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Evaluating the potential impact of fishing on demersal species in the Bay of Biscay using simulations and survey data

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Abstract:

Fishing affects fish populations through direct and indirect effects. It can change size structures and/or modify population mean weights. Reference values are thus needed to assess the status of populations in exploited ecosystems. These reference values can either be set by a historical approach, i.e. using information from before the onset of exploitation or overexploitation, or by a simulation approach. Using a model based on life-history parameters, we predicted population mean weights and length structures at equilibrium (in the absence of fishing and for fishing equal to different fishing mortalities) which we compared with contemporary data collected during scientific surveys in the Bay of Biscay. Contemporary mean weights were 88% to 30% smaller than expected for unexploited populations for 10 out of the selected 18 demersal species. Part of this difference might be explained by the survey not covering all age classes in the population, as demonstrated for *Merluccius merluccius*. We found that species with larger asymptotic length and slower growth were generally more impacted by fishing than smaller, faster growing species. Assuming that species specific life-history traits are well documented and/or easily measurable, the simulation approach can provide a useful tool for setting indicator reference levels for mean weight and size structures.

Highlights

► The study provides an evaluation of the potential impact of fishing in the Bay of Biscay. ► It compares simulated and contemporary mean weights for 18 fish populations. ► Contemporary mean weights were 88% to 30% smaller.

Keywords: Indicators ; Fishing impacts ; Ecosystem based management ; Fish community ; Reference points ; Northeast Atlantic

1 Introduction

The abundance of marine fish populations changes over time, both at local and global scales. Human activities play an important role in these variations, notably through overexploitation (Lotze and Worm, 2009), and anthropogenic-induced climate change (Hoegh-Guldberg and Bruno, 2010). Recent analyses of fishing impacts on life-history traits may underestimate the extent of these changes because (i) certain life history traits make some populations more resistant than others to fishing pressure, so that the relative short time spans of scientific surveys may not be long enough to observe these changes (Andersen and Brander, 2009); (ii) the analyses are mostly based on time series that started after the beginning and the acceleration of exploitation, which leads to a shift in the baseline used for assessments (Pauly, 1995); (iii) very few areas are not impacted by human activities which makes it unlikely to find an area of reference to set the baseline (Jackson et al., 2001).

One method to assess the impact of fishing on marine populations is to use indicators describing the studied system (Jennings, 2005). A wide range of indicators are known to describe the fisheries-induced changes in exploited populations and communities (Rochet and Trenkel, 2003; Fulton et al., 2005; Jennings, 2005; Shin et al., 2005). At the population level, impacts of fishing can either be direct: fisheries remove the oldest, largest individuals from the exploited populations (Rochet and Trenkel, 2003), or indirect: genetic selection driven by fishing affects growth rates, age- and size-at-maturation and reproductive output (Andersen and Brander, 2009). At the community level, there are potential indirect effects through habitat modification and/or food web propagation (Hiddink et al., 2011). Depletion of the largest species tends to release predation pressure which can result in a better survival of small species (Shin et al., 2005).

Reference values are needed to assess population and ecosystem status using indicators. These reference values can either be set by a historical approach, i.e. using information collected before the onset of overexploitation (Lotze and Worm, 2009), or by simulating population structures in the absence of fishing (Jennings and Blanchard, 2004). Both methods do not necessarily give the same results, as in simulation studies current environmental conditions are generally assumed while historical data were probably collected under different environmental conditions. This can lead to confounding of the effects of fishing and those caused by environmental change (Jennings and Blanchard, 2004). Simulating populations at equilibrium assuming constant recruitment means that only mortality determines population structure. If the assumed mortality corresponds to natural mortality, the simulated mean weights and sizes provide reference values for evaluating the combined direct and indirect effects of fishing on exploited populations. Studying indirect effects on non target species is a necessary step towards ecosystem-based fisheries management which requires knowledge of the relationships between the different species and compartments of the system (Hall and Mainprize, 2004).

The Bay of Biscay has been exploited for a long time, making fishing the human activity with the most widespread impact (Lorance et al., 2009). This impact persists on both the population and community level (Rochet et al., 2005). A strong increase in fishing effort occurred in the late 19th century when steam trawlers replaced sailing boats (Quéro and Cendrero, 1996). Historical documents show that some species such as large elasmobranches were already impacted at that time, and the increase of fishing effort combined with the industrialisation of fishing activities conducted to further depletion of some species. Historically, groundfishes represented most of the target species, as bottom trawls were the principal gears used in the Bay of Biscay (Quéro and Cendrero, 1996). More than a century later in the early 2000s, landings of small pelagic species such as sardine and anchovy were the most important in weight for French vessels, but a large number of groundfish species were still landed in substantial amounts, caught by a diversity of fishing gears (Daurès et al., 2009). Though French fleet size has decreased over the last decades as the result of vessel decommissioning programs aimed at reducing overcapacity, the expected positive effects for all exploited populations have not been observed (Rochet et al., 2012). Regarding environmental conditions, water temperatures have increased in the Bay of Biscay over the second half of the 20th century by on average 0.2 °C per decade (Michel et al., 2009). This might have impacted the ecosystem on several levels; improved growth conditions are compatible with the food web changes observed by Rochet et al. (2010).

Here we study the potential impact of fishing on several groundfish stocks in the Bay of Biscay by comparing mean equilibrium weight and size distribution of simulated populations with those derived from survey data. The results are then discussed at the scale of populations and the assemblage, bearing in mind the possible short comings of survey data.

2 Material and Methods

Two types of data were used: (i) scientific survey data for the calculation of contemporary mean weights of exploited populations and (ii) life history parameters for the estimation of the mean weight for simulated populations.

2.1 Survey data collection

The data were collected during the scientific survey EVHOE. Survey data for the period 1987 to 2009 were used. They were collected annually in autumn between 43.7°N and 47.9°N using a stratified random sampling design. The data covered a relatively wide bathymetric range (15 - 623 m; Figure 1). The sampling gear was a GOV trawl 36/47 with 4 m vertical opening, 20 m horizontal opening and a mesh size of 20 mm in the codend. For each haul, individuals were identified, counted, weighed and measured to the lower centimetre. A total of eighteen demersal species were selected for this study (Table 1). Length restrictions were applied to account for the size-selectivity of the gear (see section 2.3.3 for details). It is worth mentioning that not all species are commercially targeted.

2.2 Estimating mean weight

2.2.1 Mean weight from simulated populations

For each species, estimates of mean weight in the absence of exploitation were obtained in several steps. First, adult (at maturation) natural mortality M in the absence of fishing was estimated from life history parameters using the equation by Andersen et al. (2009)

$$M = 3 \; (\Phi / \alpha) \; \eta^{-1/3} K \qquad [1]$$

with Φ the geometric factor of the predation size selection function, α the assimilation efficiency of standard metabolism, η the size at maturation divided by the asymptotic size and K the growth parameter of the von Bertalanffy growth function. For this study, Φ was set to 0.12 (Andersen et al., 2009) and α to 0.8 for all species as most of the selected species are carnivorous with a relatively high assimilation efficiency (Bodiguel et al., 2009; Freitas et al., 2010; Winberg, 1956). The species specific parameters were either measured on the surveys or taken from published studies for the Bay of Biscay (Table 2). We also computed M values scaling with individual body size using the empirical model developed by Gislason et al. (2010). As the two models gave similar results, we only show those using the Andersen et al model but we briefly discuss the results from both models in the discussion.

Second, population age-structure at equilibrium (numbers-at-age $N(a)$) was simulated assuming constant recruitment R

$$N(0) = R$$

$$N(a+1) = N(a)\exp(-M) \qquad a>0 \qquad [2]$$

In practice, simulations were performed with a time increment of 0.1 years and ran for 500 years with recruitment fixed at one million individuals. This means that age *a* had a resolution of 0.1 years. The equilibrium state was verified by comparing the last simulation to the 50 preceding years.

Third, age was transformed into length-at-age $L(a)$ using the von Bertalanffy growth equation

$$L(a) = L_{\mathrm{inf}}\,(1-\exp(-K\,(a - t0))) \qquad [3]$$

and the K and L_{inf} values in table 2; $t0$ had to be set to 0 as it was missing for most species. The appropriateness of the growth function values for the Bay of Biscay was verified by comparing visually the position of the first peak in the length frequency distribution of the survey data with the expected (fractional) age at the time of the survey for the youngest age class caught by the survey (often young-of-the-year).

Fourth, length-at-age $L(a)$ was transformed into weight-at-age $W(a)$ using the length-weight relationship

$$\mathrm{W}(a) = \alpha\, L(a)^{\beta} \qquad [4]$$

with values for the coefficients α and β taken from the literature (Table 2).

Fifth, unexploited mean weight $\overline{W}_M$ was estimated using the equilibrium numbers-at-age and the calculated weight-at-age

$$\overline{W}_M = (\Sigma\, S\, N(a)\, W(a)\,)/\,(\Sigma\, S\, N(a)) \qquad [5]$$

To account for the length L_s at which the species could be assumed fully available to a given survey, the selectivity indicator variable S was set to zero for $L(a) < L_s$. The way L_s was estimated is described in section 2.2.3.

Finally, for interpreting the survey derived mean weight values, simulations assuming a total fishing mortality Z = F + M varying from 1M to 5M (steps of 0.5M) were carried out. The scenario in which Z = 2M is presented in detail with the simulated mean weight values referred to as $\overline{W}_{2M}$.

2.2.2 Mean weight from survey data

For survey data mean weight across all years y was calculated using a per station approach (Cotter, 2009) as the length of individual fishes captured in the same trawl are generally not independent, in particular for schooling species. For this calculation individual length in station i was transformed into weight using the length-weight relation in eq. [4], this was multiplied by the number of individuals in that length class $N_i(l)$ to obtain the total weight-at-length $W_i(l)$. These weight-at-length were summed across length classes to obtain the total weight W_i at station i. To take account of survey selectivity only individuals with length $l > L_s$ were included in the summation using as for the simulations the indicator variable S (see section 2.2.3). The estimators of mean survey weight $\overline{W}_{surv}$ and its variance are then

$$\overline{W}_{surv} = \frac{\sum_i^m \left(\sum_l S W_i(l) / \sum_l N_i(l) \right)}{m} = \frac{\sum_i^m \overline{W}_i}{m} \quad [6]$$

$$Var(\overline{W}_{surv}) = \sum_i^m \left(\overline{W}_i - \overline{W}_{surv} \right)^2 / \left(m(m-1) \right) \quad [7]$$

with $\overline{W_i}$ the mean weight per station (for individuals larger than L_s) and m the total number of stations. Approximate 95% confidence intervals were constructed assuming normality: $\overline{W}_{surv} \pm 2\sqrt{Var(\overline{W}_{surv})}$.

The data were pooled across all years to smooth interannual variations (see time series in Fig. S1 in electronic supplementary material).

