

Northwest Atlantic



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### Ecosystem production potential in the Northwest Atlantic

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#### Introduction

From a theoretical perspective, ecosystem production potential (EPP) is the expected biomass/carbon that the entire biological community would produce out of the primary production generated in that region in ideal conditions. In its simplest conception, the EPP would be a function of the fraction of the primary production retained in that region and available to higher trophic levels, the transfer efficiency between successive trophic levels, and the number of trophic levels through which energy must be transferred (e.g. Ryther 1969, Ware 2000). In reality, other processes (e.g. transport, state of ecosystem components, environmental conditions and variability, climate change) would affect primary production and influence realized ecosystem production of higher trophic levels.

Without disputing that many factors can and do influence ecosystem productivity, global fisheries catches still seem to be effectively constrained by the primary production available (Chassot et al. 2010). This suggests that relatively simple EPP estimates can be useful starting points to identify ceilings for overall ecosystem catches if set to a level that prevents hindering overall ecosystem functionality could guide strategies at sustainably exploiting an ecosystem.

The concept of defining caps for total catches in an ecosystem is not new; the Northwest Atlantic Fisheries Organization (NAFO) predecessor, the International Commission for the Northwest Atlantic Fisheries (ICNAF), has already explored this concept in the 1970s (ICNAF 1973, 1974), although the analyses were never fully implemented. In the context of the development and implementation of the NAFO Roadmap for an Ecosystem Approach to Fisheries (EAF) (NAFO 2010a, 2013), the identification of ceilings for the overall catch level for an ecosystem (*sensu* "ecosystem level TAC") is the first step (tier 1) in the process of defining TACs for the exploited stocks within that ecosystem.

In order to generate plausible figures for ecosystem level catch ceilings, two basic components are required; [1] a precise definition on the geographical boundaries of the areas to be considered functional ecosystems, and [2] models that produce estimates of ecosystem productivity that can be implemented for those areas. The NAFO Scientific Council Working Group on Ecosystem Science and Assessment is in the process of identifying areas that can be considered functional ecosystem production units (NAFO 2010b, 2011). The purpose of this paper is to develop simple EPP models for these candidate areas, that could serve as starting points for estimating the fisheries production potential (FPP) of these ecosystems, and serve as guidelines for setting ecosystem-level catch ceilings in the context of the NAFO Roadmap to EAF.

## Methods

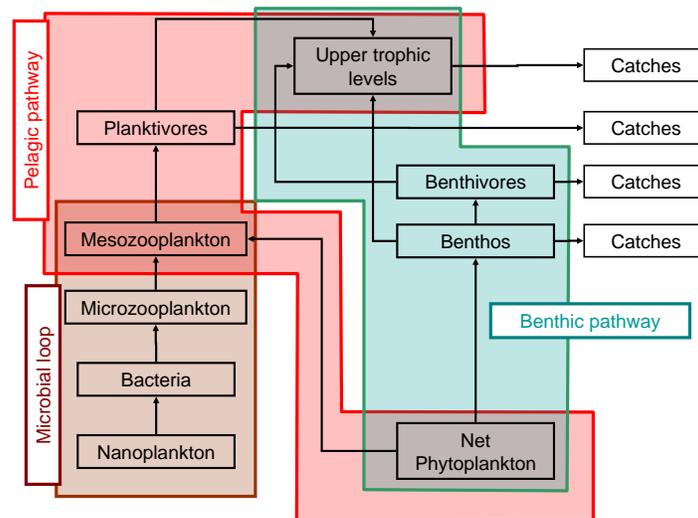
### *Ecosystem production units*

In this exercise, production units were based on some of the candidate ecosystem management units identified so far. The core ecosystem units considered in this analysis were the northern Newfoundland and Southern Labrador Shelf (NAFO Div. 2J3K), the Grand Bank (NAFO Div. 3LNO), the Flemish Cap (NAFO Div. 3M), the Scotian Shelf (NAFO Div. 4VsWX), and the Northeast US Continental Shelf (aprox. NAFO Div. 5+6ABC).

### *Ecosystem Production Potential (EPP) model structure*

The approach taken to estimating ecosystem production potential is an expansion of the Ryther-Ware method (Ryther 1969; Ware 2000) which traces production processes through a food chain (Rosenberg et al. in press; Fogarty et al. in press). Unlike the original Ryther-Ware food chain representation, in which yield is extracted at a specified mean trophic level, the version implemented here utilizes a simplified food web structure within which yield can be extracted at different trophic levels.

