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Strength and consistency of density dependence in marine fish productivity

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Abstract

The correct prediction of the shape and strength of density dependence in productivity is key to predicting future stock development and providing the best possible long-term fisheries management advice. Here, we identify unbiased estimators of the relationship between somatic growth, recruitment and density, and apply these to 80 stocks in the Northeast Atlantic. The analyses revealed density-dependent recruitment in 68% of the stocks. Excluding pelagic stocks exhibiting significant trends in spawning stock biomass, the probability of significant density dependence was even higher at 78%. The relationships demonstrated that at the commonly used biomass limit of 0.2 times maximum spawning stock size, only 32% of the stocks attained three quarters of their maximum recruitment. This leaves 68% of the stocks with less than three quarters of their maximum recruitment at this biomass limit. Significantly lower recruitment at high stock size than at intermediate stock size was seen in 38% of the stocks. Density dependence in late growth occurred in 54% of the stocks, whereas early growth was generally density-independent. Pelagic stocks were less likely to exhibit density dependence in recruitment than demersal and benthic stocks. We recommend that both the degree to which productivity is related to density and the

degree to which the relationship changes over time should be investigated. Both of these aspects should be considered in evaluations of whether sustainability and yield can be improved by including density dependence in forecasts of the effects of different management actions.

KEYWORDS
Benthic fish, demersal fish, fisheries, North Atlantic, pelagic fish, stability

1 | INTRODUCTION

Density-dependent processes are key to avoiding population extinction and explosion (Henle et al., 2004). Understanding the strength, direction and consistency of density dependence is particularly important for exploited populations, for which correctly predicting the effects is essential to avoiding over- or under-exploitation with associated loss of ecological sustainability or social benefits. The theoretical explanations of density dependence are mainly derived from resource limitation of either the species investigated or its predators. Under resource limitation, the abundance of individuals affects individual growth, reproduction and survival as competition for prey increases with abundance (Chesson, 1998). Additionally, survival and growth can be density-dependent as a result of the response of predators to changes in prey abundance in the form of satiation, diet switching or aggregation in areas of high prey abundance (Bax, 1998).

Unfortunately, the processes through which density dependence act are notoriously difficult to identify, even in populations that are clearly regulated (Murdoch, 1994). The difficulty in detection can at least partially be alleviated by using information over a long time series and analysing a large number of populations concurrently. Long time series are widely available for commercially exploited fish populations. These populations are generally managed based on short-term projections to meet long-term management aims. Information on the level of fishing that would achieve Maximum Sustainable Yield (MSY, UN, 2002) is derived from population models that include density dependence implicitly or explicitly (Quinn & Deriso, 1999). The assumptions made about the characteristics and functional form of density dependence are highly influential in determining the exploitation rate and selectivity pattern that produces MSY. Generally, long-term predictions of yield and sustainability assume density dependence in the abundance of incoming recruits by incorporating a decelerating relationship between spawning stock biomass and recruitment (Cadigan, 2013). In contrast, density dependence in individual growth is rarely incorporated and hence the effect on potential yield of such changes is largely ignored, though some analyses exist (Andersen et al., 2017; Gislason, 1999; Horbowy & Luzeńczyk, 2017). These assumptions raise questions as to how recruitment and growth depend on density within the range of stock biomass modelled and whether these relationships are consistent over time.

The objective of the present study was to determine the strength, direction and consistency of density dependence

in recruitment and body growth of fished stocks in the North Atlantic. Recruitment is defined here as the combined effect of spawning output and early life survival. The analyses aim to determine whether density dependence is present, whether the strength and direction differs between species feeding habitat types (pelagic: feeding in the water column, demersal: feeding on the bottom and in the waters above it, benthic: feeding on the bottom), and whether the relationship is consistent over time. The results of these analyses are also investigated in relation to characteristics such as the contrast in the densities observed and the variability around predicted relationships. We note that density dependence is not the only relevant driver, and that the signals from density dependence will be confounded with environmental drivers such as variation in temperature and habitat quality and food abundance, which again may be impacted by density. An increase in food abundance over time may spark increased recruitment success and increased growth and hence a positive correlation between abundance and individual growth without a causal relationship with density. In contrast, a decrease in food

abundance may lead to aggravated density-dependent effects as competition for food increases. As a result, distinguishing density-dependent effects from other variables may not be possible in individual stocks. However, by examining a large number of fish stocks, we aim to identify general patterns.

2 | METHODS

To structure our analyses, we formulated a list of specific hypotheses related to density-dependent effects pertaining to three different life stages: recruitment phase (i.e. early life stage survival), early individual growth and late individual growth in order to identify density dependence at each life stage. Furthermore, as previous studies have shown that a key factor in the determination of the strength of density dependence in growth is the choice of growth and density measures (Zimmermann et al., 2018), we performed a detailed investigation into which growth and density measures would be unbiased and sensitive to density dependence before deciding on the measures to compare. Furthermore, we expanded our analysis of the relationship between stock and recruitment to other forms than the traditionally investigated Beverton-Holt (1957) and Ricker (1954) functions, both of which through their shape have the disadvantage that the slope of the curve at low densities is highly correlated with the slope at high densities.

2.1 | Data

The data used for the analyses were derived for stocks in the North Atlantic from the ICES stock database, published literature and personal contacts (Table S1). The data covered 80 stocks and 25 species in the North Atlantic. Both recruitment and the first reliable age with data on weight at age in the stock data were derived from stock assessments. The term recruitment in this manuscript refers to the number of fish in a cohort that survive to the first age included in the stock assessment model. Recruitment in stock assessment models is determined from survey indices and the age composition of catches. The ages at which cohorts are consistently observed are most influential in determining cohort strength. The inherent assumption in most assessment models is that natural mortality is constant or at least density independent. Hence, when recruitment in the model is given at age 0, recruitment at this age is estimated under the assumption that all density dependence occurs before this age. The age at recruitment in the assessment was strongly correlated to the age at which Lorenzen and Camp (2019) suggests density dependence has fully acted (20% of asymptotic length, Supplementary Material). Based on this, we infer that the age at which recruitment occurs in our data is unlikely to bias our conclusions. The first reliable age with weight at age data is often based on samples from commercial catches. However, weight at age was based on survey data for younger ages in some of the stocks. The first reliable weight

at age was within one year of the age of recruitment for all but 7 stocks but where the reliable weight at age was 2 years from age at recruitment. We divided the stocks into pelagic, demersal, and benthic stocks based on feeding habitat derived from Fishbase (Froese & Pauly, 2000).

2.2 | Selecting the most appropriate density measure

The measure of density relevant to survival and growth of the individual varies between life stages. For initial survival of the early life stages, the abundance of cohort siblings and possibly the abundance of the preceding cohort are relevant. Cohort siblings compete for the same resources and may also compete with the preceding cohort if growth is slow. Abundance of both cohort siblings and the preceding cohort may also affect mortality from predators, either by attracting predators, by satiating them, or by cannibalism. Hence, recruitment to the first observed life stage in the stock assessment was compared to spawning stock biomass, used as an indicator of initial cohort abundance prior to observation. Though initial recruitment may not be proportional to spawning stock biomass in all stocks (Takasuka et al., 2019), we chose this approach to ensure consistency across stocks with and without information of total egg production per kg of spawning biomass. We further related recruitment to the abundance of the preceding cohort, assuming that larger fish are at a competitive advantage over smaller fish (Hoare et al., 2000). If food abundance is limited or predation mortality increases with abundance, we expect to see a decrease in recruitment success at high initial cohort size. We note that other environmental variation may also occur.

