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How benthic habitats and bottom trawling affect trait composition in the diet of seven demersal and benthivorous fish species in the North Sea

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ABSTRACT

Demersal and benthivorous fish depend on prey availability in benthic habitats for their diet. Prey availability may in turn be affected by bottom trawling. Our study attempted to link the prey consumed by fish directly to those available in the benthic environment. We test the hypothesis that bottom trawling significantly affected the trait composition of fish diets with a strong link to benthic habitats. Stomach content data were analysed for seven demersal and benthivorous fish species in the southern and central North Sea and were related to habitat fauna collected by grab and epi-benthic trawl data across the same spatial extent. Biological trait analysis was used to avoid taxonomic bias in large-scale comparisons across habitats and to quantify the effect of bottom trawling, which tends to shift prey diversity in favour of small, opportunistic and short-lived species and traits. The diets of two demersal omnivores (whiting, *Merlangius merlangus* and Atlantic cod, *Gadus morhua*) and two opportunistic benthivores (haddock, *Melanogrammus aeglefinus* and long-rough dab, *Hippoglossoides platessoides*) did not appear to reflect either infaunal or epifaunal traits that were abundant in the benthic environment. The diets of European plaice (*Pleuronectes platessa*) and Dover sole (*Solea solea*), however, showed strong links with infaunal prey trait composition in shallow sand to muddy sand habitats located in the eastern North Sea and the Dogger Bank. Such strong links were also observed for the diets of Common dab (*Limanda limanda*) and plaice in similar habitats in deeper waters. Plaice targeted small to medium sized infaunal burrowers and deeper dwelling infaunal species. Its diet was significantly affected by bottom trawling, which caused a reduction in prey biomass in their stomachs rather than a shift in trait composition. Our study showed that the diets of benthivorous fish across large spatial scales are strongly linked with the prey trait availability in their benthic habitats and that bottom trawling significantly affected the diet of plaice, a species with strong habitat-diet associations.

1. Introduction

In recent decades, a substantial amount of research has been conducted into both the acute and chronic impacts of fishing on benthic assemblages (Collie et al., 2000; Hiddink et al., 2017; Kaiser et al., 2006). Together, these studies have demonstrated large changes in the structure and functioning of benthic assemblages, with varying types and magnitudes of impacts being observed in differing habitats and from different trawl gear types (Kaiser and de Groot, 2000; Tillin et al., 2006). Decreases in faunal abundance, biomass and species richness have been empirically documented (Jennings et al., 2001; Reiss et al., 2009), together with a reduction in benthic production and size structure (Hiddink et al., 2006; Queirós et al., 2006). Traditional fisheries management has long focused on single-species approaches ignoring potential knock-on trawling effects on essential fish habitat (Link, 2002). Ecosystem-based fisheries management (Trochta et al., 2018) requires that important ecosystem interactions such as predator-prey interactions and essential fish habitat are considered in relevant legislative instruments. Given the demonstrable impacts of trawling on benthic habitats and potential trophic consequences (Frank et al., 2005; van Denderen et al., 2013; Walters et al., 2005) this is undoubtedly a positive step.

Studies that improve our understanding of the trophic relationships between the stocks of commercial fish with their prey have been undertaken, primarily based on the assessment of the contents of their stomachs (Braber and de Groot, 1973; Molinero and Flos, 1991; Pinnegar, 2014b; Steven, 1930; Wyche and Shackley, 1986). Such studies have demonstrated that reliance on benthic prey varies between

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fish species and age. Prey availability is thought to be one of the most important factors influencing fish distributions (Hinz et al., 2003), however, few studies have attempted to link the prey consumed by the predator to those available in the environment (Bizzarro et al., 2017; Hinz et al., 2005; Johnson et al., 2015) and none, to our knowledge, have attempted to make these links using a biological trait approach.

In this study, we undertake some analysis which helps bring together information on benthic prey availability and benthic prey consumed, at a functional level, in the presence and absence of fishing activity to further our understanding of the impacts of fishing on both benthic communities and the fish that consume them. We make use of the invaluable data regarding the variability in biological traits composition across the different seabed habitats that has recently been developed (Bolam et al., 2017). This approach allows us to describe changes in prey availability with respect to their inherent biological traits as opposed to their taxonomic identity that has been undertaken to date. This trait-based approach is more appropriate for large scale studies of commercial fish diet analysis as it removes geographical taxonomic biases in benthic invertebrates. To directly relate fish predation with prey availability, the changes in fish diets are described in terms of their trait composition, a novel approach in the assessment of the diets of commercial fish.

2. Materials and methods

2.1. Study area and datasets

2.1.1. Stomach datasets

Stomach content data was collated from four main data sources; ICES Year of the Stomach 1991[1] (ICES, 1997), Cefas' in-house database DAPSTOM (Pinnegar, 2014a) and data from BENTHIS partners; Institute for Marine Resources and Ecosystem Studies (IMARES), Wageningen UR (Rijnsdorp and Vingerhoed, 2001) and Institute for Agricultural and Fisheries Research (ILVO). The ICES Year of the Stomach 1991 data formed the basis of the geographical extent of the study area as it contained the most spatially extensive stomach data covering the North Sea, Skagerrak and Kattegat, ranging between 51 and 62 degrees North and 4 degrees West to 13 degrees East (Fig. 1).

