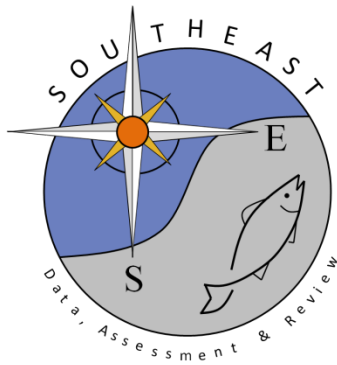


Evidence of ecosystem overfishing in U.S. large marine ecosystems

Jason S. Link

SEDAR103-RD-01

February 2026



This information is distributed solely for the purpose of pre-dissemination peer review. It does not represent and should not be construed to represent any agency determination or policy.



Original Article

Evidence of ecosystem overfishing in U.S. large marine ecosystems

Jason S. Link *

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, 166 Water St., Woods Hole, MA 02543, USA

*Corresponding author: Tel: +1-508-495-2340; e-mail: Jason.Link@noaa.gov

Link, J. S. Evidence of ecosystem overfishing in U.S. large marine ecosystems. – ICES Journal of Marine Science, 78: 3176–3201.

Received 3 May 2021; revised 28 August 2021; accepted 9 September 2021; advance access publication 4 October 2021.

Marine capture fisheries in the U.S. are important from a societal, cultural, economic, and ecological perspective. Although fisheries in the U.S. are generally well-managed, they still face some challenges as do most fisheries around the world. To address these challenges, a broader, more systematic approach is useful. There is a global need to develop measures of ecosystem overfishing (EOF) that detect overfishing of *an entire ecosystem* using readily available data and based on widely repeatable patterns. These EOF indicators extend the thinking beyond single stock overfishing to an entire ecosystem and are largely based on well-established trophic theory. Moreover, these EOF indicators need to be germane for both data rich and especially data limited situations, easily interpretable, and relatively simple to calculate. Here, I present the results of several of these indicators—the Ryther, Fogarty, and Friedland indices—as well as indices based on cumulative biomass-Trophic Level curve parameters for eight U.S. Large Marine Ecosystems (LMEs). Significantly, all these EOF indicators also have thresholds beyond which EOF is indicated, particularly when coupled with other evidence. Evidence for EOF is suggested for two of the eight U.S. LMEs. Even apart from EOF thresholds, detecting whether EOF is occurring, or how debatable the proposed EOF thresholds are, there are multiple benefits from monitoring these ecosystem-level indicators. Detecting patterns and trends in overall fishing changes for an ecosystem is chief among them. Additionally, EOF indicators detected changes in these LMEs at least 2–3 years, even up to 5 years prior to major impacts that might not be identified by piecing together fishing impacts on a stock-by-stock basis; thus, the EOF indicators could serve as an early warning signal. I propose that instead of starting with the history of which stocks have been assessed or even with what we deem most valuable, we look at the entire system of fisheries in an LME and if EOF is detected, explore means to address excess fishing pressure systematically before delving into the details of specific stocks. I conclude that EOF measures need to be monitored, EOF thresholds refined, and if EOF is detected then the means to mitigate total fishing pressure in an ecosystem should be explored.

Keywords: comparative analysis, ecosystem-level reference points, ecosystem perturbation, fisheries ecosystem, integrative metrics, sustainable fishing, systemic overfishing, thresholds.

Introduction

Fisheries and marine ecosystems that support them are important. Fisheries are clearly a valuable part of the U.S. economy; the fisheries sector represents ~1% of total economy (in terms of gross domestic product (GDP) relative to the total U.S. GDP; NMFS, 2018, 2019; NOAA 2020; BEA, 2021), has sales valued at > \$212 U.S. Billion, and contributes ~1.7 million jobs (NMFS, 2018, 2019). Fisheries also provide an important source of protein in the U.S., with

approximately 16 pounds per capita consumed per year from the > 4.5 million metric tons of fish that is commercially landed, which does not include recreational and artisanal catches (NMFS, 2018). Comparable statistics are found elsewhere in the world (e.g. World Bank, 2017; FAO, 2018, 2020; OECD, 2020). There is also the intrinsic value of the ecosystem goods and services that marine ecosystems and their associated fisheries provide (Costanza *et al.*, 1997; MEA, 2005; Guerry *et al.*, 2015). It is factually accurate to state that the large marine ecosystems (LMEs; Sherman *et al.*, 1993) in

the U.S. (and globally) and their associated marine capture fisheries have a significant societal, economic, cultural, and ecological impact.

There are broader concerns about fisheries sustainability that range from the well-known, persistent challenges to population dynamics (Schaefer, 1957; Levin *et al.*, 1997; Cadrin *et al.*, 2014; Lynch *et al.*, 2018) to a broader array of factors that influence the dynamics of these living marine resources (LMRs; Keyl and Wolff, 2008; Link, 2010; Rodhouse *et al.*, 2014; Thorson *et al.*, 2015). Not only are fish populations, fishing fleets and fishery systems impacted from overfishing (Pauly *et al.*, 2002; Hilborn *et al.*, 2015; Link, 2018), but changes to fish and fisheries can also result from, and be impacted by, broader factors acting on marine ecosystems (Jackson *et al.*, 2001; Coll *et al.*, 2008; Link, 2010, 2018). Overfishing can result in, for example, cascading effects that debilitate key habitats and taxa (Scheffer *et al.*, 2005), foster blooms of invasive species (Daskalov, 2002), impact sustainability of other exploitation efforts (Libralato *et al.*, 2004) and enhance the negative effects of climate change to the ocean (Gaines *et al.*, 2018). To address many of these challenges, a broader, more systematic means to detect and delineate overfishing is warranted, before it sequentially impacts fish population after fish population, fishery after fishery, and ultimately marine ecosystem functioning (Link, 2010, 2018; Fogarty, 2014; Link and Watson, 2019). It is clear that considering the larger impacts to the ecosystem from overfishing is not obtainable from solely a single species emphasis. Recognizing that business-as-usual, single-species management may not fully address the full array of issues that impact fisheries, nor fully address ecosystem considerations that arise from fishing, and definitely not the cumulative effects across multiple fisheries in a given ecosystem (Halpern *et al.*, 2008; Micheli *et al.*, 2014; Coll *et al.*, 2016), numerous calls to implement ecosystem-based fisheries management (EBFM) have arisen (Simberloff, 1998; Pikitch *et al.*, 2004; Beddington *et al.*, 2007; Link, 2010; Fogarty, 2014; NMFS, 2016a). The implementation of EBFM and related approaches are ultimately predicated upon knowing when we have actionable criteria (thresholds) to address these broader, more systematic concerns.

Marine capture fisheries in the U.S. are generally recognized as being well managed (Pitcher *et al.*, 2009; Hilborn *et al.*, 2015, 2020), but that does not mean all fisheries, fish stocks, and LMEs are optimally handled. Overfishing of stocks still occurs, but mostly the status of those stocks has improved over time (Methot *et al.*, 2014; Lynch *et al.*, 2018; NMFS, 2020; *c.f.*, Melnychuk *et al.*, 2017; Hilborn *et al.*, 2020 for broader context). Despite this generally positive situation, there remain challenges to the management of marine fisheries in the U.S., and many stocks in the U.S. have a remarkably unknown status (NMFS, 2020). The importance of U.S. fisheries and the continued challenges they face (beyond what can be addressed via a single species emphasis) highlights the need to estimate and explore marine ecosystem overfishing (EOF) in U.S. LMEs (and globally; Link and Watson, 2019). Even for relatively data rich situations, national and international policies are increasingly calling for ecosystem indicator thresholds. Examples include the Good Environmental Status in the Marine Strategy Framework Directive (European Parliament and Council of the European Union, 2008) context in Europe and EBFM policies in the U.S. (NMFS, 2016); the key principles thereof are paralleled internationally via some of the Sustainable Development Goals in the UN context (United Nations, 2015). The need for such thresholds is highly germane for U.S. and all LMEs (Link and Watson, 2019). Even apart from such thresholds, at the least it seems highly warranted to at least

monitor some of these system-level features. From hierarchy theory (*c.f.* Link, 2018; O'Neill *et al.*, 1986; Wu, 2013 as applied to fisheries), a routine and systematic examination of emergent features should provide standard and useful information more than what can be obtained by monitoring solely on component stocks or *ad hoc*, intermittent and non-systematic meta-analyses thereof, particularly as major pattern detectors and potentially as early warning signals.

Here, I estimate measures of EOF and evaluate them for U.S. LMEs. There have been several attempts to quantitatively characterize, and delimit, the impacts of overfishing on marine ecosystems (*e.g.* Murawski, 2000; Tudela *et al.*, 2005; Bundy *et al.*, 2005; Link, 2005; Shin *et al.*, 2010a, b; Halpern *et al.*, 2012,), including those specifically from a trophically-oriented perspective (Pauly and Christensen, 1995; Gascuel *et al.*, 2005; Coll *et al.*, 2008; Libralato *et al.*, 2008; Link *et al.*, 2015). But few of these calculations have had clear thresholds and delineation of EOF (Libralato *et al.*, 2008; Fay *et al.*, 2015; Link *et al.*, 2015) or associated tipping points (Large *et al.*, 2015; Samhuri *et al.*, 2017; Tam *et al.*, 2017). Recent definitions of EOF with limit thresholds have been proposed (Link *et al.*, 2015; Link and Watson, 2019; Libralato *et al.*, 2019), and I adopt those here for assessing U.S. LMEs relative to EOF. These include the Ryther, Fogarty, and Friedland indices that examine catch in relation to area of the ecosystem, primary productivity, and chlorophyll *a*, respectively, as well as cumulative biomass curve properties (Link *et al.*, 2015; Libralato *et al.*, 2019; Pranovi *et al.*, 2020). Here, I define EOF as an occurrence where total CPUE is declining, the sum of all catches decline after a period of increasing, total landings relative to ecosystem production exceeds suitable limits as seen in the Ryther, Fogarty, and Friedland indices (Link and Watson, 2019) over their thresholds, and the cumulative trophic curve parameters are below thresholds indicative of system-wide perturbation (Libralato *et al.*, 2019) (or at least most of the preceding is indicated). These are described further below, and have begun to be considered and used in other LME contexts (Link *et al.*, 2020). The relevant point is that these indicators of EOF are based on widely observed and repeatable patterns, use commonly available and widely reported data, and can be considered as an emerging standard to see if thresholds have been grossly exceeded. My objective in this work is to calculate, present and evaluate these indicators of EOF for U.S. LMEs, noting when EOF may be occurring, contrasting that with known fisheries histories in these LMEs, and explore if further elucidation of this systematic approach has potential utility.

A brief primer on EOF

As noted, there is now a considerable body of work to explore the ecosystem effects of overfishing (*e.g.* Murawski, 2000; Tudela *et al.*, 2005; Bundy *et al.*, 2005; Link, 2005; Shin *et al.*, 2010a, b; Halpern *et al.*, 2012), particularly from a trophically-oriented perspective (Pauly and Christensen, 1995; Gascuel *et al.*, 2005; Coll *et al.*, 2008; Libralato *et al.*, 2008; Link *et al.*, 2015). Yet only recently have there been quantifiable, repeatable, widely observed, and clearly defined facets of EOF (Link and Watson, 2019), which have associated thresholds. But prior to delving into EOF, let us review the basics of single species overfishing.

The dynamics of single population overfishing are well chronicled; as catch declines, effort increases, which is then repeated. This is Graham's "Law of Overfishing" (Graham, 1943; Smith, 1994), which implies that as catch-per-unit-effort (CPUE) declines, an increasing amount of time is spent fishing in an increasingly larger

area. For a single, discrete population, as the fishing rate (F) increases, mortality increases up to an unknown maximum, the numbers of fish, population biomass, mean individual size (weight or length), mean weight-at-age, mean age- and size-at-maturity, recruitment, somatic and population growth, and ultimately yield all decrease. Concurrently, the amount of effort and area fished increases, which results in a fishing rate that exceeds the rate for maximum sustainable yield (e.g. $F/F_{MSY} > 1$). There are several nuances to this regarding recruitment or growth overfishing (Murawski, 2000; Hilborn *et al.*, 2015), but the general patterns hold based on population dynamics theory. This theory and application of population overfishing have well-defined features (Smith, 1994; Mace, 1994; Murawski, 2000; Hilborn *et al.*, 2015), which have led to clearly demarcated thresholds of overfishing and overfished population status, representing critical decision criteria for fisheries management.

Most metrics of overfishing have focused on individual fish stocks or populations, yet the concept is applicable for groups of stocks, guilds of fish, or even an entire fisheries ecosystem to delineate EOF. By extending definitions of single population overfishing, there is an analogous suite of overfishing measures at an ecosystem level (Murawski, 2000; Link, 2005; Link *et al.*, 2015; Link and Watson, 2019). As an individual stock's catches decline and effort increases, such that CPUE declines past what is economically viable, catch shifts towards a second, often less preferred species and the cycle then repeats, *ad infinitum*.

For EOF, catch for the overall ecosystem (i.e. or group of species) increases until overall (i.e. across all species) CPUE declines, escalating to the point of systemic depletion. This is the Law of Sequential Depletion (Smith, 1994; Murawski, 2000), a corollary to Graham's Law of Overfishing (Graham, 1943; Smith, 1994). The sequence of eroding CPUE implies an expansion of both taxonomic and geographic scope as fishing fleets target more and more distinct types of fishable biomass in more and more distant and distinct habitats to maintain economic viability (Watson *et al.*, 2004, 2015; Swartz *et al.*, 2010). For an entire system of LMR stocks, as total catch (or effort) increases across all harvested taxa, the mean individual size (usually some estimate of overall, average, aggregated length; Link, 2005), total biomass and yield decline, while the size spectra slope increases (Link, 2005; Blanchard *et al.*, 2012). Besides these elements occurring across all species, other composite effects are also observed. The species composition changes, and thus biodiversity may change, but not always in a clearly predictable manner as, by definition, any particular diversity estimate can result from multiple configurations of species composition. These nuances aside, the tenets of sequential depletion generally hold from theories of the perturbation of ecological communities (Link *et al.*, 2015). For food webs and energy flows impacted by fisheries, as overall catch (or effort, or F) increases, the Loss in Production (or L) index (Libralato *et al.*, 2008), system ascendancy (*sensu* Ulanowicz, 1986), total system throughput (*sensu* Odum, 1969), biomass of apex predators of particular interest, cumulative biomass inflection points, cumulative production (Libralato *et al.*, 2008, 2019; Link *et al.*, 2015), and mean trophic level (Pauly *et al.*, 1998) all decline. Disruption in trophic linkages also often occurs (e.g. apex predators; Estes *et al.*, 2011; forage fishes; Smith *et al.*, 2011), which results in changes to ecosystem function via altered dynamics of energy flow pathways (i.e. predator-prey dynamics, competition, etc.), which additionally highlights the need for ecosystem-level indicators. Similar to the single stock situation, as EOF occurs, the effort and area fished to catch all fishes increases, resulting in a

system-level fishing rate exceeding the rate to obtain the composite, maximum sustainable yield for all caught LMRs in the ecosystem ($F_{System}/F_{SystemMSY} > 1$; c.f. Worm *et al.*, 2009; Rindorf *et al.*, 2017; Link, 2018; Thorpe, 2019).

Essentially, one can extend the usual single stock yield curve from a single population to an entire system of LMRs with the same general features and behaviors (Gaichas *et al.*, 2012; Link and Watson, 2019). Doing so ties all fisheries removals to the carrying capacity of an ecosystem. That is, fishing effort should be at a rate less than or equal to the rate of ecosystem production required to maintain the aggregate of all LMR taxa. I recognize that there are many other possible aspects of EOF relating to apex predators, bycatch, habitat, ecosystem function, biodiversity, etc. (Jackson *et al.*, 2001; Link, 2010, 2018; Smith *et al.*, 2011; Hilborn *et al.*, 2015). Here, I focus on trophic transfer as the basis for determining limitations to fisheries production because it is intuitive, has had several background studies to establish and describe these relationships both classically (Graham and Edwards, 1962; Ricker, 1969; Schaefer, 1965; Ryther, 1969) and more recently (Pauly and Christensen, 1995; Chassot *et al.*, 2010; Conti and Scardi, 2010; Blanchard *et al.*, 2012; Friedland *et al.*, 2012; Watson *et al.*, 2014; Fogarty *et al.*, 2016; Stock *et al.*, 2017), and most stock-oriented definitions of overfishing likewise focus on production of the population while simultaneously recognizing that other features of stock productivity do not usually address these other aspects explicitly (i.e. predation, links to habitat, etc.) to demarcate single stock overfishing (Mace, 1994; Hilborn *et al.*, 2015).

To place this in perspective and to delineate quantitative thresholds for EOF, it has been established that there are clear limits to oceanic primary production (Antoine *et al.*, 1996; Carr *et al.*, 2006); it then follows that there are real limits to fisheries production that are well known (Graham and Edwards, 1962; Ricker, 1969; Schaefer, 1965; Ryther, 1969; Pauly and Christensen, 1995) and continually refined (Chassot *et al.*, 2010; Conti and Scardi, 2010; Blanchard *et al.*, 2012; Friedland *et al.*, 2012; Watson *et al.*, 2014; Fogarty *et al.*, 2016; Stock *et al.*, 2017). Essentially there are legitimate limitations on how many fish any given ecosystem can produce (Pauly and Christensen, 1995), can store as biomass (Schlenger *et al.*, 2019), and hence can be caught (Libralato *et al.*, 2008). Based on these realities there are associated thresholds which can demarcate EOF. A series of trophic transfer calculations, models, and global observations have repeatedly demonstrated these real limits to fisheries production, ultimately as established by primary production (Pauly and Christensen, 1995; Chassot *et al.*, 2010; Conti and Scardi, 2010; Friedland *et al.*, 2012; Watson *et al.*, 2014) with continued refinements and nuances in this understanding (Fogarty *et al.*, 2016; Stock *et al.*, 2017; Link and Watson, 2019; Petrick *et al.*, 2019).

Material and methods

EOF, cumulative biomass indicators, and their thresholds

In short, there are three main EOF indices plus cumulative trophic curves that can be used to demarcate EOF. The main EOF indices are the Ryther, Fogarty, and Friedland index (Link and Watson, 2019). The Ryther index consists of total catch presented on a per unit-area basis for an ecosystem. The Fogarty index is the ratio of total catches to total primary productivity in an ecosystem. The Friedland index is the ratio of total catches to mean annual chlorophyll in an ecosystem. These indices are founded upon the ecological concept of trophic transfer, with specific thresholds developed for each

index to delineate whether EOF is actually occurring. One can develop and estimate thresholds for them based on first principles, trophic transfer theory, and empirical evidence.

The Ryther index is essentially catch by area, and the threshold for it is based on empirical evidence from over 70 years of observations from over 60 ecosystems (Bundy *et al.*, 2012; Tam *et al.*, 2017; Link and Watson, 2019). What emerges is that to maintain catches at a level above $\sim 3 \text{ t km}^{-2} \text{ yr}^{-1}$ (i.e. levels of excessive EOF) requires an incredibly productive ecosystem, which is not sustainable in the long-term (c.f. Supplemental Materials, *Sensitivity Analysis and EOF Thresholds- Global Calculations to Scope Potential EOF Thresholds*). Any instances where this threshold of $\sim 1 \text{ t km}^{-2} \text{ yr}^{-1}$ has been exceeded for extended periods of time have been followed, and verified, by significant and often sequential stock collapses, major stock overfishing, depletion, and lowering of average trophic level (Link and Watson, 2019).

