# The ghosts of overfishing past that haunt present day fisheries management

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# 1 Abstract

Fish biomass is the most widely used indicator of fish stock health. Stocks whose biomass is or has previously collapsed owing to overfishing, and the management systems built around them, may carry a memory of decline, even if biomass has recovered. This is because stock biomass as the main indicator of stock health does not represent all aspects of stock health and biomass can possibly become a weaker indicator of health after stock collapse. These latent weaknesses have been termed "ghosts of overfishing past". Not accounting for ghosts can impact the speed of stock recovery and susceptibility to further collapses. This concept has been popularised by Professors Jeff Hutchings, Anna Kuparinen, and others. Ghosts are varied and can include changes in vital rates, phenotypic response, fish behaviour, and aspects of the human system such as institutional inertia, fisheries subsidies and income portfolios. The presence of ghosts has implications for fisheries management: altering stock biomass objectives (dynamic reference points) may be appropriate for populations that have experienced collapse even if biomass has recovered. Ghosts should be considered when developing management strategies for populations that have previously experienced large declines.

## 2 Keywords

hysteresis, population collapse, management strategy evaluation, dynamic reference points, latent effect, social licence, epigenetics

# 3 Graphical abstract

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# 4 Introduction

The fishery science-management system in most Global North countries presently employs some variation of the precautionary approach (PA) (Hilborn et al. 2001) as their sustainable fishery decision framework. The PA sets objectives, commonly called reference points, for stock health and prescribes a level of exploitation based on the current stock health relative to reference points. Stock health is usually described as a level of biomass of mature individuals expressed as spawning stock biomass (SSB). However, this operational decision making framework can suffer from being too simplistic in that it is not well adapted to consider measures of stock health other than SSB. Prior to overexploitation, SSB may be a good overall measure of stock health and is likely closely associated with other measures of stock health. However, after overfishing and stock collapse occurs, SSB may disassociate from other measures of stock health. For example, SSB declines from overfishing are often coupled with shifts in stock age/size structure. These stocks may not recover the largest most fecund individuals even after SSB recovery if fishing selectively removed the majority of the largest individuals (Cooper et al. 2013; Hixon et al. 2014). Alternatively, the large fecund phenotype or genotype may be lost owing to past overfishing (Enberg et al. 2009). The loss of SSB as the overall best indicator of stock health can have an important influence on the speed and likelihood of stock recovery (Neubauer et al. 2013) if the specifics of how biomass decoupled from other measures of stock health have not be accounted for.

The residual effects or memories of previous stock collapses (Ogle et al. 2015) are "ghosts" in the system, in that they are present but may not be known or easily observed. These ghosts of overfishing past manifest with different mechanisms and in turn, have varying impacts on stock productivity (Hutchings and Kuparinen 2014; Frank et al. 2023). Previous work has shown how the ghosts of overfishing past can make it difficult for stocks to recover to previous levels with curtailment of fishing and can increase stock vulnerability to environmental variability and climate change (Hutchings and Reynolds 2004; Planque et al. 2010; Collie et al. 2013; Regular et al. 2022; Goto 2023).

Coupled with the biological ghosts of stock collapse are the ghosts that exist in the human dimension. Socio-economics and emotional attachments of fishers and human communities to fishing can present challenges for providing and implementing effective advice, especially during fish stock downturns. For example, when a fish stock collapses, fisheries also collapse and this can have impacts such as out-migration from fishing ports that leave communities with an older age structure, and generating marine infrastructure changes as communities change their main target species (Hamilton et al. 2004; Schrank 2005). In addition, the management system may change, including the ways stocks are assessed scientifically and the degree of risk aversion of managers and politicians (Charles 1998; King et al. 2015; Bertheussen 2022). Social licence for fisheries to operate (Robinson et al. 2021), which is the acceptability that society assigns to capture fisheries as a legitimate social and economic activity, may also change post collapse even if a stock appears to be recovered because biomass has recovered. Ultimately, there are many diffuse impacts of stock collapse on human factors associated with fisheries, and these aspects of the human system can continue to have an influence on a stock's ability to withstand fishing even if a stock recovers to previous biomass levels.

The work of Prof. Jeff Hutchings along with close colleague Prof. Anna Kurparinen, has been instrumental in popularising the concept of ghosts of overfishing past (Hutchings and Kuparinen 2014) to reflect the latent effects of past fishing that may still be acting on fish populations. This is important because most fisheries models consider fish stocks in isolation and only account for key demographic drivers without representing the mechanisms that explain variation in population productivity shifts. However, by considering latent effects as ghosts that haunt recovered fish stocks (or those undergoing recovery), Hutchings and colleagues were able to bring into the consciousness of managers, scientists and fishers that their past actions can have unknown and ongoing implications for fish stocks generations into the future (Enberg et al. 2009). The thinking behind this concept may have come from Jeff Hutchings' own experience working in Newfoundland in the 1990s where the once great northern cod stock, *Gadus morhua*, was declared collapsed in 1992. The recovery that was thought to be possible in five to nine years (Roughgarden and Smith 1996) did not materialise. Thus, examining life-history parameter correlates before and after population collapse as an explanation for lack of recovery became a key pillar of Jeff Hutchings' subsequent research (Myers et al. 1997; Hutchings and Reynolds 2004; Neubauer et al. 2013; Hutchings and Kuparinen 2014). The work of Hutchings and colleagues remains an active area of research and we suggest that these ghosts of overfishing past should be considered when fishery science advice is developed (Eddy et al. 2023). In addition, it is also timely to include other ghosts that may be apparent such as those we discuss related to the human dimension and novel but relatively unknown impacts of epigenetics. With this perspective, we reviewed ghosts of overfishing past and potential technical solutions to provide management advice in the face of some of these ghosts.

This perspective is based on an international workshop that was hosted by the authors on the use of dynamic reference points (DRP) in fisheries in January 2021 (Zhang et al. 2021). The workshop was attended by 111 participants from many countries and continents. The authors were able to glean the recurrence of ideas about latent effects of collapse on lack of recovery or increased vulnerability to future collapse from discussions amongst participants, presentations and panel discussions. Additionally, a survey of participants (82 responses) identified some of the major influences affecting the effectiveness of the science-management fisheries systems globally (Eddy et al. 2023). Ideas about fishery collapse and non-recovery based on Jeff Hutchings' research underlied many of the presentations and discussions at the workshop. The ghosts of overfishing past identified here therefore represent not just a literature search by the authors but also the informed views of many fisheries scientists who worked with Jeff Hutchings, fishery managers, fisheries policy analysts, environmental NGOs, Indigenous rights holders, and fishers themselves.

