In this study, we investigated trophic-level variability in Celtic Sea fish predators using a database of stomach content records characterized by a high level of taxonomic resolution. The predictors occupied a high position in the food web, with Atlantic cod (Gadus morhua) having a trophic level (TL) of 4.75, haddock (Melanogrammus aeglefinus) having a TL of 4.44, European hake (Merluccius merluccius) having a TL of 8.88, megrim (Lepidorhombus whiffiagonis) having a TL of 5.00, and whiting (Merlangius merlangus) having a TL of 5.27. The level of taxonomic resolution of the prey did not greatly affect the mean TL predictor values; an effect on variance was evident, with low resolution masking intra-population variability in TL. Generalized additive models (GAMs) were used to explain the variability of predator TL caused by environmental variables (International Council for the Exploration of the Sea, ICES, division and season) and predator characteristics (total length, LT). Significant year, location season, and interaction effects were found for some species and with LT at the scale of ICES subdivision. The species-specific variability of TL could be due to spatio-temporal variations in prey availability and in predator selectivity following ontogenetic changes. Omnivorous fish TL was less affected by spatio-temporal variations. In addition, results showed that the omnivory index and TL variability provide dissimilar information on predator feeding strategy. Combining information on TL 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.

Key words: food web; GAM; indicator; omnivory; predation; trophic level.

INTRODUCTION

The trophic level (TL) 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). The TL 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 (http://www.fishbase.org; Froese & Pauly, 2005) or derived from stomach content analyses or applications of Eco-path 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 (Greenstreet et al., 1997) and ontogenetic changes.

The $T_L$ 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 total length ($L_T$) through ontogenetic changes (Stergiou & Karpouzi, 2002; Pinnegar et al., 2003). Hence, $T_L$ are expected to display spatio-temporal variations according to fish age or $L_T$. In addition, estimates of $T_L$ 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* (Walbaum) 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 spatio-temporal variations in diet (Hislop et al., 1991; Hop et al., 1992; Guichet, 1995; Jiang & Jorgensen, 1996; Morte et al., 1999; Carpentieri et al., 2005). 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 five 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 sea water 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 and year), fishing depth (m) and International Council for the Exploration of the Sea (ICES) division where the fishes 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 data set 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 fishes. For each stomach, predator $L_T$ (mm), prey number, prey identity and prey mass (g) were recorded.
Because the original sampling scheme was not randomized or random stratified over space and time, in the present analysis, only fishes 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 *G. morhua* 240–1160 mm *L* _T_, 403 for *M. aeglefinus* 240–830 mm *L* _T_, 682 for *M. merluccius* 250–950 mm *L* _T_, 749 for *L. whiffiagonis* 200–630 mm *L* _T_ and 608 for *M. merlangus* 200–600 mm *L* _T_. Despite ‘rebalancing’ sample sizes varied from year to year and between divisions (Table I).

**PREY TROPHIC LEVELS**

Stable isotope methods rely on the consistent enrichment of the stable-nitrogen isotope, $^{15}$N (mean ± s.d. 3.4 ± 0.3‰), between prey and predator (Minagawa & Wada, 1984; Owens, 1987), allowing its use as a measure of an organism’s continuous trophic position. Mean $T_\text{L}$ 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 $T_\text{L}$-size relationship was available (Jennings et al., 2002a), $T_\text{L}$ 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 $T_\text{L}$ was calculated as the arithmetic mean of the values obtained from isotopic ratios for species belonging to this group. Cnidarians were assigned the mean $T_\text{L}$ ($T_\text{L}$ = 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 $T_\text{L}$ was investigated replacing the $T_\text{L}$ of each prey by the $T_\text{L}$ of their broad taxonomic group level, i.e. cephalopod, cnidarian, crustacean, echinoderm, fish, mollusc (other than cephalopod) and polychaete. Sensitivity of predator $T_\text{L}$ to prey $T_\text{L}$ was also analysed based on $T_\text{L}$ values extracted from the FishBase database. Non-parametric Wilcoxon Mann–Whitney _U_-tests were performed in both cases to analyse differences between $T_\text{L}$ distributions.

