Body condition of predatory fishes linked to the availability of sandeels

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ORIGINAL PAPER

Body condition of predatory fishes linked to the availability of sandeels

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Abstract Lesser sandeels *Ammodytes marinus* are eaten by a range of predatory fishes including commercially fished species, but are also exploited at large scale by industrial fisheries. Is availability of sandeels, as key prey source, linked to the body condition of predatory fishes? In the North Sea, the largest sandeel biomass is concentrated in the Dogger Bank region. Here we studied predator–sandeel interactions at two sites differing widely in sandeel abundance and local sandeel fishing effort. Surveys took place in 2004, 2005, and 2006, years when local sandeel densities observed at these sites were low, intermediate, and high, respectively. Five predator species—whiting, lesser weever, grey gurnard, plaice, and haddock—showed better body condition indices in either the years or study area (or both) characterised by higher local sandeel densities, when compared to sandeel-poorer conditions. Moreover, whiting, weever, and gurnard condition was better for those individuals actually observed to have eaten sandeels (based on stomach contents) than for those that had not. As body condition relates to growth, reproduction, and survival, predators in sandeel-rich conditions may be inferred to have a higher fitness. These links between sandeel availability, sandeel consumption, and predator condition hint that, if large-scale localised depletions of sandeels were to occur, negative indirect effects on predatory fish might become apparent, underlining the importance of considering the sandeel fishery in an ecosystem context.

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Introduction

In temperate shelf seas, sandeels (Ammodytidae) provide high-energy food to a wide range of predators, from fishes to seabirds and marine mammals (Reay 1970; Camphuysen 2005). But the localised, often dense schools of these small lipid-rich fish are also targeted by substantial fisheries for industrial fishmeal and fish oil: in the North Sea alone, annual landings of lesser sandeel *Ammodytes marinus* have fluctuated around 425,000 t over the past ten years (ICES 2011), higher than for any other North Sea species. So it is not surprising that the sandeel fishery has been hotly debated since it first developed in the 1950s (e.g. Macer 1966; Anonymous 2003). Off eastern Scotland and the Shetlands, a shortage of sandeels has been linked to the fishery and in turn to breeding failure and declines at seabird colonies (Frederiksen et al. 2004; Polaczanska et al. 2004). Elsewhere a lack of sandeels has been related tentatively to starvation in porpoises (MacLeod et al. 2006). But sandeels are also prey to a rather long list of piscivorous fish species, many of high commercial significance to 'human consumption' fisheries. These include cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, whiting *Merlangius merlangus*, plaice *Pleuronectes platessa*, sole *Solea solea,* and mackerel *Scomber scombrus* (Reay 1970), many of which are currently at historically low levels (ICES 2011). Much controversy is therefore on the issue to what extent large-scale, localised sandeel depletions might deprive wide-ranging predatory fish of food, so affecting their condition and survival chances.

How crucial are sandeels as prey to predatory fish? Here we address this question by studying relationships between local sandeel numbers, actual sandeel consumption, and body condition indices of eight predatory fish species. The emphasis is on body condition given its likely links with survival, growth, and reproduction, and ultimately with population dynamics (Roff 2002; Marshall et al. 2003). The predator species examined were known to have sandeels as part of their diet (Engelhard et al. 2008) and included five species highly valued commercially, namely plaice, whiting, haddock, cod, and mackerel, and three species of minor or no commercial significance, namely lesser weever *Echiichthys vipera*, grey gurnard *Eutrigla gurnardus*, and greater sandeel *Hyperoplus lanceolatus*.

Predator–sandeel interactions were studied at two study sites on the western Dogger Bank that differed widely in local sandeel abundance and fishing effort (Fig. 1). The Dogger Bank is, within the North Sea, the region where the majority of sandeel fishing takes place each year; it is also an area that has been of key importance to 'human consumption' fisheries for over a century (e.g. Jennings et al. 1999; Starkey et al. 2000). Surveys took place in 2004, 2005, and 2006 which were years when the sandeel densities at these study sites were extremely low, intermediate, and moderately high, respectively (Engelhard et al. 2008). The very low sandeel abundance in 2004 was also evident in the wider Dogger Bank region, where this was the lowest year on record in terms of spawning stock biomass of sandeels, since assessments began in 1983 (ICES 2011). In the present paper we examine the hypothesis that contrasting local sandeel availability, and actual sandeel consumption, will be significantly related to body condition indices of predatory fish.

