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Mediterranean nekton traits: Distribution, relationships and significance for marine ecology monitoring and management

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Biological traits are increasingly used in order to study aspects of ecology as they are related to the organisms' fitness. Here we use an extensive dataset of 23 traits regarding the life cycle, distribution, ecology and behavior of 235 nektonic species of the Mediterranean Sea assembled from the bibliography in order to evaluate the distribution of traits, identify rare ones and detect relationships between pairs of traits. Traits relationships were tested using correlation and non-linear regression for pairs of continuous traits, parametric and non-parametric tests (ANOVA, Kruskall-Wallis, t-test and Mann Whitney U test) for pairs of continuous-categorical traits and cooccurrence testing for categorical traits. Apart from relationships that have already been documented in the past (e.g. the relationship between longevity and size) a number of findings have significant implications concerning the potential effects of climate change (e.g. through the relationships of the trait of optimal temperature) or habitat loss (derived from the relationships of traits related to tolerance ranges). Furthermore, some unexpected relationships are documented, like the inversely proportional relationship between longevity and age at maturity expressed as a percentage of life span, the non-linear relationship between fecundity and longevity or optimal temperature with depth. For the assessment of the results, we first critically evaluate the importance of each trait at the level of the population, community, ecosystem and landscape, i.e. regarding anthropogenic effects and then propose the traits that should be monitored concerning the regulation and resilience of ecosystem functioning and the management of the marine ecosystems.

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Abstract

Biological traits are increasingly used in order to study aspects of ecology as they are related to the organisms' fitness. Here we use an extensive dataset of 23 traits regarding the life cycle, distribution, ecology and behavior of 235 nektonic species of the Mediterranean Sea assembled from the bibliography in order to evaluate the distribution of traits, identify rare ones and detect relationships between pairs of traits. Traits relationships were tested using correlation and non-linear regression for pairs of continuous traits, parametric and non-parametric tests (ANOVA, Kruskall-Wallis, t-test and Mann Whitney U test) for pairs of continuous-categorical traits and cooccurrence testing for categorical traits. Apart from relationships that have already been documented in the past (e.g. the relationship between longevity and size) a number of findings have significant implications concerning the potential effects of climate change (e.g. through the relationships of the trait of optimal temperature) or habitat loss (derived from the relationships of traits related to tolerance ranges). Furthermore, some unexpected relationships are documented, like the inversely proportional relationship between longevity and age at maturity expressed as a percentage of life span, the non-linear relationship between fecundity and longevity or optimal temperature with depth. For the assessment of the results, we first critically evaluate the importance of each trait at the level of the population, community, ecosystem and landscape, i.e. regarding anthropogenic effects and then propose the traits that should be monitored concerning the regulation and resilience of ecosystem functioning and the management of the marine ecosystems.

Introduction

Today, the characteristics of organisms, usually referred to as traits, are increasingly used in order to study aspects of biology and ecology as they are related to the organisms' ability to survive, grow and produce offspring, i.e. to increase their fitness (Violle et al., 2007). The so-called traits based approaches, comprise an arsenal of methods that use traits instead of taxonomic information to characterize ecosystems, providing various advantages like alternative ways to study biological communities and their functioning (Bellwood, Hoey & Choat, 2003; Bremner, 2008; Pecuchet et al., 2017, 2018). Furthermore, they can be used to elucidate the effects of environmental or anthropogenic stressors on ecosystem functioning (Frelat et al., 2018; McLean, Mouillot & Auber, 2018).

However, the study of biological traits is not novel in marine biology. Traits have long been studied in order to determine relationships between aspects of an organisms' physiology or ecology. Additionally, evolutionary processes have provided specific combinations of characteristics to organisms; hence the traits appearing in any given species are not random (e.g. Winemiller & Rose, 1992; Charnov, 1993). Their combination into life histories serve functions like survival, growth, sexual maturation and reproduction at the organismal level (Beverton, 1992) shaping fitness that can act at the level of populations and, ultimately, communities. However, the relationships between traits can be important, not only for understanding how evolution has shaped life into form and function (Charnov, Gislason & Pope, 2013), but also in order to assess the potential effects of environmental factors. Even more so as, apart from environmental filtering (Bejarano et al., 2017), anthropogenic stressors like fisheries can favour the selection of specific traits (e.g. de Juan et al. 2007) and thus indirectly alter future community trait composition, possibly modifying the functioning of communities or the ecosystem. As a result, there is a probability that the selection of specific traits may lead to changes in the frequencies of others that are associated with them as a side effect. This supposition gives novel importance to the study of relationships between traits. Furthermore, the study of trait frequencies and the identification of rare traits may indicate keynote species for ecosystem functioning (Violle et al., 2017).

In order to comprehend the functional aspect of traits and the implications of their relationships it is important to document their significance not only for shaping the life history of an organism at the level of the individual. Highlighting the importance of traits at the population scale comes easily, as traits are related to the adaptations of the species to its environment aiming to maximize fitness at the individual and population level (Violle et al., 2007). However, an overall evaluation of the importance or the implications of biological traits should be carried out at levels beyond that of the population, especially for nekton, where a multitude of species are under a exploitation and inter-specific interactions have raised important challenges. Thus, a brief presentation of the significance and implications of nekton traits at various ecological levels, i.e. (a) that of the population, (b) interspecific relationships and communities, (c) overall ecosystem functioning and even (d) relevance for anthropogenic effects like fisheries and climate change is presented in Table 1.

The investigation of patterns and relationships between traits are especially important for regions that host a high biodiversity like the Mediterranean Sea (Myers et al., 2000, Bianchi & Morri, 2000). Furthermore, the Mediterranean has a long history of human presence and is today facing challenges due to stressors that are either novel or are acting at unprecedented levels (Lejeusne et al., 2010). Koutsidi et al. (2016) have already studied traits relationships and rarity; however, in that work traits had been assembled only for a limited number of species (mainly commercial species targeted or caught by fisheries). Additionally, in that work traits had been evaluated only as categorical variables (i.e. with each trait being described by trait categories). This may possibly have blurred the results in the case of quantitative traits like life span or size.

The aim of the present study is to use an extensive dataset of 23 traits assembled from the bibliography for 235 nektonic species of the Mediterranean Sea in order to: (a) determine whether there are rare or important traits by evaluating the distribution of traits and (b) detect whether there are undocumented relationships between pairs of biological traits.

Materials & Methods

Information on 23 traits related to the life cycle, distribution, ecology and behaviour of 235 species of nekton occurring in the Mediterranean Sea was collected from the bibliography (Table 2). Trait information is often found in printed sources (e.g. fish identification keys) and terms are not standardized. Thus, no systematic review could be performed. Instead, the information was collected from books, review articles or journal research articles by searching using the species name and adding the name of the trait or relevant terms (e.g. "life span" instead of "longevity", "reproduction" instead of "spawning period"). These traits comprise different types of variables: continuous (e.g. size or maximum lifespan), range (e.g. optimal depth) and categorical (e.g. spawning habitat: pelagic or benthic). The information on traits as continuous variables and the definition of traits categories per species as well as the bibliographic reference for the documentation of each trait per species can be found at: https://figshare.com/articles/Koutsidi_Moukas_Tzanatos_23_traits_by_235_species_xls/8020247/1

For the detection of patterns in their distribution, the range type traits (fecundity, optimal depth, optimal temperature, trophic level) were expressed as such, while for statistical tests and the detection of relationships between trait pairs they were used as the average between the minimum and the maximum (thus used as continuous type traits). Continuous and range-type traits were investigated for outlier detection using the Grubbs test (Grubbs, 1950). As this test is parametric, it was performed after the log-transformation of the traits: longevity and maximum length, while age at maturity was transformed using the square root to achieve normality. As average fecundity and average depth could not be described by a normal distribution with any possible transformation the Grubb test was not used on these variables. Regarding the identification of rare traits, the distribution of trait values (for continuous variable-type trait) or the frequencies of trait categories (for categorical variable-type trait) allowed the identification of rare traits as these shared by less than 5 % of species.

