

Density regulation in Northeast Atlantic fish populations: Density dependence is stronger in recruitment than in somatic growth

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Abstract

1. Population regulation is a central concept in ecology, yet in many cases its presence and the underlying mechanisms are difficult to demonstrate. The current paradigm maintains that marine fish populations are predominantly regulated by density-dependent recruitment.
2. While it is known that density-dependent somatic growth can be present too, its general importance remains unknown and most practical applications neglect it. This study aimed to close this gap by for the first time quantifying and comparing density dependence in growth and recruitment over a large set of fish populations.
3. We fitted density-dependent models to time-series data on population size, recruitment and age-specific weight from commercially exploited fish populations in the Northeast Atlantic Ocean and the Baltic Sea. Data were standardized to enable a direct comparison within and among populations, and estimated parameters were used to quantify the impact of density regulation on population biomass.
4. Statistically significant density dependence in recruitment was detected in a large proportion of populations (70%), whereas for density dependence in somatic growth the prevalence of density dependence depended heavily on the method (26% and 69%). Despite age-dependent variability, the density dependence in recruitment was consistently stronger among age groups and between alternative approaches that use weight-at-age or weight increments to assess growth. Estimates of density-dependent reduction in biomass underlined these results: 97% of populations with statistically significant parameters for growth and recruitment showed a larger impact of density-dependent recruitment on population biomass.
5. The results reaffirm the importance of density-dependent recruitment in marine fishes, yet they also show that density dependence in somatic growth is not

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uncommon. Furthermore, the results are important from an applied perspective because density dependence in somatic growth affects productivity and catch composition, and therefore the benefits of maintaining fish populations at specific densities.

KEYWORDS

early life stages, fisheries ecology, life-history strategy, marine ecosystems, population dynamics, population regulation

1 | INTRODUCTION

Density dependence is a key concept in population ecology (Hassell, 1975; Hixon, Pacala, & Sandin, 2002; May, Conway, Hassell, & Southwood, 1974; Turchin, 1995). Although some form of density-dependent population regulation is nearly a logical necessity, detecting density regulation can be challenging. For instance, many insect populations fluctuate widely, without showing detectable signs of density regulation. This has prompted an ongoing debate about how density-dependent population regulation could be detected and whether it is important at all (summarized by, e.g. Brook & Bradshaw, 2006; Hixon et al., 2002; Turchin, 1995). The mechanisms involved in population regulation are highly varied. They include predation, cannibalism, disease or habitat selection, and competition for limiting resources such as food and nesting sites, manifesting themselves as increased mortality, slower somatic growth and/or reduced fertility when density increases (e.g. Anderson & May, 1978; Boutin, 1990; Pöysä & Pöysä, 2002; Pulliam, 1988; Sinclair, Mduma, & Brashares, 2003).

Two of the commonly used functions used to describe density-dependent effects, the Ricker (1954) and Beverton and Holt (1957) functions, were first used to describe density-dependent effects in fish populations. Indeed, the presence of density dependence is deeply ingrained in the thinking of fisheries scientists because some form of density-dependent compensation is necessary for fish populations to sustain the additional mortality caused by exploitation (Shepherd, Cushing, & Beverton, 1990). Against this background, it would be natural to expect that the nature of density regulation in fish populations would be well understood, but this is not the case (Andersen, Jacobsen, Jansen, & Beyer, 2017).

Marine fish populations are traditionally believed to be primarily regulated by density-dependent survival at early life stages, between spawning and first (few) years of life. It is customary to describe this density dependence with the so-called stock-recruitment relationship, of which the aforementioned Ricker and Beverton–Holt models are the most used ones (Hilborn & Walters, 1992). “Stock” (essentially, population in fisheries parlance) here refers to the reproducing parent population, and is typically measured as spawning stock biomass, i.e. the total biomass of all mature individuals, which is a proxy of the total numbers of eggs produced by the stock during one reproductive season. “Recruitment” is the

number of individuals resulting from that reproduction, typically measured one or more years after reproduction, when individuals in the new cohort are large enough to be captured by fishermen or scientists (Hilborn & Walters, 1992). The customary use of stock-recruitment relationships stands in contrast to often controversial or absent empirical evidence for the existence of such a relationship (Marshall, Kjesbu, Yaragina, Solemdal, & Ulltang, 1998; Myers & Barrowman, 1996).

