Interpreting variation in fish-based food web indicators: the importance of “bottom-up limitation” and “top-down control” processes

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Proposed indicators for the Marine Strategy Framework Directive (MSFD) food webs Descriptor focus on structural elements of food webs, and in particular on the abundance and productivity of top predators. However, the inferences that can be drawn from such indicators depend on whether or not the predators are “bottom-up limited” by the availability of their prey. Many seabird populations appear to be “bottom-up limited” so that variation in their reproductive success and/or abundance reflects changes in lower trophic levels. Here we find that gadoid fish predators off the Firth of Forth, southeast Scotland, do not appear to be “bottom-up limited” by the biomass of their main prey, 0-group sandeels; gadoid biomass and feeding performance was independent of sandeel biomass. Variability in food web indicators based on these gadoid predators seems to impart little insight into underlying processes occurring at lower trophic levels in the local food web. The implications of this in terms of how the currently proposed MSFD food web indicators should be used and interpreted are considered, and the ramifications in terms of setting targets representing good environmental status for both fish and seabird communities are discussed.

Keywords: Ammodytes marinus, food web dynamics, Marine Strategy Framework Directive, predator performance, prey limitation, wasp-waist food webs.

Introduction

The Marine Strategy Framework Directive (MSFD) identifies 11 attributes (termed Descriptors) of marine ecosystems and requires that good environmental status (GES) be achieved for each attribute by 2020 (EC, 2008). “Food webs” is one such attribute. The indicators stipulated by the EC focus heavily on structure and functioning within the upper trophic levels of food webs (EC, 2010). Such metrics are most valuable in situations of “bottom-up limitation”, where the availability of prey has a direct and overriding influence on predator population dynamics (Frederiksen et al., 2006). In such instances, variation in these top predator indicators reflects underlying changes in food web processes in lower trophic levels. But in “top-down controlled” systems, top-predator population dynamics are decoupled from events taking place in lower trophic levels. In these circumstances, indicators of top predator population dynamics provide little insight regarding food web dynamics in lower trophic levels (Rombouts et al., 2013).

In “bottom-up limited” food webs, reductions in prey abundance can have profound effects on predator population dynamics, triggering migration, raising mortality rates, affecting population condition or reducing reproductive capacity (Thompson et al., 1996; Frederiksen et al., 2004). The impact is greatest in situations where predators cannot switch to alternative prey, for example in “wasp-waist” food webs (Cury et al., 2000; Yaragina and Dolgov, 2009) where energy from species-diverse lower trophic levels is channelled to a broad range of predators in higher trophic levels via a single key species that dominates the intermediate trophic level (Rice, 1995). In the North Sea, the lesser sandeel (Ammodytes marinus) fulfils such a role, obtaining energy from a wide range of zooplankton prey (Macer, 1966; Reay, 1970) and in turn constituting a major component of the diets of many fish, seabird and marine mammal predators (Daan, 1989; Wanless et al., 1998; Santos and Pierce, 2003). Industrial fishing for sandeels is the largest single species fishery in the North Sea (ICES, 2011). Such large scale
removals of sandeels, the species fulfilling this essential role of transferring energy from lower to upper trophic levels in the North Sea, wasp-waist food web, therefore has the potential to profoundly affect food web dynamics and affect many predators in higher trophic levels (Monaghan, 1992; Rindorf et al., 2000).

In one sandeel-dependent seabird predator in particular, the black-legged kittiwake (Rissa tridactyla), a detrimental impact of industrial fisheries on kittiwake breeding success was evident over and above any environmental influence (Lewis et al., 2001; Frederiksen et al., 2004; Frederiksen et al., 2005; Scott et al., 2006). Consequently, indicators related to kittiwake reproductive productivity have been proposed to support OSPAR Ecological Quality Objectives (EcoQOs) for the North Sea concerning the supply of sandeel prey to marine top predators (Heslenfeld and Enserink, 2008). Similar indicators are likely to be adopted to support the MSFD with respect to “the performance of key predators using their production per unit biomass”. However, seabirds are not the most important predators in terms of their capacity to influence the population dynamics of sandeels. About 90% of all forage fish, including sandeels, consumed by predators in the North Sea are eaten by piscivorous fish (Bax, 1991; Mackinson and Daskalov, 2007).

