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Using the diet of fish to reflect spatial patterns of their benthic prey

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Abstract :

The ability to efficiently implement ecosystem-based fisheries management is largely dependent on data availability. As invertebrates are not included in routine monitoring programmes, data should be collected by different approaches. We assessed whether fish could be suitable biological samplers of benthic invertebrates in the Eastern English Channel by comparing spatial distributions of Galatheidae, Portunidae and Porcellanidae found in digestive tracts (DTs) from a fish survey (Channel Ground Fish Survey), and in a dedicated benthos survey (Eastern English Channel Benthic Survey, ECBS). We found a significant spatial match between the distributions of Porcellanidae, Galatheidae and Portunidae found in fish DTs, and the ECBS occurrence-based maps. The strongest overlap was found for Galatheidae. Spatial distributions of Porcellanidae based on fish DTs better overlapped those derived from dedicated benthos surveys when we assumed these prey to also be consumed in the neighbouring spatial units to where fish were sampled. This might reflect the relatively high mobility of the dominant predators of Porcellanidae (e.g. Mustelus asterias, Scyliorhinus canicula). Overall, this study demonstrated that fish diet sampling can provide valuable information on the spatial distribution of benthic organisms.

Keywords : Benthos spatial distribution, Digestive tract, Co-occurrence, Eastern English Channel

1. INTRODUCTION

The performance of marine ecosystem-based management relies on the diagnostics established for the state of exploited marine organisms and habitats. This assessment requires spatial and temporal monitoring of the key elements of the marine ecosystem, a service which scientific surveys may provide. Scientific surveys, however, are expensive and may generally not be operated at a frequency that would comprehensively and satisfactorily cover the spatial, annual and seasonal patterns of the ecosystem. The sampling of marine organisms other than commercial fish and shellfish is particularly challenging, although these species may perform essential functions in the marine ecosystem (Seibold et al. 2018). This is typically the case for benthic invertebrates, for which regular sampling is particularly time- and resource-consuming (Dauvin et al. 1991, Kiyko and Pogrebov 1997, Theroux and Wigley 1998, Thiébaut et al. 1998) or requires methodological adaptations, because fishery survey gears are not typically suitable for benthic invertebrate monitoring (Day et al. 2020).

An alternative to scientific surveys has been to collect information from the principal foragers of marine ecosystems, including fishers (Marchal et al. 2003, Maunder and Punt 2004, Bourdaud et al. 2017), but also other marine predators. Foraging fish are thus considered adequate biological samplers and their digestive tracts (DT) have been examined to infer the spatial and/or temporal dynamics of various prey, including fishes (Fahrig et al. 1993, Ng et al., 2021), crustaceans (Lasley-Rasher et al. 2015), cephalopods (Staudinger et al. 2013), common gelatinous invertebrates (Link & Ford 2006), benthic invertebrates (Frid & Hall 1999, Link 2004, Smith et al. 2013), or a combination of these (Dwyer et al. 2010). These diet-based studies provide valuable information on the distribution of a variety of species which could otherwise not have been collected by traditional sampling. The extent to which such diet-based estimates reflect actual prey distributions and abundances may, however, be questioned; particularly where no independent survey information is available to corroborate the outcomes of DT analyses (Frid & Hall 1999, Link & Ford 2006, Staudinger et al. 2013, Lasley-Rasher et al., 2015). In other studies, the temporal and/or spatial distribution of prey abundance, as revealed from fish diet, could be contrasted with net- or acoustic-based survey information (Fahrig et al. 1993, Dwyer et al. 2010), or analytical stock assessment time series (Ng et al. 2021). Still, because foraging locations are generally unknown, it was assumed that prey species were eaten (and therefore considered present) in the same location where their predator was caught by the survey gear, except in a few studies (Smith et al. 2013). There was, however, no obvious rationale to support that assumption other than a need for simplification.

In other studies, where higher-trophic-level predators (e.g., seabirds, seals) have been used as biological samplers, it has been possible to identify foraging locations and prey distributions by combining satellite-tracking and stomach contents information, with applications to various species including albatrosses, penguins, or fur seals (Cherel & Weimerskirch 1995, Barlow et al. 2002). Seabirds and seals are considered well-suited biological samplers, since they are opportunistic feeders and forage over a broad geographical area. Such an approach, however, is difficult to apply to fish. Although many fish tagging experiments have been conducted to better understand their behavior (Righton et al. 2007, Tamdrari et al. 2012, Williams et al. 2015), these are generally not designed to monitor foraging locations precisely, making it impractical to use tagged fish as biological samplers in a similar way to birds or seals.

The aim of the present study is to address two primary questions: (i) how representative are spatial distributions of selected prey species inferred from diet-based analyses relative to dedicated, survey-based estimates and, (ii) does relaxing the assumption that prey are eaten in the same location as their fish predator is sampled confer any benefit to understanding their spatial distribution? We address these two questions, with a focus on the spatial distribution of benthic invertebrates in the Eastern English Channel (EEC), by contrasting distributions derived from the analysis of benthic prey found in fish DT collected during a groundfish survey, and distributions estimated directly from a dedicated benthos survey.

2. MATERIALS AND METHODS

2.1. Study area

The EEC (International Council for the Exploration of the Sea, ICES, Division 7d) is a rich and productive ecosystem which has, for a long time, supported many human activities (Carpentier et al. 2009). The EEC is a shallow sea with strong benthic-pelagic coupling, where benthic organisms strongly support the ecosystem structure and functioning. Benthic organisms may thus be eaten not only by benthic and demersal fishes, but also by pelagic fish (Kopp et al. 2015, Giraldo et al. 2017, Cresson et al. 2020). More broadly, results of a recent modelling study demonstrated that diets of most fish species in the area are based on opportunistic, size-driven predation (Travers-Trolet et al. 2019).

Different components of the EEC ecosystem have been surveyed over various periods and geographical scales. Of particular relevance to this study are the Eastern Channel Benthic Survey (ECBS) and the Channel Groundfish Survey (CGFS), on which information is respectively provided in Sections 2.2 and 2.3.

2.2. Mapping benthic invertebrates' distributions from dedicated benthos surveys

A dedicated benthos survey was conducted in the Eastern EEC (East of 0° longitude, EEEC) over the period 2004-2007 (Foveau et al. 2013; Fig. 1), which we refer to hereafter as the ECBS (Eastern Channel Benthic Survey). All macrofauna were identified to the lowest taxonomic resolution and enumerated wherever possible at each of the 274 ECBS stations (Foveau et al. 2013). Different sampling gears were used depending on the type of sediment: grabs on soft sediments (sands and muddy sands: 170 stations; 154 were sampled with a Hamon grab, and 16 with a Van Veen grab) and Rallier du Baty dredge for coarse sediments (gravels, pebbles and cobbles: 104 stations). At each station, three replicates were collected with the Hamon grab (sampling surface of 0.25 m²); two replicates were dedicated to the evaluation of fauna, and the other one was dedicated to sediment analysis. Five replicates were collected with the Van Veen grab (sampling surface of 0.10 m^2). The duration of the dredging tow was about five minutes, corresponding to approximately 200 meters. The dredge samples were validated only if 30 L of sediments were collected; otherwise a second tow was operated until 30 L were collected. All replicates were sieved through 2 mm and 1 mm rounded mesh. The retained material was preserved for analysis in 5% buffered formaldehyde.

It is important to note that grabs and dredges have different sampling efficiencies; the Hamon grab is a quantitative benthos sampler, which allows rapid extraction of benthic fauna down to 10 cm depth in soft sediments (Dauvin 1979). However, the Hamon grab cannot be used on coarse sediments and may be difficult to operate because of its weight (400 kg) and the rough weather conditions that prevail in the Eastern English Channel. The Van Veen grab is also a quantitative sampler, but it is lighter (70 kg) and easier to handle than the Hamon grab. However, like the Hamon grab, it cannot be used on coarse sediments or when weather conditions are poor. The Rallier du Baty dredge is a semi-quantitative sampler, because the sampling surface cannot be determined directly. Nevertheless, the dredge may be operated on all types of sediments, unlike the two grabs. Since a constant volume of 30 L is collected, it is possible to compare the number of individuals collected across stations.

The analyses carried out in this study required the combination of information provided by grab and dredge samples, despite their different efficiency and selectivity properties, and some assumptions had to be made to pool these samples into a common density metric. First, a coefficient of conversion was applied to convert densities obtained with the Hamon and Van Veen grabs into the number of benthic organisms per 30L of sediments, consistent with the abundance indices derived from the Rallier du Baty dredge. This built on earlier work by Dauvin (1979), who estimated the volume corresponding to grab operations. Dauvin (1979) concluded that two Hamon grab and five Van Veen operations (total sampling surface of 0.5 m²) collected an average volume close to 30 L (i.e., the volume obtained with the dredge). We then scaled densities obtained with the grabs by 0.5 m² surface, to make them quantitatively equivalent to the densities per 30 L collected with the dredge. Second, we assumed that grabs and dredge had similar selectivity characteristics across surveyed species. While this assumption could be reasonable for species with limited escapement abilities, it was, however, more questionable for mobile species. To alleviate the effects of contrasting selectivity patterns across sampling gears, we calculated the probability of occurrence as an alternative metric to density, to reflect benthic abundances.

