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Population biology of grey gurnard (*Eutrigla gurnardus* L.; Triglidae) in the coastal waters of Northwest Wales

**Running Title:** Population biology of grey gurnard

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**Summary**

The grey gurnard *Eutrigla gurnardus* (L.) has been identified by ICES as a potential commercial species in the NE Atlantic with recommendations made to derive information on population biology for stock assessment purposes. However, data on the population biology of this species is limited. In this study, data on the age, growth and maturity of grey gurnard were collected by otter trawling in the coastal waters of northwest Wales and Eastern Anglesey. Total length (TL) of fish sampled ranged between 2.1-33.0 cm (male) and 1.9-36.9 cm (female) with the majority of female (70.8%) fish between 11-20 cm TL and male fish (70.5 %) between 11-18 cm TL. The percentage of fish >20 cm TL was larger for females (30.4%) compared to males (17.6%). Total weight (TW) for female and male
grey gurnard in the stratified subsample ranged from 1.9-499.9 g for females and 2.1-390.0 g for males, with the majority of female (66.3%) and male (76.1%) fish between 10 and 60 g. TL/TW relations for male and female fish and both sexes combined were: TW = 0.006TL^{3.07}, TW = 0.007TL^{3.03} and TW = 0.007TL^{3.05} respectively. Age structure (based on otolith reading) ranged between 0.5 and 7.5 years old for females and 0.5 to 5.5 years old for male with the majority of female (41.7%) and male (45.95%) fish aged as 1.5 years old. The age structure of female and male grey gurnards was significantly different with the majority of older fish (> 2.5 years) being female. The von Bertalanffy growth functions were calculated as \( L_t = 32.4[1-e^{-0.24(t+1.41)}] \) for males, \( L_t = 45.9[1-e^{-0.16(t+1.37)}] \) for females and \( L_t = 44.0[1-e^{-0.18(t+1.20)}] \) for both sexes combined. Instantaneous rates of total mortality were similar for males and females and the combined Z value 1.00 year\(^{-1}\) with the natural mortality rate estimated as 0.33 year\(^{-1}\). The size at 50% maturity (\( L_{50} \)) was estimated to be 25.3 cm TL for males, females and for both sexes combined. Age at 50% maturity (\( A_{50} \)) was 3.2 years for both males and females. The results of this study provide the first information on the population biology of \( E. \) gurnardus in the Irish Sea, the first detailed study in the NE Atlantic since 1985 and helps to address the data gap identified by ICES in knowledge of the population biology of this species.

1 | INTRODUCTION

The grey gurnard \( Eutrigla gurnardus \) L. (Triglidae) is a demersal teleost fish found in the Eastern Atlantic (Norway to Morocco, Madeira, Iceland, including Greenland) and also in the Mediterranean and Black Sea (Froese & Pauly, 2017). Across its range it is commonly found on sandy substrates usually at depths between 10 to 140 m, although it is recorded as deep as 340 m in the E. Mediterranean (Froese & Pauly, 2017). Grey gurnard feed predominantly on crustaceans (mostly mysids and decapods) and fishes (especially gobies, flatfish, and young gadids) with the latter becoming more important as the fish increase in size (Moreno-Amich, 1994; Montanini, Stagioni & Vallisneri, 2010; Montanini, Stagioni, Benni & Vallisneri, 2017). \( E. \) gurnardus has been described as being a Lusitanian species (Yang, 1982) with historically a predominantly southern distribution in coastal waters around the UK but its distribution is shifting, moving North with climate change (Beare et al., 2004; Perry, Low, Ellis & Reynolds, 2005). It is ranked among the 10 most dominant
species in the North Sea, where its abundance has increased since the 1980s (Heessen & Daan, 1995; Floeter et al., 2005), possibly through occupying the ecological niche of demersal gadoids that had declined through overfishing (Floeter et al., 2005).