The current EPP model recognizes two pathways for transfer of primary production in the system: the metazoan grazing food web tracing the fate of production of net phytoplankton (phytoplankton cells  $> 20 \mu\text{m}$ ; principally diatoms and large dinoflagellates) and production involving transfer through the microbial food web originating with combined nanoplankton ( $2\text{-}20 \mu\text{m}$ ) and picoplankton ( $< 20 \mu\text{m}$ ) production (i.e., nano-picoplankton; Figure 1). The metazoan pathway involves grazing by mesozooplankton and filter-feeding of diatom production by benthic invertebrates (e.g. bivalves). The microbial pathway entails ‘consumption’ of nano-picoplankton by heterotrophic bacteria (principally in the form of dissolved organic carbon –DOC–) and feeding of microzooplankton on bacteria. In this representation, carnivorous zooplankton (mesozooplankton) prey on microzooplankton. The microbial pathway therefore involves two or more trophic transfer steps before reaching mesozooplankton as a bridge to higher trophic levels. Although both dissolved and particulate organic carbon (POC) derived from other sources in the food web and are utilized by bacteria, in this simplified representation we follow the approach of Ware (2000) and assume that most of the POC and DOC utilized by bacteria are from nano-picoplankton sources. We note that the functional groups represented in the upper food web depicted in Figure 1 do not correspond to taxonomic groups. Individual taxa may feed at multiple trophic levels, reflecting both ontogenetic shifts in diet, and generalist feeding strategies.



**Figure 1.** Food web structure employed in this analysis. Nano-pico plankton, bacteria, and microzooplankton comprise the microbial food web in this representation. The classical grazing food web is fuelled by net phytoplankton production. Species characterized by ontogenetic shifts in diet and/or mixed feeding strategies can occupy multiple compartments in this representation.

Within this structure, production at a given node  $i$  is a function of the transfer efficiency from other nodes ( $j$ ) to node  $i$ , the inputs from other locations and losses from the  $i^{\text{th}}$  node:

$$P_i = \left( \sum_{j \neq i} t_{ji} x_{ji} P_j \right) + A_i - L_i$$

where  $P_i$  is the production of node  $i$ ,  $t_{ji}$  is the transfer efficiency from node  $j$  to node  $i$ , and  $x_{ji}$  is the fraction of the production of node  $j$  that is channeled into node  $i$  over all nodes (this is different from 1 when a given node feeds into two or more nodes in the next trophic level, also  $\sum_i x_{ij} = 1$ ).  $A_i$  represents the addition of production to node  $i$  from other sources outside the ecosystem (e.g. immigration).  $L$  represents a loss term from node  $i$  (e.g. advective loss, removals due to harvest etc.).

### ***Fishery Production Potential***

The model represented by Figure 1 serves to estimate the total ecosystem production potential, but the production available for fishing is only a fraction of this total production. This fraction will be a function of the production potential at the nodes being harvested, and the harvesting rate imposed on those nodes. If we discriminate between losses of production to exploitation ( $C_i$ ) (including both discarded and landed components) and all other sources of removals ( $L'_i$ ), the basic model equation can be re-written as

$$P_i = \left( \sum_{j \neq i} t_{ji} x_{ji} P_j \right) + A_i - L'_i - C_i$$

For the purposes of this analysis, we assume that inputs and losses from sources other than fishing are in balance at each node. Then, harvest extracted from node  $i$  can be expressed as

$$C_i = E_i P_i$$

where  $E_i$  is the fractional exploitation rate applied to the production at node  $i$ .

Although standard reference points have not been fully established to guide overall extraction policies for marine ecosystems, Iverson (1990) proposed that exploitation rates should not exceed the  $f$ -ratio (the ratio of new primary production to total primary production) in marine systems. This suggestion recognizes that new production (primarily by larger phytoplankton species) is more readily available to fuel production at the higher trophic levels of principal economic interest while the production derived from the nano-picoplankton is largely (but not exclusively) consumed within the microbial food web. Although direct estimates of the  $f$ -ratio are not broadly available for large marine ecosystems, we can consider the ratio of microplankton production to total primary production as a first-order approximation. On this basis, we have initially considered exploitation rates of 20-30% as our limit reference points for exploitation.

As initial step, and considering that many species included in the benthos (e.g. polychaetes, brittle stars) and planktivores (e.g. myctophids) nodes are not currently of commercial value, the fisheries production potential of those nodes was further bounded by assuming that only 10% of the benthos and 50% of the planktivores production were of interest to harvesters. The results of applying these exploitation rates are the estimates of fisheries production potential (FPP) (i.e. the production potential available to fisheries).

