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Rindorf, Anna; Henriksen, Ole; van Deurs, Mikael

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Scale-specific density dependence in North Sea sandeel

By Anna Rindorf[1], Ole Henriksen and Mikael van Deurs

Technical University of Denmark, National Institute of Aquatic Resources, Kemitorvet 1, 2800
Lyngby, Denmark.

[1]Email: ar@aqua.dtu.dk

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Local and regional density dependence

Abstract

Density dependent demographic processes occur in many marine fishes and potentially enhance the stability of local aggregations and regional populations. The degree of density dependence exhibited at the population level is a combination of local density dependent effects acting on different spatial scales. In this study, we searched for density dependence in recruitment, growth, and mortality of North Sea sandeel *Ammodytes marinus* at different spatial scales by analysing data at a spatial resolution specifically reflecting the mosaic of populated habitat patches. Two types of density dependent processes occurred: A shift in the spatial distribution towards low mortality areas when overall recruitment level was high and an increase in local mortality as local density increased. When combined, these processes largely compensated for each other and the size of the overall population had little influence on population level mortality. The study points to the necessity of considering both local and regional scale processes in analyses of density dependence.

Key words

Spatial scale-dependency, density dependent distribution, demographic processes

Introduction

Density dependent demographic processes are thought to be an essential mechanism ensuring stability, resilience, and persistence in marine fish populations, which often experience large temporal variability in productivity (Turchin 1999, Berryman et al. 2002, Lande et al. 2002). However, demonstrating density dependence in marine fish populations is challenging (Hixon et al. 2002). The challenges may relate to the open dispersive phase, that decouples local reproduction and subsequent recruitment of juveniles to the population (Webster 2003) and the fact that marine processes are difficult to observe and hence, the available data are often confounded by high variance and potential bias (Hixon & Carr 1997). An additional issue may be the mismatch between the spatial scale of population studies and the scale at which density dependent mechanisms act (Shima & Osenberg 2003, Melbourne & Chesson 2005, Einum & Nislow 2005). This mismatch could explain why studies of density dependence in reef-associated species with well-defined habitat boundaries and high local densities often reveal significant results (Anderson 2001, Rose et al. 2001, Hixon & Jones 2005), whereas effects of density dependence in species with more open population boundaries are less frequently detected (Myers

& Cadigan 1993a, b). Further, if the distribution of individual fish is density dependent (e.g. MacCalls basin theory, MacCall 1990), the combined effects of local density, local mortality and distribution can result in density dependence at population scale which differs substantially from that observed at local scale (Shima & Osenberg 2003).

Sandeels *Ammodytes spp.* form an important link between lower and upper trophic levels in many shelf ecosystems (Hedd et al. 2006, Frederiksen et al. 2006, 2007, Eliasen et al. 2011). They are entirely dependent on coarse sandy sediments as they spend a considerable part of their non-feeding periods buried (Winslade 1974a, b, c). The pelagic larvae can be transported considerable distances by currents before settling into sandy habitat (Potter & Lough 1987, Proctor et al. 1998) but the exchange of post-settled sandeels between the sandy habitat patches is low (Jensen et al. 2011). The high site fidelity after settling into fragmented habitat combined with large fluctuations in densities (Wright et al. 2000, Holland et al. 2005) makes the lesser sandeel *Ammodytes marinus* in the North Sea an ideal case for investigating the effect of density dependence on population dynamics. Previous studies of the North Sea lesser sandeel have indicated the existence of density dependent processes at a regional scale (Arnott & Ruxton 2002, van Deurs et al. 2009), acting concurrently with predation mortality, fishing pressure and climatically-induced changes in prey abundance to determine population size (Clausen et al. 2017, Lindegren et al. 2018). However, these studies did not investigate the role of density dependence acting within local habitat patches.

In the present study, we hypothesize that: (1) the spatial distribution of recruitment measured by the catch rate of 1-year old fish depends on regional density in a given year, (2) local recruitment depends on local density the previous year, (3) density dependent mortality occurs at a local scale and (4) the cumulated effect when scaling up to population level differs from the processes acting on a local scale. To investigate these hypotheses, we used a series of statistical models to analyse density dependent recruitment and mortality, taking into account both local and regional densities. The analysis was based on catch rates of lesser sandeel (*Ammodytes marinus*) in the North Sea commercial sandeel fishery and in a scientific survey at Shetland.

Materials & methods

Data

The majority of the data was derived from a self-sampling programme on commercial sandeel fishing vessels. Vessels in the programme recorded the exact location and time of shooting and hauling of the trawl, and an estimate of the total weight of the catch in each individual haul. A sample of 0.5 to 1 kg fish was collected from each haul and frozen on board. In the laboratory, the lesser sandeel were length measured to nearest half cm below (Rindorf et al. 2016). Samples were assigned to fishing grounds based on the distance between the midpoint of the haul and the nearest fishing ground (Jensen et al. 2011) and hauls with midpoints closer than 1 km to a fishing ground were assumed to be taken on that fishing ground. All fishing grounds were located in the North Sea between 54°N and 57°N (fig. 1) and all participating vessels were Danish. The collection of samples started in 1999 with between 8 and 29 vessels participating each year (on average 15) until 2014, where the number of vessels increased to between 31 and 58 (on average 44). In 2012 and 2016, the fishery was restricted to a monitoring fishery in April before the main fishing season, and hence not strictly comparable to the catch rates from the remaining years. These years were therefore excluded from the analyses.

In addition to the commercial data described above, data from a scientific survey conducted at Shetland from 1985 to 2000 were also included (Cook 2004). During this period, sandeel at Shetland were subject to zero or very low fishing pressure and the data were therefore used to study the relationship between density and natural mortality. Data on regional stock size was derived from agreed sandeel assessments (ICES 2018).

Catch rate in numbers at age a per minute fishing (C_a, in units of sandeels caught min^{-1}) was estimated by combining estimated catch in kg per minute fishing with numbers per kg of each age group. The latter was estimated by applying separate age-length keys for each fishing ground and week where possible; otherwise data from within the same statistical rectangle (1^{o}W times 0.5^{o}N) and two consecutive weeks were combined before fitting the age-length key. The age-length key analysis used the method described in (Rindorf & Lewy 2001). In some hauls, the number of large fish was too low to provide reliable estimates of the number of fish older than age 1. Hence, the number of data values for age 1 exceeded that for age 2.

To avoid violating assumptions of the statistical regression models used, a sequence of transformations and statistical modelling was used. First, the variance of catch rates tends to increase with the mean (Pennington 1983). To address this, all catch rates were transformed by taking the natural log. Secondly, if the error of the independent variable is in the same order of magnitude as that of the dependent variable, parameter estimates in standard regression models may be considerably biased (Kendall & Stuart 1979). This problem was addressed by using average catch rates across all samples in a given year whenever catch rates were used as an independent variable. This decreases the standard error of the independent variable compared to that of the dependent variable. Thirdly, the sampling design was highly unbalanced and using mean catch rates as the dependent variable in a standard linear regression would violate the assumption of constant variance of the observations. We used individual catch rates as observations in all analyses to accommodate the unbalanced sampling design and to assure that the variance of the dependent variable is considerably larger than that of the independent variable. Lastly, the data from a specific fishing ground, fishing vessel, or year are likely to be correlated due to e.g. local weather effects, skipper skills etc. To address this, random effect models were used throughout and the r^2 of the model using only fixed and both fixed and random effects given (Nakagawa & Schielzeth 2013).