The threshold derived for the Fogarty index was based on the following. Before using the trophic transfer equation (Equation (1) here; adopted from Equation (5) in Link and Watson (2019)), one can make simple assumptions of about 10% Transfer Efficiency (TE; c.f. Fogarty *et al.*, 2016; Link and Watson, 2019; Eddy *et al.*, 2021) for either 3 or 4 trophic levels (TLs), which gives a range of 0.1–1% (i.e. 10% TE for 4 TL = $0.1^4 = 0.1\%$, 10% TE for 3 TL = $0.1^3 = 1\%$). By then plugging into a simplified version of the transfer equation (repeated here; Equation (1)):

$$C_{\text{tot}} = \sum_{i=1}^{TL} \alpha \cdot PP \cdot TE_i^{TL-1}, \quad (1)$$

where PP is net primary production (often expressed as net primary production, NPP), α is a scalar for local conditions and availability of transfer, TL is trophic level, and TE is transfer efficiency, one can bracket the range of possible threshold levels. By using average values of NPP (with a range of global estimates) and set values of α (set to ~ 15 –20% for average availability of the TL, which emerges when estimated from maintaining a global average catch that has been stable for the past 30 years; Libralato *et al.*, 2008; Fogarty *et al.*, 2016; Stock *et al.*, 2017), and making average assumptions about these TE (between 6 and 20%) and TL (between 2.8 and 4.2) values gives a range of 0.3–3.0%. Thus, the range from theory and empirical examination is 0.1–3.0%. I then conducted sensitivity analyses (Supplemental Materials, *Sensitivity Analysis and EOF Thresholds- Sensitivity Analysis for EOF Threshold Context*; ranges as noted above with changes to NPP included) to explore how the behavior of Equation (1) outputs change; these results all tend to identify the main inflections on the response surface regardless of assumed TE and α , or net primary production and TL. Basically, these all show that catch declines as TL increases, or as TE and NPP decline. Since the threshold is a ratio, it ultimately scales to NPP.

I then calculated actual values for Equation (1) (c.f. Link and Watson, 2019), with more known and constrained limits of NPP, TL, α , and TE, and then compared those outputs to previously reported values of what one could expect for total, global catch (summing across all LMEs, etc.; i.e. 0.1–0.42 Gt; c.f. Supplemental Materials, *Sensitivity Analysis and EOF Thresholds- Global Calculations to Scope Potential EOF Thresholds*). That gave the range of values of what could potentially be supported between 0.22 and 0.92%, with a high level of 1 Gt (i.e. ~ 10 x what FAO reports for all global landings; FAO, 2018, 2020), resulting in 2.2%. This was then compared empirically to several individual ecosystems known to have had sequential overfishing challenges (for which this ratio

was previously and separately calculated with different, nationally or regionally-based data; Link and Watson, 2019), to see approximately at what level this Fogarty index was when conditions began to deteriorate. They all showed signs of change around 1%. As the Friedland ratio is catch to chlorophyll, and as chlorophyll is strongly correlated to NPP, I used a similar approach and line of logic as to the Fogarty index to develop the threshold level for this index. Thus, from a theoretical consideration (e.g. 10% TE for 3 TL = $0.1^3 = 1\%$; Supplemental Materials, *Sensitivity Analysis and EOF Thresholds- Simple Energy Transfer Calculations*), to sensitivity bracketed ranges (c.f. Supplemental Materials, *Sensitivity Analysis and EOF Thresholds- Global Calculations to Scope Potential EOF Thresholds*), to bracketed possible total catches, to empirically evaluated ecosystems as lines of evidence (Supplemental Materials, *Sensitivity Analysis and EOF Thresholds- Summary*), I set this threshold at $\sim 1\%$ for the Fogarty index and ~ 1 for the Friedland index.

The recommended approach to considering these three main EOF indices is as follows. When data for an ecosystem exhibits EOF index values near any one of these index thresholds, it merits additional attention. When it has values exceeding all three index thresholds, it is probable that EOF is occurring in that ecosystem. When the values are 3–5 times greater (i.e. in excess of 300%, also approximately > 1.5 –2 SD from the threshold value) than the threshold for more than one of these indices, it is probable that significant EOF is occurring. Thresholds for these three main EOF indices have been examined empirically, with thresholds being approximately and consistently at these same levels before major ecosystem changes occur (Bundy *et al.*, 2012; Link *et al.*, 2012; Large *et al.*, 2015; Tam *et al.*, 2017). The absolute value of and the uncertainty surrounding these thresholds still warrants further debate and exploration. Here I provide them as reasonable proxies from which EOF is likely indicated.

In addition to the three main EOF indicators, cumulative trophic curves emerge upon examination of cumulative biomass (cumB) and cumulative production (cumP) across TLs for an ecosystem (Link *et al.*, 2015). These emergent features are based on observations and supporting theory that biomass accumulation is (log-) normally distributed (Figure 1c) and represents transfer (even if inefficiently) of biomass and hence production up a food web to successive TLs (Figure 1b). Therefore, if production at different TLs always results in trophic pyramids because the TE is always less than 1, cumulative production curves are asymptotic, plateauing near the sum of all ecosystem productivity. Fundamental trophodynamic features—overall system limits based on primary production (Figure 1a), turn-over of populations, average growth efficiency—are the overall system limits that influence the production curve (c.f., Link *et al.*, 2015). Furthermore, biomass accumulation across TL is not inevitably pyramidal in marine systems but is more often rhomboidal due to high standing biomass at TL 2 (i.e. benthos and plankton; Figure 1b); thus, the cumulative biomass curve across trophic levels (cumB-TL) is a sigmoidal curve (i.e. a curve with a clear inflection point indicative of this rhomboidal pattern (Figure 1e). The cumB-TL curves exhibit a typical “S” shape that seems to hold regardless of type of ecosystem or type of data (biomass, catch, energy budget, etc.) used to construct these curves (Pranovi and Link, 2009; Pranovi *et al.*, 2014). The cumB-cumP curves likewise tend to exhibit “hockey stick” shapes (Figure 1f). Broader inspection of these curves has confirmed the existence and commonality of these patterns from over 200 different marine ecosystems across the globe (Link *et al.*, 2015; Libralato *et al.*, 2019); they have also confirmed repeatable, consistent and

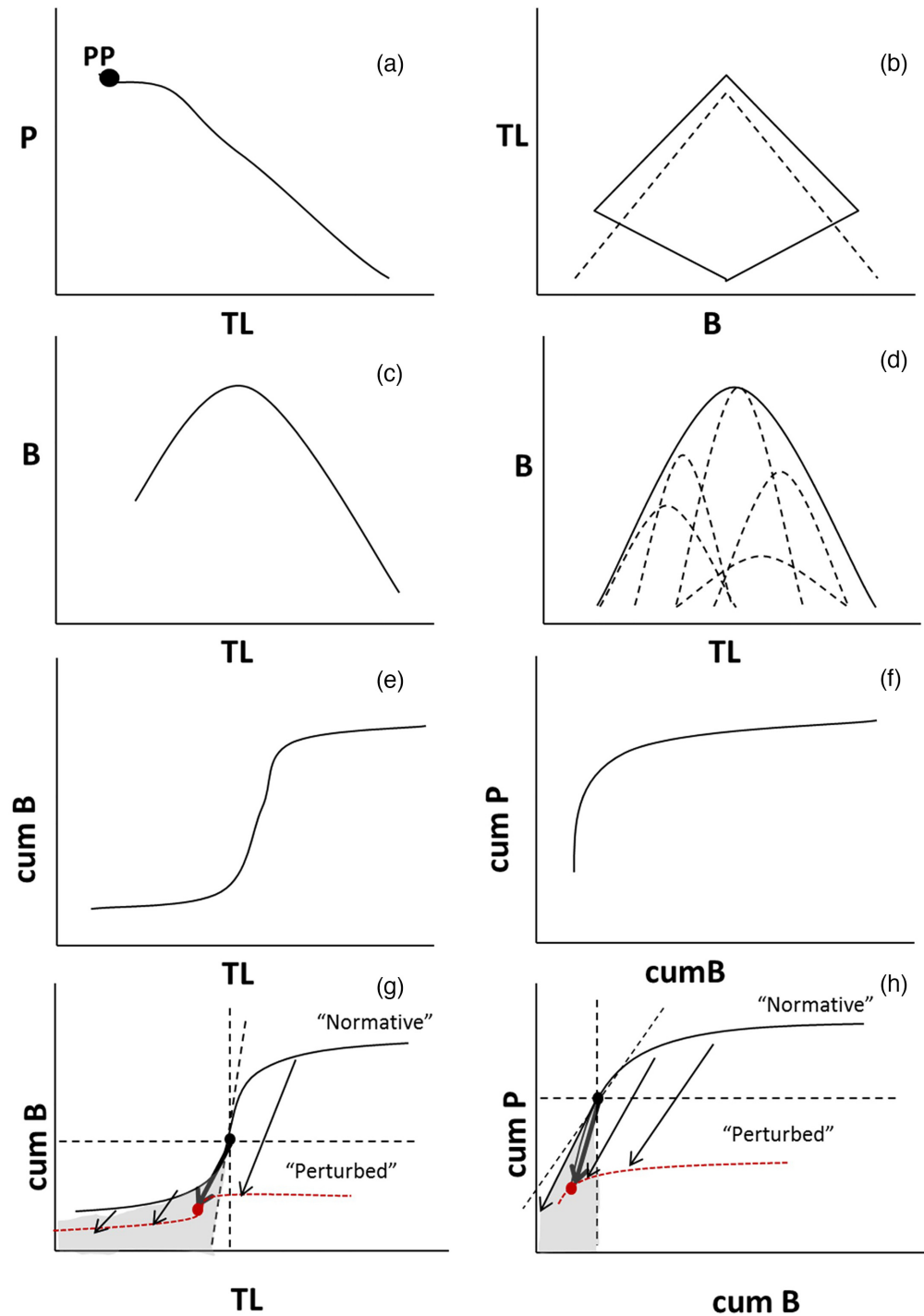


Figure 1. Schematic of general patterns of ecosystem dynamics resulting in the cumulative trophic theory (a–h). Panels (a–c) represent known theory and observations, (d) constraints, (e and f) the resultant theory, and (g and h) predictions from the theory. (a) The decline of productivity across increasing TLs, starting at the point where primary production is estimated (Pauly and Christensen, 1995; Lindeman, 1942; Strayer, 1991; Oksanen, 1997; Friedland *et al.*, 2012; Link *et al.*, 2012). (b) The trophic pyramid (dashed) and rhomboid (solid) of biomass with increasing TL (Elton, 1927; Lindeman, 1942). (c) The unimodal distribution of biomass over TLs (Lindeman, 1942; Strayer, 1991; Oksanen, 1997). (d) The trophic spectra of biomasses of individual populations within a total, systemic biomass constraint (Gascuel *et al.*, 2005, 2008; Libralato and Solidoro, 2010). (e) The cumulative biomass sigmoidal pattern across increasing TL. (f) The “hockey stick” of cumulative production across cumulative biomass. (g) Prediction showing the shift in cumulative biomass over TL from a “Normative” system as it moves (depicted by arrows) to a perturbed system. Dashed lines intercepting axes represent inflection point values, and angled dashed line represents slope of the curve at the inflection point, the dot represents the inflection point, and shaded areas represents a zone of perturbation below some ecosystem threshold. (h) Similar to (g) but for cumulative production across cumulative biomass. B = biomass, TL = trophic level, P = production, PP = primary production, cumB = cumulative biomass, and cumP = cumulative production. Adapted from Link *et al.* (2015).

predictable changes in curve shape due to perturbations that alter trophodynamics in marine ecosystems (Pranovi *et al.*, 2012, 2014, 2020; Link *et al.*, 2015; Libralato *et al.*, 2019). The schematic of the cumB-TL curve shown in Figure 1g (adapted from Link *et al.*, 2015) demonstrates that perturbations result in the “S” curve becoming less steep and moving toward lower TLs. Conversely, ecosystem recovery results in increasing steepness and the “stretching” toward upper TLs of these curves. These repeatable and predictable dynamics imply that the core facets of these curves and their parameters, which represent the primary determinants of the “S” curve shape (i.e. the biomass inflection point, TL inflection point, and steepness (or slope)) behave in ways that are useful to elucidate ecosystem recovery or perturbation. These parameters can then be tracked over time to determine major shifts in the condition of an ecosystem. These curve parameters also represent emergent properties of marine ecosystems with a surprising ability to elucidate ecosystem structure and functioning. Hence, these cumulative trophodynamic curves and their associated properties hold some promise in demarcating ecosystem conditions that require management action.

These cumulative trophic curve “S” and shrinking hockey sticks are observed in every marine ecosystem, respond consistently, repeatedly, and predictably to perturbation or recovery, and thus can inform marine EOF. From a global study of over 60 LMEs, empirical thresholds emerged for the “S” curve parameters (Libralato *et al.*, 2019). The thresholds for these are: cumB inflection point at $\sim 33\%$; TL inflection point at ~ 3.4 ; and steepness of ~ 0.5 . This implies that as these curve parameters move cross and then remain below these thresholds, the “S” shape of the curve has in fact shrunk in a manner consistent with perturbation (Figure 1g). Previous empirical estimates had slightly higher thresholds (Pranovi *et al.*, 2012; Link *et al.*, 2015), but more refined and larger sample sizes have narrowed these curve parameter values to the values noted above (Libralato *et al.*, 2019). The value of these “S” curve parameter thresholds essentially indicates that when two-thirds of the biomass in an ecosystem has been removed, when the TL has shifted below a medium TL, and when the curve becomes flatter, the conditions in the ecosystem are generally undesirable (Pranovi *et al.*, 2012, 2014; Libralato *et al.*, 2019). Libralato *et al.* (2019) further discusses the nuances of transitions approximately at or around these “S” curve parameter values, as well as interpreting hysteresis of crossing these thresholds. Again, the absolute value of and the uncertainty surrounding these “S” curve parameter thresholds still warrants further debate and exploration. Here I provide them as reasonable proxies from which EOF is likely indicated.

Three main eof indicator data sources and analysis

Marine capture fisheries data was obtained from Watson (2017); prior descriptions (Watson *et al.*, 2004, 2017; Anticamara *et al.*, 2011; Rousseau *et al.*, 2019; and references therein) provide fuller details of these data. To compare this Watson dataset, data were downloaded from FAO using the Fish-StatJ v2.12.2 software and database package and from the Sea Around Us (SAU) project, by LMEs, using the online GUI to download CSV files (Pauly *et al.*, 2020). I recognize that there have been prior disputes regarding the exact magnitude of total marine capture fisheries yield (Watson and Pauly, 2001; Watson, 2017; Pauly and Zeller, 2016; Watson *et al.*, 2014; Branch *et al.*, 2010). These debates focus on the magnitude of fishery production potential, whether the estimates are carrying capacity (K) or Biomass at MSY (K/2), whether the

estimates adequately represent Illegal, Unreported and Unregulated fishing, the degree of awareness that the data do not contain recreational fisheries catch, whether the methods for extrapolating data are germane, and related concerns over missing or misrepresented data. Despite these contested nuances regarding the magnitude and source of these catch estimates, all tend to agree that the total, global catch of marine capture fisheries has fluctuated about essentially the same level for nearly 30 years. Additionally, though there are differences among data sets in terms of magnitude, the same general trends, and order of magnitude results are repeated (Watson and Pauly, 2001; Watson, 2017; Pauly and Zeller, 2016; Watson *et al.*, 2014; Branch *et al.*, 2010). And although updates are available, I chose to retain a data set that lags contemporary estimates of catch to avoid any confusion about current catch and management advice. Though the present work focuses on U.S. LMEs, I note the comprehensiveness of the data from Watson (2017) and chose to use it to be consistent with other, comparable, international studies (Link and Watson, 2019; Link *et al.*, 2020). One could just as readily use reported national landings from the U.S., or the FAO or SAU databases, to calculate these estimates (see below; independent of these international datasets, <https://www.fisheries.noaa.gov/foss/f?p=215:200:.....>). For these reasons, I used the compiled dataset from Watson (2017) to calculate the three main EOF indicators.

Effort data were similarly tallied and examined at the LME scale (Anticamara *et al.*, 2011; Watson, 2017, R. Watson, pers. comm.). Catch and effort data (units of kw seaday⁻¹) were analyzed using LME designations. Dividing the former by the latter provides estimates of CPUE. I note that aggregation across spatial scales could obscure some signals across and among fisheries, but at the scale at which most fisheries operate (i.e. the LME scale), the main patterns should emerge. Estimates of primary production (described below) were chosen at resolutions consistent with these LME scales. I also recognize that aggregation across taxa could also obscure patterns among fisheries, but since the main purpose was to examine total catches by ecosystem, the total catch patterns should also emerge from such an approach.

Measures of chlorophyll *a* and net primary production were estimated for all U.S. LMEs, from 1998 (when satellites began providing these data) to 2014 using satellite imagery. These used a combined SeaWiFS and MODIS imagery set (<http://oceancolor.gsfc.nasa.gov/>). Chlorophyll *a* was adopted from the merged time series data (<http://hermes.acri.fr/>) at 25 km spatial resolution, and annually integrated using monthly time steps. Primary production was estimated using the Behrenfeld method (Behrenfeld and Falkowski, 1997; c.f. Eppley, 1972), and was annually integrated using daily values, converted to wet weight, and summed for each LME.

Catches assigned to LMEs are expressed as t km⁻², and are presented as the Ryther index (with km⁻² from the LME area). The catch data were compared to chlorophyll *a* values to calculate the Friedland index. The same catch data were compared to estimates of net primary production to calculate the Fogarty index (Fogarty *et al.*, 2016). I recognize that these data need to be contextualized within regional and even local conditions. Additionally, within a given LME, other sources of production may be occurring at the sub-LME scale that might not be as readily detectable via satellite (upwelling, estuarine, benthic, etc. inputs) and thus could sporadically and locally alter production estimates. Additionally, some taxa may migrate across LME boundaries. Thus, I recommend that the indices proposed here be used conscious of other, possible sources of productivity that are germane to the scale at which

fisheries management occurs in each LME. From these global LME datasets, I extracted and explored the time series for the eight U.S. LMEs.

Cumulative curve data sources and analysis

Following the methodology of Libralato *et al.* (2019), I used landings data for the eight U.S. LMEs obtained from the Sea Around Us Project (SAU) database (<http://www.seaaroundus.org/>; Pauly *et al.*, 2020). These data are used here as a proxy for ecosystem status. I used them to be semi-independent from the Watson (2017) database when providing this different perspective on potential EOF, though the data are comparable and based on some similar underlying data sets. I used this dataset to examine these curves that use a different way of treating this composite catch information to avoid biases of any one method. The data consists of landings (weight, in tons) for each taxa caught for each year from 1950 to 2010. I acknowledge that as a proxy for biomass, landings or catch data have had some difficulties (de Mutsert *et al.*, 2008; Branch *et al.*, 2010), but there remain some data deficiencies when it comes to estimates of biomass for all taxa across all TLs for all these eight LMEs, let alone all global LMEs (*sensu* Shannon *et al.*, 2014). Further, prior work has shown that for estimating the cumulative trophic curves the same patterns emerge using landings data as to biomass data, and the results are robust to underlying sources of biomass data as long as it covers a wide range of TLs and taxa; plus though TL inflection points change with the use of landings data slightly, the percentage of cumulative biomass inflection and steepness parameters have negligible change (Pranovi *et al.*, 2014; Link *et al.*, 2015; Libralato *et al.*, 2019; see further descriptions below). Hence using landings data as a proxy for cumulative trophic curves has robust precedent and, although minor differences in curve parameters may result, detects the major signals of change that one would expect. Data include LMR taxa that represent the most important commercial invertebrates and fish species, while some general groups are also presented (e.g. bony fish). These landings data for all LMEs from SAU spans the entire global ocean (c.f. Sherman *et al.*, 1993; Hempel and Sherman, 2003), but is focused on the eight U.S. LMEs here.