2.2.3 Survey selectivity determination

To compare simulated mean weights with survey derived mean weights, the length at which a species was fully selected by the survey (L_s) was estimated to create the indicator variable S used in equations [5] and [6]. Survey selectivity is defined here as a species catchability - availability, catchability being caused by net selectivity, i.e. small individuals not being caught, and availability by juvenile habitats not covered by the survey, e.g. because they are in too shallow waters. The potential case of large individuals not being covered by the survey was only considered for *M. merluccius* (see below).

Length-frequency distributions cumulated across all years were inspected to select L_S values for all species (Table 1). Most of the length-frequency distributions were multimodal, with young-of-the-year (all individuals before the dotted vertical line in Fig. S2 in electronic supplementary material) showing a first normal-like distribution. This pattern was found for 14 out of the 18 selected species. In case of the four remaining species, juveniles were too small (*L. whiffiagonisea*) or not at all present (*C. conger*, *D. labrax*) or no clear mode was visible (*S. canicula*) (Fig. S3 in electronic supplementary material). The L_S values were chosen to take into consideration these specificities. For the first group of species L_S was set at relative small sizes (between 7 and 14 cm), which in most cases corresponds to young-of-the-year or age 1. For the remaining species L_S was selected so that only individuals from age

2 and older were considered in the estimation of mean weight from the simulated populations and survey data (Fig. S2 and S3 in electronic supplementary material).

For *M. merluccius* a selectivity curve was available from the stock assessment model fitted by Bertignac et al. (2012). This selectivity curve had a dome shaped form. It was applied instead the cut off limit L_s to evaluate the reduced survey availability of both smaller and larger individuals.

2.2.4 Comparing mean weights

Simulated mean weights $\overline{W}_M$ were compared with the contemporary survey derived mean weights $\overline{W}_{surv}$ using the relative percentage difference

$$\Delta\overline{W}_{surv-M}=100(\overline{W}_{surv}-\overline{W}_M)/\overline{W}_M \qquad [8].$$

Thus, negative values indicate that the contemporary mean values were smaller compared to those simulated assuming no fishing mortality. Relative percentage differences were also calculated using the mean weights obtained from the upper ($\overline{W}_{surv}^{up}$) and lower ($\overline{W}_{surv}^{low}$) 95% confidence intervals as well as the uncertainty analysis (section 2.2.5). To gauge the impact fishing might have had on contemporary fish populations we also compared the simulated $\overline{W}_{2M}$ to simulated mean weights without fishing $\overline{W}_M$, referred to as $\Delta\overline{W}_{2M-M}$.

To try and explain species differences, the species-specific $\Delta\overline{W}_{surv-M}$ values were regressed against two explanatory life history traits, K and L_{inf}, using linear quantile regression (QR). The lower 25% quantile was modelled in the QR as it is expected that high K make species more resilient to fishing impacts (less resilient for high L_{inf}), which in turn should lead to less negative values, i.e. a positive relationship between $\Delta\overline{W}_{surv-M}$ and K (negative relationship with L_{inf}). Further, ANOVA and boxplots were performed in order to test the effects of five categorical explanatory variables: existence of a fishing quota (TAC) in the Bay of Biscay, body shape of the species, magnitude of French landings, biogeography, and maximum depth (Table 3).

2.2.5 Calculating uncertainty intervals

Uncertainty intervals incorporating parameter and sampling uncertainty into mean weight estimates and subsequently relative differences were constructed based on the most extreme mean values obtained for a set of scenarios.

For simulated mean weights ($\overline{W}_M$), in scenario 1, 10% was added and removed from the M values calculated with eq. (1), giving estimates $\overline{W}_{90\%M}$ and $\overline{W}_{110\%M}$. In scenario 2, 10% was added and removed from L_S values (Table 1) used for creating the indicator variable S (eq. 5), giving $\overline{W}_{M,90\%Ls}$ and $\overline{W}_{M,110\%Ls}$ estimates. The lower uncertainty value is then $\overline{W}_M^{low}$=min($\overline{W}_{110\%M}$,$\overline{W}_{M,90\%Ls}$) and the upper one $\overline{W}_M^{up}$ =max($\overline{W}_{90\%M}$,$\overline{W}_{M,110\%Ls}$). The same approach was applied for $\overline{W}_{2M}$.

For survey mean weights ($\overline{W}_{surv}$), 10% was added and removed from L_S values and uncertainty intervals were calculated as $\overline{W}_{surv}^{low}=\overline{W}_{surv,90\%Ls}-2\sqrt{Var(\overline{W}_{surv,90\%Ls})}$ and $\overline{W}_{surv}^{up}=\overline{W}_{surv,110\%Ls}+2\sqrt{Var(\overline{W}_{surv,110\%Ls})}$.

Similarly, uncertainty intervals for relative differences in mean weight were obtained as $\Delta\overline{W}_{surv-M}^{low} = f(\overline{W}_{surv}^{up},\overline{W}_M^{low})$ and $\Delta\overline{W}_{surv-M}^{up} = f(\overline{W}_{surv}^{low},\overline{W}_M^{up})$.

3 Results

3.1 Comparing mean weights

Simulations were carried out for the five different F values (F=1M to 5M). For 40% of the studied species, the scenario using F=M provided the best match between simulated and contemporary mean weights (Figure 2). In contrast, for *Conger conger, Chelidonichthys cuculus, Physis blennoides,* and *M. merluccius* values as high as 2.5M and 3M provided the best agreement.

When considered in details, the relative difference between simulated and survey-derived mean weight estimates $\Delta\overline{W}_{surv-M}$ was negative or close to zero for all 18 species (dark grey bars in Figure 3). Uncertainty intervals increased with relative differences. The ten species showing the largest relative difference in mean weight were: *C. conger, M. merluccius, L. piscatorius, C. cuculus, P. blennoides, Trachurus trachurus, Mullus surmuletus, Callionymus lyra, Solea solea* and *Lophius budegassa* with mean relative differences ranging from -88% to –30% (Figure 3). The largest relative difference in mean weight was found for *C. conger*, for which uncertainty intervals ranged from -92% to -83%. Thus, this suggests that the contemporary mean weight in the survey is substantially smaller than would be expected in an unexploited population. On the second rank, contemporary *M. merluccius* mean weights were 83% to 89% smaller. However, results for *C. Conger* and *M. merluccius* might partly be due to larger individuals not having been available to the survey. When using the dome-shaped selectivity curve, available for *M. Merluccius*, the relative mean weight uncertainty interval was reduced to -46% to -16% (filled circle with whiskers in Figure 3). *L. piscatorius* and *C. cuculus* ranked third and fourth, with contemporary mean weights being 52% to 72%, and 47% to 69% smaller than expected mean weights in the absence of exploitation. The species showing no difference, i.e. where the uncertainty interval included zero were: *Trisopterus* *luscus, Dicentrarchus labrax, Merlangius merlangus, Lepidorhombus whiffiagonis, Scyliorhinus canicula* and *Dicologlossa cuneata*. That means that the mean weights under exploitation were almost the same or even slightly larger (for *D. cuneata*) than mean weights simulated without exploitation (dark grey bars in Figure 3).

Looking at the comparison between length-frequency distributions in the survey data representing contemporary exploited populations and in the populations simulated with no fishing, three patterns emerge (light grey bars in Figure 4): (i) small individuals are very abundant while the larger ones are quickly eroded in the contemporary populations; (ii) the mode of the length structure is located on small length classes but larger individuals persist in the contemporary population with lower number than in the simulations; (iii) there is no difference between the size classes of the contemporary population and the simulated ones. The five species with the largest relative differences in mean weight (*C. conger*, *M. merluccius*, *L. piscatorius*, *C. cuculus* and *P. blennoides*) all showed the first pattern, though this is less pronounced for *C. cuculus* and *P. blennoides,* possibly because the two species reach a smaller asymptotic size. Presence of larger size classes but in lower abundance was characteristic for *M. surmuletus, L. budegassa*, and *C. gurnardus*. The four species with the smallest relative difference in mean weight exhibited no difference in the survey and simulated size classes (*D. labrax, L. whiffiagonis* and *S. canicula*). *D. cuneata* displayed a specific pattern, with the mode close to the asymptotic size. Unexpectedly, *M. merlangius* showed pattern (i). These length structures, combined with the species specific weight-at-length were largely in agreement with the observed relative differences in mean weight $\Delta\overline{W}$.

Turning to the comparison between the relative difference in mean weight for simulations with and without fishing mortality ($\Delta\overline{W}_{2M-M}$, white bars in Figure 3) and the relative differences discussed above for contemporary populations ($\Delta\overline{W}_{surv-M}$, grey bars in Figure 3).

Three different cases can be distinguished. In the first case, $\Delta\overline{W}_{surv-M}$ was larger than $\Delta\overline{W}_{2M-M}$ (*C. conger*, *C. cuculus*, *M. merluccius*, and *P. blennoides*). This would indicate that these species might be exploited at fishing mortalities above *M.* In the second case, the two values were almost equal (*L. piscatorius*, *C. gurnardus*, *C. lyra*, *S. solea* and *T. trachurus*), compatible with contemporary fishing mortalities about equal to *M*. In the third case, $\Delta\overline{W}_{surv-M}$ was smaller than $\Delta\overline{W}_{2M-M}$ (*D. labrax*, *D. cuneata*, *L. whiffiagonis*, *L. budegassa*, *M. merlangus*, *M. surmuletus*, *S. canicula*, *T. luscus* and *Z. faber*), which could indicate that contemporary fishing mortalities were below natural mortality. However, this interpretation is contingent on the survey covering the whole population and variations in recruitment averaging out over the twenty-three year time series. We will come back to this point in the discussion. Larger uncertainty intervals for $\Delta\overline{W}_{2M-M}$ can be explained by the sensitivity to *M*. In other words the variability (10%) on *M* was applied twice as we compare both simulated populations.

3.2 Explaining relative differences in mean weight

The quantile regression showed that the lower 25% quantile of $\Delta\overline{W}_{surv-M}$ increased, as expected, with growth rate *K* and decreased with L_{inf} even though the slopes were not significantly different from zero (Figure 5). These results seemed to be strongly influenced by *C. conger* as its asymptotic size is high compared to the other species considered. However, the same trends were found when this species was removed from the analysis, though the slopes were shallower (*K: slope*= 2.7 instead of 3.07).

Looking at the categorical explanatory variables, the ANOVA found no significant differences between levels for all explanatory variables (p-values>0.1) and no clear patterns emerged from the boxplots except for maximum depth. Relative differences in mean weight increased for species being distributed deeper (Figure 5).

4 Discussion

For size-based indicators such as mean weight, mean size or evolutionary indicators such as growth parameters or size-at-maturity, there is a clear need for historical or simulation-based studies to derive reference values. Contemporary survey data are considered unsuitable for setting reference values. This study confirms this view as the mean weights in the surveys showed a clear decrease in comparison to mean weight of simulated populations with no fishing. Similar results were found by Jennings and Blanchard (2004) at the community level for the North Sea. These authors demonstrated that mean weight of an individual in the community represented 38% of that expected without fishing.

