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Evidence of a relationship between weight and total length of marine fish in the North-eastern Atlantic Ocean: physiological, spatial and temporal variations

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Weight–Body Length relationships (WLR) of 45 fish species (37 Actinopterygii and eight Elasmobranchii) were investigated. A total of 31,167 individuals were caught and their biological parameters measured during the four quarters from 2013 to 2015, on five scientific surveys sampling the North-eastern Atlantic Ocean from the North Sea to the Bay of Biscay (ICES Divisions IVb, IVc, VIId, VIIe, VIIg, VIIh, VIIj, VIIIa and VIIIb). Among 45 tested species, all showed a significant correlation between total length (L) and total weight (W). The influence of sex on WLR was estimated for 39 species and presented a significant sexual dimorphism for 18 species. Condition factor (K) of females was always higher than for males. Moreover, a spatial effect on the WLR according to five ecoregions (the Bay of Biscay, the Celtic Sea, the Western English Channel, the Eastern English Channel and the North Sea), was significant for 18 species among 38 tested species. The temporal effect was tested according to components (year and quarter/season). The seasonality effect on WLR is more frequently significant than the year especially for the Elasmobranchii species, and can be related to the spawning season. Finally, depressiform species (skates, sharks and flatfish) are characterized by positive allometric growth, whereas there is no such clear pattern regarding roundfishes growth, whatever their body shape is.

Keywords: weight-length relationship, condition factor, Bay of Biscay, Celtic Sea, English Channel, North Sea, sexual dimorphism, seasonality

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INTRODUCTION

Biological information, such as body length and weight, constitute necessary data for assessing population structure, particularly to estimate the biomass from the length frequency distribution and to convert length-at-age to weight-at-age (Froese, 2006). However, conversely to length measurement it is difficult to obtain the weight with good accuracy during sampling at sea or from an underwater stereo-video system. Consequently, the characterization of the Weight-Length Relationship (WLR) allows for establishing the value of the unknown variable from the known variable. Moreover, this relationship is a sustainable proxy for the 'fatness' and 'general well-being' as the condition factor (Le Cren, 1951; Tesch, 1968; Weatherley & Gill, 1987). In fish species, WLR is often defined by an exponential function under conditions of isometric growth (regression follows the cube law; Ricker, 1975). However, in nature, this relationship depends on the environmental conditions – the physiological state of the fish also has to be considered (Le Cren, 1951; Froese, 2006; Pauly, 2010; Mozsar *et al*., 2015) – and the exponent or growth coefficient (b) can vary between 2.5 and 4 (Hile, 1936; Martin, 1949; Pauly & Gayanilo, 1997; Froese, 1998, 2006). In this study, the influence of factors such as sampling year and quarter, geographic area and sex were evaluated through the WLR which were estimated for 45 species, sampled during five scientific surveys operating from the North Sea to the Bay of Biscay and covering the entire length range from juveniles to adults.

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MATERIALS AND METHODS

Sampling was conducted on the research vessels 'Thalassa' and 'Gwen-Drez' each year from 2013 to 2015, totalling five bottom-trawl surveys (Figure 1):

- IBTS survey (International Bottom Trawl Survey), North Sea and Eastern English Channel, January–February (Vérin, 1992).
- CGFS survey (Channel GroundFish Survey), Eastern English Channel, October (Coppin & Travers-Trolet, 1989).
- CAMANOC survey (CAmpagne MANche Occidentale), Eastern and Western English Channel, September–October (Travers-Trolet & Vérin, 2014).