**PREDATOR TROPHIC LEVELS AND OMNIVORY**

The $T_\text{L}$ of each individual sampled was calculated as the sum of its prey $T_\text{L}$, weighted by their relative importance in the stomach following Adams _et al._ (1983):

$$T_\text{L}_{jl} = 1 + \sum_{i=1}^{n_j} r_{ijl} T_{Li}$$  \hspace{1cm} (1)

where $r_{ijl}$ represents the relative biomass of prey _i_ in the stomach of individual _l_ of predator species _j_, _i.e._ the relative mass of food _i_ in the stomach, _n_j_ is the number

**Table I.** Spatial and temporal coverage of the stomach data analysed for five species of fishes

<table>
<thead>
<tr>
<th>Year</th>
<th>Division</th>
<th><em>Gadus morhua</em></th>
<th><em>Melanogrammus aeglefinus</em></th>
<th><em>Merluccius merluccius</em></th>
<th><em>Lepidorhombus whiffiagonis</em></th>
<th><em>Merlangius merlangus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1981</td>
<td>VIIg</td>
<td>29</td>
<td>14</td>
<td>52</td>
<td>13</td>
<td>31</td>
</tr>
<tr>
<td>1983</td>
<td>VIIh</td>
<td>2</td>
<td>53</td>
<td>165</td>
<td>164</td>
<td>60</td>
</tr>
<tr>
<td>1984</td>
<td>VIIg</td>
<td>640</td>
<td>224</td>
<td>—</td>
<td>69</td>
<td>399</td>
</tr>
<tr>
<td></td>
<td>VIIh</td>
<td>67</td>
<td>66</td>
<td>166</td>
<td>118</td>
<td>52</td>
</tr>
<tr>
<td>1985</td>
<td>VIIg</td>
<td>91</td>
<td>41</td>
<td>221</td>
<td>252</td>
<td>66</td>
</tr>
<tr>
<td></td>
<td>VIIh</td>
<td>—</td>
<td>5</td>
<td>83</td>
<td>133</td>
<td>—</td>
</tr>
</tbody>
</table>
of prey in the stomach of individual $i$ of predator species $j$ and $T_{Li}$ is the mean $T_L$ of prey $i$.

The $T_L$ 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 (Jennings et al., 2002a; Pinnegar et al., 2002) and on the other hand with values available in different areas of the world extracted from the FishBase database. Omnivory indices ($O_I$) of each individual sampled were also computed following Christensen & Pauly (1992):

$$O_{Ijl} = \sqrt{\frac{1}{n_j} \sum_{j=1}^{n_j} \rho_{ijl}(T_{Lij} - T_{Ljl})^2}$$

where $T_{Lij}$ is the predator $T_L$ computed from equation (1). $O_I$ describes the range of $T_L$ consumed and masses 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 S.D. of $T_L$ (Christensen & Pauly, 1992). Non-parametric Wilcoxon Mann–Whitney $U$-tests were performed to analyse differences between $O_I$ distributions.

IDENTIFYING SOURCES OF VARIABILITY IN TROPHIC-LEVEL VALUES

Generalized additive models (GAM) were used to investigate the variability of $T_L$ over space and time and according to predator $L_T$. GAMs are non-parametric generalizations of multiple linear regressions (Hastie & Tibshirani, 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 $T_L$ computed from equation (1) were modelled as a function of year ($Y$), ICES division ($D_S$), season ($S$) and predator $L_T$. The $D_S$ was used to represent distinct areas assumed to characterize various types of habitat where prey availability changes. The $S$ was modelled as a factor, i.e. winter, spring, summer and autumn, and predator $L_T$ (mm) 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:

$$T_{Lj} = s_j(L_T) + Y + D_S + S$$

where $T_{Lj}$ is the trophic level and $s_j(L_T)$ represents a smooth function (regression spline) for species $j$. Model fitting and automatic selection of the d.f. for the regression splines were performed using the generalized cross-validation method based on minimizing 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.

RESULTS

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 $T_L$ in the size
range sampled: 3·81–5·88 for *G. morhua*, 3·50–5·95 for *M. aeglefinus*, 4·02–6·08 for *M. merluccius*, 3·88–5·95 for *L. whiffiagonis* and 3·99–5·95 for *M. merlangus*. The $T_L$ 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...
M. merlangus (Fig. 3). $T_L$ s.d. were relatively similar for the five species, the values ranging from 0·44 for G. morhua to 0·69 for M. merluccius (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 M. merlangus (Fig. 3). The discrepancy was particularly important for M. aeglefinus, M. merluccius and L. whiffiagonis 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).