Density-dependent processes at later life stages, on the other hand, have been largely ignored in population dynamics and often deemed as uncommon (Walters & Martell, 2004). However, the ecology and habitat of a species shapes its life history and therefore how and at which life-stage density dependence predominantly occurs. The spatial component of habitat size may be of particular importance in this context (Andersen et al., 2017). Although these findings suggest that density dependence early in life may dominate in marine fish, density-dependent body growth may still be relevant, as has been established by case studies in several populations of marine fish (Ivanov & Beverton, 1985; Kovalev & Yaragina, 2009; Olafsdottir et al., 2015; Rijnsdorp & Van Leeuwen, 1992; Rindorf, Jensen, & Schrum, 2008). However, there have been few attempts to systematically study the prevalence of density-dependent growth. In their review, Sánchez Lizaso et al. (2000) noted many examples of density-dependent growth in marine fish, particularly in juveniles, but also the lack of such an effect in other cases. The only unified, quantitative approach to this question (Lorenzen & Enberg, 2002) found evidence for density-dependent body growth in 9 of the 16 studied fish populations; among the nine marine populations, four had statistically significant density dependence in growth. Furthermore, the same authors provided some evidence that density-dependent growth was the primary source of population regulation in the populations where it was significant, although they did not explicitly evaluate density-dependent recruitment. Even if density-dependent recruitment is also present, density-dependent growth may still be a concern for fisheries management because of its negative effects on body size and sustainable yield (Svedäng & Hornborg, 2014).

The many demonstrations of density-dependent growth leave open two questions: how prevalent density-dependent growth really is, and how its strength compares to the strength of density-dependent recruitment. In other words, does empirical data support

the current paradigm that marine fish populations are primarily regulated by density-dependent recruitment? In this study, we performed the first comprehensive quantitative assessment of density dependence in growth and recruitment and their relative importance for a wide range of marine fish populations and species using data from commercially exploited fish populations from the Northeast Atlantic Ocean.

2 | MATERIALS AND METHODS

Stock-recruitment and size data from all European fish populations with sufficient data published in stock assessment reports from the International Council for the Exploration of the Sea (ICES) were used (ICES, 2015a, 2015b, 2015c, 2015d, 2015e, 2015f, 2015g, 2015h, 2015i, data accessible at Dryad Digital Repository: <https://doi.org/10.5061/dryad.d1458>). To reduce potential bias in the parameter estimation and comparison among populations (Dickey-Collas, Hintzen, Nash, Schön, & Payne, 2015), all data are based on analytical stock assessment models that do not include an explicit stock-recruitment relationship in the estimation process. Population size and recruitment data were based on annual spawning stock biomass (SSB) and recruitment numbers from stock summary tables, and time series of age-specific body weight allowed us to trace the growth of each cohort through cohort-specific weight per age class and year. Body weights were used because they are routinely assessed and more readily available in most commercially exploited fish population than other measurements of temporal changes in size. Weights that were corrected for potential selectivity bias and represent true weight-at-age were used preferentially where available (see Table S2) because these so-called “stock weights” represent true weight-at-age in population better than age-specific weights from fisheries catches. The study includes 70 different populations from the Northeast Atlantic Ocean. Details of the different populations used (species, stock area and assessment methodology) appear in Table S1.

We compared the strength of density dependence at two different levels. In the process-level comparisons, we assessed how the processes of growth and recruitment are influenced by population density. To make this comparison meaningful between the two processes, we used the same functional form to describe density dependence. Furthermore, to make parameter estimates comparable between age groups and populations, biomass, recruitment and weight-at-age of each population were normalized with respect to their means prior to model fitting. Consequently, all following variables and parameters are dimensionless. In the population-level comparisons, we assessed how population biomass is expected to be influenced by population density.

Growth is defined here in two alternative ways: as year-specific weight increments within each cohort and in a complementary approach as absolute year-specific body weight. The latter was done to test whether the use of weight-at-age influences the results compared to using changes in weight, and to provide the basis to

quantify directly the impact of density dependence on population dynamics.

