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4 **Investigating trophic level variability**  
5 **in Celtic Sea fish predators**  
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16 The trophic level (T<sub>L</sub>) mean and variance, and the degree of omnivory for five  
17 Celtic Sea fish predators were estimated using a database of stomach content  
18 records characterized by a high level of taxonomic resolution. The predators  
19 occupied a high position in the food web, *i.e.* 4.75 for Atlantic cod *Gadus*

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1 *morhua*, 4.44 for haddock *Melanogrammus aeglefinus*, 4.88 for European hake  
2 *Merluccius merluccius*, 5.00 for megrim *Lepidorhombus whiffiagonis* and 5.27 for  
3 whiting (*Merlangius merlangus*). The level of taxonomic resolution of the prey  
4 did not greatly affect mean  $T_L$  predator values; an effect on variance was evident,  
5 low resolution masking intra-population variability in  $T_L$ . Generalized additive  
6 models were used to explain the variability of predator  $T_L$  caused by  
7 environmental variables (ICES subdivision, season) and predator characteristics  
8 (length). Significant year, location, season, and interaction effects were found for  
9 some species and with length at the scale of ICES subdivision. The species  
10 specific variability of  $T_L$  could be due to spatio-temporal variations in prey  
11 availability and/or in predator selectivity following ontogenetic changes.  
12 Omnivorous fish  $T_L$  was less affected by spatio-temporal variations. In addition,  
13 results showed that the omnivory index and  $T_L$  variability provide dissimilar  
14 information on predator feeding strategy. Combining information on  $T_L$  variability  
15 and omnivory allowed us to separate between within-individual and between-  
16 individual components contributing to trophic niche width and to identify the type  
17 of generalization of fish predators.

18  
19 Running headline: Trophic level variability

20 Key words: food web, GAM, indicator, omnivory, predation, trophic level

## 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.

11  
12 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.

21  
22 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.

## MATERIALS AND METHODS

### 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 VIIh 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).

#### PREY TROPHIC LEVELS

Stable isotope methods rely on the consistent enrichment of the stable nitrogen isotope,  $^{15}\text{N}$  ( $3.4 \pm 0.3$  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)  $T_{LS}$  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  $T_{LS}$  to prey  $T_{LS}$  was also analysed based on  $T_L$  values extracted from the FishBase database ([www.fishbase.org](http://www.fishbase.org); Froese & Pauly, 2005). Non-parametric Wilcoxon Mann-Whitney tests were performed in both cases to analyse differences between  $T_L$  distributions.

#### 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):

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

where  $\rho_{ijl}$  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  $\overline{T_{L_i}}$  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):

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

where  $T_{L_{jl}}$  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.

## 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  $T_{LS}$  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

1 in the 'best' model were also given. The residuals in each GAM were used as a measure of  
2  $T_L$  intra-population variability.

## 4 RESULTS

### 6 TROPHIC POSITION IN THE CELTIC SEA

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

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

### 23 SENSITIVITY OF TROPHIC LEVEL ESTIMATES

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

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

#### 18 MODELLING TROPHIC LEVEL VARIABILITY

20 The covariates explaining  $T_L$  varied between species (Table II). The total deviance  
21 explained by the 'best' models was high for hake and megrim, 43.3% and 26.1%  
22 respectively, while it was 13.1%, 11.3%, and 5.9% for whiting, haddock, and Atlantic  
23 cod respectively (Table II). Comparison between the deviance of the 'best' models and the

1 deviance explained by the different covariates or factors individually showed that there  
2 were confounded effects, particularly for hake and megrim.

3  
4 Considering the 'best' model, significant year and season effects were found for all  
5 species except Atlantic cod (Table II). This indicated interannual and seasonal variations  
6 in  $T_L$  due to changes in types or relative proportions of prey consumed. Year and season  
7 effects differed between species. For instance, haddock showed estimates of  $T_L$  higher in  
8 subdivision VIIg in 1983 ( $T_L = 4.63$ ) than in 1981 ( $T_L = 4.40$ ) whereas hake showed an  
9 overall negative effect on  $T_L$  in 1983 relative to 1981 ( $-0.44 T_L$ ) and the highest  $T_L$  for  
10 hake was observed in spring 1985 in subdivision VIIIh ( $T_L = 5.72$ ). Year-to-year changes  
11 in species specific  $T_L$  led to variations in the rank of their position occupied within the  
12 food web. For instance, megrim was the 'top-predator' in subdivision VIIg in spring 1983,  
13 followed by whiting, Atlantic cod, haddock and hake. As hake's  $T_L$  increased from 1983  
14 to 1985 and whiting and haddock's  $T_L$ s decreased throughout this period, in spring 1985  
15 hake occupied a higher position than haddock and Atlantic cod, and a similar position as  
16 whiting.

17  
18 Subdivision effects were also found to vary between Celtic sea fish predators. The  
19 overall effect of subdivision VIIIh was positive for hake ( $+0.53 T_L$ ) and negative for  
20 megrim ( $-0.34 T_L$ ) relative to their respective GAM intercepts.