During the 20th century, fishing pressure in the northeast Atlantic increased markedly (Thurstan et al., 2010), causing substantial reductions in fish predator populations (Christensen et al., 2003; Myers and Worm, 2003). Such “top-down control” (reductions) in predator abundance can initiate trophic cascades in which prey populations increase in abundance by as much as an order of magnitude (Ward and Myers, 2005; Frank et al., 2007; Heithaus et al., 2008). In the North Sea, where fish predator populations have been reduced considerably by decades of heavy fishing activity (Hislop, 1996), increases in the biomass of prey-sized fish have exceeded the decline in the biomass of predatory-sized fish by a factor of at least five (Daan et al., 2005; Greenstreet et al., 2011). Over the same period, the number of seabirds using North Sea feeding grounds increased exponentially, partly due to less “top-down control” through increased protection from hunting (Mitchell et al., 2004) and partly to less “bottom-up limitation” through the increase in fish prey abundance (Montevcechi, 2002; Furness, 2002). By the end of the 20th century, the rate of increase in total seabird numbers had slowed and in some species a decline was evident (Mitchell et al., 2004), suggesting that some seabird populations had reached their environmental “carrying capacity” and were becoming “bottom-up limited” by prey abundance. Certainly evidence of prey availability limiting breeding performance was more prevalent (Harris and Wanless, 1997; Daunt et al., 2008; see also references above).

This raises two immediate issues. First, since fish predators account for such a high proportion of the natural predation mortality of sandeel and other forage fish, indicators of predatory fish abundance and performance, similar to those proposed for seabirds, will be essential to represent changes in marine food web structure and functioning within the MSFD. The proposed indicator, “abundance/distribution of key trophic groups/species” (EC, 2010), for example, might well be served by assigning fish sampled in groundfish surveys to different trophic guilds, and using trends in guild biomass to gain insight into changes in food web structure and dynamics (Greenstreet et al., 1997; Heath, 2005). Second, the extent to which seabird and fish predator populations are “top-down controlled” or “bottom-up limited” may differ. This would have implications for how seabird and predatory fish indicators should be interpreted with respect to marine food web structure and functioning. Determining whether predatory fish populations are “bottom-up limited” at current levels of forage fish abundance is therefore key to the interpretation of food web indicators.

Whiting (Merlangius merlangus) and haddock (Melanogrammus aeglefinus) are two of the more abundant demersal fish predators of sandeels in the North Sea (Daan, 1989; Greenstreet et al., 1998; Temming et al., 2004). In this study, we examine the feeding ecology of whiting and haddock in an area immediately offshore of the mouth of the Firth of Forth in southeast Scotland where sandeels, predominantly of the 0-group age class, are a key prey in late spring and early summer (Greenstreet, 2006). Crucially, it was in this area that much of the research to elucidate the processes influencing kittiwake population dynamics and the role of sandeel abundance was undertaken (Wanless et al., 1998; Frederiksen et al., 2004, 2006; Scott et al., 2006; Daunt et al., 2008). Our objectives were to assess the extent that 0-group sandeel biomass influenced whiting and haddock biomass, diet or feeding rate, and so determine whether these whiting and haddock are “bottom-up limited”.

Methods
Data collection
The study area covered most of ICES rectangles 41E7 and 41E8; an area of 4529 km², off the Firth of Forth, southeast Scotland (Figure 1). The area contains three sandbanks: the Wee Bankie, Marr Bank and Berwick’s Bank. Fishing operations were conducted at 19 equally spaced stations (station L in the inner Firth of Forth was abandoned as unfishable early in the study) every year from 1997 to 2009 except 2004 and 2007 (Figure 1). At each station a CTD (Sea-Bird Electronics 19+ V2 SEACAT PROFILER) was used to measure the water temperature at the seabed. Surveys were conducted in June of each year, a time when 0-group sandeels exhibit diurnal migration, leaving the sediment at dawn to feed and returning to the sediment at night (Macer, 1966; Reay, 1970), thus making them available to predators feeding in the water column.