Each taxon was associated with a TL as obtained from local food habits databases (e.g. Smith and Link, 2010; Simons *et al.*, 2013; Livingston *et al.*, 2017), Fishbase (www.fishbase.org), Sealifebase (www.sealifebase.org) or from local, published food webs (Northeast U.S., Link *et al.*, 2006, 2008, 2010; Lucey *et al.*, 2021; Gulf of Mexico, Walters *et al.*, 2008; de Mutsert *et al.*, 2016; Sagarese *et al.*, 2017; Chagaris *et al.*, 2020a, b; South Atlantic and Caribbean, Opitz, 1996; Okey and Pugliese, 2001; Smikle *et al.*, 2010; West Coast-California Current, Field, 2004; Field *et al.*, 2006, Brand *et al.*, 2007; Ruzicka *et al.*, 2012; Alaska, Aydin *et al.*, 2002, 2007; Heymans *et al.*, 2007; Lee *et al.*, 2010; Gaichas *et al.*, 2011; Pacific Islands, Polovina, 1984; Parrish *et al.*, 2012; Howell *et al.*, 2013; Weijerman *et al.*, 2014, 2015; plus Ecobase for further context, Colleter *et al.*, 2015); for a few taxa, TL was assigned according to available, local ecosystem model outputs. Landings by TL were then estimated for each LME and each year, which were then ordered by increasing TL. From that data, a cumulative curve of catches (biomass proxy) vs. TL was generated (i.e. the cumB-TL curve, c.f. Link *et al.*, 2015). The resultant cumB vs. TL data resemble an S-shaped curve, consistent with prior observations and theory (Pranovi *et al.*, 2012, 2014; Link *et al.*, 2015; c.f. Libralato *et al.*, 2019; Pranovi *et al.*, 2020). For each LME and each year, the data were fit independently to an S-shaped curve

using a 5-parameter logistic nonlinear regression model (Ricketts and Head, 1999; i.e. using the “drc” package (Ritz *et al.*, 2015) for R (v3.5.2; R Core Team, 2018)). The main curve parameters, steepness (or slope at the inflection point; Slope), TL at the inflection point (TL_Infl), and biomass at the inflection point (B_Infl) were estimated. Further details on the method for curve-fitting and estimating the parameters can be found in works by Pranovi (c.f. Pranovi *et al.*, 2014, 2020). From this global LME dataset, I estimated and examined time series of curve parameters for U.S. LMEs.

Comparison to major LMR taxa comprising catch

For further context, I present examples of major populations or aggregated groups of LMR catches for the Northeast U.S., Gulf of Mexico and the California Current LMEs (based on the NOAA Fisheries landings database; [https://www.fisheries.noaa.gov/foss/f?p=215:200:::~:](https://www.fisheries.noaa.gov/foss/f?p=215:200:::)). These data were for commercial fisheries landings not inclusive of recreational landings, and were also selected for the top (by weight) 20–30 landed species (though often only the approximately first 10–12 are shown). These by definition will be less than total ecosystem landings. I used these national, U.S. landings data to be semi-independent of the Watson (2017) or SAU (Pauly *et al.*, 2020) databases to present yet another perspective on the fisheries in these LMEs and to avoid any confounding or collinearity among the same datasets; that said, these should generally exhibit similar patterns across the main, aggregate features of these data. The aim of this comparison was to contrast the main EOF indicators and cumB-TL curves with more typical, stock or stock group-oriented data, particularly to compare major trends and changes, and to highlight detection of the timing related to major changes in the ecosystem.

For both the major EOF indicators and the individual taxon landings time series, I evaluated whether there were trends using the non-parametric Cox–Stuart test, which is essentially a modified signs test or Wilcoxon rank test. When coupled with a runs test, one can identify if there is a significant departure in the sequence of data from the median, and approximate the change point at which it occurred (Daniel, 1990). All tests were executed using two-tails (above or below median) with a 5% probability of detection. Since there are multiple LMEs, taxa, and hence time series (8 LMEs, ~25 stocks, + 3 EOF indicators, and ~60+ years), I simply refer to approximate periods in the time series where a major data shift occurred (c.f. Supplemental Materials, Statistical Analysis, Supplementary Tables S2 and S3 for more details of these non-parametric change statistics).

Presentation of EOF information

I present primary production, catch, effort, CPUE, and the three main EOF indicators (i.e. the Ryther index, the Fogarty index, and the Friedland index) over time for the eight U.S. LMEs. I also present the cumulative biomass-trophic level “S” curve parameters over time, specifically B_infl vs. TL_infl, and slope vs. TL_infl for the U.S. LMEs. The biomass at the inflection point is presented as a normalized percentage relative to the maximum in the time series.

I also present what are essentially modified Kobe plots for each U.S. LME. Instead of showing fishing rate compared to perturbation of biomass for individual stocks as in standard Kobe plots, I present one example index of EOF (i.e. the Ryther index) against the cumB-TL biomass inflection point (B_infl; i.e. perturbation to biomass;

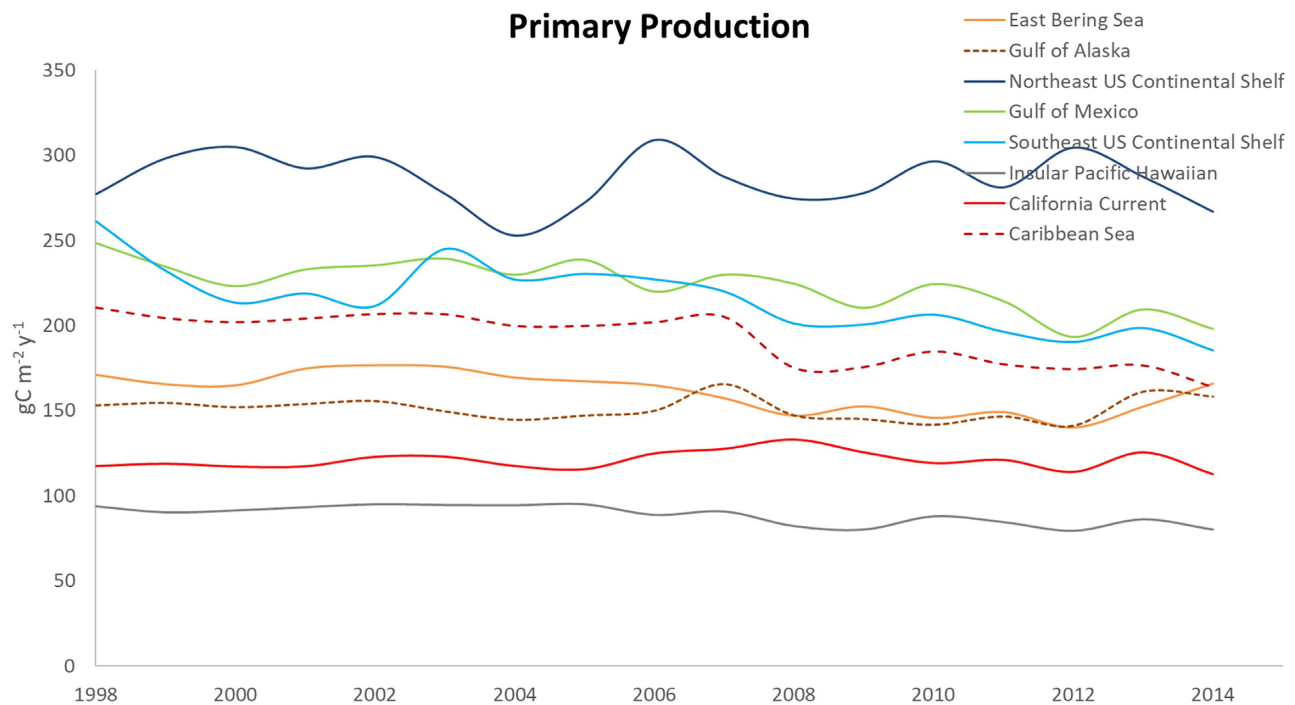


Figure 2. Primary production estimates for the eight U.S. LMEs. This sets the stage for any subsequent fisheries production.

another reason why I chose to use independent data sets) as a means to show how integrated perturbation or recovery occurs over time.

Results

The majority of measurements of primary production (PP) are on the order of 150–250 $\text{g C m}^{-2} \text{yr}^{-1}$ (Figure 2). Of note is the higher PP observed in the Northeast U.S. Continental Shelf, and lower PP observed in the California Current and Hawaiian Islands. Also noteworthy is the relative stationarity of production in these LMEs over the past 30+ years. There may be a slight downward shift for the Gulf of Mexico, Southeast U.S., and Caribbean LMEs in the 2000s; whether this represents an actual change in PP or reflects a change in source of satellite data is unclear. Based on PP alone, one would expect higher catches in the Northeast U.S., Gulf of Mexico, and Southeast U.S. Conversely, one would expect relatively lower catches in the California Current and Hawaiian Islands.

About half of the LMEs have exhibited a prominent increase in total catch over the past 60 years, including the Eastern Bering Sea, Gulf of Alaska, California Current, Hawaii, and Gulf of Mexico (Figure 3). The Northeast U.S. and Southeast U.S. LMEs have exhibited a declining trend in total catch over time, whereas the Gulf of Mexico, Caribbean, and Gulf of Alaska have exhibited an increase followed by a decrease in total catch. The three continental Pacific LMEs (Gulf of Alaska, Eastern Bering Sea, and California Current) all exhibit relatively high levels of total catch, as has the Northeast U.S. and Gulf of Mexico LMEs. A total of two of the three sub-tropical LMEs (Hawaii and Southeast U.S.) exhibited moderate to low levels of total catch, though the recreational and subsistence fisheries catches are likely (at least mildly) under-reported here. Effort in most U.S. LMEs exhibited peaks in the 1980s, followed by a decline and stabilization of total effort thereafter (Figure 3). Consistent with catch results, there have been recent declines in effort

in the Northeast, Southeast, Gulf of Alaska, Gulf of Mexico, and Caribbean LMEs. Contrary to many other LMEs (not shown here; c.f. Anticamara *et al.*, 2011; Watson, 2017), total fishing effort in U.S. LMEs has stabilized over the past 60 years and is not increasing.

The CPUE has seen spikes in recent years for most LMEs except the Gulf of Alaska and California Current (Figure 4). Many of these emerged around a stationary mean over the past 30 years (Southeast U.S., Eastern Bering Sea, Gulf of Mexico, and Hawaii), one after a steady decline (Northeast U.S.), and another (the Caribbean) after an increase. The peaks in CPUE varied for each region over time, with no clear nor nationally consistent pattern of timing that emerged. All of these LMEs are relatively quite low in CPUE (relative to other, global LMEs; Anticamara *et al.*, 2011; Watson, 2017; Link *et al.*, 2020), with none exhibiting values above 0.1 (t kWh^{-1}).

Examining the EOF indicators reveals consistent patterns. The Ryther index suggests that the Northeast U.S. LME is experiencing significant EOF (Figure 5) with values well above the global threshold, as do the Fogarty (Figure 6) and Friedland (Figure 7) indices. The Ryther index (Figure 5) also suggests that the Gulf of Mexico LME has improved but may still be experiencing EOF, which is congruent with the Friedland index (Figure 7). The Southeast U.S. may have experienced EOF in the 1980s based on the Ryther index (Figure 5), and the Friedland index suggests EOF may have occurred for the Southeast U.S. and California Current (Figure 7). These two LMEs are collectively not over the EOF threshold, but may have been near it at certain points in time (Figures 5 and 7). No other LMEs besides the Northeast U.S. LME are experiencing EOF according to the Fogarty index (Figure 6). Recognizing that the Friedland index may be highly sensitive and the Fogarty index may be just the opposite (Link and Watson, 2019), and that these indices are (due to their underlying data) shorter than the Ryther index, it is not trivial that all three indicators suggest the Northeast U.S. LME is experiencing EOF. The Ryther index (Figure 5) and Friedland index (Figure 7) also suggest that the Gulf of Mexico

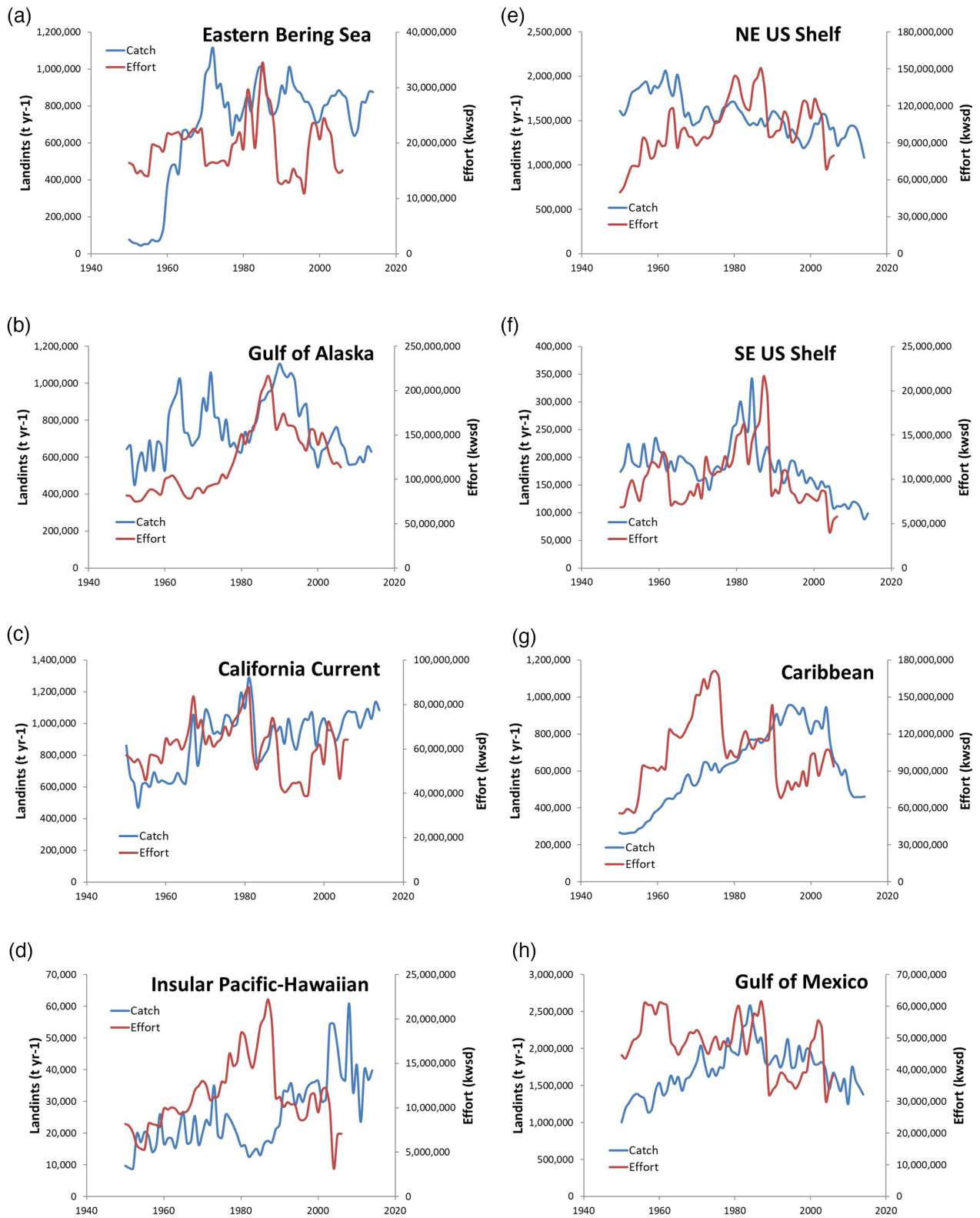


Figure 3. Total catches (blue line) and effort (red line) for the eight U.S. LMEs. (a) Eastern Bering Sea, (b) Gulf of Alaska, (c) California Current, (d) Insular Pacific–Hawaiian, (e) Northeast U.S. Continental Shelf, (f) Southeast U.S. Continental Shelf, (g) Caribbean Sea, and (h) Gulf of Mexico.

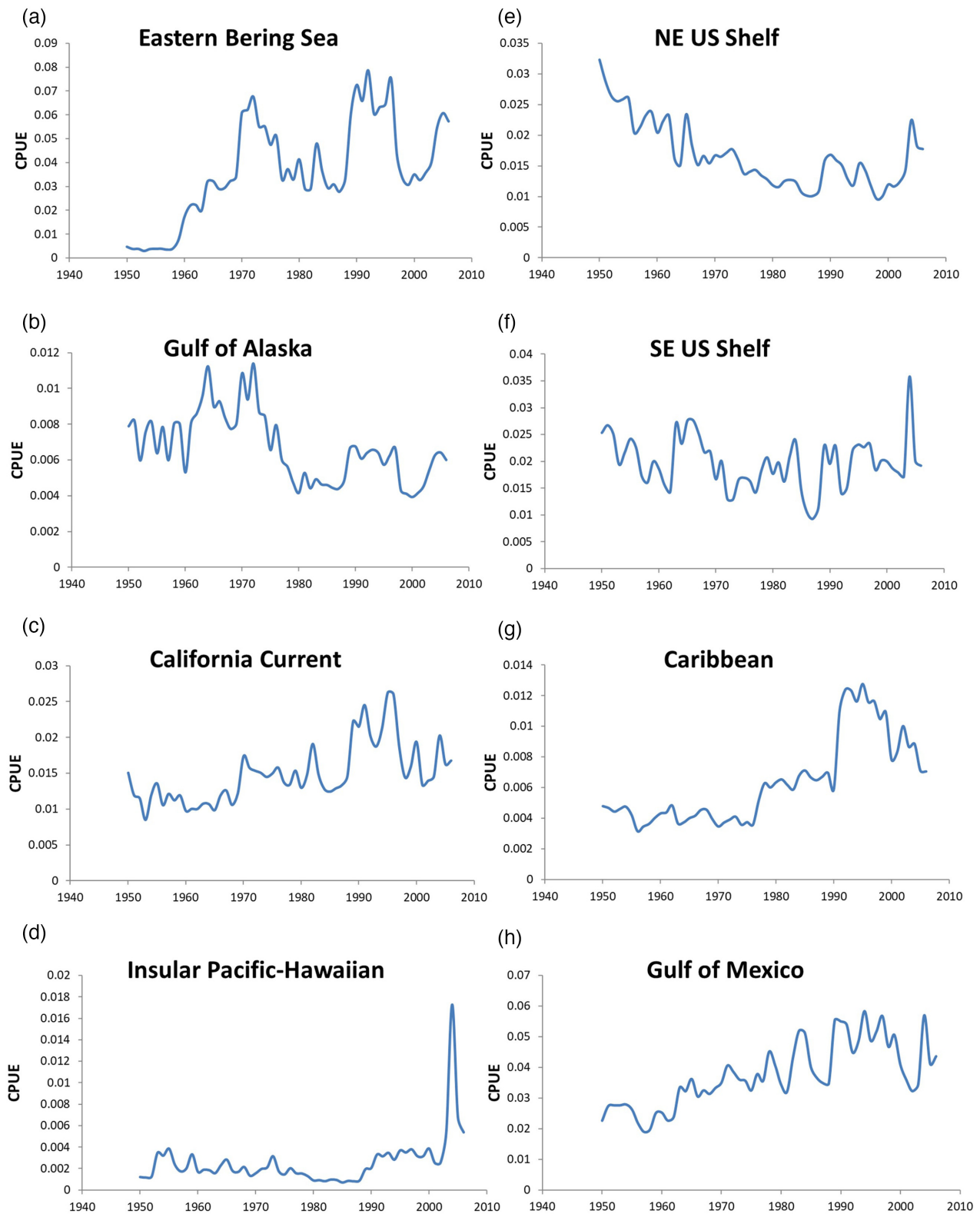


Figure 4. CPUE for the eight U.S. LMEs. (a) Eastern Bering Sea, (b) Gulf of Alaska, (c) California Current, (d) Insular Pacific–Hawaiian, (e) Northeast U.S. Continental Shelf, (f) Southeast U.S. Continental Shelf, (g) Caribbean Sea, and (h) Gulf of Mexico.

