Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution

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Summary

1. The intensive exploitation of fish communities often leads to substantial reductions in the abundance of target species, with ramifications for the structure and stability of the ecosystem as a whole.
2. We explored changes in the mean trophic level of the Celtic Sea (ICES divisions VII f–j) fish community using commercial landings, survey data and estimates of trophic level derived from the analysis of nitrogen stable isotopes.
3. Our analyses showed that there has been a significant decline in the mean trophic level of survey catches from 1982 to 2000 and a decline in the trophic level of landings from 1946 to 1998.
4. The decline in mean trophic level through time resulted from a reduction in the abundance of large piscivorous fishes and an increase in smaller pelagic species which feed at a lower trophic level.
5. Similar patterns of decline in the trophic level of both catches and landings imply that there have been substantial changes in the underlying structure of the Celtic Sea fish community and not simply a change in fishery preferences.
6. We suggest that the reported changes in trophic structure result from reductions in the spawning stock biomass of traditional target species associated with intensive fishing, together with long-term climate variability.
7. The relative distribution of fish market prices has changed significantly over the past 22 years, with high trophic level species experiencing greater price rises than lower trophic level species.
8. Although decreased abundance of high trophic level species will ultimately have negative economic consequences, the reduction in mean trophic level of the fish community as a whole may allow the system to sustain higher fishery yields.
9. Management objectives in this fishery will depend on the relative values that society attaches to economic profit and protein production.

Key-words: climate, environment, exploitation, fisheries, nitrogen, stable isotope.

Introduction

The intensive exploitation of fish communities often leads to substantial reductions in the abundance of target species and changes in species composition (Greenstreet & Hall 1996). Large or slow-growing species with late maturity decline in abundance more rapidly than their smaller, faster-growing, counterparts (Jennings, Greenstreet & Reynolds 1999), and as large species typically feed at higher trophic levels, fishing is expected to reduce the mean trophic level of exploited fish communities (Pauly et al. 2001).

Changes in the composition of landings often reflect changes in the structure of underlying fish communities (Gulland 1987). Pauly et al. (1998a) used aggregated landing statistics from the United Nations (UN) Food and Agriculture Organization (FAO) and estimates of trophic level for individual species derived from food web models, to demonstrate that the mean trophic levels of global fisheries have declined significantly since the late 1950s. This decline was found to be particularly...
marked in the north-east Atlantic (FAO area 27), and
reflects a gradual transition from long-lived high
trophic level piscivorous fish towards short-lived invertebrates and planktivorous fishes at lower trophic levels (Pauly et al. 1998a, 2000a).

Several concerns have been expressed regarding the approach and methodology used by Pauly et al. (1998a) (Caddy et al. 1998; Pauly, Froese & Christensen 1998b; Caddy & Garibaldi 2000; Pauly & Palomares 2000). These focused principally on (i) errors in assigning trophic levels to individual species; (ii) the validity of FAO landings data; and (iii) the potential influence of environmental factors.

The trophic level estimates used by Pauly et al. (1998a) for north-east Atlantic fishes were largely derived from the North Sea Ecopath model of Christensen (1995). Christensen’s (1995) estimates were based on gut contents analyses, yet these tend to provide only snapshots of diets in time and space and thus offer a poor basis for establishing trophic level. In addition, gut content analysis neglects certain dietary materials (e.g. gelatinous plankton and detritus) that are hard to identify but which are an important constituent in the diet of some fish (Deb 1997; Polunin & Pinnegar 2002). Furthermore, this tool may be particularly unsuitable for predicting trophic levels of top predators that feed intermittently and frequently regurgitate food upon capture (Bowman 1986).

The landings data used by Pauly et al. (1998a), for the north-east Atlantic, were derived by the FAO from more detailed International Council for the Exploration of the Sea (ICES) assessments based on 15 distinct subareas. The large-scale geographical aggregation of such data makes it very difficult to discern the species and fleets responsible for any observed changes in mean trophic level. There are distinct differences in the fisheries and fleets that operate in each of the ICES subareas (MAFF 1999), which were not taken into account by Pauly et al. (1998a).

The Celtic Sea is an intensively fished ecosystem and is unusual among north-east Atlantic seas in that its major fisheries were developed relatively recently, at a time when good fishery monitoring and survey programmes were in place. As a consequence the Celtic Sea offers an ideal situation for study of the indirect effects of intensive fishing on trophic structure and to compare the changes in trophic level of survey catches and commercial landings. Christensen (1998) has demonstrated apparent declines in trophic level of an ecosystem may be even more marked in survey data than in landings data from the same region.

The Celtic Sea comprises ICES statistical divisions VII f–j, and is mainly fished by France, Ireland, the UK, Spain and Belgium. The Celtic Sea supports valuable fisheries for several species, notably for Merluccius merluccius (Linnaeus), Lepidorhombus whiffiagonis (Walbaum) and Trachurus trachurus (Linnaeus) (MAFF 1999). The fisheries of the Celtic Sea are harvested by several distinct fleets (métiers), characterized by the use of different fishing gear types and different target species (Laurec, Biseau & Charuau 1991; Marchal & Horwood 1996). The recent expansion of Celtic Sea fisheries has prompted concerns about the present and future state of fish stocks (Horwood 1993), the scale of fishery discards by-catch (Perez, Trujillo & Pereda 1996; Treganza et al. 1997; Morizur et al. 1999; Roche, Trenchel & Péronnet 2001) and possible implications for the ecosystem as a whole.