Historically the grey gurnard, together with other gurnard species, has formed a major part of discards in bottom trawl fisheries in the coastal shelf seas around the UK and Ireland (Borges, Rogan & Officer, 2005; Enever, Revill & Grant, 2007, 2009), although discard rates of the grey gurnard in some fisheries, e.g. the Dutch beam trawl fishery in the North Sea, have declined as new markets for grey gurnard have developed (Catchpole, van Keeken, Gray & Piet, 2008). With increasing pressure on demersal fish stocks in the north east Atlantic, ICES has recognized the grey gurnard, along with the red gurnard Chelidonichthys cuculus and tub gurnard C. lucerna, as new potential commercial species, (‘MoU species’; ICES, 2006). As interest in all 3 gurnard species has increased, ICES has recommended that landings and discards are monitored and information regarding population biology is obtained for stock assessment purposes, however, information remains limited for all three species (ICES, 2010, 2013, 2014a, 2015, 2016), especially biological data for the grey gurnard (ICES, 2010). A knowledge of ecology and population biology is essential in the development of sustainable management plans for any exploited species (King, 2007) but to the authors’ knowledge, there has been no study of the population biology (i.e. patterns of growth, mortality and reproduction) of grey gurnard in the Irish Sea, and no detailed study on the population biology of grey gurnard since Baron (1985a, 1985b) in the Bay of Douarnenez, France. Therefore, the aims of this study are to provide data on the population biology (specifically the size/age-structure and patterns of growth, maturity and mortality) of grey gurnard Eutrigla gurnardus within the coastal waters of Eastern Anglesey and Northwest Wales.

2 | MATERIALS AND METHODS

2.1 | Sample collection

Grey gurnards were collected between 2000 and 2015 (excluding 2005 and 2008) by the RV Prince Madog in the coastal waters around Eastern Anglesey and Northwest Wales (Figure 1) as part of the ongoing survey (since 1972) of local demersal fish stocks. Surveys were conducted during October of each year in the same five areas: (A) Red Wharf Bay,
(B) Conwy Bay, (C) Inshore Colwyn Bay, (D) Offshore Point Lynas and (E) Offshore Colwyn Bay (A-C designated as ‘inshore’ sites and D-E designated as ‘offshore’ site; see Marriott, Latchford & McCarthy, 2010). During the 14 years of sampling, 275 trawls were conducted at trawl depths between 10 and 32 m in inshore sites (205 trawls in total) and between 17 and 45 m in offshore sites (70 trawls in total) respectively. The five sampling areas have similar substrate with most sites comprising of gravelly sand, medium sand and broken shells, with the sites around Point Lynas and Red Wharf Bay comprising mainly of sandy gravel and sand respectively. Trawls of approximately 1 hour duration towed at 2-3 knots were conducted using a rockhopper otter trawl (cod end stretched mesh size of 73 mm), in the five survey areas. On completion of each trawl, the catch was sorted and all grey gurnard were retained and frozen. In the laboratory, the fish were defrosted overnight and the following data were collected: TL (to nearest 0.1 mm), total weight (TW, to nearest 0.1 g), sex and maturity status (immature or mature based on macroscopic examination of the gonads; Booth, 1997; King, 2007). Finally, the sagittal otoliths were removed and stored in paper envelopes until subsequent ageing. The age of each fish was determined as described by Marriott et al. (2010) using digital imaging techniques assuming one pair of opaque/hyaline bands formed each year (Colloca, Cardinale, Marcello & Ardizzone, 2003).