21  
22 A subdivision effect in interaction with year or season was found significant for  
23 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.

#### 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.

1 Atlantic cod and haddock were the most omnivorous fish with mean values of  $O_I$  equal to  
2 0.054 and 0.041, respectively. Hake and whiting were less omnivorous than Atlantic cod  
3 and haddock with mean  $O_I$ s of 0.017 and 0.012 respectively and megrim was the least  
4 omnivorous predator with a mean  $O_I$  of 0.008.

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

## 17 18 **DISCUSSION**

19  
20 The  $T_L$  of five major predator species of the Celtic Sea was estimated based on a  
21 database of food stomachs collected in the early 1980s and characterized by a high level  
22 of taxonomic resolution ( $> 150$  prey taxa), and using mean values of prey  $T_L$ s derived  
23 from a literature review of stable isotope analyses in adjacent seas. Predator  $T_L$ s differed

1 from values available in the literature or available from FishBase. The source of  $T_L$   
2 values assigned to the prey was found to potentially strongly affect predator  $T_L$ ,  
3 depending on the species of interest. The level of taxonomic resolution of the prey did not  
4 greatly affect mean values of predator  $T_{LS}$  but did affect  $T_L$  variance, low resolution  
5 masking intra-population variability in  $T_L$ . In addition and assuming that stable isotopes  
6 correctly reflect prey  $T_{LS}$ , results provided evidence for high variability of  $T_{LS}$  in space  
7 and time, and with length at the scale of ICES subdivision. The species specific  
8 variability of  $T_L$  would be due to spatio-temporal variations in prey availability and/or in  
9 predator selectivity following ontogenetic changes (see below). Our findings also show  
10 that information available from  $T_L$  variability and omnivory is complementary and  
11 adequate to describe ecological features of fish predators such as generalization type.

## 12 13 ESTIMATING TROPHIC LEVELS

14  
15 Although stomach content data are submitted to specific limits such as differential  
16 digestion rates and tissue digestibility (Hyslop, 1980), the use of stomach content data  
17 allowed us to investigate  $T_L$  variability on relatively short time (season) and small spatial  
18 scales (ICES subdivision) as they reflect food present in the stomach over the digestion  
19 period. Prey digestion state could not be considered in the present analysis because  
20 information was generally missing. Gastric evacuation models might improve estimates  
21 of consumption rates but were not tested here (Andersen, 2001).

22  
23 The level of taxonomic resolution reached during stomach content analysis depends on  
24 the objectives of the study and can be low for pragmatic (*e.g.* time restriction for

1 identification) or ecological (*e.g.* rapid digestion) reasons. Effects of taxonomic  
2 resolution on mean  $T_L$  values were rather low and differed between predator species. On  
3 the contrary, taxonomic resolution strongly affected  $T_L$  standard deviations. Observed  
4 trophic levels as well as other major food web patterns have been shown to be sensitive to  
5 the level of resolution data (Martinez, 1991). In this context, high taxonomic resolution of  
6 prey, as in our dataset, is a major prerequisite for analysis of species specific  $T_L$   
7 variability.

8  
9 Mean  $T_{LS}$  assigned to prey in equation (1) also have a strong impact on predator  $T_{LS}$   
10 and are therefore of major concern for ecosystem analyses based on  $T_L$ -based indicators.  
11 It was assumed here that isotope values correctly characterise the  $T_L$  of the prey animals  
12 although some studies have shown that they may vary with size due to ontogenetic  
13 changes (Hentschel, 1998). The use of mean values for prey  $T_L$  constitutes the classic  
14 approach to estimate predator  $T_L$  following equation (1) and the standard deviation of  
15 prey  $T_{LS}$  were generally low in the samples of Pinnegar *et al.* (2002), Jennings *et al.*  
16 (2002b) and Le Loc'h (2004). Prey  $T_{LS}$  used were thus considered as the best current  
17 information available to analyse the variability of predator  $T_{LS}$ . Using prey  $T_{LS}$  derived  
18 from stable isotopes of nitrogen allowed us to avoid the use of default values for prey  $T_{LS}$   
19 currently used in FishBase except for cnidarians and allowed us to assign mean  $T_L$  values  
20 for small invertebrate prey groups for which diets are generally poorly known.  
21 Application of stable isotope methods to estimate cnidarians  $T_L$  in the European seas  
22 would allow better quantifying their  $T_L$  for future analyses. In addition, the use of mean  
23 prey  $T_{LS}$  provided by isotope methods seems consistent for the estimation of predator  $T_{LS}$



1 because they integrate prey diet over a period ranging from a few months to one year,  
2 depending on the turn-over rate of the tissues (O'Reilly *et al.*, 2002). Recent work has  
3 however suggested that the assumption of average enrichment of 3.4 per mil, may be  
4 problematic as isotopic fractionation can be impacted by feeding rate, nitrogen content of  
5 the food, excretion rate and assimilation efficiency (*e.g.* Olive *et al.*, 2003). Such  
6 validation has however not been completed in a complex open sea food web and Post  
7 (2002) has shown using a comparative cross-system analysis that the mean fractionation  
8 of  $\delta^{15}\text{N}$  is remarkably constant among trophic levels in many species. On the basis of the  
9 currently 'best' values of prey  $T_L$  available, species specific  $T_L$  estimates relevant at the  
10 scale of the Celtic Sea were thus provided.

