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Patchy zooplankton grazing and high energy conversion efficiency – Ecological implications of sandeel behavior and strategy

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ABSTRACT

Sandeel display strong site-fidelity, and spend most of their life buried in the seabed. This strategy carries important ecological implications. Sandeels save energy when they are not foraging but in return are unable to move substantially and therefore possibly are sensitive to local depletion of prey. Here we studied zooplankton consumption and energy conversion efficiency of lesser sandeel (*Ammodytes marinus*) in the central North Sea, using stomach data, length and weight-at-age data, bioenergetics, and hydrodynamic modeling. The results suggested: (i) lesser sandeel in the Dogger area depend largely on relatively large copepods in early spring. (ii) lesser sandeel is an efficient converter making secondary production into fish tissue available for higher trophic levels. Hence, changes in species composition towards a more herring dominated system, as seen in recent times, may lead to a decrease in system transfer efficiency. (iii) sandeels leave footprints in the standing copepod biomass as far as 100 km from the edge of their habitat, but smaller and more isolated sandeel habitat patches have a much lower impact than larger patches, suggesting that smaller habitats can sustain higher sandeel densities and growth rates per area than larger habitats.

Keywords: Sand lance · Food web · Trophic transfer efficiency · Bioenergetics · Growth · Food consumption · North Sea · Dogger

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Patchy zooplankton grazing and high energy conversion efficiency – Ecological implications of
sandeel behavior and strategy

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25 This strategy carries important ecological implications. Sandeels save energy when they are not
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27 depletion of prey. Here we studied zooplankton consumption and energy conversion efficiency of
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29 weight-at-age data, bioenergetics, and hydrodynamic modeling. The results suggested: (i) lesser
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36 suggesting that smaller habitats can sustain higher sandeel densities and growth rates per area than
37 larger habitats.

48 INTRODUCTION

49 In marine ecosystems, the main flow of energy from secondary producers to larger fish, birds and
50 mammals is often channeled through just a few key species of small schooling fish, the so-called
51 forage fishes (Cury et al. 2000). Forage fish is a functional group characterized by fast somatic
52 growth, early maturation, planktivory and schooling behaviour, and they are a major energy
53 resource to a wide variety of predators (Alder et al. 2008). In the central North Sea, the most
54 important forage fishes are lesser sandeel (*Ammodytes marinus*) and the clupeids, herring (*Clupea*
55 *harengus*) and sprat (*Sprattus sprattus*). These species act as major food-web energy conveyers,
56 grazing vigorously on the zooplankton and thereby converting secondary production into fish tissue,
57 which is in turn available to marine predators higher in the food web. If the energy conversion
58 efficiency of the forage fish community is high, more of the energy ingested in the form of
59 secondary producers will be available for production at higher trophic levels and less will be lost
60 through respiration. Energy conversion efficiency is therefore an important ecological aspect of the
61 food-web, and has been proposed as a major determinant of food-chain length (the energy-flow
62 hypothesis) and predator production (e.g. Rand and Stewart 1998, Yodzis 1984; Trussell et al.
63 2006).

64 Although sandeels share the general characteristics of a forage fish, they possess several unique
65 traits. Sandeels spent a large part of their juvenile and adult life buried in the seabed in areas with
66 well-oxygenated bottom substrate consisting of gravel or coarse sand (Reay 1970; Jensen et al.
67 2011). They remain buried throughout the diel cycle in winter, except during spawning around new-
68 year. However, in early spring they start to emerge every day to feed, and become one of the most
69 abundant fish species in the water column of the North Sea for the following three to four months
70 (Macer 1966; Winslade 1974; MacLeod et al. 2007). When burrowed, sandeel are motionless and
71 their metabolism is reduced to a minimum (e.g. Behrens et al. 2007; van Deurs et al. 2011a). This

cryptic energy saving behaviour potentially renders sandeels more efficient as food-web energy conveyers compared to forage fish with a more active behaviour.

Another unique trait of sandeels is the high degree of site fidelity resulting in a foraging behaviour resembling that of central place foragers. Feeding takes place near their nightly burying habitat (e.g. van der Kooij et al. 2008; Jensen et al. 2011; Engelhard et al. 2008). Therefore, the movement of water and associated zooplankton relative to the fixed location of the sandeels is likely to greatly influence the food available to sandeels and their impact on the local zooplankton. In contrast, fully pelagic forage fishes, such as clupeids are able to move more freely in response to food density (Dragesund et al. 1997; Corten 2001) and can effectively graze continuously on the same copepod population for prolonged periods of time.