Materials and methods

Study area

Sandeels and sandeel predators were observed during surveys, carried out from 20 April–4 May 2004, 6–17 May 2005, and 10–20 May 2006. Two study areas on the western Dogger Bank were sampled: Grid 1 (North West Riff), an area of about 800 km^2 which during spring and summer is heavily fished by sandeel fishing vessels, and Grid 2 (The Hills), an equally sized but relatively unfished area (Fig. 1). Biological sampling was carried out at 60 stations during each cruise. Because sandeels show distinct diurnal

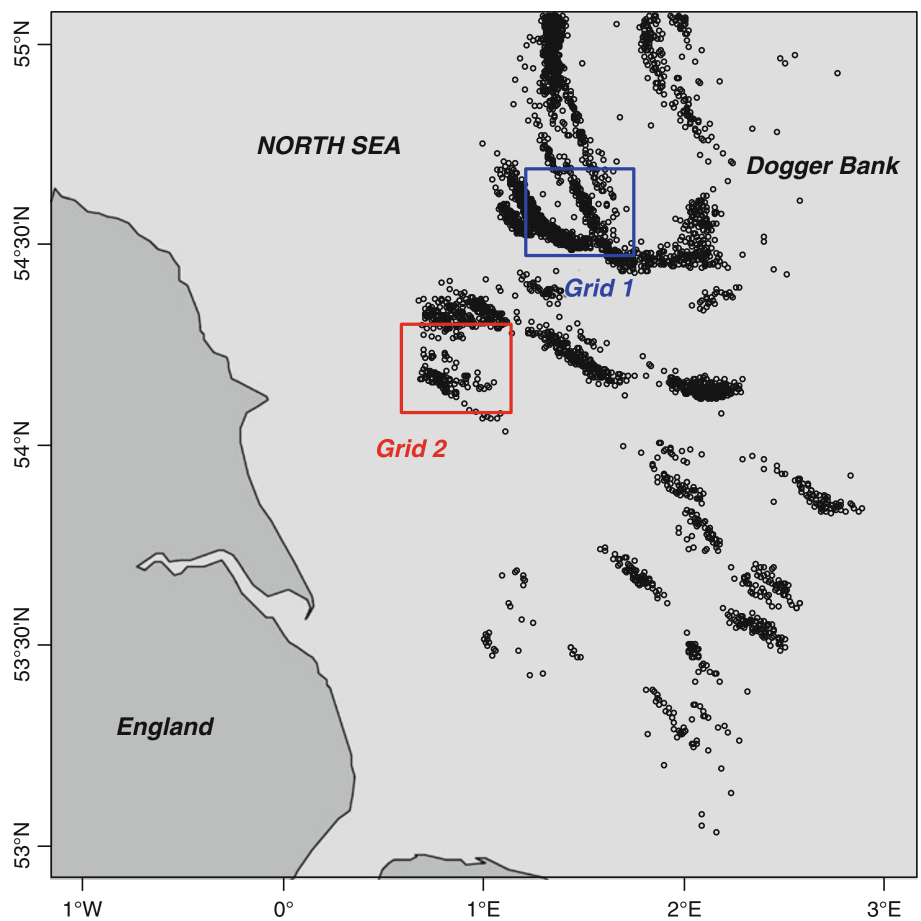

Fig. 1 North-east England and the Dogger Bank region of the central North Sea, with Grid 1 and Grid 2. *Small symbols* illustrate the distribution of sandeel fishing effort during the peak of the fishery in April–June 2006 (each point represents approximately 10 h fishing)

migrations during spring—between the seabed where they bury themselves at night, and the water column where they forage on plankton during the day (van der Kooij et al. 2008)—their availability as a potential prey source was examined using two approaches: (1) at night, sampling sandeels in the seabed by dredge and (2) from morning to midday, observing sandeels in the water column by means of acoustics. At the same sampling stations, the condition and feeding habits of potential sandeel predators were examined during morning and afternoon, by sampling piscivorous fish species (and their stomach contents) from catches taken by a Granton otter trawl.

Sandeel availability

At night, distribution of sandeels in the seabed was examined by means of a modified French scallop dredge, 1.2 m wide. Between 22:00 and 4:00 GMT, 10-min dredge tows were carried out at each station. Catch-per-tow was converted to density (sandeels per m^2) by dividing the catch by the swept area, and including an 8 % correction factor to account for the efficiency of the dredge for catching sandeels. This correction factor was based on previous estimates of sandeel dredge efficiency ranging from 1.52 to 9.6 %, provided by Mackinson et al. (2005).

During the day, acoustic surveys were carried out to examine sandeel distributions in the water column. These started at dawn and ended around 11:00 GMT; previous studies revealed that sandeels mostly forage during initial daylight hours (e.g. Freeman et al. 2004). In each survey grid, ten parallel north–south transects were surveyed, crossing the sampling stations; the transects were each 27 nautical miles (nm) long and 6.75 nm apart. Fisheries' acoustics were recorded using a dual-frequency Simrad EK60 splitbeam echosounder. Using the frequency response of sandeels at 38 and 120 kHz, algorithms were developed in Myriax Echoview processing software (Version 4.8) to automatically identify sandeel schools. The acoustic energy attributed to sandeels at 120 kHz was integrated and converted into numbers per m^2 using standard procedures (MacLennan and Simmonds 1992). Following Mackinson et al. (2005), we used a sandeel target strength defined as $TS = 20\log(L) - 90.8$ dB, with L representing the mean length of sandeels caught in night-time dredge samples in the same area. However, as the sandeel TS value has been determined indirectly, the calculated numbers should not be considered as absolute, but instead as relative abundance indices allowing comparisons between sites and years.