Production of benthivores and piscivores (labelled upper trophic levels in Fig. 1) was also combined to better reflect the overall fisheries production potential of demersal species as a generic target group for fisheries. It is important to highlight that these Standard Demersal Components (SDC) include traditional commercial groundfish species like Atlantic cod and American plaice which may vary in their reliance on benthos as they grow, but also commercial shellfish like shrimp and crab. The amalgamated SDC is better suited for comparisons with catch levels which are often dominated by groundfishes and shellfish, and because a number of piscivorous species also prey on benthic organisms and have broadly omnivorous feeding patterns.

### ***Primary production***

Composite satellite derived surface observations of chlorophyll  $a$  concentrations and temperature were a fundamental input for the estimation of primary production, but the specific models used differed depending on the location of the ecosystem under consideration. Based on the availability/quality of data and models, comparisons

among primary production models were made to the extent possible. The results of these comparative analyses were used to select which approach for estimating primary production seemed to work better for each ecosystem.

Primary production estimates for the Grand Bank, Newfoundland and Labrador Shelves, Flemish Cap, and the Scotian Shelf were based on remotely sensed satellite observations from ocean color (SeaWiFS and MODIS-Aqua) and thermal (AVHRR, MODIS-Aqua and MODIS-Terra) sensors (1997-2013). The method that most closely corresponds to *in situ* estimates of primary production consists of the Nearest-Neighbour Method (NNM) of primary production estimation (Platt et al. 2008). The approach relies on observations of surface chlorophyll *a* concentrations and temperature coupled with information from a climatological archive of photosynthesis-irradiance relationship parameters, as well parameters that describe the vertical structure of chlorophyll and temperature based on ship observations from the same region.

Primary production for the Northeast US continental shelf was also calculated on the basis of data from the Sea-viewing Wide Field-of-View Sensor (SeaWiFS, NASA); in this case a modified version of the Vertically Generalized Productivity Model (VGPM; Behrenfeld and Falkowski 1997) was applied. This modified VGPM model replaces the original temperature-dependent description of photosynthetic efficiencies with the exponential Eppley function (Eppley 1972), which was modified by Morel (1991).

The estimates of productivity from these models were coupled with phytoplankton taxonomic composition information (e.g. Uitz et al. 2009; 2010; Pan et al. 2011) to estimate size fractionated primary production. The phytoplankton community was divided into two main size categories, microplankton (>20m), and picoplankton (<20m) for their incorporation into the EPP models (labeled “Net phytoplankton” and “Nanoplankton” respectively in Fig. 1).

### ***Transfer Efficiencies***

Early laboratory studies by Slobodkin (1961) indicated that the expected transfer efficiency was on the order of 10%. Thermodynamic constraints place limits on the transfer efficiency between successive levels in the food chains comprising a reticulated food web. The canonical value of 10% as an ecological transfer efficiency was supported by Pauly and Christensen (1995), who estimated that the transfer efficiency of biomass between trophic levels in aquatic ecosystems, although variable, had a mean of 10%. However, more recent studies have suggested higher transfer efficiencies at lower levels in the food web and a general decline in transfer efficiency from lower to higher trophic levels.

To better assess trophic transfer efficiencies throughout our generic food web, we evaluated estimates of transfer efficiencies derived from published Ecopath with Ecosim (EwE) models for subarctic-boreal-temperate systems compiled by the *Sea Around Us* Project of the University of British Columbia. Rather than assume or assign trophic transfer efficiencies at different steps in the food web for the models, we used these model estimates to define probability distributions characterizing transfer probabilities at different steps in the food web. Our characterization of transfer efficiencies between discrete trophic levels based on these Ecopath models followed the approach of Ulanowicz (1993).

### ***Benthic-Mesozooplankton Pathway***

To determine transfer efficiencies from the microplankton, we examined energetic pathways from Ecopath models and assigned a proportion to the microplankton group and determined the production flowing to mesozooplankton and benthos. As there are three pathways of energy transfer from primary producers, we need the proportion of the primary production flowing to zooplankton versus the proportion flowing to benthic invertebrates in addition to the transfer efficiencies. We examined published Ecopath models for Arcto-boreal-temperate systems to infer the split between benthos and mesozooplankton from microplankton.

### ***Treating Uncertainty***

To represent uncertainty in key input parameters to the production potential model, we specified empirically derived probability distributions for primary production, transfer efficiencies, and the split between transfer of energy from microplankton to benthos and mesozooplankton.

We used truncated normal probability distributions to represent variability in microplankton and nano-picoplankton production. We computed the means and, based on an examination of the the interannual variability of the primary production combined with the uncertainty in the empirical models relating chlorophyll *a* to primary production,

coefficient of variations of 30% were used to represent the variance of interannual phytoplankton production for both phytoplankton components.