Samples of haddock and whiting were collected from 30 min trawls using a Jackson Rockhopper demersal trawl with a 10 mm codend towed at a speed of about 4 km h ¹. Net geometry monitoring equipment (SCANMAR, Norway) attached to the headline and wing ends of the trawl recorded the height and width of the trawl every 30 s. Trawls were abandoned and repeated if these data fell outside expected ranges. The data were integrated over six 5 min periods (Δ), and the width (Ω) and the length of track (Φ) towed in each time period, were used to estimate the area of seabed swept by each trawl (Ad,Y) at each station (d) in each year (Y):

\[ A_{d,Y} = \sum_{\Delta=1}^{\Delta=6} \Phi_d \Omega_\Delta \]

The catches of haddock and whiting at each station were quantified as the total numbers of fish caught per 1 cm length class. Subsamples of fish were examined to derive weight-at-length relationships and dissected for diet and food consumption analysis. The subsampling was length stratified based mainly on 5 cm length categories (12–14.9 cm, 15–19.9 cm, 20–24.9 cm, etc.; e.g. Daan, 1989) to ensure that the full size range of each species caught at each station was adequately sampled. Only fish greater than 12 cm were sampled for stomach analysis because gadoids smaller than this are not piscivorous (Robb, 1981).
Predator abundance and biomass
The total numbers \( (N) \) per 1 cm length class \( (L) \) of haddock and whiting in the area associated with each station \( (d) \) in each year \( (Y) \) was calculated as:

\[
N_{L,d,Y} = \frac{C_{L,d,Y} G_d}{A_{d,Y}},
\]

where \( C_{L,d,Y} \) is the sample catch of each species (by length class, station and year) and \( G_d \) is the discrete area of sea associated with each station determined using a nearest neighbour tessellation procedure (Greenstreet et al., 2006). The estimates of abundance were converted to biomass estimates:

\[
B_{L,d,Y} = N_{L,d,Y} W_L,
\]

using weight-at-length \( (W_L) \) relationships for each species (see below). Summing the biomass estimates across all lengths and stations provided a yearly estimate of the biomass of each predator in the study area.

Stomach contents analysis
Subsamples of fish retained for stomach analysis were re-measured to the 0.5 cm below and weighed to the nearest 0.1 g. Weight-at-length relationships of the form \( W_L = a L^b \) were derived for each species by linear regression of \( \log L \) on \( \log W \). The fish were dissected and the stomach removed, either at sea (1997–2003) or on return to the laboratory (2005–2009). When removed at sea, the stomachs were stored in a plastic bag, placed within a second zip-lock sealed bag and frozen as soon as possible. Otherwise, the fish were frozen whole as soon after removal from the trawl as possible. When processed in the laboratory, stomachs were removed as soon as defrosting allowed and the samples analysed immediately. The difference in methodology had no appreciable effect on either the appearance of the samples or on any of the measured variables. Where possible, between 10 and 20 stomachs were examined in each 5 cm size category.

Stomach contents were identified to as high a taxonomic resolution as possible or labelled as “unidentified”. Each prey item was weighed individually to the nearest 0.01 g. The total stomach contents weight \( (S) \) was the summed weights of all prey items and unidentified food material in the stomach, rather than the initial measured weight of all the prey material removed from the stomach as the latter included some water. For analytical purposes, all prey items were classified as “sandeels”, “clupeids”, “other fish prey” or “invertebrate material”. Unidentified prey items were included with the “invertebrate material” given the absence of any structures to suggest that they were vertebrates. Unidentified prey items were only 0.01% by weight of the total food consumed, so this assumption had minimal impact on our results.

