



## From traits to life-history strategies: Deconstructing fish community composition across European seas

Pécuchet, Lauréne; Lindegren, Martin ; Hidalgo, Manuel; Delgado, Marina; Esteban, Antonio; Fock, Heino O.; Gil de Sola, Luis; Punzón, Antonio; Sólmundsson, Jón; Payne, Mark R.

*Published in:*  
Global Ecology and Biogeography

*Link to article, DOI:*  
[10.1111/geb.12587](https://doi.org/10.1111/geb.12587)

*Publication date:*  
2017

*Document Version*  
Peer reviewed version

[Link back to DTU Orbit](#)

*Citation (APA):*  
Pécuchet, L., Lindegren, M., Hidalgo, M., Delgado, M., Esteban, A., Fock, H. O., Gil de Sola, L., Punzón, A., Sólmundsson, J., & Payne, M. R. (2017). From traits to life-history strategies: Deconstructing fish community composition across European seas. *Global Ecology and Biogeography*, 26(7), 812-822.  
<https://doi.org/10.1111/geb.12587>

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1   **From traits to life history strategies: deconstructing fish community composition**  
2   **across European Seas**

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23   Keywords: community composition; marine fish; life history strategies; trait; trade-off; fecundity; size;  
24   offspring survival; temperature; depth; archetypal analysis

25   Running title: Life history strategies of European fish communities

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27   Words in abstract: 300

28   Words in main body of the paper: 5,600

29   Number of references: 71

30

31   **Abstract**

32   **Aim**

33   The life history of a species is determined by trade-offs between growth, survival and reproduction to  
34   maximize fitness in a given environment. Following a theoretical model, we investigate whether the  
35   composition of marine fish communities can be understood in terms of a set of life history strategies and  
36   whether the prevalence of the strategies follows specific spatial patterns that can be related to the  
37   environment.

38   **Location**

39   European Seas

40   **Methods**

41   An extensive set of scientific bottom trawl surveys were collected to obtain the species composition of fish  
42   communities across European Seas. We complemented this data with species-specific information  
43   regarding six life history traits, reflecting reproductive, growth and feeding modes. We then calculated the  
44   optimal number of strategies needed to summarize the information contained in the traits by using an  
45   archetypal analysis. The proportion of each obtained strategy in the communities and their spatial patterns  
46   were explained as a function of the environment and their temporal changes were investigated.

47   **Results**

48   The species could be decomposed into a continuum of three life history strategies: opportunistic, periodic  
49   and equilibrium, resulting from trade-offs between traits. The strategies' marked spatial patterns could be  
50   explained by depth, temperature and its seasonality, chlorophyll and fishing effort. In recent years,  
51   opportunistic and equilibrium strategies significantly increased, likely due to an increase in temperature  
52   and decrease in fishing effort.

53   **Main conclusions**

54   Our empirical analysis supports a theoretical framework outlining three life-history strategies of fish. The  
55   strategies vary predictably in space and time in response to the environment. This highlights the underlying  
56   process whereby fitness is optimized through trade-offs between growth, feeding and reproduction under  
57   different environmental conditions. Due to their response to the environment, life history strategies  
58   provide a suitable tool to monitor and understand community changes in response to natural and  
59   anthropogenic stressors, including fishing and climate change.

60 **Introduction**

61 Trait-based study of biodiversity has been an expanding field in recent decades (Petchey & Gaston 2002,  
62 Schleuter et al. 2010, Cadotte et al. 2013). Traits are often referred to as any characteristics of an  
63 individual, or a group of organisms, which encompass morphological, demographic or physiological  
64 attributes (Violle et al. 2007). Using traits instead of taxonomic information has several advantages when  
65 studying biodiversity since they provide a more fundamental and mechanistic approach to understanding  
66 community composition (Shipley et al. 2006, McGill et al. 2006, Pecuchet et al. 2016b). Trait-based  
67 approaches also permit to reduce the complexity of community diversity by focusing on the factors that  
68 best characterize an organism's fitness (Litchman et al. 2013) and has also been successfully related to  
69 ecosystem functions and services in the terrestrial (Diaz & Cabido 2001, Flynn et al. 2011) and marine  
70 (Bellwood et al. 2003) realms.

71 Selecting a relevant set of key traits to characterize the species and ultimately the communities can,  
72 however, be difficult (Petchey and Gaston, 2006), especially when the aim is to explain ecosystem functions  
73 (McIntyre et al. 1999, Lavorel & Garnier 2002). In particular, deciding on how many traits to include is  
74 controversial since using too many traits increases complexity and may introduce redundancy due to  
75 correlation among closely related traits. Trait information can instead be reduced into combinations of  
76 particular trait values, so-called functional groups. Functional groups are defined as a unit of species  
77 sharing similar trait-attributes, for example body size and trophic guild (e.g Halpern & Floeter 2008).  
78 However, adding new traits to this analysis can substantially increase the number of functional groups.  
79 In contrast to functional groups, life history strategies are defined as a combination of trait attributes and  
80 are the result of inter-relationships and trades-offs among key traits (Winemiller et al. 2015). They are  
81 often based on a theoretical framework and are used to shed light on the evolution of the life history of  
82 organisms, as well as the environment wherein the species occur (Charnov et al. 2013). Some well-known  
83 examples of life history theories or models are the r and K-selection (Pianka 1970) or the fast-slow life

84 history continuum (Franco & Silvertown 1996). Due to their simplicity, these linear models of life history  
85 strategies have been used in numerous studies ranging from population dynamics (e.g. Oli 2004) to  
86 communities spatial pattern (e.g. Wiedmann et al. 2014). However, this approach has also been criticized  
87 for oversimplifying reality (Nichols et al. 1976, Bielby et al. 2007).

88 For fish communities, Winemiller and Rose (1992) developed the “Equilibrium-Periodic-Opportunistic”  
89 (EPO) model. This theoretical model links three strategies characterized by trades-off between fecundity,  
90 juvenile survival and generation time to environmental stability and predictability: “equilibrium species”  
91 with high juvenile survivorship; “opportunistic species” with low generation time; and “periodic species”  
92 with high fecundity. The equilibrium strategy is thought to prevail in stable and predictable environments  
93 while the opportunistic strategy prevails in unstable and unpredictable environments. The periodic strategy  
94 is thought to occur in seasonal but periodically fluctuating environments. A number of studies have used  
95 the EPO model to investigate temporal changes and spatial distribution of the composition of freshwater  
96 fish communities (Mims & Olden 2012).

