Trophic Analytical Approaches

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Summary

Energy is fixed and biomass is produced at lower trophic levels, which then transfers up the food chain to taxa of harvestable interest. Using measures or proxies of primary productivity, one can declinate how much fish could be caught in an ecosystem. One can also use those estimates of lower TL production coupled with measures of catch to delineate ecosystem overfishing indices. An extension of these methods, which is more complicated, are food web models. Though there are extant examples of food web models in the Caribbean, they often result in similar outputs. The utility of the relatively simple trophic approaches is that they can use widely available data to establish both ecosystem caps—and ascertain if ecosystem overfishing is occurring—and also estimate ecosystem production potential of how much of all fish could be caught in an ecosystem. These approaches have management applications, because they estimate ecosystem caps and provide coverage for high biodiversity, low-capacity situations that would otherwise not be able to estimate reference points for large portions of the harvested taxa.

I. Introduction

The basic tenet of renewable natural resource management is that any harvest must meet the condition of:

$R_{\text{removal}} \leq R_{\text{renewal}}$

for each rate of use to remain sustainable. That is, sustainable living marine resource (LMR) management is predicated upon utilizing (removing) a resource at a rate less than or equal to the rate of replenishment of that resource. This is obviously true and widely used at the population level in fisheries. But it is also true at the multispecies, aggregate, or system level. This is consistent with hierarchy theory but is rarely applied at levels beyond the population level. And this principle of removing less than what is replenished is also the conceptual basis for the thinking and estimation of overfishing in general (with associated reference points) and specifically ecosystem overfishing (EOF; Link and Watson 2019).

Reference points are an essential component of LMR management, providing a basis against which to measure the status of a resource and serving as a potential target or limit (trigger) for management actions (Sissenwine and Shepherd, 1987; Caddy and Mahon, 1995; Morrison et al. 2024). In traditional single-species fisheries management, reference points are usually established for the fishing mortality level that would achieve maximum sustainable yield (or some comparable proxy thereof), and above which overfishing is occurring. The target or limit is set for an individual stock, typically without consideration of species interactions, impacts on food webs, environmental changes, or other ecosystem dynamics. This approach can lead to a scenario where catch limits seem reasonable for individual stocks, but the cumulative total of removals across all individual species exceeds the system's ability to replenish removed biomass and allow for sustainable harvest across all stocks (refs). Analytically, to specifically codify EOF, one needs to calculate any one among a suite of associated ecosystem-level reference points (ELRPs; Morrison et al. 2024). Hence, for EOF considerations, an ELRP to minimize overfishing for the entire system would account for the cumulative impacts of catches, non-harvest mortality, and bycatch. This limit on the total biomass that can be sustainably removed from the ecosystem is an 'ecosystem cap' (Morrison et al., 2024; Link, 2018).

For EOF, establishing these caps is often related to primary production, because this sets the energy production for the system. For context, total oceanic primary production is on the order of 40-50 giga tonnes of carbon per year (GtC/y; Car et al. 2006). Total marine capture fishery yield is on the order of 0.1 GtC/y. Thus, there are limits to how much fish any ecosystem can produce, and hence can be (potentially) caught. Ocean changes are going to impact primary production, and with the efficiency of trophic level energy transfer (10% Transfer Efficiency is assumed; Link 2021), this ultimately affects the productivity of fisheries. Catch declines as trophic level increases, or as Transfer Efficiency and Net Primary Production decrease (Link 2021). Therefore, economically speaking, primary production constrains the revenue that can be obtained from any given marine ecosystem (Marshak and Link 2021).

Ecosystem overfishing is an ecological term that ultimately evaluates how much fish are caught in an ecosystem relative to how much can be produced. Ecosystem overfishing (EOF) indicators are developed by using landings data coupled with the total catch per unit area in the ecosystem (Ryther index), primary production (Fogarty index) and chlorophyll a (Friedland index). Link 2021 describes global thresholds to delineate EOF for eight U.S. Large Marine Ecosystems. One can also use trophic declination methods, or even sophisticated food web models, to measure productivity as it moves up the food chain (or web) into harvestable biomass of LMRs. From these, one can back out expected yields and compare that to what is being caught to delineate MMSY, Aggregate MSY, System-Level MSY, or other measures of ELRPs. This is particular useful in data limited situations.

II. Method Description

Adapted from Link et al. (in press)

Several approaches are based on the ecological principle of trophic transfer and limits of fish production as a proportion of net primary production. To cover the broad geographic range of ecosystems for this study, we utilize satellite-derived estimates of both chlorophyll a and net primary productivity as follows.

