

Trophic mechanisms underlying benthodemersal community recovery in the north-east Atlantic

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Summary

1. Bottom trawling is considered one of the greatest and most widespread causes of anthropogenic change in shelf seas, with major and prolonged impacts in areas with a long history of exploitation by fisheries such as the North Atlantic. Here, signs of recovery following the enforcement of regulations are increasingly being reported.

2. We examined the extent to which biological diversity and functionality are restored when fishing pressure is reduced by evaluating changes in species biomass and that of the main functional groups present in the continental platform, as obtained from systematic survey (IBTS) results. Moreover, we examined how this recovery is mirrored in the trophic organization of the affected communities by assessing variations in link density and strength of the main consumer species and investigating whether variations in species richness were paralleled by changes in network properties. Finally, we investigated whether reductions in fishing pressure (fishing mortality) were correlated with the abovementioned variations in community and trophic structure of the benthodemersal assemblages.

3. Our results corroborate the apparent recovery of North Atlantic fishing stocks and further substantiate the improved welfare of the benthodemersal assemblages of the Southern Bay of Biscay. Specifically, we found an increase in species richness and in the abundance of most functional groups, especially those more closely related to the benthos, following the reduction in fishing mortality. Increases in overall species richness were paralleled by an increase in the number of links and a reduction in mean interaction strength connecting the main consumer species with their prey items. This is in accordance with ecological theory and could explain the mechanism by which benthodemersal assemblages restructure their trophic network towards more stable organizations.

4. *Synthesis and applications.* Detecting patterns of recovery or change to alternative stable states following stress release is essential to unravel the effects of perturbations and to design effective management strategies. Our study shows that trophic network properties provide a convincing tool to evaluate and perceive recovery patterns. The trends shown in our study appear to be related with the decline in fishing mortality resulting from the enforcement of fisheries regulations in the area. They substantiate the efficiency of these regulations as a guarantee for an ecosystem approach to fisheries management and advocate their enforcement at a wider level as a convincing measure to preserve the sustainability of marine resources and their welfare.

Key-words: benthodemersal, bottom trawling, community recovery, diversity-stability, fisheries management, food webs, functional groups, interaction strength, resilience, trophic links

Introduction

Increasing theoretical background and empirical evidence seems to converge in the notion that diversity enhances

ecosystem stability, not through a mere addition of species numbers in balanced quantities, but through the diverse functionalities, responses and interactions these species may represent within an ecosystem (MacArthur 1955; Peterson, Allen & Holling 1998; McCann 2000; Loureau *et al.* 2001; Dunne, Williams & Martínez 2002; Steiner *et al.* 2006; O'Gorman &

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Emmerson 2009). As such, persistence of stability within ecosystems is attained by the maintenance of the networks of interactions that species create over ecologically relevant time-scales, and their ability to adapt to and resist perturbations (Rooney *et al.* 2006; McCann & Rooney 2009). Food webs are a good example of such diverse and complex networks and a good tool for understanding the distribution of species diversity and its response to disturbances (Thompson *et al.* 2007; Rooney & McCann 2012). Indeed, their high flexibility (i.e. alternation of fast and slow pathways, consumer adaptability to resource availability etc.) confers a strong stability to populations (McCann & Rooney 2009). According to various theoretical and empirical studies, this stability can be further enhanced by increased diversities as long as the incorporation of new species into a system occurs in such a manner that interaction strengths (the degree in which consumers and resources are connected) are balanced, i.e. weak interactions increase and only a few strong consumer–resource interactions prevail (May 1973; Winemiller 1989; McCann 2000; Bascompte, Melián & Sala 2005; Gellner & McCann 2012). In general, low mean interaction strengths are supposed to allow the co-existence of many species, while increases in diversity further diminish them, thus additionally increasing stability and so on (Kokkoris *et al.* 2002). On the other hand, the loss of either strong or weak interactions may lead to a reduction in diversity and increased species turnover (O’Gorman & Emmerson 2009), limiting the ability of a system to reorganize and decreasing its ecological resilience to disturbance (Peterson, Allen & Holling 1998). Specifically, strong interactors act as keystone species, their removal causing dramatic trophic cascades and loss of primary production in the system (O’Gorman & Emmerson 2009), while weak interactors have an important stabilizing role as buffering agents in production transfer processes (O’Gorman & Emmerson 2009). With this rationale, increasing the number of species should enhance stability (McCann 2000 and references therein), while species removal, especially at large scales should have dramatic effects on food webs and population stability (McCann & Rooney 2009; O’Gorman & Emmerson 2009).

Marine food webs generally show high structural robustness to species loss, probably as a result of their relatively strong connectance (Dunne, Williams & Martínez 2002; Link 2002) and the elevated levels of omnivorous and generalist organisms occurring in marine habitats (Link 2002; Dunne, Williams & Martínez 2004; Thompson *et al.* 2007). In the last century, however, increasing impacts on marine systems have put this robustness to the test, and shown that the cumulative effect of various perturbations (i.e. climate change, eutrophication, invasive species, overfishing etc.), is causing phase shifts and impacts on marine communities and their stability that are difficult to reverse (Halpern *et al.* 2007; Estes *et al.* 2011). Among these disturbances, fisheries have been considered one of the main human activities causing detrimental effects on marine ecosystems (Pauly & Watson 2003; Worm *et al.* 2009; Lassalle *et al.* 2014). Fisheries