The aim of the present study was to explore the ecological implications of the two unique traits of sandeels, with particular focus on energy conversion efficiency and site fidelity. To this aim, we studied lesser sandeel inhabiting the sand banks in the Dogger area located in the frontal region of the central North Sea (fig. 1). Firstly, the amount of zooplankton consumed by sandeels was estimated from stomach content and bioenergetics. Secondly, the energy conversion efficiency from ingested zooplankton to fish tissue was calculated for sandeels. Thirdly, the ecosystem effects of differential energy conversion efficiencies amongst forage fishes were analyzed. Lastly, the grazing pressure on local zooplankton communities was modeled by taking water movement and sandeel site-fidelity into account.

96 METHODS AND MATERIALS

97

98 **Data**

99 Sandeel samples were collected during a data collection program carried out in co-operation
100 between the Danish Fisherman's Association and the Technical University of Denmark. Samples
101 were taken at sea by the fishermen and immediately frozen. Samples were later transported,
102 together with information on haul location and time, to the Technical University of Denmark for
103 further analysis. In the laboratory, a subsample of each sample was measured and rounded down to
104 the nearest half centimeter group below and 10 sandeels per half cm group were randomly selected
105 and age determined using otoliths. For further details, see Jensen et al. (2011). Mean length-at-age
106 was estimated by combining length distributions with age-length keys. Age-length keys were
107 produced separately for each distinct fishing ground and week using the method described by
108 Rindorf and Lewy (2001). Condition was estimated as $\text{weight [g]}/\text{total length [cm]}^b$, where $b = 3.06$
109 is equal to exponent of the power law function describing fish weight as a function of total length
110 when all data is used. Only samples collected between 2001 and 2008 (a period of consistently high
111 sampling intensity throughout quarter 2) and from the major fishing grounds were used (fig. 1).
112 During the same sampling program described above, a total of 472 sandeel stomachs were analyzed.
113 Stomachs were collected between 2006 and 2008 (in April, May and June) from all over the Dogger
114 area. After taking out each stomach, it was gently dabbed on both sides with tissue before weighing
115 [g wet weight]. Roughly every third stomach was put aside after weighing for further diet analysis
116 (preserved in 98% alcohol).

117

118 **Amount of zooplankton consumed**

119 Two approaches were used to estimate consumption by sandeel: Stomach contents and bioenergetic
120 calculation. The weight of stomach content was used to estimate consumption in the period where
121 the samples were taken. This is often seen as a more accurate method than bioenergetics modeling
122 when growth is food limited (Elliott and Persson 1978). In contrast, bioenergetic modeling provides
123 the opportunity to estimate food consumption over longer periods where the sampling of stomachs
124 becomes increasingly labour intensive. Before any estimates of consumption were made, a diet
125 analysis was carried out to investigate the size distribution of copepods. This information was
126 necessary to account for different energy densities of different sized copepods (e.g. Corner and
127 O'Hara 1986).

128

129 *Diet analysis*

130 Stomach content was spread evenly out on a Petri-dish with 2 to 3 mm of water. A sub-area of 4
131 cm² in the middle of the petri-dish was photographed through a stereo-microscope. Copepods
132 completely dominated the diet. Other organisms, such as annelids, crustacean larvae, amphipods,
133 appendicularians and fish eggs each constituted ~ 1% of the diet. Further analyses therefore focused
134 on copepods. A reliable quantitative separation into copepod species was not possible due to the
135 advanced stage of digestion of the stomach content. Instead Image Pro Plus software was used to
136 digitally measure the length of all intact copepod prosomes ignoring stomach content in advanced
137 stages of digestion. Laboratory experiments have shown that sandeels prefer fish larvae over
138 copepods (Christensen 2010). Hence, to investigate whether a major proportion of the diet of
139 sandeels consists of fish larvae, we also examined the stomach contents for pieces of fish larvae.

140

141 *Energy density of copepods of different sizes*

142 Corner and O'Hara (1986) reported the monthly energy content of four North Sea copepod species
 143 in spring. Based on this data copepods were given an energy density of 3200 J g⁻¹ wet weight for
 144 individuals < 1.3 mm and 5600 J g⁻¹ wet weight for larger copepods. Average energy density of the
 145 diet, e_d , was then determined from the proportion of large (> 1.3 mm) copepods observed in the diet
 146 P_{large} as $e_d = 3200(1 - P_{large}) + 5600P_{large}$.