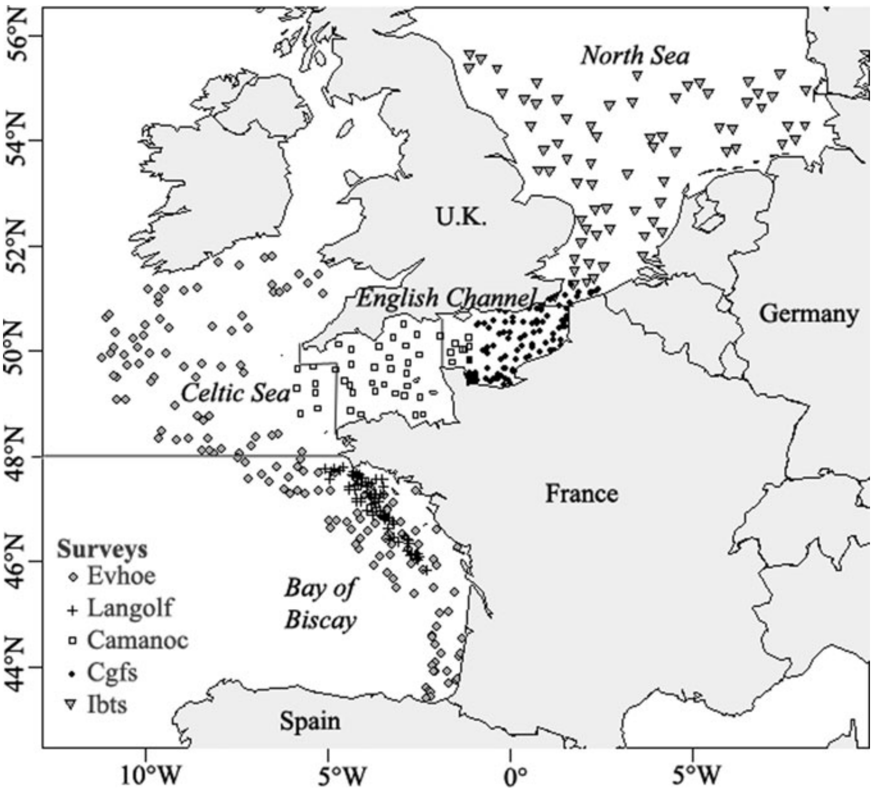

Fig. 1. Location of trawling stations from the Bay of Biscay to the North Sea sampled by the five scientific surveys (EVHOE, LANGOLF, CAMANOC, CGFS, IBTS), where the 31,167 individuals used in this study have been sampled.

- EVHOE survey (ÉValuation Halieutique de l'Ouest de l'Europe), the Celtic Sea and the Bay of Biscay, October-November (Mahé, 1987).
- LANGOLF (LANgoustine GOLFe de Gascogne), the Bay of Biscay, May (Garren & Martin, 2013).

For this study, 31,167 marine individuals were individually weighed (total weight, W to the nearest gram) and measured (Total length, L to the nearest centimetre below) on board from all daylight hauls. When possible, the sex of *Actinopterygii* and *Elasmobranchii* was determined by macroscopic observation of the gonads (ICES, 2014). A total of 45 species were determined: *Actinopterygii* ($N = 29{,}083$) represented by 37 species (28 roundfishes and nine flatfishes).

Elasmobranchii ($N = 2084$) represented by eight species (Table 1; Anonymous, 2016).

Before characterization of the WLR took place, all pairs of data for each species were plotted in order to identify and delete obvious outliers. In order to estimate the parameters of the allometric WLR (equation (1)), its base-10 logarithm (equation (2)) was fitted for each species to data using a least squared linear model:

$$W = aL^b. \qquad (1)$$

$$\log W = \log a + b \log L \qquad (2)$$

where '*a*' is the intercept or initial growth coefficient and '*b*' is the slope i.e. the growth coefficient (Le Cren, 1951; Ricker, 1975; Froese, 2006).

To investigate variations of the relationship between body length and weight for each species a completed Generalized Linear Model was performed according to the following explanatory variables:

- Geographic area (A): North Sea (ICES divisions IVb & IVc); Eastern English Channel (ICES division VIId), Western English Channel (ICES division VIIe), Celtic Sea (ICES divisions VIIg, VIIh & VIIj) and the Bay of Biscay (ICES divisions VIIIa & VIIIb).
- Sex (S): Female and Male.
- Sampling year (Y): 2013, 2014 and 2015.
- Sampling quarter (Q): 1, 2, 3 and 4.

For each species, data were deleted when the data number from explanatory variables was lower than 10. The individual weight of each species was modelled on body length as a continuous effect and geographic area, sex, sampling year and quarter as factors (equation (3)):

$$\log W \sim \log L + A + S + Y + Q + \log L \times A + \log L \times S + \log L \times Y + \log L \times Q \qquad (3)$$

with the separate influence of factors A ($\log L \times A$), S ($\log L \times S$), Y ($\log\ L \times Y$) and Q (*log* $L \times$ Q) on the relationship between body length and weight. For each species, the normality of the dataset was tested by a Quantile-Quantile Plot of the residuals (Zuur *et al.*, 2007).

To characterize the difference in the WLR for each species of fish, the condition factor, *K*, has been employed (Le Cren, 1951, equation (4)):

$$K = 1000.W/L^3 \qquad (4)$$

Table 1. Characteristics of the 45 fish species caught from the Bay of Biscay to the North Sea during 2013, 2014 and 2015: number of sampled individuals (N), mean length ± SD (cm), length range (cm), mean weight ± SD (g) and weight range (g).