Data Sources

The characterization of basal ecosystem energy requires robust estimates of Net Primary Production (NPP). Satellite-derived estimates of NPP were selected to provide a synoptic, observation-based measure of phytoplankton carbon fixation that is both spatially explicit and temporally consistent across ecosystems. A range of established NPP algorithms exist, each grounded in different representations of phytoplankton physiology and environmental controls. Chlorophyll-based approaches parameterize photosynthetic efficiency as a function of chlorophyll concentration, light, and temperature, implicitly capturing broad-scale patterns in light acclimation but with differing sensitivities to nutrient limitation at higher temperatures. In contrast, carbon-based productivity models estimate phytoplankton biomass from particulate backscatter and infer growth rates from photoacclimation-driven changes in cellular carbon-to-chlorophyll ratios, providing a more mechanistic link to physiological state under varying light and nutrient regimes. These estimates associated with primary production have been variously linked to fisheries production for decades with a host of caveats and considerations (multiple, seminal references, but see Ryther and related from 1950-60s), the salient point here being that from basic ecological principles, the base of the food web ultimately dictates the amount of fish that can be caught in an ecosystem.

Satellite-Derived Chlorophyll Concentration

Satellite estimates of chlorophyll-a concentration (Chl a) serve as the primary observational baseline for assessing ecosystem biomass. Thus satellite-derived chlorophyll-a (chl-a) was included as a complementary indicator of phytoplankton biomass, providing a simpler, observation-based metric that is widely used in ecosystem assessment frameworks. In contrast to NPP, which integrates physiological processes governing carbon fixation, chl-a reflects the standing stock of phytoplankton pigments and is more directly tied to biomass. While chl-a does not explicitly resolve variability in growth rates or photoacclimation, its long observational record and widespread use in management contexts make it a valuable and interpretable metric. Chlorophyll-a fields were obtained from the Ocean Colour Climate Change Initiative (OC-CCI) via OpenDAP (https://comet.nefsc.noaa.gov/erddap/griddap/occci_V6_8day_4km.html), using the merged, multi-mission dataset provided at 4-km spatial resolution and 8-day temporal compositing. These data are captured by optical sensors–such as SeaWiFS, MODIS, VIIRS, and OLCI–which measure ocean color at a handful of discrete wavelengths. For ecosystem-scale assessments, these individual records are often integrated into "climate-quality' merged products, such as the ESA Ocean Colour Climate Change Initiative (OC-CCI). The OC-CCI product integrates observations from multiple satellite sensors into a consistent time series, with inter-sensor biases minimized through cross-calibration and validation protocols. Note, the same underlying ocean color record also serves as the foundation for the NPP estimates, ensuring methodological consistency across productivity and biomass metrics. To generate regionally/island representative chl-a values, surface concentrations can be spatially aggregated within each Region using the geometric mean. Annual values were provided and used in subsequent calculations. This approach reduces the influence of extreme values and better reflects the log-normal distribution typically observed in chlorophyll fields, particularly in heterogeneous coastal and transitional environments.

Net Primary Production (NPP)

Because net primary production (NPP) is a rate of carbon fixation (e.g., mg C m-2 day-1) rather than a static pigment concentration, it must be derived through bio-optical models. These models, such as the Vertically Generalized Production Model or the spectral models utilized by OC-CCI, integrate environmental variables like photosynthetically active radiation and sea surface temperature (SST). By converting optical reflectance into an energetic rate, these data provide an estimate of the rate of organic matter production by primary producers (i.e., the fuel required for production by higher trophic levels), allowing a direct comparison between fisheries removals and the total energy fixed at the base of the food web.

Given the differing assumptions and known performance tradeoffs among them, no single bio-optical model can be expected to perform optimally across the full range of oceanographic conditions represented in large marine ecosystems. For a management-oriented application where consistency, transparency, and robustness are critical, reliance on a single model risks introducing systematic regional bias. Accordingly, we adopt an ensemble approach using the multi-model NPP dataset developed by Ryan-

Keogh et al. (2023), which synthesizes outputs from several widely used algorithms applied to a harmonized ocean color record (data can be found at https://zenodo.org/records/18980518). This framework provides not only a central estimate of NPP, but also a representation of model spread, enabling a more defensible characterization of uncertainty that is directly relevant for ecosystem-based decision-making. The ensemble dataset is provided as 8-day composites at 25-km spatial resolution and incorporates a suite of satellite-derived and ancillary inputs, including sea surface temperature, chlorophyll-a, particulate backscatter, absorption coefficients, diffuse attenuation (Kd490), and photosynthetically available radiation (PAR), along with mixed layer depth and nutricline depth fields. These variables collectively constrain estimates of phytoplankton biomass, light availability, and growth rates across models. The use of a consistent, multi-decadal dataset facilitates interannual comparisons, while the inclusion of multiple algorithm classes ensures that key physiological processes (e.g., light limitation, nutrient stress, and photoacclimation) are represented in aggregate.