SENSITIVITY OF TROPHIC-LEVEL ESTIMATES

The level of taxonomic resolution used for prey affected estimates of predator $T_L$ [Fig. 4(a)]. Predator $T_L$ based on prey groups were significantly lower than $T_L$ based on a high taxonomic resolution for G. morhua ($P < 0·001$), L. whiffiagonis ($P < 0·01$) and M. merluccius ($P < 0·001$), and significantly higher for M. merluccius ($P < 0·001$). Although significant, the differences between mean estimates of $T_L$ were small, i.e. $<0·10$ for G. morhua and M. merluccius, 0·12 and 0·35 for L. whiffiagonis and M. merlangus, respectively. Estimates of the $T_L$ of M. aeglefinus were not modified by a decrease in the level of prey taxonomic resolution. By contrast, s.d. of the $T_L$ were strongly modified and significantly higher for the five 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. 4(b)]. Predator $T_L$ based on prey $T_L$ derived from FishBase were significantly lower than $T_L$ estimates based on $T_L$ derived from stable-isotope methods ($P < 0·001$). These results show that prey $T_L$ 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.

Fig. 3. Comparison of trophic level ($T_L$) for five species (Gadus morhua, Melanogrammus aeglefinus, Merluccius merluccius, Lepidorhombus whiffiagonis and Merlangius merlangus) estimated in the present study (■), derived from stable isotopes of nitrogen in the Celtic Sea (□) and the North Sea (□□). Values are means ± s.d.
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 *M. merluccius* and *L. whiffiagonis*, 43.3 and 26.1% respectively, while it was 13.1, 11.3 and 5.9% for *M. merlangus*, *M. aeglefinus* and *G. morhua*, 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 *M. merluccius* and *L. whiffiagonis*.

Considering the ‘best’ model, significant year and season effects were found for all species except *G. morhua* (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, *M. aeglefinus* showed estimates of $T_L$ higher in division VIIg in 1983 ($T_L = 4.63$) than in 1981 ($T_L = 4.40$), whereas *M. merluccius* showed an overall negative effect on $T_L$ in
1983 relative to 1981 (−0.44 T_L), and the highest T_L for M. merluccius was observed in spring 1985 in division 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, L. whiffiagonis was the ‘top-predator’ in division VIIg in spring 1983, followed by M. merlangus, G. morhua, M. aeglefinus and M. merluccius. As M. merluccius T_L increased from 1983 to 1985 and M. merlangus and M. aeglefinus T_Ls decreased throughout this period, in spring 1985 M. merluccius occupied a higher position than M. aeglefinus and G. morhua and a similar position as M. merlangus.

Division effects were also found to vary between Celtic Sea fish predators. The overall effect of division VIIh was positive for M. merluccius (+0.53 T_L) and negative for L. whiffiagonis (−0.34 T_L) relative to their respective GAM intercepts. A division effect in interaction with year or season was found significant for M. aeglefinus, M. merluccius and L. whiffiagonis. For M. merluccius, a positive effect was found in autumn 1981 in division VIIg (+0.14 T_L relative to spring), whereas a negative season effect was found for autumn in division VIIh (−0.22 T_L relative to spring). For L. whiffiagonis, the 1985 effect was found positive (+0.2 T_L) in division VIIh, whereas it was negative in division VIIg. Hence, temporal changes in T_L for the Celtic Sea fish predators were not similar among habitats defined here by the ICES divisions.