Spatial distribution of recruitment depends on regional density in a given year (Hypothesis 1)

The relationship between spatial distribution of recruitment measured by the catch rate of 1-year old fish and density in the given year was investigated by relating the catch rates of 1-year old sandeel on the individual fishing grounds to that of a central reference ground. This will reveal if different grounds experience the same relative (regional) annual change in recruitment or if some grounds exhibit greater changes than others. The analysis was performed using a random effects model, where the central well-sampled fishing ground, North West Rough, was used as the reference ground and catch rate of 1-year old fish was used as recruitment proxy:

$$\ln\hat{C}_{1,g,y,v} = k_g + \gamma_g ln\bar{C}_{1,NWRough,y} + \omega_{g,y} + \varphi_v \qquad (1)$$

Here, $\ln\hat{C}_{1,g,y,v}$ is the predicted log catch rate of 1-year olds of vessel *v* at fishing ground *g* in year *y*, $ln\bar{C}_{1,NWRough,y}$ is the average log catch rate of 1-year olds on North West Rough in the given year and k_g is the theoretical catch rate at fishing ground *g* when $ln\bar{C}_{1,NWRough,y}$ is 1. The slope γ_g describes the fishing ground specific relationship with density at the reference ground and the random effects of year/fishing ground and fishing vessel ID are contained within $\omega_{g,y} \in N(0, \sigma_\omega)$ and $\varphi_v \in N(0, \sigma_\varphi)$, respectively. If y_g is close to one and σ_ω and σ_φ are small, virtually all variation is explained by the recruitment at the reference ground, North West Rough (no density dependence). If y_g values > 1, there is positive density dependence at the fishing ground, and an increased recruitment on the reference ground is accompanied by a higher than proportionally increased recruitment at other grounds. In contrast, y_g values between 0 and 1 are indicative of negative density dependence at the fishing grounds, where an increased recruitment on the reference ground is accompanied by a lower than proportionally increased recruitment at other grounds. Lastly, if y_g is close to zero and σ_ω and/or σ_φ are large, the development in local recruitment is independent of that recorded at the reference ground. Since γ_g is estimated for each fishing ground, it is possible that negative density dependence is detected on some grounds and positive density dependence on others. The model was fitted to all data as well as to a subset of data consisting only of fishing grounds within sandeel population area 1 (fig. 1). A similar model was made for population area 4 (fishing grounds close to the coast of Scotland, fig. 1) using Berwick Bank as the reference fishing ground. The areas are considered to contain separate populations (ICES 2016) and hence correlation is expected within areas but not necessarily between areas.

If recruitment to different fishing grounds is density dependent, the economic profitability of different fishing grounds may vary with density leading to a relationship between catch rates and stock size that differs from proportional at the regional scale (density dependent catchability). In order to test for density dependent catchability at the regional level, the yearly average catch rates of age 1 sandeel were compared to the number of age 1 fish on January 1st estimated in the analytical assessment (ICES 2018) using a log-linear model:

$$\ln\hat{C}_{1,g,y,v} = k_g + \eta_g \ln R_{1,y} + \omega_{g,y} + \varphi_v \quad (2)$$

where $\hat{C}_{1,g,y,v}$ is the predicted catch rate of age 1 sandeel of vessel *v* at fishing ground *g* in year *y*, the constant k_g represents the average catch rate at the fishing ground at a theoretical abundance of 1 (not related to k_g in eq. 1), $R_{1,y}$ is number of age 1 fish on January 1st in year *y* taken from the analytical assessment, and η_g describes the ground-specific dependence of catch rates on $R_{1,y}$. $\omega_{g,y} \in N(0, \sigma_\omega)$ describes the random effect of year and fishing ground and $\varphi_v \in N(0, \sigma_\varphi)$ describes the random effect of vessel ID. For catchability to be density independent, η_g must be one. If η_g is larger than one, catch rates decrease faster than proportionally as abundance decreases (hyperdepletion, (Hilborn & Walters 1992)). If η_g is less than one, catch rates decrease slower than proportionally as abundance decreases (hyperstability, (Hilborn & Walters 1992)). Temporal trends in catchability at age 1 was analysed by making η_g a linear function of year and testing whether this improved model fit significantly.

Local recruitment depends on local density the previous year (Hypothesis 2)

Recruitment can be temporally density-dependent if the recruitment on a given fishing ground in a given year depends on the recruitment to that specific ground in the preceding year. This type of density dependent recruitment was tested using the following model:

$$\ln\hat{C}_{1,g,y,v} = k_y + \kappa_g ln\bar{C}_{1,g,y-1} + \omega_{g,y} + \varphi_v \quad (3)$$

Here, $\ln\hat{C}_{1,g,y,v}$ is still the predicted log catch rate of 1-year olds of vessel *v* at fishing ground *g* in year *y* and $ln\bar{C}_{1,g,y-1}$ is log catch rate of 1-year old fish (used as a proxy for recruitment) for a given fishing ground in the preceding year (*y*-1). The intercept k_y describes the predicted catch rate at a theoretical average recruitment in the preceding year equal to 1, κ_g describes the effect of the recruitment in the preceding year and the random effects of year/fishing ground and fishing vessel ID are again contained within $\omega_{g,y} \in N(0, \sigma_\omega)$ and $\varphi_v \in N(0, \sigma_\varphi)$, respectively. Note that the density dependent effect was estimated for each fishing ground separately.

Density dependent mortality occurs at local scale (Hypothesis 3)

The density of a cohort will decrease exponentially from year *y* to year *y*+1 as fish are removed by mortality, according to the population decay function:

$$N_{a+1,y+1} = N_{a,y}e^{-Z_y}$$

Where $N_{a,y}$ is the number of fish in the population of a given age class *a* at the beginning of the year *y* and Z_y denotes the total mortality rate for a given year. Using catch rates as indicators of abundance, we can adapt the above equation:

$$\hat{C}_{2,y+1} = \frac{q_{2,y+1}}{q_{1,y}}\hat{C}_{1,y}e^{-Z_y}$$

Hence, if the relative difference in catchability of the two age groups and mortality remain constant over time, the catch rate of a given cohort in a particular year is directly proportional to the catch rate of the same cohort in the preceding year. Note that when we use catch rates rather than abundance, catch rates of e.g. 2-year olds (C_2) may exceed that of 1-year olds (C_1) the year before if catchability of 2-year olds (q_2) is higher than of 1-year olds (q_1). If mortality is density dependent, Z_y is a function of the population density in that year. Assuming that mortality is linearly related to log abundance with the proportionality factor β, this relationship can be described as:

$$Z_y = Z_0 + \beta lnN_{1,y} = Z_0 - \beta \ln q_{1,y} + \beta \ln \hat{C}_{1,y}$$

Where Z_0 is the theoretical mortality at $\ln \hat{C}_{1,y} = \ln q_{1,y}$ or $\beta = 0$. When inserting this relationship and taking the natural logarithm on both sides, we get

$$\ln \hat{C}_{2,y+1} = k_{y+1} + (1-\beta) ln\hat{C}_{1,y}$$

where $k_{y+1} = \ln\left(\frac{q_{2,y+1}}{(q_{1,y})^{1-\beta}}\right) - Z_0$

Estimates from the stock assessment of sandeel in area 1 indicate that the ratio $\frac{q_{2,y}}{q_{1,y-1}}$ is increasing over time (ICES 2018), and this was accounted for in the model based on the equation above:

$$\ln \hat{C}_{2,\mathrm{g},y+1,v} = k_0 + k_1 y + (1-\beta_g) ln\bar{C}_{1,\mathrm{g},y} + \omega_{g,y} + \varphi_v \qquad (4)$$

where $k_0 = \ln\left(\frac{q_{2,2000}}{(q_{1,1999})^{1-\beta}}\right) - Z_0$, $k_1 = \Delta \ln\left(\frac{q_2}{(q_1)^{1-\beta}}\right)$ describes the annual change in the ratio of catchabilities, β_g describes the density dependent effect of last year's geometric average catch rate of 1-year olds, $ln\bar{C}_{1,y}$, on mortality at fishing ground g, allowing us to determine if mortality differs between high and low survival grounds as suggested by Shima and Osenberg (2003). Random effects of year/fishing ground and fishing vessel ID are again contained within $\omega_{g,y} \in N(0, \sigma_\omega)$ and $\varphi_v \in N(0, \sigma_\varphi)$, respectively. Mortality is independent of density when β =0. If β is greater than zero, mortality increases with density. β was estimated at the two fishing grounds with 8 or more years of data (North West Rough and Southernmost Rough). Due to the very limited catches of fish of age 3 and older, only mortality from 1-year olds to 2-year olds was investigated. To allow comparison of mortality levels between fishing grounds, mortality indices for fishing grounds with at least 5 years data were estimated assuming $\beta = 0$ as $\ln\bar{C}_{2,y+1} - ln\bar{C}_{1,y}$.

Catch rates from a scientific survey around Shetland was analysed using a slightly different model without random effect terms and time trend in catchability:

$$\ln\hat{C}_{a+1,y+1} = k_0 + (1-\beta)ln\bar{C}_{a,y}$$

These simplifications were required since only one value per year was available and it is reasonable to assume that catchability in a scientific survey is constant over time. More ages were available than in the commercial samples and the analysis therefore included ages 0 to 4. Since $ln\bar{C}_{a,y}$ is observed with error, ordinary regression is not appropriate. Instead, Deming regression was used to estimate β assuming the error in the dependent and independent variable to be equal (Linnet 1993). The 95% confidence limits of β were estimated using jackknife.