# 5 Unmasking the ghosts

To enable greater consideration in science-management systems, ghosts of overfishing past first need to be identified. Some ghosts are less obvious than others and may be more apparent during the stock recovery than ones that have shown biomass recovery. Several ghosts can be present at any one time, and their relative influence may change with time. In this study, ghosts were identified by the author group based on an analysis of discussions from the workshop (Zhang et al. 2021). A description of each ghost and how they impact populations is provided (Table 1). There are undoubtedly other ghosts, some of which we may not even be aware of yet.

The ghosts identified here have been divided into population intrinsic and extrinsic categories. Population intrinsic ghosts are those either present within individuals of a population or within collective population rates or characteristics. Extrinsic ghosts are those present within the physical environment e.g., water temperature, the biological community abundance of prey species, the broader socio-ecological system, employment opportunities or the specific socio-economic/fisheries management system, management culture. Many population intrinsic ghosts can be the manifestation of fisheries induced evolution (FIE). FIE is an umbrella process that can manifest in specific measures such as age at maturity, truncated age structure, lost phenotypic plasticity and loss of sub-populations (Laugen et al. 2014). It can be difficult to identify FIE through field collections based on phenotype alone (Heino et al. 2015) and we have instead concentrated on these lower-level mechanisms rather than the phenomenon of FIE as a specific process.

## 5.1 Population intrinsic

### 5.1.1 Truncation of age structure

The nature of fisheries that target large fish can lead to a truncation of age structure leaving predominantly younger age classes (Barnett et al. 2017). Age-truncated populations are more sensitive to environmental variability and recruitment deviations, increasing the risk of population collapse and decreasing population recovery potential (Hsieh et al. 2006). Furthermore, the selection of larger and older individuals can lead to a loss of big, old, fat, fecund, female fish (BOFFFF) that are disproportionately important contributors to population growth (Enberg et al. 2009; Barneche et al. 2018). Even after fishing pressure is reduced, age/size structure may not recover, particularly for the largest, old fish (Charbonneau et al. 2019). Age truncation is a common ghost and is well studied (Brunel and Piet 2013), with several examples including groundfish, e.g., Atlantic cod from Canada, Iceland, the Barents Sea and the North Sea, and pelagics, e.g., western Atlantic bluefin tuna (Secor et al. 2015) and Norwegian herring (Rouyer et al. 2011).

### 5.1.2 Loss of subpopulations & rescue effects

As local populations of fish become depleted, fishers expand the spatial extent of their fishing to maintain catch levels (Berkes 2006). As the spatial scale of effort expands, locally-adapted sub-populations can be depleted (DeYoung and Rose 1993; Hayden et al. 2015; Okamoto et al. 2020). Overfished populations can show a 12% reduction in allelic richness, while simulations suggest that the reduction in allelic richness can be much greater (Pinsky and Palumbi 2014). In situations of local population depletion, subpopulations may be "rescued" with the influx of individuals from adjacent populations that increase abundance and genetic diversity (Carlson et al. 2014; Draghi et al. 2024). While a simple influx of new immigrants might be enough to restore population biomass, simulations of northern cod suggest that immigrant genetic composition can significantly affect the rate of recovery (Kuparinen and Uusi-Heikkilä 2020). This is because increased genetic diversity can promote recolonisation of previously occupied areas (Smedbol and Wroblewski 2002) and can help overcome negative growth trends, inbreeding, and possible Allee effects (Carlson et al. 2014; Kuparinen and Uusi-Heikkilä 2020). As such, fisheries managers must be cognizant that maintaining and restoring population genetic diversity may be as important as restoring biomass (Smedbol and Wroblewski 2002; Hilborn et al. 2003; Kuparinen and Uusi-Heikkilä 2020).

### 5.1.3 Reproductively driven Allee effect

The Allee effect is defined as a decline in per-capita population growth with decreasing population size i.e., depensatory population growth (Stephens et al. 1999), that can cause a population to become extirpated when there appears to be a sufficient number of adults to allow the population to recover (Walters and Kitchell 2001). The Allee effect has been observed in terrestrial populations of passenger pigeon (Courchamp et al. 2008) and caribou (Festa-Bianchet et al. 2011). Allee effects in marine populations are usually attributed to an inability to find mates (Gascoigne et al. 2009) or to increased predation pressure e.g., predator pits, more below (Gascoigne and Lipcius 2004b; Bakun 2006). Although reproductively driven Allee effects are often discussed, observations of reductions in reproductive success i.e., fertilisation rates, number of breeding aggregations at low population size/density have only been observed in a few marine species, including Atlantic cod (Rowe et al. 2004), south Australian abalone (Shepherd and Brown 1993), and sea urchins (Levitan et al. 1992). In general, it is expected that reproductively driven Allee effects are more important for less mobile species that depend on the proximity of individuals for mating rather than species that actively move and congregate to reproduce.

#### 5.1.4 Loss of phenotypic plasticity

Phenotypic plasticity is an adaptation to survive in variable environments, where genotypes produce different phenotypes when exposed to a range of environmental conditions, allowing for a greater chance of survival (Hidalgo et al. 2014). A phenotypic response will occur with size selective harvesting in just a few generations and well before a genetic response is likely to arise through continuous selection (Matte et al. 2023). Size selective fishing may decrease the age at maturity in a population (Kuparinen and Festa-Bianchet 2017) through a phenotypic response. Similarly, behavioural phenotypic plasticity may be expressed through modifications to migration timing and routes, given that older fish may train younger conspecifics (Petitgas et al. 2010). This type of learned behaviour can be lost during periods when stocks have collapsed due to overfishing (Hidalgo et al. 2014), as fisheries often selectively exploit older individuals. The result is that spawning or feeding grounds that were formerly occupied may become vacant for a period of time, ultimately reducing available habitat. Loss of phenotypic plasticity has been observed in Newfoundland Northern cod that lost subpopulation ecotypes (Petitgas et al. 2010). The North Sea and Georges Bank herring showed a behavioural loss from using certain spawning areas (Petitgas et al. 2010). California sardine experienced social disruption and cessation of migration (Petitgas et al. 2010). Bay of Biscay anchovy lost contingents and the connectivity between the contingents (Petitgas et al. 2010). European hake showed a changed maturation schedule (Hidalgo et al. 2014). Petitgas et al. (2010) makes the useful distinction between depleted and collapsed populations in this context. Despite the potential loss of phenotypic plasticity with population collapse, there may be sufficient plasticity to recover demographic rates in reduced populations when fisheries pressure is reduced or eliminated (Eriksson and Rafajlović 2022).

