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1 **Scale-specific density dependence in North Sea sandeel**

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6

7 **Running page head**

8 Local and regional density dependence

9

10 **Abstract**

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

21 the necessity of considering both local and regional scale processes in analyses of density
22 dependence.

23

24 **Key words**

25 Spatial scale-dependency, density dependent distribution, demographic processes

26

27 **Introduction**

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

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

46 Sandeels *Ammodytes spp.* form an important link between lower and upper trophic levels in many
47 shelf ecosystems (Hedd et al. 2006, Frederiksen et al. 2006, 2007, Eliassen et al. 2011). They are
48 entirely dependent on coarse sandy sediments as they spend a considerable part of their non-
49 feeding periods buried (Winslade 1974a, b, c). The pelagic larvae can be transported considerable
50 distances by currents before settling into sandy habitat (Potter & Lough 1987, Proctor et al. 1998)
51 but the exchange of post-settled sandeels between the sandy habitat patches is low (Jensen et al.
52 2011). The high site fidelity after settling into fragmented habitat combined with large fluctuations
53 in densities (Wright et al. 2000, Holland et al. 2005) makes the lesser sandeel *Ammodytes marinus*
54 in the North Sea an ideal case for investigating the effect of density dependence on population
55 dynamics. Previous studies of the North Sea lesser sandeel have indicated the existence of density
56 dependent processes at a regional scale (Arnott & Ruxton 2002, van Deurs et al. 2009), acting
57 concurrently with predation mortality, fishing pressure and climatically-induced changes in prey
58 abundance to determine population size (Clausen et al. 2017, Lindegren et al. 2018). However,
59 these studies did not investigate the role of density dependence acting within local habitat
60 patches.

61 In the present study, we hypothesize that: (1) the spatial distribution of recruitment measured by
62 the catch rate of 1-year old fish depends on regional density in a given year, (2) local recruitment
63 depends on local density the previous year, (3) density dependent mortality occurs at a local scale

64 and (4) the cumulated effect when scaling up to population level differs from the processes acting
65 on a local scale. To investigate these hypotheses, we used a series of statistical models to analyse
66 density dependent recruitment and mortality, taking into account both local and regional
67 densities. The analysis was based on catch rates of lesser sandeel (*Ammodytes marinus*) in the
68 North Sea commercial sandeel fishery and in a scientific survey at Shetland.

69

70 **Materials & methods**

71 **Data**

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

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

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

99 To avoid violating assumptions of the statistical regression models used, a sequence of
100 transformations and statistical modelling was used. First, the variance of catch rates tends to
101 increase with the mean (Pennington 1983). To address this, all catch rates were transformed by
102 taking the natural log. Secondly, if the error of the independent variable is in the same order of
103 magnitude as that of the dependent variable, parameter estimates in standard regression models
104 may be considerably biased (Kendall & Stuart 1979). This problem was addressed by using average
105 catch rates across all samples in a given year whenever catch rates were used as an independent
106 variable. This decreases the standard error of the independent variable compared to that of the
107 dependent variable. Thirdly, the sampling design was highly unbalanced and using mean catch

108 rates as the dependent variable in a standard linear regression would violate the assumption of
109 constant variance of the observations. We used individual catch rates as observations in all
110 analyses to accommodate the unbalanced sampling design and to assure that the variance of the
111 dependent variable is considerably larger than that of the independent variable. Lastly, the data
112 from a specific fishing ground, fishing vessel, or year are likely to be correlated due to e.g. local
113 weather effects, skipper skills etc. To address this, random effect models were used throughout
114 and the r^2 of the model using only fixed and both fixed and random effects given (Nakagawa &
115 Schielzeth 2013).