Changes in fishery preferences are often driven by economic forces, and the value of a species will determine the investment that fishermen are willing to make in order to catch it, and thus how heavily it is fished at low abundance. Existing evidence suggests that the average market price of a species will increase as it becomes scarce (Murawski & Serchuk 1989; OECD 1997), and Sumaila (1998) has demonstrated that markets are good at giving value to previously undesirable fish when target species become unavailable. On a world-wide basis, between 1952 and 1994 the average price of low trophic level species apparently increased relative to the price of high trophic level species (Sumaila 1998). Long-term price data are available for the Celtic Sea fishery, and these provide an opportunity to examine how market prices might relate to changes in the composition of landings at a local scale.

Stable isotopes of nitrogen have been widely used for establishing trophic level in aquatic organisms (Cabana & Rasmussen 1996; Vander Zanden, Cabana & Rasmussen 1997; Post, Pace & Hairston 2000). The isotope method relies on the general observation that with every trophic step, there is bioaccumulation of the heavier isotope $^{15}$N (Minagawa & Wada 1984). Trophic level estimates resulting from stable isotope analysis (SIA) largely corroborate trophic level data derived from steady-state modelling (Kline & Pauly 1998; Pinnegar 2000) and/or gut contents analysis (Vander Zanden, Cabana & Rasmussen 1997), but offer advantages because they integrate diet over a year or more in many fish species (Hesslein, Hallard & Ramal 1993) and thus they are much less subject to seasonal bias. Moreover, isotopes in tissues of a consumer reflect materials that are assimilated and not merely ingested.

Because the average transfer efficiency between trophic levels in marine systems is $c. 10\%$ (Pauly & Christensen 1995), Pauly, Christensen & Walters (2000b) predicted that a fall of 1 in the level at which a fishery operates would lead to a 10-fold increase in potential catches. To study this effect Pauly, Christensen & Walters (2000b) and Christensen (2000) introduced the fishing-in-balance (FIB) index:

$$FIB = \log\left(\frac{\text{Catch}_y \times TE^{TL-1}}{\text{Catch}_1 \times TE^{TL+1}}\right)$$

where $y$ is the year of the time-series, $TL$ is the trophic level of the catch, $TE$ is the mean energy-transfer efficiency between trophic levels (assumed to be $10\%$), and 1 refers to the first year in a time-series that is used
as a baseline. If catches increase 10-fold for every full trophic level decline, the FIB index will remain constant and fishing can be deemed ‘in balance’.

The objectives of the present study were to: (i) describe changes in the mean trophic level of survey catches and fishery landings using stable isotope-derived estimates of trophic level; and (ii) examine whether changes are reflected in the relative market price distribution of fish species.

**Methods**

**Stable isotope measurements**

Individual species were sampled in the Celtic Sea from the research vessel Cirolana using the standard bottom trawl gear utilized for annual ground-fish surveys. This gear consisted of a modified Portuguese High-Headline Trawl (Warnes & Jones 1995), and tows of 30-min duration were made at a speed of approximately 4 knots. Sixty-one standard survey stations were fished throughout the Celtic Sea (Fig. 1) during February and March 2000. Where possible, three fish of each species, between 60% and 80% of their maximum recorded size, were selected from the survey hauls (Jennings et al. 2001a), and these animals were dissected aboard ship to obtain tissue samples for nitrogen stable isotope analysis. Approximately 2 g of white muscle was dissected from the dorsal musculature of each fish, placed in a vial and immediately frozen at −30 °C. On return to the laboratory, the frozen tissue was freeze-dried and ground to a fine powder (particles < 60 µm). This was thoroughly mixed and a 1-mg sample was weighed into a tin capsule for stable isotope analysis (Pinnegar & Polunin 1999).

The $^{15}$N composition of the samples was determined using continuous-flow isotope ratio mass spectrometry (CF-IRMS). The weighed samples were oxidized and the resulting $N_2$ passed to a single-inlet dual collector mass spectrometer (automated nitrogen carbon analysis, ANCA; SL 20–20 system, PDZ Europa, Crewe, UK). Two samples of an internal reference material (homogenized cod white muscle) were analysed after every six tissue samples in order to calibrate the system and compensate for drift with time. The conventional delta notation was used to express stable isotope ratios and these are reported (in ‰) relative to an international standard (atmospheric nitrogen):

$$
\delta^{15}N = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000
$$

where $R$ is the ratio $^{15}$N:$^{14}$N. Experimental precision (based on the standard deviation of replicates of the internal standard) was < 0·1‰.

**Trophic level estimates**

Stable isotope-based estimates of trophic level were calculated assuming a constant per trophic level fractionation of 3·4‰ (Minagawa & Wada 1984). The adductor muscle of Celtic Sea scallops *Pecten maximus* (Linnaeus) (shell length 11·37 cm, SD 0·06; $n = 6$) was used as a reference material. Scallops were caught by dredge from the research vessel *Corystes* in November 2000 (Fig. 1). The mean $\delta^{15}$N of adductor muscle was 7·21‰ (SD 0·18) and this value was used to predict the trophic levels of other species whereby:

$$
\text{TL}_{Ni} = \left( \frac{\delta^{15}N_i - \delta^{15}N_{\text{ref}}}{3·4} \right) + 2
$$

$\text{TL}_{Ni}$ is the trophic level of species $i$, $\delta^{15}$N$_i$ is the mean $\delta^{15}$N of species $i$, and $\delta^{15}$N$_{\text{ref}}$ is the mean $\delta^{15}$N of the scallops, which were assumed to be herbivorous/detrivorous and consequently feeding at trophic level 2. Although in the present study we assigned specific trophic levels to species, it equally would have been sufficient to report only their $\delta^{15}$N values and simply assume linearity in the relationship between $\delta^{15}$N and trophic level (Jennings et al. 2001b). We have...
converted $\delta^{15}$N values to trophic level simply for ease of comparison with those of Pauly et al. (1998a).