can affect the entire food web, causing profound shifts in species abundance at various trophic levels, and a reduction of the number and length of pathways linking fish to primary producers (Pauly *et al.* 2002; Pauly & Watson 2003). Moreover, fishing has been shown to be increasingly selective across functional groups as high trophic levels (the major ‘couplers’ and thus the strongest interactors) have been depleted (Essington, Beaudreau & Wiedenmann 2006; McCann & Rooney 2009; Rochet, Collie & Trenkel 2013). The effects of fisheries are particularly damaging in demersal and benthic habitats (Halpern *et al.* 2007; Clark *et al.* 2015), where the direct physical impact of trawling gears causes losses in species abundance, biomass, and richness at large scales, ultimately leading to substantial changes in community structure and productivity (Kaiser *et al.* 2006; Hinz, Prieto & Kaiser 2009; Rochet, Collie & Trenkel 2013). Undeniably, bottom trawling is considered one of the greatest and most widespread causes of anthropogenic change in shelf seas (Kaiser *et al.* 2006; Hinz, Prieto & Kaiser 2009), with major and prolonged impacts in areas with a long history of exploitation by fisheries such as the North Atlantic (Kaiser *et al.* 2006; Hinz, Prieto & Kaiser 2009). Here, fishing mortality increased over time from slightly above sustainable levels (MSY), until a maximum was reached in the late 1990s, when fishing mortality was on average more than double that of sustainable levels (EEA 2015). Fortunately, progressive reductions in quotas and an overall decrease of the level of fishing pressure back to sustainable levels since the early 2000s, have mirrored in the recovery of certain stocks in the north-east Atlantic Ocean and the Baltic Sea (Collie, Rochet & Bell 2013; EEA 2015). The Southern Bay of Biscay is no exception. After a long history of overexploitation by fisheries and trawling activities with a very impacted system by the mid-90s (Sánchez & Olaso 2004) the bay is now beginning to show promising signs of recovery (Modica *et al.* 2014; Punzón *et al.* 2016). It would be expected that this reduction in fishing activities and more specifically, trawling activities would also be paralleled by a recovery of the benthic assemblages inhabiting the trawling-released areas and that this would, in turn, have beneficial effects in the functional and trophic structure of the benthic-demersal domain.

Our study examines the extent to which biological diversity and functionality are restored when fishing pressure is reduced and how this recovery is mirrored in the trophic organization of the affected communities. Specifically, we examine trends in community and functional structure of the benthic-demersal assemblage of the Southern Bay of Biscay over a 22-year period (1992–2013) covering the years of maximum depletion of fish stocks by fisheries and their recovery over time. We analyse whether there have been any variations in the diet and the trophic relationships of the main consumer species, and whether these variations can be related to changes in fishing pressure. As a response to reduced fishing pressure, we

hypothesized an increase in species richness, diversity and biomass of the benthic-demersal domain, with an increase in benthic-related functional groups (FG) and changes in community structure at the species and functional level. Additionally, we expected these variations to be paralleled by changes in the trophic habits of the main consumers, with an increase in diet diversity and in the number of interactions, which in the light of stability maintenance processes, would likely be skewed towards weak interaction strengths.

Materials and methods

SAMPLING AND STANDARDIZATION PROCEDURES

Sampling was conducted along the Cantabrian continental shelf (Southern Bay of Biscay), in ICES subdivisions VIIIc and IXa, from years 1992 to 2013 (Fig. 1). Samples belong to random stratified bottom trawl surveys which are conducted for demersal fishery assessments in the study area every year during autumn ('Demersales' surveys), following IBTS (International Bottom Trawl Surveys) standards (ICES 2012). Stomach content and diet analyses were conducted following the standardized procedures described in Olaso, Velasco & Pérez (1998) and Velasco, Olaso & Sánchez (2001), in 22 predator species. Since hake is one of the main target species and its feeding habits are intimately related to its size, we established two categories for this species, i.e. <20 cm in total length and >19 cm (tl), and examined specimens as two different species.

CHANGES IN THE DEMERSAL ASSEMBLAGE AND FUNCTIONAL GROUP STRUCTURE OVER TIME

First, we investigated variations in mean biomass, mean abundance, species richness and diversity (H' loge) per haul, and

variations in species/group assemblage structure over time. We also grouped all taxa appearing during the study years into functional groups (Appendix S1, Supporting Information), and evaluated variations in their biomass, functional group number, diversity (H' loge) and assemblage structure over time. Functional group assignment was adapted from the categorization proposed by Sánchez & Olaso (2004) and further revised for the initial assessment of environmental status for the Marine Strategy Framework in the Spanish North Atlantic demarcation (Fig. 2, see Appendix S1). The following functional groups were created: BC = benthic carnivores; BD = benthivore decapods; Bceph = benthic cephalopods; BF = benthivorous fish; CE = carnivorous echinoderms; CP = carnivorous polychaetes; DD = detritivore decapods; DDF = deep demersal fish; DFE = deposit feeding echinoderms; DS = deep sea sharks; G = gastropods; GZ = gelatinous zooplankton; LDF = large demersal fish; MM = migrating macrozooplankton; NF = necrophagous fish; PC = pelagic crustaceans; PF = planktivorous fish; POL = *Polybius henslowii* Leach 1820; M = megrims; R = rays; SF = benthic invertebrate suspension feeders; SPB = detritivore suprabenthos; SQ = squids and ZP = zooplanktivorous shrimps. Following Sánchez & Olaso (2004), we also separated the main commercial species (hake, *Merluccius merluccius* Linnaeus 1858 (HKE), blue whiting *Micromesistius poutassou* Risso, 1827 (WHB), megrims *Lepidorhombus boschii* Risso, 1810 (M1) and *Lepidorhombus whiffiagonis* Walbaum, 1792 (M2) and monkfish *Lophius piscatorius* Linnaeus, 1758 and *Lophius budegassa* Spinola 1807 (MNZ), Norwegian lobster *Nephrops norvegicus* Linnaeus 1758 (NPH) and catshark *Scyliorhinus canicula* Linnaeus 1758 (SCY)).

Changes in the structure of the benthic-demersal assemblage (i.e. species caught during the 'Demersales' surveys) over time were analysed by means of multivariate analyses. Mean biomass per 30 min haul data of species/groups appearing throughout the period surveyed (1992–2013) were used to construct the data matrix. Only those species appearing in at least 5 of the studied years were included in the data matrix.