If food production is constant, the relevant measure of density for impacts on growth is the food consumption by the competing fish. Most fish show pronounced ontogenetic shifts from early life to later life, and hence, the recruiting cohort is likely to compete mainly with individuals in the same cohort (Hoare et al., 2000). While there may be some variation in the weight of individuals within the cohort, this is likely to be much less than the variation in number of recruits. Hence, for the youngest age group observed, weight at age was compared to the number of individuals in the cohort. This test retains the statistical independence between the dependent and independent variables which is not the case if the biomass of recruits is used instead of the number of recruits (Supplementary Material).

For older age groups, the diet often overlaps to a greater degree with that of adjacent cohorts and hence inter-cohort competition can be of importance. If we assume that consumption in a given year (B_y) is proportional to weight$^{3/4}$ (Brown et al., 2004), this makes the relevant density index

$$B_y = \sum_{a=a_{\min}}^{a_{\max}} N_{a,y} W_{a,y}^{3/4}$$

where $N_{a,y}$ is the number of fish of age a in year y, and $W_{a,y}$ is the body weight of fish of age a in year y. Total consumption reflects body

weight; however, annual estimates of B_y are not statistically independent of annual estimates of weight at age and hence the analyses of growth as a function of B_y are likely to be biased. The correlation between weight at age and total consumption each year can be reduced by estimating total consumption using mean weight at age throughout the time series

$$B_y^* = \sum_{a=a_{\min}}^{a_{\max}} N_{a,y} \overline{W}_a^{3/4}.$$

Simulation analyses showed that these measures were indeed unbiased and sensitive to the presence of density dependence when compared to the growth measures listed below (Supplementary Material).

An overview of the hypotheses and the associated tests are given in Table 1. In all cases, the effects may persist over time or may occur only in restricted periods of time and may relate to the temporal contrast in data or the direction of the development in density (increasing, decreasing or fluctuating stock size). For all three measures of density (SSB, recruitment, B_y^*), the contrast in the data was defined as the difference in the 90th and 10th percentiles of the log-transformed density measure (large values indicate large contrast in data, zero indicates no contrast). Stock trends were identified based on the significance level and direction of the correlation between the density measure and year (Figure S1).

In addition to the contrast and long-term stock development, a measure of inter-annual variability was derived as the r^2 of a loess fit to the log-transformed density measure (indicating the proportion of variation explained by long-term changes, Spencer & Collie, 1997). We used the loess.as function in the fANCOVA package in R to automate the selection of the 'span' smoothing parameter. We expect that density dependence is most easily determined where contrast and long-term change is large and inter-annual variability is small.

2.3 | Recruitment

The dominant models for the relationship between stock size and recruitment, Beverton-Holt and Ricker, are very similar in their prediction of the relationship between recruitment and stock size at low abundance. However, they differ in the predicted relationship at high stock size, the Ricker model predicting a decrease in recruitment, whereas the Beverton-Holt relationship predicts no change or a slight increase in recruitment as stock size continues to increase and carrying capacity is approached. We do not wish to prejudge the shape of this relationship in this study, and therefore we employ a more general model suggested by Cadigan (2013). The Cadigan model encompasses both decreasing, constant and increasing recruitment at high stock size (Cadigan, 2013, Supplementary material) and can mimic both proportional increase, Ricker and Beverton-Holt type relationships (Figure 1).

The model was formulated with smoothing parameters $k = 20$ and $sp = 0.01$ to provide enough flexibility to capture the trends in the data. In some cases, this resulted in unrealistic model behaviour, with recruitment increasing, then decreasing, and then increasing again as SSB increased. In these cases, sp was set to 0.1 to increase the amount of smoothing. For comparison, we included a model with a proportional relationship between recruitment and spawning stock biomass ($\hat{R} = aSSB$) as this is the relationship that should appear in the absence of any density dependence. Subsequently, we evaluated which of the two models resulted in the lowest AIC. One stock, for which recruitment occurred at age 5 was not included in the analysis of recruitment as by this time, the number of fish in the cohort may have been affected by large differences in mortality due to reasons unrelated to density.

The Cadigan model assumes that the variance of SSB estimates are negligible compared to those of recruitment estimates. If this assumption is not valid this could potentially affect the estimated stock recruitment relationship (Walters and Ludwig, 1981; Kehler et al., 2002; Kope, 2006; Cadigan, 2009). To address this issue, the stock recruitment relationship can be estimated within the assessment model, thereby accounting for variance and covariance of recruitment and SSB in the estimation of the stock recruitment function. This was possible for a selection of stocks assessed using the state-space assessment model (SAM, Nielsen & Berg, 2014) at stockassessment.org or through personal correspondence. For these cases, a stock recruitment relationship similar to the Cadigan model (compensatory mortality property or CMP spline, Albertsen & Trijoulet, 2020) was estimated internally in SAM and the resulting steepness and overcompensation compared to those derived when estimating the relationship externally from the stock assessment using both the CMP spline and the Cadigan model.

We analysed the probability that a stock is best fitted by a non-proportional (density-dependent) relationship using general linear models assuming binomial distributed observations. We included model effects for species, ecotype and SSB (decline/no trend/increase across all observations) and continuous effects of interannual variation and contrast in SSB.

As additional measures of the strength of density dependence, we estimated the steepness h of the estimated Cadigan relationship:

$$h = \frac{\hat{R}(0.2 * \max(SSB))}{\max(\hat{R}(SSB))}$$

where $\max(\hat{R}(SSB))$ is the maximum recruitment predicted from the estimated relationship and $\hat{R}(0.2 * \max(SSB))$ is the predicted recruitment at a spawning stock biomass of 0.2 times the maximum observed spawning stock biomass, $\max(SSB)$ (Punt & Dorn, 2014). Steepness can only take values from 0.2 to 1, and h was transformed to produce a measure that is continuous on $(-\infty, \infty)$ for further analyses:
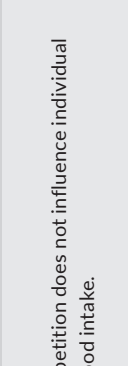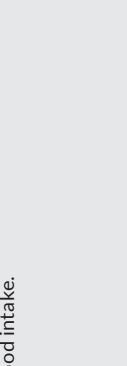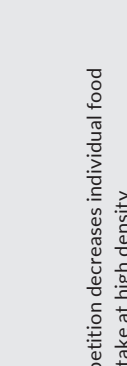
$$logit(h) = ln\left(\frac{h}{1-h} - 0.25\right).$$

TABLE 1 Overview of hypotheses of density-dependent effects on recruitment and growth and associated tests

	Hypothesis	Prediction	Test	Example
Recruitment				
No density dependence	Mortality in the pre-recruit stage is not density-dependent	Recruitment increases proportionally with initial cohort abundance, indicated by spawning stock biomass	AIC of a proportional relationship exceeds that of non-proportional relationships	
Compensation	Density dependence leads to increased mortality at higher abundance.	Recruitment increases with initial cohort abundance to an asymptote, after which there is no significant change	AIC of a non-proportional relationship exceeds that of proportional relationships. Further, low steepness indicates small distance of the stock from the proportional relationship and vice versa	
Over-compensation	Density dependence leads to decreased survival as abundance increases.	Recruitment increases with initial cohort abundance up to a maximum, after which there is a significant decrease with cohort abundance	Predicted recruitment at maximum observed biomass is smaller than lower confidence interval of maximum predicted recruitment	
Depensation	Predator satiation leads to increased survival beyond the satiation level	Recruitment at low stock size is lower than expected in the stock recruitment relationship	The mean of residuals from the predicted stock recruitment relationship at low SSB significantly less than zero	