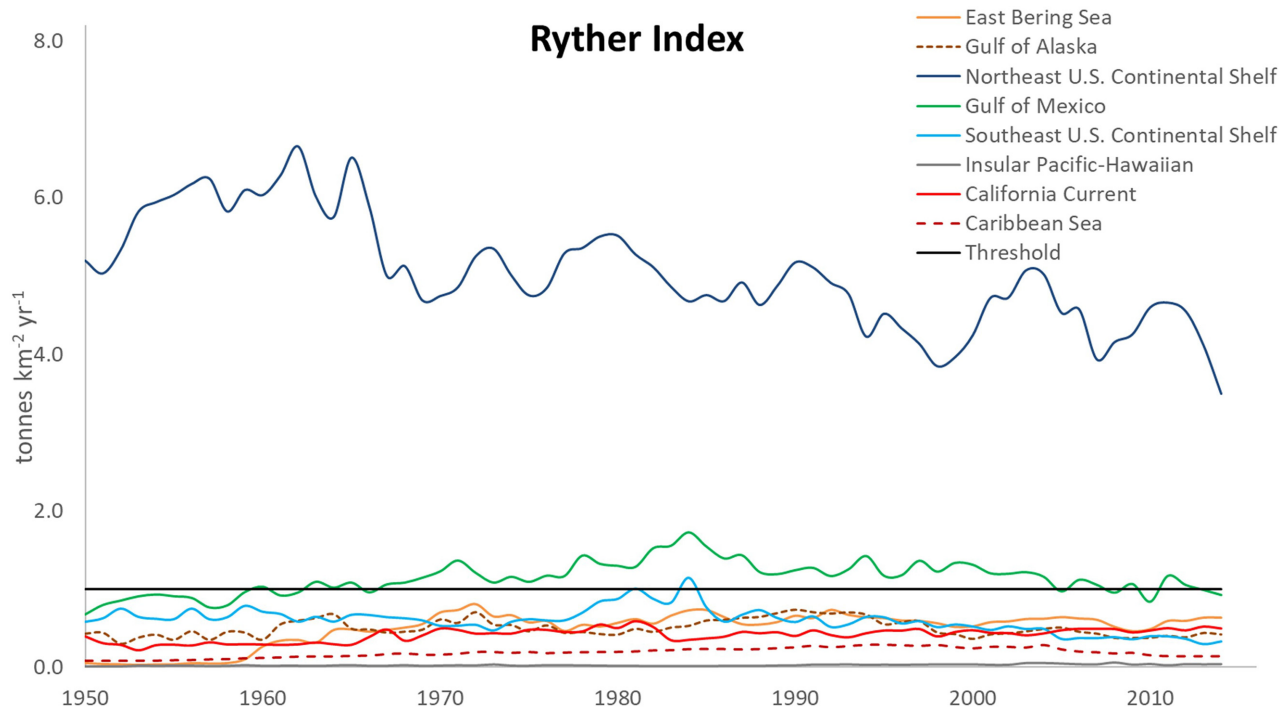


Figure 5. The Ryther index of EOF for the eight U.S. LMEs. The black line corresponds to globally derived thresholds of EOF as determined by Link and Watson (2019).

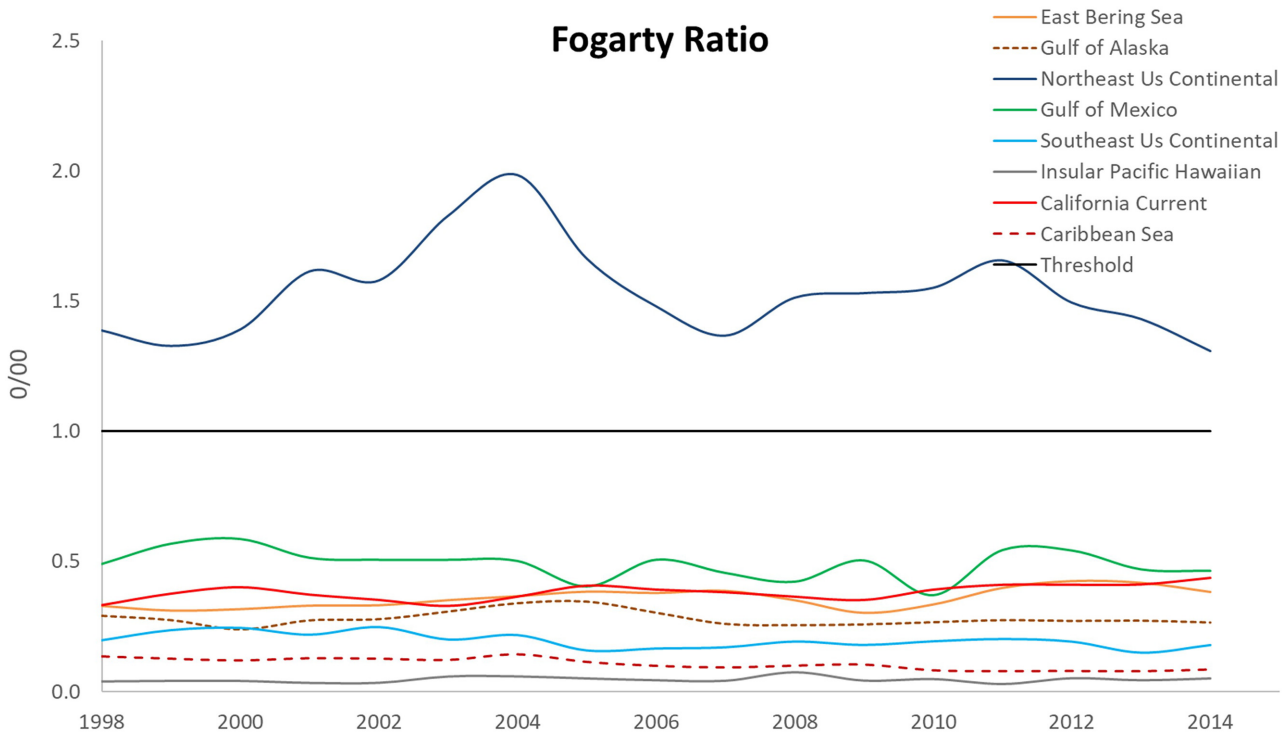


Figure 6. The Fogarty index of EOF for the eight U.S. LMEs. The black line corresponds to globally derived thresholds of EOF as determined by Link and Watson (2019).

LME is experiencing EOF approximately at the threshold to a level even twice the threshold, suggesting that this LME may also be subject to EOF. So, one of the eight U.S. LMEs is experiencing significant EOF, another is likely experiencing EOF, and the other LMEs

likely are not. That is, two out of eight U.S. LMEs exhibit symptoms of EOF (not only these EOF indicators, but also other metrics as well; e.g. declines in aggregate CPUE (Figure 4) and catch (Figure 3)).

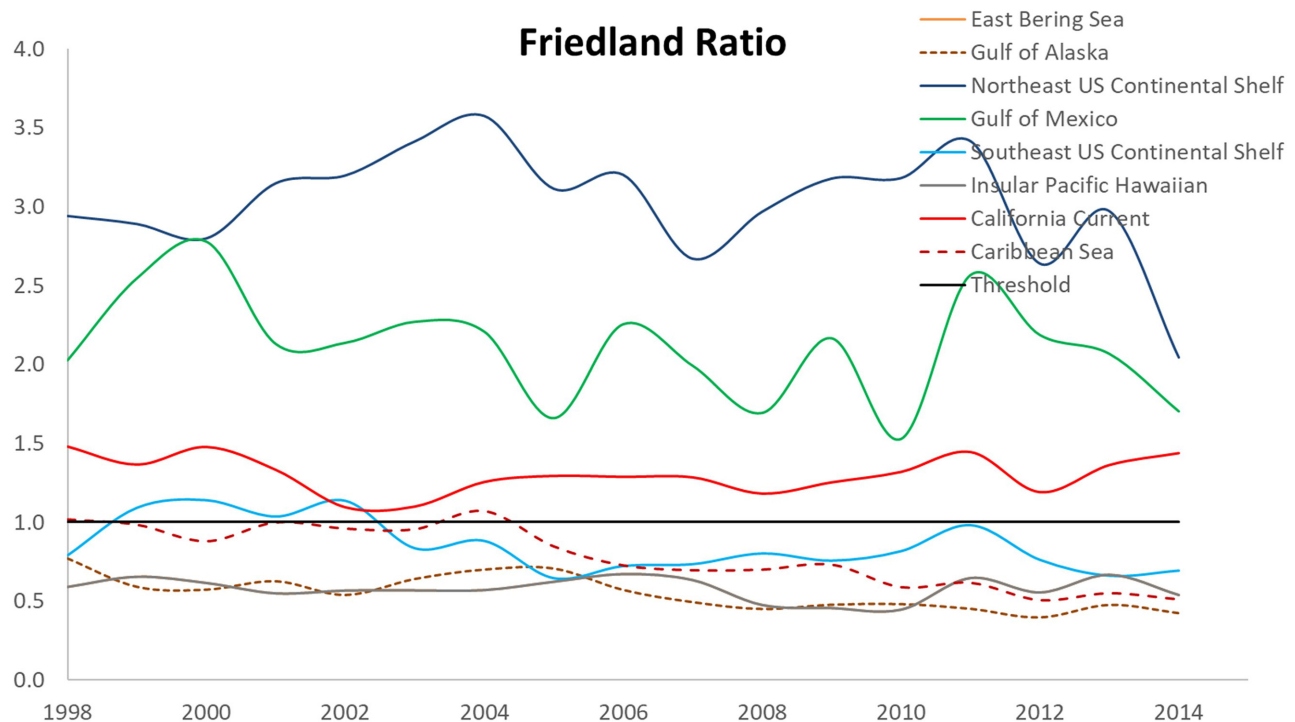


Figure 7. The Friedland index of EOF for the eight U.S. LMEs. The black line corresponds to globally derived thresholds of EOF as determined by Link and Watson (2019).

The cumulative biomass and trophic level “S” curves were again commonly observed in U.S. LMEs, with prominent dynamics over time (not shown here). The cumulative biomass and TL curve parameter graphics demonstrate that many of the U.S. LMEs, except the Northeast U.S., Southeast U.S., and Gulf of Mexico, tend to be above the global TL inflection point threshold near TL 3.4 (Figure 8). Of interest is that the trajectories of these curves demonstrate that there have been notable shifts across TL over time, indicative of a shift in ecosystem dynamics. Few of these LMEs, except the Northeast U.S. and Gulf of Mexico, are consistently below the cumB threshold of around 33% (Figure 8). The slope and TL at inflection point graphic exhibits the notable phase shift (i.e. near perpendicular shift in curve parameters; Libralato *et al.*, 2019; Link *et al.*, 2015) for the Eastern Bering Sea, Gulf of Alaska, Northeast U.S., Southeast U.S., and Gulf of Mexico, with a particular change in the magnitude of the slope (Figure 9). These are indicative of major ecosystem changes, as the “S” curve has compressed towards the origin due to perturbation. Three of these LMEs show signs of recovery (Gulf of Alaska, Eastern Bering Sea, and Southeast U.S.) and the Gulf of Mexico and Northeast U.S. do exhibit a mild hint of a return trajectory, but not to the extent exhibited by the other LMEs (Figures 8 and 9). The other three LMEs exhibit much smaller shifts in the magnitude of the slope over time, implying stability of ecosystem structure (e.g. Hawaii and Caribbean) or routinely reset-dynamics (e.g. upwelling and California Current) in these LMEs. Collectively, these cumB-TL results are consistent with the other EOF indicators (Figures 5–7) for all the U.S. LMEs. Thus, one can infer that although the ecosystems are dynamic for all these marine ecosystems, for five of the eight there has been directional change towards a more perturbed state,

albeit with three (Gulf of Alaska, Eastern Bering Sea, and Southeast U.S.) on a recovery trajectory (Figure 9). That indications of EOF are similarly detected for the same LMEs using both this cumB-TL approach (Figures 8 and 9) and the EOF indices (Figures 5–7) confirms that both methodologies are consistent. Furthermore, both can detect EOF given a different set of underlying datasets, data treatments, data types, and theoretical bases.

Examining some of the more specific dynamics for the fisheries in these LMEs, I present landings for major taxa and taxa groups from the Northeast U.S. (Figure 10). Certainly, whenever the EOF indicators are presented, it begs the question of species composition of the catch; thus the data for EOF and representative taxa in this LME and the following examples (c.f. Supplemental Materials, *Statistical Analysis*) are informative for multiple reasons. Of note is a major decline in the 1950s–mid-1960s in the amount of various LMR caught, which stabilizes in the 1970s–1990s, and has exhibited a slight decline in more recent years. This is consistent with total landings of all taxa in this LME (Figure 3e). The dominant taxa landed in terms of weight was the Atlantic menhaden (*Brevoortia tyrannus* Latrobe), which followed the same overall trends noted. Besides menhaden, it also merits noting that other targeted and landed taxa have shifted over time. The emphasis was on Acadian redfish (*Sebastes fasciatus* Storer), flounders, Atlantic cod (*Gadua morhua* Linnaeus), and haddock (*Melanogrammus aeglefinus* L.), and has shifted towards Atlantic herrings (*Clupea harengus* L. and other Clupeidae), Atlantic sea scallops (*Placopecten magellanicus* Gmelin), crabs (Decapoda: Brachyura) and American lobster (*Homarus americanus* Milne Edwards; Figure 10). Of interest is that EOF indicators (Figures 5–7) track these patterns, especially the Ryther index. In particular, EOF was already extant in the 1950s,

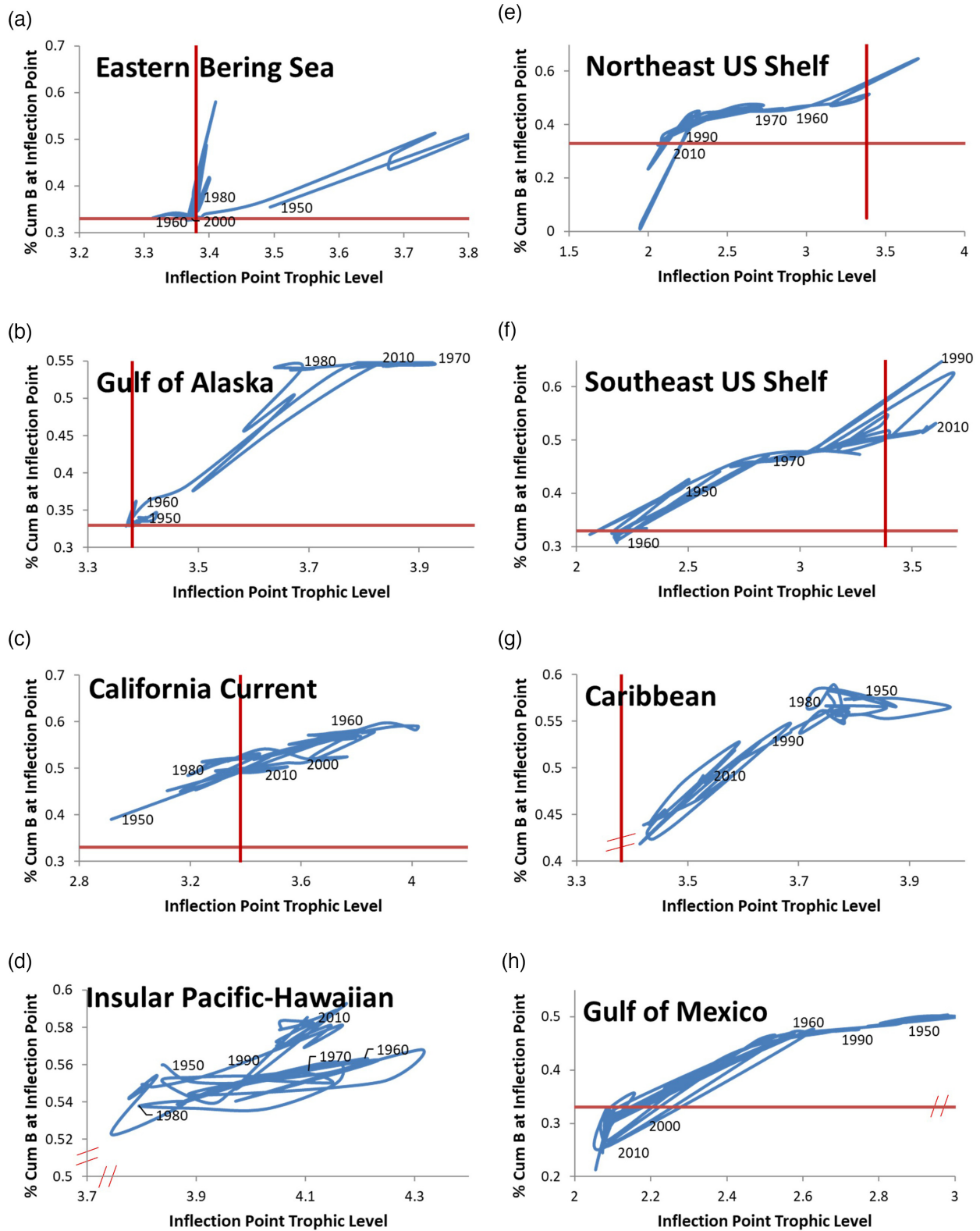


Figure 8. Percent of the total biomass vs. TL at the inflection point of the “S” curve over time for the eight U.S. LMEs. The lines correspond to globally derived thresholds of perturbation/recovery as determined by Libralato *et al.* (2019). (a) Eastern Bering Sea, (b) Gulf of Alaska, (c) California Current, (d) Insular Pacific–Hawaiian, (e) Northeast U.S. Continental Shelf, (f) Southeast U.S. Continental Shelf, (g) Caribbean Sea, and (h) Gulf of Mexico.

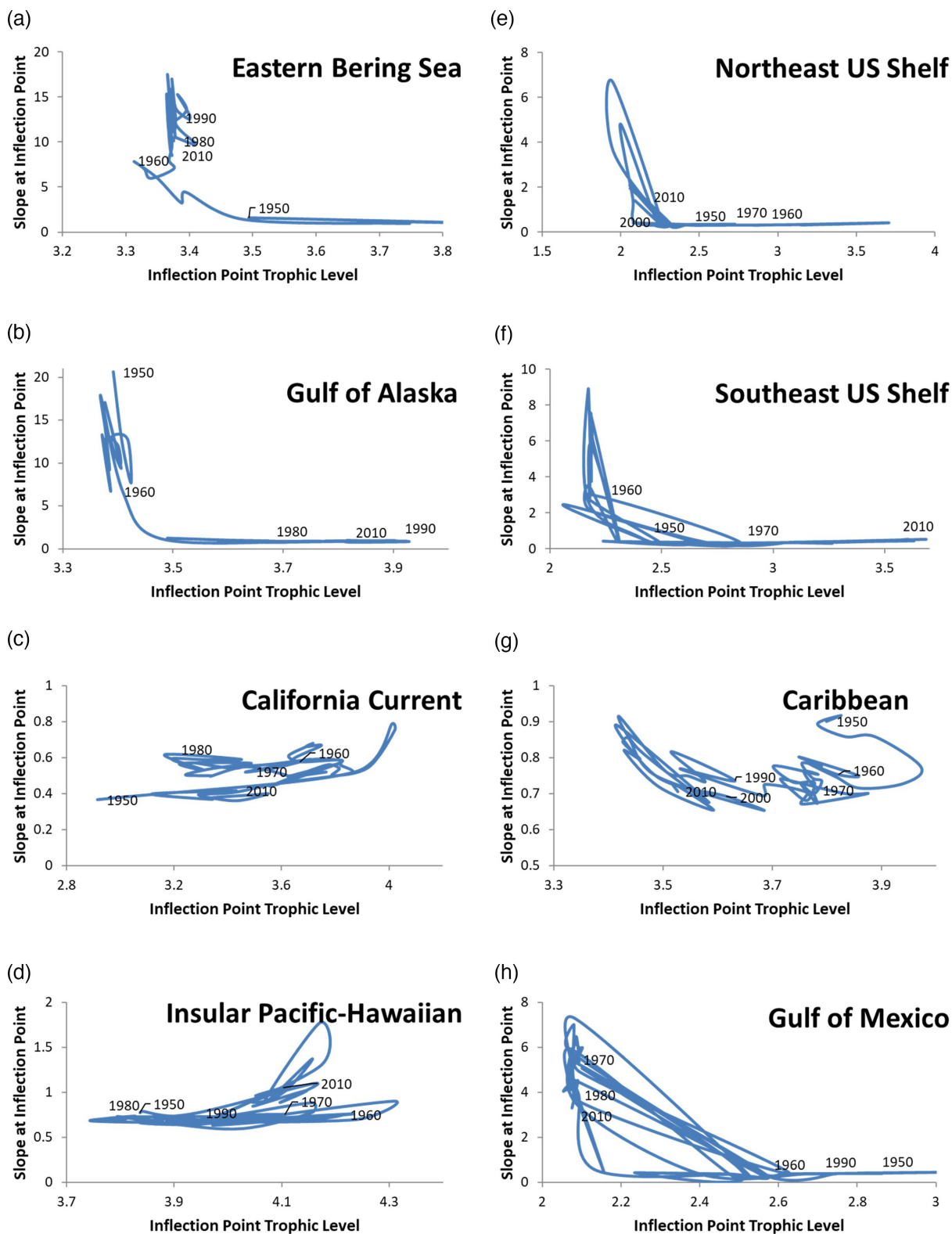


Figure 9. Slope vs. TL at the inflection point of the “S” curve over time for the eight U.S. LMEs. (a) Eastern Bering Sea, (b) Gulf of Alaska, (c) California Current, (d) Insular Pacific–Hawaiian, (e) Northeast U.S. Continental Shelf, (f) Southeast U.S. Continental Shelf, (g) Caribbean Sea, and (h) Gulf of Mexico.

