
Investigating trophic-level variability in Celtic Sea fish predators

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Abstract:

The trophic level (T_L) mean and variance, and the degree of omnivory for five Celtic Sea fish predators were estimated using a database of stomach content records characterized by a high level of taxonomic resolution. The predators occupied a high position in the food web, i.e. 4.75 for Atlantic cod *Gadus morhua*, 4.44 for haddock *Melanogrammus aeglefinus*, 4.88 for European hake *Merluccius merluccius*, 5.00 for megrim *Lepidorhombus whiffiagonis* and 5.27 for whiting *Merlangius merlangus*. The level of taxonomic resolution of the prey did not greatly affect mean T_L predator values; an effect on variance was evident, low resolution masking intra-population variability in T_L . Generalized additive models (GAM) were used to explain the variability of predator T_L caused by environmental variables (International Council for the Exploration of the Sea, ICES, division and season) and predator characteristics (total length, L_T). Significant year, location season and interaction effects were found for some species and with L_T at the scale of ICES subdivision. The species-specific variability of T_L could be due to spatio-temporal variations in prey availability and in predator selectivity following ontogenetic changes. Omnivorous fish T_L was less affected by spatio-temporal variations. In addition, results showed that the omnivory index and T_L variability provide dissimilar information on predator feeding strategy. Combining information on T_L variability and omnivory allowed between within-individual and between-individual components contributing to trophic niche width to be separated and the type of generalization of fish predators to be identified.

Keywords: food web • GAM • indicator • omnivory • predation • trophic level

1. Introduction

The trophic level (T_L) reflects the position of an organism, species, population, or trophic group within the food web as it traces the path lengths for energy in an ecosystem (Lindeman, 1942). T_L plays a major role in theoretical and applied ecology (Post, 2002; Williams & Martinez, 2004) and appears relevant for an ecosystem approach to fisheries management (EAF; Garcia *et al.*, 2003). In particular, T_L constitutes the basis for the measurement of several indicators for evaluating the ecosystem effects of fishing (Pauly *et al.*, 1998, 2000; Gascuel *et al.*, 2005; Stergiou *et al.*, 2007). Among the six trophodynamic indicators selected by Cury *et al.* (2005) in an EAF perspective, three are based on T_L values: primary production required to support catches, mean T_L of the catch and the Fishing-In-Balance index. In addition, the mean T_L of the catch has been proposed as a measure of biodiversity, following the Conference of the Parties to the Convention on Biological Diversity (Pauly & Watson, 2005). All these indicators are generally calculated based on mean T_L values for each species that are either provided by FishBase, or derived from stomach content analyses or applications of Ecopath models (Christensen & Pauly, 1992). Mean T_L values, averaged over time and area, may conceal potentially high T_L variability associated with food web dynamics (e.g. Greenstreet *et al.*, 1997) and ontogenetic changes.

T_L results from the predation process and depends on the combination of different factors that determine prey availability and vulnerability (Sih & Christensen, 2001) including predator morphological and behavioural characteristics (Mérigoux & Ponton, 1998; Karpouzi & Stergiou, 2003). For a given species, diet composition has notably been shown to vary with time (Albert, 1995; Adlerstein & Welleman, 2000), season (du Buit, 1995, 1996; Cabral & Murta, 2002) and predator length through ontogenetic changes (Stergiou & Karpouzi, 2002; Pinnegar *et al.*, 2003). Hence, T_L s are expected to display spatio-temporal variations according to fish age or length. In addition, estimates of T_L s based on stomach content data rely on the T_L values assigned to the prey and the level of taxonomic resolution of the prey. Therefore, it is important to study the relative contribution of different sources of variability of T_L to understand how T_L -based indicators are sensitive to fish feeding behaviours and ecosystem characteristics in addition to fishing.

In the present analysis, the amount and sources of T_L variability is investigated for a selection of representative predator fish species in the Celtic Sea, Atlantic cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.), European hake (*Merluccius merluccius* L.), megrim (*Lepidorhombus whiffiagonis* W.) and whiting (*Merlangius merlangus* L.). The feeding habits of these five predator species greatly differ and they all have been shown to display, to varying extents, ontogenetic and/or spatio-temporal variations in diet (e.g. Hislop *et al.*, 1991; Hop *et al.*, 1992; Jiang & Jorgensen, 1996; Morte *et al.*, 1999; Carpentieri *et al.*, 2005; Guichet 1995). Such changes might be reflected in their T_L and omnivory.

This paper follows the works of Pinnegar *et al.* (2003) and Trenkel *et al.* (2005) who studied the relationships between prey availability and predator diets, and the spatio-temporal structure of predator-prey relationships in the Celtic Sea. The main outcome of the first analysis (Pinnegar *et al.*, 2003) was that the diet of predator species changed as the animals grew larger, but generally did not reflect fish prey availability. This analysis provided evidence of the existence of interannual changes in prey importance and strong prey preferences in certain predators. By contrast, the results of the second study (Trenkel *et al.*, 2005) suggested spatial and seasonal prey-switching behaviour by some fish predators and concluded that the Celtic Sea fish community is globally characterized by opportunistic predators and weak interspecific predator interactions. In the present study, knowledge of feeding relationships in the Celtic Sea was used to address the following objectives: (1) estimate the T_L for the 5 predators and the corresponding T_L variance, (2) investigate predator T_L sensitivity to prey T_L and level of taxonomic resolution, and (3) identify, quantify and order the factors that affect T_L by species to better understand the sensitivity of this indicator to species ecological features and food web dynamics.

2. Material and methods

2.1. Stomach content data

Fish stomachs were collected from 1981 to 1985 aboard nine French commercial trawlers during routine fishing operations in the Celtic Sea (Fig. 1). Samples were briefly investigated and only 'full' stomachs were preserved in seawater containing 10% formalin (du Buit, 1982, 1992, 1995, 1996). Empty stomachs and those with partially regurgitated or unidentifiable contents were excluded. Time period (day, month, year), fishing depth (m), and International Council for the Exploration of the Sea (ICES) subdivision where the fish were caught were recorded. Prey items were identified and sorted into taxonomic groups, to the species level whenever possible. The state of digestion of the prey was not considered in the analysis. For the selected dataset of stomachs, 57 prey taxa were identified at the species level, 32 were identified at the genus level and prey items that could not be identified beyond the sub-order level were pooled into broad taxonomic group levels, *i.e.* polychaete, echinoderm, cnidarian, cephalopod, mollusc (other than cephalopod), crustacean and fish. For each stomach, predator total length (cm), prey number, prey identity and prey weight (g) were recorded.

Because the original sampling scheme was not randomized or random-stratified over space and time, in the present analysis, only fish sampled in years 1981, 1983, 1984, and 1985 and in ICES subdivisions VIIg and VIIIh were considered in order to 'rebalance' the sampling design. This resulted in a total of 3271 stomachs sampled, *i.e.* 829 for Atlantic cod 24-116 cm in length, 403 for haddock 24-83 cm in length, 682 for hake 25-95 cm in length, 749 for megrim 20-63 cm in length and 608 for whiting 20-60 cm in length. Despite 'rebalancing' sample sizes varied from year to year and between subdivisions (Table I).