Benthos densities and probabilities of occurrence derived from the ECBS were both used as a reference, against which the distributions of prey found in fish DTs collected during the CGFS were compared. CGFS fish DT benthic prey data were averaged at the genus level, within a 15’ × 15’ spatially-resolved grid (Delavenne et al. 2013; Fig. 1), and three benthic decapod families were well-represented in both the ECBS and CGFS fish DTs: Galatheidae, Portunidae and Porcellanidae. Both Porcellanidae and Galatheidae are filter-feeding decapods, which are characteristic and abundant in coarse substrata, while Portunidae are scavenging decapods, which may be found in finer sediments (Moyse and Smaldon 1990, Carpentier et al. 2009, Foveau 2009).

The taxonomic and spatial resolutions of ECBS benthos data were made consistent with those inferred from CGFS fish DT analyses, to make inter-survey comparisons easier. As a result, for each spatial unit i, ECBS benthic densities (b_i) of Galatheidae, Portunidae and Porcellanidae were averaged at the genus level within a 15’ × 15’ spatially-resolved grid (with a total of B=40 EEEC spatial units). In addition to b_i, we calculated the probability of occurrence (r_i) as an alternative metric reflecting benthic prey abundance; r_i is the proportion of sampling stations located in spatial unit i where prey are present. We thus produced two complete, spatially and taxonomically resolved, datasets for each metric from ECBS: a *benthos occurrence dataset* (including r_i) and a *benthos density dataset* (including b_i). The spatial structure of both datasets was analyzed by examining the empirical semi-variograms for r_i and b_i. The occurrence semi-variograms could be better fitted than density semi-variograms for a wide range of models (exponential, Matern, Gaussian, spherical; Fig. S1 in Supplementary Material #1, model fit not shown). Considering occurrence semi-variograms only, the model fit was better for Galatheidae and Porcellanidae than for Portunidae. This preliminary analysis overall suggested that a stronger spatial structure was found in benthos occurrence data relative to benthos density data, and for Galatheidae and Porcellanidae relative to Portunidae probability of occurrence data. Finally, we calculated the relative distributions of benthic prey abundance for each of the B=40 EEEC spatial units using two metrics, one for the *benthos occurrence dataset* (h_r_i in Equation (1a)), and another for the *benthos density dataset* (h_b_i in Equation (1b)):

$$h\_r_i = \frac{r_i}{\sum_{i=1}^{B} r_i} \tag{1a}$$

$$h\_b_i = \frac{b_i}{\sum_{i=1}^{B} b_i} \tag{1b}$$

2.3. Mapping benthic invertebrate distributions from fish diet-based sampling

An extensive digestive tract (DT) trawl survey was conducted, covering the EEC (ICES Division 7d) and the neighboring grounds of the Southern North Sea (SNS, ICES Division 4c), during the Channel Ground Fish Survey (CGFS) in October 2009 (Cachera et al. 2017, Le Roy 2009). The CGFS is conducted by Ifremer, the French Research Institute for the Exploitation of the Sea; it covers the whole Eastern English Channel every year in October using a GOV “Grande Ouverture Verticale” otter trawl, rigged with a 20 mm codend and towed at a speed of 3.5 knots for 30 minutes. The CGFS survey domain was structured according to a 15’ × 15’ spatially-resolved grid

(Delavenne et al. 2013), which was also used to group ECBS information (Section 2.2, Fig. 1). During the 2009 CGFS, sixteen fish species belonging to diverse trophic groups (Tab. 1) were caught and immediately frozen onboard using liquid nitrogen. Those fish were defrosted, measured and dissected after the survey (Cachera et al. 2017). The stations where the DTs used in this study were sampled are shown in Fig. 1. The level of DT sampling was variable across areas, and the best-sampled spatial units were located to the east of 0°15’ longitude east. To reduce standard error due to low sampling and homogenize it across spatial units, while maintaining a coherent set of inter-connected spatial units in the region under consideration, we retained 26 square-shaped spatial units in total where more than 9 DTs had been collected (Fig. S2 in Supplementary Material #2), all located to the east of 0°15’ longitude east. Between 1 and 4 stations were grouped in each of those 26 spatial units (Fig. 1). We used frequency of occurrence instead of diet composition as index of abundance, since it is considered less sensitive to predator density and also less biased than other metrics, especially those that require counting a number of prey species based on body fragments (Link 2004, Link & Ford 2006).

Benthic invertebrates represented the bulk of the diet in the DTs collected from 16 fish. We retained Portunidae (N=135 DT, *Liocarcinus* representing 84% of identified genera), Galatheidae (N=91 DT, *Galathea* representing the only identified genus) and Porcellanidae (N=50 DT, *Pisidia* representing 89% of identified genera), which were also well represented in the ECBS.

The 16 fish species for which the DTs were analysed were grouped into five functional groups, following the classification proposed by Giraldo et al. (2017) (Table 1). We first assumed all fish had the capacity to predate the three benthic prey under consideration with a similar selectivity (*comprehensive feeders dataset*). This assumption is supported by the strong benthic-pelagic coupling that has been found in the Eastern English Channel ecosystem (Kopp et al. 2015, Giraldo et al. 2017, Cresson et al. 2020, Timmerman et al. 2020), but we also considered the possibility of predator-dependent selectivity by considering only benthos- and endobenthos-feeding fish (*benthos-*

feeders dataset).

The frequency of occurrence of each prey family in DTs (q_i) was then counted for each spatial unit i as the number of DTs where this family was recorded at least once, relative to the total number of DTs sampled in this spatial unit. q_i was calculated based on the DT from either all predator fish sampled (*comprehensive feeders dataset*), or only benthos- and endobenthos-feeding fish (*benthos-feeders dataset*)

Inferring prey spatial distribution from their predator's DTs builds on a *co-occurrence assumption*: prey are eaten where their predators are fished. There is, however, no strong rationale to justify this assumption as prey residence time in DTs may be several days, and increases for indigestible fragments and when temperature is low (Daan 1973, Dos Santos & Joblings 1990a, Dos Santos & Joblings 1990b). In this study, we relaxed the *co-occurrence assumption*, and considered that a prey could have been eaten either in the same or in a directly neighbouring spatial unit to that where its predator was caught. This range corresponds to the maximal range that most benthic feeders considered in this study could cover before their prey are fully digested, except starry smooth-hound and small-spotted catshark, which could potentially travel longer distances (Text S2 in Supplementary Material #3).

The probability that a prey is found in a DT collected in square i (where i varies between 1 and S=26 EEC-SNS spatial units) is assumed to equate to the observed frequency of occurrence of that prey (q_i). Finding a prey in a DT of a fish collected in square i requires that, (1) the prey actually occurs in square i (with probability p_i) and that it has been eaten in square i (with probability $1 - \alpha$) or, (2) the prey actually occurs in square j, which refers to any of the N_i spatial units directly neighbouring square i (with probability p_j) and that it has been eaten in square j by a fish which subsequently moved to square i where it was caught (with probability α/N_i). The *co-occurrence coefficient*, α, reflects the extent to which the *co-occurrence assumption* applies, and varies between 0 and 1. When $\alpha = 0$, the prey has been eaten in the same spatial unit to that where its predator was caught (q_i = p_i). When α = 1, the prey has been eaten, with an equal probability, in any of the spatial units located in the direct neighbourhood of that being surveyed (square *i*), but never in square *i* itself. The frequency of occurrence q_i was then formulated as:

$$q_i = (1-\alpha)p_i + \left(\frac{\alpha}{N_i}\right)\sum_{j=1}^{N_i} p_j \qquad (2)$$

The maximum value of N_i is theoretically 8 (all squares surrounding square *i* are at sea), and is reduced by the number of surrounding squares either located on land or for which no DT information was available.

To derive the actual probability of occurrence p_i of a prey in all *i* spatial units, it is necessary to solve a system of *S* linear equations building on Equation (2), subject to $0 \leq p_i \leq 1$, where $0 \leq \alpha \leq 1$. Although that system could be solved with exact solutions, we found, using a simpler case, that some p_i values may be out of the range [0, 1] for different α values, and may hence not be interpreted as probabilities (Text S3 in Supplementary Material #4). We therefore used a different approach to estimate proxies for the different p_i, by minimizing the sum of squares (*SSQ*) using the PROC NLIN procedure of the SAS/STAT package (SAS 2010):

$$SSQ = \sum_{i=1}^{S}\left(q_i - (1-\alpha)p_i - \left(\frac{\alpha}{N_i}\right)\sum_{j=1}^{N_i} p_j\right)^2, \text{ subject to } p_i \in [0, 1], \text{ where } \alpha \in [0, 1] \qquad (3)$$

Finally, we calculated the relative distribution of prey abundance (d_i) for each of the *S*=26 EEEC spatial units, assuming it is proportional to probability of occurrence (p_i):

$$d_i = \frac{p_i}{\sum_{i=1}^{S} p_i} \qquad (4)$$

2.4. Measuring the spatial overlap between benthic decapod distributions derived from digestive tract survey and from dedicated benthos survey

Spatial overlap was calculated to measure the extent to which fish diets could reflect benthos distributions. If spatial overlap between benthic decapod distributions derived from fish diets and benthic survey was high, then DTs were considered as adequate samplers. We calculated the spatial overlap between the relative distributions of the three benthic prey families found in CGFS fish DTs (d_i in Equation (4)) and in the reference ECBS (h_r_i in Equation (1a), or h_b_i in Equation (1b)) using the Horn index (Horn 1966) for the A spatial units (15’ × 15’) i where benthic distributions from both surveys were reported. A=24 spatial units had benthos abundance available from both ECBS (B=40 spatial units) and CGFS fish diet sampling (S=26 spatial units). Two Horn indices were then calculated, one for the *benthos occurrence dataset* (HI_r, building on h_r_i), and another one for the *benthos density dataset* (HI_b, building on h_b_i):

$$HI\_r = \frac{2\sum_{i\in A} d_i h\_r_i}{\sum_{i\in A} d_i^2 + \sum_{i\in A} h\_r_i^2}$$

(5a)

$$HI\_b = \frac{2\sum_{i\in A} d_i h\_b_i}{\sum_{i\in A} d_i^2 + \sum_{i\in A} h\_b_i^2}$$

(5b)

HI_r is bounded between 0 and 1, and increases with the degree of spatial overlap. $HI\_r = 1$ corresponds to a full match between the prey’s distributions ($d_i = h\_r_i, \forall\ i$), while $HI\_r = 0$ corresponds to no overlap ($d_i = 0$ if $h\_r_i > 0$, $d_i > 0$ if $h\_r_i = 0$, $\forall\ i$). This also applies to HI_b, substituting h_r_i by h_b_i.