For transfer efficiencies between microplankton and higher components of the food web we used Beta distributions at each level based on our compilation of EwE results as described above. Transfer efficiency estimates are constrained between 0 and 1 and are appropriate for application of the Beta distribution. To obtain reasonable sample sizes to characterize these probability distributions, we pooled model estimates over major ocean biomes (Subarctic Boreal Shelf and Temperate Shelf systems).

Energetic pathways involving the benthos differed substantially in different food web models we examined. In recognition of the limitations in using these models to characterize uncertainty in energetic pathways involving the benthos, we used uniform probability distributions bounded by the upper and lower quartiles of the range of observed splits between the benthos and mesozooplankton in our analyses.

Many of the EwE models we examined did not partition phytoplankton production by size class and therefore did not allow treatment of the microbial food web as specified in our model (Figure 1). In those cases, we used literature values for ecotrophic efficiencies (proportion of production consumed within the microbial food web and the gross growth efficiency of bacteria and microzooplankton (Straile 1997; Ware 2000)). It was not possible to define these elements according to Ecotype or to fully represent the uncertainty in these estimates.

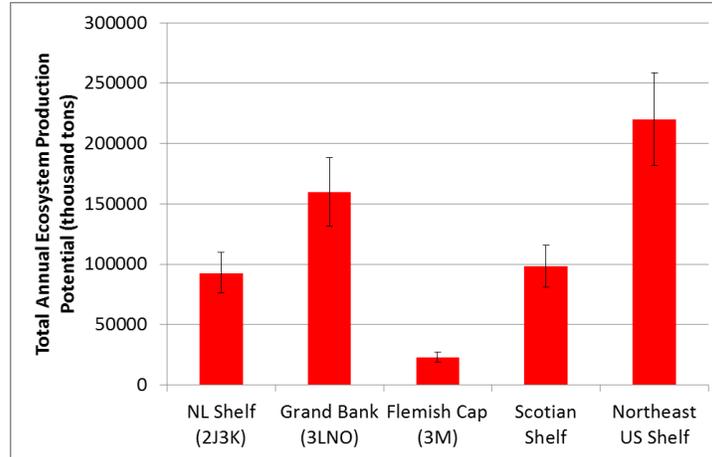
## Results

For the five ecosystems under consideration, total annual ecosystem production potential (EPP) for trophic levels 2+ (i.e. not primary producers) varied from 23 to 322 million tonnes (Fig. 2, Table 1). Although absolute differences in EPP across ecosystems are essentially driven by the areal extent of the ecosystems, temperate shelf systems like the Scotian Shelf and the Northeast US shelf showed higher production potential per unit area than the subarctic-boreal systems.

The exploitation rates of 20 and 30% were applied to all nominally fishable nodes in the EPP model (benthos, planktivores, benthivores, and piscivores); this allowed inclusion of the impact of fishing lower in the trophic web on the productivity of higher trophic levels. In the same sense that considering the  $f$ -ratio as an initial proxy for exploitation rate could be interpreted, in a financial analogy, as living from the interest without touching the capital of the investment, the simultaneous exploitation of all fishing nodes allows incorporating the effect of “lost revenue” in the higher trophic level nodes (i.e. the production that will not occur because the required input production from lower trophic levels has already been reduced by fishing).

Table 1 summarizes the key results for a baseline run without exploitation and the two exploitation rate scenarios considered; for the runs with exploitation, the production potential available to fisheries (i.e. fisheries production potential) and available to the ecosystem (i.e. for sustaining ecosystem functioning –non-provisioning ecosystem services-) is differentiated.

In terms of FPP, the two exploitation rate scenarios provide an initial envelope for the level of fishing that these Northwest Atlantic ecosystems could tolerate in a sustainable manner (Fig. 3). It is clear that SDC components only represent around 30% of the total FPP, the remainder being associated with planktivores and benthos (Fig. 3, Table 1).



**Figure 2.** Median values for the estimates Total Annual Ecosystem Production Potential in trophic levels 2+ (not primary producers) for Northwest Atlantic ecosystems. The error bars correspond to the 25-75% quantile intervals.

**Table 1.** Ecosystem production potential (EPP) estimates for Northwest Atlantic ecosystems. These estimates are based on three scenarios: a) base case with no exploitation, b) ecosystem exploitation rate set at 20%, and c) ecosystem exploitation rate set at 30%. For those nodes in the EPP model with exploitable species, EPP is discriminated between what is estimated as potentially available for the ecosystem (to allow ecosystem functioning), and what is potentially available to fisheries (i.e. fisheries production potential). The “Standard Demersal Component” was defined as the sum of the piscivores and benthivores nodes in the EPP model (Figure 1). Each estimate of EPP is characterized by its median and 25-75% quantile range. All EPP estimates are in thousands of tonnes.