Whereas acoustic data were collected along transects, data on night sandeel (and predator) distributions were collected at sampling stations. To facilitate comparisons, we used the acoustic data to provide a measure of sandeel daytime abundance for each station (as in Engelhard et al. 2008). First, rectangles surrounding the midpoint of each sampling station were delineated as 0°3′ latitude by 0°3′ longitude. Next, relative sandeel day abundance was calculated by station as the mean of the acoustic abundance estimates that fell within the corresponding rectangle (1–4 observations per station).

Linear mixed effects models were used to test for significant differences in sandeel densities between study years. These models included the sampling station as random effect, to account for repeated sampling of stations over three seasons, and log sandeel density as the dependent variable, which showed a normal distribution. Before log transformation, a small value ($+0.001\ m^{-2}$) was added to all values to allow inclusion of zero sandeel densities. Thus, models were of the form:

$$\log(N_{y,s} + 0.001) \sim \text{year}_y + \text{station}_s + \varepsilon_{y,s} \quad (1)$$

where $N_{y,s}$ represents the sandeel density observed in year y at station s, year_y is the fixed effect of year y, station_s is the random station effect, and $\varepsilon_{y,s}$ is the error term.

Sandeel predators

At the same sampling stations but later, between 11:00 and 19:00 GMT, the potential predators of sandeels were sampled using a Granton trawl fitted with a codend liner with 20 mm mesh. The horizontal and vertical opening of the net averaged 18 and 1.8 m, respectively, and the spread between the trawl doors 41 m; the duration of each tow averaged 20 min (net in contact with the seafloor). Catches were sorted by species and all individuals (or a subsample, in case of very large catches) counted and their length measured (rounded down to the nearest cm).

The reliance of predatory fish on sandeels was investigated. At each station, five fish from each 5 cm length class were subsampled from the total catch of a given species. Their stomach contents were identified and weighed. For all prey items, identity and digestion stage (on a four-point scale) were recorded, and where possible individual prey length and weight.

The body condition of predatory fishes was assessed based on length and weight measurements, where weight was defined as the total weight excluding the weight of the stomach contents. Le Cren's (1951) condition index was used as a proxy for body condition. This index can be described, for a given fish, as the ratio of its observed weight (W) to the weight predicted from its length (L) and the population-level (here the Dogger Bank population) length–weight relationship. First, for each species, a traditional exponential length–weight relationship was estimated based on all data, using standard linear regression:

$$\ln W \sim a + b \ln L + \varepsilon \quad (2)$$

Next, for each individual *i*, Le Cren's condition index was calculated as the observed divided by predicted weight. The procedure was illustrated in Fig. 2 for one particular predator species, lesser weever. Thus, a fish with condition index 1.1 is 10 % heavier than expected for its length, and one with index 0.9 is only 90 % of its expected weight.

Linear mixed effects models were used to test for significant differences in predator condition indices between study grids and years. Models were of the form:

$$\text{Condition}_{y,a,s}\text{year}_y + \text{area}_a + \text{station}_s + \varepsilon_{y,a,s} \quad (3)$$

where the subscripts *a* and *y* denote the fixed effects of area (Grid 1 or 2) and year (2004, 2005 or 2006). The subscript *s* denotes the random effects of sampling stations, to account for repeated sampling of stations over three seasons and for multiple fish sampled from the same station. Condition indices were normally distributed. Linear mixed effects models were also used to test whether condition indices of predators that had consumed sandeels (sandeel reported in stomach contents of individual fish) differed significantly from those that had not. Nonparametric correlation analysis (Kendall's τ rank correlation) was used to test for associations between predator condition and the number of sandeels eaten by the fish. All analyses were carried out in *R* (The *R* Foundation for Statistical Computing 2009).

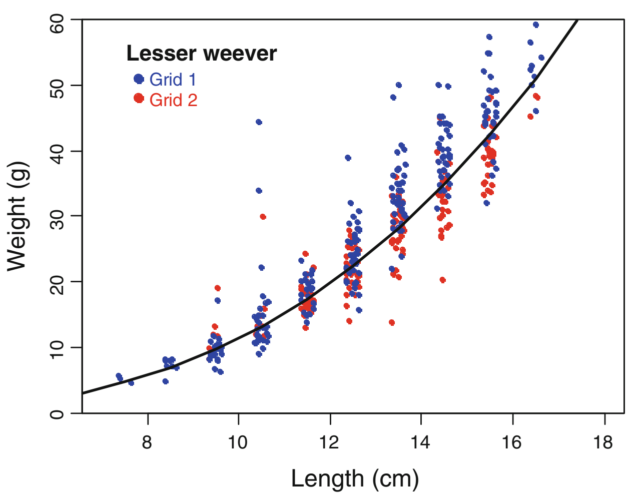

Fig. 2 Illustration of calculation of Le Cren's condition index for individual fish. First, the population-level length–weight relationship (*black curve*) is predicted from all data for the species using eq 1. Next, for each individual, observed weight is divided by the weight predicted from the length–weight curve. *Blue* and *red dots* represent fish from the two study grids (notice that fish from Grid 1 were more often heavier, from Grid 2 more often lighter than expected for their length)

