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Published in:
Marine Ecology - Progress Series

Link to article, DOI:
10.3354/meps10390

Publication date:
2013

Citation (APA):
Deurs, M. V., Christensen, A., & Rindorf, A. (2013). Patchy zooplankton grazing and high energy conversion efficiency: ecological implications of sandeel behavior and strategy. *Marine Ecology - Progress Series*, *487*, 123-133. https://doi.org/10.3354/meps10390

Marine Ecology Progress Series
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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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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.

INTRODUCTION

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

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

METHODS AND MATERIALS

Data

Sandeel samples were collected during a data collection program carried out in co-operation between the Danish Fisherman´s Association and the Technical University of Denmark. Samples were taken at sea by the fishermen and immediately frozen. Samples were later transported, together with information on haul location and time, to the Technical University of Denmark for further analysis. In the laboratory, a subsample of each sample was measured and rounded down to the nearest half centimeter group below and 10 sandeels per half cm group were randomly selected and age determined using otoliths. For further details, see Jensen et al. (2011). Mean length-at-age was estimated by combining length distributions with age-length keys. Age-length keys were produced separately for each distinct fishing ground and week using the method described by Rindorf and Lewy (2001). Condition was estimated as weight [g]/total length $[cm]^b$, where $b = 3.06$ is equal to exponent of the power law function describing fish weight as a function of total length when all data is used. Only samples collected between 2001 and 2008 (a period of consistently high sampling intensity throughout quarter 2) and from the major fishing grounds were used (fig. 1).

During the same sampling program described above, a total of 472 sandeel stomachs were analyzed. Stomachs were collected between 2006 and 2008 (in April, May and June) from all over the Dogger area. After taking out each stomach, it was gently dabbed on both sides with tissue before weighing [g wet weight]. Roughly every third stomach was put aside after weighing for further diet analysis (preserved in 98% alcohol).

Amount of zooplankton consumed

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

Diet analysis

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

Energy density of copepods of different sizes

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

Daily ration estimated from stomach data

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

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

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

Bioenergetic modeling of consumption

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

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

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

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

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

$$M = 24SMR[t2-t1] + 33SMR[t2-t1] \tag{3}$$

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

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

$$C_W = \frac{C_B / W^*}{(t2-t1)} \tag{4}$$

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

Population level consumption rate per surface area (C_R [g wet weight d^{-1} m^{-2}]) were estimated as

$$C_R = \frac{C_B \times N \times (t2-t1)}{15 \times 10^9} \tag{5}$$

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:

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

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: $CE_{annual(\text{sandeel})} = (\Delta E_S+\Delta E_R - \textit{cost of overwintering})/C_E \times 100\%$, where $\textit{cost of overwintering} = 18.69L_{t2}^{2.66}$ [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:

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

where *CE* is conversion efficiency and *B* is the stock biomass in a given year ($B_{\text{(clupeid)}}$ 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). $CE_{\text{(foragefish)}}$ was calculated using either annual values or growth period specific *CE* values. $CE_{growthperiod\text{(sandeel)}}$ and $CE_{annual\text{(sandeel)}}$ 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 $CE_{growthperiod\text{(clupeids)}} = 15\%$. 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:

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

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 $C_{R(\mathrm{age}\ 1)}$ plus $C_{R(\mathrm{age}\ 2)}$ 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^{o}E and 53.5 to 56^{o}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: $\rho_2=\textit{sandeel grazing}/\textit{total grazing}$ (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).

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

Conversion efficiency

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

The sensitivity of the model to the activity multiplier (α), daily activity period (β), timing of the growth period ($t2$-$t1$), and temperature (T) was low. Estimated consumption and energy conversion efficiency varied no more than 5% in response to decreasing/increasing these parameter values +/- 15%, except for T, which varied between 5 and 8% depending on the age of the fish (8% for age 2).

Ecosystem effects

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

Grazing pressure on local zooplankton communities

The grazing pressure exerted by sandeels relative to total copepod grazing was estimated to ρ_1 = 0.697 (s.d. = 0.032) inside sandeel habitats and ρ_2 = 0.367 (s.d. = 0.031) for the study area as a whole (including the spaces between sandeel habitats). Assuming that sandeels are evenly distributed within sandeel habitats, copepod concentrations drifting over sandeel habitats with a large surface area or dense habitat clusters were effectively diluted (by grazing) and distinct local gradients in copepod concentrations appeared with a heterogeneity length scale of ~150 km (fig. 7).