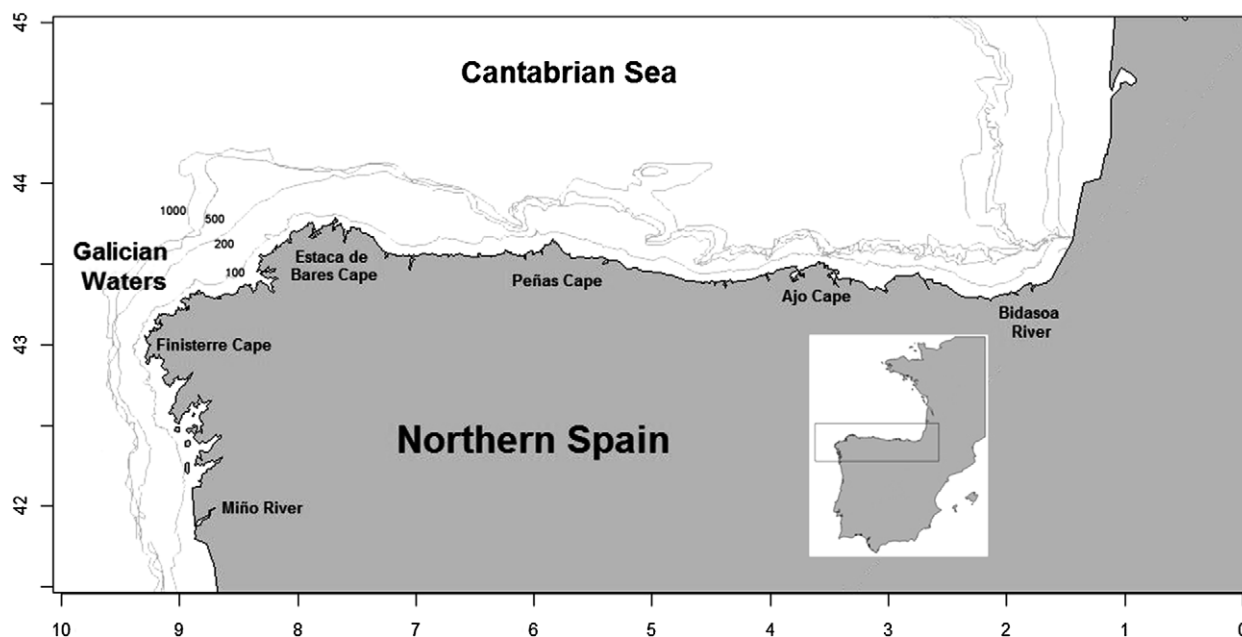


Fig. 1. Map of the study area. International Bottom Trawling (IBT) Surveys are conducted every year during autumn along the Galician and Cantabrian coasts.

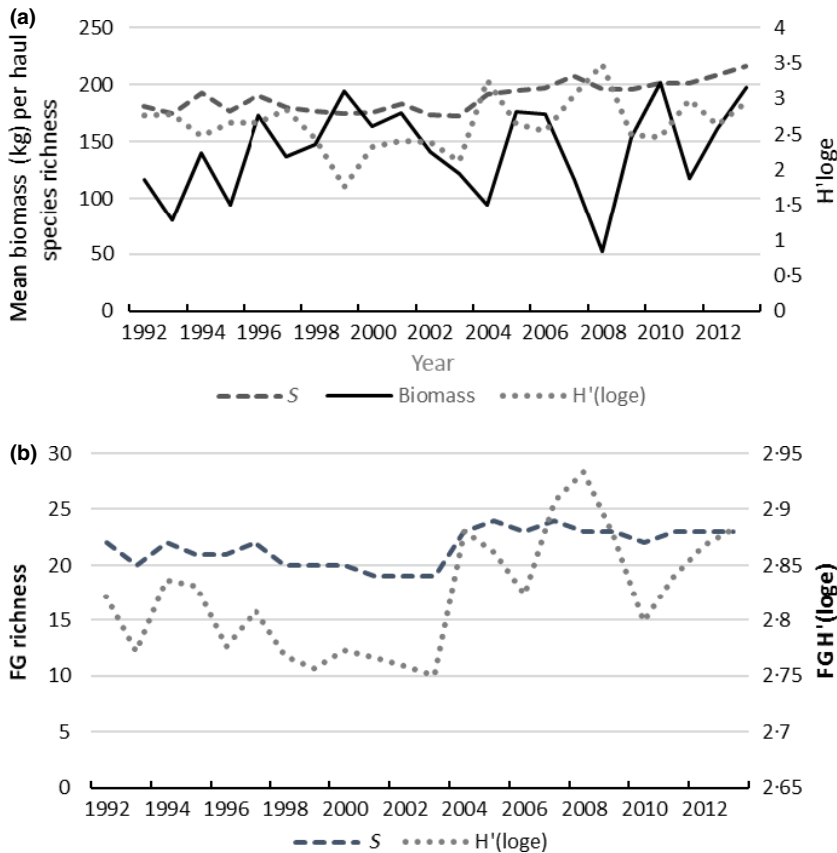


Fig. 2. Variations in richness, biomass and diversity ($H'(\log_e)$) over the study period (1992–2013) at species (a) and functional group (b) level. Values are the mean per haul for each year during Demersales IBT surveys.

In both cases (demersal assemblage and functional group structure), the resulting data matrices were double-root transformed to down-weight the importance of the most abundant species and the Bray-Curtis similarity index calculated between sampling years. nMDS analysis was applied and the results plotted bidimensionally. Significant differences among the resulting groups of years were investigated by means of ANOSIM and species responsible for major differences between years identified using the SIMPER analysis. All these procedures were conducted using PRIMERv6 software (Clarke & Gorley 2006).

VARIATIONS IN CONSUMER NETWORK STRUCTURE

To assess network structure variations of the main predators in the demersal assemblage, we calculated link number and the mean and the variance of the interaction strength for the 22 consumer species for whom gut contents were analysed over time. These species represent the consumer compartment of the Southern Bay of Biscay's demersal ecosystem, and were the most abundant and frequent during the 'Demersales' surveys throughout the study period.

First, we calculated link number (L) by counting the number of prey items identified to species level for each consumer species each year and used it to calculate variations in consumer mean link number over time. We also grouped the 22 species into the aforementioned functional groups and analysed the evolution of mean number of links for the resulting groups, analysing large and small hake, monkfish, blue whiting and megrims (the main commercial species), independently. Since the proportion of consumed volume that was not identified to species level did not vary significantly

over time (Mann–Kendall, $P > 0.05$), and most of it was composed of prey items which were already in the identified species list, the number of actual links for a given species should not have been significantly altered by excluding the unidentified volume.