Results

Sandeel abundance: grids and years compared

There were marked interannual and grid differences in sandeel abundance, as observed by day in the water column using acoustics (Fig. 3a) and by night in the seabed using the dredge (Fig. 3b). Sandeel densities, observed in the water column during daylight hours, were significantly higher in Grid 1 than in Grid 2 during each of the 3 study seasons (2004: $W = 630$, $P < 0.0005$; 2005: $W = 584$, $P < 0.0005$; 2006: $W = 446$, $P < 0.0005$). Daytime sandeel densities were, moreover, significantly higher in 2005 and 2006 than in 2004, in both study grids (Table 1), and this increase was far more marked in Grid 1 than in Grid 2 (Fig. 3a).

Sandeel densities, observed at night in the seabed, were very low in 2004 and 2005, and although on average slightly higher in Grid 1 than in Grid 2, not significantly different between these areas in either year (2004: $W = 450.5$, $P > 0.8$; 2005: $W = 450.5$, $P > 0.8$). In Grid 1, a strong increase in the night-time sandeel densities in the seabed was observed in 2006, when they were significantly higher here than in Grid 2 ($W = 565$, $P = 0.010$). As a result, night-time densities in the seabed were significantly higher in 2006 than in 2004 and 2005 (Table 1). In Grid 2, interannual differences in night-time sandeel densities in the seabed were not significant (Table 1).

In summary, Grids 1 and 2 could be characterised as having comparatively high and low sandeel abundance, respectively, and the seasons of 2004, 2005, and 2006 as years of very low, intermediate, and high local sandeel densities, with the increase in sandeel abundance mainly being observed in Grid 1. Most of the increase in daytime densities in the water column was observed from 2004 to 2005, and most of the increase by night in the seabed was from 2005 to 2006.

Predator condition: grids and years compared

Body condition indices of various sandeel predator species were significantly different between sandeel-rich and sandeel-poor study grids, and/or between comparatively sandeel-rich and sandeel-poor years (Fig. 4). Where significant grid or year differences in predator condition were found, the direction of differences was almost always such that better condition was associated with higher sandeel numbers (compare with Fig. 3).

The body condition of two species—lesser weever and plaice—was significantly better in the years *and* study grid characterised by higher sandeel densities (Fig. 4a, b). A linear mixed effects model (Table 2) revealed that these interyear and intergrid differences in condition were

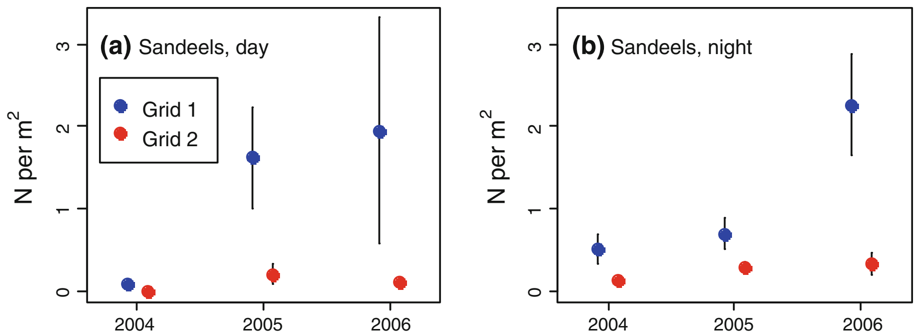

Fig. 3 Sandeel abundance compared between study grids and years, as observed **a** during daytime (in the water column) and **b** at night (in the seabed). Means ± 1 SE of values by station are shown

Table 1 Observed sandeel densities compared between three study seasons, for Grids 1 and 2 and for the combined study sites

Area	Mean density ± SE			Year effect		Direction of year effect
	2004	2005	2006	*F*	*P*	
Day sandeel densities						
Grid 1	0.10 ± 0.04	1.62 ± 0.62	1.95 ± 1.37	**10.40**	**<0.0001**	04 < (05, 06)
Grid 2	0.00 ± 0.00	0.11 ± 0.12	0.11 ± 0.04	**5.46**	**0.008**	04 < (05, 06)
Combined grids	0.05 ± 0.02	0.94 ± 0.33	1.22 ± 0.76	**19.05**	**<0.0001**	04 < (05, 06)
Night sandeel densities						
Grid 1	0.50 ± 0.18	0.70 ± 0.19	2.26 ± 0.61	**9.77**	**<0.0001**	(04, 05) < 06
Grid 2	0.13 ± 0.03	0.29 ± 0.07	0.32 ± 0.14	0.62	0.544	–
Combined grids	0.32 ± 0.09	0.50 ± 0.10	1.34 ± 0.34	**8.49**	**0.0004**	(04, 05) < 06

Linear mixed effects models were used to test for interannual differences in densities. Models included log density as the dependent variable, and year as fixed effect. The 60 sampling locations were included as random effects, given that the same stations were sampled repeatedly over three seasons. A small value (+0.001 m^{-2}) was added to all densities, to allow log transformation of zero values. *F* and *P* values significant at the 0.05 level are shown in bold type

Direction of year effects: the notation 04 < (05, 06) implies that densities were significantly higher in 2005 and 2006 than in 2004, but not significantly different between 2005 and 2006

significant at the $P < 0.0001$ level, although in plaice the condition difference between years 2004 and 2005 was nonsignificant (and in weever, data were lacking for 2004).