<b>Ecosystem</b>	<b>NL Shelf (2J3K)</b>	<b>Grand Bank (3LNO)</b>	<b>Flemish Cap (3M)</b>	<b>Scotian Shelf</b>	<b>Northeast US Shelf</b>
<b>Ecosystem type</b>	Subarctic-Boreal Shelf	Subarctic-Boreal Shelf	Subarctic-Boreal Shelf	Temperate Shelf	Temperate Shelf
<b>Area (thousand km<sup>2</sup>)</b>	238.944	305.854	46.197	181.589	321.974

#### **Scenario: No Exploitation**

Total EPP in trophic levels 2+ (not primary producers)	median	92481	159534	23004	98348	219955
	25% quantile	76144	131866	18966	81027	181822
	75% quantile	109624	188272	27086	115769	258483
EPP of fishable nodes available to Ecosystem	median	6945	10218	1493	7618	12012
	25% quantile	4020	5986	878	4388	6927
	75% quantile	11413	16767	2440	12492	19739
EPP of fishable nodes available to Fisheries	median	0	0	0	0	0
	25% quantile	0	0	0	0	0
	75% quantile	0	0	0	0	0
EPP of Standard Demersal Components (SDC) available to Ecosystem	median	847	1246	180	890	1377
	25% quantile	488	730	106	478	748
	75% quantile	1420	2086	302	1562	2453

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<b>Ecosystem</b>		<b>NL Shelf (2J3K)</b>	<b>Grand Bank (3LNO)</b>	<b>Flemish Cap (3M)</b>	<b>Scotian Shelf</b>	<b>Northeast US Shelf</b>
EPP of Standard Demersal Components (SDC) available to Fisheries	median	0	0	0	0	0
	25% quantile	0	0	0	0	0
	75% quantile	0	0	0	0	0
EPP of planktivores available to Ecosystem	median	2466	3714	541	1917	3281
	25% quantile	1516	2312	342	1103	1977
	75% quantile	3838	5840	841	3202	5299
EPP of planktivores available to Fisheries	median	0	0	0	0	0
	25% quantile	0	0	0	0	0
	75% quantile	0	0	0	0	0
EPP of benthos available to Ecosystem	median	3632	5259	772	4811	7353
	25% quantile	2016	2944	430	2807	4201
	75% quantile	6155	8841	1297	7728	11988
EPP of benthos available to Fisheries	median	0	0	0	0	0
	25% quantile	0	0	0	0	0
	75% quantile	0	0	0	0	0

**Scenario: ecosystem exploitation rate at 20%**

Total EPP in trophic levels 2+ (not primary producers)	median	92103	157823	22892	97522	220165
	25% quantile	76200	130093	18812	80841	180451
	75% quantile	108682	187709	27004	114836	256781
EPP of fishable nodes available to Ecosystem	median	6405	9524	1371	6971	10978
	25% quantile	3690	5591	805	3984	6309
	75% quantile	10455	15477	2219	11646	18107
EPP of fishable nodes available to Fisheries	median	475	713	103	444	724
	25% quantile	283	431	62	249	412
	75% quantile	765	1145	165	759	1222
EPP of Standard Demersal Components (SDC) available to Ecosystem	median	634	941	134	650	1013
	25% quantile	364	545	78	346	543
	75% quantile	1052	1570	226	1163	1814
EPP of Standard Demersal Components	median	158	235	34	163	253
	25% quantile	91	136	20	87	136

**Table 1.** Ecosystem production potential (EPP) estimates for Northwest Atlantic ecosystems. These estimates are based on three scenarios: a) base case with no exploitation, b) ecosystem exploitation rate set at 20%, and c) ecosystem exploitation rate set at 30%. For those nodes in the EPP model with exploitable species, EPP is discriminated between what is estimated as potentially available for the ecosystem (to allow ecosystem functioning), and what is potentially available to fisheries (i.e. fisheries production potential). The “Standard Demersal Component” was defined as the sum of the piscivores and benthivores nodes in the EPP model (Figure 1). Each estimate of EPP is characterized by its median and 25-75% quantile range. All EPP estimates are in thousands of tonnes.