DISCUSSION

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

Daily ration estimated from stomach data agreed well with daily consumption estimated from bioenergetics, although during late spring, the stomach data gave values that were generally lower than values derived from bioenergetics. The difference was particularly pronounced in late spring, indicating that the fish length at the end of this period was underestimated. This could be caused by size selective burial, where longer sandeel with a high condition tended to enter the sediment earlier than smaller sandeel (Pedersen et al. 1999). However, the overestimation is considerably less than experienced in previous studies of forage fish, where the bioenergetic calculations provided estimates 2 to 4 times higher than methods based on stomach content (Arrhenius and Hansson 1994; Maes et al. 2005).

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

In line with the present findings, Macer (1966) found the diet of lesser sandeel on Dogger Bank to consist predominantly of copepods. Genus and species was not identified here, yet the size distributions show a clear change in the diet composition from early to late spring. In early spring copepods smaller than 1 mm was absent and size distribution peak around 2 mm, suggesting a major contribution from late *Calanus* stages. *Calanus* is the only genus common to the North Sea, which reaches an average lengths >1.5 mm (Pitois et al. 2009) and *Calanus finmarchicus* tend to reach a maximum in abundance earlier in the season than other common North Sea species (Fransz et al. 1991).

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

The high energy conversion efficiency of sandeels was also evident at system level, suggesting that 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 g wet weight d^{-1} m^{-2} is close to the daily copepod production rate reported for the Dogger area in May (1.5 g wet weight d^{-1} 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 because large patches of zooplankton may remain unused if they are too far from suitable sandeel habitat. Hence, changes in species composition towards a more herring dominated system, as seen in recent times, could potentially lead to a decrease in system level energy transfer efficiency. It was further demonstrated that sandeels effectively leave footprints in the standing copepod biomass as far as 100 km from the edge of the habitat, but also that smaller and more isolated sandeel habitat patches have much less influence on the copepod biomass than larger patches.

ACKNOWLEDGEMENT

This research has been supported by EU FP7 grant FACTS (Forage Fish Interactions), Grant Agreement No. 244966. We would also like to thank the laboratory personnel at DTU Aqua for having put aside samples since 2006, and Henrik Mosegaard and Henrik Gislason for constructive feedback along the way.

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Table 1. Parameter values used in the bioenergetic calculations. Condition factor and length of fish 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 the calculation period (*t1* and *t2*), mean water temperature (*T*), and the energy density of prey (e_d). Values outside parentheses were used when calculating the entire growth period and values inside the parentheses were used when modeling the first half (early spring) and second half (late spring) 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)

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

	Early spring		Late spring		Summer
Measures of consumption:	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
CEgrowthperiod (%)	56	54	40	32	47
CEannual (%)	22	18	16	11	25

