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Review and Assessment of the Ecosystem Production Potential (EPP) model structure, sensitivity, and its use for fisheries advice in NAFO

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Abstract

In support of the development and implementation of the NAFO Roadmap, a synthesis, review and assessment of the Ecosystem Production (EPP) model and its applicability in providing guidance for ecosystem level total catches was undertaken. Ecosystem Production Potential (EPP) models are simple network models that track the production generated by primary producers and ultimately limits fish production in the marine ecosystem. The EPP model represents productivity conditions integrated over a medium term horizon (e.g. 3-5 years), it is not intended to be dynamic but rather provides snapshot of productivity given current conditions, and includes three main energy channels in the ecosystem, the pelagic, benthic, and microbial loop pathways. It is implemented as a Monte Carlo simulation to account for the uncertainty in inputs and model parameters. Total heterotrophic ecosystem production is highly dominated by production associated with the microbial loop, while the nodes [functional guilds] associated to fisheries, even those targeting highly productive species like small pelagic fish (i.e. planktivore node), have productions orders of magnitude lower. Production within the pelagic pathway is highly coherent, while production along the benthic pathway is more diffuse. Estimates of the Fisheries Production Potential (FPP), the production that can be sustainably taken by fishing, were produced for three Ecosystem Production Units (EPUs) within the NAFO Convention Area, the Newfoundland Shelf (2J3K), the Grand Bank (3LNO), and the Flemish Cap (3M) using a 20% exploitation rate. This exploitation rate is linked to the fraction of new primary production, which is considered a proxy for maximum sustainable exploitation in the context of the EPP model. FPP estimates obtained from the EPP model are highly consistent with MSY estimates obtained from more traditional analyses of aggregate biomass surplus production. FPP estimates assume that the ecosystem is fully functional and relatively stable, but it does not assume equilibrium, it is simply tracking flows through the system. Therefore, practical use of FPP estimates requires adjusting them to better reflect the realized productivity state of the ecosystem. This adjustment was based on the total biomass estimated from research surveys, and only applied to the Newfoundland Shelf (2J3K), and the Grand Bank (3LNO) because only these ecosystems have experienced substantial and sustained changes in total biomass over time. The evaluation of the history of catches in these areas reveals that that in the 1960-1995 period, catches from the piscivore guild were consistently above Total Catch Index (TCI) levels in all ecosystems, while the other functional guilds were mostly within their sustainability envelope. After 1995 and

the collapse of the fish community in the Newfoundland-Labrador ecosystems, catches from the benthivore guild, mostly driven by shellfish species, have also been above the TCIs in all three ecosystems, while piscivore guild catches above the TCIs keep occurring in 3LNO and 3M. Evaluation of the effectiveness of TCI as guidance level for total catches revealed that catches above TCI levels are clearly associated to negative biomass trends in functional guilds, while catch levels below TCI show a fairly even distribution of positive and negative biomass trends. Furthermore, the Catch/TCI ratio and environmental conditions were found to be significant drivers of the functional guilds biomass trends, with the TCI-based indicator being the dominant driver. Overall, the EPP model provides a good approximation to ecosystem production based on primary production, while the FPP distributions, corrected for differences in ecosystem functionality, and TCI values are reasonable metrics to characterize the upper boundary to sustainable fisheries exploitation.

Introduction

The Northwest Atlantic Fisheries Organization (NAFO) has been embarked in a process to develop and implement an ecosystem approach for the management of its fisheries since 2007 (NAFO, 2007a; NAFO, 2007b). As part of this process a template for how this implementation should look like has evolved over time. This template is known as the NAFO Roadmap for an Ecosystem Approach to Fisheries, or simply the "Roadmap" for short (Koen-Alonso et al., 2019).

The Roadmap lays out the key elements and connections that would be necessary for a true to form implementation of an Ecosystem-based Fisheries Management (EBFM) framework in NAFO (Koen-Alonso et al., 2019). Its core principles are: a) the approach has to be objective-driven, b) it should consider long-term ecosystem sustainability, c) it must be place-based, and d) the consequences of trade-offs in managing human activities have to be explicitly defined. In terms of exploitation rates, the Roadmap approaches their definition through a hierarchical sequence that considers ecosystem state, species interactions, and stock-level processes. This would be implemented through a series of nested assessments focused on ecosystem (Tier 1), multispecies (Tier 2), and stock (Tier 3) sustainability. The goal is that by considering these assessments together, tactical management measures ultimately put in place at the stock level will effectively be informed by and integrate the requirements for sustainability from all levels of ecological organization.

One question that has historically received a lot of attention, and that also arises within the Roadmap implementation, is how much fish can we safely extract from the ocean based on the observed primary production. This question links two aspects relevant to fishing. On one side, we know from first principles that primary production represents the ultimate limit for fish production, while empirical analyses show that this is effectively the case in many real ecosystems (Clarke et al., 1946; Schaefer, 1965; Ryther, 1969; Pauly and Christensen, 1995; Ware and Thomson, 2005; Chassot et al., 2010). On the other, fisheries sustainability rely on the services provided by a functioning ecosystem (Palumbi et al., 2009), and excessive fishing can hinder this functionality leading to ecosystem overfishing (Murawski, 2000; Coll et al., 2008; Link and Watson, 2019; Link, 2021).

The initial conversation about how to define ecosystem overfishing examined multiple aspects related to ecosystem structure and function expected to be impacted by fishing (Murawski, 2000). As the conversation evolved, the joint examination of the two aspects of the question posed above led to operational definitions of ecosystem overfishing that relate fisheries catches with primary production or proxies for it (Coll et al., 2008; Link and Watson, 2019; Link, 2021).

This idea of ecosystem overfishing is not only embedded in current concepts of ecosystem approaches (Link, 2010; Fogarty, 2014), but has proven effective in concrete fisheries management implementations (Link, 2017), and to the extent that primary production has been found limiting fisheries economic performance (Marshak and Link, 2021).

Within the Roadmap, the implementation of these concepts is at the centre of Tier 1 assessments, and it has primarily taken the shape of guidelines for total catches, discriminated by functional feeding guilds, at the functional ecosystem level (NAFO, 2016b; NAFO, 2018). These guidelines rely on Ecosystem Production Potential (EPP) models for the estimation of the Fisheries Production Potential (FPP) on which the guidelines are based.

EPP models are simple network models that track the production generated by primary producers up the food web (Koen-Alonso et al., 2013; Rosenberg et al., 2014; Fogarty et al., 2016). Conceptually, these models represent an expansion of the basic Ryther (1969) model where the original linear food chain is replaced by a more realistic food web network. The food web considered in EPP models remains simplified in the sense that the model nodes represent functional trophic guilds aimed at capturing the basic energy pathways and trophic levels, but without resolving to species.

Even though the work on developing EPP models and guidelines for total catches has been in development in NAFO for many years (NAFO, 2010; NAFO, 2013; NAFO, 2015b; NAFO, 2019; NAFO, 2020), these guidelines have yet to be used to inform management decisions. Furthermore, a recent recommendation by NAFO Scientific Council (SC) to formalize the use of these guidelines toward the implementation of some aspects of the Roadmap (NAFO, 2020; NAFO, 2021c) has brought to the surface a number of managers' reservations about the validity of the scientific underpinnings of the guidelines, and about their adequacy for the intended management applications (NAFO, 2021b; NAFO, 2021a).

To resolve these issues, the NAFO Commission (COM) requested SC to convene independent experts to do a scientific review of the estimation of fisheries production potential and related work, and of the adequacy of these analyses for their proposed use within the Roadmap (NAFO, 2021a).

In order to facilitate this review process, here we summarize and consolidate the EPP modeling work, the related derivation of guidelines for total catches, and the evaluation of their effectiveness. This includes a description of the model itself, how is parameterized, and a characterization of its behavior and key aspects of structural uncertainty. We then describe how fisheries production potential is estimated from the model, and adjusted to reflect the realized level of productivity of the ecosystem. Based on the principles guiding the existing NAFO Precautionary Approach framework (NAFO, 2004), we define the indicator used to produce the guidelines for total catches, and analyze how NAFO fisheries have performed over time from an aggregate catches perspective, and use trends in functional guilds to assess how effective this approach is at identifying an upper bound for sustainable aggregate catches.

We also provide some final comments on the adequacy of this work for its intended application within the Roadmap, and how it relates to other Roadmap elements like multispecies and stock-level assessments.

Material and Methods

The Ecosystem Production Potential (EPP) model

Concept, model structure, and parametrization

The basic premise of the EPP model is that the primary production generated by phytoplankton is the ultimate limit for fish production in the marine ecosystem. If we track how this production moves up the food chain, we can estimate the production of the trophic levels that support fisheries, providing an upper bound for total fisheries catches. In order to track this productivity, the model estimates the production of a trophic level as a fraction of the production of the trophic level that feeds into it. This fraction is the transfer efficiency. If we expand this idea to a food web in a real ecosystem, with potential imports and exports of production, the production of any given node in the EPP model can be described by the following master equation:

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

where *Pi* is the production in node [functional guild] *i*, t_{ji} is the transfer efficiency between a lower trophic level node [functional guild] *j*, a food source, and an upper trophic level node [functional guild] *i*, the predator, and where x_{ji} is the fraction of the production of the prey node *j* (P_j) available to the predator node *i*. This fraction allows splitting the total production of any prey node into multiple predator pathways while respecting the conservation of biomass principle (i.e. $\sum_j x_{ji} = 1$). The parameters A_i and L_i represent the imports/exports of production to/from node *i* and other neighboring ecosystems. C_i is the production of node *i* taken as catch, and can also be represented as $C_i = F_i P_i$, where F_i is the exploitation rate of node *i*.

The EPP basic equation is not dynamic; the EPP model does not represent changes in productivity over time, it simply tracks production from primary producers through the food web. In practical terms, this means that primary production in a given year will not become production of the highest trophic levels that same year. The EPP model, at least it its current form, represents productivity conditions integrated over a medium term horizon (e.g. 3-5 years).

Another important feature of the model is that all available production in a trophic level becomes production in the next one via the transfer efficiencies; there is no other functional limitation or constraint to production when the ecosystem is a closed system (i.e. no exports/imports). This assumes that the ecosystem is fully functional, that each node [functional guild] has full capacity to utilize the production available to it. The EPP model estimates the full potential (i.e. maximum) production of an ecosystem; if there are other factors beyond transfer efficiencies that limit the functionality of the ecosystem, the actual production would be lower than the potential estimated by the model.

The food web structure in the EPP model represents three main energy channels in the ecosystem, the pelagic, benthic, and microbial loop pathways. The current version of the EPP model (v2) (Fig. 1) builds upon the original EPP model (v1) (Koen-Alonso et al., 2013; Rosenberg et al., 2014; Fogarty et al., 2016). Some key improvements in the current model are a more resolved microbial loop, the splitting of benthos into suspension and deposit feeders, and the direct connection between bacteria and deposit-feeding benthos (detritus pathway).

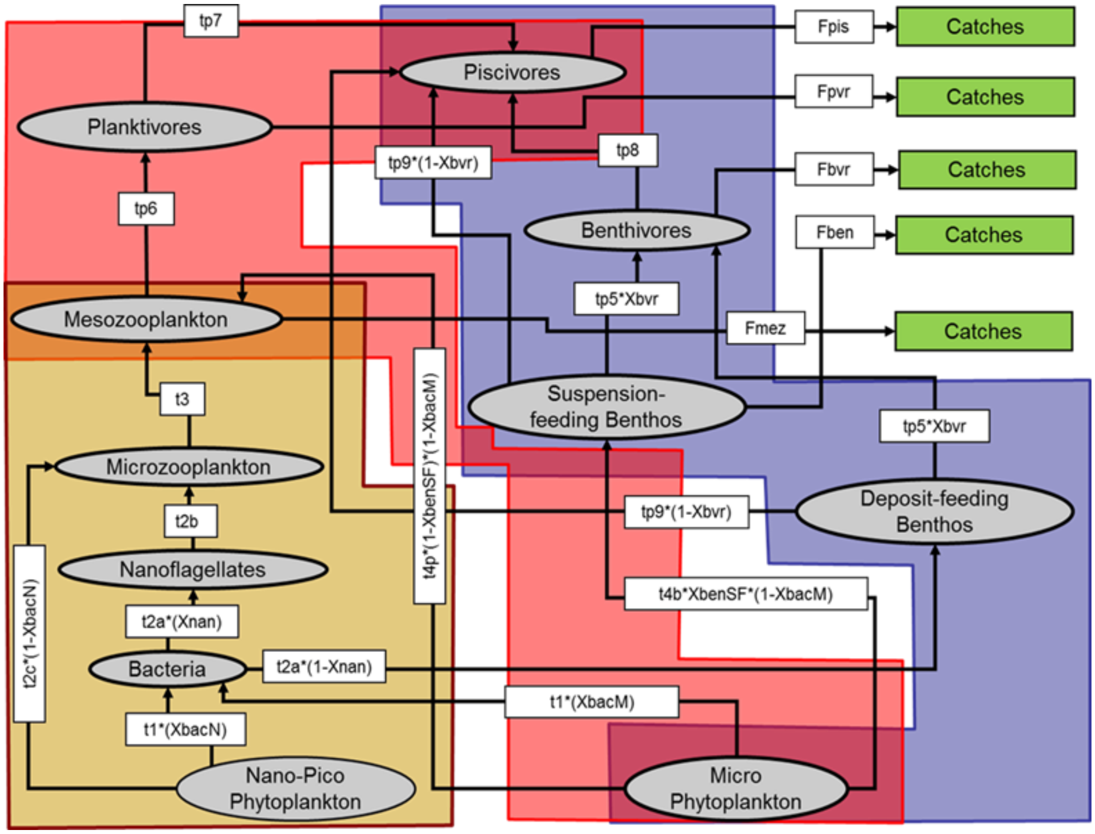


Figure 1. Structure of the EPP model (v2). Ovals represent nodes [functional guilds], and arrows indicate the trophic flows between nodes. The equations along the flows indicate the parameters/factors in each flow (i.e. transfer efficiency, transfer efficiency times fraction available, or exploitation rate). The red, blue, and brown backgrounds indicate the pelagic, benthic, and microbial loop energy pathways. The current model implementation allows fishing on five (5) nodes [functional guilds], mesozooplankton, planktivores, suspension feeding benthos, benthivores, and piscivores.

The EPP model is implemented as a Monte Carlo simulation to account for the uncertainty in inputs and model parameters, which defines the underlying "error" in the estimates of EPP. Transfer efficiencies outside the microbial loop are modeled using beta distributions whose parameters were derived from a compilation of existing network models (35 models for Arcto-Boreal ecosystems, 58 models for Temperate ecosystems) (Rosenberg et al., 2014; Fogarty et al., 2016). There is more limited information to parameterize the microbial loop, and hence, transfer efficiencies within this pathway and some fractions (t1, t2a-c, t3, XbacM, XbacN) were set as fixed parameters based on general ecological literature on bacterial and microzooplankton gross growth efficiency, and utilization of primary production carbon in marine ecosystems (Azam et al., 1983; Cole et al., 1988; Straile, 1997; Rivkin and Legendre, 2001). Other fractions (XbenSF, Xnan) were modeled using uniform distributions to characterize the range of their expected variability. The default settings for the model (base run) include Fmez=0 (i.e. no fishing on mesozooplankton), and Xbvr=1 (i.e. no direct link between deposit-feeding benthos and piscivores functional guilds). The full list of model parameters is presented in Appendix 1.

The EPP model was coded in JAGS, using the package R2JAGS as interface between JAGS and R (Plummer, 2003; Plummer, 2017; Su and Yajima, 2021). A total of 10,000 iterations were used to characterize the behavior of each model run.

Ecosystem-specific inputs and outputs

The analysis of the spatial structure of NAFO ecosystems has identified three nested spatial scales relevant for the development of ecosystem summaries and management plans (NAFO, 2014b; Pepin et al., 2014; NAFO, 2015b). Bioregions represent the larger spatial scale and are conceptually equivalent to Large Marine Ecosystems. Within a bioregion, Ecosystem Production Units (EPUs) represent major geographical subunits characterized by distinct productivity and a reasonably well defined major marine community/food web system, making them an appropriate spatial scale for the implementation of ecosystem level management plans, including the analyses of ecosystem production potential (Pepin et al., 2014; NAFO, 2015a; Koen-Alonso et al., 2019). Within the NAFO Convention Area, the EPUs that include most of the fisheries resources under NAFO management and/or for which NAFO provides advice are the Newfoundland Shelf (2J3K), Grand Bank (3LNO), and Flemish Cap (3M) EPUs (Fig. 2). EPP models were constructed for each of these EPUs.

These ecosystems units can be classified as Subarctic-Boreal Shelf ecotypes (Rosenberg et al., 2014), so the basic model parameterization is the same for all of them. However, the main model input is size-partitioned primary production derived from remote sensing data and associated analyses, which differs among EPUs (Koen-Alonso et al., 2013; Rosenberg et al., 2014; Fogarty et al., 2016). Mean size-partitioned primary production in $gCm^{-2}y^{-1}$ for each EPU was used as input (Koen-Alonso et al., 2013), and transformed into wet weight units within the model using a carbon to biomass ratio of 1:9 (Pauly and Christensen, 1995). Variability in primary production was incorporated using truncated normal distributions to avoid extreme lows or highs, and using a generic 30% coefficient of variation (CV) which was defined based on the examination of primary production estimates for multiple years and EPUs (Koen-Alonso et al., 2013).

Another obvious difference among EPUs is their geographical extent. Ecosystem area in thousand km^2 is a required input that allows scaling model outputs to the size of the EPU.

Model outputs are production of the functional guilds in thousand tonnes per year and ecosystem. The Monte Carlo implementation implies that these outputs are full distributions. Results are typically reported using the median and/or percentile ranges of these distributions to display the variability around the median.