(Continues)

TABLE 1 (Continued)

|	Hypothesis	Prediction	Test	Example
Growth				
No density dependence	Competition does not influence individual food intake.	No relationship between growth and density	Correlation between density and growth measure not significantly different from zero	
Weak negative density dependence	Competition decreases individual food intake at high density	Decreased growth at high density, random variation at low density	Probability of having above median growth at above median density less than 0.25	
Strong negative density dependence	Competition decreases individual food intake at all densities	Decreased growth as density is increased	Correlation between density and growth significantly less than zero	
Apparent positive density dependence	Increased food availability leads to increased recruitment, increased growth and increased biomass	High recruitment success initially co-occurs with high growth as increased food abundance enhances both. The correlation between the two disappears if the new state persists long enough for food abundance and stock size to once again be in balance around a new level.	Correlation between density and growth significantly greater than zero	
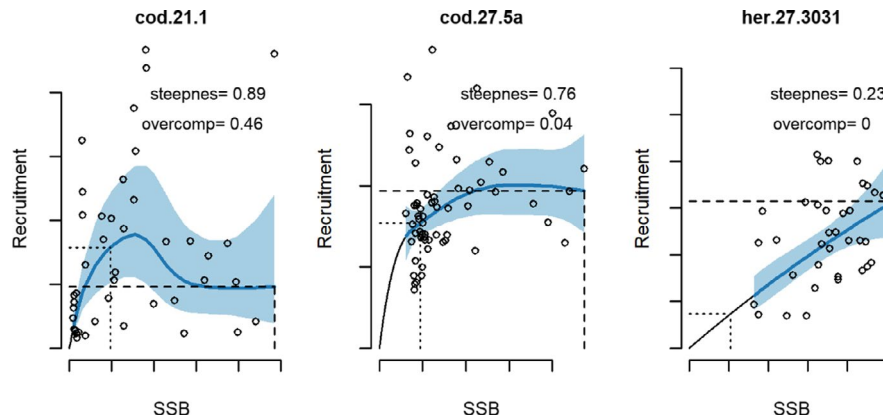
FIGURE 1 Examples of the fit of the Cadigan model (thick blue line), with 95% confidence interval around the curve (shaded) and the resulting steepness (vertical dotted line) and overcompensation (difference between the maximum recruitment and the predicted recruitment at maximum biomass (broken horizontal line). Examples are chosen to represent overcompensation in a Ricker-like relationship (left panel: West Greenland cod), compensation in a Beverton-Holt-like relationship (middle panel: Cod around Iceland) and an almost proportional relationship (right panel: Gulf of Bothnia herring)

The effects were analysed in a general linear model assuming the logit was normally distributed, analysing fixed effects of species, ecotype and stock decline/no trend/increase and continuous effects of interannual variation and contrast in SSB.

Overcompensation (OC) of the estimated relationship was defined as:

$$OC = 1 - \frac{\widehat{R}\left(\max(SSB)\right)}{\max\left(\widehat{R}(SSB)\right)}.$$

Overcompensation was analysed in two models, one for the probability of a stock exhibiting significant overcompensation (assuming binomial distributed observations) and one for the logit transformed OC:

$$logit(OC) = ln\left(\frac{OC}{1 - OC}\right).$$

Stocks with $OC = 0$ were omitted from the analyses using logit transformed data. Both the probability of exhibiting significant overcompensation and the degree of overcompensation were analysed in a general linear model with effects described above. Estimated values were transformed back to OC before presenting the results. In the proportional model, h is 0.2 and OC is 0 by definition. Overcompensation was recorded as significant if the predicted recruitment at the maximum observed stock size max(SSB) was below the confidence interval of the maximum recruitment predicted within the range of observed spawning stock biomass. After deriving estimates of steepness and the probability of significant overcompensation, these were tested for significant differences between habitat types, asymptotic length of the species (derived from Rindorf et al., 2020), contrast and trend in spawning stock observations using general linear models with a normal and binomial error distribution respectively.

We investigated evidence of depensation (lower recruitment than proportional at low stock size) by testing if the average log

residual at SSB less than 0.2 times the maximum observed biomass was significantly less than zero, analysing the 47 stocks that had at least five SSB values below 0.2 max (SSB). We also tested if recruitment decreased following a large cohort, which can be caused by e.g. competition for low mortality habitat, by estimating the autocorrelation in log recruitment. The length of the time series affects estimates of steepness and overcompensation by changing the maximum observed spawning stock, and hence estimates of temporal changes in steepness and overcompensation were not conducted.

2.4 | Growth

The growth measure used must be responsive to changes caused by density in any individual year but preferably not the previous or subsequent year. This is particularly important for species where the biomass may fluctuate greatly between years, as is often the case for short lived species. Furthermore, it is important that the measure has a high power to detect density dependence with high precision. We distinguish between measures to detect growth changes early in life (growth to the age of first occurrence in the fishery data) and subsequent growth (growth after the age of first occurrence in the fishery). This eliminates any impact of growth later in life on estimates of early growth, in contrast to using methods based on estimating cohort growth curves (e.g. von Bertalanffy, 1938). Furthermore, it allows us to use all data regardless of the number of times a cohort has been observed whereas estimation of the von Bertalanffy curves rely on the observation of a minimum of three age groups (one for each parameter to be estimated). To determine the most appropriate combination of growth and density measures, we first conducted a simulation study to determine the combination that provides high power to detect density dependence when it occurs and the lowest risk of detecting it where it is not (Supplementary Material).

2.4.1 | Early growth

The effect of density dependence on juvenile growth was analysed by relating the weight at age of each species at the youngest age consistently observed to recruitment numbers of the cohort. To obtain reliable results, weight at age must be consistently sampled and reflect cohort growth rather than differences in catchability due to changes in survey time relative to the growth period. This was ensured by eliminating ages for which weight at age was not significantly correlated to the weight at age of the same cohort in the subsequent year. The analyses were performed on log transformed data as variance of both numbers and weight at age increased with the mean. A drawback to this method is that the initial age will depend on how sampling was conducted as well as the biology of the fish stock. Recruitment and weight at age were matched to be that of the cohort.

2.4.2 | Late growth

Based on the results of the simulation analyses (Supplementary Material), we chose the growth measure expressing weight at age in units of standard deviations from the mean as done by Shephard et al. (2014):

$$G_{\text{late},y} = \frac{1}{A} \sum_{a=a\min}^{a=a\max A} \left(\frac{w_{a,y} - \overline{w_a}}{\text{std}(w_a)} \right)$$

This measure has the advantage of integrating annual effects in a single measure. However, by doing so, the measure tends to smear out cohort effects caused by rapid or slow growth in the first year of life. To avoid this affecting longer time periods, we used only three age classes for all stocks. The ages were chosen as 1–3 ages above the youngest age with consistent weight at age data.