#### 5.1.5 Epigenetic effects

Epigenetic effects are a form of phenotypic plasticity that may be triggered by conditions experienced by individuals during their lifetimes that can lead to the expression or repression of parts of the existing genome, with intergenerational consequences (Ryu et al. 2020; Kelley et al. 2021). Epigenetic effects are to some degree heritable, and external conditions can induce or inhibit the transcription of different gene sequences (Wellband and Heath 2017). Epigenetic changes associated with predation risk experienced by parents have been implicated in behavioural shifts in their offspring (Donelan et al. 2020). Similarly, climate change may trigger epigenetic effects (Eirin-Lopez and Putnam 2019) and theoretically, the expression of an environmentally induced epigenetic trait may come to dominate when a population has been reduced dramatically in size, perhaps owing to fisheries induced depletion, during a time of environmental change. Epigenetic plasticity may be a mechanism by which low fecundity, long-lived species are able to adapt relatively quickly to changing selective pressures (Lighten et al. 2016), thereby inferring a fitness advantage. In some cases, it may be prudent to consider these epigenetic traits as ghosts to test plausible mechanisms (Bell and Hellmann 2019; Donelan et al. 2020) impacting fishery sustainability, but the mechanisms of how this might influence recovery and persistence of populations would be speculative given the current state of knowledge.

#### 5.1.6 Loss of population genetic diversity

Intense fishing can reduce the genetic diversity of exploited populations (Heino 1998; Jorgensen et al. 2007; Pinsky and Palumbi 2014). This effect has been referred to as “Darwinian Debt” (Pandolfi 2009) because genetic recovery after exploitation may take many generations. This can arise through fisheries selection of large individuals and individuals that grow faster to fishable sizes. This creates a selection pressure for individuals that achieve their contributions to fitness at small size and younger age (Therkildsen et al. 2019). There may also be physiological selection of phenotypes that move more and therefore they become more susceptible to passive gear because encounter rates are higher, or have a lower capability to escape active fishing gear (Alos et al. 2012; Diaz Pauli et al. 2015; Hollins et al. 2018). This loss of genetic diversity in these populations, even after recovery, may lead to a reduced capacity to adapt to changes in the environment (Vasseur et al. 2014). It is not clear, however, whether intense fisheries and stock collapse will always lead to a loss of genetic diversity to the extent that recovery may not be possible (Pinsky et al. 2021). Notably, however, loss of distinct genetic units such as salmon runs from particular tributaries or loss of sub-populations should be considered a hidden biodiversity crisis (Des Roches et al. 2021) that could potentially result from past overfishing. Although it is necessary to be averse to this loss of genetic diversity as the consequences for it are severe and potentially irreversible, phenotypic changes may be reversible through well aimed management actions. It is not straightforward to disentangle genotypic from phenotypic change (Swain et al. 2007; Heino et al. 2008; Uusi-Heikkilä et al. 2015).

### 5.1.7 Spatial Behaviour and Social Learning

Social learning is hypothesized to play a key role in transferring information from knowledgeable older individuals to younger ones (MacCall et al. 2019). It has been suggested that fishing, by removing larger, older individuals, could disrupt the guidance of newcomers to spawning, feeding, and wintering grounds (Corten 2002; Petitgas et al. 2010). This disruption may lead to changes in migration patterns, potentially affecting fisheries catches. Some argue that this ghost may linger even after stock biomass recovers to pre-collapse levels (Vilhjálmsson 1997; Petitgas et al. 2010). Examples of changes in spatial behaviour include Norwegian herring (Vilhjálmsson 1997), North Sea herring (Corten 2002), northern cod, and Californian sardine (Petitgas et al. 2010). The concept of leader individuals and their critical role in population-level behaviour may not have strong empirical evidence. While this has been documented in the bird migration literature (Mueller et al. 2013), direct evidence for such processes in fish remains limited. The negative impacts of losing leaders may be overstated without more concrete evidence that these older individuals are essential for maintaining migration routes or ingrained behaviours.

In the context of climate change, the absence of leaders could theoretically foster greater behavioural plasticity. High abundances of behaviourally naïve individuals might encourage innovation and colonisation of new habitats (Huse et al. 2002), potentially aligning with shifting environmental conditions. While this redistribution could lead to novel life-cycle patterns, such outcomes depend on sufficient population fecundity and fertility to support such experimentation. Given the difficulty in proving these mechanisms, the role of social learning and leadership in fish populations warrants cautious interpretation.

## 5.2 Population extrinsic

### 5.2.1 Alternate trophic pathways

Altered trophic structure is a ghost that is observed in ecosystems where fisheries target species at high trophic levels, leading to a food web dominated by small, short-lived species (Szuwalski et al. 2017). This new type of food web structure may emerge as an alternative stable state and persist after a reduction of fishing mortality (Collie et al. 2013). As a result, the high trophic level target species may not recover due to the stabilizing interactions within the alternative state of the food web, particularly following the loss of top predators (Berkes 2002). For example, the depletion of cod can increase the abundance of its prey species which are competitors/predators of juvenile cod, which can further inhibit the recovery of cod (Walters and Kitchell 2001; Fauchald 2010; Gårdmark et al. 2015).

### 5.2.2 Habitat fragmentation and range contraction

Range contraction is a common response to fish population decline (Rose and Kulka 1999; Post et al. 2002; Shackell et al. 2005; Dassow et al. 2020), observed through decreased area of occupancy (Frisk et al. 2011). This phenomenon can arise through schooling mechanisms, mate searching, and can be influenced by intraspecific niche widths (Faulks et al. 2015). The terrestrial metapopulation literature, however, tends to view abundance as a function of occupancy and shows that fragmented landscapes tend to have lower occupancy than non-fragmented ones, and therefore lower abundance (Webb et al. 2007). This is consistent with the theory of extinction debt (Tilman et al. 1994), where ecosystems that have experienced habitat fragmentation show a loss of occupancy of competitor species over time, independent of declines in abundance. Such declines in occupancy have been observed in several fish stocks such as Newfoundland cod (Rose and Kulka 1999), Scotian Shelf cod (Shackell et al. 2005), and fish in Wisconsin lakes (Dassow et al. 2020). These could be consistent with an extinction debt, though defining marine habitat fragmentation is not simple. Once an extinction debt has been incurred, it can be difficult to slow the decline of the population and this can lead to decreased resilience and increased vulnerability to fishing or localised environmental and ecosystem impacts (Duplisea et al. 2016). Multiple uses of marine systems, a history of habitat destructive fishing practices, and a concurrent decline in occupancy, even if abundance has recovered to previous levels, can be an indication that an extinction debt could be present, even if not apparent from abundance estimates alone.

