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Describing ecosystem contexts with single-species models: a theoretical synthesis for fisheries

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Abstract

Fished populations exist within complex ecosystems but are typically assessed using single-species models. It is often lamented that stock assessments rarely account for other ecosystem components explicitly, but in most fisheries there are clear difficulties in implementing data-intensive ecosystem-based assessment approaches. Addressing these competing challenges requires prioritizing investments in expanded assessment frameworks. To provide high-level conceptual guidance to such prioritization, here we use general analytical theory to identify (i) characteristics of fish stocks that tend to facilitate or inhibit the precision and accuracy of reference points from single-species assessments, (ii) characteristics of ecosystem components that introduce the greatest bias/imprecision into single-species reference points and (iii) warning signs within single-species frameworks that important ecosystem components may not be adequately accounted for. We synthesize and expand on theories from various branches of applied mathematics addressing analogous questions. Our theory suggests that (i) slow population dynamics (relative to the dynamics of other ecosystem components) and a wide range of abundance observations promote precision and accuracy of single-species reference points; (ii) ecosystem components that strongly influence the focal stock's growth, and change on similar timescales as the focal stock's abundance, introduce the greatest bias/imprecision to single-species reference points; and (iii) signs of potential challenges for single-species assessment include fast population dynamics, 'hydra effects' (i.e. abundance and fishing pressure simultaneously increase), and recently detected extinctions, invasions or regime shifts in closely connected ecosystem components. Our results generalize to other levels of abstraction and provide strategic insights complementing tactical simulation approaches such as management strategy evaluation.

Keywords Complexity, dimensionality, ecosystem-based fishery management, stock assessment

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Introduction

Harvested fish populations exist within diverse and complex ecosystems, but their sustainable harvests are almost always estimated using single-species population models (Hilborn and Walters 1992; Skern-Mauritzen *et al.* 2016). Many have called for a transition away from single-species assessment and management approaches and towards ecosystem-based fishery management (EBFM) (e.g. Pikitch *et al.* 2004; Fletcher *et al.* 2010; Fulton *et al.* 2014), while others have argued that such a transition is not necessarily pressing, citing the many recent examples of success in traditional single-species fisheries management (Hilborn 2011; Hilborn and Ovando 2014).

We argue that there is conceptual merit to both of these perspectives. Single-species approaches clearly may fail to capture critical fishery-relevant ecosystem properties (Link 2002a), but fisheries science is also highly data-limited. A large fraction of the world's fisheries do not even have sufficient data for traditional single-species assessments (Costello *et al.* 2012, 2016), and those for which whole ecosystem models (e.g. Link 2002b; Christensen and Walters 2004) – or even 'models of intermediate complexity' (MICE) (Plagányi *et al.* 2014; Collie *et al.* 2016) – can be applied empirically are an even smaller minority (Hilborn 2011). Complexity and data limitation in fisheries exemplify the common conflicting challenges of wanting to make high-value predictions, but having relatively little information to base these on – challenges that demand pragmatism in prioritizing investments in new information and maximizing the value of available information.

To prioritize investments in transitions towards multispecies approaches, it is important to identify conditions *a priori* under which we would expect single-species assessment and management to fail. For example, single-species management could be problematic if (a) single-species models are likely to provide inaccurate predictions of a stock's response to fishing pressure, or (b) multispecies management objectives are unlikely to be achieved through independent pursuits of single-species management objectives that fail to consider multispecies trade-offs (e.g. see Walters *et al.* 2005; Smith *et al.* 2011).

Here, we focus on the first of these problems. Specifically, we use general analytical theory to identify (i) characteristics of fish stocks that tend to facilitate or inhibit the precision and accuracy of reference points from single-species assessments, (ii) characteristics of ecosystem components linked to the focal stock that introduce the greatest bias/imprecision into single-species reference points and (iii) warning signs, detectable within single-species frameworks, that important ecosystem components may not be adequately accounted for. Our results are summarized heuristically in Table 1.

For specific stocks or ecosystems, management strategy evaluation (MSE) (see Punt *et al.* 2016 for

Table 1 Heuristic summary of properties of the focal stock and its ecosystem that promote or inhibit single-species assessment.

Focal stock traits promoting precision and accuracy in single-species reference points:	Ecosystem component traits that introduce bias/imprecision into single-species reference points:	Warning signs for single-species assessment:
• Slow turnover (precision and accuracy), generally associated with large body size and long lifespan • Large range of abundances observed (precision)	• Strong influence on the growth of the focal stock, *and* one or both of: • Non-stationarity (bias and imprecision), or stationary cycling with large amplitude (imprecision) and long period (bias and imprecision) • A state that changes on a similar timescale as the focal stock's abundance (bias and imprecision), especially if there is also nonzero covariance (bias)	• Fast turnover in the focal stock (suggests bias and imprecision likely) • Hydra effect (i.e. fish harder and abundance increases; suggests future change in productivity likely) • Recently detected invasion, local extinction or regime shift (suggests abrupt recent change in productivity possible)

review) and related multispecies simulation approaches could provide tactical advice on similar questions (i.e. advice that is 'focused on management actions on short timescales', see Plagányi *et al.* 2014; see Fogarty 2013; Fulton *et al.* 2014; Link and Browman 2014 for conceptual overviews; see Holsman *et al.* 2015 for a worked example). Our objective is to provide complementary strategic insights (in the spirit of 'big picture, direction-setting and contextual', see Plagányi *et al.* 2014) – demonstrating *why* certain stocks or ecosystems are less amenable to single-species assessment, and how to identify these stocks and ecosystems in advance of doing system-specific MSEs, so that more complex MSE efforts can be better targeted.

Our analysis is underpinned by two basic conceptual questions. First, under what conditions can single-species population models abstractly describe (hereafter 'abstract') the short- and long-term responses of a stock to fishing even though the stock exists in a complex ecosystem context? Such abstraction would occur if the focal stock's response to fishing followed a pattern consistent with a single-species model, and the effects of the stock's interactions with other species and abiotic factors were therefore captured implicitly when estimating the parameters of the assumed single-species model (Schaffer 1981). Second, when abstraction fails, which characteristics of stocks and their ecosystem contexts lead to the greatest reductions in the precision and accuracy of fishery reference points derived from single-species model fits?

Although it is implicitly central to much of fisheries science, the concept of abstraction has received relatively little formal treatment in a fisheries context. A few studies in ecology, economics and other branches of applied mathematics have explored related concepts (e.g. Schaffer 1981; Iwasa *et al.* 1987, 1989; Abrams 2009a,b,c,d; Tschirhart 2012; Reynolds and Brassil 2013; Wolpert *et al.* 2015). Our analysis draws and expands on these results, aiming to provide a general synthesis for a fisheries context. Our goal is to provide a primer that links these conceptually rich but abstract analytical theories to the practical experience of assessing and managing fisheries.

Model

We assume that a fish stock of interest – having abundance $N(t)$ at time t – exists within a larger ecosystem made up of A additional components (including other species/populations, abiotic factors and even other fishing fleets), whose dynamics are represented by the vector $\boldsymbol{M}(t) = \{M_1(t),\ldots, M_A(t)\}$. The (true) dynamics of the focal stock are determined by the difference between its per-capita fishing mortality rate, $F(t)$ at time t, and its per-capita production rate (growth + recruitment – natural mortality) – which is denoted $g[N(t), \boldsymbol{M}(t)]$ and is potentially a function of both the stock's own abundance [N(t)] and the other ecosystem components' states [$\boldsymbol{M}(t)$].

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = N(t)(g[N(t),\boldsymbol{M}(t)] - F[t]) \qquad (1)$$

So the stock's dynamics are in reality connected to other ecosystem components, but we assume that these interconnections are (explicitly) ignored in a single-species stock assessment, which assumes a production model of the form:

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = N(t)(\hat{g}[N(t)] - F[t]). \qquad (2)$$

Here, $\hat{g}[N(t)]$ is the single-species per-capita production function being used to abstract the stock's dynamics; in general, $\hat{g}[N(t)] \neq g[N(t),\boldsymbol{M}(t)]$. For simplicity, we do not explicitly consider age structure, but incorporating it would be a straightforward extension of our analysis (where $\boldsymbol{N}$ and $\boldsymbol{F}$ would now be vectors of age-specific abundance and fishing mortality, instead of being scalars), one unlikely to significantly impact the general results (Discussion). To our knowledge, single-species models always specify unique mappings from N to $\hat{g}(N)$ [in other words, given N, there is a unique value of $\hat{g}(N)$], which in our framework without age structure implies an assumption that:

$$\hat{g} : \Re^1 \to \Re^1. \qquad (3)$$

We formally consider the exercise of fitting a single-species model (2) to data produced by the ecosystem context (1) using the following simplified framework, which is designed to be tractable but still capture the essence of a realistic assessment. We assume the fitting exercise involves measuring catch [$C(t)$] and abundance $N(t)$ (if an index proportional to abundance is observed instead, as is generally the case, we are in effect assuming that the proportionality of the index is estimated without bias; see Appendix 1 for further discussion) – and thereby also its rate of change, $\mathrm{d}N(t)/\mathrm{d}t$ – over time, and estimating the parameters of $\hat{g}(.)$, using a method that minimizes the sum of squares, based on the following equation:

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t}\left[\frac{1}{N(t)}\right] = \hat{g}[N(t)] - \frac{C(t)}{N(t)}. \qquad (4)$$

Here, the fractional change in abundance [the left-hand side of (4)] is the response variable, $C(t)/N(t) = F(t)$, and the sum of squares over a data set (i.e. a set of observations, having time indices $\boldsymbol{T} = \{t_1, t_2, \ldots\}$), denoted $\mathrm{SSQ}_{\boldsymbol{T}}$, is given by:

$$\mathrm{SSQ}_{\boldsymbol{T}} = \sum_{t \in \boldsymbol{T}} (\hat{g}[N(t)] - g[N(t),\boldsymbol{M}(t)])^2. \qquad (5)$$

For simplicity, we assume no observation error or process noise, that is, any apparent noise in the single-species model fit is a result of its failure to capture the true dynamics of the larger ecosystem rather than genuinely random error. We assume sum-of-squares-based estimation because of its analytical tractability, but other more commonly used estimators (e.g. maximum-likelihood and Bayesian methods; Methot and Wetzel 2013 described a common modern estimation approach) would likely produce similar qualitative results.