Cumulated density dependent effects differ from the processes acting on a local scale (Hypothesis 4)

Following the analyses of density dependence in recruitment and mortality, the predictions from the two analyses were combined to assess the integrated effect of local density dependence in mortality and spatial distribution of recruitment on regional mortality (summed across local fishing grounds). Three different combinations were examined:

1. Spatial distribution of recruitment depends on regional density and local mortality is independent of local density
2. Spatial distribution of recruitment is independent of regional density and local mortality depends on local density
3. Spatial distribution of recruitment depends on regional density and local mortality depends on local density

For options one and three, an index of abundance at each fishing ground, I_g, was estimated as the product of local density estimated from the relationship with density at North West Rough and the surface area of the fishing ground, A_g:

$$\mathrm{I}_{1,g,y} = A_g e^{(k_g+\gamma_g ln\bar{C}_{1,NWRough,y})}$$

Where k_g and γ_g are estimated in model 1. For option 2, the ground specific index of abundance was estimated as the ground specific median abundance index multiplied by area of the ground.

As the aim is to investigate the impact of the each of the density dependent components distribution and mortality, the observed abundance at age 2 cannot be used as this includes both effects. Instead, the index of abundance of 2-year old fish at each ground for this analysis was estimated as $I_{2,g,y} = I_{1,g,y}\exp(-Z_{1,g,y})$. For option 1, the average mortality index at each ground, $Z_{1,g,y}$, was assumed equal to the observed $k_{0,g} = \ln\bar{C}_{a+1,y+1,g} - ln\bar{C}_{a,y,g}$ averaged across years. For options 2 and 3, the annual mortality index at a ground was assumed equal to $k_{0,g} - \beta ln\bar{C}_{a,y,g}$ where the value of β was estimated in model 4.

The total mortality index across fishing grounds was estimated as:

$$Z_{pop,y} = \ln\left(\sum_{g} I_{1,g,y}\right) - \ln\left(\sum_{g} I_{2,g,y}\right)$$

This was compared to an index of total abundance of age 1 fish across fishing grounds estimated as:

$$I_{pop,y} = \ln\left(\sum_{g} I_{1,g,y}\right)$$

As the abundance and mortality are indices rather than absolute values, both are given relative to the value at median density.

Results

Spatial distribution of recruitment depends on regional density in a given year (Hypothesis 1)

The fixed effects model for fishing grounds in assessment area 1 explained 57% of the variation, and the combined fixed and random effects explained 66% (fig. S1 in supplementary material). The standard deviation of the random effect of fishing ground and year (0.31) was much larger than that of vessel ID (0.18), but smaller than the residual deviation (1.84). The fishing ground Lisborgs Revle had a slope (γ_g) >1 (table 2). The remaining fishing grounds in assessment area 1 showed no significant difference in γ_g (P=0.6031). The joint slope at these grounds was 0.62 (table 3), which was significantly different from both 0 and 1 (P<0.001 in both cases). Hence, when recruitment at age 1 increased by 100% at North West Rough, recruitment at Lisborgs Revle increased by 155% and recruitment at fishing grounds other than Lisborgs Revle increased by only 54% (fig. 2). These density dependent differences in catch rates across grounds meant that when catch rates were low on average across all grounds (i.e. low regional population density), North West Rough and Lisborgs Revle catch rates were low relative to other grounds, while catch rates at these grounds were the highest observed when average catch rates were high (fig. 3). In spite of these differences, strong year-classes were detectable across all grounds as above average densities, while weak year-classes provided below average densities across all grounds (i.e. note the difference in scale in fig. 2).

Annual recruitment at fishing grounds in assessment areas 2 and 4 was not related to catch rates at North West Rough (γ_g not different from zero, P=0.0604, fig. 3). However, catch rates at Wee Bankie were significantly related to those at Berwick Bank (area 4, P=0.0158).

Catch rate in area 1 was highly correlated to abundance estimated from the analytical assessment (P<0.0001, r^2 of fixed and random effects together=59%, (fig. 4 and fig. S2)). The estimated slope (η_g) of the relationship between catch rate and abundance was 1.24 with a standard error of 0.13, not significantly different between fishing grounds (P=0.3355). The value is not significantly different from one (P=0.0718) and hence there was a non-significant tendency towards density dependent catchability at a population level. There was no significant trend over time in catch rate divided by stock abundance (i.e. index of catchability at age 1) (P=0.1226).

Local recruitment depends on local density the previous year (Hypothesis 2)

Recruitment at age 1 to a given fishing ground was not significantly related to the recruitment in the previous year (P=0.1170).

Density dependent mortality occurs at local scale (Hypothesis 3)

Only North West Rough and Southernmost Rough were sampled sufficiently to allow the estimation of density dependence in mortality while seven grounds were sampled sufficiently to allow the estimation of a ground specific mortality index (fig. 5 and 6). Among the seven grounds sampled, Lisborgs revle had the lowest mortality, S.W. Patch and Elbow Spit the highest while the remaining grounds had intermediate values. The catch rate at age 2 was highly related to catch rate of 1-year old fish (P<0.0001) and the model explained 51% and 65% of the variation by fixed and fixed plus random effects, respectively (fig. S3). The effect of year, k_1, was significantly positive (P=0.0364), indicating that catch rates at age 2 increased over time even if catch rate of 1-year old fish remained unchanged. β was 0.19 and 0.21 at North West Rough and Southernmost Rough, respectively and neither β nor k_0 differed between the two fishing grounds (P>0.0795). The joint density dependent term β was significantly positive (β=0.21, std=0.09, P=0.0218). The model used for the Shetland data revealed a common β of 0.27 (std=0.07), significantly greater than 0 (P=0.0003) (fig. 7).With this strength of density-dependence, the smallest average catch rate of 1-year olds at North West Rough resulted in a 230% higher catch rate when the fish were 2-year olds, corresponding to a higher catchability of 2-year olds compared to 1-year old fish masking the effects of mortality. In contrast, the largest average catch rate of 1-year olds at North West Rough resulted in 58% lower catch rate when the fish were 2-year olds, corresponding to an 8-time reduction in survival between the smallest and the largest year-class (assuming constant catchability at age). The density dependence at Shetland was sufficient to reduce the survival of the largest and smallest index by a factor 5. This could potentially be contributing to the stabilization of the population by increasing mortality of large year-classes.

Cumulated density dependent effects differ from the processes acting on a local scale (Hypothesis 4)

While density dependent mortality led to increased mortality at higher densities (fig. 8, dark grey broken lines), density dependent distribution of recruitment to age 1 led to the opposite result, as the proportion of fish settling to recruit at age 1 at grounds showing high mortality decreased when the overall recruitment in the population was high (fig. 8, light grey dotted lines). Combining the two for fishing grounds in the Dogger Bank area resulted in a mortality index, which was virtually independent of abundance (solid black line in fig. 8). Excluding S. W. Patch, which had a very high estimated mortality index and a very large area, changed the result so the combined effect of density dependent recruitment and mortality was an increase in mortality with abundance, acting to decrease fluctuations in stock abundance at age 2 compared to age 1. If we assume that catchability of age 1 and 2 are equal, this corresponds to a reduction in survival from 47% at the lowest observed abundance to 18% at the highest observed abundance. The results of all density dependence investigations are summarised in table 4.

Discussion

The regional population processes of North Sea sandeel were a combination of density dependent spatial distribution of recruitment on a regional scale and density dependent mortality on a local scale. In years characterized by a large overall population, a large fraction of the population occurred at low mortality fishing grounds while local mortality increased. Depending on the balance between these two factors, this potentially leads to either increasing or decreasing mortality as abundance increases.