2.2 | Data analysis

The length-weight relationship was described using the power function $TW = aTL^b$ (King, 2007), where $a$ and $b$ are constants, with data for females and males examined separately and the slopes of the regression lines for the log-transformed data compared using a GLM to test for differences between the sexes. The $b$-values for males and females were also tested against a value of $b=3$ to test for isometric growth. The age structure of male and female fishes was compared using a chi-squared test. The relationship between mean length at age for male and female grey gurnard was described using the von Bertalanffy growth (VBG), $L_t = L_\infty[1-e^{-kt}]/(1-e^{-ko})$ (King, 2007), where $L_t$ is the average TL (cm) at age $t$ (years), $k$ is the growth coefficient (year$^{-1}$), $L_\infty$ is the asymptotic total length and $t_0$ is the theoretical age at length zero (year). The total instantaneous mortality rates ($Z$, year$^{-1}$) were calculated from the linearised catch curve data (King, 2007) for females and males and the slopes of the regression lines for the log-transformed data were compared using a GLM to test for
differences between the sexes. The instantaneous rates of natural mortality \((M, \text{ year}^{-1})\) were estimated using the Pauly (1980) equation based on growth in length and the average surface seawater temperature for the area (10.66°C; Moelfre and Amlwch stations; Joyce, 2006). The exploitation ratio, \(E = F/Z\) (King, 2007), was calculated for males and females combined where \(F\) (year\(^{-1}\)) is the instantaneous rate of fishing mortality (estimated as \(Z - M\)). The TL \((L_{50}, \text{ cm})\) and age \((A_{50}, \text{ years})\) at 50% maturity were calculated using the logistic equation \(Y = \frac{1}{1+e^{-r(L-X_{50})}}\) (King, 2007), where \(Y\) is the proportion of mature fish in the total length class \(L\) (cm), \(r\) is a constant and \(X_{50}\) is the TL or age at 50% maturity. In order to determine whether population biology parameters had changed over time, the correlation between year and length-weight coefficients, average/maximum size, or minimum/maximum age were determined using Pearson’s correlation coefficient. Data were grouped into three time periods: 2000-2004, 2006-2010 and 2011-2015 and differences in size at age in each age group examined using ANOVA or t-test and b-values of the log-transformed TL/TW relations examined using GLM. All data are presented as mean values ± SD with statistical analyses conducted in SPSS v22.

3 | RESULTS

In total, 1268 grey gurnard (732 females and 536 males) were caught with males and females ranging in TL between 2.1-33.0 cm and 1.9-36.9 cm (Figure 2A) respectively. The majority of female (70.8%) were between 11-20 cm TL and the majority of male fish (70.5%) were between 11-18 cm TL (Figure 2A). The percentage of fish >20 cm TL was larger for females (30.4%) compared to males (17.6%). TW for female and male grey gurnard in the stratified subsample ranged from 1.9-499.9 g for females and 2.1-390.0 g for males, with the majority of female (66.3%) and male (76.1%) fish between 10 and 60 g.

A total of 1021 fish could be aged (614 female, 407 male) with the age structure ranging between 0.5 and 7.5 years old for females and 0.5 to 5.5 years old for male fish (Figure 2B). For both females (41.7%) and males (45.9%), the majority of fish were 1.5 years old. The age structures of female and male grey gurnards in the subsample were significantly different \((\chi^2=34.8, P<0.001)\), with the older age classes consisting predominantly of female fish (Figure 2B).
The length-weight relationships for female and male grey gurnard and for both sexes combined are presented in Figure 3. Males exhibited positive allometric growth with a $b$ value significantly different from 3 ($\hat{b}=3.077$ [SE $b=0.033$]; $t_{534}=2.33$, $P=0.02$) whereas females exhibited isometric growth ($\hat{b}=3.030$ [SE $b=0.021$]; $t_{731}=1.43$, $P=0.15$). The slope values for the log-transformed linearised length-weight data for both female and male grey gurnard were similar ($F_{1,1266}=1.33$, $P=0.25$). The length-weight relationship for the combined data was described by $TW = 0.007T^{3.05}$ (SE $b=0.015$, $r^2=0.970$, $P<0.001$), with the $b$ value significantly different from 3 ($t_{1269}=3.0$, $P<0.001$).