116 **Spatial distribution of recruitment depends on regional density in a given year** 117 **(Hypothesis 1)**

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

$$125 \quad \ln \hat{C}_{1,g,y,v} = k_g + \gamma_g \ln \bar{C}_{1,NWRough,y} + \omega_{g,y} + \varphi_v \quad (1)$$

126 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
127 y , $\ln \bar{C}_{1,NWRough,y}$ is the average log catch rate of 1-year olds on North West Rough in the given
128 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
129 describes the fishing ground specific relationship with density at the reference ground and the

130 random effects of year/fishing ground and fishing vessel ID are contained within $\omega_{g,y} \in N(0, \sigma_\omega)$
131 and $\varphi_v \in N(0, \sigma_\varphi)$, respectively. If γ_g is close to one and σ_ω and σ_φ are small, virtually all variation
132 is explained by the recruitment at the reference ground, North West Rough (no density
133 dependence). If γ_g values > 1 , there is positive density dependence at the fishing ground, and an
134 increased recruitment on the reference ground is accompanied by a higher than proportionally
135 increased recruitment at other grounds. In contrast, γ_g values between 0 and 1 are indicative of
136 negative density dependence at the fishing grounds, where an increased recruitment on the
137 reference ground is accompanied by a lower than proportionally increased recruitment at other
138 grounds. Lastly, if γ_g is close to zero and σ_ω and/or σ_φ are large, the development in local
139 recruitment is independent of that recorded at the reference ground. Since γ_g is estimated for
140 each fishing ground, it is possible that negative density dependence is detected on some grounds
141 and positive density dependence on others. The model was fitted to all data as well as to a subset
142 of data consisting only of fishing grounds within sandeel population area 1 (fig. 1). A similar model
143 was made for population area 4 (fishing grounds close to the coast of Scotland, fig. 1) using
144 Berwick Bank as the reference fishing ground. The areas are considered to contain separate
145 populations (ICES 2016) and hence correlation is expected within areas but not necessarily
146 between areas.

147 If recruitment to different fishing grounds is density dependent, the economic profitability of
148 different fishing grounds may vary with density leading to a relationship between catch rates and
149 stock size that differs from proportional at the regional scale (density dependent catchability). In
150 order to test for density dependent catchability at the regional level, the yearly average catch

151 rates of age 1 sandeel were compared to the number of age 1 fish on January 1st estimated in the
152 analytical assessment (ICES 2018) using a log-linear model:

153 $\ln \hat{C}_{1,g,y,v} = k_g + \eta_g \ln R_{1,y} + \omega_{g,y} + \varphi_v \quad (2)$

154 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 ,
155 the constant k_g represents the average catch rate at the fishing ground at a theoretical abundance
156 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
157 analytical assessment, and η_g describes the ground-specific dependence of catch rates on $R_{1,y}$.

158 $\omega_{g,y} \in N(0, \sigma_\omega)$ describes the random effect of year and fishing ground and $\varphi_v \in N(0, \sigma_\varphi)$
159 describes the random effect of vessel ID. For catchability to be density independent, η_g must be
160 one. If η_g is larger than one, catch rates decrease faster than proportionally as abundance
161 decreases (hyperdepletion, (Hilborn & Walters 1992)). If η_g is less than one, catch rates decrease
162 slower than proportionally as abundance decreases (hyperstability, (Hilborn & Walters 1992)).
163 Temporal trends in catchability at age 1 was analysed by making η_g a linear function of year and
164 testing whether this improved model fit significantly.

165

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

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

170 $\ln \hat{C}_{1,g,y,v} = k_y + \kappa_g \ln \bar{C}_{1,g,y-1} + \omega_{g,y} + \varphi_v \quad (3)$

171 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
 172 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
 173 given fishing ground in the preceding year ($y-1$). The intercept k_y describes the predicted catch
 174 rate at a theoretical average recruitment in the preceding year equal to 1, κ_g describes the effect
 175 of the recruitment in the preceding year and the random effects of year/fishing ground and fishing
 176 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
 177 the density dependent effect was estimated for each fishing ground separately.

