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Wageningen University &  
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Wageningen Marine Research



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Client: Ministry of Agriculture, Nature and Food Quality  
Attn.: Mw. E. Smith  
Postbus 20401  
2500 EK Den Haag

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# Samenvatting

Er bestaat al enige tijd het vermoeden dat de afnemende groei van schol wordt veroorzaakt door toegenomen concurrentie tussen de vissen, die wordt versterkt door de grote aantallen in het bestand (zogenaamde dichtheids-afhankelijke groei). Als de toename van het aantal schollen hun groei remt, dan kan ook het omgekeerde effect ontstaan: door de aantallen te verlagen, groeien de overgebleven vissen harder. Als dit effect belangrijk is kan het vangstverlies aan maatse vis door bijvangst van ondermaatse schol kleiner zijn dan verwacht, of zelfs helemaal omkeren, zodat meer bijvangst leidt tot meer vangbare schol later. In dat uiterste geval zou het voorkomen van sterfte van ondermaatse vis leiden tot minder, in plaats van meer vangbare schol.

Om dit te onderzoeken hebben we een nieuw ontwikkelde statistische methode ingezet, waarmee we duidelijk een aan de aantallen gerelateerde groeisnelheid vinden voor schollen tussen 17 en 27 centimeter. Precies de grootteklasse van de ondermaatse bijvangst dus. Voor de andere maten vonden we dit niet. De gevonden relatie hebben we gebruikt in een model wat erg lijkt op dat waarmee referentiepunten voor de visserij, zoals Fmsy en Blim, worden bepaald door ICES. Met dat model hebben we vervolgens gekeken wat het effect op de vangst is, wanneer de overleving van ondermaatse schol wordt verhoogd of verlaagd ten opzichte van de huidige overleving.

We vinden een beperkt effect van het hierboven beschreven mechanisme. Als we doen alsof er geen relatie is tussen groei en aantallen (de huidige praktijk) en we zetten de bijvangst van ondermaatse schol helemaal op nul, dan vinden we voor de huidige visserij een toename in de vangst van ongeveer 17.5% ten opzichte van de voorspelde vangst met de huidige overleving van ondermaatse bijvangst. Wanneer we de gevonden relatie tussen aantallen en groei gebruiken, is deze toename ongeveer 11.5%. De verwachting is dus nog steeds een hogere vangst dan nu, als geen ondermaatse bijvangst meer plaatsvindt, maar het voordeel is niet zo groot als tot nog toe aangenomen.

De sterkte van de relatie tussen groei en aantallen varieert in de tijd. Omdat die relatie sterk bepalend is voor de uitkomsten die we hier vinden, is het belangrijk deze ook in de toekomst te blijven meten. Zo houden we zicht op de uiteindelijke effecten van maatregelen zoals de aanlandplicht, en uitzonderingen daarop.

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# 1 Introduction

The models used to calculate thresholds and reference points for the management of exploited fish stocks generally assume that growth of individuals after recruitment does not depend on the abundance of these individuals, the availability of resources or other environmental factors. Commonly, the models used are age-structured, and a fixed age-weight relationship is used to determine stock biomass from numbers at age. This assumption has been questioned (Lorenzen and Enberg 2001), but it has been argued that density-dependent individual growth is irrelevant when stocks are far below their maximum abundance, which would be the case under intensive harvesting.

More recently however, density dependent individual growth in post-recruit size and age classes has been shown to be common in harvested fish stocks (Zimmerman et al, 2018; Rindorf et al, 2022). The recency of this observation could be the result of the rebuilding of many fish stocks in the last decades (Cook and Fernandes, 2015), but this hypothesis remains untested.

It has been demonstrated that such late in life density dependent individual growth has important consequences for fisheries yield, as well as the occurrence and location of reference points like Maximum Sustainable Yield (Lorenzen and Enberg, 2001; Horbowy and Luzencyk, 2017; van Gemert et al, 2018; Croll et al, 2023). Despite its common occurrence and the consequences for fisheries and fisheries management, density-dependent growth has to date not been incorporated into stock management and stock assessment procedures (Rindorf et al, 2022).

Density dependent growth can be very important in the management of exploited stocks. It introduces a compensatory mechanism, where increased individual growth at low abundance compensates for some of the biomass lost to fishery (Lorenzen and Enberg 2001). The strength of this mechanism depends strongly on the size selectivity of the fishery (van Gemert et al). Here, we show how the phenomenon affects the potential consequences of one of the largest changes in recent fishing regulations in the European Union, implementation of the landing obligation (EU, 2013). The landing obligation stipulates that all catches count towards the quatum for that stock, irrespective of the size of individuals, and must be landed. Discarding of undersized fish at sea for stocks for which there are quota is no longer allowed. However, exceptions for certain species are allowed if it can be shown that survival of discarded undersized individuals of that species in a specific fishery is sufficiently high. The objective of the landing obligation is to provide a strong incentive for the fishery to become more size-selective and avoid catching undersized individuals. This would reduce the mortality of undersized fish, which is perceived as wasteful and inefficient. On the short term, while innovations for more selective fishing practices are not yet available, the obligation to land all undersized fish could in fact increase their mortality because for many species, at least some individuals survive the catching, handling, and discarding process (van Beek et al, 1990; Depestele et al, 2014; Van der Reijden et al, 2017). For plaice caught with beam trawls in the North Sea, survival is sufficiently high that a survival-based exception is in place.

We study the effects of both these phases of the landing obligation on the North Sea plaice (*Pleuronectes platessa*) stock. This is one of the largest flatfish stocks in the North Sea, and is important to a variety of fishing communities, across countries and fishing methods (ICES, 2023). Plaice has a history of high undersized discards, because it is caught in the small-mesh sole fishery. The first assessments of density-dependent growth in North Sea plaice show density-dependent individual growth up to ~25 cm, but not for larger individuals (Rijnsdorp and van Leeuwen, 1992; 1996). A later analysis found no evidence for density-dependent individual growth (Lorenzen and Enberg, 2001). Interestingly, the first analyses included a period when the plaice stock was large and fishing mortality relatively low, and the later analysis used data including the 1980's and 1990's, a period of intensive fishing and small stock size. The North Sea plaice stock has grown strongly since ~2005, and two recent analyses using data including the post-rebuilding period find clear density-

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dependent individual growth in the North Sea plaice stock (Zimmerman et al, 2018; Rindorf et al, 2022).

We use weight at age data from fishery-independent surveys to estimate the environmental growth limitation over time, which we relate to stock abundance to obtain a relationship between individual growth and stock size. We then implement that relationship in a size-structured population model using a density-dependent version of Von Bertalanffy growth. Using that model, we explore the implementation of the landing obligation. We start by assuming an empirically derived fishery size selectivity, including discarding of undersized fish. We vary the survival from no survival up to complete survival. No survival is when the landing obligation would be strictly imposed, without exception, while fishery would continue without any other changes to selectivity. Complete survival of undersized bycatch, which is equivalent to no undersized bycatch, reflects what could be seen as the original idea behind imposing the landing obligation: to completely prevent the fishing mortality on undersized fish. The trajectory between these extremes indicates how the expected landings change, dependent on bycatch survival. This predicts the effect of an exception to the landing obligation for any value of the discard survival, on the landings of the fishery. We compare this result with and without density-dependent growth, to understand the strength of its effect on landings at each possible discard survival fraction.