VBG curves for female and male grey gurnard are presented in Figure 4 with the growth parameters presented in Table 1. Female grey gurnard attained a larger $L_{\infty}$ value than males ($\hat{L}_{\infty}^f=45.9$ cm; $\hat{L}_{\infty}^m=32.4$ cm). The growth curve for the combined male and female data is described by $L_t = 44.0[1-e^{-0.18(t+1.20.)}]$ ($r^2=0.948$, $P<0.001$).

There were no differences in the instantaneous rates of total mortality for males and females ($\hat{Z}^f=0.94$ year$^{-1}$, $\hat{Z}^m=1.13$ year$^{-1}$; $F_{1,6}=4.81$, $p = 0.07$) and the instantaneous rate of total mortality for males and females combined was $Z=1.00$ year$^{-1}$ with the instantaneous rates of natural mortality estimated as $M=0.33$ year$^{-1}$ and the exploitation ratio as $E=0.67$.

Length maturity ogives for male and female grey gurnard are presented in Figure 5. The calculated $L_{50}$ values for female, male and combined sexes were calculated as 25.34 cm ($\hat{L}_{50}^f$), 25.28 cm ($\hat{L}_{50}^m$) and 25.31 cm and the $A_{50}$ values for female and male grey gurnard were both calculated as 3.2 years respectively.

When the population biology data were examined to determine any temporal changes, there was no indication of changes in length-weight coefficients over time (Figure 6A) and the slope values for the log-transformed linearised length-weight data for the 5-year groupings were similar ($F_{1,1266}=0.19$, $P=0.83$; Table 2). Decreases in average length ($r=0.61$, $p=0.02$), maximum length ($r=0.47$, $p=0.09$) (Figure 2B) and maximum age (Figure 2C) were observed over time but these decreases coincided with an increase in the proportion of inshore fishing conducted in any given year ($r=0.54$, $p=0.04$) (Figure 2D). VBG curves could not be fitted to the size at age data for each 5 year grouping, however the average size for each time group were similar for each age group (0.5-2.5 years, ANOVAs, all $p=0.13-0.56$; 3.5-4.5 years, t-tests, $p=0.98$ and $p=0.23$ respectively) suggesting that patterns of growth were similar over time (Figure 6E). Patterns of maturity...
appeared similar over time (Figure 6F) with calculated $L_{50}$ values for 2000-2004 and 2011-2015 of 25.00 and 25.81 cm respectively (Table 2).

4 | DISCUSSION

ICES has identified the three main gurnard species in the NE Atlantic, red gurnard $C$. *cuculus*, tub gurnard, $C$. *lucerna* and grey gurnard *E. gurnardus* as potential new species for commercial exploitation (ICES 2006, 2013). However, detailed information on the population biology and landings/discard data for stock assessment purposes for each species within the different ICES subareas of the NE Atlantic is currently lacking. To help address this data gap, data from surveys conducted on all three triglid species in northwest Wales have been recently published: red gurnard (Marriott et al., 2010), tub gurnard (McCarthy & Marriott, 2017) and grey gurnard (this study). Population biology data for grey gurnard is limited. Although there have been many published studies presenting length-weight relationships for the species in the NE Atlantic and the Mediterranean (see Table 3), however, the number of published studies where multiple biological parameters, e.g. growth and reproduction, are co-reported is limited to studies in Brittany and the Faroe Islands (Table 1).

The maximum sizes reported in the literature for grey gurnard range from 50-60 cm depending on the population, although these values are for studies published between 1913 and 1969 (data from Algeria, English Channel, North Sea and Mediterranean reported in Table 2 of Baron, 1985a). More recent studies report maximum sizes of ca. 40-46 cm [Brittany, Baron (1985a); North Sea and Skaggerak, ICES (2010, 2014c); Bay of Biscay, ICES (2014d); Celtic Sea, ICES (2014b)]. In the present study, grey gurnard in the inshore coastal waters of NW Wales attained a maximum size of 37 cm TL and, since sampling was conducted at <45 m water depth, it is possible that larger fish may be located further offshore in deeper water. However, beam trawl surveys conducted at multiple sites within the Irish Sea report similar TL size-frequency distributions to that observed in the present study with a maximum size of 37 cm TL in Parker-Humphreys (2004) and 34 cm TL in ICES (2014b) indicating that the full size range for the species in the Irish was sampled within the study area. In addition, Parker-Humphreys (2004) presents data on the distribution and abundance of grey gurnards at 66 sites within the Irish Sea indicating that
in the eastern Irish Sea grey gurnards are caught at depths < 40 m and so the full depth range over which fish are likely to be found has also been sampled in the present study.