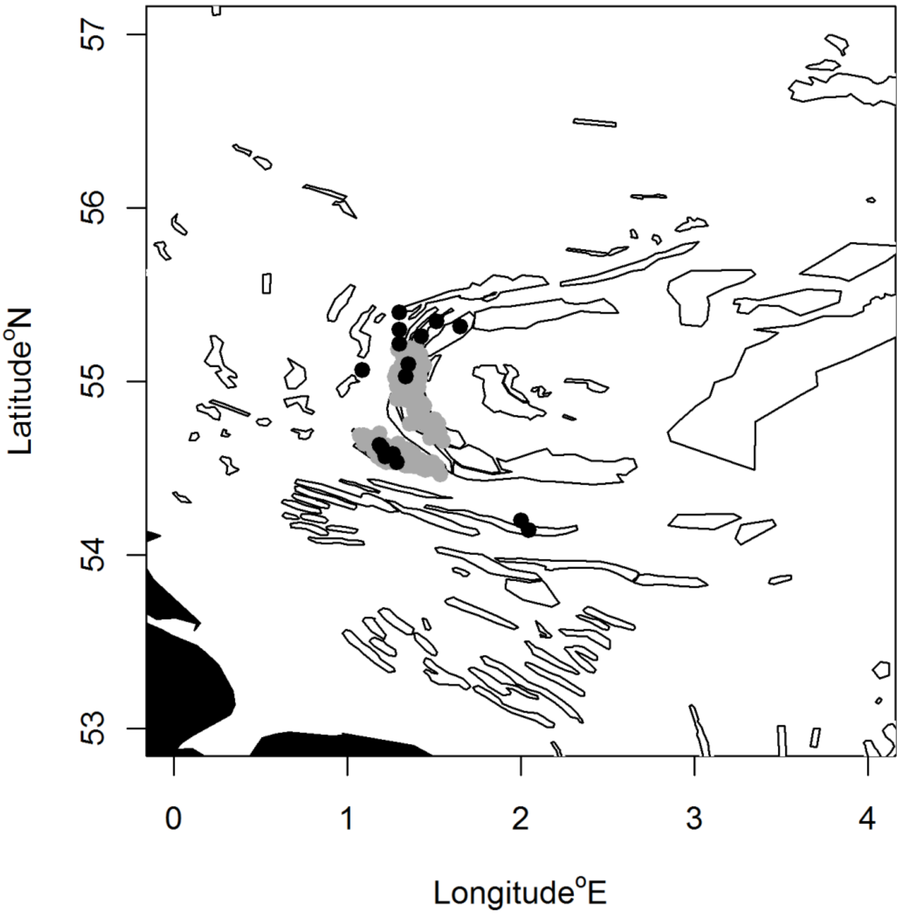

Figure 1. Study area. White patches represent sandeel habitats (Jensen et al. 2011). Grey clusters of bullet points represent the locations of the commercial hauls providing information on growth. Black bullet points represent locations of stomach sampling. Black surfaces are land (southern UK).

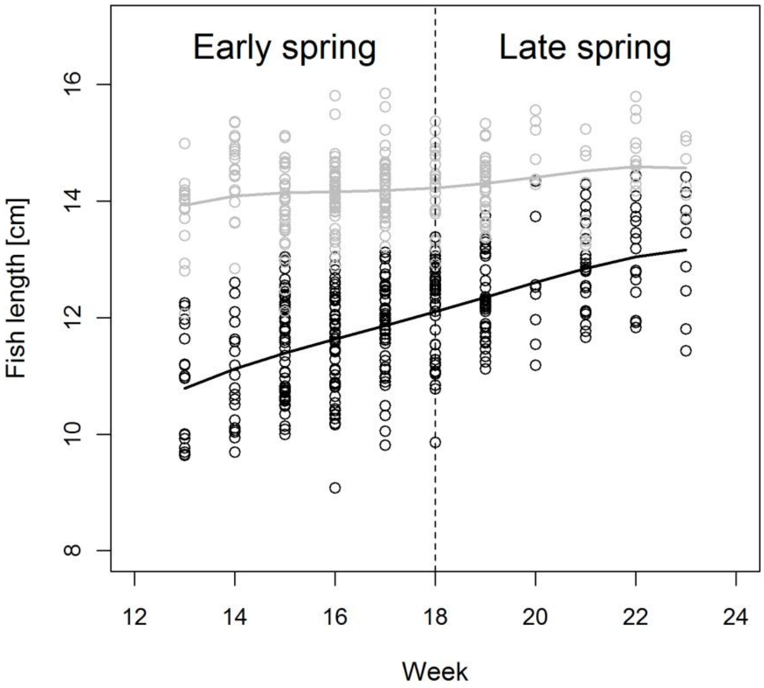

Figure 2. Length of lesser sandeels during the growth period of adults (black: age 1; grey: age 2). Curves were created by fitting a 4th order polynomial to data. Vertical dashed line represents the split between early and late spring (week 18 is included in late spring).

