# Supplementary material

## Recruiting age compared to age at 20% of

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. According to Lorenzen and Camp (2019), the biologically relevant age at recruitment at which density dependence has fully acted is the age at which 20% of asymptotic length, , is attained. This age is smaller for rapidly growing (southern stocks or species with high intrinsic growth rate, ) stocks than for slowly growing (northern stocks or species with low )(Brander 1995). For example, the age at which individuals exceed 20% is 0.8 year for North Sea cod, 1.8 years for Barents Sea cod, 0.4 years for North Sea sprat and 1.9 years for ling (Supplementary material). In general, the age at recruitment in the assessment is also higher for northern and slow growing stocks than for southern and rapid growing stocks. For example, North Sea cod recruits in the assessment at age 0, whereas Barents Sea cod recruits at age 3. As a consequence, the age at recruitment and the age at which individuals exceed 20% showed a correlation of 0.96 when comparing values for North Sea cod, plaice, sole, herring and sprat, Barents Sea cod and the widespread stocks of tusk and ling:

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Stock |  | *K* | Age at 20% | Recruitment age in assessment |
| Atlantic cod, North Sea | 119 | 0.27 | 0.8 | 0 |
| European plaice, North Sea | 48 | 0.23 | 1 | 1 |
| Sole, North Sea | 39 | 0.32 | 0.7 | 1 |
| European sprat, North Sea | 14 | 0.63 | 0.4 | 0 |
| Atlantic herring, North Sea | 30 | 0.33 | 0.7 | 0 |
| Atlantic cod, Barents Sea | 129 | 0.126 | 1.8 | 3 |
| Ling | 183 | 0.118 | 1.9 | 3 |
| Tusk | 84 | 0.109 | 2 | 3 |

Growth parameters are derived from Garrod (1967) and Rindorf et al. (2020). Based on this, we infer that the age at which recruitment occurs in our data is unlikely to bias our conclusions.

## Cadigan model implementation

The Cadigan model is implemented using the *scam* R package. This package allows for a variety of shape constraints on the component functions of the linear predictor of the GAM. The constraints involve monotonicity (increasing or decreasing) with options to specify convex or concave shapes. *Scam* use spline smoothers for nonparametric regression. Data are assumed to be independent and from an exponential family distribution with mean μ that is a partially linear function of covariates, , where *g* is a smooth monotone link function and the ’s are unknown smooth functions of the covariates. ’s and ’s must be estimated.

The *scam* package uses spline approximations for the ’s; , where ,…, are unknown spline parameters to estimate and *,…,* are known spline basis functions. The package uses B-spline basis functions. Knots determine the location and shape of the polynomial. The knots are evenly spaced and cover the range of *x*. The shape constraints are based on evenly spaced knots; these constraints are difficult to specify otherwise. A penalty function is used to control the variation in the *γ*‘s. A smoothing parameter determines the contribution of the smoothing penalty function to the total fit function. The *scam* package uses generalized cross-validation or the Akaike information criterion to determine the value of the smoothing parameter. P-splines are penalized B-splines. The package uses various shape restrictions on the spline parameters to ensure the correct shape restrictions on *f.* For example, if *f(x)* is strictly monotone increasing in *x,* and since all B-spline basis functions are nonnegative, then a sufficient condition for this shape constraint (i.e. monotone increasing) is *γi > γi-1*. This is achieved by redefining the parameters as , for *j = 2,…,q*. The *βi‘s* are unconstrained parameters to estimate. The penalty function is based on the squared differences of *β2*,… *βq*. However, the shape restrictions themselves add smoothing and model results are usually not that sensitive to the choice of smoothing parameter.

The scam package option *bs=’mpd*’ produces a monotone decreasing spline smoother. The scam code is simple to use. If the SR data are contained in a R dataframe called dat, then the R code

*scam(log.recruit ~ s(stock.size,bs="mpd"* *,m=2) + offset(log(stock.size)),data=dat)*

will provide nonparametric estimates of a SR curve with the CMP. This R code is more appropriate than the default when recruitment is lognormally distributed. The *s(.)* term represents *log{μ(S)/S}* which is assumed to be a monotonic decreasing function of spawning biomass *S*. The offset term is added to *s(.)* so that the right-hand side of the scam equation represents *log{μ(S)}*.

## Simulation study to determine the most appropriate combination of measures of growth and density

A simulation study was conducted to determine the combination of growth and density measures that provides the greatest probability of detecting density dependence where this is present and the lowest probability of detecting it where it is not present.

### Growth measures

We investigated seven measures of growth as listed below. We investigated their relationship with density and growth by simulating weight at age from the von Bertalanffy growth equation (1938):

Where is asymptotic length, *a*0 is the theoretical age at which length is zero and is instantaneous growth rate at *L*=0 which occurs at *a*=*a*0.

The equation is transformed to weight assuming the relationship where *b* is the condition factor and *α* is the allometric scaling factor.

If condition *b*, allometric scaling *α* or asymptotic length vary over time, this will lead to temporal variation in . If is constant, instantaneous growth rate can vary if *K* varies with time. Both of these factors may change with density. In contrast, *a*0 seems less likely to be affected by density and will hence be assumed constant in the following.

Our requirement is that the metric must be responsive to changes 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 such as is the case for short lived species. This eliminates the benefit of methods estimating cohort specific growth parameters in the von Bertalanffy equation as a general approach (Cook et al. 1999) as these determine a single set of cohort specific growth parameters. It is not of importance to our analysis whether the density dependence acts through a change in *K*, or , so the metric should ideally respond to changes in all three.

Three sets of data were simulated, one with growth independent of density, one with *K* a linear function of ln(density) and one with a linear function of ln(density. For each set, the seven indicators of growth below were estimated.

#### Annual weight change assuming K to be constant

This measure is estimated as

The formulation = *wa*+1*,y*+1 – *wa,y*  is also sometimes used but is not investigated further here. is frequently used in the literature (e.g. Rindorf et al. 2008) and is simple to estimate and explain. If annual changes affect *K* in the von Bertalanffy rather than the other parameters, the measure will not reflect these changes. The measure is more prone to noise than estimates based on a single age because errors occur in both components. The actual value of the measure depends on the initial weight when fish grow according to a von Bertalanffy curve, leading the measure to decrease with age. This issue can be removed by expressing the weight at age relative to the mean weight at age correcting *G2* for dependency on initial weight:

It also holds for this measure that annual changes in *K* will not be reflected. Similar to *G2*, this measure is more prone to noise than estimates based on a single age because errors occur in both components.

An alternative measure based on the same assumption is

This measure is proportional to *W∞* and can be used as an indicator of change in this parameter. If *K* is not constant or incorrectly estimated, the measure depends on weight at age and hence on age.