2.2. Prey trophic levels

Stable isotope methods rely on the consistent enrichment of the stable nitrogen isotope, ^{15}N (3.4 ± 0.3 per mil), between prey and predator (Minagawa & Wada, 1984; Owens, 1987), allowing its use as a measure of an organism's continuous trophic position. Mean T_L values of prey were extracted from a literature review of stable isotopes in the North Sea, Celtic Sea and Bay of Biscay (Jennings *et al.*, 2002a,b; Pinnegar *et al.*, 2002; Le Loc'h, 2004). When the T_L -size relationship was available (Jennings *et al.*, 2002a) T_L s assigned to fish prey were estimated corresponding to the median prey length of fish predators (Pinnegar *et al.*, 2003). For prey identified at a broad taxonomic group level, the mean T_L was calculated as the arithmetic mean of the values obtained from isotopic ratios for species belonging to this group. 'Cnidarians' were assigned the mean T_L ($T_L = 2.5$) value available in FishBase (<http://www.fishbase.org>; Froese & Pauly, 2005) because no information was available for this group based on stable isotope methods.

The impact of the level of taxonomic resolution on estimates of predator T_L was investigated replacing the T_L of each prey by the T_L of their broad taxonomic group level, *i.e.* cephalopod, cnidarian, crustacean, echinoderm, fish, mollusc (other than cephalopod) and polychaete. Sensitivity of predator T_L s to prey T_L s was also analysed based on T_L values extracted from the FishBase database (www.fishbase.org; Froese & Pauly, 2005). Non-parametric Wilcoxon Mann-Whitney tests were performed in both cases to analyse differences between T_L distributions.

2.3. Predator trophic levels and omnivory

The T_L of each individual sampled was calculated as the sum of its prey T_L , weighted by their relative importance in the stomach following Adams *et al.* (1983):

$$T_{Ljl} = 1 + \sum_{i=1}^{n_{jl}} \rho_{ijl} \times \overline{T_{Li}} \quad (1)$$

where ρ_{ijl} represents the relative biomass of prey i in the stomach of individual l of predator species j , *i.e.* the relative weight of food i in the stomach, n_{jl} is the number of prey in the stomach of individual l of predator species j and $\overline{T_{Li}}$ is the mean T_L of prey i .

T_L s estimated for the five predator species of interest were compared on the one hand with values estimated by stable isotope methods in the Celtic Sea and in the North Sea (Pinnegar *et al.*, 2002; Jennings *et al.*, 2002a) and on the other hand with values available in different areas of the world extracted from the FishBase database (<http://www.fishbase.org>; Froese & Pauly, 2005).

Omnivory indices (O_i) of each individual sampled were also computed following Christensen & Pauly (1992):

$$O_{ljl} = \sum_{j=1}^{n_{jl}} \rho_{ijl} \times (T_{Lijl} - T_{Ljl})^2 \quad (2)$$

where T_{Lijl} is the predator T_L computed from equation (1). O_i describes the range of T_L s consumed and weights each prey item by its relative biomass in the stomach. The square root of O_i has been proposed as a preliminary estimate of the standard deviation of T_L (Christensen & Pauly, 1992). Non-parametric Wilcoxon Mann-Whitney tests were performed to analyse differences between O_i distributions.

2.4. Identifying sources of variability in trophic level values

Generalized additive models (GAMs) were used to investigate the variability of T_L over space and time and according to predator length. GAMs are non-parametric generalizations of multiple linear regressions (Hastie & Tibschirani, 1990). In particular, GAM fitting methods do not rely on a rigid parametric shape, expressing the dependence between the response variable and the covariates, but on local smoothers. Individual predator T_L s computed from equation (1) were modeled as a function of year, ICES subdivision, season and predator length. ICES subdivision was used to represent distinct areas assumed to characterize various types of habitat where prey availability changes. Season was modeled as a factor, *i.e.* winter, spring, summer, and autumn, and predator length (in cm) as a continuous variable. Interaction effects were tested when possible. The general form of the model fitted for each predator species j and without interaction was then:

$$T_{Lj} = s_j(\text{length}) + \text{year} + \text{subdivision} + \text{season}$$

where T_L is the trophic level and $s_j()$ represents a smooth function (regression spline) for species j . Model fitting and automatic selection of the degrees of freedom for the regression splines, were performed using the generalized cross-validation method based on minimising the jackknifed squared prediction error in the mgcv package in R (R Development Core Team, 2007) as described in Wood & Augustin (2002). The assumption of Gaussian error distributions was checked through the residuals. Selection of the 'best' model was based upon the Akaike information criterion (AIC). For each species, the AIC and percentage of deviance explained by each factor and covariate kept in the 'best' model were also given. The residuals in each GAM were used as a measure of T_L intra-population variability.

3. Results

3.1. Trophic position in the Celtic sea

The distributions of estimated individual T_L values were rather asymmetric for all predator species (Fig. 2). All five species exhibited a range of T_L s in the size range sampled: 3.81-5.88 for Atlantic cod, 3.50-5.95 for haddock, 4.02-6.08 for hake, 3.88-5.95 for megrim, and 3.99-5.95 for whiting. T_L values estimated in the present study showed that the five species had a high position in the food web, the highest value of mean T_L being 5.27 for whiting (Fig 3). T_L standard deviations were relatively similar for the five species, the values ranging from 0.44 for Atlantic cod to 0.69 for hake (Fig. 3).

Estimated mean T_L for the five predator species were higher than those available from FishBase (Fig. 3). T_L estimates were also higher than values estimated from stable isotope methods in the Celtic Sea except for whiting (Fig. 3). The discrepancy was particularly important for haddock, hake and megrim with differences in T_L values close or higher than 1 T_L , *i.e.* 0.88, 0.73 and 1.09 respectively. Differences were less marked with T_L estimated from stable isotope methods in the North Sea (Fig. 3).

3.2. Sensitivity of trophic level estimates

The level of taxonomic resolution used for prey had impacts on estimates of predator T_L (Fig. 4a). Predator T_L s based on prey groups were significantly lower than T_L s based on a high taxonomic resolution for Atlantic cod ($P < 0.001$), megrim ($P < 0.01$), and whiting ($P < 0.001$) and significantly higher for hake ($P < 0.001$). Although significant, the differences between mean estimates of T_L were small, *i.e.* less than 0.1 for Atlantic cod and hake, 0.12 and 0.35 for megrim and whiting respectively. Estimates of the T_L of haddock were not modified by a decrease in the level of prey taxonomic resolution. By contrast, standard deviations of the T_L were strongly modified and significantly higher for the 5 species when considering a high level of taxonomic resolution.

Values of T_L assigned to the prey strongly affected estimates of predator T_L (Fig. 4b). Predator T_L based on prey T_L derived from FishBase were significantly lower than T_L estimates based on T_L s derived from stable isotope methods ($P < 0.001$). These results show that prey T_L s are important to estimate mean values of predator T_L and that the level of resolution attained during stomach content analysis is essential for analysis of T_L variability.