The Von Bertalanffy growth model we use, extended to include a density-dependent factor in the maximum length, is a common way to model fish growth and population dynamics, and hence we expect our results to hold for many species where density dependent growth beyond very small sizes is relevant.

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## 2 Methods

### 2.1 Analysis

The goal of our analysis here is to understand how density-dependent growth affects the relationship between discard survival, stock size and yield in the North Sea plaice population. The analysis breaks down into several steps:

1. Based on survey data, estimate the change in growth of plaice over time.
2. Relate the changes in growth to changes in abundance of plaice.
3. Use the relationship from 2. in a population model and use that model to simulate the effects of undersized bycatch survival on yield and stock size.
4. Relate the outcome of 3. to a model with fixed growth (no relationship between growth and abundance).

Below we describe this process in more detail.

### 2.2 Survey data

We used survey data from the Beam Trawl Survey (BTS). This is an annual survey using a beam trawl similar to that used in commercial fisheries, which is specifically designed to survey plaice and sole. The survey covers the entire North Sea and has been conducted in its current form since 1996. It is carried out in August-September each year. Each sample consist of the catch of a 30-minute trawl at a fixed speed. The catch is then sorted by species, and the length of all plaice individuals is determined. A length-stratified subsample of plaice is then weighted and aged. Using the net width, haul duration and the vessel speed, a catch per unit effort (CPUE, # of individuals/m<sup>2</sup>) is calculated for each sample and length group (see below), which we use as a proxy for the local abundance of plaice. This data was obtained from ICES (Database on Trawl Surveys (DATRAS), 2023). Because we are interested in processes governing the plaice population development in recent years, we restrict our analysis to data from 2000 onwards. We have tested our analysis also with the full data set and found only marginal differences.

### 2.3 Estimation of growth rate

To estimate the growth rate of plaice, we used the VBGFIT R package (Croll and van Kooten, 2022). This package contains a method to fit a von Bertalanffy growth function to size-age data. It can do so for the entire stock at once, or separately for different size- or age groups within the stock. Because differently sized plaice have different diets and different spatial distribution in the North Sea, we split the population into several size groups: <17 cm, 17 to 27 cm, 27 to 37 cm and >37 cm. The smallest group are generally found closer to the coast and the commercial gears have low catchability for this size range. The 17-27 group make up the bulk of the discarded size group. The gear is suitable to catch them, they occur together with the next larger group (27-37 cm), which form the majority of the catches, but they are below the minimum landing size. The largest group are individuals which the gear catches well, except that the bulk of these large and old individuals occur nowadays in a geographical range (in the northern North Sea off the coast of Scotland) where not much fishing occurs (ICES, 2022). While this distinction is loosely based on diet and spatial distribution, it is somewhat arbitrary. However, we tried many different size groupings, and the results of our analysis were highly similar. The von Bertalanffy growth equation (1) is used routinely in fishery management to conduct for example the simulations to determine reference points such as  $F_{MSY}$ . It describes the change in length ( $L$ ) of an individual of age  $a$ , and has the following form:



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$$\frac{dL}{da} = K(L_{\infty} - L) \quad (1)$$

It takes as parameters  $L_{\infty}$ , the length which an individual ultimately reaches and  $K$ , a parameter which scales the change in the effect of current individual length  $L$  on growth. The parameter  $L_{\infty}$  affects both the growth rate at a given size  $L$  (because smaller  $L_{\infty}$ , decreases the value of  $(L_{\infty} - L)$ ), but also determines the maximum size (when current length  $L$  equals  $L_{\infty}$ , the right-hand-side of equation (1) becomes zero and growth stops).

Generally,  $L_{\infty}$  is assumed to be constant in fisheries applications. However, the value of  $L_{\infty}$  is ultimately determined by the environment. In a low-food environment, individuals are more likely not to find enough food, grow more slowly and attain a smaller maximum size.

For each year, the fitting procedure in VBGFIT estimates the environmental limitation of a fixed physiological maximum  $L_{\infty}$  for each year and each size group in the model, based on the observed growth from year to year in the survey data. The maximum value of this environment-corrected  $L_{\infty}$  is 780 mm, the maximum size based on physiological limitations of plaice (van der Veer et al, 2001). It simultaneously fits a value for the parameter  $K$ , but this value is independent of time or size group. The fitted values of environment-corrected  $L_{\infty}$  can be taken as an estimate of the environmental quality experienced by individuals in each size group that year.

## 2.4 Relating growth rate to stock size

In this study, we are not just interested in the variation of growth over time, but in the relationship between this growth and the stock size. The hypothesis is that part of the variation in growth is caused by competition for food or space, which becomes more intense when the plaice stock is large and/or concentrated in a smaller spatial extent, resulting in slower growth and smaller individuals at high plaice abundance. To study the presence of such a relationship, we relate the  $L_{\infty}$  values which are produced by the fitting procedure to the stock abundance, as indexed by the Catch Per Unit Effort in the survey data for the same size groups as used for the von Bertalanffy parameter fit.

The size-specific CPUE is the measure of stock abundance most directly related to the fitted values of  $L_{\infty}$ , since they are derived from the same data set. However, for our population model, we need a relationship between population size itself, and not an index thereof. Therefore, for each size group where we find a relationship between CPUE and  $L_{\infty}$ , we relate  $L_{\infty}$  to the stock abundance as estimated in the ICES stock assessment report (ICES, 2023). We search for the combination of age-specific stock biomass which gives the best-fitting linear relationship with  $L_{\infty}$ .

## 2.5 Population model

We use a cohort-based population model, running in the Escalator Boxcar Train framework (de Roos, 1988), built in the EBTTOOL software (de Roos, 2023). We simulate an annually reproducing plaice population, with a size-dependent natural mortality function identical to that assumed in the ICES stock assessment for plaice (ICES 2022; 2023). We use an empirically derived size-based fishery selectivity function, which covers both the undersized mortality (bycatch) and landings. Growth of each year-class follows the von Bertalanffy growth function, with fixed growth rate  $K$  and  $L_{\infty}$  either fixed or linearly dependent on a measure of stock size, as derived from the fitting procedure. We model the same part of the fish population which is used in the stock assessment, assuming that fish enter the stock at age 1 and a length of 140 mm, approximately corresponding to the long-term mean length converted from weight at age 1 used in the stock assessment. To determine the recruitment to the one-year-old cohort, we use the same stock-recruitment relationship used in the North Sea plaice

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stock assessment, which assumes a linear increase in recruitment from zero to  $3e^9$  individuals for an SSB between zero and  $3.41e^{11}g$  (or 341000 tonnes; ICES, 2022).

The model keeps track of daily landings and undersized discards, and we can vary the fraction of undersized discards which survives the fishing process.