Positive allometric growth has been reported in the majority of grey gurnard studies (Tables 1 and 3) and average ‘a’ and ‘b’ values for the length-weight relationship from these studies are 0.007 and 3.06 respectively. The ‘a’ and ‘b’ values obtained for grey gurnard in northwest Wales are similar to this average (Table 1). The maximum age reported in the present study (8 years) is the same as that reported by Damm (1987) for grey gurnard in the North Sea, with a maximum age of 16 years reported by Baron (1985a) for grey gurnard in the Bay of Douarnenez, Brittany. The available data indicates that females grow faster than males and that the majority of larger individuals in the population are female (Baron 1985a; Damm, 1987; present study). Variability in size at age increased with increasing age class for both sexes (Figure 4) and it is possible that this could be due to dietary specialisation by some grey gurnards. An ontogenetic diet switch has been reported for the species with a change in dominant prey taxa from crustaceans (mostly mysids and decapods) to fishes (especially gobies, flatfish, and young gadids) as the fish increase in size (Moreno-Amich, 1994; Montanini et al., 2010). However, there is evidence to suggest individual dietary specialisation in grey gurnard with three putative feeding types (Weinert, Floeter, Krönke and Sell, 2010): a predator specialised on fish (FP), on invertebrates (IP) or having a mixed diet (MDP). Recent work by Montanini et al. (2017) also indicates increasing individual dietary specialisation in grey gurnard with increasing size. Weinert et al. (2010) found that fish condition, in terms of the length-specific individual weight, increased with specialisation on fish prey (FP > MDP > IP) and, although size at age and growth rates were not considered in their study, it is possible that the increased energy intake observed with specialisation on fish may translate into differences in growth (FP > MDP > IP) that may explain the larger size range observed with increasing age.

Although the population biology presented in this study was collected over a 16 year time period (2000-2015), there is little evidence for changes in length-weight relations and patterns of growth and maturity over time (Figure 6, Table 2) with changes in the size and age distributions over time related to an increase in inshore fishing in recent years. The population biology data for grey gurnards are limited (Table 1), however, the VBG
parameters (k and $L_\infty$) for northwest Wales are similar to those reported for the North Sea. Growth performance of grey gurnards from different populations can be compared using the phi prime growth performance index ($\Phi' = 2\log_{10}L_\infty + \log_{10}k$; Pauly and Munro, 1984) and the data are presented in Table 1. The average $\Phi'$ value for the three grey gurnard populations from the NE Atlantic studied is $2.84 \pm 0.24$ (range 2.53 - 2.96). The value recorded in the present study (2.53) is at the lower end of the $\Phi'$ values reported but within the range of published values.

For an accurate assessment of $L_{50}$, it is recommended that sampling should be conducted at the start of the reproductive season (Lowerre-Barbieri et al., 2011). Although this was not the case in the present study as the spawning season for grey gurnard is thought to be between February-August (Froese & Pauly, 2017), the $L_{50}$ values obtained in the present study were very similar to those obtained by most other studies in the NE Atlantic (Table 1. In contrast, Valisineri, Montanini & Stagioni (2012) observed a much smaller length at 50% maturity, 12 or 15 cm TL (♀ or ♂) for the single published study from the Mediterranean with Montanini et al. (2017) stating that grey gurnard may start to mature as small as 10 cm TL in the Mediterranean.