To estimate the relative strength of the predator–prey interaction, we estimated the fraction that each diet item identified to species level contributed to the diet of each of the 22 predator species by dividing the total volumetric contribution of this item in the stomachs of a given consumer species by the total amount of stomach content of this consumer species, analysed during each year. Following Rossberg *et al.* (2011), a list of the numerical values of all the diet fractions of the 22 consumers for each year was compiled, without regard for the identities of the resources or the consumers. The number of links surpassing specific threshold levels (contributions to the diet of a specific predator, or interactions) was then quantified. Thus, in this case, L stood for the number of links with $l_{jk} \geq \theta$, for pre-defined thresholds θ , and l_{jk} represented the interaction strength between predator and prey, formulated as the volume diet contribution (m_{jk}) of species j to the diet (gut content) of consumer species k :

$$l_{jk} = m_{jk} / \sum_h m_{hk}$$

We established a suite of thresholds ranging from 0.001 prey percentage contribution to 1 and examined variations in their trends over time.

Since a considerable amount of volume may be unidentified when concentrating on identified species, we corrected link density values for those resource species not included in the list (Rossberg *et al.* 2006). We calculated the average amount

(volume) of non-identified resources among the 22 consumer species for each year and calculated the amount of 'lost links (N)' by using the formula:

$$N = (u * l) / r,$$

where u stands for the percentage of unidentified volume, l is the number of links identified to species level above a particular threshold and r is the percentage of identified volume.

The total number of links for each specific threshold was thus calculated as:

$$L = N + l$$

We examined the relationship between mean interaction strength and species richness by correlation analysis, using the Spearman correlation.

CHANGES IN DIET DIVERSITY OVER TIME

We examined variations in diet diversity of the 22 consumer species for which gut contents were identified using the Gini-Simpson diversity index. We considered only those prey items which were identified to species level, disregarding species lumped into higher taxa groups. As before, a high amount of volume was lost in the calculations, but inconsistencies in species identifications among years were minimized. We used the formula:

$$d_k = 1 - \sum_j p_{jk}^2,$$

where p_{jk} stands for the proportional contribution of species j to the diet of consumer species k . We corrected for the elimination of those items that were not identified to species level by using the same rationale as before, and calculated overall diet diversity (D) as:

$$G = D + d$$

where $D = (u * d) / r$, u stands for the percentage of unidentified volume, d is the diversity of identified species and r is the percentage of identified volume.

Finally, to discern whether changes in mean diet diversity and that of the main consumer species or FG were related with variations in species richness or diversity in the demersal community, we conducted correlation analyses between variables. Since we expected a monotonic relationship, but not necessarily a linear one, we used the Spearman rank correlation analysis.

For all analyses, significances of observed trends over time were examined by using a modified version of the Mann-Kendall trend test for autocorrelated data based on Hamed & Rao (1998), and developed by the Santander Meteorology Group (<http://www.meteo.unican.es>). (<https://cran.r-project.org/src/contrib/Archive/fume/>). This package provides both the uncorrected (Z) and corrected (Z_c) statistic, calculates the slope according to Sen's (1968) test, and allows determining whether any autocorrelation has a clear effect on the significance of the Mann-Kendall correlation by providing the adjusted sample size after the correction. Trends were judged significant when $P < 0.05$. Given the high amount of comparisons/analyses performed and in order to prevent Type I error occurrence, we adjusted significance levels by using the Sequential Bonferroni correction (Quin & Keough 2002) on each family of analyses. Considering the high degree of

conservativeness of this type of correction, when relevant, significant values found before the adjustment were also indicated.

RELATIONSHIP WITH FISHING PRESSURE

To investigate whether trends in link number and interaction strength were related to variations in fishing pressure, we conducted a Spearman correlation analysis between mean link number, link density values at various thresholds and mean interaction strength, and fishing mortality (F_{com}), as a surrogate of fishing pressure in the area.

Estimates of assemblage-averaged fishing mortality (F_{com}) were generated using data from the five main commercial demersal species, i.e. hake *M. merluccius*, angler *Lophius piscatorius*, black-bellied angler *Lophius budegassa*, and the two megrim species *L. boscii* and *L. whiffagonis*, using $F_{s,msy}$ as reference point (Modica *et al.* 2014), and calculated as:

$$F_{com,Y} = \frac{\sum_{s=1}^4 F_{s,Y} / F_{s,msy}}{5}$$

where $F_{s,y}$ is the annual fishing mortality for each species in each year. Values of $F_{s,Y}$, and $F_{s,msy}$ were obtained from stock assessment data at the ICES data portal.

TRAFFIC LIGHT PLOT (TLP)

To visualize overall systematic patterns of community and network structure parameters over time, we generated a TLP in which all values were categorized into quintiles and each of them was assigned a specific colour following a colour gradation scheme. F_{com} values were also incorporated into the graph following the same procedure to allow the direct comparison of the observed values against this measure of fishing pressure.

All statistical analyses were conducted using R software (R Core Team, 2015), except where otherwise specified.

Results

Approximately 300 species, gathered into 23 functional groups were recorded over the 22 years investigated, including fish and macroinvertebrates. All species recorded and included in our analyses were consumers ranging from detritivores to top predator species feeding solely on fish (Appendix S1).

CHANGES IN THE DEMERSAL ASSEMBLAGE AND FUNCTIONAL GROUPS STRUCTURE OVER TIME

Mean biomass and abundance values per haul fluctuated over time (Fig. 2a), but no significant increasing or decreasing trend was discernible (Mann Kendall, $P > 0.05$). On the other hand, species richness per year (S), increased significantly over time (MK, $Z = 3.44$, $P < 0.001$, $sen = 1.59$), while Shannon-Wiener's diversity (H'/\log_e), or evenness (J') whether based on biomass or abundance (number of individuals) values, did not (MK, $P > 0.05$).

The biomass of 10 of the total number of functional groups/commercial species varied significantly over time

(Fig. 3). Detritivore decapods (DD) also showed a marginally significant increasing trend ($P = 0.055$) at the end of the time series (Fig. 3). Notably, most demersal-related and benthic feeding groups, and particularly those including large predators such as large demersal fish (LDF) or deep demersal fish (DDF) increased significantly. Sharks (DS) and rays (R) also showed a progressive increase in their biomass per haul over time, as well as carnivore (CE) and deposit-feeding (DFE) echinoderms, while only the biomass of nectophagous fish (NF) decreased significantly through the years. When the trend in the biomass of specific commercially important species was evaluated separately, significant values were found for hake (HKE), megrim (M) and catshark (SCY), all of which increased their biomasses, and *Nephrops norvegicus* (NPH), whose biomass decreased significantly over time (Fig. 3). These variations were mirrored in significant trends in Shannon diversity of FG (MK, $Z_c = 2.22$, $P < 0.05$), but not their richness (MK, $P > 0.05$), over time (Fig. 2b). As regards diversity, the trend declined until 2003, when it was reversed

into an increasing tendency which prevailed until the end of the time series (Fig. 2b).