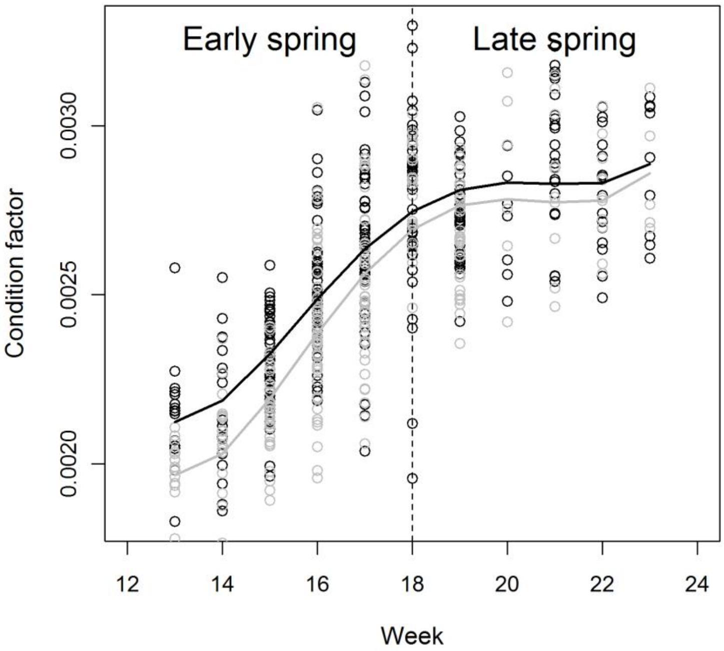

Figure 3. Condition factor ($W/L^{3.06}$) of lesser sandeels during the growth period of adults (black: age 1; grey: age 2). Curves were created by fitting a 4th order polynomial to data. Vertical dashed line represents the split between early and late spring.

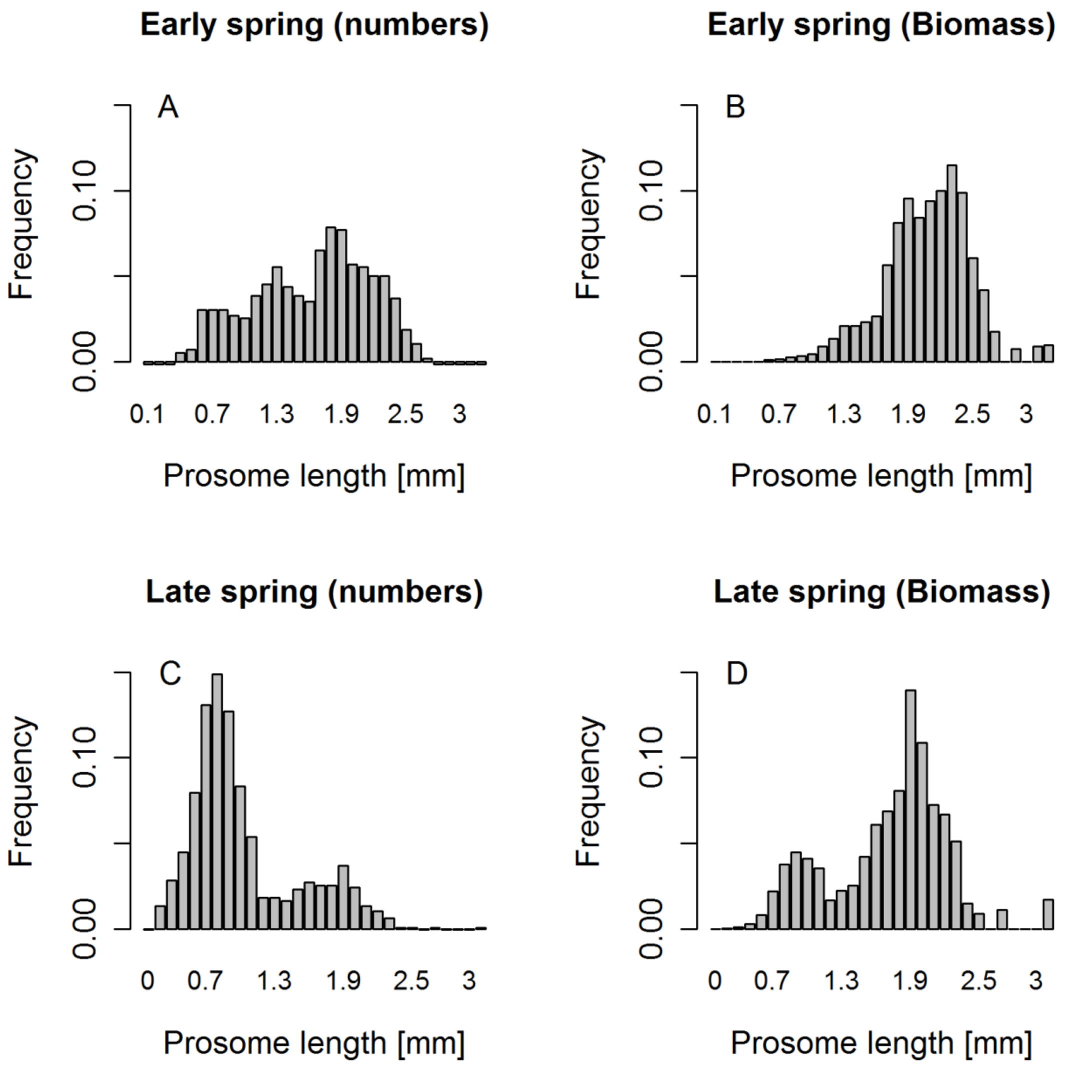

Figure 4. Size composition of copepods in the diet. Early spring (A, B), late spring (C, D). Relative diet size distributions are expressed both in numbers (left graphs) and biomass (right graphs).