GROUND FISH SURVEY DATA

The relative abundance of Celtic Sea demersal fishes has been monitored since 1981 (Warnes & Jones 1995). The original purpose of the surveys was to investigate the distribution and biology of mackerel, but subsequently, with an increasing need for fishery-independent data on western stocks, the objectives were widened to include the biology, distribution and abundance of all species that could be sampled representative by bottom trawl. From 1982 onwards, catch numbers, weight and length compositions were recorded routinely, thus giving a time-series of 18 years. The area of coverage extends from 47°30’S to 52°30’S and from 3°W to 12°W, and includes ICES Divisions VII f,g,h,j and the northern part of VII e (Fig. 1). In the earlier years two surveys were carried out each year, one in the spring (March–April) and one in winter (December). However, from 1989 onwards only the spring survey has been undertaken, and thus only data for the spring surveys were utilized in the present analysis. No spring survey data were available for 1983.

NOMINAL INTERNATIONAL FISHERY LANDINGS

Nominal landings of fish and shellfish are officially submitted to ICES by each of the 19 member countries on an annual basis. ICES has published these data in Bulletin Statistique des Pêches Maritimes from 1903 to 1987 (ICES 1906–90) and from 1988 onwards in ICES Fisheries Statistics (in electronic form). We used aggregated data from ICES divisions VII j–k (Fig. 1). Data for the period 1946–72 were obtained directly from Bulletin Statistique and data for 1972–98 were downloaded from the ICES web site, http://www.ices.dk. Landings were expressed in tonnes live weight equivalent. Bulletin Statistique describes the limitations of the annual data sets, and notable discrepancies over the time-series include the occasional aggregation of Limanda limanda (Linnaeus) with Microstomus kitt (Walbaum) in French reports and the separation of Micromesistius potassou (Risso) from non-specified gadoids in 1975.

RELATIVE PRICE INDEX

The weight and value of fishery landings by English, Welsh and Northern Ireland vessels are recorded annually by the Centre for Environment, Fisheries and Aquaculture Sciences (CEFAS, formerly MAFF Fisheries Directorate). We estimated the average price of 26 fish species (in £ per tonne) landed from the Celtic Sea (ICES regions VII f–k) between 1979 and 2000, as landings (in tonnes) divided by value (in UK £). For these 26 species (Table 1) there was a complete time-series of price estimates; species where a complete time-series did not exist were excluded. Within each individual year, we examined the relationship between price and trophic level using linear regression. The slope of the regression ($b$) was taken as the relative price index (RPI) for that particular year. If the RPI decreases, then the prices of lower trophic level species can be interpreted as having increased relative to higher trophic level species (sensu Sumaila 1998), and conversely if RPI increases then the top predators have increased in value relative to the low trophic level species. If the RPI remains constant then the relationship between the prices of low and high trophic level species has also remained constant, although in absolute terms prices may have increased due to inflation.

STATISTICAL ANALYSIS

To test for significant long-term trends in time-series data, non-parametric Mann–Kendall tests were performed (Gilbert 1987). The Mann–Kendall test is particularly useful because data need not conform to any particular distribution. Where a significant linear trend was indicated, the true slope (change per unit time) was estimated using the procedure developed by Sen (1968). This non-parametric estimator is not greatly affected by outliers and can be computed when data for individual years (e.g. 1983 in Celtic Sea survey data) are missing (Gilbert 1987). Differences were judged significant when $P < 0.05$. For some analyses, species were grouped into ISSCAAP (International Standard Statistical Classification of Aquatic Animals and Plants) categories.

Results

Nitrogen stable isotope compositions were determined for 48 fish species, which represented 99.7% of the biomass in the year 2000 groundfish survey. $\delta^{15}$N values ranged from 10.2‰ in Gadilus argenteus Guichenot to 17.2‰ in Merluccius merluccius, and trophic level ranged from 2.88 to 4.94 (Table 1). The unweighted mean trophic level of all fish combined was 3.86.

SURVEY DATA

There was a significant decline in the mean (weighted by species abundance) trophic level of the fish caught in trawl surveys from 1982 to 2000 (Mann–Kendall $Z = -2.01$, $P = 0.04$; Fig. 2a). Sen’s non-parametric estimator of slope indicated that the average rate of trophic level decline was around 0.04 year$^{-1}$. This decline coincided with substantial changes in the composition of survey catches, whereby the proportion represented by ‘cods and hakes’ and ‘sharks and rays’ (high trophic level species) seems to have decreased markedly (Fig. 2b), as did the proportion represented by Trachurus trachurus [trophic level (TL) = 3–94]. In contrast the relative abundance of Scomber scombrus Linnaeus (TL = 3–61) increased (Fig. 2b), as did the proportion represented by ‘seabasses, redfishes and congers’
Table 1. Fish species collected in the Celtic Sea during the spring 2000 groundfish survey, mean total length, $\delta^{15}$N and calculated trophic level of samples. Three individuals were sampled from each species except * where $n = 1$; trophic levels were calculated assuming a fractionation step of 3.4‰ and against a baseline of Pecten maximus (7.21 ± 0.18‰). †Species included in the relative price analysis.