We consider the accuracy of single-species assessments in terms of their ability to estimate the reference point F_{MSY} – the maximum sustainable yield (MSY) fishing mortality rate (Fig. 1a) – but we note that considering other reference points would be an analogous exercise with qualitatively similar results. The fitted estimate of F_{MSY}, denoted $\hat{F}_{\mathrm{MSY}}$, is equal to $\hat{g}(N)$ at the abundance, N, maximizing $N\hat{g}(N)$, given the fitted parameters. The precision of the single-species assessment, for our purposes, is the consistency with which $\hat{g}(N)$ – and by extension $\hat{F}_{\mathrm{MSY}}$ – would be estimated across different possible samples [i.e. sets of times at which $N(t)$, $C(t)$ and $\mathrm{d}N(t)/N(t)\mathrm{d}t$ were measured].

Results

Effective dimensionality and timescale separation

If the focal stock's true dynamics [from (1)] were perfectly described by model (2), it would have to be the case that:

$$\hat{g}[N(t)] = g[N(t),\boldsymbol{M}(t)]|N(t), \text{at any } t. \qquad (6)$$

This follows from equations (1) and (2), and assumption (3). For this to literally be true – for N to map uniquely to $g(\ldots)$ – N would almost certainly have to also map uniquely to all M_j (i.e. the states of all other species, abiotic factors and fishing fleets) ecologically connected to the focal stock. In other words, it would be possible to

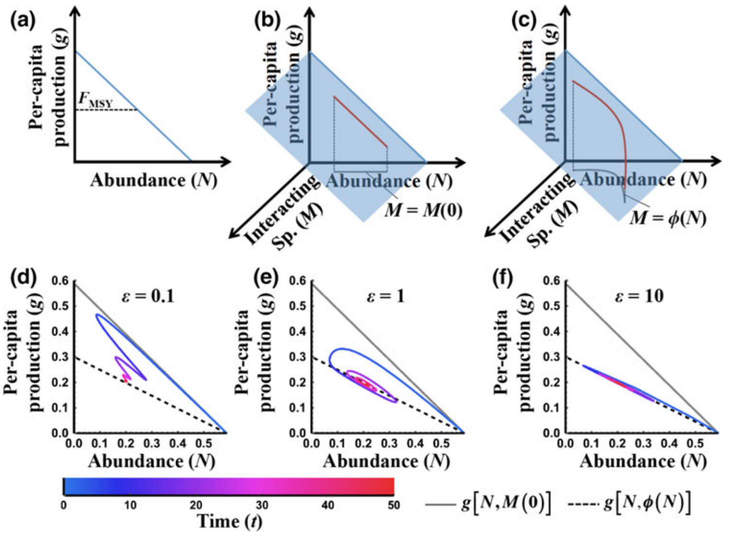

Figure 1 Timescale separation promotes capturing ecosystem contexts with single-species models – illustrated in panels a-c, and demonstrated in a simulated example in panels d-f, with a single additional species [having abundance $M(t)$] interacting with the focal stock. (a) A single-species production model specifies an $\mathfrak{R}^1 \to \mathfrak{R}^1$ mapping (blue line) from focal stock abundance (N) to per-capita production (g): $N \to g$. (b) $M(t)$ is approximately constant if its dynamics are very slow relative to $N(t)$, which implies an approximate $\mathfrak{R}^1 \to \mathfrak{R}^1$ mapping from $N(t) \to M(t)$ [$N(t) \to M(0)$] (grey line) and therefore also an $\mathfrak{R}^1 \to \mathfrak{R}^1$ mapping from $N \to g$ (blue plane) ($g[N(t), M(t)] \approx g[N(t), M(0)]$) (red curve, which sits in the blue plane); this is effectively a single-species model. (c) Similarly, if the dynamics of $M(t)$ are very fast relative to $N(t)$ – and if $M(t)$ converges to $\phi(N)$ (grey) with fixed N – $M(t)$ approximately tracks $N(t)$, that is $g[N(t), M(t)] \approx g[N(t), \phi(N[t])]$) (red curve in the blue plane), which is also effectively a single-species model. (d)-(f): Simulated example where $g[N(t), M(t)] = 1 - N(t) - c_{MN}M(t)$, $\mathrm{d}F(t)/\mathrm{d}t = F(t)[5N(t) - 1]$ (i.e. open-access fishing [Clark 1976], with F proportional to fishing effort, price per-unit harvest 5 and cost per-unit fishing mortality 1), and $\mathrm{d}M(t)/\mathrm{d}t = \varepsilon M(t)[1 - M(t) - c_{NM}N(t)]$ (i.e. N and M are ecological competitors, with c_{MN} and c_{NM} determining strength of competition); c_{MN} and $c_{NM} = 0.7$, $F(0) = 0.01$ and $N(t)$, $M(t)$ are initialized at their unharvested equilibrium values, in all three panels. Parameter ε determines the relative timescales of $N(t)$ and $M(t)$ dynamics and is varied in value across (d)-(f) as indicated. When $M(t)$ is fast (f: large ε), the dynamics of $g[N(t), M(t)]$ (coloured by time, as indicated) are well approximated by single-species model $g[N(t), \phi(N[t])]$ (black, dashed); when $M(t)$ is slow (d: small ε), the dynamics of $g[N(t), M(t)]$ are well approximated by single-species model $g[N(t), M(0)]$ (grey) in the short term, but they eventually drift away. [Color figure can be viewed at wileyonlinelibrary.com]

express each M_j as a function of only N [i.e. $M_j(t) = M_j(N[t])$ at all t]. In Appendix 2, we show that if this were not the case – for example, if there were multiple possible abundances for a set of interacting species at a given N – the effects of these discrepancies (either direct or indirect through the food web) on $g(N, \boldsymbol{M})$ would have to exactly cancel one another out, which, as we discuss in Appendix 2, is far-fetched.

In other words, the stock's density dependence (i.e. the relationship between its per-capita growth rate and abundance) will only perfectly resemble a single-species model if it is effectively one-dimensional. Put another way, a single-species model can perfectly abstract the response of a stock to fishing pressure if the fishing pressure is the only free parameter in the system at the timescale in question. Other degrees of freedom (from interacting species, fleets or exogenous drivers such as climate [see Szuwalski *et al.* 2015]) make the system of larger effective dimension than a single-species model can describe. Clearly, a stock's density dependence will never be exactly one-dimensional; indeed, one study (Glaser *et al.* 2014) estimating the effective dimensionality of the dynamical systems producing several fish stock abundance time series found most to have effective dimension larger than 2 (the dimension implied by a single-species model subject to fishing).

However, if the focal stock interacts with other species and abiotic factors whose dynamics occur on significantly different timescales (i.e. their dynamics are much faster or much slower than those of the focal stock), the focal stock's dynamics may approximately have the dimensions of a single-species system (see Heineken *et al.* 1967; Schaffer 1981 for expanded analogous demonstrations in chemistry and ecology, respectively). The dynamic 'speed' or timescale of biological populations is determined roughly by their turnover rates (see Rinaldi and Muratori 1992 for an illustrative example); for example, a forage fish has faster dynamics than a whale, because it has higher birth and death rates. For abiotic factors, the timescale is determined by their average absolute-value rates of change.

The basic intuition of timescale separation is the following (illustrated in Fig. 1b,c): if the dynamics of the focal stock's abundance, $N(t)$, are much faster than the dynamics of the rest of its ecosystem, $\boldsymbol{M}(t)$, then the rest of the ecosystem ($\boldsymbol{M}$) is approximately constant relative to the focal stock in the short term (Fig. 1b), that is,

$$g[N(t), \boldsymbol{M}(t)] \approx g[N(t), \boldsymbol{M}(0)]. \qquad (7)$$

Conversely, if the dynamics of the focal stock's abundance, $N(t)$, are much slower than the dynamics of the rest of its ecosystem, $\boldsymbol{M}(t)$ – and if $\boldsymbol{M}(t)$ asymptotically approaches an attractor, $\boldsymbol{\phi}(N)$, which is only a function of N, if N is held constant – then the rest of the ecosystem ($\boldsymbol{M}$) approximately tracks the focal stock (N), (Fig. 1c), that is,

$$g[N(t), \boldsymbol{M}(t)] \approx g[N(t), \boldsymbol{\phi}(N[t])]. \qquad (8)$$

Both $g[N(t), \boldsymbol{M}(0)]$ and $g[N(t), \boldsymbol{\phi}(N[t])]$ are single-species models (because they are functions of only $N[t]$ and constants). However, an important difference (e.g. from the standpoint of fishery reference points) is that if the dynamics of the focal stock are fast relative to other factors, the quality of the single-species approximation ($g[N(t), \boldsymbol{M}(0)]$) decays over time (see example in Fig. 1d), whereas quality of the single-species approximation ($g[N(t), \boldsymbol{\phi}(N[t])]$) does not decay over time if the dynamics of the focal stock are slow relative to other factors (see example in Fig. 1f).

To state the concept of timescale separation more precisely, if the dynamics of $\boldsymbol{M}$ can be written as:

$$\frac{\mathrm{d}\boldsymbol{M}(t)}{\mathrm{d}t} = \varepsilon \boldsymbol{f}[N(t), \boldsymbol{M}(t)], \qquad (9)$$

then:

$$\lim_{\varepsilon \to \infty} g[N(t), \boldsymbol{M}(t)] = g[N(t), \boldsymbol{\phi}(N[t])], \qquad (10a)$$

$$\lim_{\varepsilon \to 0} g[N(t), \boldsymbol{M}(t)] = g[N(t), \boldsymbol{M}(0)], \qquad (10b)$$

where (10a) follows from Tikhonov's (1952) theorem, assuming that $\boldsymbol{\phi}(N)$ is an asymptotically stable solution of $\boldsymbol{f}[N, \boldsymbol{M}] = 0$ for $\boldsymbol{M}$, over the domain of attraction including $\boldsymbol{M}(0)$. We relax this assumption in the section below on model fitting.