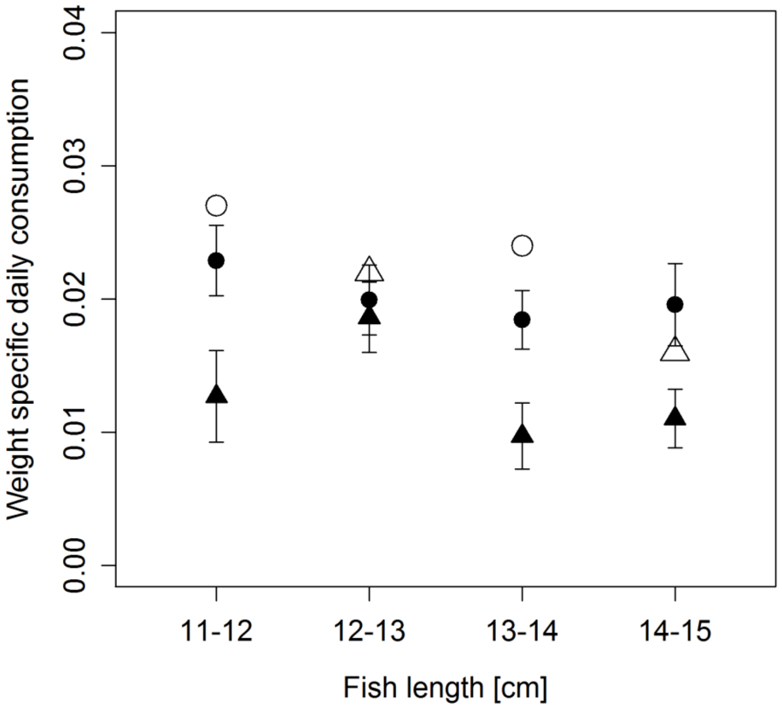

Figure 5. Comparison of weight specific daily consumption (in proportions of body weight) estimated from stomach content (D_R) and bioenergetic calculations (C_W). Black symbols: Geometric mean of D_R (± s.e.) for each of four length groups and early spring (black bullets) and late spring (black triangles) 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.

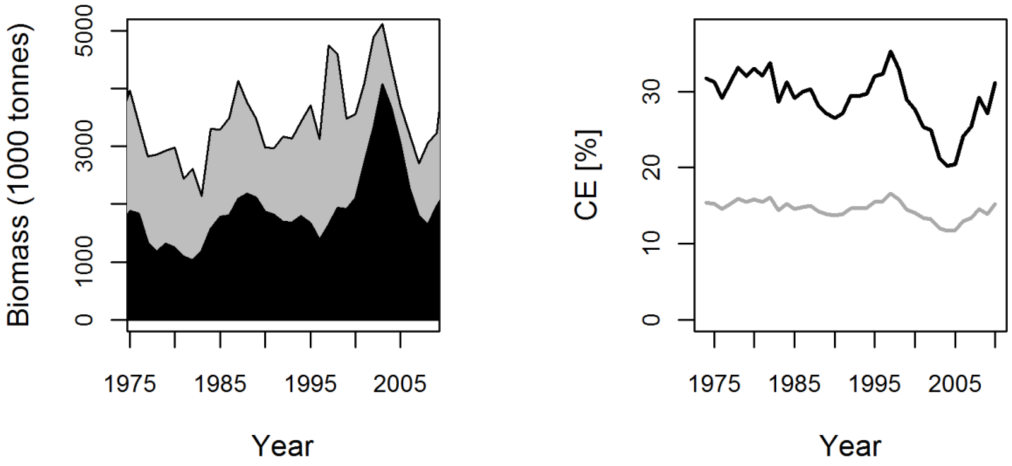

Figure 6. Changes over time in the energy conversion efficiency of the forage fish community. A: Inter-annual variation in forage fish biomass in the North Sea separated into clupeids (black) and lesser sandeel (grey). B: Inter-annual variation in the energy conversion efficiency (*CE*) calculated for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