Sandeel recruitment in all areas increased as overall recruitment increased, but the increase was substantially greater at North West Rough and Lisborgs Revle. Consequently, the relative contribution of these grounds shifted from supporting the lowest sandeel densities in years where the overall population size was small to supporting the highest densities when the overall population size was large. This density dependence in the distribution of recruitment across fishing grounds does not follow the most commonly referenced distribution hypotheses. For example, the basin theory (MacCall 1990) and the theory on cryptic density dependence (Shima & Osenberg 2003) predicts that high quality habitat is always occupied and exhibits the highest densities. This is not the case in our data, as the two grounds switch from having the lowest relative density to the highest relative density. Sutherland's (1983) theory of fish distribution, based on a different parametrization of the Ideal Free Distribution (Fretwell & Lucas 1969), predicts that as the overall population size goes up, local densities throughout the population range increase proportionally. However, this prediction does not match our results either. An alternative explanation for our observations could be spatio-temporal variation in the environmental conditions for recruitment. If oceanographic features, such as advection and retention, vary in different years, this might affect recruitment of settling larvae by shaping the trophodynamic arena that regulate survival through food availability and the physical settings that determine transport into and retention within an area (Henriksen et al. 2018). For example, if the recruitment conditions such as food availability and drift pattern are highly variable in the northwest corner of Dogger Bank but more stable in other areas and large food availability only occurs in the northwest corner of Dogger Bank when there is a high food supply overall, this could explain the greater variation at North

West Rough and Lisborgs Revle. Alternatively, the number of sandeel dying from predation before age 1 in these two areas is a constant number rather than a constant fraction. This would lead to a greater mortality up to age 1 at low abundance than at high abundance and could be the result of a predator stock which remains approximately constant and is capable of feeding at approximately the same rate regardless of overall sandeel density (i.e. limited by handling time rather than search time (Stephens & Krebs 1986)).

The distribution of sandeel recruitment was not affected by the density of the previous cohort. This is in contrast to studies on sandeel abundances reporting negative correlations between the recruitment in a given year and that in the previous (Arnott & Ruxton 2002, van Deurs et al. 2009, Lindegren et al. 2018). It is possible that the residual variation in our data was too large for the density dependent effect to be detected at the local scale. Alternatively, the autocorrelation seen in earlier studies was caused by factors relating to the assessment model output used. If the commercial fishery targets fishing grounds with high abundance of specific cohorts, this can introduce an overrepresentation of these cohorts and an underrepresentation of the adjacent cohorts in the regional catch data, leading to the impression that there is negative autocorrelation at the population level, even though there is no autocorrelation at the local scale.

Density dependent mortality substantially reduced the difference between large and small local cohorts at the local level, potentially contributing to the stability of local aggregations. The density dependent mortality seemed to be a result of predation rather than fishing, as it was present at approximately the same level in unfished (Shetland) and fished areas (North West Rough and Southernmost Rough). Density dependent natural mortality of fish such as damselfish (*Dascyllus flavicaudus*) and bridled goby (*Coryphopterus glaucofraenum*) acts through exposing individuals to higher predation rates once the carrying capacity of an area has been reached (Forrester & Steele 2004, Schmitt & Holbrook 2007). In the case of sandeel, carrying capacity may refer to the availability of suitable burying substrate rather than to refuges as in reef fish (Hobson 1986). Different substrates may offer different overwintering survival or increased food competition may lead to delayed onset of the overwintering period, increasing predation mortality (van Deurs et al. 2011). There was no significant difference in the level of density dependent mortality at the three sites examined, indicating that either the sites are similar in quality or the factors inducing density dependence are not related to quality of the sites as found for coral reef fish, such as *Thalassoma Hardwicke* (Shima & Ostenberg 2003).

Density dependence in natural mortality occurs if natural predators switch between different prey types according to their abundance, either by changing their consumption or by exhibiting an aggregative response (Murdoch et al. 1975, Anderson 2001). Large-scale studies of the diet of predatory fish in the North Sea and Celtic Sea have generally failed to produce evidence of more than proportional increases in consumption of individual predators with increasing prey density (Pinnegar et al. 2003, Rindorf & Gislason 2005, Rindorf et al. 2006). However, as areas of sandeel habitat are characterised by highly stationary features (gravelly substrate and limited depth range), they can potentially be targeted accurately by aggregating natural predators (Temming et al. 2004, van der Kooij et al. 2008, Engelhard et al. 2008). Hence, it is possible that extensions in the period in which the predators feed on sandeel and aggregation of predators in areas with high densities of sandeel lead to the observed density dependence of mortality from age 1 to 2.

If the fishery optimises revenue by seeking out the highest catch rates, the density dependent distribution of recruitment will lead to a widespread fishery with low catch rates and little fishing activity at North West Rough and Lisborgs Revle when the overall population is small. When the population is large, the fishery will exhibit high catch rates and concentrate at North West Rough and Lisborgs Revle. This general pattern seems to be confirmed by the distribution of commercial catches in 2003-2005, where abundance was low compared to later years (ICES 2018). The generally reported form of density dependence of catch rates is hyperstability, where catch rates decrease slower than abundance (Saville & Bailey 1980, Winters & Wheeler 1985, Beverton 1990). This has been suggested to be a major cause of overfishing (Erisman et al. 2011). In contrast, the pattern in our data is likely to lead to hyperdepletion of catch rates, where catch rates decrease faster than fish abundance at a regional scale. This is also indicated by the analysis of density dependent catchability, where the slope (η) (eq. 2) was estimated to be 1.24, consistent with hyperdepletion. Alternatively, local catchability depends on local density. If this is the case, it would bias the analysis of density dependence of mortality. However, to produce the impression of mortality increasing with density where no such underlying process exists, catchability for age 1 must increase with density more than that of age 2. This is consistent with hyperdepletion for age 1 rather than the more commonly reported hyperstability. It is not clear by which process the catchability at a local fishing ground would increase with density. The opposite relationship however, where catchability decreases with increasing stock size is consistent with fisheries targeting prime habitat into which the fish are aggregating to a greater degree when stock size is low.

In summary, the population dynamics of lesser sandeel in the North Sea rely on a mosaic of local habitats determining density dependence at the regional population level. Local density dependent mortality led to increasing mortality at higher densities. Concurrently, density dependent distribution of recruitment led to a shift in distribution towards low mortality fishing grounds when recruitment at the regional scale was high. As a result, hyperdepletion of catch rates was more likely than hyperstability. Combining the two density dependent effects for fishing grounds in the Dogger area resulted in a mortality index, which was virtually independent of abundance. Our study demonstrated the necessity of considering both local and regional processes in analyses of density dependence (Shima & Osenberg 2003, Einum & Nislow 2005): had the analysis considered only local density dependent effects on mortality, the conclusion of the study would have been in complete opposition to an analysis considering only density dependent effects on the spatial distribution of recruitment.

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Tables

Table 1. Overview of models and density dependent terms used. In the following, *k* is used to denote a constant in the specific model and hence, though *k* appears in several models, the estimate of *k* differs in each case.

Hypothesis	Model	Density dependence analysed	Tests performed
1	$\ln\hat{C}_{1,g,y,v} = k_g + \gamma_g ln\bar{C}_{1,NWRough,y} + \omega_{g,y} + \varphi_v$ (1)	The regional effect of recruitment to North West Rough (used as reference fishing ground) on the recruitment to other fishing grounds.	$\gamma_g \neq 0$ $\gamma_g \neq 1$
1	$\ln\hat{C}_{1,g,y,v} = k_g + \eta_g \ln R_{1,y} + \omega_{g,y} + \varphi_v$ (2)	The regional effect of population abundance of age 1 fish on the catch rates of age 1 fish on the individual fishing grounds.	$\eta_g \neq 0$ $\eta_g \neq 1$
2	$\ln\hat{C}_{1,g,y,v} = k_{y,g} + \kappa_g ln\bar{C}_{1,g,y-1} + \omega_{g,y} + \varphi_v$ (3)	Dependence of local recruitment in year *y* on local recruitment in the	$\kappa_g \neq 0$ $\kappa_g \neq 1$

		previous year to the same fishing ground.	
3	$\ln\hat{C}_{2,g,y+1,v} = k_0 + k_1 y + (1 - \beta_g) ln\bar{C}_{1,g,y} + \omega_{g,y} + \varphi_v$ (4)	Dependence of local mortality on local cohort density.	$\beta \neq 0$

Table 2. Parameter estimates of the model $\ln\hat{C}_{1,g,y} = k_{0,g} + \gamma_g ln\bar{C}_{1,NWRough,y} + \omega_{g,y} + \varphi_v$ describing the relationship between catch rates of 1-year olds at North West Rough and other fishing grounds in assessment area 1. Significant probabilities (P) are in bold. N denotes number of observations used, Year denotes number of years where data were available from that fishing ground.