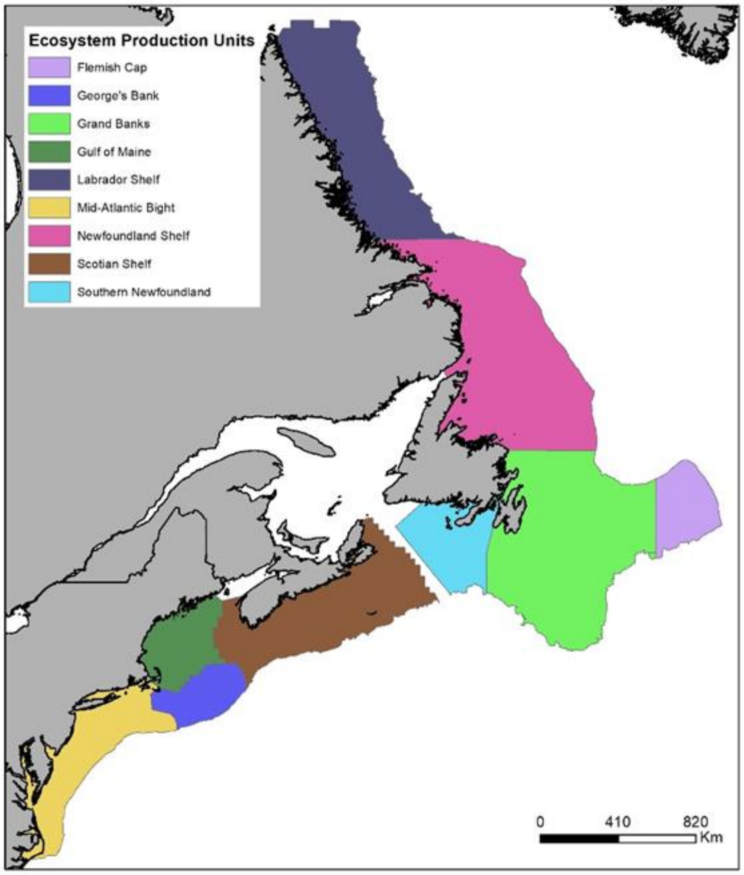


Figure 2. Ecosystem Production Units (EPUs) delineated in the NAFO Convention Area. Only the Newfoundland Shelf (2J3K), Grand Bank (3LNO), and Flemish Cap (3M) EPUs were considered for analyses of Ecosystem Production Potential (EPP) and derived estimates.

Characterizing EPP model behavior

The behavior of the EPP model was examined using the Grand Bank (3LNO) EPU model as a case study. While this ecosystem unit was selected because it was the target EPU for the pilot development of Ecosystem Summary Sheets within NAFO (NAFO, 2019), the general EPP model structure and parameterization does not differ among ecosystem units, so these results can also be considered representative of the behavior of the EPP model (v2) more generally.

The EPP model behavior was characterized by examining the distribution of production among nodes [functional guilds], the correlation among productivities within energy pathways, and the correlation between primary production and fishable nodes (i.e. suspension-feeding benthos, benthivores, planktivores, and piscivores).

Correlations within main energy pathways (i.e. pelagic, benthic, and microbial loop) were evaluated by estimating the pairwise correlation between connected nodes within the pathway, and then taking the average of these within-pathway correlations as an indicator of the coherence of production within the pathway. Correlations between primary production and fishable nodes were evaluated using total primary production (i.e. the sum of nano-pico and micro phytoplankton production). All pairwise correlations were calculated using the Pearson correlation coefficient, and estimated on the basis of 10,000 iterations of the model using the default (base run) configuration without fishing.

Sensitivity analysis

The previous analysis of the relationships in productivity among model nodes [functional guilds] and energy pathways provides a general characterization of the EPP model behavior. However, a comprehensive examination of the model also requires an evaluation of its structural uncertainty; how the model responds to changes in the topology of the food web.

From first principles we know that total heterotrophic production is dominated by production associated with lower trophic levels, especially the microbial loop. While changes in these lower trophic levels can have substantial impacts on trophic nodes relevant to fishing, our understanding on energy flows and transfer efficiencies for these trophic levels is more limited. Therefore, we conducted a sensitivity analysis focused on topological changes impacting the microbial loop to explore more fully how uncertainties at this level may impact model results.

This analysis was also based on the Grand Bank (3LNO) EPU model, and involved a series of runs where specific combinations of parameters were used in order to remove, weaken, or strengthen the microbial loop production and/or microbial loop input to the pelagic and benthic pathways (Table 1). The results from each sensitivity run were represented as fractions of the base run calculated using the median of the corresponding distributions; this allows direct comparisons in the relative changes in productivity across model nodes as well as easy visualization if the changes trigger an increase (ratio >1) or decrease (ratio<1) in node [functional guild] productivity.

Table 1. Description of the EPP model (v2) runs conducted as part of the sensitivity analysis of the model. Sensitivity runs have been order in this table as a function of increasing strength of the microbial loop. The color coding in the "Run name" column is intended to represent the strength of the microbial loop, with dark grey indicating no microbial loop in the model, and red indicating a very strong microbial loop. The same color coding is used in the results.

Run name	Parameter changes	Description of effect	Ecological Scenario
Run 0	No changes	Base run for comparisons. Used as denominator for all comparisons	Normal conditions
Run 7	XbacM=0 and XbacN=0	No input to bacteria; removes the microbial loop from the system	Microbial loop removed
Run 6	t2b=0 and XbacM=0	No micro-phytoplankton to bacteria and removes microbial loop input to micro-zooplankton	Weak microbial loop with no input to pelagic pathway
Run 1	XbacM = 0	No micro-phytoplankton to bacteria	Weak microbial loop
Run 4	XbacM=0 and Xnan=1	No micro-phytoplankton to bacteria, and no bacteria to deposit-feeding benthos	Weak microbial loop, and weak bentho-pelagic coupling by removing the detritus pathway
Run 5	t2b=0	No microbial loop input to micro-zooplankton	Normal microbial loop, but no microbial loop input to pelagic pathway
Run 2	Xnan=1	No bacteria to deposit-feeding benthos; all bacteria goes to nanoflagellates	Stronger microbial loop, but weak bentho-pelagic coupling by removing the detritus pathway
Run 3	XbacN=1	No nano-pico plankton to microzooplankton (no jumping around the microbial loop)	Strong microbial loop

Application of the EPP model to fisheries management

Ecosystem Production Potential (EPP), Fisheries Production Potential (FPP) and Total Catch Indices (TCIs)

The NAFO Roadmap defines a 3-tiered structure to achieve sustainable catch levels, where Tier 1 involves evaluating sustainability of total catches at the ecosystem level (Koen-Alonso et al., 2019). EPP models and derived metrics are intended to inform the Tier 1 assessment.

The EPP model estimates the potential production of the ecosystem under the assumption that the ecosystem is fully functional (i.e. its maximum potential for production). Also, since the model is not dynamic, model estimates represent an integrated period of time sufficient for the primary production to reach the upper trophic levels (e.g. 3-5 years). While the model does not assume equilibrium *per se* nor impose mass balance constraints, it does assume that general conditions during that time horizon are somewhat stable. This implies that any practical application derived from EPP model outputs would be strategic in nature, informing management actions within 3-5 yr time blocks.

In this context, generating practical guidance on sustainable catch levels from the EPP model requires some important additional steps: 1) defining what is a sustainable catch level in the context of an EPP model, 2) evaluate the level of ecosystem functionality and, if required, scale down the model results to consider the realized ecosystem state, and 3) based on the previous steps, and accepted management principles, identify and calculate a suitable indicator to be used in the provision of science advice.

Following these steps will render related but different metrics. Step 1 estimates the fraction of the EPP that can be sustainably extracted as catch; this is the Fisheries Production Potential (FPP). Like EPP estimates, FPP also corresponds to the maximum FPP if the ecosystem is fully functional. Step 2 adjusts the FPP estimates from its original fully functional ecosystem context to the realized productivity conditions of the ecosystem, generating the adjusted Fisheries Production Potential (FPP_{adj}). If the ecosystem is indeed fully functional, FPP and FPP_{adj} would be the same. Step 3 calculates a single value from the FPP_{adj} distribution, the Total Catch Index (TCI) that can be used to evaluate if aggregate fisheries catches for a given node [functional guild] are consistent with sustainable levels of catch.

Sustainable catch level

In traditional fisheries science the idea of sustainability is often related to the Maximum Sustainable Yield (MSY) concept. In its simplest representation, MSY emerges from simple surplus-production dynamic models and corresponds to the maximum level of catch that can be annually extracted from the stock while keeping the stock size at a stable level; other catch levels that can keep the stock stable over time would also be sustainable, but they would be lower than MSY, while sustained catches above MSY will drive the stock down. Most importantly, the whole idea of sustainability is built around stock dynamics; it is about reliably extracting the most catch possible while keeping the stock size within some acceptable margins.

Because the EPP model is not dynamic this idea of sustainability cannot be directly explored; we cannot derive a sustainability metric from the model itself. However, the EPP model tracks the fate of primary production within the food web, and looking at sustainability from the perspective of primary production can provide an avenue to define what could be sustainable within the context of the EPP model. This rationale was originally developed by Iverson (1990), who indicated that fish production appears to be "controlled by the amount of new nitrogen incorporated into phytoplankton biomass", and later applied in an EPP model context by Rosenberg et al. (2014) and Fogarty et al. (2016).

The basic idea builds upon the concepts of new, regenerated/recycled, and total primary production, which are related to the nitrogen cycle in the ocean. Nitrogen is a typically a limiting nutrient in the ocean. Organic material generated by phytoplankton using nitrogen from nitrate ($NO3^-$) is using a "fresh/new" source of nitrogen (i.e. an inorganic source of nutrient). Organic material generated by phytoplankton using ammonium ($NH4^+$), a product from organisms' metabolism, is using "recycled" nitrogen. New production is generally associated to large phytoplankton (e.g. diatoms) that feed more directly into the pelagic pathway, and fish production.

The *f*-ratio (or similar metrics) can be seen as the upper limit of the production that can be extracted sustainably because it is the fraction of primary production that relies on a "fresh/new" source of nutrients. The assumption here is that the bacteria involved in nitrification will never become a bottleneck for primary production, and that other sources of inorganic nitrogen would replenish what is removed by fisheries.

Estimates of the *f*-ratio are not that commonplace, but given its general link to micro-phytoplankton production (i.e. large phytoplankton), the ratio between micro-phytoplankton production and total primary production can be used as proxy. Rosenberg et al (2014) compiled these ratios for 54 Large Marine Ecosystems around the world. The median of those ratios is 0.205, and hence, a generalized exploitation rate of 20% can be used to define the upper limit for sustainable fishing in the context of the EPP model.

While the above rationale provides an upper limit for sustainable exploitation in the context of production analyses like the EPP model, practical applications of this exploitation rate requires some additional considerations. Production in the EPP model is estimated for each node [functional guild] in the modeled food web, but not all nodes contain species targeted by fisheries, and for those nodes that do, their species complement may not be fully relevant to fisheries. Defining sustainable upper bounds for total catches requires both, an exploitation rate that can be considered sustainable, as well as an idea of what fraction of the production of the node [fishing guild] is of potential fisheries relevance.

Only four nodes [functional guilds] in the EPP model are considered to contain species targeted by fisheries or of potential fisheries relevance: piscivores, benthivores, planktivores, and suspension-feeding benthos. Most traditional commercial groundfish and shellfish species in the NAFO Convention Area, like Atlantic cod, redfish, Greenland halibut, American plaice, yellowtail flounder, Northern shrimp, and snow crab are included in the piscivore and benthivore nodes, commercial small pelagic fish like capelin and herring are included in the planktivore node, while scallops and clams are included in the suspension-feeding benthos node.

Considering that current and historical commercial species within the piscivores and benthivore nodes constitute a substantial fraction of the total biomass estimated from bottom trawl surveys in these EPUs it was deemed acceptable to assume, at least as a first approximation, that 100% of the production of these functional guilds was of relevance to fishing.

In the case of planktivores the information from bottom trawl surveys is less reliable given the more pelagic nature of the species within this functional guild. However, the number of planktivore species of commercial relevance is more limited, with capelin representing the bulk of the catches, followed by Atlantic herring and Atlantic mackerel. Bottom trawl survey information indicates that capelin dominates the planktivore biomass in the Newfoundland shelf (2J3K), but non-commercial species (e.g. sandlance) are as important or more than capelin in the Grand Bank (3LNO) and Flemish Cap (3M). In the absence of pelagic surveys in these ecosystems, and taking into account that pelagic surveys in a similar Subarctic-boreal ecosystem like the Barents Sea indicated that 50% or more of the pelagic biomass was associated with 0-group fishes (Eriksen et al., 2011), it was deemed appropriate to assume that only 50% of the planktivore production was of relevance to fishing.

In the case of suspension-feeding benthos, only few species of clams and scallops are exploited in these EPUs, and mostly in the Grand Bank (3LNO). While the true catchability of different invertebrate species in the bottom trawl surveys is unknown, an initial examination of Canadian bottom trawl survey catches of suspension-feeding invertebrate species indicated that the biomass of commercial species was consistently below 10%. Given the many uncertainties and caveats involved, it was assumed that up to 10% of the suspension feeding benthos production was of potential relevance to fishing.

Overall, these assumptions about the fraction of the production of the functional guilds that is of fisheries relevance were guided by the premise that the goal of the analysis is to delineate reasonable upper limits for sustainable catches, but without necessarily imposing overly restrictive limits. The Tier 1 of the Roadmap is intended to provide an overall envelope for sustainable catch levels that would inform and complement the results obtained from other assessment tiers (Koen-Alonso et al., 2019).

Fisheries Production Potential (FPP) for key NAFO Ecosystem Production Units (EPUs)

Estimates of FPP were produced for the Newfoundland Shelf (2J3K), the Grand Bank (3LNO), and the Flemish Cap (3M) EPUs. FPP levels for the fishable nodes were estimated using a 20% exploitation rate and the fractions of fishing relevance described above. In addition to the FPP by fishable node [functional guild], the FPPs for the piscivore and benthivore nodes were also presented as an aggregate, the Standard Demersal Component (SDC). This SDC aggregate provides an integrated FPP metric to complement the node-specific estimates, especially considering that part of the production for some commercial species can be shared between the benthivore and piscivore nodes given their trophic plasticity. The SDC aggregate also provides a more direct point of comparison with other analyses, like aggregate biomass surplus production models (Bundy et al., 2012).

Adjustment for ecosystem functionality

While FPP estimates assume that the ecosystem is fully functional and relatively stable, real ecosystems are often away from equilibrium, and relatively stable conditions do not necessarily imply full functionality.

Therefore, practical use of FPP estimates requires adjusting FPP estimates to better reflect the realized productivity state of the ecosystem.

The Newfoundland Shelf (2J3K), Grand Bank (3LNO) and Flemish Cap (3M) EPUs have experienced important changes in total biomass over time (Fig. 3). The Flemish Cap appears to have maintained a relatively stable total biomass level, with a temporary but significant increase in biomass during the late 2000s mostly linked to unusually high recruitment events for redfish (Perez-Rodriguez et al., 2012; Koen-Alonso et al., 2018). On the other hand, the Newfoundland Shelf (2J3K), and Grand Bank (3LNO) currently have total biomass levels that are far lower than the ones observed before the early 1990s, when a regime shift took place in the Newfoundland-Labrador (NL) bioregion (Koen-Alonso et al., 2010; Buren et al., 2014a; Dempsey et al., 2017; Pedersen et al., 2017; Dempsey et al., 2018; Koen-Alonso and Cuff, 2018; Pedersen et al., 2020).

These observations would suggest that the Flemish Cap appears to be fully functional, while the functionality of the Newfoundland Shelf (2J3K) and Grand Bank (3LNO) EPUs appears impaired to some degree. The failure of these ecosystems to rebuild to pre-1990 levels clearly indicates reduced productivity for, at the very least, the functional guilds predominately surveyed by bottom trawl multispecies surveys (i.e. benthivore and piscivore nodes).

Consequently, while the Flemish Cap (3M) EPU could be assumed fully functional and the FPP estimates for this system could be directly used to provide guidance, the FPP estimates for the Newfoundland Shelf (2J3K) and Grand Bank (3LNO) EPUs need to be adjusted to reflect their reduced productivity state before they can be used to inform the sustainability of total catches in these ecosystem units.

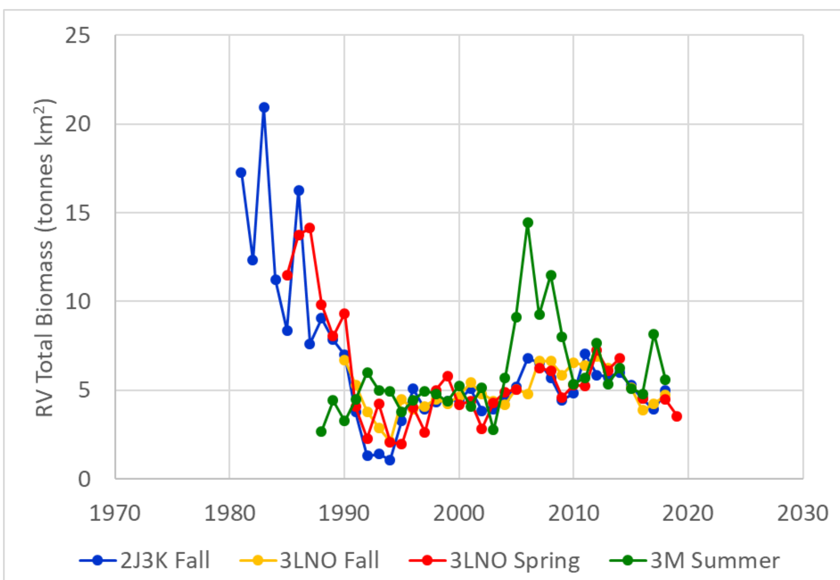


Figure 3. Total RV Biomass Density indices for the Newfoundland Shelf (2J3K) (Fall), the Grand Bank (3LNO) (Spring and Fall), and Flemish Cap (3M) (Summer). The 2J3K and 3LNO series have been scaled pre-1995/1996 to correct for the change in the survey gear in the DFO surveys.

From a system perspective, the production estimated by the EPP model is limited by the primary production inputs and transfer efficiencies, and we can consider these first order constraints. However for this production to actually happen, each one of the nodes in the EPP model needs to have sufficient biomass to actually utilize the production available from lower trophic levels. If this is not the case, the flow of production up the food web gets reduced. Therefore, having sufficient biomass in each model node to process available production becomes a second order constraint to production, and something that is not factored in within the EPP model structure. However, while tracking the fate of any "unused" available production is not possible using the EPP model itself, and becomes a question to be tackled with other analyses, we can still adjust the outputs of the EPP model by considering overall system biomass level.