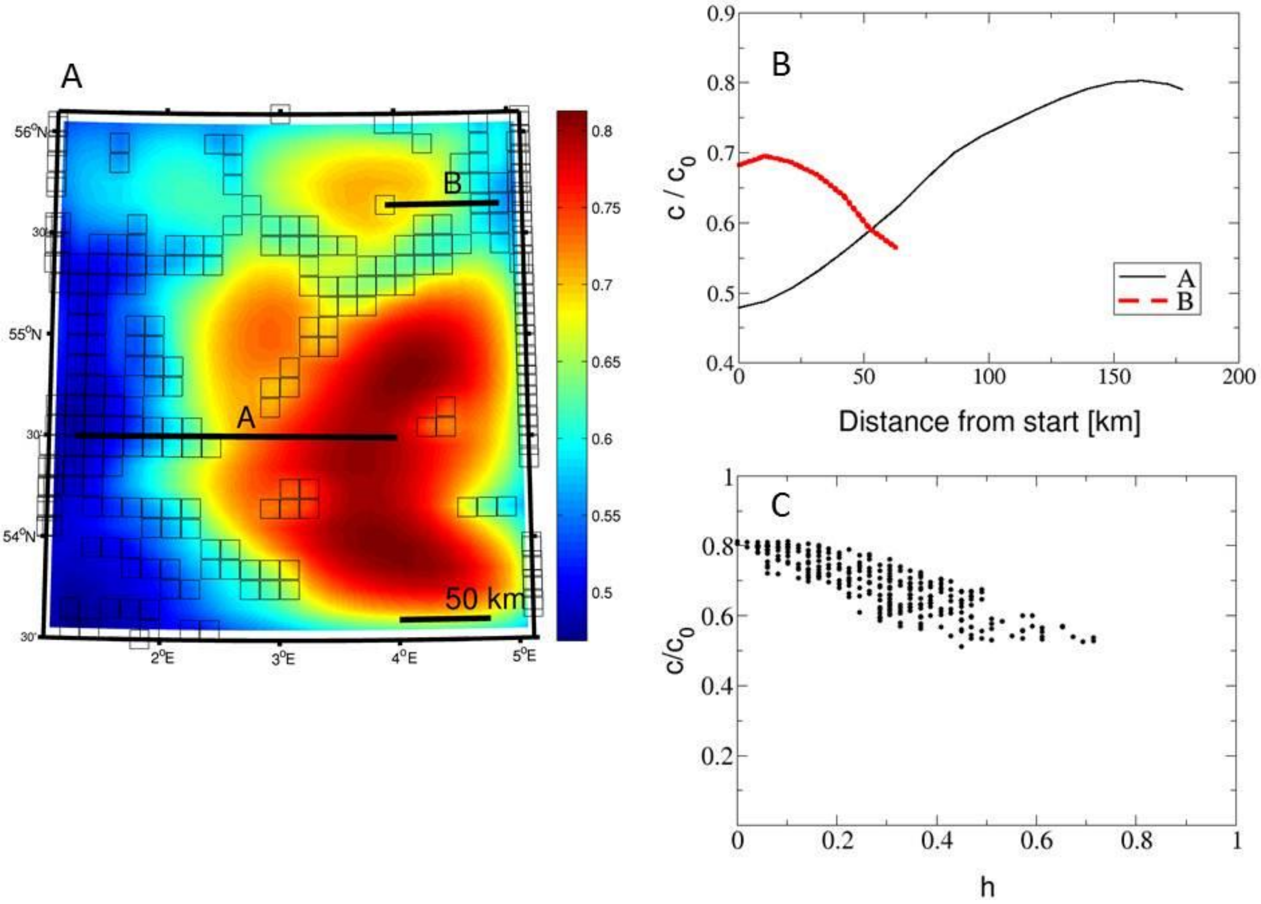

Figure 7. Simulation of grazing impact from patchily distributed sandeels in the Dogger area. A: Spatial heterogeneity in grazing impact depicted as copepod concentration relative to carrying capacity (c/c_0) (averaged over the simulation period April 1-July 1). B: Two-dimensional cross sections corresponding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