Fishing ground	Ass. area	N	Years	γ_g	P(γ=0)	$k_{0,g}$ in reduced model	γ_g in reduced model
Lisborgs Revle	1	313	11	1.35 (0.13)	**<0.0001**	-4.07 (1.12)	1.35 (0.12)
Stenkanten	1	124	11	0.74 (0.10)	**<0.0001**	3.15 (0.41)	0.62 (0.04)
Rute 18	1	61	7	0.72 (0.13)	**<0.0001**	2.88 (0.42)	0.62 (0.04)
Southernmost Rough	1	234	14	0.67 (0.09)	**<0.0001**	3.61 (0.40)	0.62 (0.04)
S. W. Patch	1	169	11	0.49 (0.10)	**<0.0001**	3.91 (0.39)	0.62 (0.04)
Sorel	1	115	7	0.78 (0.30)	**0.0093**	3.47 (0.47)	0.62 (0.04)
Outer Well	1	85	6	0.48 (0.17)	**0.0057**	4.05 (0.44)	0.62 (0.04)
Elbow Spit	1	220	10	0.62 (0.12)	**<0.0001**	3.83 (0.43)	0.62 (0.04)
Tail End	1	94	8	0.55 (0.10)	**<0.0001**	3.92 (0.41)	0.62 (0.04)

Table 3. Proportion of individuals found in the Dogger Bank area present at each fishing ground.

Fishing ground	Area (km2)	Average $ln\hat{C}_{1,y-1}$- $ln\hat{C}_{2,y}$	Proportion of all at minimum density at North West Rough	Proportion of all at median density at North West Rough	Proportion of all at maximum density at North West Rough
Lisborgs Revle	250	0.59	0.000	0.030	0.129
N.W. Rough	593	1.28	0.018	0.192	0.367
Southernmost Rough	204	1.64	0.048	0.085	0.074
Stenkanten	216	1.79	0.023	0.060	0.062
S. W. Patch	1285	2.76	0.911	0.634	0.368

Table 4. Summary of results

Hypothesis number	Density dependence analysed	Tests results
1	The regional effect of the recruitment to North West Rough (used as reference fishing ground) on the recruitment to other fishing grounds.	Sandeel area 1: γ_g>1 at Lisborgs Revle (P=0.0012). Remaining fishing grounds had 0< γ_g< 1 (P<00001 in both cases).
1	The regional effect of population abundance of age 1 fish on the catch rates of age 1 fish on the individual fishing grounds.	η_g was significantly different from zero (P<0.0001) but not significantly different from 1 (P=0.0718).
2	Dependence of local recruitment in year *y* on local recruitment in the previous year to the same fishing ground.	No significant effect of local recruitment the previous year (P=0.1170, $\kappa = 0$)
3	Dependence of local mortality on local cohort density.	N. W. Rough and Southernmost Rough: β significantly greater than zero (β=0.21, P=0.0218), indicating that mortality increased with increasing density. Shetland: β significantly greater than zero (β = 0.27, P=0.0003), indicating

		that mortality increased with increasing density.

Figures

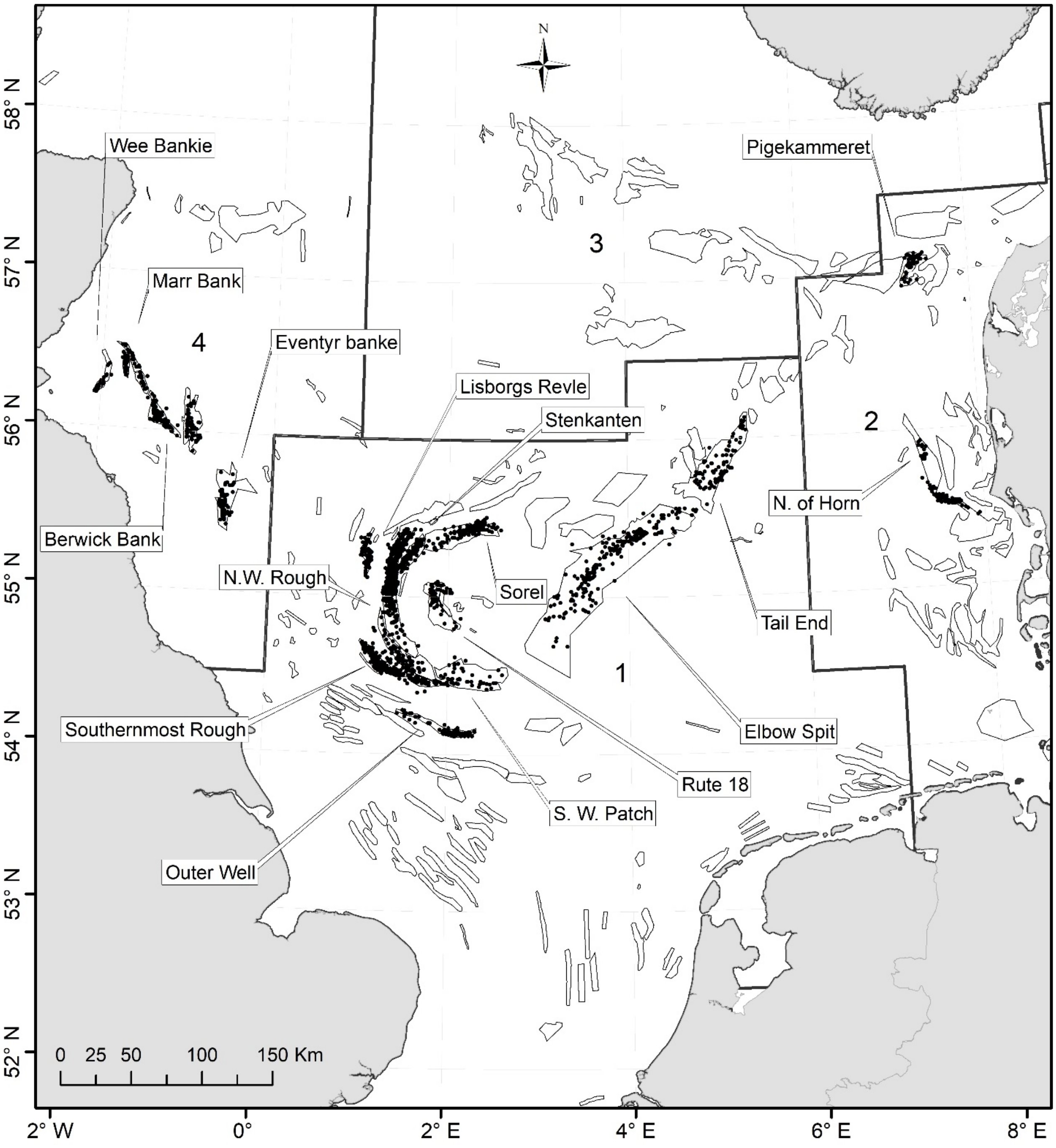


Fig. 1. Named fishing grounds and numbered sandeel areas referred to in the study.