This adjustment can be derived from the production/biomass ratio (P/B ratio) concept. The P/B ratio emerges from the study of the relationship between production and biomass (Allen, 1971), and while is typically calculated for a given taxa, there is no conceptual impediment to calculate it for other levels of aggregation (Mertz and Myers, 1998). While P/B ratios would *a priori* be expected to be variable depending on a number of factors (e.g. age, size and/or taxa composition of the aggregate considered, organism biology, environmental conditions), they are typically found to be a relatively stable trait, with most of the observed variability being across taxa and explained by differences in body size, physiology, life history, and environmental conditions (Banse and Mosher, 1980; Dickie et al., 1987; Randall and Minns, 2000; Brey, 2012). Furthermore, the general stability of P/B ratios indicates that changes in overall production would be expected to be more associated to changes in biomass levels than changes in the P/B ratio itself (Boudreau and Dickie, 1989), while its underlying allometric structure (Banse and Mosher, 1980) highlights that its first order scaling is defined by physiological constraints (Dickie et al., 1987), which justifies using P/B ratios as an effective parameter to characterize productivity of species and/or species groups in ecosystem modelling and other applications (Christensen and Pauly, 1992; Randall and Minns, 2000; Christensen and Walters, 2004; Link et al., 2008; Heymans et al., 2016).

Based on this pattern of relative stability in P/B ratios, and taking into account that functional guilds can exhibit compensatory dynamics (i.e. guild dynamics are more stable than the dynamics of the species within) (Auster and Link, 2009), it is reasonable to assume the existence of a relatively stable ecosystem-level P/B ratio. Even without knowing its actual value, it follows from this argument that production and biomass are directly proportional $\left(\frac{P}{B} \approx k \rightarrow P \approx kB \Longrightarrow P \propto B\right)$. Based on this approximation, we can use the relative changes in total biomass to map the expected relative changes in overall productivity. If total ecosystem biomass is relatively stable over time, we can assume that that the system is fully functional, and no adjustment for realized productivity is required. On the other hand, if total ecosystem biomass show important and sustained changes over time, then these changes would be indicators of reduced productivity in those periods with lower biomass, suggesting that ecosystem functionality is somehow impaired. In these cases, the ratio between the maximum total ecosystem biomass and the observed lower biomass can be used as penalty factor to adjust the FPP estimates from the EPP model.

A recent analysis looking at identifying regime shifts has shown that the fish community in the NL bioregion has not been in a stable regime within the last 40 years, with the only possible exception of the early 1980s (Pedersen et al., 2020). While this bioregion has experience substantial fishing prior the 1980s, there are no comprehensive surveys to evaluate if the total biomass had already suffered significant declines before this time. Considering that the available evidence indicates some stability in the early 1980s, the initial years of the available time series were used to define an assumed fully functional state for the EPUs in the NL bioregion. The median of total RV Biomass between 1981-1985 for 2J3K, and between 1985-1987 for 3LNO were used as proxies for maximum biomass. Revisiting the trajectories of total biomass in the Newfoundland Shelf (2J3K) and Grand Bank (3LNO) EPUs, we can express the estimated total RV biomass as a fraction of these proxies for maximum biomass (Fig. 4).

Considering that the EPP model results represent an integrated view of ecosystem productivity over a medium term horizon (e.g. 3-5 yr), adjustment of FPP values to realized conditions also needs to be based on some reasonable integration over a medium term period. A 5-yr running median was used to characterize the trajectory of biomass state over time, as a proxy for productivity state (Fig. 4). These running median trajectories where then used to abstract a pattern of adjustment over time that can be applied, as a factor, to the estimated FPP values (Fig. 4). If the abstracted penalty factor is 1, it implies that the ecosystem is fully functional, and no real adjustment is required; if the penalty factor is less than 1, then full ecosystem functionality is compromised to some degree, and fisheries productivity has to be adjusted down accordingly.

The application of these penalty factors to the FPP estimates allows to calculate an adjusted FPP that more closely represents the realized fisheries productivity at a given time; these "adjusted FPP estimates" (FPP_{adj}) are the ones to be used to generate guidelines for total catches.

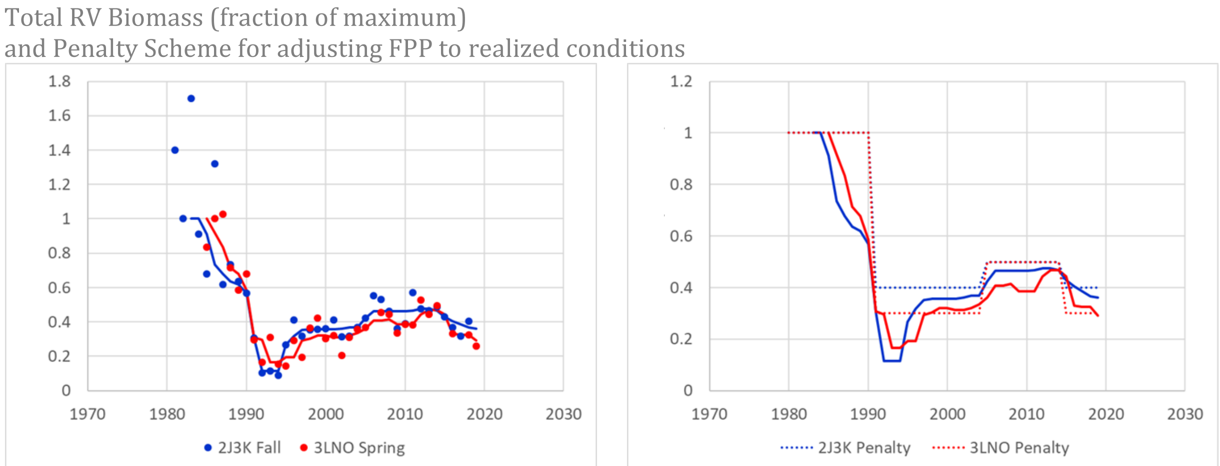


Figure 4. Total RV biomass for the Newfoundland Shelf (2J3K) (Fall survey) and Grand Bank (3LNO) (Spring Survey), and corresponding penalty scheme used for adjusting the FPP estimates to realized productivity state. Left: Total RV Biomass expressed as a fraction of the 1981-1985 median for 2J3K and the 1985-1987 median for 3LNO; lines correspond to the 5yr running median. Right: Filled lines correspond to the running medians from the left panel, and dotted lines represent the abstracted penalty scheme to represent the productivity state over time, where 1 corresponds to a fully functional ecosystem. Blue dots and lines: 2J3K; Red dots and lines: 3LNO.

Total Catch Indices (TCIs) and Guidelines for Total Catches

The analyses described so far generate a framework to estimate fisheries production potential for a given ecosystem, and to adjust these estimates to better represent the realized ecosystem productivity conditions. The only remaining element is to define how to use these results to generate any related science advice in a way that is consistent with NAFO management principles and practices. Since this work is intended to start making the Tier 1 level of the NAFO Roadmap operational (Koen-Alonso et al., 2019), there is no pre-existing practice to guide how the science advice needs to be framed. However, NAFO Precautionary Approach (PA) framework (NAFO, 2004) provides guidance on how stocks are to be managed, and the elements in this framework can inform the development of guidelines for total catches.

FPP_{adj} is derived by considering an exploitation rate that is consistent with the upper bound for sustainable catch levels from an ecosystem perspective. The NAFO PA indicates that the probability of exceeding a limit should be low, and nominally characterizes low probability of around 20% (although the actual value is to be set by managers). Following a similar rationale, guidelines for total catches should be provided in a way that the probability of exceeding FPP_{adj} is also low. Considering that the estimated FPP_{adj} is a distribution, a simple way to ensure that the probability of exceeding FPP_{adj} is low is to select as guideline reference a percentile of the FPP_{adj} distribution that satisfies this condition (e.g. 20-25th percentiles of the FPP_{adj} distribution). Based on these arguments, the 25th percentile of the FPP_{adj} distribution was selected as guideline reference for total catch. This reference value has been labelled "Total Catch Index" (TCI) (Fig. 5).

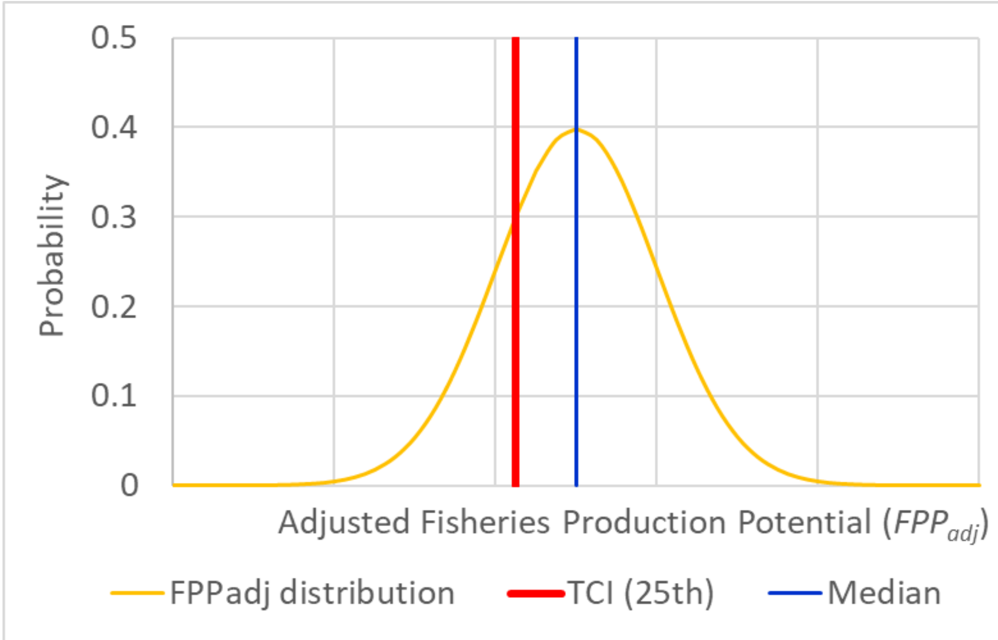


Figure 5. Schematic representation the FPP_{adj} distribution, highlighting the median of the distribution in blue, and the 25th percentile in red. This 25th percentile is used to define the Total Catch Index (TCI) reference value.

While TCIs provide a reference guideline for the upper bound of total catches that are consistent with sustainability, evaluating if catches are within this envelope also requires mapping the species being caught to the functional guilds represented in the EPP model nodes. While this mapping typically assigns species to functional guilds, catches for some important commercial species need to be split between different EPP model nodes. Small sizes of cod, and redfish functionally operate more as planktivores than piscivores based on their life history characteristics. In these cases, available diet information was used to define the fractions of the catches allocated to these two model nodes. In the Newfoundland-Labrador bioregion EPUs (2J3K and 3LNO), 90% of the cod and 70% of the redfish catches were mapped to the piscivore guild, with the remaining being mapped to the planktivore guild (NAFO, 2014a; NAFO, 2017). In the Flemish cap (3M) catches, the cod and redfish fractions mapped to the piscivore guild were 85% and 65% respectively (Pérez-Rodríguez et al., 2011; NAFO, 2016a; NAFO, 2017). All catches considered in this analysis are the ones reported in the NAFO STATLAN 21A database.

Evaluating the effectiveness of TCI as guidance level for total catches

TCIs are developed to inform the implementation of Tier 1 within the NAFO Roadmap. This implies that their use is strategic in nature, aiming at providing guidance in terms of the sustainability of the aggregate level of catch at the ecosystem level. TCIs by themselves are not intended as the basis for providing direct stock-level tactical advice, but their integration with the advice derived from Tier 2 (multispecies assessments), and Tier 1 (stock assessments), once the Roadmap is fully implemented, should provide a robust framework for the production of tactical advice that is consistent with an ecosystem approach.

Within their strategic scope, the effectiveness of TCIs will be given by their ability to associate catches above TCIs with negative outcomes in ecosystem performance, like declines in the biomass of functional guilds. Furthermore, declines in functional guilds may not be solely driven by fishing pressure, but if TCIs properly map the boundary for sustainable aggregated catches at the ecosystem level, sustained fishing above TCIs would be expected to erode ecosystem functionality, and be consistently associated with negative ecosystem trends. This basic rationale provides an avenue to evaluate the performance of TCIs. If TCIs are effective as a reference level for sustainability, fishing above TCIs would be more associated with negative trends in the corresponding functional guilds than fishing below TCIs.

Given that most catches in the Newfoundland Shelf (2J3K), Grand Bank (3LNO), and Flemish Cap (3M) EPUs are mapped onto the piscivore and benthivore functional guilds, we focused our evaluation of the above prediction on catches and trends for these two functional guilds. The catch data was obtained from the NAFO STATLAN 21A database, and trends in biomass for the functional guilds were derived from Fisheries and Oceans Canada (DFO) RV surveys for 2J3K (Fall, 1981-2018) and 3LNO (Spring, 1983-2018), and from the European Union (EU) survey for 3M (Summer, 1990-2018).

For each functional guild in each EPU, the slope of the biomass index between consecutive years ($slope_t = (B_t - B_{t-1})/\Delta_t$, effectively the change in biomass), after smoothing the trajectory using a 3-yr running average to minimize year effects, was use as indicator of trend. Since the magnitude of these slopes would be a function of the functional guild and EPU, they were standardized by dividing them by the corresponding time series standard deviation (SD); this re-scales all slope values in relative SD units and allows comparability among functional guilds and ecosystems, with negative values indicating declines and positive values indicating increases in functional guild biomass.

Since TCIs are derived from a non-dynamic model intended to represent conditions integrated over a medium term horizon (e.g. 3-5 years), it would not be reasonable to simply pair yearly catch/TCI ratios with functional guild trends; ecosystem erosion would be expected to arise from a sustained level of fishing above the TCI over a number of years. To represent this feature the times series of catch/TCI were smoothed using a 5-yr running mean before pairing functional guild trends with catch/TCI ratios. This smoothed catch/TCI ratio constitutes an indicator of integrated fishing pressure for a functional guild and ecosystem unit relative to the upper bound guideline for sustainability. Values below one indicate catch levels within the sustainability envelope for total catches, while values above one represent fishing pressures beyond that envelope, indicating conditions consistent with those of ecosystem overfishing.

Given that functional guild trends are standardized by SD, and the catch/TCI ratio is by definition standardized as "fraction of the corresponding TCI", the data from all functional guilds and EPUs can be integrated for analysis.

Two analyses were performed using this integrated dataset of functional guild trend and catch/TCI ratio. The first analysis was a simple comparison of the functional guild biomass trend above and below a catch/TCI ratio equal to 1. If TCIs are a sensible boundary for sustainability, trends above a catch/TCI ratio of one would be expected to be significantly lower than those associated with catches within the sustainability envelope. This hypothesis was evaluated using a one-sided two-sample Mann-Whitney test.

The second analysis explored the relationship between functional guild trend and catch/TCI ratio taking into account the ecosystem unit, functional guild, and the possibility that environmental conditions may influence functional guild trends beyond fishing pressure. For this analysis, general environmental conditions were represented using the NL Climate Index (NLCI) (Cyr and Galbraith, 2021). This is a composite index which characterizes the large scale ocean climate state in the broad NL bioregion, and hence, it was also considered adequate to capture general environmental conditions in the Flemish Cap (3M) given its geographical proximity to the Grand Bank (3LNO). A precursor of this index has been used to investigate the role of environmental conditions as a driver of stock trajectories (Koen-Alonso et al., 2010). This analysis was done using a general linear model with identity link, where the functional guild trend was the response variable, and the independent variables were EPU and functional guild as factors, and year and NLCI as continuous variables. A single term deletion procedure was also used to identify the significant independent variables.

TCI sensitivity to the underlying trade-offs among functional guilds

A defining feature of ecosystem approaches is the open recognition that trade-offs among objectives need to be explicitly addressed. In the context of fisheries, considering the trophic interactions among exploited species is a prime example of trade-off that would need direct and explicit management attention. The NAFO Roadmap mainly focuses on these trade-offs in its Tier-2 assessment (Koen-Alonso et al., 2019), but the EPP model also allows us to perform some initial scoping of trade-offs.

This is of relevance in the context of TCIs because the calculation of TCIs relies on FPP estimates that assume that all nodes of relevance to fishing will be fished up to their sustainability limit. Given the food web structure of the EPP model, this implies that fishing on lower trophic level nodes like the planktivore and suspension-feeding benthos functional guilds will reduce the fisheries production potential of upper trophic level nodes like the benthivore and piscivore functional guilds. It follows from this, that if lower trophic level nodes are not actually fully fished, that would increase the fisheries production potential of the upper trophic level ones, making the TCIs as calculated an underestimate of the actual upper bounds for sustainability for these nodes. Therefore, assessing trade-offs within the context of the EPP model is not only important as a scoping exercise for the broader discussion about trade-offs and management objectives, but it is also useful to evaluate the potential impact of the implicit trade-offs underlying the TCI calculation.

FPP calculations can be done assuming that not all the fishable nodes will be fished. In fact, this assumption is already implemented, albeit trivially, in the base calculation of FPP; the EPP model allows for fishing on the mesozooplankton guild (e.g. a fishery on copepods or krill) but the exploitation rate for this model node is set to zero in the default setting of the EPP model.

While fishing on mesozooplankton may not be of particular management relevance at the present time in NAFO, considering the potential impact of reduced fishing on the planktivore and suspension-feeding benthos nodes is very relevant. Most catches in NAFO ecosystems are associated with the benthivore and piscivore functional guilds, so a potential boost in their fisheries production potential due to more limited fishing on the planktivore and suspension-feeding benthos functional guilds is a very real possibility.

We evaluated the potential impact of this effect by performing a sensitivity analysis consisting in estimating FPP under two scenarios, one forfeiting fishing on the planktivore functional guild, and the other forfeiting fishing on both the planktivore and suspension-feeding benthos functional guilds. In both scenarios all fished nodes were exploited at F=20%. The results from these sensitivity runs were compared with the base run (all nodes exploited at F=20%) by taking the ratio between the median FPPs between the scenario and the base case. These sensitivity runs were done for all three EPUs and based on FPP (i.e. assuming the ecosystem is fully functional).