In two further predator species—whiting and grey gurnard—no area differences, but highly significant ($P < 0.0001$) interannual differences in condition were found. In whiting, condition indices differed between each of the years 2004, 2005, and 2006, consistent with the increasing sandeel abundance over these three years (Fig. 4c; Table 2). Gurnard condition was higher in the sandeel-richest year 2006 than in both earlier years (Fig. 4e; Table 2).

Haddock showed smaller but still significant grid and year differences in body condition (Fig. 4d; Table 2). Condition was lower ($P < 0.05$) in Grid 2 than in Grid 1 if analysed over all years combined but not in each of the three years separately; the grid difference was most marked in 2006. Haddock condition was lower in the sandeel-poor year 2004 than in both following years (Table 2).

Greater sandeel (Fig. 4f) showed a year difference in condition that was opposite to the expected: condition was lower in 2006 than in 2005, despite higher numbers of (lesser) sandeels in the later year ($P = 0.046$, Table 2). Greater sandeel condition was on average marginally lower in Grid 2 than in Grid 1; however, this difference was not statistically significant ($P = 0.076$, Table 2).

In mackerel, no significant grid differences ($P = 0.320$) or year differences ($P = 0.930$) in body condition were found. Likewise in cod there was no evidence of differences in condition between grids ($P = 0.492$) or years ($P = 0.779$).

Links between predator condition and actual sandeel consumption

For three out of eight predator species examined, the body condition of those fish observed to have eaten sandeel (i.e. where sandeel was recorded in the stomach contents) was significantly higher than for those fish that had not eaten sandeel (Fig. 5). In each of these, condition indices of individuals that had eaten sandeels were significantly higher than those of individuals that had not eaten sandeels (lesser weever: mean condition indices, respectively, 1.066 versus 0.997; linear mixed model with station as random