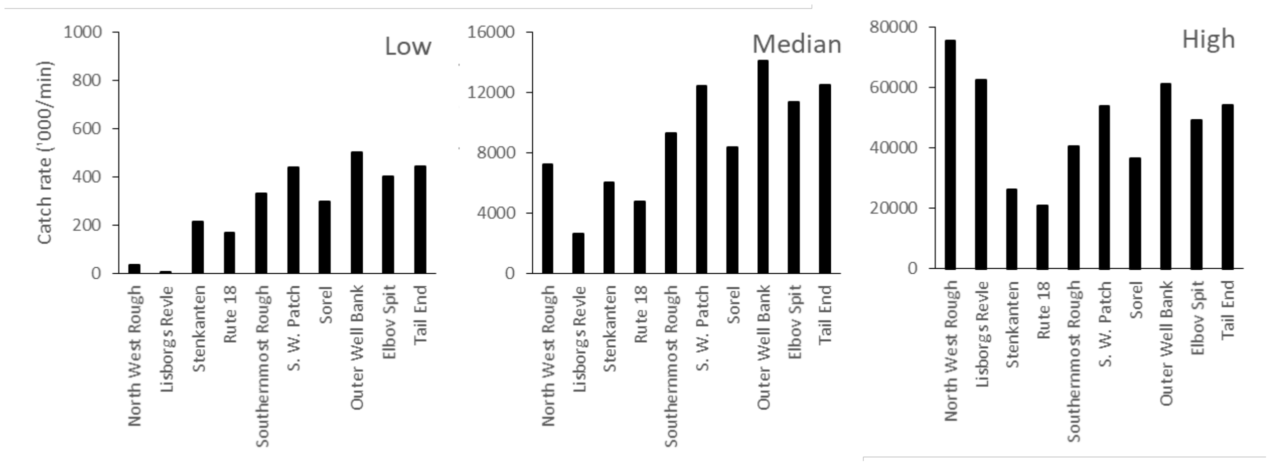
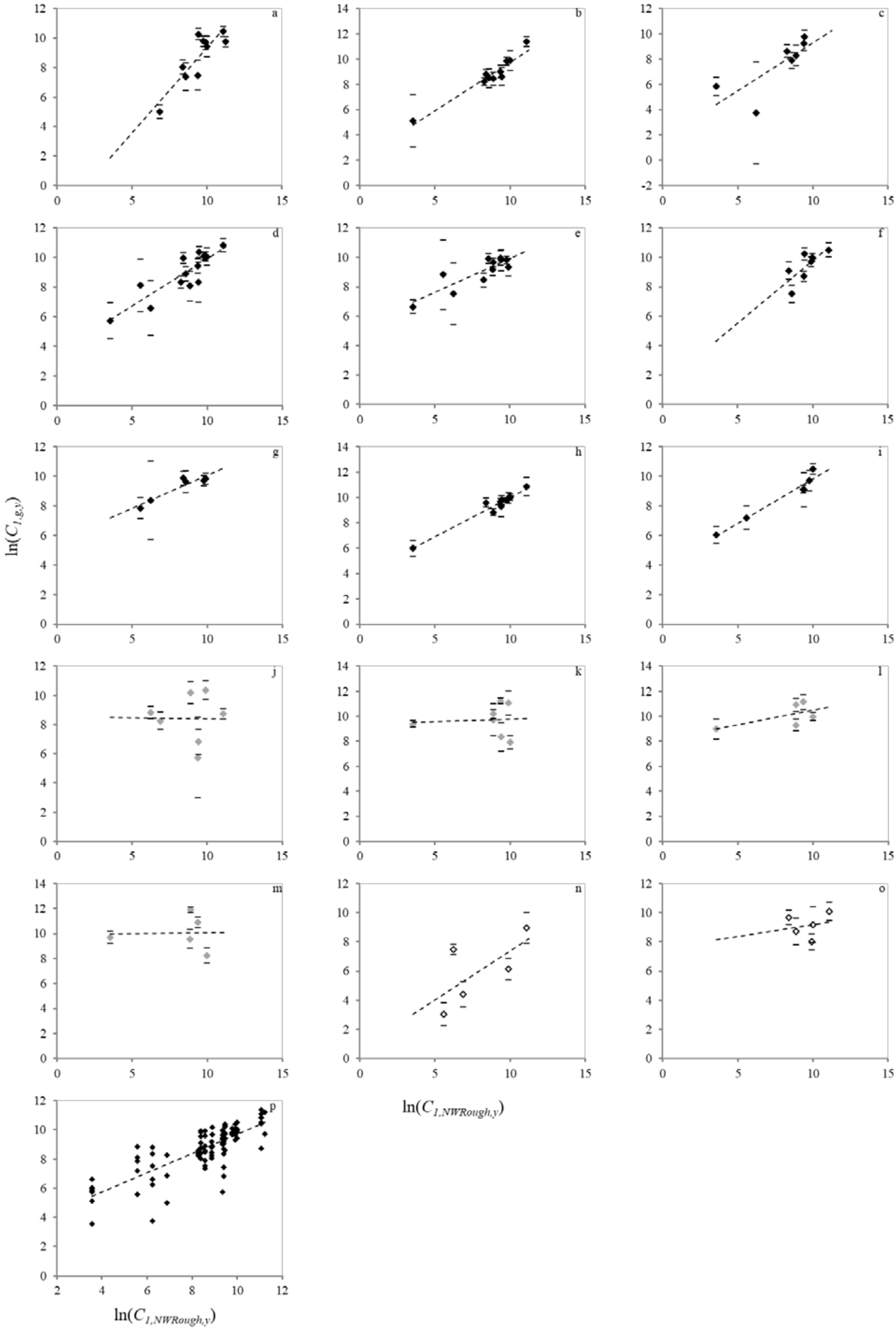


Fig. 2. Catch rates by fishing ground in area 1 at low, median and high densities at North West Rough. Note difference in scale of the three plots. Fishing grounds are ordered according to increasing distance to North West Rough. Catch rates did not differ significantly between fishing grounds more distant than Rute 18.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ln(C1,NWRough,y)

Fig. 3. Average catch rate of 1-year olds (‘000/min) at 14 fishing grounds as a function of average catch rate at N. W. Rough. Fishing grounds are ordered according to distance to North West Rough, with letters higher in the alphabet indicating more distant fishing grounds: In assessment area 1 (black diamonds), Lisborgs Revle (a), Stenkanten (b), Rute 18 (c), Southernmost Rough (d), S.W. Patch (e), Sorel (f), Outer Well Bank (g), Elbow Spit (h), Tail End (i). In assessment areas 4 (grey diamonds), Eventyr Banke (j), Berwick Bank (k), Marr Bank (l), Wee Bankie (m), and in 2 (open diamonds), N. of Horn (n) and Pigekammeret (o). All fishing grounds in assessment area 1 plotted in one panel are also shown (p). Each symbol represents one year, bars indicate confidence limits of the mean, broken lines are ground specific regressions.

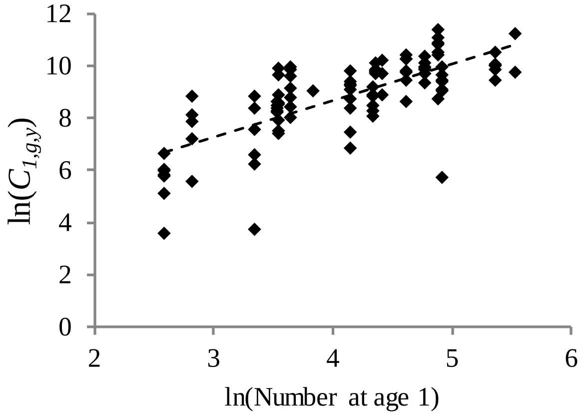

Fig. 4. Catch rates at all grounds as function of number of 1-year olds according to the ICES assessment in area 1 (10^9). Hatched line shows the predicted average catch rate.

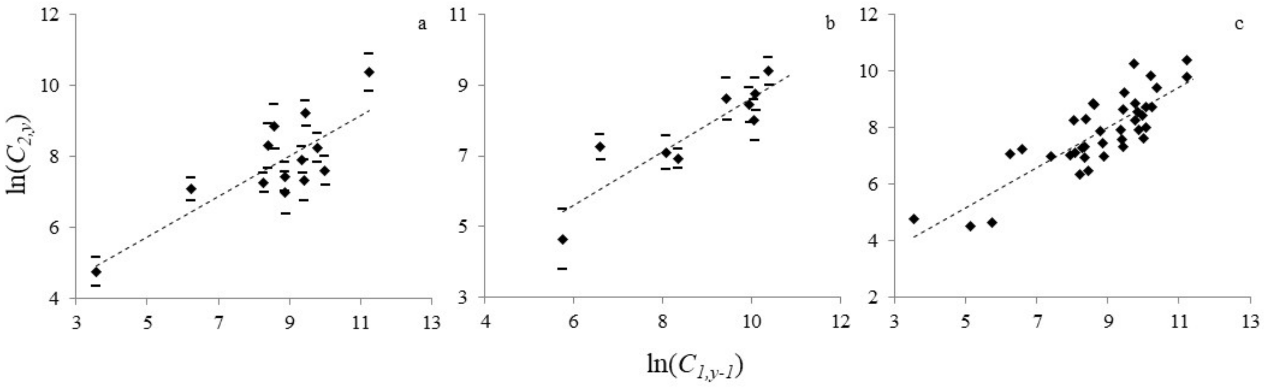

Fig. 5. Average log catch rate (catch in numbers per minute) in the current year of 2-year olds as a function of average log catch rate of 1-year olds the preceding year. N. W. Rough (a), Southernmost Rough (b) and all fishing grounds with at least 5 years of data (c). Horizontal lines represent 95% confidence limits of the mean, lines are ground specific average predictions.