Results and Discussion

The EPP model

Concept and implementation

The characterization of the EPP model behavior was based on the Grand Bank (3LNO) EPU model, but since the basic structure and parameterization of the model is common to all three EPUs considered (i.e. all EPUs are classified as Subarctic-boreal ecotypes), these results are representative for the other EPUs.

The Monte Carlo implementation of the EPP model generates distributions for each model node, which allows characterizing the uncertainty in the estimation of production for the different functional guilds (Fig. 6). These distributions reflect the compounding effects of the variability in the individual transfer efficiencies, as well as in the partitioning of production among the different energy pathways. For mid to upper trophic levels these distributions reflect the longer right tails associated with the underlying beta distributions of the transfer efficiencies, the distributions within the microbial loop reflect the underlying normal distributions representing the variability in primary production inputs, while the "flat top" in the deposit-feeding benthos production is a reflection of the larger uncertainty in the magnitude of the bentho-pelagic coupling (Fig 6). Overall, the range of variability in the estimated production for each functional guild is generally bounded within 0.5-1.0 order of magnitude (Fig. 6).

The distribution of production among nodes [functional guilds] generated by the model is consistent with our current understanding of marine ecosystems, with most heterotrophic production associated with lower trophic level nodes (Fig 7). Total heterotrophic ecosystem production is highly dominated by production associated with the microbial loop, while the nodes [functional guilds] associated to fisheries, even those targeting highly productive species like small pelagic fish (i.e. planktivore node), have productions orders of magnitude lower. Therefore, even small relative changes in these lower trophic levels could potentially have substantial impacts on trophic nodes relevant to fishing.

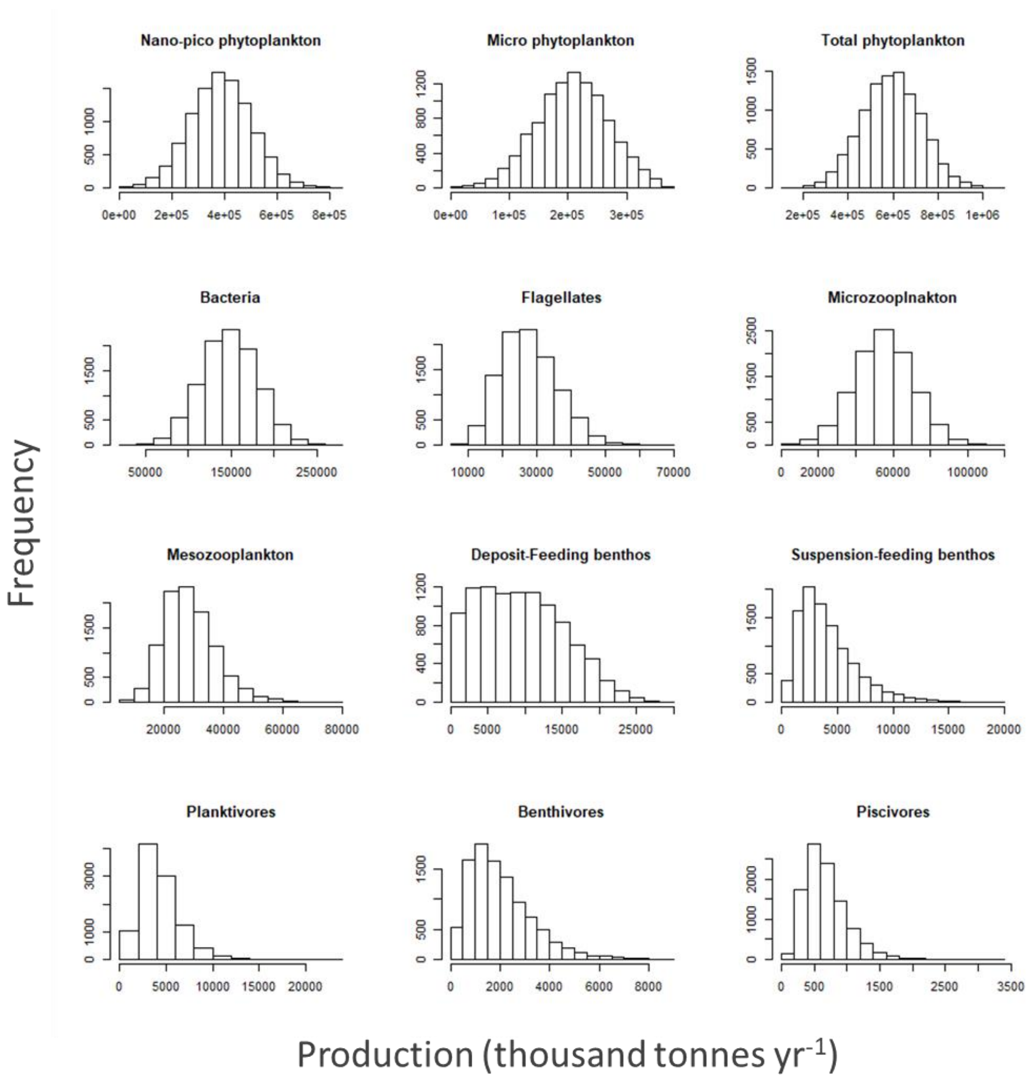
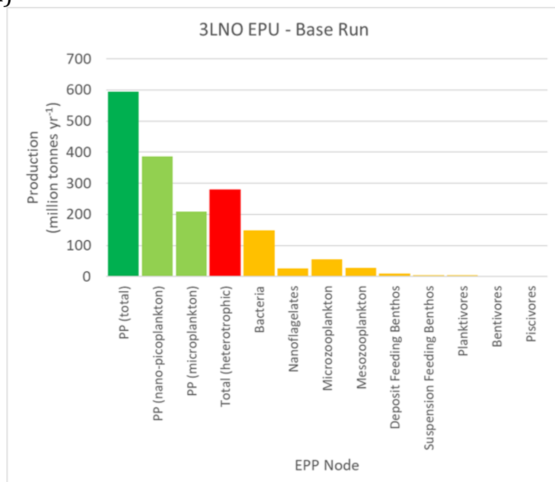


Figure 6. EPP model (v2) distributions of production for inputs (including the aggregated total primary production) and model nodes [functional guilds] for the base run of the Grand Bank (3LNO) EPU model. These distributions are derived from 10,000 iterations of the model.

A)



B)

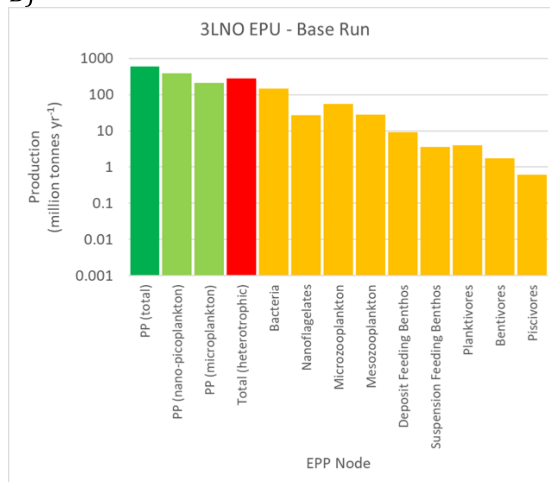


Figure 7. EPP model (v2) estimated median production for each model node [functional guild] and some relevant aggregates for the Grand Bank (3LNO) EPU. Green bars correspond to primary production (total and discriminated by phytoplankton size-fraction), the red bar indicate the aggregated total heterotrophic production, and the orange bars correspond to individual model nodes [functional guilds]. Production estimates are coarsely ordered by increasing trophic level, with production estimates presented in linear (A, left hand side plot), and logarithmic (B, right hand side) scales to facilitate visualization.

The incorporation of uncertainty in the EPP model (Monte Carlo implementation) also permits uncovering the strength of the links in productivity between nodes [functional guilds] (Table 2). While total primary production and total heterotrophic production are, as expected, highly correlated, most correlations between individual nodes [functional guilds] are on the weak side (overall average r=0.35) (Table 2).

From a fisheries perspective, the correlations between total primary production and fishable nodes indicate that the EPP model predicts a weak and diffuse linear connection between total primary production and fisheries production. The average correlations were 0.33 and 0.36, depending on the inclusion or not of suspension-feeding benthos among the fishable nodes, and it is consistent with the overall average correlation between nodes. At first sight this could suggest that total primary production (or variations in total primary production) would only have a limited influence, an hence predictive scope, on the production of ecosystem components relevant to fishing. However, the examination of the correlations within energy pathways shows a much better defined structure. The pelagic pathway (which includes planktivores and piscivores as fishable nodes) shows strong internal coherence in productivity (average r=0.67), while production along the benthic pathway (which includes suspension feeding benthos, and benthivores as fishable nodes) is more diffuse (average r=0.47) but still clearly stronger than the simple and direct link between total primary production and fishable nodes.

These results are consistent with recent studies which indicate that the connection between primary production and fisheries productivity is not necessarily linear, and that reconciling the differences in catches across Large Marine Ecosystems (LMEs) requires, in addition to primary production, consideration of the variability in food web structure/pathways, and transfer efficiencies (Friedland et al., 2012; Stock et al., 2017). These results are also well aligned with theoretical ecology concepts which indicate that ecosystems are characterized by a majority of weak links, and asymmetric energy channels which differ in productivity and turnover rate (e.g. a fast pelagic pathway vs a slow benthic pathway) (McCann et al., 1998; McCann et al., 2005; Rooney et al., 2006; Koen-Alonso, 2009). This coherence between the EPP model behavior and other analyses exploring related questions suggests that the model is capturing important features of real ecosystems.

In terms of the magnitude of the estimated productivity, even though our understanding of fish production and its relationship with primary production has advanced since Ryther (1969), current perspectives still build upon the basic principles and ideas encapsulated in the original Ryther model, which remains relevant to this day (Friedland et al., 2012; Stock et al., 2017; Link and Watson, 2019; Eddy et al., 2021). With this in mind, and within the context of further characterizing the EPP model behavior, a comparison between the outputs of the EPP model and the Ryther model can be useful.

The Ryther model relies on a very simple equation, $P_i = PP\tau^{TL_i - 1}$, where the production (P_i) at a given trophic level i (TL_i) is a function of the total primary production (PP), and the transfer efficiency (τ), which is often assumed as 10%. Unlike the EPP model, the Ryther model represents a linear food chain and, in its simplest formulation, with a common transfer efficiency. If we use this model to calculate the production at TL 3 and 4 for the Grand Bank (3LNO) EPU, which coarsely correspond to the planktivores plus benthivores (TL_3) and piscivores (TL_4) functional guilds in the EPP model, the estimated productions are 5,937 and 594 thousand tonnes y^{-1} respectively, which are very consistent with the corresponding production estimates from the EPP model, which are 5, 690 and 620 thousand tonnes y^{-1} respectively. These results indicate that the estimated order of magnitude for production from the EPP model is well aligned with a benchmark model that still underpins more complex and modern applications (Stock et al., 2017; Eddy et al., 2021).

Overall, and despite its simplicity, the EPP model architecture and emergent behavior encapsulates features identified as necessary to effectively link primary production with fisheries production (e.g. food web structure, variability in transfer efficiencies), and more general properties of real ecosystems (e.g. asymmetry in energy pathways), while delivering estimates of production with appropriate orders of magnitude and where the variability around these estimates is also characterized. Based on these observations, the EPP model appears in line with current ecological understanding of productivity of marine systems.

Table 2. Pairwise correlations among estimated node [functional guild] productions, and including some relevant aggregates (Total primary production, Total heterotrophic production), from the EPP model (v2) for the Grand Bank (3LNO) EPU. All correlations are calculated using the Pearson correlation coefficient and based on 10000 runs of the model. The background color indicate the value of the correlations, with dark green indicating high negative correlations, and strong orange high positive correlations.

Correlation Matrix (3LNO EPU, Base Run)	Primary Production (nano-picoplankton)	Primary Production (microplankton)	**Primary Production (total)**	Bacteria	Nanoflagellates	Microzooplankton	Mesozooplankton	Deposit Feeding Benthos	Suspension Feeding Benthos	Planktivores	Benthivores	Piscivores	**Total (heterotrophic)**
Primary Production (nano-picoplankton)	1.00												
Primary Production (microplankton)	0.02	1.00											
Primary Production (total)	0.89	0.48	1.00										
Bacteria	0.89	0.48	1.00	1.00									
Nanoflagellates	0.67	0.37	0.76	0.76	1.00								
Microzooplankton	1.00	0.07	0.90	0.90	0.74	1.00							
Mesozooplankton	0.45	0.54	0.64	0.64	0.52	0.47	1.00						
Deposit Feeding Benthos	0.32	0.16	0.35	0.35	-0.34	0.24	0.18	1.00					
Suspension Feeding Benthos	0.01	0.48	0.23	0.23	0.18	0.04	0.19	0.07	1.00				
Planktivores	0.28	0.33	0.40	0.40	0.33	0.30	0.61	0.09	0.09	1.00			
Benthivores	0.21	0.25	0.30	0.30	-0.19	0.17	0.17	0.70	0.35	0.09	1.00		
Piscivores	0.28	0.33	0.40	0.40	0.16	0.28	0.50	0.35	0.21	0.75	0.47	1.00	
Total (heterotrophic)	0.90	0.44	0.99	0.99	0.76	0.92	0.71	0.33	0.24	0.46	0.30	0.45	1.00

Sensitivity analysis

The results of the sensitivity analysis show that overall ecosystem heterotrophic production is directly linked to the microbial loop production, but increased overall heterotrophic production does not necessarily translates into higher production in all models nodes [functional guilds], or the nodes [functional guilds] that support fisheries (Fig. 8).

The microbial loop has a key role in driving deposit-feeding benthos production through benthic-pelagic coupling (detritus pathway). However, overall benthic production does not respond homogeneously to changes in production at lower trophic levels. Weakening the microbial loop boosts suspension-feeding benthos production, but has negative impacts on deposit-feeding benthos (Fig. 8).

A stronger microbial loop generally reduces productivity in the pelagic pathway, and consequently on some fishable nodes like planktivores and piscivores, while the effect on benthivores is less consistent and depends on how the different pathways are affected (Fig. 8).

Overall, these results emphasized the notion that production along the pelagic pathway is highly correlated, while production along the benthic pathway is more diffused.

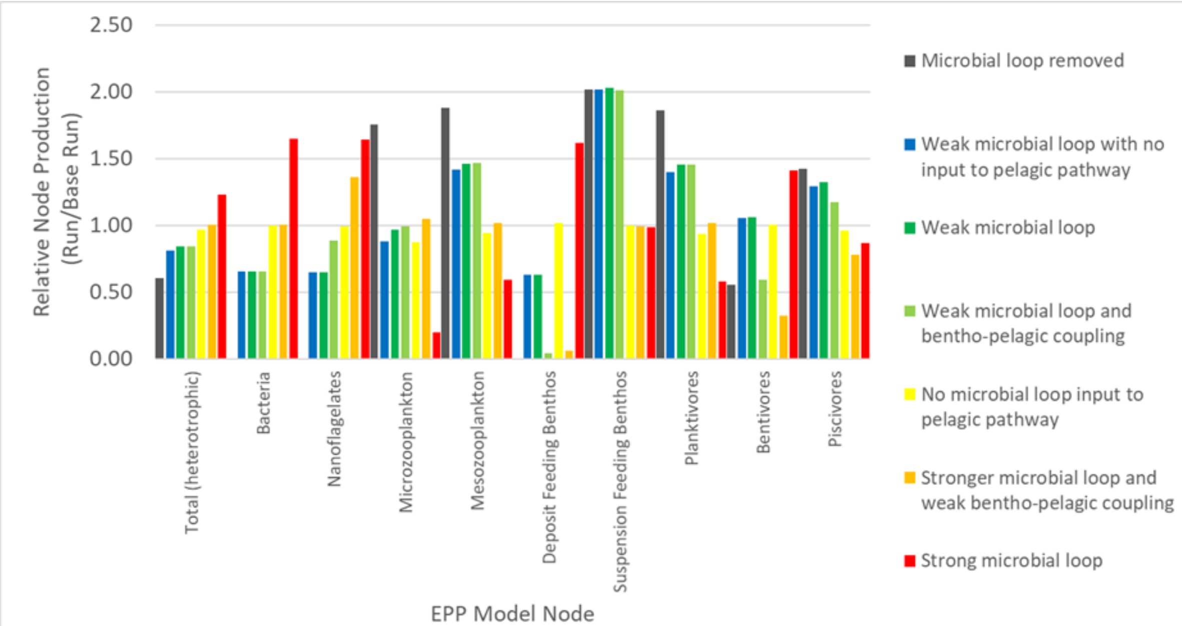


Figure 8. Results from the EPP model (v2) sensitivity runs for the Grand Bank (3LNO) EPU. Runs are ordered by increasing strength of the microbial loop, and the colors correspond to the run descriptions provided in Table 5.

Another important observation from this sensitivity analysis is that the structural changes explored affected the energy pathway that has the biggest impact on overall heterotrophic ecosystem production (Fig. 7), and even though these structural changes were substantive, their impacts on production of fishable nodes were generally bounded by a factor of two; production either doubled or was reduced by half (Fig. 8). Considering that the current uncertainties in parameterizing the microbial loop are not expected to trigger drastic scenarios like the ones explored in this sensitivity analysis, these results provide useful information on the potential extreme outer bounds for the estimated production derived from the Monte-Carlo implementation, and would suggest that the current EPP model is capturing an important fraction of the overall uncertainty in production.

Furthermore, the current implementation of the EPP model also allows for considering some aspects of marine production that can become particularly important as the impacts of climate change increases. Recent studies have predicted that the increased stratification of the ocean as a result of climate change could lead to reduced primary production and/or increases in the fraction of small phytoplankton, leading to reductions in fisheries production (Lotze Heike et al., 2019; Friedland et al., 2021; Tittensor et al., 2021). The EPP model, by considering size-fractioned primary production as input, provides a straightforward framework to explore these climate change effects, and eventually incorporate these considerations in the Tier 1 advice within the Roadmap.