The feeding status of each fish was assessed as “full”, “regurgitate” or “empty” (Daan, 1989). “Full” fish had food material in the stomach but none in the buccal cavity. Fish with digested food material in the buccal cavity were deemed to have regurgitated at least part of their stomach contents. Fish with no food material in either the stomach or the buccal cavity, and with a small stomach with tight walls, were deemed to be “empty”. Fish with no food material in either the stomach or the buccal cavity, but where the stomachs were large with flaccid walls were generally considered to have regurgitated the whole of their stomach contents. In these latter cases, the colour and size of the gall bladder was also used to determine whether these fish should be classified as “empty” or “regurgitate” (Robb, 1992).

By definition “regurgitate” fish were feeding, but because food material was lost, these fish were not used in the estimation of diet or daily food intake rates. However, when estimating intake rates at the predator population level, “regurgitate” fish were assumed to have the same diet and individual daily food intake rates as...
“full” fish of the same species and length. Table 1 lists the number of “full” F, “empty” E, and “regurgitated” R haddock and whiting in each year Y. The vast majority of fish were actively feeding, and preliminary analysis found negligible differences between stations or lengths, so it was assumed that the proportion feeding was length and station independent. Table 1 therefore also gives the proportion of fish within each population considered to be actively feeding (P), calculated as

\[ P_Y = \frac{F_Y + R_Y}{E_Y + R_Y + E_Y}. \]

### Food intake rates

#### Modelling individual stomach contents weight

Changes in stomach weight (S) were investigated using a generalized linear mixed-effect model (GLMM) with gamma errors and a log link. Potential explanatory variables were predator length (L), year (Y), bottom temperature (T), time of day (V), habitat (H), 0-group sandeel biomass (the predominant age group consumed by haddock and whiting) (Z) and station (d). Year was treated as a continuous variable to examine temporal trends in stomach weight, and as a categorical variable (Y) for some random effects (see Model 1 below). Bottom temperature ranged from 6.7–10.9°C and averaged 8.8°C, with higher mean temperatures between 1997 and 1999. Bottom temperature was negatively correlated with depth. Time of day was grouped as early morning (0400 to 0930 h) and daytime (0930 to 1600 h) to assess feeding periodicity. (The research vessels used in this study are 12 working vessels, which precluded the possibility of sampling throughout the 24 h period.) Habitat was classified as “inshore”, “sandbank” or “offshore”; trawl stations within the coastal 50 m depth contour were classed as “inshore”; beyond this point, stations were classed as “offshore” unless they were < 50 m deep, in which case they were classed as “sandbanks”. Annual 0-group sandeel biomass estimates were derived from a combination of acoustic survey and demersal trawl survey data given in Greenstreet et al. (2006, 2010).

First, a model was fitted with all the explanatory variables included as main effects (Model 1). Length was log-transformed since preliminary analysis showed that, on the log link, stomach weight varied linearly with log length. Following preliminary analysis, the model included three random effects, allowing the length effect to vary between years (log L|Y) and between stations within years (L|Yd; d) and the year effect (temporal trend) to vary between stations (Y|d).

Model 1. Response variable \( \sim \) S

Fixed effects \( \sim \log L + Y + T + V + H + Z \)

Random effects \( \sim \log L | Y \) + (log L | Yd: d) + (Y | d)

The model was then modified in a forwards and backwards stepwise selection procedure in which the effect of adding/removing main effects and two-way interactions was considered at each step using Wald tests (multivariate generalizations of the t-test, expressed as F-statistics on the appropriate degrees of freedom) (e.g. McCulloch and Searle, 2001).

#### Daily intake rates

Daily food intake rates (I) by individual fish were estimated using Andersen’s (2001) gastric evacuation model:

\[ I_{L,d,Y} = 24 \times 0.00132L^{1.44}e^{-0.078T_d}K - 0.875 \sum_{m,L,d,Y}^{S_{0}} \]