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
<th>Fish length (mm) mean ± SD</th>
<th>$\delta^{15}$N (%) mean ± SD</th>
<th>Trophic level mean ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scyliorhinus canicula</td>
<td>Lesser spotted dogfish</td>
<td>647 ± 18</td>
<td>15.0 ± 0.91</td>
<td>4.29 ± 0.27</td>
</tr>
<tr>
<td>Galeorhinus galeus†</td>
<td>Tope</td>
<td>1090 ± 164</td>
<td>17.0 ± 0.82</td>
<td>4.88 ± 0.24</td>
</tr>
<tr>
<td>Mustelus asterias</td>
<td>Starry smooth hound</td>
<td>1115 ± 15</td>
<td>14.0 ± 0.22</td>
<td>4.00 ± 0.06</td>
</tr>
<tr>
<td>Squalus acanthias†</td>
<td>Spurdog</td>
<td>628 ± 40</td>
<td>12.0 ± 0.57</td>
<td>3.41 ± 0.17</td>
</tr>
<tr>
<td>Raja montagui†</td>
<td>Spotted ray</td>
<td>626 ± 18</td>
<td>13.7 ± 0.93</td>
<td>3.91 ± 0.27</td>
</tr>
<tr>
<td>Leucoraja naevus</td>
<td>Cuckoo ray</td>
<td>641 ± 30</td>
<td>13.6 ± 0.44</td>
<td>3.88 ± 0.13</td>
</tr>
<tr>
<td>Clupea harengus</td>
<td>Sardina pilchardus</td>
<td>280 ± 40</td>
<td>13.5 ± 0.73</td>
<td>3.85 ± 0.21</td>
</tr>
<tr>
<td>Gadus morhua</td>
<td>Microchirus variegatus</td>
<td>38 ± 14</td>
<td>13.0 ± 0.21</td>
<td>3.85 ± 0.21</td>
</tr>
<tr>
<td>Melanogrammus aeglefinus†</td>
<td>Whiting</td>
<td>306 ± 15</td>
<td>17.2 ± 1.24</td>
<td>4.94 ± 0.36</td>
</tr>
<tr>
<td>Micromesistius poutassou</td>
<td>Blue whiting</td>
<td>240 ± 10</td>
<td>11.1 ± 0.64</td>
<td>3.14 ± 0.19</td>
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<tr>
<td>Molva molva†</td>
<td>Ling</td>
<td>1107*</td>
<td>15.3</td>
<td>4.38</td>
</tr>
<tr>
<td>Physic hennoides</td>
<td>Fordike</td>
<td>426 ± 31</td>
<td>13.3 ± 0.50</td>
<td>3.79 ± 0.15</td>
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<tr>
<td>Pollachius virens†</td>
<td>Saithe</td>
<td>1054 ± 28</td>
<td>14.4 ± 0.60</td>
<td>4.11 ± 0.18</td>
</tr>
<tr>
<td>Trisopterus esmarki</td>
<td>Norway pout</td>
<td>168 ± 12</td>
<td>13.7 ± 1.03</td>
<td>3.91 ± 0.30</td>
</tr>
<tr>
<td>Trisopterus minutus</td>
<td>Poor cod</td>
<td>146 ± 5</td>
<td>12.9 ± 1.12</td>
<td>3.67 ± 0.33</td>
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<tr>
<td>Merluccius merluccius†</td>
<td>Hake</td>
<td>863 ± 120</td>
<td>13.5 ± 0.29</td>
<td>3.85 ± 0.09</td>
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<td>Beryx splendidus</td>
<td>Beryx</td>
<td>241 ± 2</td>
<td>10.8 ± 0.85</td>
<td>3.06 ± 0.25</td>
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<tr>
<td>Zeus faber†</td>
<td>John dory</td>
<td>356 ± 40</td>
<td>14.7 ± 0.74</td>
<td>4.20 ± 0.22</td>
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<tr>
<td>Capros aper</td>
<td>Boarfish</td>
<td>116 ± 5</td>
<td>10.4 ± 0.20</td>
<td>2.94 ± 0.06</td>
</tr>
<tr>
<td>Helicolenus dactylopterus</td>
<td>Dab</td>
<td>59 ± 13</td>
<td>12.9 ± 0.80</td>
<td>3.61 ± 0.12</td>
</tr>
<tr>
<td>Aspitrigla cuculus†</td>
<td>Lemon sole</td>
<td>35 ± 13</td>
<td>13.5 ± 0.73</td>
<td>3.85 ± 0.21</td>
</tr>
<tr>
<td>Etiolirigia gurnard</td>
<td>Bass</td>
<td>639 ± 3</td>
<td>15.8 ± 0.42</td>
<td>4.53 ± 0.12</td>
</tr>
<tr>
<td>Trachurus trachurus†</td>
<td>Horse-mackerel</td>
<td>347 ± 22</td>
<td>13.8 ± 0.41</td>
<td>3.94 ± 0.12</td>
</tr>
<tr>
<td>Sponyllosoma canthusrus†</td>
<td>Black sea bream</td>
<td>302 ± 22</td>
<td>15.2 ± 0.85</td>
<td>4.35 ± 0.25</td>
</tr>
<tr>
<td>Mullus surmuletus</td>
<td>Red mullet</td>
<td>280 ± 20</td>
<td>15.3 ± 0.82</td>
<td>3.48 ± 0.24</td>
</tr>
<tr>
<td>Echiichthys vipera</td>
<td>Lesser weaver</td>
<td>106 ± 8</td>
<td>15.1 ± 0.21</td>
<td>4.32 ± 0.06</td>
</tr>
<tr>
<td>Hyperolus immaculatus</td>
<td>Corvina sandeal</td>
<td>267 ± 5</td>
<td>12.2 ± 0.87</td>
<td>3.47 ± 0.26</td>
</tr>
<tr>
<td>Callionymus lyra</td>
<td>Dragonet</td>
<td>158 ± 14</td>
<td>12.7 ± 0.40</td>
<td>3.61 ± 0.12</td>
</tr>
<tr>
<td>Scomber scombrus†</td>
<td>Mackeral</td>
<td>289 ± 4</td>
<td>12.7 ± 1.26</td>
<td>3.61 ± 0.37</td>
</tr>
<tr>
<td>Lepidorhombus boscii</td>
<td>Four-spot megrim</td>
<td>284 ± 17</td>
<td>11.9 ± 0.12</td>
<td>3.38 ± 0.04</td>
</tr>
<tr>
<td>Lepidorhombus whiffiagonis†</td>
<td>Megrin</td>
<td>394 ± 38</td>
<td>15.7 ± 0.74</td>
<td>3.56 ± 0.22</td>
</tr>
<tr>
<td>Arnoglossus imperialis</td>
<td>Imperial scadfish</td>
<td>165 ± 8</td>
<td>10.9 ± 0.14</td>
<td>3.09 ± 0.04</td>
</tr>
<tr>
<td>Glyptocephalus cyanoglossus†</td>
<td>Witch</td>
<td>299 ± 24</td>
<td>13.6 ± 0.51</td>
<td>3.88 ± 0.15</td>
</tr>
<tr>
<td>Hippoglossidae platessaoides</td>
<td>Long rough dab</td>
<td>180 ± 10</td>
<td>14.1 ± 0.16</td>
<td>4.03 ± 0.05</td>
</tr>
<tr>
<td>Limanda limanda†</td>
<td>Dab</td>
<td>193 ± 17</td>
<td>14.7 ± 1.66</td>
<td>4.20 ± 0.49</td>
</tr>
<tr>
<td>Microstomus kitt†</td>
<td>Lemon sole</td>
<td>239 ± 14</td>
<td>12.9 ± 2.00</td>
<td>3.67 ± 0.59</td>
</tr>
<tr>
<td>Platicthys fluvius†</td>
<td>Flounder</td>
<td>315 ± 3</td>
<td>13.5 ± 1.17</td>
<td>3.85 ± 0.34</td>
</tr>
<tr>
<td>Pleuronectes platessa†</td>
<td>Plaice</td>
<td>336 ± 13</td>
<td>12.9 ± 0.97</td>
<td>3.67 ± 0.29</td>
</tr>
<tr>
<td>Microcris variegatus</td>
<td>Thick back sole</td>
<td>202 ± 3</td>
<td>13.5 ± 0.73</td>
<td>3.85 ± 0.21</td>
</tr>
<tr>
<td>Solea solea†</td>
<td>Sole</td>
<td>328 ± 38</td>
<td>14.6 ± 0.71</td>
<td>4.17 ± 0.21</td>
</tr>
</tbody>
</table>