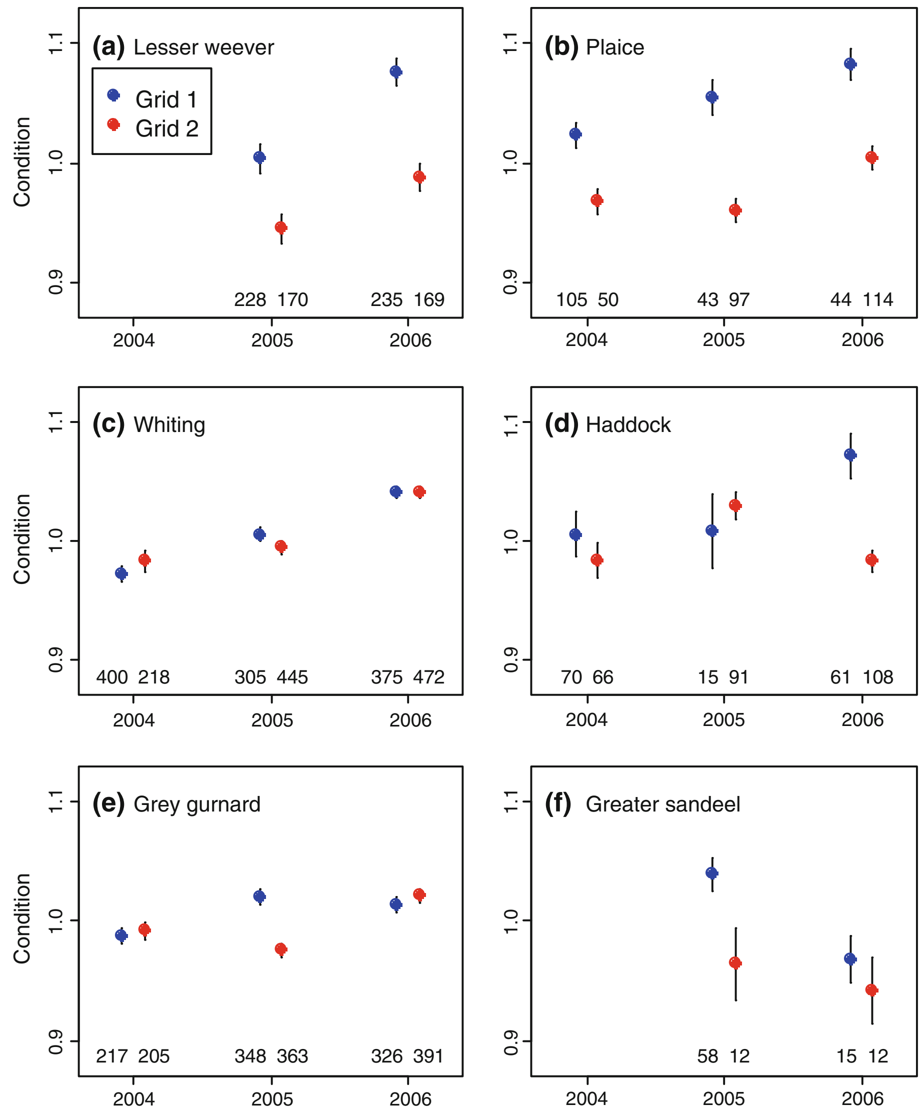

Fig. 4 Mean Le Cren's condition index (±1 SE) of six predatory fish species, compared between grids and years of contrasting sandeel availability. Grids 1 and 2 characterised by high and low sandeel numbers, respectively; years 2004, 2005, and 2006 by low, medium, and high local sandeel density. *Numbers* below the *symbols* indicate the sample sizes

effect, $F = 10.07$, $P < 0.005$; whiting: condition indices 1.038 versus 1.000, $F = 44.81$, $P < 0.0001$; grey gurnard: condition indices 1.050 versus 0.997, $F = 40.88$, $P < 0.0001$). In the other five species, differences were not significant ($P > 0.1$).

Moreover, in various predator species, the average body condition at sampling stations was significantly correlated with the per capita sandeel consumption (i.e. the number of sandeels recorded per stomach). The correlation was significant ($P < 0.05$) for four out of the eight predator species examined (Table 3), that is, lesser weever, whiting, grey gurnard, and greater sandeel, and approached significance ($P = 0.0501$) for a fifth species, haddock. In each of these cases the correlation was positive, higher condition being associated with a higher number of sandeels consumed. There was no evidence for this correlation in plaice, mackerel, or cod ($P > 0.3$).

Discussion

For the Dogger Bank, an area where an extensive industrial sandeel fishery takes place (Jensen et al. 2011), the present study shows that sandeel availability was linked to the body condition of a variety of predatory fish species in a number of ways. Several of these predator species, in turn, support important commercial fisheries supplying the 'human consumption' market (ICES 2011).

Condition indices were significantly better in year(s) characterised by higher sandeel availability, in five out of eight predator species examined (lesser weever, plaice, whiting, haddock, and grey gurnard); the reverse was found for a sixth predator (greater sandeel). In three of these species (weever, plaice, and haddock), condition indices were better in the sandeel-rich study area (Grid 1) than in the sandeel-poor site (Grid 2). Condition was

Table 2 Results of linear mixed effects models comparing body condition of predators between 2 study grids and 3 years of contrasting sandeel abundance

Predator species	Sample	Grid effect		Year effect		Direction of year effect
		F	*P*	*F*	*P*	
Lesser weever	805	**40.8**	**<0.0001**	**27.5**	**<0.0001**	05 < 06
Plaice	453	**31.5**	**<0.0001**	**10.8**	**<0.0001**	(04, 05) < 06
Whiting	2215	1.2	0.276	**62.6**	**<0.0001**	04 < 05 < 06
Haddock	411	**6.0**	**0.019**	**3.1**	**0.048**	04 < (05, 06)
Grey gurnard	1850	3.6	0.063	**10.1**	**<0.0001**	(04, 05) < 06
Greater sandeel	97	3.5	0.076	**4.1**	**0.046**	05 > 06
Mackerel	223	1.0	0.320	0.01	0.930	–
Cod	71	0.5	0.492	0.25	0.779	–

For each predator species, the model included grid and year as fixed effects. The 60 sampling locations were included as random effects, given that the same stations were sampled in three years and that multiple individual fish could have been sampled from the same station. For each species, the total sample size, *F* statistic, and *P* value for the area and year effects are given, as well as indication of the direction of significant year effects. *F* and *P* values significant at the 0.05 level are shown in bold type

Direction of year effects: the notation (04, 05) < 06 implies that condition was similar in years 2004 and 2005, but significantly higher in 2006 than in both earlier years. *Direction of grid effects*: in all species where the grid effect was significant, condition was higher in Grid 1 than in Grid 2

moreover significantly, and positively, correlated with the number of sandeel actually consumed by the predators, in four of the eight species (weever, whiting, gurnard, and greater sandeel), and there were significant differences in condition between those fish that had, and those that had not, eaten sandeel in three predator species (weever, whiting, and gurnard). These results are in line with earlier studies that highlighted extensive feeding on sandeels by larger, predatory species (e.g. Hobson 1986; Furness 1990; Greenstreet et al. 1998; Temming et al. 2004), although these studies did not report links with body condition.