Order	Family	Species	*N*	Mean length ± SD	Length range (cm)	Mean weight ± SD	Weight range (g)
Actinopterygii							
Roundfishes	*Ammodytidae*	*Hyperoplus immaculatus*	139	23.28 ± 3.30	13/36	34.2 ± 12.9	6/90
	Carangidae	*Trachurus trachurus*	244	19.11 ± 8.13	7/39	99.7 ± 101.3	4/540
		Clupea harengus	1342	20.93 ± 5.21	9/34	70.2 ± 51.0	5/292
	Clupeidae	*Sardina pilchardus*	111	18.30 ± 3.31	9/26	53.3 ± 29.7	7/138
		Sprattus sprattus	627	10.81 ± 2.16	5/15	12.4 ± 55.8	1/1400
	Congridae	*Conger conger*	94	90.50 ± 38.80	32/220	3 279.3 ± 6 185.3	46/45,000
	Engraulidae	*Engraulis encrasicolus*	289	13.62 ± 2.26	8/20	17.6 ± 10.9	1/66
		Gadus morhua	1452	45.80 ± 18.43	11/126	1 567.4 ± 2 172.2	15/24,020
		Melanogrammus aeglefinus	1476	36.50 ± 12.66	12/77	698.0 ± 753.7	17/4900
		Merlangius merlangus	6820	27.28 ± 8.13	8/62	220.0 ± 211.6	1/2348
	Gadidae	*Micromesistius poutassou*	52	15.77 ± 2.94	13/27	30.2 ± 25.5	15/149
		Pollachius pollachius	50	54.36 ± 14.16	15/82	1 815.2 ± 1 156.5	38/3894
		Trisopterus esmarkii	121	14.02 ± 3.60	9/25	3 756.1 ± 7 301.3	5/40,000
		Trisopterus luscus	506	24.79 ± 6.23	9/41	230.1 ± 156.4	8/900
		Trisopterus minutus	164	14.73 ± 3.25	7/20	38.4 ± 19.8	4/88
	Lophiidae	*Lophius budegassa*	489	29.94 ± 14.95	5/82	726.4 ± 1 054.8	2/7800
		Lophius piscatorius	375	41.61 ± 22.53	9/115	2 007.9 ± 2 878.3	10/19,720
	Merlucciidae	*Merluccius merluccius*	2038	39.37 ± 19.79	6/121	799.4 ± 1 283.4	1/11,100
	Moronidae	*Dicentrarchus labrax*	417	46.11 ± 11.35	16/83	1 221.8 ± 969.1	43/7140
	Mullidae	*Mullus surmuletus*	904	19.34 ± 5.99	8/39	122.9 ± 111.8	6/880
	Phycidae	*Phycis blennoides*	579	31.43 ± 10.25	13/60	323.7 ± 308.5	14/1870
	Scombridae	*Scomber scombrus*	43	31.33 ± 4.77	19/43	301.0 ± 174.9	56/830
	Sparidae	*Spondyliosoma cantharus*	209	21.62 ± 10.06	5/48	294.4 ± 353.6	4/2190
	Trachinidae	*Trachinus draco*	62	33.66 ± 6.74	12/47	291.8 ± 145.6	10/682
	Triglidae	*Eutrigla gurnardus*	266	24.04 ± 6.47	8/38	147.8 ± 109.5	5/480
		Chelidonichthys cuculus	1343	25.5 ± 5.9	7/42	186.1 ± 124.5	10/796
		Chelidonichthys lucerna	176	31.18 ± 8.30	3/64	380.5 ± 422.2	1/3080
Flatfishes	*Zeidae*	*Zeus faber*	251	32.55 ± 13.24	4/67	773.3 ± 727.3	3/4900
	Scophthalmidae	*Lepidorhombus whiffiagonis*	977	29.85 ± 10.11	7/58	271.9 ± 277.6	5/1450
		Scophthalmus maximus	74	39.92 ± 10.99	17/63	1 613.1 ± 1 332.0	92/6070
		Scophthalmus rhombus	61	36.07 ± 7.23	21/57	741.8 ± 523.2	175/2750
	Soleidae	*Solea solea*	945	26.14 ± 7.35	9/49	206.5 ± 184.6	4/1300
	Pleuronectidae	*Glyptocephalus cynoglossus*	117	32.42 ± 5.62	18/43	257.1 ± 135.1	30/592
		Limanda limanda	985	20.85 ± 5.10	5/37	114.4 ± 85.2	2/620
		Microstomus kitt	503	25.98 ± 5.27	10/45	238.9 ± 152.3	10/1175
		Platichthys flesus	98	28.15 ± 5.15	15/39	280.2 ± 175.8	35/960
		Pleuronectes platessa	4684	28.08 ± 7.09	10/57	257.0 ± 209.1	5/1945
Elasmobranchii							
	Arhynchobatidae	*Raja brachyurops*	45	60.98 ± 20.93	30/103	2 075.6 ± 2 235.1	142/10,650
		Raja clavata	608	62.25 ± 17.69	3/112	2 082.7 ± 1 597.0	50/7340
	Rajidae	*Raja montagui*	82	47.94 ± 15.23	12/74	943.2 ± 733.3	5/2700
		Raja undulata	144	68.08 ± 20.51	27/100	2 892.9 ± 2 206.7	200/7860
	Scyliorhinidae	*Scyliorhinus canicula*	176	50.93 ± 11.12	10/67	504.0 ± 377.1	18/3900
		Scyliorhinus stellaris	250	70.76 ± 23.84	17/113	2 095.8 ± 1 746.8	48/6660
	Trakidae	*Galeorhinus galeus*	87	93.14 ± 20.32	48/150	4 116.8 ± 3 163.7	514/17,040
		Mustelus asterias	692	80.78 ± 16.68	33/127	2 328.8 ± 1 552.5	116/8660

Within each class, species are listed in alphabetical order of their family.