### 5.2.3 Predator driven Allee effects

Predation driven Allee effects, commonly referred to as predator pits, are driven by increased predation mortality at low population sizes (Gascoigne and Lipcius 2004a). If remaining individuals in a declining population aggregate, their overall abundance is not a reflection of the local abundance and a predator can still consume them in large numbers with increasing impacts on the total population, i.e., scarcity is not a naturally protective mechanism as encounter rates may not change as the prey population decreases. Examples of increases in predation mortality at small population sizes have been observed in a number of species including salmonids (Wood 1987; Falkegård et al. 2023), crown of thorns starfish (Dulvy et al. 2004), and Atlantic cod (Swain and Sinclair 2000; Fauchald 2010; Swain and Benoît 2015; Neuenhoff et al. 2019). Predator pits leading to local extinction may be more likely when the stochasticity of predation rates is high due to high environmental variation (Clark et al. 2021).

### 5.2.4 Institutional inertia

Sustainable harvest of marine species requires the establishment of appropriate governance institutions. Although there is no perfect governance structure (Ostrom 2007; Ye and Gutierrez 2017; Young et al. 2018), inappropriately defined access structures, spatial scales, and decision making processes can increase the risk of unsustainable harvest and vulnerability to climate and environmental change that can haunt collapsed and recovered populations (Ostrom 1990, 2009; Hilborn et al. 2005; Khan and Neis 2010; Fulton 2021; Eddy et al. 2023). Institutional ghosts have been implicated in the collapse of New England groundfish (Hennessey and Healey 2000; Brewer 2011) where fishers overcapitalise leading to stock declines followed by compensation after collapse and the cycle repeats. This institutional and economic driver has been termed "Ludwig's ratchet". The boom-bust and serial depletion of sea cucumber stocks globally may be partially a result of the insufficient speed with which institutional management structure can keep up with fisheries exploitation (Anderson et al. 2011; Purcell et al. 2013).

### 5.2.5 Fishery subsidies and socio-economics

Fisheries subsidies are a financial contribution that are used to support programs and activities that benefit and increase the profit of, or participation in, the fishing sector (Sumaila et al. 2010). Global subsidies to fisheries can contribute to overcapacity of fishing fleets and overfishing (Cisneros-Montemayor et al. 2016; Sumaila et al. 2016). However, eliminating fisheries subsidies is a controversial issue because of the trade-off between employment, fish catch and ecosystem sustainability (Worm et al. 2009). Globally, subsidies for the fishing sector are around $35.4 billion (2018 USD) (Sumaila et al. 2016; Sumaila et al. 2019). It is clear that fisheries subsidies can be considered ghosts that are different from ecological ghosts but can similarly lead to declines in fish stocks and prevent their recovery. Subsidies can come in many different forms, and it may not be clear when a subsidy is in place; thus, their impacts can remain hidden to conventional analysis.

Employment maximisation has often been pursued as a socio-economic goal in fisheries management. However, it can result in higher fishing costs and lower profit, undermining long-term economic viability of the fishing sector (Grafton et al. 2012). Higher fishing capacity makes it more difficult for decision-makers to reduce harvests when required, i.e. declining or collapsing stocks (Grafton et al. 2012). For example, the Fishermen's Employment Insurance (FEI) provided by the Canadian federal government kept capacity for cod fishing in Newfoundland that otherwise would have reduced owing to poor economic prospects (Schrank 2005). In 1990, FEI accounted for 80% of the income of fishers in Atlantic Canada (Feehan 1994). This may have slowed sustainable transformation in the fishery (Parsons 2010; Grafton et al. 2012). Although the sustainability of rural coastal communities require fisheries managers to consider a multi-dimensional concept of sustainability (Seghezzo 2009), socio-economic ghosts discussed here are interpreted primarily in terms of how they impact ecological sustainability rather than economic and social sustainability (Stephenson et al. 2017).

### 5.2.6 Emotional attachment

Fishers and fishing communities have emotional bonds to fishing and the way of life it entails (Ross 2013; Cline et al. 2017; Andrews et al. 2021), which is often inherited from ancestors, and passed on to children (Nightingale 2013). Fishers in these communities may compensate for lost income during low stock biomass periods by taking up alternate or temporary employment until fishing prospects return. If fishers subsidize their fishing ability, for example they upgrade their boat, with other income streams, this can lead to a break in the feedback between income from fishing and fishing effort expended. Furthermore, a fisher waiting for the return of a stock, exerts a certain pressure on government regulators to re-open fisheries when stocks show just small improvements in status. This could potentially be an important driver of stock reduction and lack of recovery in the case of social programs that may subsidize incomes during down-swings in fish stock biomass and productivity. Low mobility of local fishers in Thailand led to cooperation and even to under-exploit fishery resources in danger of rapid stock productivity shifts (Lindahl and Jarungrattanapong 2023). It was also found that non-local fishers, with weaker links to the local community or fishers with alternative income sources, were more likely to over-exploit stocks. In the Global North, where catch allocations between groups are often specified, fishers may be reluctant to sell their licences even when future economic prospects for fisheries are poor and buy-back programs are in place (Pollnac and Poggie 2008). This may be particularly true in places where alternative income streams allow rural resource-based communities to invest in fishing even when fishery income prospects are poor. Incentives towards emotional decisions by fishers rather than economic ones can be a result. Likewise, fisheries with a strong social component may continue even when fish population sizes are low or cannot withstand just moderate removal levels. There are many reasons why fishers continue to fish or leave fisheries altogether that are not simply related to fishery economic returns (Arias Schreiber and Gillette 2021). Understanding these reasons and the emotional response, sense of self or community that fishers attach to fishing, or lack of alternative careers can be a ghost that can lead to overfishing or hinder recovery of collapsed stocks. On the contrary, we are aware of the positive aspects of community that arise from the same attachment to fishing and community (Jentoft and Kristoffersen 1989; Castello et al. 2009). Furthermore, the attachment to place and fishing activities in fishing communities can allow fishers to quickly take advantage of upswings in fish resources when they occur which is a form of human community resilience. As with subsidies, there is a balance to be struck by managers and politicians setting fishery policy and who must be sensitive to both fishing community health and fish stock health.