In this study all studied species showed some level of response to fishing, the larger species being the most impacted, as four out of the five most impacted species in terms of mean weight reduction were large species (*C. conger, L. piscatorius, M. merluccius* and *P. blennoides*). These results are consistent with many studies showing that larger individuals are usually more impacted by fishing (Bianchi et al., 2000; Jennings et al., 2002, 1999; Myers and Worm, 2003; Rogers and Ellis, 2000). Large species have low natural mortality, low fecundity and low growth rates and therefore have less chances of repopulating than smaller species with a high reproductive strategy and fast growth (Denney et al., 2002).

No clear differences were found between target and bycatch species. Indeed, several species displaying strong or medium response to fishing (*C. cuculus* and *C. gurnardus, C. lyra*) are not targeted by any fisheries but may represent large bycatches (Dubé et al., 2012). Dubé et al. (2012) estimated the bycatch rate for *C. cuculus* at over 18% (in weight) for large bottom trawlers (> 18 m) the Bay of Biscay in 2011. For this species and several other species, incidental fishing mortality is often the consequence of similar habitat requirements as target species. For instance, Triglidae and *C. lyra*, inhabit sandy, muddy or gravely grounds (Griffin et al., 2012; Marriott et al., 2010) which are also preferred by *L. piscatorius* (soft to hard sand and gravel substrata, (Fariña et al., 2008)), which is one of the target species.

For several species (incl. *L. whiffiagonis* and *Z. faber*), the simulated mean weights without fishing were about the same than contemporary mean weights, suggesting that these species might be either underexploited or not well sampled by the bottom trawl survey gear. The first interpretation is supported by the fact that the simulated size distributions were similar to the survey distributions. In contrast, the ICES stock assessment working group (WGHMM, 2008), considered *L. whiffiagonis* as being within or slightly outside safe biological limits in the Iberian region or northern Bay of Biscay, which supports the second interpretation.

Although their lower uncertainty interval spanning negative values does not allow for clear interpretation, two species, *D. cuneata* and *S. canicula*, were found to have slightly larger contemporary mean weights compared to those derived from simulations with no fishing. It is commonly assumed that the removal of top predators in a community should be beneficial for their preys (Daan et al., 2005; Shin et al., 2005), which could explain the result for *D. cuneata*, a small flatfish. Lesser spotted dogfish (*S. canicula*) has become more dominant in abundance among the elasmobranchs in British waters during the last century (Rogers and Ellis, 2000), which might imply a change in recruitment strength and thus explain smaller contemporary mean weight.

Other factors than fishing could explain the seemingly large differences in mean weight between contemporary and simulated populations: i) bias induced by the survey sampling protocol, ii) absence of size- or age-selective mortality in the model, and iii) environmental effects on growth. All of these will lead to overestimating mean weight differences between the surveys and the simulations. We will now discuss each issue in turn.

4.1 Survey size selectivity and species catchability

Survey data such as those used in this study are inevitably selective for specific size classes. Smaller size classes may escape through the meshes or may be inhabiting shallower habitats than those surveyed whereas larger individuals or species (with a greater swimming ability) may rise up and escape from the GOV trawl (Main and Sangster, 1981). In the study the youngest individuals were removed from the calculations of mean weight for both the simulations and survey to account for smaller fish being underrepresented in the survey catches. A correction for any selectivity bias for larger size classes was however more difficult to apply due to the scarcity of GOV selectivity curves for the species included in our study. When we corrected for size selectivity on larger individuals of *M. merluccius* using the selectivity curve estimated by Bertignac et al. (2012), the difference in mean weight reduced substantially. For this species not having sampled the larger individuals probably led to overestimating the mean weight difference.

C. conger displayed an excessively high response to fishing mortality. It is uncertain whether or not this response is entirely due to fishing or to a low level of catchability during the bottom trawl surveys. *C. conger* inhabits the continental shelf and the rocky shelf-slope areas, where it displays a high degree of fidelity to obtain refuge in rocks (Xavier et al., 2010). Rocky habitats are inadequately sampled using bottom trawls and this may thus explain, at least partially, our results.

4.2 Modelling hypotheses

The mean weight and size distributions obtained in our simulations depend on the life history parameter values and the underlying assumptions of the model for natural mortality (Andersen et al., 2009). A strong assumption of the model is the absence of size-selective natural mortality. Theoretical and empirical results suggest that natural mortality should scale with individual body size (Gislason et al., 2010). We computed natural mortality values using Gislason et al. empirical model and found the results highly similar to those of the Andersen et al. model (Spearman r = 0.98, $p<0.01$). Thus, failing to consider size-selective natural mortality cannot explain the greater proportion of larger individuals in our simulations.

The natural mortality values used in this study (Table 2), did not necessarily agreed with those assumed in contemporary stock assessment models. For example, for *M. merluccius* we used M=0.31 while Bertignac et al. (2012) used M=0.4 for all sizes. Using the smaller value for M in the simulations might have led to overestimating differences in mean weight. Another example is for *S. solea* where the natural mortality value found in the literature and used in this study (M=0.48) was larger than the one used by the ICES assessment group (M=0.1; ICES 2012). In that case, using larger M value for *S. solea* in the simulations might have led to underestimating differences in mean weight.

4.3 Environment

Among the expected responses of fish to climate change and the warming of waters is the deepening of large individuals and changes in species growth rates according to depth (Thresher et al. 2007). Macpherson and Duarte (1991) showed that large individuals migrate toward deeper waters during ontogeny where they physiologically benefit from lower temperature (lower metabolism). Using eight species displaying different depth ranges, Thresher et al. (2007) observed increased growth rate for species living above 250 m and the opposite trend for deeper species (i.e. below 250 m). Slower growth rate may thus lead to lower mean weight. Observations of larger individuals inhabiting deeper habitats have been documented for *L. piscatorius* (Garcia-Rodriguez et al., 2005) and *M. merluccius* (Woillez et al., 2007).

Dulvy et al. (2008) highlighted that the North Sea winter bottom temperature has increased by 1.6°C over the last 25 years. During that period, the demersal fish assemblage deepened by ~3.6 m decade^{-1}. Warming trends in the Bay of Biscay in modelled and *in situ* temperatures were 0.23°C and 0.30°C decade^{-1} respectively (Huret et al. 2013, Michel et al. 2009). However, no changes in spatial distribution with bottom water temperature were found for any of the eight species studied by Persohn et al. (2009) in the Bay of Biscay, six of which were also part of this study. So changes in bottom temperature might have increased growth rates, which go in the direction of compensating fishing impacts rather than explain the estimated differences in mean weight.

The absence of explanatory power for most of the categorical variables can be explained by (i) the relatively low number of species and low diversity in life history traits among the selected species in this study, this low count being notably due to the fact that life-history trait parameters are not always easy to obtain for non commercial species, and (ii) that fishing sensitivity seems to be caused by multifactorial combinations rather than one dominant factor. Nevertheless, the shapes of the relationships between the difference in mean weight and maximum length L_{inf} or maximum depth range, though not statistically significant), strengthen our conclusions regarding the effects of fishing on larger species.

5 Conclusion

We showed that in the Bay of Biscay the demographic structure of most of the 18 selected species seemed to be impacted by fishing, with the larger species displaying larger reduction in mean weight. Using *M. merluccius*, we demonstrated the sensitivity of the results to the assumed survey selectivity. While no clear differences between target and bycatch species were found, it is important to note that two important commercial species in the Bay of Biscay, *M. merluccius* and *L. piscatorius*, were among the top species with the largest relative reduction in mean weight.

Assuming that the mortality in fish populations corresponded exclusively to natural mortality, we obtained reference values for mean weights and sizes which are free from any effects of fishing. Hence these simulated reference values can be used for setting limit reference points but not target reference points for exploited populations. In contrast empirical contemporary values already include the effects of fishing and are therefore unsuitable for setting reference points.

6 Acknowledgement

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Figure captions

Fig. 1 : Map of the EVHOE survey conducted in the Bay of Biscay for the period 1987-2009 .

Fig. 2 : Relative difference in species mean weights (%) between survey-derived and simulated estimates for different values of fishing mortality F. The dotted line represents the case where simulated estimates were most similar to the contemporary estimates from the survey.

Fig. 3 : Relative difference in species mean weights (%) between survey-derived estimates (EVHOE) and estimates for populations simulated with no fishing (F=0, grey bars), and between simulated populations with fishing at $F=M$ and estimates with no fishing (white bars). The whiskers represent uncertainty intervals that include survey and parameter uncertainty (see text). The black filled circle characterises the relative difference of mean weight for hake with a dome-shaped selectivity curve (see text).

Fig. 4 : Length-frequency distributions above the cut off length of survey selectivity (L_s in table 2) for contemporary survey data (dark grey) and populations simulated with no fishing (light grey). The species are ordered as in Fig. 2.

Fig. 5 : Relative difference in species mean weight (%) between contemporary survey data and values simulated without fishing mortality as a function of explanatory variables. Linear quantile regression (25th percentile) for the continuous variables and boxplots (outliers not drawn) for categorical variables.

Tables

Table 1 : Number of individuals caught and length range in the EVHOE survey (1987 : 2002) (species are ordered as in Fig. 2). L_s is the cut off length, i.e. individuals < L_s were removed from mean weight calculations. NA: no data.

	Number of individual caught	**Length range (cm)**	**L_s (cm)**
Species			
Conger conger	1390	27-210	40
Merluccius merluccius	254045	3-108	9
Lophius piscatorius	1935	6-124	13
Chelidonichthys cuculus	9010	1-45	15
Phycis blennoides	3567	6-66	12
Trachurus trachurus	7602332	3-56	8
Mullus surmuletus	9322	3-45	9
Callionymus lyra	14955	4-32	12
Solea solea	1405	6-52	17
Lophius budegassa	1047	5-91	7
Chelidonichthys gurnardus	1519	5-49	15
Zeus faber	1624	3-58	15
Trisopterus luscus	181545	5-46	8
Dicentrarchus labrax	956	27-87	30
Merlangius merlangus	34058	4-55	9

Lepidorhombus whiffiagonis	5503	3-56	15
Scyliorhinus canicula	22883	9-82	26
Dicologlossa cuneata	1409	6-29	14
Total / Range	**8148505**	**1-210**	**7-40**

Table 2 : Life-history trait estimates used for simulating population structure at equilibrium A median L_{inf} value was used when more than one value was available (species are ordered as in Figure 2). K and L_{inf} : von Bertalanfy growth and asymptotic length; Lmat length-at-maturity; α and β parameters of length-weight relationship $W=\alpha L^{\beta}$; M natural mortality.