2.4.3 | Analyses of density dependence of growth

The presence of density dependence in growth (weight at the youngest age and ln$R$ for early growth and G_{late} and lnB^* for late growth) was investigated in two analyses: (1) estimation of correlation between the growth and the density measure and (2) quadrant analysis of the frequency of data points in each of the combinations of above median/below median of growth and density measures. If there is no evidence of density dependence at low and high density, we expect the correlations to be insignificant. If there is no evidence of density dependence at high density, we expect the probability of each combination of above or below average of growth measures and density to have the same probability (all quadrants are equally likely corresponding to 25% probability of a point being in a given quadrant). Furthermore, to investigate the effect of density dependence on growth, we estimated a linear relationship between early and late growth and the relevant density measure and used this to predict relative weight change when density increased from the minimum to the maximum observed:

$$\Delta w_{\text{early}} = \sigma \left(G_{\text{early,}} (\max(R)) - G_{\text{early}}(\min(R)) \right)$$

and

$$\Delta w_{\text{late}} = \sigma \left(G_{\text{late}}(\max(B^*)) - G_{\text{late}}(\min(B^*)) \right)$$

where σ is the average coefficient of variation as described in the Supplementary Material. For comparison, density dependence in recruitment including both steepness and overcompensation was estimated as 1-R(max(SSB))/(5*R(0.2*max(SSB)), corresponding to assuming that no density dependence would result in a proportional relationship through the point (0.2*max(SSB), R(0.2*max(SSB))) on the estimated stock recruitment relationship.

We repeated the correlation analyses for a moving window of 20 years, resulting in measures revealing the long-term variation in the density dependence of growth. The moving window analyses will identify positive relationships between survival and growth without reacting to long-term correlations between the number of recruits and the mean weight at age of the youngest age caused by environmental changes increasing both factors simultaneously.

In addition to the above analysis of early growth and density, we investigated the evidence for positive effects of growth on survival of juveniles by relating mean weight to residuals from the stock-recruitment relationship, as positive residuals indicate greater than average survival. After deriving estimates of correlation between growth and density for each of the two measures as well as the probability of significant negative and positive correlations, these were tested for significant differences between habitat types, range and trend in density using general linear models with a normal and binomial error distribution.

3 | RESULTS

3.1 | Recruitment

Among the stocks investigated, the relationship between recruitment and spawning stock biomass was better described by a density-dependent (non-proportional) relationship in 54 out of 79 stocks, corresponding to significant density dependence in 68% of the stocks (Figure 2, Table S2, Figure S2). The probability of the relationship being density-dependent differed significantly between pelagic stocks exhibiting different trends in SSB ($p = 0.0006$). This was not the case for the other two ecotypes ($p = 0.1784$). No other factor had a significant effect. The probability of no density dependence was 0.22 (confidence interval 0.14–0.34) for benthic/demersal and pelagic stocks exhibiting no significant trend, 0.50 (confidence interval 0.20–0.80) for significantly declining pelagic stocks and as high as 0.87 (confidence interval 0.46–0.98) for significantly increasing pelagic stocks. Correspondingly, the probability of significant compensatory density dependence was 0.78 (confidence interval

FIGURE 2 Steepness (left) and overcompensation (middle) of the stock-recruitment relationship for each species group (benthic, demersal, pelagic) for all stocks and for stocks where density dependence or overcompensation is significant (right). Numbers in the top of the boxplots refer to the numbers of stocks included
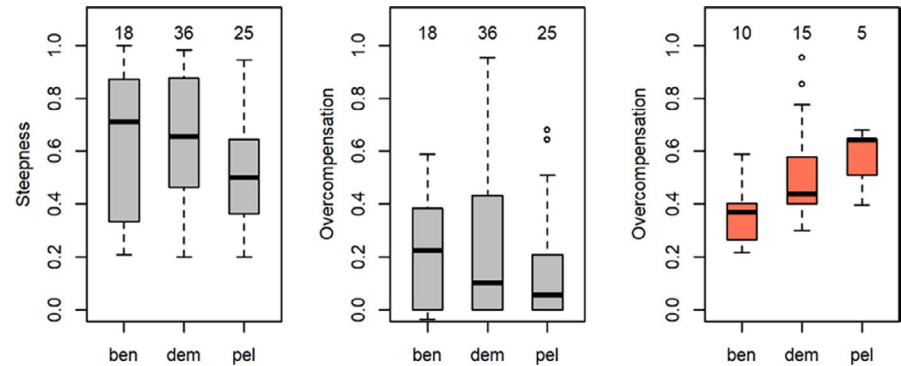

TABLE 2 Overview of density-dependent effects on recruitment and growth

	Pelagic	Benthic	Demersal	All	Depends on
Recruitment					
Total number of stocks	25	18	36	79	
No density dependence (recruitment proportional to SSB)	48%	11%	31%	32%	Pelagic stocks exhibiting significant trends in SSB significantly less likely to exhibit density dependence than other stocks.
Compensation (Beverton-Holt- type)	44%	39%	31%	37%	Pelagic stocks exhibit significantly lower steepness and hence weaker density dependence than benthic/demersal stocks
Over-compensation (Ricker-type)	8%	50%	39%	32%	Benthic/demersal stocks significantly more likely to exhibit strong density dependence than pelagic stocks
Early growth	Pelagic	Benthic	Demersal	All	
Total number of stocks	22	17	30	69	
No density dependence	73%	88%	70%	75%	No significant differences
Weak negative density dependence (quadrant)	9%	6%	10%	9%	No significant differences
Negative density dependence (correlation)	23%	12%	13%	16%	No significant differences
Positive density dependence	5%	0%	17%	9%	No significant differences
Later growth	Pelagic	Benthic	Demersal	All	
Total number of stocks	20	14	27	61	
No density dependence	50%	21%	41%	39%	No significant differences
Weak negative density dependence (quadrant)	20%	14%	19%	18%	No significant differences
Negative density dependence (correlation)	50%	71%	48%	54%	No significant differences
Positive density dependence	0%	7%	11%	7%	Within range expected from type−1 error

Note: Percentage of stocks for which the hypothesis provided the best fit to data/total number of stocks in group.

0.66–0.86) for benthic/demersal stocks and pelagic stocks exhibiting no significant trend in SSB, 0.50 (confidence interval 0.20–0.80) for significantly declining pelagic stocks and 0.13 (confidence interval 0.02–0.54) for significantly increasing pelagic stocks. Among the 54 species showing significant density dependence, the steepness of the stock recruitment curves ranged from 0.29 to 1 with a median

of 0.79 (Figure 2). A total of 10 and 25 stocks of the 79 had a steepness greater than 0.90 or 0.75, respectively, corresponding to at least 90% and 75% of the maximum recruitment being attained at only 20% of the maximum spawning biomass. There was no significant effect of species, asymptotic length, contrast in spawning stock biomass, interannual variability, stock development or ecotype.

A total of 30 of the 79 stocks (38%) showed statistically significant overcompensation (i.e. decreased recruitment at high stock sizes) (Figure 2). Although the degree of overcompensation ranged from 0 to 0.95, with a median of 0.08 when examining all stocks (Figure 2), the average overcompensation was 0.22 and 0.44 among the stocks which showed significant density dependence and significant overcompensation, respectively. Significant overcompensation was only observed in stocks with a steepness greater than 0.33 (Figure S3). Among the stocks with density-dependent recruitment, the probability of a stock exhibiting significant overcompensation did not differ between benthic and demersal stocks ($p = 0.9874$) but pelagic stocks were significantly less likely to exhibit overcompensation (probability 0.15, 95% CI 0.04–0.45) than demersal/benthic stocks (probability 0.56, 95% CI 0.41–0.70) ($p = 0.0211$)(Figure 2). There were no significant differences between species or types of stock development in the degree of overcompensation (*OC*).