To analyse the effects of harvesting and undersized bycatch survival, we use simulation-based equilibrium analysis. This means that we run the model for a long time ( $\sim 50$  years), then look at the population state in the last period ( $\sim 20$  years), when the system has reached equilibrium, meaning that it shows the same dynamics from year to year. We then take the last state (the output at the end of year 50), change the parameter under study by a small amount, and rerun the simulation. By plotting the end state of the model against the value of the parameter under study, we obtain insight into the ultimate effect of the parameter on the stock state. This procedure is similar to that used to determine  $F_{MSY}$  for stock assessments.

## 3 Results

### 3.1 Dynamics of $L_{\infty}$

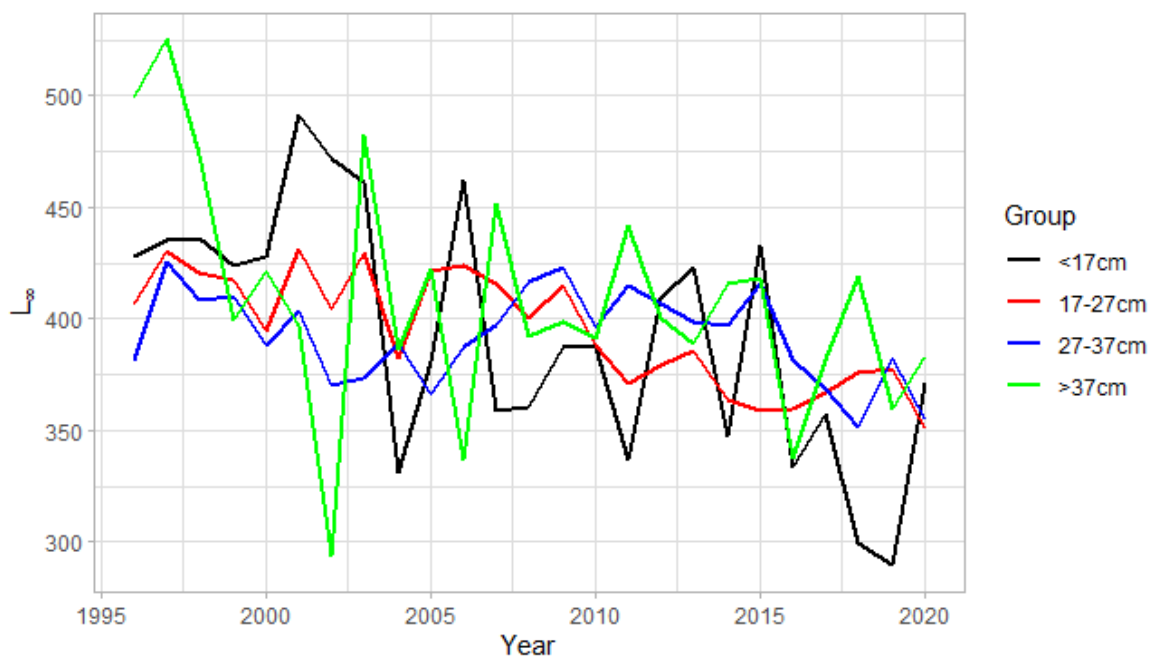


Figure 1: Environmental limitation as expressed in asymptotic maximum size ( $L_{\infty}$ ) over time for the four size groups used in the statistical model.

The output from the VBGFIT procedure shows that the realized  $L_{\infty}$  is approximately half of the theoretical maximum for all size groups, indicating strong environmental limitation (Figure 1). There appears to be a slight increase in the degree of environmental limitation (toward lower values of  $L_{\infty}$ ) over time for all size groups. Although there is year-to-year variation between groups, no differential trend among groups is visible.

### 3.2 Density dependent growth

We found a clear and highly significant negative correlation ( $R=-0.75$ ,  $p<1\times 10^{-4}$ ) between  $L_{\infty}$  and catch per unit effort in the survey data for the size group 17-27 cm, but not for the other groups (Figure 2). This correlation indicates that  $L_{\infty}$  is lower when survey CPUE (and hence stock size) is higher, indicating density-dependent growth of individuals in that size range.

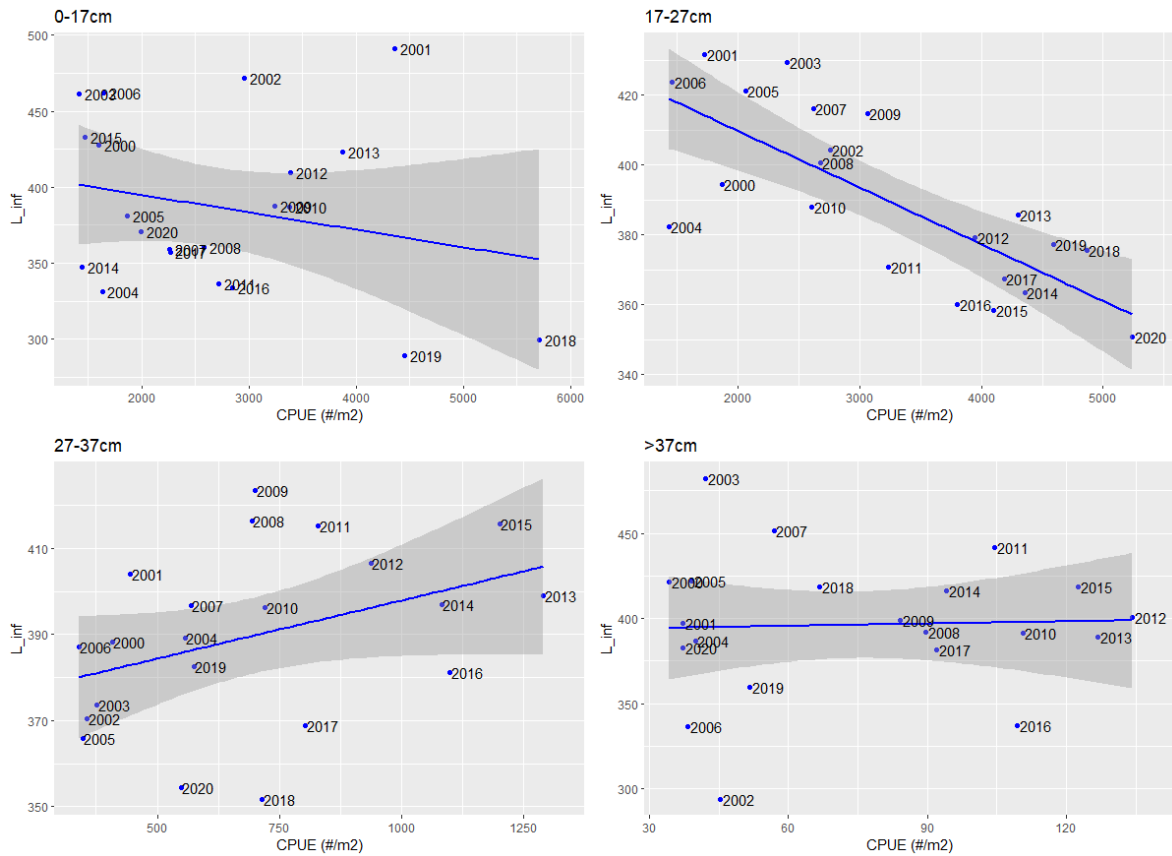


Figure 2: Effect of CPUE (numbers per square meter seafloor trawled) on the  $L_{\infty}$  ( $L_{\infty}$ , mm) of four plaice size groups in 2000 to 2020. Individual points are annotated by the observation year. Blue lines indicate linear regressions and shaded areas indicate 95% confidence limits. The regression is significant only for the 17-27cm group.