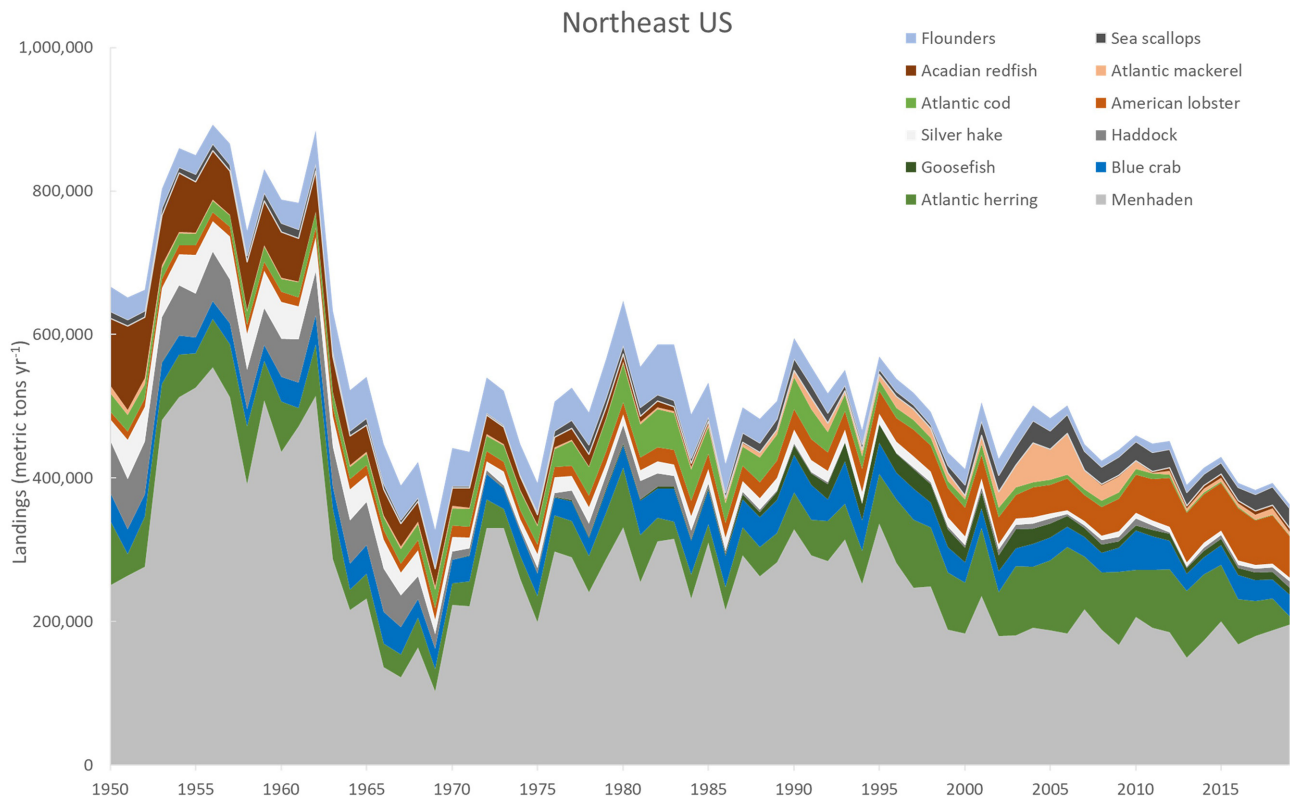


Figure 10. Catches from the Northeast U.S. LME for major taxa or taxa groups over time.

which has declined over time; yet peaks in the mid-1970s, late 1980s-early 1990s, and early 2000s were seen (Figure 5). These peaks were prior to the increase in catches seen here in the late 1970s-early 1980s, mid-1990s, and mid-2000s (Figure 10) by at least three, and sometimes 5 years (c.f. Supplemental Materials, Statistical Analysis, Supplementary Table S4). As the targeted species shifted in the late 1980s and early 1990s, the EOF index (Figure 5) exhibited an earlier peak in the late 1970s to early 1980s, then declined thereafter. The patterns stabilize and persist, with a generally declining trend for the rest of the time series, with other, ancillary species comprising a larger portion of the catch over time. Hence, there also appears to be not necessarily sequential overfishing, but certainly a shift to targeting other LMRs over time (i.e. fishing through, not necessarily down, the food web; Essington *et al.*, 2006; Pauly *et al.*, 1998). Although shorter time series, the other EOF indicators (Figures 6 and 7) similarly exhibit comparable patterns of increase in the early 2000s, presaging major changes in the amount of what is caught (Figure 10). Thus, it appears that the EOF indices for the Northeast U.S. LME detect major changes at least 2–3 years, if not more (c.f. Supplemental Materials, Statistical Analysis, Supplementary Table S4), prior to what can be pieced-together on a stock-by-stock basis.

A similar example is seen for the Gulf of Mexico (Figure 11). There is a clear increase in catch in the late 1970s to early 1980s. These are consistent with the total landings seen for this LME (Figure 3h). Like the Northeast U.S., the primary landed species was menhaden (Gulf; *Brevoortia patronus* Goode), which after peaking in the 1980s exhibited a decline and then stabilization. The catches for the other taxa exhibit variable patterns over time. These data do

not show recreational landings for this LME, which may be substantial. Also noteworthy is that EOF indicators (Figures 5–7) likewise detected shifts in this ecosystem and that EOF was occurring. The Ryther index (Figure 5) detected signs of EOF in the early 1970s, much earlier than the peak and then collapse seen in the early 1980s; the peak in the Ryther index in the mid- to late-1970s certainly precedes the peak in catches seen 3–5 years later. The Fogarty and Friedland indices detect less of a clear pattern due their shorter duration time-series (Figures 6 and 7), but the Friedland index might presage increases in catch (Figure 11) in the mid-2000s by 2–3 years. Hence, it also appears that the EOF indices for the Gulf of Mexico can detect major changes at least 2–3 years, maybe five (c.f. Supplemental Materials, Statistical Analysis, Supplementary Table S4), prior to what can be pieced together on a stock-by-stock basis.

I also present landings for selected taxa from the California Current LME (Figure 12). There is a decline in taxa landed in the 1950s (largely due to declines in sardine [Pacific; *Sardinops sagax* Jenyns] catches), followed by a moderate peak in landings in the early to mid-1970s (largely due to increases in anchovy [Northern; *Engraulis mordax* Girard] catches), and then an increase in landings beginning in the 2000s (largely due to notable increases in whiting [Pacific; *Merluccius productus* Ayres] and sardine landings). There was also a notable decline in landings in the early 1960s and mid-1980s, followed by a shift in what was targeted and caught (Figure 12). These patterns exemplify potential sequential depletion, albeit in the context of a shifting upwelling ecosystem with various oceanographic and climatological regimes (Huyer, 1983; Bograd and Lynn, 2003; Chhak and Di Lorenzo, 2007). The patterns

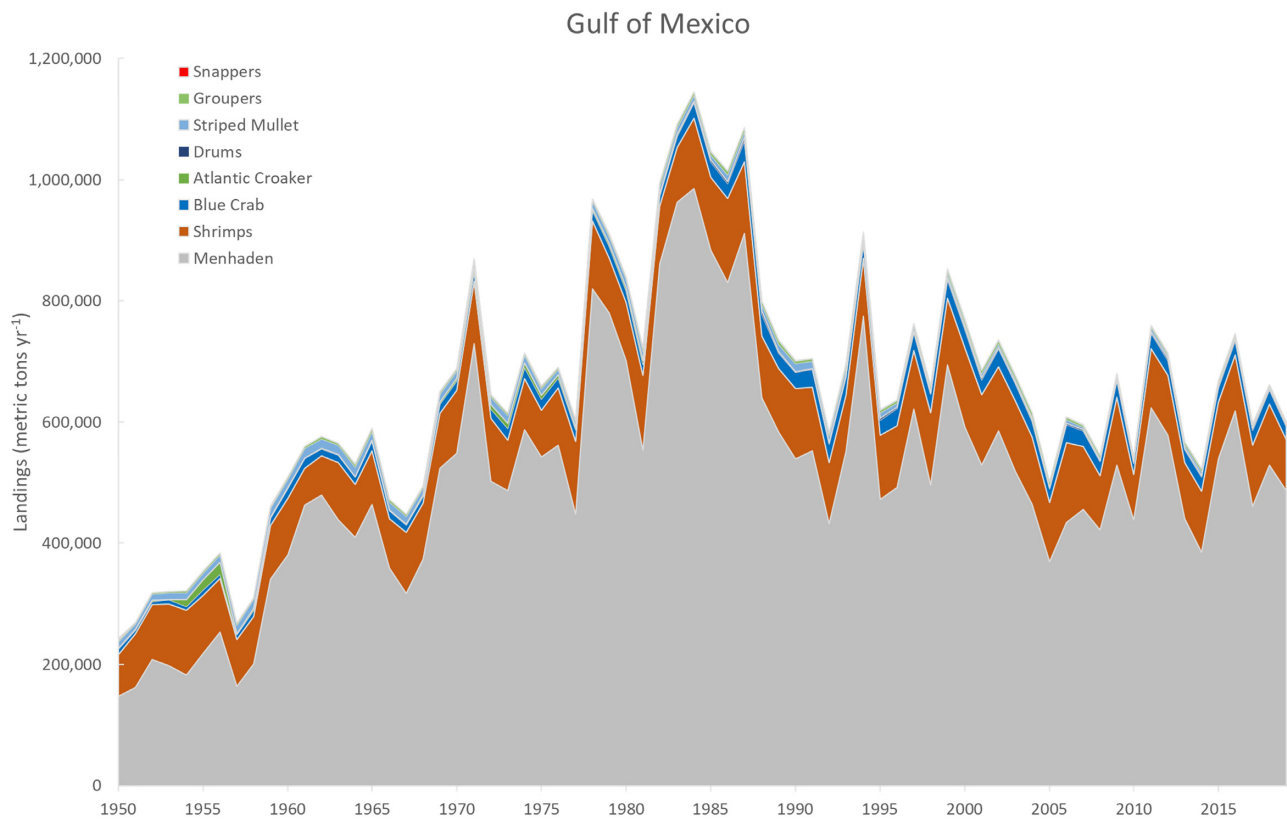


Figure 11. Catches from the Gulf of Mexico LME for major taxa or taxa groups over time.

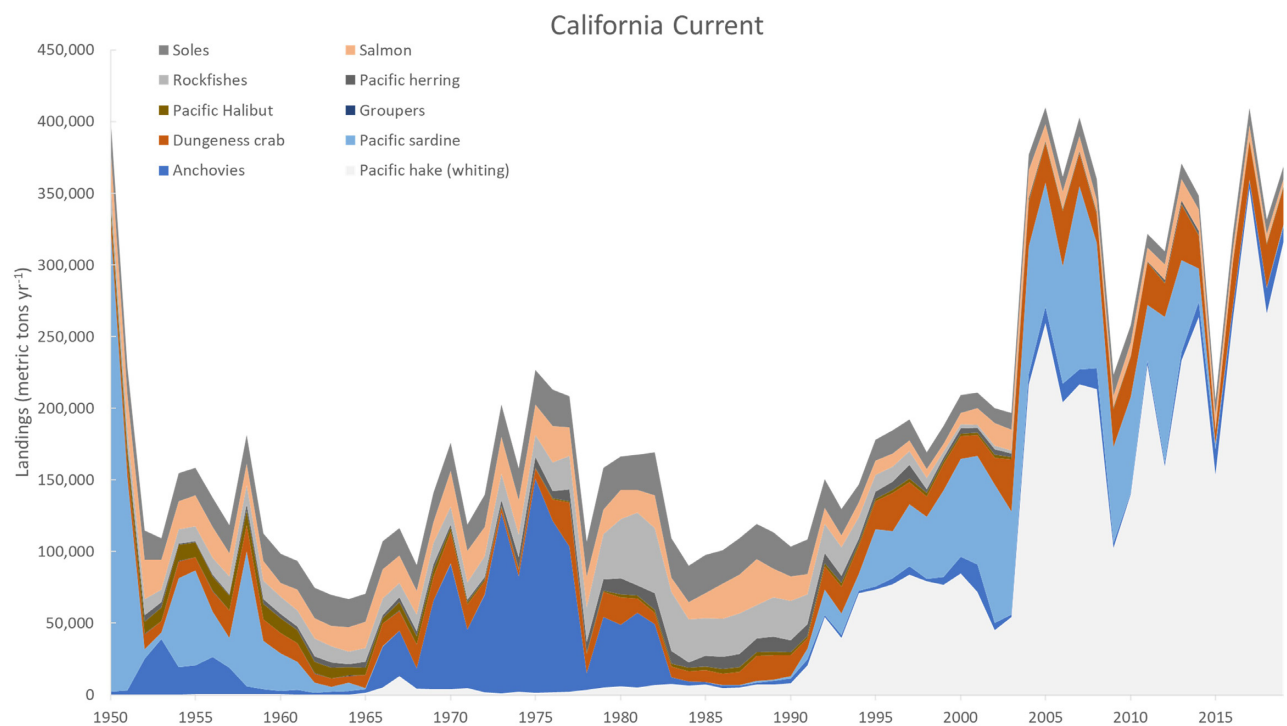


Figure 12. Catches from the California Current LME for major taxa or taxa groups over time.

shown here for select taxa are consistent for total landings seen for this LME (Figure 3c). Minimal evidence for EOF was observed for this LME (Figures 5–7), although the Friedland index did indicate the possibility of mild EOF throughout the last 20 years. Even though minimal evidence of EOF was detected for this LME, shifts in EOF indicators were detected. For example, there was an increase in the late 1960s to early 1970s, and then a decline in early 1980s for the Ryther index (Figure 5); these presaged what was detected for individual taxa (Figure 12) by approximately 5 years (c.f. Supplemental Materials, Statistical Analysis, Supplementary Table S4). These did not foreshadow the increase in catches in the 2000s, but did hint at the decline to come in the mid-1980s. The U.S. West Coast ocean is known to have experienced a major regime shift during the late 1970s to mid-1980s, which then impacted the component biota (Francis *et al.*, 1998; Hare and Mantua, 2000; Bograd and Lynn, 2003; Peterson and Schwing, 2003). These three LME examples demonstrate the potential value of these EOF indicators as an early detection signal. They also show that explaining the patterns of sequential depletion, shift in what was targeted, and details of the catch composition are highly complemented by the more systematic EOF indices, particularly in instances where EOF is suspected.

The ecosystem Kobe plots demonstrate that for six of the eight U.S. LMEs, the indication of EOF coupled with major perturbations has been moderate and not exceeded the proposed thresholds (Figure 13). Though three LMEs (Eastern Bering Sea, Gulf of Alaska, and Southeast U.S.) have been on the borderline of perturbation at times, none of these six are experiencing EOF. Yet two LMEs, the Northeast U.S. and Gulf of Mexico, have exhibited dynamics that would be flagged by these Kobe plots. The degree of perturbation has shifted between above or below the proposed threshold, but both LMEs exhibit clear signals of EOF over time.

Discussion

EOF in U.S. ecosystems

A total of two out of eight U.S. LMEs have exhibited evidence consistent with EOF, a result which is not surprising and generally consistent with what is known about the Northeast U.S. (e.g. Fogarty and Murawski, 1998; Link *et al.*, 2011; NEFSC 2020a, b) and Gulf of Mexico (e.g. Cowan *et al.*, 2011; Karnauskis *et al.*, 2017) LMEs. Some regions with notable histories of regimes shifts (e.g. California Current or Eastern Bering Sea; Francis *et al.*, 1998; Hare and Mantua, 2000; Conners *et al.*, 2002; Bograd and Lynn, 2003; Peterson and Schwing, 2003) also had major periods of change detected in the EOF indicators, prior to the shift to different targeted taxa in what was caught for those LMEs. The cumulative biomass curve parameters are also consistent with over half of these eight LMEs being classified as in a transition state regarding the “S” curves (Pranovi *et al.*, 2020; Libralato *et al.*, 2019). All have exhibited histories of notable single stock overfishing and changes to the ecosystem; thus, evidence for EOF, and in some cases recovery, is not surprising.

Of the two U.S. LMEs that have exhibited consistent signals of EOF, at least one continues to experience significant EOF. Clearly the Northeast U.S. is exhibiting evidence of EOF. That EOF is detected and highly probable for this LME is not surprising given what is known from other, independent sources about this LME. There has been notable and enduring fishing pressure in this LME for several decades, primarily for gadoids, flatfish, and other demersals,

then small pelagic fishes, then back to demersals (e.g. Fogarty and Murawski, 1998; Link *et al.*, 2011; NEFSC 2020a, b). The EOF indices for this LME are consistently 3–5x higher than the proposed thresholds. Furthermore, the Northeast U.S. LME’s primary and secondary production have been explored relative to fisheries production, with the recognition that some of that production is subject to significant variability due to positional shifts in major currents and gyres, shifts in phenology of bloom events, and related physical oceanographic phenomena (Friedland *et al.*, 2012; NEFSC 2020a, b). Thus, I appreciate that this could result in some uncertainty regarding the amount of what one could reasonably be expected to be harvested in that ecosystem. But this LME is also well known for a highly productive fishing environment (Fogarty and Murawski, 1998); therefore, the patterns detected here are likely reflective of the overall fishing pressure being experienced in this LME. It may be wise to review EOF, and perhaps scenarios to address it, in the various management contexts (e.g. Fisheries Commissions, Councils, Marine Sanctuaries, and Mammal Review Groups) for the Northeast U.S. LME.

One other U.S. LME has likely experienced conditions that are at levels consistent with EOF over time, the Gulf of Mexico LME. Whether the more recent declines in EOF measures are accurate or are subject to underreported or misreported catch due to the limited inclusion of recreational landings in this study is uncertain (Coleman *et al.*, 2004; de Mutsert *et al.*, 2008; Karnauskis *et al.*, 2017). I admit that for those circumstances, and perhaps for all these LMEs, data sufficiency and corroboration certainly need to temper the interpretation of these results. But it does seem that the data are sufficient to detect EOF when evidence for it emerges, even given these possible data limitations. For the Gulf of Mexico LME, that EOF was even detected without an important facet (and perhaps substantial fraction; i.e. recreational fisheries) of its total catches is not trivial. The results of a history and perhaps levels close to EOF thresholds are again not surprising for the Gulf of Mexico given what is known of its collective exploitation history from other sources (Cowan *et al.*, 2011; Karnauskis *et al.*, 2017). This possible EOF finding might warrant further attention in that region.