Considering the full suite of results from the model characterization and sensitivity analysis, we conclude that the EPP model properly captures basic ecosystem features, and can serve as a simple and practical platform to explore changes in productivity at different trophic levels, including some basic impacts of climate change. It allows linking primary production with those trophic levels of interest to fisheries, and hence, can provide a first order approximation to the production potential of these trophic guilds.

Application of the EPP model to fisheries management

Fisheries Production Potential (FPP) for key NAFO Ecosystem Production Units (EPUs)

The Fisheries Production Potential (FPP) was derived under the assumption of fully functional ecosystems, and considering an exploitation rate of 20%. The results indicate that the Newfoundland Shelf (2J3K), the Grand Bank (3LNO), and the Flemish Cap (3M) EPUs would be able of sustaining total fisheries catches up to 577, 889, and 157 thousand tonnes per year respectively, but traditional groundfish and shellfish fisheries would represent less than half of these yields, and piscivore yields around 10% (Fig. 9). Differences in FPP estimates across ecosystems are mostly driven by differences in ecosystem area.

These FPP estimates are consistent with MSY estimates from aggregate biomass surplus production models. A comparative analysis of 12 Northern hemisphere marine ecosystems, which also included the Newfoundland-Labrador Shelves, found that MSY ranged between 1-5 tonnes km^{-2} yr^{-1} and that the associated exploitation rates were 0.1-0.4 yr^{-1}, with most ecosystems showing values around 0.2 yr^{-1} (Bundy et al., 2012). These results for exploitation rate are consistent with the F=20% derived from the *f*-ratio rationale, while the MSY range fully encompass the FPP estimates for the EPUs considered here (Fig. 10).

Furthermore, the specific results from Bundy et al. (2012) for the Newfoundland-Labrador system show MSY values around 1 tonne km^{-2} yr^{-1}, which if we consider that their analysis relied on bottom trawl survey data, makes the similarity between their results and the SDC FPP estimate (Fig. 10) particularly remarkable. Their analysis also shows a highly variable Fmsy for the Newfoundland-Labrador system in the range of 0.1-0.4 yr^{-1}.

The high consistency between FPP estimates and MSY estimates obtained from more traditional aggregate biomass surplus production models is reassuring. This level of coherence from two completely different and independent approaches provides additional support for the reliability of the estimated FPP values.

While this consistency between these modelling exercises could question the need for using FPP estimates in the first place, some key advantages of the FPP model estimates are that they are derived from a model architecture that allows estimating these values from primary production, permits approximating FPP for guilds that are not necessarily well captured by aggregate biomass surplus production models due to the limitations in the underlying surveys (e.g. planktivores and suspension-feeding benthos), and provide a suitable framework to explore how changes in size distribution and magnitude of the primary production could impact FPP. Still, the Roadmap calls for a multi-model approach to inform its different assessment tiers (Koen-Alonso et al., 2019), therefore, as Tier 1 implementation progresses, aggregate biomass surplus production models can also become part of the ensemble of models informing this assessment level.

Overall, the similar magnitudes between the FPP estimates and independently derived estimates of MSY for those aggregates that can be reasonably compared gives credence to the rationale behind FPP calculations. If we consider that in an MSY framework catches above MSY are by definition unsustainable, and that within the EPP framework FPP aims at identifying the upper bound for sustainable catches, this emerging consistency in magnitude from both frameworks would indicate that FPP appears to be effective at mapping the sustainability boundary at the ecosystem level. More generally, the agreement between two frameworks that build the concept of sustainability from very different perspectives seems to suggest that, like the blindmen and the elephant, both frameworks are effectively uncovering a more fundamental underlying property of ecosystem organization that defines the functional boundary for sustainable catches at the ecosystem level.

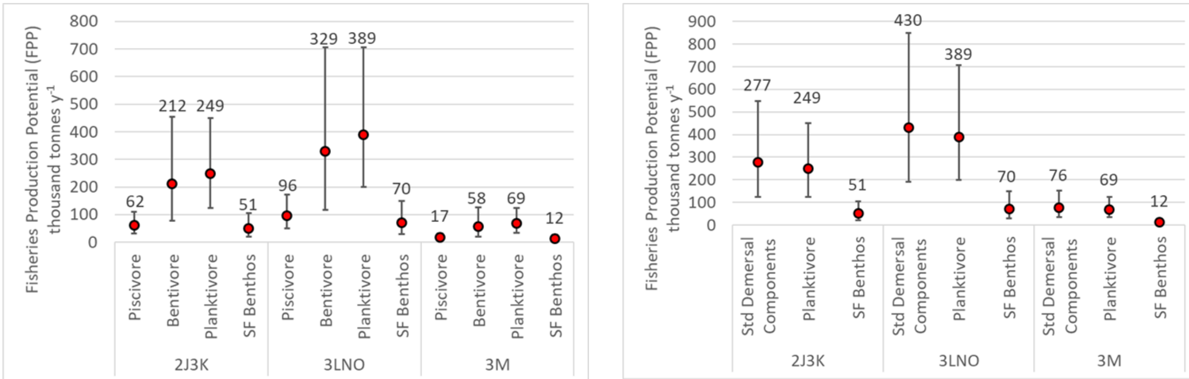


Figure 9. Fisheries Production Potential (FPP) for the Newfoundland Shelf (2J3K), Grand Bank (3LNO), and Flemish Cap (3M) EPUs. Left: FPP by fishable node [functional guild], Right: FPP with piscivore and benthivore nodes aggregated into Standard Demersal Components (SDC). Red dots indicate the medians, whiskers the 10-90% range, and the numbers above are the numerical value of the medians. The differences in magnitude across EPUs is mostly a reflection of the differences in areal extent of these ecosystems. All these estimates assume these ecosystems are fully functional.

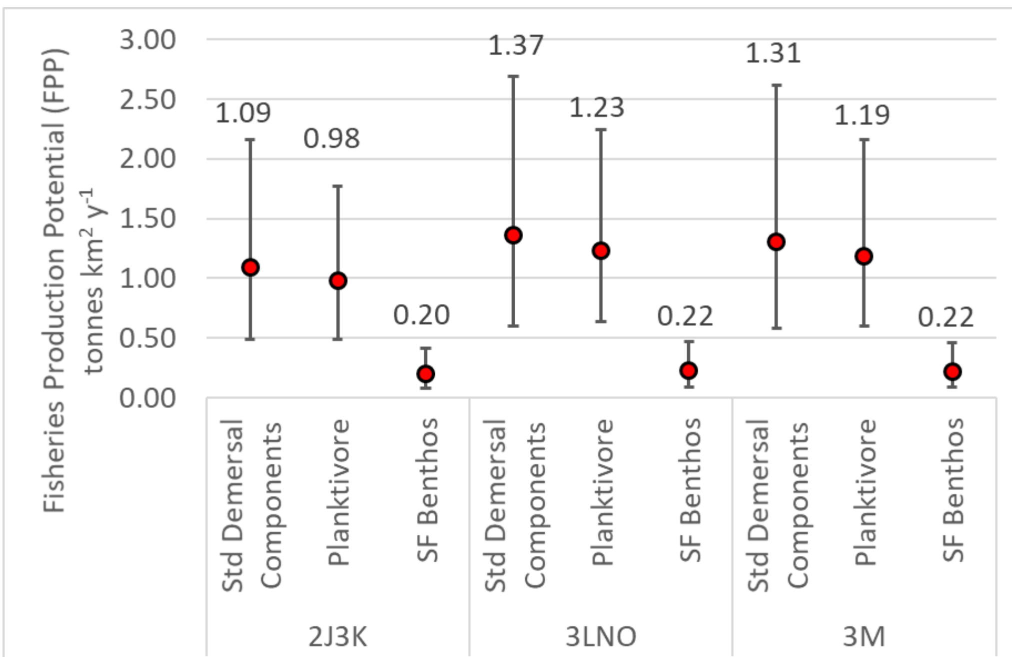


Figure 10. Fisheries Production Potential (FPP) per unit area for the Newfoundland Shelf (2J3K), Grand Bank (3LNO), and Flemish Cap (3M) EPUs, with the FPP for piscivores and benthivores aggregated into Standard Demersal Components (SDC). Red dots indicate the medians, whiskers the 10-90% range, and the numbers above are the numerical value of the medians. All these estimates assume these ecosystems are fully functional.

Adjustment for ecosystem functionality

The approach taken to adjust FPP estimates to realized levels of ecosystem productivity is based on a number of assumptions. The fundamental assumption of a relatively constant P/B ratio at the ecosystem level, is consistent with analog assumptions made for individual taxa in other ecosystem modelling exercises (Banse and Mosher, 1980; Dickie et al., 1987; Christensen and Pauly, 1992; Randall and Minns, 2000; Christensen and Walters, 2004; Link et al., 2008; Brey, 2012; Heymans et al., 2016), and certainly in line with the assumption of a common intrinsic growth rate in aggregate biomass surplus production modelling exercises (Bundy et al., 2012).

Considering that the model integrates the entirety of the food web, it seems reasonable to assume that changes in community composition within functional guilds would be compensatory (e.g. Auster and Link 2009) keeping the overall P/B ratio somewhat stable over time. This actually seems to be the case. A recent Ecopath modelling exercise of the NL shelves focusing on two time periods, one prior to the 1990s regime shift and another in the early 2010s, capturing differences in community composition and total biomass level, rendered remarkably close average P/B ratios for both periods (Tam and Bundy, 2019). The unweighted average P/B ratio for heterotrophic components were 5.80 and 5.78 for the 1985-1987 and the 2010-2013 models respectively, while the corresponding biomass-weighted averages were 0.109 and 0.098 (Tam and Bundy, 2019). These results provide further credence to the adopted approach, and to the rationale that changes in total biomass would be expected to track changes in total productivity.

A reasonable criticism to the current implementation of this adjustment is the fact that bottom trawl surveys are used to represent the trajectory of total ecosystem biomass. Many ecosystem components (e.g. benthos, pelagic fish, zooplankton) are not properly sampled by traditional bottom trawl surveys. However, some important pelagic components, like capelin, a key forage species in the NL bioregion, also experienced a drastic collapse during the regime shift without really recovering since (Buren et al., 2014a; Buren et al., 2019; Murphy et al., 2021), and this capelin collapse and lack of recovery has been a driver in the lack of recovery of Atlantic cod (Buren et al., 2014b; Koen-Alonso et al., 2021). These observations indicate that the signal in total biomass from bottom trawl surveys does indeed match a more general signal, making the bottom trawl surveys an acceptable first approximation for other important components, even if the surveys themselves do not sample those components particularly well. More importantly, these analyses indicate that overall productivity in the NL bioregion appears bottom-up driven (Koen-Alonso et al., 2010; Buren et al., 2014a; Buren et al., 2014b; Dempsey et al., 2018; Koen-Alonso et al., 2021; Murphy et al., 2021; Regular et al., 2022), and tracking higher trophic levels (as bottom trawl surveys do) would indeed integrate the changes in the lower trophic levels that feed them. While this rationale may be more diffuse for some ecosystem components (e.g. deposit-feeding benthos) and does not provide insights on where within the food web the bottlenecks for production are, the current implementation does capture the consequences of those bottlenecks on the trophic levels relevant to fishing, and hence, allows for a credible adjustment of FPP estimates to realized productivity conditions for at least those functional guilds that sustain fisheries.

Another aspect that also needs consideration is that by using bottom trawl surveys, the implemented adjustment can only consider the changes in total biomass since the 1980s. These ecosystems were intensely fished in the 1960s and 1970s, and while individual stock-assessments indicate important declines for some key commercial stocks during these years (e.g. Atlantic cod), it is unclear how much the overall ecosystem biomass may have declined given the possibility of compensatory dynamics. The use of the early period in the available time series as a representation of a fully functional ecosystem would certainly reflect total biomass values closer to full ecosystem functionality, but they may still be an underestimate, which would make any guidance on total catches to be an optimistic one. Still, given the absence of clear evidence of total biomass declines prior to the 1980s, and the finding that the NL ecosystems have not been demonstrably stable in the last 40 years, with the possible exception of the early 1980s (Pedersen et al., 2020), suggest that using the early 1980s as a reference biomass level for full functionality is the only defensible choice at the moment.

The abstracted penalty scheme was drawn based on the smoothed trajectory of total biomass, and using general knowledge of the changes in structure and dynamics of the ecosystem units in the NL bioregion to identify key points in time where some clear changes in structure and trend were observed (Koen-Alonso et al., 2010; Dawe et al., 2012; Buren et al., 2014a; Dempsey et al., 2017; Dempsey et al., 2018; Koen-Alonso and Cuff, 2018; Pedersen et al., 2020; Koen-Alonso et al., 2021). This expert-based approach to the abstracting process was chosen because of the multifaceted nature of the information considered (changes in fish community structure, diet compositions, trajectories in key stocks, environmental information) and the caveats within each one (e.g. completeness of time series, changes of sampling over time, etc), which does not lend itself to a straightforward full analytical integration. The key points in time identified for the abstracted penalty scheme correspond to the collapse of the fish community during the 1990s regime shift (1991), the start of rebuilding signals in the fish community (2005), and the consistent declines in fish biomass in the mid-2010s (2015). This type of abstracted step-wise penalty scheme may not be ideal, but captures periods of time where there is consistent evidence from multiple sources that indicate likely changes in productivity conditions, and reasonably maps onto the observed trends in total biomass from bottom trawl surveys. This schematic approach to the adjustment of FPP estimates is also more consistent with the non-dynamic nature of the EPP model; a more continuous adjustment of FPP would be implicitly attaching to the EPP model a temporal resolution that the model does not necessarily provides.

While the specific details of the adjustment procedure implemented here can be further revised and improved, there is an explicit rationale behind each step taken, and the overall process builds on both, general ecological knowledge on the relationships between productivity and biomass in marine ecosystems, as well as evidence from direct studies of the NL marine ecosystems. In this context, further advances on these aspects would be expected to be refinements within the general theme developed here, so any changes derived from these refinements would not be expected to substantially alter the tone and magnitude of the results obtained from the application of the current approach.

Total Catch Indices (TCIs) and Guidelines for Total Catches

Putting all these pieces together allows calculating Total Catch Indices (TCIs) for the different functional guilds in the Newfoundland Shelf (2J3K), Grand Bank (3LNO), and Flemish Cap (3M) EPUs, and plotting the Catch/TCI ratio over time provides a simple way of examining how fishing levels compared with the upper bounds for sustainability encapsulated in the TCIs. The results clearly show that most catches in these EPUs come from the piscivore and benthivore functional guilds, and indicate that in the 1960-1995 period, catches from the piscivore guild were consistently well above TCI levels in all ecosystem units (Fig. 11). Catches of other functional guilds were mostly within their sustainability envelope but with some incursions above the TCIs, like some mid-1970s planktivore guild catches in 2J3K (Fig. 11). After 1995 and the collapse of the fish community in the Newfoundland-Labrador ecosystems, catches from the benthivore guild, mostly driven by shellfish species, have also been above the TCIs in all three ecosystem units, while piscivore guild catches above the TCIs kept occurring in 3LNO and 3M (Fig. 11). These results indicate that piscivore guild catches have seldom being within a sustainable level from an ecosystem perspective, while benthivore guild catches are showing runs of years above TCI levels. Overall the results indicate that all EPUs have experienced levels of fishing which would be consistent with ecosystem overfishing.

It is also worth noting that catches above TCIs after 1995 have rarely exceeded twice the TCI level, while earlier catch levels were consistently above 2*TCI for the main functional guild targeted by fishing. This would suggest that management measures taken since the collapse of many groundfish stocks in the 1990s have been effective in reducing excessive fishing, even though their aggregate may still fall above the sustainability envelope defined by the TCIs. These individual stock management decisions were deemed sustainable (or sustainably enough) in isolation, but their emerging aggregate is of sufficient magnitude to represent a non-trivial risk to ecosystem-level sustainability.

This highlights the practical need for considering fishing impacts at the ecosystem level, and the relevance of Tier 1 level assessments. In this context, and to inform the development of guidance for total catches, the current TCIs (25th percentile), and the median for the corresponding FPP_{adj} distributions for the Newfoundland Shelf (2J3K), Grand Bank (3LNO) and Flemish Cap (3M) EPUs are summarized in Table 3.