More generally, suppose that the ecosystem contains some components – with states denoted $\boldsymbol{M}_X$ – having significantly faster dynamics than the focal stock; some components – with states denoted $\boldsymbol{M}_Z$ – having significantly slower dynamics than the focal stock; and some components – with states denoted $\boldsymbol{M}_Y$ – varying on a similar timescale as the focal stock [$\boldsymbol{M}(t) = \{\boldsymbol{M}_X(t), \boldsymbol{M}_Y(t), \boldsymbol{M}_Z(t)\}$], such that the dynamics of $\boldsymbol{M}(t)$ can be written as:

$$\varepsilon \frac{\mathrm{d}\boldsymbol{M}_X(t)}{\mathrm{d}t} = \boldsymbol{f}_X[N(t), \boldsymbol{M}(t)], \qquad (11a)$$

$$\frac{\mathrm{d}\boldsymbol{M}_Y(t)}{\mathrm{d}t} = \boldsymbol{f}_Y[N(t), \boldsymbol{M}(t)], \qquad (11b)$$

$$\frac{\mathrm{d}\boldsymbol{M}_Z(t)}{\mathrm{d}t} = \varepsilon \boldsymbol{f}_Z[N(t), \boldsymbol{M}(t)]; \qquad (11c)$$

and suppose that $\boldsymbol{\phi}_X(N, \boldsymbol{M}_Y, \boldsymbol{M}_Z)$ is an asymptotically stable (holding N, $\boldsymbol{M}_Y$, $\boldsymbol{M}_Z$ constant) solution to $\boldsymbol{f}_X[N, \{\boldsymbol{M}_X, \boldsymbol{M}_Y, \boldsymbol{M}_Z\}] = 0$ for $\boldsymbol{M}_X$. In this case,

$$\lim_{\varepsilon \to 0} g[N(t), \boldsymbol{M}(t)] = g[N(t), \{\boldsymbol{\phi}_X[N(t), \boldsymbol{M}_Y(t), \boldsymbol{M}_Z(0)], \boldsymbol{M}_Y(t), \boldsymbol{M}_Z(0)\}], \qquad (12a)$$

$$\lim_{\varepsilon \to 0} \boldsymbol{f}_Y[N(t), \boldsymbol{M}(t)] = \boldsymbol{f}_Y[N(t), \{\boldsymbol{\phi}_X[N(t), \boldsymbol{M}_Y(t), \boldsymbol{M}_Z(0)], \boldsymbol{M}_Y(t), \boldsymbol{M}_Z(0)\}]. \qquad (12b)$$

Thus, in general, the dynamics of the focal stock can be approximately described by a model which excludes components of the ecosystem that either are approximately constant or very closely track the abundance of the focal stock on timescales relevant for assessment and management. In the next section, we expand on this general concept of timescale separation – and relax its underlying assumptions – to provide more specific insights concerning the precision and accuracy of fitted single-species models and the reference points derived from them.

Model fitting: The 'signal' and the 'noise'

The previous section provided a high-level overview of the concept of timescale separation, which suggested that ecosystem processes operating on similar timescales as the focal stock were most important to incorporate into assessments and that assessments ignoring slow components could be accurate in the short term but would need to be regularly updated. In this section, we refine these insights by explicitly considering the precision and accuracy of single-species model [$\hat{g}(.)$] fitting and reference point (F_{MSY}) estimation.

Precision

A single-species model (see above and Appendix 2) will only perfectly describe the dynamics of a focal stock if there is perfect timescale separation – all interacting ecosystem components are either infinitely fast or infinitely slow relative to the focal stock [$\boldsymbol{M}_X$ and $\boldsymbol{M}_Z$ include all components of $\boldsymbol{M}$ and $\varepsilon = 0$ in equations (11)]. By the same logic, assessing a stock using a single-species model implicitly assumes perfect timescale separation, and treats deviations from this as noise. The larger this 'noise' is, the less precise the model fit will be (assuming that the attracting 'signal' exists and is estimated without bias – an assumption we relax in the section on accuracy below).

For example, suppose that if N is held constant, each other ecosystem component's state, M_j for component j, converges to $\phi_j(N)$ at a rate λ_j, that is,

$$\frac{\mathrm{d}M_j(t)}{\mathrm{d}t} = -\lambda_j M_j(t)\left[M_j(t) - \phi_j(N[t])\right]. \tag{13}$$

(This assumption is equivalent to assuming linear interactions among all components of $\boldsymbol{M}$, whereby the resulting interaction, or Jacobian, matrix, as in May (1973), has only negative eigenvalues.) In this case, the single-species model, $\hat{g}(.)$, which would accurately predict F_{MSY} (or any other reference point) for the focal stock (i.e. the 'signal'), is given by:

$$\hat{g}[N(t)] = g[N(t), \boldsymbol{\phi}(N[t])], \tag{14}$$

and the squared deviation of the actual per-capita production from this function (measuring the 'noise') at time t is given by:

$$\begin{aligned}&(\hat{g}[N(t)] - g[N(t), \boldsymbol{M}(t)])^2\\ &= (g[N(t), \boldsymbol{\phi}(N[t]) - g[N(t), \boldsymbol{M}(t)])^2.\end{aligned} \tag{15}$$

This squared deviation decreases through time (i.e. $\frac{\mathrm{d}}{\mathrm{d}t}(g[N(t), \boldsymbol{\phi}(N[t])] - g[N(t), \boldsymbol{M}(t)])^2 < 0$) if:

$$\begin{aligned}&(g[N(t), \boldsymbol{\phi}(N[t])] - g[N(t), \boldsymbol{M}(t)])\\ &\sum_{j=1}^{A}\left[\left(\frac{\partial g}{\partial M_j}\Big|_{M_j=\phi_j[N(t)]}\right)\phi'_j(N[t])\frac{\mathrm{d}N(t)}{\mathrm{d}t} - \frac{\partial g}{\partial M_j}\right.\\ &\left.\lambda_j M_j(t)(\phi_j[N(t)] - M_j[t])\right] < 0.\end{aligned} \tag{16}$$

Parsing inequality (16) (see Appendix 3 for expanded discussion): (i) ecosystem component $M_j(t)$ is approaching the ('signal') attractor $\phi_j[N(t)]$ at time t if (but not only if) $\left|\phi'_j(N[t])\frac{\mathrm{d}N(t)}{\mathrm{d}t}\right| < \left|\lambda_j M_j(t)\left(\phi_j[N(t)] - M_j[t]\right)\right|$, where $\left|\phi'_j(N[t])\frac{\mathrm{d}N(t)}{\mathrm{d}t}\right|$ measures the rate at which attractor $\phi_j[N(t)]$ is changing due to changes in $N(t)$, and $|\lambda_j M_j(t)\left(\phi_j[N(t)] - M_j[t]\right)|$ measures the rate at which $M_j(t)$ is being pulled towards $\phi_j[N(t)]$; (ii) $\frac{\partial g}{\partial M_j}$ measures the magnitude with which changes in ecosystem component j's state, M_j, impact the per-capita production [$g(.,.)$] of the focal stock; and (iii) $(g[N(t), \boldsymbol{\phi}(N[t])] - g[N(t), \boldsymbol{M}(t)])$ measures the current difference (and its sign) between $g[N(t), \boldsymbol{\phi}(N[t])]$ (the 'signal') and $g[N(t), \boldsymbol{M}(t)]$ (the 'noise').

Assuming each ecosystem component has a monotonic effect on the growth of the focal stock (i.e. for each j, either $\frac{\partial g}{\partial M_j} \geq 0$ for all values of M_j, or $\frac{\partial g}{\partial M_j} \leq 0$ for all values of M_j), inequality (16) implies bounds on how far $g[N(t), \boldsymbol{M}(t)]$ (the 'noise') can deviate from $g[N(t), \boldsymbol{\phi}(N[t])]$ (the 'signal'). This is because $\left|\lambda_j M_j(t)\left(\phi_j[N(t)] - M_j[t]\right)\right|$ (the strength of the pull of M_j towards $\phi_j[N]$) increases as the difference between M_j and $\phi_j[N]$ increases (Appendix 3). Ecosystem components with slow dynamics relative to the focal stock (i.e. small λ_j relative to $|\mathrm{d}N[t]/\mathrm{d}t|$) (Fig. 1d,e; Fig. 2a), and strong coupling to the focal stock (i.e. large $\left|\frac{\partial g}{\partial M_j}\right|$ – implying a strong effect of M_j on the focal stock – and/or large $|\phi_j{}'(N[t])|$ – implying a strong effect of the focal stock on M_j) (Fig. 2b, c, d vs. a) will allow the largest outward expansions in these bounds (of deviations of noise from signal) and will therefore most greatly reduce the precision with which $\hat{g}(.)$ is fit [assuming that the fitted $\hat{g}(.)$

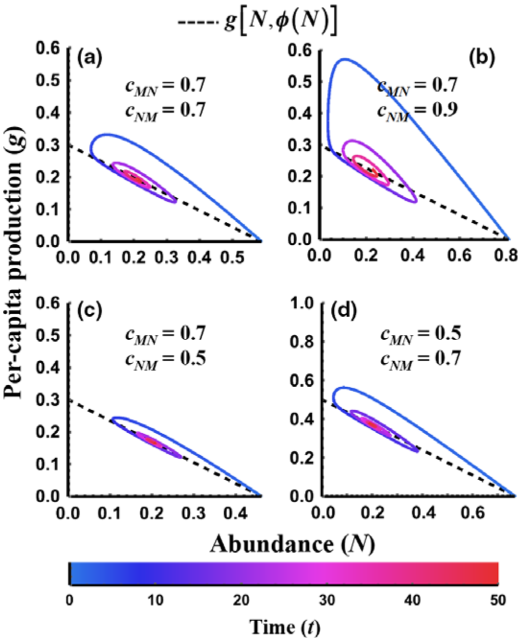

Figure 2 Simulations (of the same model shown in Figure 1d, e, f) illustrating the impacts on single-species model precision of the strength of influence of biotic factor *M* on the production of *N* (*g*) (measured by c_{MN}), and the strength of influence of *N* on the dynamics of *M* (measured by c_{NM}). In all panels, the dynamics of $g[N(t), M(t)]$ (coloured by time, as indicated) are compared to the long-term attractor, $g[N(t), \phi(N[t])]$ (black, dashed), that is effectively a single-species model. Precision (and likely also accuracy in this particular model) is negatively impacted by strong influence of *M* on the production of *N* (a vs. d) and by strong influence of *N* on the dynamics of *M* (a vs. b and c). [Color figure can be viewed at wileyonlinelibrary.com]

satisfies equation (14) without bias; we discuss sources of bias below].