Species	***K***	**L_{inf}**	***L*mat**	**α [4]**	**β [4]**	**M_{study}**	**M_{Ander}**
Conger conger	0.0680 [4]	265 [13]	200 [11]	0.00023	3.4991	0.098	0.03
Merluccius merluccius	0.181 [4]	106 [4] [10]	48.5 [3]	0.00438	3.1130	0.31	0.11
Lophius piscatorius	0.0882 [4]	134.5 [4] [10] [3]	65 [4]	0.02457	2.85612	0.15	0.05
Chelidonichthys cuculus	0.46 [2]	46 [4] [10] [3]	25 [11]	0.00325	3.31963	0.74	0.25
Phycis blennoides	0.217 [6]	69.25 [4] [10]	33 [11]	0.213006	2.103422	0.36	0.13
Trachurus trachurus	0.2 [8]	50 [4] [10] [3]	24.5 [3]	0.00733	3.02544	0.33	0.11
Mullus surmuletus	0.3 [2]	44.5 [4] [10] [3]	17 [3]	0.00512	3.29558	0.54	0.19
Callionymus lyra	0.47 [1]	40 [10]	13 [1]	0.014	2.70900	0.89	0.31
Solea solea	0.278 [4]	58.5 [4] [10] [3]	25.5 [4]	0.00475	3.18094	0.48	0.16
Lophius budegassa	0.1102 [4]	88 [4] [10]	58.5 [4]	0.015	3.00400	0.16	0.06
Chelidonichthys gurnardus	0.48 [12]	44.5 [4] [10] [3]	21 [4]	0.00671	3.06235	0.80	0.28
Zeus faber	0.2085 [9]	58 [4] [10] [3]	37 [3]	0.01809	2.98270	0.31	0.11
Trisopterus luscus	0.47 [4]	44.5 [4] [10] [3]	20 [4]	0.00738	3.15608	0.8	0.28
Dicentrarchus labrax	0.13 [4]	85 [4] [10]	37 [4]	0.01248	2.94846	0.22	0.08
Merlangius merlangus	0.238 [4]	55 [4] [10] [3]	21 [4]	0.00455	3.16690	0.43	0.15
Lepidorhombus whiffiagonis	0.104 [4]	57.5 [4] [10]	22.5 [4]	0.00307	3.24460	0.19	0.06

Scyliorhinus canicula	0.21 [7]	74 [4] [10] [3]	57 [4]	0.00342	2.99468	0.3	0.3
Dicologlossa cuneata	0.47 [5]	27.75 [10] [3]	15 [4]	0.0066	3.00000	0.75	0.75

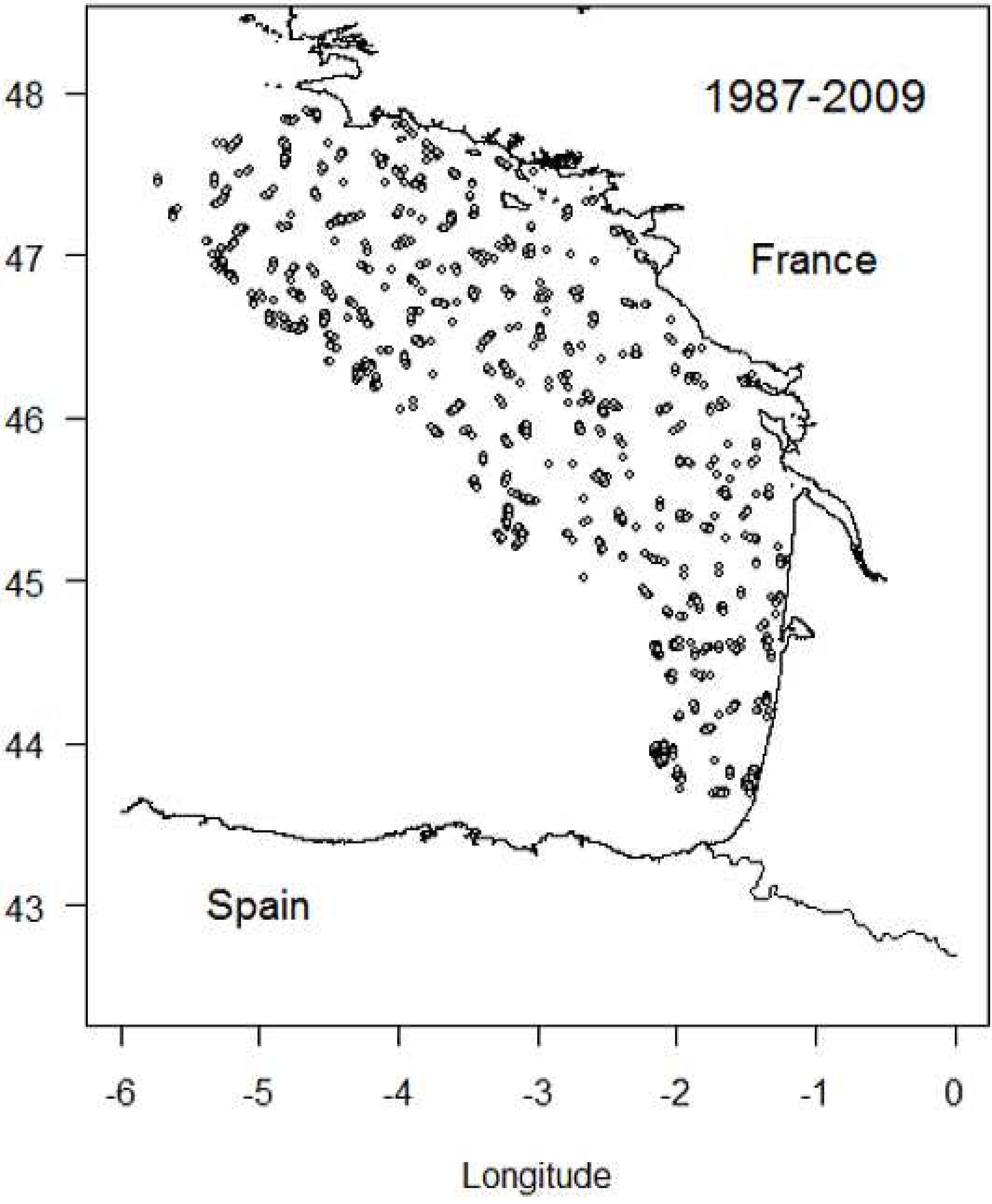
[1] Jennings et al., 1999; [2] Mahé et al., 2006; [3] Dorel, 1986; [4] Dorel et al., 1998; [5] Félix et al., 2011; [6] Casas and Piñeiro, 2000; [7] Rodriguez-Cabello et al., 2005; [8] Cubillos and Arancibia, 1995; [9] Pauly, 1978; [10] Maximum lenght from EVHOE surveys; [11] http://www.fishbase.org; [12] Magnussen, 2007; [13] Correia et al., 2009.

Table 3 : Categorical variables used to investigate the relationship between management measures, habitat or life history traits and relative differences in mean weight between populations at equilibrium or under fishing pressure (species are ordered as in Fig. 2). Depth category : Coastal = 0m-100m ; Shelf = 100m-450m ; Slope = > 450m.

Species	**TAC [1]**	**Shape**	**Landings [2]**	**Latitudinal distribution [3]**	**Depth category[4]**
Conger conger	No	Round	Low	Subtropical	Shelf
Merluccius merluccius	Yes	Round	High	Temperate	Slope
Lophius piscatorius	Yes	Flat	High	Temperate	Slope
Chelidonichthys cuculus	No	Round	Low	Subtropical	Shelf
Phycis blennoides	No	Round	Low	Boreal	Slope
Trachurus trachurus	Yes	Round	Medium	Subtropical	Slope
Mullus surmuletus	No	Round	Medium	Subtropical	Shelf
Callionymus lyra	No	Round	Low	Temperate	Shelf
Solea solea	Yes	Flat	High	Subtropical	Coastal
Lophius budegassa	Yes	Flat	High	Subtropical	Slope
Chelidonichthys gurnardus	No	Round	Low	Temperate	Shelf
Zeus faber	No	Round	Medium	Subtropical	Slope
Trisopterus luscus	No	Round	Low	Temperate	Shelf
Dicentrarchus labrax	Yes	Round	High	Subtropical	Coastal
Merlangius merlangus	Yes	Round	Medium	Boreal	Shelf
Lepidorhombus whiffiagonis	Yes	Flat	Medium	Temperate	Slope

Scyliorhinus canicula	No	Round	Low	Subtropical	Coastal
Dicologlossa cuneata	No	Flat	Low	Subtropical	Coastal

[1] European commission : http://ec.europa.eu/fisheries/cfp/fishing_rules/tacs/index_en.htm; [2] French landings for the year 2009; [3] Blanchard et al., 2001; [4] Quéro and Vayne, 1997.


1987-2009
France
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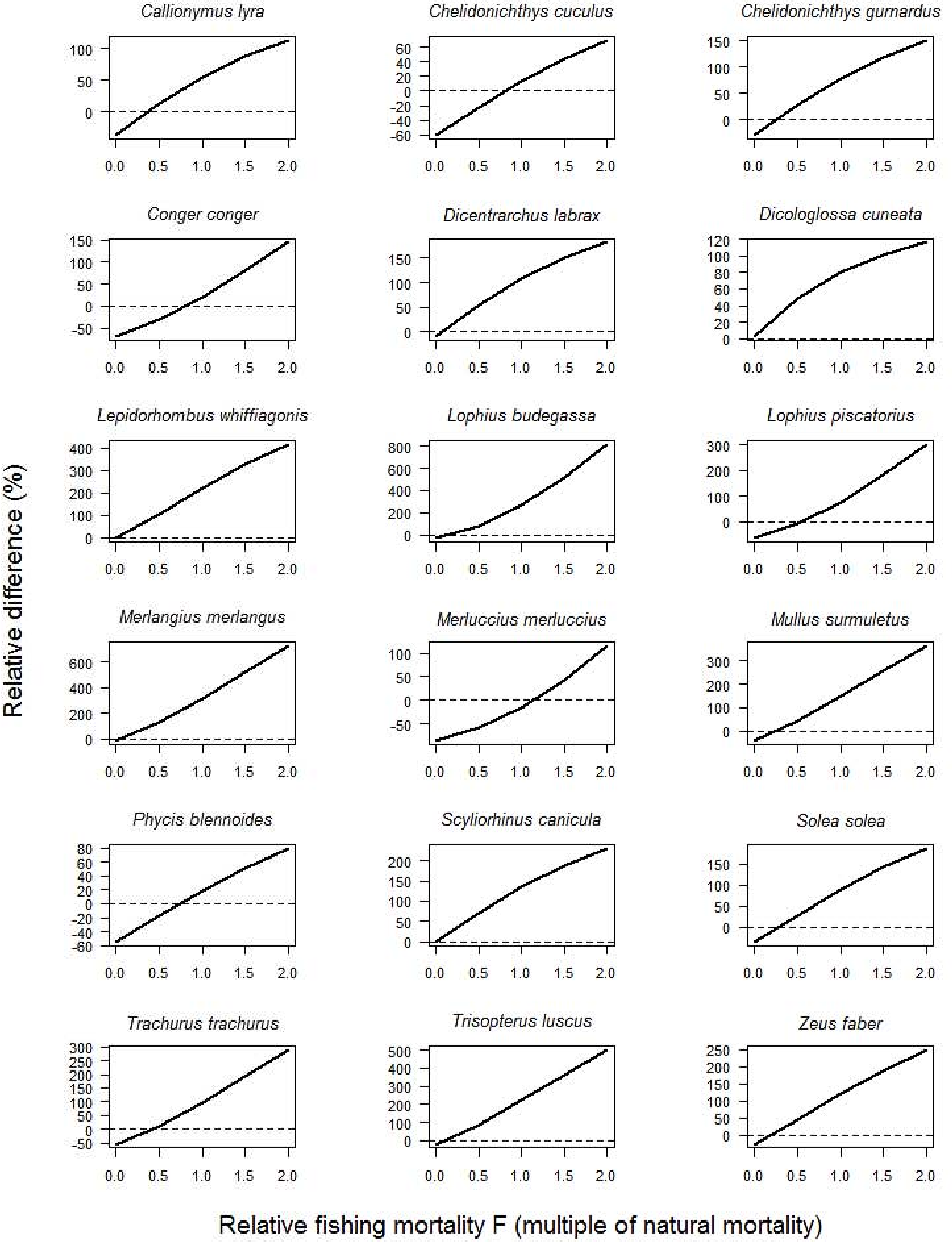
Longitude