# 6 Ghostbusters

## 6.1 Technical solutions

We explore two technical solutions to provide advice for fisheries management in the presence of ghosts of overfishing past (Table 2): (1) management strategy evaluation (MSE) approaches that consider the presence of the ghosts in the development of a robust operating model suite and (2) the use of dynamic reference points to reflect the time-varying productivity conditions that stocks experience.

MSE is an approach that allows one to simulation test the efficacy of management actions for achieving objectives, under the assumption that successful management actions under simulation are likely to work well in reality. The use of MSE in fisheries was relatively uncommon prior to 2010 and it is presently only applied to a fraction of assessed stocks in most jurisdictions (Goethel et al. 2019). MSE uses simulations of fish stock population dynamics, called operating models, to represent varying hypotheses about stock, fishery and ecosystem dynamics. For example, to consider the hypothesis that climate change would lead to reduced reproductive success in the future, an operating model with a depressed reproductive rate linked to a climate variable could be employed. If this hypothesis was considered credible, any management action tested may have to perform to high standards under this operating model. In this way, ghosts of overfishing past could be considered in the operating model suite. There have been studies that have explored this (Lee et al. 2020; Szuwalski et al. 2023) but it is not clear that they had impacts on fishery management decisions.

DRPs may also be a means of accounting for the ghosts of overfishing past in fisheries management so that reference points match current fish stock productivity (Lee et al. 2020; Zhang et al. 2021; Eddy et al. 2023). This can be done without simulation testing e.g., MSE, but should demonstrate that the new reference points align with current stock productivity, thus correcting the mismatch between reference points and actual stock productivity. This is somewhat easier to conceptualise than do in practice (Eddy et al. 2023) but guidance exists (Duplisea and Cadigan 2012; Silvar-Viladomiu et al. 2021), and it may be one of the most operational ways to provide useful management advice outside the MSE paradigm to achieve management objectives.

The main trade-off in MSE vs DRP approaches is in expertise required, time consumption and complexity where MSE is generally more demanding in all three. It is also important to note that they are not exclusive. One could incorporate a DRP approach in an MSE as part of the management procedure. And though not strictly MSE, one could and perhaps should simulate the potential impacts of implementing DRP approach.

# 7 Perspectives for managing recovering and recovered populations

We are currently in a period where many stocks around the world have collapsed, some have recovered, and many remain in a low biomass state (Hilborn et al. 2020; Britten et al. 2021). Some nations such as Canada have legally mandated that stocks not fall below safe biological limits, where the regulatory body is obliged to recover collapsed stocks (Justice-Canada 2019). Once a fish stock collapses, it may not simply be biomass alone that has been impacted but that other aspects of the population or ecosystem may have changed in addition to reduced biomass (Collie et al. 2013; Hutchings and Kuparinen 2014). The role that a stock plays in the ecosystem may change after collapse and recovery of biomass may not mean recovery of their previous role in the ecosystem. Finally, stock biomass recovery may not be a linear relationship with external forces like fisheries and the environment, as stocks and ecosystems often follow a nonlinear pathway hysteresis (Fauchald 2010; Durant et al. 2021; Robertson et al. 2021; Frank et al. 2023), or perhaps not recover at all (Sguotti et al. 2022).

Since the groundfish stock collapses in eastern Canada in the 1990s (Hutchings and Reynolds 2004), the idea of changing reference points in response to the perceived productivity regime shift for a stock has been considered but not often implemented. The reason it has not often been implemented is that it usually requires that scientists assessing a stock make the choice to leave out some historical data in model fitting because they feel it is not relevant to current stock dynamics. In peer-review processes for assessments, this can seem like willful ignorance and giving up on the ability of a stock to achieve past biomass levels. In more recent years, the discussion on changing reference points has become more nuanced. Ecosystem and stock productivity may undergo abrupt regime shifts (alternative stable state), suggesting tipping points that need to be accounted for (Blöcker et al. 2023), or they may simply never experience prolonged periods of stationary productivity (Britten et al. 2021; Bessell-Browne et al. 2024). The accelerating rate of climate change and its influence in the short and medium term on stocks has contributed to this broadening of the conversation into DRPs (Eddy et al. 2023; Punt et al. 2024). We now have more methods and perhaps more licence to consider other ways of adding modified reference points, for both fishing intensity and stock biomass, into the suite of operational management tools for stock assessment and advice.

The two overarching approaches of DRP and MSE can include specific technical implementations. DRP is an approach that attempts to align the biomass objectives to the biological realities of stock productivity (Silvar-Viladomiu et al. 2021). DRP may change biomass reference points continuously or in regimes (alternative stable states) and deciding when and how to change reference points accordingly is critical (Pélissié et al. 2024). MSE seeks to find strategies to safely exploit a stock that is robust to uncertainties in the methods, data, biology and ecology of a stock, and the fisheries management process itself (Goethel et al. 2019). MSE can therefore encompass a wide range of ghosts where the robustness is determined via performance of management strategies in simulation. DRP and MSE are not mutually exclusive and DRP have been tested in the MSE framework (Bessell-Browne et al. 2024). Both approaches may be means where ghosts of overfishing past can be accounted for when providing fisheries advice (e.g. Figure 1).

It is important that when DRP approaches are implemented, they follow a systematic process of deciding when and how to change with consideration of their stability and the credibility of the process if reference points vary widely and often (Duplisea and Cadigan 2012; Silvar-Viladomiu et al. 2021). For example, if a ghost has changed a life history parameter leading to a long term or permanent decrease in a stock's productivity, then it makes sense to alter biomass and fishing pressure reference points accordingly. A useful characteristic of DRP is that they can be almost purely phenomenological. That is, they are the result of a calculation or a level chosen and they are not necessarily mechanistic hypotheses. Allowing modified reference points to vary without a clear mechanism has limitations and dangers however, as reference point changes are usually premised on implicit assumptions about ecosystem stability and relatively constant external forces, i.e., a new stationarity (Punt et al. 2024). It is important that scientist and managers remain aware that changing goal posts (reference points) too much or too frequently can undermine credibility in the whole science and management process.