(ISSCAAP group 33), largely due to increased catches of the boarfish Capros aper (Linnaeus) (Fig. 2c), which feeds at a low trophic level (TL = 2.94). Among species of ‘seabasses, redfishes and congers’, the proportion represented by monkfish (Lophius spp.), which feed at a high trophic level (Lophius piscatorius Linnaeus TL = 4.09), declined markedly, from 22.8% of the group’s biomass in 1986 to only 0.7% in 2000 (Fig. 2c). The mean trophic level of the groundfish survey was relatively stable until 1988 (Fig. 2a), but in subsequent years it became more variable, largely due to variation in Scomber scombrus and Trachurus trachurus abundance, with very low catches of these species in 1993–95.

**LANDINGS DATA**

The mean trophic level of fish landed from the Celtic Sea declined significantly from 1946 to 1998.
(Mann–Kendall $Z = -3.25$, $P = 0.01$; Fig. 3a), and Sen's non-parametric estimator of slope indicated a decline of around 0.03 TL each year. For the period 1982–98 (the years covered by the groundfish survey), there was no significant overall trend in the mean trophic level of landings (Mann–Kendall $Z = 0.48$, $P = 0.63$; Fig. 3a).

There was a significant negative correlation (Spearman $r_s = 0.49$, $P < 0.01$) between mean trophic level and total landings (in tonnes) (Fig. 3b). From 1946 to 1968 the

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**Fig. 2.** Patterns of changing (a) trophic level, (b) catch composition and (c) catch composition of the ‘seabasses, redfishes and congers’ in an 18-year time-series of fishery-independent survey data for the Celtic Sea (scientific names given in Table 1).
mean trophic level and landings varied relatively little from year to year (TL 3.86–4.01, landings 51 235–201 494 tonnes); however, from 1969 to 1976 landings increased greatly (up to 489 776 tonnes in 1976) and this was accompanied by a decline in mean trophic level (TL = 3.78 in 1976; Fig. 3b). Between 1976 and 1977 landings fell dramatically (to only 155 131 tonnes) and this coincided with a slight increase in the mean trophic level until 1985–88, when landings began to increase again and trophic level declined (to TL = 3.65, landings 304 792 tonnes). In recent years (1989–98) landings have varied relatively little from year to year (232 501–364 942 tonnes), and the mean trophic level of the landed fish has ranged from 3.80 to 3.91 (Fig. 3b).