Callionymus lyra
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Chelidonichthys cuculus
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-40
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Chelidonichthys gurnardus
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100
50
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Conger conger
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50
0
-50
Dicentrarchus labrax
150
100
50
0
Dicologlossa cuneata
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Lepidorhombus whiffiagonis
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Lophius budegassa
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Lophius piscatorius
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100
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Merlangius merlangus
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400
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Merluccius merluccius
100
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-50
Mullus surmuletus
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Phycis blennoides
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-20
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-60
Scyliorhinus canicula
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Solea solea
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Trachurus trachurus
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0
-50
Trisopterus luscus
500
400
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100
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Zeus faber
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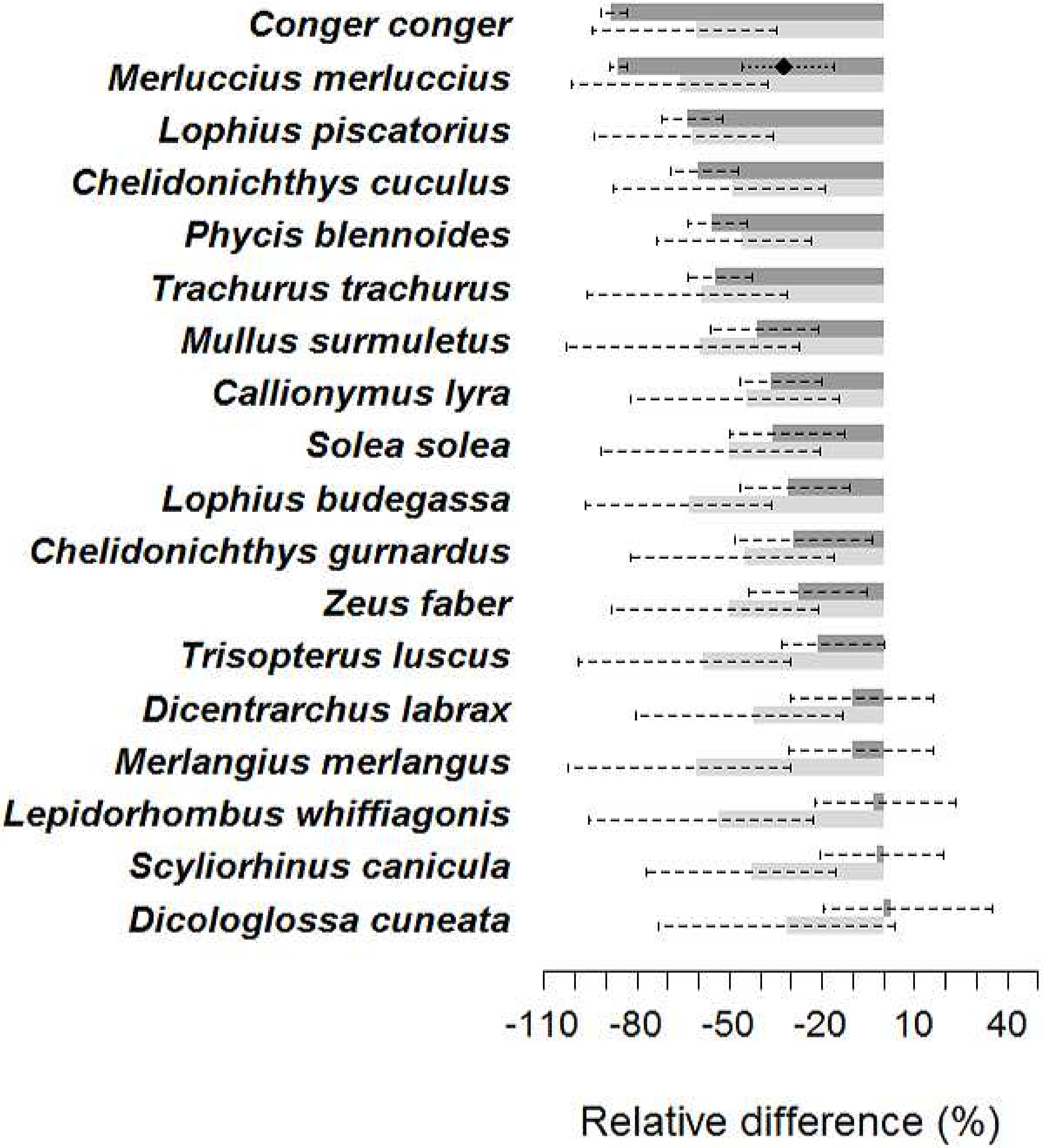
Relative difference (%)
Relative fishing mortality F (multiple of natural mortality)


Conger conger
Merluccius merluccius
Lophius piscatorius
Chelidonichthys cuculus
Phycis blennoides
Trachurus trachurus
Mullus surmuletus
Callionymus lyra
Solea solea
Lophius budegassa
Chelidonichthys gurnardus
Zeus faber
Trisopterus luscus
Dicentrarchus labrax
Merlangius merlangus
Lepidorhombus whiffiagonis
Scyliorhinus canicula
Dicologlossa cuneata
-110
-80
-50
-20
10
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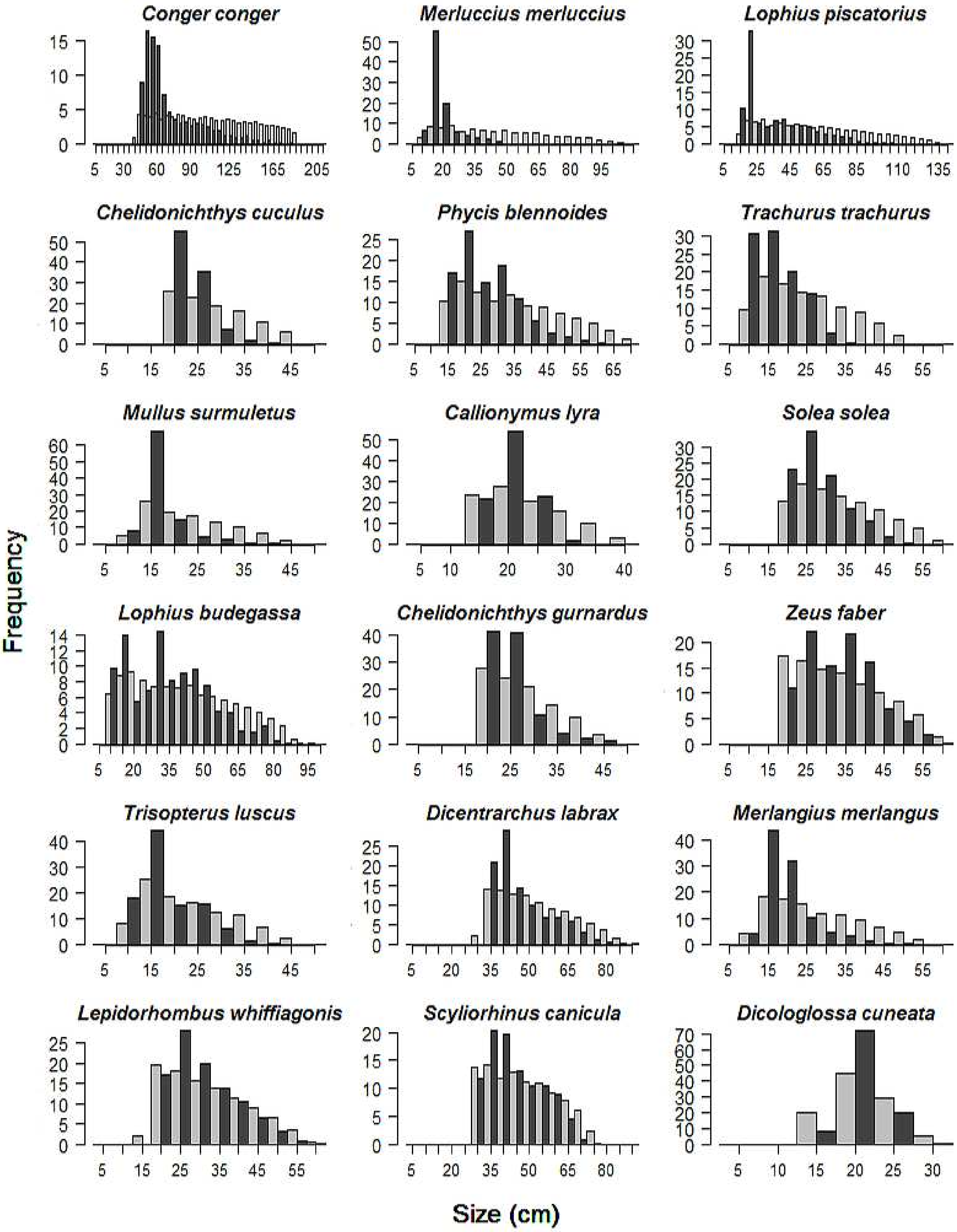
Relative difference (%)