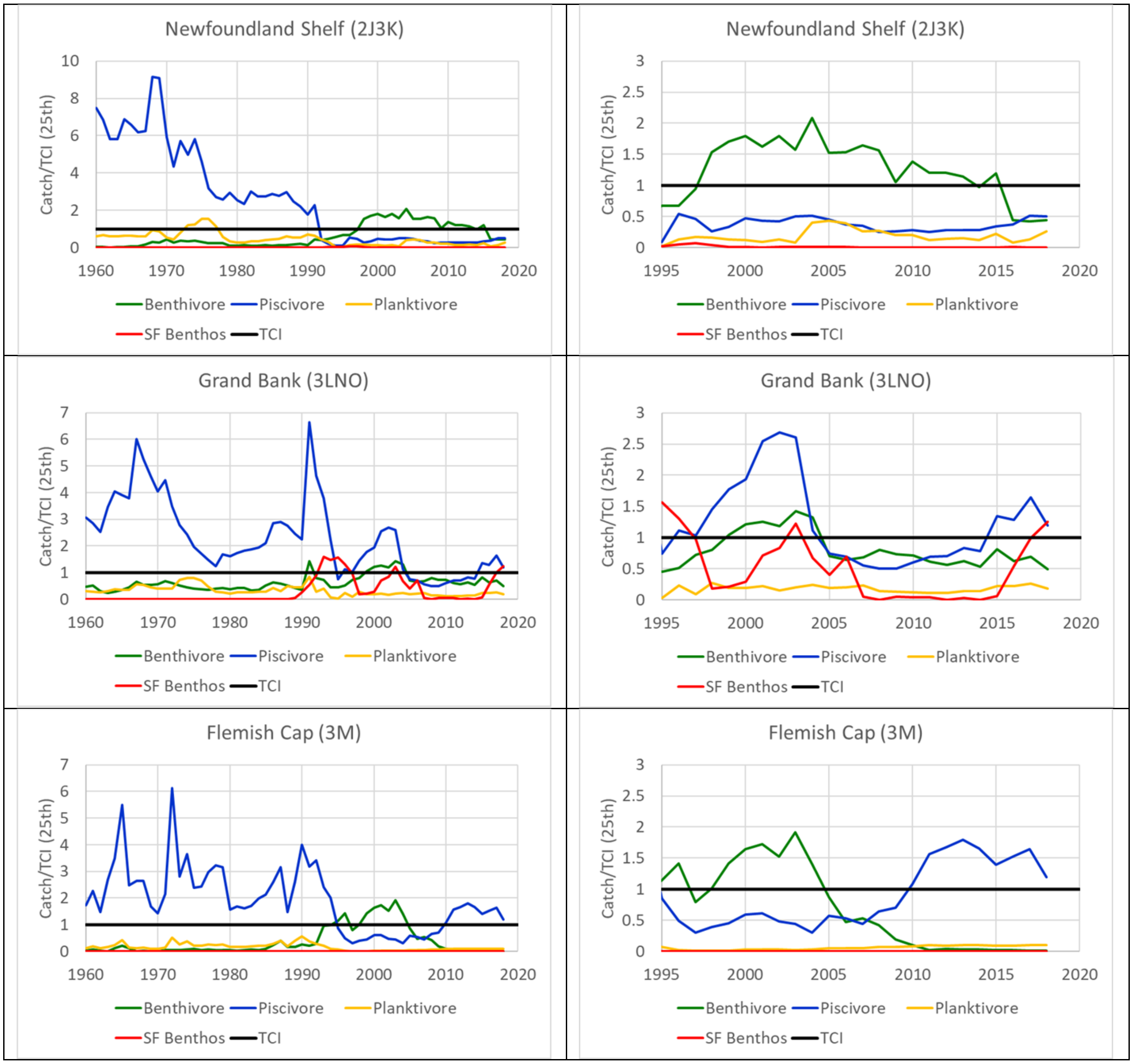


Figure 11. Time series of Catch/Total Catch Index (TCI) by functional guild for the Newfoundland Shelf (2J3K), Grand Bank (3LNO), and Flemish Cap (3M) EPUs. Left panels shown the full time series, while right panels zoom in on the most recent decades.

Table 3. Current Total Catch Indices (25th percentile) and medians of the adjusted Fisheries Production Potential (FPP_{adj}) distributions for each fishable model node [functional guild] and Standard Demersal Components (SDC) aggregate (SDC=benthivore+piscivore) for the Newfoundland Shelf (2J3K), Grand Bank (3LNO), and Flemish Cap (3M) EPUs. Penalty factors were applied for 2J3K (0.4) and 3LNO (0.3).

		Total Catch Index (TCI)			
		Total (thousand tonnes y^{-1})		Density (tonnes km^2 y^{-1})	
		TCI (25th)	Median	TCI (25th)	Median
2J3K	SDC	74	111	0.29	0.44
	Piscivore	18	25	0.07	0.10
Area:	Benthivore	51	85	0.20	0.33
254.32	SF Benthos	13	20	0.05	0.08
thousand km^2	Planktivore	70	100	0.28	0.39
	Total FPP_{adj}	416	543	1.63	2.14
3LNO	SDC	86	129	0.27	0.41
	Piscivore	21	29	0.07	0.09
Area:	Benthivore	59	99	0.19	0.31
315.18	SF Benthos	14	21	0.04	0.07
thousand km^2	Planktivore	83	117	0.26	0.37
	Total FPP_{adj}	468	612	1.49	1.94
3M	SDC	50	76	0.86	1.31
	Piscivore	12	17	0.21	0.30
Area:	Benthivore	35	58	0.60	1.00
57.83	SF Benthos	8	12	0.14	0.22
thousand km^2	Planktivore	49	69	0.84	1.19
	Total FPP_{adj}	274	359	4.74	6.21

Evaluating the effectiveness of TCI as guidance level for total catches

The pattern emerging between functional guild trends and Catch/TCI ratio was consistent with the expectation of TCI being a reasonable boundary for sustainability (Fig. 12). Catches above TCI levels are clearly associated to negative trends in functional guild biomass, while catch levels below TCI show a fairly even distribution of positive and negative biomass trends (Fig. 12). The average trend for catch levels above TCI was -0.457, while the average trend for catch levels below TCI was 0.041. Trends above the boundary defined by TCI=1 were significantly smaller than those below this boundary (Mann-Whitney test, p-value < 0.006).

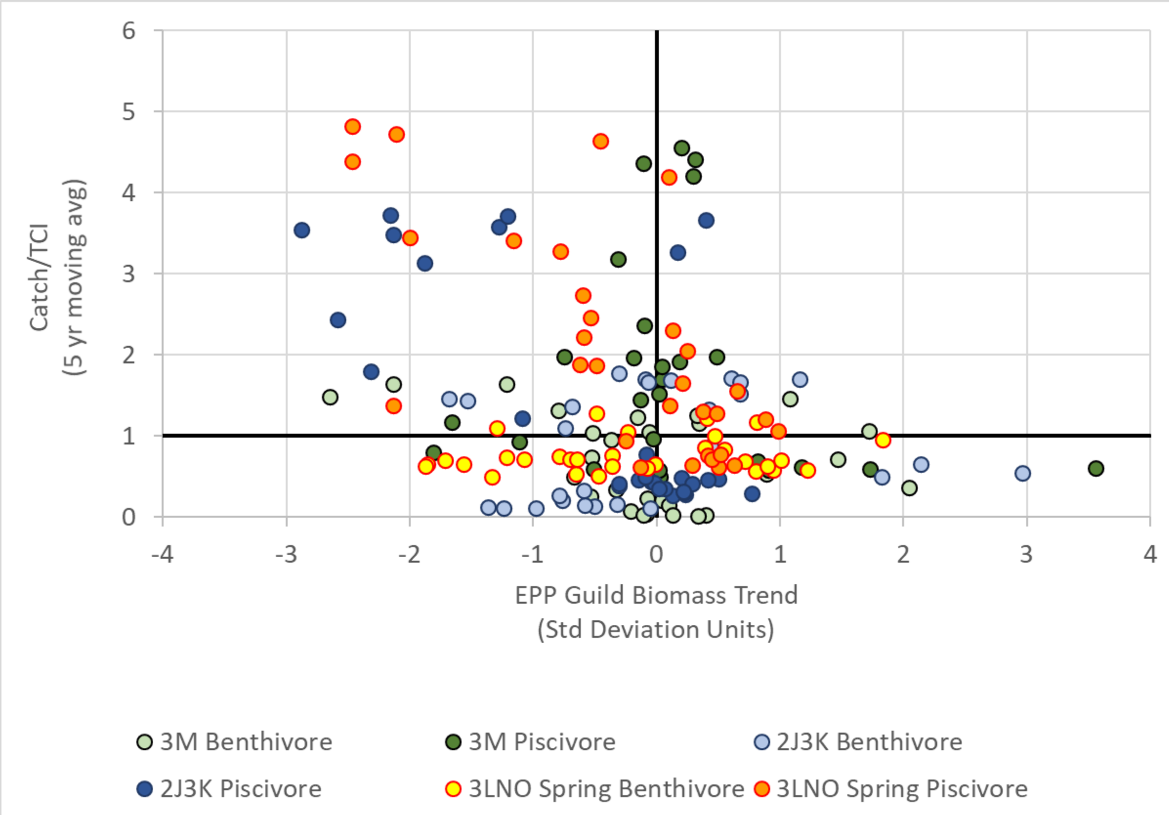


Figure 12. Relationship between functional guild biomass trends and catch level expressed as a fraction of the corresponding Total Catch Index (TCI) for the piscivore and benthivore guilds in the Newfoundland Shelf (2J3K), Grand Bank (3LNO), and Flemish Cap (3M) EPUs. Catch levels below 1 indicate sustainable exploitation levels from the perspective of TCI.

These results indicate that fishing above TCI is clearly associated with negative trends, while fishing below TCI improves the odds of positive growth. The even distribution of positive and negative trends when fishing below TCI (Fig. 12) is also consistent with the premise that, if fishing is sustainable, other factors would control functional guild trajectories.

Using the data from Figure 12 is also possible to construct empirical cumulative distributions of the probability of functional guild growth under different ranges of Catch/TCI ratios. These empirical probability distributions provide a more clear perspective of the risk of decline under different Catch/TCI scenarios. Looking at the results from this perspective, it becomes clear that the probability of negative trends increases consistently as the Catch/TCI ratio increases (Fig. 13). Conversely, the probability of positive trends increases with declining Catch/TCI ratio (Fig. 13). It also seems clear that TCIs are properly mapping an operational boundary in functional guilds trends in relation to fishing pressure, where plots like Figure 13 can be particularly useful to inform risk levels. For example, using TCI as a boundary for sustainability renders an even distribution between positive and negative growth but with a reduced probability of steep declines and an increased probability of steep biomass build-ups. Catch levels between 1-2 TCI may still be considered generally sustainable given that they still shows a fairly even partition between positive and negative trends, but these higher catches come with an increased probability of steeper declines, and it would be up to managers to decide if these increased risks of negative outcomes are deemed acceptable or not. Catch levels above 2*TCI are clearly unsustainable with very high probability of negative outcomes.

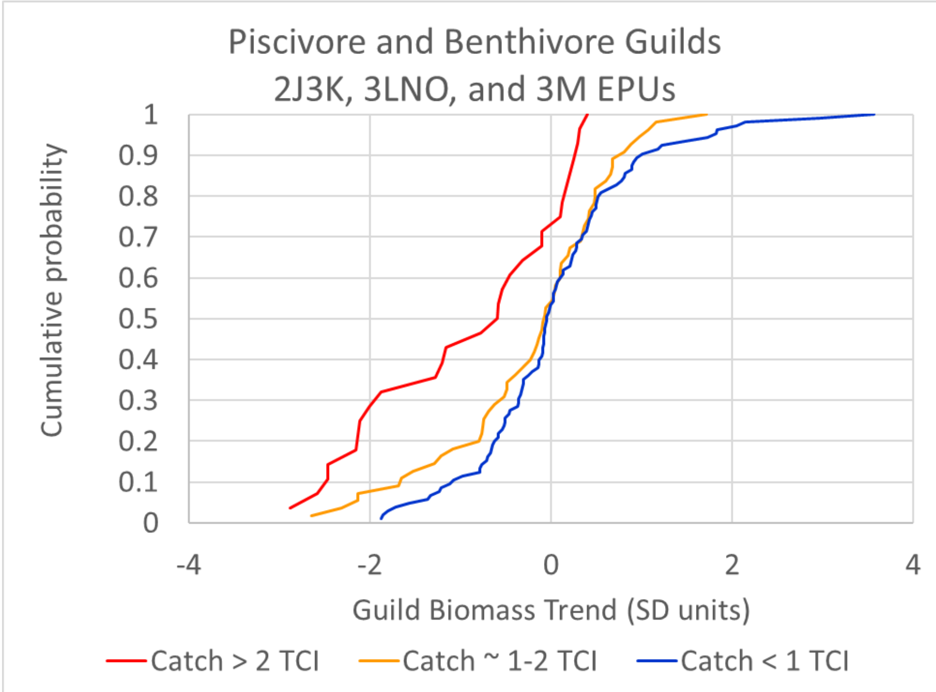


Figure 13. Empirical cumulative probability distributions for functional guild trends under three catch scenarios: catch below TCI, catch between 1 and 2 times TCI, and catch above 2*TCI. The data used to build these empirical distributions is the one presented in Fig. 12. These distributions do not discriminate by EPU or functional guild.

While these results show a clear association between ecosystem responses and TCI levels, we still need to examine the influence of factors other than fishing on functional guild trends before concluding on the effectiveness and reliability of TCIs as a valid metric to evaluate sustainability of aggregate catch levels.

Current understanding of the marine ecosystem in the NL and Flemish Cap bioregions indicate the both fishing pressure and environmental conditions have been important drivers of the changes observed (Koen-Alonso et al., 2010; Pérez-Rodríguez et al., 2011; Dawe et al., 2012; Perez-Rodriguez et al., 2012; Buren et al., 2014b; Dempsey et al., 2017; Dempsey et al., 2018; Koen-Alonso and Cuff, 2018; Koen-Alonso et al., 2018). Furthermore, while the changes in these systems have had similarities, these changes have not been homogeneous nor perfectly synchronized across all ecosystem units. For example, the Flemish Cap did not experienced a fish community collapse like the EPUs in the NL bioregion did, even if some important stocks showed severe declines (Perez-Rodriguez et al., 2012; Koen-Alonso et al., 2018), and the increase in shellfish biomass started earlier and was more important in the Newfoundland Shelf (2J3K) than in the Grand Bank (3LNO) EPU (Dempsey et al., 2017; Dempsey et al., 2018; Koen-Alonso and Cuff, 2018). Still, despite their differences, signals linking many of these changes to fishing and environmental conditions have been detected in all ecosystem units (Koen-Alonso et al., 2010; Pérez-Rodríguez et al., 2011; Perez-Rodriguez et al., 2012; Buren et al., 2014a; Dempsey et al., 2018; Dempsey et al., 2020).

In the context of functional guild trends and TCIs, this general premise of fishing and environmental conditions as overarching signals driving changes in these ecosystems was explored by constructing a general linear model using functional guild trend as dependent variable, and EPU, functional guild, year, Catch/TCI ratio, and the Newfoundland and Labrador Climate Index (NLCI) as explanatory variables. The results from this analysis indicate that both Catch/TCI ratio and NLCI are statistically significant drivers of functional guild trends, while functional guild, EPU, and year are not, but there is a hint in the coefficients results that the Flemish Cap (3M)

EPU could have somewhat higher functional guild trends than the Newfoundland Shelf (2J3K) and Grand Bank (3LNO) EPUs (Table 4).

Table 4. General Linear Model results for the model considering functional guild trend as a function of Catch/TCI Ratio, EPU, functional guild, year, and NLCI (trend~Catch_TCI+EPU+funct_guild+year+NLCI), where EPU and Functional guild were considered as factors and the remaining as continuous variables. This model was fitted with an identity link (i.e. gaussian distribution).

Analysis of Deviance

Term	df	Deviance	Residual df	Residual Deviance	F statistic	p-value
Null model			187	187.17		
Catch/TCI Ratio	1	19.81	186	167.36	22.624	**4.01E-06**
EPU	2	3.35	184	164.01	1.913	0.151
Functional guild	1	1.45	183	162.56	1.654	0.200
Year	1	0.63	182	161.94	0.715	0.399
NLCI	1	3.44	181	158.50	3.925	**0.049**

Coefficients

Term	Estimate	Std. Error	t statistic	p-value
Intercept	2.494	18.303	0.136	0.892
Catch/TCI Ratio	-0.280	0.074	-3.781	**2.12E-04**
EPU (3LNO)	0.085	0.167	0.511	0.610
EPU (3M)	0.297	0.171	1.737	*0.084*
Funct. guild (piscivore)	0.150	0.150	0.998	0.320
Year	-0.001	0.009	-0.139	0.890
NLCI	0.261	0.132	1.981	**0.049**

Single term deletion analysis

Term	df	Deviance	AIC	F statistic	p-value
Full model		158.50	517.43		
Catch/TCI Ratio	1	171.02	529.72	14.293	**2.12E-04**
EPU	2	161.25	516.67	1.572	0.210
Functional guild	1	159.37	516.46	0.996	0.320
Year	1	158.52	515.45	0.019	0.890
NLCI	1	161.94	519.46	3.925	**0.049**

These results are also consistent with the expected directions of the impacts from the different drivers; fishing has a negative effect on guild trends while NLCI has a positive effect. The NLCI result meets expectations because NLCI is constructed using properly signed anomalies so that the resulting index increases when the ocean climate is dominated by conditions generally associated with a warmer ocean state, and decreases with conditions more associated with a colder ocean state (Cyr and Galbraith, 2021). These warmer ocean states have been found to be more favorable for some key groundfish stocks (Koen-Alonso et al., 2010). Furthermore, there is evidence indicating declines in chlorophyl concentration and changes in phytoplankton size structure in large marine ecosystems over the last 30 years (Friedland et al., 2021), as well as long term indicators derived from ice core analyses indicating declining primary production in the North Atlantic since the 1800s (Osman et al., 2019). The NLCI, which starts in 1951, is positively correlated with the ice core-derived indicator of primary productivity (5-yr running means of NLCI and [MSA]PCI1 productivity index from Osman et al. 2019, Spearman Rho=0.55, p-value<0.001), suggesting that NLCI could also potentially reflect changes in primary production. Considering that TCIs are derived from average values of primary production, the mechanisms underlying the statistical significance of NLCI would be expected to be diverse, from tracking changes of underlying physical conditions that promote primary production, to reflecting a generally more favorable environment for fish production.

It is also interesting to note that neither year nor functional guild were identified as significant drivers. Any variation over time in fish functional group trends is being explained by the variations in both fishing pressure and ocean climate conditions, while any potential difference between functional guilds was likely factored out by the standard deviation scaling applied to the trends. While EPU was also found not significant, the results hint at the possibility that the Flemish Cap (3M) EPU may have higher functional group trends than the EPUs in the NL bioregion. Such potential difference would not be surprising; the marine community in the Flemish Cap did not experience a collapse, and this ecosystem, unlike those in the NL bioregion, is considered fully functional. Even if we do not fully understand the exact nature of the processes involved in the erosion of functionality of the Newfoundland Shelf (2J3K) and Grand Bank (3LNO) ecosystem units, the hint at higher trends in the Flemish Cap (3M) would be consistent with the expected differences arising from different levels of ecosystem functionality.

Based on the results of the initial general linear model, a reduced model was constructed using solely Catch/TCI ratio and NLCI as independent variables. An examination of this model diagnostics indicates an adequate model fit, with model predictions generally well aligned with the observations but not overly tight, and an even distribution of the standardized residuals above and below the zero line, mostly bound between ±2 standard deviations, and without any obvious pattern (Fig. 14). The results from this reduced model confirms the conclusions from the initial general linear model, indicating that both fishing pressure and environmental conditions are significant drivers of functional guild trends (Table 5). The examination of the single term deletion analysis indicates that fishing pressure is a more significant driver of functional guild trends than environmental conditions; if we examine the Akaike Information Criterion (AIC) from a goodness of fit perspective, removing any driver significantly worsens the goodness of fit of the model, but removing fishing has a far more substantive impact on model adequacy than removing the ocean climate signal (Table 5). These results suggest that fishing pressure, scaled by ecosystem productivity, has been the dominant driver of functional guild trends for piscivores and benthivores, with ocean climate playing a more modulating role.