The ICES Year of the Stomach data were mainly collected during the quarterly International Bottom Trawl Surveys of the North Sea (IBTS), which involved nine research vessels belonging to seven nations, with additional samples collected during other research surveys and by commercial vessels (ICES, 1991). Samples were obtained from ICES statistical rectangles, measuring approximately 30 × 30 nautical miles (one degree longitude x 0.5 degree latitude), using a Grande Ouverture Verticale (GOV) trawl (ICES, 2012). The DAPSTOM data were collected over a number of years and during several different sampling campaigns, using a variety of fishing gears, but particularly on the Dogger Bank between 2004 and 2006 using a Granton Trawl (see Engelhard et al., 2013). DAPSTOM data used in the current study spanned a 20-year period (1991–2010) to encompass sampling dates of both the ICES data and the available infauna and epifauna data. The IMARES data was collected in April, June and August–September 1996 using 8 m and 12 m beam trawls (see Rijnsdorp and Vingerhoed, 2001 for detailed methodology) across various parts of the North Sea. The ILVO data was collected using 4 m beam trawls from within one ICES rectangle in 2013.

Demersal and benthivorous fish species with a diet comprising benthic invertebrates at some stage of their life history, and that were represented by a sufficient number of stomachs containing food, were selected for inclusion in the data analysis. From the ICES Year of the Stomach database four fish species were identified: haddock (*Melanogrammus aeglefinnus*), Atlantic cod (*Gadus morhua*), whiting (*Merlangius merlangus*), and long rough dab (*Hippoglossoides platessoides*). No information was available for other flat fish species within this database due to selective sampling of predatory ground fish species during this survey (ICES, 1991). From the DAPSTOM database, prey information was extracted for haddock, cod, whiting, long rough dab (LRD), plaice (*Pleuronectes platessa*), sole (*Solea solea*) and Common dab (*Limanda limanda*). The data from ILVO contained prey information from stomachs of plaice, sole and dab, whilst the IMARES dataset comprised prey information from stomachs of sole and plaice. In total the stomach contents of seven commercial fish species were analysed in relation to the traits composition of the benthic invertebrate prey only Table 1 (Fig. 2).

2.1.2. Macrofaunal datasets

To determine links between prey selectivity and prey availability we used macrofaunal data collected between 2000 and 2010 across the study area. In total, data collected from 419 infaunal grab stations and 821 epifaunal trawl stations were used in the analyses (Fig. 3). Data were classified as unfished (UF) (according to Bolam et al., 2017) and fished (F) (defined by station location according to trawling intensity (as determined by Eigaard et al., 2017, see also section 2.3.1)). Trawling intensity was based on data collated between 2010 and 2012 and whilst we recognise the mismatch between datasets we are confident that the broad spatial patterns of fishing effort have not changed significantly over the study period. In fact, Hiddink et al. (2006) found a relatively strong correlation between trawling effort as calculated from recent Vessel Monitoring Systems (VMS) and older over-flight data, which showed that fishing distribution patterns in an area of the North Sea were relatively stable.

2.1.3. Habitat composition and clustering

The habitat composition of each ICES rectangle within our study area was determined using EUSeaMap 2012 modelled habitat map[2] (Fig. 4). For each ICES rectangle, information relative to the 42 European Nature Information System (EUNIS) habitat-related parameters was used to reduce the number of habitat-related groups (henceforth called “habitat cluster”) into a more manageable comprehensive number at a scale relevant to fisheries. To do so, the K-means partitioning technique was used. Each ICES rectangle was partitioned into a k group or cluster based on the proportion of each habitat type present within each rectangle, such that the ICES rectangles within each cluster are more similar to one another than to those from other clusters (with respect to the 42 habitat-related parameters). This method is non-hierarchi8cal and is based on least-squares methods. It is ideal when a “simple” reduction of information to a few groups is sought without any specific reference to gradients or hierarchy in the data. This method, however, requires the number of k groups to be defined a priori and determines which k gives the best fit. Milligan and Cooper (1985) recommend maximising the Calinski-Harabasz criterion (classic F-statistic comparing the among-group to the within-group sum of squares of the k clusters). Here we tested from k = 2 to 10 cluster and a “best” compromise of 6 clusters was yielded by the analysis (Fig. 5 and Table 2).

2.1.4. Biological traits

A biological trait database (see Bolam et al., 2017) was utilised to assign trait scores to the benthic prey species identified from the fish stomachs and to infauna and epifauna present within the environment. Where taxa were absent from the database, further research was undertaken to acquire trait information. Each of ten trait categories was subdivided into multiple ‘modalities’ chosen to encompass the range of possible attributes of all the taxa (Table 3).

Many taxa display multi-faceted behaviour depending upon, for example, the specific conditions and resources available (Usseglio-

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[1] http://ecosystemdata.ices.dk/stomachdata

[2] http://www.emodnet-seabedhabitats.eu/