Fish with a high value of K are heavy for their length, while fish with a low value are light for their length.

All statistical analyses were carried out using the 'CAR' package (Fox & Weisberg, 2011) in the statistical environment R (R Core Team, 2016).

RESULTS

Data relative to each species are presented in Table 1 with the number of measured specimens and the minimum, maximum and mean ± SD of length and weight. For *Actinopterygii*, measured length (29.0 ± 13.4 cm) and weight (401.3 ± 925.6 g) ranged respectively from 3 cm (*Chelidonichthys lucerna*) to 220 cm (*Conger conger*) and from 1 g (several species) to 45,000 g (*Conger conger*) and for *Elasmobranchii*, measured length (69.6 ± 21.4 cm) and weight (2173.8 ± 1967.8 g) ranged respectively from 3 cm (*Raja clavata*) to 150 cm (*Galeorhinus galeus*) and from 1 g (*Raja clavata*) to 19,000 g (*Mustelus asterias*) (Table 1). The samples were distributed by sex, sampling year, sampling quarter and by geographic area (Supplementary Table 1). Among the 45 tested

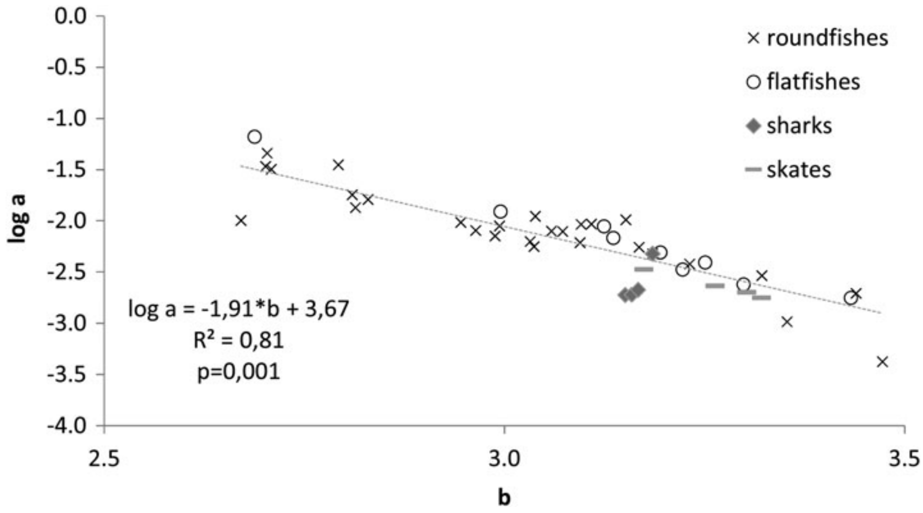

Fig. 2. Relationship between the WLR parameters showed by a scatter plot of mean log a over mean b for 45 fish species by distinguishing the *Actinopterygii* (roundfishes and flatfishes) and the *Elasmobranchii* (sharks and skates) with body shape information. The regression line was realized from 45 fish species.

species, all showed a significant correlation ($P < 0.05$) between body length and weight. The parameters of the WLR are given in Supplementary Table 2. The initial growth coefficient '*a*' varied from $4.2 \times 10^{-4} \pm 1.0 \times 10^{-5}$ in *Conger conger* to $6.6 \times 10^{-2} \pm 4.8 \times 10^{-2}$ in *Scophthalmus maximus*, while the growth coefficient '*b*' ranged from $2.7 \pm 1.2 \times 10^{-2}$ in *Hyperoplus immaculatus* to $3.5 \pm 8.2 \times 10^{-3}$ in *Conger conger*. The coefficients of the WLR are significantly correlated (Figure 2). Among the 45 tested species, the value of b was under 3 for 14 species (31.1%) with 12 roundfishes and two flatfishes (Supplementary Table 2). All *Elasmobranchii* species presented positive allometric growth (coefficient b higher than 3) (Supplementary Table 2; Figure 2).