First, the Ricker stock-recruitment model was used to describe density dependence in both growth and recruitment. The model is traditionally formulated as:

$$R = \alpha_R \cdot B \cdot e^{\beta_R \cdot B},$$

where R denotes recruitment, B spawning stock biomass, α_R maximum production of recruits per unit biomass obtained when $B=0$, and β_R the density-dependent reduction in recruits (i.e. usually $\beta_R < 0$). The Ricker model was selected due to its greater flexibility and generally better model fits over all populations compared to Beverton–Holt models or constant recruitment. The model can also be expressed as density-dependent per unit biomass recruit production:

$$r = \frac{R}{B} = \alpha_R \cdot e^{\beta_R \cdot B}$$

The same functional form can be used to describe density dependence in growth:

$$g_a = \alpha_{G,a} \cdot e^{\beta_{G,a} \cdot B},$$

where g denotes growth (weight increment), a the age group, B population biomass, $\alpha_{G,a}$ maximum growth when $B=0$, and $\beta_{G,a}$ the density-dependent reduction in growth. Parameters β_R and $\beta_{G,a}$ allow to compare directly which source of density regulation is stronger. Because β can take on both positive and negative values (implying positive/negative density dependence), the metric $\beta_{G,a} - \beta_R$ was used as measurement to compare strength of density dependence, i.e. $\beta_{G,a} - \beta_R < 0$ suggests that (age-specific) density dependence in growth is stronger than density dependence in recruitment, and vice versa.

Stock-recruitment and growth models were fitted to time series, and parameter values of α_x and β_x were estimated, with likelihood functions using a maximum likelihood method assuming a normal distribution (Haddon, 2010). Standard deviation and significance of parameters were obtained as part of the parameter estimation. All analyses were conducted using R version 3.4 (R: Development Core Team, 2016) with the TMB package (Kristensen, Nielsen, Berg, Skaug, & Bell, 2016). Spawning stock biomass (SSB) was used as a measure of population biomass and year-specific numbers of recruits were offset to match the year when the cohort was formed. The age at recruitment is stock-specific but is typically 1 year (range: 0–5 years, see Table S2).

Growth models were fitted to two alternative measurements of growth: (1) relative change in weight-at-age per year within a cohort ($g_a = \left(\frac{w_{a+1,t+1}}{w_{a,t}} \right) / T$), where t is the year and $T = 1$ year and (2) weight-at-age ($g_a \equiv w_{a+1,t+1}$). The former measures growth directly, whereas the latter measures the cumulative effect of growth, rather than growth per se. This metric was used because it allows estimating the effect of density dependence at the population level (see below). Furthermore, it is potentially less influenced by observation error because reported weights-at-age can be used directly, while it

suffers from being affected by a cohort's whole growth history, not just the focal time interval.

Growth was represented alternatively either as the average growth across all ages ($G_a = G_{all}$), or for three representative age groups: the youngest age group present in the data, one at the average between youngest and oldest age group, and the oldest age group, representing young ($G_a = G_1$), intermediate ($G_a = G_2$) and old fish ($G_a = G_3$) respectively. Figure S1 shows an example of the input data and the estimated relationships. All age groups used in the analysis and recruitment ages are detailed in Table S2.

Population biomass is the sum of abundance at each (mature) age class times the corresponding weights. Because abundance at age is the product of initial recruitment and mortality experienced in previous years, density dependence in both growth and recruitment affects population biomass. When density dependence in growth is age-independent, both density-dependent growth and recruitment have direct, multiplicative effects on population biomass after exponentiation (see Appendix S1). Therefore, as first approximation, the coefficients β_G and β_R have similar, directly comparable effects on population biomass. Their relative effect is calculated here as ratio $e^{(\beta_R \bar{B})} / e^{(\beta_G \bar{B})}$, with \bar{B} as mean population biomass. This argument applies for both total population biomass and mature biomass. However, this comparison is only approximate because it ignores the effects of growth on survival and maturation. The net effect of these confounding factors is case specific, difficult to evaluate without detailed models and not attempted here; see Appendix S1 for detailed discussion.

