that the New World waters are less resilient to fishing pressure than those in the Old World. The maps of hydrographic and productivity patterns in Figure 5 lends some credibility to such a hypothesis. If this observation has any merit, it means that care should be exercised when transferring experience on managing Northeastern Atlantic stocks to the Northwestern Atlantic.

We were in the present study not able to reliably estimate the abundance of forage fishes, and chose to omit these from the results. This is reflective of our limited knowledge of these groups, and is indicative of fisheries science focusing on the exploited target species, and largely ignoring the ecology of the systems on which the fisheries rely.

Ecosystem models may indeed help one to draw inferences about prey abundance from predator demand. We can conclude that if the biomasses of predatory fishes were indeed much higher in past ecosystems (as all evidence points to) they must have been consuming more than today's impoverished fauna would lead one to think. However, we do not know if this demand was met by a higher biomass of the forage species and/or by higher mortality rates for the groups. On the other hand, we can be certain that the product of these two, i.e., the production of prey species must have been higher. We note in passing that there are ways of obtaining supporting evidence – egg and larval surveys have been conducted for a century, and even if they were rather sporadic in the early part of the 20th Century, there is a widespread coverage of standardized egg surveys from the 1960s through to the 1980s. Unfortunately, the surveys have typically focused on target species only, and the eggs or larvae of the species of lower trophic-level species may not have been analyzed. Since the samples are stored in many laboratories, it is at least in principle still possible to obtain such information given sufficient interest and resources. Another source of evidence may come from the size compositions of forage species from 'old' diet composition studies of predatory fishes. Based on the size distributions, mortality rates can be estimated given growth parameters (which are readily available, e.g., from FishBase). However, old diet compositions studies have a tendency to focus on presence or absence, and not much on prey size compositions.

We have developed and applied a methodology to assess the state of the high trophic-level fish populations of the North Atlantic, and have concluded that the biomass of these commercially and ecologically important species are dwindling rapidly. We stress that what happens to the high trophic-level species serves as an indicator for what we do to the ocean, and hence we conclude that all is not well with the ocean.

REFERENCES

ACFM, 2001. Report of the ICES Advisory Committee on Fisheries Management.

Anon., 2001a. Report of the North-Western Working Group. ICES, CM 2001/ACFM:20.

Anon., 2001b. S-Plus 6 for Windows Guide to Statistics, Volume 1. Insightful Corporation, Seattle, WA,

Baird, D., and Ulanowicz., R. E. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. Ecological Monographs, 59(4):329-364.

Behrenfeld, M. J., and Falkowski, P. G. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnology and Oceanography, 42:1-20.

Beverton, R. J. H., and Holt, S. J., 1957. On the dynamics of exploited fish populations. Chapman and Hall, London., 533 pp.

Blalock, H. M., 1972. Social Statistics. McGraw-Hill, New York. 583 pp.

Brattey, J., Cadigan, N. G., Lilly, G. R., Murphy, E. F., Shelton, P. A., and Stansbury, D. E., 2000. An assessment of

the cod stock in NAFO Subdiv. 3Ps in October 2000. DFO Canadian Stock Assessment Secretariat, Research Document 2000/134.

Bundy, A., Lilly, G., and Shelton, P. A., 2000. A mass balance model of the Newfoundland-Labrador Shelf. Canadian Technical Report of Fisheries and Aquatic Sciences 2310.

Carscadden, J. E., Frank, K. T., and Leggett, W. C. 2001. Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. Canadian Journal of Fisheries and Aquatic Sciences, 58(1):73-85.

Christensen, V. 1995. A model of trophic interactions in the North Sea in 1981, the Year of the Stomach. Dana, 11(1):1-28.

Christensen, V. 1996. Managing fisheries involving predator and prey species. Reviews in Fish Biology and Fisheries, 6(4):417-442.

Christensen, V., and Pauly, D. 1998. Changes in models of aquatic ecosystems approaching carrying capacity. Ecological Applications, 8(1):S104-S109.

Christensen, V., and Walters, C. J., 2000. Ecopath with Ecosim: methods, capabilities and limitations. pp 79-105. In: Methods for assessing the impact of fisheries on marine ecosystems of the North Atlantic. Ed. by D. Pauly and T. J. Pitcher. Fisheries Centre Research Report 8(2).

Cole, K. C., 1998. The universe and the teacup: The mathematics of truth and beauty. Harcourt Brace and Co., New York. 214 pp.

Daskalov, G. M. 2002. Overfishing drives a trophic cascade in the Black Sea. Marine Ecology Progress Series, 225:53-63.

Heymans, J.J. in prep.a). A Picasso-esque view of the marine ecosystem of Newfoundland and southern Labrador in 1500 and 1900. In: Ecosystem Models of Past and Present in the Hecate Strait and Newfoundland Shelf. Ed. by J. J. Heymans, C. Ainsworth, and T. J. Pitcher, Fisheries Centre Research Reports.