To identify potential relationships the continuous traits longevity, fecundity, maximum length and depth were transformed using the natural logarithm. Each of the total of 23 traits was examined for the existence of a potential relationship with all other ones, depending on their types. Regarding pairs of continuous traits, Pearson correlation between all pairs of continuous traits was used. As carrying out a test for multiple hypotheses increases the probability of a rare event, the likelihood of incorrectly rejecting the null hypothesis (Type I error) increases; hence in the results the Bonferroni correction was incorporated. Correlation has the advantage of investigating relationships without assuming causality, however it can only detect linear relationships. To investigate the existence of non-linear relationships, a polynomial regression was additionally used (e.g. where the residuals indicated a non-linear pattern) and, in cases of better fit, these relationships are presented instead.

For the detection of relationships between continuous and categorical traits, the t-test or Analysis of Variance (ANOVA) was used, depending on the number of categories of the categorical trait. In the cases where the parametric prerequisites (normality and homogeneity of variance) were not fulfilled, the Mann-Whitney or Kruskal-Wallis tests were used instead (Zar, 1999). Similarly, we incorporated the Bonferroni correction here.

To detect relationships between categorical traits, we followed the approach by Koutsidi, et al. (2016) that had been used for a smaller number of traits (21) and species (86). This approach investigates pairwise patterns of traits co-occurrence and compares these co-occurrences to the number of randomly expected ones, characterizing them thus as positive (the pair of traits tends to co-occur more than expected by the product of their independent frequencies), negative (the pair of traits tends to co-occur less than expected by the product of their independent frequencies) or random co-occurrences. For this analysis we used the library "co-occur" (Griffith, Veech & Marsh, 2016) in R-language.

The significance level $\alpha=0.05$ was used for all inferential tests, subsequently incorporating the Bonferroni correction as stated above.

Results

Trait frequencies and distributions allowed the identification of dominant and rare traits in the 235 species examined. Regarding continuous traits, 89,6% of the species examined were found to have a maximum life span of up to 25 years, but life cycles can reach up to ~120 years with the rare high longevity frequency classes shared in most cases by only a few species (Figure 1A). Concerning age at maturity, both early and late age at maturity (in comparison to life span) come as outliers with low frequencies. Finally, regarding size, nekton species with a maximum length over ~80 cm is uncommon (~78 % of species examined may reach below this size), while nekton reaching 2-8 metres is scarce. Slightly over 5% are the number of nekton species with a maximum size below 10 cm. No outliers were found in the log-transformed longevity (Grubbs test, G=2,82, p=0.91) and maximum length data (Grubbs test, G=3.25, p=0.23) or in the square root age at maturity (Grubbs test, G=3.44, p=0.10).

For range type traits (Figure 1B), fecundity shows a distribution that, in both low and high values, follows a different angle compared to intermediate ones. Especially the values of low fecundity are mostly associated with Chondrichthyes (the 20 species with the lowest fecundity values are all cartilaginous fish). The highest values of fecundity were obtained by a heterogeneous group of species (*Thunnus thynnus, Labrus merula, Psetta maxima, Scophthalmus rhombus, Polyprion americanus*). Distribution across depth is relatively continuous with many species being distributed in shallow depths (40 species with an average depth more shallow than 20 m and 86 above 50 m). Only a few species were found to be distributed in deep habitats (only 17 had an average depth deeper than 500 m, but the case is that deep-living nekton generally includes species whose traits are relatively unknown and, as a result, were generally not included in the dataset of 235 species examined here). The distribution of trophic level indicated the rarity of low (reaching up to trophic level 3) trophic level species among the nekton, while the distribution of optimal temperatures did not indicate important outliers. The Grubbs test indicated no outliers regarding average trophic level (Grubbs test, G=3.14, p=0.34) and optimal temperature (Grubbs test, G=2.15, p=0.99).

Regarding categorical traits (Figure 2), gonochorism (86%), subtropical distribution (64%), summer spawning (61%), free exposure type (67%), benthopelagic habitat use (63%), grazing feeding type (60%), eurythermal temperature range (66%), stenohaline salinity range

(61%) and solitary behavior (57%) were dominant trait categories among the species examined. Flat (9%) and long body shape (7%), tropical (9%) and cosmopolitan geographic distribution (3%), autumn (3%), winter (7%) and all year spawning (6%), hard substrate seabed type (9%), ambusher mobility (6%), ambushing predation feeding behaviour (7%) and herbivorous (2%) and zooplankton diet (9%) were found to be shared by below 10% of the total species.

The relationships between continuous traits indicated eight statistically significant correlations, incorporating the Bonferroni correction (Table 3, Figure 3). Longevity had most correlations, with three positive ones (large organisms have long life expectancy, high trophic level and dwell deeper) and one negative (large organisms have lower age at maturity –as a percentage of life span). Fecundity was found to increase with optimal temperature, while maximum length increased with both trophic level and depth. Depth and trophic level were also positively correlated. Finally, three variable pairs were found to show non-linear patterns that best described their relations: fecundity had highest values in intermediate depths, optimal temperature was highest in species of intermediate depths, while fecundity was highest in species of low and high longevity.

The relationships between continuous and categorical traits indicated 20 cases where there are significant statistical differences in the value of a continuous trait between the different modalities incorporating the Bonferroni correction (Table 4). The main findings are summarized in Table 5 (but see Supplementary Figure S1 for pairwise comparisons between trait categories). Longevity was highest in flat-shaped species, in ambushing and active predators, piscivorous species and pelagic spawners. Fecundity was higher in atractoid and pelagic species; however, if seabed type is also taken into account apart from open sea species hard substrate ones had higher values. Maximum length had significant variation across six categorical traits, with the most striking being the highest values in pelagics, pelagic spawners and non-migratory species. Regarding depth, eurybathic species and benthic spawners were found to occur deeper, herbivore diet/grazing behavior and euryhaline species were found shallower. Highest trophic level was naturally found in piscivorous species, ambushing predators (and mobility type) and eurybathic species. Optimal temperature was found to be higher in species of high and medium mobility, stenothermal species and species of tropical distribution.

The trait co-occurrence analysis documented 170 (17.4 %) positive, 183 (18.8 %) negative, and 622 (63.8 %) random modality associations (Figure 4). The modalities with the highest number of positive co-occurrences are associated with the pelagic (e.g. free exposure with 13 positive co-occurrences) or the benthic way of living (e.g. flat body shape with 12 positive co-occurrences). The modalities with the highest number of negative co-occurrences are associated mostly with the pelagic way of living (atractoid body shape, formation of schools and pelagic habitat, had 16-17 negative co-occurrences). Deep body shape had relatively many positive and negative co-occurrences (12 and 15 respectively). Relatively rare trait categories (e.g. tropical distribution, autumn spawning) had a small number of co-occurrences.