The demersal assemblage structure of the Southern Bay of Biscay, based on species biomass data showed significantly different year groupings over time (global $R = 0.791$, $P = 0.001$, Fig. 4a, Table 1). These corresponded to chronological groupings from years 1992–1997 (group 1), 1998–2003 (group 2) and 2004–2013 (group 3), respectively. Pair-wise differences were found between all groups (groups 1–2, $R = 0.761$, $P < 0.01$; groups 1–3, $R = 0.96$, $P = 0.001$; groups 2–3, $R = 0.682$, $P = 0.001$). The SIMPER analysis based on these groupings, did not identify any species or group clearly responsible for them, but rather the whole assemblage as contributing to variations among groups of years (i.e. more than 70 species contributed to 50% variation in all cases, results not shown).

The nMDS on the biomass of the various functional groups (Fig. 4b) did not show such clear groupings among years, though still a chronological trend was discernible. In this case, two main groups including years

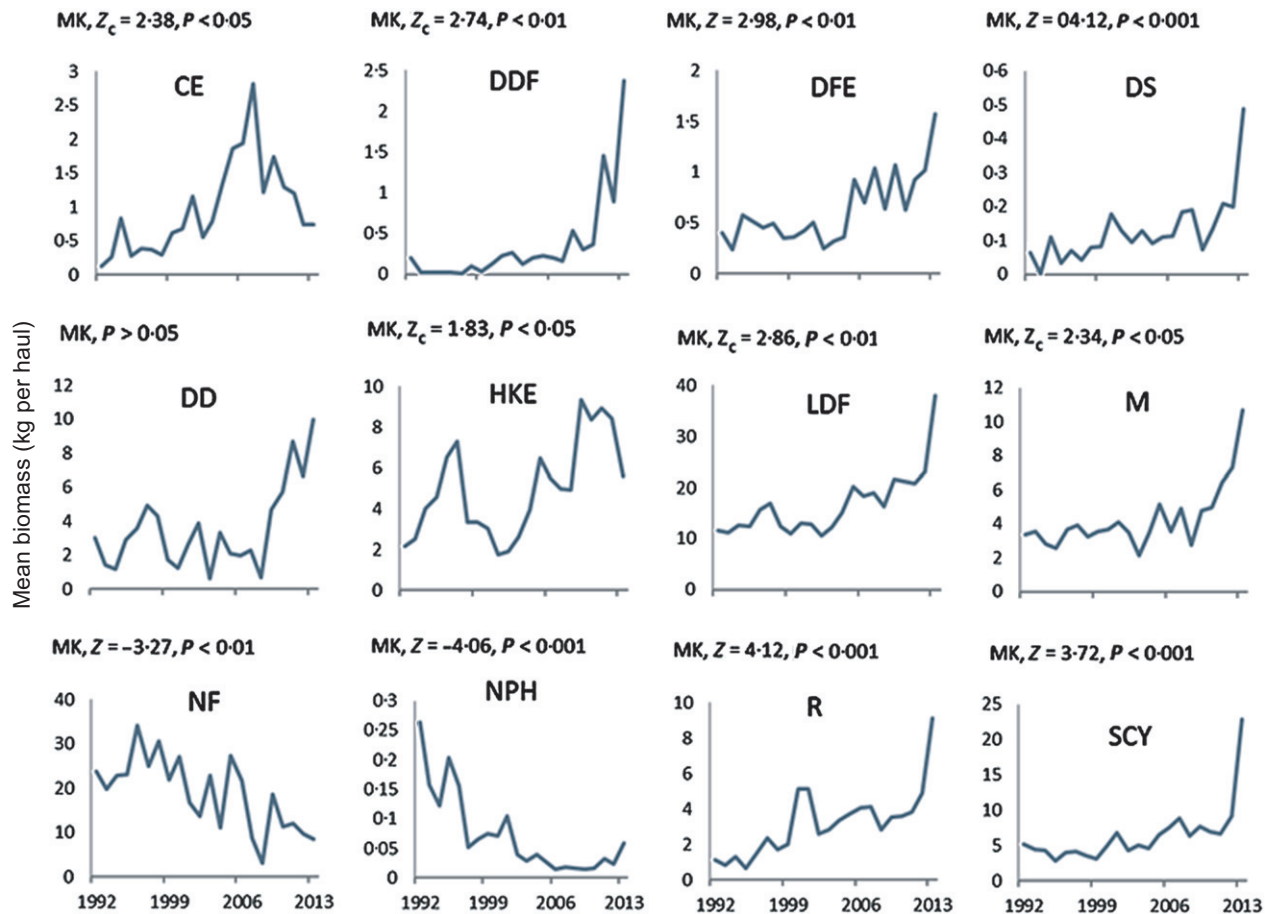


Fig. 3. Trends in the biomass of functional groups and commercial species with significant variations over time, shown by Mann Kendall (MK) trend analyses. All values significant after Bonferroni correction. CE = carnivorous echinoderms; DDF = deep demersal fish; DFE = deposit feeding echinoderms; DS = deep sea sharks; DD = detritivore decapods; HKE = hake; LDF = large demersal fish; M = megrims; NF = nectophagous fish; NPH = *Nephrops norvegicus*; R = rays; SCY = *Scylliorhinus canicula*.

