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Challenges to fisheries advice and management due to stock recovery

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During the 20th century, many large-bodied fish stocks suffered from unsustainable fishing pressure. Now, signs of recovery are appearing among previously overfished large-bodied fish stocks. This new situation raises the question of whether current fisheries advice and management procedures, which were devised and optimized for depleted stocks, are well-suited for the management of recovered stocks. We highlight two challenges for fisheries advice and management: First, recovered stocks are more likely to show density-dependent growth. We show how the appearance of density-dependent growth will make reference points calculated with current procedures inaccurate. Optimal exploitation of recovered large-bodied fish stocks will therefore require accounting for density-dependent growth. Second, we show how a biomass increase of large-bodied piscivorous fish will lead to a reverse trophic cascade, where their increased predation mortality on forage fish reduces forage fish productivity and abundance. The resulting decrease in maximum sustainable yield of forage fish stocks could lead to conflicts between forage and large-piscivore fisheries. Avoiding such conflicts requires that choices are made between the exploitation of interacting fish stocks. Failure to account for the changed ecological state of recovered stocks risks creating new obstacles to sustainable fisheries management.

Keywords: density dependence, ecosystem-based management, fisheries management, stock recovery

Introduction

The 20th century saw the decline of many fish stocks due to the effects of overfishing. In an attempt to counteract this decline, a great number of measures have since been taken to make fishing more sustainable and prevent future stock collapse. Widespread survey programmes have been set up that provide a wealth of data for scientific advice (e.g. the European Union’s Data Collection Framework), there is an increasing focus on sustainable exploitation in management tools (e.g. harvest control rules) and strategies (e.g. landing obligations), and there is an increasing cooperation between science and industry (e.g. Pastoors, 2016) meant to build trust and integrate the knowledge of fishers and scientists to the benefit of fisheries science and management (Kaplan and McCay, 2004; Hartley and Robertson, 2008). Due to these and other factors, an increasing percentage of ICES-assessed stocks have had their exploitation rate reduced to a more sustainable level (Fernandes and Cook, 2013). This decrease in exploitation rate should result in the recovery of many previously overfished stocks.

For stocks of small forage fish, a biomass recovery would be expected to occur rapidly after fishing mortality is reduced, due to their short generation time. Especially clupeids adhere to this expectation (Hutchings, 2000), aided by them being often targeted by pelagic gear that leaves their habitat intact (Hutchings and Reynolds, 2004).

It takes a longer time for large-bodied fish stocks to recover. We here define large-bodied fish as those whose adult life stages do not rely mainly on planktivory. Large-bodied fish generally...
have a longer generation time, slowing their recovery. Furthermore, they may be caught up by changes in the ecosystem that impede recovery, either through competition (Bundy and Fanning, 2005; Van Leeuwen et al., 2008) or predation (Trzcinski et al., 2006; Cook et al., 2015), with gadoid stocks as a notable example (Hutchings, 2000; Shelton et al., 2006). Despite these challenges, we will provide an indication that large-bodied fish stocks are starting to recover, at least in the Northeast Atlantic waters.

Almost all advice calculations and management approaches have been devised while large-bodied fish stocks were overexploited, begging the question of whether they will still work optimally when those stocks are recovered. Density-dependent growth, for instance, is almost always disregarded when calculating target reference points (e.g. Hilborn and Walters, 1992; Rijnsdorp and Van Leeuwen, 1992). Furthermore, a recovery of large-bodied stocks could trigger far-reaching community responses in the form of reverse trophic cascades, where an increased predator biomass leads to lower prey biomass. This may be especially problematic if it affects commercially valuable prey species such as forage fish.

Against this background we ask whether fisheries management, and its advisory bodies, are fully prepared for a recovery of large-bodied fish stocks. We address this question in three separate sections, each with its own methodology, results, and discussion. In the first section, we show that stocks of large-bodied fish in the Northeast Atlantic are starting to recover. In the second section, we argue how an increase in stock biomass may well make density-dependent reductions in growth more common among large-bodied fish stocks. For example, the absence of fishing during the Second World War led to recovery of several North Sea fish stocks, which resulted in slower growth rates (Margetts and Holt, 1948; Rijnsdorp and Van Leeuwen, 1992). Furthermore, a recovery of large-bodied stocks could trigger far-reaching community responses in the form of reverse trophic cascades, where an increased predator biomass leads to lower prey biomass. This may be especially problematic if it affects commercially valuable prey species such as forage fish.