We tested how CPUE in the survey is related to SSB of various age groups in the stock assessment timeseries. A good fit was found between the CPUE of individuals in the 17-27 cm group and the total biomass of age 3 and older individuals in the stock ( $R=0.67$ ,  $p<1^{-3}$ ). We fitted a linear relationship between  $L_{\infty}$  and the biomass of age 3+ individuals in the stock (Figure 3). We found a significant negative linear relationship:  $L_{\infty} = 439 - 1.646E-8 \cdot \text{biomass\_age\_3+}$  ( $p<1e^{-3}$ ,  $R^2=0.64$ ).

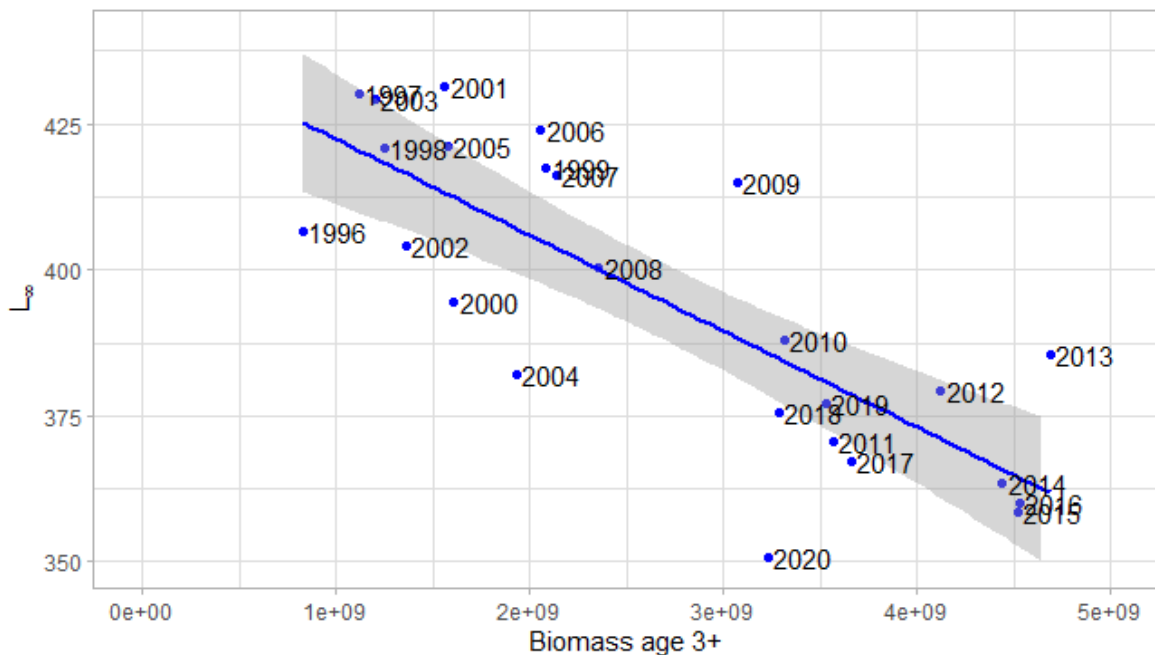


Figure 3: Relationship between the fitted  $L_{\infty}$  (in mm) values for individuals between 17 and 27 cm in the survey data and the biomass (g) of age 3 and older individuals in the North Sea plaice stock as reported in the ICES stock assessment. The drawn line is a linear regression, shaded areas indicate the 95% confidence interval.

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### 3.3 Effects of fishing

The VBGFIT package returns, for each size group, a growth rate parameter  $K$  and an annual estimate of  $L_{\infty}$ . The growth rate parameter was similar for all groups, and varied around 0.0008 per day, which we used for all plaice, independent of size. For plaice individuals between 17 and 27 cm, we used the relationship between the biomass of individuals age 3+ and  $L_{\infty}$  as stated in 3.2 above, which means  $L_{\infty}$  equals 439mm when the biomass would be zero, and declines to 373mm when the biomass reaches 4.5E9 g, which is approximately the highest value in the stock assessment time series (Figure 3). A lower  $L_{\infty}$  means growth is slower, which occurs at high total biomass of age 3+ individuals. For all other plaice individuals, we used a  $L_{\infty}$  of 390mm which approximates the mean of the VBGFIT estimates.

To study how undersized discard survival and density dependence affect stocks and landings with varying fishing mortality, we compare two extreme scenarios: zero discard survival and 100% discard survival, with and without density dependence. Zero discard survival would be a situation where the landing obligation is perfectly enforced, but there is no change in fishing gear or strategy. A 100% survival on the other hand is a situation where plaice below the legal size suffer zero fishing mortality. This could be interpreted to represent the zero-discard state which was the idea behind developing the landing obligation. While these extremes do not reflect reality, with many exceptions to the landing obligation in place, they are useful to understand the possible outcomes. In general, landings with density-dependent growth are higher for given fishing mortality compared to the non-density dependent equivalent (compare left and right hand side panels of Figure 4). The results also clearly indicate that zero discard mortality lead to much higher landings, with and without density-dependent growth, and that the effect of discard survival on landed biomass of fish above the legal landing size limit (compare plots between upper and lower row in Figure 4; Figure 5) is much greater than the effect of density-dependent growth (compare plots in left and right columns of Figure 4; Figure 5). Complete discard survival leads to a population which can sustain an almost four times higher harvesting mortality before collapsing. At low harvesting rates ( $<0.0005$  1/d in the model), the patterns in SSB and annual landings appear similar for all cases: SSB decreases exponentially, and landings as well as discards (where relevant) increase rapidly. At higher harvest rates, the effect levels off but catches are still increasing. The effect of density-dependent growth is to shift the maximum sustainable yield (the highest point of the red curve in Figure 4) to higher harvesting mortality and higher annual catches.