The four explanatory variables presented a significant effect on the WLR (Table 2), but only for whiting (*Merlangius merlangus*) and striped red mullet (*Mullus surmuletus*), were all four effectively significant at the same time. The influence of sex was estimated on the 39 species for which macroscopic observation was sufficient to determine sex identification. Slopes of WLR were significantly different between males and females for only 18 species (46.1%) of which 14 were *Actinopterygii* (Family *Pleuronectidae: Pleuronectes platessa, Limanda limanda, Microstomus kitt, Platichthys flesus*; Family *Soleidae: Solea solea*; Family *Scophthalmidae: Scophthalmus maximus*; Family *Moronidae: Dicentrarchus labrax*; Family *Merlucciidae: Merluccius merluccius*; Family *Gadidae: Merlangius merlangus, Trisopterus esmarkii*; Family *Mullidae: Mullus surmuletus*, Family *Trachinidae: Trachinus draco*; Family *Phycidae: Phycis blennoides*; Family *Triglidae: Chelidonichthys cuculus*) and four were *Elasmobranchii* (Family *Trakidae: Mustelus asterias*; Family *Scyliorhinidae: Scyliorhinus canicula*; Family *Rajidae*: *Raja clavata, Raja montagui*) (Table 1). The effect of the sex factor is more often observed in *Elasmobranchii* (50%) than in *Actinopterygii* (35.1%). Nevertheless, in *Actinopterygii*, this result fluctuated according to the fish shape (66.6% of flatfishes *vs* 21.9% of roundfishes). The geographic factor of dividing the results into five sampling ecoregions from the Bay of Biscay to the North Sea, was significant on WLR of only 18 species among 38 tested species (where species occur in sufficient number in these areas) (47.4%). These species were composed of 17 *Actinopterygii* (*Hyperoplus immaculatus, Limanda limanda, Merlangius merlangus, Chelidonichthys cuculus, Lophius piscatorius, Sardina pilchardus, Gadus morhua, Lophius budegassa, Microstomus kitt, Phycis blennoides, Merluccius merluccius, Melanogrammus aeglefinus, Dicentrarchus labrax, Solea solea, Mullus surmuletus, Pollachius pollachius, Pleuronectes platessa*) and only one *Elasmobranchii* (*Raja undulata*) (Table 2). Contrary to the sexual dimorphism, the spatial effect on the WLR was measured essentially for the *Actinopterygii.* The temporal effect on the WLR must be divided at two observation scales with the variations inter-years and intra-year (seasonality effect represented by the quarters). Among the 29 tested species with both temporal effects, only five (17.2%, *Gadus morhua, Merlangius merlangus, Lophius piscatorius, Mullus surmuletus, Mustelus asterias*) presented both significant variations inter-years and intra-year. Additionally, the year effect and the seasonality effect were significant at the level of 32.4 and 35.3% respectively. In *Elasmobranchii* the seasonality effect (42.8%) was more significant than between years (11.1%; Table 2).

To compare the fatness of each fish species according to geographic area, sex, sampling year and quarter, the condition factor (*K*) was estimated (Table 3). In the event of significant sexual dimorphism, all condition factors (*K*) of females were higher than those of males (Table 3). For the other tested factors, the highest values of *K* were distributed between all sampled years, areas and quarters; there was no observable trend (Table 3).

DISCUSSION

The large sample data (N = 31,167) used in this study allows exploration of the possible effects of factors influencing the allometric WLR. According to Hile (1936); Martin (1949); Pauly & Gayanilo (1997) and Froese (1998, 2006), '*b*' values may range from 2.5 to 4 for fish, which is the case for the values estimated in our study. Moreover, the study showed

Table 2. *P*-value for the relationship between weight and body length (W-L) and for the influence of sex.