We expect the measures *G*2, *G*3 and *G*5 to be more noisy than measures based on a single year as they are based on the difference between two observations which both contain observation error. We expect that the measure will be biased if *K* rather than other parameters in the von Bertalaffy is changing.

#### Annual weight change assuming W∞ to be constant

If the von Bertalanffy parameter *W∞* is constant and known and *W*=*bL*3, the measure

is equal to *K*. If the assumptions are fulfilled and correctly estimated, this metric is independent of age. If *W∞* changes over time or is incorrectly estimated, the metric depends on weight at age and hence on age. As was the case with the measures assuming *K* to be constant, we expect these measures to be more noisy than measures based on a single year as they are based on the difference between two observations which both contain observation error. The measure will be biased if *W∞* rather than other parameters in the von Bertalanffy is changing.

#### Average weight anomaly across age groups

This measure has been used by e.g. Clausen et al. (2017) and is estimated as

This measure is likely to show strong results where growth in a year is impacted by a common factor for several ages (e.g. changes in the amount of plankton for planktivorous fish as in the case studied by Clausen et al 2017). The ages are given equal weight, thereby assuming that they carry equal information. If some (younger) ages vary greatly in weight whereas others vary less, the greatly varying age group will determine the average, even if this is caused by e.g. greater measurement uncertainty in this age group.

This problem can be removed by expressing the weight at age in units of standard deviations from the mean and averaging across ages as done by Shephard et al. (2012)

This measure should react to changes in either of *K* and or .

#### Annual weight up to the youngest age observed

Effect of density dependence on juvenile growth can analysed by the weight at the youngest age consistently observed.

= w1,y

This measure responds to changes in both *K* and or .

### Density measures

The relevant density to compare to measures of growth when seeking to detect density dependence is the density relevant to the growth of the individual. If we assume that the abundance of prey is constant, the relevant measure of density is the consumption of the competing fish. If we assume for simplicity in the simulation that consumption is proportional to weight, the relevant density estimate is the total biomass of competitors. 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. While there may be some variation in the weight of individuals within the cohort, this effect is likely to be much less than the large variation in number of recruits. Hence, for the youngest age group observed, it is most appropriate to compare weight at age directly to the number of individuals in the cohort.

For older age groups, the diet often overlaps to a greater degree and hence intercohort competition can be of importance. A common way to address this is to compare weight at age with the total biomass of fish estimated as the product of numbers and age and weight at age. However, these two measures are not statistically independent and hence this approach may introduce relationships where none exists, in particular in cases where one large cohort is dominating the biomass. To eliminate this correlation between weight at age and total biomass in a given year, we estimated total biomass as

Where is the number of fish of age *a* in year *y*.

## Simulation study

We simulated number of incoming recruits (*Na*=0) each year (*y*) for 100 years as 109 times a log-normal distributed error with a mean of 1 and a standard deviation of 0.3. Following this, the number at older ages was calculated as

corresponding to a total annual mortality of 0.5.The first five years and last five years of the timeseries were discarded as these only contain data for some age groups.

Length and weight was estimated using the von Bertalanffy equation (assuming *a*0=0) with year-specific growth parameters. The year-specific growth parameters, *Ky* and *L∞,y*, was calculated as 0.4 and 90 (cm), respectively, times a random normal distributed error with a mean of 1 and a standard deviation of 0.1 (a separate pair of error-values were produced each year, one for K and one for *L∞*) and used to estimate length at age 1. Length () and weight at age at subsequent ages was then estimated as

Biomass was estimated as

Where is the number of fish of age *a* in year *y*.

The growth measures *G*0 to *G*6 were then compared to *B*y to determine if a correlation was detected in this case where none was present. Subsequently, the process was repeated making either the mean of *Ky* or *L∞,y* proportional to ln*B*y.

## Results

The correlation between density and each of the 7 measures is shown in the table below. All measures fulfilled the criteria of having a low correlation between density and the measure when no density dependence is present. The measures *G*1, *G*6 and *G*7 were all highly correlated to *KyL∞,y* regardless of whether the variability was caused by changes in *Ky* or *L∞,y*. These measures also detected the highest negative correlation between the measure and density. The correlation was less strong when the density dependence was in *Ky* than when it was in *L∞,y*. Among the other measures, only *G*3 responded to density dependence and only in *L∞,y*. Based on this investigation, it was decided to proceed with the measure *G*7 for the youngest age group and *G*6 for the older age groups.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Correlation between measure and *KyL∞,y* (probability in brackets) | | | Correlation between measure and ln*B*y (probability in brackets) | | |
| Measure | No density dependence | Density dependence in *Ky* | Density dependence in *L∞,y* | No density dependence | Density dependence in *Ky* | Density dependence in *L∞,y* |
| *G*1 | 0.84 | 0.85 | 0.9 | 0.06 | -0.39 | -0.84 |
| *G*2 | -0.51 | -0.52 | -0.32 | 0.01 | 0.16 | 0.07 |
| *G*3 | -0.03 | 0.13 | 0.63 | 0.06 | -0.16 | -0.75 |
| *G*4 | -0.03 | -0.23 | -0.20 | -0.11 | 0.18 | 0.20 |
| *G*5 | -0.51 | -0.52 | -0.32 | 0.01 | 0.16 | 0.07 |
| *G*6 | 0.78 | 0.80 | 0.89 | 0.05 | -0.37 | -0.84 |
| G7 | 0.96 | 0.96 | 0.97 | 0.04 | -0.39 | -0.75 |

## Deriving relative change in weight at age from minimum to maximum density

Estimating the average relative change in mean weight at age of a stock from minimum to maximum density, from G6 is possible under the assumption that the standard deviation is proportional to weight at age across ages (constant CV). First, the relative change in mean weight of age *a* is estimated as

Note that in this formulation, the relative change can exceed 1. For example, if , 155 and =100, is 1.1. Using the ages 1 to 3 in the example for simplicity, the average relative change across ages is

can be estimated as

where is the average coefficient of variation across the three ages:

The relative change across ages is estimated separately for each stock.