We then used permutation tests to find values of α for which actual Horn indices would significantly differ from Horn indices derived from the null distribution. To that purpose we compared, for each value of α (21 values in total, ranging between 0 and 1 by 0.05 steps), the actual Horn index value with hypothetical indices obtained by reshuffling the CGFS-based values from their original spatial unit to other spatial units drawn randomly from a uniform probability distribution. 1000 distributions were drawn and the basic statistics (median, 5th and 95th percentiles) of the resulting simulated Horn index values were derived and contrasted with the actual Horn index for each benthic family, and for α ranging between 0 and 1. Overlap strength was measured as the distance between the actual Horn index and the 95th percentile of the simulated Horn index values, with larger values indicating stronger overlap.

We also compared the benthic prey spatial distributions derived from ECBS and CGFS diet surveys considering the corresponding cumulative distributions per spatial unit for each prey family. To produce the cumulative distributions, we sorted the A=24 spatial units for each benthic prey by decreasing (ECBS-based) h_r_i. (for the *benthos occurrence dataset*) or h_b_i (for the *benthos density dataset*). We then compared the ECBS- and the CGFS-based cumulative prey distribution functions (Y-axis) with the A sorted spatial units (X-axis). We also drew a reference straight line representing the cumulative proportion of the region covered when adding each supplementary spatial unit. The ECBS-based cumulative distribution functions have a typical convex shape due to the sorting of the spatial units. An overlap between CGFS- and ECBS-based spatial distributions would be reflected by a convex CGFS-based cumulative prey distribution function positioned close to the ECBS-based cumulative prey distribution function and above the reference line. The closer the CGFS- and ECBS-based cumulative prey distribution curves, the larger the overlap between spatial distributions derived from fish diets and the benthos survey. With little or no correlation between CGFS- and ECBS-based spatial distributions, the CGFS-based cumulative prey distributions would be aligned with or fluctuate around the reference line. A negative correlation between CGFS- and ECBS-based spatial distributions would be reflected by a concave CGFS-based cumulative prey distribution function, positioned symmetrically to the ECBS-based curve relative to the reference line.

3. RESULTS

Under the co-occurrence assumption, the DT-based distributions of Galatheidae, Portunidae and Porcellanidae prey derived from the *comprehensive feeders dataset* significantly ($p<0.05$) overlapped the ECBS-based distributions when these were calculated based on probabilities of occurrence (Fig. 2a). When ECBS-based distributions were calculated using the *benthos density dataset*, a significant overlap was found for Galatheidae and Porcellanidae, but not for Portunidae (Fig. 2b). Selecting benthic-feeders did not enhance overlap strength (Figs. 2c-d).

The effects of relaxing the co-occurrence assumption are shown in Figs. 3-5. The shape of the relationship between the Horn index and the weight (α) given to the co-occurrence assumption was neither monotonic, nor convex. However, it presented some common features across the different benthic families and datasets under consideration. The Horn index thus decreased when α increased until α reached some value α_{min} greater than 0.5. When α increased beyond α_{min}, the Horn index overall increased and reached a maximum (local or absolute) at some case-dependent value of α_{max} greater than 0.65. When α was greater than α_{max}, the Horn index overall decreased until α equalled 1, except for Porcellanidae when considering ECBS occurrence and the *comprehensive feeders dataset* (Fig. 5a), where the Horn index decreased, reached a second minimum, and finally increased steeply.

For Galatheidae, the spatial overlap between both survey distributions measured with the Horn index was always significant ($p < 0.05$) when α was low ($\alpha \leq 0.50$; Figs. 3a-d), and it was maximum with the DT-based *comprehensive* and the *ECBS-based benthos occurrence dataset*s, and when assuming full co-occurence (Fig. 3a). The spatial overlap was almost always higher when retaining all CGFS-sampled fish (Figs. 3a & 3b) than when selecting benthic feeders only

(Figs. 3c & 3d). The spatial overlap obtained with both ECBS-based datasets were similar, although it was slightly higher using occurrences at low α (Figs. 3a & 3c), and densities at high α (Figs. 3b & 3d).

When Portunidae distributions were derived from the ECBS-based *benthos occurrence dataset*, the spatial overlap between both survey distributions was significant ($p < 0.05$) for a range of α values when all CGFS fish were retained ($\alpha \leq 0.5$) and highest when assuming full co-occurrence (Fig. 4a). The spatial overlap was only significant when α was in the range [0.65, 0.70] when CGFS benthos-feeders were selected (Fig. 4c). Finally, the spatial overlap was never significant when ECBS-based Portunidae distributions were derived from the *benthos density dataset* (Figs. 4b & 4d). When Porcellanidae distributions were derived from the ECBS-based *benthos occurrence dataset*, the spatial overlap between ECBS- and DT-based benthos distributions was significant for most α values (Figs. 5a & 5c), and more particularly when $\alpha > 0.80$. When Porcellanidae distributions were derived from the ECBS-based *benthos density dataset*, the spatial overlap between ECBS- and DT-based distributions was significant for low (≤ 0.3) and high (≥ 0.6) α values when all feeders sampled by CGFS were considered, with a maximum at $\alpha = 0.75$ (Fig. 5b). The overlap was significant for most α values ($\alpha < 0.90$), when considering CGFS-sampled benthic feeders only, with a maximum at $\alpha = 0.75$ (Fig. 5d). Overall, selecting CGFS-sampled benthic feeders (Figs. 5c & 5d) did not enhance the spatial overlap derived when retaining all feeders (Figs. 5a & 5b), irrespective of the ECBS-based dataset being considered.

We mapped and compared the benthos distributions derived from ECBS and CGFS surveys and the corresponding cumulative distributions per spatial unit for each prey family (Galatheidae, Portunidae, Porcellanidae), the CGFS *all feeders* dataset, and combinations of ECBS benthos (occurrence or density) datasets and of α values leading to the largest between-surveys spatial overlap (Figs. 6 & 7).

Of the three benthic prey under consideration, the highest spatial overlap was found for Galatheidae, with several hotspots and low density areas being found with both surveys, when co-occurrence was assumed (Figs. 6a & 6b). This is well-reflected by the similar cumulative prey distributions per spatial unit obtained with the ECBS-based *benthos occurrence dataset* and the CGFS-based *all feeders dataset* (Fig. 6c). The top twelve DT-based Galatheidae hotspots (representing 12/24 = 50% of the total EEEC area) thus concentrated 75% of the overall DT- and 83% of ECBS-estimated abundance (Fig. 6c). Several Galatheidae hotspots were in particular found by both surveys off the “Pays de Caux” (one spatial unit centred on [49°52’30”N, 0°52’30”E]) and to the west of a line joining Dieppe and Hastings (six spatial units [50°37’30”N, 0°22’30”E], [50°22’30”N, 0°22’30”E], [50°07’30”N, 0°22’30”E], [50°22’30”N, 0°37’30”E], [50°07’30”N, 0°37’30”E], [50°22’30”N, 0°52’30”E]). The seafloor of these seven “agreed” spatial units were largely dominated by gravels, except [50°22’30”N, 0°37’30”E] and [50°22’30”N, 0°52’30”E], which were substantially covered by coarse sands (see Fig. 1 in Foveau et al. (2013)). While one Galatheidae hotspot was revealed by the ECBS survey in the spatial unit located off Dover [51°07’30”N, 1°07’30”E], no Galatheidae could be found in the DTs sampled by the CGFS. In addition, one Galatheidae hotspot found by the CGFS method could not be confirmed by the ECBS [50°37’30”N, 0°37’30”E].

There was less overlap between Portunidae distributions, with few hotspots agreed by both surveys (Figs. 6d-e), which was reflected by a DT-based cumulative prey distribution well below the ECBS-based distribution and close (although still above) to the reference line. 56% of DT-estimated Portunidae abundance was thus concentrated in twelve spatial units (representing 50% of the total EEEC area, the proportion that would have been expected if all EEEC spatial units had the same average abundance value), while the Portunidae ECBS-estimated abundance from these twelve spatial units represented 90% of the overall EEEC abundance (Fig. 6f). Both surveys agreed on three major Portunidae hotspots found in spatial units where coarse sands were dominant ([50°37’30”N, 0°37’30”E], [50°22’30”N, 0°52’30”E]), or covered part of the seafloor [50°22’30”, 0°37’30”E] between Hastings and Dieppe (see Fig. 1 in Foveau et al. (2013)). A major Portunidae hotspot revealed by the ECBS survey off Dover [51°07’30”N, 1°07’30”E] could not, however, be confirmed using DT information.