Order	Family	Species	W-L	Area	Year	Quarter	Sex
Actinopterygii							
Roundfishes	*Ammodytidae*	*Hyperoplus immaculatus*	<0.001	<0.001	–	0.646	–
	Carangidae	*Trachurus trachurus*	<0.001	0.602	–	0.186	–
		Clupea harengus	<0.001	0.139	<0.001	–	0.918
	Clupeidae	*Sardina pilchardus*	<0.001	<0.001	0.026	–	0.621
		Sprattus sprattus	<0.001	0.562	0.174	–	0.099
	Congridae	*Conger conger*	<0.001	0.092	0.097	0.745	–
	Engraulidae	*Engraulis encrasicolus*	<0.001	0.322	0.725	0.002	0.778
	Gadidae	*Gadus morhua*	<0.001	<0.001	0.092	<0.001	0.729
		Melanogrammus aeglefinus	<0.001	0.004	0.191	<0.001	0.585
		Merlangius merlangus	<0.001	<0.001	0.018	<0.001	0.008
		Micromesistius poutassou	<0.001	–	–	–	–
		Pollachius pollachius	<0.001	0.045	0.120	0.443	0.413
		Trisopterus esmarkii	<0.001	–	<0.001	–	0.049
		Trisopterus luscus	<0.001	0.745	<0.001	0.934	0.225
		Trisopterus minutus	<0.001	0.616	–	0.053	–
	Lophiidae	*Lophius budegassa*	<0.001	<0.001	0.289	0.438	0.764
		Lophius piscatorius	<0.001	<0.001	<0.001	0.039	0.562
	Merlucciidae	*Merluccius merluccius*	<0.001	0.002	0.392	0.003	0.008
	Moronidae	*Dicentrarchus labrax*	<0.001	0.005	0.403	0.162	0.002
	Mullidae	*Mullus surmuletus*	<0.001	0.020	<0.001	<0.001	0.047
	Phycidae	*Phycis blennoides*	<0.001	0.001	0.731	–	0.040
	Scombridae	*Scomber scombrus*	<0.001	–	–	–	–
	Sparidae	*Spondyliosoma cantharus*	<0.001	0.123	–	0.586	0.225
	Trachinidae	*Trachinus draco*	<0.001	–	–	–	0.016
	Triglidae	*Eutrigla gurnardus*	<0.001	0.600	0.611	0.629	0.233
		Chelidonichthys cuculus	<0.001	<0.001	0.001	0.583	0.047
		Chelidonichthys lucerna	<0.001	0.544	0.327	0.850	0.498
	Zeidae	*Zeus faber*	<0.001	0.944	0.565	<0.001	0.585
Flatfishes		*Lepidorhombus whiffiagonis*	<0.001	0.971	<0.001	0.909	0.867
	Scophthalmidae	*Scophthalmus maximus*	<0.001	0.808	0.322	0.446	0.016
		Scophthalmus rhombus	<0.001	0.280	0.137	0.279	0.288
	Soleidae	*Solea solea*	<0.001	0.007	0.274	0.119	0.016
		Glyptocephalus cynoglossus	<0.001	–	0.650	–	0.542
	Pleuronectidae	*Limanda limanda*	<0.001	<0.001	0.041	0.188	<0.001
		Microstomus kitt	<0.001	0.001	<0.001	0.222	0.001
		Platichthys flesus	<0.001	0.882	–	–	0.009
		Pleuronectes platessa	<0.001	0.045	0.127	<0.001	<0.001
Elasmobranchii							
	Arhynchobatidae	*Raja brachyurops*	<0.001	–	0.077	–	0.404
		Raja clavata	<0.001	0.366	0.078	0.584	0.005
	Rajidae	*Raja montagui*	<0.001	0.334	0.667	0.171	0.009
		Raja undulata	<0.001	0.019	0.181	0.020	0.428
	Scyliorhinidae	*Scyliorhinus canicula*	<0.001	0.180	0.139	<0.001	<0.001
		Scyliorhinus stellaris	<0.001	0.564	0.669	0.592	0.237
	Trakidae	*Galeorhinus galeus*	<0.001	–	0.406	0.686	0.382
		Mustelus asterias	<0.001	0.643	0.000	0.011	0.000

Geographic area, Sampling year and Quarter on the WLR ($P < 0.05$ in grey cell) of the 45 fish species caught from the Bay of Biscay to the North Sea during 2013, 2014 and 2015. No value in the cell (–) indicates that the factor was not tested because there was only one modality.

that the coefficients of the WLR were significantly correlated. The growth coefficient (b) reflected firstly the shape and the fatness of the fish species. Consequently, the *Elasmobranchii* (sharks and skates) and the flatfishes presented only one body shape, known as depressiform, and consequently the weight growth was higher than the length growth ($b > 3$; Figure 2). This result corroborated the results obtained for *Elasmobranchii* (Pallaoro *et al*., 2005; Yeldan & Avsar, 2007; Yığın & Ismen, 2009) and for *Soleidae* (Torres *et al*., 2012). Among 28 roundfish species, the b values were within the range of 2.5–3.5 and there was no observed trend in body shape due to its large range of shapes as fusiform (i.e. *Gadus morhua*), arrow-like (i.e. *Hyperoplus immaculatus*), ribbon-like (*Conger conger*) or laterally flattened (i.e. *Trachurus trachurus*). The difference of shapes could be characterized by the 'form factor' equation of the log a–b relationship (Froese, 2006; Verreycken *et al*., 2011).

For all 45 species, the body length-weight relationship was significant. Our analyses confirmed those observed in the North-eastern Atlantic Ocean (Dorel, 1986; Coull *et al*., 1989; Silva *et al*., 2013; Wilhelms, 2013), in Greek waters (Petrakis & Stergiou, 1995), in the Persian Gulf (Naderi *et al*., 2013) and in the Aegean Sea (Moutopoulos & Stergiou, 2002). Consequently, it is possible for these marine

Table 3. Mean value of condition factor (K) of the 45 fish species according to each modality of the explanatory factors (Geographic area, Sex, Sampling year and Quarter) on the WLR. Grey cells indicate that a factor appears to have a significant effect ($P < 0.05$) on the WLR (see Table 2 for P-values).