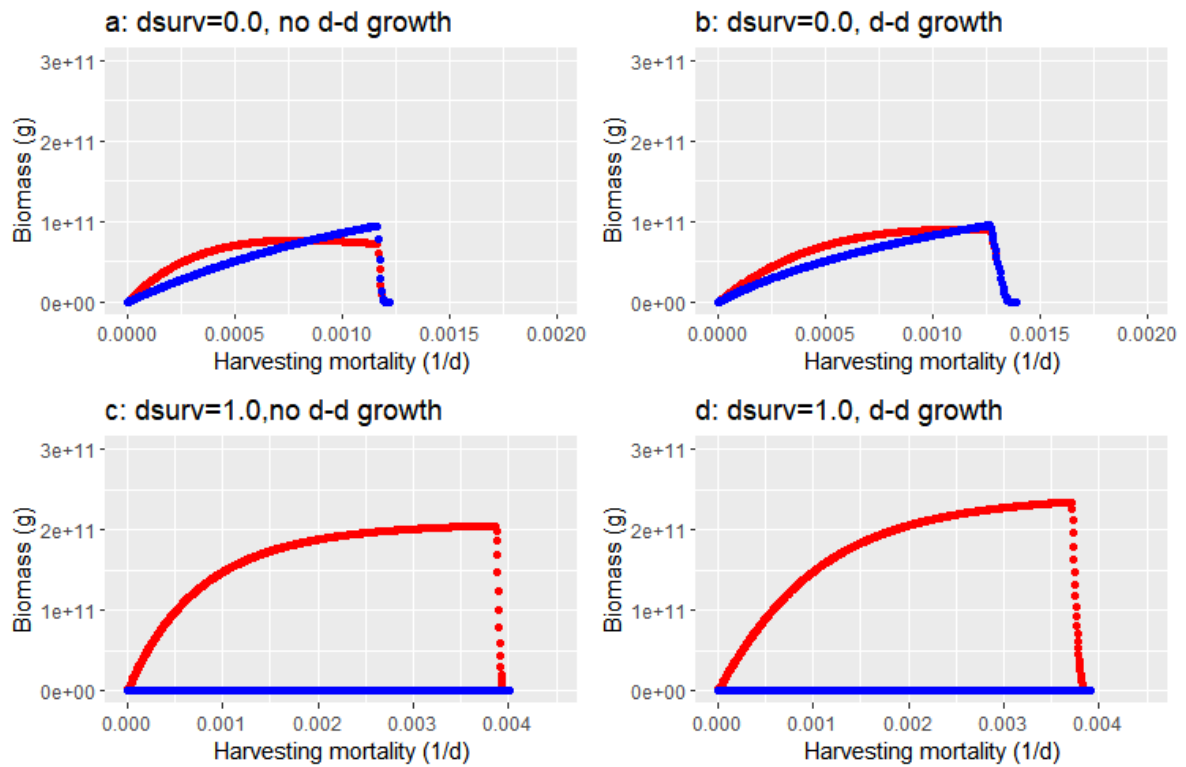


Figure 4: Effects of density dependence and discard survival on equilibrium annual landings (red) and discards (blue) with varying harvesting mortality. Left hand panels (a, c) are without density-dependent growth, right hand panels (b, d) are with density dependent growth. In the top panels (a, b) no discards survive, in the bottom panels (c, d) all discards survive.

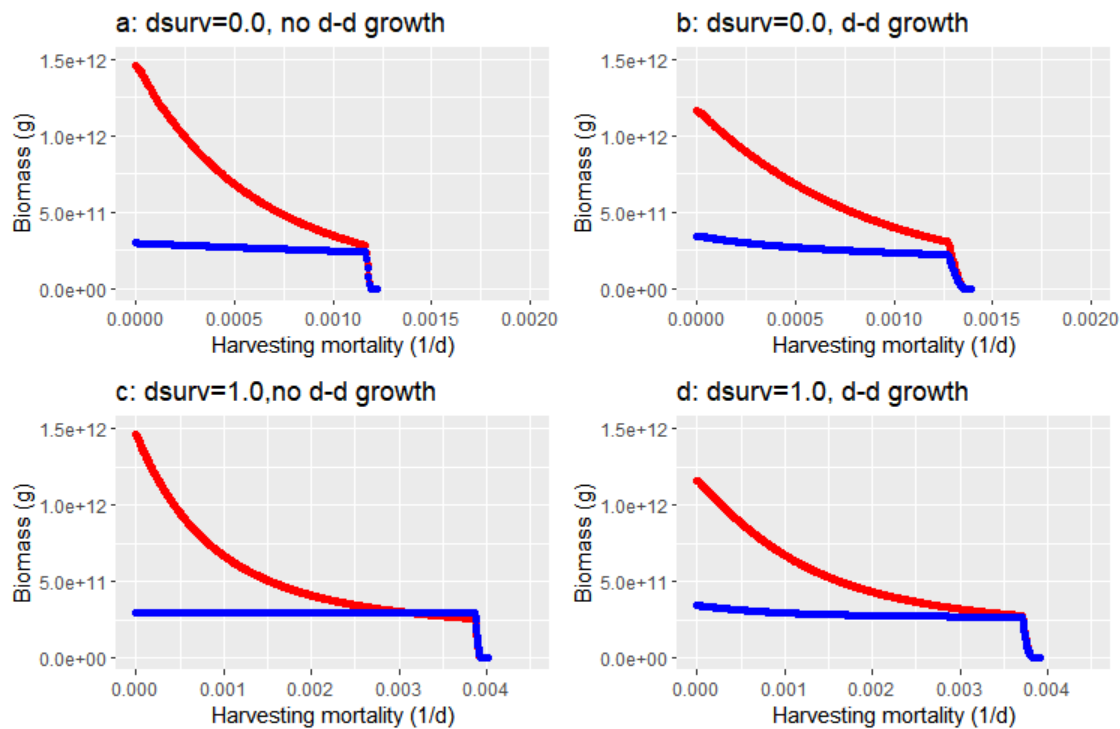


Figure 5: Effects of density dependence and discard survival on equilibrium SSB (red) and juvenile stock biomass (blue) with varying harvesting mortality. Left hand panels (a, c) are without density-dependent growth, right hand panels (b, d) are with density dependent growth. In the top panels (a, b) no discards survive, in the bottom panels (c, d) all discards survive.

To compare the effect of density-dependent growth on the catches with and without density-dependent growth, we calculated the equilibrium annual catches, for the entire range of discard survival from 0 to 1 (or 100%). We did this for a fishing mortality of 0.085 per year (or  $2.3 \times 10^{-4}$  per day), corresponding to that calculated from the current fishery (ICES, 2023), and both with and without density-dependent growth (Figure 4). To be able to compare the results to the current situation, we first calculated the relationship between discard survival and annual landings with density-dependent growth, and then extracted the  $L_{\infty}$  at discard survival of  $\sim 0.15$ , which approximates the current situation with the derogation from the landing obligation. We then used this  $L_{\infty}$  as fixed maximum length in the calculation without density dependence for individuals between 17 and 27 cm length. By doing so, we ensure that the landings in the current situation (with a landing obligation exception based on a discard survival of 15%) are identical with and without density dependent growth (Figure 6).

Increasing discard survival from zero to one always increases landings, irrespective of density dependence. However, we see that with density dependence, the increase is less steep than without. This is the compensatory effect of density dependence: higher discard survival means higher abundance of small individuals, which in turn means slower growth, which ultimately translates into a reduction in catches. The difference between density-dependent and density-independent growth (Figure 7) increases as discard survival increases. When growth is density-dependent, complete elimination of all undersized discards would lead to 11.5% higher landings, while without density-dependent growth this increase is 17.5%. The net effect of density-dependence is hence a 6% lower gain in catches than under density-independent growth. Zero survival would lead to slightly lower catch loss than with density-independent growth. The results shown here for catches are very similar for SSB (results not shown).