To translate gridded NPP fields into ecosystem-scale metrics, the 8-day composite data were first temporally resolved to daily values and integrated over each time step. Spatial aggregation was performed by applying region-specific masks derived from management polygons, summing NPP across all grid cells within each region, and scaling by pixel area to convert areal rates (e.g., mg C m^{-2} d^{-1}) into total daily carbon production. Daily totals were then accumulated over the course of each year to yield annual NPP estimates (g C yr^{-1}) for each region. This workflow preserves the native spatial structure of the satellite data while producing regionally integrated metrics that are directly interpretable within an ecosystem management context. By combining physiologically diverse models within a consistent processing framework, this approach provides a transparent and extensible pathway for incorporating satellite-based primary productivity into ecosystem-scale assessments. We also acknowledge that these satellite-based methods may not capture mid-water or deeper water chlorophyll or production, but should capture most of what is seen in near surface waters. We also acknowledge that in some of the more shallow systems (e.g. Caribbean Islands) other productivity may play an important factor in reef fish communities; but we do not provide such estimates here; although in the paragraph below we provide a methodology to do so.

As fish biomass in the shallow waters of the Caribbean is largely dependent upon benthic productivity we propose using literature values of productivity per unit area from seagrass beds and coral reefs. Douglas et al. (2001) estimates coral reef productivity to be 1-15 g C m^{-2} d^{-1} and Gomis et al. (2025) estimates seagrass productivity to be 5,833 kg C ha^{-1} yr^{-2}. We can multiply these values by the areal extent of seagrass beds and coral reefs in the region to get the total productivity from critical benthic habitats in the region. While these values are global averages, we could also explore Caribbean specific productivity values in an attempt to better parameterize these estimates for our region.

Trophodynamic Approaches

Trophodynamics track the flow of energy and thus biomass through trophic levels. The trophic efficiency is a measure of how much productivity is transferred from one trophic level to the next highest trophic level. Hence, it uses estimates of NPP or chlorophyll a (as noted above) and "declinates" that production (or biomass) as one ascends the food chain. That is, this approach can be used in conjunction with the primary productivity estimates noted above to estimate how much productivity is being produced annually and hence provide a theoretical maximum annual harvest at that trophic level.

Most fishery species harvested within U.S. waters function between trophic level 3 or 4. Thus, the amount of annual productivity at trophic level 3 or 4 would theoretically represent the total maximum catch that could be sustainably achieved for the ecosystem. The amount of productivity and thus sustainable catch at each trophic level can be calculated using the following equation (c.f. Link and Watson 2019):

$$C\_total*(1/9) = \alpha*NPP* 〚TE〛^(TL-1) \qquad (1)$$

where NPP is the net primary productivity calculated as noted in the section above (in g C km^{-2}), TE is the trophic efficiency, TL is the mean trophic level of the catch, and α is the fraction of energy at TL that is realized as catch (Stock et al. 2017). The catch in tons per km^{-2} is converted to carbon by multiplying by 1/9 (Stock et al. 2017; often it is simply 10, but the literature suggests this more caveated approach from global studies). We term this trophic transfer model approach a trophic declination method.

Ideally, the α, trophic efficiency, and trophic level of the catch should be calculated for each ecosystem based on local conditions and measurements (Stock et al. 2017). However, there are some generalities that can be used to estimate this value when data is lacking. The value for α has been found to be between 0.14 - 0.20 based on the value that emerges from maintaining a stable global average catch for the past 30 years (Link and Watson 2019, though 0.1 to 1 have been used). Similarly, the TE has been estimated to be 0.08-0.18 based on global marine ecosystem analyses (Pauly and Christensen 1995, Link and Watson 2019, refs). The more detailed trophic transfer model uses the global averages for these variables and the NPP in each given ecosystem to calculate the maximum total ecosystem catch. The values used for the trophic transfer model were α=0.175, TE=0.13, and TL=3.4. A sensitivity analysis is shown for some of these parameters, indicating the directionality from changes in the variables in EQ. 1 (Fig. 1).