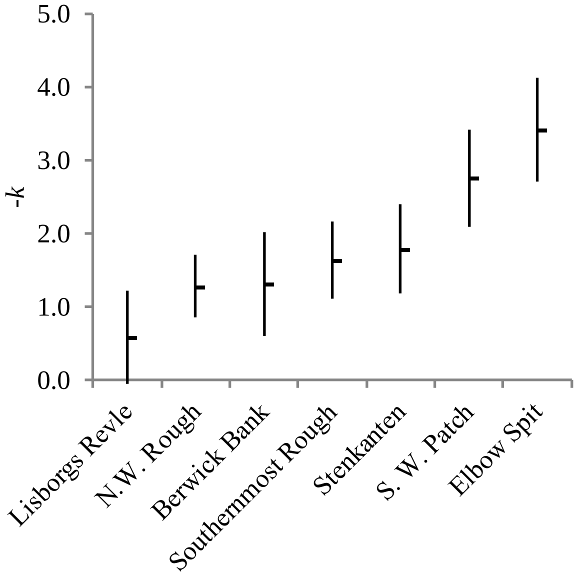

Fig. 6. Average $-k = ln\hat{C}_{1,y-1}$- $ln\hat{C}_{2,y}$, an indicator of total mortality combined with relative catchability of ages 2 and 1.

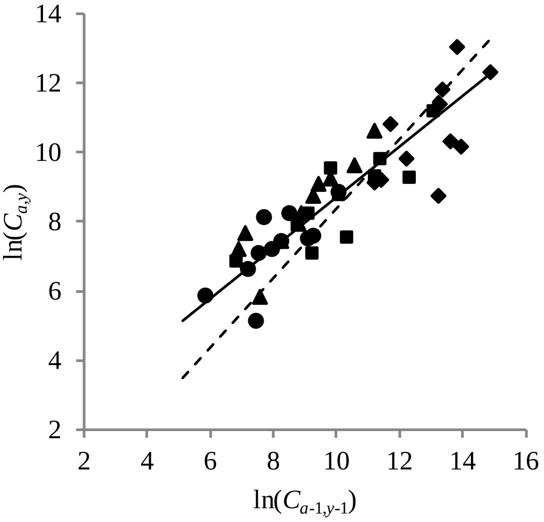

Fig. 7. Index of abundance of sandeel of age *a* in year *y* as a function of the abundance of 1-year younger fish the previous year. Diamonds: 1-year olds, squares: 2-year olds, triangles: 3 year olds and circles: 4 year olds. Hatched line indicates a slope of 1, solid line is a regression line common for all ages assuming gamma error distribution of $C_{a,y}$. Data from sandeel at Shetland by Cook (2004).

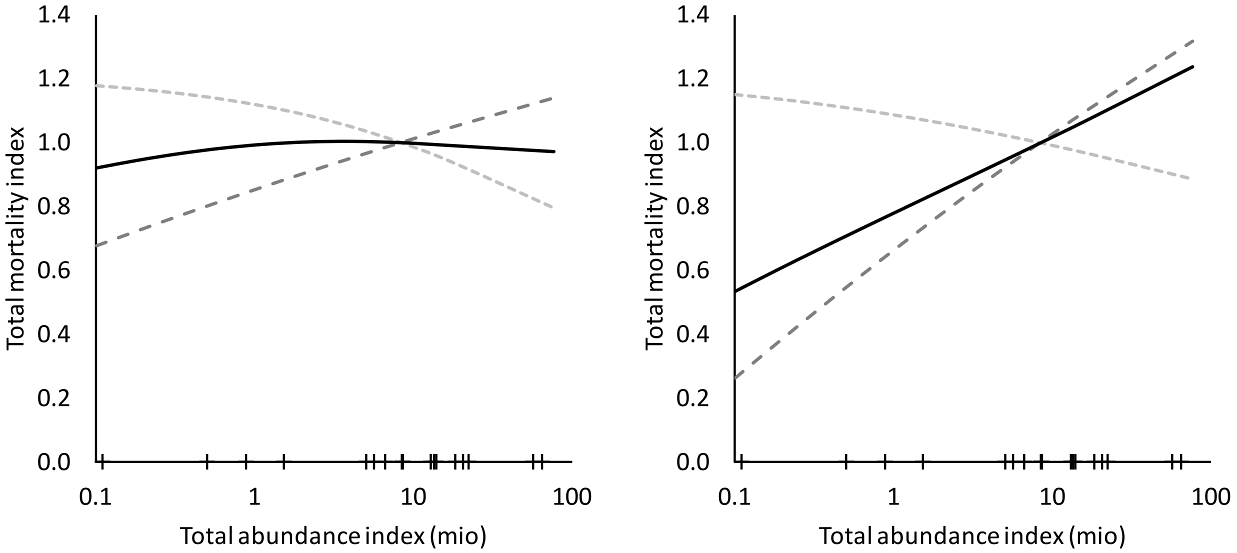

Fig. 8. The combined effect of local density dependent recruitment and mortality. Index of total mortality as a function of an index of total abundance of sandeel in area 1. Left panel: estimated for all fishing grounds. Right panel: estimated for all fishing grounds except S. W. Patch. Light grey dotted line: density dependent recruitment and density independent local mortality. Dark grey broken line: density independent recruitment and density dependent local mortality. Black solid line: density dependent recruitment and density dependent local mortality. Vertical lines at the axis indicate annually observed abundance indices. Lines are scaled to be 1 at the median abundance index.

Supplementary material

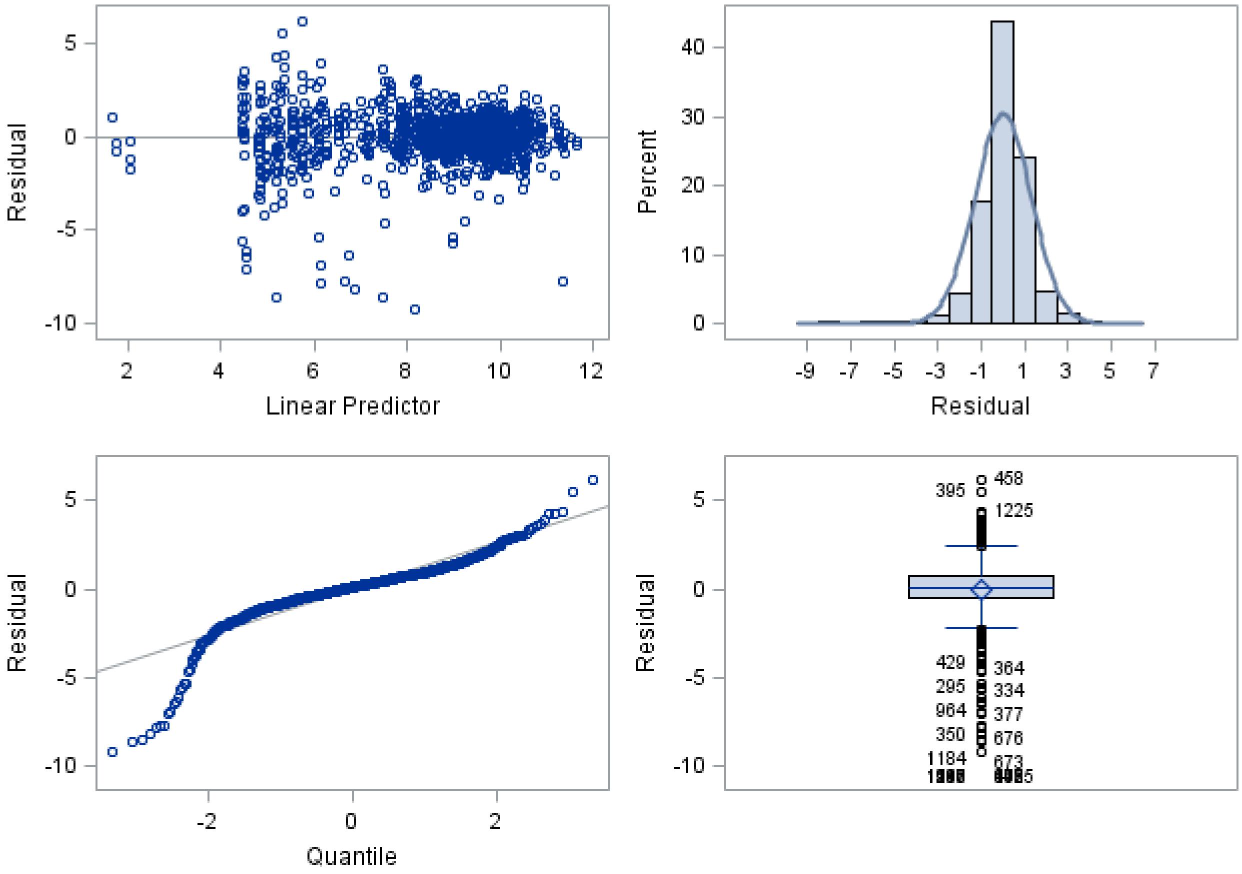

Fig. S1. Residual plots for reduced model 1 ($\ln\hat{C}_{1,g,y} = k_g + \gamma_g ln\bar{C}_{1,NWRough,y} + \omega_{g,y} + \varphi_v$) for grounds in assessment area 1.