The overlap between Porcellanidae distributions derived from both surveys was intermediate (higher than for Portunidae, lower than for Galatheidae), with or without the co-occurrence assumption (Figs. 7a-c). The overlap was slightly higher when relaxing the co-occurrence assumption (Fig. 7d), as could be expected from Fig. 5. Under the co-occurrence assumption (α = 0), the top half of DT-based Porcellanidae abundance concentrated 83% of the overall DT-estimated abundance and 99% of the ECBS-estimated abundance (Fig. 7d). When the co-occurrence assumption was relaxed (α = 0.7), the top 50% of DT-based Porcellanidae abundance concentrated 87% of the overall DT-estimated abundance (Fig. 7d). Three major Porcellanidae hotspots were in particular found by both surveys in the northeast (entrance of the Dover Strait) of the EEEC ([51°07’30”N, 1°37’30”E], [51°07’30”N, 1°52’30”E], [50°52’30”N, 1°22’30”E]), an area dominated by gravels (see Fig. 1 in Foveau et al. (2013)). A major Porcellanidae hotspot revealed by the ECBS survey off Dover [51°07’30”N, 1°07’30”E] could not, however, be confirmed using DT information, while two Porcellanidae hotspots identified using DT information to the west of the line joining Hastings and Dieppe, in spatial units characterized by gravelly sediments ([50°22’30”N, 0°22’30”E], [50°07’30”N, 0°37’30”E]), could not be retrieved from the ECBS survey.

4. DISCUSSION

In this study, we quantitatively compared overlap between the spatial distributions of benthic decapods inferred from a dedicated benthos survey and from fish DTs sampled during a trawl survey within a similar timeframe. We found significant overlap between diet and benthic survey information for the three prey families under consideration (Fig. 2).

Our study focused on three decapod families: Galatheidae, Porcellanidae and Portunidae. The main reason for restricting our analysis to those three families was that they were well-represented both in the benthic survey and in fish diets. Many more benthic taxa were adequately sampled by the benthic survey, but infrequently found in fish DTs (Foveau et al. 2013). This particularly applied to soft-bodied organisms, which are rapidly digested, and to large benthic animals, which cannot be ingested by fish. In contrast, highly mobile crustaceans Caridea and *Crangon crangon* were abundant in fish diets, but they were rarely caught in the benthic survey due to their ability to escape from the survey gear. While our results overall suggest that diet sampling could be useful for benthos monitoring, one limitation is the ability to identify prey in digestive tracts at the lowest taxonomic level. Greater possibilities should be offered with the increased application of genetics and DNA metabarcoding to taxonomic sorting (Hansen et al. 2018, Beentjes et al. 2019). Substrate was found to be an important factor for areas of high benthic decapod occurrence. Galatheidae and Porcellanidae hotspots were found by both diet and benthic survey sources in areas mostly dominated by gravelly sediments: off the “Pays de Caux”, to the west of a line joining Hastings and Dieppe, or in the entrance of the Dover Strait (Larsonneur et al. 1982, Foveau et al. 2013), which concurs with knowledge on the habitat preferences of these decapods (Carpentier et al. 2009). Portunidae are less dependent on gravelly sediments compared to Galatheidae and Porcellinidae (Moyse and Smaldon 1990). This may explain why both surveys agreed on Portunidae hotspots between Hastings and Dieppe, in spatial units where coarse sands were either dominant, or well represented. One spatial unit [50°22’30”, 0°37’30”E] was characterized by geographically distinct patches of gravelly and sandy sediments, which are preferred by Galatheidae and Portunidae respectively. This may explain why both surveys agreed that Galatheidae and Portunidae hotspots were found on this spatial unit, despite their contrasted sediment preferences. Distinct hotspots might have been revealed for these two decapod families with a spatial resolution finer than 15’ x 15’. It was more surprising that both surveys agreed on a Galatheidae hotspot in a spatial unit dominated by coarse sands [50°22’30”N, 0°52’30”E]. This could, however, be explained by the high level of sediment heterogeneity in that area, which could not be fully captured at the spatial resolution of our analysis.

Although diet and benthic surveys generally agreed on the locations of hotspots, there were several cases where they provided contrasted information. One significant Galatheidae, Portunidae and Porcellanidae hotspot revealed by the benthic survey off Dover [51°07’30”N, 1°07’30”E] was not retrieved using DT contents. When checking diet information, we found that the percentage of crustaceans identified down to the family level was the lowest in this particular spatial unit (29%), which may explain this discrepancy. In contrast, one Galatheidae hotspot [50°37’30”N, 0°37’30”E] and two Porcellanidae hotspots ([50°22’30”N, 0°22’30”E], [50°07’30”N, 0°37’30”E]) inferred by diet information could not be confirmed by the benthic survey. This could result from the different geographical locations of fish and benthic surveys, which may have sampled different benthic communities within each of these spatial units, possibly combined with fish movements.

We found prey family-specific differences in the utility of predator diets, which may be due to a combination of ecological or methodological differences between prey families. Considering cumulative spatial distributions, we found the strongest overlap between survey methods for Galatheidae (Fig. 6c), followed by Porcellanidae (Fig. 7d) and finally Portunidae (Fig. 6f) families. Differences in overlap strength may be due to different catch selectivity between predatory fishes and sampling gears used in benthic surveys (Day et al. 2020), and differing spatial structures across the three prey distributions (Fig. S1 in Supplementary Material #1). More specifically, Galatheidae and Porcellanidae species have limited escapement capacities, which make them more accessible to benthic survey gears than mobile Portunidae species. In addition, some Portunidae species investigated in this study, e.g., *Liocarcinus holsatus*, migrate to estuaries in spring and move back to deeper waters in winter to avoid low temperatures (Venema et Creutzberg, 1973), which may blur their sampling distributions in the ECBS, since this benthic survey has been operated over different years and seasons.

Beyond their presence and easy identification in fish diet, knowledge on the distribution of the decapod families investigated in this study provides valuable information on other components of the Eastern English Channel ecosystem. *Galathea intermedia* and *Pisidia longicornis*, respectively the main Galatheidae and Porcellanidae species, are characteristic of, and abundant in, coarse sediments. As filter-feeding decapods, they are particularly sensitive to perturbations in their environment. These two species also belong to a benthic assemblage of species from different taxa, characteristic of gravelly sediments in the Eastern English Channel, which is mainly composed of other crustaceans (*Pilumnus hirtellus*, *Balanus crenatus*), echinoderms (*Psammechinus miliaris*, *Ophiothrix fragilis*), gastropods (*Calliostoma zizyphinum*) and Polychaeta (*Pomatoceros triqueter*). This assemblage has been shown to be relatively stable in terms of species composition and geographic distribution over three decades (Cabioch and Glaçon 1975, Cabioch and Glaçon 1977, Foveau 2009). As a result, spatial distributions of Galatheidae and Porcellanidae inferred from fish diets may also be useful in providing information on the benthic habitats distribution

of the other taxa belonging to the gravelly sediments assemblage. Portunidae are more ubiquitous and mobile than Galatheidae and Porcellanidae, and, as scavengers, may characterize disturbed sediments.

A possible bias to using fish DTs as a biological sampling tool for the spatial distribution of their benthic prey is that the precise location of where these prey were consumed is unknown. This issue has been overlooked in previous studies, where co-occurrence was assumed. Smith et al. (2013) did test the statistical correlation between benthos survey abundances and fish diet compositions within and across spatial areas. They found that fish diet composition was in most cases correlated with benthic survey abundance within areas, although not systematically. They also suggested the possibility that haddock (*Melanogrammus aeglefinus*), one of the benthivorous fishes under investigation, might have foraged in a different area to where it was sampled.

Our study is one of the first to investigate systematically whether and the extent to which relaxing the co-occurrence assumption could improve the capacity of fish DTs to adequately sample benthic invertebrates. We showed in particular that the spatial distributions of Porcellanidae found in DTs better overlapped those derived from ECBS when we assumed prey to be consumed either in the same, or in a neighbouring spatial unit to that where their predators were caught. Relaxing the co-occurrence assumption did not strengthen the overlap between fish DT- and ECBS-based distributions for Galatheidae and Portunidae, which might reflect differences in the mobility of their predators. The bulk of Porcellanidae (44%) occurred in the DTs of starry smooth-hound (34%) and small-spotted catshark (10%), two specialist crustacean feeders some individuals of which have been shown to travel long distances (Walker et al. 1980, Ellis et al. 1996, Brevé et al. 2016) (Table 1, Text S2 in Supplementary Material #3). In contrast, the bulk of Portunidae and Galatheidae occurred in the DTs of fishes with a more restricted foraging range, including thornback ray (Walker et al. 1997, Hunter et al., 2005a, Hunter et al. 2005b), cod (ICES 1970), bass (Holden & Williams 1974), red gurnard and red mullet, while starry smooth-hound and small-spotted catshark only contributed 11-15% of occurrence. We also explored the possibility that contrasted digestion durations across predators could explain why spatial distributions of Porcellanidae found in DTs better overlapped those derived from ECBS when the co-occurrence assumption was relaxed, but the results were not conclusive (Text S1 in Supplementary Material #3).