Other U.S. LMEs do not appear to have experienced EOF in a consistent and persistent manner, with evidence limited to only a few indicators or periods thereof. Yet an important rationale when considering this approach is that if in fact the confidence in these data is reasonably high, such a situation might actually indicate the potential under-utilization of fisheries resources if values of EOF indicators were notably below thresholds, thereby suggesting the potential for further fishing opportunities. If so, such under-utilization could have significant social, cultural, economic (Sanchirico *et al.*, 2008; Jin *et al.*, 2016; Carmona *et al.*, 2020), and even global food security implications (Jennings *et al.*, 2016). Such situations might also warrant further systematic fisheries exploration, albeit for different reasons than those LMEs experiencing EOF. I am not stating that if values of the EOF indicators are below the thresholds that fishing pressure should necessarily be increased, rather that there may be more production in the system available for harvest that could warrant additional exploration. How applicable this is in the US, let alone the global suite of LMEs, warrants further examination.

Changes in more recent years for many of the LMEs exhibit declines in the value EOF indicators, even for LMEs still exhibiting EOF. This is consistent with major management interventions in the fisheries of these regions (Methot *et al.*, 2014; Melnychuk *et al.*, 2017; Lynch *et al.*, 2018; Hilborn *et al.*, 2020). These instances

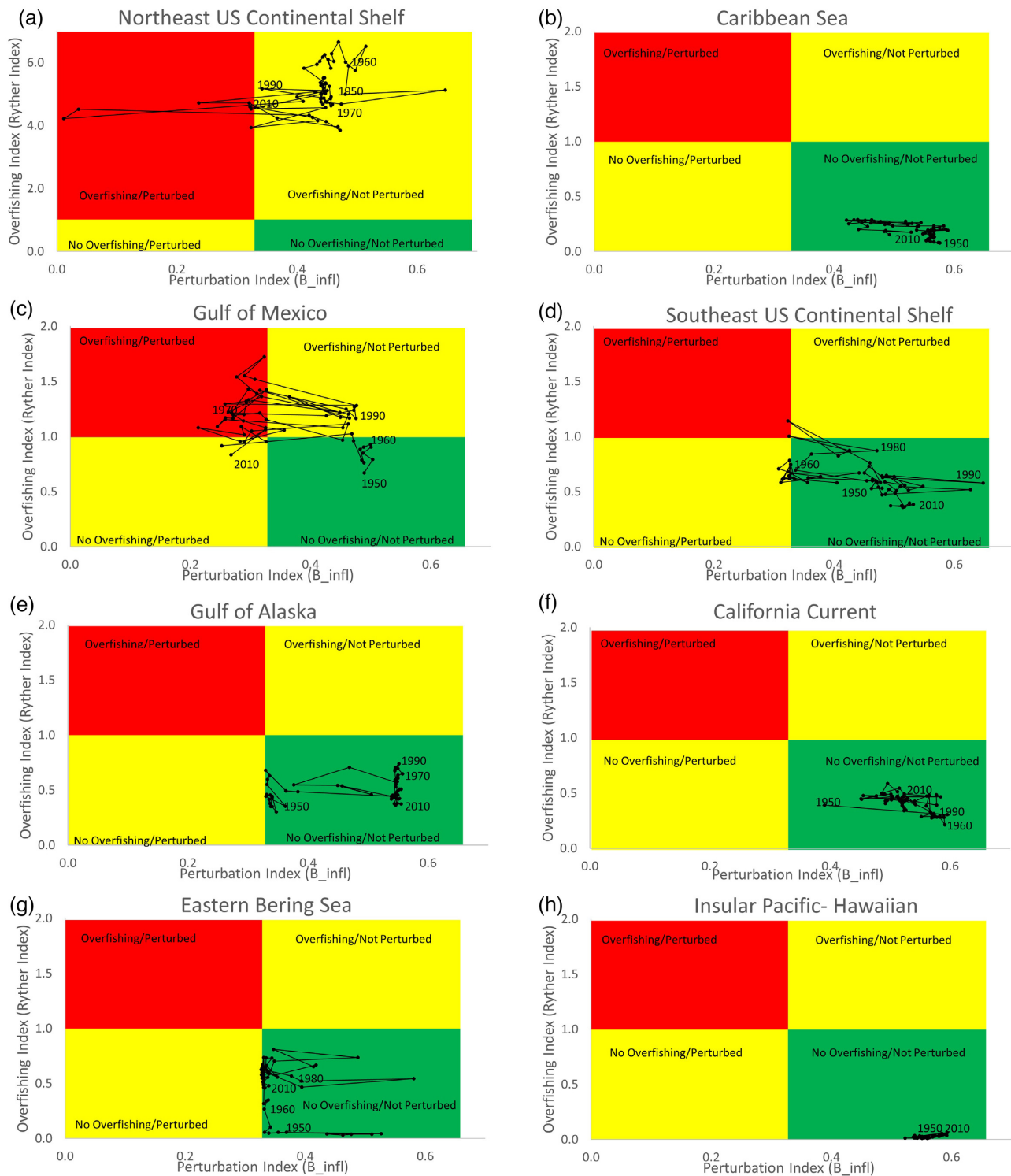


Figure 13. Ecosystem-level Kobe plots of EOF and ecosystem perturbation. The trajectories show the values for each year in each LME. Thresholds represent level of EOF (using the Ryther index) and perturbation (using the cumB-TL biomass inflection point). (a) Northeast U.S. Continental Shelf, (b) Caribbean Sea, (c) Gulf of Mexico, (d) Southeast U.S. Continental Shelf, (e) Gulf of Alaska, (f) California Current, (g) Eastern Bering Sea, and (h) Insular Pacific–Hawaiian.

should be viewed as a positive sign such that with some management intervention, LMEs and their associated fisheries can recover (as seen in these EOF metrics) and the effects are detected at the ecosystem level.

Caveats of EOF

One important caveat, especially about the three main EOF indicators, pertains to the TL of the catch. There has been notable debate about how to interpret TL impacts in a fisheries context

(Pauly *et al.*, 1998; Essington *et al.*, 2006; Libralato *et al.*, 2008; de Mutsert *et al.*, 2008; Branch *et al.*, 2010) and although cognizant of those considerations, I do not wish to reiterate that debate here. Rather, the TL of catch could influence how EOF thresholds are estimated and EOF determinations are interpreted. In the two regions that have exhibited symptoms consistent with EOF (Gulf of Mexico and Northeast U.S. Continental Shelf), some notable fraction of the catch has been on lower TL LMRs (e.g. menhaden, invertebrates). Based on Equation (1) and sensitivity analyses surrounding it, given a slightly lower overall TL it is possible that the potential for overall catch, and hence EOF thresholds, could be slightly higher in those regions. That said, while lower overall than global averages, the decline in average TL for these two LMEs did not occur until much later in the time series. Furthermore, other indicators of EOF still suggest systematic symptoms of overall, excessive fishing pressure in those LMEs. And even if TL were lower by one level, exceeding current EOF thresholds by a factor of five would still not be explained by the lower TL. Hence, this caveat merits consideration in interpreting EOF determinations, but also highlights the need for multiple indicators and fuller context when examining evidence for EOF.

It is worth noting that EOF was detectable at least 2–3, and perhaps up to 5 years, prior to major taxa or taxa group declines or collapses in several of these LMEs. Even if EOF was not detected, EOF indicators still provided early warning signals several years prior to other observable changes in the ecosystem. An important facet to remember is that this is highly expected from hierarchy theory (O'Neill *et al.*, 1986; Wu, 2013; Link, 2018), whereby monitoring phenomena at higher levels of organization can detect major features much more consistently and obviously than trying to track all the dynamics at lower levels of the hierarchy, which is consistent with major ecosystem changes that have been documented for some of these LMEs on both the West or Arctic (Francis *et al.*, 1998; Hare and Mantua, 2000; Bograd and Lynn, 2003; Peterson and Schwing, 2003; Harvey *et al.*, 2020), and East or Gulf coasts (Karnauskis *et al.*, 2017; NEFSC 2020a, b). Instead of attempting to piece together major, significant shifts in ecosystems by a single taxa-at-a-time, meta-analytic approach, it seems more effective and efficient to monitor what are essentially early warning signals of major ecosystem shifts, an emergent feature supported by hierarchy theory (O'Neill *et al.*, 1986; Wu, 2013; Link, 2018). Invoking hierarchy theory (O'Neill *et al.*, 1986; Wu, 2013) implies that measures of system properties at a level above the focal level can be more stable, tend to operate more slowly and at a lower frequency than lower levels (and thus pick up macro-temporal signals more obviously), and by their definition of aggregation tend to dampen frequencies of dynamics at lower levels (O'Neill *et al.*, 1986; Wu, 2013; Link, 2018). That is, delineating precision of a property at a higher, aggregated, emergent level is important, but less important than even doing so at all and certainly less important than ignoring that major shifts in those aggregate levels are apt to be representative of larger, system-wide dynamics, which if detected can have major overall consequences, and usually detected more rapidly than those occurring at lower levels. Thus, I assert that even if the specific levels of the proposed thresholds for these EOF metrics are debatable, there remains high value in monitoring these indicators as early warning signals to detect major trends and patterns of potential fisheries change, ecosystem change, or possible overfishing before subsequent and significant impact has occurred. Detecting and acting on this ecosystem-level information can prevent both continued EOF and sequential stock overfishing, identify upcoming regime

shifts, most probably save money, and even stave off other potential impacts.

I reiterate that fisheries management in the U.S. is generally well done (Pitcher *et al.*, 2009; Hilborn *et al.*, 2015, 2020). The rebuilding and recovery of many overfished stocks has continued to progress in the U.S., and collective evidence for this is detected in the recent downward trends of EOF indicators for many LMEs. So why would one even need another consideration of overfishing, especially EOF? There are a few reasons. These EOF measures can be particularly helpful for data poor situations, such as in the Caribbean or Pacific Island territories where detailed, age-structured, single species approaches are challenging to develop given limited data and limited local analytical capacities relative to high biodiversities (Barlow *et al.*, 2018); these EOF indices can provide a total backstop for all fishing in the system absent such detailed information. Additionally, these ecosystem-level measures are relatively simple, and can be used to set the context for other types of information that may be missing or difficult to obtain. For example, with satellite-based information, one can back-calculate and then set the stage for approximate total catch levels, and then adjust monitoring and management expectations accordingly. Plus, they can act as early warning signals as noted above.

The other main reason to consider EOF in light of the observation that fisheries are generally well managed in the U.S. (Pitcher *et al.*, 2009; Hilborn *et al.*, 2015, 2020; Lynch *et al.*, 2018) is that of all the fisheries and fish stocks that are formally monitored, of all those stocks rebuilt, and of all the stocks under fisheries management plans (Methot *et al.*, 2014; Lynch *et al.*, 2018; NMFS, 2020), that does not include all the LMRs targeted and landed in the country. The major, national indicator of U.S. marine fisheries status is the fish stock sustainability index (FSSI; <https://www.fisheries.noaa.gov/national/population-assessments/status-us-fisheries#fish-stock-sustainability-index>; NMFS, 2020). Although FSSI scores have improved dramatically over the past 20 years, they still only account for approximately 200 stocks, and a high number of them have unknown status. And although those ~200 stocks are major components of U.S. fisheries landings, they do not represent all fishes landed and certainly not all that are of local, cultural or ecological importance in every U.S. LME. For context, there are often that many fish taxa (~200) in a given LME, and some LMEs easily have double or triple that number of taxa. Furthermore, there are many “ecosystem component” stocks or species that are considered but not accounted for in official statistics nor directly and explicitly managed. Hence, an approach like that represented by the EOF measures presented here captures a more exhaustive look at the marine capture fisheries in the U.S., and provides the backstopping to ensure that no entire ecosystem, and by extension all stocks *in toto* therein, are fished at levels beyond what an ecosystem can produce. There are obvious, parallel extensions to many other fisheries systems in the world with even less well-known stock status.

I note that a major challenge for many parties involved in fisheries science and management regarding the concept of EOF is that they have been trained to think about one stock (taxa, population, species, fleet, etc.) at a time, largely from a population dynamics perspective, rather than a more systemic approach (Fogarty, 2014; Link, 2018). Treating the entire set of fleets and catches as an amalgamated system may be an intellectual or philosophical stretch, even though a more systemic approach has been shown to have notable, even improved, value (c.f. Link, 2018; Fulton *et al.*, 2019). Hence, from experience I would argue that any objections

to EOF are not typically about the evidence for whether EOF is actually occurring, but rather about the perspective underlying actually being able to define and determine overfishing for an entire ecosystem in the first place. We can define and detect EOF, and there may in fact be evidence for it in a particular situation. It is simply that many in our discipline reject the concept outright, *a priori*, because it is not familiar nor based on more typical stock dynamics, and thus many are not used to thinking in terms of the entire system of fisheries. Which once that objection is surpassed is then closely followed by objections related to practical considerations about how to estimate and implement any associated thresholds. I trust that most in our discipline will at least be able to appreciate the concept and objectively consider the evidence for EOF that is provided.

The thresholds noted herein can be debated, and they should be. Sensitivity analyses have demonstrated that of all the factors that can impact the calculation of an EOF value and associated thresholds, none are particularly dominant and the magnitude scales with primary production and total catch. The theoretical levels of the thresholds are robust, but can still span nearly an order of magnitude. For a given application in a particular LME, it would be wise to estimate these values more rigorously than the national, comparative approach demonstrated here. The salient point herein is that apart from the precision and estimation of the actual thresholds, and apart from any given value of an EOF at a given point in time, the key question is whether the concept of EOF as a threshold is even useful. Presuming it can be, the usual debates about the statistical details of how to aggregate, precision of estimation for EOF thresholds and values, assumptions about estimating primary production, if there is missing catch, and related caveats can and certainly should occur, but they need to be done so cognizant of the context of emergent, higher level properties. Thus, in the context of evaluating EOF values against thresholds, it must be kept in mind the relative value of examining them in the first place and that the thresholds may not be precise at this time, but can certainly be loosely indicative of major ecosystem change.

Thus, one might fairly ask whether these measures are ultimately worthwhile, are useful and can indicate EOF, particularly given the caveats about the thresholds and then using those thresholds to delineate EOF. I assert these measures are probably indicative of EOF, at least where there is some degree of confidence in the data. By definition, when effort has increased until it is no longer profitable, the sum of all catches declines following a notable increase, total CPUE is declining, total landings relative to ecosystem production exceeds suitable limits for the Ryther, Fogarty and Friedland indices, and the cumulative trophic curve parameters fall below thresholds that are known to indicate system-wide perturbation, the evidence of EOF becomes pretty compelling. For instance, if $> \frac{2}{3}$ of the biomass has been removed from an ecosystem, if CPUE has dropped to $< 90\%$ of what it was, and if LMRs are being caught at a rate $> 10x$ what can be reasonably produced by lower TLs, it is likely that EOF is occurring. I am not suggesting that if only one of these EOF indicators exceeds its threshold by a very little and precise amount that EOF is occurring, rather that the compound body of evidence needs to be consistent across multiple indicators and multiple contributing data inputs. If an LME is consistently exceeding EOF thresholds for all indicators by a factor of 2–5X, then it is more probable that EOF is occurring. The coherence of assessing EOF using both the cumB-TL approach and the EOF indices (i.e. the Ecosystem Kobe plots, based on relatively independent data sets) confirms the robustness of the approaches presented here, and also confirms that there is

compelling evidence that EOF has occurred for at least a couple of U.S. LMEs.

Proposed protocols for using EOF indicators

How might one operationally use EOF measures, particularly in the context that most fisheries management in the U.S. (and elsewhere) is conducted on a stock-by-stock, or at least fishery-by-fishery, basis (Methot *et al.*, 2014; Link, 2018; Lynch *et al.*, 2018)? I propose monitoring the entire system and major changes first, rather than piecemealing any such picture by some form of meta-analysis across multiple taxa examined separately and independently; such cross-taxa syntheses are rare and when they do occur they are often done too late, such that collectively a regional set of interested parties misses bigger signals. Even apart from EOF measures, this reinforces the value of ecosystem status reports that set the broader context for stocks in a region (e.g. Karnauskis *et al.*, 2017; Harvey *et al.*, 2020; NEFSC 2020a, b). I propose that once the overall ecosystem-level of catch is evaluated, then risk or susceptibility analyses (Patrick *et al.*, 2009; Gaichas *et al.*, 2014, 2018; Hare *et al.*, 2016) could be conducted, and high risk, high value, and otherwise high priority stocks could be monitored and assessed more closely (Methot, 2015; Lynch *et al.*, 2018). In some ways this represents a shift in order and focus of how one would conduct fisheries science and management. That is, instead of starting with the history of which stocks have been assessed or even with what we deem most valuable, we look at the entire system of fisheries in an LME and if EOF is detected, explore means to address excess fishing pressure systematically before delving into the details of specific stocks. And then we explore evaluations of a select few specific stocks, with the EOF evaluation in place for all others that we do not have time, data or resources to assess. In other ways, this proposed approach codifies and more formally acknowledges that we already prioritize stock assessments, monitoring and analyses, but just in a less systematic manner. The key distinction is that it checks the higher-level system of all fisheries first to determine if there are not broader concerns warranting attention prior to delving into more specific stock analyses.

These EOF measures can also set the stage for what might be expected for all fisheries landings in an LME given what we know about ecosystem productivity related to catches (Pauly and Christensen, 1995; Chassot *et al.*, 2010; Conti and Scardi, 2010; Friedland *et al.*, 2012; Watson *et al.*, 2014; Stock *et al.*, 2017; Petrick *et al.*, 2019) and possible EOF (Fogarty *et al.*, 2016; Link and Watson, 2019). On the one hand, this sets limits of what can be caught from an entire ecosystem, and from that tradeoffs can be explored among the component fisheries cognizant of the total limits to what can be produced (Link, 2018). On the other hand, and returning to the point raised earlier, it could be that for some regions the fisheries remain under-utilized, as has been implied by sporadic portfolio analyses on U.S. fisheries (Edwards *et al.*, 2004; Sanchirico *et al.*, 2008; Schindler *et al.*, 2015; Jin *et al.*, 2016; Carmona *et al.*, 2020). If EOF values remain consistently below even $\frac{1}{2}$ of EOF thresholds, some exploration of why this is the case is warranted (are fisheries focused on high TL species, could the ecosystem have low TE, etc.). And if after that the evidence leads to a reasonable understanding and if EOF values still remain consistently below even $\frac{1}{2}$ of EOF thresholds, and if ecological, oceanographic, or economic explanations for the low value are accounted for, some exploration of other fishing options might warrant consideration. If this evaluation still suggests the ecosystem productivity could support more

fishing pressure, then other fishing options could be considered. I am not proposing increasing fishing effort to the level of what are admittedly potentially imprecise EOF thresholds. Nor am I implying that increasing fishing on any taxa is necessarily the best option. Rather that the potential exists for some careful fisheries expansions relative to the production potential of an ecosystem, and examination of possibilities to explore that potential might be considered. This again may have positive implications for global food security (Jennings *et al.*, 2016).

Considerations if EOF is detected

The question begs, what is an appropriate course of action if EOF is detected? As previously noted (Link and Watson, 2019), I think it unwise to be too prescriptive given local policy and governance considerations. Yet a few simple, generic suggestions emerge. First would be to (continue to) monitor these EOF metrics and disseminate both the methods to calculate them, data to estimate them, and the resulting values broadly to all interested parties. Effectively, if one can monitor landings (I acknowledge that can be a big *if* but global fishery datasets are improving (e.g. Watson, 2017; Pauly and Zeller, 2016; FAO, 2018; Rousseau *et al.*, 2019; and certainly in the U.S. datasets have begun to reasonably bound this challenge), and one can obtain satellite primary productivity data for the area being fished, the three main EOF indicators can be readily calculated and evaluated. Admittedly the data are more involved for calculating cumulative biomass curve parameters, but there are numerous LME landings and catch data from which those curves can also be estimated. Thus, I recommend implementation and ongoing monitoring of these EOF metrics. Second, if EOF is strongly implied (e.g. the Northeast U.S. LME), then regional fisheries management organizations somehow need to limit the total fishing pressure in an ecosystem. The best way to do that is not a suite of specific recommendations that I will propose here for several reasons, but again in general it amounts to lowering the overall fishing pressure in the ecosystem. Executing management to ultimately lower fishing pressure has many potential avenues (Mace, 1994; Hilborn *et al.*, 2015), and all options should be explored given a local or regional context. I am sensitive to the challenges, specifics and nuances of governance and infrastructure in many of these U.S. (and global) LMEs. That said, the methods proposed herein are rather simple to implement and monitor. Thus, I am proposing that if EOF is detected, then at least some means to lower fishing pressure might need to be considered.