However, while strong coupling between an ecosystem component, *j*, and the focal stock will always reduce precision (assuming, as above, that precision is reduced by large deviations of noise from signal), very slow dynamics of an interacting component, *j*, can also increase precision if the dynamics are slow enough that the component's state, M_j, can be considered approximately constant when fitting the model, $\hat{g}(.)$. To illustrate this, now suppose that some ecosystem components are so slow that $\hat{g}(.)$ is fit as:

$$\hat{g}[N(t)] = g[N(t), \{\boldsymbol{\phi}_X(N[t]), \bar{\boldsymbol{M}}_Z\}], \qquad (17)$$

where $\bar{\boldsymbol{M}}_Z$ is the vector of mean states of slow components, $\boldsymbol{M}_Z$, over the time series in which the model is fit. With this assumption, the condition for the squared deviation to be decreasing through time is:

$$\begin{aligned}&(\hat{g}[N(t)] - g[N(t), \boldsymbol{M}(t)])\\&\left(\sum_{j\in X}\left[\left(\frac{\partial g}{\partial M_j}\Big|_{M_j=\phi_j[N(t)]}\right)\phi_j'(N[t])\frac{\mathrm{d}N(t)}{\mathrm{d}t}\right.\right.\\&\left.-\frac{\partial g}{\partial M_j}\lambda_j M_j(t)(\phi_j[N(t)] - M_j[t])\right]\\&\left.-\sum_{l\in Z}\frac{\partial g}{\partial M_l}\frac{\mathrm{d}M_l(t)}{\mathrm{d}t}\right) < 0. \qquad (18)\end{aligned}$$

In this case, very slow dynamics of component *l*'s state, M_l, [i.e. small $\mathrm{d}M_l(t)/\mathrm{d}t$] increases precision – at the extreme, where $\mathrm{d}M_l(t)/\mathrm{d}t = 0$ for all *t*, $M_l(t) = \bar{M}_l$ for all *t*.

What if an ecosystem component has a one-way interaction with the focal stock (e.g. an abiotic factor such as sea surface temperature, which influences – but is generally not influenced by – fish growth)? A component, *j*, having this type of one-way interaction with the focal stock would imply $\frac{\partial g}{\partial M_j} \neq 0$ but $\frac{\partial}{\partial N}\left(\frac{\mathrm{d}M_j}{\mathrm{d}t}\right) = 0$. Thus, if $M_j(t)$ was stably attracted to a fixed point, $\phi_j(N)$, given *N*, as is assumed above for example, it would now be the same point for all *N* ($\phi_j[N] = \phi_j$), and $M_j(t)$ would be constant (implying component *j* could be safely ignored in a single-species assessment), assuming it had reached ϕ_j before the data collection for fitting the single-species model started.

A more interesting case for an abiotic factor, *j*, is one where it does not converge to a fixed point (ϕ_j), but instead has short-term cyclic behaviour and/or a long-term trend (Fig. 3). For example, suppose:

$$M_j(t) = M_{j,0} + a\sin\left(\frac{2\pi}{b}t\right) + ct, \qquad (19)$$

where $M_{j,0}$, *a*, *b* and *c* are constants, respectively determining initial value, amplitude, period and long-term trend of $M_j(t)$ (see left panels in Fig. 3); suppose (for simplicity) that component *j* was the only factor affecting the focal stock's production other than the focal stock itself (i.e. $\frac{\partial g}{\partial M_l} = 0$ for all $l \neq j$) and that the effect of $M_j(t)$ on the focal stock's growth was linear and separable, i.e.:

$$g[N(t), \boldsymbol{M}(t)] = g_N[N(t)] + \gamma\left[M_{j,0} + a\sin\left(\frac{2\pi}{b}t\right) + ct\right], \qquad (20)$$

where $g_N[N(t)]$ describes the focal stock's effect on its own production, and γ is a constant representing the effect of $M_j(t)$ on the focal stock's production. Since we are only considering precision, for

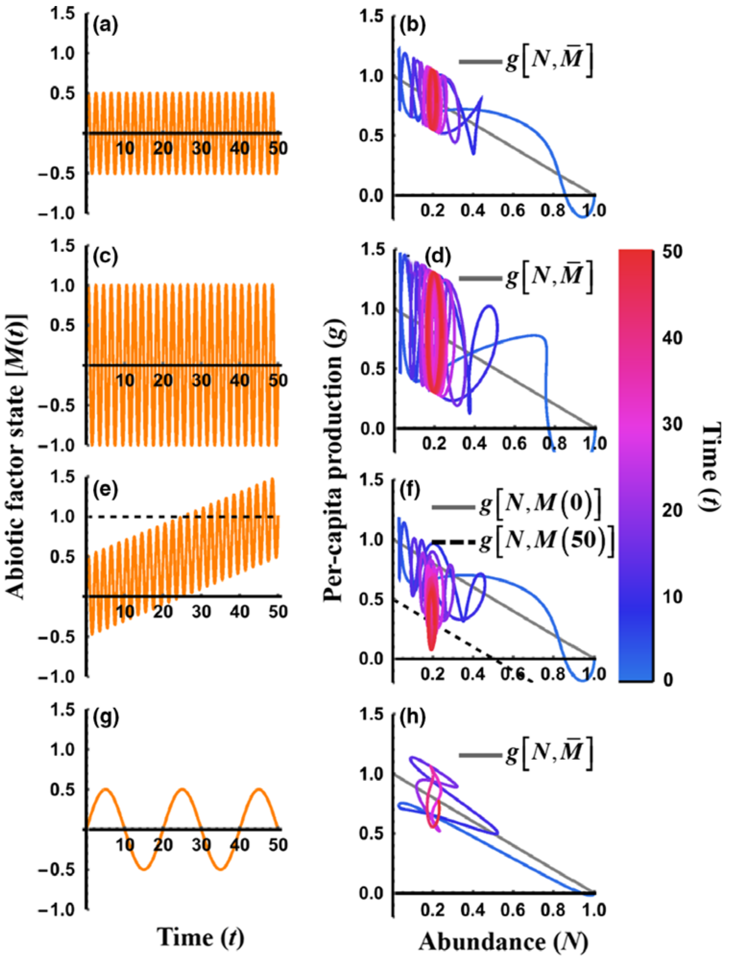

Figure 3 Simulations illustrating the impacts of the dynamics of a cycling abiotic factor, $M(t)$ [which influences, but is not influenced by, $N(t)$], on the precision with which a single-species model is estimated. In all panels, $g[N(t), M(t)]$ and $dM(t)/dt$ are given by equations (19) and (20), with $M_{j,0} = M_0 = 0$ and $\gamma = 0.5$ in all panels, and the dynamics of $F(t)$ are the same as in Figure 1. Each row of panels represents a single simulation with dynamics of $M(t)$ (orange) shown at left, and $N(t)$ and $g[N(t), M(t)]$ (coloured by time, as indicated) shown at right. Compared to panels a and b (where $a = 0.5$, $b = 2$, $c = 0$), lower rows of panels illustrate the negative effects on precision of: (c and d) increased amplitude ($a = 1$) of cycles, (e and f) non-stationarity ($c = 0.02$) (which also affects accuracy) and (g and h) long period of cycles ($b = 20$). Simulations in all panels are initialized at $N(0) = 1$. [Color figure can be viewed at wileyonlinelibrary.com]

the moment, let us assume that $\hat{g}(.)$is estimated without bias as:

$$\hat{g}[N(t)] = g_N[N(t)] + \gamma\bar{M}_j, \qquad (21)$$

where $\bar{M}_j$ is the mean value of $M_j(t)$ over the sample period – with respective start and end points T_1 and T_2 – which is given by $\bar{M}_j = M_{j,0} + \frac{c}{2}(T_1 + T_2) + \frac{a}{(T_2-T_1)}\int_{T_2-Rb}^{T_2}\sin\left(\frac{2\pi}{b}t\right)dt$, where R denotes the decimal remainder, as a fraction of the oscillation period b, resulting from dividing $(T_2 - T_1)$ by b. With this assumption, the absolute deviation of $g(.)$ from $\hat{g}(.)$ is given by:

$$|\hat{g}[N(t)] - g[N(t),\boldsymbol{M}(t)]| = \left|\gamma\left[\frac{c}{2}(T_1 + T_2 - 2t) - a\sin\left(\frac{2\pi}{b}t\right) + \frac{a}{(T_2 - T_1)}\int_{T_2-Rb}^{T_2}\sin\left(\frac{2\pi}{b}t\right)dt\right]\right|. \qquad (22)$$

From (22), we can see that large deviations of $g(.)$ ('noise') from $\hat{g}(.)$ ('signal') – and therefore imprecise fitting – would occur if ecosystem component j

had a large impact on the growth of the focal stock (i.e. large $|\gamma|$) and one or more of: large amplitude cycles (i.e. large $|a|$, which increases the magnitude of the second and third terms in [22]) (Fig. 3c, d vs. a, b), a large time trend (i.e. large $|c|$, which increases the magnitude of the first term in [22]) (Fig. 3e,f vs. a,b), or a long period of oscillations (i.e. large $|b|$, which increases the magnitude of the third term in [22]) (Fig. 3g,h vs. a,b).

Though not the focus of this study, precision in estimating the relationship between production and abundance [i.e. $\hat{g}(.)$] is of course also heavily influenced by the range of observed abundances (N) – the larger the range of observed N, the more precision in fitting $\hat{g}(.)$, all else equal (e.g. see Magnusson and Hilborn 2007).

Accuracy

In the previous section, we assumed that the 'signal' – the single-species production model (i.e. the relationship between abundance, N and per-capita production, $g[.,.]$) that would exist for the focal stock under perfect timescale separation (if one existed) (e.g. equation [14]) – was estimated without bias, in order to consider precision. We now relax this assumption and consider the implications of different types of ecosystem contexts on the accuracy of estimated reference points – using F_{MSY} as the prototypical example reference point. To do this analytically, we must make an assumption about the specific functional form of the fitted model, $\hat{g}(N)$, assumed in the assessment. For simplicity, we assume a linear model, because the fitted parameter values in a linear model – given the data – can be derived analytically in the general case; we then discuss alternate assumptions.