In this study, we relaxed the co-occurrence assumption and found a complex relationship between the estimated probabilities of occurrence and co-occurrence, particularly when probability of co-occurrence was low, which confirmed theoretical findings building on a simple case (Text S3 in

Supplementary Material #4). This complex relationship could also reflect violation of the assumption that the probability for a prey to be eaten in the *N* neighboring spatial units was equal across these spatial units (“space-invariant assumption”). In reality, some of these neighboring spatial units may provide more suitable habitat for benthic prey than others, which would cause the space-invariant assumption to be at fault.

Several refinements could be enacted to relax the assumption that all spatial units neighboring that where fish diet was sampled have equal probabilities to be the source of a prey (space-invariant assumption). Firstly, knowledge on preferred benthic habitats could be applied to assign different weightings to the spatial units, instead of using a flat rate materialized by one parameter (α). These weightings could be derived from current knowledge of the spatial heterogeneity of the distribution of benthic habitats in the Eastern English Channel (Foveau 2009, Carpentier et al. 2009, Foveau et al. 2013). For instance, a strong weighting could be allotted to those spatial units where coarse sediments are dominant when deriving the spatial distributions of Galatheidae and Porcellanidae based on fish diets. In addition, where information on the digestion stage of prey in each fish diet is available, which was not the case in this study, the likely geographical range where the prey was consumed could be inferred more precisely. For instance, if a fish was caught in the upper left corner of a spatial unit and its diet is minimally digested, it appears unlikely that prey were consumed in spatial units located in the direct vicinity of the lower right corner.

While the results shown in this study provided a novel framework to evaluate the extent to which fish DTs can be considered suitable biological samplers for the distribution of benthic invertebrates, given the patchy nature of benthos we would recommend that future investigations build on DT sampling programs using a spatial grid size smaller than (15’ x 15’). In addition, some benthic species may have strong individual patterns that may have been diluted through aggregation into broader families. Including indicators of predator selectivity could also be beneficial. Some prey within a genus may have higher nutritional value, or be easier to catch, so these would be overrepresented in DTs compared to the environment. Similarly, ascertaining the actual width of fish trophic niches may provide a future improvement of the present approach, by identifying generalist fish species that could be considered as optimal samplers of the benthic community in future studies.

We assumed that the 2004-2007 benthos spatial distributions derived from ECBS were comparable to 2009 values, *i.e.*, the year when stomach contents were comprehensively sampled by the CGFS. This assumption is supported by evidence that the spatial distribution of benthic communities is strongly determined by their general habitat, and that the EEEC benthos spatial distribution has been subject to only limited changes over decades (Foveau et al. 2013, Dauvin 2015, Saulnier et al. 2019). However, this assumption may be questionable for species that undertake seasonal migrations and move across habitats (e.g., Portunidae; Venema and Creutzberg, 1973).

Our study offers a valuable methodological framework to examine the spatial dimension of how closely fish diets reflect the actual distribution of their benthic prey, and an important follow-up would be to investigate the temporal consistency of benthic abundance trends across surveys. Examining the time correlation between abundances derived from fish diet and benthic surveys would be a necessary second step to apply our methodological framework in support of ecosystem-based assessment. That step would require concurrent and regular sampling of fish diets and of their benthic prey fields over several years and/or seasons (Smith et al. 2013), which was not available to our study but could be promoted as part of marine data collection programmes, such as those operated in EU waters under the Marine Strategy Framework Directive (EC 2008). We combined fishes of different guilds and assumed they all had the capacity to forage the three benthic prey families; although this may be seen as a strong assumption, restricting the list of predator species to benthivorous fishes did not improve overlap strength. Strong benthic-pelagic coupling structures the EEC ecosystem, a shallow sea where benthic prey are accessible to most predators of the water column, including the large proportion of demersal fish (i.e., cod, whiting, bass), which were filtered out when selecting benthic feeders, possibly explaining the lack of improvement in overlap strength (Kopp et al. 2015, Giraldo et al. 2017, Cresson et al. 2020, Timmerman et al. 2020). A complementary explanation is that the functional groups considered in this study, which built on the detailed analysis carried out by Giraldo et al. (2017), were not disaggregated to a level that would allow identification of predators feeding (or not) specifically on the three benthic decapod families investigated in this study. For instance, cod and whiting have been identified as demersal piscivorous fish. It has been shown in different maritime regions, however, that these species feed on fish, but also on other types of prey such as benthic decapods, and also that the contribution of prey types in their diet depends on their ontogeny (Worm and Myers 2003, Thompson et al. 2020, Timmerman et al. 2020). In contrast, the diet of sole and plaice, which have hereby been categorized as benthos feeders, is more based on deposit feeders such as polychaeta and amphipods than on benthic decapods (Girardin et al. 2018). Overall, the main effect of selecting benthic feeders was then to increase sampling gaps in space, rather than to refine diet information. This is mainly due to the withdrawal of demersal piscivorous fish which contributed as much as the benthic feeders to the consumption of Galatheidae, Portunidae and Porcellanidae, while the other planktivorous and pelagic piscivorous fish had a more limited contribution (Tab. 1). Refining functional groups to categorize benthic decapod feeders could be used to test whether and the extent to which spatial distributions of Galatheidae, Portunidae and Porcellanidae found in DTs would better overlap those derived from ECBS. With the data available to our study, refining functional groups would remove information useful to this study, and would increase the gaps in our spatial sampling grid. It should be stressed, however, that a finer species functional grouping would likely be necessary to apply our approach to deeper ecosystems, where benthic-pelagic coupling is less prevalent, e.g., Mediterranean Sea, Bay of Biscay (Cresson et al. 2020). Overall, this study showed that fish diet sampling may provide valuable information on the spatial distribution of benthic organisms belonging to Galatheidae, Porcellanidae and Portunidae families. In doing so, we took into account for the first time the potential spatial mismatch between diet and benthos survey sampling locations. We found that results were generally robust to neglecting that mismatch possibility, although relaxing the co-occurrence assumption led to a slightly better overlap of the Porcellanidae spatial distributions derived from both surveys. Our results did not suggest that diet sampling could substitute dedicated benthos surveys, but they showed that diet sampling could help to either identify areas where a benthos survey should operate, or question benthos sampling methods if some prey is found in diet tracts but not in the survey.

SUPPLEMENTARY MATERIAL:

The following supplementary material is available online: Spatial structure of observed benthos occurrences and densities drawn from the Eastern English Channel Benthic Survey (#1), Standard error of the frequency of occurrence of each prey family found in fish digestive tracts sampled from the Channel Groundfish Survey (#2), Calculation of the maximal distance covered by fish before their prey are fully digested (#3), Structure of the system of equations used to estimate probability of occurrence of benthic prey (#4).

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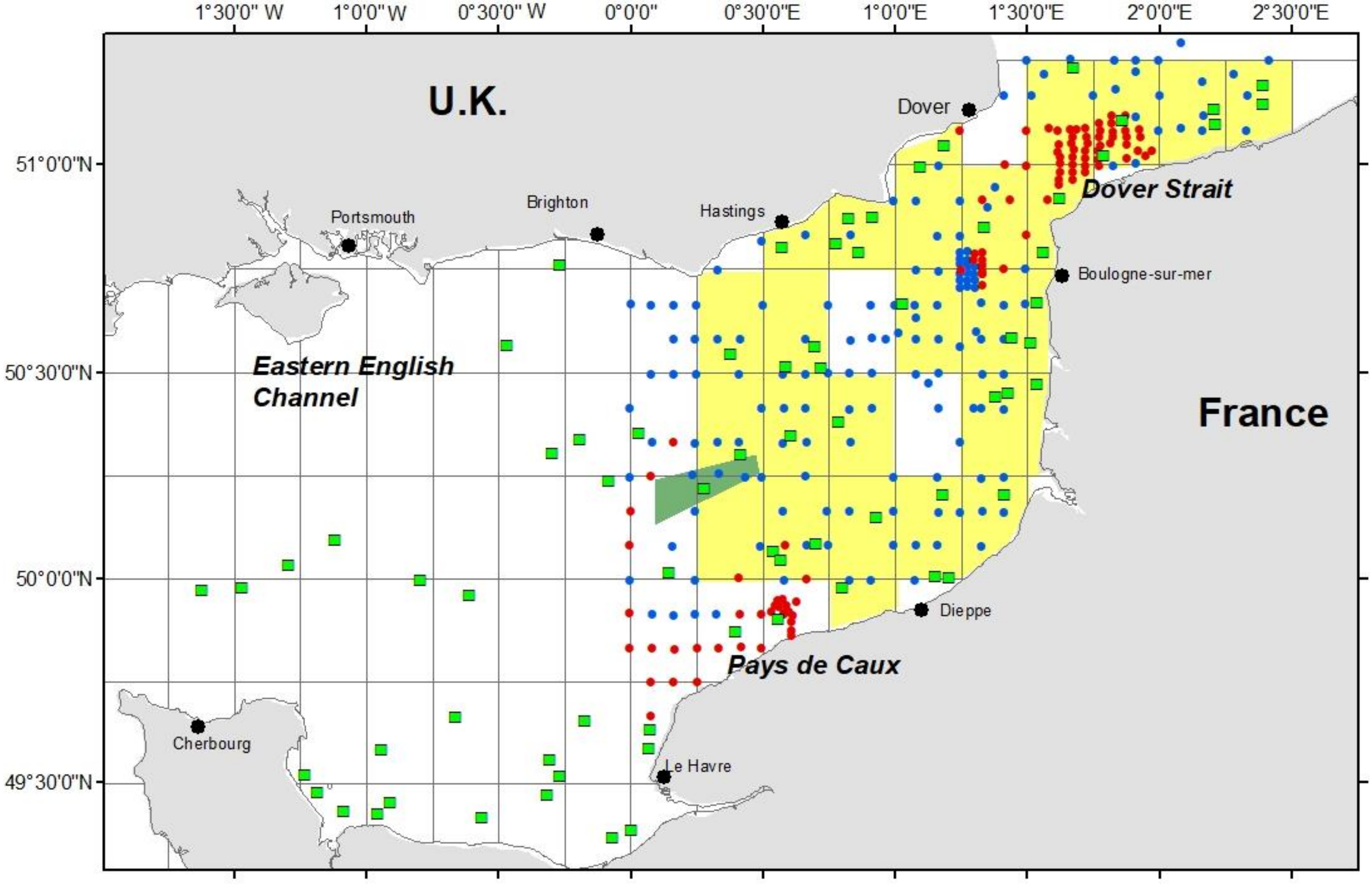
Table 1. Contribution of the different functional groups and predator species to prey occurrence: for each predator species, number (and %) of Digestive Tracts (DTs) where at least one individual from a given prey family has been recorded [e.g., Portunidae species have occurred in 135 fish DTs, of which 13 (10%) were red gurnards, and 61 (45%) were benthos-feeding fish].