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Stock recovery

In 2000, Hutchings offered a grim prospect of little to no recovery amongst stocks of large marine fish. Myers and Worm (2003) followed up by concluding that the biomass of large predatory fish stocks had been reduced with 90% when compared with pre-industrial levels. More recently, Fernandes and Cook (2013) provided us with a more positive outlook for stock recovery in the Northeast Atlantic, although they mainly looked at levels of exploitation rather than biomass. Here we use spawning stock biomass (SSB) data from ICES assessments, to look for signs of recovery among stocks of large-bodied piscivorous fish stocks can affect the marine community, and what this would mean for the fisheries that exploit this community. We conclude by summarizing the challenges that stock recovery presents to current fisheries advice and management and suggesting preparatory measures.

Density dependence

Increased stock biomass will lead to stronger density-dependent processes. Generally speaking, density dependence influences three vital rates: reproduction, growth, and mortality. Density dependence within reproduction is usually incorporated in fisheries advice through the use of stock–recruitment relationships. Similarly, density-dependent mortality can also be incorporated in stock–recruitment relationships, if it takes place in the pre-recruit life stage. Cannibalism can for instance be incorporated by a Ricker stock–recruitment relationship, or by changing natural mortality according to stock size, which is for example done for Arctic cod (ICES, 2016b). We can therefore expect that, in future advice, density-dependent changes in recruitment and mortality that arise due to changes in stock biomass will be described fairly well. The same cannot be said about density dependence in growth.

In the past decades, most large-bodied commercial stocks had a biomass that was too low for a noticeable density-dependent growth effect. Nevertheless, increasing evidence shows that marine fish can experience density-dependent growth not only in the pre-recruit phase but also as older juveniles and adults (e.g. Lorenzen and Enberg, 2002; Corman et al., 2016; Zimmermann et al., in press). In adult North Sea placide for instance, van der Sleen et al. (in press) observed both a significant effect of density on growth, and a growth decrease overlapping with the biomass recovery in Figure 1d. Similarly, ICES (2018) finds a negative relationship between biomass and weight-at-age not only for adult
Challenges due to stock recovery

(25 examined stocks. (c) SSB/parametric bootstrap with 1000 samples. (b) Summed-up SSB of all the 95% confidence interval of the mean, as calculated by a non-aeglefinus limanda North Sea plaice, but also for adult North Sea dab (Limanda limanda) in the North Sea, Eastern English Channel, and Skagerrak. (d) SSB/trigger of plaice (P. platessa) in the North Sea. (e) SSB/trigger of hake (M. merluccius), Northern stock.

Figure 1. Recovery of large-bodied stocks in the Northeast Atlantic. The thin dotted lines show the MSY Btrigger reference point, as determined by ICES in 2016. Note that the scales on the y-axes vary. (a) Mean SSB/Btrigger of all 25 examined stocks. The grey area shows the 95% confidence interval of the mean, as calculated by a non-parametric bootstrap with 1000 samples. (b) Summed-up SSB of all 25 examined stocks. (c) SSB/Btrigger of cod (G. morhua) in the North Sea, Eastern English Channel, and Skagerrak. (d) SSB/Btrigger of plaice (P. platessa) in the North Sea. (e) SSB/Btrigger of hake (M. merluccius), Northern stock.

North Sea plaice, but also for adult North Sea dab (Limanda limanda) and adult Georges Bank haddock (Melanogrammus aeglefinus). With stocks of large-bodied fish starting to recover, it is therefore likely that density-dependent growth will become a more prominent process within large-bodied fish stocks, and it should thus be considered when calculating fisheries advice. Density-dependent growth is partly covered by current advice when changes in observed weight-at-age are used to update reference points. However, the process of density-dependent growth is rarely included directly in the calculation of reference points.