3.3. Modelling trophic level variability

The covariates explaining T_L varied between species (Table II). The total deviance explained by the 'best' models was high for hake and megrim, 43.3% and 26.1% respectively, while it was 13.1%, 11.3%, and 5.9% for whiting, haddock, and Atlantic cod respectively (Table II). Comparison between the deviance of the 'best' models and the deviance explained by the different covariates or factors individually showed that there were confounded effects, particularly for hake and megrim.

Considering the 'best' model, significant year and season effects were found for all species except Atlantic cod (Table II). This indicated interannual and seasonal variations in T_L due to changes in types or relative proportions of prey consumed. Year and season effects differed between species. For instance, haddock showed estimates of T_L higher in subdivision VIIg in 1983 ($T_L = 4.63$) than in 1981 ($T_L = 4.40$) whereas hake showed an overall negative effect on T_L in 1983 relative to 1981 ($-0.44 T_L$) and the highest T_L for hake was observed in spring 1985 in subdivision VIIh ($T_L = 5.72$). Year-to-year changes in species specific T_L led to variations in the rank of their position occupied within the food web. For instance, megrim was the 'top-predator' in

subdivision VIIg in spring 1983, followed by whiting, Atlantic cod, haddock and hake. As hake's T_L increased from 1983 to 1985 and whiting and haddock's T_L s decreased throughout this period, in spring 1985 hake occupied a higher position than haddock and Atlantic cod, and a similar position as whiting.

Subdivision effects were also found to vary between Celtic sea fish predators. The overall effect of subdivision VIIh was positive for hake (+0.53 T_L) and negative for megrim (-0.34 T_L) relative to their respective GAM intercepts.

A subdivision effect in interaction with year or season was found significant for haddock, hake and megrim. For hake, a positive effect was found in autumn 1981 in subdivision VIIg (+0.14 T_L relative to spring) whereas a negative season effect was found for autumn in subdivision VIIh (-0.22 T_L relative to spring). For megrim, the 1985 effect was found positive (+0.2 T_L) in subdivision VIIh whereas it was negative in subdivision VIIg. Hence, temporal changes in T_L s for the Celtic Sea fish predators were not similar among habitats defined here by the ICES subdivisions.

Length was significant for all species except haddock. T_L increased with body length for Atlantic cod and megrim, and for hake from a 50 cm length (Fig. 5). Maximum changes in T_L predicted by the GAMs for the range of length observed were +0.43, +0.45, +0.80, and -0.21 T_L for Atlantic cod, hake, megrim, and whiting respectively. For whiting, no clear relationship was found, though there might be an indication of a decreasing pattern of T_L with length over the size range 30-60 cm.

3.4. Trophic level variability and omnivory index

Overall GAM results showed that T_L standard deviation reflected on the one hand T_L variations due to differences in area or season, and on the other hand between-individual (intra-population) variations. T_L intra-population variability, derived from GAM residuals, was higher for megrim and hake (0.47 and 0.40 respectively) than for haddock (0.37), and Atlantic cod and whiting that showed a similar value of 0.30. Results on T_L intra-population variability differed from information provided by the omnivory indices. O_i distributions were highly skewed and characterized by a high proportion of 0 values corresponding to predators with only 1 type of prey in their stomach (Fig. 6). Statistical tests showed that O_i distributions were significantly different ($P < 0.001$) in all cases. Atlantic cod and haddock were the most omnivorous fish with mean values of O_i equal to 0.054 and 0.041, respectively. Hake and whiting were less omnivorous than Atlantic cod and haddock with mean O_i s of 0.017 and 0.012 respectively and megrim was the least omnivorous predator with a mean O_i of 0.008.

Megrim's diet could then be characterized by a high between-individual variability of T_L s with most of the individuals preying upon a small range of T_L s at any given time. By contrast, Atlantic cod showed a lower T_L variability but individual fish tended to consume on average a larger range of T_L s. In other terms, it was shown that Atlantic cod dietary niche width was mainly explained by generalist individuals all taking a wide range of food types (Type A generalization) whereas the larger dietary niche width for megrim resulted from individuals specializing on a different but narrow range of food types (Type B generalization). Whiting displayed both a low T_L variability and a low degree of omnivory, suggesting it was the most specialist species among the 5 predators. Haddock and hake appeared in intermediate positions in terms of both T_L variability and omnivory.

4. Discussion

The T_L of five major predator species of the Celtic Sea was estimated based on a database of food stomachs collected in the early 1980s and characterized by a high level of taxonomic

resolution (> 150 prey taxa), and using mean values of prey T_L s derived from a literature review of stable isotope analyses in adjacent seas. Predator T_L s differed from values available in the literature or available from FishBase. The source of T_L values assigned to the prey was found to potentially strongly affect predator T_L , depending on the species of interest. The level of taxonomic resolution of the prey did not greatly affect mean values of predator T_L s but did affect T_L variance, low resolution masking intra-population variability in T_L . In addition and assuming that stable isotopes correctly reflect prey T_L s, results provided evidence for high variability of T_L s in space and time, and with length at the scale of ICES subdivision. The species specific variability of T_L would be due to spatio-temporal variations in prey availability and/or in predator selectivity following ontogenetic changes (see below). Our findings also show that information available from T_L variability and omnivory is complementary and adequate to describe ecological features of fish predators such as generalization type.

4.1. Estimating trophic levels

Although stomach content data are submitted to specific limits such as differential digestion rates and tissue digestibility (Hyslop, 1980), the use of stomach content data allowed us to investigate T_L variability on relatively short time (season) and small spatial scales (ICES subdivision) as they reflect food present in the stomach over the digestion period. Prey digestion state could not be considered in the present analysis because information was generally missing. Gastric evacuation models might improve estimates of consumption rates but were not tested here (Andersen, 2001).

The level of taxonomic resolution reached during stomach content analysis depends on the objectives of the study and can be low for pragmatic (e.g. time restriction for identification) or ecological (e.g. rapid digestion) reasons. Effects of taxonomic resolution on mean T_L values were rather low and differed between predator species. On the contrary, taxonomic resolution strongly affected T_L standard deviations. Observed trophic levels as well as other major food web patterns have been shown to be sensitive to the level of resolution data (Martinez, 1991). In this context, high taxonomic resolution of prey, as in our dataset, is a major prerequisite for analysis of species specific T_L variability.