Functional group	Predator species		Prey family		
			Portunidae	Galatheidae	Porcellanidae
Benthos-feeding fish	Red gurnard	*Aspitrigla cuculus*	13 (10%)	19 (21%)	4 (8%)
	Red mullet	*Mullus surmuletus*	7 (5%)	23 (25%)	0 (0%)
	Starry smooth-hound	*Mustelus asterias*	12 (9%)	11 (12%)	17 (34%)
	Thornback ray	*Raja clavata*	21 (16%)	4 (4%)	1 (2%)
	Small-spotted catshark	*Scyliorhinus canicula*	3 (2%)	3 (3%)	5 (10%)
	Greater-spotted dogfish	*Scyliorhinus stellaris*	1 (<1%)	0 (0%)	0 (0%)
	Tub gurnard	*Trigla lucerna*	4 (3%)	1 (1%)	0 (0%)
	SUB-TOTAL		61 (45%)	61 (67%)	27 (54%)
Endobenthos-feeding fish	Plaice	*Pleuronectes platessa*	1 (<1%)	0 (0%)	0 (0%)
	Sole	*Solea solea*	3 (2%)	5 (5%)	6 (12%)
	SUB-TOTAL		4 (3%)	5 (5%)	6 (12%)
Demersal piscivorous fish	Bass	*Dicentrarchus labrax*	26 (19%)	1 (1%)	2 (4%)
	Cod	*Gadus morhua*	32 (24%)	7 (8%)	14 (28%)
	Whiting	*Merlangius merlangus*	2 (1%)	11 (12%)	0 (0%)
	SUB-TOTAL		60 (44%)	19 (21%)	16 (32%)
Planktivorous fish	Herring	*Clupea harengus*	1 (<1%)	0 (0%)	0 (0%)
	Sardine	*Sardina pilchardus*	2 (1%)	0 (0%)	1 (2%)

	Sprat	*Sprattus sprattus*	4 (3%)	0 (0%)	0 (0%)
	SUB-TOTAL		7 (5%)	0 (0%)	1 (2%)
Pelagic piscivorous fish	Horse mackerel	*Trachurus trachurus*	3 (2%)	6 (7%)	0 (0%)
	SUB-TOTAL		3 (2%)	6 (7%)	0 (0%)
TOTAL			135 (100%)	91 (100%)	50 (100%)

Fig. 1. Map of the Eastern English Channel and Southern North Sea (EEC-SNS), including the 2009 Channel Ground Fish Survey (CGFS) stations where fish digestive tracts used in this study were collected (green squares), and the 2004-2007 Eastern Channel Benthic Survey (ECBS) stations, where benthos was sampled in the Eastern part of the Eastern English Channel (EEEC) with a (Hamon or Van Veen) grab (blue) or a dredge (red dots). The 26 EEEC CGFS spatial units (15’ x 15’) where more than nine digestive tracts have been sampled are highlighted in yellow. The dark green polygon delineates an intensively investigated site (high ECBS station density), for which the exact position of stations cannot be shown for confidentiality reasons (see Foveau et al., 2013).


1°30'0" W
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50°0'0"N
49°30'0"N
U.K.
Dover
Portsmouth
Brighton
Hastings
Dover Strait
Boulogne-sur-mer
Eastern English Channel
France
Dieppe
Pays de Caux
Cherbourg
Le Havre

Fig. 2. Horn indices measuring the spatial overlap between benthos distributions estimated under the co-occurrence assumption (α = 0) from Channel Ground Fish Survey (CGFS) DT-based [(a, b) *comprehensive feeders*, (c, d) *benthos-feeders*] datasets, and from Eastern Channel Benthic Survey (ECBS)-based [(a, c) *benthos occurrence*, (b, d) *benthos density*] datasets. A Horn index H = 1 corresponds to a hypothetical full match between the prey distributions while H = 0 corresponds to a complete mismatch. The actual Horn index (blue dot) is compared with the median (black dot), the 5th and the 95th percentiles (black circles) of Horn index values resulting from 1000 random simulations. Three benthic families are considered: Galatheidae, Portunidae and Porcellanidae.

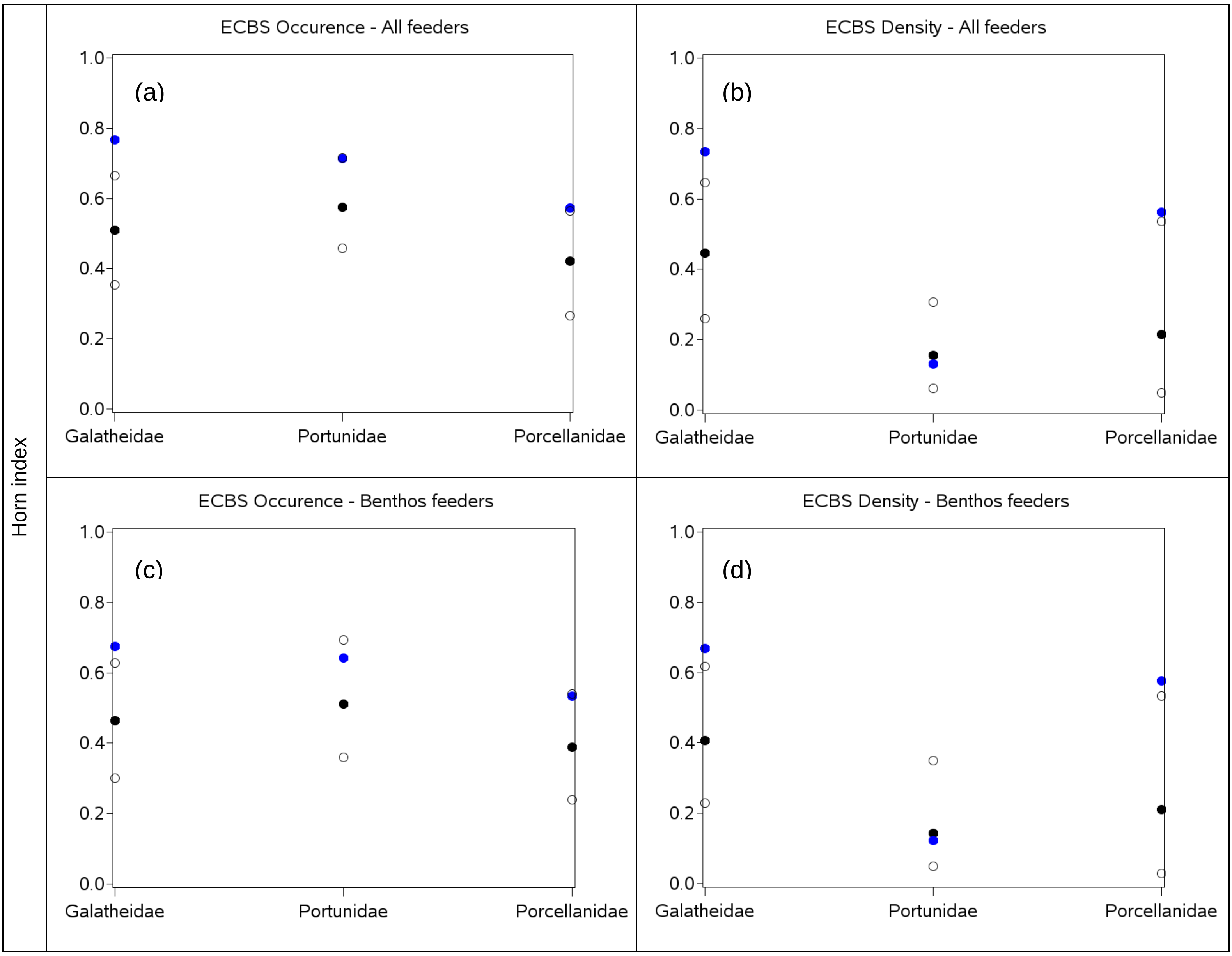

Fig. 3. Horn indices measuring the spatial overlap between Galatheidae distributions estimated for different weightings (α) given to the co-occurrence assumption, from Channel Ground Fish Survey (CGFS) DT-based [(a, b) *comprehensive feeders*, (c, d) *benthos-feeders*] datasets, and from Eastern Channel Benthic Survey (ECBS)-based [(a, c) *benthos occurrence*, (b, d) *benthos density*] datasets. The actual Horn index (blue dots) is compared with the median (black dot), the 5th and the 95th percentiles (black circles) of Horn index values resulting from 1000 random simulations.