147

148 *Daily ration estimated from stomach data*

149 We assumed a simple Bajkov type relationship between the amount of food consumed and the
 150 amount of food in the stomach (e.g. Eggers 1977) and calculated the weight specific daily ration
 151 [weight of daily food intake relative to body weight] as:

152

$$153 \quad D_R = \frac{24\phi(T) \times W_S}{W^*} \quad (1)$$

154

155 $\phi(T)$ is the evacuation coefficient as a function of temperature and was adopted from van Deurs et
 156 al. (2010). W_S is the net weight of the stomach [g wet weight] (total weight of the stomach minus
 157 the weight of the emptied stomach; weights of empty stomachs was estimated based on a curve
 158 fitted to 30 empty stomachs). W^* is the mean body weight of the fish defined as the body weight
 159 half way through the growth period. D_R was calculated for each fish separately to allow us to
 160 calculate the geometric mean and standard error for various length intervals and for early and late
 161 spring. Note that D_R is directly comparable to daily consumption as derived from bioenergetics in
 162 the section below. Stomach data were only available for adults.

163

164 *Bioenergetic modeling of consumption*

165 Conventional bioenergetic calculations consider growth over time as a function of consumption,
 166 respiration, egestion and excretion (e.g. Hansen et al. 1993). However, in the present study the
 167 calculations were inverted in order to find the amount of energy required to obtain observed
 168 changes in growth and condition over time. Input values to the bioenergetics calculations were
 169 therefore observed total length (L [cm]) and condition (K) on the first ($t1$) and last Julian day ($t2$) of
 170 the calculation period. Calculation periods for adults (age 1 and age 2) were taken as the entire
 171 growth period (April 1 – June 30) and early and late spring separately (April 1 to May 15 and May
 172 15 to June 30) corresponding to the first and second half of the growth period (Macer 1966;
 173 Winslade 1974c; MacLeod et al. 2007). For juveniles (age 0) we assumed a summertime growth
 174 period of one hundred days (not split into early and late growth/spring as was done for the adults).
 175 L_{t1} , L_{t2} , K_{t1} and K_{t2} for adults were determined by fitting a 4th order polynomial to observed weekly
 176 mean length or weekly mean condition as a function of week (fig. 2 & 3), except for early spring
 177 age 2 where we assumed $L_{t1(\text{age } 2)} = L_{t2(\text{age } 1)}$. Juveniles (age 0) were poorly represented in the
 178 samples, since they metamorphose and settle to the sand banks after the main fishing season has
 179 ended. We therefore chose to define $L_{t1(\text{juveniles})}$ and $L_{t2(\text{juveniles})}$ as the size at metamorphosis (5 cm,
 180 Wright and Bailey 1996) and $L_{t2(\text{juveniles})} = L_{t1(\text{age } 1)}$, and values of $K_{t1(\text{juveniles})}$ and $K_{t2(\text{juveniles})}$ were
 181 assumed identical to those of age 1 sandeels.

182

183 Individual food consumption in terms of energy (C_E [J]) for a given age-class and period was
 184 calculated as:

185

$$186 \quad C_E = \frac{\Delta E_S + \Delta E_R + M}{0.7} \quad (2)$$

187

188 where ΔE_S and ΔE_R are the change in body energy [J] attributable to structural growth (length
 189 growth) and energy reserves (condition increase) respectively taking place over the calculation
 190 period, M is metabolism [$\text{J ind}^{-1} \text{h}^{-1}$] (see equation 3) and 0.7 is the universal assimilation efficiency
 191 for fish (Chianelli et al. 1998). ΔE_S and ΔE_R were calculated from the change in mass of structural
 192 tissue (Δm_S [g]) and energy reserves (Δm_R [g]) over the time period: $\Delta E_S = 4500\Delta m_S$ and
 193 $\Delta E_R = 8600\Delta m_R$, where the coefficients 4500 and 8600 represent energy densities [J g^{-1}] of
 194 structural tissue and energy reserves, respectively. Energy density of structural tissue was derived
 195 from table 2 in Hislop et al. (1991) (data from March/April when reserves of lesser sandeel are at
 196 their minimum) and energy density of reserves from van Deurs et al. (2011a). Δm_S and Δm_R were
 197 calculated as $\Delta m_S = (K_{t2}L_{t2}^{3.06}) - (K_{t1}L_{t1}^{3.06})$ and $\Delta m_R = (K_{t2}L_{t2}^{3.06}) - (K_{t1}L_{t1}^{3.06})$. The exponent 3.06
 198 corresponds to the b exponent mentioned previously. The latter equation is more accurate when K_{t1}
 199 approaches K_{minimum} . $C_{E(\text{late spring})}$ was therefore approximated from $C_{E(\text{entire growth period})} - C_{E(\text{early spring})}$
 200 rather than using the equation.