Here we present three approaches for this method. The first two are simple trophic transfer declination results using a TL of 3, and 4 to bracket the range of potential fish production. The third is a more detailed trophic transfer efficiency method using the global averages noted above. These are in addition to other trophodynamic index methods noted below. Since these primarily use only NPP as the input data and rely on theoretical declinations (as noted in EQ 1), these should be considered as bracketing the range of ecosystem caps estimated from other methods. If an estimate exceeds one of these extremes, that would warrant further examination, exploration, or explanation.

Fogarty and Friedland Indices

The Fogarty-based estimate (Fig. 2) is calculated based on underlying trophodynamics (EQ 1) and the NPP values as described above. Link and Watson (2019) suggest that ecosystem overfishing may be occurring when the ratio of total weight of catch:net primary productivity (both in tons of wet weight) exceeds 1 ‰ (0.001). We use this threshold value to estimate maximum catch from estimated net primary productivity by simply multiplying net primary productivity (g wet weight y^{-1}) by 0.001.

The Friedland Index (Fig. 3) is similar to the Fogarty Index, but is based upon chlorophyll a in mg m^{-3} instead of NPP. Link and Watson (2019) suggested an ecosystem overfishing threshold value of 1 for the ratio of total weight of catch:total chlorophyll a. We use this threshold value to estimate maximum catch from estimated chlorophyll a in the manner used for the Fogarty Index.

Ryther Index

The Ryther index (Fig. 4) is based on the theoretical maximum catch in the ocean per unit area based on the typical primary productivity in the ocean and observed catches. Based on a global fishery yield of 0.1 to 0.42 Gt $year^{-1}$, the value per unit area in the ocean ranges from 0.3 - 1.1 t km^{-2} $year^{-1}$, with an extreme limit of 3 t km^{-2} $year^{-1}$ in some systems (Link and Watson 2019, Ryther 1969). We recognize that reef ecosystems may have different production dynamics and hence ranges of total productivity. We utilize a maximum yield of 1 t km^{-2} $year^{-1}$ to calculate our Ryther-based estimate where the ecosystem cap estimate for each region is simply calculated as 1 t km^{-2} $year^{-1}$ across the full spatial extent of the region.

Ecosystem Model Outputs

Both static and dynamic food web and ecosystem models can inform ecosystem caps. Throughout most U.S. regions Ecopath food web models (Walters et al. 1997; Christensen and Walters 2004) have been constructed to quantify predator-prey interactions and fishing, tracing the flow of production to predators, fishing, and other losses. Additional, mass-balance related approaches have been implemented via the Rpath (Lucey et al. 2020) and ECOTRAN (Steele and Ruzicka 2011) modeling approaches, which, like Ecopath, begin with a static accounting of biomasses, productivity, and catch.

Data Needs
Static ecosystem models including Ecopath, Rpath, and ECOTRAN, have common data requirements (Walters et al. 1997; Christensen and Walters 2004, Lucey et al. 2020, Steele and Ruzicka 2011, Heymans et al. 2011). These include specification of biomass, production rates, consumption rates, catches, diet composition, and losses due to non-specified causes ('1-ecotrophic efficiency'). One of these values per species (or species groups) can be unknown, and solved for via the Ecopath/Rpath equations. For instance, often species that are data-poor will require "top-down" estimation of biomass, after specifying other parameters. ECOTRAN generally starts with estimates of primary production, e.g. from satellite observations, and traces this up through the food web as donor-driven flow to consumers (Ruzicka et al. 2024), rather than imposing a top-down estimation of biomass. *In situ* observations to support specification of these parameters typically include fisheries independent surveys for common target species, life history information related to size and age, and consumption estimates based on detailed bioenergetic or feeding studies, or at least rough proxies for feeding demand. Diet studies are necessary and often sporadic or opportunistic, but typically can approximate diets sufficiently to inform our static estimates here; there exist methods to estimate diet from rank ordering of known or suspected prey fields (Link 2002). Fishery dependent estimates of catches, and often bycatch, are also used as inputs to these models. In short, static ecosystem models can be constructed and are available for most U.S. LMEs, including parts of the Caribbean, largely due to their use of data collected routinely for stock assessment, supplemented with information on feeding and local expertise on primary production and non-harvested species such as lower trophic levels.