The utility of these main EOF measures lies in their simplicity. Apart from any specific action, I assert that they are useful to routinely monitor. The relevant point here is there is value in having national and even international standards of EOF. Any interested party can obtain and calculate these estimates from widely available, public sources, and if the indicator values exceed the proposed thresholds herein by significant amounts, then a clear agreement and obvious consensus on whether (ecosystem) overfishing was occurring, or not, would then not be debatable. Rather, it would shift the debate to the most appropriate actions to best mitigate EOF (beyond generally a lowering of fishing pressure to a discussion that specifically evaluated particular means to systematically do so via a suite of management measures), and that in turn would shift the burden of proof to one better emphasizing ecosystem-level sustainability. I am in no way implying that adopting these EOF measures will be easy nor be a simple cure-all. Rather, I propose them as an approach that is easy to understand and can help address bigger,

systemic, LME-wide challenges for U.S. fisheries. Doing so will help to better operationalize EBFM.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

Data availability statement

The data used in this article are available at the duly cited references and associated webpages noted herein for each of the specific instances.

Acknowledgements

I thank FAO and SAU for making their data widely available, and Reg Watson for sharing his dataset. I thank Wendy Morrison, Jameal Samhoury, Ryan Rykaczewski, and anonymous reviewers for their very helpful comments on prior versions of the manuscript. I thank Reg Watson for collaboration and thinking on the EOF indicators, and I thank Fabio Pranovi and Simone Libralato for their long-standing collaborations on the cumulative trophic biomass curves. I thank Alexander Ilich for the Ecosystem Kobe plot idea.

References

- Anticamara, J. A., Watson, R., Gelchu, A., and Pauly, D. 2011. Global fishing effort (1950–2010): trends, gaps, and implications. *Fisheries Research*, 107: 131–136.
- Antoine, D., André, J. - M., and Morel, A. 1996. Oceanic primary production: 2. Estimation at global scale from satellite (Coastal Zone Color Scanner) chlorophyll. *Global Biogeochemical Cycles*, 10: 57–69.
- Aydin, K. Y., Lapko, V. V., Radchenko, V. I., and Livingston, P. A. 2002. A comparison of the eastern and western Bering Sea shelf and slope ecosystems through the use of mass-balance food web models. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-130, 78 p.
- Aydin, K., Gaichas, S., Ortiz, I., Kinzey, D., and Friday, N. 2007. A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands large marine ecosystems through food web modeling. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-178, 298 p.
- Barlow, J., França, F., Gardner, T. A., Hicks, C. C., Lennox, G. D., Berenguer, E., Castello, L. *et al.* 2018. The future of hyperdiverse tropical ecosystems. *Nature*, 559: 517–526.
- Beddington, J. R., Agnew, D. J., and Clark, C. W. 2007. Current problems in the management of marine fisheries. *Science*, 316: 1713–1716.
- Behrenfeld, M. J., and Falkowski, P. G. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography*, 42: 1–20.
- Blanchard, J., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J. I., Holt, J. *et al.* 2012. Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367: 2979–2989.
- Bograd, S. J., and Lynn, R. J. 2003. Long-term variability in the Southern California Current system. *Deep Sea Research Part II: Topical Studies in Oceanography*, 50: 2355–2370.
- Branch, T. A., Watson, R., Fulton, E. A., Jennings, S., McGilliard, C. R., Pablico, G. T., Ricard, D. *et al.* 2010. The trophic fingerprint of marine fisheries. *Nature*, 468: 431–435.
- Brand, E. J., Kaplan, I. C., Harvey, C. J., Levin, P. S., Fulton, E. A., Herrmann, A. J., and Field, J. C. 2007. A spatially explicit ecosystem

- model of the California Current's food web and oceanography. U.S. Dept. Commerce, NOAA Technical Memorandum NMFS-NWFSC-84, 145 p.
- Bundy, A., Bohaboy, E. C., Hjermann, D. O., Mueter, F. J., Fu, C., and Link, J. S. 2012. Common patterns, common drivers: comparative analysis of aggregate systemic surplus production across ecosystems. *Marine Ecology Progress Series*, 459: 203–218.
- Bundy, A., Fanning, P., and Zwanenburg, K. C. T. 2005. Balancing exploitation and conservation of the eastern Scotian Shelf ecosystem: application of a 4D ecosystem exploitation index. *ICES Journal of Marine Science*, 62: 503–510.
- Bureau of Economic Analysis (BEA). 2021. https://www.bea.gov/sites/default/files/2021-01/gdp4q20_adv.pdf (last accessed 28 August 2021).
- Cadrin, S. X., Kerr, L. A., and Mariani, S. 2014. *Stock Identification Methods: Applications in Fishery Science*, 2nd edn. Academic Press, New York, NY.
- Carmona, I., Ansuategi, A., Chamorro, J. M., Escapa, M., Gallastegui, M. C., Murillas, A., and Prellezo, R. 2020. Measuring the value of ecosystem-based fishery management using financial portfolio theory. *Ecological Economics*, 169: 106431.
- Carr, M. E., Friedrichs, M. A. M., Schmeltz, M., Noguchi Aita, M., Antoine, D., Arrigo, K. R., Asanuma, I. *et al.* 2006. A comparison of global estimates of marine primary production from ocean color. *Deep Sea Research Part II: Topical Studies in Oceanography*, 53: 741–770.
- Chagaris, D. D., Patterson, W. F., and Allen, M. S. 2020a. Relative effects of multiple stressors on reef food webs in the Northern Gulf of Mexico revealed via ecosystem modeling. *Frontiers in Marine Science*, 7: 513. doi:10.3389/fmars.2020.00513
- Chagaris, D., Drew, K., Schueller, A., Cieri, M., Brito, J., and Buchheister, A. 2020b. Ecological reference points for Atlantic Menhaden established using an ecosystem model of intermediate complexity. *Frontiers in Marine Science*, 7: 606417. doi:10.3389/fmars.2020.606417
- Chassot, E., Bonhommeau, S., Dulvy, N. K., Mélin, F., Watson, R., Gascuel, D., and Le Pape, O. 2010. Global marine primary production constrains fisheries catches. *Ecology Letters*, 13: 495–505.
- Chhak, K., and Di Lorenzo, E. 2007. Decadal variations in the California current upwelling cells. *Geophysical Research Letters*, 34:L14604, doi:10.1029/2007GL030203.
- Coleman, F. C., Figueira, W. F., Ueland, J. S., and Crowder, L. B. 2004. The impact of United States recreational fisheries on marine fish populations. *Science*, 305: 1958–1960.
- Coll, M., Libralato, S., Tudela, S., Palomera, I., and Pranovi, F. 2008. Ecosystem overfishing in the ocean. *Plos ONE*, 3: e3881, doi:10.1371/journal.pone.0003881.
- Coll, M., Shannon, L. J., Kleisner, K. M., Juan-Jordá, M. J., Bundy, A., Akoglu, A. G., Banaru, D. *et al.* 2016. Ecological indicators to capture the effects of fishing on biodiversity and conservation status of marine ecosystems. *Ecological Indicators*, 60: 947–962.
- Colleter, M., Valls, A., Guitton, J., Gascuel, D., Pauly, D., and Christensen, V. 2015. Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. *Ecological Modelling*, 302: 42–53
- Connors, M. E., Hollowed, A. B., and Brown, E. 2002. Retrospective analysis of Bering Sea bottom trawl surveys: regime shift and ecosystem reorganization. *Progress in Oceanography*, 55: 209–222.
- Conti, L., and Scardi, M. 2010. Fisheries yield and primary productivity in large marine ecosystems. *Marine Ecology Progress Series*, 410: 233–244.
- Costanza, R., D'Arge, R., de Groot, R. S., Farber, S., Grasso, M., Hannon, B., Limburg, K. *et al.* 1997. The value of the world's ecosystem services and natural capital. *Nature*, 387: 253–260.
- Cowan, J. H., Grimes, C. B., Patterson, W. F., Walters, C. J., Jones, A. C., Lindberg, W. J., Sheehy, D. J. *et al.* 2011. Red snapper management in the Gulf of Mexico: science- or faith-based? *Reviews in Fish Biology and Fisheries*, 21: 187–204.
- Daniel, W. W. 1990. *Applied Nonparametric Statistics*. PWS-Kent Publ. Co., Boston, MA.
- Daskalov, G. M. 2002. Overfishing drives a trophic cascade in the Black Sea. *Marine Ecology Progress Series*, 225: 53–63.
- De Mutsert, K., Cowan, J. H., Essington, T. E., and Hilborn, R. 2008. Re-analyses of Gulf of Mexico fisheries data: landings can be misleading in assessments of fisheries and fisheries ecosystems. *Proceedings of the National Academy of Sciences*, 105: 2740–2744.
- De Mutsert, K., Steenbeek, J., Lewis, K., Buszowski, J., Cowan, J. H., and Christensen, V. 2016. Exploring effects of hypoxia on fish and fisheries in the northern Gulf of Mexico using a dynamic spatially explicit ecosystem model. *Ecological Modelling*, 331: 142–150.
- Eddy, T. D., Bernhardt, J. R., Blanchard, J. L., Cheung, W. W. L., Colléter, M., du Pontavice, H., Fulton, E. A. *et al.* 2021. Energy flow through marine ecosystems: confronting transfer efficiency. *Trends in Ecology and Evolution*, 36: 76–86.
- Edwards, S. F., Link, J. S., and Rountree, B. P. 2004. Portfolio management of wild fish stocks. *Ecological Economics*, 49: 317–329.
- Elton, C. S. 1927. *Animal Ecology*. Sidgwick and Jackson, London.
- Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. *Fishery Bulletin*, 70: 1063–1085.
- Essington, T. E., Beaudreau, A. H., and Wiedenmann, J. 2006. Fishing through marine food webs. *Proceedings of the National Academy of Sciences*, 103: 3171–3175.
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R. *et al.* 2011. Trophic downgrading of planet Earth. *Science*, 333: 301–306.
- European Parliament, and Council of the European Union. 2008. Directive 2008/56/EC of the European Parliament and of the Council. *Official Journal of the European Union*, 164: 19–40.
- FAO. 2018. *The State of World Fisheries and Aquaculture 2018, Meeting the Sustainable Development Goals*. FAO, Rome.
- FAO. 2020. *The State of World Fisheries and Aquaculture 2020. Sustainability in action*. FAO, Rome. doi: 10.4060/ca9229en.
- Fay, G., Link, J. S., Large, S. I., and Gamble, R. J. 2015. Management performance of ecological indicators in the Georges Bank finfish fishery. *ICES Journal of Marine Science*, 72: 1285–1296.
- Field, J. C. 2004. *Application of Ecosystem-Based Fishery Management Approaches in the Northern California Current*. Doctoral Dissertation, University of Washington, Seattle, WA.
- Field, J. C., Francis, R. C., and Aydin, K. 2006. Top-down modeling and bottom-up dynamics: linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. *Progress in Oceanography*, 68: 238–270.
- Fogarty, M. J. 2014. The art of ecosystem-based fishery management. *Canadian Journal of Fisheries and Aquatic Sciences*, 71: 479–490.
- Fogarty, M. J., and Murawski, S. A. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecological Applications*, 8: S6–S22.
- Fogarty, M. J., Rosenberg, A. A., Cooper, A. B., Dickey-Collas, M., Fulton, E. A., Gutiérrez, N. L., Hydeg, K. J. W. *et al.* 2016. Fishery production potential of large marine ecosystems: a prototype analysis. *Environmental Development*, 17: 211–219.
- Francis, R. C., Hare, S. R., Hollowed, A. B., and Wooster, W. S. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fisheries Oceanography*, 7: 1–21.
- Friedland, K. D., Stock, C., Drinkwater, K. F., Link, J. S., Leaf, R. T., Shank, B. V., Rose, J. M. *et al.* 2012. Pathways between primary production and fisheries yields of large marine ecosystems. *Plos ONE*, 7: e28945.
- Fulton, E. A., Punt, A. E., Dichmont, C. M., Harvey, C. J., and Gorton, R. 2019. Ecosystems say good management pays off. *Fish and Fisheries*, 20: 66–96.
- Gaichas, S. K., Aydin, K. Y., and Francis, R. C. 2011. What drives dynamics in the Gulf of Alaska? Integrating hypotheses of species, fishing, and climate relationships using ecosystem modeling. *Canadian Journal of Fisheries and Aquatic Sciences*, 68: 1553–1578.
- Gaichas, S. K., DePiper, G. S., Seagraves, R. J., Muffley, B. W., Sabo, M. G., Colburn, L. L., and Loftus, A. J. 2018. Implementing ecosystem approaches to fishery management: risk assessment in

- the US mid-Atlantic. *Frontiers in Marine Science*, 5: 442. doi:10.3389/fmars.2018.00442.
- Gaichas, S. K., Link, J. S., and Hare, J. A. 2014. A risk-based approach to evaluating northeast US fish community vulnerability to climate change. *ICES Journal of Marine Science*, 71: 2323–2342.
- Gaichas, S., Gamble, R., Fogarty, M., Benoit, H., Essington, T., Fu, C., Koen-Alonso, M. *et al.* 2012. Assembly rules for aggregate-species production models: simulations in support of management strategy evaluation. *Marine Ecology Progress Series*, 459: 275–292.
- Gaines, S. D., Costello, C., Owashi, B., Mangin, T., Bone1, J., García Molinos, J., Burden, M. *et al.* 2018. Improved fisheries management could offset many negative effects of climate change. *Science Advances*, 4: eaao1378.
- Gascuel, D., Bozec, Y. - M., Chassot, E., Colomb, A., and Laurans, M. 2005. The trophic spectrum: theory and application as an ecosystem indicator. *ICES Journal of Marine Science*, 62: 443.
- Gascuel, D., Morissette, L., Lourdes, M., Palomares, D., and Christensen, V. 2008. Trophic flow kinetics in marine ecosystems: toward a theoretical approach to ecosystem functioning. *Ecological Modelling*, 217: 33.
- Graham, H. W., and Edwards, R. L. 1962. The world biomass of marine fishes. In *Fish in Nutrition*. eds Heen, E., and Kreuzer, R. Fishing News Books, London.
- Graham, M. 1943. *The Fish Gate*. Faber, London.
- Guerry, A. D., Polasky, S., Lubchenco, J., Chaplin-Kramer, R., Daily, G. C., Griffin, R., Ruckelshaus, M. *et al.* 2015. Natural capital and ecosystem services informing decisions: from promise to practice. *Proceedings of the National Academy of Sciences*, 112: 7348–7355.
- Halpern, B. S., Longo, C., Hardy, D., McLeod, K. L., Samhouri, J. F., Katoana, S. K., Kleisner, K. *et al.* 2012. An index to assess the health and benefits of the global ocean. *Nature*, 488: 615–620.
- Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'agrosa, C., Bruno, J. F. *et al.* 2008. A global map of human impact on marine ecosystems. *Science*, 319: 948–952.
- Hare, J. A., Morrison, W. E., Nelson, M. W., Stachura, M. M., Teeters, E. J., Griffis, R. B., Alexander, M. A. *et al.* 2016. A vulnerability assessment of fish and invertebrates to climate change on the northeast U.S. continental shelf. *Plos ONE*, 11:1–30.
- Hare, S. R., and Mantua, N. J. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, 47: 103–145.
- Harvey, C., Garfield, N., Williams, G., Tolimieri, N., Andrews, K., Barnas, K., Bjorkstedt, E. *et al.* 2020. Ecosystem status report of the California Current for 2019–20: a summary of ecosystem indicators compiled by the California Current Integrated Ecosystem Assessment Team (CCIEA). U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-160.
- Hempel, G., and Sherman, K. (eds) 2003. *Large Marine Ecosystems of the World: Trends in Exploitation, Protection and Research*. Elsevier, Amsterdam.
- Heymans, J. J., Guénette, S., and Christensen, V. 2007. Evaluating network analysis indicators of ecosystem status in the Gulf of Alaska. *Ecosystems*, 10: 488–502.
- Hilborn, R., Fulton, E. A., Green, B. S., Hartmann, K., Tracey, S. R., and Watson, R. A. 2015. When is a fishery sustainable? *Canadian Journal of Fisheries and Aquatic Sciences*, 72: 1433–1441.
- Hilborn, R., Oscar Amoroso, R., Anderson, C. M., Baum, J. K., Branch, T. A., Costello, C., de Moor, C. L. *et al.* 2020. Effective fisheries management instrumental in improving fish stock status. *Proceedings of the National Academy of Sciences*, 117: 2218–2224.
- Howell, E. A., Wabnitz, C. C. C., Dunne, J. P., and Polovina, J. J. 2013. Climate-induced primary productivity change and fishing impacts on the Central North Pacific ecosystem and Hawaii-based pelagic longline fishery. *Climatic Change*, 119: 79–93.
- Huyer, A. 1983. Coastal upwelling the California Current system. *Progress in Oceanography*, 12: 259–284.
- Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H. *et al.* 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293: 629–637.
- Jennings, S., Stentiford, G. D., Leocadio, A. M., Jeffery, K. R., Metcalfe, J. D., Katsiadaki, I., Auchterlonie, N. A. *et al.* 2016. Aquatic food security: insights into challenges and solutions from an analysis of interactions between fisheries, aquaculture, food safety, human health, fish and human welfare, economy and environment. *Fish and Fisheries*, 17: 893–938.
- Jin, D., DePiper, G., and Hoagland, P. 2016. Applying portfolio management to implement Ecosystem-Based Fishery Management (EBFM). *North American Journal of Fisheries Management*, 36: 652–669.
- Karnauskis, M., Kelble, C. R., Regan, S., Quenée, C., Allee, R., Jepson, M., Freitag, A. *et al.* 2017. 2017 Ecosystem Status report Update for the Gulf of Mexico. NOAA Technical Memorandum NMFS-SEFSC-706 51 p.
- Keyl, F., and Wolff, M. 2008. Environmental variability and fisheries: what can models do? *Reviews in Fish Biology and Fisheries*, 18: 273–299.
- Large, S. I., Fay, G., Friedland, K. D., and Link, J. S. 2015. Critical points in ecosystem responses to fishing and environmental pressures. *Marine Ecology Progress Series*, 521: 1–17.
- Lee, S. I., Aydin, K. Y., Spencer, P. D., Wilderbuer, T. K., and Zhang, C. I. 2010. The role of flatfishes in the organization and structure of the eastern Bering Sea ecosystem. *Fisheries Science*, 76: 411–434.
- Levin, S. A., Grenfell, B., Hastings, A., and Perelson, A. S. 1997. Mathematical and computational challenges in population biology and ecosystems science. *Science*, 275: 334–343.
- Libralato, S., Coll, M., Tudela, S., Palomera, I., and Pranovi, F. 2008. Novel index for quantification of ecosystem effects of fishing as removal of secondary production. *Marine Ecology Progress Series*, 355: 107–129.
- Libralato, S., Pranovi, F., Raicevich, S., Da Ponte, F., Giovanardi, O., Pastres, R., Torricelli, P. *et al.* 2004. Ecological stages of the Venice Lagoon analysed using landing time series data. *Journal of Marine Systems*, 51: 331–344.
- Libralato, S., Pranovi, F., Zucchetto, M., Monti, M. A., and Link, J. S. 2019. Global Thresholds in properties emerging from Cumulative Curves of Marine Ecosystems. *Ecological Indicators*, 103: 554–562.
- Libralato, S., and Solidoro, C. 2010. Comparing methods for building trophic spectra of ecological data. *ICES Journal of Marine Science*, 67: 426–434.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology*, 23: 399–417.
- Link, J. S. 2005. Translation of ecosystem indicators into decision criteria. *ICES Journal of Marine Science*, 62: 569–576.
- Link, J. S. 2010. *Ecosystem-Based Fisheries Management: Confronting Tradeoffs*. Cambridge University Press, Cambridge, UK.
- Link, J. S. 2018. System-level optimal yield: increased value, less risk, improved stability, and better fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, 75: 1–16.
- Link, J. S., Bundy, A., Overholtz, W. J., Shackell, N., Manderson, J., Duplisea, D., Hare, J. *et al.* 2011. Northwest Atlantic ecosystem-based fisheries management. *Fish and Fisheries*, 12: 152–170.
- Link, J. S., Fulton, E. A., and Gamble, R. J. 2010. The Northeast US Application of ATLANTIS: a full system model exploring marine ecosystem dynamics in a living marine resource management context. *Progress in Oceanography*, 87: 214–234.
- Link, J. S., Gaichas, S., Miller, T. J., Essington, T., Bundy, A., Boldt, J., Drinkwater, K. F. *et al.* 2012. Synthesizing lessons learned from comparing fisheries production in 13 Northern Hemisphere ecosystems: emergent fundamental features. *Marine Ecology Progress Series*, 459: 293–302.
- Link, J. S., Griswold, C. A., Methratta, E. M., and Gunnard, J. (eds) 2006. *Documentation for the Energy Modeling and Analysis eExercise (EMAX)*. Northeast Fisheries Science Center Reference Document, 06-15. 166 pp.
- Link, J. S., Pranovi, F., Libralato, S., Coll, M., Christensen, V., and Solidoro, C. 2015. Delineating marine ecosystem perturbation and recovery. *Trends in Ecology and Evolution*, 30: 649–661.