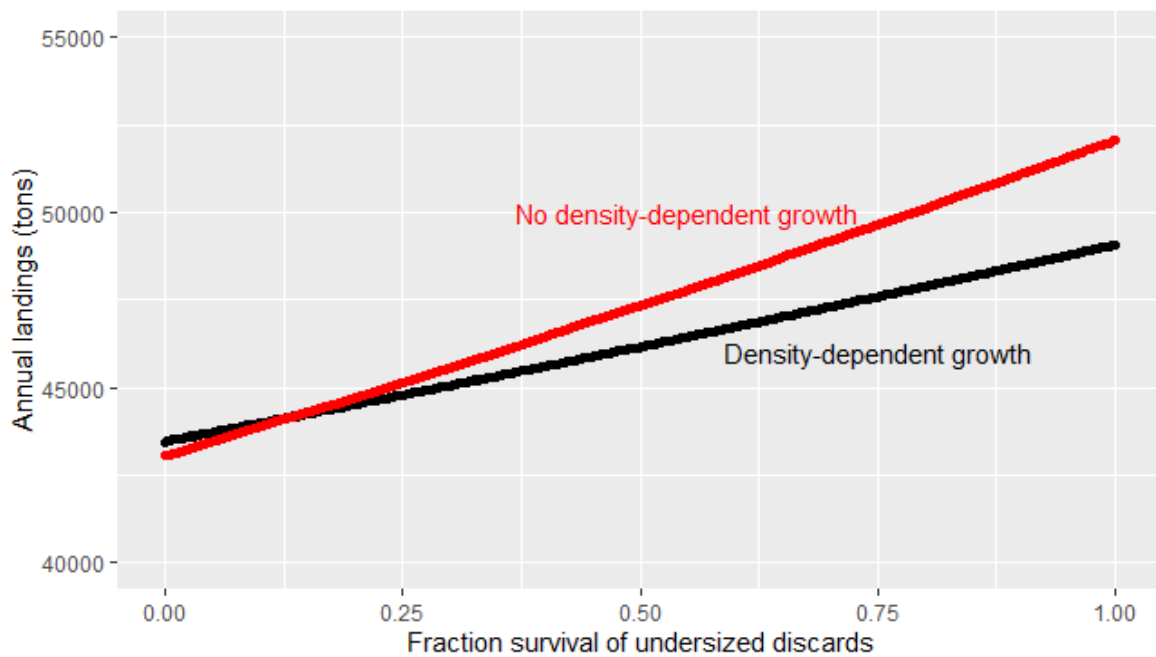


Figure 6: Annual landings as a function of undersized discard survival with (black) and without (red) density-dependent growth. For the density-independent case we used  $L_{\infty}=372\text{mm}$ , which corresponds to  $L_{\infty}$  in the density-dependent model at a discard survival of  $\sim 0.15$ , the current situation. As a result, the models produce identical catches at that value of discard survival.

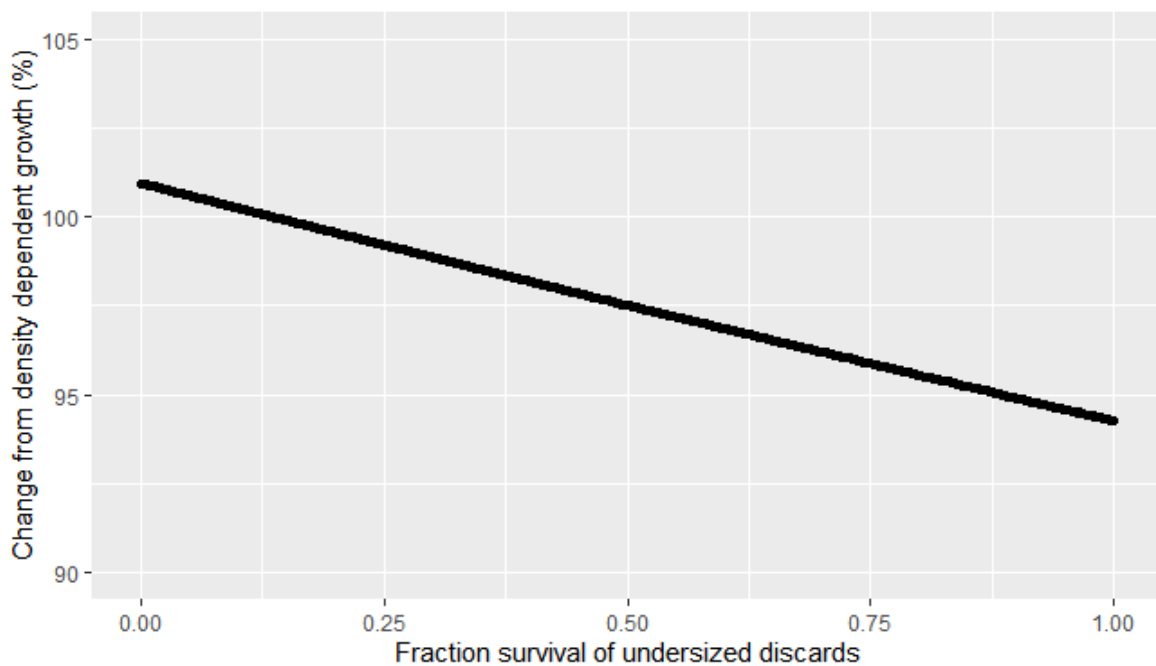


Figure 7: Catch with density dependent growth as a percentage of catches without density-dependent growth. A value over 100% implies higher catches with density-dependent growth, a value below 100% means catches are lower for density-dependent growth than for density-independent growth. Actual catches shown in Figure 6.



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## 4 Discussion

We have used fishery-independent survey data to estimate the strength of density-dependent growth of North Sea plaice (*Pleuronectes platessa*). Density-dependent growth has the potential to reverse (from a positive to a negative effect) the relationship between undersized discard mortality and Spawning Stock Biomass (SSB), as well as landings, because the 'thinning' effect of undersized mortality causes the remaining individuals to grow faster and to larger sizes. We found clear evidence of density-dependent growth in the size range between 17 and 27 cm, where most of the undersized discarding of plaice occurs. We used the found relationship between growth and density in a population dynamical model to study how it changes the effect of undersized discard survival on SSB and landings. We found that the empirical relationship between growth and SSB was not strong enough to reverse the effect of undersized discard survival on SSB and landings, but it did reduce the positive effect of discard survival on catches by a maximum of ~6%.

### 4.1 Dynamics of $L_{\infty}$

Using plaice data from the Beam Trawl Survey, which is conducted each 3<sup>rd</sup> quarter throughout the North Sea, we estimated the temporal changes in  $L_{\infty}$ , which we defined as the environment-mediated maximum size that individuals can reach. We determined this parameter for a number of size groups, roughly corresponding to 'not affected by the fishery' (0-17cm), 'undersized discard size' (17-27cm), harvest size (27-37cm) and very large (>37cm). While this last group is caught in the fishing gears, the bulk of these large and old individuals occur nowadays in a geographical range (in the northern North Sea off the coast of Scotland) where not much fishing occurs. As a result, fishing mortalities for these fish are very low (ICES, 2023). This geographical separation limits competition with smaller individuals, which is why they are in a separate group.