## Comparison between internally fitted CMP, externally fitted CMP and Cadigan models

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. Two stocks (mac.27.nea and whg.27.47d) were fitted by CMP with local minima in the relationship and maximum recruitment predicted below the lowest observed spawning stock. These were excluded from further comparisons. A further 3 stocks showed developments at high spawning stock biomass that were highly dependent on knot locations and these were included in comparisons of steepness but excluded from comparisons of overcompensation. Steepness estimated internally with CMP was on average 0.007 less than when estimated externally with CMP (range -0.029 to 0.015, Table S3) and overcompensation on average 0.032 greater when estimated externally, largely driven by a single value of 0.147 (range -0.027 to 0.147, average when excluding the value of 0.147 was 0.009). Neither steepness nor overcompensation differences were significantly different from zero (P=0.1742 and 0.2538, respectively). Steepness from the Cadigan model was on average 0.028 less than that estimated externally by CMP (range -0.06 to 0.122), but the difference was not significant (P=0.1465). Overcompensation in the Cadigan model was on average 0.0273 less than that estimated externally by CMP (range -0.30 to 0.043), but again, the difference was not significant (P=0.2172). 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.

## References

Brander, K. M. (1995). The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). *ICES journal of Marine Science*, 52(1), 1-10.

Clausen, L. W., Rindorf, A., van Deurs, M., Dickey‐Collas, M., & Hintzen, N. T. (2018). Shifts in North Sea forage fish productivity and potential fisheries yield. *Journal of Applied Ecology*, 55(3), 1092-1101. doi: 10.1111/1365-2664.13038

Cook, R. M., Kunzlik, P. A., Hislop, J. R. G., & Poulding, D. (1999). Models of growth and maturity for North Sea cod. *Journal of Northwest Atlantic Fishery Science*, 25, 91-99.

Garrod, D.J., (1967). Population dynamics of the Arcto-Norwegian cod. *Journal of the Fisheries Research Board Canada* 24(1), 145-190.

Rindorf, A., Jensen, H., & Schrum, C. (2008). Growth, temperature, and density relationships of North Sea cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 65(3), 456-470. doi: 10.1139/F07-150

Rindorf, A., Gislason, H., Burns, F., Ellis, J. R., & Reid, D. (2020). Are fish sensitive to trawling recovering in the Northeast Atlantic?. Journal of Applied Ecology, 57(10), 1936-1947.

Shephard, S., Rindorf, A., Dickey-Collas, M., Hintzen, N. T., Farnsworth, K., & Reid, D. G. (2014). Assessing the state of pelagic fish communities within an ecosystem approach and the European Marine Strategy Framework Directive. *ICES Journal of Marine Science*, 71(7), 1572-1585. doi: 10.1093/icesjms/fsu005

von Bertalanffy, L. 1938. A quantitative theory of organic growth. *Human Biology*, 10: 181–213.

Table S1. Data included in the analyses and assessment for each stock. Stocks are identified using ICES/NAFO area codes in combination with a species name abbreviation. Numbers refer to the time-series length (number of years) available for the analysis. For each stock the species group (popular names) and ecotype is given: pelagics (pel), demersal (dem), and bottom dwelling (ben).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| ICES/NAFO Stock code | Species | Ecotype | SR analysis | Growth-R analysis | Growth-B\* analysis |
| 3LNO\_plaice | American plaice | ben |  |  | 57 |
| ldb.27.8c9a | Megrim | ben | 32 | 32 | 32 |
| meg.27.7b-k8abd | Megrim | ben | 34 | 35 | 36 |
| meg.27.8c9a | Megrim | ben | 32 | 32 | 32 |
| mon.27.78abd | Monkfish | ben | 33 | 32 |  |
| mon.27.8c9a | Monkfish | ben | 39 |  |  |
| ple.27.420 | Plaice | ben | 61 | 61 | 61 |
| ple.27.7a | Plaice | ben | 37 | 36 | 36 |
| ple.27.7d | Plaice | ben | 38 | 38 | 38 |
| ple.27.7e | Plaice | ben | 37 | 38 | 38 |
| sol.27.20-24 | Sole | ben | 34 | 34 | 34 |
| sol.27.4 | Sole | ben | 61 | 54 | 54 |
| sol.27.7a | Sole | ben | 47 | 48 | 48 |
| sol.27.7d | Sole | ben | 36 | 36 |  |
| sol.27.7e | Sole | ben | 48 | 49 | 49 |
| sol.27.7fg | Sole | ben | 47 | 47 | 47 |
| sol.27.7h-k | Sole | ben | 22 | 25 |  |
| sol.27.8ab | Sole | ben | 33 | 34 | 34 |
| tur.27.4 | Turbot | ben | 35 | 36 |  |
| 3NO\_cod | Cod | dem | 56 | 46 | 46 |
| bss.27.4bc7ad-h | Seabass | dem | 34 |  |  |
| cod.21.1 | Cod | dem | 42 | 42 | 42 |
| cod.2127.1f14 | Cod | dem | 44 | 44 | 44 |
| cod.27.1-2 | Cod | dem | 70 | 72 | 72 |
| cod.27.22-24 | Cod | dem | 24 | 24 | 24 |
| cod.27.47d20 | Cod | dem | 55 | 56 | 56 |
| cod.27.5a | Cod | dem | 61 | 64 | 64 |
| cod.27.5b1 | Cod | dem | 59 | 60 | 60 |
| cod.27.6a | Cod | dem | 36 | 37 | 37 |
| cod.27.7a | Cod | dem | 51 | 36 | 36 |
| +-cod.27.7e-k | Cod | dem | 47 | 37 | 37 |
| cod3m | Cod | dem | 40 | 24 | 31 |
| cod3pn4R | Cod | dem | 39 | 39 | 46 |
| codKat2020\_SAM | Cod | dem | 23 | 24 | 24 |
| had.27.1-2 | Haddock | dem | 65 | 38 | 39 |
| had.27.46a20 | Haddock | dem | 47 | 46 | 46 |
| had.27.5a | Haddock | dem | 38 | 37 | 37 |
| had.27.5b | Haddock | dem | 61 | 41 | 41 |
| had.27.6b | Haddock | dem | 27 | 27 |  |
| had.27.7a | Haddock | dem | 26 | 25 |  |
| had.27.7b-k | Haddock | dem | 26 | 23 | 23 |
| hke.27.3a46-8abd | Hake | dem | 41 |  |  |
| hke.27.8c9a | Hake | dem | 37 |  |  |
| lin.27.5a | Ling | dem | 34 |  |  |
| pok.27.1-2 | Saithe | dem | 56 | 38 | 38 |
| pok.27.3a46 | Saithe | dem | 49 | 51 | 51 |
| pok.27.5a | Saithe | dem | 36 | 38 | 38 |
| pok.27.5b | Saithe | dem | 55 | 58 | 56 |
| reb.27.1-2 | Redfish | dem | 23 | 25 | 25 |
| reg.27.1-2 | Redfish | dem | 22 | 23 |  |
| usk.27.5a14 | Tusk | dem | 34 |  |  |
| whg.27.47d | Whiting | dem | 41 | 40 | 40 |
| whg.27.6a | Whiting | dem | 37 | 37 | 37 |
| whg.27.7a | Whiting | dem | 38 | 38 | 38 |
| whg.27.7b-ce-k | Whiting | dem | 20 |  |  |
| ane.27.8 | Anchovy | pel | 30 |  |  |
| cap-icel | Capelin | pel | 36 |  |  |
| cap.27.1-2 | Capelin | pel | 36 | 37 | 46 |
| her.27.1-24a514a | Herring | pel | 28 | 30 | 31 |
| her.27.20-24 | Herring | pel | 28 | 27 | 27 |
| her.27.25-2932 | Herring | pel | 44 | 44 | 44 |
| her.27.28 | Herring | pel | 41 | 41 | 41 |
| her.27.3031 | Herring | pel | 38 | 38 | 38 |
| her.27.3a47d | Herring | pel | 72 | 34 | 34 |
| her.27.5a | Herring | pel | 29 | 31 | 31 |
| her.27.6a7bc | Herring | pel | 61 | 26 | 26 |
| her.27.irls | Herring | pel | 60 | 61 | 61 |
| her.27.nirs | Herring | pel | 38 | 38 | 38 |
| hom.27.2a4a5b6a7a-ce-k8 | Horsemackerel | pel | 38 | 36 |  |
| hom.27.9a | Horsemackerel | pel | 27 | 26 |  |
| mac.27.nea | Mackerel | pel | 38 | 38 | 39 |
| nop.27.3a4 | Norwaypout | pel | 34 | 33 | 33 |
| pil.27.8c9a | Pilchard | pel | 41 |  |  |
| san.sa.1r | Sandeel | pel | 36 | 35 | 35 |
| san.sa.2r | Sandeel | pel | 36 | 35 | 35 |
| san.sa.3r | Sandeel | pel | 33 | 32 | 32 |
| san.sa.4 | Sandeel | pel | 26 | 25 | 25 |
| spr.27.22-32 | Sprat | pel | 44 | 44 | 44 |
| spr.27.4 | Sprat | pel | 45 | 44 | 44 |
| whb.27.1-91214 | Blue whiting | pel | 36 | 37 | 38 |