where \( I_{L,d,Y} \) is the daily food intake rate (g d\(^{-1}\)) of a fish of length L given a water temperature of T°C at the seabed at each station (d) in each year (Y). \( S_{0} \) is the fitted stomach weight derived from the GLMM, and K the overall energy density of stomach contents, for which an average value of 4 kJ g\(^{-1}\) was used as this best represented the energy densities of the main prey items consumed, including 0-group sandeels (Andersen, 2001). Samples were not collected over the full 24 h range, so night-time feeding was assumed to be equivalent to daytime feeding. There was no evidence of differences in feeding during the studied time period (0400–1600 h) for either predator. Daily food intake by each predator population (\( I_{tot,Y} \)) was determined by:

\[ I_{tot,Y} = \sum_d \sum_L I_{L,d,Y} N_{L,d,Y} \frac{P_Y}{Y} \]

with \( P_Y \) accounting for the proportion of fish considered to be actively feeding (calculated above).

A generalized linear model assuming quasi-binomial errors was used to investigate the relationship between total daily food intake

### Table 1. Total numbers of haddock and whiting sampled for stomach contents analysis in each year, with the numbers in each feeding category (“full” F; “empty” E; and “regurgitated” R), and the proportion considered to be actively feeding (P).

<table>
<thead>
<tr>
<th>Year</th>
<th>FY</th>
<th>EY</th>
<th>RY</th>
<th>Total</th>
<th>PY</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>5</td>
<td>960</td>
<td>276</td>
<td>1241</td>
<td>&gt;0.99</td>
</tr>
<tr>
<td>1998</td>
<td>16</td>
<td>708</td>
<td>41</td>
<td>765</td>
<td>0.98</td>
</tr>
<tr>
<td>1999</td>
<td>0</td>
<td>13</td>
<td>2</td>
<td>15</td>
<td>1</td>
</tr>
<tr>
<td>2000</td>
<td>2</td>
<td>618</td>
<td>32</td>
<td>652</td>
<td>&gt;0.99</td>
</tr>
<tr>
<td>2001</td>
<td>0</td>
<td>659</td>
<td>22</td>
<td>681</td>
<td>1</td>
</tr>
<tr>
<td>2002</td>
<td>33</td>
<td>443</td>
<td>18</td>
<td>494</td>
<td>0.93</td>
</tr>
<tr>
<td>2003</td>
<td>33</td>
<td>408</td>
<td>5</td>
<td>446</td>
<td>0.93</td>
</tr>
<tr>
<td>2005</td>
<td>2</td>
<td>69</td>
<td>0</td>
<td>71</td>
<td>0.97</td>
</tr>
<tr>
<td>2006</td>
<td>8</td>
<td>183</td>
<td>0</td>
<td>191</td>
<td>0.96</td>
</tr>
<tr>
<td>2008</td>
<td>2</td>
<td>264</td>
<td>0</td>
<td>266</td>
<td>0.99</td>
</tr>
<tr>
<td>2009</td>
<td>0</td>
<td>166</td>
<td>2</td>
<td>168</td>
<td>1</td>
</tr>
</tbody>
</table>

In all years the large majority of individuals were deemed to be actively feeding.
by each predator population, as a percentage of predator biomass, and 0-group sandeel biomass.

**Diet Composition**
The proportion of the stomach contents (by weight) that consisted of sandeels was modelled in the same way as the individual stomach weights, but assuming quasi-binomial errors and a logistic link.

**Results**

**Biomass**
The biomasses of haddock and whiting were both greatest at the start of the study and were positively correlated; Spearman’s rho 0.72, \( p = 0.02 \) (Figure 2). However, there was no evidence of a relationship between 0-group sandeel biomass and haddock or whiting biomass; indeed the point estimates of Spearman’s rho were both negative (Figure 3a). The biomass of haddock and whiting in the Firth of Forth study area was positively correlated with the biomass of these two species in the North Sea (Figure 3b).

**Stomach weight**
Predator length was the only variable that significantly affected the stomach weight of either predator (Table 2, Figure 4). In particular, there was no evidence that sandeel biomass or water temperature at the seabed affected the stomach weight of either haddock or whiting.