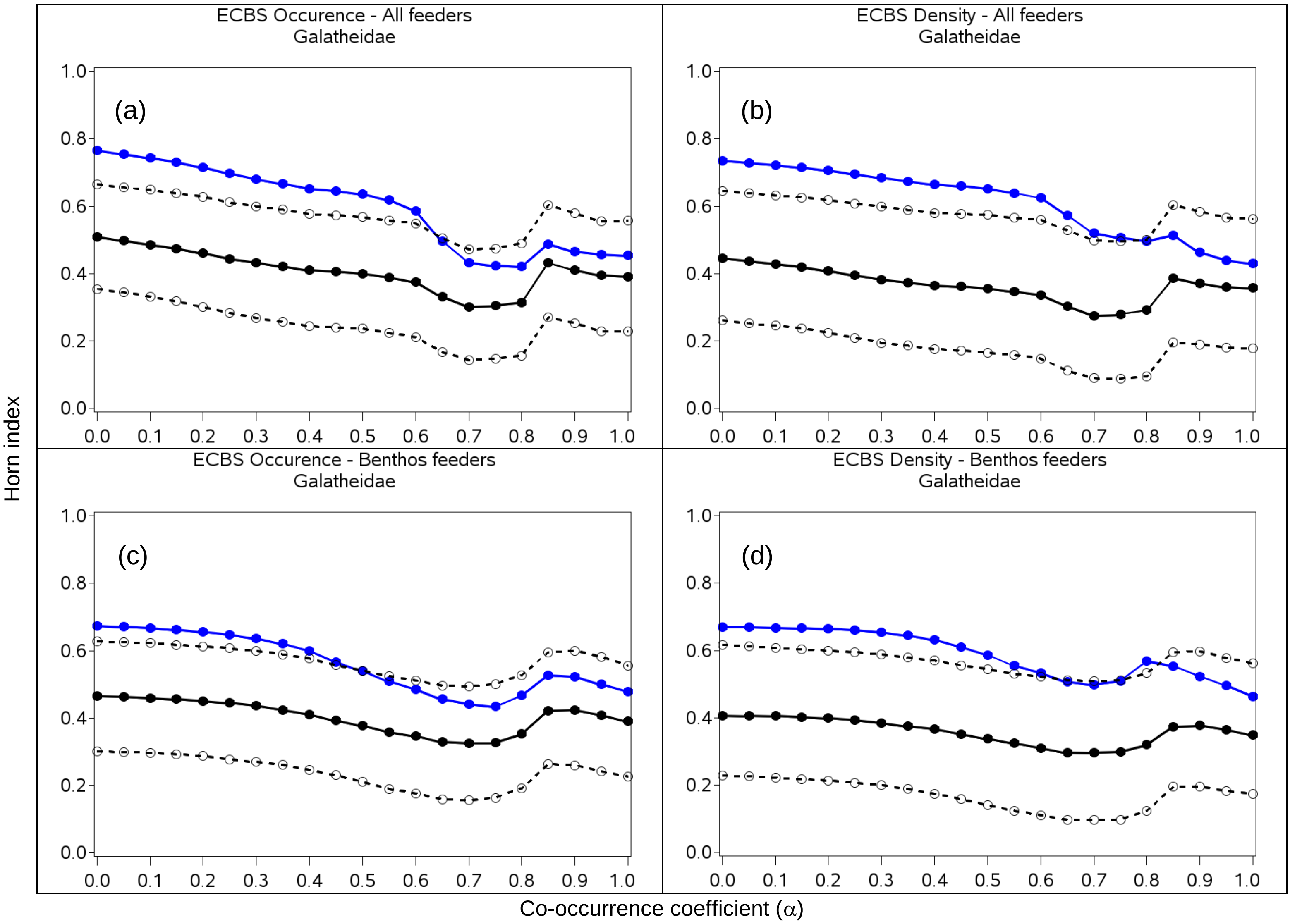

Fig. 4. Horn indices measuring the spatial overlap between Portunidae distributions estimated for different weightings (α) given to the co-occurrence assumption, from Channel Ground Fish Survey (CGFS) DT-based [(a, b) *comprehensive feeders*, (c, d) *benthos-feeders*] datasets, and from Eastern Channel Benthic Survey (ECBS)-based [(a, c) *benthos occurrence*, (b, d) *benthos density*] datasets. The actual Horn index (blue dot) is compared with the median (black dot), the 5th and the 95th percentiles (black circles) of Horn index values resulting from 1000 random simulations.

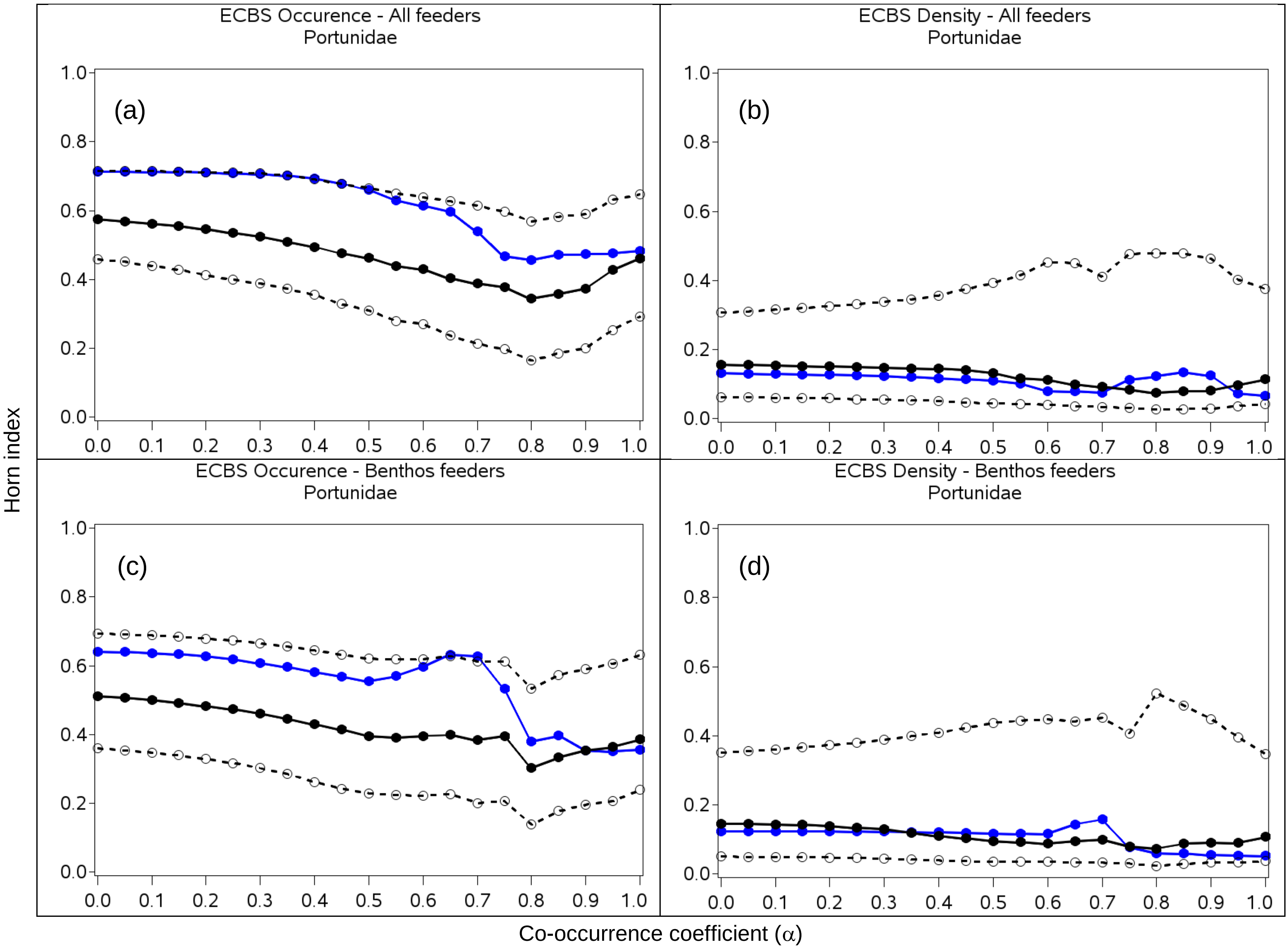

Fig. 5. Horn indices measuring the spatial overlap between Porcellanidae distributions estimated for different weightings (α) given to the co-occurrence assumption, from Channel Ground Fish Survey (CGFS) DT-based [(a, b) *comprehensive feeders*, (c, d) *benthos-feeders*] datasets, and from Eastern Channel Benthic Survey (ECBS)-based [(a, c) *benthos occurrence*, (b, d) *benthos density*] datasets. The actual Horn index (blue dot) is compared with the median (black dot), the 5th and the 95th percentiles (black circles) of Horn index values resulting from 1000 random simulations.