Table S2. AIC of the Cadigan SR model and the proportional model and values of steepness and overcompensation. Significant overcompensation and trend is indicated by \*.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Stock | AIC proportional model - AIC Cadigan | steepness | Overcompensation | Trend in stock biomass (significant trends in bold) |
| ldb.27.8c9a | 0.32 | 0.31 | -0.01 | 0.00 |
| meg.27.7b-k8abd | 20.70 | 0.67 | 0.05 | 0.00 |
| meg.27.8c9a | -1.10 | 0.21 | -0.04 | -0.02\* |
| mon.27.78abd | 14.78 | 0.87 | 0.30\* | 0.00 |
| mon.27.8c9a | 17.01 | 1.00 | 0.38\* | 0.02 |
| ple.27.420 | 14.74 | 0.76 | 0.02 | 0.00 |
| ple.27.7a | 59.89 | 0.85 | 0.59\* | 0.02\* |
| ple.27.7d | 18.11 | 0.64 | 0.11 | 0.03\* |
| ple.27.7e | 10.73 | 0.75 | 0.23\* | 0.00 |
| sol.27.20-24 | 16.44 | 1.00 | 0.40\* | 0.00 |
| sol.27.4 | 18.18 | 0.88 | 0.52\* | -0.01\* |
| sol.27.7a | -3.92 | 0.33 | 0.22\* | -0.04\* |
| sol.27.7d | 7.60 | 0.55 | 0.35\* | 0.00 |
| sol.27.7e | 0.63 | 0.30 | 0.00 | 0.00 |
| sol.27.7fg | 38.39 | 0.95 | 0.39\* | -0.01\* |
| sol.27.7h-k | 4.51 | 0.53 | 0.00 | -0.02\* |
| sol.27.8ab | 0.40 | 0.29 | 0.00 | -0.01\* |
| tur.27.4 | 60.61 | 0.85 | 0.26\* | -0.01\* |
| 3NO\_cod | -10.19 | 0.20 | 0.00 | -0.05\* |
| bss.27.4bc7ad-h | 11.84 | 0.46 | 0.95\* | -0.02\* |
| cod.21.1 | 27.41 | 0.89 | 0.46\* | 0.00 |
| cod.2127.1f14 | 7.41 | 0.98 | 0.25 | -0.03 |
| cod.27.1-2 | 38.08 | 0.96 | 0.56\* | 0.02\* |
| cod.27.22-24 | -2.96 | 0.20 | 0.00 | -0.05\* |
| cod.27.47d20 | -1.08 | 0.20 | 0.00 | -0.02\* |
| cod.27.5a | 54.15 | 0.76 | 0.04 | -0.01\* |
| cod.27.5b1 | 12.43 | 0.64 | 0.44\* | -0.02\* |
| cod.27.6a | 1.83 | 0.34 | 0.00 | -0.09\* |
| cod.27.7a | 0.00 | 0.20 | 0.00 | -0.05\* |
| cod.27.7e-k | -7.41 | 0.46 | 0.08 | -0.02\* |
| cod3m | 0.00 | 0.20 | 0.00 | -0.04\* |
| cod3pn4R | 11.52 | 0.33 | 0.00 | -0.09\* |
| codKat2020\_SAM | 2.23 | 0.63 | 0.00 | -0.09\* |
| had.27.1-2 | -6.12 | 0.63 | 0.39\* | 0.01\* |
| had.27.46a20 | 4.52 | 0.98 | 0.59\* | 0.00 |
| had.27.5a | -0.93 | 0.88 | 0.09 | 0.01 |
| had.27.5b | 12.53 | 0.57 | 0.78\* | -0.02\* |
| had.27.6b | -5.94 | 0.51 | 0.00 | -0.03 |
| had.27.7a | 10.40 | 0.73 | 0.49\* | 0.05\* |
| had.27.7b-k | 17.00 | 0.96 | 0.85\* | 0.05\* |
| hke.27.3a46-8abd | 60.34 | 0.98 | 0.00 | 0.03\* |
| hke.27.8c9a | 63.67 | 0.94 | 0.30\* | -0.02\* |
| lin.27.5a | 0.82 | 0.47 | 0.12 | 0.03\* |
| pok.27.1-2 | 51.25 | 0.87 | 0.03 | 0.00 |
| pok.27.3a46 | 13.63 | 0.79 | 0.00 | -0.01\* |
| pok.27.5a | 1.71 | 0.58 | 0.11 | 0.00 |
| pok.27.5b | 42.17 | 0.85 | 0.43\* | -0.01\* |
| reb.27.1-2 | -0.06 | 0.86 | 0.00 | 0.09\* |
| reg.27.1-2 | -8.87 | 0.20 | 0.00 | -0.02\* |
| usk.27.5a14 | 6.80 | 0.87 | 0.34\* | -0.03\* |
| whg.27.47d | 15.85 | 0.76 | 0.00 | -0.02\* |
| whg.27.6a | 12.53 | 0.60 | 0.44\* | -0.08\* |
| whg.27.7a | 62.73 | 0.67 | 0.41\* | -0.12\* |
| whg.27.7b-ce-k | 16.64 | 0.91 | 0.32\* | 0.02 |
| ane.27.8 | -1.88 | 0.53 | 0.03 | 0.02 |
| cap-icel | 8.11 | 0.74 | 0.08 | 0.02 |
| cap.27.1-2 | 3.16 | 0.54 | 0.23 | 0.01 |
| her.27.1-24a514a | -2.10 | 0.48 | 0.40\* | 0.02\* |
| her.27.20-24 | -2.26 | 0.23 | 0.00 | -0.04\* |
| her.27.25-2932 | 18.83 | 0.57 | 0.09 | -0.02\* |
| her.27.28 | -4.01 | 0.26 | 0.00 | 0.02\* |
| her.27.3031 | -3.12 | 0.23 | 0.00 | 0.02\* |
| her.27.3a47d | 59.77 | 0.87 | 0.06 | 0.00 |
| her.27.5a | -1.03 | 0.95 | 0.51\* | 0.01\* |
| her.27.6a7bc | -0.38 | 0.20 | 0.00 | -0.01\* |
| her.27.irls | 9.67 | 0.47 | 0.00 | -0.01\* |
| her.27.nirs | 1.90 | 0.36 | 0.00 | 0.01\* |
| hom.27.2a4a5b6a7a-ce-k8 | 3.88 | 0.51 | 0.00 | -0.05\* |
| hom.27.9a | -1.52 | 0.35 | 0.06 | 0.03\* |
| mac.27.nea | 7.00 | 0.66 | 0.00 | 0.00 |
| nop.27.3a4 | 11.80 | 0.52 | 0.64\* | 0.01 |
| pil.27.8c9a | -1.56 | 0.30 | 0.00 | -0.05\* |
| san.sa.1r | 8.14 | 0.78 | 0.64\* | -0.03\* |
| san.sa.2r | -0.78 | 0.44 | 0.68\* | -0.05\* |
| san.sa.3r | 7.58 | 0.88 | 0.21 | 0.00 |
| san.sa.4 | 0.33 | 0.65 | 0.06 | -0.02 |
| spr.27.22-32 | -3.64 | 0.50 | 0.00 | 0.01\* |
| spr.27.4 | 4.65 | 0.38 | 0.00 | 0.01 |
| whb.27.1-91214 | -3.50 | 0.45 | 0.08 | 0.03\* |