201 Metabolism M (used in equation 2) was modelled as the standard metabolic rate (SMR [$\text{J ind}^{-1} \text{h}^{-1}$])
 202 plus the metabolic cost of swimming during the daily foraging period. Specific dynamic action (the
 203 metabolic cost associated with digesting a meal) is accounted for in the assimilation coefficient in
 204 equation 2. Standard metabolic rate in the period $t1$ to $t2$ is simply $24SMR \times (t2 - t1)$ where $t1$ and $t2$
 205 are given in Julian days. The metabolic cost of swimming was estimated as the product of the hours
 206 spent swimming per day (β), an activity multiplier (α), and the duration of the calculation period $t1$
 207 to $t2$: $\alpha SMR \beta \times (t2 - t1)$, where α was given the default value 3.3 (from: van Deurs et al. 2010). This
 208 activity multiplier is in agreement with Boisclair and Sirois (1993). The duration of the daily
 209 activity period was set to $\beta = 10$ h in accordance with laboratory experiments (van Deurs et al.
 210 2011b). Together this resulted in an estimate of M in the calculation period $t1$ to $t2$ of:

211

$$M = 24SMR[t_2 - t_1] + 33SMR[t_2 - t_1] \quad (3)$$

213

214 *SMR* was modeled as a function of body mass and temperature and was adopted directly from van
 215 Deurs et al. (2011a): $SMR = 1.36W^{0.8} \times (0.08T - 0.25)$, where W is the weight of the fish [g wet
 216 weight] (here defined as the weight half way through the calculation period, back calculated from
 217 figure 2 & 3 using $W = K \times L^{3.06}$). T is the mean sea surface temperature during the calculation period
 218 and provided by the Danish Meteorological Institute.

219

220 Weight specific daily consumption (C_w [in proportion of body weight]) was estimated as:

221

$$C_w = \frac{C_B / W^*}{(t_2 - t_1)} \quad (4)$$

223

224 where C_B is the total biomass consumed per individual during the calculation period [g ind⁻¹]
 225 calculated as: $C_B = C_E / e_d$, where e_d corresponds to the energy content of the diet (from the section
 226 above about energy density of different sized copepods). W^* is the mean body weight of the fish
 227 defined as the body weight half way through the growth period.

228

229 Population level consumption rate per surface area (C_R [g wet weight d⁻¹ m⁻²]) were estimated as

230

$$C_R = \frac{C_B \times N \times (t_2 - t_1)}{15 \times 10^9} \quad (5)$$

232

where C_B corresponds to the definition given under equation 4. N is the average stock number for the period 2001-2008 and for the sandeel stock assessment area 1 (corresponding to the Dogger area) in ICES (2011) and 15×10^9 is roughly the combined surface area [m^2] of sandeel habitats in the Dogger area (Jensen et al. 2011).

Conversion efficiency of sandeels

The energy conversion efficiency during the growth period [% of ingested energy that is converted to fish tissue via structural growth or reserve accumulation] was calculated as:

$$CE_{\text{growthperiod}} = \frac{\Delta E_S + \Delta E_R}{C_E} \times 100 \quad (6)$$

where ΔE_S , ΔE_R and C_E are taken from equation 2. In the literature energy conversion efficiency is either given specifically for the growth period or the entire year. For zooplanktivorous fishes in seasonal environments the annual value is expected to be lower since some of the reserves accumulated during the growth period fuels metabolism outside the growth period. To allow a comparison we also estimated annual energy conversion efficiency for sandeels. This was done by including the metabolic cost of overwintering in equation 6 in the following way: $CE_{\text{annual(sandeel)}} = (\Delta E_S + \Delta E_R - \text{cost of overwintering}) / C_E \times 100\%$, where $\text{cost of overwintering} = 18.69 L_t^{2.66}$ [J] (derived from table 2 in van Deurs et al. 2011a).