<table>
<thead>
<tr>
<th>Species Variable</th>
<th>Variables</th>
<th>d.f.</th>
<th>Significance</th>
<th>Deviance (%)</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gadus morhua</td>
<td>T_L = s (L_T)</td>
<td>4-0</td>
<td>***</td>
<td>5-9</td>
<td>828-6</td>
</tr>
<tr>
<td></td>
<td>s (L_T)</td>
<td>3</td>
<td>NS</td>
<td>9-9</td>
<td>576-2</td>
</tr>
<tr>
<td>Melanogrammus aeglefinus</td>
<td>T_L = year × division</td>
<td>5</td>
<td>**</td>
<td>11-3</td>
<td>576-7</td>
</tr>
<tr>
<td>Merluccius merluccius</td>
<td>T_L = s (L_T) + year × division × division</td>
<td>5</td>
<td>***</td>
<td>16-6</td>
<td>1312-7</td>
</tr>
<tr>
<td>Lepidorhombus whiffiagonis</td>
<td>T_L = s (L_T) + year × division + season</td>
<td>5</td>
<td>***</td>
<td>26-1</td>
<td>1246-2</td>
</tr>
<tr>
<td>Merlangius merlangus</td>
<td>T_L = s (L_T) + year + season</td>
<td>5-6</td>
<td>*</td>
<td>13-1</td>
<td>728-3</td>
</tr>
</tbody>
</table>

*Note: T_L = trophic level; d.f. = degrees of freedom; AIC = Akaike information criterion*
The $L_T$ was significant for all species except $M.\ aeglefinus$. The $T_L$ increased with $L_T$ for $G.\ morhua$ and $L.\ whiffiagonis$, and for $M.\ merluccius$ from a 500 mm $L_T$ (Fig. 5). Maximum changes in $T_L$ predicted by the GAMs for the range of $L_T$ observed were $+0.43$, $+0.45$, $+0.80$ and $-0.21$ $T_L$ for $G.\ morhua$, $M.\ merluccius$, $L.\ whiffiagonis$ and $M.\ merlangus$, respectively. For $M.\ merlangus$, no clear relationship was found, though there might be an indication of a decreasing pattern of $T_L$ with $L_T$ over the size range 300–600 mm.

TROPHIC-LEVEL VARIABILITY AND OMNIVORY INDEX

Overall GAM results showed that $T_L$ S.D. reflected on the one hand $T_L$ variations due to differences in area or season, and on the other hand

![Graph showing smooth functions of $T_L$ and $L_T$ for different species.](https://example.com/graph.png)

Fig. 5. Smooth functions (—) mean ± s.e. (····) estimated by GAM regression describing the dependence of trophic level ($T_L$) and total length ($L_T$) in (a) $Gadus\ morhua$, (b) $Merluccius\ merluccius$, (c), $Lepidorhombus\ whiffiagonis$ and (d) $Merlangius\ merlangus$. No significant effect of $L_T$ on the $T_L$ of $Melanogrammus\ aeglefinus$ was detected. Whiskers on the abscissa axis indicate data presence.

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between-individual (intra-population) variations. $T_L$ intra-population variability, derived from GAM residuals, was higher for $L.\ whiffiagonis$ and $M.\ merluccius$ (0·47 and 0·40, respectively) than for $M.\ aeglefinus$ (0·37), and $G.\ morhua$ and $M.\ merlangus$ 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 zero values corresponding to predators with only one type of prey in their stomach (Fig. 6). Statistical tests showed that $O_I$ distributions were significantly different ($P < 0·001$) in all cases. $Gadus\ morhua$ and $M.\ aeglefinus$ were the most omnivorous fish with mean values of $O_I$ equal to 0·054 and 0·041, respectively. $Merluccius\ merluccius$ and $M.\ merlangus$ were less omnivorous than $Gadus\ morhua$ and $M.\ aeglefinus$ with mean $O_I$ of 0·017 and 0·012, respectively, and $L.\ whiffiagonis$ was the least omnivorous predator with a mean $O_I$ of 0·008.

The diet of $L.\ whiffiagonis$ could then be characterized by a high between-individual variability of $T_L$ with most of the individuals preying upon a small range of $T_L$ at any given time. By contrast, $Gadus\ morhua$ showed a lower $T_L$ variability but individual fish tended to consume on average a larger range of $T_L$. In other words, it was shown that $Gadus\ morhua$ 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 $L.\ whiffiagonis$

![Fig. 6. Boxplots for all individual omnivory indices [$O_I$; see equation (2)] analysed for the Celtic Sea fish predators. The boxplot has lines at the lower quartile, median (bold) and upper quartile values. The whiskers extend to 1·5 times the interquartile range from the box. ⭕ outliers, i.e. data with values beyond the end of the whisker.](image-url)
resulted from individuals specializing on a different but narrow range of food types (type B generalization). *Merlangius merlangus* displayed both a low $T_L$ variability and a low degree of omnivory, suggesting it was the most specialist species among the five predators. *Melanogrammus aeglefinus* and *M. merluccius* appeared in intermediate positions in terms of both $T_L$ variability and omnivory.