Heymans, J.J. in prep.b) The marine ecosystem of Newfoundland and southern Labrador (2J3KLNO) in 1985-1987 and 1995-1997. In: Ecosystem Models of Past and Present in the Hecate Strait and Newfoundland Shelf. Ed. by J. J. Heymans, C. Ainsworth, and T. J. Pitcher, Fisheries Centre Research Reports.

Hoepffner, N., Bouvet, M., and Mélin., MS, F., Global marine primary production from space. Joint Research Center of the European Commission, (nicolas.hoepffner@jrc.it)

ICCAT, 2001. Report of the ICCAT SCRS. West Atlantic Bluefin tuna stock assessment session, (Madrid, Spain - September 18 to 22, 2000). Detailed Report.

Kaschner, K., Watson, R., Christensen, V., Trites, A. W., and Pauly, D., 2001. Modeling and Mapping Trophic Overlap between Marine Mammals and Commercial Fisheries in the North Atlantic. pp 35-45. In: Fisheries Impacts on North Atlantic Ecosystems: Catch, Effort, and National and Regional Data Sets. Ed. by D. Zeller, R. Watson, and D. Pauly, Fisheries Centre Research Report 9(3).

Lilly, G. R., Shelton, P. A., Brattey, J., Cadigan, N., Murphy, E. F., Stansbury, D. E., Davis, M. B., and Morgan, M. J., 1998. An assessment of the cod stock in NAFO Divisions 2J+3KL. DFO Canadian Stock Assessment Secretariat, Research Document 98/15. 102 pp.

Lilly, G. R., Shelton, P. A., Brattey, J., Cadigan, N. G., Healey, B. P., Murphy, E. F., and Stansbury, D. E., 2001. An assessment of the cod stock in NAFO Divisions 2J+3KL. DFO, Canadian Stock Assessment Research Document 2001/044.

NAFO, 2000. Report on Standing Committee on Fisheries (STACFIS), June 2000.

O'Brien, L., and Munroe, N. J., 2001. A Report of the 4th Transboundary Resources Assessment Committee Meeting Assessment of the Georges Bank Atlantic Cod Stock for 2001. Northeast Fisheries Science Center, Reference Document 01-10.

Pace, M. L., Cole, J. J., Carpenter, S. R., and Kitchell, J. F. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution, 14(12):483-488.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology & Evolution, 10(10):430.

Pauly, D. 1996. One hundred million tonnes of fish, and fisheries research. Fisheries Research (Amsterdam), 25(1):25-38.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F., Jr. 1998. Fishing down marine food webs. Science, 279(5352):860-863.

Pauly, D., Christensen, V., and Walters, C. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES Journal of Marine Science, 57(3):697-706.

Pauly, D., and Palomares, M. L. D., MS, Fishing down marine food web: it is far more pervasive than we thought. Presented at the Conference of Sustainability of Fisheries, held on November 26-28, 2001 at the Rosenstiel School of Marine Sciences, University of Miami.

Pauly, D., and Pitcher, T. J., 2000. Assessment and Mitigation of Fisheries Impacts on Marine Ecosystems: A Multidisciplinary Approach for Basin-Scale Inferences, Applied to the North Atlantic. pp 1-12. In: Methods for assessing the impact of fisheries on marine ecosystems of the North Atlantic. Ed. by D. Pauly and T. J. Pitcher. Fisheries Centre Research Report 8(2)

Pinnegar, J. K., Polunin, N. V. C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M. L., Hereu, B., Milazzo, M., Zabala, M., D'Anna, G., and Pipitone, C. 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environmental Conservation, 27(2):179-200.

Sokal, R. R., and Rohlf, F. J., 1995. Biometry: The Principles and Practice of Statistics in Biological Research. W. H. Freeman Company, 877 pp.

Sumaila, U. R., and Watson, R., 2001. Mapping catch values from marine ecosystems with emphasis on the North Atlantic. pp 12-17. In: Fisheries impact on North Atlantic marine ecosystems: Catch, effort and national and regional data sets. Ed. by D. Zeller, R. Watson, and D. Pauly, Fisheries Centre Research Report 9(3).

Walters, C., Christensen, V., and Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries, 7(2):139-172.

Walters, C., and Kitchell, J. F. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. Canadian Journal of Fisheries and Aquatic Sciences, 58:39-50.

Walters, C., Pauly, D., and Christensen, V. 1999. Ecospace: Prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems, 2(6):539-554.

Walters, C., Pauly, D., Christensen, V., and Kitchell, J. F. 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. Ecosystems, 3(1):70-83.

Watson, R., Gelchu, A., and Pauly, D., 2001. Mapping fisheries landings with emphasis on the North Atlantic. pp 1-11. In: Fisheries impact on North Atlantic marine ecosystems: Catch, effort and national and regional data sets. Ed. by D. Zeller, R. Watson, and D. Pauly. Fisheries Centre Research Report 9(3).

Watson, R., and Pauly, D. 2001. Systematic distortions in world fisheries catch trends. Nature, 424:534-536.