The comparison between the internally fitted CMP model and the externally fitted CMP and Cadigan models was complicated by the large sensitivity of the estimated relationships to choices of smoothing parameters in the CMP. For the stocks where robust results were attained, neither steepness nor overcompensation differences between internal and externally estimated CMP and the Cadigan model were significantly different from zero ($p > 0.1465$). The confidence intervals of the estimated curves were slightly larger in internal than external CMP. In conclusion, there may be minor effects of estimating the stock recruitment relationship externally, with overcompensation and the occurrence of significant overcompensation likely to be slightly more affected than steepness.

Only two of the 79 stocks (2.5%) showed significantly negative residuals below 20% of maximum spawning stock, a pattern consistent with depensation, which supports our decision not to include a depensatory recruitment model, as the proportion is less than the 5% expected by type 1 error. The results are summarised in Table 2.

3.2 | Early growth

Only 17 of the 69 stocks (25%) exhibited a significant correlation between recruitment and weight of the cohort at the youngest age observed (Figure 3, Table S4, Figure S4). Among these, negative relationships were more frequent than positive relationships (11 negative and 6 positive significant relationships). The effect on early growth was closely related to the correlation coefficient. There was no significant effect of trend in recruitment, species, ecotype or stock development on the correlation ($p > 0.05$). The probability of achieving a negative correlation between early growth and recruitment was significantly higher than the 0.05 expected from type-1 error (probability 0.17, 95% confidence interval (0.10, 0.28)) with no difference between species, ecotypes or stock development ($p > 0.05$). The probability of achieving a significant positive correlation did not exceed that expected by type-1 error significantly (probability 0.09, 95% confidence interval (0.04, 0.18)). There was no

significant over-occurrence of above-average growth at below average abundance (Figure S5).

The correlation between growth and abundance of benthic and demersal stocks was centered around 0 for the stocks having sufficient observations to perform the moving window analyses (Figures 4 and 5). In contrast, the correlation of pelagics showed considerable changes over time (range of loess 0.7 on average), varying from a correlation close to 0 to a substantial negative correlation (Figure 5). Investigating the evidence for individual growth enhancing cohort survival, there was a significant positive relationship between growth and residuals from the stock recruitment curve in four out of 69 stocks, corresponding to 5.8% and hence the level expected by type 1 error alone. In contrast, 14 of the 69 stocks showed a significant negative relationship between growth and residuals from the stock recruitment curve, indicating that a higher than expected year class generally experienced less than average growth. There were no clear tendencies when comparing fish groups (Supplementary Material, Fig. S6).

3.3 | Late growth

Thirty-seven of the 61 stocks (61%) investigated exhibited a significant correlation between total stock biomass and late growth (Figure 6, Table S5). Negative relationships were much more frequent than positive relationships (33 negative and 4 positive significant relationships) (Figure 6). The probability of obtaining a significant negative correlation was 0.54 (95% confidence interval (0.42, 0.66), significantly larger than the 5% expected from type-1 error, and it did not differ significantly between any of the factors tested. The probability of significant positive correlations was 0.07 (95% confidence interval (0.03, 0.14)), which is not significantly different from the 5% expected from type-1 error.

The quadrant analysis supported the occurrence of strong density dependence in late growth in many stocks, as 45 of the 61 showed lower than average growth at higher than average biomass (benthic: 13 out of 14 stocks, demersal: 19 out of 27 stocks and pelagic: 13 out of 20 stocks). At below average abundance, an over-occurrence of above average growth was seen in 40 out of 61 stocks (benthic: 12 out of 14 stocks, demersal: 15 out of 27 stocks and pelagic: 13 out of 20 stocks) (Figure S7).

The correlations of the demersal stocks having sufficient numbers of observations to perform the moving window analyses showed a very large variation in the correlation over time, with both large negative and moderate positive correlations (Figure 7). In contrast, the correlation of benthic and pelagic stocks changed little over time and were almost exclusively negative (Figure 7).

There was a tendency for the correlations between density and growth to be positively correlated for early and late growth of a stock, but the correlation was not significant ($p > 0.08$, Figures S8–S12). There were no significant correlations between steepness, overcompensation and the change in relative growth of a stock at observed densities ($p > 0.39$, Figures 8, S12). Of 60 stocks,

FIGURE 3   Relationship between weight at the youngest observed age and cohort abundance. Top left: correlations estimated between growth and recruitment by species group. Remaining plots: Change in growth from minimum to maximum observed recruitment as a function of correlation (top right, red indicates significant correlations ($p < 0.05$)), by species groups for all species (bottom left) and by species groups where the correlation is significant (bottom right). Ranged from +34% to −33% with neither of these extremes being significant correlations. The effect on early growth ranged from −5% to −29% among the significant negative correlations
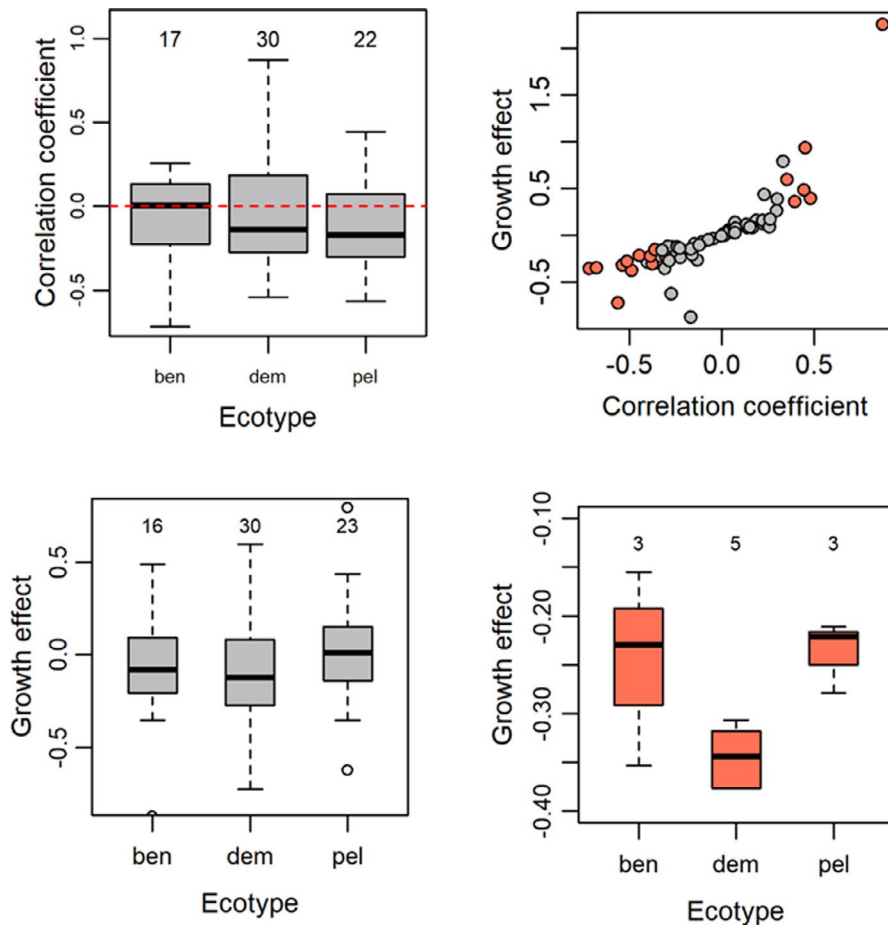
24 showed both significant negative density dependence in growth and significant density dependence in recruitment whereas 14 out of 60 stocks showed both significant negative density dependence in growth and significant overcompensation. Only 8 stocks of the 60 examined did not show significant density dependence in any of the analyses. Comparing predicted density dependence in recruitment and growth in the range from 0.2 to 1 times the maximum observed biomass and hence correcting for differences in the range of densities included in the analyses of recruitment and growth (Figure 8, right panel), the effect of density on recruitment exceeded the effect of density on growth in 50 out of 60 stocks.

