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

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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.

107

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 (L_{max}) 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 (L_{inf}) parameters
135 from the Von Bertalanffy growth equation. L_{inf} is calculated from empirical growth data for the majority of
136 the species but is inferred from L_{max} 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 ovoviviparous. 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 ½ degree grid
156 cells, 95% of the species present and 97% of the individuals recorded in each grid cell had trait information.

157

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 ...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) 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) 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)
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°x0.05° 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 ½ 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 & Thureau
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

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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

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

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^2 is the adjusted
 619 R^2 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^2 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^2	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**

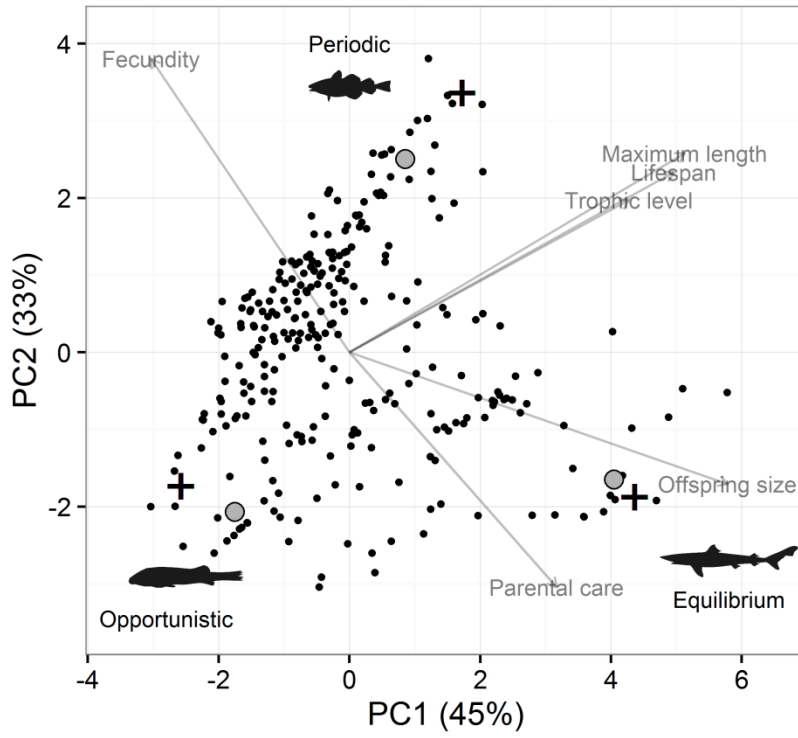
626 Figure 1. Plot of the first and second principal component (PC1 and PC2) based on a principal
627 component analysis (PCA) on the six selected traits. Each species used in the study is represented
628 by a black dot. The three extreme points (archetypes) that encompass the trait-space are
629 represented 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 ½ 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.