3 | RESULTS

The Ricker model was successfully fitted to describe density dependence in recruitment for the 70 populations analysed in our study. The Ricker model was also successfully fitted to describe density dependence in growth for most age groups; the fitting process failed to converge in few specific populations and age groups. Density dependence parameters in growth (for all age groups G_{all}) and recruitment were statistically significant ($p < .05$) in 26% and 70% of the populations respectively (Tables S3 and S4). Of these, 13 populations (19%) showed statistical significance ($p < .05$) in both growth and recruitment parameters. The proportions increased substantially when growth models were fitted to weight-at-age: in 69% of populations, parameter estimates were statistically significant in growth, and in 47% in both growth and recruitment parameters. The degree and direction of density dependence varied greatly among populations, ranging from very strong negative to no or even positive density dependence (Figure 1). Variability within populations was similarly large for growth and recruitment as well as for growth among all age groups and different specific age groups. Parameter estimated from all age groups together represented the results from specific age groups well, except for showing fewer values on the extremes and thus a slightly narrower distribution. The results from the complementary method that used annual weight-at-age to describe growth confirmed the results based on weight increments (Figure 2, Tables S5 and S6) with in general very similar results, although

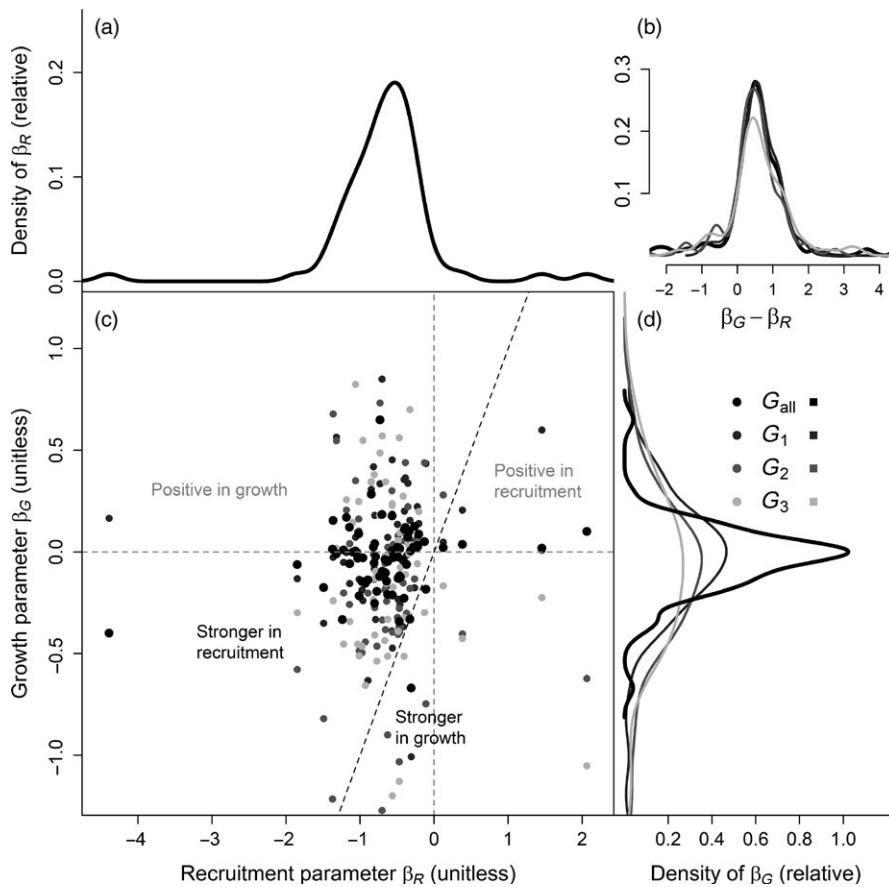


FIGURE 1 Process-level comparison of the strength of density dependence in recruitment and somatic growth in 70 fish populations based on the density dependence parameters β_R and $\beta_{G,a}$ for recruitment and growth respectively. The latter is defined for all ages combined (G_{all}) as well as for three representative age groups (G_1 = low age, G_2 = intermediate age and G_3 = high age). Negative values indicate negative density dependence that contributes to population regulation. In the scatterplot (c) subdiagonal points indicate that density dependence in growth is stronger than in recruitment. The immediately adjacent panels show the marginal density distributions of recruitment parameter β_R (a) and growth parameter $\beta_{G,i}$ (d). All parameter values are unitless. The top right panel (b) shows the density distributions of the metric $\beta_{G,i} - \beta_R$