Thus, we assume

$$\hat{g}[N(t)] = \hat{r}\left[1 - \frac{N(t)}{\hat{K}}\right], \quad (23)$$

where $\hat{r}$ and $\hat{K}$ are, respectively, the estimated maximum per-capita growth rate and carrying capacity (Fig. 4) of the focal stock, and therefore:

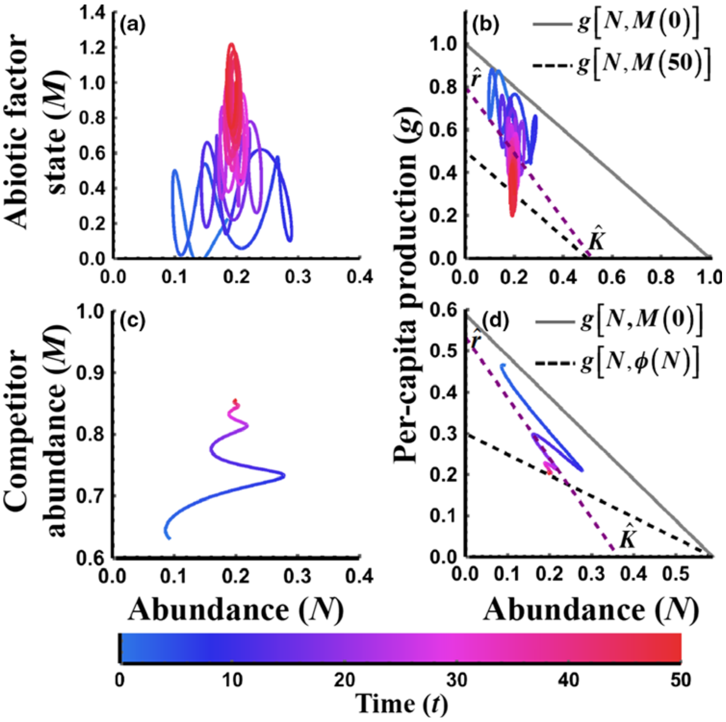

Figure 4 Simulations illustrating the negative impacts on fitted single-species model accuracy of: (a, b) long-term time trends (i.e. non-stationarity) in an abiotic factor (M) that covary with the focal stock's abundance, and (c, d) convergence of an interacting biotic factor (M) towards its attractor, $\phi(N[t])$, on timescales similar to changes in focal stock abundance, $N(t)$, with covariance between N and M. The model in panel a is identical to Figure 3f, with the logistic model fit (purple dashed line) using observations at each integer value of t from t = 11 to t = 50. The model in panel b is identical to Figure 1d, with the logistic model fit (purple dashed line) using observations at each integer value of t from t = 5 to t = 50. [Color figure can be viewed at wileyonlinelibrary.com]

$$\hat{F}_{\mathrm{MSY}} = \frac{\hat{r}}{2}, \tag{24}$$

(Schaefer 1954). The parameter estimates minimizing sum of squares (5) in a given sample is given by:

$$\hat{r} = \bar{g} - \bar{N}\left(\frac{\mathrm{Cov}[N(t), g(N[t], \boldsymbol{M}[t])]}{\mathrm{Var}[N(t)]}\right), \tag{25a}$$

$$\hat{K} = \bar{N} - \bar{g}\left(\frac{\mathrm{Var}[N(t)]}{\mathrm{Cov}[N(t), g(N[t], \boldsymbol{M}[t])]}\right), \tag{25b}$$

where $\bar{N}$ is the mean value of $N(t)$, $\bar{g}$ is the mean value of $g[N(t), \boldsymbol{M}(t)]$, and $\mathrm{Var}[N(t)]$ and $\mathrm{Cov}[N(t), g(N[t], \boldsymbol{M}[t])]$ are, respectively, the variance of $N(t)$ and the covariance between $N(t)$ and $g[N(t), \boldsymbol{M}(t)]$, each over the sample of observations used in fitting. The ratio of $\mathrm{Cov}[N(t), g(N[t], \boldsymbol{M}[t])]$ and $\mathrm{Var}[N(t)]$ defines the estimated slope of $\hat{g}(N)$ [i.e. $\hat{g}'(N)$, equal to $-\hat{r}/\hat{K}$].

There are two basic potential sources of bias in an estimate of $\hat{F}_{\mathrm{MSY}}$:

First, a 'true' long-term F_{MSY} may not exist. This would occur if one or more influential ecosystem components do not converge to a stationary point or cycle, given N [i.e. there is no $\phi_j(N)$ for one or more components j]. For example, if the state of an abiotic factor, M_j, has a long-term trend ($c \neq 0$ if its dynamics are governed by equation [19]), its mean value, $\bar{M}_j$, would have a trend as the sample grew. In this case, there would be no long-term F_{MSY}, and the mortality rates producing sustainable yield at each abundance would change over time. Moreover, the effect of a trend in $M_j(t)$ on focal stock production [$g(.,.)$] might be difficult to separate statistically from the stock's density dependence [i.e. the effect of N on $g(.,.)$] if there were covariance between the trends in $M_j(t)$ and $N(t)$ (e.g. if both increased or decreased together on similar timescales) (see Fig. 4a,b for an illustrated example of this phenomenon). Bias in reference point estimation resulting from non-stationary ecosystem components would be more pronounced, the more influential the non-stationary components were on the growth of the focal stock [$g(.,.)$] and the faster their trends were in comparison with the dynamics of the focal stock's abundance [$N(t)$].

Second, there is a 'true' long-term F_{MSY}, but the 'noise' contributes significantly to the covariance between $N(t)$ and $g[N(t), \boldsymbol{M}(t)]$, such that the parameters given by (24) and (25) do not match the 'signal'. This may occur, for example, if the effect on $g(.,.)$ of one or more ecosystem components' convergence towards their attractor, $\boldsymbol{\phi}(N[t])$], is large and covaries significantly with the focal stock's abundance, $N(t)$ (see Fig. 4c,d for illustrated example).

A third potential source of bias that we do not consider explicitly here is that there is a true 'signal', but it is nonlinear. We discuss the general implications of mismatch between the assumed $\hat{g}(.)$ form and the true 'signal's form in the Discussion.

Sudden disruptions to the signal

In the previous sections, we examined focal stock and ecosystem characteristics that can either make single-species model fitting imprecise by causing large-magnitude deviations in focal stock production from an attractor (i.e. the 'signal'; e.g. $g[N(t), \boldsymbol{\phi}(N[t])]$) that determines medium-/long-term reference points (if one exists), or make single-species model fits inaccurate by causing significant mismatch between the true attractor (if one exists) and the one estimated by least squares. A final challenge we consider – that ecosystem contexts can create for single-species assessments – is sudden ecosystem changes, which cause the true attractor to either be locally non-differentiable or discontinuous (i.e. the value – $g[N(t), \boldsymbol{\phi}(N[t])]$ – or the slope – $\mathrm{d}g[N(t), \boldsymbol{\phi}(N[t])]/\mathrm{d}N$ – of $g[N(t), \boldsymbol{\phi}(N[t])]$ abruptly changes over a small range of N) (see Fig. 5 for examples).

Sudden ecosystem changes that disrupt the production of fish stocks – and their causes and prevalence – are the subject of a sizeable literature (e.g. see Vert-pre *et al.* 2013; King *et al.* 2015; Szuwalski *et al.* 2015), so we will only briefly highlight their most salient features for our purposes. The basic consequence of any sudden disruption in focal stock production (or its slope or curvature in relation to focal stock abundance) is that relationships between abundance (N) and production [$g(.,.)$] estimated using only data from before the disruption will have little to no ability to predict the medium-/long-term production at either later times, out-of-sample abundances, or both. Below, we briefly discuss the consequences and detectability associated with some of the possible causes of such disruptions.

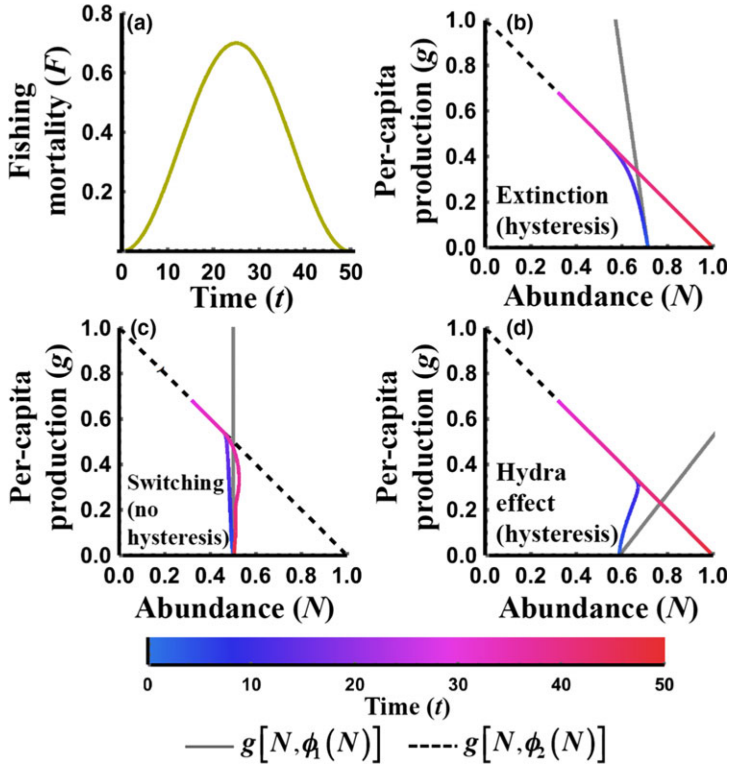

Figure 5 Sudden disruptions to the 'signal' (i.e. the effectively single-species attractor, $g[N(t), \phi(N[t])]$, of the production of the focal stock, $g[N(t), M(t)]$), with each of three different causes, are shown (b-d), with dynamics of $F(t)$ (dark yellow) identical in all simulations (a) [$F(t) = 0.35(1 - \cos[0.04\pi t])$]. In each case, something causes the attractor $g[N(t), \phi(N[t])]$ to abruptly shift from one form, denoted $g[N, \phi_1(N)]$ (grey), to another, denoted $g[N, \phi_2(N)]$ (black, dashed). In some cases (example in c), the shift is reversible; in other cases (examples in b and d), it does not reverse (there is hysteresis). In panels b and d, the focal stock has an ecological competitor that is caught as by-catch in its fishery ($g[N(t), M(t)] = 1 - N(t) - c_{MN}M(t)$, $dM(t)/dt = \varepsilon M(t)[1 - M(t) - c_{NM}N(t) - q_{NM}F(t)]$; in b, $\varepsilon = 10$, $c_{MN} = 0.8$, $c_{NM} = 0.9$, $q_{NM} = 1.2$; in d, $\varepsilon = 10$, $c_{MN} = c_{NM} = 0.7$, $q_{NM} = 2$). In panel d, there is a 'hydra effect' – where N increases as F increases – initially. In both b and d, the disruption in $g[N(t), \phi(N[t])]$ is caused by extinction of the competitor at moderate fishing pressure (F). This shift does not reverse as F decreases because the competing species is not resurrected from extinction. In panel c, there are two interacting species: a predator that eats the focal stock, and an alternate prey. The predator hunts whichever prey is more abundant. As fishing pressure increases from low to moderate levels, it is offset by reduced predation ($g[N, \phi_1(N)]$) resulting in a net-neutral effect on abundance. Eventually, the predator is only targeting the alternate prey, at which point the production of the focal stock shifts to $g[N, \phi_2(N)]$. Importantly, this abrupt shift in the growth of the focal stock – caused by the predator's switching behaviour – reverses itself when fishing pressure returns to low levels. The dynamics of the focal stock, $N(t)$, the predator, $M_1(t)$, and the other prey, $M_2(t)$, shown are given by: $g[N(t), M(t)] = 1 - N(t) - 0.4\alpha(t)M_1(t)$, $dM_1(t)/dt = 10M_1(t)[0.4\alpha(t)N(t) + 0.4(1 - \alpha[t])M_2(t) - 0.2]$; $dM_2(t)/dt = 10M_2(t)[1 - M_2(t) - 0.4(1 - \alpha[t])M_1(t)]$. The function $\alpha(t)$, which describes the switching, is given by: $\alpha(t) = \mathrm{Exp}[100N(t)/M_2(t)]/(\mathrm{Exp}[100] + \mathrm{Exp}[100N(t)/M_2(t)])$. [Color figure can be viewed at wileyonlinelibrary.com]

Causes and hysteresis

The implications of a sudden ecosystem change for a single-species assessment are largely determined by two factors: the magnitude of the impact of the change on the focal stock's production, and whether or not the change results in hysteresis.