Possibly the preferred current technical solution for considering ghosts of overfishing past is with MSE (Kaplan et al. 2021; Bessell-Browne et al. 2024). MSE allows one to test how a particular ghost or suite of ghosts might affect the efficacy of management decisions taken in their presence. MSE could also allow one to develop management strategies that are in theory robust to a particular ghost. MSE, however, depends on how one implements hypotheses about the world, what kind of uncertainties to include, and how much uncertainty to include. The robustness of the management strategy chosen depends on these decisions. The MSE paradigm requires that one hypothesize and implement mechanistic formulations of how a ghost would operate in a population. Though MSE can be a very powerful tool, it is not without costs. MSE requires a very high level of biological, statistical and coding expertise, it can be time-consuming and in some cases the costs of doing the MSE may not be justified by the value of the fishery, when simpler, cautious fishery management may suffice without necessarily forsaking too much yield (Walter et al. 2023). MSEs are becoming more commonplace and tools now exist that can allow one to develop a MSE type of simulation (i.e. at a worker's desk rather than requiring full stakeholder input) much faster than just a few years ago, for example using MSEtool (Hordyk et al. 2024). However, because MSE is a conceptually and technically complex approach, 'black-boxing' it too much into easy-to-use wrapper code has limitations.

Developing plausible operating models (Punt et al. 2014) and hypotheses for MSE could be difficult when considering the range and diversity of ghosts of overfishing past. For example, most operating models do not have an explicit spatial component to them and therefore if one were trying to simulate a ghost related to loss of a subpopulation, they would need to implement an explicit mechanism in how the loss of a particular subpopulation affects the recruitment rate, growth rate or mortality rate of the larger population. This makes MSE more difficult and more speculative, yet on the other hand, it requires that researchers make clear hypotheses that can be criticised and tested and be the focus for more work. This is good scientific practice because it is based upon falsifiable hypotheses. MSE with multiple operating models that represent different hypotheses about the system, such as the presence of a ghost of overfishing past, requires an unambiguous statement of what constitutes a "pass" or a "fail" for management strategies. If the criteria are too strict, an operating model with a speculative ghost mechanism could potentially prevent any management procedure from passing. That is, the MSE paradigm presents what can appear to be a "silver bullet" solution that continually challenges the practitioners with subjective decisions to advance to the point of advice provision.

The 2019 changes to Canada's Fisheries Act (Justice-Canada 2019) specify that environmental and ecological conditions should be accounted for when setting reference points and developing recovery plans. Updating stock assessments to account for environmental and ecological conditions means that there will naturally be a tracking of productivity changes that could impact MSE and reference points from one assessment to the next. This, however, is not often done in the spirit of addressing ghosts of overfishing past but just a consequence of data updates. Even when an MSE process contains operating models that may encompass changes in something like life-history parameters, they are usually not included owing to their changes resulting from past overfishing but to represent another hypothesis or uncertainty. That said, there has been consideration of changed stock recovery targets in southern bluefin tuna to account for changes to stock production that may have arisen owing to previous overfishing (Hillary et al. 2016). It is challenging to find studies where aspects of the stock productivity or management system have been expressly adapted to account for ghosts of overfishing past.

Previous fishery collapses are an unintended experiment that can help uncover how and why changes in stock productivity occur and identify ghosts. Continuous monitoring of stocks and their productivity through scientific surveys and also through monitoring catch rates and spatial distribution of fishing fleets can also provide directions for how to best consider ghosts. There may be particular ghosts that would be better handled by MSE or DRP or a combination of the two (Table 2). Understanding historical levels (baselines) for biomass and productivity of stocks provides a basis for evaluating what are appropriate stock biomass levels (McClenachan et al. 2024).

## 7.1 Conclusion

In this perspective, we have summarized how ghosts of overfishing past may influence recovery of collapsed and recovered populations. The biased perception of a fish stock as an aggregation of exploitable biomass with other characteristics (e.g. size structure, life history rates) being static underlies a precautionary approach to fisheries management. Fish stocks are rather adaptive biological systems, and they have the potential to leave hidden ghosts when we oversimplify their dynamics. Fishers, managers and scientists know that these systems are more complex than are accounted for in various steps of the science-management system; however, considering this complexity can be very difficult in practice and can lead to the problem of being precisely wrong rather than generally right. We have provided a general description of some ghosts and how DRP or MSE might consider them in practice when developing fisheries advice. Of course, the best strategy to avoid ghosts is to prevent population collapse to start with. We are now, however, in a situation where climate change is affecting fisheries (Roux et al. 2022), and may even increase the potential for particular ghosts to affect stocks. Allowing a system whereby both fishery exploitation pressure and biomass reference points can be altered in response to climate change (Duplisea et al. 2021; Punt et al. 2024) and the presence of ghosts should be considered when scientists and managers consider fishery sustainability.

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# 9 Data availability statement

There was no new ecological or environmental data generated by this work.

# 10 Competing interests statement

None of the authors declare any competing interests.