FIGURE 2 Process-level comparison of the strength of density dependence in recruitment and somatic growth based on growth models fitted to weight-at-age (complementary method) in 70 fish populations. The distributions of density dependence parameters β_R and $\beta_{G,a}$ for recruitment and growth, respectively, are shown. The latter is defined for all ages combined (G_{all}) as well as three representative age classes (G_1 = low age, G_2 = intermediate age and G_3 = high age). Negative values indicate negative density dependence that contributes to population regulation. In the scatterplot (c) subdiagonal points indicate that density dependence in growth is stronger than in recruitment. The immediately adjacent panels show the marginal density distributions of recruitment parameter β_R (a) and growth parameter $\beta_{G,i}$ (d). All parameter values are dimensionless. The top right panel (b) shows the density distributions of the difference $\beta_{G,i} - \beta_R$

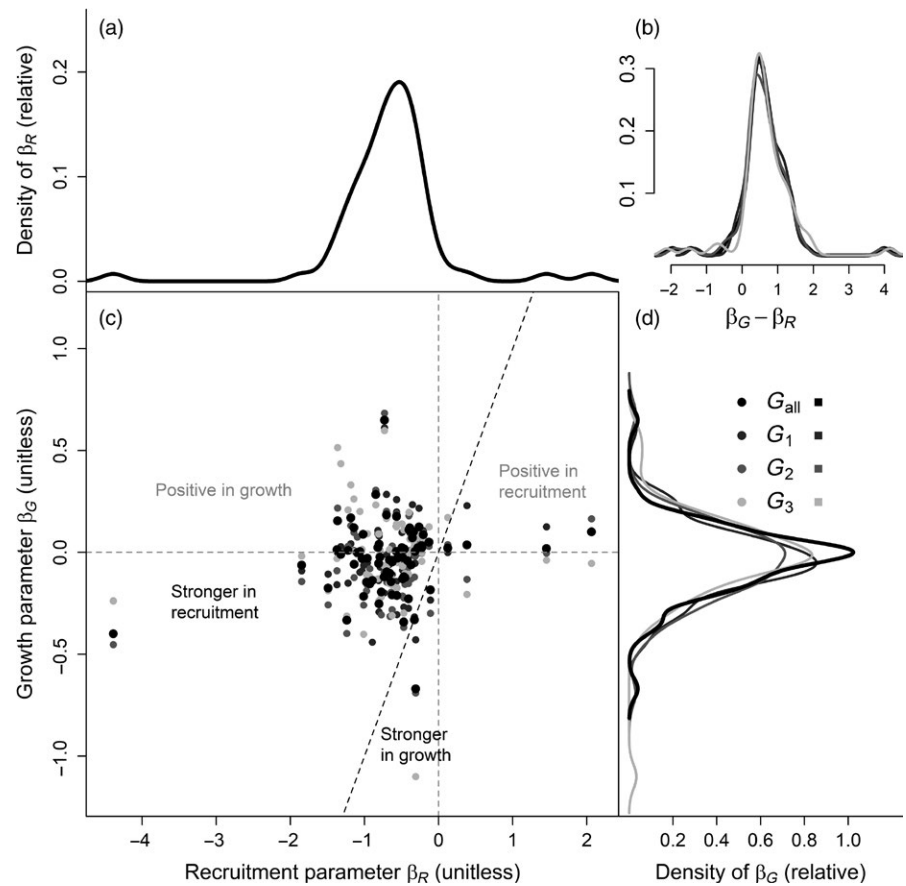


TABLE 1 Percentages of populations with stronger density dependence in recruitment ($\beta_{G,i} - \beta_R > 0$) or in growth ($\beta_{G,i} - \beta_R < 0$) for all age groups together (G_{all}) and three stock-specific representative age groups (G_1 = low age, G_2 = intermediate age, G_3 = high age). Results are shown for populations with statistically marginally significant estimates ($p < .1$) in both parameter values as well as for all 70 populations. When significance level is set to $p < .05$, the proportion of populations with stronger density dependence in growth falls to 0% in all age groups. Percentages of all populations where no successful model fit to either growth or recruitment data was possible are detailed in a separate column

Age class	Stronger in recruitment		Stronger in growth		No model fit
	Populations with significant estimates	All populations	Populations with significant estimates	All populations	All populations
G_{all}	95%	90%	5%	10%	0%
G_1	87%	86%	13%	9%	5%
G_2	94%	87%	6%	13%	0%
G_3	91%	81%	9%	16%	3%

statistical significance was higher and variability among age groups lower (Figure S2).