178

179 **Density dependent mortality occurs at local scale (Hypothesis 3)**

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

$$182 \quad N_{a+1,y+1} = N_{a,y} e^{-Z_y}$$

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

$$186 \quad \hat{C}_{2,y+1} = \frac{q_{2,y+1}}{q_{1,y}} \hat{C}_{1,y} e^{-Z_y}$$

187 Hence, if the relative difference in catchability of the two age groups and mortality remain
 188 constant over time, the catch rate of a given cohort in a particular year is directly proportional to
 189 the catch rate of the same cohort in the preceding year. Note that when we use catch rates rather
 190 than abundance, catch rates of e.g. 2-year olds (C_2) may exceed that of 1-year olds (C_1) the year

191 before if catchability of 2-year olds (q_2) is higher than of 1-year olds (q_1). If mortality is density
 192 dependent, Z_y is a function of the population density in that year. Assuming that mortality is
 193 linearly related to log abundance with the proportionality factor β , this relationship can be
 194 described as:

$$195 \quad Z_y = Z_0 + \beta \ln N_{1,y} = Z_0 - \beta \ln q_{1,y} + \beta \ln \hat{C}_{1,y}$$

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

$$198 \quad \ln \hat{C}_{2,y+1} = k_{y+1} + (1 - \beta) \ln \hat{C}_{1,y}$$

$$199 \quad \text{where } k_{y+1} = \ln \left(\frac{q_{2,y+1}}{(q_{1,y})^{1-\beta}} \right) - Z_0$$

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

$$202 \quad \ln \hat{C}_{2,g,y+1,v} = k_0 + k_1 y + (1 - \beta_g) \ln \bar{C}_{1,g,y} + \omega_{g,y} + \varphi_v \quad (4)$$

203 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
 204 catchabilities, β_g describes the density dependent effect of last year's geometric average catch
 205 rate of 1-year olds, $\ln \bar{C}_{1,y}$, on mortality at fishing ground g , allowing us to determine if mortality
 206 differs between high and low survival grounds as suggested by Shima and Osenberg (2003).
 207 Random effects of year/fishing ground and fishing vessel ID are again contained within $\omega_{g,y} \in$
 208 $N(0, \sigma_\omega)$ and $\varphi_v \in N(0, \sigma_\varphi)$, respectively. Mortality is independent of density when $\beta = 0$. If β is
 209 greater than zero, mortality increases with density. β was estimated at the two fishing grounds

210 with 8 or more years of data (North West Rough and Southernmost Rough). Due to the very
211 limited catches of fish of age 3 and older, only mortality from 1-year olds to 2-year olds was
212 investigated. To allow comparison of mortality levels between fishing grounds, mortality indices
213 for fishing grounds with at least 5 years data were estimated assuming $\beta = 0$ as $\ln\bar{C}_{2,y+1} - \ln\bar{C}_{1,y}$.

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

$$216 \quad \ln\hat{C}_{a+1,y+1} = k_0 + (1 - \beta)\ln\bar{C}_{a,y}$$

217 These simplifications were required since only one value per year was available and it is
218 reasonable to assume that catchability in a scientific survey is constant over time. More ages were
219 available than in the commercial samples and the analysis therefore included ages 0 to 4. Since
220 $\ln\bar{C}_{a,y}$ is observed with error, ordinary regression is not appropriate. Instead, Deming regression
221 was used to estimate β assuming the error in the dependent and independent variable to be equal
222 (Linnet 1993). The 95% confidence limits of β were estimated using jackknife.

223

224 **Cumulated density dependent effects differ from the processes acting on a local scale** 225 **(Hypothesis 4)**

226 Following the analyses of density dependence in recruitment and mortality, the predictions from
227 the two analyses were combined to assess the integrated effect of local density dependence in
228 mortality and spatial distribution of recruitment on regional mortality (summed across local fishing
229 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 :

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

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:

250
$$Z_{pop,y} = \ln\left(\sum_g I_{1,g,y}\right) - \ln\left(\sum_g I_{2,g,y}\right)$$

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

253
$$I_{pop,y} = \ln\left(\sum_g I_{1,g,y}\right)$$

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

256

257 **Results**

258 **Spatial distribution of recruitment depends on regional density in a given year**