Table S3. Comparison of internal CMP, external CMP and Cadigan model estimates from analyses of recruitment as a function of SSB. St: Steepness, OC: overcompensation. Overcompensation is not included in comparison where this was highly dependent on knot choice in CMP.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Internal CMP | | External CMP | | External Cadigan | | External CMP-internal CMP | | External CMP-External Cadigan | |
| Stock | St | OC | St | OC | St | OC | St | OC | St | OC |
| cod.21.1 | 0.997 | 0.714 | 0.969 | 0.490 | 0.886 | 0.456 | -0.029 |  | 0.083 |  |
| cod.27.1-2 | 0.989 | 0.477 | 0.985 | 0.450 | 0.955 | 0.563 | -0.004 | -0.027 | 0.030 | -0.113 |
| cod.27.47d20 | 0.238 | 0.199 | 0.222 | 0.110 | 0.200 | 0.000 | -0.016 |  | 0.022 |  |
| had.27.1-2 | 0.735 | 0.059 | 0.749 | 0.085 | 0.627 | 0.385 | 0.015 | 0.026 | 0.122 | -0.300 |
| had.27.5b | 0.598 | 0.757 | 0.611 | 0.803 | 0.573 | 0.776 | 0.013 | 0.046 | 0.038 | 0.027 |
| pok.27.1-2 | 0.866 | 0.002 | 0.868 | 0.006 | 0.870 | 0.026 | 0.002 | 0.004 | -0.002 | -0.020 |
| pok.27.5b | 0.892 | 0.328 | 0.878 | 0.440 | 0.846 | 0.429 | -0.014 |  | 0.032 |  |
| sol.27.20-24 | 0.956 | 0.298 | 0.937 | 0.445 | 0.997 | 0.402 | -0.019 | 0.147 | -0.060 | 0.043 |
| whb.27.1-91214 | 0.456 | 0.012 | 0.441 | 0.011 | 0.452 | 0.083 | -0.015 | -0.002 | -0.011 | -0.072 |
| Average |  |  |  |  |  |  | -0.007 | 0.032 | 0.028 | -0.073 |