The results of all analyses are summarised in Table 2.

4 | DISCUSSION

Density dependence in recruitment and late growth occurred in the majority of stocks, whereas density dependence was uncommon in early growth. Benthic stocks were more likely to exhibit density-dependent growth than demersal and pelagic stocks, and pelagic stocks with trends in stock size had lower probabilities of density dependence in their stock-recruitment relationship than benthic and demersal stocks. If habitat size of pelagic species is larger than that of benthic species, the pattern in density dependence confirms the predictions of Andersen et al. (2017) that density dependence of

larger species in medium sized habitats may occur later than that of smaller species in larger habitats.

Density dependence in stock recruitment was by far the most common relationship. Across all stocks, 68% exhibited significant density dependence, and the probability of occurrence was even higher (78%) when pelagic stocks exhibiting significant trends in spawning stock biomass were excluded. This level is the same order of magnitude as that found in a study of 16 marine and freshwater fish populations (Lorenzen, 2008) and a meta-analysis of recruits per spawning biomass as a function of spawning biomass (assuming a Ricker curve, Zimmermann et al., 2018). The relationships estimated here were significantly density-dependent when tested against the null model of proportional recruitment. Considering the degree of curvature of the stock-recruitment relationships, 13% of the stocks of the stocks had steepness values above 0.9 and 32% were above 0.75. For the remaining 55% of the stocks, recruitment would therefore already be seriously impaired before biomass fell below $20\%B_{max}$ and presumably therefore also 20% of the average unfished biomass, a reference point that is frequently used as lower limit (AFMA, 2007). Likewise, limits of 0.40–0.60 times virgin biomass would not ensure full recruitment of all stocks (AFMA, 2007; Pikitch et al., 2012). In fact, in 22%–32% of the stocks, there was no density dependence in recruitment success, indicating that a decrease in stock density would lead to a decrease in average recruitment regardless of the density at which it occurred. We did not find a
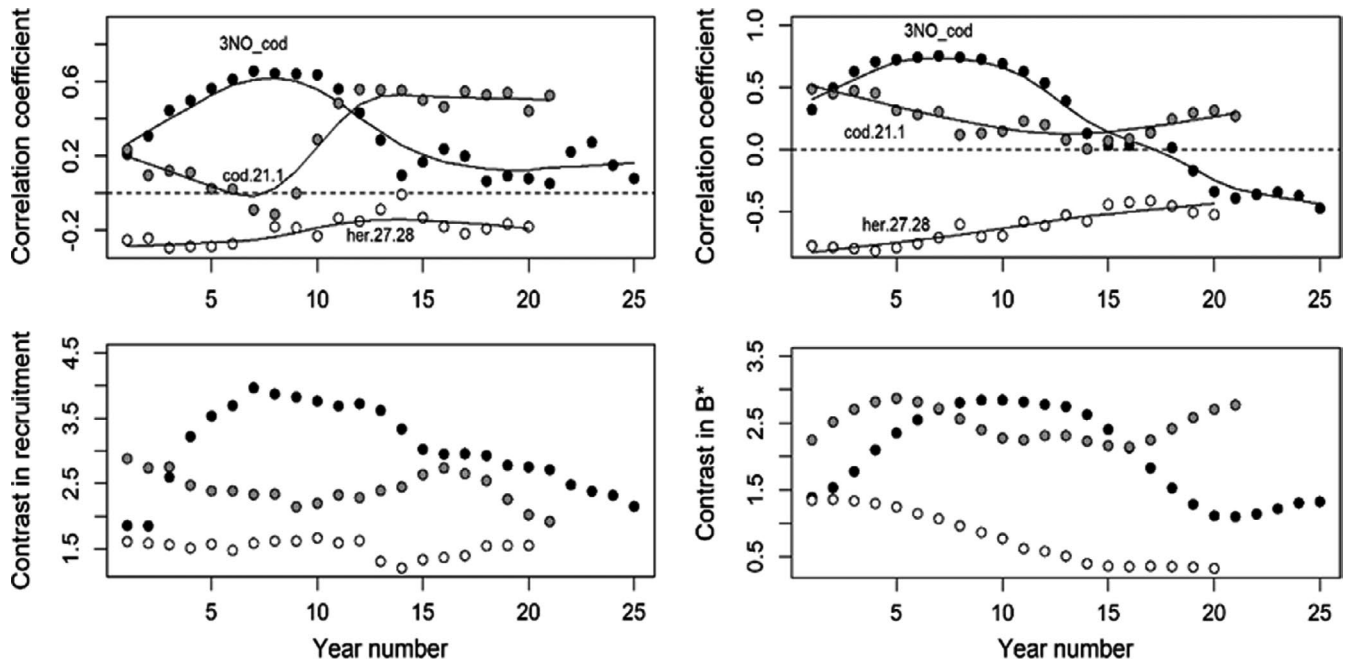
FIGURE 4 Examples of moving window analyses of early (upper left) and late (upper right) growth and density. Lower left and lower right panel show the contrast in density (recruitment and B^* respectively). Black: Cod.3NO. Grey: Cod.21.1. Open circles: Her.27.28
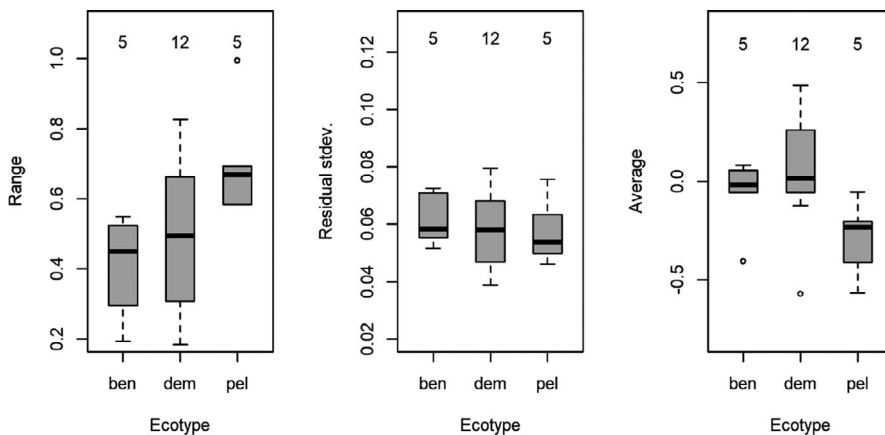

FIGURE 5 20-year moving window analyses of correlation coefficients between early growth and cohort abundance. Range denotes the range (maximum-minimum) of the loess of correlation as a function of start year of the moving window, residual standard deviation is the variation around the loess and finally, average is the average correlation across all moving window analyses for a stock. Numbers above boxes denote number of stocks included

significant effect of asymptotic length on steepness or overcompensation, in accordance with Thorson (2020) but contrary to Goodwin et al. (2006), whose analysis examined derivatives of fitted Ricker and 'hockey stick' stock recruitment relationships. It is unclear if the difference in results is related to our use of a more flexible stock recruitment relationship and hence in effect a structural effect rather than an underlying biological difference. There was no significant evidence for depensation occurring more frequently than what is expected by chance, confirming previous results of Myers et al. (1995) and Hilborn et al. (2014).