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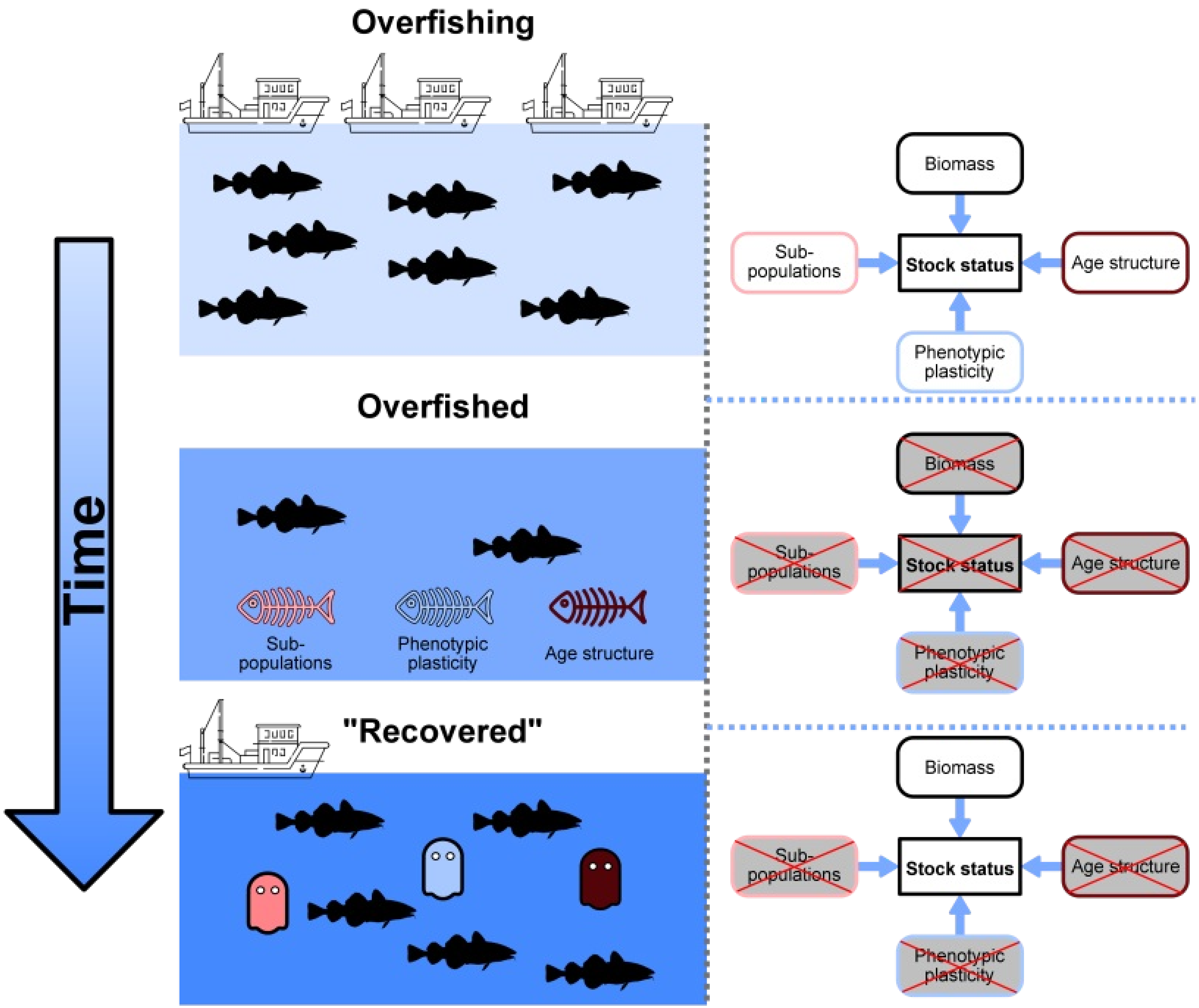
# 12 Figure and Table captions

Figure 1: Conceptual diagram of the application of management strategy evaluation and dynamic reference points for dealing with ghosts of overfishing past. The true dynamics panel represents alternative possibilities for a stock's true dynamics (dB/dt = population growth rate, B = biomass, R = recruitment, t= time) with an Allee effect (dashed blue line) and without an Allee effect (solid red line). Each of the lower panels represent either a situation in which the Allee goes unnoticed, a management strategy evaluation is used to identify the potential effects of an Allee effect, or dynamic reference points are used to account for an Allee effect. Each of these panels visualises the stock perception by managers (in terms of recruitment and biomass over time), how this perception affects the determination of reference points (F = fishing pressure, Blim = biomass limit reference point, Bpa = biomass precautionary limit reference point), and finally the outcome of perception and reference points on future stock status (in terms of biomass change and fishing rates).

Table 1: an overview of the 13 ghosts considered here and a key reference for each of them.

Table 2: model processes by which ghosts of overfishing past might be accounted for in advice through dynamic reference point methods or through the testing of management procedures in management strategy evaluation simulations.



Overfishing
Overfished
"Recovered"
Time
Sub-
populations
Phenotypic
plasticity
Age structure
Biomass
Sub-
populations
Stock status
Age structure
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plasticity
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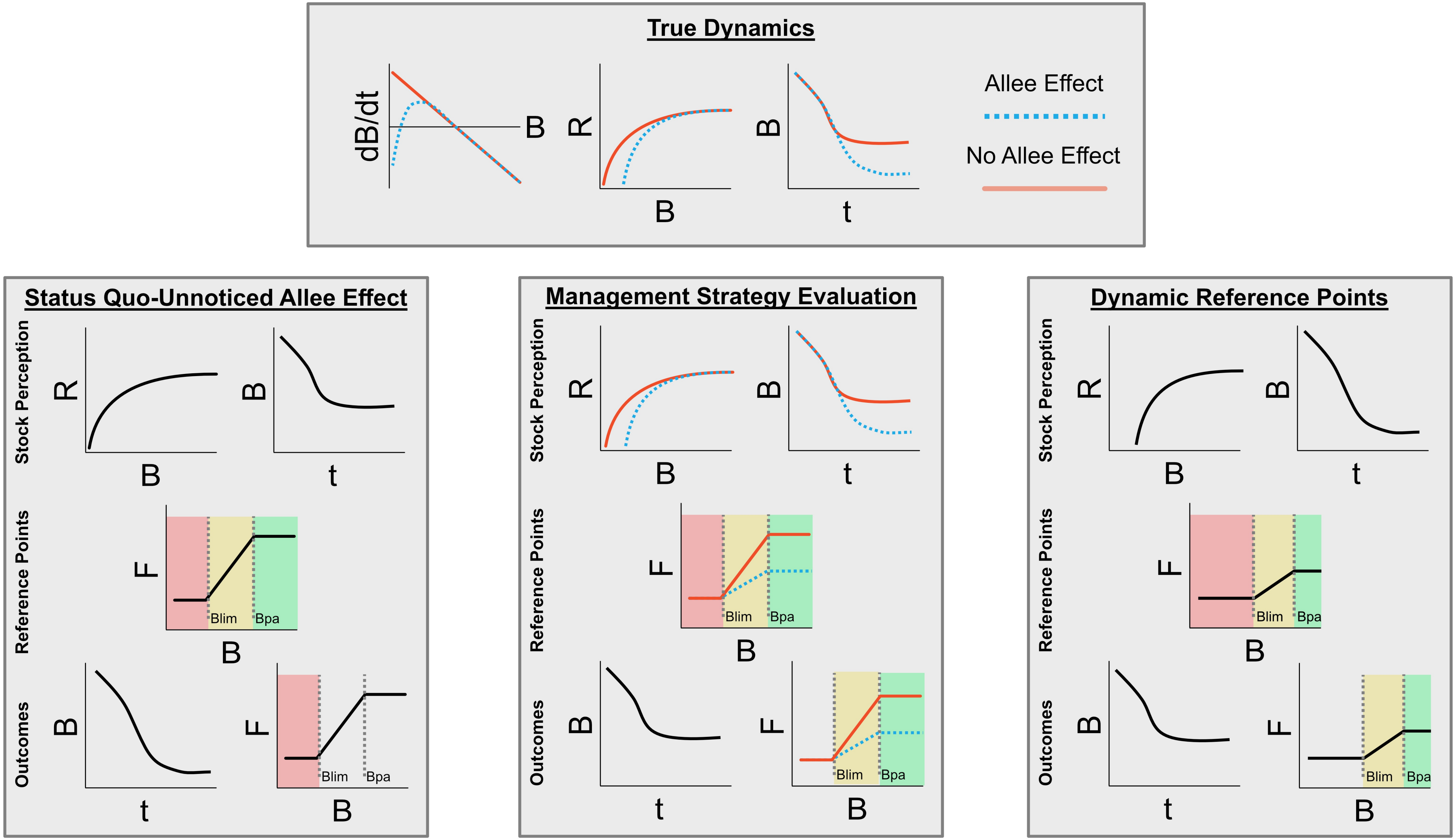
True Dynamics
dB/dt
B
R
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Allee Effect
No Allee Effect
Status Quo-Unnoticed Allee Effect
Stock Perception
R
B
B
t
Reference Points
F
Blim
Bpa
B
Outcomes
B
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Management Strategy Evaluation
Stock Perception
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Dynamic Reference Points
Stock Perception
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Table 1