Still, caution must be taken to not over-interpret these results. This analysis is a proof of concept for the utility of TCI. This index summarizes a lot of information at a high level of aggregation, and has proven useful for uncovering relationships between system-level fishing pressure and large scale responses of ecosystem components, but the dispersion around the 1:1 predicted vs observed line in Figure 14 is a clear reminder that other factors and processes are also at play. Understanding fully the processes that ultimately drive trends in functional groups requires more detailed analyses, likely including species interactions, more appropriate consideration of the dynamics (this is a simple linear model after all), and more nuanced characterizations of both, the impacts of fishing and environmental factors. Those are the types of analysis that would be expected from the multispecies (Tier 2) and stock (Tier 3) level assessments within the Roadmap. The goal of TCIs is to inform ecosystem level assessments about the sustainability of aggregate catch levels, and within that context, if follows from these results that if a TCI-based indicator can be effective for predicting general responses in the trends of functional guilds, they can also be useful for supporting guidance on total catches in relation to the likely impacts of those catch levels on ecosystem functioning, at least as measured by the functional guild trends.

Overall, the results from all the above analyses validate the logic behind, and the effectiveness of TCIs as a metric for identifying the upper bound for sustainability of aggregate catches at the ecosystem level. We can never entirely dismiss the possibility that these results appear sensible but for the wrong reasons, but given the step-wise process used to build the TCIs, the explicit rationale behind each one of these steps, and the ability of TCI-based metrics to explain the response of ecosystem components, it seems reasonable to conclude that TCIs emerge as a robust guideline reference for informing Tier 1 assessments within the Roadmap.

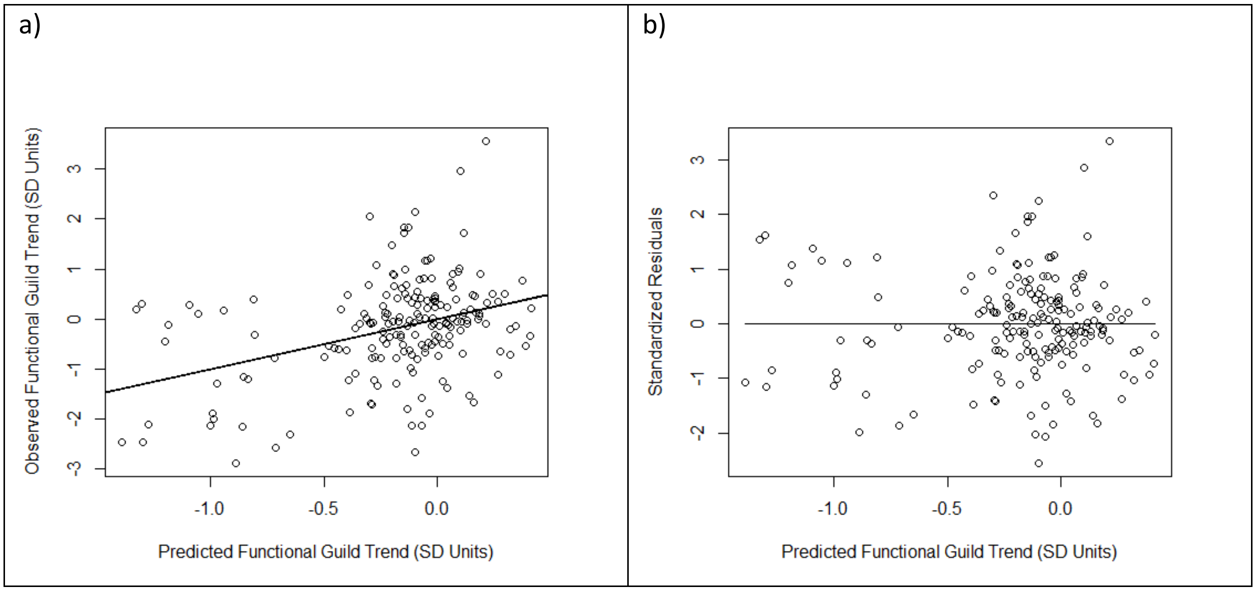


Figure 14. Diagnostics for the reduced general linear model considering functional guild trend as a function of Catch/TCI Ratio, and NLCI (trend~Catch_TCI+ NLCI). a) Predicted vs observed functional guilds trend values; the line indicates the 1:1 relationship. b) Standardized residuals as a function of observed functional guilds trend values, including the zero line for reference.

Table 5. General Linear Model results for the reduced model considering functional guild trend as a function of Catch/TCI Ratio, and NLCI (trend~Catch_TCI+ NLCI). Both independent variables were considered as continuous. This model was fitted with an identity link (i.e. gaussian distribution). df: degrees of freedom, AIC: Akaike Information Criterion

Analysis of Deviance

Term	df	Deviance	Residual df	Residual Deviance	F statistic	p-value
Null model			187	187.17		
Catch/TCI Ratio	1	19.81	186	167.36	22.615	**3.97E-06**
NLCI	1	5.29	185	162.07	6.040	**0.015**

Coefficients

Term	Estimate	Std. Error	t statistic	p-value
Intercept	0.098	0.107	0.916	0.361
Catch/TCI Ratio	-0.245	0.064	-3.816	**1.85E-04**
NLCI	0.285	0.116	2.458	**0.015**

Single term deletion analysis

Term	df	Deviance	AIC	F statistic	p-value
Full model		162.07	513.62		
Catch/TCI Ratio	1	174.82	525.86	14.559	**1.85E-04**
NLCI	1	167.36	517.66	6.040	**0.015**

TCI sensitivity to the underlying trade-offs among functional guilds

While TCI is emerging as a robust metric to inform the bounds of sustainable aggregated catches at the ecosystem level, there is no denying that estimates like this need to contend with non-trivial levels of uncertainty. Some of this uncertainty is associate to our current knowledge about parameters like transfer efficiencies (Eddy et al., 2021), or it is the consequence of the many details we discount by representing full ecosystems in a formulation as condensed and stylized as the EPP model. The fact that the results still appear informative and useful is a testament that understanding is actually advanced by learning which details are somewhat safe to ignore.

Still, part of the uncertainty in linking TCI-based metrics with ecosystem responses is also emerging from some of the underlying considerations in the calculation of FPP from the EPP model. As a default approach, FPP is calculated using a 20% exploitation rate for all functional guilds of relevance to fishing. This default is justified on the premise that FPP is intended to be an estimate of the upper bound for sustainable catches, and hence, it assumes that all functional guilds amenable to be fished will be fished at the limit of sustainable exploitation.

This assumption represents an implicit trade-off; catches from any functional guild are deemed equally desirable. However, fishing at lower trophic levels reduces the production available to upper trophic levels, effectively limiting the FPP that could be derived from those upper trophic levels. If catches from upper trophic levels are considered more desirable, their FPP can be boosted by forfeiting FPP at lower trophic levels.

The fact that some functional guilds have not been actually exploited up to their adjusted FPPs (Fig. 11) means that observed exploitation patterns have realized a trade-off configuration that is different from the one assumed as a default for the calculation of FPPs. This is no indictment to the default FPPs; assuming that all possible catches within a sustainable envelope will be taken is a reasonable assumption to make in a world where a pervasive concept in fisheries management is MSY. However, this difference implies that, if some of the lower trophic levels have not been fully exploited, the boosting of upper trophic levels would be expected to have occurred to some degree. A consequence of this is that the calculated TCIs for upper trophic levels may represent an underestimate of the realized bounds for sustainability. These discrepancies would add to the uncertainty around the relationship between the calculated Catch/TCI ratios and functional guild trends, and could influence the dispersion around the 1:1 line in Figure 14. They could also be behind some of the positive trends for TCI values above 1 observed in Figure 12. The fact that despite these potential effects the relationship between fishing pressure and ecosystem response is still clear and strong is a good indicator of the robustness of the approach, but still begs the question of how much the fisheries potential can be influenced by making explicit the trade-offs underlying the default FPP calculation.

This question is at the center of any implementation of an ecosystem approach. The explicit treatment of trade-offs is a core feature of ecosystem-based management (Link, 2002; Link, 2010), and it is certainly identified as such in the Roadmap (Koen-Alonso et al., 2019). Within the context of the EPP model, this issue was examined by exploring two scenarios, one involving the forfeiting of fishing on the planktivore guild, and a second one where fishing was forfeited from both, the planktivore and suspension-feeding benthos functional guilds. These scenarios effectively assume that piscivore and benthivores are preferred functional guilds for fisheries, which is consistent with the catch history of the ecosystem units under consideration here (Fig. 11). The results of these explorations indicate that there is potential to achieve gains in some preferred functional guilds by managing these trade-offs (Fig. 15). Piscivore and benthivore FPP increased by 10-20% depending on the fishing scenario. As it could be expected, forfeiting planktivore fishing had a stronger impact in boosting piscivore FPP, while forfeiting suspension-feeding benthos fishing had a stronger positive impact on benthivores (Fig. 15). However, these gains were achieved at a substantial loss in total FPP.

Regardless of how realistic or not these scenarios might be, they represent extreme trade-off cases, and as such they provide insights on the expected changes in FPP for the preferred functional guilds under these extreme scenarios. The expected boosting in FPP in piscivores and benthivores does not appear trivial from a fishing industry perspective, changes up to 20% in yields are nothing to sneeze at, but changes in the order of 10-20% in FPP are well within the range of variability of current estimates. This would suggest that while these effects may be a measurable contributor to the uncertainty around the relationship between fishing pressure and ecosystem responses, they are unlikely to severely confound or blur the underlying signal. This would mean that TCIs are indeed robust to the underlying trade-offs assumptions used in the default calculation of FPP.

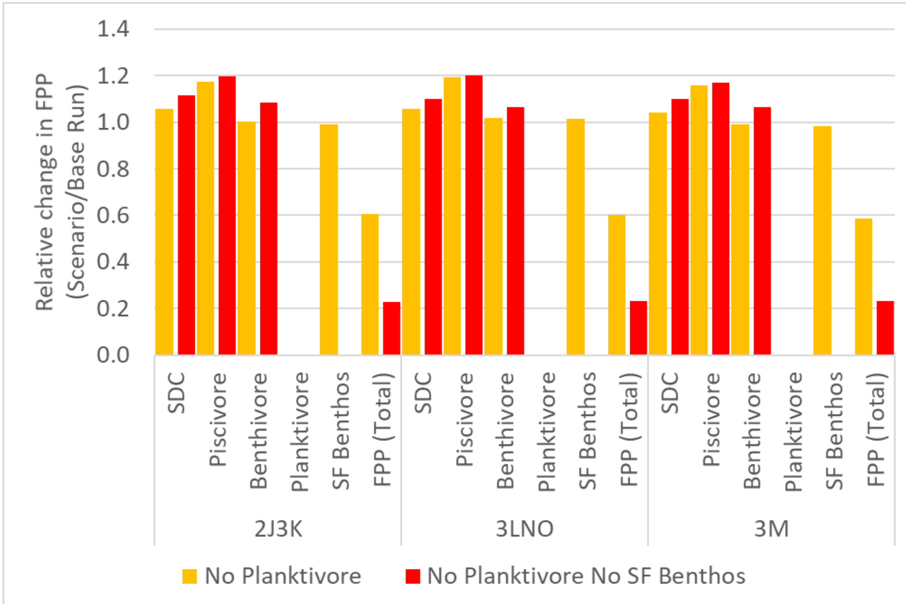


Figure 15. Relative change in median FPP for all fishable nodes and relevant aggregates (SDC and total FPP) between the base run (all fishable nodes exploited at F=20%), and the two alternative scenarios (no planktivore fishing, and no planktivore nor suspension-feeding benthos fishing).

From EPP to TCI: A quick recap and implications

When taken together, the different steps and analyses presented here provide a framework to answer the question posed in the introduction: how much fish can we safely extract from the ocean based on the observed primary production? We answer this question by using the EPP model to estimate how primary production becomes FPP. The upper bound for sustainability that defines FPP is justified on the fraction of primary production supported by the inventory of nitrogen, a generally limiting nutrient in the ocean, that is annually added to the system from fresh sources. This FPP is adjusted to realized productivity conditions using changes in total biomass in the ecosystem, under the premise that total biomass tracks changes in productivity. Finally, we use the 25th percentile of the FPP_{adj} distribution to define TCI, and indicator that allows evaluating if total catches are within the sustainability envelope while keeping a low probability of exceeding the upper bound for total catches.

As part of this process we characterize the uncertainty in the estimates derived from the EPP model, and in doing so we show that this simple model encapsulates features that have been identified by empirical studies as necessary to link primary production with fisheries production, as well as others emerging from theoretical studies about the structure of food webs. We also found that, despite the differences in the underlying frameworks, FPP estimates are consistent with MSY ones, which indicates that the FPP estimates are likely robust. We also indicate how the available data supports the type of adjustment to realized productivity conditions implemented in the framework.

From the perspective of reliability for management applications, we demonstrate that TCI does indeed provide an effective boundary for total catches by showing that catches exceeding TCI are consistently associated with negative trends in the exploited functional guilds. We also show that fishing pressure, scaled by ecosystem productivity, has been a significant driver of functional guild trends, which have also been influenced by ocean climate conditions.

Perhaps more importantly, our analyses show that after many groundfish collapses, the management measures implemented by NAFO at the stock level were effective at significantly reducing the overall fishing pressure. However, these measures, driven by single stock considerations, where insufficient to consistently keep aggregate catches within the sustainability envelope defined by TCIs. Given this shortcoming, and the demonstrated significance of fishing pressure as a driver of negative outcomes at the scale of functional guilds, it becomes evident that additional management measures beyond single stock management are required to ensure that exploitation levels are sustainable at the ecosystem level. TCIs not only work, they -or conceptually similar approaches- appear necessary for sustainable fisheries in an ecosystem context.

Adequacy of TCIs for their proposed used within the Roadmap

The Roadmap is the general template being followed by NAFO to develop and implement an ecosystem-based fisheries management approach (Koen-Alonso et al., 2019). Within its general structure, the definition of sustainable catch levels is constructed by the integration of a system of hierarchically integrated assessments. The theoretical foundations of this tiered approach is the consideration of ecosystems as nested hierarchical structures where higher level structures would affect lower level ones, acting as constraints to the levels within (O'Neill et al., 1986; Wu and David, 2002; Fogarty, 2014; Link, 2017). In relation to the definition of sustainable catch levels, its tiered approach focusing on ecosystem, multispecies, and stock sustainability is intended to promote that the catch rates implemented on the individual stocks would integrate the requirements for sustainability emerging from multiple levels of ecological organization.

At the present time, only the traditional single species stock-assessment (Tier 3) is being used to define sustainable catch rates. Even though guidelines for total catches based on TCIs have been available for a number of years (NAFO, 2013; NAFO, 2015b; NAFO, 2019; NAFO, 2020), and NAFO Scientific Council (SC) has recently recommended an initial formalization of TCIs as part of the implementation of Tier 1 assessments (NAFO, 2020; NAFO, 2021c), the NAFO Commission has been reluctant to act on this recommendation. Some of the stated reasons behind this reluctance, beyond the inherent inertia of large organizations to move away from *status quo* practices, is the concern that the science behind TCIs is not good enough for the provision of science advice. These concerns include the quality of the scientific work itself (i.e. the EPP model, the FPP estimation, its adjustment for productivity, the derivation of TCIs, and its effectiveness as a metric for identifying upper bounds for aggregate catches), as well as the adequacy of TCIs as a reliable tool for the provision of the intended level of science advice (i.e. is TCI fit for purpose?).

In terms of the quality of the scientific work, the results presented here provide a detailed description of how TCIs are constructed, what are the ecological principles behind them, the assumptions made, and how well TCI-based metrics perform in terms of mapping and explaining ecosystem-level responses relevant to the impacts of fishing at the ecosystem level. The analyses performed explicitly investigated the uncertainties involved, providing a thorough examination of the expected consequences from different sources of uncertainty. As we went through the different steps of the process of constructing and evaluating TCIs, we have also placed this scientific work in the context of relevant scientific literature, showing how the work here relates and builds upon past and present developments in this field of research. Like any scientific work, improvements can always be made. Some relevant avenues for this future work include, for example, the incorporation of trends in the input primary production, or the investigation of temperature effects on transfer efficiencies, just to name a couple. Notwithstanding these potential future endeavors, we consider that the scientific work done to date meets current scientific standards, and the conclusions made logically follow from the results obtained. Based on the work presented here, we consider TCIs to be a reasonable and scientifically defensible metric to characterize the upper bounds of aggregate catches at the functional ecosystem level.

In terms of the adequacy of TCIs for the provision of the intended level of science advice, it is relevant to examine the most recent advice from NAFO Scientific Council (SC) on this topic. In 2020, NAFO SC advised :

"The NAFO Roadmap toward an Ecosystem Approach to Fisheries is organized around two general components dealing with a) sustainability of the fisheries exploitation (i.e. impacts on fished stocks), from an ecosystem (Tier 1), multispecies (Tier 2) and single species (Tier 3) perspective, and b) the effects of fishing on other ecosystem elements (i.e. impacts of fishing on habitats). In practice, work toward implementing Tier 1 principles has involved, among other things, the development of guidance for aggregated total catches based on Ecosystem Production Potential (EPP) models. To address existing concerns about the reliability of this approach, SC conducted a detailed review of the EPP model, the process used to derive the Fishery Production Potential (FPP), the adjustment for ecosystem productivity conditions that renders the current FPP (FPPc)[1], and the associated Total Catch Index (TCI) which serves as an operational metric in the guidance for total catches.

Results indicate that the EPP model provides a good approximation to ecosystem production, that it is necessary to consider basic food web structure and energy pathways to adequately track how primary production becomes fisheries production, and that this model can provide a first order approximation to the production potential of trophic guilds relevant to fisheries. SC also notes that total FPP estimates are consistent with MSY estimates from aggregate biomass surplus production models from 12 Northern hemisphere marine ecosystems, including the Newfoundland Shelf. This coherence with independent analyses gives further support to FPP and TCI as a reliable basis for the provision of strategic (3-5yr) guidance. Furthermore, the results also indicate that catches above TCI levels are more often associated with negative biomass trends in functional guilds, particularly when catches were 2-5 times greater than TCI guidance. This indicates that TCIs perform reasonably well at mapping catch levels associated with negative trends in growth of functional guilds among ecosystem units.