**Diet**
The proportion of sandeels in the diet of both predators was highest in sandbank habitats (Table 2, Figure 5a and b). For example, the estimated proportions in 2003 (the median year) and for haddock and whiting of lengths 24 and 19 cm (the median lengths) were 45% and 87% in sandbank habitats, falling to 14% and 62% in offshore habitats and 4% and 50% in inshore habitats, respectively. For haddock, habitat was the only significant explanatory variable. However, for whiting the proportion of sandeels in the diet decreased with increasing predator length as whiting diet became more varied. This was driven by greater consumption of sprat (**Sprattus sprattus**) and larger crustaceans (Table 2, Figure 5c). There was also a temporal decline in the proportion of sandeels in the diet of whiting over the course of the study (Table 2, Figure 5d). For example, the estimated proportion for a 19 cm whiting in sandbank habitats fell from 93% to 57% during the study period.

**Intake rate**
Because predator length was the only variable to significantly affect stomach contents weight, and because the age and length compositions of the two predator populations were relatively consistent from year to year, the total quantity of prey consumed daily by each predator population is primarily related to predator biomass (compare the trend lines in Figure 6a with those in Figure 2). The total quantity of sandeels consumed daily by each predator population did not track quite so closely the trends in predator biomass (Figure 2) because of year-to-year variation in the proportion of sandeels in the diet. However, the total daily intake of sandeels as a function of predator biomass, 2 years aside, remained relatively stable (Figure 6b). In terms of the objectives of the study, neither the total daily intake rate, nor the intake rate of sandeels prey, both expressed as a fraction of predator population biomass, were significantly influenced by the biomass of 0-group sandeels (Figure 6b).

**Discussion**
All the evidence we present suggests that in the Firth of Forth study area, two predatory demersal fish populations, whiting and haddock, were not “bottom-up limited”. The biomasses of the two species were positively correlated, and had they been competing for a limiting food resource one might have expected an inverse correlation (Hssu et al., 1978). The biomass of haddock and whiting in the Firth of Forth were also correlated with the biomass of the two species in the North Sea. It is likely therefore that predator biomass in the study area was primarily influenced by factors external to the study area, in particular recruitment and fishing mortality. High levels of fishing mortality combined with lower than average recruitment over recent decades have reduced North Sea haddock and whiting population biomass to less than half the levels seen during the 1970s and early 1980s (Hislop, 1996). These “top-down control” processes appear to have reduced stocks to the point where haddock and whiting in the Firth of Forth are no longer “bottom-up limited”. Their prey resources are no longer

![Figure 2. Haddock, whiting, and 0-group sandeel biomass in the Firth of Forth study area from 1997–2009.](https://academic.oup.com/icesjms/article-abstract/71/2/406/784513)
limiting so prey density has ceased to influence their feeding performance and population dynamics.

There was no evidence that either haddock or whiting stomach weight depended on 0-group sandeel (from here on referred to as sandeel) biomass. Consequently, the estimates of food intake rates were unrelated to sandeel density. Predator intake rates generally increase with increasing prey density, associated with a reduction in “search time” as encounters with prey items become more frequent. This continues until the “handling time” associated with processing each prey item becomes limiting and gives rise to the classic asymptotic Holling type II feeding response relating predator food intake rates to prey density (Holling, 1959). The lack of a relationship between intake rates and sandeel biomass suggests that the sandeel biomasses observed in this study were within the asymptotic region of a Holling type II relationship. However, as haddock and whiting also eat other prey, more conclusive statements about functional response cannot be made without estimates of the availability of other prey.

In demersal fish predators, “handling time” is determined by their capacity to digest prey in their stomachs, evacuate the products into their hindgut, and so make room in their stomachs to consume new prey. Evacuation rates are positively related to both the weight of food material in the stomach and to water temperature (Bromley, 1994). The conclusions we draw from this are that all else being equal, rising water temperature should therefore increase the rate of evacuation of food material from the stomach into the hindgut, causing stomach contents weight to decline. This in turn should reduce the evacuation rate. Eventually a new equilibrium between the food intake and stomach evacuation rates would be reached, which would be associated at higher water temperatures with a lower stomach contents weight. For both haddock and whiting, there was no evidence of a relationship between stomach weight and water temperature at the seabed. This implies that in years, or in locations, where water temperature was higher, both predators were able to compensate for the direct effect of temperature on gastric evacuation rates by raising their food intake rates and so maintaining the weight of prey in their stomachs. If these predators were food limited they would not be expected to be able to balance the effect of elevated evacuation rates.