259 **(Hypothesis 1)**

260 The fixed effects model for fishing grounds in assessment area 1 explained 57% of the variation,
261 and the combined fixed and random effects explained 66% (fig. S1 in supplementary material). The
262 standard deviation of the random effect of fishing ground and year (0.31) was much larger than
263 that of vessel ID (0.18), but smaller than the residual deviation (1.84). The fishing ground Lisborgs
264 Revle had a slope (γ_g) >1 (table 2). The remaining fishing grounds in assessment area 1 showed no
265 significant difference in γ_g (P=0.6031). The joint slope at these grounds was 0.62 (table 3), which
266 was significantly different from both 0 and 1 (P<0.001 in both cases). Hence, when recruitment at
267 age 1 increased by 100% at North West Rough, recruitment at Lisborgs Revle increased by 155%
268 and recruitment at fishing grounds other than Lisborgs Revle increased by only 54% (fig. 2). These

269 density dependent differences in catch rates across grounds meant that when catch rates were
270 low on average across all grounds (i.e. low regional population density), North West Rough and
271 Lisborgs Revle catch rates were low relative to other grounds, while catch rates at these grounds
272 were the highest observed when average catch rates were high (fig. 3). In spite of these
273 differences, strong year-classes were detectable across all grounds as above average densities,
274 while weak year-classes provided below average densities across all grounds (i.e. note the
275 difference in scale in fig. 2).

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

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

286

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

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

290

291 **Density dependent mortality occurs at local scale (Hypothesis 3)**

292 Only North West Rough and Southernmost Rough were sampled sufficiently to allow the
293 estimation of density dependence in mortality while seven grounds were sampled sufficiently to
294 allow the estimation of a ground specific mortality index (fig. 5 and 6). Among the seven grounds
295 sampled, Lisborgs revle had the lowest mortality, S.W. Patch and Elbow Spit the highest while the
296 remaining grounds had intermediate values. The catch rate at age 2 was highly related to catch
297 rate of 1-year old fish ($P < 0.0001$) and the model explained 51% and 65% of the variation by fixed
298 and fixed plus random effects, respectively (fig. S3). The effect of year, k_1 , was significantly
299 positive ($P = 0.0364$), indicating that catch rates at age 2 increased over time even if catch rate of 1-
300 year old fish remained unchanged. β was 0.19 and 0.21 at North West Rough and Southernmost
301 Rough, respectively and neither β nor k_0 differed between the two fishing grounds ($P > 0.0795$).
302 The joint density dependent term β was significantly positive ($\beta = 0.21$, $\text{std} = 0.09$, $P = 0.0218$). The
303 model used for the Shetland data revealed a common β of 0.27 ($\text{std} = 0.07$), significantly greater
304 than 0 ($P = 0.0003$) (fig. 7). With this strength of density-dependence, the smallest average catch
305 rate of 1-year olds at North West Rough resulted in a 230% higher catch rate when the fish were
306 2-year olds, corresponding to a higher catchability of 2-year olds compared to 1-year old fish
307 masking the effects of mortality. In contrast, the largest average catch rate of 1-year olds at North
308 West Rough resulted in 58% lower catch rate when the fish were 2-year olds, corresponding to an
309 8-time reduction in survival between the smallest and the largest year-class (assuming constant
310 catchability at age). The density dependence at Shetland was sufficient to reduce the survival of
311 the largest and smallest index by a factor 5. This could potentially be contributing to the
312 stabilization of the population by increasing mortality of large year-classes.

313

314 **Cumulated density dependent effects differ from the processes acting on a local scale**

315 **(Hypothesis 4)**

316 While density dependent mortality led to increased mortality at higher densities (fig. 8, dark grey
317 broken lines), density dependent distribution of recruitment to age 1 led to the opposite result, as
318 the proportion of fish settling to recruit at age 1 at grounds showing high mortality decreased
319 when the overall recruitment in the population was high (fig. 8, light grey dotted lines). Combining
320 the two for fishing grounds in the Dogger Bank area resulted in a mortality index, which was
321 virtually independent of abundance (solid black line in fig. 8). Excluding S. W. Patch, which had a
322 very high estimated mortality index and a very large area, changed the result so the combined
323 effect of density dependent recruitment and mortality was an increase in mortality with
324 abundance, acting to decrease fluctuations in stock abundance at age 2 compared to age 1. If we
325 assume that catchability of age 1 and 2 are equal, this corresponds to a reduction in survival from
326 47% at the lowest observed abundance to 18% at the highest observed abundance. The results of
327 all density dependence investigations are summarised in table 4.