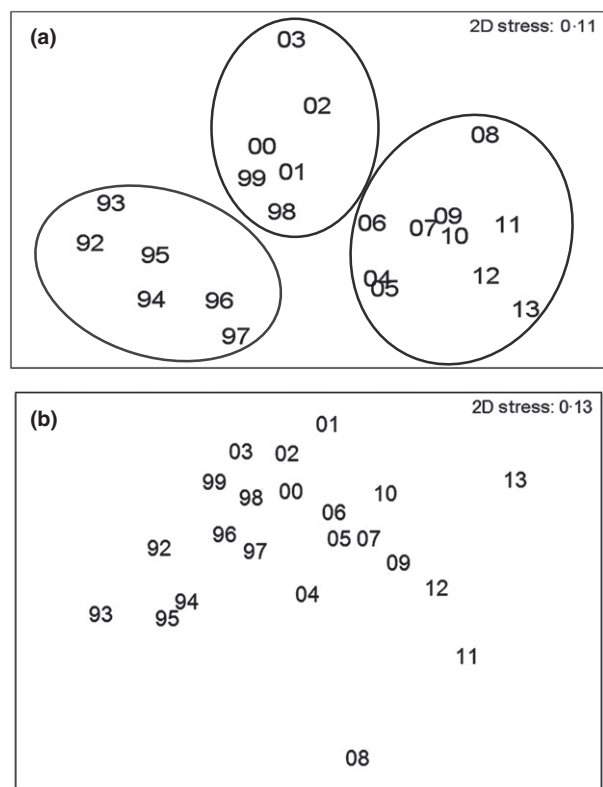


Fig. 4. Results of the nMDSs based on Bray–Curtis similarities of double root transformed values of mean biomass per haul data of the benthic-demersal assemblage at (a) species and (b) functional group level. Ellipses in A indicate significantly different groups of years as confirmed by the ANOSIM.

Table 1. Results of Mann Kendall trend analyses on the mean and the variance of global interaction strengths, and the amount of interaction strength above specific thresholds, for the 22 consumer species analysed. Significant values are highlighted in bold. ***Significant after Bonferroni correction

| Interaction strength | Z | P-value | Tau | Sen's slope |
|----------------------|--------------|-------------------|--------------|----------------|
| Mean | -4.56 | 0.000005 | -0.67 | -0.001 |
| Variance | -2.36 | 0.02 | -0.35 | -0.0003 |
| Threshold value | | | | |
| 0.001 | 3.94 | 0.00008*** | 0.58 | 0.32 |
| 0.005 | 2.75 | 0.006 | 0.40 | 0.15 |
| 0.007 | 2.65 | 0.008 | 0.39 | 0.15 |
| 0.009 | 2.50 | 0.01 | 0.37 | 0.14 |
| 0.01 | 2.50 | 0.01 | 0.37 | 0.11 |
| 0.02 | 2.10 | 0.03 | 0.31 | 0.08 |
| 0.05 | 1.51 | 0.13 | 0.22 | 0.03 |
| 0.1 | 0.91 | 0.36 | 0.14 | 0.008 |
| 0.2 | 0.37 | 0.71 | 0.06 | 0.002 |
| 0.4 | 0.02 | 0.98 | 0 | 0.001 |
| 0.6 | 0.22 | 0.82 | 0.04 | -0.001 |
| 0.8 | -1.44 | 0.15 | -0.21 | -0.002 |
| 0.9 | 0.33 | 0.74 | 0.05 | 0 |
| 1 | -0.33 | 0.74 | -0.04 | 0 |

before 2000 and from 2000 onwards, respectively, were apparent, and identified as significantly different by the ANOSIM (Global $R = 0.377$, $P < 0.05$).

VARIATIONS IN PREDATOR NETWORK STRUCTURE OVER TIME

There was a significant increasing trend in the mean number of links shown by the consumer species analysed (MK, $Z = 4.69$, $P < 0.001$, Fig. 5). This trend was maintained for benthic feeding fish (BF, MK, $Z_c = 3.564$, $P < 0.001$), rays (R, MK, $Z = 4.51$, $P < 0.001$), and large demersal fish (Fig. 5). Among megrims, *L. boschii* also showed a significant increasing trend (M1, MK, $Z = 4.50$, $P < 0.001$) while *L. whiffiagonis* did not. Neither did *M. poutassou* nor small hake ($P > 0.05$). Adult hake (MK, $Z = 2.37$, $P < 0.05$) and *Scyliorhinus canicula* (MK, $Z = 3.72$, $P < 0.05$) also showed significant increasing trends over time, but not after the Bonferroni correction. Overall, *Scyliorhinus canicula* showed the highest number of links over time (Fig. 5).

Moreover, there was a significant positive correlation between the number of species recorded each year and the mean number of links for the main consumer species in the study area ($S = 609.79$; $P < 0.05$; $\rho = 0.735$), but not between mean link number and Shannon's diversity ($P > 0.05$).

In general, weak interactions predominated over the whole study period, indicating a majority of generalist species within the 22 consumers considered (Fig. 5). When variations in consumer-prey relations were examined quantitatively over time, a clear increasing trend was only discernible for low threshold values (i.e. below a 20% contribution, less than 1% contribution after Bonferroni correction, Fig. 5, Table 1), indicating a significant increase only in weak interactions (<20% contribution) over time. The mean and the variance of overall interaction strengths decreased significantly over time (Table 1) and mean interaction strength was negatively correlated with species richness (Fig. 5, Spearman $\rho = -0.73$; $P < 0.001$).

CHANGES IN DIET DIVERSITY OVER TIME

No changes in mean diet diversity values of the 24 consumer species were detected over time after correcting for unidentified species in stomach contents (Table 2). However, significant variations were found for some functional groups which increased (LDF), or decreased (R, SCY), their mean diet diversity values over time (Table 2). The remaining functional groups or species analysed showed no significant variations (Table 2).

RELATIONSHIP BETWEEN SPECIES RICHNESS, DIVERSITY AND DIET DIVERSITY

The Spearman correlation test based on ranks did not detect any significant relationship between mean diet diversity and species richness or diversity ($P > 0.05$). When specific species and FG were analysed, the test detected a significant positive relationship between the diet diversity of large hake and species diversity ($\rho = 0.5$, $P < 0.05$), and a negative one between the diversity of the catshark's diet and overall species richness ($\rho = -0.65$, $P < 0.001$).