Mean T_L s assigned to prey in equation (1) also have a strong impact on predator T_L s and are therefore of major concern for ecosystem analyses based on T_L -based indicators. It was assumed here that isotope values correctly characterise the T_L of the prey animals although some studies have shown that they may vary with size due to ontogenetic changes (Hentschel, 1998). The use of mean values for prey T_L constitutes the classic approach to estimate predator T_L following equation (1) and the standard deviation of prey T_L s were generally low in the samples of Pinnegar *et al.* (2002), Jennings *et al.* (2002b) and Le Loc'h (2004). Prey T_L s used were thus considered as the best current information available to analyse the variability of predator T_L s. Using prey T_L s derived from stable isotopes of nitrogen allowed us to avoid the use of default values for prey T_L s currently used in FishBase except for cnidarians and allowed us to assign mean T_L values for small invertebrate prey groups for which diets are generally poorly known. Application of stable isotope methods to estimate cnidarians T_L in the European seas would allow better quantifying their T_L for future analyses. In addition, the use of mean prey T_L s provided by isotope methods seems consistent for the estimation of predator T_L s because they integrate prey diet over a period ranging from a few months to one year, depending on the turn-over rate of the tissues (O'Reilly *et al.*, 2002). Recent work has however suggested that the assumption of average enrichment of 3.4 per mil, may be problematic as isotopic fractionation can be impacted by feeding rate, nitrogen content of the food, excretion rate and assimilation efficiency (e.g. Olive *et al.*, 2003). Such validation has however not been completed in a complex open sea food web and Post (2002) has shown using a comparative cross-system analysis that the mean fractionation of $\delta^{15}\text{N}$ is remarkably constant among trophic levels in many species. On the basis of the currently 'best' values of prey T_L available, species specific T_L estimates relevant at the scale of the Celtic Sea were thus provided.

Predator T_L s estimated in this study were generally higher than estimates obtained by Pinnegar *et al.* (2002) using stable isotopes. The differences between our estimates and T_L s derived from $\delta^{15}N$ data are difficult to interpret regarding the assumptions made in both methods. Among other causes, this could be inherent to the nominal 'baseline' organisms with known T_L used to estimate prey T_L s in stable isotope analyses. If the 'baseline' is wrong then all values will be shifted upwards or downwards incorrectly. The low sample size used by Pinnegar *et al.* (2002), whose study mainly focused on large fishes, could also be responsible for the underestimation observed in predator T_L estimates.

T_L s estimated in the present analysis were higher than FishBase values. These differences can result both from the T_L s assigned to the prey and to the predator size-range sampled. Prey T_L s used were based on a review of stable isotope methods that showed that default values available for species groups from FishBase (bivalves, cephalopods, crustaceans, echinoderms and polychaetes) were always underestimated.

4.2. Factors influencing trophic level variability

T_L values were found to vary with respect to different variables according to the predator species considered. Deviance explained by GAMs was the lowest for Atlantic cod and haddock that displayed the most omnivorous feeding strategy. This could suggest that spatio-temporal changes in prey abundance and composition in the ecosystem might affect omnivorous species less than more specialist predators.

ICES subdivision was used here to characterize distinct habitats described by differences in prey availability and/or composition. It was shown that T_L could significantly vary at the scale of ICES subdivision for haddock, hake, and megrim. Atlantic cod did not show significant change in T_L between ICES subdivisions although they are generalist predators that have been shown to display variations in diet according to area (du Buit, 1995; Hanson & Chouinard, 2002; Link & Garrison, 2002). The type A generalization (Van Valen, 1965) observed for Atlantic cod could explain that spatial variations in diet composition were not reflected in T_L as Atlantic cod consumed a wide diversity of prey in each area of the Celtic Sea. No significant spatial effect on T_L was found for whiting whereas they were found to show geographical differences in diet composition in the North Sea and the Sea of Marmara (Hislop *et al.*, 1991; Artüz, 2005). In the Celtic Sea, whiting mainly consumed fish prey such as sprat (*Sprattus sprattus*), *Trisopterus* spp., and blue whiting (*Micromesistius poutassou*) that are distributed all over the area. This could explain the absence of variations in T_L between ICES subdivisions. In operational terms for an EAF, showing significant spatial variations in T_L for particular species emphasizes the need to consider ecosystem specific predator T_L . Considering spatialized T_L s would seem of major importance for specialist predators with prey showing a limited geographic distribution.

Hake have been shown to display large seasonal diet variations in the Bay of Biscay (Guichet, 1995) but not in the Cantabrian Sea (Velasco & Olaso, 1998). Major prey of hake, *i.e.* blue whiting (*Micromesistius poutassou*), mackerel (*Scomber scombrus*) and horse mackerel (*Trachurus trachurus*) were found to be consumed in accordance with their higher densities in the Celtic Sea (Pinnegar *et al.*, 2003; Trenkel *et al.*, 2005). Megrim has also been shown to consume more blue-whiting when this prey was at higher abundance in the environment (Pinnegar *et al.*, 2003; Trenkel *et al.*, 2005). Density related prey selection seems therefore to explain seasonal changes in T_L for hake and megrim. For hake, the interaction effect between season and subdivision showed that seasonal changes in T_L could vary according to area. The diet of whiting has also been shown to display seasonal variations, with some prey such as sandeel (*Ammodytes* spp.) being more prominent in whiting diets during the summer, which coincided with their peak abundance (Greenstreet *et al.*, 1998).

The absence of a seasonal effect for haddock was not expected as different studies have evidenced considerable seasonal variation in their diet (Jiang & Jorgensen, 1996, Greenstreet *et al.*, 1998; Adlerstein *et al.*, 2002). These variations might not be reflected in terms of T_L for

haddock as they are omnivorous fish and their diet is mostly composed of echinoderms, molluscs and polychaetes that were assigned similar T_L values comprised between 3.0 and 3.4. This could indicate that although there are marked changes in the types of invertebrate prey targeted by haddock, these fishes may actually select prey with similar T_L s (Deudero *et al.*, 2004). Finally, the absence of seasonal effect for Atlantic cod could again be explained by the wide diversity of prey they consumed in the Celtic Sea.

The increase in T_L for Atlantic cod is mainly explained by the increasing proportion of fish in their diet with age, although crustaceans always remain a major component in the food, even for older specimens (du Buit, 1995; Pinnegar *et al.*, 2003). Hake are opportunistic consumers mostly piscivorous that do not seem to have a selective predatory behaviour (du Buit, 1996). Nevertheless, larger fish (> 50 cm) tend to target horse-mackerel (*Trachurus* spp.; $T_L = 4.95$) and pilchard (*Sardina pilchardus*; $T_L = 3.59$) whereas small predators exploit blue whiting ($T_L = 3.14$), *Argentina* spp. ($T_L = 3.44$) and *Trisopterus* spp. ($T_L = 4.52$) (Pinnegar *et al.*, 2003; Mahé *et al.*, 2007). This might be the reason for the increasing relationship between T_L and size observed for hake larger than 50 cm. Megrim was also found to show increasing T_L with length with a plateau from 50 cm that is related to the increasing proportion of fish in their diet with length.

Changes in prey targeted with size is a well known phenomenon for marine fish predators and is mostly associated with increase in mouth size and improved swimming performance (Karpouzi & Stergiou, 2003; Scharf *et al.*, 2000). For hake and Atlantic cod, the fact that large predators continued to select small benthic prey of lower T_L throughout their lives explained why the size- T_L relationships were not as strong as shown in the North Sea (Jennings *et al.*, 2002a). In this context, the weak interactions inherent to the large opportunism characterizing the Celtic Sea fish community (Trenkel *et al.*, 2005) led here to a smaller variation in T_L with length compared to the North Sea fish community.