Sandeels are a key prey of both haddock and whiting (Daan, 1989; Greenstreet et al., 1998; Temming et al., 2004). In this study, the proportion of sandeels in the diet was higher in sandbank habitats, where sandeels were most likely to be encountered (Holland et al.,

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**Table 2.** Significant explanatory variables and Wald test $p$-values for each predator’s stomach weight and diet proportion model ($L = \text{predator length}, Y = \text{year}, H = \text{habitat}$).

<table>
<thead>
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</tr>
</thead>
<tbody>
<tr>
<td>Stomach weight</td>
<td>Whiting</td>
<td>$L$</td>
<td>1</td>
<td>10.2</td>
<td>118.88</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Haddock</td>
<td>$L$</td>
<td>1</td>
<td>8.6</td>
<td>0.69929</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Diet proportion</td>
<td>Whiting</td>
<td>$L$</td>
<td>1</td>
<td>9.8</td>
<td>8.39</td>
<td>0.016</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$Y$</td>
<td>1</td>
<td>9.7</td>
<td>6.85</td>
<td>0.026</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$H$</td>
<td>2</td>
<td>15.5</td>
<td>11.25</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Haddock</td>
<td>$H$</td>
<td>2</td>
<td>16.1</td>
<td>10.64</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Numerator (n.d.f.) and denominator (d.d.f.) degrees of freedom, $F$ test statistics, and associated probability values are indicated.
than in inshore and offshore habitats. That there was no significant change in stomach weight between habitats suggests that away from sandbanks stomach weight was maintained by the consumption of other prey. Generally predators switch to an alternative prey when the abundance of their primary prey declines and starts to become limiting (Hubbard et al., 1982; Stephens and Krebs, 1986). However, the sandeel fraction of the diet of both predators was independent of sandeel biomass suggesting that, aside from the spatial switch in prey, this was not the case.

Whilst our results suggest that all aspects of predator feeding performance were independent of sandeel biomass, the variability in the data means that such effects might be present but not detected. Table 3 quantifies the possible relationships with sandeel biomass compatible with the data by giving estimates and standard errors when sandeel biomass is reintroduced to the models. The point estimates are very close to zero in the stomach weight model, but are more suggestive of a positive relationship in the diet proportion model. The size of the standard errors, despite the intensive sampling undertaken in this study, highlights the difficulties of such work. Indeed a major international sampling effort would be needed to get a meaningful improvement in statistical power. However, our non-significant results are still very pertinent in the debate surrounding MSFD indicators.

Interpreting variation in indicators

Proposed indicators to support the MSFD food webs descriptor focus heavily on marine top predators: top predator guild biomass; the proportion of top predators in fish communities, and various aspects of the population dynamics of top predators. The explanation for this lies in the long-argued premise that changes in top predator populations provides insight into underlying changes in the lower trophic levels of marine food webs (Cairns, 1987; Montevecchi, 1993). Studies of seabird populations have provided the bulk of the evidence supporting this contention (e.g. Monaghan and Zonfrillo, 1986; Harris and Wanless, 1997; Frederiksen et al., 2004). In all these studies, some aspect of the population dynamics or abundance of a seabird top predator was shown to be related to prey density. In other words “bottom-up limitation” through limiting prey resources was established. Thus high top predator abundance or reproductive success could be interpreted as implying high levels of prey availability, and vice versa. In the absence of “bottom-up limitation” though, such an interpretation would be fallacious. Food web indicators based, for example, on the biomass of haddock and whiting in the Firth of Forth study area would suggest a marked decline after the first two years of the study, but to interpret this as implying a marked decline in local sandeel abundance would be erroneous given neither predator appears to be limited by their sandeel prey.