Ecosystem effects

To explore the potential ecosystem effects of the contribution of sandeels to the forage fish community, we calculated the combined annual energy conversion efficiency of the North Sea forage fish community (sandeels and clupeids) for each year from 1974 – 2010 as:

$$CE_{(foragefish)} = \frac{B_{(sandeel)} \times CE_{(sandeel)} + B_{(clupeid)} \times CE_{(clupeid)}}{B_{(foragefish)}} \quad (7)$$

where CE is conversion efficiency and B is the stock biomass in a given year ($B_{(clupeid)}$ include both herring and sprat). Stock biomasses of all species were derived from the multispecies model (SMS) of the North Sea (Lewy and Vinther 2004, ICES 2011) using data downloaded from ICES (http://wet.weightw.ices.dk/reports/SSGSUE/2011/WGSAM/SMS_summary.csv). $CE_{(foragefish)}$ was calculated using either annual values or growth period specific CE values. $CE_{growthperiod(sandeel)}$ and $CE_{annual(sandeel)}$ is calculated above (we used the average across age-classes). The growth period specific value for clupeids was derived from values for Atlantic herring (*Clupea harengus*) given in Varpe et al. (2005) and De Silva and Balbontin (1974) resulting in $CE_{growthperiod(clupeids)} = 15\%$. Annual values were not available for Atlantic herring, sprat or any closely related species. We therefore chose 10% for the purpose of these calculations, assuming herring spent accumulated reserves during overwintering and spawning migration.

Grazing pressure on local zooplankton communities

Grazing pressure and local gradients in copepod concentrations resulting from patchy distribution of sandeels were investigated using a simple logistic grazing/production model coupled to a 3 dimensional operational ocean circulation model, the Danish Meteorological Institute

hydrodynamical operational model BSHCmod. Details about performance and model results verification of this model are reported in Larsen et al. (2007), She et al. (2007a) and She et al. (2007b).

The grazing/production model was formulated as a differential equation:

$$\frac{\Delta c}{\Delta t} = \lambda c \left(1 - \frac{c}{c_0} \right) - (\mu_s + \mu_0) c \quad (8)$$

Where c is copepod concentration, c_0 is the copepod carrying capacity (given as a concentration) of the system in the absence of grazing, λ is 1/(production time scale), μ_s is grazing pressure exerted by sandeels, and μ_0 is a background grazing level provided by other grazers in the region. The first term on the right hand side of the equation can be interpreted as the copepod production p and provides a production time scale ($1/\lambda$) and a copepod concentration (c) that equals carrying capacity of the system (c_0) in the absence of grazing. The second term on the right hand side of the equation is the grazing term. The equation was parameterized by assuming (i) a copepod vertical distribution (δ) of 0 - 8 m from the surface, (ii) production maximum = $0.5c_0$, (iii) a regional characteristic copepod production $p\delta = 1.5$ g wet weight m^{-2} day^{-1} and copepod concentration $c\delta = 15$ g wet weight m^{-2} (Nielsen and Munk (1998); see also Berggren et al. (1988)), (iv) total grazing (sandeels plus other) equals total copepod production, and (vii) grazing rate of sandeels ($\mu_s\delta c$) equals the sum of $C_{R(age\ 1)}$ plus $C_{R(age\ 2)}$ from equation 5.

The differential equation was solved using Eulerian forward simulations performed by solving mass balance equations for each grid cell (6x6 nautical miles) on a computational grid. Mass fluxes over grid cells were derived from spatially and temporally varying water currents provided by the circulation model. The Eulerian simulation period was April 2007 – June 2007 (corresponding to

the growth period for adult sandeels). The computational grid was restricted to the Dogger area (1 to 5°E and 53.5 to 56°N) and Dirichlet boundary conditions were applied. Information about the geographical distribution of sandeel habitat (Christensen et al. 2009, Jensen et al. 2011) was used to constrain grazing to defined grid cells within the computational grid. As a simplification, spatio-temporal variation in sandeel consumption rate and copepod production rate were neglected. Grazing pressure was quantified as (i) the average fraction of the copepod biomass grazed by sandeels inside sandeel habitats relative to the total grazing of copepods inside sandeel habitats: $\rho_1 = \mu_s / (\mu_s + \mu_o)$ (averaged over the simulation) and (ii) the bulk grazing ratio averaged over the entire simulation area: $\rho_2 = \text{sandeel grazing} / \text{total grazing}$ (averaged over the simulation). Lastly, the spatial heterogeneity scale in copepod concentrations, resulting from patchy distribution of grazing sandeels, was investigated by depicting the average copepod concentration (averaged over the entire simulation period) for each grid cell in a color gradient map.

RESULTS

Zooplankton consumption

During early spring larger copepods dominated the stomach content of adult sandeels. Copepods with prosome lengths around 2.25 mm were the most important. Juvenile sandeels were not available for stomach sampling. In late spring smaller copepods dominated in terms of numbers, but biomass-wise relatively large copepods (>1.5 mm) were still the more important food source (fig. 4).