Table S4. Density dependence in early growth. Correlation between recruitment and early growth. 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 | p-value | Correlation coefficient | Contrast in recruitment |
| ldb.27.8c9a | 0.80 | 0.05 | 0.77 |
| meg.27.7b-k8abd | 0.97 | 0.01 | 0.50 |
| meg.27.8c9a | 0.23 | 0.22 | 1.76 |
| mon.27.78abd | 0.94 | 0.01 | 1.24 |
| ple.27.420 | 0.08 | -0.23 | 1.25 |
| ple.27.7a | 0.07 | -0.31 | 0.57 |
| ple.27.7d | 0.78 | -0.05 | 1.23 |
| ple.27.7e | 0.09 | -0.27 | 0.59 |
| sol.27.20-24 | 0.00 | -0.72 | 1.13 |
| sol.27.4 | 0.76 | 0.04 | 1.57 |
| sol.27.7a | 0.48 | -0.10 | 2.17 |
| sol.27.7d | 0.20 | 0.22 | 1.06 |
| sol.27.7e | 0.36 | 0.13 | 0.90 |
| sol.27.7fg | 0.32 | 0.15 | 0.97 |
| sol.27.7h-k | 0.21 | 0.26 | 0.45 |
| sol.27.8ab | 0.00 | -0.68 | 0.67 |
| tur.27.4 | 0.67 | -0.07 | 0.30 |
| 3NO\_cod | 0.02 | 0.35 | 3.71 |
| cod.21.1 | 0.06 | 0.30 | 2.54 |
| cod.2127.1f14 | 0.82 | 0.04 | 4.34 |
| cod.27.1-2 | 0.72 | 0.04 | 1.89 |
| cod.27.22-24 | 0.06 | -0.40 | 2.56 |
| cod.27.47d20 | 0.28 | -0.15 | 2.17 |
| cod.27.5a | 0.99 | 0.00 | 0.88 |
| cod.27.5b1 | 0.16 | 0.19 | 1.96 |
| cod.27.6a | 0.00 | 0.45 | 2.45 |
| cod.27.7a | 0.12 | -0.27 | 3.11 |
| cod.27.7e-k | 0.00 | 0.48 | 2.34 |
| cod3m | 0.11 | -0.35 | 6.09 |
| cod3pn4R | 0.16 | -0.24 | 2.59 |
| codKat2020\_SAM | 0.11 | -0.34 | 2.31 |
| had.27.1-2 | 0.42 | 0.14 | 3.38 |
| had.27.46a20 | 0.38 | -0.13 | 3.68 |
| had.27.5a | 0.00 | -0.54 | 2.00 |
| had.27.5b | 0.01 | 0.39 | 2.87 |
| had.27.6b | 0.01 | -0.49 | 4.38 |
| had.27.7a | 0.92 | 0.02 | 1.98 |
| had.27.7b-k | 0.46 | -0.16 | 2.27 |
| pok.27.1-2 | 0.13 | -0.25 | 1.08 |
| pok.27.3a46 | 0.00 | -0.51 | 1.12 |
| pok.27.5a | 0.11 | -0.27 | 1.39 |
| pok.27.5b | 0.07 | -0.24 | 1.08 |
| reb.27.1-2 | 0.04 | -0.45 | 2.36 |
| reg.27.1-2 | 0.34 | 0.23 | 2.65 |
| whg.27.47d | 0.09 | -0.27 | 0.82 |
| whg.27.6a | 0.33 | 0.17 | 2.65 |
| whg.27.7a | 0.00 | 0.87 | 1.87 |
| cap.27.1-2 | 0.02 | -0.38 | 3.43 |
| her.27.1-24a514a | 0.74 | 0.06 | 2.49 |
| her.27.20-24 | 0.16 | -0.29 | 1.40 |
| her.27.25-2932 | 0.64 | 0.07 | 0.94 |
| her.27.28 | 0.01 | -0.39 | 1.68 |
| her.27.3031 | 0.66 | 0.07 | 1.32 |
| her.27.3a47d | 0.06 | 0.33 | 1.10 |
| her.27.5a | 0.38 | -0.17 | 1.46 |
| her.27.6a7bc | 0.73 | 0.07 | 2.00 |
| her.27.irls | 0.02 | -0.30 | 1.52 |
| her.27.nirs | 0.03 | -0.36 | 1.34 |
| hom.27.2a4a5b6a7a-ce-k8 | 0.32 | -0.17 | 2.12 |
| hom.27.9a | 0.03 | 0.45 | 1.54 |
| mac.27.nea | 0.16 | -0.24 | 1.05 |
| nop.27.3a4 | 0.21 | -0.23 | 2.03 |
| san.sa.1r | 0.13 | 0.26 | 2.20 |
| san.sa.2r | 0.49 | -0.12 | 2.93 |
| san.sa.3r | 0.98 | 0.00 | 2.71 |
| san.sa.4 | 0.15 | 0.30 | 3.02 |
| spr.27.22-32 | 0.06 | -0.28 | 1.87 |
| spr.27.4 | 0.00 | -0.56 | 1.84 |
| whb.27.1-91214 | 0.05 | -0.32 | 2.06 |

Table S5. Density dependence in late growth. Correlation between B\* and growth. 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 | p-value | correlation coeffcient | contrast in total stock biomass |
| 3LNO\_plaice | 0.02 | 0.31 | 3.32 |
| ldb.27.8c9a | 0.02 | -0.40 | 0.64 |
| meg.27.7b-k8abd | 0.00 | -0.68 | 0.60 |
| meg.27.8c9a | 0.07 | -0.32 | 1.01 |
| ple.27.420 | 0.00 | -0.58 | 0.93 |
| ple.27.7a | 0.00 | -0.71 | 1.14 |
| ple.27.7d | 0.30 | -0.17 | 1.33 |
| ple.27.7e | 0.02 | -0.39 | 1.07 |
| sol.27.20-24 | 0.01 | -0.42 | 0.73 |
| sol.27.4 | 0.00 | -0.39 | 0.93 |
| sol.27.7a | 0.00 | -0.40 | 1.67 |
| sol.27.7e | 0.93 | 0.01 | 0.44 |
| sol.27.7fg | 0.00 | -0.56 | 0.85 |
| sol.27.8ab | 0.00 | -0.80 | 0.48 |
| 3NO\_cod | 0.01 | 0.36 | 2.65 |
| cod.21.1 | 0.13 | 0.24 | 2.57 |
| cod.2127.1f14 | 0.07 | -0.28 | 3.59 |
| cod.27.1-2 | 0.01 | -0.30 | 1.26 |
| cod.27.22-24 | 0.04 | -0.42 | 1.36 |
| cod.27.47d20 | 0.71 | -0.05 | 1.73 |
| cod.27.5a | 0.51 | 0.08 | 0.86 |
| cod.27.5b1 | 0.13 | 0.20 | 1.37 |
| cod.27.6a | 0.00 | 0.57 | 2.31 |
| cod.27.7a | 0.51 | -0.11 | 2.43 |
| cod.27.7e-k | 0.26 | 0.19 | 1.32 |
| cod3m | 0.00 | -0.70 | 4.03 |
| cod3pn4R | 0.00 | -0.53 | 2.88 |
| codKat2020\_SAM | 0.01 | -0.49 | 2.54 |
| had.27.1-2 | 0.01 | -0.44 | 2.25 |
| had.27.46a20 | 0.00 | -0.47 | 2.07 |
| had.27.5a | 0.71 | 0.06 | 1.04 |
| had.27.5b | 0.00 | -0.51 | 1.84 |
| had.27.7b-k | 0.14 | 0.32 | 1.19 |
| pok.27.1-2 | 0.00 | -0.45 | 1.19 |
| pok.27.3a46 | 0.15 | -0.20 | 0.75 |
| pok.27.5a | 0.07 | -0.30 | 0.85 |
| pok.27.5b | 0.00 | -0.62 | 0.93 |
| reb.27.1-2 | 0.00 | -0.61 | 0.61 |
| whg.27.47d | 0.00 | -0.50 | 0.84 |
| whg.27.6a | 0.02 | -0.39 | 2.77 |
| whg.27.7a | 0.00 | 0.94 | 2.77 |
| cap.27.1-2 | 0.00 | -0.57 | 3.15 |
| her.27.1-24a514a | 0.00 | -0.73 | 0.97 |
| her.27.20-24 | 0.07 | -0.35 | 1.16 |
| her.27.25-2932 | 0.06 | 0.29 | 0.49 |
| her.27.28 | 0.00 | -0.80 | 1.18 |
| her.27.3031 | 0.33 | -0.16 | 1.12 |
| her.27.3a47d | 0.00 | -0.49 | 0.48 |
| her.27.5a | 0.70 | 0.07 | 0.43 |
| her.27.6a7bc | 0.14 | 0.30 | 1.08 |
| her.27.irls | 0.02 | -0.31 | 1.32 |
| her.27.nirs | 0.05 | -0.31 | 1.05 |
| mac.27.nea | 0.01 | -0.43 | 0.77 |
| nop.27.3a4 | 0.02 | -0.39 | 1.57 |
| san.sa.1r | 0.18 | 0.23 | 1.34 |
| san.sa.2r | 0.97 | 0.01 | 2.04 |
| san.sa.3r | 0.70 | 0.07 | 1.67 |
| san.sa.4 | 0.75 | 0.07 | 2.09 |
| spr.27.22-32 | 0.00 | -0.75 | 1.40 |
| spr.27.4 | 0.00 | -0.54 | 1.71 |
| whb.27.1-91214 | 0.01 | -0.41 | 1.38 |