Order	Family	Species	Areas					Sex			Year			Quarter			
			VIIIa, b	VIIg, h, j	VIIe	VIId	4	F	M	−1	2013	2014	2015	1	2	3	4
Actinopterygii																	
Roundfishes	*Ammodytidae*	*Hyperoplus immaculatus*			0.25	0.21				0.27		0.27				0.25	0.27
	Carangidae	*Trachurus trachurus*			0.94	0.92				0.93		0.93				0.94	0.91
		Clupea harengus				0.68	0.61	0.63	0.62	0.64	0.64	0.63	0.61	0.62		0.63	0.61
	Clupeidae	*Sardina pilchardus*	0.77			0.88		0.79	0.75	0.78	0.79	0.77	0.85			0.87	0.78
		Sprattus sprattus				0.72	0.70	0.73	0.72	0.74	0.74	0.70	0.69	0.71		0.82	0.87
	Congridae	*Conger conger*	0.21	0.24	0.22	0.25		0.22		0.22	0.22	0.22	0.23			0.23	0.22
	Engraulidae	*Engraulis encrasicolus*	0.61		0.63	0.62		0.62	0.62	0.63	0.61	0.63	0.65			0.64	0.62
		Gadus morhua		1.05	1.10	1.03	1.02	1.04	1.03	1.01	1.04	1.02	1.04	1.03		1.01	1.04
		Melanogrammus aeglefinus	1.02	1.03	1.09	1.09	0.90	1.02	1.00	1.03	0.99	1.03	0.98	0.90		1.09	1.03
		Merlangius merlangus	0.79	0.85	0.80	0.83	0.83	0.84	0.82	0.82	0.85	0.83	0.83	0.84		0.80	0.83
	Gadidae	*Micromesistius poutassou*			0.69					0.69		0.69				0.69	
		Pollachius pollachius			0.93	0.97		0.96	0.94	1.02		0.97	0.94	0.97		0.94	0.97
		Trisopterus esmarkii					0.71	0.75	0.69	0.70	0.75		0.70	0.71			
		Trisopterus luscus			1.26	1.27		1.29	1.27	1.31	1.31	1.31	1.23			1.27	1.30
		Trisopterus minutus			1.12	1.06				1.08		1.08				1.09	1.05
	Lophiidae	*Lophius budegassa*	1.57	1.46				1.55	1.49	1.59	1.52	1.61			1.55		1.53
		Lophius piscatorius	1.28	1.45				1.31	1.31	1.48	1.46	1.02			1.51		1.31
	Merlucciidae	*Merluccius merluccius*	0.71	0.71	0.77			0.71	0.69	0.78	0.73	0.70				0.77	0.71
	Moronidae	*Dicentrarchus labrax*	1.02	1.09	0.90	1.08	0.99	1.08	1.04	1.05	1.07	1.05	1.07	1.04		1.06	1.06
	Mullidae	*Mullus surmuletus*	1.28	1.30	1.32	1.09	1.08	1.31	1.28	1.25	1.29	1.31	1.26	1.11	1.22	1.31	1.33
	Phycidae	*Phycis blennoides*	0.76	0.79				0.80	0.73	0.73	0.75	0.79	0.77				0.77
	Scombridae	*Scomber scombrus*			0.89					0.89		0.89				0.89	0.87
	Sparidae	*Spondyliosoma cantharus*			1.76	1.80		1.75	1.76	1.78	1.80	1.76	1.79			1.77	1.80
	Trachinidae	*Trachinus draco*				0.66		0.68	0.64	0.65	0.64	0.66	0.64			0.65	0.68
	Triglidae	*Eutrigla gurnardus*	0.83	0.84		0.87	0.88	0.88	0.88	0.86	0.85	0.87	0.88	0.88			0.85
		Chelidonichthys cuculus	0.98	0.92	0.93	0.97		0.97	0.92	0.97	0.97	0.94	0.98	0.95		0.95	0.96
		Chelidonichthys lucerna	0.99	0.99		1.00		0.97	0.96	1.09	0.97	1.00	1.00	0.94		1.00	1.00
	Zeidae	*Zeus faber*	1.82	1.89	1.89	1.94		1.78	1.72	1.83	1.72	1.63	1.75			1.51	1.94
Flatfishes	*Scophthalmidae*	*Lepidorhombus whiffiagonis*	0.72	0.73	0.78			0.73	0.70	0.85	0.72	0.77			0.73	0.74	0.73
		Scophthalmus maximus	1.86	1.85	1.89	1.92	1.93	2.00	1.91	2.04	2.00	2.00	1.89	1.99	2.01	1.93	1.99
		Scophthalmus rhombus		1.46		1.43	1.41	1.43	1.36	1.41	1.33	1.41	1.34	1.41		1.40	1.46
	Soleidae	*Solea solea*	0.87	0.99	1.03	0.93	0.94	0.92	0.88	0.91	0.92	0.95	0.97	0.93	0.87	0.88	0.91
		Glyptocephalus cynoglossus		0.67				0.68	0.67	0.68	0.70	0.68	0.67				0.67
	Pleuronectidae	*Limanda limanda*			1.14	1.11	1.02	1.07	0.98	1.19	1.06	1.04	1.07	1.04		1.11	1.12
		Microstomus kitt	1.11	1.15	1.23	1.29		1.24	1.16	1.20	1.12	1.21	1.29			1.22	1.20
		Platichthys flesus				1.13	1.09	1.18	1.06	1.14	1.11	1.14	1.06	1.10			1.15
		Pleuronectes platessa		1.08	1.00	0.98	0.91	0.97	0.93	1.00	0.96	0.94	0.97	0.92		1.00	1.04