Conger conger
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Merluccius merluccius
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Lophius piscatorius
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Mullus surmuletus
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Callionymus lyra
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Solea solea
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Frequency
Lophius budegassa
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Chelidonichthys gurnardus
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Dicologlossa cuneata
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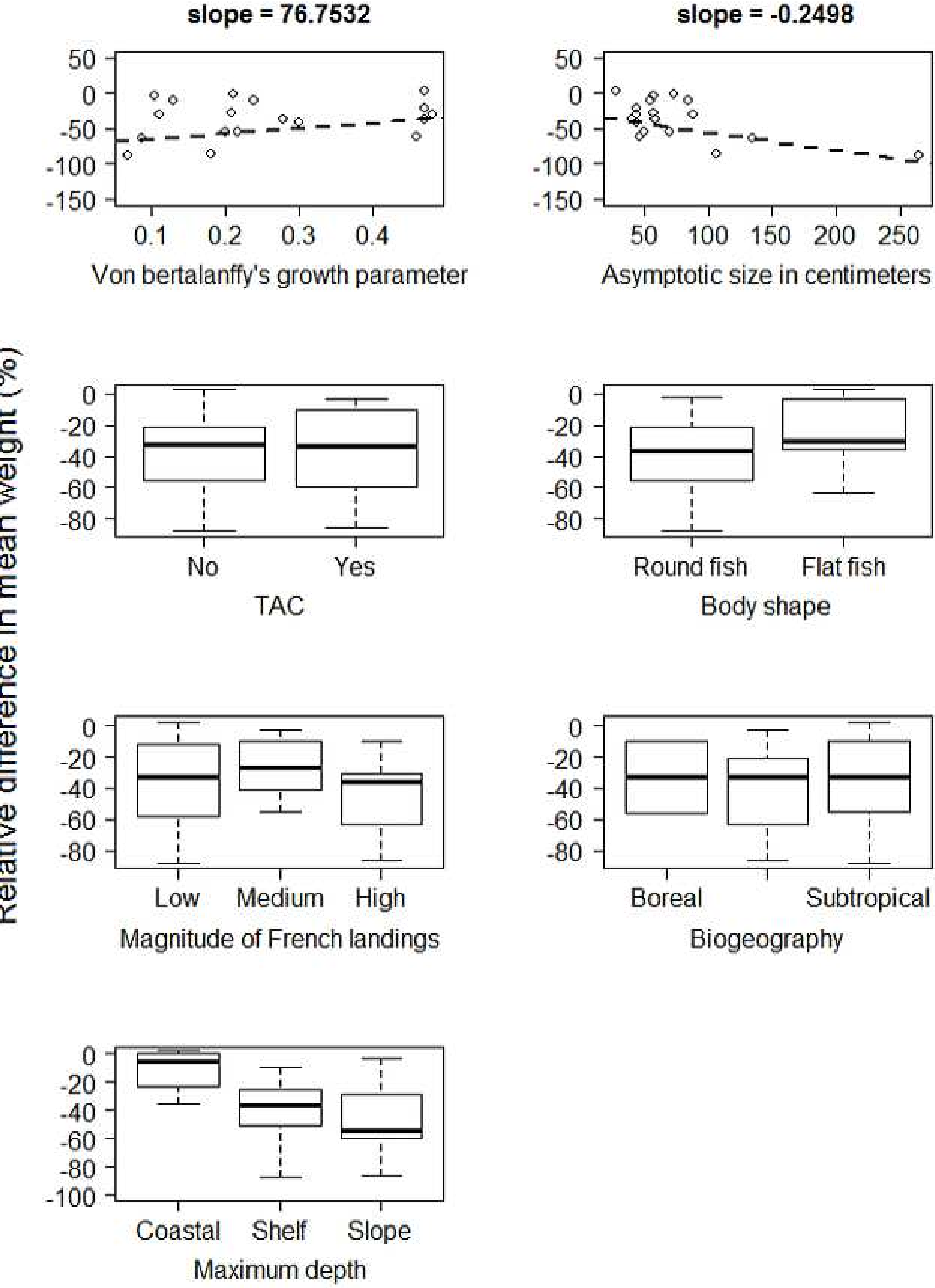
40
30
20
10
0
5
10
15
20
25
30
Size (cm)


Relative difference in mean weight (%)
slope = 76.7532
50
0
-50
-100
-150
0.1
0.2
0.3
0.4
Von bertalanffy's growth parameter
slope = -0.2498
50
0
-50
-100
-150
50
100
150
200
250
Asymptotic size in centimeters
0
-20
-40
-60
-80
No
Yes
TAC
Round fish
Flat fish
Body shape
Low
Medium
High
Magnitude of French landings
Boreal
Subtropical
Biogeography
-100
Coastal
Shelf
Slope
Maximum depth

Corrigendum to: Evaluating the potential impact of fishing on demersal species in the Bay of Biscay using simulations and survey data

An error was detected in the calculation of natural mortality values using the model by Andersen et al. in equation (1). The corrected M values ($M_{\text{Andersen et al.}}$) and those used in the study (M_{study}) are given in Table 2. A revised version of the table is provided below:

Table 1 : Life-history trait estimates used for simulating population structure at equilibrium A median L_{inf} value was used when more than one value was available (species are ordered as in Figure 2). K and L_{inf} : von Bertalanfy growth and asymptotic length; Lmat length-at-maturity; α and β parameters of length-weight relationship $W=\alpha L^{\beta}$; M_{study} natural mortality used in this study; $M_{Andersen\ at\ al.}$ natural mortality estimated using Andersen's formula (i.e. equation (1) in the paper).

Species	***K***	***L***L_{inf}	***L*mat**	**α [4]**	**β [4]**	M_{study}	$M_{Andersen\ et\ al.}$
Conger conger	0.0680 [4]	265 [13]	200 [11]	0.00023	3.4991	0.098	0.03
Merluccius merluccius	0.181 [4]	106 [4] [10]	48.5 [3]	0.00438	3.1130	0.31	0.11
Lophius piscatorius	0.0882 [4]	134.5 [4] [10] [3]	65 [4]	0.02457	2.85612	0.15	0.05
Chelidonichthys cuculus	0.46 [2]	46 [4] [10] [3]	25 [11]	0.00325	3.31963	0.74	0.25
Phycis blennoides	0.217 [6]	69.25 [4] [10]	33 [11]	0.213006	2.103422	0.36	0.13
Trachurus trachurus	0.2 [8]	50 [4] [10] [3]	24.5 [3]	0.00733	3.02544	0.33	0.11
Mullus surmuletus	0.3 [2]	44.5 [4] [10] [3]	17 [3]	0.00512	3.29558	0.54	0.19
Callionymus lyra	0.47 [1]	40 [10]	13 [1]	0.014	2.70900	0.89	0.31
Solea solea	0.278 [4]	58.5 [4] [10] [3]	25.5 [4]	0.00475	3.18094	0.48	0.16
Lophius budegassa	0.1102 [4]	88 [4] [10]	58.5 [4]	0.015	3.00400	0.16	0.06
Chelidonichthys gurnardus	0.48 [12]	44.5 [4] [10] [3]	21 [4]	0.00671	3.06235	0.80	0.28

Zeus faber	0.2085 [9]	58 [4] [10] [3]	37 [3]	0.01809	2.98270	0.31	0.11
Trisopterus luscus	0.47 [4]	44.5 [4] [10] [3]	20 [4]	0.00738	3.15608	0.8	0.28
Dicentrarchus labrax	0.13 [4]	85 [4] [10]	37 [4]	0.01248	2.94846	0.22	0.08
Merlangius merlangus	0.238 [4]	55 [4] [10] [3]	21 [4]	0.00455	3.16690	0.43	0.15
Lepidorhombus whiffiagonis	0.104 [4]	57.5 [4] [10]	22.5 [4]	0.00307	3.24460	0.19	0.06

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Evaluating the potential impact of fishing on demersal species in the Bay of Biscay using simulations and survey data

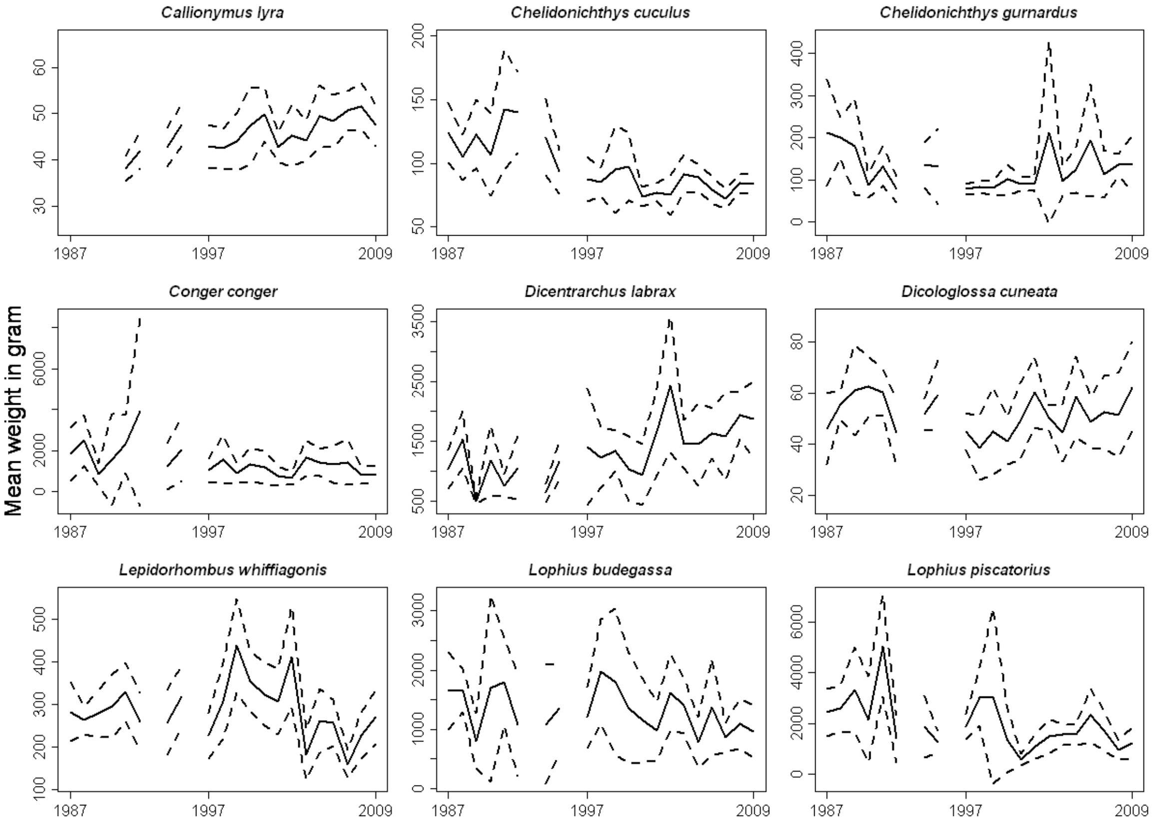
Electronic supplementary material

Figure legends:

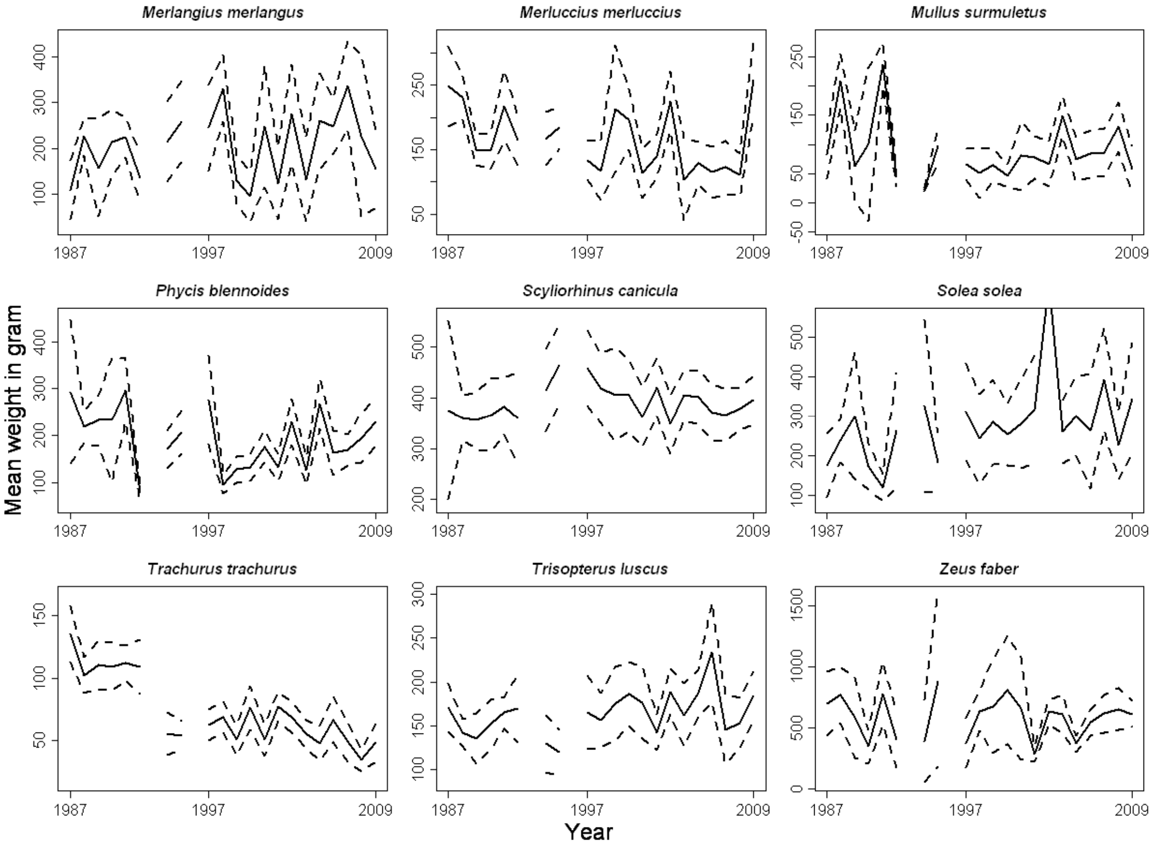
Fig. S1: Annual mean weight for nine groundfish species from EVHOE surveys (1987-2009). Solid line represents the annual mean weight by station (see text), dashed lines represent 2 standard deviations around the mean.

Fig. S2: Size structure of the firsts nine species (in alphabetical order) sampled by EVHOE surveys between 1987 and 2009, all year pooled. Solid line (i.e. L_s) represents the mean level of truncation that was applied for each species. All individuals below L_s were removed before mean weight calculation. Dotted lines represent the age at size of species (i.e. 0,5 year / 1 year / 1,5 years and 2 years).

Fig. S3: Size structure of the firsts nine species (in alphabetical order) populations at equilibrium. Solid line (i.e. L_s) represents the mean level of truncation that was applied for each species. All individuals below L_s were removed before mean weight calculation. Dotted lines represent the age at size of species (i.e. 0,5 year / 1 year / 1,5 years and 2 years).



Mean weight in gram
Callionymus lyra
30
40
50
60
Chelidonichthys cuculus
50
100
150
200
Chelidonichthys gurnardus
0
100
200
300
400
Conger conger
0
2000
6000
Dicentrarchus labrax
500
1500
2500
3500
Dicologlossa cuneata
20
40
60
80
Lepidorhombus whiffiagonis
100
200
300
400
500
Lophius budegassa
0
1000
2000
3000
Lophius piscatorius
0
2000
4000
6000
1987
1997
2009



Mean weight in gram
Merlangius merlangus
100
200
300
400
Merluccius merluccius
50
150
250
Mullus surmuletus
-50
0
50
150
250
Phycis blennoides
100
200
300
400
Scyliorhinus canicula
200
300
400
500
Solea solea
100
200
300
400
500
Trachurus trachurus
50
100
150
Trisopterus luscus
100
150
200
250
300
Zeus faber
0
500
1000
1500
1987
1997
2009
Year

Fig. S1: Annual mean weight for nine groundfish species from EVHOE surveys (1987-2009). Solid line represents the annual mean weight by station (see text), dashed lines represent 2 standard deviations around the mean.

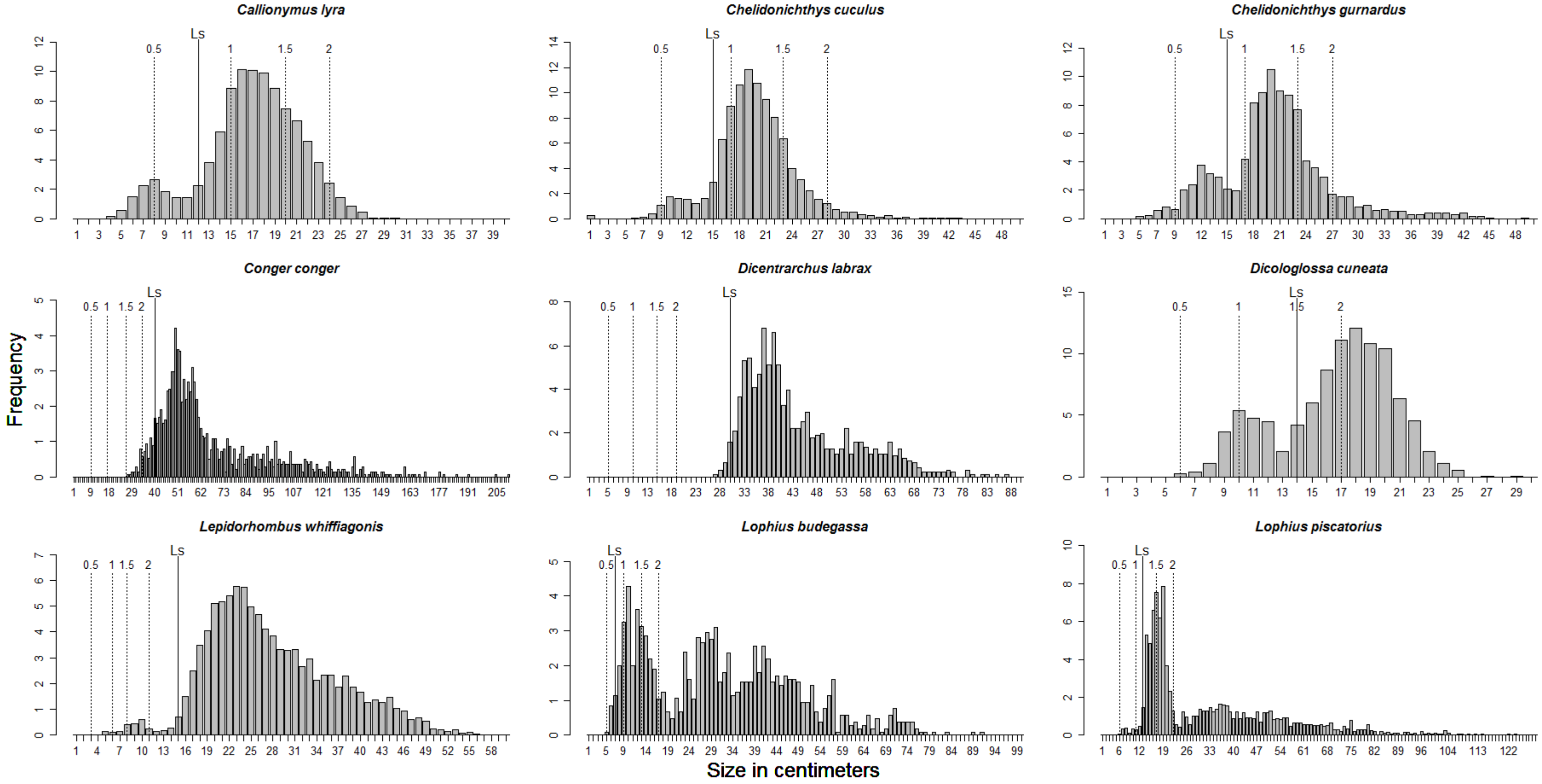


Fig. S2: Size structure of the firsts nine species (in alphabetical order) sampled by EVHOE surveys between 1987 and 2009, all year pooled. Solid line (i.e. L_s) represents the mean level of truncation that was applied for each species. All individuals below L_s were removed before mean weight calculation. Dotted lines represent the age at size of species (i.e. 0,5 year / 1 year / 1,5 years and 2 years).