With the growing interest in gurnard species as MoU species, ICES has recommended that landings and discards are monitored and information on population biology is obtained for stock assessment purposes, however, information remains limited for red, tub and grey gurnards (ICES, 2010, 2013, 2015, 2016). Previously, gurnard landings were not sorted by species and were often reported as the generic category ‘gurnards’ and thus, species-specific data are only available from countries participating in gurnard fisheries since 2010 (ICES, 2015). The issue of accurately quantifying discard rates for each gurnard species in other demersal fisheries still remains unresolved although discard rates are thought to be very high (ICES, 2015, 2016). For example, the average discard rate for grey gurnards in the North Sea is estimated at 80% (ICES, 2016). As a result, the management advice provided for grey gurnard is limited and advises a precautionary approach with reduced landings until more detailed information on population biology, stock size, fishing pressure and discard rates are determined as these are currently unknown (ICES 2014b, 2014c, 2014d, 2016). The results of this study provide the first information on the population biology of $E.\ gurnardus$ in the Irish Sea, the first detailed study in the NE Atlantic since
1985 and helps to address the data gap identified by ICES in knowledge of the population biology of this species.

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The authors wish to thank the crew of the RV Prince Madog and the staff and students from the School of Ocean Sciences who conducted the fisheries surveys and collected much of the raw data used in this study.

REFERENCES


**FIGURE LEGENDS**

**FIGURE 1** Location of sampling sites trawled for grey gurnard *E. gurnardus* (L.) in the coastal waters of Eastern Anglesey and Northwest Wales. Inshore sites: (A) Red Wharf Bay; (B) Conwy Bay; (C) Colwyn Bay; Offshore sites: (D) Colwyn Bay (North of the Constable Bank); (E) Offshore Point Lynas.

**FIGURE 2** (A) Length-frequency distributions (Total Length, cm) and (B) Age-frequency distribution for male and female grey gurnard *E. gurnardus* (L.) sampled in October in the coastal waters of Northwest Wales, UK, between 2000 and 2015 (excluding 2005 and 2008).

**FIGURE 3** Length-weight relationships for (A) female and (B) male grey gurnard *E. gurnardus* (L.) sampled in October in the coastal waters of Northwest Wales, UK, between 2000 and 2015 (excluding 2005 and 2008).

**FIGURE 4** Length-at-age relationships for female (solid circles) and male (open circles) grey gurnard *E. gurnardus* (L.) sampled in October in the coastal waters of Northwest Wales, UK, between 2000 and 2015 (excluding 2005 and 2008).

**FIGURE 5** Maturity ogives (Total length at 50% maturity, *L*$_{50}$) for (A) female and (B) male grey gurnard *E. gurnardus* (L.) sampled in October in the coastal waters of Northwest Wales, UK, between 2000 and 2015 (excluding 2005 and 2008).

**FIGURE 6** Temporal changes in population biology data for grey gurnard *E. gurnardus* (L.) (both sexes combined) sampled in October in the coastal waters of Northwest Wales, UK, between 2000 and 2015 (excluding 2005 and 2008). Data are presented for (A) the a/b-values for the length-weight relationship, (B) mean and maximum Total length, (C) maximum and minimum age, (D) proportion of fishing tows conducted inshore, (F) length-at-age relationships and (F) maturity ogives (Total length at 50% maturity, *L*$_{50}$).
TABLE 1. Summary of studies where multiple population biology measures have been studied for grey gurnard *Eutrigla gurnardus*. Data are presented for the coefficients from the length-weight relationship (a, b), the von Bertalanffy growth function \( [L_\infty \text{ (cm)}, k \text{ (year}^{-1}), t_0 \text{ (years)}] \), the growth performance index \( \Phi' \) (Pauly & Munro, 1984) and length at 50% maturity \( (L_{50}) \). All length values are Total Length.