Only half the pelagic stocks exhibited significant density dependence in recruitment and only 8% showed significant overcompensation. This difference from benthic and demersal stocks seemed to be linked to lower density dependence when there were significant trends in stock size. These trends can occur when there are changes in stock productivity, effectively meaning that two stock recruitment

relationships are overlayed in the relationship for the full period. If one productivity period has low SSB and low recruitment and the other high SSB and high recruitment, overlaying the two in one relationship gives the appearance of a linear relationship (Szuwalski et al., 2015). Hence, a higher frequency of changes in early survival rates of pelagic fish than occur in the more stable demersal communities may be the cause of the difference between the ecotypes.

Overcompensation occurred most frequently for benthic and demersal stocks. These stocks often settle to bottom habitat that is already inhabited by older conspecifics. Furthermore, most demersal stocks feed on larger items than pelagic fish of the same size, which allows them to be opportunistic cannibals (Bogstad et al., 1994; Link et al., 2009; Uzars & Plikshs, 2000). Pelagic fish often school together with individuals of similar size (Hoare et al., 2000), thereby effectively limiting the interaction between adults and juveniles. Their smaller mouth gape width further limits cannibalism and

FIGURE 6 Relationship between late growth and total stock biomass. Top left: correlations estimated between late growth and total stock biomass by species group. Remaining plots: Change in growth from minimum to maximum observed total stock biomass as a function of correlation (top right, red indicates significant correlations ($p < 0.05$)), by species groups for all species (bottom right) and by species groups where the correlation is significant (bottom left)
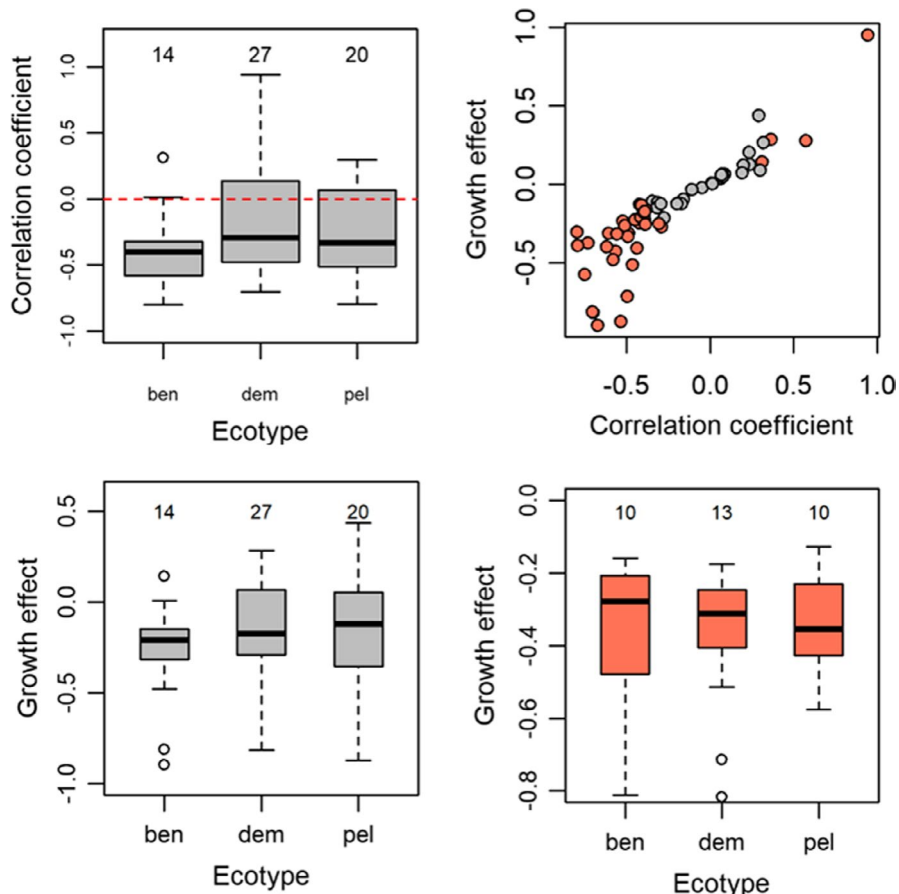

FIGURE 7 20-year moving window analyses of correlation between late growth and total biomass. Range denotes the range (maximum-minimum) of the loess of correlation as a function of start year of the moving window, residual standard deviation is the variation around the loess and finally, average is the average correlation across all moving window analyses for a stock. Numbers above boxes denote number of stocks included
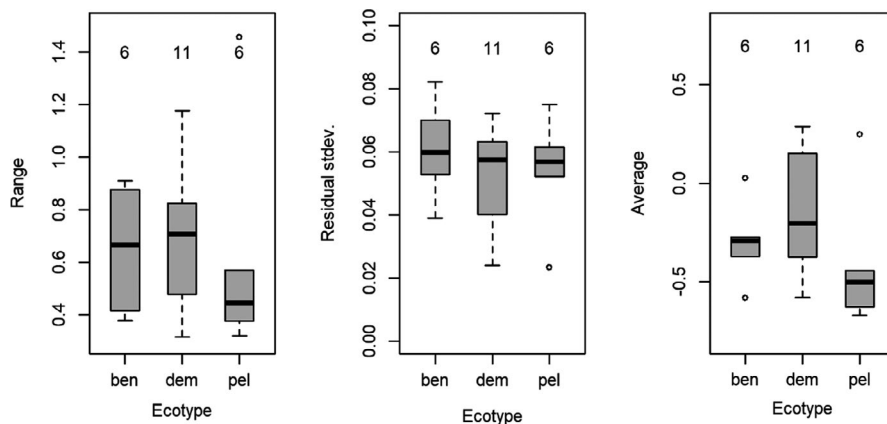
thereby potential overcompensation. In benthic fish, overcompensation must be linked to competition for either food or space or both (Biro et al., 2003) as most benthic fish have insufficient gape width to cannibalise settling juveniles.

Lack of density dependence in early growth is consistent with the food competition hypothesis if food abundance varies greatly between years for reasons unrelated to fish density. Most fish stocks feed on zooplankton at some stage during the recruitment phase, but only pelagic planktivores continue this diet throughout their life span. Zooplankton biomass is often considered highly variable, even if the variation between years seems lower after accounting for the various sampling artefacts (Beaugrand & Reid, 2003). The recent interdecadal changes in planktonic food abundance (Mackas &

Beaugrand, 2010) may confound the use of the observed long-term density dependence in growth as a predictor of early growth.