Dynamic ecosystem models such as Ecosim, Atlantis, OSMOSE, and some implementations of ECOTRAN generally build on static ecosystem models but require time series of catches, often biomass, and may also be forced with time series of primary production or physical oceanography. Alternatively, Ecosim may be used to estimate time-varying trends in productivity, which can be compared to observed time series (e.g., satellite estimates of chl-a). Dynamic ecosystem models are also typically fitted or calibrated to (time series) observations, such as annual abundance estimates from fishery independent surveys, fishery-dependent estimates of catch-per-unit-effort, seasonal estimates of productivity or spatial distribution, or estimates of growth and size-at-age (Kaplan and Marshall 2016, Perryman et al. 2025, Fulton et al. 2012). Overall, many of the additional data required to translate static ecosystem models to dynamic models are already extant (and available) from other calculation methods for ecosystem caps. However, the time and expertise necessary to construct and execute these dynamics models means that while dynamic ecosystem models are available for specific regions they are not uniformly applied across all U.S. LMEs. As noted above, outputs from dynamic ecosystem models such as Ecosim and Ecospace can also be used in surplus production models to estimate multispecies maximum sustainable yields (MMSY), which is another approach for setting total ecosystem caps.

A. Data Inputs

- Primary production or chl a
- and
- Landings data of all/most species;
- OR
- The above with estimates of trophic transfer efficiency
- And estatimates or approximations of the trophic level of catches
- OR
- The above, with additional information needed for Food web models, which can be quite extensive

B. Analyses/Data Outputs

- Trophic declination
- Trophic-based EOF Indices
- Limits on Fisheries Production Potential
- Balanced model outputs of landings

When combined with other measures

- Can serve as comparable “Kobe” plots to delineate EOF
- Can provide insights into system dynamics
- Can provide backstopping to all fisheries removals
- Expectations of what Fisheries Removals could be
- Also provide early warning signals of system-wide events

C. Implications for Management

- Potential Indicator of EOF, ELRPs
- Can provide theoretical limits of the amount of total fish that should be caught in an Island ecosystem/region
- Can provide thresholds for how much fishing, in total, is too much
- Can provide estimates of how much fish could *potentially* be caught

D. Caveats

- Various methods in Primary Production ensemble estimation
- for trophic declination, assumptions about TL and TE values
- inclusion of benthic/coral production - other sources of production (benthic, coral) may be occurring at the sub-LME scale and not as readily detectable by satellite (Link 2021)

III. Applications of the Method

- Has been used to test and inform policy on good environmental status in the EU under their MSFD auspices (ICES 2014, Tam et al. 2017).
- Backstopping and testing for EOF, especially with ecosystem-level Kobe plots, in the US (Link 2021; e.g. Fig. 3).
- Identified EOF for African LMEs and used to inform sustainable development decisions (Link et al. 2020).
- Reported on in various national and regional Ecosystem Status Reports

IV. Discussion

Besides the full ecosystem models, the specific methods noted herein are simple, robust, well-known, well-tested, and rely on rather basic input data or literature values. The application we recommend is calculation of some of these as a back-stop, per island, as the data are readily available and the computational/analytical costs are minimal. These can then delineate whether an Island ecosystem is experiencing excessive ecosystem overfishing, or is close to its production potential, and then be used to ensure that there are SDCs and BRPs for all/most taxa without having to worry about conducting detailed analyses for every taxa in these ecosystems. In conjunction with other approaches, these simple landings or production-based methods provide a limit to fishing in each island ecosystem and can provide the basis for further evaluations of higher priority species.

Ecosystem caps are estimates that attempt to relate the removal of all harvested stocks (or at least most of them) to the underlying production capacity of a given ecosystem.

The thinking from hierarchy theory is that though important and problematic, it is one thing if lower level (e.g., a couple of populations) components are perturbed, but if the entire system (large aggregate groups or the entire ecosystem) is perturbed there are much bigger concerns and issues occurring cannot be rectified by resolving issues at lower levels in the hierarchy (refs). Ecosystem caps have a solid theoretical backing, particularly via the principle of carrying capacity for an entire suite of species, and can provide a strategic backstop by reverting to the first principles of said carrying capacity (Link, 2018; Morrison et al., 2024). By utilizing ELRPs, managers can evaluate harvestable biomass to account for larger system dynamics. This range of methods serve as ecosystem-level reference points that act as a reality check on the sustainability of total removals. While single-species approaches remain valuable for a limited sub-set of specific allocations, these broader ecosystem-level caps offer a relatively inexpensive and robust safeguard, ensuring that the cumulative pressure of all fisheries does not exceed the fundamental energetic limits of the marine environment (Link, 2018; Morrison et al. 2024). The ecosystem cap estimates also have utility for management as indicators of system-level trends, the likelihood of ecosystem overfishing, and as context for discussing tradeoffs of various management approaches and decisions.