<table>
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<th>a</th>
<th>b</th>
<th>( L_\infty )</th>
<th>k</th>
<th>( t_0 )</th>
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TABLE 2. Summary the population biology data for grey gurnard *Eutrigla gurnardus* sampled in October in the coastal waters of Northwest Wales, UK, between 2000 and 2015 (excluding 2005 and 2008). Data are presented for the coefficients from the length-weight relationship (a, b), average and maximum Total Length (cm), maximum and minimum ages (years) and length at 50% maturity (L\(_{50}\)). The proportion of inshore tows conducted in each time period is also presented with the total number of tows in parentheses (see Figure 1 and Methods text for definition of ‘inshore’ versus ‘offshore’).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sample size</td>
<td>352</td>
<td>179</td>
<td>737</td>
</tr>
<tr>
<td>a</td>
<td>0.008 (0.099)</td>
<td>0.007 (0.099)</td>
<td>0.007 (0.095)</td>
</tr>
<tr>
<td>b</td>
<td>3.00 (0.033)</td>
<td>3.04 (0.034)</td>
<td>3.01 (0.035)</td>
</tr>
<tr>
<td>Average TL</td>
<td>20.7 (5.2)</td>
<td>14.3 (5.0)</td>
<td>15.8 (3.9)</td>
</tr>
<tr>
<td>Maximum TL</td>
<td>36.9</td>
<td>32.9</td>
<td>32.4</td>
</tr>
<tr>
<td>Minimum age</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Maximum age</td>
<td>7.5</td>
<td>2.5</td>
<td>4.5</td>
</tr>
<tr>
<td>L(_{50})</td>
<td>-</td>
<td>25.0</td>
<td>-</td>
</tr>
<tr>
<td>Proportion inshore</td>
<td>0.66 (n=66)</td>
<td>0.69 (n=101)</td>
<td>0.81 (n=118)</td>
</tr>
</tbody>
</table>

TABLE 3. Summary of studies presenting data on the Total Length-Total Weight relationship for grey gurnard *Eutrigla gurnardus*. Data are presented for males and females separately or for both sexes combined. Data are taken from Fishbase (Froese & Pauly, 2017) except where indicated by asterisks.

<table>
<thead>
<tr>
<th>Location</th>
<th>♂ a</th>
<th>♂ b</th>
<th>♀ a</th>
<th>♀ b</th>
<th>♂+♀ a</th>
<th>♂+♀ b</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scotland (N. Sea &amp; West Coast)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.006</td>
</tr>
<tr>
<td>North Sea</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.011</td>
</tr>
<tr>
<td>Portugal (S.coast)</td>
<td>0.024</td>
<td>2.72</td>
<td>0.017</td>
<td>2.86</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Pagassitikos Gulf, Greece</td>
<td>0.006</td>
<td>3.08</td>
<td>0.005</td>
<td>3.17</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Trikeri Channel, Greece</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.004</td>
</tr>
<tr>
<td>South Aegean Sea, Turkey*</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.004</td>
</tr>
<tr>
<td>Edremit Bay, Turkey**</td>
<td>0.007</td>
<td>3.08</td>
<td>0.006</td>
<td>3.17</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Sea Of Marmara, Turkey***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.011</td>
</tr>
</tbody>
</table>

* Bilge et al. (2014), ** Uçkun (2005), *** Bok et al. (2011)
Figure 2

(a) Distribution of fish by total length (cm) for males (solid bars, n = 536) and females (open bars, n = 732).

(b) Distribution of fish by age class (years) for males (solid bars, n = 407) and females (open bars, n = 614).
Figure 3

(a) Male
\[ W = 0.006L^{3.07} \]
\[ r^2 = 0.972, n = 536, p < 0.001 \]

(b) Female
\[ W = 0.007L^{3.03} \]
\[ r^2 = 0.967, n = 732, p < 0.001 \]
Figure 4

- Males (n = 407)
- Females (n = 614)
Figure 5

(a) Female
L_{50} = 25.34 cm
r^2 = 0.973
p < 0.001

(b) Male
L_{50} = 25.28 cm
r^2 = 0.979
p < 0.001
Figure 6