326 There was a large degree of similarity between daily consumption (C_W ; bioenergetic approach) and
327 daily ration (D_R ; stomach data) (fig. 5). Both methods resulted in lower estimates of consumption in
328 late spring compared to early spring. Parameter values used in the bioenergetics calculations are
329 summarized in table 1. At the individual level, juvenile sandeels (summer) had higher weight
330 specific consumption compared to adults (spring), but lower absolute consumption due to their
331 lower weight. For adults, consumption rates were highest during early spring (table 2).

332

333 **Conversion efficiency**

334 The consumed secondary production was converted to sandeel biomass with an energy conversion
335 efficiency of 32 - 56% within the growth period. Energy conversion efficiency was lowest for age 2
336 in late spring and in general highest during early spring. Annual energy conversion efficiencies
337 were considerably lower (table 2).

338 The sensitivity of the model to the activity multiplier (α), daily activity period (β), timing of the
339 growth period (t_2-t_1), and temperature (T) was low. Estimated consumption and energy conversion
340 efficiency varied no more than 5% in response to decreasing/increasing these parameter values +/-
341 15%, except for T , which varied between 5 and 8% depending on the age of the fish (8% for age 2).

342

343 **Ecosystem effects**

344 The results suggest that the proportion of sandeels in the forage fish community has ecosystem
345 implications, although the extent depends on whether calculations are based on the growth period
346 efficiency or the annual efficiency. The combined forage fish energy conversion efficiency (of the
347 growth period) varied markedly between 1974 and 2010 and decreased by 35% in the period 2003 –
348 2005 (a period of low sandeel stock biomass) compared to the average level from 1974 – 2000. This
349 was approximately halved (17%) when annual efficiencies were used (fig. 6).

350

351 **Grazing pressure on local zooplankton communities**

352 The grazing pressure exerted by sandeels relative to total copepod grazing was estimated to $\rho_1 =$
353 0.697 (s.d. = 0.032) inside sandeel habitats and $\rho_2 = 0.367$ (s.d. = 0.031) for the study area as a
354 whole (including the spaces between sandeel habitats). Assuming that sandeels are evenly
355 distributed within sandeel habitats, copepod concentrations drifting over sandeel habitats with a
356 large surface area or dense habitat clusters were effectively diluted (by grazing) and distinct local
357 gradients in copepod concentrations appeared with a heterogeneity length scale of ~150 km (fig. 7).

358

359

360

361 **DISCUSSION**

362

363 In the present study we estimated the food consumption and energy conversion efficiency for Lesser
364 sandeel inhabiting the Dogger area in the North Sea. Based on this information we demonstrated the
365 ecological implications of (a) fluctuating proportions of sandeels in the forage fish community and
366 (b) sandeel habitat patchiness.

367

368 Daily ration estimated from stomach data agreed well with daily consumption estimated from
369 bioenergetics, although during late spring, the stomach data gave values that were generally lower
370 than values derived from bioenergetics. The difference was particularly pronounced in late spring,
371 indicating that the fish length at the end of this period was underestimated. This could be caused by
372 size selective burial, where longer sandeel with a high condition tended to enter the sediment earlier
373 than smaller sandeel (Pedersen et al. 1999). However, the overestimation is considerably less than

374 experienced in previous studies of forage fish, where the bioenergetic calculations provided
375 estimates 2 to 4 times higher than methods based on stomach content (Arrhenius and Hansson 1994;
376 Maes et al. 2005).

377

378 The weight specific consumption of 1.6 - 2.7% of body weight for adults was considerably lower
379 than reported for other forage fishes (i.e. clupeids). Biomass and production estimates for pelagic
380 planktivorous fishes in the North Sea suggested a daily weight specific consumption of 4%
381 (Greenstreet et al. 1997). Average daily weight specific consumption for adult Norwegian spring
382 spawning herring during its growth period is roughly 7% (derived from values in Varpe et al. 2005).
383 Likewise, age 0 herring and sprat consume between 3.6 and 11% of their body weight per day (De
384 Silva and Balbontin 1974; Arrhenius 1998; Maes et al. 2005), a range which contains the value
385 estimated here for juvenile sandeel (6.1%). Relatively lower consumption rates, in particular for
386 adults, may relate to the foraging strategy of sandeels, which resembles that of a central place
387 forager. Compared to migratory fish like herring, that can move to areas of high food concentration
388 (Dragesund et al. 1997; Corten 2001) sandeels have a rather limited foraging range as they are
389 obliged to stay near suitable burying habitat. Both stomach data and bioenergetics showed that food
390 consumption decreased from early to late spring, indicating that food limitation was more important
391 in late spring/early summer when copepods were smaller.