The maximum size including the environmental effect which we find here is substantially less than the theoretical maximum of 780mm, which has been reported for plaice in ideal conditions (van der Veer et al, 2001). This suggests that plaice in the North Sea grow more slowly and reach substantially smaller sizes than they could, due to the environmental conditions. It is not clear which specific conditions (e.g. food availability and quality, temperature) are the cause, but temperature has been suggested to be important (Teal et al, 2014; Baudron et al, 2014).

For all groups, there appears to be a temporal trend towards smaller  $L_{\infty}$  in the studied period (1995-2020). Although we did not test the significance of the trend, it seems less obvious before ~2010. The downward trend coincides with a strong increase in the SSB between 2005 and 2015, when SSB more than doubled in estimated size (ICES, 2023). However, in the period 2015-2020, SSB became smaller again, while the downward trend in  $L_{\infty}$  continues.

The environmental limitation we find brings the environment-mediated maximum size of plaice (~39cm) close to 34 cm, which is reported as the size at first reproduction in female plaice (Rijnsdorp, 1989). A further reduction of  $L_{\infty}$  towards the size at maturation, could jeopardize population reproduction, as an increasing fraction of female plaice would be unable to reproduce. This could have important negative effects for stock abundance in the areas where adult plaice currently occur. However, it has also been argued that size-selective fishing leads to a continuing evolution towards smaller size at maturity and first reproduction (Mollet et al, 2016), even though it is debated whether the speed of fisheries-induced evolution is fast enough for it to be relevant (Andersen and Brander, 2009).

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## 4.2 Density dependent growth

We find a clear relationship between  $L_{\infty}$  and the density in the survey data for the discarded size group (17-27 cm), but not for the other size groups. For the smallest individuals, the BTS survey does not sample the areas where they are likely to be most numerous, and therefore even if there is a relationship between growth and abundance, it is unlikely to be present in our data set. For the larger size ranges, we can hypothesize on the absence of a relationship.

One possibility why density-dependent growth could be absent for larger individuals (>27 cm) is that they have a different diet than their smaller conspecifics, which is abundant enough not to limit their growth. Diet data suggests that larger plaice have broader diets than smaller individuals (Rijnsdorp and Vingerhoed, 2001), implying that even when the size classes have spatial overlap, there may be food sources which are exclusive to the larger individuals.

Alternatively, there could be an effect of density-dependent growth in smaller individuals on the likelihood of observing it at larger sizes. If growth of small individuals slows down, the mean size of individuals in the population will also shift towards smaller sizes. This strengthens any density-dependent growth at those smaller sizes, but because it reduces the abundance of larger sized individuals, it reduces the competition among them and hence the likelihood that density-dependent growth reduction plays a role for these larger-sized individuals.

## 4.3 Effects of fishing

The effects of fishing in our population model largely correspond to what is expected from operational fisheries models (ICES, 2022). Starting from zero, landings and discards (if relevant) rapidly increase at low values of harvesting intensity. As harvesting intensity increases, the increase in catches levels off. Eventually, a maximum sustainable yield occurs, after which catches start to decrease with further increasing harvesting intensity, and eventually the stock collapses to extinction. SSB decreases exponentially from zero harvest mortality to the point of stock collapse. This pattern is, at least qualitatively, independent of the presence of density-dependent growth or the survival of undersized discards. We find that with higher survival of undersized discards, the stock can sustain a higher harvesting intensity before collapsing. Density-dependent growth, in the strength and size ranges where we detected it, generally increases catches at a given harvesting intensity, but does not qualitatively affect the pattern.

## 4.4 Effects of undersized discard survival

We find that density-dependent growth as we detected it from North Sea plaice data was not strong enough to reverse the effect of discard survival on landings (from more landings at higher survival to less landings at higher survival). It did however dampen the beneficial effect of higher discard survival on catches and SSB. We found that with no mortality on undersized fish (no discards, or 100% discard survival), a situation reflective of the goal of the landing obligation, density-dependent growth leads to 6% lower landings and SSB than what would be predicted based on density-independent growth. Currently, the measured survival of undersized discards is ~15%, and this is the reason for a derogation from the landing obligation for this stock. If that derogation would be revoked, it would, in the short term, lead to a 0% survival of undersized plaice, as all would have to be landed. Based on our model calculations, we expect this to lead to a slightly smaller catch and SSB reduction than expected using density-independent models.

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## 5 Conclusion and recommendations

The results of our analysis indicate that density-dependent growth occurs in North Sea plaice in the size range of 17 to 27 cm. We find that it weakens the beneficial effects of survival of undersized discards, but is not strong enough to reverse the effect: Reducing undersized discard mortality still leads to higher catches (although the increase is not as strong as if we assume no density-dependent growth). We have calculated these effects in such a way that we can make a direct comparison with the current situation (an exception from the landing obligation based on a measured discard survival of ~15%). We show that any increase in the survival, with or without density dependent growth, leads to higher landings at the current fishing mortality. This increased landing can be interpreted as an incentive for fishers to further increase the survival of undersized bycatch, even under an exception from the landing obligation.

We conclude that density-dependent growth as we have measured it here is not at odds with the ideas behind the landing obligation: more selective fishing leads to higher catches, with or without density-dependent growth. The effects of density dependence we find here are relatively minor. Based on this conclusion, increased survival of undersized plaice, either by increased discard survival or more selective fishing, is an appropriate way to promote the abundance and persistence of the plaice stock in the North Sea. This strongly depends on the exact result found here. To check this further, it would be prudent to do a more thorough comparison between the output of our model and the patterns in the data, particularly of the growth trajectories of plaice in the model and in the survey data.

It is important to continue to monitor the environmental growth limitation and the strength of density-dependent growth in plaice, because these recommendations depend on the current findings. These are likely to change in the future, especially if the North Sea becomes warmer. A second reason to do so is the finding that the current maximum size (~39cm) is not very far from the reported maturation size for females (~34 cm). A further reduction in maximum size for female plaice could jeopardize the reproductive capacity of the plaice stock, causing a stock size reduction and/or a northward shift in distribution. Because maturation size has also been shown to vary, it is important to include that parameter in the monitoring as well.

Such monitoring can be conducted by regularly repeating the analysis conducted in this report, but based on new data collected as part of the BTS survey. Data on size at maturation cannot be taken from the BTS survey, as this is conducted in the 3<sup>rd</sup> quarter of the year, and plaice maturation and spawning occur during winter. Other sources of data should be explored to monitor this quantity.

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## 6 Quality Assurance

Wageningen Marine Research utilises an ISO 9001:2015 certified quality management system. The organisation has been certified since 27 February 2001. The certification was issued by DNV.

All computer code used to produce the results presented in this report is available upon request from the authors.