Hysteresis means, in this context, that the change in focal stock production does not reverse itself even if the conditions that caused it reverse themselves. If a shift in production results in hysteresis, then a single-species model fitted before the shift will have limited ability to predict the focal stock's production at later times over both observed and unobserved ranges of abundance, whereas without hysteresis, a single-species model fitted before the shift may still be able to predict the production at later times over previously observed ranges of abundance.

Fig. 5 illustrates examples of this distinction. First (illustrated in Fig. 5a,b), suppose a focal stock's competitor is caught as by-catch in the focal stock's fishery. If fishing effort increased to a level great enough to cause the extinction of the competitor, the focal stock's production function would change abruptly ($dg[N(t),\ \phi(N[t])]/dN$ would become shallower, because fishing would no longer have the indirect benefit of also killing competitors; Fig. 5b), but subsequent reductions in fishing effort would not reverse the shift (because the extinct competitor would not be raised from the dead). Conversely, suppose (illustrated in Fig. 5a,c) that the focal stock is one of multiple prey species eaten by a predator, but is only targeted by the predator when it is relatively abundant (see Stephens and Krebs 1986 for review of this type of predation). In this case, the focal stock's production would abruptly shift when its abundance reached a level where the predator had incentive to shift its diet towards or away from the focal stock, but this shift would reverse itself as soon as the predator's incentives were reversed (Fig. 5c), implying no hysteresis. Abrams (2009b) and Tschirhart (2012) provide more in-depth worked examples of sudden shifts in production caused by switching or extinctions in food web models. Other possible causes of sudden shifts that are likely to cause hysteresis include (but are not limited to): biological invasions, ecosystem-wide regime shifts caused by positive feedbacks (see Scheffer *et al.* 2001 for review and examples) and sudden changes in climate or other abiotic factors that are unimpacted by the focal stock (and therefore unlikely to revert in response to changes in focal stock abundance or fishing pressure).

The magnitude of impact of a sudden shift on the focal stock's production is important in determining its impact – on the predictive ability of pre-shift single-species assessments – for obvious reasons. In short, a sudden change in the ecosystem that has a trivial impact on both the production of the focal stock ($g[N(t),\ \boldsymbol{\phi}(N[t])]$), and the relationship between production and abundance ($dg[N(t),\ \boldsymbol{\phi}(N[t])]/dN$), will result in a bias of trivial magnitude in forecasts of sustainable harvest rates (and vice versa).

Detectable warning signs

Many of the drivers of sudden shifts in a focal stock's production are detectable without explicit multispecies modelling. For example, both invasions and extinctions can be detected, and often there is contextual ecological information with which to infer the importance of the (locally) extinct or invading species to the production of the focal stock. Similarly, ecosystem-wide regime shifts are often apparent, and can in some cases be detected in advance (see Scheffer *et al.* 2012; but see also Boettiger and Hastings 2012). Prey-switching behaviour may be harder to detect, but the fact that it is unlikely to cause hysteresis (Fig. 5c) may limit its adverse impacts on single-species assessments.

One final noteworthy warning sign of possible future disruptions to a focal stock's production pattern ($g[N(t),\ \boldsymbol{\phi}(N[t])]$) is a 'hydra effect' (as coined by Abrams 2009d) – whereby a stock's abundance (and per-capita production) increases as its harvest rate increases (example illustrated in Fig. 5d). Hydra effects are caused (see Abrams 2009d for review) by indirect positive effects of harvesting on the focal stock's growth – via the ecosystem – that are larger than the direct negative effect of harvesting via morality. Hydra effects are noteworthy because: (a) they are detectable (a stock increasing in abundance as it is fished harder can be observed), and (b) they are very likely to be associated with eventual sudden shifts in production – because a hydra effect cannot possibly persist indefinitely (infinite harvest pressure has to eventually cause extinction), meaning that the indirect effect fuelling the hydra effect (e.g. a competing species or predator more greatly harmed by the fishery, as illustrated in Fig. 5d) is often unsustainable.

Discussion

Summary of main results

In this study, we use general mechanistic theory to examine the traits of a stock and its surrounding ecosystem that may cause one of three potential problems for single-species assessments: (a) imprecision of estimated fishery reference points (and the production–abundance relationships they derive from), (b) inaccuracy of reference points and (c) sudden shifts in the production or production–abundance relationship that limit the predictive power of reference points from pre-shift assessments, especially when there is hysteresis associated with the shifts. We specifically aim to identify key focal stock and ecosystem traits that lead to these problems and can be qualitatively spotted in any system without first requiring system-specific simulation modelling or detailed ecosystem-wide monitoring; we thereby hope to provide high-level conceptual insights complementing more tailored tactical approaches – to link the analytical mechanistic theory of abstraction to the practice of stock assessment and management. Table 1 heuristically summarizes some of our most salient results.

Our theory suggests that reference point 'accuracy' can only be defined in a long-term equilibrium sense if all ecosystem components impacting the growth of the focal stock approach a fixed point or stationary cycle if focal stock abundance is held constant. If this is not the case (as is likely typical), then reference points would need to be updated regularly, more heavily weighting more recent data. The faster the dynamics of non-converging, non-stationary ecosystem components are – especially those with a large influence on the focal stock's production – the more regularly reference points would need to be updated and the more heavily recent data would need to be weighted in their estimation.

Our theory predicts that the speed of the focal stock's dynamics – relative to the ecosystem components it interacts with –is important for both precision and accuracy. It also predicts that the strength of interaction between an ecosystem component and the focal stock is important in determining its impact on single-species assessments. Ecosystem components that converge to a fixed point or stationary cycle, and that have much faster dynamics than the focal stock, are unlikely to significantly bias an assessment or affect its precision (unless they stationarily cycle with large amplitude) – even if they strongly impact the growth of the focal stock. Ecosystem components that have much slower dynamics than the focal stock may not hinder the precision or short-term accuracy of a single-species assessment (which will likely treat them as approximately constant), but they will eventually create bias – if they strongly influence the production of the focal stock – as they drift away from their initial state. Ecosystem components with dynamics of similar speed to those of the focal stock can adversely affect both precision and accuracy of single-species reference points – especially if their dynamics have covariance with those of the focal stock's abundance, and their effect on the focal stock's production is strong.

Our theory suggests that slow dynamics (e.g. top predators with long generation times) is a trait in focal stocks that may promote both precision and accuracy of single-species reference points (because it makes other ecosystem components relatively fast). We note however that slow dynamics may also be associated with smaller ranges of abundance variation – which hinders precision (see Magnusson and Hilborn 2007) – with short timescale data sets. We also note that even very slow-growing species are likely to interact with slower abiotic processes, which may in some cases (e.g. climate change) be fast enough to create biases in single-species assessments. Our theory suggests that fast dynamics in focal stocks (e.g. forage fish with short generation times) may create challenges for single-species reference point accuracy.

Lastly, our theory suggests that sudden shifts in focal stock production can inhibit single-species assessment accuracy – especially when the shifts exhibit hysteresis – but we posit that many drivers of sudden shifts in production are identifiable. In particular, we posit that recent (local) extinctions, invasions, sudden climactic changes and positive-feedback-driven ecological regime shifts are each likely to result in hysteresis when they impact important drivers of focal stock production. Observing a hydra effect (i.e. increases in focal stock abundance under increased exploitation) (Abrams 2009d) is also a likely sign of production shifts at later times of higher fishing pressure. A sudden shift in production that exhibits hysteresis may severely limit the utility of pre-shift data in predicting post-shift production.

Caveats

The modelling frameworks we use – and consequentially our results – are quite general, but a few simplifications are worth discussing. First, we neglect age structure in the focal stock, although many of our results would extend analogously with this added complexity. For example, condition (6) would now specify unique mappings from a vector of age-specific abundances of the focal stock to another vector of age-specific growth rates and would impose analogous dimensionality constraints on the system. This said, we note that because we omit age structure, a modern stock assessment model could not be defined as a $\hat{g}(.)$ that can be inserted directly into our analysis, nor could reference points be reliably estimated from aggregate production in practice (e.g. see Punt and Szuwalski 2012).

Second, our hypothetical model fitting exercise – based on sum of squares – is simplistic relative to modern maximum-likelihood and Bayesian methods (e.g. Methot and Wetzel 2013). Our framework also does not consider errors in estimating abundance, and implicitly assumes that such errors do not interact with errors in estimating production (Appendix 1). The possibility and implications of such interaction are important areas for further study; errors in abundance estimation certainly are known to affect reference points (e.g. see Hurtado-Ferro *et al.* 2015).

Lastly, we do not explicitly consider the importance of the choice of specific functional form [of $\hat{g}(.)$ or its age-structured analogue] for an assessment, and the possibility that the chosen form may not match the true long-term production–abundance relationship, even if such a relationship exists. This is a potential source of further bias in assessments, one which may be widespread (for specific examples, see Abrams 2009a,b,c; Reynolds and Brassil 2013), although its severity is unclear and likely varies on a case-by-case basis.

Thus, the insights of our analysis are primarily qualitative, general, mechanistic and strategic, rather than being quantitative, system-specific or tactical. In the concluding sections below, we briefly discuss our theory in context with recent advances in stock assessment, multispecies modelling, MSE and other methods for prioritizing transitions away from single-species assessment and management, towards ecosystem-based approaches.

Implications for stock assessment

Among the conditions we identify as inhibitive to single-species reference point accuracy (e.g. influential ecosystem components that are slow or non-converging), the common thread is that they cause biological processes that single-species models assume to be stationary (e.g. stock–recruitment relationships, natural mortality, selectivity) to be non-stationary. The most advanced stock assessment methods used to manage many of the world's most valuable fisheries explicitly model each of these processes (e.g. Stewart *et al.* 2013; Ianelli *et al.* 2014) and are therefore somewhat more complicated than the models presented here. The problem of biases in estimates of biomass or reference points when these population processes are non-stationary has been recognized in the stock assessment community for many years (e.g. Butterworth 1981; Mohn 1999; Collie *et al.* 2016; Szuwalski and Hollowed 2016). Our primary contribution is to identify *which* ecosystem and focal stock properties are likely to make these processes non-stationary, and *why*.