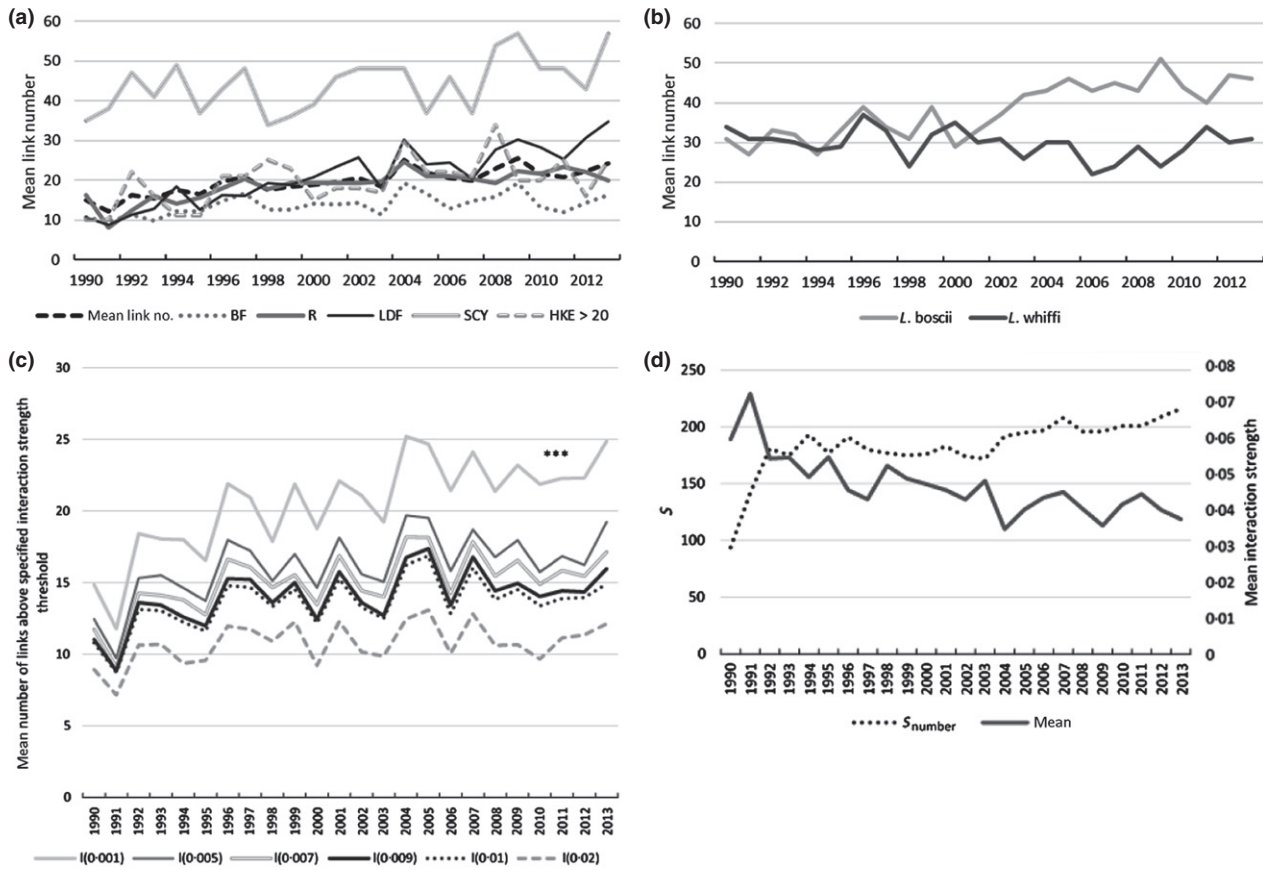


Fig. 5. Trends in mean link number of those groups/species with significant variations (a), in mean link number of the two megrim species sampled in the Southern Bay of Biscay (b), in mean number of links above specific interaction strength thresholds (c), and in species number and mean interaction strength (d) over time. BF = benthivorous fish; R = rays; LDF = large demersal fish; SCY = *Scyliorhinus canicula*; HKE >20 = large hake (*Merluccius merluccius*). In c, only thresholds below 20% are shown. ***Significant after Bonferroni correction.

Table 2. Results of Mann Kendall trend analyses of mean diet diversity and diet diversity of the main functional groups and the main commercial species under analyses. Corrected and uncorrected values are presented when serial correlation occurred. Significant values are highlighted in bold (**significant after Bonferroni's correction). M1, *Lepidorhombus boscii*; M2, *Lepidorhombus whiffiagonis*

| Group | Z | P-value | Zcorr | P-value-corr | Tau | 'N/N*s' | Sen's slope |
|-----------|---------------|------------------|-------|--------------|--------------|---------|---------------|
| Mean | 0.22 | 0.82 | | | 0.04 | | 0.0002 |
| BF | -0.57 | 0.57 | | | -0.08 | | -0.001 |
| R | -2.009 | 0.04 | | | -0.29 | | -0.004 |
| HKElarge | 0.72 | 0.47 | 1.36 | 0.17 | 0.11 | 0.28 | 0.003 |
| HKE small | 0.025 | 0.98 | | | | | |
| M1 | -0.27 | 0.78 | -0.21 | 0.83 | -0.04 | 1.71 | -0.0007 |
| SCY | -3.74 | 0.0002*** | | | | | -0.008 |
| LDF | 2.60 | 0.009 | | | 0.38 | | 0.008 |
| WHB | 0.87 | 0.38 | 0.99 | 0.32 | 0.13 | 0.76 | 0.004 |
| M2 | -0.97 | 0.33 | | | -0.14 | | -0.003 |

RELATIONSHIP WITH FISHING PRESSURE

As for the relationship between network structure properties (number of links, interaction strength) and fish mortality indicators, there was a significant negative correlation between fishing mortality and link number (Spearman $\rho = -0.58$, $P < 0.01$) and a positive one

between fishing mortality and mean interaction strength (Spearman $\rho = 0.71$, $P < 0.01$).

TRAFFIC LIGHT PLOT

The traffic light plot (Fig. 6) confirmed the year groupings obtained with the nMDS analysis and highlighted even

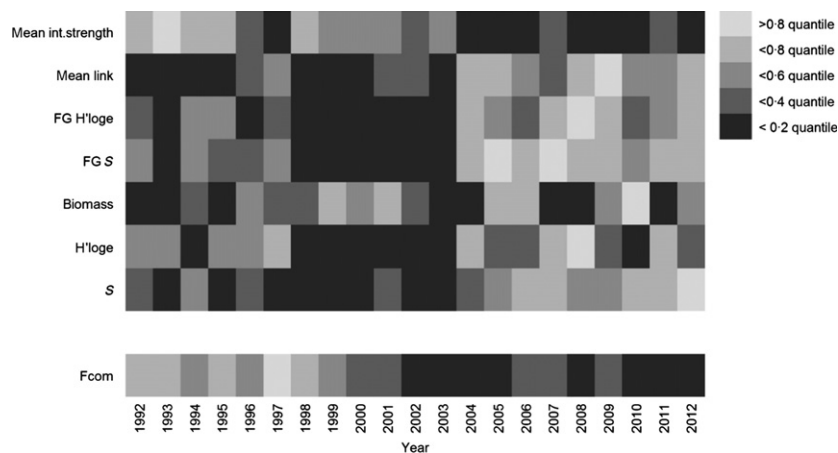


Fig. 6. Traffic light plot representing community indices over time based on quintile classifications of species and functional group (FG) biomass data, and Fcom values calculated on the main commercial demersal species.

further the different structure in terms of species and functional group richness and diversity during the middle period between 1998 and 2003, and the opposed trends in mean link values and mean interaction strength with a reduction in mortality values.