SC notes that the overall results of the analyses are promising, and **recommends** that, *as an interim measure in the implementation of the NAFO Roadmap, the particular circumstances in the state of stocks and the potential consequences to fishery sustainability be considered and addressed in management decisions when the combined TACs can result in overall catches about two-fold greater than the TCI guidance. Total catches above TCIs would require more frequent ecosystem monitoring/reporting*. SC also **recommends** *the development of simulation-based analyses (Management Strategy Evaluation, or analogous processes), to evaluate the reliability of specific decision rules for species-aggregated catch levels based on the TCI, though recognizing that this will be a complex exercise requiring considerable time, resources and stakeholder involvement, and hence the need for interim measures as indicated above.* Furthermore, SC **recommends** that *priority be given for the development of multispecies dynamic models to a) complement the recommended simulation-based exercises and investigate the consequences of time-dependent dynamics on the operational reliability of the TCIs as guidance for ecosystem-level advice, and b) contribute to the development of tools toward implementation of the Tier-2 level of the Roadmap.*"

This SC advice was supported by the analyses included here up to Figure 12; additional analyses like the general linear modelling exercises were developed after 2020, and have only been presented at the NAFO Working Group on Ecosystem Science and Assessment (WGESA).

In the years leading to this advice, SC had produced guidelines for total catches based on TCIs (or its precursors), and has used the Catch/TCI ratio as one of the indicators included in the development of Ecosystem Summary Sheets. However, it wasn't until 2020 that SC formally recommended the use of TCIs as an interim measure to start the formal implementation of Tier 1 assessments. In 2021 NAFO SC reiterated this advice, and it was as part of the ensuing discussion between scientists and managers that the need for a scientific review by independent experts on TCIs and its adequacy for advice was identified.

Within the context of the above SC advice, it is clear that the current SC recommendation for implementation of TCIs is strategic in nature. The pattern emerging from Figure 12 is used to identify operational ranges of Catch/TCI that are expected to trigger different actions. If the aggregate of recommended catches (i.e. aggregated Total Allowable Catches -TACs-) is above 2*TCI, the expected action is a formal consideration by managers of the potential consequences to fishery sustainability of this level of fishing pressure. In practice this is calling for considering the risk of ecosystem overfishing when making the stock-level TAC decisions. The advice does not prescribe any specific action, but logic dictates that reductions on one or many TACs would be

[1] FPPc is the adjusted FPP to realized productivity conditions referred in this document as FPP_{adj}

one of the potential courses of action. If aggregated TACs are above TCIs but not exceeding the 2*TCI level, the advice only recommends more frequent ecosystem monitoring and reporting, but no explicit action by managers. The overall structure of these elements of the advice is analogous to a traffic light approach; red if catches are above 2*TCI, actions need to be consider by managers to address the risk of ecosystem overfishing, yellow if catches are between 1 and 2 TCIs, the increasing risk of ecosystem overfishing requires more close attention and monitoring, and green if the catches are below TCI, conditions indicate a low risk of ecosystem overfishing and regular ecosystem monitoring is sufficient.

The advice also indicates that simulation-based quantitative applications would likely be required for implementing more formulaic advice based on TCIs (e.g. harvest control rules to reduce overall fishing pressure and determine the distribution of the reductions across stocks), but also recognizes that time and resource limitations may hinder the development of these tools. Furthermore, this type of quantitative exercises also requires an active involvement by stakeholders; many of the decisions needed go beyond the ecology, and would require consideration of social and economic factors. Finding acceptable common grounds on this front within a multilateral organization like NAFO is a challenging task that would require both, time and stakeholders willingness to engage in this kind of discussion.

Under this light, the need for an interim implementation of Tier 1 assessments to incorporate some responsiveness to the risk of ecosystem overfishing within NAFO becomes apparent. Simulation-based solutions can take a long time to get off the ground, and the risks of potential reductions in ecosystem productivity due to factors like climate change appear to be approaching faster than ever.

In this context, the semi-quantitative and strategic approach recommended by SC only relies on the ability of TCIs to effectively map the upper boundary for sustainable aggregate catches. The results presented here (e.g. Figs. 12 and 13) indicate that TCIs indeed perform well in delineating such boundary. Furthermore, the general linear modelling exercises suggest that there is room for these types of analysis to provide a platform for a more quantitative evaluation of the joint effects of fishing pressure and ocean climate on the risk of negative ecosystem outcomes (i.e. probability of negative functional guild trends), while the flexibility provided by the EPP model (i.e. including trends in magnitude and size structure of the primary production inputs) could allow exploring the impacts of alternative climate scenarios on the risk of negative outcomes due to ecosystem overfishing.

Overall, TCIs not only appear perfectly appropriate for the currently proposed strategic implementation of Tier 1 assessments, but their effectiveness at explaining functional guild trends, and the underlying EPP model structure that supports them, provide a potentially useful analytical foundation to construct more quantitative applications going forward.

While more quantitative applications developed from the TCI foundations are certainly possible, it is important to avoid the trap of trying to transform TCIs or their underlying EPP models into Swiss army knives. These tools cannot be, and are not meant to be, the be all end all of the implementation of the Roadmap. Sometimes the discussions between scientists and managers get so focused on a specific topic or application, that it is often forgotten that Tier 1 is only one of the assessment tiers required for a full Roadmap implementation, and that TCIs are just one of the tools that can be used to inform Tier 1 assessments.

Given the modular structure of the Roadmap, and the step-wise approach to the development of its different elements, especially given the limited human and logistical resources available to this process, some tunnel vision effects are to be expected. For this reason it is particularly useful, when discussing a specific aspect like TCIs, to put those specific aspects in the context of the Roadmap at large.

Tier 1 assessments include the definition of functional ecosystem units, the evaluation of ecosystem state, the consideration of large scale forcing and patterns on ecosystem structure and functionality, and the evaluation of the aggregate effects of fishing on ecosystem sustainability. It is at this scale of organization where TCIs play a role by informing the risk associated to ecosystem overfishing arising from the combine impacts of multiple fisheries operating within the same functional ecosystem. In this context, the practical value of TCIs comes from its simple theoretical structure, relative ease of parameterization, calculation and maintenance, ability to encompass a range of functional guilds, and relative simplicity of communication to a diversity of stakeholders. Of course, other tools can also be informative (e.g. aggregate surplus production models, other ecosystem models) and these should also be pursued to complement TCI-based analyses, but our results indicate that TCIs perform well, and are already available. In line with the modular implementation of the Roadmap, Tier 1 assessments can start to be implemented on the basis of TCIs, and the scope of their supporting tools expanded as other analyses become available.

The strategic advice produced by Tier 1 assessments provides the background against which the multispecies analyses that are the focus of Tier 2 assessments need to be contrasted. Tier 2 assessments are focuses on multispecies interactions, and intended to evaluate potential trade-offs emerging from those interactions, as well as to consider management objectives related to multispecies sustainability (e.g. ecosystem resilience under perturbations). In this context, Tier 2 models are aimed at capturing intermediate levels of ecological complexity (e.g. Minimum-Realistic Models –MRM-, Models of Intermediate Complexity for Ecosystem assessments –MICE-)(Plaganyi, 2007; Koen-Alonso, 2009; Plagányi et al., 2014; Collie et al., 2016). Tier 2 serves as a bridge between the large scale ecosystem features and characteristics (e.g. ecosystem-level production), and the individual stock-level status and trends which are the focus of Tier 3 assessments. This implies that Tier 2 assessments can provide support for strategic and/or tactical decisions, depending on the specifics of the assessment and the models it relies upon.

At the present time, the development of tools for Tier 2 assessments is only starting. There are some models available (Pérez-Rodríguez et al., 2016) or in development that can support Tier 2 assessments, but there is still a need for a formal framework to help guide the development of models for Tier 2 applications, and to triage and prioritize model development. The initial steps toward building such framework have recently been taken at the 2021 NAFO WGESA meeting, but there is still significant work to do to make Tier 2 assessments operational.

Until Tier 1 assessments start getting implemented, and Tier 2 assessment development gains more momentum, the tactical advice in NAFO will continue relying on traditional single-species stock assessments (Tier 3). However, despite the slow progress in making Tier 1 and 2 formally operational, many results from this ongoing work is presently being used and/or informs the Tier 3 stock assessments.

Finally, it is important to keep in mind that the general architecture, concepts, and workflows encapsulated in the Roadmap structure is what represents the vision for the implementation of an ecosystem approach in NAFO. The tools that we use deliver on the Roadmap elements, like TCIs, are transient. They are expected to be replaced by better versions as our understanding and science capacity advances. At the present time, we believe TCIs are mature enough for their use in the formal implementation of Tier 1 assessments, but if we wait for better versions down the road, we may be risking that their arrival would come too late to be useful.

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Appendix 1. List of input parameters to the EPP model for each one of the Ecosystem Production Units (EPUs) considered. All these EPUs are considered Subarctic-Boreal Shelf ecotype (Rosenberg et al., 2014; Fogarty et al., 2016)

Parameter name	Description	Unit	Implementation	EPU		
				2J3K	3LNO	3M
PPsmp_prior_1	Mean of primary production nano-pico phytoplankton	$gCm^{-2}y^{-1}$	Truncated normal distribution	96.5	136.3	130.4
PPsmp_prior_2	CV for primary production nano-pico phytoplankton	fraction		0.3	0.3	0.3
PPsmp_prior_3	Lower bound for primary production nano-pico phytoplankton	$gCm^{-2}y^{-1}$		10	10	10
PPsmp_prior_4	Upper bound for primary production nano-pico phytoplankton	$gCm^{-2}y^{-1}$		300	300	300
PPlgp_prior_1	Mean of primary production micro phytoplankton	$gCm^{-2}y^{-1}$	Truncated normal distribution	64.4	73.4	70.2
PPlgp_prior_2	CV for primary production micro phytoplankton	fraction		0.3	0.3	0.3
PPlgp_prior_3	Lower bound for primary production micro phytoplankton	$gCm^{-2}y^{-1}$		5	5	5
PPlgp_prior_4	Upper bound for primary production micro phytoplankton	$gCm^{-2}y^{-1}$		130	130	130

Rsmp_prior_1	Lower bound for Retention fraction of primary production nano-pico phytoplankton within the ecosystem	fraction	Fixed parameter= 1 Assumes a closed system	1	1	1
Rsmp_prior_2	Upper bound for Retention fraction of primary production nano-pico phytoplankton within the ecosystem	fraction		1	1	1
Rlgp_prior_1	Lower bound for Retention fraction of primary production micro phytoplankton within the ecosystem	fraction	Fixed parameter= 1 Assumes a closed system	1	1	1
Rlgp_prior_2	Upper bound for Retention fraction of primary production micro phytoplankton within the ecosystem	fraction		1	1	1
Wsmp_prior_1	Mean dry to wet weight conversion of primary production nano-pico phytoplankton	$gm^{-2}y^{-1}$/ $gCm^{-2}y^{-1}$	Fixed parameter= 9 Additional parameters (greyed out) implemented for future development	9	9	9
Wsmp_prior_2	CV for dry to wet weight conversion of primary production nano-pico phytoplankton	fraction		NA	NA	NA

Wsmp_prior_3	Lower bound for dry to wet weight conversion of primary production nano-pico phytoplankton	$gm^{-2}y^{-1}$/ $gCm^{-2}y^{-1}$		NA	NA	NA
Wsmp_prior_4	Upper bound for dry to wet weight conversion of primary production nano-pico phytoplankton	$gm^{-2}y^{-1}$/ $gCm^{-2}y^{-1}$		NA	NA	NA
Wlgp_prior_1	Mean dry to wet weight conversion of primary production micro phytoplankton	$gm^{-2}y^{-1}$/ $gCm^{-2}y^{-1}$	Fixed parameter= 9 Additional parameters (greyed out) implemented for future development	9	9	9
Wlgp_prior_2	CV for dry to wet weight conversion of primary production micro phytoplankton	fraction		NA	NA	NA
Wlgp_prior_3	Lower bound for dry to wet weight conversion of primary production micro phytoplankton	$gm^{-2}y^{-1}$/ $gCm^{-2}y^{-1}$		NA	NA	NA
Wlgp_prior_4	Upper bound for dry to wet weight conversion of primary production micro phytoplankton	$gm^{-2}y^{-1}$/ $gCm^{-2}y^{-1}$		NA	NA	NA
XbacN_prior	Fraction of nano-pico phytoplankton production available to bacteria	fraction	Fixed parameter= 0.5	0.5	0.5	0.5

XbacM_prior	Fraction of micro phytoplankton production available to bacteria	fraction	Fixed parameter= 0.5	0.5	0.5	0.5
XbenSF_prior_1	Lower bound for the fraction of primary production micro phytoplankton available to Suspension Feeding benthos	fraction	Uniform distribution	0.102	0.102	0.102
XbenSF_prior_2	Upper bound for the fraction of primary production micro phytoplankton available to Suspension Feeding benthos	fraction		0.33	0.33	0.33
XbenDF_prior_1	Lower bound for the fraction of primary production micro phytoplankton available to Deposit Feeding benthos	fraction	Parameter not used in the model. Included as input as part of the model development process.	0.102	0.102	0.102
XbenDF_prior_2	Upper bound for the fraction of primary production micro phytoplankton available to Deposit Feeding benthos	fraction		0.33	0.33	0.33
Xnan_prior_1	Lower bound for the fraction of bacterial production available to Nanoflagellates	fraction	Uniform distribution	0.5	0.5	0.5
Xnan_prior_2	Upper bound for the fraction of bacterial production available to Nanoflagellates	fraction		0.99	0.99	0.99

Xbvr_prior	Fraction of Deposit Feeding benthos production available to Benthivores	fraction	Fixed parameter= 1 Assumes no direct link between Suspension Feeding Benthos and Piscivores	1	1	1
t1_prior	Transfer efficiency from phytoplankton to bacteria	fraction	Fixed parameter= 0.5	0.5	0.5	0.5
t2a_prior	Transfer efficiency from Bacteria to Nanoflagellates and Deposit Feeding benthos	fraction	Fixed parameter= 0.25	0.25	0.25	0.25
t2b_prior	Transfer efficiency from Nanoflagellates to Bacteria	fraction	Fixed parameter= 0.25	0.25	0.25	0.25
t2c_prior	Transfer efficiency from Nano-Pico phytoplankton to Microzooplankton	fraction	Fixed parameter= 0.25	0.25	0.25	0.25
t3_prior	Transfer efficiency from Microzooplankton to Mesozooplankton	fraction	Fixed parameter= 0.25	0.25	0.25	0.25
Area_prior	Area of the Ecosystem Production Unit	thousand km^2	This is used to scale results for the area	254.32	315.183	57.829
t4b_prior_1	Alpha parameter for Transfer efficiency from Micro phytoplankton to Suspension Feeding Benthos	dimensionless	Beta distribution	5.081	5.081	5.081

t4b_prior_2	Beta parameter for Transfer efficiency from Micro phytoplankton to Suspension Feeding Benthos	dimensionless		22.845	22.845	22.845
t4p_prior_1	Alpha parameter for Transfer efficiency from Micro phytoplankton to Mesozooplankton	dimensionless	Beta distribution	5.081	5.081	5.081
t4p_prior_2	Beta parameter for Transfer efficiency from Micro phytoplankton to Mesozooplankton	dimensionless		22.845	22.845	22.845
t5_prior_1	Alpha parameter for Transfer efficiency from Suspension Feeding Benthos to Benthivores	dimensionless	Beta distribution	6.1	6.1	6.1
t5_prior_2	Beta parameter for Transfer efficiency from Suspension Feeding Benthos to Benthivores	dimensionless		34.895	34.895	34.895
t6_prior_1	Alpha parameter for Transfer efficiency from Mesozooplankton to Planktivores	dimensionless	Beta distribution	6.1	6.1	6.1
t6_prior_2	Beta parameter for Transfer efficiency from Mesozooplankton to Planktivores	dimensionless		34.895	34.895	34.895

t7_prior_1	Alpha parameter for Transfer efficiency from Planktivores to Piscivores	dimensionless	Beta distribution	10.163	10.163	10.163
t7_prior_2	Beta parameter for Transfer efficiency from Planktivores to Piscivores	dimensionless		84.4	84.4	84.4
t8_prior_1	Alpha parameter for Transfer efficiency from Benthivores to Piscivores	dimensionless	Beta distribution	10.163	10.163	10.163
t8_prior_2	Beta parameter for Transfer efficiency from Benthivores to Piscivores	dimensionless		84.4	84.4	84.4
t9_prior_1	Alpha parameter for Transfer efficiency from Suspension Feeding Benthos to Piscivores	dimensionless	Parameter not used in the model. Included as input as part of the model development process.	NA	NA	NA
t9_prior_2	Beta parameter for Transfer efficiency from Suspension Feeding Benthos to Piscivores	dimensionless		NA	NA	NA
f_mez_prior	Exploitation Rate for Mesozooplankto n	fraction	Fixed parameter= 0 While implemented within the model, all scenarios assume no fishing on this functional guild	0	0	0

f_ben_prior	Exploitation Rate for Suspension Feeding benthos	fraction	Fixed parameter= 0.2 This is the baseline value with fishing. Scenarios with no fishing for this functional guild set this value to 0	0.2	0.2	0.2
f_bvr_prior	Exploitation Rate for Benthivores	fraction	Fixed parameter= 0.2 This is the baseline value with fishing. Scenarios with no fishing for this functional guild set this value to 0	0.2	0.2	0.2
f_pvr_prior	Exploitation Rate for Planktivores	fraction	Fixed parameter= 0.2 This is the baseline value with fishing. Scenarios with no fishing for this functional guild set this value to 0	0.2	0.2	0.2
f_pis_prior	Exploitation Rate for Piscivores	fraction	Fixed parameter= 0.2 This is the baseline value with fishing. Scenarios with no fishing for this functional guild set this value to 0	0.2	0.2	0.2