<b>Ecosystem</b>		<b>NL Shelf (2J3K)</b>	<b>Grand Bank (3LNO)</b>	<b>Flemish Cap (3M)</b>	<b>Scotian Shelf</b>	<b>Northeast US Shelf</b>
(SDC) available to Fisheries	75% quantile	263	393	56	291	454
EPP of planktivores available to Ecosystem	median	2195	3333	490	1684	2952
	25% quantile	1365	2110	303	967	1742
	75% quantile	3420	5170	753	2808	4807
EPP of planktivores available to Fisheries	median	244	370	54	187	328
	25% quantile	152	234	34	107	194
	75% quantile	380	574	84	312	534
EPP of benthos available to Ecosystem	median	3576	5250	746	4637	7013
	25% quantile	1961	2936	424	2671	4024
	75% quantile	5983	8737	1241	7674	11486
EPP of benthos available to Fisheries	median	73	107	15	95	143
	25% quantile	40	60	9	55	82
	75% quantile	122	178	25	157	234

**Scenario: ecosystem exploitation rate at 30%**

Total EPP in trophic levels 2+ (not primary producers)	median	91316	157966	22810	96377	220849
	25% quantile	75047	129338	18732	79626	181767
	75% quantile	107785	186921	26930	113677	257621
EPP of fishable nodes available to Ecosystem	median	6097	9039	1319	6797	10603
	25% quantile	3554	5302	771	3844	6179
	75% quantile	10045	14758	2146	11214	17597
EPP of fishable nodes available to Fisheries	median	700	1053	152	659	1072
	25% quantile	420	636	92	366	619
	75% quantile	1130	1690	245	1130	1815
EPP of Standard Demersal Components (SDC) available to Ecosystem	median	533	785	115	551	861
	25% quantile	306	452	66	292	464
	75% quantile	893	1311	190	1003	1537
EPP of Standard	median	229	337	49	236	369

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<b>Ecosystem</b>		<b>NL Shelf (2J3K)</b>	<b>Grand Bank (3LNO)</b>	<b>Flemish Cap (3M)</b>	<b>Scotian Shelf</b>	<b>Northeast US Shelf</b>
Demersal Components (SDC) available to Fisheries	25% quantile	131	194	28	125	199
	75% quantile	383	562	81	430	659
EPP of planktivores available to Ecosystem	median	2058	3168	453	1581	2763
	25% quantile	1294	2009	287	902	1670
	75% quantile	3191	4891	706	2638	4530
EPP of planktivores available to Fisheries	median	363	559	80	279	488
	25% quantile	228	355	51	159	295
	75% quantile	563	863	125	466	799
EPP of benthos available to Ecosystem	median	3506	5086	751	4665	6979
	25% quantile	1954	2841	418	2650	4045
	75% quantile	5960	8556	1251	7573	11529
EPP of benthos available to Fisheries	median	108	157	23	144	216
	25% quantile	60	88	13	82	125
	75% quantile	184	265	39	234	357