- Link, J. S., and Watson, R. A. 2019. Global ecosystem overfishing: clear delineation within real limits to production. *Science Advances*, 5:eaaav0474. doi: 10.1126/sciadv.aav0474.
- Link, J. S., Watson, R. A., Pranovi, F., and Libralato, S. 2020. Comparative production of fisheries yields and ecosystem overfishing in African Large Marine Ecosystems. *Environmental Development*, 36: 100529.
- Link, J., Overholtz, W., O'Reilly, J., Green, J., Dow, D., Palka, D., Legault, C. *et al.* 2008. An overview of EMAX: the Northeast U.S. continental shelf ecological network. *Journal of Marine Systems*, 74: 453–474.
- Livingston, P. A., Aydin, K., Buckley, T. W., Lang, G. M., Yang, M., S., and Miller, B. S. 2017. Quantifying food web interactions in the North Pacific—a data-based approach. *Environmental Biology of Fishes*, 100: 443–470.
- Lucey, S. M., Aydin, K. Y., Gaichas, S. K., Cadrin, S. X., Fay, G., Fogarty, M. J., and Punt, A. 2021. Evaluating fishery management strategies using an ecosystem model as an operating model. *Fisheries Research*, 234: 105780. <https://doi.org/10.1016/j.fishres.2020.105780>.
- Lynch, P. D., Methot, R. D., and Link, J. S. (eds.) 2018. Implementing a next generation stock assessment enterprise. *In* An Update to the NOAA Fisheries Stock Assessment Improvement Plan. NOAA Tech. Memo, NMFS-F/SPO-183, U.S. Department of Commerce. 127pp.
- Mace, P. M. 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 110–122.
- Melnichuk, M. C., Peterson, E., Elliott, M., and Hilborn, R. 2017. Fisheries management impacts on target species status. *Proceedings of the National Academy of Sciences*, 114: 178–183.
- Methot, R. D. (ed.) 2015. Prioritizing Fish Stock Assessments. NOAA Tech. Memo, NMFS-F/SPO-152, U.S. Department of Commerce. 31p.
- Methot, R. D., Tromble, G. R., Lambert, D. M., and Greene, K. E. 2014. Implementing a science-based system for preventing overfishing and guiding sustainable fisheries in the United States. *ICES Journal of Marine Science*, 71: 183–194.
- Micheli, F., De Leo, G., Butner, C., Martone, R. G., and Shester, G. 2014. A risk-based framework for assessing the cumulative impact of multiple fisheries. *Biological Conservation*, 176: 224–235.
- Millennium Ecosystem Assessment (MEA). 2005. *Ecosystems and Human Wellbeing: A Framework for Assessment*. Washington, DC: Island Press.
- Murawski, S. A. 2000. Definitions of overfishing from an ecosystem perspective. *ICES Journal of Marine Science*, 57: 649–658.
- National Marine Fisheries Service (NMFS). 2016. NOAA fisheries ecosystem-based fisheries management road map. NMFS 01-120-01: 1–50.
- National Oceanic and Atmospheric Administration (NOAA). 2020. Office for Coastal Management. NOAA Report on the U.S. Marine Economy. Charleston, SC: NOAA Office for Coastal Management. Available at <http://coast.noaa.gov/digitalcoast/training/econreport.html> (last accessed 28 August 2021).
- NEFSC. 2020b. State of the Ecosystem 2020: New-England. 25923/4tdk-eg57.
- NMFS. 2018. Fisheries of the United States, 2017. U.S. Department of Commerce, NOAA Current Fishery Statistics No. 2017.
- NMFS. 2019. Fisheries Economics of the United States, 2017. U.S. Dept. of Commerce, NOAA Tech. Memo. NMFS-F/SPO.
- NMFS. 2020. Status of Stocks 2019: Annual Report to Congress on the Status of U.S. Fisheries. U.S. DOC NOAA NMFS, Silver Spring, MD. <https://www.fisheries.noaa.gov/national/sustainable-fisheries/status-stocks-2019> (last accessed 28 August 2021).
- Northeast Fisheries Science Center (NEFSC). 2002a. State of the Ecosystem 2020: Mid-Atlantic. doi: 10.25923/1f8j-d564.
- O'Neill, R. V., DeAngelis, D. L., Waide, J. B., and Allen, T. F. H. 1986. *A Hierarchical Concept of Ecosystems*. Princeton University Press, Princeton, NJ.
- Odom, E. P. 1969. The strategy of ecosystem development. *Science*, 164: 262–270.
- OECD (Organisation for Economic Cooperation and Development). 2020. *OECD Review of Fisheries 2020*, OECD Publishing, Paris. doi: 10.1787/7946bc8a-en.
- Okey, T. A., and Pugliese, R. 2001. A Preliminary Ecopath Model of the Atlantic Continental Shelf Adjacent to the Southeastern United States. Pages 9: pp. 167–181. Ed. by Guenette, S., Christensen, V., and Pauly, D.. University of British Columbia, Fisheries Centre Research Reports. University of British Columbia, Fisheries Centre Research Reports.
- Oksanen, L. 1991. Trophic levels and trophic dynamics: a consensus emerging? *Trends in Ecology & Evolution*, 6: 58–60.
- Opitz, S. 1996. Trophic interactions in Caribbean Coral Reefs. *In* Trophic Models of Aquatic Ecosystems, 43. pp. 259–267, eds Christensen, V., and Pauly, D. ICLARM Technical Report 43.
- Parrish, F. A., Howell, E. A., Antonelis, G. A., Iverson, S. J., Littnan, C. L., Parrish, J. D., and Polovina, J. J. 2012. Estimating the carrying capacity of French Frigate Shoals for the endangered Hawaiian monk seal using Ecopath with Ecosim. *Marine Mammal Science*, 28: 522–541.
- Patrick, W., Spencer, P., Ormseth, O., Cope, J., Field, J., Kobayashi, D., Gedamke, T. *et al.* 2009. Use of productivity and susceptibility indices to determine the vulnerability of a stock, with example applications to six U.S. Fisheries NOAA Tech. Memo. MFS-F/SPO-101, 90 p.
- Pauly, D., and Christensen, V. 1995. Primary production required to sustain global fisheries. *Nature*, 374: 255–257.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. 1998. Fishing down marine food webs. *Science*, 279: 860–863.
- Pauly, D., Christensen, V., Guénette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., Watson, R. *et al.* 2002. Towards sustainability in world fisheries. *Nature*, 418: 689–695.
- Pauly, D., and Zeller, D. 2016. Catch reconstructions reveal that global fisheries catches are higher than reported and declining. *Nature Communications*, 7: 10244.
- Pauly, D., Zeller, D., and Palomares, M. L. D. (Editors). 2020. *Sea Around Us Concepts, Design and Data* (www.seaaroundus.org) (last accessed 28 August 2021).
- Peterson, W. T., and Schwing, F. B. 2003. A new climate regime in north-east Pacific ecosystems. *Geophysical Research Letters*, 30: 1896. doi:10.1029/2003GL017528.
- Petrick, C. M., Stock, C. A., Andersen, K. H., van Denderen, P. D., and Watson, J. R., 2019. Bottom-up drivers of global patterns of demersal, forage, and pelagic fishes. *Progress in Oceanography*, 176: 102124.
- Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P. *et al.* 2004. Ecosystem-based fishery management. *Science*, 305: 346–347.
- Pitcher, T. J., Kalikoski, D., Short, K., Varkey, D., and Pramod, G. 2009. An evaluation of progress in implementing ecosystem-based management of fisheries in 33 countries. *Marine Policy*, 33: 223–232.
- Polovina, J. J. 1984. Model of a coral reef ecosystem I. The ECOPATH model and its applications to French Frigate Shoals. *Coral Reefs*, 3: 1–11.
- Pranovi, F., Libralato, F. S., Zucchetto, M., and Link, J. 2014. Biomass accumulation across trophic levels: analysis of landings for the Mediterranean Sea. *Marine Ecology Progress Series*, 512: 201–216.
- Pranovi, F., Libralato, S., Zucchetto, M., Monti, M. A., and Link, J. S. 2020. Cumulative biomass curves describe past and present conditions of Large Marine Ecosystems. *Global Change Biology*, 26: 786–797.
- Pranovi, F., and Link, J. S. 2009. Ecosystem exploitation and trophodynamic indicators: a comparison between the Northern Adriatic Sea and Southern New England. *Progress in Oceanography*, 81: 149–164.
- Pranovi, F., Link, J., Fu, C., Cook, A., Liu, H., Gaichas, S., Friedland, K. *et al.* 2012. Trophic-level determinants of biomass accumulation in marine ecosystems. *Marine Ecology Progress Series*, 459: 185–201.

- R Core Team. 2018. R: A language and environment for statistical computing, RFoundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/> (last accessed 12 September 2019).
- Ricker, W. E. 1969. Food from the sea. in U.S. National Academy of Sciences Series- Resources and man. W.H. Freeman, San Francisco, CA.
- Ricketts, J. H., and Head, G. A. 1999. A five-parameter logistic equation for investigating asymmetry of curvature in baroreflex studies. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 277:R441–R454.
- Rindorf, A., Dichmont, C. M., Levin, P. S., Mace, P., Pascoe, S., Prelezo, R., Punt, A. E. *et al.* 2017. Food for thought: pretty good multispecies yield. *ICES Journal of Marine Science*, 74: 475–486.
- Ritz, C., Baty, F., Streibig, J. C., and Gerhard, D. 2015. Dose-response analysis using R. *Plos ONE*, 10: 1–13.
- Rodhouse, P. G., Pierce, G. J., Nichols, O. C., Sauer, W. H., Arkhipkin, A. L., Laptikhovskiy, V. V., Lipiński, M. R. *et al.* 2014. Environmental effects on cephalopod population dynamics: implications for management of fisheries. *Advances in Marine Biology*, 67: 99–233.
- Rousseau, Y., Watson, R. A., Blanchard, J. L., and Fulton, E. A. 2019. Evolution of global marine fishing fleets and the response of fished resources. *Proceedings of the National Academy of Sciences*, 116(25):12238–12243.
- Ruzicka, J. J., Brodeur, R. D., Emmett, R. L., Steele, J. H., Zamon, J. E., Morgan, C. A., Thomas, A. C. *et al.* 2012. Interannual variability in the Northern California Current food web structure: changes in energy flow pathways and the role of forage fish, euphausiids, and jellyfish. *Progress in Oceanography*, 102: 19–41.
- Ryther, J. H. 1969. Photosynthesis and fish production from the sea. *Science*, 166: 72–76.
- Sagarese, S. R., Lauretta, M. V., and Walter, J. F. 2017. Progress towards a next-generation fisheries ecosystem model for the northern Gulf of Mexico. *Ecological Modelling*, 345: 75–98.
- Samhuri, J. F., Andrews, K. S., Fay, G., Harvey, C. J., Hazen, E. L., Hennessey, S. M., Holsman, K. *et al.* 2017. Defining ecosystem thresholds for human activities and environmental pressures in the California Current. *Ecosphere*, 8: e01860.
- Sanchirico, J. N., Smith, M. D., and Lipton, D. W. 2008. An empirical approach to ecosystem-based fishery management. *Ecological Economics*, 64: 586–596.
- Schaefer, M. B. 1957. Some considerations of population dynamics and economics in relation to the management of the commercial marine fisheries. *Journal of the Fisheries Research Board of Canada*, 14: 669–681.
- Schaefer, M. B. 1965. The potential harvest of the sea. *Transactions of the American Fisheries Society*, 94: 123–128.
- Scheffer, M., Carpenter, S., and de Young, B. 2005. Cascading effects of overfishing marine systems. *Trends in Ecology and Evolution*, 20: 579–581.
- Schindler, D. E., Armstrong, J. B., and Reed, T. E. 2015. The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, 13: 257–263.
- Schlenger, A. J., Libralato, S., and Ballance, L. T. 2019. Temporal variability of primary production explains marine ecosystem structure and function. *Ecosystems*, 22: 331–345.
- Shannon, L., Coll, M., Bundy, A., Gascuel, D., Heymans, J. J., Kleisner, K., Lynam, C. P. *et al.* 2014. Trophic level-based indicators to track fishing impacts across marine ecosystems. *Marine Ecology Progress Series*, 512: 115–140.
- Sherman, K., Alexander, D. G., and Gold, B. D. 1993. Large Marine Ecosystems. Stress, Mitigation and Sustainability. Science, American Association for the Advancement of, Washington, DC. 376pp.
- Shin, Y. - J., Shannon, L. J., Bundy, A., Coll, M., Blanchard, J. L., Borges, M. - F., Cotter, J. *et al.* 2010b. Using indicators for evaluating, comparing, and communicating the ecological status of exploited marine ecosystems. 2. Setting the scene. *ICES Journal of Marine Science*, 67: 692–716.
- Shin, Y. - J., Bundy, A., Shannon, L. J., Simier, M., Coll, M., Fulton, E. A., Link, J. S. *et al.* 2010a. Can simple be useful and reliable? Using ecological indicators for representing and comparing the states of marine ecosystems. *ICES Journal of Marine Science*, 67: 717–731.
- Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation*, 83: 247–257.
- Simons, J. D., Yaun, M., Carollo, C., Vega-Cendejas, M., Shirley, T., Palomares, M. L. D., Roopnarine, P. *et al.* 2013. Building a fisheries trophic interaction database for management and modeling research in the Gulf of Mexico large marine ecosystem. *Bulletin of Marine Science*, 89: 135–160.
- Smikle, S. G., Christensen, V., and Aiken, K. A. 2010. A review of Caribbean ecosystems and fishery resources using ECOPATH Models. *Études Caribéennes*, 15: 4529. doi: 10.4000/etudescaribeennes.4529.
- Smith, A. D. M., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-Montes, H. *et al.* 2011. Impacts of fishing low-trophic level species on marine ecosystems. *Science*, 333: 1147–1150.
- Smith, B. E., and Link, J. S. 2010. The trophic dynamics of 50 Finfish and two squid species on the Northeast U.S. continental shelf. NOAA Technical Memorandum NMFS-NE-216, 640pp.
- Smith, T. D. 1994. *Scaling Fisheries: The Science of Measuring the Effects of Fishing, 1855-1955*. Cambridge University Press, New York, NY.
- Stock, C. A., John, J. G., Rykaczewski, R. R., Asch, R. G., Cheung, W. W. L., Dunne, J. P., Friedland, K. D. *et al.* 2017. Reconciling fisheries catch and ocean productivity. *Proceedings of the National Academy of Sciences*, 114: E1441–E1449.
- Strayer, D. 1991. Notes on Lindeman's progressive efficiency. *Ecology*, 72:348–350.
- Swartz, W., Sala, E., Tracey, S., Watson, R., and Pauly, D. 2010. The spatial expansion and ecological footprint of fisheries (1950 to present). *Plos ONE*, 5:e15143.
- Tam, J., Link, J. S., Large, S. I., Andrews, K., Friedland, K., Gove, J., Hazen, E. *et al.* 2017. Comparing apples to oranges: common trends and thresholds in anthropogenic and environmental pressures across multiple marine ecosystems. *Frontiers in Marine Science*, 4: 282.
- Thorpe, R. B. 2019. What is multispecies MSY? A worked example from the North Sea. *Journal of Fish Biology*, 94: 1011–1018.
- Thorson, J. T., Cope, J. M., Kleisner, K. M., Samhuri, J. F., Shelton, A. O., and Ward, E. J. 2015. Giants' shoulders 15 years later: lessons, challenges and guidelines in fisheries meta-analysis. *Fish and Fisheries*, 16: 342–361.
- Tudela, S., Coll, M., and Palomera, I. 2005. Developing an operational reference framework for fisheries management on the basis of a two-dimensional index of ecosystem impact. *ICES Journal of Marine Science*, 62: 585–591.
- Ulanowicz, R. E. 1986. *Growth and Development: Ecosystem Phenomenology*. Springer-Verlag, New York, NY.
- United Nations. 2015. *Transforming our world: the 2030 agenda for sustainable development*. General Assembly 70 Session, 16301: 1–35.
- Walters, C., Martell, S. J. D., Christensen, V., and Mahmoudi, B. 2008. An Ecosim model for exploring ecosystem management options for the Gulf of Mexico: implications of including multistanza life-history models for policy predictions *Bulletin of Marine Science*, 83: 251–271.
- Watson, R. A. A. 2017. Database of global marine commercial, small-scale, illegal and unreported fisheries catch 1950–2014. *Scientific Data*, 4: 170039.
- Watson, R. A., Nowara, G. B., Hartmann, K., Green, B. S., Tracey, S. R., and Carter, C. G. 2015. Marine foods sourced from farther as their use of global ocean primary production increases. *Nature Communications*, 6: 7365.
- Watson, R., Kitchingman, A., Gelchu, A., and Pauly, D. 2004. Mapping global fisheries: sharpening our focus. *Fish and Fisheries*, 5: 168–177.
- Watson, R., and Pauly, D. 2001. Systematic distortions in world fisheries catch trends. *Nature*, 414: 534–536.

- Watson, R., Zeller, D., and Pauly, D. 2014. Primary productivity demands of global fishing fleets. *Fish and Fisheries*, 15: 231–241.
- Weijerman, M., Fulton, E. A., Kaplan, I. C., Gorton, R., Leemans, R., Mooij, W. M., and Brianard, R. E. 2015. An integrated coral reef ecosystem model to support resource management under a changing climate. *Plos ONE*, 10: e0144165. doi: 10.1371/journal.pone.0144165.
- Weijerman, M., Kaplan, I., Fulton, E., Gordon, B., Grafeld, S., and Brainard, R. 2014. Design and Parameterization of a Coral Reef Ecosystem Model for Guam. U.S. Department of Commerce, NOAA Technical Memorandum, NOAA-TM-NMFS-PIFSC-43, 113p.
- World Bank. 2017. *The Sunken Billions Revisited: Progress and Challenges in Global Marine Fisheries*. Washington, DC: World Bank. Environment and Sustainable Development series. doi:10.1596/978-1-4648-0919-4.
- Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J. *et al.* 2009. Rebuilding global fisheries. *Science*, 325: 578–585.
- Wu, J. G. 2013. Hierarchy theory: an overview. In *Linking Ecology and Ethics for a Changing World: Values, Philosophy, and Action*. pp.281–301 Ed. by Rozzi, R., Pickett, S. T. A., Palmer, C., Armesto, J. J., and Callicott, J. B. Springer, New York, NY.

Handling Editor: Morgane Travers-Trolet