The trends apparent in the composition of fishery landings were somewhat similar to those we have reported for survey catches (Fig. 4a). In both data series, there was a marked decline in the importance of high trophic level groups such as the ‘cods and hakes’ (78.1% of landings in 1946, 13.9% in 1998) and ‘sharks and rays’ (7.5% in 1946, 3.3% in 1998). However, in fishery landings data the importance of small pelagic species has increased more markedly. In 1946, reported landings of *Trachurus trachurus* were only 0.03% of the total, but after 1967 the fishery expanded greatly and represented 50.4% of total landings in 1998. Similarly the fishery for *Scomber scombrus* was very small in the early years of the time-series (6.6% in 1946) but expanded throughout the 1960s and 1970s, peaking in 1976, after which its importance was eclipsed by that of *Trachurus trachurus* (Fig. 4a). The proportion of flatfishes (ISSCAAP group 31) and ‘seabreams, redfishes and congers’ (ISSCAAP group 33) remained relatively unchanged over the course of the whole time-series. However, the proportion of ‘herrings and anchovies’ (ISSCAAP group 35) was less consistent and peaked in 1958–59, 1962–64 and 1966–70. Between 1984 and 1990, the proportion of ‘cods and hakes’ in the landings (ISSCAAP group 32) rose slightly, largely due to catches of low trophic level (TL = 3.14) blue whiting *Micromesistius poutassou* (Risso). This peak in blue whiting landings was reflected in a decrease in the mean trophic level of landings (Fig. 3a) for these years. Subsequently, the proportion of ‘cods and hakes’ in the

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**Fig. 3.** A 53-year time-series of aggregated fisheries landings (fish only) for the Celtic Sea: (a) changes in mean trophic level; (b) relationship between mean trophic level and total international landings (individual years indicated).
Fig. 4. A 53-year time-series of aggregated fisheries landings for the Celtic Sea: (a) changes in relative composition of landings; (b) changes in the absolute quantities of fish landed; (c) changes in the fishing-in-balance index (FIB).
landings continued to decline (Fig. 4a), largely due to reduced catches of high trophic level species such as cod and hake (TL = 3.85).

Overall, between 1946 and 1998, there was a significant increase (Mann–Kendall Z = 7.48, P < 0.0001) in fishery landings from the Celtic Sea (Fig. 4b), and landings of most fish groups increased in absolute terms (Fig. 4b). Particularly high landings of Scomber scombrus and Trachurus trachurus were taken in 1976. A clear and strongly significant increase was observed (Mann–Kendall Z = 4.32, P < 0.0001) in the FIB index, based on total landings and the mean trophic level (Fig. 4c).

**Discussion**

Our study clearly demonstrates that there have been significant changes in the structure of fish communities and fishery landings in the Celtic Sea over the past 50 years, and these have coincided with a period of considerable fishery expansion. The response of markets has been a marked switch away from high trophic level, high price, species, to greater demand for low trophic level, low price, species.

Our results support the assertion of Pauly et al. (1998a) that there have been major changes in the fish communities of the north-east Atlantic generally. The decline we observed in the survey data (0.04 TL year\(^{-1}\)) was slightly stronger than the decline we observed in the landings data (0.03 TL year\(^{-1}\)), and in both cases this decline was more marked than that given by Pauly et al. (1998a) for the north-east Atlantic as a whole (c. 0.02 TL year\(^{-1}\)). The fact that we found a significant decline in the fishery-independent survey data over the past 19 years, when there was no apparent trend in the landing data over this same period, suggests that the changes occurring in the underlying ecosystem may be stronger than any changes observable in fishery preferences, as demonstrated by Christensen (1998).

Our trophic level estimates for the 48 fish species (Table 1) in many cases differed from those used by Pauly et al. (1998a). There are several possible explanations for this phenomenon, including the use of ‘default’ values by Pauly et al. (1998a) to represent certain species. Of the 48 species for which we have isotope-derived trophic level estimates (Table 1), 18 estimates in Pauly et al. (1998a) were allocated a trophic level of 3.5, the default for ‘demersal percomorphs’, five were given the default value for ‘gadiformes’ (TL = 3.8), and two were given the default for ‘clupeiformes’ (TL = 2.8). Most of these default values were obtained from Pauly & Christensen...
The use of default values was necessary because no locally derived estimates for the particular species were available, thus values for related species from around the world were averaged and utilized as a substitute. Feeding behaviour, and therefore trophic level, can range markedly within most fish families, for example among the gadoids where blue whiting are planktivorous but cod and hake are primarily piscivorous. Thus the use of default values by Pauly et al. (1998a) to represent species groups may lead to unrealistic conclusions concerning the trophic structure of the fish assemblage. We have provided species-specific and geographically relevant trophic level estimates for 99-7% (by biomass) of the Celtic Sea fish community (based on the 2000 survey data).

Another possible explanation for the discrepancies between our trophic level estimates and those of Pauly et al. (1998a) stems from the different abilities of gut contents analysis vs. stable isotope analyses. In the present study, several species of flatfishes and mullet (notably Solea solea (Linnaeus), Limanda limanda, Hippoglossoides platessoides Fabricius and Mullus surmuletus) possessed higher trophic levels than might have been expected for species feeding primarily on benthic invertebrates (Table 1). Soft bottom ecosystems can be very complex, such that many polychaete species, for example, feed exclusively on other polychaetes, thus giving them a high trophic level (Jennings, for example, feed exclusively on other polychaetes, thus giving them a high trophic level (Jennings et al. 2001). Some soft bottom fish species are known to suggest by Pauly et al. (1998a). However, the relative commercial value. Discards and by-catch are reported to be substantial in the Celtic Sea, and may represent as much as one-third of total catches in some years (Rochet, Trenkel & Péronnet 2001).