## Discussion

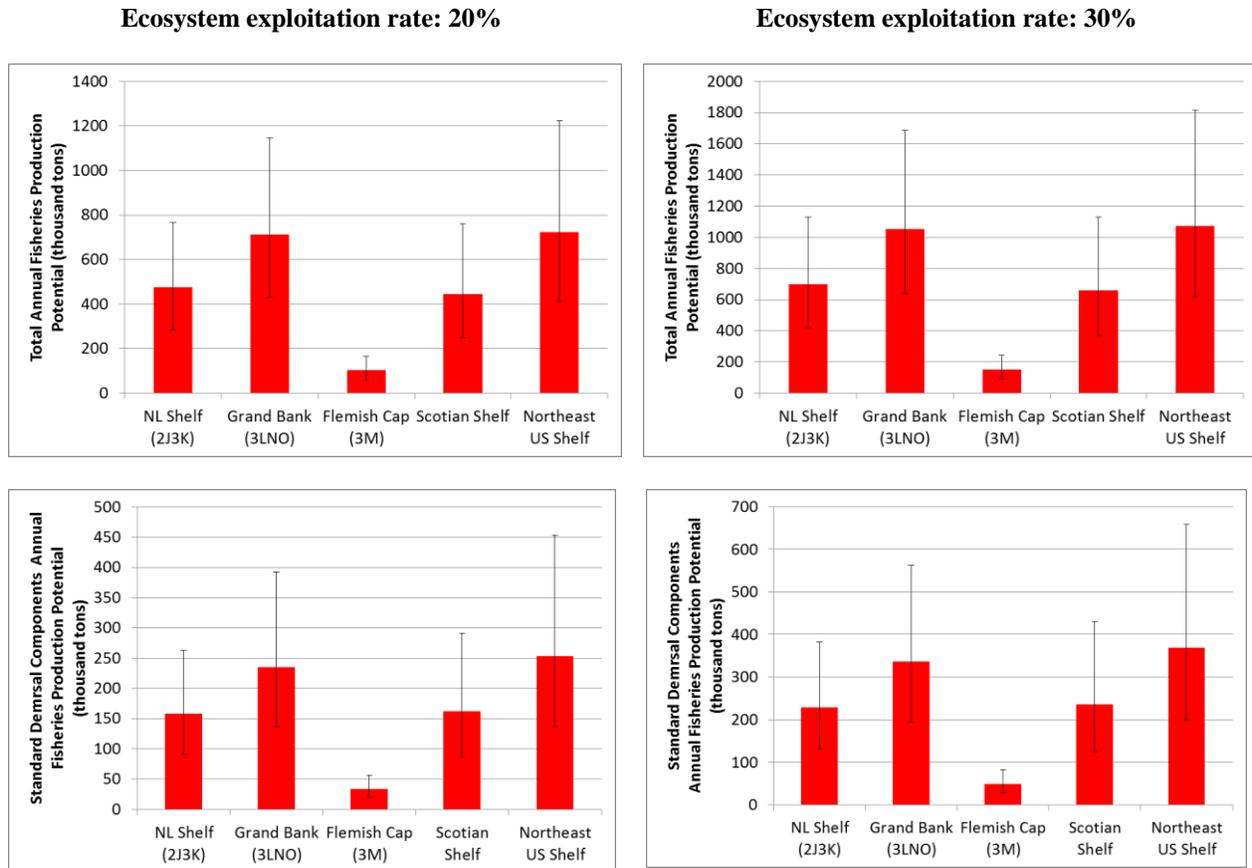
Our model structure assumes that the ultimate bottleneck in productivity at each node is the transfer efficiency. This implies that each node in the model is capable of fully utilizing the available production that reaches the node from lower trophic levels. This would be expected to be the case in a fully functional, mature and unperturbed ecosystem; actual ecosystems on the other hand, are likely to be limited by other factors (e.g. the existing biomass in each node), which may impose additional limitations to productivity. This difference between realized and potential ecosystem productivity is non-trivial, especially for practical management applications. The EPP model structure considered here would provide the expected theoretical maximum for ecosystem productivity, and as such, any reference point derived from it should be considered a limit (not a target) reference point. Furthermore, if the ecosystem under analysis cannot be considered to be fully functional (e.g. experienced major structural changes, suffered significant collapses of major stocks, etc.), estimates from EPP models would likely be overestimates of the current production levels, and hence, the limits derived from the EPP model would have to be adjusted to reflect the lower productivity level of the ecosystem that result from lower standing stocks at different trophic levels.

Previous estimates of fishery production potential typically assumed that 50-70% of production at a defined mean trophic level could be extracted as catch (e.g. Graham & Edwards 1962; Ryther 1969; Schaefer 1965; Ricker 1969; but see Moiseev 1994). These proposed extraction rates were predicated on prevailing single-species recommendations based on the (implicit) assumption that fishing mortality rates could equal natural mortality for the stock (Pauly & Christensen 1995). We now recognize that these earlier target levels for single-species management were too high and led to risk-prone decisions (Pauly & Christensen 1995). As a result we considered that sustainable ecosystem exploitation rates cannot be higher than the ratio of new primary production to total primary production, following Iverson (1990).

It is important to highlight that FPP estimates effectively are the maximum fishing production that these ecosystems could generate within a context of general ecosystem sustainability. Fishing above these levels would be expected to start hindering the capacity of the system to function fully, because it would start eroding the biomass structure needed to generate the production.

In this context, there is a significant and important difference between the FPP for an ecosystem, and the actual level of exploitation that the system can sustainably tolerate at a given point in time. These initial estimates of FPP are derived from a model that has a purposely simple (but still reasonable) structure, and where several approximations and assumptions are made regarding the values, distribution and variability of its parameters. Key to it all is the assumption that transfer efficiencies are the proximal limiting factor in production at each node; this is what it defines the “potential” of the system. However, if the biomass level in a particular node is not adequate, the capacity of that node to utilize all the production available from lower trophic levels could be impaired. In such a case, the “standing stock” biomass of the node would become the proximal limiting factor for production (e.g. if there is not enough piscivores to eat/process all the planktivore production available, the potential production of piscivores - which assumes that all the planktivore production will be used- would not be realized). Therefore, these FPP levels can only be achieved if the ecosystem is “healthy” in the sense that there is enough biomass in each node to process all the production that feeds into that node. If this is not the case, the actual fishing production that the system can generate sustainably would be lower.