Discussion

Violle et al. (2017) underline the importance of functional rarity and the ecology of outliers as complementary to the concept of the traditional taxonomic rarity. While rare species may share traits with more abundant ones, in the case that the traits (and resulting functions) are rare, loss of the species that have them may significantly alter ecosystem functioning (Jain et al., 2014). This is also relevant to the concept of keystoneness (a keystone species being a species whose importance for its community is disproportionally high in comparison to its abundance -Bond, 2001). Here we document the rarity (even below 5% of the species total) of autumn spawning (but also winter and all year spawning) as well as that of herbivory. Herbivory is anyway considered a crucial aspect of ecosystem functioning as alterations in herbivory may cause community phase shifts where the main habitat-formers are lost or substituted by very different ones (Verges et al., 2014), e.g. in coral reefs (Hughes et al., 2010) or in temperate algal forests (Steneck et al., 2002). Thus, it is important to maintain and regulate the abundance and the rate of renewal of this trait, especially taking into account the fact that some of the invading species (e.g. *Siganus* sp.) in the Mediterranean are herbivorous and competing with resident species (M. Koutsidi, unpublished data). It is true that herbivory is also carried out by other, benthic, biota (e.g. echinoderms); however they have different traits (e.g. mobility) that may change this function. Successful seasonal spawning, like autumn and winter spawning -and also the success of the recruitment that follows it- may be prone to various environmental factors, also possibly affected by anthropogenic effects like fisheries (that are characteristically seasonal in the Mediterranean) or climate change that may decrease the duration of the window-period suitable for spawning (Table 1). The above indicate the clear need for a holistic assessment evaluation of traits including all biotic elements of the ecosystem (plankton, nekton and benthos).

The rarity of other traits like hard seabed type preference may be related to the relatively small extent of this habitat type in the marine environment. Similarly, the low occurrence of long body shape may be related to the scarcity in characteristics of the habitat (e.g. structurally complex habitat for long body shape which here was indeed found to cooccur with cryptic exposure). However, the similarly rare flat body shape cooccurs with soft seabed preference which is a relatively common trait, indicating that trait relationships may be less straightforward.

It is important to note that trait rarity should not only be evaluated at the species level, but also weighted with species abundance to indicate the actual “abundance” of traits in the ecosystem (Violle et al., 2017). E.g. the planktivorous diet trait category may be rare if evaluated using the number of species but very abundant as the small pelagic or benthopelagic species that possess it have very high abundances. Still, the fact that it is shared by only a handful of species may be a risk for ecosystem functioning, especially taking into account the fact that these species are known to have interannual abundance fluctuations. Even more so, some of these species like the European anchovy *Engraulis encrasicholus* and the European pilchard *Sardina pilchardus* are under intense fishing pressure and have been shown to be affected by climate (Tzanatos et al., 2013).

The present work confirms that the combinations of functional traits in species of Mediterranean fisheries resources are not random (e.g. Jennings et al., 2002), since the evolutionary process has provided species with certain trait combinations (Gislason et al., 2010). Here we reconfirm that species with a long lifespan also have large body size (Vila-Gispert, Alcaraz & Garcia-Berthou 2005). Charnov, Gislason & Pope (2013) note that species only grow to a large body size if natural mortality rates are low, thus their life span is long.

In the present work, longevity and age at maturity are negatively correlated, contrary to previous studies documenting a positive relationship (Froese & Binohlan, 2000; Jarić & Gavcić, 2012). Contrary to these works (where age at maturity is expressed in years), here age at maturity was examined as a percentage of the species lifespan to indicate a proportion of life duration. Therefore, species with a short life span tend to mature relatively late in their lifetime. This can be interpreted, if we take into account that even a short-lived species needs to have completed an amount of growth to reach a minimum size and biomass for reproduction (Beverton, 1963).

The positive relationship between size and trophic level found in this study has also been documented in other works (e.g. Romanuk, Hayward, & Hutchings 2011). Trophic level increases with increasing body size, because most predators are larger than their prey (Kaiser et al., 2005). Jennings et al. (2002) also point out that, in benthic communities, trophic level and body mass of species have a strong relationship. Additionally, in this study we found a relationship between maximum body length and average depth species distribution. Finally, in this study, non-linear (polynomial) relationships between traits are indicated perhaps because of the existence of sharks and rays in the dataset. Especially their high longevity and low fecundity, result in deviations from the linear pattern.

The co-occurrence analysis indicates some positive and negative associations between pairs of trait modalities. The main characteristics of small pelagic fish (e.g. *Sardina pilchardus, Engraulis encrasicolus*) have the highest number of positive and negative associations with the other modalities. The traits of the family Sparidae, such as deep body shape, hermaphroditism (e.g. *Sparus aurata*) and grazing feeding (e.g *Sarpa salpa*), were found to have a relatively high number of positive associations with other modalities. The detection of relationships between traits is important not only as a way to explore the relationships of characteristics shaping life, but also because it could be useful to predict the possible effects of anthropogenic pressures on these traits. For example, climate change can be expected to favour thermophilic species, thus traits related to high optimum temperatures (high fecundity, deep body shape, high mobility) may be favoured as well. Koutsidi et al. (2016) have documented the removal of specific traits by fisheries; this could also result in modification of traits composition depending on fisheries management.

The current work has some findings differing from those of Koutsidi et al. (2016), as e.g. the associations of depth with fecundity and optimal temperatures documented here are not reported there. This can be a result of the inclusion of many more species here, but also because of the treatment of traits according to the variable type here and not as categories in all cases. Many rare traits identified like ambushing feeding behavior, flat and long body shape, autumn spawning, cosmopolitan and tropical distribution and low trophic level and fecundity are common in both works while others like long lifespan and distribution in deep water are novel here and again indicate that continuous traits are better analyzed as such.

Naturally (and as shown also here) traits are related. This is not only with regard to life strategies shaped by evolutionary processes (e.g. larger species having longer life duration too), but also as they may be relevant (e.g. diet and trophic level). Still, apart from the trait affinity, and despite the fact that there is the tendency to try to include only “hard” traits (i.e. more relevant to life cycle and resource use), different traits may still convey different information and still vary (e.g. as shown here piscivorous fish tend to have higher trophic level, but may still span a range of trophic level values depending on their prey). Furthermore, even relevant traits may incorporate information with different significance for ecosystem functioning or resilience (see e.g. the significance of traits regarding tolerance range for variables like temperature and depth in comparison to the optimal values of these factors in Table 5). Thus, depending on the research question, some, even relevant traits can be useful for the evaluation of findings.

Still, the question as to which traits constitute more fundamental information for ecosystem functioning still pertains. As ecosystem functioning is related to the transfer of energy and mater and the regulation and maintenance of ecological processes (Naeem et al. 1999; Bremner, Rogers & Frid 2006; Paterson, Defew & Jabour, 2012), traits related to trophic interactions like diet and trophic level are of direct significance. Traits affecting these interactions in space and time, such as habitat and depth distribution, migration, spawning season and even fecundity are also relevant (Table 1).

With the global ocean being under a multitude of anthropogenic effects (e.g. Crain et al., 2009), it is crucial to identify traits that are significant for monitoring human induced alterations in the structure and dynamics of the marine ecosystem. These traits are not only important as descriptors of the marine community (see e.g. the "mean temperature of the catch" -Cheung, Watson & Pauly, 2013) useful in monitoring, but should also be maintained to some minimum levels, to avoid function loss or the creation of too many empty ecological niches that could more easily be colonized, e.g. by alien species (Givan et al., 2017). Thus, regarding climate change, traits like optimal temperature and temperature range are significant, yet all range-type traits and also distribution seem to have important implications for ecosystem dynamics and resilience. Regarding fisheries effects, size (also because of the various significant relationships it has with other traits) and its implications for management is a crucial trait. Other core biological traits like longevity, fecundity and age at maturity are also important for fisheries management, but also some behavioural traits relevant for the interaction of nekton with fishing gear may bear some importance. The relationships between traits documented here and elsewhere may help explaining the dynamics of nektonic communities and marine ecosystems and also make predictions for future scenarios, as anthropogenic stressors may alter trait composition indirectly, through selection of associated traits.

Conclusions

This work investigates the major patterns in the traits distribution of 235 Mediterranean nekton species with the aim to identify rare traits and attempts to detect undocumented relationships between pairs of traits. Autumn spawning and herbivory are highlighted as important because of their rarity and their significance for ecosystem functioning. Apart from traits relationships already known, the approaches used here, not only illuminated novel relations, but also documented some non-linear relationships like these of fecundity with depth, depth with temperature and longevity with fecundity. It has to be noted, however, the distribution of traits should be evaluated against the actual abundance of species in specific habitats. The significance of nekton traits for species interactions/community assembly, ecosystem functioning and even their implications for anthropogenic effects indicate that the relationships of traits may lead to the selection of some due to their correlation with others (thus selection of traits related with high optimal temperature due to climate change or others associated with elements selected by fisheries). Furthermore, the significance of traits at various levels indicates thosee most important for future monitoring and maintenance to ensure ecosystem resilience

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Table 1(on next page)

Significance of traits at the level of species, community, ecosystem functioning and anthropogenic effects.

NR: Not relevant. References with explanation/examples are indicated with numbers corresponding to in-text citations following and are listed in detail in the Reference list.

[1]Ballesteros (2006), [2]Bamber (1995), [3]Beauchard et al. (2017), [4]Charnov, Gislason & Pope (2013), [5]Cheung, Watson & Pauly D. (2013), [6]Coll et al. (2010), [7]Costello et al. (2015), [8]Côté & Poulin (1995), [9]Dutil (1986), [10]Edworthy & Strydom (2016), [11]Engelhard & Heino (2005), [12]Erisman et al. (2017), [13]Ferno & Olsen (1994),[14]Floeter et al. (2007), [15]Galil (2007), [16]Gerlach, Hahn & Schrage (1985), [17]Giacomini, Shuter & Baum (2016), [18]Givan et al. (2017), [19]Godin, Classon & Abrahams (1988), [20]Henriques et al. (2017), [21]Henseler et al. (2019), [22]Hoare et al. (2005), [23]Jennings (2005), [24]Jennings, Kaiser & Reynolds (2001), [25]Jonsson & Jonsson (1993), [26]Kaiser et al. (2005), [27]Kaiser et al. (2006), [28]Kalogirou et al. (2010), [29]Katselis et al. (2003), [30]Kerr & Dickie (2001), [31]Krause & Godin (1995), [32]Krause & Ruxton (2002), [33]Leis (2006), [34]Lejeusne et al. (2010), [35]Loreau et al. (2001), [36]Mariani et al. (2013), [37]Martino & Able (2003), [38]Matheson et al. (2017), [39]McLusky & Elliott (2007), [40]Moyle & Cech (2004), [41]Occhipinti-Ambrogi & Savini (2003), [42]Park et al. (2019), [43]Pasquaud et al. (2015), [44]Pauly et al. (1998), [45]Paxton et al. (2018), [46]Pereira (2018), [47]Pianka (1970), [48]Pitcher & Parrish (1993), [49]Rideout, Morgan & Lilly (2006), [50]Rijnsdorp et al. (2016), [51]Schrandt et al. (2018), [52]Secor (2015), [53]Solan, Aspden & Paterson (2012), [54]Tserpes, Tzanatos & Peristeraki (2011), [55]Tzanatos et al. (2006), [56]Vasilakopoulos et al. (2017), [57]Vega-Cendejas & de Santillana (2019), [58]Winemiller &

Rose (1992), [59]Wooton (1999)

		Significance or implications at the level of:			
a/a	Trait (example)	Population/species	Community	Ecosystem	Anthropogenic effects
1	Longevity (5 years)	Longer lifespan increases reproductive success over time[3] May indicate population stability over time and potential of the various life stages to disperse[7]	Higher longevity renders individual more important both as prey and as a predator as more instances of predation	Longevity is related with natural mortality and thus with energy transfer in the ecosystem[4]	Longevity and age at maturity are related with the ability to recover from anthropogenic disturbance[27, 50]
2	Age-at-maturity (30% of lifespan)	Early maturity may increase resilience in unfavourable environmental conditions[2] Associated with cessation of growth[25]	NR	Ecosystem characteristics (e.g. productivity) may enhance or delay maturation	Longevity and age at maturity are related with the ability to recover from anthropogenic disturbance[50] Early maturation may increase resilience in high exploitation rates. Maturity significant for fisheries management (measures planned to ensure population part achieves sexual maturity)
3	Fecundity (5-10 eggs)	If low should ensure offspring survival-population fitness, as energy allocated to survival of offspring or fecundity (K-strategy vs. r-strategy)[47]	High fecundity means higher abundance of young "defenceless" stages (eggs, larvae) that are possible prey for other populations, but higher inter-specific competition later on[2]	As it provides easy-to-capture and rich in energy prey (compared to adult prey) may influence energy flow rates	Together with mortality until recruitment may affect stock size which is very relevant for fisheries[24]
4	Hermaphroditism (gonochoristic)	Sexual maturity of the second (in succession) sex must be achieved through survival to guarantee successful spawning and recruitment Size is important in determining male reproductive success[59]	NR	NR	As both sex ratio and gear selectivity change with size, exploitation of one size part of the population may affect sex ratio and possibly reproductive success.

		Significance or implications at the level of:			
a/a	Trait (example)	Population/species	Community	Ecosystem	Anthropogenic effects
5	Maximum length (20 cm)	Related to individual biomass, food web position, abundance, metabolic rates, and dispersal[7]	As in the marine ecosystem there is an "eat what is smaller" pattern, there has to be some variability in species sizes to support a community[17,30]	Related to energy flow in the ecosystem (because of association with trophic level/diet) and resulting food webs[16,23]	Relevant for fisheries (with regard to body shape) for selectivity[24]
6	Body form (flat)	Related to position in the water column/habitat, diet/potential prey, activity[21,59]	Because of association with habitat, specific communities may have higher frequencies of some body forms	Not relevant	Related to the way fishing gear may affect selectivity (together with size)[24]
7	Optimal depth (0-50 m)	Physical factor determining potential species habitat[7]	Depth is a major factor shaping marine communities[46,57]	Depth may affect productivity and energy flow as e.g. below the euphotic zone the lack of primary production modifies trophic links. Also effects of elements like critical depth or seagrass bed distribution[27]	Different gears and fishing sectors are often operating in different depths resulting in different communities prone to exploitation and resulting catch composition[54]
8	Optimal temperature (25-30oC)	Defines optimal temperature conditions for population fitness. May affect movement between water masses (behavioural thermoregulation) and thus abundance and distribution[40]	Due to climate change can shift to dominance of more thermophilic species[34]	NR	More thermophilic species may appear more frequently in the catches[5,56]
9	Habitat type (benthic)	Populations are closely associated to pelagic or benthic habitat or migrate between them[21,59]	Specific habitats are characterised by specific communities[1,28]	Effect of seabed type on ecosystem functioning expected to be significant as both are related to biodiversity and its attributes[35]	Has implications for target species abundance and bycatch (thus fishing gear use)[55]
10	Distribution (tropical)	Related to proximity to the geographic distribution of the area examined (if e.g. through Gibraltar or Suez in the Med) and could be associated to favourable environmental conditions[6]	Species of alien distribution (invasive) species may dominate the community through colonisation of empty niches/lack of "natural enemies"[18]	NR	Climate change or other environmental changes may be forcing changes in distribution paterns[15,41]

		Significance or implications at the level of:			
a/a	Trait (example)	Population/species	Community	Ecosystem	Anthropogenic effects
11	Sea bed type (hard)	Physical factor determining potential species habitat[7]	Specific habitats host and are characterized by specific communities[1,28]	Effect of seabed type on ecosystem functioning expected to be significant as both are related to biodiversity and its attributes[35,53]	Has implications for target species abundance and bycatch (thus gear use)[55]
12	Spawning habitat (pelagic)	Spawning habitat determines the nature and intensity of hazards encountered by eggs and larvae[33,59]	May determine seasonal communities as a result of spawning seasonality and also of populations feeding on eggs and juveniles	If spawning habitat different from adult stage habitat may be relevant to benthopelagic coupling[33,52]	May create aggregations prone to fisheries[12]
13	Temperature range (eurythermal)	May increase population resilience to abrupt temperature changes or ability to change environment	Eurythermal species may dominate community under climate change/frequent weather changes	NR	May increase population resilience to climate change, invasion rates and appearance in the fisheries catch Eurythermal species may be favoured in thermal pollution sites[2]
14	Salinity range (stenohaline)	May be related to population ability to approach/enter productive habitats like estuaries & lagoons[40]	Shapes communities of brackish waters, e.g. along salinity gradients[20,39,43]	Relevant to matter & energy transfer between the ocean and brackish waters through euryhaline species[37]	Shapes the resources exploited by fisheries in brackish environments (e.g. lagoon fisheries)[29]
15	Depth range (eurybathic)	Eurybathic species have more potential habitat and might be more resilient to habitat loss[7]	Communities dominated by eurybathic species may be more resilient to environmental changes and disturbance	Eurybathic species may transfer energy through depth zones and contribute to benthopelagic coupling	More eurybathic species may be more resilient to habitat degradation by fisheries or other anthropogenic effects
16	Seasonal migrations (migratory)	Can change the population ecological status, may lead to a seasonal (periodic) life strategy and shape seasonal energy needs[52,58]	Community will change seasonally, qualitatively and quantitatively[42]	Can have impact on energy flow, creating seasonal dynamics[52]	Many fisheries are based on seasonal migrations for fishing grounds or even operation of specific gears (e.g. lagoon fisheries)[29]
17	Trophic level (3.5-4.2)	Derived from the type and frequency of trophic objects in its diet[7]	Influence on other species abundance and community structure and dynamics[7]	May alter nutrient cycling in the ecosystem[3]	Depending on exploitation removing part of the trophic network may result in fishing down the food web[44]
18	Diet (zooplankton)	Determines food web position[7]	Influence on other species abundance and community structure and dynamics[7]	May alter nutrient cycling in the ecosystem[3]	Relevant to fishing gear mode of operation exploiting diet (hook and line gears e.g. longlines) and associated target species & catch composition

		Significance or implications at the level of:			
a/a	Trait (example)	Population/species	Community	Ecosystem	Anthropogenic effects
19	Spawning period (spring)	Shapes the period that the population must feed to prepare spawning and non-feeding period. May be associated with "weak" period (bad condition) after spawning[9,11]	May shape feeding interactions and trophic links within the community seasonally, both as a result of preying on eggs and larvae and, secondarily, because of the seasonal pattern of recruitment[10]	Is affected by suitability of the environmental conditions for eggs & larvae. Is affected by energy supply (low energy may result in delay or skipping spawning). As the spawning period generates eggs and larvae it provides potential prey[49,59]	Seasonality of fisheries may lead to unsuccessful spawning and result in few individuals recruited
20	Feeding type (plankton)	Related to the diet and the trophic level through the relative size and mobility of the prey in comparison to the predator[7]	By shaping diet can affect the community composition	Related to prey community composition and lower trophic level succession patterns[36]	Relevant to fishing gear mode of operation exploiting feeding behaviour (hook and line gears e.g. trolling lines, longlines) and associated target species & catch composition[24]
21	Sociability (schools)	Benefits like predation avoidance, food location and foraging strategy, improvement of reproductive success[59] Costs like competition for food or mate, predator attraction, disease transmission[8,31]	Schooling important in shaping communities regarding hydrodynamic characteristics[14]	Schooling/pelagic fish may colonise new habitats (e.g. reefs) more easily[45]	Relevant to fishing gear mode of operation exploiting gregarious fish behaviour (e.g. purse seines) and associated target species & catch composition[24] Schooling/pelagic fish may colonise new artificial habitats (e.g. reefs) more easily[45]
22	Exposure (cryptic-temporarily)	Population must balance ability to graze/predate and predation avoidance Population (especially cryptic) may have developed diel activity rhythms[38]	Depending on conditions (e.g. habitat type) cryptic species may dominate communities[51] Level of exposure and cryptic behaviour relevant to differences in diel community composition[38]	NR	NR
23	Mobility (high)	Indicates a dispersal potential and a more or less mobile lifestyle[7]	Might differentiate pelagic (more motile) from benthic (more static) communities	May be relevant to transfer of energy between ecosystems or benthopelagic coupling	Relevant to fishing gear mode of operation exploiting fish motility behaviour (e.g. nets) and associated target species & catch composition[13,24]

Table 2(on next page)

List of traits used in the analyses, trait type and categories/modalities used for categorical traits.

CON: Continuous. RAN: Continuous, provided as a range for most/all species. CAT: Categorical. *as % of maximum age. **scale of eggs/juveniles per spawn, maximum value indicated. ***indicating that food items have negligible or low mobility related to predator.

Trait	Trait type	Trait categories/modalities (in case of categorical trait)					
Longevity	CON						
Age at maturity*	CON						
Fecundity**	RAN						
Gonochorism	CAT	Gonochoristic	Hermaphrodite				
Maximum length	CON						
Body shape	CAT	Flat	Long	Deep	Atractoid	Rounded	
Optimal depth	RAN						
Optimal temperature	RAN						
Habitat type	CAT	Pelagic	Benthic	Benthopelagic			
Distribution	CAT	Global	Temperate	Tropical	Subtropical		
Seabed morphology	CAT	Open sea	Soft	Hard	Variable		
Spawning habitat	CAT	Pelagic	Benthic				
Temperature range	CAT	Stenothermal	Eurythermal				
Salinity range	CAT	Stenohaline	Euryhaline				
Depth range	CAT	Eurybathic	Stenobathic				
Seasonally migratory	CAT	Migratory	Non-migratory				
Trophic level	RAN						
Diet	CAT	Herbivore	Zoobenthivore	Zoobenthivore-Hyperbenthos	Omnivore	Zooplankton	Piscivore
Spawning period	CAT	Winter	Spring	Summer	Autumn	All year	
Feeding behaviour***	CAT	Grazer***	Active predator	Ambushing predator			
Sociability	CAT	Schools	Shoals-large groups (>10)	Small groups (<~10)	Solitary		
Exposure	CAT	Free	Cryptic (permanently)	Cryptic (temporarily)			
Mobility	CAT	Ambusher	Small	Medium	High		

1

Table 3(on next page)

Pearson correlation coefficients between continuous traits.

Statistically significant correlations without taking into account the Bonferroni correction are denoted in red color, while these incorporating the Bonferroni correction are indicated in green. Pairs of traits where non-linear regression indicated that a non-linear relationship was better than a linear one in describing trait fluctuations are framed (in all these cases the non-linear $p<0.01$ remained significant after the Bonferroni correction).

1

Trait	ln(Longevity)	Age at maturity	ln(Fecundity)	ln(Maximum length)	ln(Depth)	Trophic level	Optimal temperature
ln(Longevity)	-	-0.34	0.16	0.65	0.22	0.27	-0.08
Age at maturity	-0.34	-	-0.19	-0.14	0.10	0.03	-0.01
ln(Fecundity)	0.16	-0.19	-	0.11	0.01	-0.06	0.23
ln(Maximum length)	0.65	-0.14	0.11	-	0.30	0.50	0.07
ln(Depth)	0.20	0.08	0.01	0.30	-	0.36	-0.13
Trophic level	0.27	0.03	-0.06	0.50	0.38	-	-0.04
Optimal temperature	-0.08	-0.01	0.23	0.06	-0.10	-0.04	-

2

3

Table 4(on next page)

Results of the statistical analyses between continuous and categorical traits.

Test (A: ANOVA, T: t-test, K: Kruskal-Wallis, M: Mann-Whitney) indicated as superscript next to result. *p<0,05, **p<0,01, ***p<0,001. Statistically significant differences between groups (categorical traits) without taking into account the Bonferroni correction are denoted in red color, while these incorporating the Bonferroni correction are indicated in green.

Trait	ln(Longevity)	Age-at-maturity	ln(Fecundity)	ln(Maximum length)	ln(Depth)	Trophic level	Optimal temperature
Gonochorism	-1.21^{T}	-339.50^{M}	391.5^{M}	-75.50^{M}	214.50^{M}	0.21^{T}	-1.23^{T}
Body shape	**17.71^{K}	1.81^{A}	***24.28^{K}	***8.58^{A}	8.67^{K}	7.05^{K}	**4.04^{A}
Habitat type	0.79^{A}	0.8^{A}	***13.43^{K}	***9.38^{A}	0.13^{A}	**10.32^{A}	*3.34^{A}
Seasonally migratory	629.50^{M}	-0.34^{T}	*-2.45^{T}	***-5.27^{T}	0.10^{T}	-1.61^{T}	-0.73^{T}
Distribution	2.08^{A}	*2.75^{A}	1.52^{A}	2.00^{A}	*3.42^{A}	0.83^{A}	***12.17^{A}
Seabed morphology	0.96^{A}	0.48^{A}	***16.97^{K}	2.57^{A}	1.58^{A}	3.57^{A}	*4.22^{A}
Diet	***6.16^{A}	0.57^{A}	10.58^{K}	***30.41^{A}	***49.43^{K}	***143.7^{K}	1.65^{A}
Feeding behaviour	***27.29^{K}	0.72^{A}	2.65^{A}	***42.98^{K}	***21.38^{K}	***76.18^{A}	1.64^{A}
Spawning period	4.65^{K}	0.83^{A}	0.65^{A}	1.13^{A}	*3.00^{A}	0.86^{A}	*2.49^{A}
Spawning habitat	**1276.50^{M}	1.03^{T}	**-2.85^{T}	***1664^{M}	***1762^{M}	-1.53^{T}	-0.8^{T}
Depth range	0.11^{T}	**-1222^{M}	-1.18^{T}	*2.5^{T}	***-63.65^{M}	***3.53^{T}	-0.76^{T}
Temperature range	1.59^{T}	-0.49^{T}	-1.83^{T}	-0.95^{T}	0.03^{T}	681.5^{M}	***-4.8^{T}
Salinity range	0.81^{T}	-1.3^{T}	1.37^{T}	1.51^{T}	***-5.47^{T}	-1.58^{T}	-0.31^{T}
Sociability	0.23^{A}	1.98^{A}	**12.72^{K}	0.18^{A}	2.24^{A}	7.6^{K}	2.16^{A}
Exposure	0.11^{A}	*3.78^{A}	2.22^{A}	0.81^{A}	*4.25^{A}	0.89^{A}	*3.02^{A}
Mobility	**4.31^{A}	0.82^{A}	**4.23^{A}	**4.44^{A}	*3.48^{A}	**15.25^{K}	**4.79^{A}

Table 5(on next page)

Summary of the main findings of the significant relationships between continuous and categorical traits.

For pairwise contrasts between trait categories see Supplementary Figure S1.

Continuous trait	Categorical trait	Main findings
Longevity	Body shape	Highest in flat species, lowest in rounded species
	Feeding type	Highest in ambushing & active predators, lowest in grazers
	Spawning habitat	Higher in pelagic spawners
	Diet	Highest in piscivorous species, lowest in zooplanktivorous-zoobentivorous
Fecundity	Body shape	Higher in atractoid and deep-bodied, lower in flat and long species
	Habitat type	Highest in pelagic species, intermediate in benthopelagic, lowest in benthic
	Seabed type	Highest in the open sea and over hard substrate, lowest over soft substrate
Maximum length	Body shape	Higher in long, atractoid and flat body shape, lowest in rounded body shape
	Habitat type	Highest in pelagic species, intermediate in benthic, lowest in benthopelagic
	Seasonal migrations	Higher in non-migratory species
	Diet	Highest in piscivorous species
	Feeding type	Highest in active & ambushing predators, lowest in grazers
	Spawning habitat	Higher in pelagic spawners
Depth	Depth range	Eurybathic species deeper
	Diet	Herbivores most shallow, piscivores and zoobenthivores deeper
	Feeding type	Active predators deepest, grazers shallowest
	Spawning habitat	Benthic spawners deeper
	Salinity range	Euryhaline species in shallower depth
Trophic level	Diet	Herbivores have lowest trophic level, piscivores the highest
	Feeding type	Highest in ambushing predators, lowest in grazers
	Habitat type	Highest in pelagic species
	Depth range	Eurybathic species have higher trophic level
	Mobility	Ambushers have highest trophic level
Optimal temperature	Mobility	Higher in species of high & medium mobility, lower in small mobility species
	Temp/ture range	Higher in stenothermal species
	Distribution	Highest in tropical species, lowest in temperate

Figure 1

A. Distribution of continuous traits, B. Arrangement from minimum to maximum of range-type traits.

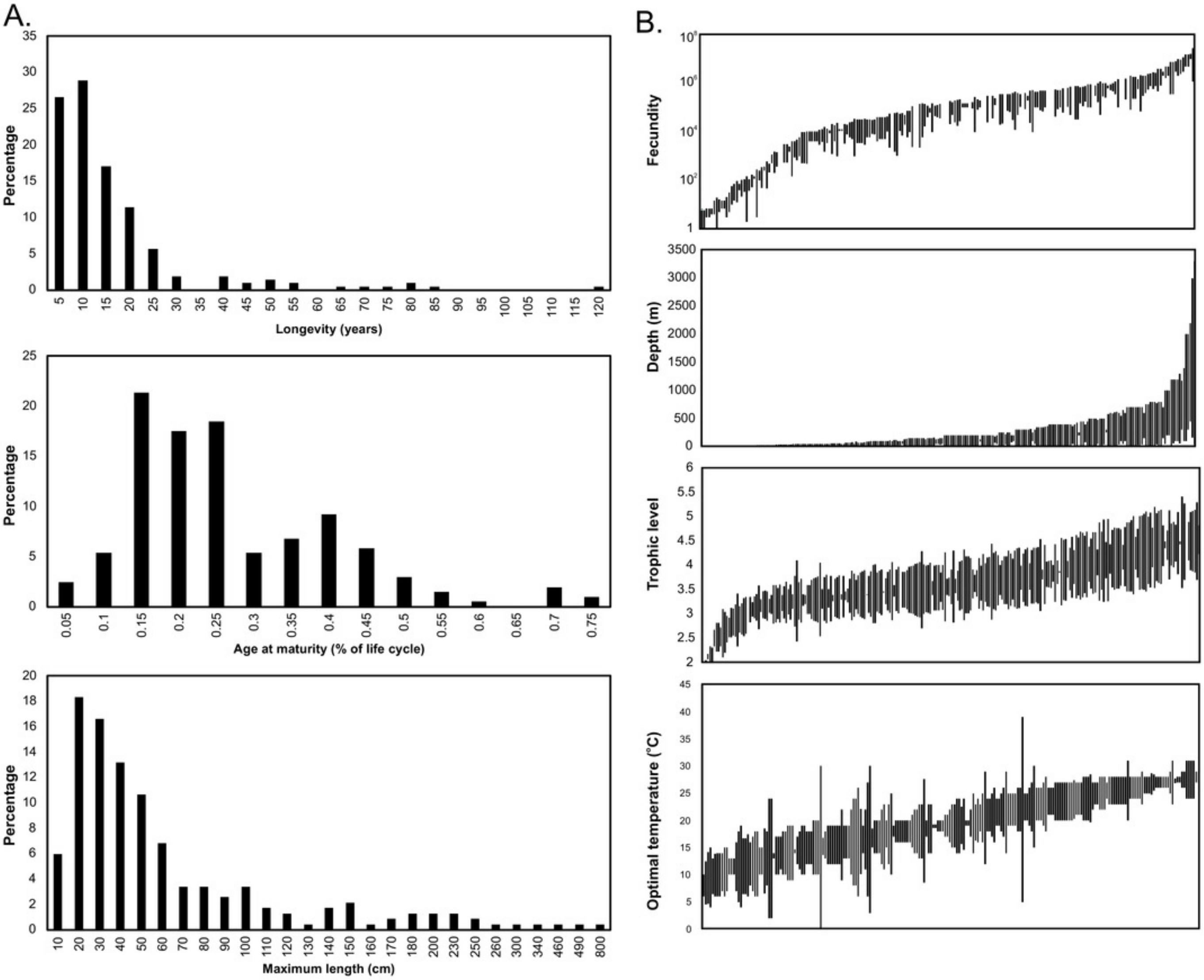


Figure 2

Frequency distribution of categorical traits

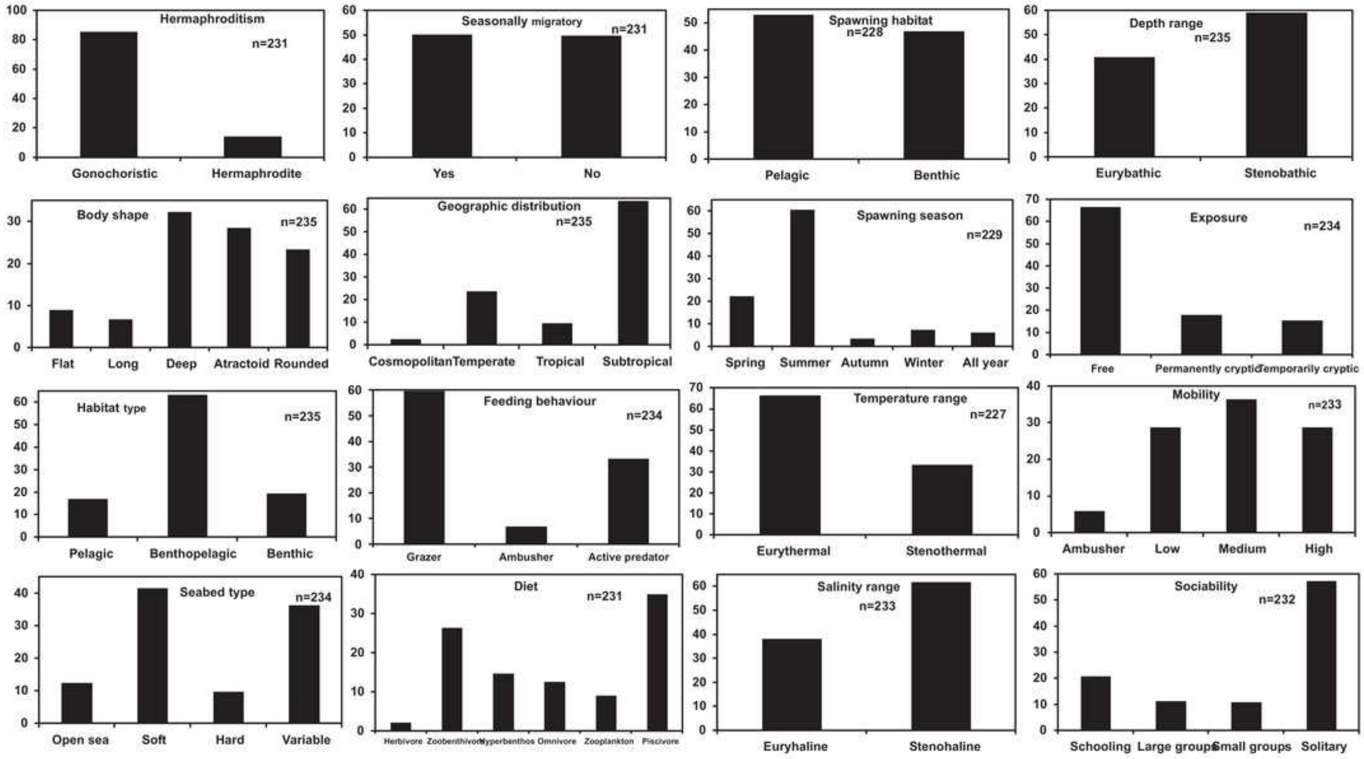


Figure 3

The statistically significant correlations or non-linear relationships between continuous traits after incorporating the Bonferroni correction.

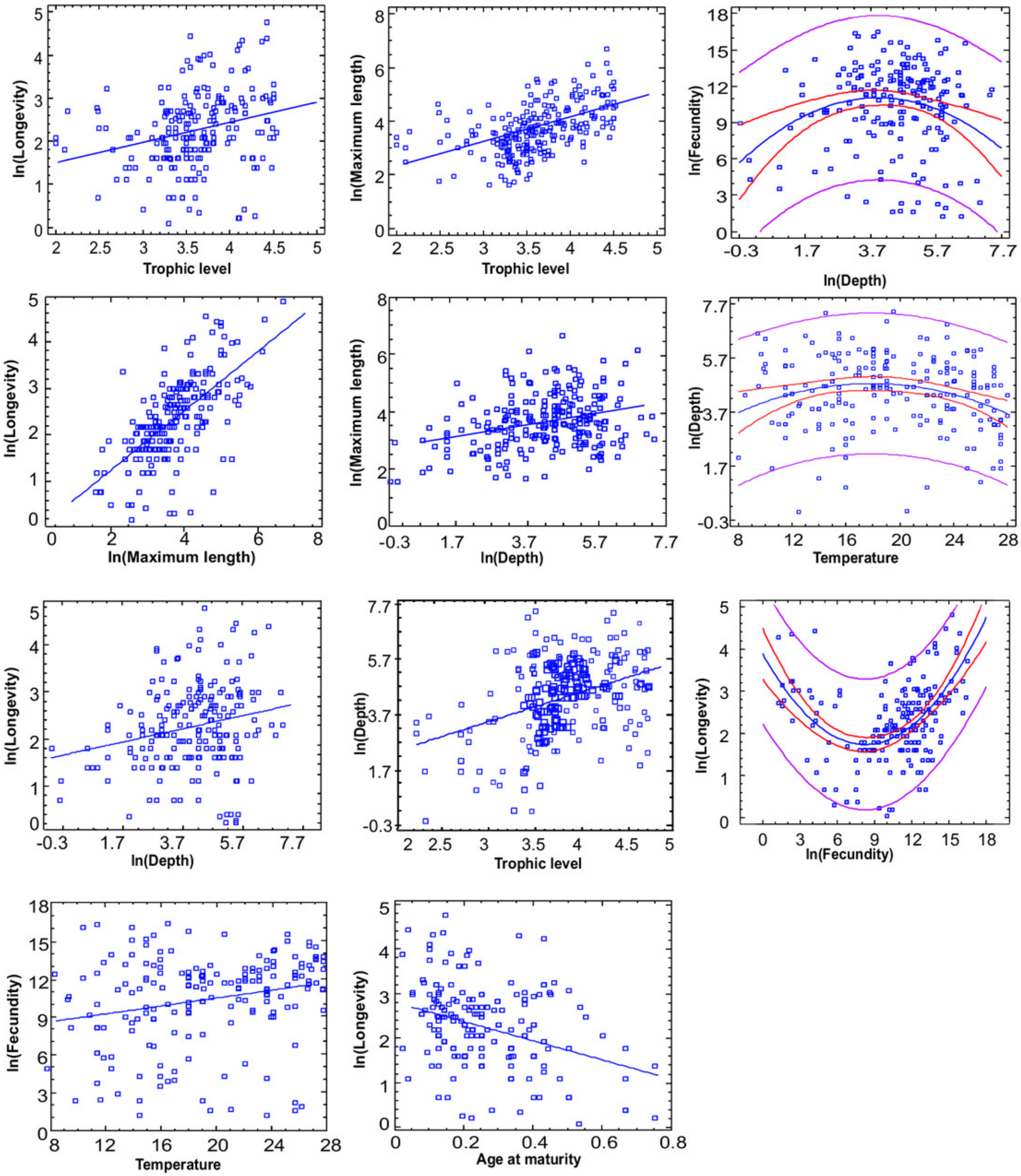
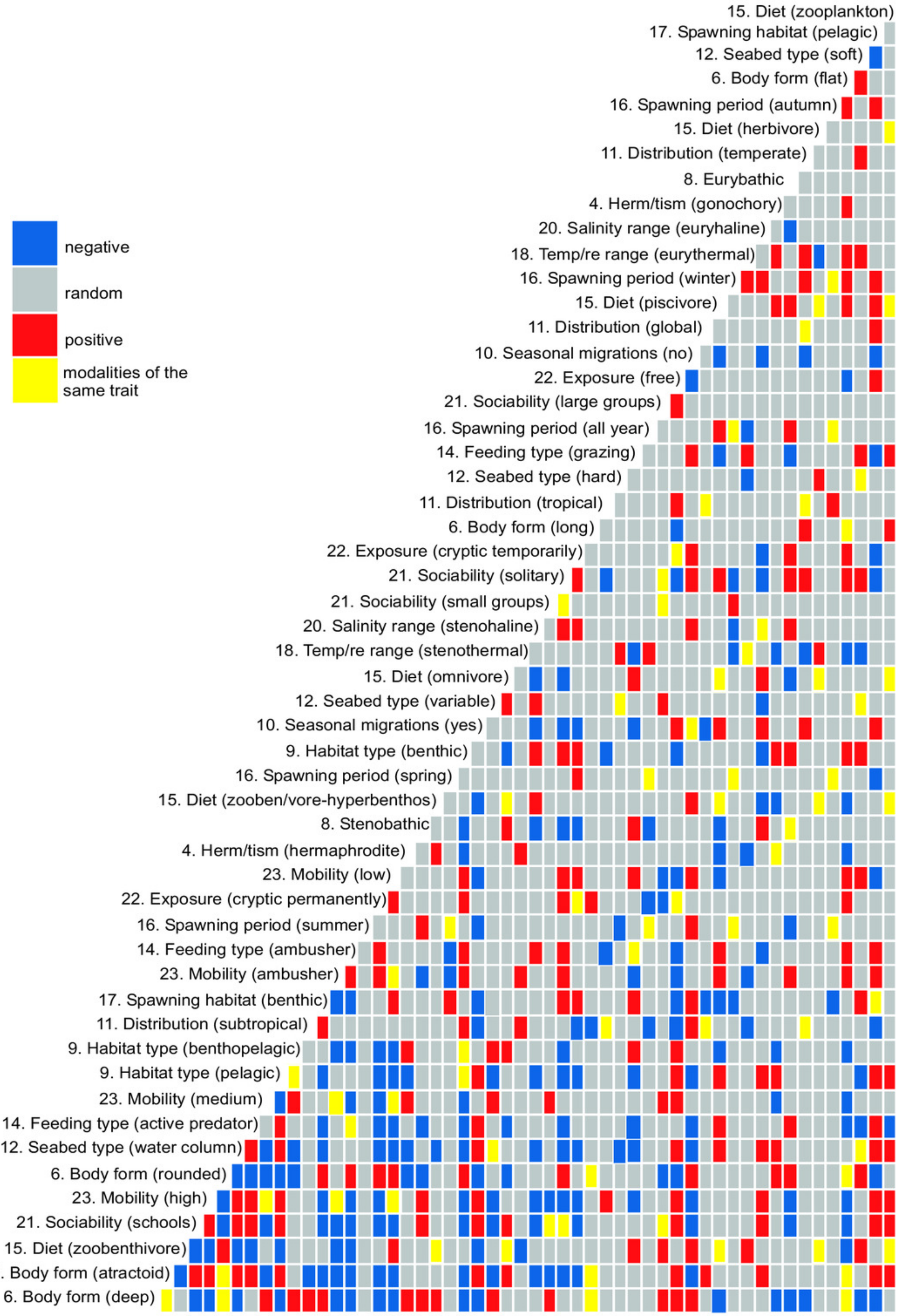

ln(Longevity)
Trophic level
ln(Maximum length)
Trophic level
ln(Fecundity)
ln(Depth)
ln(Longevity)
ln(Maximum length)
ln(Maximum length)
ln(Depth)
ln(Depth)
Temperature
ln(Longevity)
ln(Depth)
ln(Depth)
Trophic level
ln(Longevity)
ln(Fecundity)
ln(Fecundity)
Temperature
ln(Longevity)
Age at maturity

Figure 4

Diagonal matrix of positive, random, and negative co-occurrence between the trait category pairs.


negative
random
positive
modalities of the same trait
15. Diet (zooplankton)
17. Spawning habitat (pelagic)
12. Seabed type (soft)
6. Body form (flat)
16. Spawning period (autumn)
15. Diet (herbivore)
11. Distribution (temperate)
8. Eurybathic
4. Herm/tism (gonochory)
20. Salinity range (euryhaline)
18. Temp/re range (eurythermal)
16. Spawning period (winter)
15. Diet (piscivore)
11. Distribution (global)
10. Seasonal migrations (no)
22. Exposure (free)
21. Sociability (large groups)
16. Spawning period (all year)
14. Feeding type (grazing)
12. Seabed type (hard)
11. Distribution (tropical)
6. Body form (long)
22. Exposure (cryptic temporarily)
21. Sociability (solitary)
21. Sociability (small groups)
20. Salinity range (stenohaline)
18. Temp/re range (stenothermal)
15. Diet (omnivore)
12. Seabed type (variable)
10. Seasonal migrations (yes)
9. Habitat type (benthic)
16. Spawning period (spring)
15. Diet (zooben/vore-hyperbenthos)
8. Stenobathic
4. Herm/tism (hermaphrodite)
23. Mobility (low)
22. Exposure (cryptic permanently)
16. Spawning period (summer)
14. Feeding type (ambusher)
23. Mobility (ambusher)
17. Spawning habitat (benthic)
11. Distribution (subtropical)
9. Habitat type (benthopelagic)
9. Habitat type (pelagic)
23. Mobility (medium)
14. Feeding type (active predator)
12. Seabed type (water column)
6. Body form (rounded)
23. Mobility (high)
21. Sociability (schools)
15. Diet (zoobenthivore)
6. Body form (atractoid)
6. Body form (deep)