More specifically, our results highlight and conceptually underpin three key challenges for stock assessment. First, our results highlight the challenge of assessing fast-growing species (e.g. forage fish), which tend to track their surrounding ecosystems rather than the converse (see Sugihara *et al.* 2012 for an example; Szuwalski *et al.* 2015 for review). A recent simulation study by Hurtado-Ferro *et al.* (2015) found 'retrospective bias' (i.e. systematic changes in estimates of biomass in a given year as more years of data are added to the assessment that can be caused by changes in population processes) to be largest for a fast-growing, short-lived species [e.g. Pacific sardine (*Sardinops sagax caeruleus*, Clupeidae)], when compared to longer-lived, slower growing species [e.g. cod (*Gadus morhua*, Gadidae) or flatfish]. Butterworth (1981) first described a retrospective bias in Southwest African pilchard (*Sardinops ocellatus*, Clupeidae), a small pelagic species.

Second, because many abiotic processes are slow, climate change and multidecadal oscillations (e.g. see Haltuch and Punt 2011) can pose assessment challenges to even slow-growing species. For example, retrospective biases have also been identified in Pacific Halibut (*Hippoglossus stenolepis*, Pleuronectidae) (Parma 1993) and Atlantic groundfish (Sinclair *et al.* 1991) – both of which have slow dynamics relative to other species in the system.

Third, our results demonstrate how (either positive or negative) covariance between the focal stock's abundance and the states of interacting ecosystem components changing at similar speeds can pose challenges to reference point accuracy. This challenge may be especially acute in ecosystems with multiple significant and accelerating human impacts, as these may cause coincident one-way trips for multiple interacting species, creating covariance between them. For example, a top predator whose fishery development coincides with the development its prey's fisheries might seem less resilient to fishing than it would be if prey fishing slowed, and vice versa. Moreover, if there is also covariance between the ecosystem process and the focal stock's fishing pressure, explicitly including the process in a statistical model will not necessarily improve the assessment's accuracy, as the effects of fishing and the ecosystem will be difficult to statistically separate (e.g. see Haltuch and Punt 2011; Szuwalski and Punt 2012)

The stock assessment community is cognizant that population processes can be non-stationary and that this can introduce large biases in estimates of quantities important to management (Hurtado-Ferro *et al.* 2015); this has been one of the major motivations for more ecosystem-based approaches (e.g. Mangel and Levin 2005; Salomon *et al.* 2010; Nyström *et al.* 2012; Steneck *et al.* 2013). Short of this, some recent studies have developed single-species stock assessment approaches that allow processes to vary over time (e.g. Thorson 2011; Martell and Stewart 2013), which have allowed for improved estimation of current biomass. Our results (Table 1) shed light on where such innovations may be most needed.

Implications for ecosystem-based management

Recognizing the limitations of single-species approaches, fisheries scientists are increasingly making use of the whole spectrum of modelling approaches between single-species assessment models and whole ecosystem models such as Atlantis (Fulton *et al.* 2011). Multispecies and ecosystem models are often complex and still mostly used for strategic advice (e.g. Jacobsen *et al.* 2016; Skern-Mauritzen *et al.* 2016), but there has recently been considerable attention paid to building MICE (i.e. models of a small subset of ecosystem components chosen based on the management question and data availability) that can be fit to data (rather than parameterized) and have an explicit tactical focus (Plagányi *et al.* 2014).

Our results provide strategic insights that may be useful in designing MICE. Specifically, they suggest – purely from the standpoint of avoiding bias in predicting a stock's response to fishing – properties of focal stocks and ecosystem observations that suggest MICE are likely needed, and properties making ecosystem components especially important to include in MICE (Table 1). Moreover, it would be easy to show that many of our results qualitatively generalize to higher levels of abstraction. In other words, our theory would provide similar qualitative advice (summarized in Table 1) for prioritizing transitions from simple to complex multispecies models as for prioritizing transitions from single-species models to MICE. At any level of abstraction, such strategic advice could be quantitatively refined using management strategy evaluation (MSE) – simulating the application of various assessment models and harvest control rules to data drawn from a simulated range of possible 'true' ecosystems, to determine which combinations of assessment strategies and harvest control rules are most robust with respect to management objectives (see Punt *et al.* 2016 for general review of MSE; see Punt *et al.* 2014 for a review of MSEs incorporating climate forcing) – and/or risk analysis to address deep structural uncertainties (e.g. see Sethi 2010).

Of course, avoiding potential statistical bias – the focus of this study – is but one of many important considerations in prioritizing transitions from single-species to ecosystem-based management approaches (see Dickey-Collas *et al.* 2014; Plagányi *et al.* 2014 for a more detailed discussion of some of the other considerations designing models and their scope). For example, one of most important functions of ecosystem modelling approaches is to quantify trade-offs between multiple competing objectives, which are often created in large part by the interactions between different ecosystem components (see Jacobsen *et al.* 2016; Rindorf *et al.* 2016; Weijerman *et al.* 2016, for recent examples from diverse ecosystems). Getting the most value from limited data collection and management budgets is another important consideration.

Conclusion

Reconciling the need for EBFM with the data limitations and complexity of most fisheries demands a pragmatic approach – one that prioritizes transitions from single-species assessment and management towards EBFM. One (though not the only) aspect of this prioritization is determining which stocks are most likely to be assessed with bias as a result of excluding ecosystem components from the assessment, and which ecosystem components are most important to include in expanded assessments. We provide a general, analytically tractable, mechanistic theory addressing this question, which identifies salient and readily detectable characteristics of both focal stocks and their ecosystems that are likely to promote or prevent precise and accurate single-species reference point estimation. Our results provide a conceptual scaffolding that can guide simulation- and data-based approaches aimed at providing more precise system-specific advice.

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Appendix 1: Indices of abundance and the sum of squares

In the main text, we assume that the focal stock's abundance, $N(t)$, is observed directly. More typically in reality, an index of abundance – assumed to be proportional to abundance – is observed or inferred from other observations such as catch and fishing effort (see Maunder and Punt 2004 for review). Let $I(t)$ denote an index of abundance observed, and β denote its proportionality to abundance, that is $N(t) = \beta I(t)$. If $I(t)$, $\mathrm{d}I(t)/I(t)/\mathrm{d}t$ and catch $[C(t)]$ were observed, the estimator – now for both the parameters of $\hat{g}(.)$ and β – would be:

$$\frac{\mathrm{d}I(t)}{\mathrm{d}t}\left[\frac{1}{I(t)}\right] = \hat{g}[\beta I(t)] - \frac{C(t)}{\beta I(t)}, \qquad (1.1)$$

and the sum of squares over a data set $\boldsymbol{T}$, denoted $\mathrm{SSQ}_{\boldsymbol{T}}$, would be given by (where $\hat{\beta}$ denotes the estimate of β):

$$\mathrm{SSQ}_{\boldsymbol{T}} = \sum_{t\in\boldsymbol{T}} \left(\hat{g}[\hat{\beta} I(t)] - g[\beta I(t), \boldsymbol{M}(t)] - \frac{C(t)}{\hat{\beta} I(t)} + \frac{C(t)}{\beta I(t)} \right)^2. \qquad (1.2)$$

If we assume that the forms of $g(.,.)$ and $\hat{g}(.)$ always allow for unbiased estimation of β and that this estimation does not interact with the estimation of the parameters of $\hat{g}(.)$ [i.e. $\sum_{t\in T} (\hat{g}[\hat{\beta} I(t)] - g[\beta I(t), \boldsymbol{M}(t)])^2$ is minimized where $\hat{\beta} = \beta$], then we can assume $\hat{\beta} = \beta$, and the sum of squares given by (1.2) becomes sum of squares (5) from the main text:

$$\mathrm{SSQ}_{\boldsymbol{T}} = \sum_{t\in\boldsymbol{T}} \left(\hat{g}[N(t)] - g[N(t),\boldsymbol{M}(t)]\right)^2. \tag{5}$$

Thus, our assumption that abundance $[N(t)]$ is directly observed could also be thought of as assuming that an unbiased index of abundance was observed, whose estimation did not interact with the estimation of $\hat{g}(.)$.

Appendix 2: Why condition (6) requires all M_j ecologically connected to the focal stock to be slaved to N [i.e. $M_j(t) = M_j(N[t])$]

This statement applies on any timescale (e.g. either transiently, i.e. at any t, or at equilibrium) – so we hereafter omit timescale notation – and the statement can be shown mathematically by contradiction and induction. Let $\boldsymbol{\Psi}$ denote the state of the system $[\boldsymbol{\Psi} = \{N, \boldsymbol{M}\}]$. Suppose that given N, multiple states of the other ecosystem components were possible, where each possible state is denoted by a superscript $\boldsymbol{\Psi}^k = \{N, \boldsymbol{M}^k\}$, $k = \{1, 2, \ldots\}$. In other words, we assume that N^k is the same for all k: $(N^k = N)$; condition (6) therefore requires $g(N, \boldsymbol{M}^k)$ to be equal for all k.

Consider two specific k $(k = 1, 2)$, and suppose that $\boldsymbol{\Psi}^1$ and $\boldsymbol{\Psi}^2$ are infinitesimally separated in a direction, $\boldsymbol{v}$ (where $\boldsymbol{v} = \{0, v_1,\ldots, v_A\}$ is a vector of unit magnitude in $\{N, \boldsymbol{M}\}$ space, with an N-component equal to 0 because $N^1 = N^2$). The change in $g(.,.)$ moving from $\boldsymbol{\Psi}^1$ to $\boldsymbol{\Psi}^2$ would then be given by the directional derivative, $\nabla_{\boldsymbol{v}} g(N,\boldsymbol{M})|_{\boldsymbol{\Psi}=\boldsymbol{\Psi}^1}$, which must be equal to 0 [by condition (6)]:

$$\nabla_{\boldsymbol{v}} g(N,\boldsymbol{M})|_{\boldsymbol{\Psi}=\boldsymbol{\Psi}^1} = \sum_{j=1}^{A} v_j\left[\frac{\partial g(N,\boldsymbol{M})}{\partial \boldsymbol{M}_j}|_{\boldsymbol{\Psi}=\boldsymbol{\Psi}^1}\right] = 0, \tag{2.1}$$

where v_j defines the change in M_j in direction $\boldsymbol{v}$ (i.e. moving from $\boldsymbol{\Psi}^1$ to $\boldsymbol{\Psi}^2$). Notice that $v_j\left[\frac{\partial g(N,\boldsymbol{M})}{\partial M_j}\right] = 0$ for any ecosystem component, j, that either does not interact with the focal stock $\left(\left[\frac{\partial g(N,\boldsymbol{M})}{\partial M_j}\right] = 0\right)$ or does not change from $\boldsymbol{\Psi}^1$ to $\boldsymbol{\Psi}^2$ $(v_j = 0)$.