Continued

Table 3. Continued

Order	Family	Species	Areas					Sex			Year			Quarter			
			VIIIa, b	VIIg, h, j	VIIe	VIId	4	F	M	−1	2013	2014	2015	1	2	3	4
Elasmobranchii																	
	Arhynchobatidae	*Raja brachyurops*				0.69	0.76	0.71	0.70		0.75	0.69	0.72	0.76		0.69	0.72
	Rajidae	*Raja clavata*			0.68	0.71	0.70	0.73	0.68	0.59	0.65	0.73	0.70	0.70		0.69	0.71
		Raja montagui			0.64	0.61	0.63	0.65	0.58	1.12	0.59	0.64	0.63	0.63		0.64	0.61
		Raja undulata			0.75	0.71		0.74	0.73		0.72	0.75	0.68		0.86	0.74	0.70
	Scyliorhinidae	*Scyliorhinus canicula*	0.35	0.37	0.33	0.36		0.36	0.30	0.34	0.39	0.34	0.37			0.33	0.38
		Scyliorhinus stellaris			0.47	0.45		0.46	0.44	1.26	0.42	0.46	0.45		0.45	0.46	0.45
	Trakidae	*Galeorhinus galeus*		0.47	0.45	0.45		0.45	0.45	0.47	0.47	0.45	0.45			0.43	0.46
		Mustelus asterias		0.37	0.36	0.39		0.41	0.36	0.35	0.37	0.40	0.36		0.35	0.38	0.40

Only the individuals where the sex was determined were tested (F: female; M: male; -1: no sex information available).

species to use WLR to estimate weight from length or vice versa. For each species, significant differences could nevertheless be observed according to sex, sampled year, seasonality and geographic area. The first tested factor is the sex. The sexual dimorphism influenced significantly the WLR of a few species as observed in the Azores Islands (Morato *et al.*, 2001). The difference observed between males and females for striped red mullet (*Mullus surmuletus*) corroborated the previous study on this species during 2004 in the Eastern English Channel (Mahé *et al.*, 2013). The results of sexual dimorphism effect on the WLR were similar in the Eastern Adriatic Sea, except for *Mustelus asterias*, but the low number of data in the Mediterranean Sea for one species could be one explanation (Pallaoro *et al.*, 2005). According to the value of *K*, sexual dimorphism manifests as females being heavier than the males at the same length. This trend was observed both in the *Actinopterygii* and *Elasmobranchii*. The current study was realized using five surveys covering all ecoregions, from the Bay of Biscay to the North Sea. Consequently, significant differences in their WLR were observed for many widely distributed species across their distribution area. These differences were a result of many morphotypes within a species or a family. For striped red mullet (*Mullus surmuletus*), there were two morphotypes according to the head shape between South and North populations (Bay of Biscay/Eastern English Channel; Mahé *et al.*, 2014), which could explain the observed difference of condition factors. The head morphological variation, for one species between two geographic areas or habitats, is influenced by feeding behaviour (Hyndes *et al.*, 1997; Janhunen *et al.*, 2009). Within a family, values or the trend of condition factors between two similar species could be opposite. This has been observed between *Lophius budegassa* and *Lophius piscastorius* and between *Scophthalmus maximus* and *Scophthalmus rhombus* during the same sampling years and quarters. Seasonal or annual differences in WLR and therefore in condition factor may be generally related to reproduction (gonad development and spawning period) or feeding activities (food availability and feeding rate) (Bagenal & Tesch, 1978; Weatherley & Gill, 1987; Wootton, 1990) but also attributed to differences in sampling, particularly length ranges. Throughout a year, significant difference of the condition factor according to the spawning period for each species (Supplementary Table 3), showed that the specimens were heaviest just before and during the spawning period. This seasonal oscillation of the WLR and the condition factor could be explained by environmental factors such as temperature but also by the availability of food and the physiological state of the fish (i.e. degree of gonad development) (Le Cren, 1951; Froese, 2006; Pauly, 2010; Mozsar *et al.*, 2015).

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at https://doi.org/10.1017/S0025315416001752

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