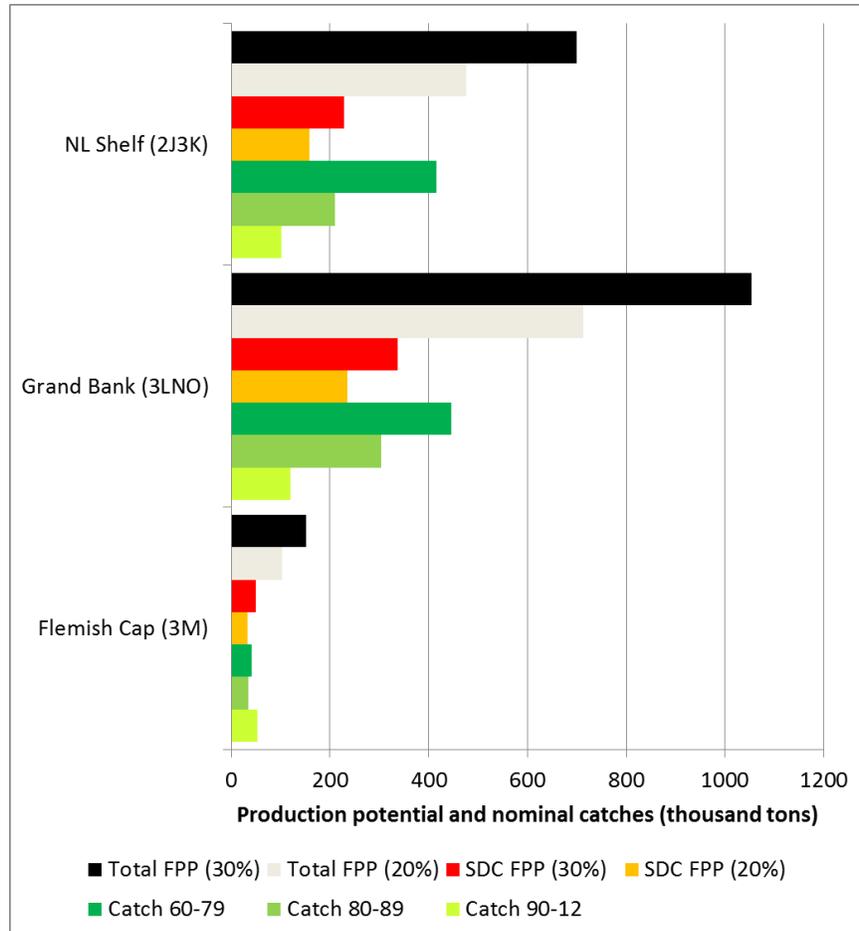
We compared the median annual nominal catches for the Newfoundland-Labrador Shelf, the Grand Bank, and Flemish Cap during three time periods (1960-1979, 1980-1989, and 1990-2012), with the corresponding median Total and SDC FPPs for these systems (Fig. 4). For these systems, total catches never exceeded the estimated envelopes of Total FPP, but they systematically exceed the SDC FPP in the earlier period for all systems, they were at par during the 1980s, and during the most recent period they have been below SDC FPP for the NL Shelf and Grand Bank, and slightly above it for the Flemish Cap. Even though some pelagic species have had important catches, most of the catches in these systems corresponded to groundfishes and shellfish.



**Figure 3.** Median values for the estimated Total (top row) and Standard Demersal Components (bottom row) Fisheries Production Potential for Northwest Atlantic ecosystems under a 20% (left column) and 30% (right column) ecosystem exploitation rates scenarios. The error bars correspond to the 25-75% quantile intervals.

If we consider that these systems underwent dramatic changes in the late 1980s and early 1990s, when among other things the overall fish biomass of the systems declined, these results suggest that these ecosystems have been under excessive fishing pressure overall. Ecosystem erosion resulting from overfishing of groundfish components would likely have reduced the production capacity of the systems, and hence have led to the maintenance of these systems in an overfished state irrespective of reductions in catches. The further reductions in overall catch in the more recent years in the NL shelf and Grand Bank may have been a contributing factor, together with changing environmental conditions, to the recent increases in biomass observed in the groundfish community for these regions.

Although these are only preliminary observations, they are compelling indications that these systems not only have been systematically overfished in the past, but overexploitation may have continued even after the collapses in the late 1980s and early 1990s. Furthermore, our results suggest that the current overall levels of exploitation are either close to the current capacity of these ecosystems, or perhaps above. Although further work is required to fully explore and develop these models, the results from this analysis suggest that at present, increases in overall catch would not be advisable from an ecosystem sustainability perspective.



**Figure 4.** Comparison between catch levels and the corresponding fisheries production potential (FPP) for Newfoundland-Labrador and Flemish Cap ecosystems. Catch levels are characterized by the median nominal total catches in three time periods (1960-1979, 1980-1989, and 1990-2012). Fisheries production potential is characterized by the estimated Total and Standard Demersal Components (SDC) Fisheries Production Potential for these ecosystems under a 20% and 30% ecosystem exploitation rates scenarios.

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