Discussion

The mechanisms through which communities recover after disturbances are many and in many instances, still poorly understood. Recent alarming global trends of marine biodiversity loss and increases in marine ecosystem collapses have provoked putting into practice measures to try to regain stability and resilience of these systems. Ironically, ways to define or determine the extent to which this stability is recovered after their implementation are still difficult to standardize, despite a growing body of empirical and modelling studies on the matter (Scheffer *et al.* 2012). In this sense, detecting patterns in natural communities released from stress when they start giving unequivocal signs of recovery or change to alternative stable states is essential to unravel the effects of these perturbations and design effective management strategies. Our study shows that trophic network properties may provide a convincing tool to evaluate and perceive recovery patterns even in highly impacted areas such as the Southern Bay of Biscay.

Indeed, our results highlight the clear bottom-up linkage from benthivores to piscivores emphasized by other studies on the Bay of Biscay (Sánchez & Olaso 2004; Heath 2005b; Lassalle *et al.* 2011; Rochet, Collie & Trenkel 2013), and point at the benthic-demersal link from detritus-based crustaceans to large demersal fish as a possible mechanism instigating the recovery of large fish populations and important commercial stocks (Moore *et al.* 2004), which is in accordance with theoretical predictions made in the study area (Rooney & McCann 2012). Moreover, trends of increased species richness and diversity of FG were paralleled by an increase in links per species and a decrease in the mean and the variance of interaction strengths between the main consumer species and their potential prey. Theoretically, these patterns should be an

indication of a path towards increased stability of the benthic-demersal assemblages in this area (Kokkoris *et al.* 2002; Rooney & McCann 2012), as well as a buffer to trophic cascades and species loss in case of further disturbances (Dunne, Williams & Martínez 2002).

Overall, our system showed high numbers of links for the main consumer species, which as expected, increased over time with species richness (Peterson, Allen & Holling 1998; Dunne *et al.* 2005). Most food webs having more than 40 species have a connectance of approximately 10% of species richness, i.e. in a given food web a species is supposed to eat 10% of the species present (Dunne, Williams & Martínez 2002; Link 2002). Our system showed species richness values ranging from 181 species in 1992 to 216 in 2013, and average link numbers which oscillated from 10 to 20 at the beginning of the time series to 20–30 at the end, which is more in agreement with the number of species present, and the generalist diet of most consumers analysed (Velasco, Olaso & Sánchez 2001; Serrano *et al.* 2003; Preciado, Velasco & Olaso 2008). Notably, of the two megrim species, *L. boschii*, the species which is most trophically linked to benthic habitats (Serrano *et al.* 2003), was the one showing increasing trends in link number over our study period. This complication of the network was in general, not paralleled by increases in diet diversity of the main consumer species, although significant and opposing trends were found for some species, i.e. hake (increasing diet diversity) vs. catshark (decreasing).

The fact that the Bay of Biscay's shelf ecosystem is mainly regulated by a detrital energy pathway has been stressed beforehand (Sánchez & Olaso 2004; Le Loc'h, Hily & Grall 2008), and could contribute to explain the relative rapidity of the recovery trends shown here, as well as the high diversity found in our study area (Moore *et al.* 2004; Yaragina & Dolgov 2009; Lassalle *et al.* 2011; Rooney & McCann 2012). Increases in large predator biomasses are particularly relevant as regards trophic implications, since they are the ones involved in trophic cascades, and representing strong interactions in food chains (McCann 2000; Bascompte, Melián & Sala 2005). The coincidence of the central period identified by our multivariate analysis, with

declines in species richness and functional group diversity with years in which hake abundance was low may be indicative of a trophic cascade and needs further investigation. Top predators (such as hake) have historically been selectively targeted by fisheries, typically rebuilding more slowly, and are particularly prone to be at risk of long-term depletion (Neubauer *et al.* 2013), so their recovery should be a convincing sign of restructuring of the food network. On the other hand, some particularly vulnerable groups such as large demersal (piscivorous) fish or rays, or sea urchins, which have been identified as indicators of the negative effects of trawling in the Cantabrian Sea (Serrano *et al.* 2011; González-Irusta, Punzón & Serrano 2012), also showed signs of recovery, which were more pronounced around 2010, 10 years after the reduction in mean mortality values.

Whether our time series was initiated during a stable or an unstable state remains questionable, but all signs and metrics analysed seem to indicate that our system is evolving into increased stability already – 10 years after the regulations were put into force. Neubauer *et al.* (2013) confirmed theoretical models predicting that most overfished stocks should recover to B_{MSY} in less than a decade provided that fishing mortality was sufficiently reduced, which has also been recently shown by Costello *et al.* (2016). They warned, however, that regardless of their depletion level, at current fishing mortality rates, recovery to B_{MSY} remains a distant target for the majority of stocks that are now depleted, which is in accordance with recent alarming global predictions of overexploitation trends (Worm 2016). In general, measures to affect resilience and guarantee stable domains rather than simply control disturbance and fluctuations have been summoned (Scheffer *et al.* 2001), and indicators of these processes are called for in order to evaluate recovery rates specifically, at the network level. Our results provide promising evidence of the efficiency of specific fishery regulations as a guarantee for the recovery of assemblages at the community level and the assurance of energy pathways to upper trophic compartments, which lie at the base of an ecosystem approach to fisheries management.

Authors' contributions

N.L.A. and I.P. conceived the ideas and designed the methodology, N.L.A. analysed the data and led the writing of the manuscript. L.L. collected the data and contributed to the analyses. I.M. and A.P. collected the data. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5bf86> (Arroyo *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Species recorded during the 22 years of Demersales (IBTS) surveys in the Southern Bay of Biscay and their functional group assignment.