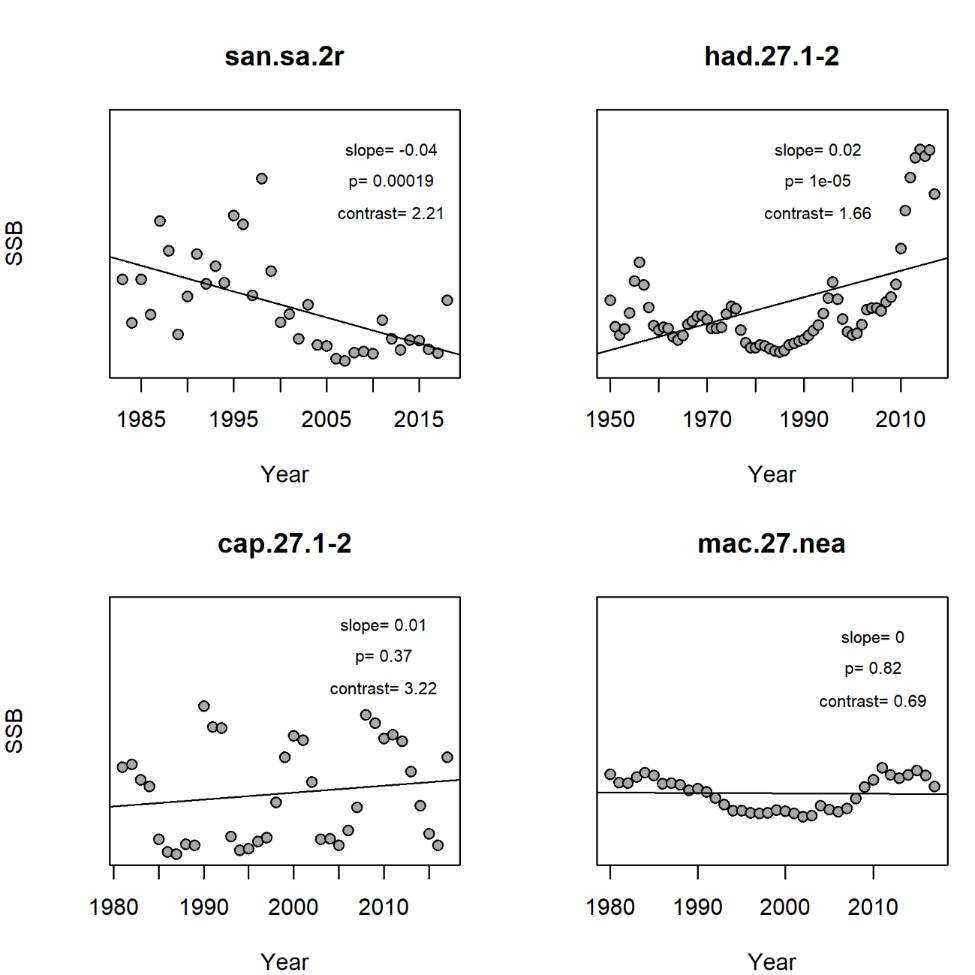


Fig. S1. Examples of different types of temporal development in density. Significant decreasing (top left), significant increasing (top right), fluctuating with large contrast (bottom left), fluctuating with low contrast (bottom right).



Fig. S2. Stock recruitment plots of all stocks and fitted Cadigan model. Vertical line is 0.2 times maximum biomass (the point where steepness is determined). Shaded area indicates 95% confidence interval of the mean.

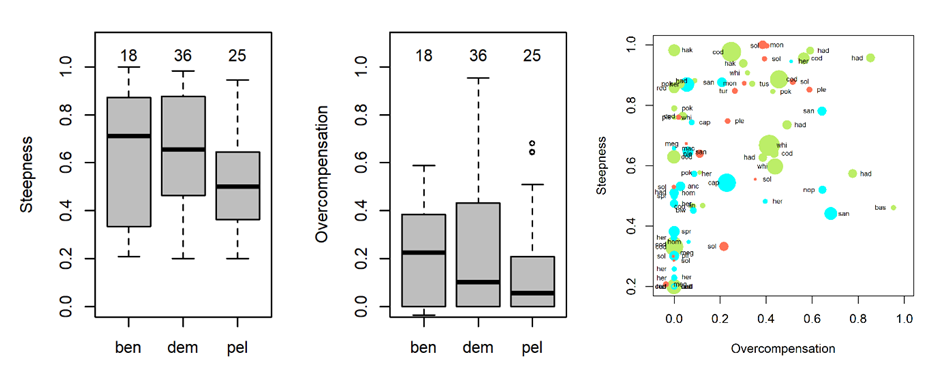


Fig. S3. Relationship between steepness and overcompensation of the stock recruitment relationship for each species group (benthic, demersal, pelagic). Blue: pelagics, red: benthic and green: demersal. Bubble size refers to the contrast in SSB.