| | Ghost | Description | Key references |
|---|---|---|---|
| **Population intrinsic** | | | |
| 1 | Truncation of age structure, life history parameters | Occurs when fisheries disproportionately target larger, older fish, leaving populations dominated by younger age classes | Brunel and Piet 2013 |
| 2 | Loss of subpopulations & rescue effect | Overharvesting of locally adapted subpopulations, reducing genetic diversity and allelic richness | Pinsky and Palumbi, 2014 |
| 3 | Reproductively driven Allee effect | Refers to a phenomenon where per-capita population growth decreases as population size declines, known as depensatory population growth | Rowe et al. 2004 |
| 4 | Epigenetics | Phenotypic plasticity allows a single genotype to produce different phenotypes in response to environmental conditions, enhancing survival chances | Hidalgo et al. 2014 |
| 5 | Phenotypic plasticity lost | Represent a form of phenotypic plasticity where environmental conditions experienced during an individual's lifetime can modify the expression or repression of genes | Donelan et al. 2020 |
| 6 | Selection for less intraspecific variation | Occurs when intense fishing reduces the genetic variability within exploited populations, a phenomenon referred to as "Darwinian Debt" | Therkildsen et al. 2019 |
| 7 | Loss of migration memory and social learning | Refers to the transfer of critical information about migration routes, spawning, feeding, and wintering grounds from older, knowledgeable individuals to | Petitgas et al. 2010 |
| **Population extrinsic** | | | |
| 8 | Alternate trophic pathways | Refer to shifts in the trophic structure of ecosystems due to fisheries targeting species at higher trophic levels. | Gårdmark et al., 2015 |
| 9 | Habitat fragmentation and range contraction | Refers to the reduction in the spatial distribution of fish populations as they decline, often observed as a decreased area of occupancy | Shackell et al. 2005 |
| 10 | Predation driven Allee effect | Occur when increased predation mortality at low population sizes exacerbates population decline. | Neuenhoff et al. 2019 |
| 11 | Institutional inertia | Refers to the challenges in achieving sustainable harvests of marine species due to poorly designed governance structures. | Healey, 2000 |
| 12 | Fishery subsidies and socio-economics | Refer to financial contributions that support programs aimed at increasing the profitability or participation in the fishing sector | Sumaila et al., 2016 |
| 13 | Emotional fisheries incentives | Refers to the deep emotional bonds that fishers and fishing communities have to fishing as a way of life, often passed down through generations | Pollnac and Poggie 2008. |

| | Ghost | How changing reference points considers this | How to include in an MSE |
|---|---|---|---|
| **Population intrinsic** | | | |
| 1 | Truncation of age structure, life history parameters | It may be more appropriately considered via the harvest control rule and F reference points | Change in vital rates in a selection of operating models such as maturity ogive, growth rate, maximum size |
| 2 | Loss of subpopulations & rescue effect | Lower Blim and Bmsy in proportion to sub-population loss and contribution to production. F will also need to change | One needs to develop an hypothesis related to the role of subpopulations in total population dynamics and consider how losses are affecting production. This is likely to be quite a speculative operating model |
| 3 | Reproductively driven Allee effect | Depensation type reference points. But if it is ghost and not a large population then this stock is already on the road to extirpation | Hypothesis related to decreased recruitment and perhaps the inclusion of a depensatory stock-recruitment model in the OM suite |
| 4 | Epigenetics | - | - |
| 5 | Phenotypic plasticity lost | large uncertainty buffer | Permanent change in vital rates |
| 6 | Selection for less intraspecific variation | large uncertainty buffer | Decreased variance in sampling distribution for life history parameters. Perhaps a shifted mean as well and consider skewed distributions where only one tail of the distribution has been affected |
| 7 | Loss of migration memory and social learning | - | Size selective harvesting allowing escape or avoidance of large or old individuals in catch |
| **Population extrinsic** | | | |
| 8 | Alternate trophic pathways | Depensatory Blim in all stocks. Include a community limit reference point in addition to single stock points. Consider a functional community reference point (connectivity, trophic energy flow conservation) | change in vital rates |
| 9 | Habitat fragmentation and range contraction | large uncertainty buffer | change in vital rates |
| 10 | Predation driven Allee effect | Large Blim and more aggressive ramp-down in F as stock decreases in size: depensatory Blim | Increasing natural mortality with decreasing stock size, continuous or perhaps best as a step function |
| 11 | Institutional inertia | large uncertainty buffer | Restrict the management procedures to allow only 'stiff' harvest control rules |
| 12 | Socio-economics | large uncertainty buffer | Non-compliance to advice |
| 13 | Emotional fisheries incentives | More aggressive ramp down in F strategy or decreased Flim | - |