V. References

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Ryther 1969

Sissenwine and Shepherd, 1987

Steele and Ruzicka 2011

Stock et al. 2017

Tam et al. 2017

Walters et al. 1997

VI. Tables and Figures

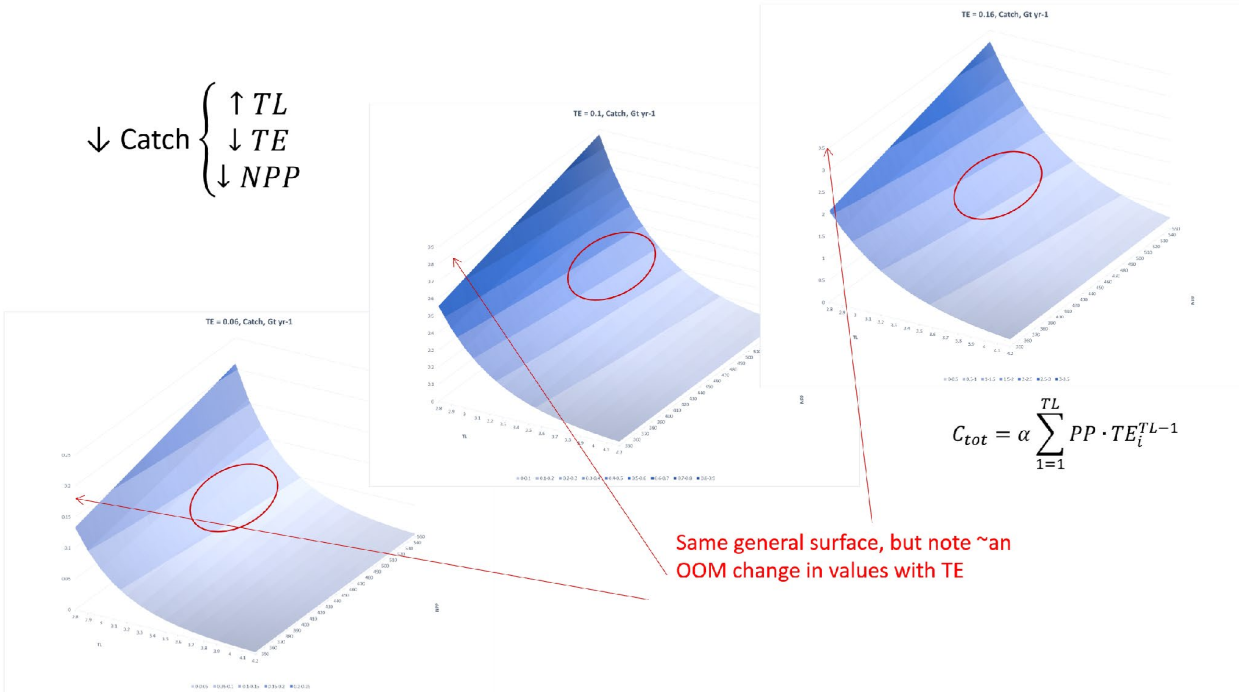

Figure 1. Sensitivity analysis of key parameters in trophic declination approaches.