11  
12 Predator  $T_L$ s estimated in this study were generally higher than estimates obtained by  
13 Pinnegar *et al.* (2002) using stable isotopes. The differences between our estimates and  
14  $T_L$ s derived from  $\delta^{15}\text{N}$  data are difficult to interpret regarding the assumptions made in  
15 both methods. Among other causes, this could be inherent to the nominal 'baseline'  
16 organisms with known  $T_L$  used to estimate prey  $T_L$ s in stable isotope analyses. If the  
17 'baseline' is wrong then all values will be shifted upwards or downwards incorrectly. The  
18 low sample size used by Pinnegar *et al.* (2002), whose study mainly focused on large  
19 fishes, could also be responsible for the underestimation observed in predator  $T_L$   
20 estimates.

21  
22  $T_L$ s estimated in the present analysis were higher than FishBase values. These  
23 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.

#### 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*),

1 *Trisopterus* spp., and blue whiting (*Micromesistius poutassou*) that are distributed all  
2 over the area. This could explain the absence of variations in  $T_L$  between ICES  
3 subdivisions. In operational terms for an EAF, showing significant spatial variations in  $T_L$   
4 for particular species emphasizes the need to consider ecosystem specific predator  $T_L$ .  
5 Considering spatialized  $T_L$ s would seem of major importance for specialist predators with  
6 prey showing a limited geographic distribution.

7  
8 Hake have been shown to display large seasonal diet variations in the Bay of Biscay  
9 (Guichet, 1995) but not in the Cantabrian Sea (Velasco & Olaso, 1998). Major prey of  
10 hake, *i.e.* blue whiting (*Micromesistius poutassou*), mackerel (*Scomber scombrus*) and  
11 horse mackerel (*Trachurus trachurus*) were found to be consumed in accordance with  
12 their higher densities in the Celtic Sea (Pinnegar *et al.*, 2003; Trenkel *et al.*, 2005).  
13 Megrim has also been shown to consume more blue-whiting when this prey was at higher  
14 abundance in the environment (Pinnegar *et al.*, 2003; Trenkel *et al.*, 2005). Density  
15 related prey selection seems therefore to explain seasonal changes in  $T_L$  for hake and  
16 megrim. For hake, the interaction effect between season and subdivision showed that  
17 seasonal changes in  $T_L$  could vary according to area. The diet of whiting has also been  
18 shown to display seasonal variations, with some prey such as sandeel (*Ammodytes* spp.)  
19 being more prominent in whiting diets during the summer, which coincided with their  
20 peak abundance (Greenstreet *et al.*, 1998).

21  
22 The absence of a seasonal effect for haddock was not expected as different studies  
23 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  $T_{LS}$  (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).

## 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

1  $T_L$  as proposed by Christensen and Pauly (1992).  $O_{IS}$  however provide information  
2 regarding the range of  $T_L$ s targeted by individual predators and seem very useful to  
3 estimate the trophic niche width of a population. In complement with  $T_L$  variability  
4 derived from GAM residuals,  $O_{IS}$  were used to identify generalization type (Van Valen,  
5 1965) and separate between within-individual and between-individual components  
6 contributing to niche width. The assessment of feeding strategy and measure of  
7 individual-level niche variation is a major issue both in theoretical and applied ecology  
8 (Amundsen *et al.*, 1996; Bolnick *et al.*, 2003; Bearhop *et al.*, 2004) and combining  
9 information on  $T_L$  variability and omnivory seems a promising approach to address such  
10 questions.

11  
12 Quantifying  $T_L$  variability is also useful for estimating ecosystem indicators and  
13 improving trophodynamic models. For instance, the weighted smoothing technique  
14 adopted to spread biomass or catches of a species along a range of fractional  $T_L$  in trophic  
15 spectra assumes constant and symmetrical distribution of  $T_L$  among species (Gascuel *et*  
16 *al.*, 2005). Here our results suggest that the distribution of individual  $T_L$  is neither  
17 symmetric nor constant between species and that the range of 0.7  $T_L$  used by Gascuel *et*  
18 *al.* (2005) underestimates  $T_L$  variability observed for Celtic Sea fish predators, the 95%  
19 reference range being comprised between 1.6 for Atlantic cod and 2.0 for haddock. In the  
20 same way, application of trophodynamic models based on  $T_L$  to real case-studies  
21 (Chassot *et al.*, 2005; Gascuel, 2005) requires information on species  $T_L$  distribution to  
22 spread the biomass among trophic groups.

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