**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 $T_L$ derived from a literature review of stable-isotope analyses in adjacent seas. Predator $T_L$ differed from values available in the literature or available from FishBase. The source of $T_L$ values assigned to the prey was found potentially to 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 $T_L$ 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 $T_L$, results provided evidence for high variability of $T_L$ in space and time, and with $L_T$ at the scale of ICES division. The species-specific variability of $T_L$ would be due to spatio-temporal variations in prey availability and in predator selectivity following ontogenetic changes (see below). The present 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.

**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 $T_L$ variability to be investigated on relatively short time (season) and small spatial scales (ICES division) 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 $T_L$ s.d. 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 the present data set, is a major prerequisite for analysis of species-specific $T_L$ variability.

Mean $T_L$ assigned to prey in equation (1) also have a strong effect on predator $T_L$ and are therefore of major concern for ecosystem analyses based on $T_L$-based indicators. It was assumed here that isotope values correctly characterize...
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 s.d. of prey $T_L$ were generally low in the samples of Pinnegar et al. (2002), Jennings et al. (2002b) and Le Loc’h (2004). Prey $T_L$ used were thus considered as the best current information available to analyse the variability of predator $T_L$. Using prey $T_L$ derived from stable-isotopes of nitrogen allowed the use of default values for prey $T_L$ currently used in FishBase except for cnidarians to be avoided and allowed mean $T_L$ values for small invertebrate prey groups for which diets are generally poorly known to be assigned. Application of stable-isotope methods to estimate cnidarians $T_L$ in the European seas would allow better-quantified $T_L$ for future analyses. In addition, the use of mean prey $T_L$ provided by isotope methods seems consistent for the estimation of predator $T_L$ because they integrate prey diet over a period ranging from a few months to 1 year, depending on the turnover rate of the tissues (O’Reilly et al., 2002). Recent work has, however, suggested that the assumption of average enrichment of 3-4% may be problematic as isotopic fractionation can be affected by feeding rate, nitrogen content of the food, excretion rate and assimilation efficiency (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 $\delta^{15}N$ 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 $T_L$ estimated in this study were generally higher than estimates obtained by Pinnegar et al. (2002) using stable isotopes. The differences between the present estimates and $T_L$ 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 $T_L$ 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.

The $T_L$ estimated in the present analysis were higher than FishBase values. These differences can result both from the $T_L$ assigned to the prey and to the predator size range sampled. Prey $T_L$ 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

The $T_L$ values were found to vary with respect to different variables according to the predator species considered. Deviance explained by GAMs was the lowest for G. morhua and M. aeglefinus 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.
The ICES division was used here to characterize distinct habitats described by differences in prey availability and composition. It was shown that $T_L$ could vary significantly at the scale of ICES division for *M. aeglefinus*, *M. merluccius* and *L. whiffiagonis*. *Gadus morhua* 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 *G. morhua* could explain that spatial variations in diet composition were not reflected in $T_L$ as *G. morhua* consumed a wide diversity of prey in each area of the Celtic Sea. No significant spatial effect on $T_L$ was found for *M. merlangus*, whereas they were found to show geographical differences in diet composition in the North Sea and the Sea of Marmara (Hislop et al., 1991; Artúz, 2005). In the Celtic Sea, *M. merlangus* mainly consumed fish prey such as sprats *Sprattus sprattus* (L.), *Trisopterus* spp. and blue whiting *Micromesistius poutassou* (Risso) that are distributed throughout the area. This could explain the absence of variations in $T_L$ between ICES divisions. 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 $T_L$ would seem of major importance for specialist predators with prey showing a limited geographic distribution.

*Merluccius merluccius* 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 *M. merluccius*, i.e. *M. poutassou*, mackerel *Scomber scombrus* (L.) and horse mackerel *Trachurus trachurus* (L.) were found to be consumed in accordance with their higher densities in the Celtic Sea (Pinnegar et al., 2003; Trenkel et al., 2005). *Lepidorhombus whiffiagonis* has also been shown to consume more *M. poutassou* 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 *M. merluccius* and *L. whiffiagonis*. For *M. merluccius*, the interaction effect between season and subdivision showed that seasonal changes in $T_L$ could vary according to area. The diet of *M. merlangus* has also been shown to display seasonal variations, with some prey such as sandeel *Ammodytes* spp. being more prominent in *M. merlangus* diets during the summer, which coincided with their peak abundance (Greenstreet et al., 1998).