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393 In line with the present findings, Macer (1966) found the diet of lesser sandeel on Dogger Bank to
394 consist predominantly of copepods. Genus and species was not identified here, yet the size
395 distributions show a clear change in the diet composition from early to late spring. In early spring
396 copepods smaller than 1 mm was absent and size distribution peak around 2 mm, suggesting a
397 major contribution from late *Calanus* stages. *Calanus* is the only genus common to the North Sea,

398 which reaches an average lengths >1.5 mm (Pitois et al. 2009) and *Calanus finmarchicus* tend to
399 reach a maximum in abundance earlier in the season than other common North Sea species (Fransz
400 et al. 1991).

401

402 During the growth period, lesser sandeel converted consumed secondary production to sandeel
403 tissue with an energy conversion efficiency of ~ 50%, resulting in an annual average of 20%. This
404 finding is consistent with what has been found for other species of sandeel: 38% for *A. personatus*
405 in growth experiments (Sun et al. 2010) and an annual efficiency of 20% for *A. dubius* based on
406 comparable bioenergetics calculations (Gilman 1994). These values imply that sandeel is more
407 energy efficient than for example clupeids, where 17% has been reported during the growth period
408 for Norwegian spring spawning herring using comparable methodology (Varpe et al. 2005) and 5-
409 12% for North Sea herring in growth experiments (De Silva and Balbontin 1974). The present
410 estimates of energy conversion efficiency derived from bioenergetics is considered accurate or in
411 worst case a slight underestimation as stomach data resulted in lower consumption rates than that
412 found using bioenergetics. It should, however, be noted that excess metabolic cost of spawning
413 activity was not accounted for when converting from growth period efficiency to annual efficiency.
414 The behaviour of Lesser sandeel during spawning has never been documented, although the general
415 consensus is that the individual sandeel only leaves the sediment for a brief period to spawn and
416 spawning migration behaviour is absent. Hence, the energetic cost associated with spawning
417 activity is most likely small, and the sensitivity analysis showed that results changed only by 5 %
418 when daily activity in the model was raised by 15 %

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420 The high energy conversion efficiency of sandeels was also evident at system level, suggesting that
421 the relative proportion of sandeels in the forage fish community has important implications for the

ecosystem. For example, during the period of reduced sandeel biomass in 2003 - 2005 our calculations indicated a reduction in the forage fish conversion efficiency of 15 - 35% compared to the average level up until 2000. This result implies that the production available for higher trophic levels (i.e. birds and Atlantic cod) is reduced when clupeids dominate the forage fish community, provided total forage fish consumption is bottom-up controlled as suggested by Frederiksen et al. (2006).

Population level consumption rates of $1.2 \text{ g wet weight d}^{-1} \text{ m}^{-2}$ is close to the daily copepod production rate reported for the Dogger area in May ($1.5 \text{ g wet weight d}^{-1} \text{ m}^{-2}$) (Nielsen and Munk 1998). However, the hydrodynamic simulations showed that the average grazing pressure for the study area was only moderate when the spaces between sandeel habitats were included. The simulations further suggested that sandeels effectively leave footprints in the standing copepod biomass as far as 100 km from the edge of the habitats, but also that smaller and more isolated sandeel patches have much less influence on the copepod biomass. The latter finding indicates that small habitats can sustain higher densities of sandeels or higher growth rates, provided that sandeel feeding rate is limited by search time (i.e. higher copepod concentration leads to higher feeding rates). Hence, if adult sandeels do not move between habitats, as Jensen et al. (2011) concluded, sandeel carrying capacity for the Dogger area as a whole depends on how recruits are being distributed amongst habitats during the larval and juvenile phase (i.e. high carrying capacity is achieved if small habitats receives more recruits per area than large habitats).

In conclusion, these results suggest that lesser sandeel in the North Sea Dogger area represents a rapid and efficient converter of secondary production to fish tissue readily available to higher trophic levels, although this may be partly counterbalanced by the greater mobility of clupeids

446 because large patches of zooplankton may remain unused if they are too far from suitable sandeel
447 habitat. Hence, changes in species composition towards a more herring dominated system, as seen
448 in recent times, could potentially lead to a decrease in system level energy transfer efficiency. It was
449 further demonstrated that sandeels effectively leave footprints in the standing copepod biomass as
450 far as 100 km from the edge of the habitat, but also that smaller and more isolated sandeel habitat
451 patches have much less influence on the copepod biomass than larger patches.