Regarding haddock, it has been reported elsewhere that the proportion of fish in their diet increased as their size increased (Greenstreet *et al.*, 1998). The absence of significant effect on T_L is due to the similar range of fish prey T_L consumed with increasing length of haddock. Variations in T_L with length for whiting differ from the increasing T_L -size relationship observed by Jennings *et al.* (2002a) in the North Sea. The increase in T_L from 20 cm to 30 cm whiting seems mainly due in our analysis to the switch from sprats ($T_L = 4.28$) to *Trisopterus* spp. ($T_L = 4.52$) in their diet as they grew. Such a switch has also been observed for whiting in the Moray Firth, NE Scotland, and could be linked to a change from pelagic to demersal habits as they grow older (Greenstreet *et al.*, 1998). The progressive increase of blue whiting ($T_L = 3.14$) in the diet of whiting with length could explain the decreasing trend in T_L from 30 cm (Fig.5).

4.3. Trophic level variability and omnivory

Our results show that mean values of T_L mask a high intra-population T_L variability that can differ between species. In addition, O_i appears to be a bad proxy for T_L variability therefore its square root should not be a good estimate of the standard error of T_L as proposed by Christensen and Pauly (1992). O_i s however provide information regarding the range of T_L s targeted by individual predators and seem very useful to estimate the trophic niche width of a population. In complement with T_L variability derived from GAM residuals, O_i s were used to identify generalization type (Van Valen, 1965) and separate between within-individual and between-individual components contributing to niche width. The assessment of feeding strategy and measure of individual-level niche variation is a major issue both in theoretical and applied ecology (Amundsen *et al.*, 1996; Bolnick *et al.*, 2003; Bearhop *et al.*, 2004) and combining information on T_L variability and omnivory seems a promising approach to address such questions.

Quantifying T_L variability is also useful for estimating ecosystem indicators and improving trophodynamic models. For instance, the weighted smoothing technique adopted to spread biomass or catches of a species along a range of fractional T_L in trophic spectra assumes constant and symmetrical distribution of T_L among species (Gascuel *et al.*, 2005). Here our

results suggest that the distribution of individual T_L is neither symmetric nor constant between species and that the range of 0.7 T_L used by Gascuel *et al.* (2005) underestimates T_L variability observed for Celtic Sea fish predators, the 95% reference range being comprised between 1.6 for Atlantic cod and 2.0 for haddock. In the same way, application of trophodynamic models based on T_L to real case-studies (Chassot *et al.*, 2005; Gascuel, 2005) requires information on species T_L distribution to spread the biomass among trophic groups.

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Table I. Spatial and temporal coverage of the stomach data analysed

Year	Division	<i>Gadus</i>	<i>Melanogrammus</i>	<i>Merluccius</i>	<i>Lepidorhombus</i>	<i>Merlangius</i>
		<i>morhua</i>	<i>aeglefinus</i>	<i>merluccius</i>	<i>whiffiagonis</i>	<i>merlangus</i>
1981	VIIg	29	14	52	13	31
1983	VIIh	2	53	165	164	60
1984	VIIg	640	224	-	69	399
	VIIh	67	66	166	118	52
1985	VIIg	91	41	221	252	66
	VIIh	-	5	83	133	-

Table II. 'Best' models (i.e. smallest Akaike information criterion; AIC) for explaining T_L of predator species in the Celtic Sea. Explanatory variables, deviance explained, and AIC value for each species 'best' GAM model are given. Significance level is indicated by asterixes: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Degrees of freedom (df), deviance explained, and AIC are also given for GAM models with each significant variable of the 'best' model considered individually

Species	Variables	df	Significance	Deviance	AIC
Cod	$T_L = s(\text{length})$			5.9%	828.6
	$s(\text{length})$	4.0	***	5.9%	828.6
Haddock	$T_L = \text{year} \times \text{subdivision}$			11.3%	576.7
	year	3	***	9.9%	579.2
	subdivision	1	ns	0.8%	613.9
	year*subdivision	5	***	11.3%	576.7
Hake	$T_L = s(\text{length}) + \text{year} + \text{season} \times \text{subdivision}$			42.3%	1065.7
	$s(\text{length})$	6.0	***	16.6%	1312.7
	year	3	***	28.4%	1202.4
	season	1	***	1.8%	1413.8
	subdivision	1	***	21.7%	1259.8
	season*subdivision	3	***	27.2%	1213.8
Megrim	$T_L = s(\text{length}) + \text{year} \times \text{subdivision} + \text{season}$			26.1%	1246.2
	$s(\text{length})$	8.2	***	7.7%	1409.5
	year	3	***	4.0%	1428.4
	subdivision	1	***	2.7%	1434.8
	season	2	***	3.9%	1427.6
Whiting	$T_L = s(\text{length}) + \text{year} + \text{season}$			13.1%	728.3
	$s(\text{length})$	5.6	*	2.8%	785.7
	year	3	***	8.0%	746.6
	season	3	***	4.4%	770.4

Figure captions

Figure 1. Location of the ICES subdivisions (VIIIf,g,h,j) of the Celtic Sea

Figure 2. Density histograms for all individual trophic levels (T_L) analysed of the Celtic Sea fish predators

Figure 3. Comparison of trophic level for the five species of interest as estimated in the present study (■), derived from stable isotopes of nitrogen in the celtic Sea (□) and the North Sea (▨), and extracted from the FishBase database (▣). Cod = Atlantic cod; Had = Haddock; Hke = Hake; Meg = Megrim; Whg = Whiting. Vertical lines indicate standard deviation when available

Figure 4. Comparison of trophic levels (mean \pm standard deviation) estimated for the Celtic Sea fish predators: (a) Different levels of taxonomic resolution for the prey: high resolution in abscissa and low resolution (broad taxonomic group) in ordinate; (b) Different sources of prey T_L s: prey T_L s derived from stable isotopes in abscissa and extracted from the FishBase database in ordinate. Cod = Atlantic cod; Had = Haddock; Hke = Hake; Meg = Megrim; Whg = Whiting

Figure 5. Trophic level (T_L) as a function of length (generalized additive model GAM, gaussian family, identity link function). No significant effect of length on the T_L of haddock was detected. Whiskers on the abscissa axis indicate data presence

Figure 6. Boxplots for all individual omnivory indices (O_I) analysed of the Celtic Sea fish predators