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# References

- Andersen, K.H. and Brander, K. 2009. Expected rate of fisheries-induced evolution is slow. *Proc. Nat. Acad. Sci.*,106(28):11657–11660.
- Baudron AR, Needle CL, Rijnsdorp AD, Marshall CT. Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Glob Chang Biol.* 2014 Apr;20(4):1023-31. doi: 10.1111/gcb.12514. Epub 2014 Jan 28. PMID: 24375891.
- van Beek F. A., van Leeuwen P. I. and Rijnsdorp A. D. 1990. On the survival of plaice and sole discards in the otter-trawl and beam-trawl fisheries in the North Sea. *Journal of Sea Research*, 26: 151–160.
- Croll, J. C., & van Kooten, T. 2022. Accounting for temporal and individual variation in the estimation of Von Bertalanffy growth curves. *Ecology and Evolution*, 12, e9619. <https://doi.org/10.1002/ece3.9619>
- Croll, J.C., van Kooten, T., and de Roos, A.M. 2023. The consequences of density-dependent individual growth for sustainable harvesting and management of fish stocks. *Fish and Fisheries*, 24(3), 427-438. <https://doi.org/10.1111/faf.12736>
- Depestele J., Desender M., Benoît H. P., Polet H. and Vincx M. 2014. Short-term survival of discarded target fish and non-target invertebrate species in the 'eurocutter' beam trawl fishery of the southern North Sea. *Fisheries Research*, 154: 82–92.
- EU. 2013. Regulation (EU) No 1380/201308 of the European Parliament and of the Council of 11 December 2013 on the Common Fisheries Policy. *Official Journal of the European Union*, 354: 22–61.
- Fernandes PG and Cook RM. 2013. Reversal of fish stock decline in the Northeast Atlantic. *Curr Biol.* 5;23(15):1432-7. doi: 10.1016/j.cub.2013.06.016. Epub 2013 Jul 18. PMID: 23871238.
- van Gemert, R. and Andersen, K. H. 2018. Implications of late-in-life density-dependent growth for fishery size-at-entry leading to maximum sustainable yield. *ICES Journal of Marine Science*, 75(4), 1296-1305.
- Horbowy, J. and Luzeńczyk, A. 2017. Effects of multispecies and density- dependent factors on MSY reference points: example of the Baltic Sea sprat. *Canadian Journal of Fisheries and Aquatic Sciences*, 74, 864–870. <https://doi.org/10.1139/cjfas-2016-0220>
- ICES. 2023. Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK). ICES Scientific Reports. 5:39. 1072 pp. <https://doi.org/10.17895/ices.pub.22643143>
- ICES. 2022. Benchmark Workshop on North Sea and Celtic Sea stocks (WKNSSC). ICES Scientific Reports. 5:04. 324 pp. <https://doi.org/10.17895/ices.pub.21558681>
- ICES. 2023. Plaice (*Pleuronectes platessa*) in Subarea 4 (North Sea) and Subdivision 20 (Skagerrak). Replacing advice provided in 2022. In Report of the ICES Advisory Committee, 2023. ICES Advice 2023, ple.27.420. <https://doi.org/10.17895/ices.advice.22548568>
- ICES Database on Trawl Surveys (DATRAS), 2023, ICES, Copenhagen, Denmark. <https://datras.ices.dk>
- Lorenzen, K. and Enberg, K. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proc. R. Soc. Lond. B.*26949–54 <http://doi.org/10.1098/rspb.2001.1853>
- Mollet F.M., Dieckmann U., Rijnsdorp A.D. 2016. Reconstructing the effects of fishing on life-history evolution in North Sea plaice *Pleuronectes platessa*. *Mar Ecol Prog Ser* 542:195-208. <https://doi.org/10.3354/meps11441>
- van der Reijden K. J., Molenaar, P., Chen, C., Uhlmann, S.S., Goudswaard, P.C. and van Marlen, . 2017. Survival of undersized plaice (*Pleuronectes platessa*), sole (*Solea solea*), and dab (*Limanda limanda*) in North Sea pulse-trawl fisheries, *ICES Journal of Marine Science*, 74(6) pp.1672–1680, <https://doi.org/10.1093/icesjms/fsx019>

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- Rindorf, A., van Deurs, M., Howell, D., Andonegi, E., Berger, A., Bogstad, B., Cadigan, N., Elvarsson, B. P., Hintzen, N., Savina Roland, M., Taylor, M., Trijoulet, V., van Kooten, T., Zhang, F., and Collie, J. 2022. Strength and consistency of density dependence in marine fish productivity. *Fish and Fisheries*, 23, 812–828. <https://doi.org/10.1111/faf.12650>
- D. Rijnsdorp, Maturation of male and female North Sea plaice (*Pleuronectes platessa* L.) , *ICES Journal of Marine Science*, Volume 46, Issue 1, 1989, Pages 35–51, <https://doi.org/10.1093/icesjms/46.1.35>
- Rijnsdorp, A.D. and Vingerhoed, B. 2001. Feeding of plaice *Pleuronectes platessa* L. and Sole *Solea solea* L. in relation to the effects of bottom trawling. *Journal of Sea Research*, 45: 219-229, 2001. 45. 10.1016/S1385-1101(01)00047-8.
- Rijnsdorp, A.D. and van Leeuwen, P.I. 1992. Density dependent and independent changes in somatic growth of female North Sea plaice *Pleuronectes platessa* between 1930 and 1985 as revealed by back-calculation of otoliths. *Marine Ecology Progress Series*, 88:19-32.
- Rijnsdorp, A.D., and van Leeuwen, P.I. 1996. Changes in growth of North Sea plaice since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature. *Ices Journal of Marine Science*, 53, 1199-1213.
- de Roos, A.M. 1988. Numerical methods for structured population models: The Escalator Boxcar Train. *Numer. Methods Partial Differential Eq.*, 4: 173-195. <https://doi.org/10.1002/num.1690040303>
- de Roos, A.M. 2023. <https://staff.fnwi.uva.nl/a.m.deroos/EBT/Software/index.html>
- Teal, L.R., van Hal, R., van Kooten, T., Ruardij, P. and Rijnsdorp, A.D. 2012, Bio-energetics underpins the spatial response of North Sea plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.) to climate change. *Glob Change Biol*, 18: 3291-3305. <https://doi.org/10.1111/j.1365-2486.2012.02795.x>
- van der Veer, H.W., Kooijman, S.A.L.M., van der Meer, J. 2001. Intra-and inter species comparison of energy flow in North Atlantic flatfish species by means of dynamic energy budgets. *J. Sea Res.* 45,303–320.
- Zimmermann F, Ricard D, and Heino M. 2018. Density regulation in Northeast Atlantic fish populations: Density dependence is stronger in recruitment than in somatic growth. *J Anim Ecol.* 87(3):672-681. doi: 10.1111/1365-2656.12800.

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# Justification

Report C063/23

Project Number: 4311400052

The scientific quality of this report has been peer reviewed by a colleague scientist and a member of the Management Team of Wageningen Marine Research

Approved: Vincent Hin  
Scientist

Signature:

Date: 16th October 2023

Approved: Dr.ir. T.P. Bult  
Director

Signature:

Date: 16th October 2023

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Wageningen Marine Research  
T +31 (0)317 48 7000  
E: [marine-research@wur.nl](mailto:marine-research@wur.nl)  
[www.wur.eu/marine-research](http://www.wur.eu/marine-research)

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With knowledge, independent scientific research and advice, **Wageningen Marine Research** substantially contributes to more sustainable and more careful management, use and protection of natural riches in marine, coastal and freshwater areas.

Visitors' address

- Ankerpark 27 1781 AG Den Helder
- Korringaweg 7, 4401 NT Yerseke
- Haringkade 1, 1976 CP IJmuiden



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