Ln(Recruitment)

Early growth

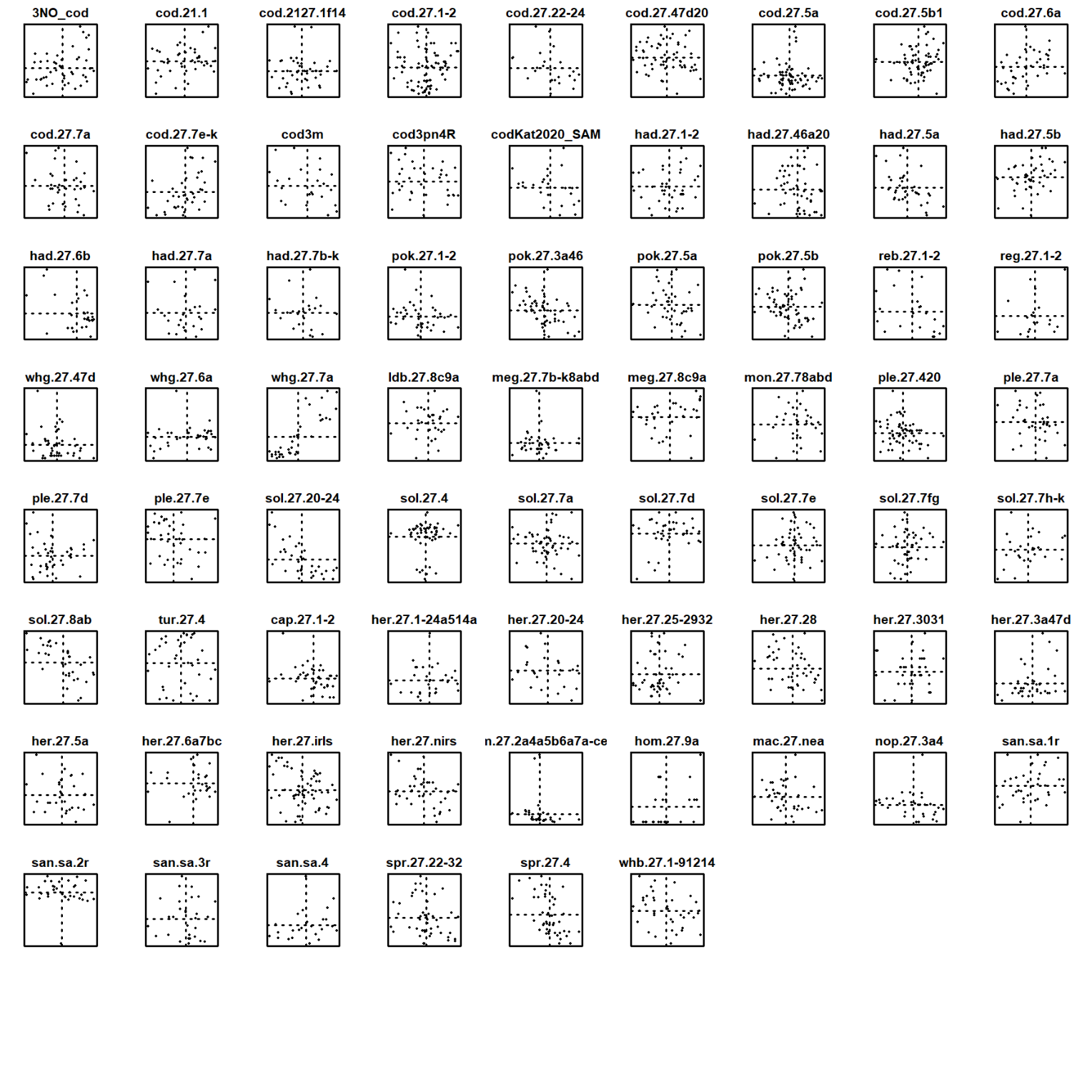


Fig. S4. Early growth as a function of cohort abundance. Hatched lines indicate medians.



Fig. S5. Top right: proportion of stocks where below average cohort abundance co-occurs with above average early growth. Top left: proportion of stocks where above average cohort abundance co-occurs with above average early growth. Bottom: Graphical representation of the numbered quadrants.

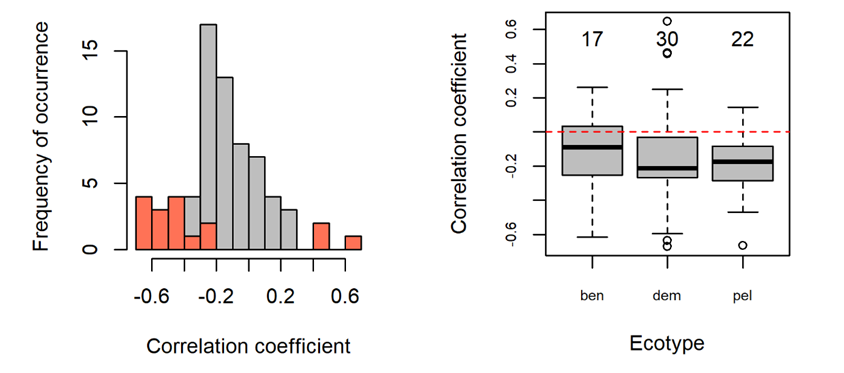


Fig. S6. Growth of youngest age-class vs. recruitment residuals from stock-recruitment curves. Red bars are significant correlations.



Fig. S7. Top right: proportion of stocks where below average density co-occurs with above average late growth. Top left: proportion of stocks where above average density co-occurs with above average late growth. Bottom: Graphical representation of the numbered quadrants.

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Fig. S8. Upper panels: Correlations between recruitment and early growth. Lower panels: Correlations between B\* and late growth. Black edge on horizontal bar indicate that the correlation is significant. Thickness of bars represent contrast in data. The contrast in the data was defined as the difference in the 90th and 10th percentiles of the log-transformed density measure (large value indicate large contrast in data, zero indicates no contrast).



Fig. S9. Moving window analysis, early growth vs. recruitment. Green line: Max recruitment, Grey line: recruitment range, Black line: moving window of correlation coefficient. Red number: P-value for the correlation between Rec and G1 (applies to the full time-series and the correlation estimate represented by the red dashed line. Black number: P-value for the correlation between Rec-range and the moving-window correlation estimate (represented by black line)



Fig. S10. Moving window analysis, late growth vs. B\*. Green line: Max recruitment, Grey line: recruitment range, Black line: moving window of correlation coefficient. Red number: P-value for the correlation between Rec and G1 (applies to the full time-series and the correlation estimate represented by the red dashed line. Black number: P-value for the correlation between Rec-range and the moving-window correlation estimate (represented by black line)



Fig. S11. Density dependence in late growth of a stock as a function of density dependence in early growth.



Fig. S12. Density dependence in early (top row) and late (bottom row) growth and overcompensation (left column) and steepness (right column) in the stock recruitment relationship.