The absence of a seasonal effect for *M. aeglefinus* 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 *M. aeglefinus* as they are omnivorous fish and their diet is mostly composed of echinoderms, molluscs and polychaetes that were assigned similar $T_L$ values ranging between 3.00 and 3.40. This could indicate that although there are marked changes in the types of invertebrate prey targeted by *M. aeglefinus*, these fishes may actually select prey with similar $T_L$ (Deudero et al., 2004). Finally, the absence of seasonal effect for *G. morhua* could again be explained by the wide diversity of prey they consumed in the Celtic Sea.

The increase in $T_L$ for *G. morhua* is mainly explained by the increasing proportion of fishes 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.,...
Merluccius merluccius are opportunistic consumers mostly piscivorous that do not seem to have a selective predatory behaviour (du Buit, 1996). Nevertheless, larger fish (>500 mm) tend to target horse mackerel (Trachurus spp.; TL = 4.95) and pilchard Sardina pilchardus (Walbaum) (TL = 3.59), whereas small predators exploit M. poutassou (TL = 3.14), Argentina spp. (TL = 3.44) and Trisopterus spp. (TL = 4.52) (Pinnegar et al., 2003; Mahé et al., 2007). This might be the reason for the increasing relationship between TL and LT observed for M. merluccius >500 mm. Lepidorhombus whiffiagonis was also found to show increasing TL with LT with a plateau from 500 mm that is related to the increasing proportion of fishes in their diet with LT.

Changes in the range of prey size eaten with increasing predator LT is a well-known phenomenon for marine fish predators and is mostly associated with increase in mouth size and improved swimming performance (Scharf et al., 2000; Karpouzi & Stergiou, 2003). For M. merluccius and G. morhua, the fact that large predators continued to select small benthic prey of lower TL throughout their lives explained why the LT and TL 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 TL with LT compared to the North Sea fish community.

It has been reported elsewhere that the proportion of fishes in the diet of M. aeglefinus increased as their size increased (Greenstreet et al., 1998). The absence of significant effect on TL is due to the similar range of fish prey TL consumed with increasing LT of M. aeglefinus. Variations in TL with LT for M. merlangus differ from the increasing TL and LT relationship observed by Jennings et al. (2002a) in the North Sea. The increase in TL from 200 mm to 300 mm M. merlangus seems mainly due in the analysis to the switch from S. sprattus (TL = 4.28) to Trisopterus spp. (TL = 4.52) in their diet as they grew. Such a switch has also been observed for M. merlangus in the Moray Firth, north-east 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 M. poutassou (TL = 3.14) in the diet of M. merlangus with LT could explain the decreasing trend in TL from 300 mm (Fig. 5).

TROPHIC-LEVEL VARIABILITY AND OMNIVORY

The present results show that mean values of TL mask a high intra-population TL variability that can differ between species. In addition, O1 appears to be a bad proxy for TL variability therefore its square root should not be a good estimate of the s.e. of TL as proposed by Christensen & Pauly (1992). The O1, however, provides information regarding the range of TL targeted by individual predators and seem very useful to estimate the trophic niche width of a population. To complement TL variability derived from GAM residuals, O1 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 measurement 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 TL 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, the 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 $G.\ morhua$ and 2-0 for $M.\ aeglefinus$. 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.

We are grateful to M. H. du Buit for collecting and analysing all stomach contents. We thank A. Colomb, Y.-M. Bozec and E. Rivot (Agrocampus) for stimulating and fruitful discussions on the variability of trophic level and J. K. Pinnegar (CEFAS) for insightful comments on an earlier version of the manuscript. J. Guitton and S. Bonhommeau (Agrocampus) helped with map drawing. We also thank A. Caskanette (DFO) for the English corrections. Anonymous reviewers helped to improve the manuscript. This work was financed by the EU funded RTD project QLRT-2000-02277 ‘PECHDEV’.

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