Were the significant area and year differences in predator condition, corresponding to differences in sandeel numbers, really due to cause–effect relationships (sandeel being a limiting food source) or simply the result of a common underlying cause, for example, generally higher productivity in one area or year compared to the other? We cannot exclude the latter possibility for each of the predator species, especially for plaice and haddock where grid and year differences in condition were significant, but relationships between condition and actual sandeel consumption based on stomach analysis were not. In other predators, however, notably weever, whiting, and gurnard, year and grid differences in condition were not only consistent with those in sandeel densities, but condition was also significantly correlated with the sandeel numbers consumed by the fish, supporting a causative relationship. Further, we previously reported that at the finer spatial scale within each study grid, predators showed 'aggregative responses' to local sandeel numbers; this implies that predators aggregated locally at the sites where sandeels were most abundant (Engelhard et al. 2008; see also Temming et al. 2004). Combined, this lends strong support for sandeel availability itself being linked to predator condition.

The feeding behaviour of whiting and lesser weever was previously shown to be particularly tightly linked to sandeels (Temming et al. 2004; Pinnegar et al. 2006; Engelhard et al. 2008), and likewise, their condition indices were closely associated with local sandeel numbers and sandeel consumption (Figs. 4 , 5; Table 2). This is relevant given the status of whiting as important commercial fish species to various European countries, and the current relatively low abundance in the North Sea, although perceived to be at higher abundance at certain locations (ICES 2011). In whiting, clear year differences in condition but no grid differences were found, in spite of a significant correlation between condition and sandeel consumption; perhaps, the absence of grid differences relates to the high mobility of this actively hunting species (Pedersen 2000). In lesser weever, close matches between body condition and sandeel availability may be expected, given the high proportion of sandeel in this predator's diet (Pinnegar et al. 2006) and its similar habitat requirements to sandeels, clean medium-grain sands at fairly shallow depths (Lewis 1980).

In grey gurnard, interannual differences in condition were significant and in line with changing sandeel densities, and although area differences were not consistently found for all years (Fig. 4e), condition was closely linked to sandeel consumption (Fig. 5e; Table 3). Fairly high predation levels by grey gurnard on sandeels were reported previously (Engelhard et al. 2008; Weinert et al. 2010), supporting importance of sandeels for the diet of this species.