To interpret the top-predator based food web indicators suggested in the MSFD Decision document (EC, 2010), an essential step is to establish whether the predator in question is “bottom-up limited”. If so, inferences regarding changes in lower trophic levels are perhaps justified, but if not, where does that leave us? Are food web indicators based on predators for which food resources are not limiting, i.e. “top-down controlled” rather than “bottom-up limited”, of little use for implementing the MSFD? When food resources are not limiting and the quantity of prey consumed daily is primarily related to predator biomass, indicators of top-predator abundance can provide a good indication of the total predation loading imposed on lower trophic levels (e.g. Greenstreet et al., 1997). Where predators are “bottom-up limited” similar predation loadings can still be inferred from predator abundance, but prey switching associated with variation in prey abundance might mean that the allocation of these loadings to particular prey, and perhaps trophic levels, might be less precise.
Our results could have serious implications for the setting of targets representing GES for both Descriptors 1 (biodiversity is maintained) and 4 (food webs), and for meeting OSPAR EcoQOs with respect to seabird and fish communities, fisheries and commercial fish stocks. Essentially, current targets for seabirds focus on maintaining the *status quo*, such that declining trends in seabird abundance are considered indicative of “deteriorating” status (Parsons *et al.* 2008). Conversely, targets for fish communities and commercial stocks aim to restore conditions to some desired historical state, by restoring fish community size composition and increasing the percentage of top-predatory fish (Greenstreet *et al.*, 2011), increasing the abundance of sensitive species believed to have declined as a consequence of fishing mortality (Greenstreet *et al.*, 2012), and ensuring that commercial fish stocks exceed precautionary biomass limits (Piet and Rice, 2004; Heslenfeld and Enserink, 2008). Our results suggest that these two sets of objectives may be incompatible. For example, were haddock biomass to reach three times the level seen in 1997 (as a result of stricter management of their stocks) it might be expected that the estimated 200 t of sandeels consumed daily by haddock in 1997 would triple to ~600 t. During a critical window from May–June, a period of 61 days, this may equate to a total consumption of ~36 000 t by haddock alone, a figure equivalent to the sandeel fishery during most years of its operation (Greenstreet, 2006; Greenstreet *et al.*, 2006). This level of sandeel removal would likely have a similar impact on kittiwake breeding success to that which the industrial fishery had (Lewis *et al.*, 2001; Frederiksen *et al.*, 2004, 2005; Scott *et al.*, 2006).

Tilman (1982) suggests that for a species to exist at a constant equilibrium population size, the amount of a limiting resource available must be sufficient to support a population birth rate that is equal to the population mortality rate, termed the “equilibrium resource requirement”. If resources exceed the “equilibrium resource requirement” the population will increase, if lower the population will decrease. Tilman maintains that the outcome of competition by two or more species for a single limiting resource is predictable on the basis of the “equilibrium resource requirements” of each species; the species with the lowest “equilibrium resource requirement” will win, the other species will lose and
decline in abundance. The evidence suggests that in the Firth of Forth study area, over the same period and experiencing the same range of sandeel biomass, kittiwake populations were food limited (Frederiksen et al., 2004; Daunt et al., 2008), while populations of haddock and whiting were not. This implies that the two gadoid species have a lower “equilibrium resource requirement” and should therefore win in a competition with kittiwakes for sandeels.

If management measures to achieve ecological and fisheries objectives for fish stocks and communities are successful, populations of haddock and whiting, both across the North Sea and in the Firth of Forth, are likely to increase, possibly to levels well above those observed during our study. Such an increase in predator fish abundance could have a far greater impact on the availability of sandeels to kittiwakes than the industrial fishery had in the past (Furness, 2002). In a situation of markedly raised competition for an increasingly limiting resource, kittiwakes would appear to be the likely losers. This is of particular importance as during the chick-raising period kittiwakes are almost entirely obligate sandeel specialists (Daunt et al., 2008). Achieving management objectives for fisheries, fish stocks and fish communities may mean that objectives currently being set for seabird populations need to be reassessed.

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