We illustrate how density-dependent growth can influence an exploited stock’s yield, biomass, and asymptotic length, by using a population model that is based on Lorenzen and Enberg (2002). The model introduces density-dependent growth into the von Bertalanffy growth equation through a dependency of asymptotic length $L_{\infty,B}$ on the total stock biomass $B$:

$$L_{\infty,B} = L_{\infty,L} - gB$$

where $L_{\infty,L}$ is asymptotic length for $B = 0$ (i.e. without density dependence), and $g$ is a coefficient that determines the reduction in asymptotic length per unit of population biomass (Lorenzen and Enberg, 2002). The other model equations are standard: recruitment is described with a Beverton-Holt stock–recruitment relationship, natural mortality decreases with individual size, and fishing mortality $F$ follows a trawl-selectivity curve (Supplementary Appendix S2). For the coefficient $g = 0$, no density-dependent growth takes place and the model therefore corresponds to a standard age-based fish demographic model.

We show how density-dependent growth can affect the way a fish stock recovers from overfishing, and how this influences both MSY and the fishing mortality and stock biomass at which MSY is obtained ($F_{MSY}$ and $B_{MSY}$, respectively). We do this by running the model with a range of $F$ values for four stocks with identical parameter settings (Supplementary Appendix S2), except for their value of $g$.

Density-dependent growth can influence how a stock recovers from overfishing. After fishing mortality is lowered, stocks that experience stronger density-dependent growth (higher value of $g$) will not have as great of an increase in yield and stock biomass as stocks that experience weaker density-dependent growth (Figure 2a and b). This is because the increased stock biomass reduces $L_{\infty,B}$ (Figure 2c), which in turn slows individual growth, impairing a further increase of stock biomass.

Furthermore, stocks that experience stronger density-dependent growth will have a higher $F_{MSY}$, while MSY and $B_{MSY}$ will be lower. This increase in $F_{MSY}$ is not an unexpected result. An increase in fishing mortality will reduce stock biomass, thereby increasing $L_{\infty,B}$ which in turn will increase individual growth, which increases biomass productivity.

Based on the results from Figure 2, two important consequences of ignoring density-dependent growth in recovering stocks can be identified. First of all, the expected increase in yield and stock biomass that results from reducing fishing mortality may be overestimated. This will lead to unrealistic expectations of recovery and could prevent recognition of when a stock has fully recovered from overfishing. Second, $F_{MSY}$ may be underestimated. If $F_{MSY}$ is set too low, the yield of the fishery will be below MSY, and the fishery will therefore lose out on potential yield. Such an underestimation of $F_{MSY}$ has for instance already been reported for Baltic sprat (Horbowy and Luzeńczyk, 2017).

Figure 2 also provides insight into why, up until now, density-dependent growth has been little observed in marine stocks. The differences among stock $B$, yield, and $L_{\infty,B}$ are small while stocks are overexploited, even though the value of $g$ greatly varies between the modelled stocks. This shows that observations from a
past overfished state are a poor basis for making assumptions on whether or not recovered stocks will experience density-dependent growth.

How, then, can we identify which stocks are susceptible to density-dependent growth, and to what extent? The magnitude of density-dependent growth will likely be highly stock-specific (see, e.g. Lorenzen and Enberg, 2002; van Gemert and Andersen, 2018; Zimmermann et al., in press). Therefore, for most stocks we will simply have to wait for recovery to see whether density-dependent growth is observed. Nevertheless, we can expect that stocks with a larger asymptotic size will be more susceptible to density-dependent growth than those with a small asymptotic size, due to the former’s higher degree of density-dependent regulation in total (Andersen and Beyer, 2015; Andersen et al., 2017). This does not mean that the occurrence of density-dependent growth is limited to only large-bodied stocks, as indicated by, e.g. Northeast Atlantic mackerel (Olafsdottir et al., 2016) and Baltic sprat (Écro, 2012). The existence of density-dependent growth should be taken into account in the advice of both large- and small-bodied fish.