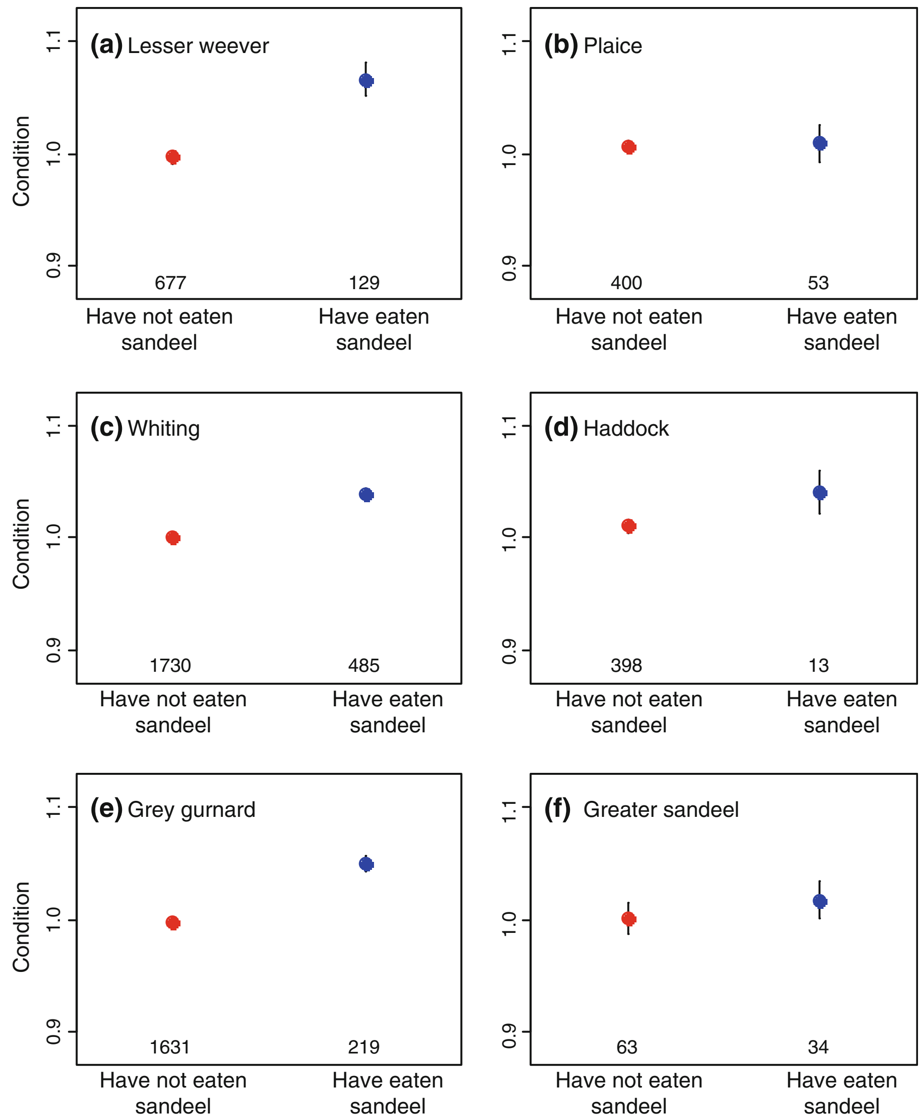

Fig. 5 Mean Le Cren's condition index (±1 SE) of six predatory fish species, compared between those individuals that had and those that had not eaten sandeels (based on the presence of sandeel in stomach contents). *Numbers below the symbols* indicate the sample sizes

Table 3 Overview of correlations between body condition, averaged by sampling station, and the number of sandeels consumed per fish, for eight predatory fish species

Predator species	Kendall's rank correlation		
	df	Kendall's τ	*P*
Lesser weever	104	**0.219**	**0.002**
Plaice	115	0.067	0.352
Whiting	137	**0.122**	**0.037**
Haddock	74	0.182	0.050
Grey gurnard	148	**0.193**	**0.001**
Greater sandeel	26	**0.309**	**0.033**
Mackerel	46	−0.017	0.879
Cod	32	−0.130	0.341

Nonparametric rank correlations were used, to reflect non-normal distribution of number of sandeels recorded in stomachs. Correlations significant at the 0.05 level are shown in bold

In plaice and haddock, grid and year differences in condition coincided with different sandeel densities (Figs. 3, 4), but other factors than sandeel availability per se might explain this, as no links between condition and sandeel numbers consumed were found (Fig. 5; Table 3). Plaice is better known as a benthivorous species feeding on polychaetes and the siphons of bivalves (e.g. de Goeij et al. 2001) than as a sandeel predator. On the Dogger Bank, the proportion of sandeels in plaice diet was previously reported to be around 15 % (Pinnegar et al. 2006), and the species might simply benefit from sandeels when and where these are available without being reliant on them (Reay 1970; this study). In haddock, sandeels comprised only 3 % of the total number of prey items consumed (Engelhard et al. 2008), and sandeels were found in only 13 out of 411 stomachs examined (Fig. 5). Indeed, haddock are known to prey on a broad variety of invertebrates and some small fish species (Pinnegar et al. 2006). Conversely, studies off Scotland have found haddock to prey extensively on sandeels (Greenstreet et al. 1998; Temming et al. 2004), and the reliance of haddock on sandeel might differ widely between areas of the North Sea.

In greater sandeel, the condition difference between 2005 and 2006 was opposite to the expected: lower in the later year despite higher densities of (lesser) sandeels (Fig. 5). Average greater sandeel condition was only marginally, but not significantly ($P = 0.076$) higher in the area of high lesser sandeel densities. Although greater sandeel do eat lesser sandeel, they share a variety of food types with the smaller species (Macer 1966) and the direction of a relationship between the two species is therefore not easy to predict. Competition effects are possible as are positive correlations caused by dependence on a common external factor (e.g. copepods abundance). A degree of reliance by greater sandeel on lesser sandeel was suggested by this study, based on the positive correlation between its condition and the number of lesser sandeels consumed (Table 3). In corroboration, we reported previously that greater sandeel, amongst all predators examined at these sites, was the species that consumed (lesser) sandeels most exclusively: the smaller species comprised 70 % of the diet of its larger relative (Engelhard et al. 2008).

The importance of sandeels as key food source for many seabird species, especially during the breeding season, is well established (Furness 1990; Rindorf et al. 2000; Polaczanska et al. 2004; Camphuysen 2005; Frederiksen et al. 2004), and there is awareness amongst the wider public about reliance of seabirds on sandeels. In marine mammals, availability of sandeels has been related to condition (and lack of sandeels to starvation) of harbour porpoises *Phocoena phocaena* (MacLeod et al. 2006; see also Pinnegar et al. 2011), and the diet of both grey seals *Halichoerus grypus* and harbour seals *Phoca vitulina* often shows a predominance of sandeels (Hammond et al. 1994; Thompson et al. 1996). This study adds to a body of work underscoring that not only seabirds and marine mammals but also many marine fish are on the long list of predator species reliant on sandeels. Not only do they feed extensively on this small forage fish, at the localised patches where these are available (e.g. Reay 1970; Temming and Mergardt 2002; Temming et al. 2004; Engelhard et al. 2008); there is now evidence that high sandeel availability is linked to a better body condition. As body condition relates to growth, reproduction, and survival chances (Roff 2002; Marshall et al. 2003), we would expect that fish in good condition would likely have a better fitness. These links between sandeels, sandeel consumption, and predator condition hint that if large-scale localised depletions of sandeels were to occur, negative indirect effects on predatory fish species might become apparent. This underlines the importance of considering the sandeel fishery in an ecosystem context.

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