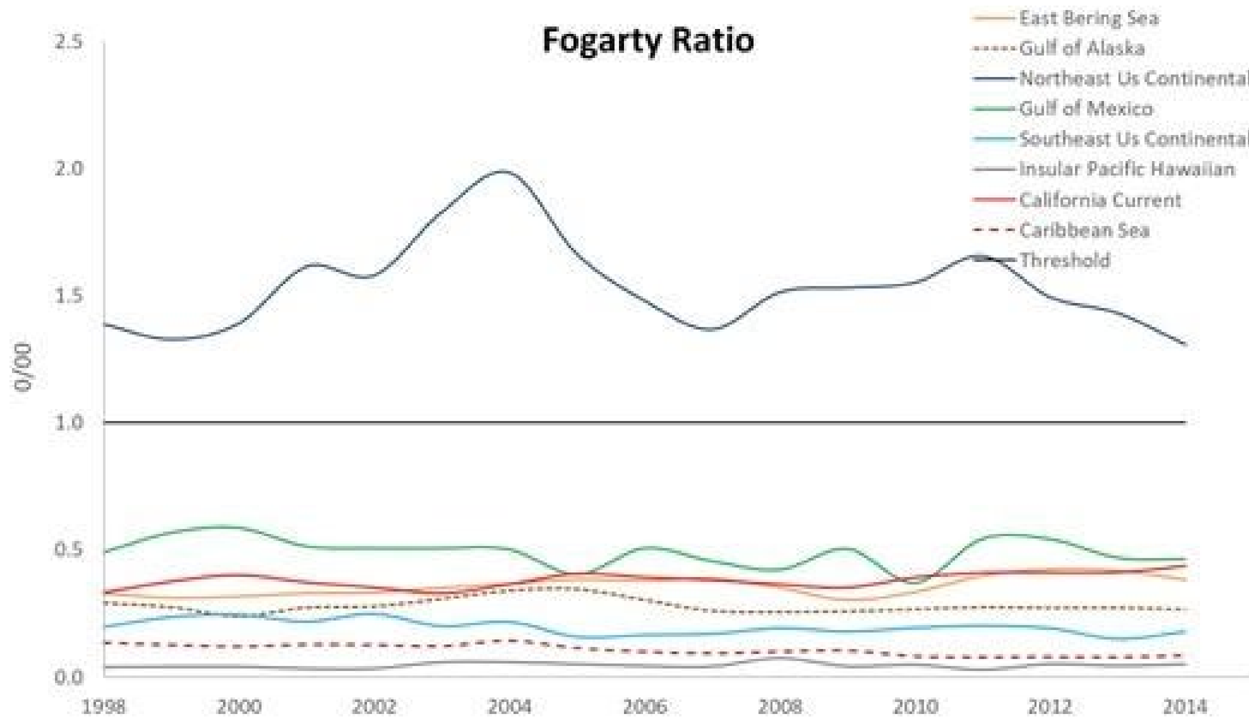

Figure 2. The Fogarty index of EOF for the eight U.S. LMEs. The black line corresponds to globally derived thresholds of EOF as determined by Link and Watson 2019 (Link 2021).