Another consequence of density-dependent growth is how it influences the size-at-entry into the fishery that maximises sustainable yield. Without density-dependent growth, fishery size-at-entry should be at a large size, above size of maturation (Froese et al., 2008), which is the logic supporting most mesh size regulations. However, recent theoretic developments have shown that if there is sufficiently strong density-dependent growth, yield may be maximised by fishing juveniles (Svedäng and Hornborg, 2014; Andersen et al., 2017; van Gemert and Andersen, 2018). Nevertheless, an analysis of three stocks by van Gemert and Andersen (2018) showed that for these stocks the levels of density-dependent growth were not strong enough to make fishing juveniles advantageous for yield maximisation.

The challenge to advisory bodies is to devise a widely-accepted method to estimate and incorporate density-dependent growth into calculations for target reference points. Some advisory bodies, such as ICES, do use updated weight-at-age data in their stock assessments and subsequent reference point estimations. However, this approach still disregards the density-dependent mechanism, and would assess stock productivity according to the most recent growth data. A reduction in individual growth would then be seen as reducing stock productivity, which would result in a reduction of the estimated $F_{MSY}$. However, if that growth reduction were due to density dependence, our results demonstrate that $F_{MSY}$ should be increased instead to relieve part of the density dependence and thereby increase stock productivity. Only updating weight-at-age data is therefore not enough to account for density-dependent growth in stock assessments. Recently an effort to incorporate density-dependent growth in reference point calculations has already been made for Northeast Atlantic mackerel (Scomber scombrus) (ICES, 2015; Pastoors et al., 2015), but more approaches should be developed.

**Reverse trophic cascades**

Fisheries advice is predominantly given from a single-stock perspective. There are a few notable exceptions to this, such as the calculation of natural mortality of most stocks in the North Sea, which takes changes in predator biomass into account (ICES, 2017a). Generally, though, reference points are calculated independently from the exploitation regimes and biomasses of other stocks. In reality however, the changes in exploitation of one stock will influence the vital rates of other stocks, and thereby their reference points, through predation and interspecific density dependence. Food availability of a stock may decrease if exploitation increases on the stock’s main prey, or it might increase instead if exploitation is increased on its main competitor. The main effect, though, is that exploitation changes of a given stock’s
main predator change the predation mortality that the stock is subject to. These dynamics are not limited to the interactions between a few stocks, but can reverberate throughout the ecosystem as trophic cascades (e.g. Daskalov, 2002; Daan et al., 2005; Frank et al., 2005).

Trophic cascades are often described as resulting from a removal of large-predator biomass (e.g. Schmitz et al., 2000; Myers et al., 2007), and there are well-documented examples where the overexploitation of large-bodied predatory fish stocks has resulted in such trophic cascades (e.g. Frank et al., 2005; Casini et al., 2008; Altieri et al., 2012). However, now that the stocks of large-bodied fish appear to be recovering in the Northeast Atlantic, we can expect to see a reversal of this process in the form of reverse trophic cascades.

We illustrate a reverse trophic cascade with an existing community size spectrum model (Andersen et al., 2016). The model has previously been used to simulate direct trophic cascades (Andersen and Pedersen, 2009) and interactions between fisheries of different components of the fish community (Houle et al., 2013; Andersen et al., 2015). The model resolves all species in a community with asymptotic weights ($W_{\infty}$) in the range of 4 g–100 kg. Both inter- and intraspecific density dependence are incorporated in the form of predation/cannibalism and competition for food, according to the mechanism of “big eats small”.

We applied two different types of exploitation regimes to the community (Figure 3a) and observed how fishing impacted the SSB and natural mortality of each stock. The first exploitation regime is one of “high $F$”, where fishing mortality is allocated according to a trawl selectivity curve, with a mean fishery size-at-entry of 0.05 $W_{\infty}$ (Andersen et al., 2016). A third exploitation regime, without fishing, was used as a baseline for comparison.