If there is any set of ecosystem components, S, not satisfying either of these criteria, then equation (2.1) requires that $\sum_{j\in S} v_j\left[\frac{\partial g(N,\boldsymbol{M})}{\partial M_j}|_{\boldsymbol{\Psi}=\boldsymbol{\Psi}^1}\right] = 0$. This means that the effects on $g(.,.)$ of the changes in all of these abiotic factors and species' abundances from $\boldsymbol{\Psi}^1$ to $\boldsymbol{\Psi}^2$ would have to exactly cancel each other out (for all possible N). Though mathematically possible, such exact compensation is far-fetched on any timescale. Among biotic factors, some degree of functional redundancy in a biodiverse ecosystem might promote partial compensation (e.g. where species are ecologically similar to one another and aggregately coupled to the focal stock), but aggregation theory (Iwasa *et al.* 1987) predicts that exact compensation would require the compensating species to be ecologically identical, and ecological theory generally predicts strict ecological redundancy (i.e. where multiple species in the same system have the exact same ecological niche) to be unlikely (MacArthur and Levins 1967; Loreau 2004). Exact compensation among abiotic factors seems even less likely.

Equation (2.1) thus implies that abstraction of the focal stock's production requires at least a 1:1 mapping from N to M_j, for any ecosystem component, j, directly influencing the growth of the focal stock.

What about other ecosystem components (including biotic and abiotic factors and even other fishing fleets) interacting directly with component j but not the focal stock? We can follow the same logic as above, considering now the dynamics of component j. Suppose the dynamics of component j follow:

$$\frac{\mathrm{d}M_j(t)}{\mathrm{d}t} = f_j[N(t),\boldsymbol{M}(t)]. \tag{2.2}$$

Moving from $\boldsymbol{\Psi}^1$ to $\boldsymbol{\Psi}^2$, we know that $M_j^{\,1} = M_j^{\,2}$ [from (2.1) and following discussion]. Given this, we also know that $f_j(N^1, \boldsymbol{M}^1) = f_j(N^2, \boldsymbol{M}^2)$. Were this not the case, then $\frac{\mathrm{d}M_j(t)}{\mathrm{d}t}|_{\boldsymbol{\Psi}=\boldsymbol{\Psi}^1} \neq \frac{\mathrm{d}M_j(t)}{\mathrm{d}t}|_{\boldsymbol{\Psi}=\boldsymbol{\Psi}^2}$ and $M_j(t)$ [and by extension $g(.,.)$] would have different values at an infinitesimal time step following state $\boldsymbol{\Psi}^1$ than at an infinitesimal time step following state $\boldsymbol{\Psi}^2$, despite the fact that $N(t)$ would be the same [assuming $F^1 = F^2$], which would violate condition (6). If we were instead focusing on the equilibrium state, then we know that the right-hand side (RHS) of equation (2.2) would be equal to 0 at both $\boldsymbol{\Psi}^1$ and $\boldsymbol{\Psi}^2$, which implies $f_j(N^1, \boldsymbol{M}^1) = f_j(N^2, \boldsymbol{M}^2)$.

Thus, the directional derivative of the RHS of equation (2.2) in direction $\boldsymbol{v}$ must also be equal to 0:

$$\nabla_{\boldsymbol{v}} f_j(N,\boldsymbol{M})|_{\boldsymbol{\Psi}=\boldsymbol{\Psi}^1} = \sum_{l=1}^{A} v_l \left[\frac{\partial f_j(N,\boldsymbol{M})}{\partial M_l}|_{\boldsymbol{\Psi}=\boldsymbol{\Psi}^1}\right] = 0, \tag{2.3}$$

We also know that $v_l = 0$ for $l = j$ and for all l directly interacting with the focal stock [from equation (2.1) and the discussion following]. From here, the logic is the same as above: for equation (2.3) to hold, either $v_l\left[\frac{\partial f_j(N,\boldsymbol{M})}{\partial M_l}\right] = 0$ for all ecosystem components l (i.e. they either do not interact with component j or they do not change from $\boldsymbol{\Psi}^1$ to $\boldsymbol{\Psi}^2$) or there is a far-fetched compensation scenario in which $v_l\left[\frac{\partial f_j(N,\boldsymbol{M})}{\partial M_l}\right] \neq 0$ for a set of components, B, but still $\sum_{l\in B} v_l\left[\frac{\partial f_j(N,\boldsymbol{M})}{\partial M_l}|_{\boldsymbol{\Psi}=\boldsymbol{\Psi}^1}\right] = 0$. This line of reasoning could be continued, by further induction, to show that N must map uniquely – over the timescale in question [at every time period to satisfy condition (6)] – onto any ecosystem component connected through the food web to the focal stock, except under the extraordinary circumstances (leading to perfect compensation) discussed above.

Appendix 3: Note on inequality (16) and text that follows

We briefly discuss some of the nuances of inequality (16) to clarify our interpretation of it in the paragraphs following its statement in the main text. Restating inequality (16), the squared deviation of $g[N(t),\boldsymbol{M}(t)]$ from $g[N(t),\boldsymbol{\phi}(N[t])]$ decreases through time (i.e. $\frac{\mathrm{d}}{\mathrm{d}t}(g[N(t),\boldsymbol{\phi}(N[t])] - g[N(t),\boldsymbol{M}(t)])^2 < 0$) if (and only if):

$$(g[N(t),\boldsymbol{\phi}(N[t])] - g[N(t),\boldsymbol{M}(t)]) \sum_{j=1}^{A}\left[\left(\frac{\partial g}{\partial M_j}|_{M_j=\phi_j[N(t)]}\right)\phi'_j(N[t])\frac{\mathrm{d}N(t)}{\mathrm{d}t} - \frac{\partial g}{\partial M_j}\lambda_j M_j(t)\left(\phi_j[N(t)] - M_j[t]\right)\right] < 0. \tag{16}$$

If all ecosystem components, $\boldsymbol{M}(t)$, are at their attractor, $\boldsymbol{\phi}(N[t])$, then $g[N(t),\boldsymbol{\phi}(N[t])] = g[N(t),\boldsymbol{M}(t)]$ and the squared deviation is equal to 0. If component j is not at its attractor, $M_j(t) \neq \phi_j(N[t])$, then it is approaching it at rate $|\lambda_j M_j(t)\left(\phi_j[N(t)] - M_j[t]\right)|$ (as assumed in equation [13]), and $\phi_j(N[t])$ is changing at a rate $\phi_j'(N[t])\frac{\mathrm{d}N(t)}{\mathrm{d}t}$ because of changes in $N(t)$. The change in $N(t)$ may either be moving $\phi_j(N[t])$ closer to $M_j(t)$ or moving it further away. If the former, then both forces acting on $M_j(t)$ are causing it to approach $\phi_j(N[t])$. If the latter, then the forces are opposing and $M_j(t)$ is approaching $\phi_j(N[t])$ only if $\left|\phi'_j(N[t])\frac{\mathrm{d}N(t)}{\mathrm{d}t}\right| < |\lambda_j M_j(t)\left(\phi_j[N(t)] - M_j[t]\right)|$. Thus, the statement from the main text – that $M_j(t)$ is approaching $\phi_j(N[t])$ if (but not only if) $\left|\phi'_j(N[t])\frac{\mathrm{d}N(t)}{\mathrm{d}t}\right| < |\lambda_j M_j(t)\left(\phi_j[N(t)] - M_j[t]\right)|$ – captures both cases.

It is also worth noting that $\left|\phi'_j(N[t])\frac{\mathrm{d}N(t)}{\mathrm{d}t}\right| < |\lambda_j M_j(t)\left(\phi_j[N(t)] - M_j[t]\right)|$ does not necessarily imply that changes in $M_j(t)$ are reducing the squared deviation of $g[N(t),\boldsymbol{M}(t)]$ from $g[N(t),\boldsymbol{\phi}(N[t])]$ (i.e. $g[N(t),\boldsymbol{\phi}(N[t])] - g[N(t),\boldsymbol{M}(t)]$ and $\left[\left(\frac{\partial g}{\partial M_j}|_{M_j=\phi_j[N(t)]}\right)\phi'_j(N[t])\frac{\mathrm{d}N(t)}{\mathrm{d}t} - \frac{\partial g}{\partial M_j}\lambda_j M_j(t)\left(\phi_j[N(t)] - M_j[t]\right)\right]$ do not necessarily have opposite sign). As in the main text, we assume that $g[N(t),\boldsymbol{M}(t)]$ is monotonic in each ecosystem component ($\frac{\partial g}{\partial M_j} \geq 0$ for all values of M_j, or $\frac{\partial g}{\partial M_j} \leq 0$ for all values of M_j). With this assumption, if ecosystem component j was the only other component interacting with the focal stock, $\left|\phi'_j(N[t])\frac{\mathrm{d}N(t)}{\mathrm{d}t}\right| < |\lambda_j M_j(t)\left(\phi_j[N(t)] - M_j[t]\right)|$ would necessarily imply changes in $M_j(t)$ are reducing the squared deviation of $g[N(t),\boldsymbol{\phi}(N[t])]$ from $g[N(t),\boldsymbol{M}(t)]$. However, with multiple ecosystem components, it is possible for movement of $M_j(t)$ towards its attractor, $\phi_j(N[t])$, to increase the squared deviation of $g[N(t),\boldsymbol{M}(t)]$ from $g[N(t),\boldsymbol{\phi}(N[t])]$, if the deviation in $g[N(t),\boldsymbol{M}(t)]$ from $g[N(t),\boldsymbol{\phi}(N[t])$ caused directly by the difference between $M_j(t)$ and $\phi_j(N[t])$ was previously compensating for a larger deviation (in $g[N(t),\boldsymbol{M}(t)]$ from $g[N(t),\boldsymbol{\phi}(N(t))]$) of opposite sign caused by another ecosystem component. The fact that $|\lambda_j M_j(t)\ \left(\phi_j[N(t)] - M_j[t]\right)|$ increases as $|\phi_j[N(t)] - M_j[t]|$ increases – coupled with the assumption that $g(.,.)$ is monotonic in all M_j – bounds the squared deviation of $g[N(t),\boldsymbol{M}(t)]$ from $g[N(t),\boldsymbol{\phi}(N(t))]$, as asserted in the main text.