The results suggested that density dependence in recruitment is generally stronger than density dependence in growth (Table 1 and Table S7). Nonetheless, at least when considering statistically marginally significant ($p < .1$) parameter estimates, there were several populations in which density dependence in growth outweighed the density-dependent effects in recruitment (Figure 1, Tables S8 and S9). Furthermore, in a number of populations density dependence in growth was comparable to recruitment. For example, $\beta_{G_{all}} - \frac{\beta_R}{4} < 0$ was found in 46% of populations with statistically

significant parameters and in 33% of all populations. The few cases in which density dependence in growth was stronger than in recruitment include Atlantic herring (*Clupea harengus*) in the Gulf of Riga, western Baltic cod (*Gadus morhua*) and ling (*Molva molva*) on the Faroes grounds, as well as specific age groups in golden redfish (*Sebastes norvegicus*) and beaked redfish (*Sebastes mentella*), the southern stock of megrim (*Lepidorhombus whiffiagonis*), sprat (*Sprattus sprattus*) in the Baltic Sea and various populations of plaice (*Pleuronectes platessa*) and sole (*Solea solea*). Stronger density dependence in growth typically coincides with statistically insignificant and/or positive parameters in recruitment. Fitting

growth models to weight-at-age instead of weight increments resulted in very similar results except for a lower proportion of populations with stronger density dependence in growth, particularly for older ages (Table 1 and Table S7).

In the majority of populations, we detected positive density dependence in at least one parameter estimate (Tables S3–S6). Statistically significant positive point estimates were much more frequent for growth (22% for G_{all} and from 29% (G_2) to 55% (G_3)) than for recruitment (4%). We found positive density dependence in growth in, among others, various populations of Atlantic cod, Atlantic herring, haddock (*Melanogrammus aeglefinus*), plaice, sandeel (*Ammodytes* spp.) and sole, as well as ling on the Faroes grounds, sprat in the Baltic Sea and turbot (*Scophthalmus maximus*) in the North Sea (Tables S3 and S4). In recruitment, only beaked redfish and ling on the Faroes grounds showed statistically significant positive parameter values.

In the population-level assessment, density-dependent impacts on population biomasses correspond (Figure 3) to the results found for the process-level assessment (Figures 1 and 2). Overall, density-dependent recruitment was estimated to reduce population biomass to a larger degree than density-dependent growth in all but a few populations (Table S10). Of 33 populations with statistically significant parameter values for both growth and recruitment, only beaked redfish (*Sebastes mentella*) showed stronger effects of growth, caused by strongly positive density dependence in recruitment. Even including populations without statistically significant parameter values for recruitment did not affect these results substantially; of 15 populations in this subgroup, just in 3 density-dependent growth reduced the biomass to a

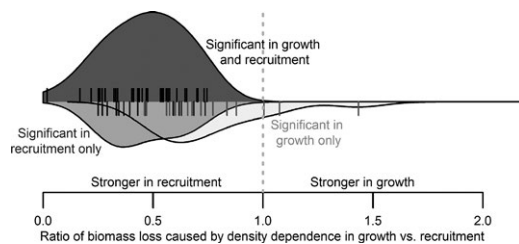


FIGURE 3 Population-level comparison of the strength of density dependence in recruitment and somatic growth. The distributions give the estimated ratio $e^{(\beta_R \cdot \bar{B})} / e^{(\beta_G \cdot \bar{B})}$ in relative density-dependent biomass reduction between recruitment and growth in 62 fish populations, based on the estimates presented in Figure 2 (two strongly positive outliers, ling on Faroes grounds and beaked redfish, and six populations without statistically significant parameter estimates in neither growth nor recruitment were excluded). Values of $e^{(\beta_R \cdot \bar{B})} / e^{(\beta_G \cdot \bar{B})} < 1$ indicate larger biomass loss due to density-dependent recruitment compared to density-dependent growth and vice versa. The ratio distribution in populations with statistically significant parameter estimates for both growth and recruitment is shown above the line (dark grey area, black bars, $n = 32$), those for populations with only statistically significant parameter estimates for growth (light grey area, grey bars, $n = 15$) or recruitment (medium grey area, black bars, $n = 15$) below; all distributions have been scaled to the number of populations included

larger degree, namely, in Atlantic herring in the Gulf of Riga, plaice in the Baltic Sea and whiting (*Merlangius merlangus*) in the North Sea.