In general, total landings from the Celtic Sea have continued to increase over the past 50 years. This is not the case elsewhere in the north-east Atlantic (e.g. North Sea), where most stocks have been exploited for a considerable period of time. After the Second World War, Celtic Sea fisheries targeted mainly gadoids, but throughout the 1960s and 1970s new fisheries opened up that targeted pelagic species. Mackerel stocks were exploited at a low level before the Second World War; however, in the mid-1960s a major winter fishery began adjacent to the Cornish peninsula, operated by the USSR (Lockwood & Shepherd 1984). The fishery for horse-mackerel developed as a potential alternative to mackerel in the late 1960s (Lockwood & Johnson 1977), again largely operated by the USSR, with small catches by UK, French, Norwegian, Polish, Spanish and Portuguese vessels. With the exclusion of the Eastern Bloc countries in 1977, the dominant pelagic fleet became that of the Netherlands, and their landings of horse-mackerel rose from 2000 tonnes to more than 40 000 tonnes in 1981 (Eaton 1983). Prior to 1974, there was very little fishing by any country on blue whiting Micromesistius poutassou, however, in the late 1970s Norwegian industrial fisheries targeted this species, largely for use as fishmeal (Pawson 1979).

The increased importance of small pelagic species in Celtic Sea landings may, in part, be a response to scarcity of more traditional target species such as cod, but it might also be related to technical innovation and the development of new fishing gear designs. The incorporation of synthetic fibres into fishing gears in the 1950s and 1960s allowed large-scale mid-water trawling and purse-seining by industrial fleets for the first time. This, in turn, greatly increased the vulnerability of small pelagic stocks world-wide (Caddy & Garibaldi 2000).

Almost all the new Celtic Sea fisheries of the last 30 years or so (blue whiting, mackerel, horse-mackerel) have targeted species that feed mainly on zooplankton (Sorbe 1980; Mehl & Westgård 1983; Ben-Salem 1988). This is in contrast to the post-war fisheries, which targeted high trophic level species such as cod, hake, haddock and small sharks. Indeed, many of these predatory fishes feed primarily on those species which were included then the observed trends in mean trophic level might have been even more marked, as suggested by Pauly et al. (1998a). However, the relative
The observation that the FIB index significantly increased over the 53-year time-series (Fig. 3c), confirms that fisheries have expanded at a rate of more than 150 tonnes year\(^{-1}\), the factor that would have been necessary to result in no change in the FIB, assuming a trophic level decline of c. 0·03 year\(^{-1}\) and a 10-fold increase in fishery productivity for each full trophic level decline (Pauly, Christensen & Walters 2000b). Christensen (2000) observed that the FIB index for the north-east Atlantic as a whole increased greatly up until 1976, but has subsequently declined, indicating that the decrease in mean trophic level is no longer being matched by a sufficient increase in landings.

**ENVIRONMENTAL INFLUENCES**

There is very little evidence that low trophic level species (such as *Capros aper*) increase in abundance as a result of an easing of predatory pressure (a top-down trophic cascade effect) (Pinnegar et al. 2000). However, climate is thought to have a major impact on low trophic level pelagic fish abundances. Southward, Boalch & Maddock (1988) demonstrated that the abundance of herring *Clupea harengus* and pilchard *Sardina pilchardus* (Walbaum) occurring off the south-west of England closely corresponded with fluctuations in water temperature. Pilchard were generally more abundant and extended further to the east when climate was warmer, whilst herring were generally more abundant in cooler times. This pattern has apparently been occurring for at least 400 years, and major changes were noted in the late 1960s as waters cooled and spawning of pilchard was inhibited. During this time mackerel *Scomber scombrus*, another cold-water arctic-boreal species, started to become very abundant, and these environmental changes coincided with the development of the mackerel and subsequently other pelagic fisheries (Lockwood & Shepherd 1984; Southward, Boalch & Maddock 1988). Changes in the distribution of other Celtic Sea fish species have been observed to coincide with cold periods (Coombs 1975; Cushing 1982; Planque & Frédoù 1999), including declines in *Merluccius merluccius*, *Trachurus trachurus*, *Lophius piscatorius*, *Mullus surmuletus*, Conger conger (Linnaeus) and *Pollachius pollachius* (Linnaeus), which are considered warm-water species (Cushing 1982), and increases in *Gadus morhua*, *Molva molva*, *Pleuronectes platessa* Linnaeus, *Scyliorhinus canicula* (Linnaeus) and *Microstomus kitt*, which are considered cold-water species.

Since 1988, mean temperatures in the Celtic Sea, and north-east Atlantic generally, have been higher than during the three previous decades, and this has coincided with declines in the abundance of cold-water species including cod and haddock. O’Brien et al. (2000) showed that a combination of reduced spawning stock biomass due to overfishing and warm conditions resulting in reduced rates of recruitment were probably responsible for the recent near-collapse of cod stocks in the North Sea. Many of the species that increase in abundance during cool periods (e.g. cod, dogfish and ling) feed at high trophic levels, whilst many that increase during warm periods feed at lower trophic levels (e.g. horse-mackerel, pilchard and *Argentinia* spp.). Thus warming can exacerbate apparent declines in trophic level caused by fishing.