Late growth showed strong density dependence in pelagic, benthic, and demersal stocks. Significant negative relationships between growth and density were common both when modelled as linear relationships and when using quadrant analyses. The relationship was highly consistent over time for pelagic and benthic species, whereas demersal stocks showed greater variability with both large negative and moderate positive correlations. This consistency may indicate a greater predictability over time of the density-dependent relationships of pelagic and benthic stocks. The proportion of stocks showing strong density dependence (54%) is very similar to the 56% of 16 stocks found by Lorenzen
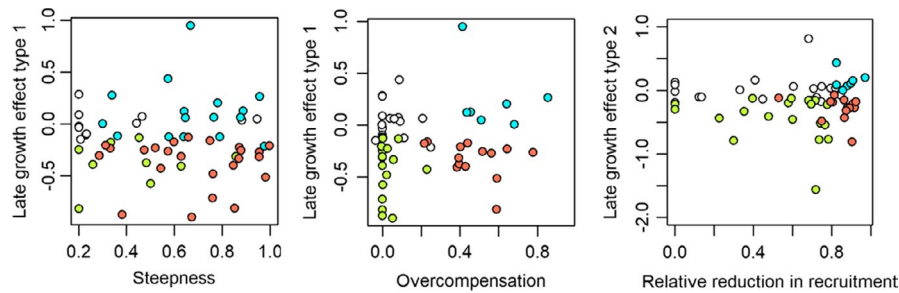
FIGURE 8 Change in late weight at age relative to average weight at age from minimum to maximum observed total stock biomass as a function of steepness (left) and overcompensation (middle) and change in relative weight and recruitment as density changes from 0.2 to 1 times maximum observed stock density (right). Red: density dependence in growth (declines only) and recruitment (left) and growth and overcompensation (right) significant. Green: Only density dependence in growth (declines only) significant. Blue: Density dependence in recruitment (left) and overcompensation (right) but no density dependence in growth. Open: No significant density dependence in growth (declines only) or recruitment

and Enberg (2002) even after including 4 times as many stocks in our analysis. Furthermore, the proportion of stocks with density-dependent growth is substantially higher in our study than in that of Zimmermann et al. (2018), possibly because of our effort to define the most suitable indicator for growth. The consistency of density dependence indicates that at least every second stock is likely to have significant density-dependent growth, and often the effect is at a level exceeding that of overcompensation.

A number of issues could affect our conclusions, and these should be investigated further in the future. Weights at age in our study were derived from stock assessment input data, which are often positively biased for younger ages that are not fully recruited to survey and commercial fishing gear (Du Pontavice et al., 2018, Claireaux et al., 2018). Hence, greater power may be attained in the analysis of early growth by using more consistent information on size, for example derived from scientific surveys. Some of the stocks show trends in mean weight at age, and as prey availability depends on the size of the individual rather than age, density-dependent effects may not be constant over time. This could be one of the reasons for the greater variability in the density dependence in growth of demersal stocks. A more difficult issue is whether growth and survival act together in ways we cannot observe in our analyses of survivors to the age of recruitment to the fishery and beyond. This would be the case if a large recruiting year class experiences food shortage and therefore has a larger proportion of small individuals, which subsequently die from size-dependent mortality. This would leave our observed mean weights unchanged but recruitment decreased as strong size-selective mortality in early life prevents observable effects of food competition on weight. Other methods would be necessary to untangle such situations. The choice of shape of the stock-recruitment relationship has substantial impact on results, as some shapes constrain the types of density dependence that can occur. We used the Cadigan model due to the flexibility it allows and hence its capacity to follow data with few constraints on the shape. The Cadigan model is the same as the Ricker model when the smoothing parameter is very large and may therefore have a tendency to conclude Ricker-type over-compensation when data are noisy.

Our measures of steepness and overcompensation both depend on the observed maximum SSB: if the stock has only been observed at less than half the unfished biomass, steepness will be estimated as half that of a stock which has been observed at near unfished biomass and overcompensation is unlikely to be detected. Other studies (Lorenzen, 2008) have addressed this issue by predicting the biomass in the absence of fishing, but as there are generally no data from periods with sustained lack of fishing, this requires predictions of population dynamics well outside the observed range of densities, potentially introducing structural errors (Miller & Brooks, 2021). Furthermore, the estimated biomass in the absence of fishing is highly dependent on the estimated density dependence, thus leading to circularity in conclusions. In addition to the average relationships between SSB and recruitment, some stocks show occasional very high recruitments which rather unexpectedly succeed in bringing the stock size back from very low levels. Such patterns were not specifically accounted for in our analysis. In addition, our analysis does not correct for the effect that changes in size selectivity in the fishery may have had on both survival and observed mean weight at age (Kvamme & Bogstad, 2007). Where fishing pressure has varied significantly, overall biomass of a stock may be confounded with changes in the age structure, which may result in changes in the nature of any density-dependent relationship. Finally, any changes in productivity related to an expansion of the distribution area need to be carefully examined to determine how the expansion affects density dependence.

Density dependence affects the management of exploited stocks through effects on productivity and reference points. Interestingly, the approach to estimating recruitment in the short-term forecast for the coming one or two years is often a simple long-term geometric mean, even for stocks that are below levels at which recruitment is expected to be impaired. This assumption results in higher estimates of future recruitment and stock size than accounting for the expected decline in recruitment. The higher estimated biomass leads to higher estimates of future catch opportunities, which if implemented work to maintain the stock at low stock size if the recruitment as expected is below the geometric

mean in the coming year. Pelagic stocks showed lower levels of density dependence in recruitment. Hence, pelagic stocks will exhibit greater fluctuations and lower self-regulatory capabilities than benthic and demersal stocks unless mortality is lower at low density and this effect is greater in pelagic than benthic and demersal stocks. Though not considered in this analysis, there is accumulating evidence of time-varying productivity (Tableau et al., 2019), which may affect the estimation of density dependence in recruitment (Claireaux et al., 2022). Time-varying productivity can be implemented in the management system through dynamic reference levels, which may improve performance in terms of both sustainability and yield (Zhang et al., 2020).

While the long-term simulations used to derive reference points such as F_{MSY} and B_{MSY} usually account for density dependence in recruitment, there is typically no accounting for density-dependent growth. A key reason for this may be the effect that including density-dependent growth has on exploitation levels providing MSY; including density dependence means that the gains of having a large population are less. As a result, the level of exploitation that produces MSY is higher than previously thought (Gislason, 1999; Kovalev & Bogstad, 2005; Sparholt et al., 2021) and the selectivity that attains this may involve catching a higher proportion of smaller and younger individuals than at present, particularly in cases where density dependence occurs late in life (Gemert 2018a, 2018b). While increasing the exploitation rate at high stock size may be desirable, including density-dependent growth at low stock size is risky because it will lead to predictions of higher than average growth in the coming two years and higher estimates of catch opportunities, thereby potentially keeping the stock at low levels of biomass for prolonged periods. Hence, it may be preferable for precautionary reasons to assume that density dependence in growth acts at high densities only (equivalent to the 'weak density dependence' in growth examined here). It should also be noted that the negative bias of assuming constant growth may cancel the positive bias of assuming constant recruitment when projecting catch opportunities at low stock size. An improved prediction of stock response to catch levels relies on an adequate understanding of the historical development in the stock, but also requires acknowledging that density-dependent relationships may change over time (Claireaux et al., 2022; Howell et al., 2013). Density-dependent growth implies food limitation, which depends, not only on consumer density, but also on prey density, which may change over time. Based on the results of this study, we recommend routine testing for density dependence in recruitment and growth, especially the late growth period. As even significant relationships between density and growth do not necessarily impact the stocks greatly (Lorenzen, 2008; Stawitz & Essington, 2019), we further recommend evaluating the potential importance of the different sources of density dependence on both productivity and variability (Rose et al., 2001). When warranted, both density-dependent recruitment and growth should be included in calculating reference points and providing short-term catch advice in a way that is compatible with policy principles such as the precautionary principle and MSY.

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