4 | DISCUSSION

Our results show that density-dependent effects are prevalent in growth and recruitment for a large proportion of Northeast Atlantic fish populations. Density dependence was clearly stronger in recruitment and had larger impacts on population biomass than in growth, yet density-dependent growth was also relatively common and in a few cases of comparable strength or stronger. The detailed patterns are diverse, ranging from instances where both mechanisms of density dependence were clearly present to where neither one could be detected. In growth, there is variability in the strength of density dependence between all age groups pooled and specific age groups as well as among the latter, but the general patterns are age independent.

Strength of density dependence was quantified at two levels, at process and population levels. In the former, after standardizing biomass across populations, the coefficients β_G and β_R express the effect of density dependence on growth and recruitment in a way that is comparable between both populations and the two processes. Nevertheless, process-level comparability does not guarantee comparable population-level impacts. Under simplifying assumptions, however, our estimates of density-dependent growth and recruitment directly translate into the effect on population and mature biomass (see Appendix S1 for derivation and detailed discussion). Without further studies, it is difficult to assess whether and how the simplifying assumptions will affect the quantification of the population-level impacts. It remains therefore an important challenge to explore further the practical implications of our findings for population dynamics. Nevertheless, given the much stronger overall impact of density-dependent recruitment compared to density-dependent growth, it is unlikely that relaxing the simplifying assumptions would qualitatively affect our conclusions.

Much of the literature on detecting density dependence has focused on univariate time series of overall population size. Moreover, the time series typically available are relatively short. For example, Brook and Bradshaw (2006) collated almost 1,200 time series, but the median length of those time series was around 20 years only. Availability of population data on marine fishes is relatively good compared to invertebrates or terrestrial vertebrates, with data often spanning several decades and containing life-stage-specific information. This has allowed us to find some form density dependence in all but one of the studied populations and to pinpoint where in the life cycle it occurs. In contrast, among the 115 fish populations studied by Brook and Bradshaw (2006), between 26% and 90% of cases showed density dependence, depending on the chosen methods and criteria; detection rates were generally somewhat lower for fish than for invertebrates or other vertebrates.

Stock assessment data, in particular information on population biomass and abundance, as those that were used here, are not

primary data but model-derived estimates (Brooks & Deroba, 2015) and thus subject to structural and parameter uncertainty (Haddon, 2010; Patterson et al., 2001). This might introduce a bias into any further analysis. Furthermore, although time series from commercially exploited fish populations are long compared to most other sources, they typically span not more than a few decades and contain a restricted range of population sizes. Key information for the density-dependent models is mostly found in areas of low (for maximum growth rates) and high stock sizes (for density-dependent compensation) (Haddon, 2010). Collection of population abundance data for commercial fish has almost always started after fishing had already depressed population abundance, and hence, high population sizes near carrying capacity are underrepresented or absent. Consequently, our parameter estimates might be biased.

Density-dependent regulation emerges from the life-history strategies within a population as adaptations to a limited environment (Reznick, Bryant, & Bashey, 2002; Winemiller, 2005), linking somatic growth and recruitment through individual life history and shared environmental drivers. Food availability in particular determines both growth and survival of early life stages in fish (Husebø, Slotte, & Stenevik, 2007). Mortality from harvesting may cause similarly confounding effects by, for instance, reducing the recruitment capacity of populations (Britten, Dowd, & Worm, 2016) and distorting population demographics with effects on density dependence in growth (Svedäng & Hornborg, 2014). Furthermore, common environmental and trophic drivers may also influence growth and fecundity of adult fish (Kjesbu, Witthames, Solemdal, & Walker, 1998). Because growth is a key life-history trait that is tightly connected with reproductive output and survival in fish (Enberg et al., 2012), changes in size-at-age affect maturity and fecundity, and therefore the overall productivity of the population (Hixon, Johnson, & Sogard, 2014). Through changes in size-at-age, density-dependent changes in growth may therefore alter the size at maturity (Helser & Almeida, 1997), reproductive output and the mature population biomass. Our assessment of population-level impacts of density dependence did not account for effects of growth on maturity and thus SSB, which is a limiting assumption. Similarly, survival in fish is commonly size dependent (Gislason, Daan, Rice, & Pope, 2010), in particular for early life stages. As a consequence, density-dependent growth in larval and juvenile fish can alter their chance of surviving to recruitment age (Cowan, Rose, & DeVries, 2000). Such feedbacks among growth, recruitment and SSB imply that available information on (mature) population biomass, numbers of recruits and size-at-age are confounded, thus potentially obscuring the detected signals of density dependence. Our results can be interpreted in this light as the strongest density dependence in growth tends to occur in populations where little to none was found in recruitment (and vice versa). However, conclusions are constrained by our specific assumptions about density dependence and not explicitly accounting for mortality.