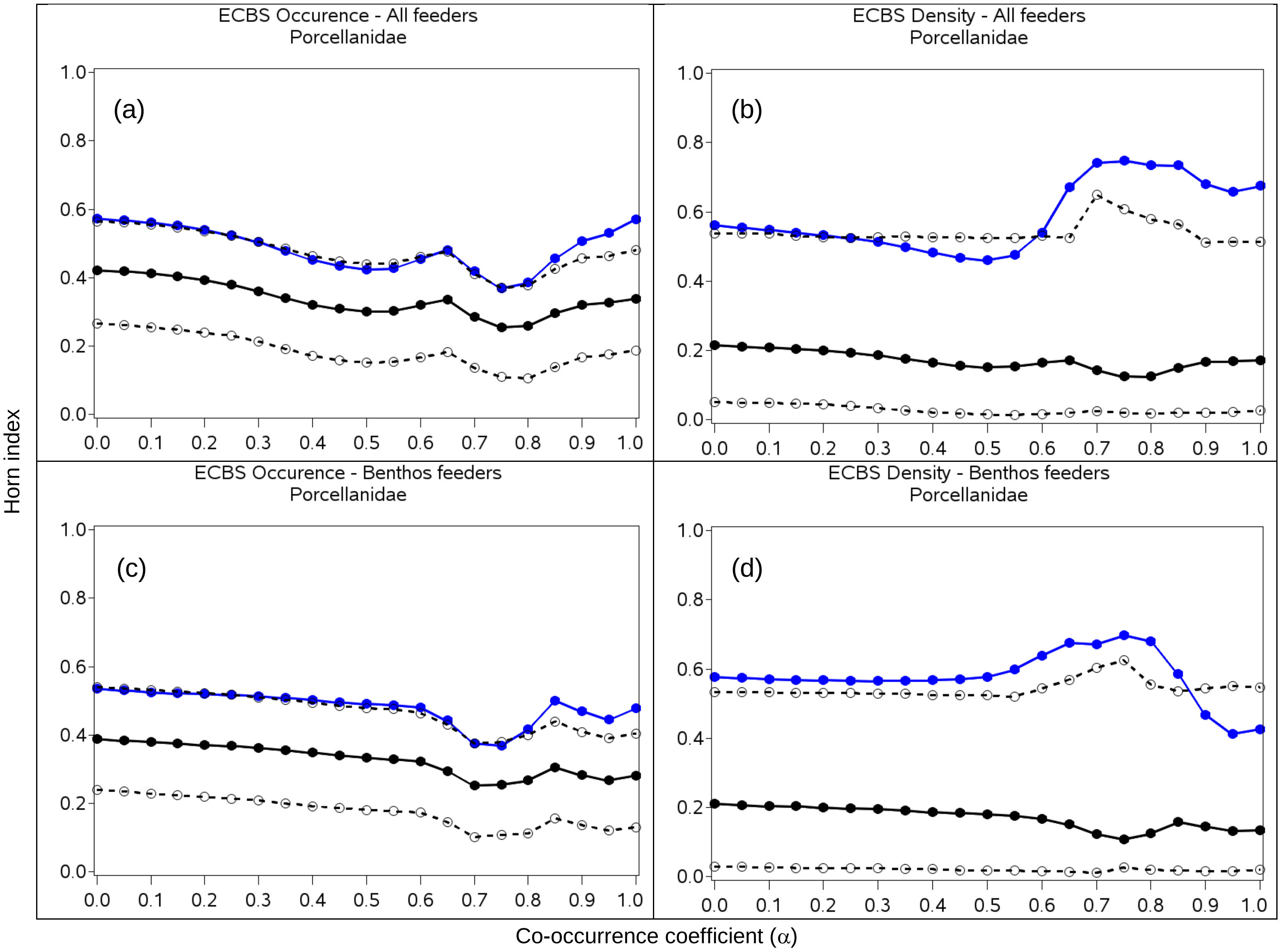

Fig. 6. Maps showing the most strongly overlapping spatial distributions of (a, b) Galatheidae and (d, e) Portunidae, derived from (a, d) Eastern Channel Benthic Survey (ECBS)-based *benthos occurrence dataset*, and from (d, e) Channel Ground Fish Survey (CGFS) DT-based *all feeders dataset*. The corresponding cumulative prey distributions per spatial unit are shown for (c) Galatheidae and (f) Portunidae (black and dotted line: reference; blue line: ECBS-based *benthos occurrence dataset*; red line: CGFS DT-based *all feeders dataset*); each of the 24 spatial units are sorted by decreasing ECBS-based densities (X-axis). Full co-occurrence ($\alpha = 0.00$) is assumed in all figures.

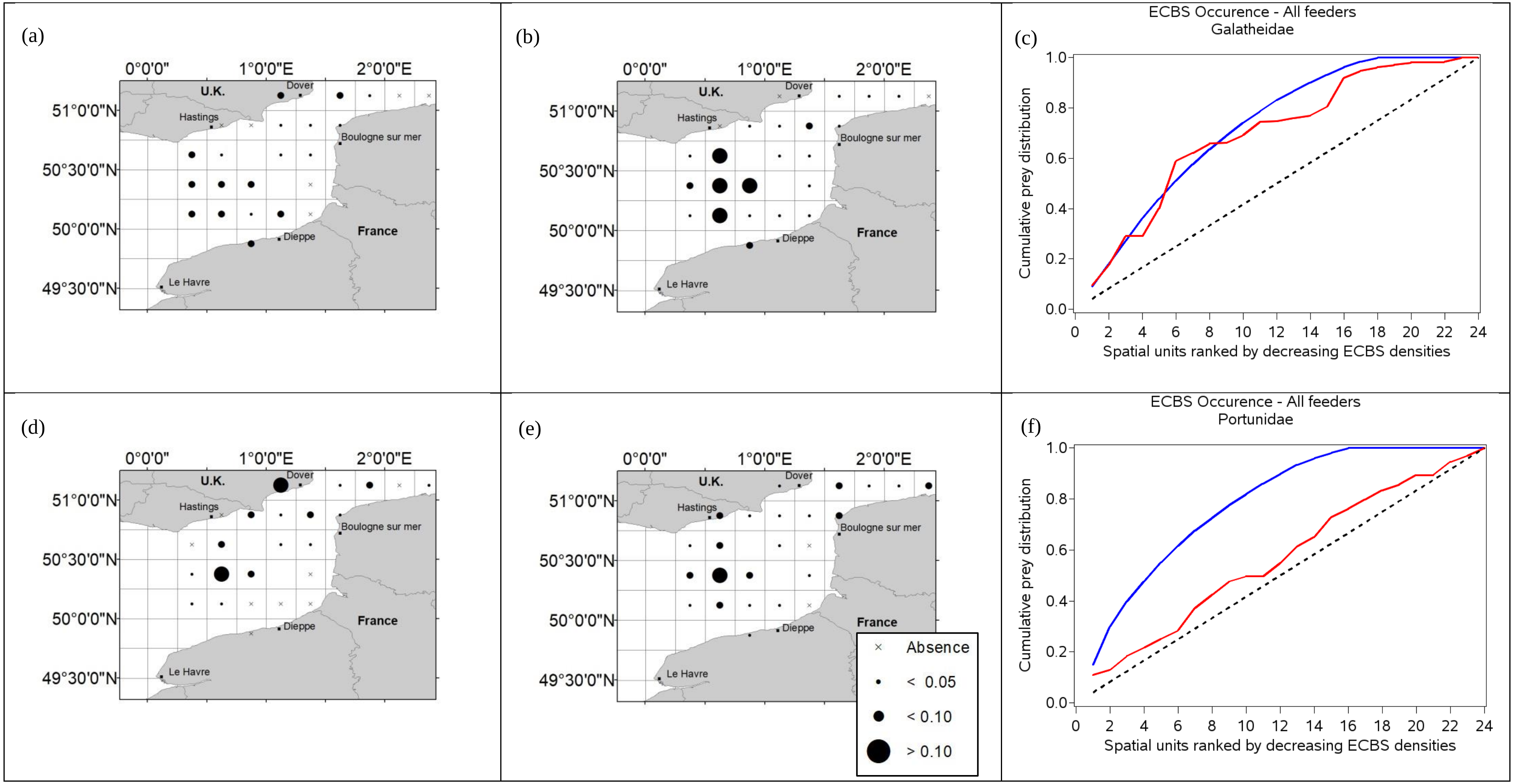

Fig. 7. Maps showing the most strongly overlapping spatial distributions of Porcellanidae, derived from Eastern Channel Benthic Survey (ECBS)-based (a) *benthos occurrence dataset* and from (b, c) Channel Ground Fish Survey (CGFS) DT-based *comprehensive feeders dataset* with α set to (b) 0.0 or (c) 0.7. The corresponding cumulative prey distributions per spatial unit are represented for (d) Porcellanidae (black and dotted line: reference; blue line: ECBS-based *benthos occurrence dataset*; red line: CGFS-based *all feeders dataset* with α = 0.0; green line: CGFS DT-based *all feeders dataset* with α = 0.7); each of the 24 spatial units are sorted by decreasing ECBS-based densities (X-axis).