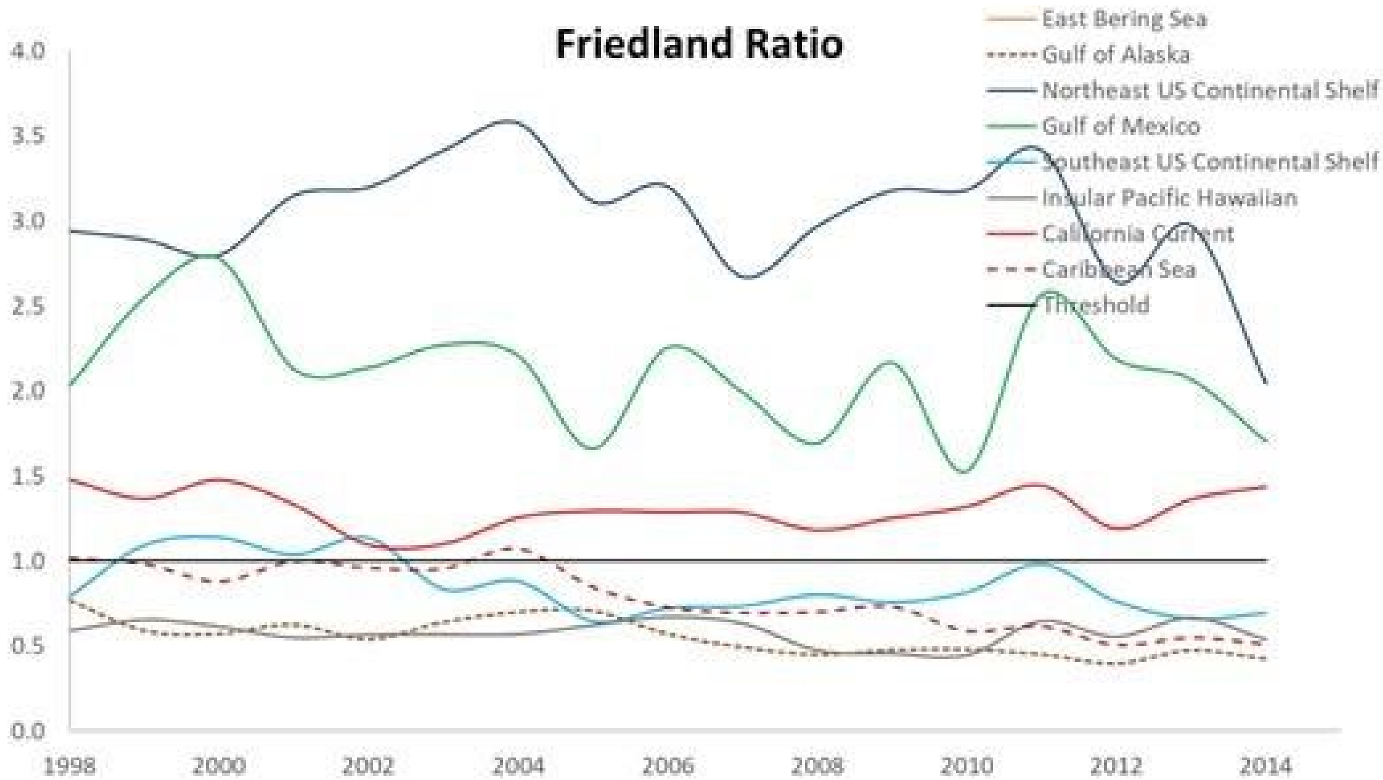

Figure 3. The Friedland index of EOF for the eight U.S. LMEs. The black line corresponds to globally derived thresholds of EOF as determined by Link and Watson 2019 (Link 2021).

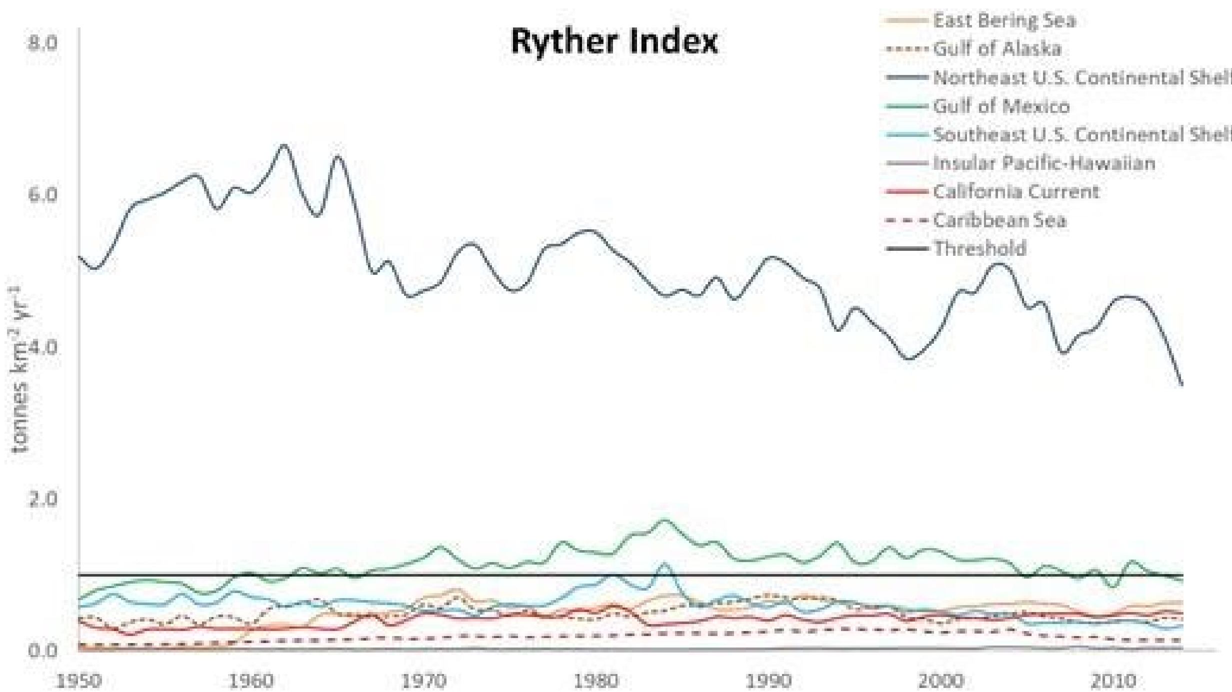

Figure 4. The Ryther index of EOF for the eight U.S. LMEs. The black line corresponds to globally derived thresholds of EOF as determined by Link and Watson 2019 (Link 2021).