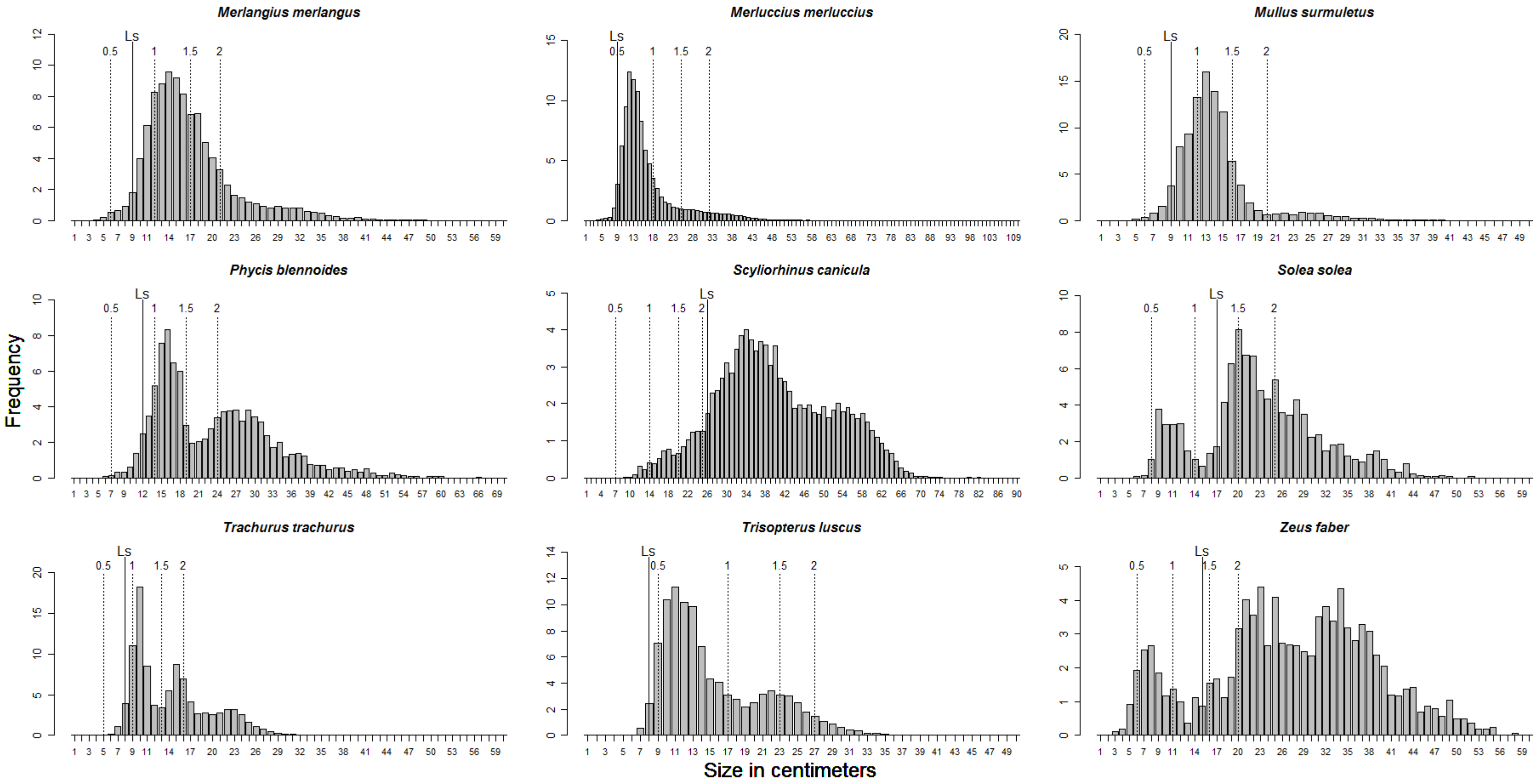


Fig. S2 continued: Size structure of the lasts nine species (in alphabetical order) sampled by EVHOE surveys between 1987 and 2009, all year pooled. Solid line (i.e. L_s) represents the mean level of truncation that was applied for each species. All individuals below L_s were removed before mean weight calculation. Dotted lines represent the age at size of species (i.e. 0,5 year / 1 year / 1,5 years and 2 years).

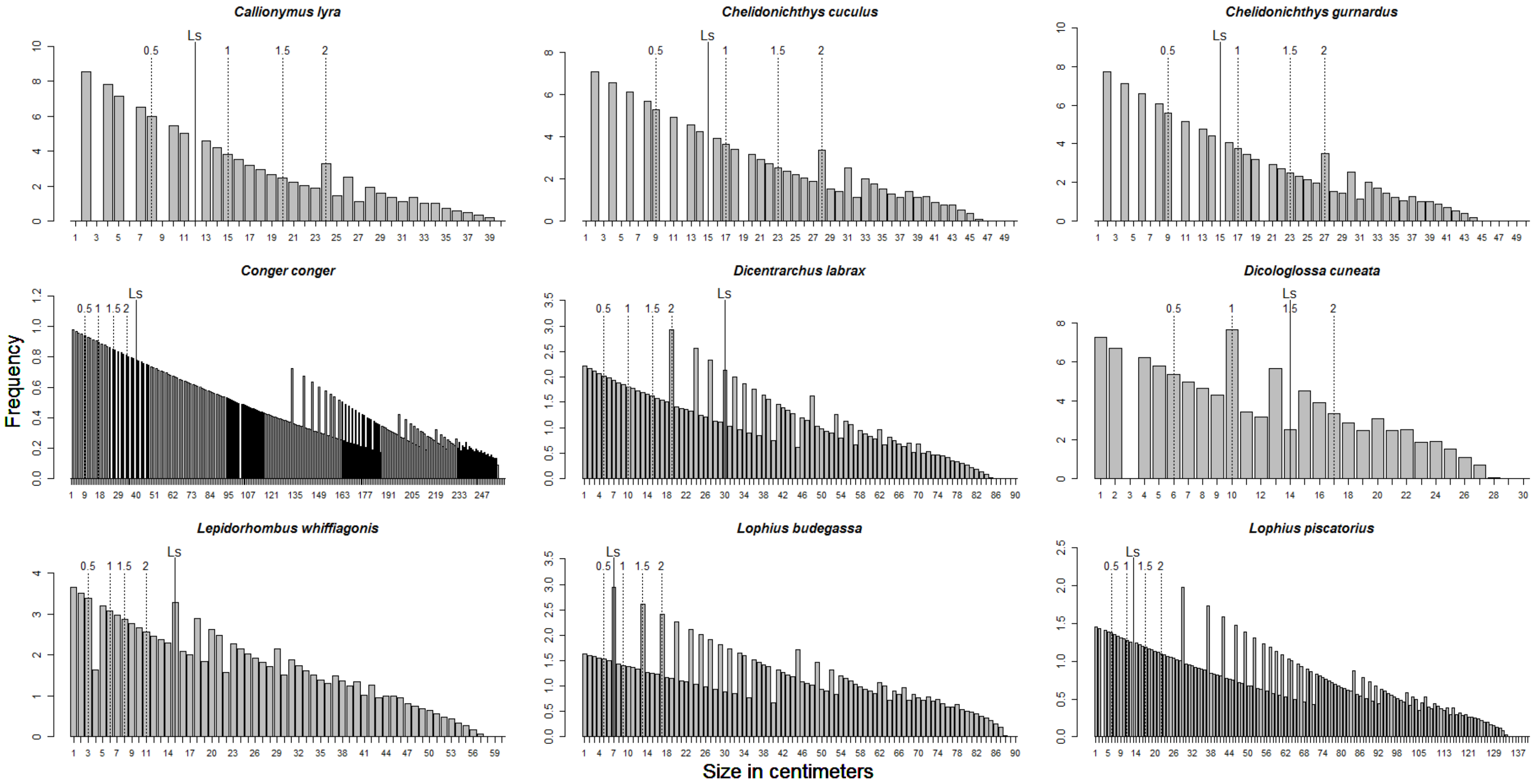


Fig. S3: Size structure of the firsts nine species (in alphabetical order) populations at equilibrium. Solid line (i.e. *L_s*) represents the mean level of truncation that was applied for each species. All individuals below *L_s* were removed before mean weight calculation. Dotted lines represent the age at size of species (i.e. 0,5 year / 1 year / 1,5 years and 2 years).

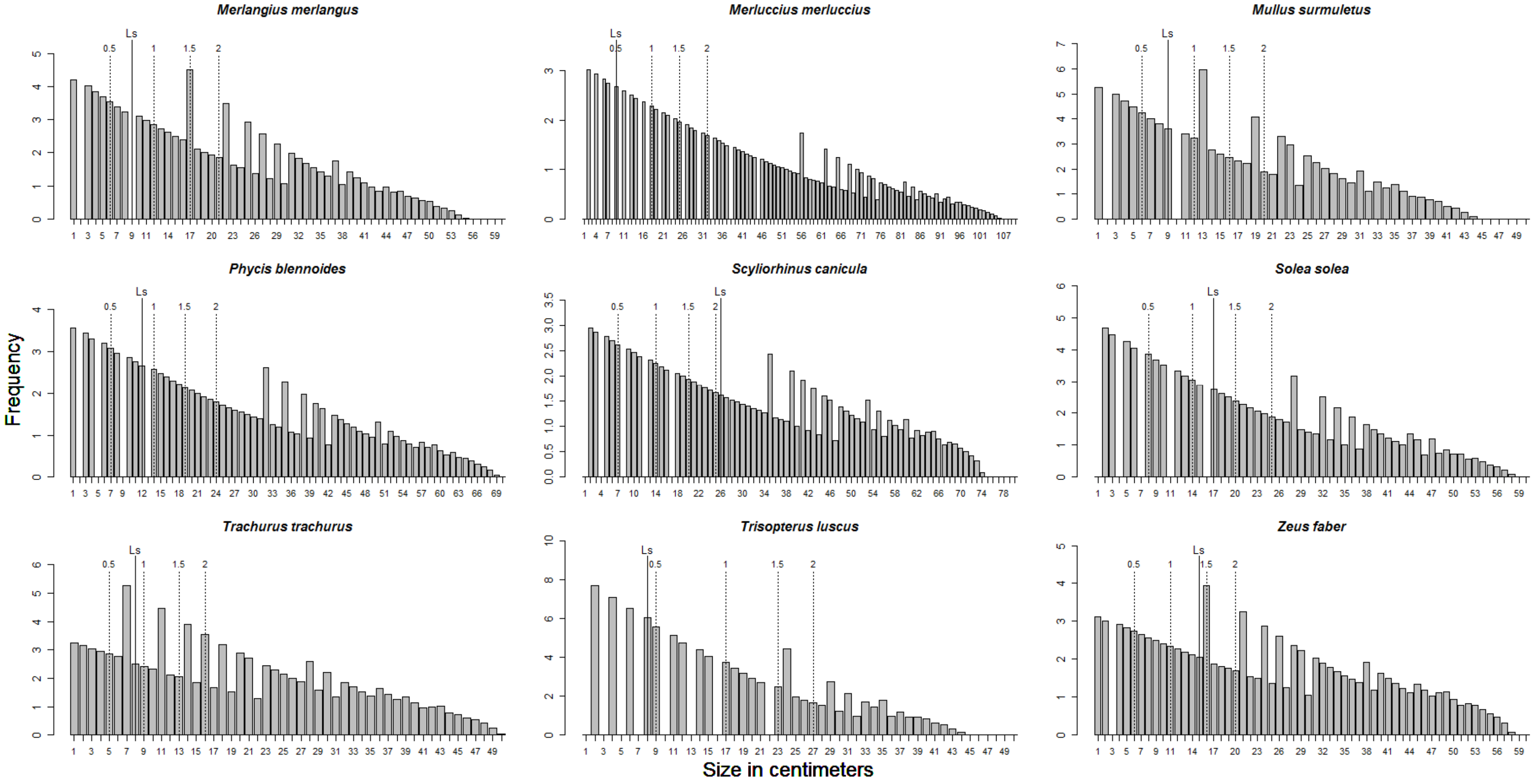


Fig. S3 continued: Size structure of the lasts nine species (in alphabetical order) populations at equilibrium. Solid line (i.e. L_s) represents the mean level of truncation that was applied for each species. All individuals below L_s were removed before mean weight calculation. Dotted lines represent the age at size of species (i.e. 0,5 year / 1 year / 1,5 years and 2 years).