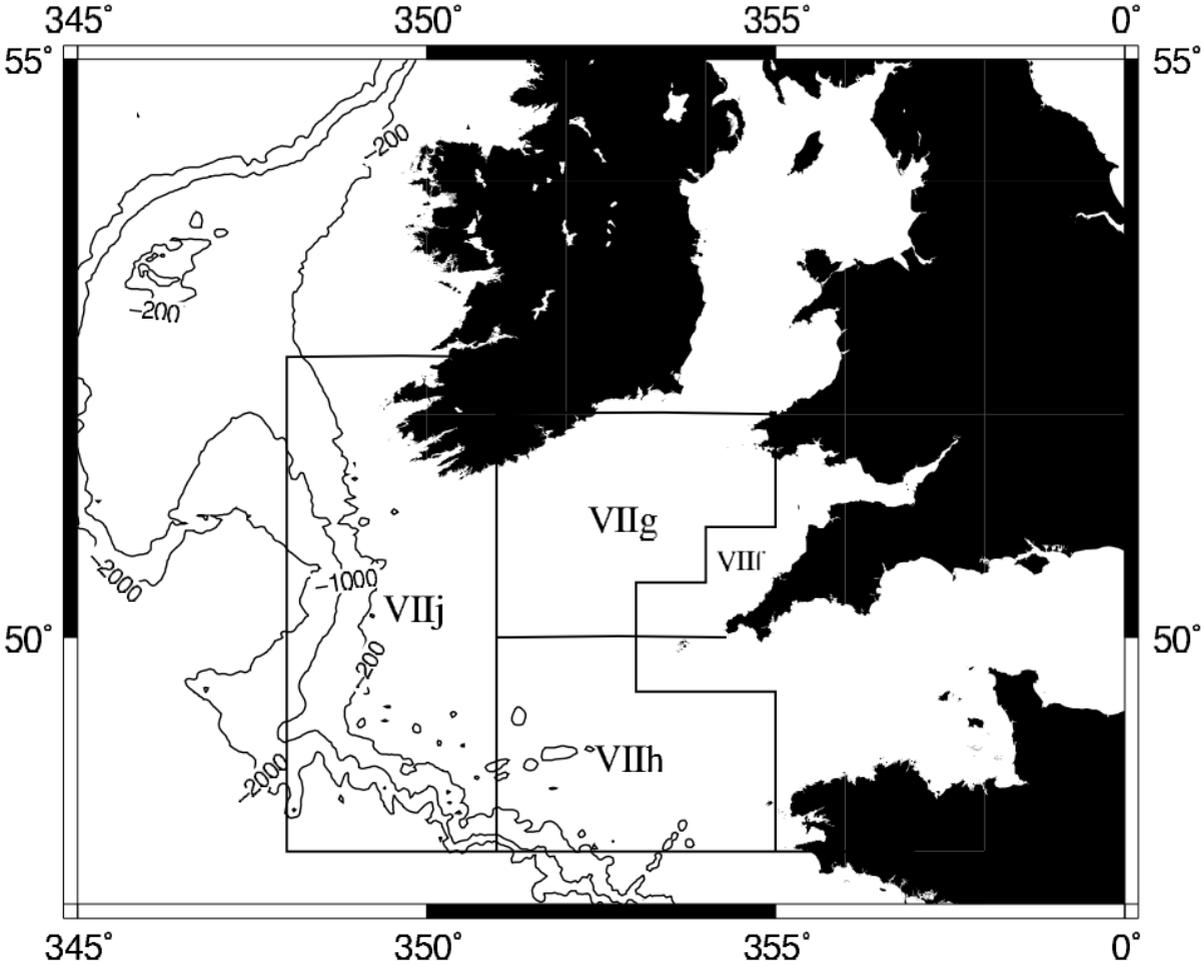
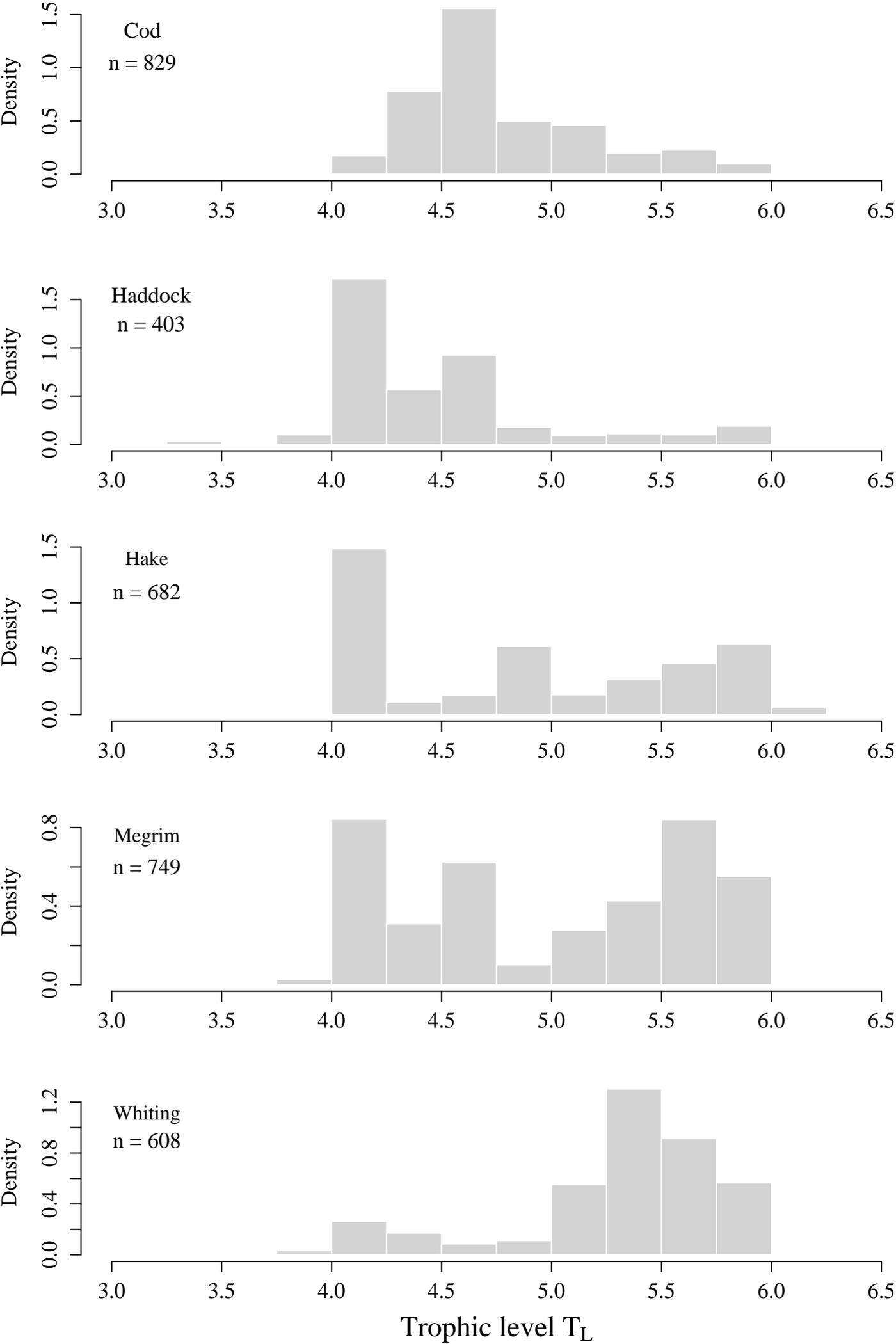


Figure 1:



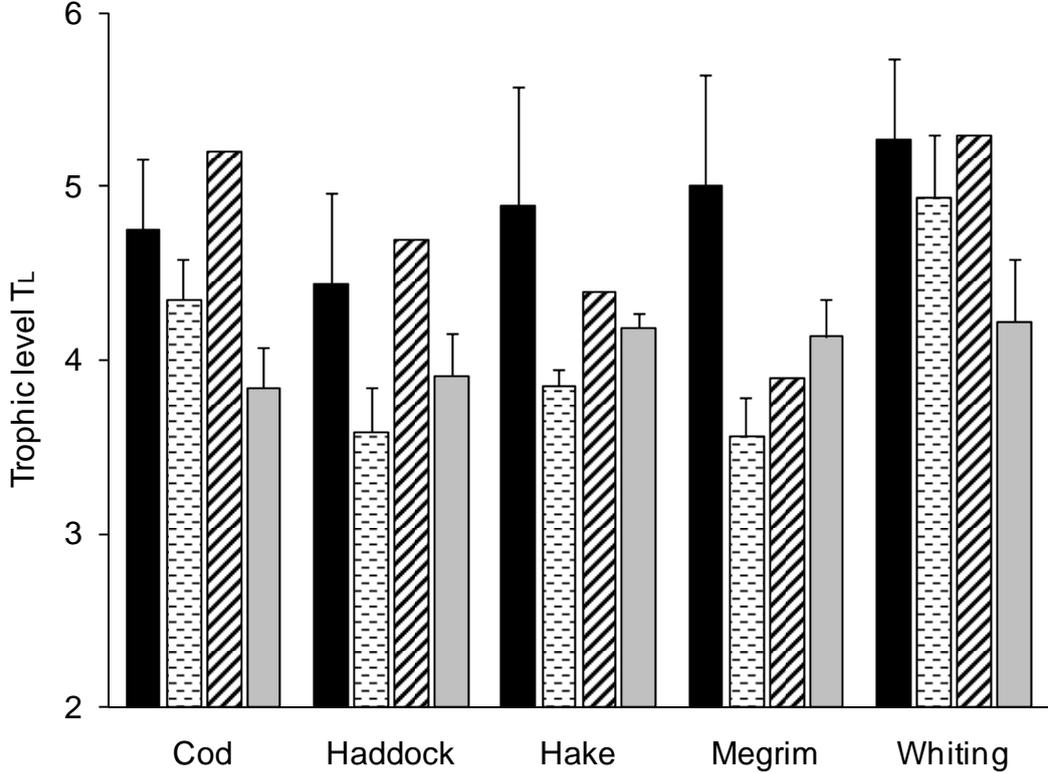


Figure 3

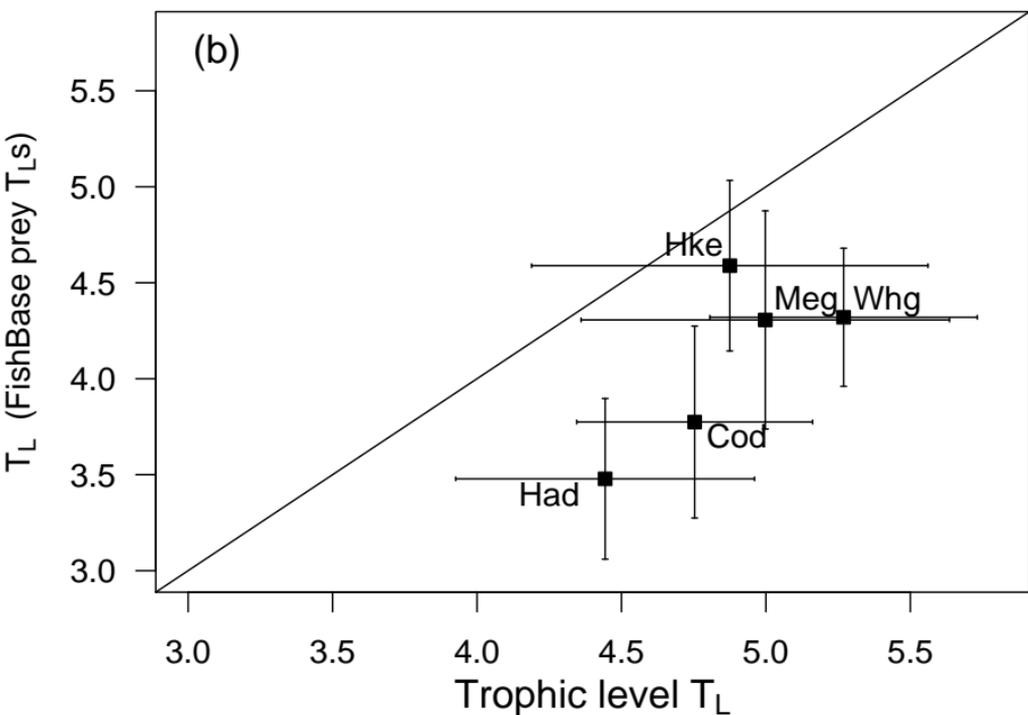
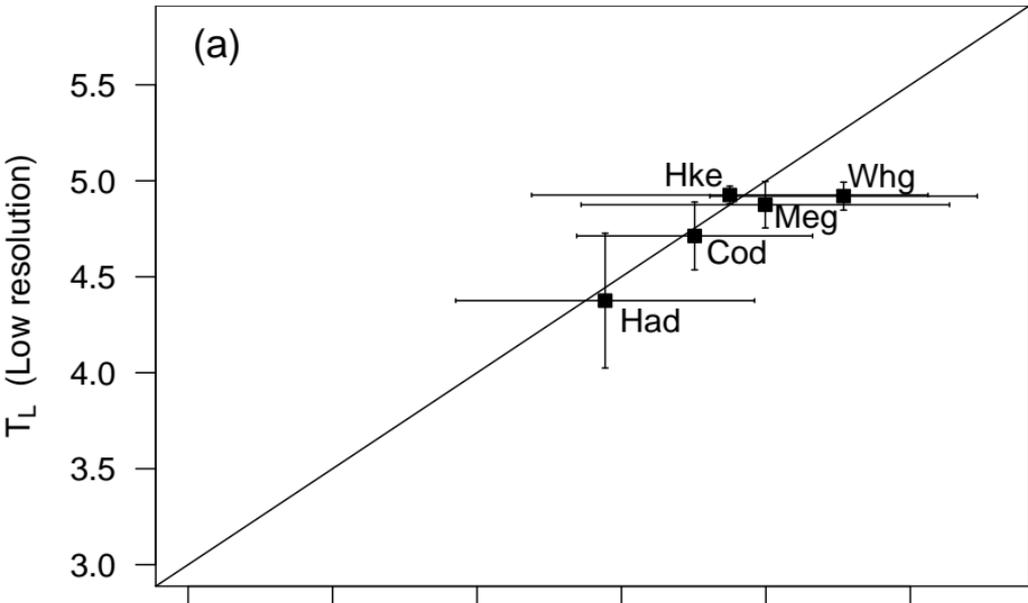