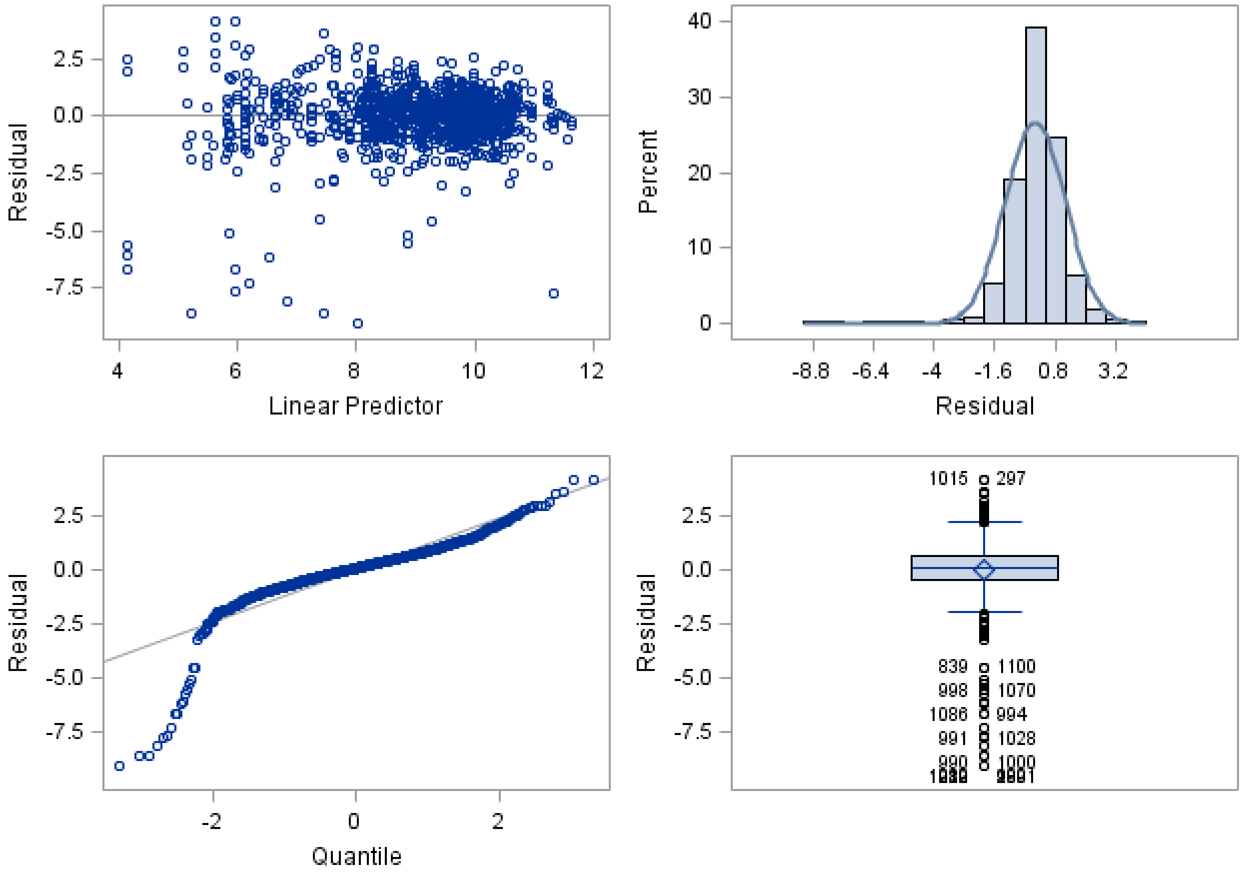

Fig. S2. Residual plots for reduced model 2 ($\ln\hat{C}_{1,g,y} = k_g + \eta_g \ln R_{1,y} + \omega_{g,y} + \varphi_v$) for grounds in assessment area 1.

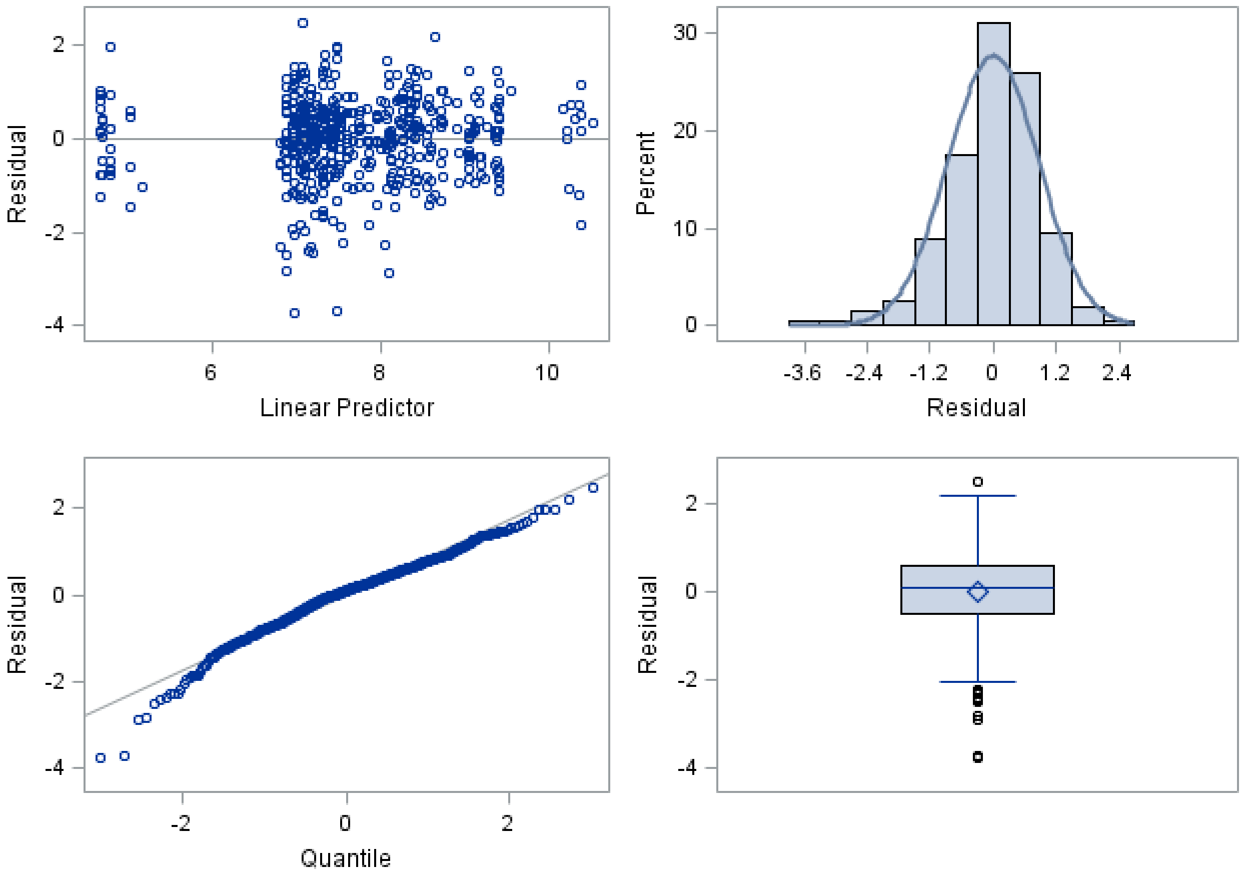

Fig. S3. Residual plots for reduced model 4 ($\ln\hat{C}_{2,y+1} = k_0 + k_1 y + (1 - \beta) ln\bar{C}_{1,y} + \omega_{g,y} + \varphi_v$) for N. W. Rough and Southernmost Rough.