The “high $F$” exploitation regime results in a clear trophic cascade when compared with an unfished system (compare dashed and dotted lines in Figure 3), as would be expected. Large-bodied fish stocks with a high trophic level become severely depleted, causing the small-bodied fish stocks at a lower trophic level to increase in SSB substantially above their unfished SSB due to reduced predation (panel b). Changing from “high $F$” to “low $F$” in turn triggers the expected reverse trophic cascade in the community (solid lines). Large-bodied fish stocks become more abundant, which increases predation mortality on the smaller-bodied prey species. As a result, these small-bodied stocks decrease in SSB.

The simulations reflect the typical development in fully exploited marine ecosystems: when large-bodied piscivorous fish stocks are overfished, forage fish stocks will have a higher productivity due to a reduced predation mortality. This higher productivity facilitates the development of highly profitable forage fisheries. An extreme example of this effect occurred in the East China Sea, where the near-obliteration of larger-bodied fish stocks lead to a large increase in biomass yield of small-bodied fish (Szuwalski et al., 2017).

When large-bodied stocks have recovered, the higher predation mortality on forage fish stocks will also reduce the $F_{\text{MSY}}$ reference point of forage fish stocks. If this reduction in $F_{\text{MSY}}$ is not recognized by the advice, the stocks of forage fish will become overexploited. Therefore, a situation with recovering large-bodied piscivorous stocks requires that reference points of their prey species are frequently updated to reflect the continuous changes in predation mortality. Failure to take a more dynamic approach to calculating the reference points of forage fish stocks will lead to increased risk of their overexploitation and collapse.

A continued recovery of large piscivorous fish stocks may also lead to conflicts between fisheries. Whereas fleets that target large piscivorous fish will welcome the recovery of these stocks, fleets...
targeting forage fish should ideally like to see a return to a situation with depleted large piscivorous fish stocks and the associated higher productivity of their forage fish stocks. Forage fish fleets may see a lesser return, or no return at all, on their investments if forage fish productivity were to decrease. A reverse trophic cascade as a result of large-piscivore stock recovery may therefore lead to conflicts between the fisheries of forage fish and large piscivorous fish.

The potential conflict between fisheries needs to be addressed by regulatory bodies. A first step is simply to acknowledge the conflict. The next step is to set a desired exploitation state for the ecosystem. Formulating such a desired exploitation state will require quantifying the magnitude of interdependence of the system’s fish stocks, both in terms of biomass production and economic rent (Ravn-Jonsen et al., 2016). This will require a fair degree of biological knowledge on the ecological interactions within the given ecosystem and how these are affected by exploitation, as well as economic knowledge on how different exploitation regimes translate into financial returns. If such knowledge is available, the regulatory body can then start to define their desired ecosystem state and the associated exploitation regimes.

Setting a desired exploitation state should include stakeholder participation. However, as previously shown, not all stakeholders will be affected positively by such a new exploitation state. The concept of fairness plays a large role in determining fisher compliance with regulations (Jentoft, 1989), and negatively-affected fishers will be unlikely to voluntarily agree with new regulations without some form of compensation for their reduced revenue, for instance in the form of subsidies. Obtaining compliance using enforcement is possible, but carries its own economic cost. More importantly, the punitive measures associated with stronger enforcement could come at the cost of a reduced perception of legitimacy of the regulatory body, especially if the regulations are perceived as unfair.

Conclusion

Undoing the consequences of decades of unsustainable fishing has been one of the major goals of fisheries management in recent years. As a result, signs are now appearing that large-bodied stocks are recovering from overfishing. We have identified three actions needed to prepare for a future with recovered stocks of large-bodied fish: (i) Density-dependent growth must be explicitly considered in stock assessments, reference point calculations, and management strategy evaluations. (ii) Reference points must be dynamically updated, to include the community changes that result from a reverse trophic cascade. (iii) The possible conflict between fisheries of forage fish and those of large piscivorous fish resulting from a reverse trophic cascade should be addressed: decision makers need to be aware that management actions can favour some fisheries whilst hurting others, and make appropriate decisions based on this information. Ignoring the challenges that arise due to the recovery of large-bodied stocks could jeopardize one of the major success stories of recent fisheries management.

Supplementary data

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

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Challenges due to stock recovery


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