*Capros aper* is a species with a southerly distribution, and therefore we might expect increases in abundance during periods of warming, as has been observed here (Fig. 2c). Farina, Freire & Gonzalez Gurriaran (1997) also observed a recent increase in *Capros aper* at sites in the Bay of Biscay. These authors suggested that increased productivity associated with upwelling might have been responsible for such an influx, and several other non-commercial and low trophic level species were similarly observed to have increased over recent years (e.g. *Argentinia sphyraena* Linnaeus). Monkfishes *Lophius piscatorius* and *Lophius budegassa* Spinola, by contrast, declined in abundance, as was observed for the Celtic Sea (Fig. 2c). Bakun (1990) has demonstrated that the warming of the north-east Atlantic, by intensifying wind stress over the ocean surface, has led to an acceleration of coastal upwelling, which may have brought about the observed changes in demersal and pelagic fish distributions (Farina, Freire & Gonzalez Gurriaran 1997).

Caddy (2000a,b) and De Leiva Moreno et al. (2000) have proposed that pelagic resources of the north-east Atlantic have greatly benefited from anthropogenic nutrient inputs in recent years, and that Pauly et al. (1998a) may have underestimated the importance of bottom-up effects, particularly with reference to semi-enclosed seas. Eutrophication may render benthic habitats less suitable for demersal predatory and piscivorous species (e.g. cod), due to reduced oxygen levels in bottom waters. This can contribute to the establishment of an ecosystem dominated by small pelagic species (De Leiva Moreno et al. 2000). The Irish Sea (ICES area VII a), which adjoins the Celtic Sea (Fig. 1), was specifically highlighted by De Leiva Moreno et al. (2000) because plankton productivity has increased in this region markedly. Although the Celtic Sea is less enclosed, and is open to the north-east Atlantic, we cannot discount the possibility that eutrophication might also have contributed to the long-term trends we observed in this region. *Capros aper* has recently appeared in much greater numbers in the western Mediterranean (Abad & Giráldez 1990), a semi-enclosed sea, highly impacted by nutrient inputs (Caddy & Garibaldi 2000).
Fish prices are greatly influenced by changes in consumer income, current tastes or preferences and the price of alternative products on the market. They are also influenced by the ability of suppliers (fishermen) to land desirable fish, which in turn is reliant upon the availability of target species in the environment, capture restrictions and/or quotas, technological innovation as well as the weather (Lawson 1984; Ludicello, Weber & Wieland 1999). Analysis of our 22-year time-series of market prices for Celtic Sea fish demonstrated that high trophic level species have become relatively more expensive in comparison with low trophic level species, i.e. the steepness of the slope in the relationship between trophic level and price (the RPI) has increased. This is evidently because the expanding pelagic fisheries flooded the market with low trophic level fish and forced their prices down (e.g. horse-mackerel prices fell by 35% between 1984 and 1985). Conversely, many high trophic level fish, e.g. hake, cod, haddock, monkfish and small sharks, have become scarce (supply has declined but demand remains high) and their prices have risen. Similar trends have been observed on a world-wide basis and, as a group, the price of cod, hake and haddock (ISSCAAP group 32) rose from $714 per tonne in 1989 to $1080 per tonne in 1994 (accounting for inflation), reflecting world-wide declines in their abundance (OECD 1997; Ludicello, Weber & Wieland 1999). Sumaila (1998) suggested that, globally, low trophic level species have become more valuable in relation to high trophic level species over the past 50 years, which would result in a declining global RPI. Our analysis does not support this theory for the Celtic Sea; however, it is possible that in regions with a longer history of intensive exploitation the RPI might begin to decline, as surmised. The decline in the mean trophic level of landings we observed suggests some substitution has occurred, but this has not yet greatly affected fish prices. Increases in the price of previously less desirable species (but still high trophic level), such as saithe Pollachius virens, relative to other gadoids, does, however, point towards changes in the targeting of species within some ISSCAAP groups.

Fig. 6. Conceptual model illustrating how the relative price index (RPI) might develop over time, assuming increasing fishing effort. (1) Prices of high trophic level species increase as they become scarce, and there may be some substitution within high trophic level species. (2) Increases in the price of high trophic level species are partly offset by substitution with low trophic level species, i.e. the increase in both cancels out, and thus the slope of the relationship between trophic level and price (the RPI) stays the same. (3) High trophic level species become so scarce that they become commercially extinct. The fishery switches to targeting low trophic level species, forcing the price of these species up and thereby reducing the slope (RPI) until eventually negative. (4) Prices of low trophic level species become higher than prices of higher trophic level species, e.g. Sumaila (1998). Therefore RPI < 0.

or was due to environmental change which, in turn, led to increases in pelagic stocks, thus making the fisheries viable for the first time, or indeed whether the fishery only became viable because of improvements in gear technology.

In the past fish prices were largely governed by local patterns of demand and supply (e.g. cod and haddock in the UK; Taylor 1960), thus the RPI would be a useful indicator of trends in the underlying ecosystem. With increasing globalization, however, prices, particularly of high value species, tend to reflect relative abundance or scarcity on global markets. Asche, Bremnes & Wessells (1999) found that salmon prices were globally integrated, and that different salmon species (from the US and Norway) exhibited similar trends, irrespective of national boundaries. Hannesson (1999) reported similar integration among whitefish prices (e.g. cod and haddock) across US and European markets.

Our analysis indicates that fisheries typically will target species at high trophic levels. Although decreased abundance of high trophic level species will ultimately have negative economic consequences, the reduction in mean trophic level of the fish community may allow the system to sustain higher fishery yields overall. Management objectives for a particular fishery will depend on the relative value that society attaches to either economic profit or protein production. In developed western societies such as those surrounding the Celtic Sea, fish are primarily viewed as a luxury food and managers are
more likely to restrict fishing mortality on high trophic level species in an attempt to maximize long-term economic yields (e.g. by catch or effort control). This is less likely to be the case in developing nations where fish remain an essential source of protein (Kent 1998).

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