328

329 **Discussion**

330 The regional population processes of North Sea sandeel were a combination of density dependent
331 spatial distribution of recruitment on a regional scale and density dependent mortality on a local
332 scale. In years characterized by a large overall population, a large fraction of the population
333 occurred at low mortality fishing grounds while local mortality increased. Depending on the

334 balance between these two factors, this potentially leads to either increasing or decreasing
335 mortality as abundance increases.

336 Sandeel recruitment in all areas increased as overall recruitment increased, but the increase was
337 substantially greater at North West Rough and Lisborgs Revle. Consequently, the relative
338 contribution of these grounds shifted from supporting the lowest sandeel densities in years where
339 the overall population size was small to supporting the highest densities when the overall
340 population size was large. This density dependence in the distribution of recruitment across fishing
341 grounds does not follow the most commonly referenced distribution hypotheses. For example, the
342 basin theory (MacCall 1990) and the theory on cryptic density dependence (Shima & Osenberg
343 2003) predicts that high quality habitat is always occupied and exhibits the highest densities. This
344 is not the case in our data, as the two grounds switch from having the lowest relative density to
345 the highest relative density. Sutherland's (1983) theory of fish distribution, based on a different
346 parametrization of the Ideal Free Distribution (Fretwell & Lucas 1969), predicts that as the overall
347 population size goes up, local densities throughout the population range increase proportionally.
348 However, this prediction does not match our results either. An alternative explanation for our
349 observations could be spatio-temporal variation in the environmental conditions for recruitment.
350 If oceanographic features, such as advection and retention, vary in different years, this might
351 affect recruitment of settling larvae by shaping the trophodynamic arena that regulate survival
352 through food availability and the physical settings that determine transport into and retention
353 within an area (Henriksen et al. 2018). For example, if the recruitment conditions such as food
354 availability and drift pattern are highly variable in the northwest corner of Dogger Bank but more
355 stable in other areas and large food availability only occurs in the northwest corner of Dogger
356 Bank when there is a high food supply overall, this could explain the greater variation at North

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

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

373 Density dependent mortality substantially reduced the difference between large and small local
374 cohorts at the local level, potentially contributing to the stability of local aggregations. The density
375 dependent mortality seemed to be a result of predation rather than fishing, as it was present at
376 approximately the same level in unfished (Shetland) and fished areas (North West Rough and
377 Southernmost Rough). Density dependent natural mortality of fish such as damselfish (*Dascyllus*
378 *flavicaudus*) and bridled goby (*Coryphopterus glaucofraenum*) acts through exposing individuals to

379 higher predation rates once the carrying capacity of an area has been reached (Forrester & Steele
380 2004, Schmitt & Holbrook 2007). In the case of sandeel, carrying capacity may refer to the
381 availability of suitable burying substrate rather than to refuges as in reef fish (Hobson 1986).
382 Different substrates may offer different overwintering survival or increased food competition may
383 lead to delayed onset of the overwintering period, increasing predation mortality (van Deurs et al.
384 2011). There was no significant difference in the level of density dependent mortality at the three
385 sites examined, indicating that either the sites are similar in quality or the factors inducing density
386 dependence are not related to quality of the sites as found for coral reef fish, such as *Thalassoma*
387 *Hardwicke* (Shima & Ostenberg 2003).

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

399 If the fishery optimises revenue by seeking out the highest catch rates, the density dependent
400 distribution of recruitment will lead to a widespread fishery with low catch rates and little fishing