Besides density-dependent processes analysed in this study, major drivers of population dynamics are environmental conditions (Borja, Fontan, Sáenz, & Valencia, 2008; Skagseth, Slotte, Stenevik, & Nash, 2015; Stachura et al., 2014), ecological interactions (Huse,

Salthaug, & Skogen, 2008; Skaret, Bachiller, Langøy, & Stenevik, 2015), additional intraspecific feedbacks (Ricard, Zimmermann, & Heino, 2016) and fishing (Anderson et al., 2008). Growth is sensitive to various factors that cause inter- and intra-annual variations, confounding estimation of density dependence. Modelling such effects explicitly would help to disentangle the different density-dependent and -independent drivers of recruitment variability and population dynamics.

This study underlines that density dependence in growth is less common and weaker than it is in recruitment in most commercial fish populations. At the same time, our analysis and the earlier literature also indicate that density dependence in growth is often not negligible, with practical implications for fisheries management. In stock assessments that aim to reconstruct the recent history of populations, both density-dependent growth and recruitment are implicitly accounted for through historic estimates of weight- and abundance-at-age data. However, management advice and therefore policy decisions depend on forward-looking predictions. While density-dependent recruitment is accounted for through the use of stock-recruitment models, the predictions typically assume constant weights-at-age, thus ignoring density-dependent growth. Our findings call for more attention to density-dependent growth in fisheries management.

Density-dependent growth may affect management decisions due to its compensatory effect on total biomass and productivity. Growth determines size-at-age and, therefore, along with mortality, the size structure within the stock, with ecological and economic implications. Varying growth rates modulate the nonlinear relationship between the numbers of fish within a stock and their total biomass: higher size-at-age due to density-dependent growth can result in a larger total biomass despite fewer fish and vice versa. As density-dependent recruitment compensates low stock sizes, so does density-dependent growth. This may therefore shift reference points of maximum sustainable yield and be of relevance for management decisions. Because in most fisheries size is directly associated with fish prices (Asche, Chen, & Smith, 2015; Zimmermann & Heino, 2013), density-dependent growth affects catch value and therefore optimal harvest strategies (Zimmermann, Heino, & Steinshamn, 2011).

Details of density-dependent effects are important for population dynamics and will affect their stability, such as presence of chaotic dynamics or multiple equilibria (Åström, Lundberg, & Lundberg, 1996; Claessen, de Roos, & Persson, 2000; Hellriegel, 2000; Neubert & Caswell, 2000). The nature of density dependence will also affect the course of life-history evolution (Mylius & Diekmann, 1995), with more than one source of density-dependent effects required for frequency-dependent selection to maintain stable polymorphisms (Heino, Metz, & Kaitala, 1998). Furthermore, the traditional fitness maximization approach in life-history theory is only valid when a population is regulated by a single source of density dependence (Metz, Mylius, & Diekmann, 2008; Mylius & Diekmann, 1995). This study has shown that population regulation through density-dependent recruitment is typical for marine fish populations and has stronger effects on population

biomass, in agreement with the common assumption that density-dependent recruitment tends to be most important source of population regulation. The results, however, also underline that density-dependent growth is not uncommon and often co-occurs with density-dependent recruitment. This challenges the prevailing paradigm of supremacy of population regulation through density-dependent recruitment, with important theoretical and practical implications.

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AUTHORS' CONTRIBUTIONS

M.H. conceived the study, all authors contributed to the design of the study, F.Z. and D.R. analysed the data, and all authors contributed to the interpretation of the results and writing of the manuscript.

DATA ACCESSIBILITY

All data used in this study are publicly available at the International Council for the Exploration of the Sea (ICES) (www.ices.dk) and the Dryad Digital Repository: <https://doi.org/10.5061/dryad.d1458> Zimmermann, Ricard, and Heino (2018).

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