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596 Table 1. Parameter values used in the bioenergetic calculations. Condition factor and length of fish
597 at the beginning and end of the calculation period (K_{t1} , K_{t2} , L_{t1} and L_{t2}), the first and last year-day of
598 the calculation period ($t1$ and $t2$), mean water temperature (T), and the energy density of prey (e_d).
599 Values outside parentheses were used when calculating the entire growth period and values inside
600 the parentheses were used when modeling the first half (early spring) and second half (late spring)
601 separately.

Input parameter	Age 0	Age 1	Age 2
$K1$	0.0021	0.0021 (0.0021;0.00275)	0.00195(0.00195;0.0027)
$K2$	0.0029	0.0029 (0.00275;0.0029)	0.00285 (0.0027;0.00285)
$L1$	5	10.8 (10.8;12.1)	13.2 (13.2;14.2)
$L2$	10.8	13.2 (12.1;13.2)	14.6 (14.2;14.6)
$t1$	150	80 (80;123)	80 (80;123)
$t2$	250	165 (123;165)	165 (123;165)
T	14	10 (8;12)	10 (8;12)
e_d	5150	5350 (5550;5150)	5350 (5550;5150)

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605 Table 2. Food consumption of Lesser sandeel derived from the bioenergetic calculations. Total
606 amount of energy consumed per individual during the calculation period (C_E), daily consumption
607 relative to body mass (C_W), population level consumption rate per surface area (C_R), and energy
608 conversion efficiency during the growth period ($CE_{growthperiod}$) and for the entire year (CE_{annual}).

Measures of consumption:	Early spring		Late spring		Summer
	age 1	age 2	age 1	age 2	age 0 (juvenile)
C_E (J)	31080	49287	33119	33220	44964
C_W (in proportion of body weight)	0.027	0.024	0.022	0.016	0.061
C_R (g wet weight m ⁻² d ⁻¹)	0.89	0.23	1.02	0.17	1.31
$CE_{growthperiod}$ (%)	56	54	40	32	47
CE_{annual} (%)	22	18	16	11	25

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Figure 1. Study area. White patches represent sandeel habitats (Jensen et al. 2011). Grey clusters of bullet points represent the locations of the commercial hauls providing information on growth. Black bullet points represent locations of stomach sampling. Black surfaces are land (southern UK).

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618 Figure 2. Length of lesser sandeels during the growth period of adults (black: age 1; grey: age 2).

619 Curves were created by fitting a 4th order polynomial to data. Vertical dashed line represents the

620 split between early and late spring (week 18 is included in late spring).

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Figure 3. Condition factor ($W/L^{3.06}$) of lesser sandeels during the growth period of adults (black: age 1; grey: age 2). Curves were created by fitting a 4th order polynomial to data. Vertical dashed line represents the split between early and late spring.

Figure 4. Size composition of copepods in the diet. Early spring (A, B), late spring (C, D). Relative diet size distributions are expressed both in numbers (left graphs) and biomass (right graphs).

Figure 5. Comparison of weight specific daily consumption (in proportions of body weight) estimated from stomach content (D_R) and bioenergetic calculations (C_W). Black symbols: Geometric mean of D_R ($\pm$ s.e.) for each of four length groups and early spring (black bullets) and late spring (black triangles) separately. Open symbols: C_W in early spring (open circles) and late spring (open triangles). C_W for age 1 and age 2 adults during early spring corresponded to length group 11-12 and 13-14, and was therefore placed accordingly in the graph. Likewise did age 1 and age 2 correspond to length group 12-13 and 14-15 during late spring.

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Figure 6. Changes over time in the energy conversion efficiency of the forage fish community. A: Inter-annual variation in forage fish biomass in the North Sea separated into clupeids (black) and lesser sandeel (grey). B: Inter-annual variation in the energy conversion efficiency (CE) calculated for the forage fish community as a whole using either $CE_{growthperiod}$ (black) or CE_{annual} (grey).

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665 Figure 7. Simulation of grazing impact from patchily distributed sandeels in the Dogger area. A:
 666 Spatial heterogeneity in grazing impact depicted as copepod concentration relative to carrying
 667 capacity (c/c_0) (averaged over the simulation period April 1-July 1). B: Two-dimensional cross
 668 sections corresponding to line A and B in graph A. C: Grazing impact in a given grid cell as a
 669 function of relative sandeel habitat coverage h within a radius of 45 km. Sandeel habitat is
 670 represented by 10 x 10 km square cells.

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