401 activity at North West Rough and Lisborgs Revle when the overall population is small. When the
402 population is large, the fishery will exhibit high catch rates and concentrate at North West Rough
403 and Lisborgs Revle. This general pattern seems to be confirmed by the distribution of commercial
404 catches in 2003-2005, where abundance was low compared to later years (ICES 2018). The
405 generally reported form of density dependence of catch rates is hyperstability, where catch rates
406 decrease slower than abundance (Saville & Bailey 1980, Winters & Wheeler 1985, Beverton 1990).
407 This has been suggested to be a major cause of overfishing (Erisman et al. 2011). In contrast, the
408 pattern in our data is likely to lead to hyperdepletion of catch rates, where catch rates decrease
409 faster than fish abundance at a regional scale. This is also indicated by the analysis of density
410 dependent catchability, where the slope (η) (eq. 2) was estimated to be 1.24, consistent with
411 hyperdepletion. Alternatively, local catchability depends on local density. If this is the case, it
412 would bias the analysis of density dependence of mortality. However, to produce the impression
413 of mortality increasing with density where no such underlying process exists, catchability for age 1
414 must increase with density more than that of age 2. This is consistent with hyperdepletion for age
415 1 rather than the more commonly reported hyperstability. It is not clear by which process the
416 catchability at a local fishing ground would increase with density. The opposite relationship
417 however, where catchability decreases with increasing stock size is consistent with fisheries
418 targeting prime habitat into which the fish are aggregating to a greater degree when stock size is
419 low.

420 In summary, the population dynamics of lesser sandeel in the North Sea rely on a mosaic of local
421 habitats determining density dependence at the regional population level. Local density
422 dependent mortality led to increasing mortality at higher densities. Concurrently, density
423 dependent distribution of recruitment led to a shift in distribution towards low mortality fishing

424 grounds when recruitment at the regional scale was high. As a result, hyperdepletion of catch
425 rates was more likely than hyperstability. Combining the two density dependent effects for fishing
426 grounds in the Dogger area resulted in a mortality index, which was virtually independent of
427 abundance. Our study demonstrated the necessity of considering both local and regional
428 processes in analyses of density dependence (Shima & Osenberg 2003, Eium & Nislow 2005): had
429 the analysis considered only local density dependent effects on mortality, the conclusion of the
430 study would have been in complete opposition to an analysis considering only density dependent
431 effects on the spatial distribution of recruitment.

432

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439

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576 **Tables**

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

Hypothesis	Model	Density dependence analysed	Tests performed
1	$\ln\hat{C}_{1,g,y,v} = k_g + \gamma_g \ln\bar{C}_{1,NWRough,y} + \omega_{g,y} + \varphi_v \quad (1)$	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	$\ln\hat{C}_{1,g,y,v} = k_g + \eta_g \ln R_{1,y} + \omega_{g,y} + \varphi_v \quad (2)$	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	$\ln\hat{C}_{1,g,y,v} = k_{y,g} + \kappa_g \ln\bar{C}_{1,g,y-1} + \omega_{g,y} + \varphi_v \quad (3)$	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	$\ln \hat{C}_{2,g,y+1,v} = k_0 + k_1 y + (1 - \beta_g) \ln \bar{C}_{1,g,y} + \omega_{g,y} + \varphi_v \quad (4)$	Dependence of local mortality on local cohort density.	$\beta \neq 0$

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581

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

Fishing ground	Ass. area	N	Year s	γ_g	P($\gamma=0$)	$k_{0,g}$ 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)

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589 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

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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: $\gamma_g > 1$ at Lisborgs Revle ($P=0.0012$). Remaining fishing grounds had $0 < \gamma_g < 1$ ($P < 0.00001$ 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 ($\beta=0.21$, $P=0.0218$), indicating that mortality increased with increasing density. Shetland: β significantly greater than zero ($\beta = 0.27$, $P=0.0003$), indicating

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		that mortality increased with increasing density.
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597 Fig. 1. Named fishing grounds and numbered sandeel areas referred to in the study.

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

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

619
 620 Fig. 4. Catch rates at all grounds as function of number of 1-year olds according to the ICES
 621 assessment in area 1 (10^9). Hatched line shows the predicted average catch rate.

623

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

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

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636 Fig. 7. Index of abundance of sandeel of age a in year y as a function of the abundance of 1-year
637 younger fish the previous year. Diamonds: 1-year olds, squares: 2-year olds, triangles: 3 year olds
638 and circles: 4 year olds. Hatched line indicates a slope of 1, solid line is a regression line common
639 for all ages assuming gamma error distribution of $C_{a,y}$. Data from sandeel at Shetland by Cook
640 (2004).

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642

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

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653

654 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

655 grounds in assessment area 1.

656

657 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
 658 assessment area 1.

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661 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

662 N. W. Rough and Southernmost Rough.

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