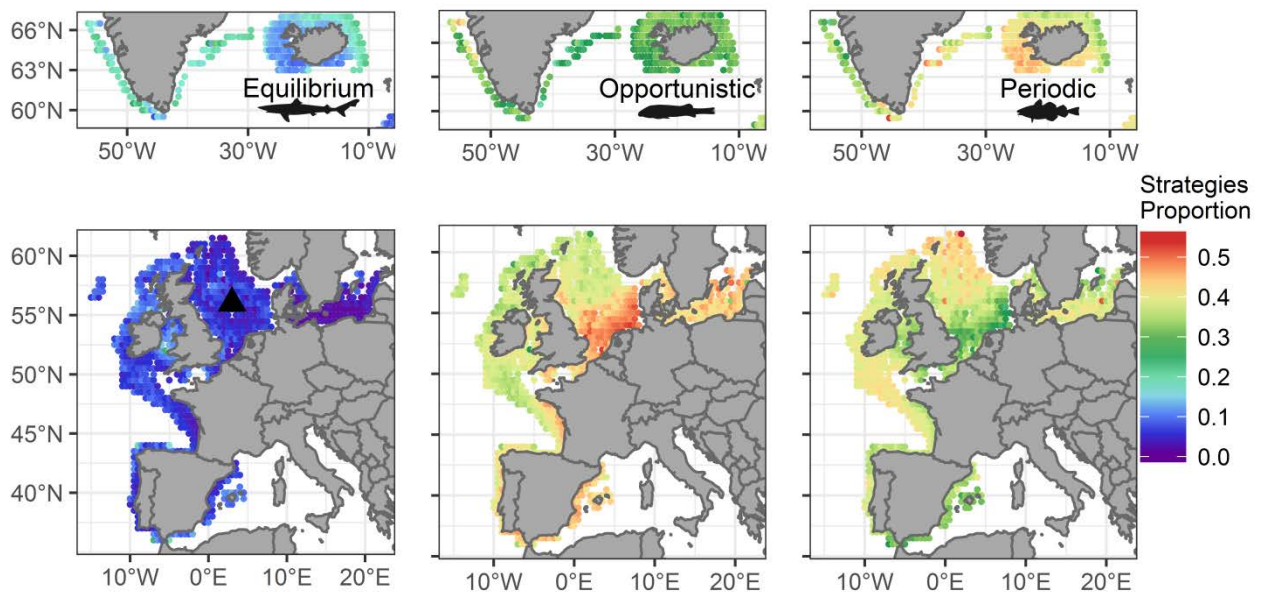
650 **Figures**



651

652 **Figure 1.**

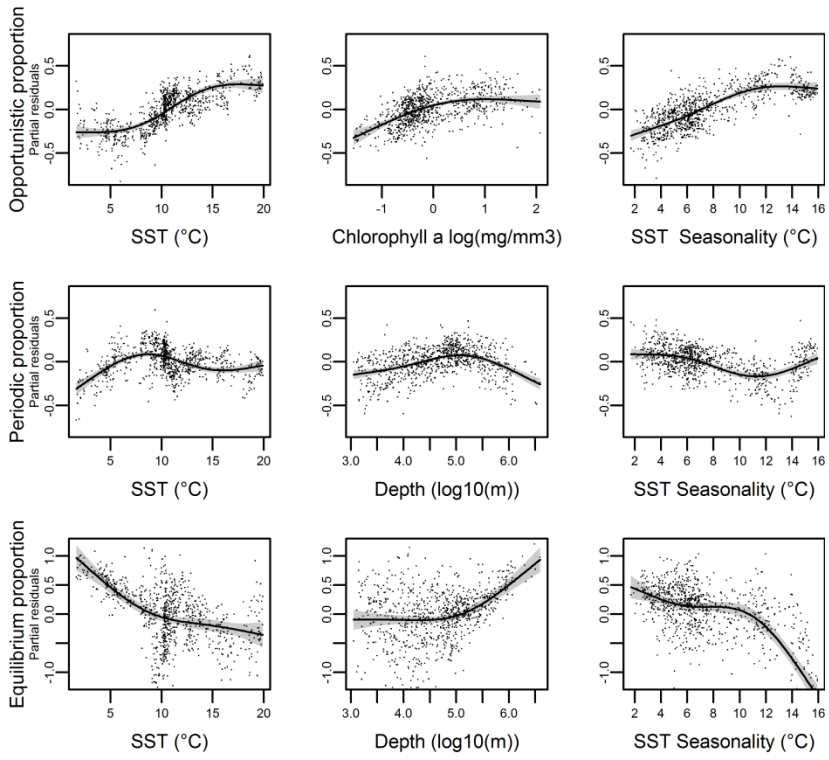
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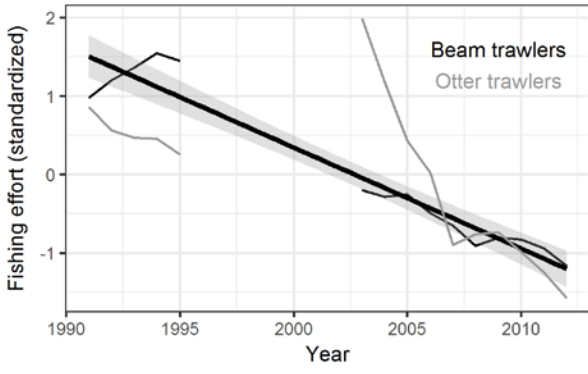
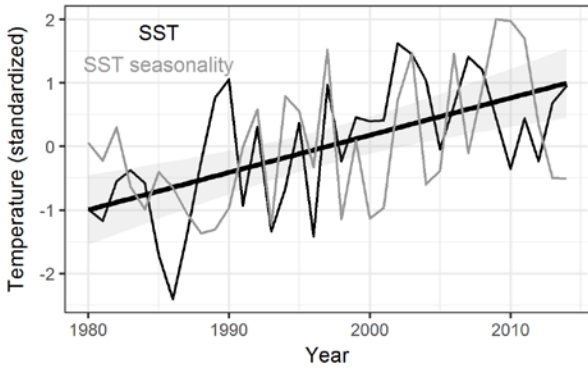
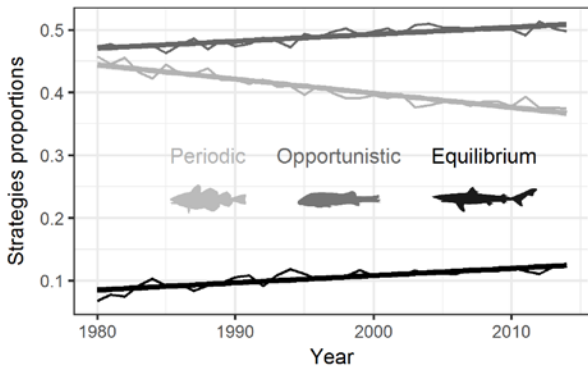
655 Figure 2.

656



657

658 Figure 3.



659

660 Figure 4.