97 In this study, we investigate whether marine fish species present in European Seas can be categorized into  
98 similar life history strategies based on their trait attributes. Furthermore, we investigate whether there are  
99 any consistent geographical and temporal patterns in the prevalence of life history strategies within fish  
100 communities across Europe and whether the patterns and trends can be explained by external  
101 (environmental) factors. For this analysis, the shelf seas of the North-east Atlantic provide an excellent  
102 study area since they contain pronounced natural gradients in terms of e.g. temperature, productivity and  
103 biodiversity, and are subjected to various anthropogenic pressures including fishing and eutrophication  
104 (Grizzetti et al. 2012). Furthermore, these seas are also rich in data, and therefore an ideal area to test the  
105 life history strategies hypothesis on the fish communities using standardized datasets with a high  
106 taxonomic and spatial resolution.

108 **Materials and Methods**

109 **Bottom trawl surveys**

110 Fifteen scientific bottom trawl surveys covering ecosystems from the Mediterranean Sea to Greenland and  
111 spanning on average ten recent years (2002-2012) were collated (Appendix S1 in Supporting Information).

112 As our focus was on offshore fish communities, and due to different survey sampling schemes, hauls  
113 sampled at a depth shallower than 20 meters were excluded to avoid the inclusion of coastal fish species.

114 The refined data set contained approximately 20.000 individual hauls (i.e. stations) that lasted on average  
115 30 minutes and covered 3 nautical miles. Not all surveys used the same taxonomic recording, therefore

116 species scientific names were checked against the World Register of Marine Species and updated by the  
117 ‘accepted’ scientific name when appropriate. For some species that are difficult to identify, taxonomic

118 recording was specified to the genus level. For each  $\frac{1}{2}$  degree latitude and longitude cell covered by the  
119 surveys, we derived the relative abundances of all the species present, calculated as the sum of its

120 abundance in all the hauls performed in a grid cell divided by the total abundance of all the species in that  
121 grid cell. The species’ abundances were log transformed prior to the calculation. A species was noted

122 present in a grid cell if it was ever recorded in one of the hauls performed in the grid. In order to study  
123 temporal changes in the prevalence of life history strategies, we calculated relative abundances and

124 presence of species using the same method but for each year separately. Due to the limited time-span of  
125 many surveys, we restricted the temporal analysis to the North Sea where time series are available from

126 1980 onwards.

127 **Trait information**

128 Six traits were selected to cover the fundamental Darwinian objectives of an organism: to feed, survive and  
129 reproduce. These traits were also selected as they were previously used to describe the theoretical life

130 history strategies of fish species based on the EPO model (Winemiller 2005, Mims et al. 2010). These traits  
131 are: maximum length, lifespan, trophic level, fecundity, offspring size and parental care. The first three

132 traits were extracted from FishBase (Froese & Pauly 2012). Maximum length (Lmax) represents the longest  
133 total length ever recorded for a given species. Lifespan is defined as the theoretical maximum expected age  
134 for a species and is estimated within FishBase using the growth (K) and length at infinity (Linf) parameters  
135 from the Von Bertalanffy growth equation. Linf is calculated from empirical growth data for the majority of  
136 the species but is inferred from Lmax for data-poor species, hence creating a dependency between these  
137 variables for some species in FishBase. Trophic level represents the position of a species in the food chain,  
138 ranging from a value of 2 when the diet is based on plant or detritus to 4.5 for top predators. Trophic level  
139 is primarily calculated from empirical diet studies or inferred from taxonomically related species. Fecundity  
140 is the average total number of offspring produced per mature female per year, usually calculated as the  
141 number of oocytes in the ovary. Fecundity can be either determinate, where the annual potential fecundity  
142 is set before the onset of the spawning season, or indeterminate, where the species continuously produces  
143 eggs during the spawning season and the annual potential fecundity is not fixed. Since information on  
144 fecundity type and the number of batches spawned per year is largely lacking, the average total number of  
145 offspring produced per year for batch spawners is likely underestimated. The offspring size corresponds to  
146 the average size of the offspring released in the water, i.e. eggs for oviparous or larvae/juveniles for  
147 ovoviparous. Parental care relates to the investment of the parents in the survival of their offspring.  
148 Parental care was transformed from categorical to continuous values, using a similar approach to  
149 Winemiller (1989), as follow: (1) pelagic egg, (2) benthic egg, (3) hidden brood, (4) guarded brood and (5)  
150 bearer. These three traits values were primarily derived from literature (Pecuchet et al. 2016a). For each  
151 species, only one value per trait was used assuming that inter-species variability is higher than intra-species  
152 variability. There were approximately 600 unique species or genus recorded in the surveys. Out of these,  
153 260 species and 29 genera had complete information for all six traits and were used in the analysis.  
154 Although representing only half of the entire species pool recorded in the surveys, the species retained  
155 were the most frequently occurring and the most abundant. Hence, on average across all the  $\frac{1}{2}$  degree grid  
156 cells, 95% of the species present and 97% of the individuals recorded in each grid cell had trait information.

158 **Life history strategies**

159 We used the unsupervised learning method Archetypal analysis (AA) to characterize European marine fish  
160 species. AA is similar to a cluster analysis, but focuses on identifying extreme values that can be used as  
161 archetypes, rather than on the means or medians of the cluster (Cutler & Breiman 1994). The core of the  
162 AA approach is the identification of points (archetypes) forming the corners of the convex hull volume  
163 encompassing the trait space (Mørup & Hansen 2012): points are then represented by the proportions  
164 based on the proximity of the point to each archetype. AA has several advantages compared to traditional  
165 cluster analysis, such as k-mean and k-medoid since these can result in an arbitrary grouping of  
166 neighbouring points when the data are continuous. For example, two data points which are at the limits of  
167 the space defined by two clusters might be categorized differently. Instead, AA gives similar values to the  
168 points that are close to each other in traits space (Hart et al. 2015) resulting in a continuous grouping  
169 instead of a categorical (Cutler & Breiman 1994). Therefore, AA is a suitable tool to identify atypical species  
170 in a dataset, which makes it useful to characterize life history strategies based on traits.

171 Trait data was normalized before input to AA by log10 transforming fecundity, offspring size, body size and  
172 lifespan and then all six traits were standardized (i.e. to a mean of 0 and a variance of 1) to ensure equal  
173 weights in the AA. The AA was performed on the traits matrix for  $k = 1, 2, 3 \dots 10$  fixed number of strategies  
174 and the residuals sum of squares (RSS) of 10 iterations was calculated for each  $k$  using the package  
175 ‘archetypes’ in R (Eugster & Leisch 2009). A robust, iteratively reweighted least squares fitting algorithm  
176 was used to down-weight the influence of the outliers (Eugster & Leisch 2011). We used the ‘elbow  
177 criterion’ to select the optimal number of strategies permitting to minimize the RSS while minimizing the  
178 number of strategies. This is done visually by assessing the number corresponding to a significant drop in  
179 the RSS. The result of the AA, and notably the position in the traits space of the archetypes, was visualised  
180 using a principal component analysis (PCA) biplot performed on the six traits. The prevalence of the optimal

181 strategies was then mapped as a proportion weighted by the species relative abundances or based on  
182 species presence only. The proportions were calculated as the mean of each life history strategy from the  
183 species composition in each grid cell. Hence, each grid cell has:  $p_{LHS1} + p_{LHS2} + p_{LHS3} = 1$ , where  $p$  is the  
184 proportion of the corresponding life history strategy (LSH).

185 **Environmental predictors**

186 In order to explain the observed spatial patterns of the life history strategies, several environmental  
187 variables were collected. Annual, winter (January-March) and summer (July-September) mean sea  
188 temperature and salinity at the surface and bottom were obtained on a  $\frac{1}{4}$  degree grid resolution from the  
189 World Ocean Atlas ([www.nodc.noaa.gov/OC5/woa13](http://www.nodc.noaa.gov/OC5/woa13)) for the period 2005-2012 and averaged on a  $\frac{1}{2}$   
190 degree grid. Surface and bottom temperature seasonality was calculated as the difference between the  
191 summer and winter mean temperatures. Chlorophyll data, used as a proxy for primary production, were  
192 obtained from the GlobColour database ([hermes.acri.fr](http://hermes.acri.fr)) as monthly averages for the years 2002-2012 on a  
193  $\frac{1}{2}$  degree grid resolution. All the chlorophyll concentrations were log transformed prior to calculations.  
194 Several metrics were derived from the dataset, including mean annual chlorophyll concentration and mean  
195 chlorophyll concentration during spring, i.e. March to May. Furthermore, chlorophyll variability during the  
196 year (proxy for seasonality and resource stability) was calculated as the standard deviation of the mean  
197 chlorophyll concentration of each month across years, while variability of the chlorophyll concentration  
198 during the spring bloom (proxy for resource predictability) was estimated as the standard deviation of  
199 mean spring chlorophyll concentrations between years. Minimum, maximum and variability (standard  
200 deviation) of depth were obtained for each  $\frac{1}{2}$  degree cell from ETOPO1 ([www.ngdc.noaa.gov/mgg/global](http://www.ngdc.noaa.gov/mgg/global))  
201 whereas mean depth was calculated directly from the depth of the hauls performed.

202 Fishing has an important impact on the composition of a community by favouring small and fast growing  
203 species relative to large and slow growing species (Jennings et al. 1999b, De Juan et al. 2007, Sguotti et al.  
204 2016). Fishing intensity can thus be an important variable explaining the spatial prevalence of the

205 strategies. Unfortunately, extensive data on fishing effort is scarce and only available for a subset of the  
206 area. As a proxy for bottom fishing intensity, we used the ratio of the area of the seabed swept by bottom  
207 trawl fishing gear, derived from Vessel Monitoring System (VMS) intensity data (ICES 2015). The swept area  
208 ratio was calculated per  $0.05^\circ \times 0.05^\circ$  grid cell per year for vessels greater than 12 meters in length, and can  
209 be interpreted as the percentage of grid cell-equivalent area swept per year. For this study, the swept area  
210 ratio was aggregated to the  $\frac{1}{2}$  degree grid cell and averaged over the four years 2009-2012.

211 For the temporal case study in the North Sea, sea surface temperature data were gathered for the years  
212 1980-2014 from a hydrographic analysis product (AHOI, Núñez-Riboni & Akimova 2015). For each year, the  
213 mean temperature was calculated as the mean of all the months, and temperature seasonality was  
214 calculated as the difference between the summer and winter months. Fishing effort, calculated as the  
215 number of hours fished by beam trawlers or otter trawlers in the North Sea, was obtained for the years  
216 1991-1995 and 2003-2012 (Jennings et al. 1999a, Engelhard et al. 2015).

## 217 **Modelling of the life history strategies**

218 The different species strategies emerge from life history evolution and as such their prevalence has been  
219 hypothesized to be non-randomly distributed and intimately linked to the environment (Grime, 1977;  
220 Winemiller and Rose, 1992). We hence tested the hypothesis that the prevalence of the life history  
221 strategies could be explained by environmental variables using generalized additive mixed models (gamm),  
222 which allows for curvilinear relationships between the response and explanatory variables (Wood 2006),  
223 e.g. in case of an environmental optimum or saturation, and permits to correct for spatial autocorrelation.  
224 In a prior analysis, we reduced the number of environmental variables to avoid problems with correlation  
225 among predictors and retained only unclustered or not highly correlated ( $r < 0.8$ ) variables (Dormann et al.  
226 2013). Eight abiotic variables were retained for the analysis: mean depth of the sampled hauls, maximum  
227 and variability of depth in each grid cell; mean and seasonality of sea surface temperature; mean and  
228 variability of annual chlorophyll concentration and sea surface salinity (Appendix S2).

229 We modelled the life history strategies as a function of the abiotic variables. The life history strategies  
230 proportion were logit transformed prior to the analysis to normalize the data and then fitted as the  
231 response variable with a Gaussian (Normal) error distribution (Warton & Hui 2011). Spatial auto-correlation  
232 was incorporated into this model with a Gaussian structure chosen from visual assessment of the  
233 variogram. The smoothing spline functions (s) were constrained to four degrees of freedom (k=4), allowing  
234 for third-order relationships, but restricting flexibility during model fitting. The strategy proportions were  
235 corrected for sampling effort by including the number of hauls performed in each grid cell as an additional  
236 explanatory variable smoother in each model and only grid cells with more than two hauls were included  
237 (n=885). All the possible models containing from zero to a maximum of three environmental variables were  
238 fitted and evaluated using the package ‘MuMIn’ in R (Barton 2016) and the best model, i.e. defined as the  
239 one with the lowest Akaike’s Information Criterion (AIC), was retained. For each strategy the predictors of  
240 the best model were plotted against the response variable. Standard model checking diagnostics were  
241 applied. We calculated the relative variable importance (RVI) to assess the contribution of each variable to  
242 the performance of the final multivariate gamm. RVI was quantified for each variable of the final models by  
243 randomly permuting the values of the variable of interest across grid cells and measuring the difference  
244 between the adjusted  $r^2$  of the newly fitted model in comparison to the original model, i.e. measuring the  
245 drop in the quality of the model fit. Thus, a variable that caused a large decrease in model performance  
246 when randomized contributed greatly to the fit of the model.

247 To explore the potential impacts of fishing on the strategies’ prevalence, a second model which integrated  
248 both environmental variables and fishing intensity were performed on a sub-area of the study for which  
249 fishing data was available. The same environmental variables used in the main model were tested as  
250 explanatory variables alongside fishing intensity using the same gam modelling method.

251 For the temporal study in the North Sea, changes in the life history strategies and environmental variables  
252 were modelled using a linear model corrected for first order temporal auto-correlation (i.e. AR1).

253 **Results**

254 **Summarizing traits variability into life history strategies**

255 The optimal number of archetypes (k) needed to encompass the spatial volume of trait-space was found to  
256 be three (Appendix S3). The largest drop in the RSS occurred when passing from two to three archetypes  
257 and adding a fourth one did not significantly reduce the RSS. The three corresponding life history strategies  
258 were represented in a biplot where the first two axes of the underlying principal component analysis (PCA)  
259 explained most of the trait variability (77%, Fig. 1). The first axis (PC1) explained almost half of the total  
260 variability (45%) and was driven by offspring size, maximum length, lifespan and trophic level. The second  
261 axis was driven by fecundity and parental care. Several traits were clustered (maximum length, lifespan and  
262 trophic level), while others were negatively correlated (fecundity against parental care and offspring size).  
263 The three life history strategies could be visualized as a triangle in trait space with each extreme point  
264 representing a unique combination of traits characteristics (Fig. 1). These strategies and their relations with  
265 traits corresponded closely with the theoretical model of Winemiller and Rose (1992), and are henceforth  
266 referred to as opportunistic, periodic and equilibrium strategies, respectively. The opportunistic strategy  
267 was characterized by species with small size, low trophic level and short lifespan but with relatively high  
268 fecundity and parental care, such as species of gobidae and ammodytidae, including the sand goby  
269 (*Pomatoschistus minutus*) and lesser sand eel (*Ammodytes tobianus*), as well as small pelagic fish, e.g.,  
270 European anchovy (*Engraulis encrasicolus*). The periodic strategy was characterized by species with  
271 medium to high lifespan, length and trophic level, high fecundity but low parental care and offspring size,  
272 such as sunfish (*Mola mola*), conger eel (*Conger conger*) and several species of gadoids including blue ling  
273 (*Molva dypterygia*) and Atlantic cod (*Gadus morhua*). The equilibrium strategy was characterized by species  
274 with high length, lifespan and trophic level, low fecundity but large offspring size and high parental care,  
275 such as rays and sharks, e.g. marbled electric ray (*Torpedo marmorata*) and spiny dogfish (*Squalus*  
276 *acanthias*), as well as rabbitfish (*Chimaera monstrosa*).

277 The species were not clustered around the three strategies end-points but instead demonstrated a  
278 continuum between the strategies (Fig. 1). A species could therefore have characteristics of more than one  
279 strategy at the same time, and were thus characterized by the proportions expressed in each strategy  
280 (Appendix S4). Both the opportunistic and the periodic strategies were prominent in the species pool, while  
281 few species showed an equilibrium strategy

282 **Patterns of life history strategies**

283 The distribution of life history strategies exhibited clear spatial patterns (Fig. 2). The proportion of the  
284 equilibrium strategy was generally much lower than the periodic and opportunistic strategies with values  
285 ranging between 0% and 36%. On the contrary, the proportions of the periodic and opportunistic strategies  
286 were never lower than 25% and 23%, and reached a maximum of 66% and 64%, respectively. The  
287 proportion of the equilibrium strategy was highest at high latitudes, in Iceland and Greenland, as well as in  
288 the Balearic and Irish Seas. The opportunistic strategy displayed a North-West to South-East gradient,  
289 prevailing notably in the Baltic Sea, the southern North Sea and the Mediterranean while less abundant in  
290 Iceland and Greenland. The periodic strategy did not exhibit strong spatial patterns as it had a relative high  
291 prevalence in most of the studied area, notably south of Iceland, in the northern offshore of the North Sea  
292 and in the Celtic Sea.

293 We found the same overall spatial pattern when using presence data (Appendix S5) and the strategies  
294 prevalence in the communities calculated using abundance and presence were highly correlated. A notable  
295 change was a shift to a lower prevalence of the equilibrium strategies when using abundance compared to  
296 presence (Appendix S5). The spatial patterns were robust to different seasons, as seen for example in the  
297 North Sea (Appendix S6).

298 **Environmental predictors of life history strategies**

299 The best models with maximum three abiotic predictors explained 53%, 70% and 78% of the variability of  
300 the periodic-, opportunistic- and equilibrium strategy, respectively (Table 1). Sea surface temperature (SST)

301 and sea surface temperature seasonality (SST season) were retained in all the final models. SST was the  
302 variable explaining most of the variability in the opportunistic strategy, with a positive relationship, while it  
303 followed a negative relationship for the equilibrium strategy (Fig. 3). SST seasonality was the most  
304 important variable explaining the variability of the equilibrium strategy, and followed a negative  
305 relationship. On the other hand, the opportunistic strategy had a positive and saturating relationship with  
306 SST seasonality. Depth was also an important predictor of the equilibrium and periodic strategy, with a  
307 positive and hump-shape relationship, respectively. Chlorophyll concentration was also retained in the  
308 opportunistic strategy and followed a positive relationship. The same explanatory variables were found  
309 when using presence only, at the exception of the equilibrium strategy for which chlorophyll concentration  
310 was retained instead of depth (Appendix S5). For the subarea where both environmental variables and  
311 fishing intensity was available, the best predictors of the opportunistic strategy were depth, temperature  
312 and temperature seasonality, explaining 78% of the variability, while for the periodic strategy they were  
313 depth, temperature and chlorophyll, explaining 63% of the variability. For the equilibrium strategy, fishing  
314 intensity, depth and sea surface temperature were the most important variables explaining 48% of the  
315 variability with fishing demonstrating a negative relationship with prevalence (Appendix S7).

316 During the period 1980-2014 in the North Sea, the proportion of the periodic strategy declined ( $p<0.001$ )  
317 while it increased for the equilibrium ( $p<0.001$ ) and opportunistic ( $p<0.001$ ) strategies. Although  
318 demonstrating significant temporal trends the magnitudes of change in prevalence were rather moderate,  
319 amounting to a decrease in the periodic strategy from 46% in 1980 to 38% in 2014 and an increase in the  
320 equilibrium and opportunistic strategies from 7% to 12% and 47% to 50%, respectively. During the same  
321 time period SST increased ( $p<0.01$ ), whereas for the recent period (1990-2012) fishing effort showed a  
322 marked decline, especially for beam trawlers ( $p<0.05$ ).

323

324 **Discussion**

325 Characterizing ecological communities by a set of biological traits is challenging since the selected traits are  
326 often correlated and therefore contain similar information. In this study, we show that several key traits of  
327 marine fish are correlated and that the variability of these traits could be reduced into three main  
328 components based on archetypal analysis (AA). AA has several advantages compared to traditional cluster  
329 analysis, especially when the data are continuous, as it gives similar values to the points that are close to  
330 each other in trait-space (Hart et al. 2015). Each point in the trait-space, e.g. a species, is defined as a  
331 convex combination (i.e. a proportion that sums to one) of the archetypes (in this case, the three life  
332 history strategies) rather than being assigned to a single class or cluster (Cutler & Breiman 1994).  
333 Furthermore, the results of the AA are also easily interpretable thanks to the more pronounced contrasts  
334 between the extreme archetypes compared to cluster analysis. AA has been used in different research  
335 fields, such as economics, astrophysics and pattern recognition for some years now (Bauckhage & Thurau  
336 2009) but has only recently been applied in biology and ecology (Hart et al. 2015). Using this novel  
337 approach the three main trait components identified are well in accordance with the theoretical model of  
338 Winemiller and Rose (1992), where the trait-space is encompassed by a triangular shape with endpoints  
339 corresponding to a life history strategy - opportunistic, equilibrium and periodic. At the community level  
340 the proportion of the strategies expressed followed a strong spatial pattern in the European seas. These  
341 spatial patterns can be explained by the abiotic variables where each strategy prevails under different  
342 environmental conditions, largely depending on sea surface temperature and its seasonality, as well as  
343 depth. The prevalence of the strategies is not fixed through time, and the last 30 years have seen a slight  
344 increase in the opportunistic and equilibrium strategies in the North Sea while the periodic strategy has  
345 decreased. These changes paralleled a period of change in the abiotic environment of the North Sea, with  
346 an increase in temperature and a decrease in fishing effort.

347 For large species, two distinctive strategies were dominant: either the periodic strategy producing many  
348 small offspring at the cost of offspring survival, or the equilibrium strategy producing few large offspring  
349 but with high survival. The periodic strategy is composed mainly of bony fish species, e.g. large flatfish and

350 gadoids species, while the equilibrium strategy is mainly composed of elasmobranchs, e.g. sharks and rays.  
351 These strategies reflect the evolutionary and environmental constraint and trade-offs shaping variability in  
352 life history strategies (Neuheimer et al. 2015). High fecundity balances high pre-adult mortality while  
353 longevity balances unfavourable periods for reproduction in typical poor environmental conditions  
354 (Gunderson 1997, Longhurst 2002). In contrast to the large species, the small and short lived species, such  
355 as gobies and clupeids, largely followed the opportunistic strategy producing many small offspring. The  
356 lifetime reproductive value of these short lived species is often compensated by fast growth, early  
357 maturation and indeterminate spawning (Tsoukali et al. 2016). The simpler, and often used, slow-fast  
358 continuum model was not appropriate here and would have failed to explain some of the trait-variability.  
359 However, in smaller and extreme ecosystems or in smaller samples of species with a wide geographical  
360 range, the slow-fast continuum model can sufficiently explain the life history variation (Juan-Jordá et al.  
361 2013, Wiedmann et al. 2014).

362 The strategies prevalence in the communities was linked to the environment and its variability. Notably, we  
363 found that the opportunistic strategy prevailed in environments with high temperature and strong  
364 temperature-seasonality while the equilibrium strategy prevailed in environments with lower and more  
365 stable temperatures. The opportunistic reproductive strategy, corresponding to the production of many  
366 small eggs, is favourable in seasonal environments to compensate for the short time where resources are  
367 available (Boyce 1979) and in warm environments to balance the higher egg mortality resulting from  
368 thermal stress (Pepin 1991). The strong negative relationship between the opportunistic strategy and  
369 temperature is verified by the recent distributional shift of mostly small and short-lived species in response  
370 to warming (Perry et al. 2005, Magurran et al. 2015), where these opportunistic seasonal migrants take  
371 advantage of newly disturbed conditions in these areas (Collie et al., 2008). The opportunistic species are  
372 physiological generalists; they are the first to respond to disturbance and can quickly attain high densities  
373 thanks to their life-history characteristics (e.g. high fecundity, short generation time and wide dispersal  
374 ability; Levinton 1970). The opportunistic strategy prevails in lower latitudes in areas with high thermal

375 seasonality and primary productivity while the equilibrium species prevails in higher latitudes and in areas  
376 with comparatively lower seasonality. According to MacArthur (1960), the opportunistic species are  
377 considered not to be resource-limited and are thriving in environment where the population size is below  
378 the carrying capacity of the habitats, while the communities composed of equilibrium species are often  
379 resource-limited and at, or near the carrying capacity of the environment.

380 Abiotic variables explained a lower degree of variability in the prevalence of the periodic strategy. This is  
381 likely due to its relatively moderate spatial contrast compared to the more pronounced spatial pattern of  
382 the equilibrium and opportunistic strategies throughout the study areas. Since we assess the strategies  
383 prevalence in the communities as proportions, the three strategies are related with each other: as one  
384 strategy proportion increase, the other decline. Therefore, the moderate response of the periodic strategy  
385 to the environment might also be due to the fact that its relative proportion is affected by the more  
386 pronounced changes in the opportunistic and equilibrium strategies.

387 Fishing can impact community composition by affecting the relative abundance of both commercial and  
388 non-commercial species, as well as by physical impacts on the seabed (Myers & Worm 2003, Hiddink et al.  
389 2006). Fishing impacts on individual species is dependent on their traits and life history strategies (Jennings  
390 et al. 1999b, Winemiller 2005). As fishing increases disturbance, it will most likely benefit opportunistic  
391 species while disadvantaging the equilibrium species (Jennings et al. 1999b, Stevens et al. 2000). In our  
392 study, we found a negative effect of fishing effort on the prevalence of the equilibrium strategy. This  
393 negative relationship is expected, as equilibrium species, e.g. sharks and rays, are particularly vulnerable to  
394 fishing and habitat disturbance due to their low productivity arising from their life history characteristics,  
395 e.g. low fecundity and slow growth (Dulvy et al. 2008, Sguotti et al. 2016). Although the variability  
396 explained by the final model was low, the negative relationship with fishing is supported by the temporal  
397 changes in the equilibrium strategy in the North Sea, where it has increased since the 1980s, in synchrony  
398 with a general decrease in fishing effort. Recent findings showing that the decline in fishing effort in the

399 North Sea and the neighbouring Kattegat coincided with an increase in the number of large fish in the  
400 communities (Fock et al. 2013, Engelhard et al. 2015; Lindegren et al. 2012) also support this explanation.

401 Life history strategies permit trait information to be reduced into a few ecologically-meaningful  
402 components. Our empirical findings of marine fish communities clearly support the theoretical framework  
403 by Winemiller and Rose (1992) demonstrating three main life-history strategies of fish: opportunistic,  
404 equilibrium and periodic. The proportion of the strategies showed pronounced spatio-temporal patterns  
405 across European Seas in response to varying environmental conditions. This highlights the underlying  
406 ecological mechanisms whereby fitness is optimized through natural selection, conditioned on the key  
407 trade-offs between growth, feeding and reproduction that ultimately determine the success or failure of a  
408 given life-history strategy under certain environmental conditions. However, our study also show that while  
409 marine fish communities can be characterized by three life-history strategies, a significant fraction of  
410 species do not abide strictly to any given strategy but rather reflect a combination of strategies.  
411 Interestingly, this is particularly evident for a number of small-pelagic species primarily distributed along  
412 the axis from opportunistic to periodic strategies (e.g., sprat, herring and mackerel). Although size is  
413 arguably a strong predictor of the position of species along a life-history continuum (Brown and Sibly 2006),  
414 it should be worthwhile exploring other more proximate traits explaining the presence and success of these  
415 intermediate strategies (Sibly and Brown 2007). In terms of marine fish, one such trait might be swimming  
416 performance which determines the range and extent of migratory behaviour and that ultimately allow  
417 species to successfully explore, forage and reproduce in very different habitats across pronounced  
418 environmental gradients. This may suggest that while for sedentary species it may be advantageous to  
419 more closely follow a given strategy, highly mobile species may rather optimize fitness through  
420 intermediate strategies, reflecting a compromise between the traits and trade-offs suitable across a large  
421 range of environments. Finally, we wish to stress that life history strategies can be implemented in various  
422 type of studies, e.g. to investigate population dynamics (Mims & Olden 2012), colonization (Olden et al.  
423 2006), fisheries management (King & McFarlane 2003), or biological succession (Silvertown & Franco 1993).

424 Due to their strong dependence on the environment, life history strategies can therefore be a suitable  
425 management tool to deconstruct and characterize communities' composition and monitor changes in the  
426 communities in response to exploitation and climate change.

427

## 428 **Acknowledgments**

429 This work was funded by the Centre for Ocean Life, a VKR center of excellence supported by the Villum  
430 foundation, as well as a VILLUM research grant to ML (13159). This work has received funding from the  
431 European Community's Seventh Framework Programme (FP7 2007-2013) under grant agreement no.  
432 308299 (NACLIM) and the European Union's Horizon 2020 research and innovation programme under grant  
433 agreement No 678193 (CERES, Climate Change and European Aquatic Resources). We acknowledge the  
434 ICES Working Group on Comparative Analyses between European Atlantic and Mediterranean marine  
435 ecosystems to move towards an Ecosystem-based Approach to Fisheries (WGCOMEDA) during which the  
436 study was initiated and are thankful to all the WGCOMEDA participants for their valuable comments. The  
437 WGCOMEDA meeting was supported by a European Consortium EUROMARINE grant. We thank Georg  
438 Engelhard for the fishing effort data in the North Sea as well as Cefas project MF1228 Fizzyfish and STECF.  
439 We are also grateful to all the scientific and crew members engaged in the International Scientific Trawl  
440 Surveys. Finally, we thank three anonymous referees and the editor for their helpful comments.

## 441 **Supporting Information**

442 Appendix S1 Information on the Bottom trawl surveys.

443 Appendix S2 Spatial patterns of the selected abiotic variables.

444 Appendix S3 Residuals sum of squares in function of the number of strategies.

445 Appendix S4 Species strategy: proportions expressed in each strategy.

446 Appendix S5 Spatial pattern and environmental predictors based on species presence.

447 Appendix S6 Seasonality and life history strategies pattern in the North Sea.

448 Appendix S7 Fishing intensity and strategies' prevalence.

449 **Biosketches**

450 The work presented here was made possible thanks to collaboration between different European institute

451 through the 'Working Group on Comparative Analyses between European Atlantic and Mediterranean

452 marine ecosystems to move towards an Ecosystem-based Approach to Fisheries' (WGCOMEDA). Further

453 information on the expert group activities can be found at

454 [www.ices.dk/community/groups/Pages/WGCOMEDA.aspx](http://www.ices.dk/community/groups/Pages/WGCOMEDA.aspx)

455 The research was conducted primarily at the Centre for Ocean Life at the Technical University of Denmark,

456 which uses the trait-based approach to study life in a changing ocean. Further information on the research

457 group can be found at [www.ocean-lifecentre.dk](http://www.ocean-lifecentre.dk)

458 **DATA ACCESSIBILITY**

459 The species list, their reproductive traits and their literature sources used for this study are available from  
460 the Pangaea database: <https://doi.pangaea.de/10.1594/PANGAEA.868610>.

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616 **Table**

617 Table 1. Variables and parameters of the best final generalized additive mixed models (gamm),  
 618 with a maximum of three abiotic variables and corrected for the sampling effort. R<sup>2</sup> is the adjusted  
 619 R<sup>2</sup> of the final model and RVI is the estimated relative variable importance of each variable present  
 620 in the final model, it corresponds to the drop in the model R<sup>2</sup> when the variable is randomized. All  
 621 variables in the final model are significant (p<0.001). SST refers to sea surface temperature, SST  
 622 *seasonality* to the seasonality in sea surface temperature, *Depth* to the mean depth of the hauls  
 623 performed and *CHL* to the chlorophyll a concentration.

Life history strategies	Best model	R <sup>2</sup>	RVI
Opportunistic	SST + SST seasonality + CHL	0.78	
	SST	0.38	
	SST Seasonality	0.34	
	CHL	0.26	
Periodic	SST + Depth + SST seasonality	0.53	
	SST	0.13	
	Depth	0.12	
	SST Seasonality	0.09	
Equilibrium	SST seasonality + SST + Depth	0.70	
	SST Seasonality	0.20	
	SST	0.09	
	Depth	0.04	

624

625 **Figures legends**

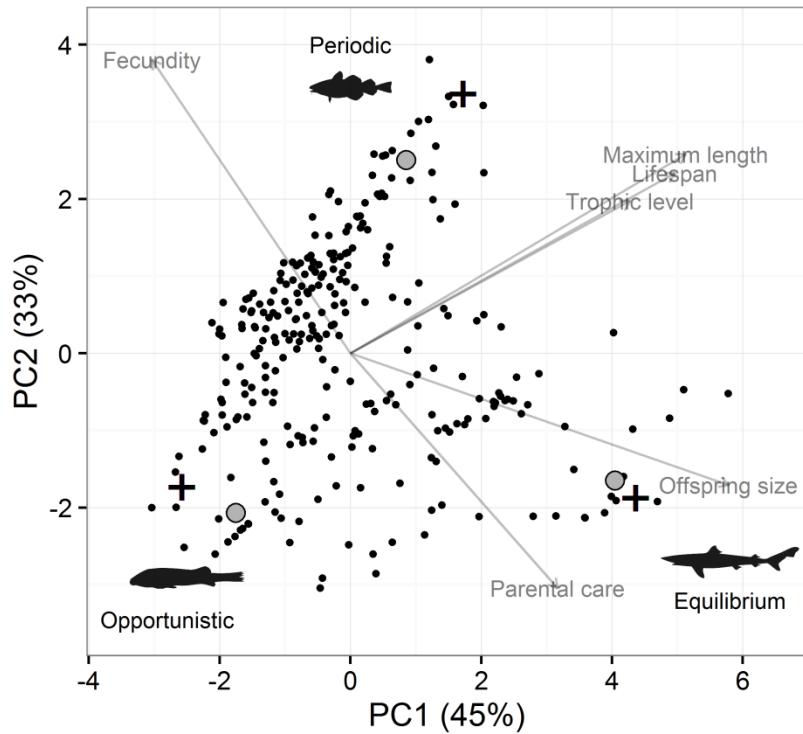
626 Figure 1. Plot of the first and second principal component (PC1 and PC2) based on a principal  
627 component analysis (PCA) on the six selected traits. Each species used in the study is represented  
628 by a black dot. The three extreme points (archetypes) that encompass the trait-space are  
629 represented by black crosses, corresponding to the equilibrium, opportunistic and periodic  
630 strategies, respectively. Furthermore, each of the strategies are illustrated by one characteristic  
631 species marked by grey dots, namely cod (*Gadus morhua*) a periodic species, sand goby  
632 (*Pomatoschistus minutus*) an opportunistic species, and school shark (*Galeorhinus galeus*) an  
633 equilibrium species.

634 Figure 2. Proportion of the life history strategies (left) equilibrium, (middle) opportunistic and  
635 (right) periodic in each  $\frac{1}{2}$  degree cell across the European Seas calculated from species abundance.  
636 At each grid cell, the sum of the three life history strategies proportion adds to one. The top panel  
637 represents Greenland and Iceland while the bottom panel shows Western Europe. On the bottom  
638 left panel, the black triangle represents the location of the North Sea, the ecosystem used in the  
639 temporal case study.

640 Figure 3. Relationships between the life history strategies proportion in the communities and their  
641 environmental predictors retained in the best gam model. SST refers to sea surface temperature,  
642 SST season to the seasonality in sea surface temperature.

643 Figure 4. Time series of relative proportions of equilibrium (black), opportunistic (dark grey) and  
644 periodic strategies (grey) in the North Sea from 1980 to 2014 (top panel). The lower panels show  
645 the concomitant trends in sea surface temperature (SST) and SST seasonality for 1980-2014  
646 (middle) and fishing effort by otter- and beam trawlers for 1991-1995 and 2003-2012 (bottom).  
647 The regression lines and their confidence interval (shaded area) are displayed when the temporal  
648 pattern is significant at  $p < 0.05$ . Due to different scale, the fishing effort and temperature variables  
649 were standardized to facilitate the comparison.

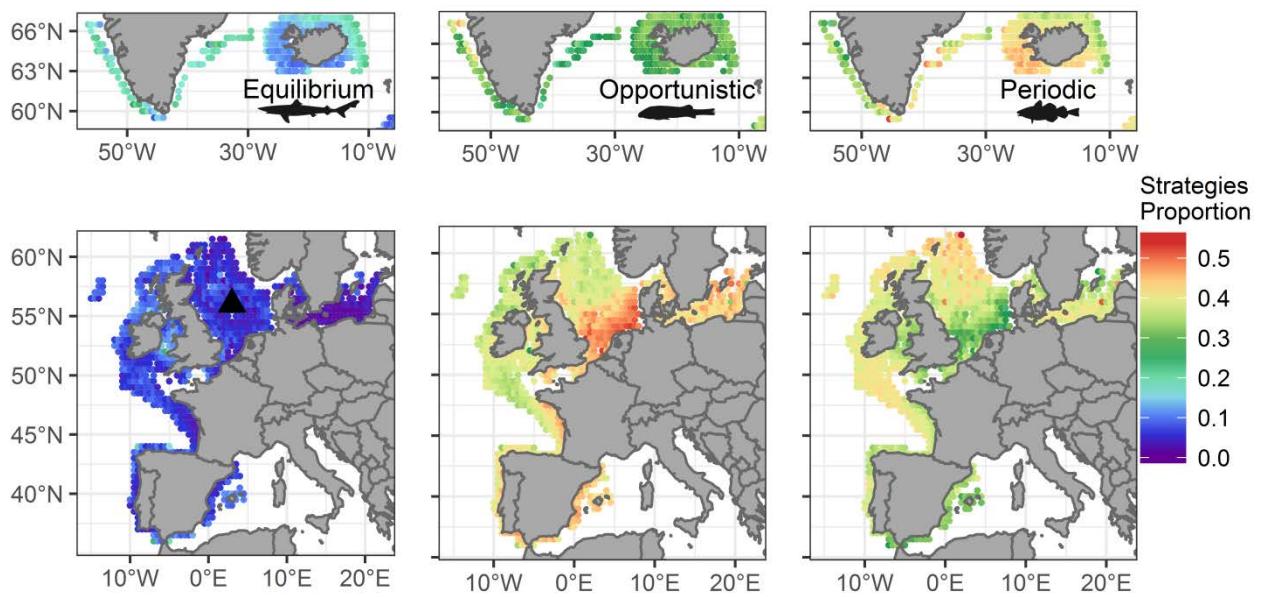
650 **Figures**



651

652 Figure 1.

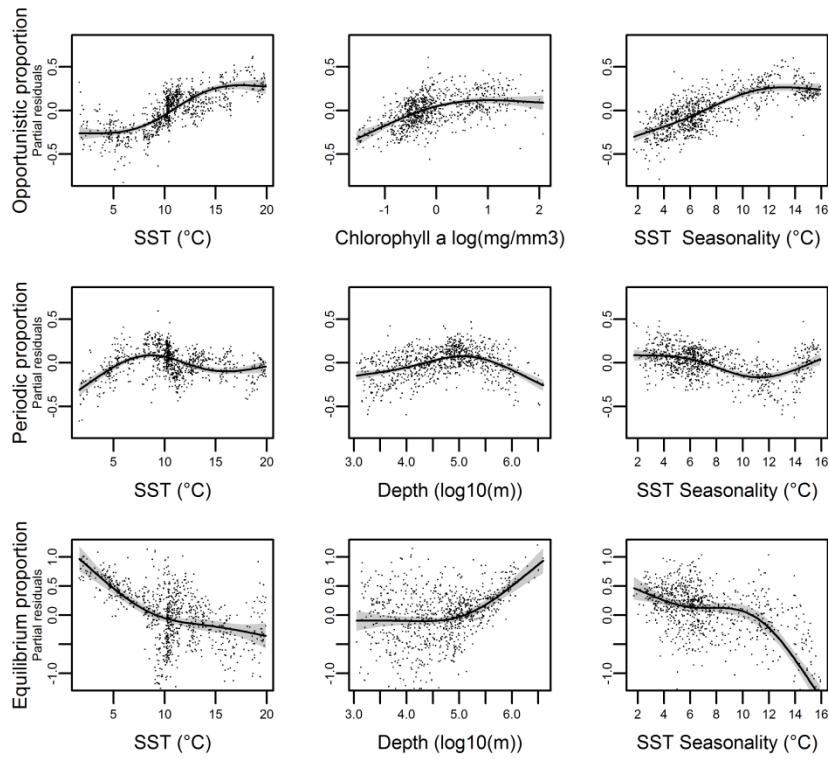
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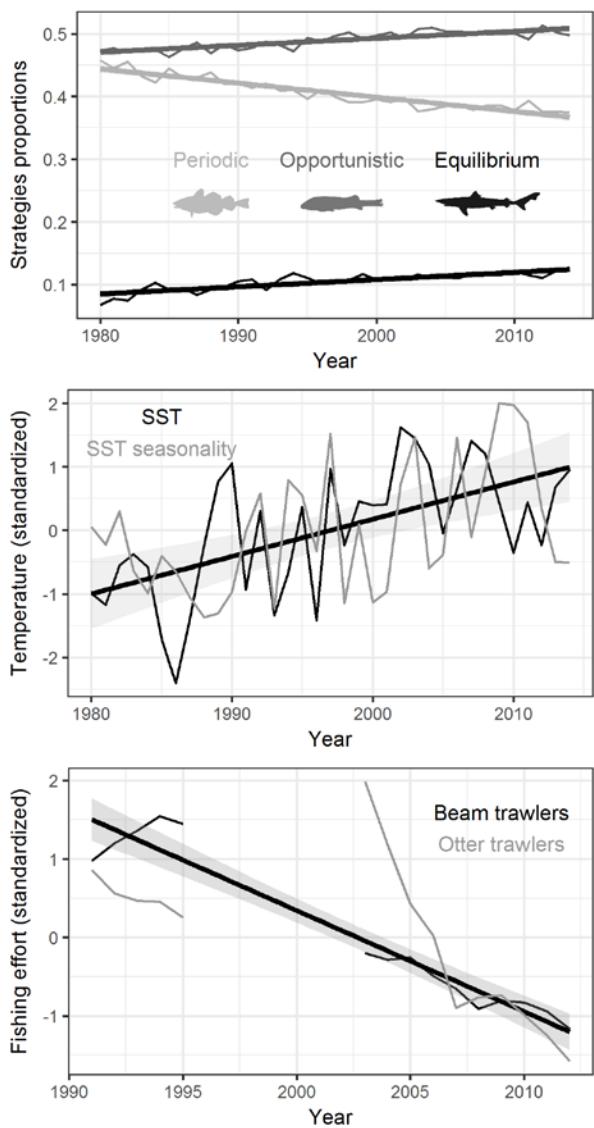
655 Figure 2.

656



657

658     Figure 3.



659

660 Figure 4.