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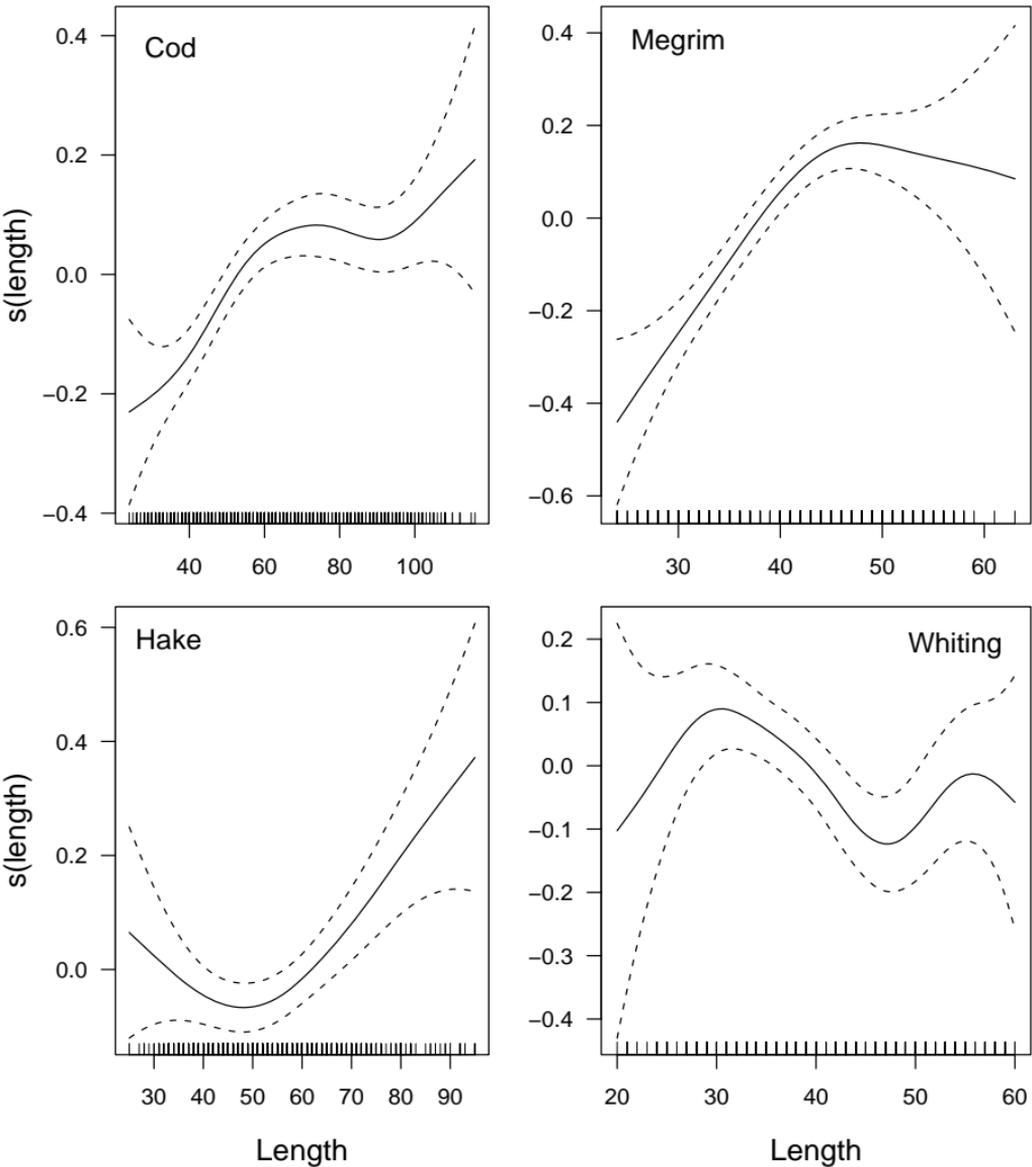


Figure 5:

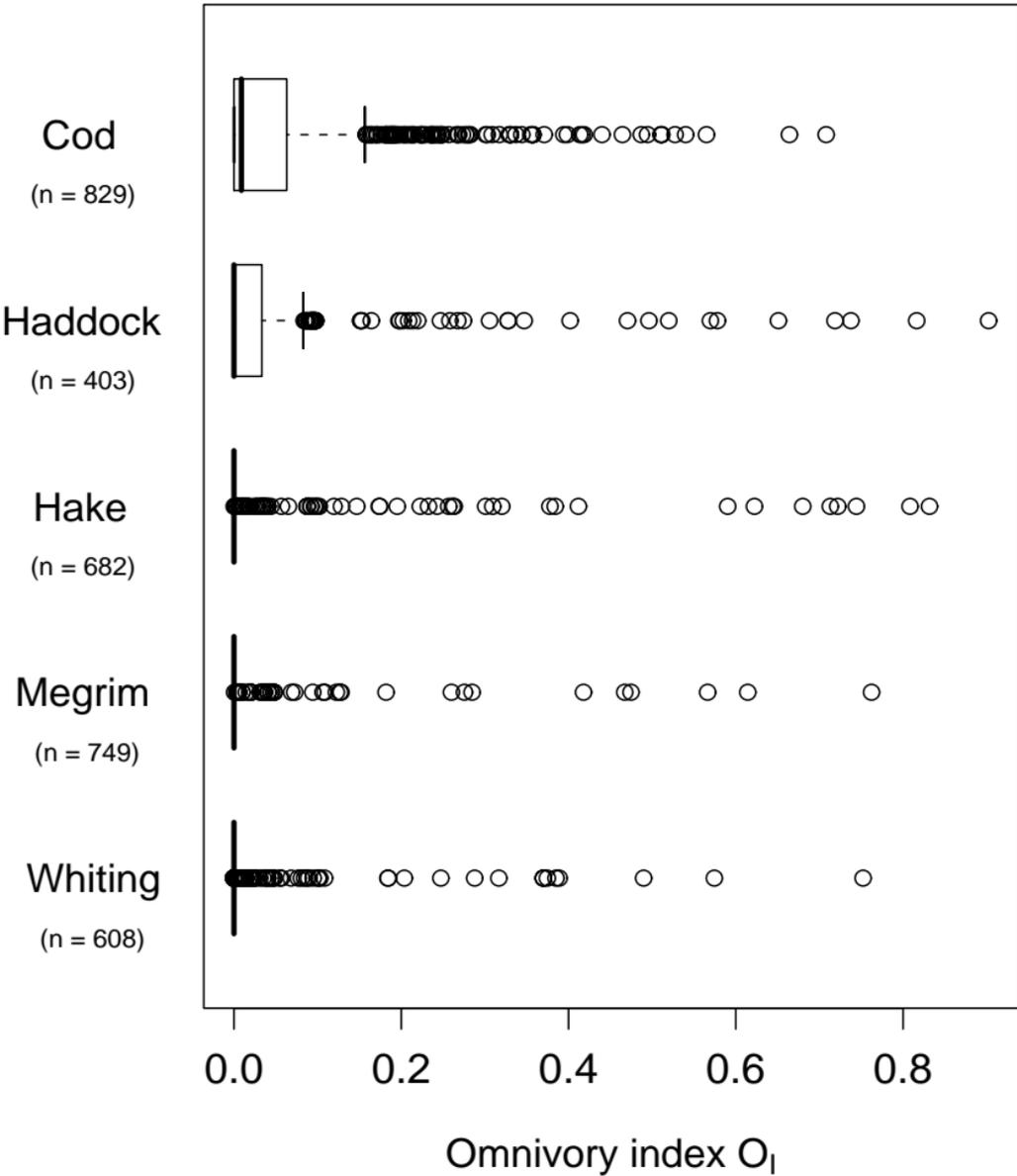


Figure 6: