Ecological and life history traits explain a climate induced shift in a temperate marine fish community

Mc Lean Matthew James [1, *], Mouillot David [2], Auber Arnaud [1]

[1] IFREMER, Unité Halieutique de Manche et mer du Nord, 150 quai Gambetta, BP699, 62321 Boulogne-sur-Mer, France
[2] MARBEC, Université de Montpellier, CNRS, IFREMER, IRD, 34095 Montpellier Cedex, France

* Corresponding author : Matthew James Mc Lean, email address : mcleamj@gmail.com

Abstract :

A better understanding of community dynamics and ecosystem functioning can be achieved by describing how community functional structure responds to environmental change over both time and space and by identifying which functional groups best mediate community responses. Here, we used a trait-based approach in combination with a newly developed application of principal response curves to functionally characterize a rapid taxonomic shift in the eastern English Channel fish community in the late 1990s. We identified the functional groups with the greatest contributions to the overall shift in fish functional structure and uncovered significant trait−environment relationships. We found that pelagic species with rapid life history cycles, characterized by broadcast spawning, small offspring size, and early maturation, declined considerably in abundance following an increase in sea surface temperature associated with a warming phase of the Atlantic Multidecadal Oscillation, which was likely exacerbated by historical fishing pressure. In contrast, species with late maturation, high parental care, and few, well-developed offspring increased in abundance, reinforcing that fish community responses to climate warming are strongly mediated through life history traits. By examining how environmental factors drove a community shift at the trait level, we provide a mechanistic understanding of how fish functional structure responds to rapid environmental change.

Keywords : Atlantic Multidecadal Oscillation, Climate warming, English Channel, Functional ecology, Principal response curves, Response traits

Introduction

41 Sustainably managing natural resources requires a greater understanding of community dynamics

42 and ecosystem functioning under changing environmental conditions (Kremen 2005, Carpenter et

43 al. 2009, Cheung et al. 2016). Examining community dynamics on a species by species basis is

44 useful for stock assessments and population management; however, such taxonomic approaches

45 are less insightful for understanding ecological mechanisms and processes (Díaz & Cabido 2001,

46 Mcgill et al. 2006, Mouillot et al. 2013). By contrast, trait-based ecology links community

47 dynamics and ecosystem processes by identifying how organismal traits respond to

48 environmental change (Mcgill et al. 2006, Winemiller et al. 2015, Gross et al. 2017), which can

49 generate predictive relationships that are not taxon or ecosystem specific (Díaz & Cabido 2001,

50 Lavorel & Garnier 2002, Winemiller et al. 2015). This approach has gained progressive support

51 and is now recognized as an essential step forward in community ecology and natural resource

52 management (Hooper et al. 2005). Thus, a better understanding of community dynamics can be

53 achieved by describing how community functional structure responds to environmental factors

54 over both time and space, and identifying which ecological traits best mediate community

55 responses.

56 Rapid and pronounced shifts in community structure have been documented in many

57 ecosystems worldwide and are often related to rapid environmental change (Scheffer & Carpenter

58 2003, Beaugrand 2004, Verges et al. 2014, Wernberg et al. 2016). In fish communities, such

59 shifts have been documented in response to extreme climatic events and climate cycles that alter

60 sea surface temperatures and oceanographic processes. For example, Wernberg et al. (2016)

61 documented an increase in subtropical fishes following a heatwave along southwestern Australian

62 and Reid et al. (2001) documented an increase in horse mackerel landings following a phase

63   change of the North Atlantic Oscillation. Fluctuations of sardine and anchovy landings have also

64   been linked to alternating cycles of the Pacific Decadal Oscillation (Chavez et al. 2003,

65   Lindegren et al. 2013). Yet, such community shifts are classically examined using taxonomic

66   approaches, which are limited in explaining biological responses and their consequences for

67   ecosystem functioning (Reid et al. 2001, Chavez et al. 2003, Clare et al. 2015). Auber et al.

68   (2015) previously documented a rapid shift in the Eastern English Channel fish community in

69   response to a warming phase of the Atlantic Multidecadal Oscillation (AMO), which induced

70   substantial decreases in the abundance of several dominant species and moderate increases in

71   some subordinate species. Such taxonomy-based findings can describe major ecosystem changes

72   with potential impacts on ecosystem services but cannot identify the functional mechanisms that

73   underpin how and why certain organisms respond strongly to climatic changes while others are

74   unaffected. Rather, greater understanding of fish community responses to rapid environmental

75   change could be achieved by functionally characterizing community shifts and identifying the

76   most responsive functional groups.

77   While a better understanding of community shifts can be achieved by describing spatio-

78   temporal changes in functional groups, statistical methods for such studies are limited (Leps et al.

79   2006, Petchey & Gaston 2006, Violle et al. 2007). Auber et al. (2017) recently proposed a new

80   application of Principal Response Curves (PRC) for examining community shifts between time

81   frames. PRC is a multivariate method that simultaneously describes spatial and temporal changes

82   in community structure and identifies the most responsive species (Van den Brink & Ter Braak

83   1999, Auber et al. 2017). Despite the utility of PRC for describing community shifts, this method

84   has been largely underused and has not yet been applied to ecological traits.

85   Here we used a trait-based approach with PRC to functionally characterize the shift in the

86   Eastern English Channel fish community, specifically answering i) did changes in taxonomic

87   community structure correspond to a pronounced shift in functional structure, ii) which functional

88   groups were most contributive to overall changes in functional structure, and iii) which

89   environmental factors were most associated to changes in functional structure through time? By

90   examining the underlying functional changes behind the taxonomic shift, we provide a

91   mechanistic understanding of changes in fish functional structure in response to rapid

92   environmental warming.

93

Methods

Fish community data

96   The fish community of the Eastern English Channel (EEC, area VIId defined by the International

97   Council for the Exploration of the Sea, ICES) has been sampled every October since 1988 during

98   the Channel Ground Fish Survey (CGFS). Here, we focused on the study period of 1988 – 2011.

99   The CGFS sampling scheme is spatially stratified by subdividing the EEC into 15'×15'

100   rectangles where at least one 30-min haul is made during daylight hours at an average speed of

101   3.5 knots. A high (3 m) vertical opening bottom trawl (GOV) with a 10-mm-stretched-mesh-size

102   codend is used. The stratified sampling scheme manages to complete 90 to 120 hauls per year

103   depending on weather conditions, and we removed all sites that had not been visited for at least

104   three consecutive years (Auber et al. 2017). After each haul, all captured fishes are identified and

105   the number of individuals per species is counted. Abundance indices at each sampling station

106 were obtained from the ICES data portal and were standardized to numbers of individuals per

107 km^2 (ICES).

108

109 **Ecological traits**

110 Ecological trait data for 73 taxa (67 species and 6 genera not identified to species level) were

111 collected from FishBase (Froese & Pauly 2012), the Ocean Biogeographic Information System

112 (http://www.iobis.org/), the Global Biodiversity Information Facility (https://www.gbif.org/),

113 Engelhard et al. (2011), Pecuchet et al. (2017), and a search of primary literature. Nine ecological

114 traits were used for this study related to life history, habitat use, and trophic ecology (Table 1).

115 Traits were chosen if they were i) readily available, ii) deemed accurate by comparison of

116 multiple sources and iii) potentially implicated in the response of communities to environmental

117 change. Categorical or binary traits included parental care, water column position, and trophic

118 guild, while continuous traits included length and age at maturity, fecundity, offspring size,

119 temperature preference, and trophic level. Temperature preference was calculated as the median

120 temperature of a species across its global range of observations for which data were available.

121

122 **Table 1.** Ecological traits and their corresponding functional groups (i.e., trait attributes).

Ecological Trait	Functional (Trait) Groups
Length at Maturity (cm)	2.65-11.03, 11.04-18.69, 18.70-26.63, 26.64-40.13, ≥40.14
Age at Maturity (years)	0.33-1.39, 1.40-2.31, 2.32-2.99, 3.0-4.49, ≥4.5
Parental Care	Pelagic Egg, Benthic Egg, Clutch Hider, Live Bearer
Offspring Size (mm)	0.34-0.89, 0.90-1.09, 1.10-1.39, 1.40-2.67, ≥2.68
Fecundity	2-879, 880-9999, 10000-106399, 106400-406589, ≥406590
Water Column Position (Engelhard et al. 2011)	Demersal, Reef-Associated, Benthopelagic, Pelagic
Temperature Preference (°C)	4.62-10.41, 10.42-11.29, 11.30-11.72, 11.73-12.49, ≥12.5
Trophic Guild	Detritivore, Planktivore, Benthivore, Carcinophage, Benthopiscivore, Piscivore
Trophic Level	2.2-3.23, 3.24-3.39, 3.4-3.69, 3.7-3.99, ≥4

123

124

125   When combining species' abundances and traits, ecologists generally have two choices:

126 calculate community-weighted mean (CWM) trait values or use the abundances of functional

127 groups. The advantage in using CWM trait values is that continuous data are not broken into

128 categories and thus no information is lost, however examination of the underlying changes in trait

129 values is not possible. For instance, CWM trait values could reveal that, on average, maximum

130 length of fishes decreased over time, but could not reveal whether this was driven by an increase

131 in small fishes, a decrease in large fishes, or both. In order to characterize the EEC fish

132 community shift in terms of changes in the actual abundance of different functional groups, we

133 categorized continuous traits, making all traits categorical. Continuous traits were therefore put

134 into five groups by using quintiles of the continuous trait data for all individuals with each trait

135 (Table 1). The abundances of all functional groups (i.e., each trait category or attribute) were then

136 $\log 10(x+1)$ transformed.

137

138 **Environmental factors**

139 Environmental factors included both ocean-wide climate oscillations and local environmental

140 parameters. The North Atlantic Oscillation (NAO) is an intra-decadal alternation of atmospheric

141 mass over the North Atlantic, which is known to influence sea surface temperatures (SST) and

142 oceanographic processes (Dickson 2000). The NAO index used here is based on the difference of

143 normalized sea-level atmospheric pressure between Lisbon, Portugal and Reykjavik, Iceland

144 (Dickson 2000). The annual NAO index for the period 1988–2011 was obtained from NOAA

145 (https://www.ncdc.noaa.gov/teleconnections/nao/). The Atlantic Multidecadal Oscillation (AMO)

146   refers to a 60–80 year cycle of North Atlantic SST (Edwards et al. 2013). The AMO index is

147   computed as a monthly area-weighted mean of SST anomalies over the North Atlantic (from 0 to

148   70°N), which is detrended to remove the effect of global warming. This index is correlated to air

149   temperature and rainfall over the Northern hemisphere, and positive phases are associated with

150   warm, dry conditions, while negative phases are associated with cool, wet conditions (Enfield et

151   al. 2001). AMO values were also derived from NOAA, US

152   (https://www.esrl.noaa.gov/psd/data/timeseries/AMO/).

153   Local environmental parameters included SST, salinity, chlorophyll-*a*, and dissolved

154   oxygen. Mean annual SST data were derived from the Hadley Centre for Climate Prediction and

155   Research's freely available HadISST1 database (Rayner et al. 2003). Mean annual chlorophyll-*a*

156   data came from the Sir Alister Hardy Foundation for Ocean Science's Continuous Phytoplankton

157   Recorder database (SAHFOS). Surface salinity and dissolved oxygen were extracted from

158   outputs of the NORWegian ECOlogical Model (http://www.ii.uib.no/~morten/norwecom.html,

159   Skogen et al. 1995). NORWECOM is a coupled 3D physical, bio-chemical model for the North

160   Sea and the English Channel that provides monthly averages of environmental parameters at a

161   geographical resolution of 0.1 degree. For salinity and dissolved oxygen, data were averaged

162   across months and spatial locations to obtain mean annual values for the entire EEC. Non-algal

163   suspended matter was obtained from satellite data (Gohin 2011) for each survey, which were then

164   averaged across years to obtain mean annual values.

165

166   **Fishing pressure**

167   Fishing pressure was assessed using three different fishing mortality indices: $F_{pelagic}$, $F_{demersal}$, and

168    $F_{benthic}$, for pelagic, demersal and benthic species, respectively. These were estimated annually as

169   the 1-year-lagged landing-weighted average fishing mortality rates for stocks assessed by ICES

170   working groups, namely mackerel and herring for pelagic, cod and whiting for demersal, and

171   plaice and sole for benthic. The fishing mortality rates of these 6 stocks (the only stocks

172   analytically assessed in the EEC) were considered representative of the global fishing pressure on

173   the EEC fish community, as these species account for more than 60% of total landings in the

174   EEC (Auber et al. 2015). The 1-year lagging accounted for the fact that annual instantaneous

175   fishing mortality rates of a given year are expected to affect the abundance of fish stocks the year

176   after (Auber et al. 2015). Each fishing mortality index was calculated as the average fishing

177   mortality of the two corresponding stocks weighted by their landings. We considered pelagic,

178   demersal and benthic fishing mortality to account for mixed types of fishing gear, and to

179   encompass the totality of fishing pressure throughout all habitat zones in the EEC. The EEC is a

180   mixed-gear fishery where pelagic stocks are generally targeted by midwater trawls and demersal

181   and benthic stocks are targeted by a mix of otter trawls, beam trawls, nets, pots, and dredges

182   (Pascoe & Coglan 2002, Ulrich et al. 2002). Thus by computing three different fishing mortality

183   indices, we account for fishing pressure across several stocks and gear types, within the

184   limitations of ICES-assessed stocks. Fishing mortality rates of the different stocks, as well as

185   landing statistics, were extracted from the ICES Stock Assessment Summary database and Catch

186   Statistics   database   (http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-

187   stock-assessment.aspx).

188

189   **Data Analysis**

190   **Principal Response Curves**

191   Temporal and spatial changes in fish functional structure were assessed using Principal Response

192   Curves (PRC). PRC is a special case of partial redundancy analysis (pRDA) with a single tested

193   factor as the explanatory variable and a single dimension of repeated observations as the co-

194   variable (Van den Brink & Ter Braak 1999). Auber et al. (2017) recently adapted the PRC

195   analysis to examine spatiotemporal changes in community structure, specifically between two

196   time periods (i.e., a 'baseline period' and a 'tested period'), by using spatial sites as repeated

197   observations and time as a tested factor. The PRC analysis generates canonical regression

198   coefficients (c_{dt}) for each sampling site, as well as contribution weights (b_k) for each species (or

199   functional group in this study). The absolute values of canonical coefficients c_{dt} quantify, at each

200   sampling site, the magnitude of change between the two tested time periods, and the absolute

201   values of functional group weights b_k quantify the contribution of each functional group to the

202   overall change of community structure; groups with weights near zero have little or no response,

203   while groups with high weights have strong responses. For a given functional group; the sign (+/-

204   ) of the canonical coefficients c_{dt} indicates the type of community response and is interpreted by

205   comparing with the sign (+/-) of weights b_k. When the signs of b_k and c_{dt} coefficients are

206   identical, the abundance of the corresponding functional group is higher in the tested period than

207   the baseline period, and when the signs of b_k and c_{dt} are opposite the abundance is higher in the

208   baseline period than the tested period. For a complete description of the original PRC method and

209   the new application of the PRC, see Van den Brink & Ter Braak (1999) and Auber et al. (2017).

210   In correspondence with the taxonomic community shift in the EEC (Auber et al. 2015),

211   we considered the years 1988 to 1997 as the pre-shift period (baseline period), and 1998 to 2011

212   as the post-shift period (tested period). We then applied the PRC analysis to examine changes in

213   functional community structure at each site between the two time periods, and to identify the

214   functional groups with the highest contributions to overall change. The PRC analysis was

215   performed using the function *prc* in the R package *vegan*. Significant changes in functional

216   structure between the two periods were then tested at each sampling site using Monte-Carlo

217   permutation tests designed to correct for the increase in the family-wise type 1 error rate due to

218   multiple comparisons across sampling sites (see Auber et al. [2017] for full details and R code).

219

220   **Influence of environmental factors and fishing mortality**

221   We identified the influences of environmental factors on temporal changes in fish functional

222   structure using RLQ and fourth corner analyses, where we considered environmental factors

223   across years rather than across sites. RLQ is a method that integrates environmental data (R),

224   species abundance data (L), and species' ecological traits (Q) to examine how environmental

225   factors influence trait variation (Dray et al. 2014). RLQ examines the co-inertia between three

226   separate ordination analyses (i.e., R, L, and Q), while fourth-corner analysis assess statistical

227   associations between each environmental factor and each functional group individually (Dray &

228   Legendre 2008, Dray et al. 2014). Thus RLQ analysis was first used to reveal major

229   environmental drivers of temporal variation in fish functional structure, while fourth corner

230   analysis then identified significant correlations between individual functional groups and

231   environmental factors. For both the RLQ and fourth corner analyses, species abundance data

232   were the mean time series of species composition averaged over the entire EEC, thus the species

233   abundance table (L) consisted of species mean abundances in columns and years in rows. While

234   RLQ is generally applied to spatial data, as the analysis functions through co-inertia of three

235 individual ordinations, alternative species abundance structures, including temporal, are

236 permissible (see Dolédec et al. 1996, Dray & Legendre 2008). Temporal environmental drivers

237 included in RLQ analysis were mean annual AMO, NAO, SST, salinity, chlorophyll-*a*, oxygen,

238 and fishing mortality (pelagic, demersal, and benthic). Thus the environmental table consisted of

239 mean environmental factors in columns and years in rows. A potential concern with RLQ and

240 fourth corner analysis was the influence of temporal autocorrelation among variables.

241 Autocorrelation can bias statistical tests by inflating type-1 error, leading to spurious correlations.

242 However, RLQ analysis is purely descriptive and does not test for significant relationships (see

243 Thuiller et al. 2006). To account for potential autocorrelation in fourth corner analysis, which

244 does test for significant relationships, we used both the standard fourth corner analysis and an

245 extended version of fourth corner that integrates Moran spectral randomization to account for

246 autocorrelation (Wagner & Dray 2015). MSR is a constrained randomization procedure that

247 compares observed values against a null model that preserves the autocorrelation of the data

248 (Wagner & Dray 2015). Due to missing environmental data in 2009, 2010, and 2011, RLQ and

249 fourth corner analysis were calculated for the time series 1988 – 2008.

250

Results

252 The PRC analysis revealed that sampling sites explained 34% of spatio-temporal variance in fish

253 functional structure (horizontal axis Fig. 1a), while time explained 13.4%, 71% of which is

254 represented by the first canonical axis of the PRC analysis (vertical axis Fig. 1a). All sites in the

255 EEC were characterized by positive c_{dt} values, indicating that the type of community change was

256 the same at every site (Fig. 1a). However, c_{dt} values were highly variable across sites, indicating

that while all sites experienced the same type of change, the magnitude of change was spatially

heterogeneous (Fig. 1a,b). Monte-Carlo permutation tests further revealed that 36 out of 79 sites

had a significant change in fish functional structure between the two time periods (Fig. 1b).
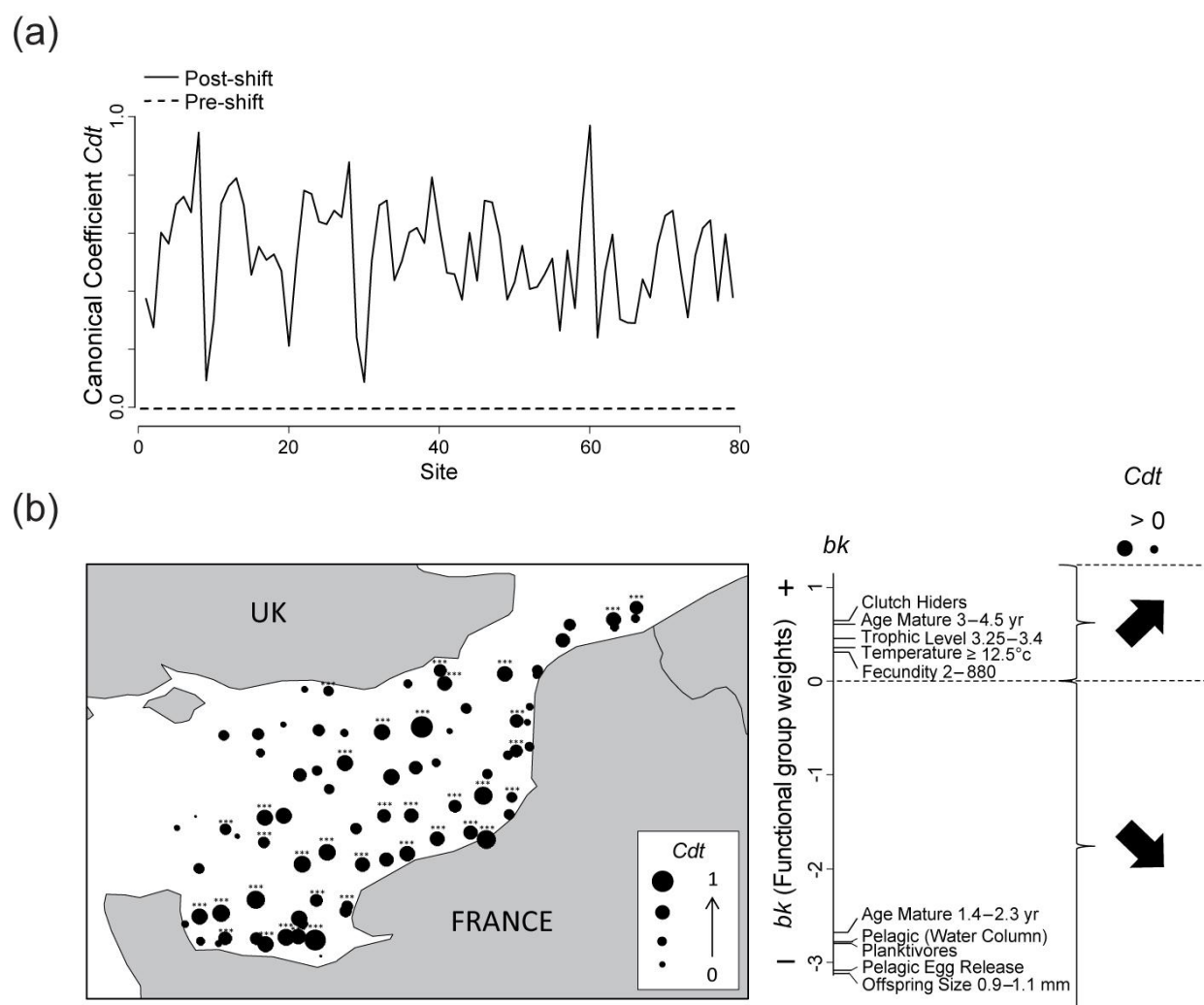
Figure 1. **a**) Principal Response Curve (PRC) showing changes in fish community structure across sampling sites between the baseline period [1988-1997] (pre-shift) and tested period [1998-2011] (post-shift), with the most contributive functional groups ranked by their b_k coefficients. For clarity, only traits with b_k coefficients in the first or last decile are shown. **b**) Map showing the amplitude of temporal changes in fish functional structure (i.e., c_{dt} values) at each sampling site and the trend (increase or decrease) of abundance for each functional group. Sampling sites with significant change are shown by asterisks (***: $p < 0.001$; **: $0.001 < p < 0.01$; *: $0.01 < p < 0.05$).

271   Functional group weights b_k revealed that changes in fish functional structure were

272   primarily driven by decreases in species with small offspring size (0.9 – 1.1 mm), pelagic egg

273   release (broadcast spawning), planktivory, pelagic water column position, and low age at

274   maturity (1.4 – 2.3 years), as the absolute values of b_k were much higher for functional groups

275   with negative values (decreasing) (Fig. 1). Concurrently, there was an increase in clutch hiders

276   (i.e., high parental care) and species with high age at maturity (3 – 4.5 years), moderate trophic

277   level (3.25 – 3.4), high temperature preference ($\geq$12.5°C), and low fecundity (2 – 880) (Fig. 1).

278   Thus, the taxonomic shift in the EEC fish community in the late 1990's was generally

279   characterized by a strong decrease in pelagic and planktivorous species with opportunistic, 'r-

280   selected' life history traits, and a moderate increase in species with equilibrium, 'K-selected' life

281   history traits.

282

Influence of environmental factors

284   RLQ analysis identified AMO, demersal and pelagic fishing mortality, SST, and NAO as the

285   primary drivers of temporal variability in fish functional structure, as AMO and fishing mortality

286   had the highest correlations with the first RLQ axis, and SST and NAO were both highly

287   correlated with the first RLQ axis and had the highest correlations with the second RLQ axis

288   (Figure 2, Figure 3).

289

290
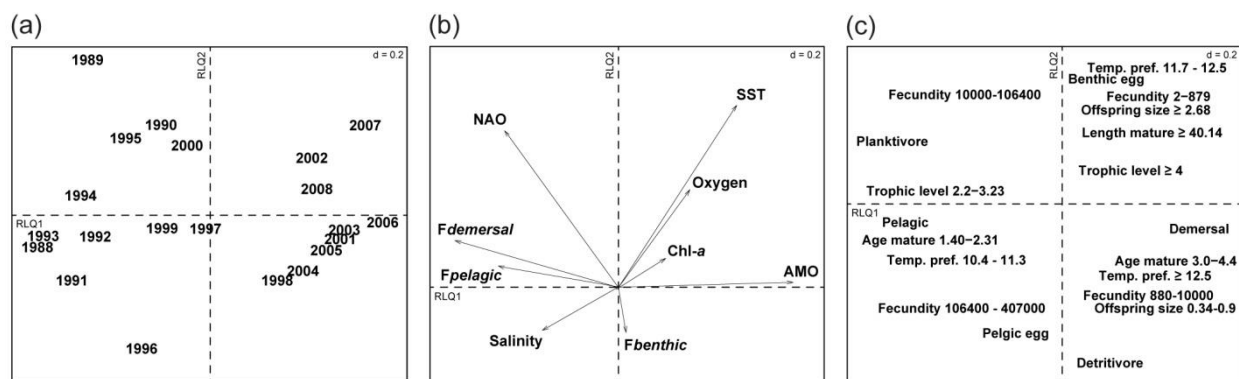
Figure 2. RLQ biplots showing temporal (**a**) associations between environmental factors (**b**) and functional groups (**c**). For clarity, only functional groups with the greatest correlations (first or last decile) to the first and second RLQ axes are plotted (**b**). Environmental factor acronyms: Atlantic Multidecadal Oscillation (AMO), sea surface temperature (SST), chlorophyll-*a* (Chl-*a*), pelagic fishing mortality (F*pelagic*), demersal fishing mortality (F*demersal*), benthic fishing mortality (F*benthic*). Temp. pref. = temperature preference. The first two RLQ axes preserved 87% of environmental variation and 71% of trait variation.

298

299
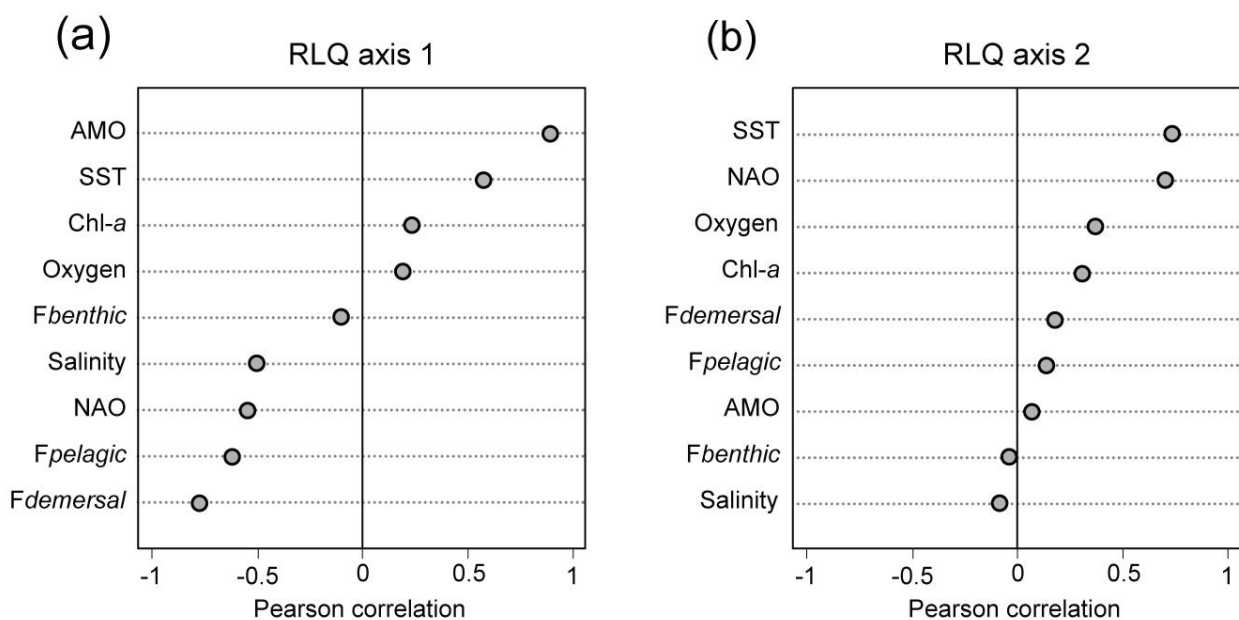
Figure 3. Contribution of environmental factors to temporal variation in fish functional structure according to Pearson correlations between environmental factors and the first (**a**) and second (**b**) axes of the RLQ analysis. Environmental factor acronyms: Atlantic Multidecadal Oscillation (AMO), North Atlantic Oscillation (NAO), sea surface temperature (SST), chlorophyll-*a* (Chl-*a*),
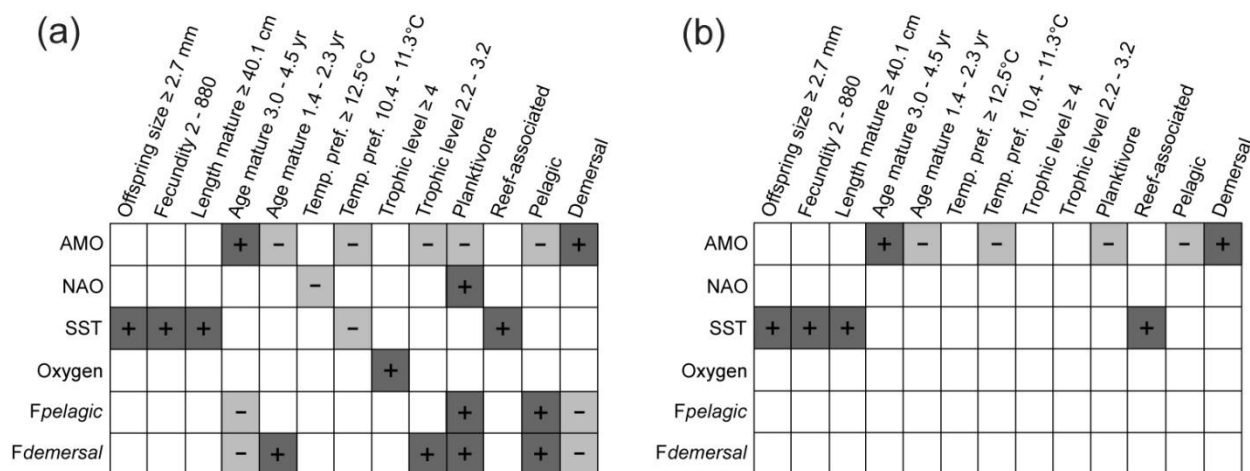
304 pelagic fishing mortality ($F_{pelagic}$), demersal fishing mortality ($F_{demersal}$), benthic fishing mortality
305 ($F_{benthic}$).

306

307   Initial fourth corner analysis, without MSR, indicated that AMO had positive

308 relationships with demersal species and species with high age at maturity (3 − 4.5 years), and

309 negative relationships with pelagic and planktivorous species and species with low trophic level

310 (2.2 − 3.25), low age at maturity (1.4 − 2.3 years), and low temperature preference (10.4 −

311 11.3°C) ($p < 0.05$, Fig. 4). In contrast, NAO was positively correlated with planktivores and

312 negatively correlated with species with high temperature preferences (≥12.5°C). SST was

313 positively correlated with species with the largest length at maturity (≥40.1 cm), lowest fecundity

314 (2 − 880), largest offspring size (≥2.7 cm), and reef-associated species, and negatively correlated

315 with species with low temperature preference (10.4 − 11.3°C) ($p < 0.05$, Fig 4). Dissolved oxygen

316 had a single, positive association with high trophic level species (≥4) ($p < 0.05$, Fig 4). Pelagic

317 and demersal fishing mortality had nearly identical relationships with functional groups; however

318 pelagic mortality had fewer significant associations. Both pelagic and demersal mortality were

319 positively associated with pelagic and planktivorous species, and negatively associated with

320 demersal species and species with high age at maturity (3 − 4.5 years) ($p < 0.05$, Fig 4). Demersal

321 fishing mortality was also positively related to species with the lowest trophic level (2.2 − 3.25)

322 and lowest age at maturity (1.4 − 2.3 years) ($p < 0.05$, Fig 4). However, re-running the fourth

323 corner analysis with MSR to account for temporal autocorrelation revealed that only AMO and

324 SST had significant associations with any of the functional groups, indicating potential spurious

325 correlations for fishing mortality, oxygen, and NAO due to high autocorrelation (Fig 4). The

326 relationships between AMO, SST, and functional group dynamics remained nearly identical, with

327 only the associations between AMO and low trophic level, and between SST and low temperature

328 preference no longer significant.

329

(a)

	Offspring size ≥ 2.7 mm	Fecundity 2 - 880	Length mature ≥ 40.1 cm	Age mature 3.0 - 4.5 yr	Age mature 1.4 - 2.3 yr	Temp. pref. ≥ 12.5°C	Temp. pref. 10.4 - 11.3°C	Trophic level ≥ 4	Trophic level 2.2 - 3.2	Planktivore	Reef-associated	Pelagic	Demersal
AMO				+	−		−	−	−			−	+
NAO					−				+				
SST	+	+	+				−				+		
Oxygen								+					
Fpelagic				−					+			+	−
Fdemersal				−	+			+	+			+	−

(b)

	Offspring size ≥ 2.7 mm	Fecundity 2 - 880	Length mature ≥ 40.1 cm	Age mature 3.0 - 4.5 yr	Age mature 1.4 - 2.3 yr	Temp. pref. ≥ 12.5°C	Temp. pref. 10.4 - 11.3°C	Trophic level ≥ 4	Trophic level 2.2 - 3.2	Planktivore	Reef-associated	Pelagic	Demersal
AMO				+	−				−			−	+
NAO													
SST	+	+	+								+		
Oxygen													
Fpelagic													
Fdemersal													

330

331 **Figure 4**. Results of fourth corner analyses of trait-environment correlations without (**a**) and with
332 (**b**) Moran spectral randomization (white = no significant relationship, dark grey = positive
333 relationship, light grey = negative relationship. Environmental factor acronyms: Atlantic
334 Multidecadal Oscillation (AMO), North Atlantic Oscillation (NAO), sea surface temperature
335 (SST), pelagic fishing mortality ($F_{pelagic}$), demersal fishing mortality ($F_{demersal}$). Temp. pref. =
336 temperature preference.

337

Discussion

339 Here, we found that a previously documented taxonomic shift in a temperate marine fish

340 community also corresponded to a considerable shift in fish functional structure. This is a major

341 finding as community functional structure can be relatively unaffected by temporal species

342 replacement or turnover (Villéger et al. 2010, Clare et al. 2015). Examining the taxonomic shift

343 through the lens of ecological traits provided more pronounced results and greater insight into the

344 biological mechanisms behind the shift. We found that the shift was characterized by a large

345　decrease in the abundance of pelagic, planktivorous species with low temperature preferences and

346　opportunistic, 'r-selected' life histories such as low age and size at maturity and low trophic level,

347　and a concurrent increase in species with moderate to high temperature preferences and

348　equilibrium, 'K-selected' life histories such as high size and age at maturity, few large offspring,

349　and high parental care. Interestingly, we found significant temporal change in functional

350　community structure at roughly half of all sites (36 of 79), whereas Auber et al. (2017) found

351　significant temporal change for only 13 sites when using PRC with taxonomic data, highlighting

352　that changes in community structure are better identified using ecological traits regardless of

353　species identity.

354　　　The finding that the type of community change was similar across all sites indicates a

355　regionally-consistent response across the entire EEC. Indeed, we found that changes in fish

356　functional structure are strongly correlated with the Atlantic Multidecadal Oscillation and

357　associated increases in sea surface temperature. While sea surface temperature has been

358　progressively rising in the North Atlantic during the past few decades, the switch from a cool to a

359　warm phase of the AMO lead to unusually-rapid warming (Ting et al. 2009, Moore et al. 2017).

360　This rapid warming likely amplified ongoing 'tropicalisation' throughout the Channel, causing an

361　abrupt decrease of species sensitive to higher sea surface temperatures, and a concurrent increase

362　in tolerant species (Rijnsdorp et al. 2009, Cheung et al. 2013, Verges et al. 2014). Indeed, we

363　identified increases in species with high temperature preferences as contributive to the overall

364　change in fish functional structure, and also identified correlations between AMO, SST, and

365　temperature preference. While the North Atlantic Oscillation (NAO) was also correlated to

366　changes in fish functional structure, the NAO is a regional index of atmospheric pressure that was

367　associated with ocean warming in the late-1980s (Reid et al. 2001), but has progressively

368　declined in parallel to the AMO increase.

369   While AMO appeared the primary driver of changes in fish functional structure, RLQ

370   analysis also identified substantial correlation between fishing mortality and functional group

371   dynamics. However, both demersal and pelagic fishing pressure declined in parallel to decreasing

372   fish abundances, and both fishing indices had identical relationships with the abundance of small

373   pelagic fishes. Thus, fishing mortality was likely not a primary driver of changes in fish

374   functional structure, as pelagic fishing mortality declined in parallel to a pronounced decrease in

375   small pelagic fishes. The community shift being characterized by a rapid decrease in species with

376   fast life history cycles also indicates an environmental response rather than progressive fishing

377   impacts (Perry et al. 2005, Rijnsdorp et al. 2009). However, given that demersal fishing pressure

378   was positively correlated with pelagic and planktivorous fishes and negatively correlated with

379   demersal fishes, it is likely that historically high demersal fishing increased the relative

380   abundance of pelagic fishes with rapid growth and generation times, rendering the community

381   more susceptible to climate stress (Thurstan et al. 2010, Molfese et al. 2014, Auber et al. 2015,

382   McLean et al. In press). Indeed the English Channel has been heavily exploited for decades,

383   particularly following intense industrialization of commercial fisheries in the early to mid-1900s

384   (Pauly et al. 2002). Long-term overfishing and fishing down the food web in the English Channel

385   have progressively shifted the ecosystem from historical dominance by large demersal species

386   such as cod and ling toward increased dominance by small pelagic and demersal species with

387   higher fishing tolerances, and commercially-untargeted species like catsharks (McHugh et al.

388   2011, Molfese et al. 2014). Thus, while the rapid shift in fish functional structure appeared most

389   strongly associated with climate-driven ocean warming, the long history of exploitation in the

390   EEC clearly reinforced this shift by rendering the ecosystem susceptible to a climatic disturbance.

391   Furthermore, the observed functional shift also reflects reduced contemporary fishing effort, as

392   we observed an increase in larger and higher trophic level species through time (Pauly et al.

393   2002). Altogether it appears that historical overfishing in combination with rapid environmental

394   change induced a major shift in fish functional structure, as the EEC was dominated by species

395   with environmentally-sensitive life history traits in the early 1990s, which were highly responsive

396   to the shift in AMO.

397   While high temperature preference was identified as an influential trait, temperature

398   preference is a 'soft' (i.e., easily measured but less informative) trait that serves as a proxy for

399   'hard' (i.e., informative but difficult to measure) physiological traits influencing species'

400   distributions and habitat preferences (Leps et al. 2006, Violle et al. 2007, Pakeman 2011). More

401   interesting was the finding that increasing and decreasing species contrast strongly in life history

402   traits related to offspring survival, population growth, and generation time. Species with r-

403   selected life histories follow type III survivorship curves, where many small offspring are

404   produced and given little to no parental investment (Pianka 1970, Gadgil & Solbrig 1972,

405   Southwood et al. 1974). This strategy employs the trade-off that while survivorship is extremely

406   low among progeny, larval dispersal and population turnover are high, allowing populations to

407   quickly respond to unfavorable environmental conditions (Pianka 1970, Gadgil & Solbrig 1972,

408   Southwood et al. 1974). Alternatively, K-selected strategists make large energetic investments in

409   few, well-developed offspring. While such a strategy limits dispersal and colonization abilities,

410   progeny are strong competitors and have high individual fitness (Pianka 1970, Gadgil & Solbrig

411   1972, Southwood et al. 1974). Beyond the classical distinction of r and K-selected strategies,

412   recent work using ecological traits suggests a continuum of three life history strategies where r-

413   selected species are considered 'opportunistic' and K-selected species can be split into 'periodic'

414   and 'equilibrium' based on tradeoffs in fecundity, parental care, and offspring size (Winemiller &

415   Rose 1992, King & McFarlane 2003, Pecuchet et al. 2017). Opportunistic species are

416   characterized by low size and trophic level and short lifespans, but with high fecundity

417 (Winemiller & Rose 1992, King & McFarlane 2003, Pecuchet et al. 2017). Both periodic and

418 equilibrium species have larger size, higher trophic level, and longer lifespans, but periodic

419 species have high fecundity and low parental care, whereas equilibrium species have low

420 fecundity and high parental care (Winemiller & Rose 1992, King & McFarlane 2003, Pecuchet et

421 al. 2017). In the context of the three-strategy life history continuum, our results suggest that

422 opportunistic species are the most susceptible to rapid environmental change, notably warming,

423 due to their shorter life cycles, while equilibrium species with few, well-developed offspring and

424 longer life cycles, appear less responsive. Prior studies examining the relationship between life

425 history strategies and climate change have shown that opportunistic species can be highly

426 impacted by climate warming because short generation times enable rapid population responses

427 (Jiguet et al. 2007, Hoffmann & Sgro 2011, Pearson et al. 2014). For example, Perry et al. (2005)

428 and DeVictor et al. (2012) documented faster and more pronounced distribution shifts among

429 species with faster life cycles and smaller size in fishes, birds and butterflies, while Simpson et al.

430 (2011) showed that smaller fish species responded faster to warming across European shelf seas.

431   While prior studies have documented rapid responses in opportunistic species, few

432 examples have shown that such responses can drive major community shifts in entire species

433 assemblages over large temporal and spatial scales (Perry et al. 2005, Devictor et al. 2012). Here,

434 our results suggest that temperature warming, amplified during the late 1990s by the combination

435 of man-made climate change and the AMO (Ting et al. 2009), led to an abrupt decrease in

436 opportunistic species with fast life histories throughout the EEC, likely as an evolutionary

437 response to a rapidly changing environment (Pianka 1970, Stearns 1989, Bradshaw & Holzapfel

438 2006). It further appears that this decrease allowed equilibrium species to expand their

439 populations under new environmental conditions. However, although opportunistic species are

440   highly responsive to environmental change and can thus be heavily impacted over short time-

441   scales, over evolutionary time opportunistic species should have higher capacity to adapt given

442   their rapid evolutionary responses (Rijnsdorp et al. 2009).

443   Among potential explanations for the shift in functional structure, temperature rise likely

444   affected larval and juvenile mortality rates through changes in dispersion and recruitment

445   (Blaxter 1991, Drinkwater et al. 2014, Young et al. 2018) or through match-mismatches with

446   food sources (Kristiansen et al. 2011, McQueen & Marshall 2017). Additionally, as proposed by

447   Auber et al. (2015), this community shift may have been influenced by density-dependent

448   interactions such as predation and competition. Temperature rise is also known to drive species

449   emigrations, and the community shift could have resulted from the rapid displacement of existing

450   individuals (Day et al. 2018, Pinsky et al. 2013, McLean et al. In press). Finally, while

451   opportunistic species can rapidly track environmental changes, allowing quick recovery when

452   conditions return to normal, the community has not returned to the initial pre-shift state,

453   suggesting environmental conditions are no longer favorable for the impacted species, inhibiting

454   their recovery.

455   While we found interesting patterns linking ecological and life history traits to rapid

456   environmental change, our study has several important limitations. As we examined changes in

457   the abundance of functional groups, our results are influenced by both trait choice and

458   categorization (Leps et al. 2006, Mcgill et al. 2006, Violle et al. 2007). Such methods remain

459   subjective, and there is no universal approach for choosing traits or defining groups. Binning

460   species also leads to a necessary loss of trait information and can potentially combine species

461   with different environmental responses. Our approach further cannot account for intra-specific

462   trait variability, and thus cannot examine how changes in ontogeny or population demographics

463   influence functional structure (Petchey & Gaston 2006, Violle et al. 2007). We also used RLQ

464   analysis to examine the potential drivers of temporal changes in fish functional structure;

465   however RLQ is unable to identify statistical significance due to potential autocorrelation, and

466   can only reveal associations among variables.

467   By using a trait-based approach, we were able to uncover the ecological characteristics

468   linking species that drove a rapid shift in the EEC fish community. These findings increase our

469   understanding of how organisms respond to environmental change and help anticipate how

470   ecosystems might change in the future. Growing evidence shows it is essential to adopt a trait-

471   based approach as it provides better understanding of biological mechanisms and because global

472   change will have drastic impacts on biodiversity, which will be mediated through species'

473   functional characteristics.

474

Author contributions

476   AA and MM conceived the ideas and designed the methodology. MM analyzed the data and led

477   the writing of the manuscript. DM played an advisory role, reviewed the methods and results, and

478   revised the manuscript. All authors contributed critically to the drafts and gave final approval for

479   publication.

480

Acknowledgements

487

References

489   Auber A, Travers-Trolet M, Villanueva MC, Ernande B (2015) Regime Shift in an Exploited Fish
490   Community Related to Natural Climate Oscillations. PLoS One 10

491   Auber A, Travers-Trolet M, Villanueva MC, Ernande B (2017) A new application of principal
492   response curves for summarizing abrupt and cyclic shifts of communities over space.
493   Ecosphere 8:e02023

494   Beaugrand G (2004) The North Sea regime shift: evidence, causes, mechanisms and
495   consequences. Prog Oceanogr 60:245–262

496   Blaxter J (1991) The effect of temperature on larval fishes. Neth J Zool 42:336–357

497   Bradshaw WE, Holzapfel CM (2006) Evolutionary response to rapid climate change. Science
498   312:1477–1478

499   Carpenter SR, Mooney HA, Agard J, Capistrano D, DeFries RS, Díaz S, Dietz T, Duraiappah
500   AK, Oteng-Yeboah A, Pereira HM (2009) Science for managing ecosystem services:
501   Beyond the Millennium Ecosystem Assessment. Proc Natl Acad Sci 106:1305–1312

502   Chavez FP, Ryan J, Lluch-Cota SE, Ñiquen M (2003) From anchovies to sardines and back:
503   multidecadal change in the Pacific Ocean. Science 299:217–221

504   Cheung WW, Reygondeau G, Frölicher TL (2016) Large benefits to marine fisheries of meeting
505   the 1.5 C global warming target. Science 354:1591–1594

506   Cheung WW, Watson R, Pauly D (2013) Signature of ocean warming in global fisheries catch.
507   Nature 497:365–368

508   Clare DS, Robinson LA, Frid CLJ (2015) Community variability and ecological functioning: 40
509   years of change in the North Sea benthos. Mar Environ Res 107:24–34

510   Day PB, Stuart-Smith RD, Edgar GJ, Bates AE (2018) Species' thermal ranges predict changes in
511   reef fish community structure during 8 years of extreme temperature variation. Divers
512   Distrib 24:1036–1046

513   Devictor V, Van Swaay C, Brereton T, Chamberlain D, Heliölä J, Herrando S, Julliard R,
514   Kuussaari M, Lindström Å, Roy DB (2012) Differences in the climatic debts of birds and
515   butterflies at a continental scale. Nat Clim Change 2:121

516   Dickson R (2000) The NAO: the dominant atmospheric process affecting oceanic variability in
517   home, middle and distant waters of European Salmon. In book: The Ocean Life of
518   Atlantic Salmon. Fishing News Books, Blackwell Science

519   Díaz S, Cabido M (2001) Vive la difference: plant functional diversity matters to ecosystem
520   processes. Trends Ecol Evol 16:646–655

521   Dolédec S, Chessel D, Braak CJF ter, Champely S (1996) Matching species traits to
522   environmental variables: a new three-table ordination method. Environ Ecol Stat 3:143–
523   166

524   Dray S, Choler P, Dolédec S, Peres-Neto PR, Thuiller W, Pavoine S, ter Braak CJF (2014)
525   Combining the fourth-corner and the RLQ methods for assessing trait responses to
526   environmental variation. Ecology 95:14–21

527   Dray S, Legendre P (2008) Testing the species traits-environment relationships: the fourth-corner
528   problem revisited. Ecology 89:3400

529   Drinkwater KF, Miles M, Medhaug I, Otterå OH, Kristiansen T, Sundby S, Gao Y (2014) The
530   Atlantic Multidecadal Oscillation: Its manifestations and impacts with special emphasis
531   on the Atlantic region north of 60 N. J Mar Syst 133:117–130

532   Edwards M, Beaugrand G, Helaouët P, Alheit J, Coombs S (2013) Marine ecosystem response to
533   the Atlantic Multidecadal Oscillation. PLoS One 8:e57212

534   Enfield DB, Mestas-Nuñez AM, Trimble PJ (2001) The Atlantic multidecadal oscillation and its
535   relation to rainfall and river flows in the continental US. Geophys Res Lett 28:2077–2080

536   Engelhard GH, Ellis JR, Payne MR, Hofstede R ter, Pinnegar JK (2011) Ecotypes as a concept
537   for exploring responses to climate change in fish assemblages. ICES J Mar Sci 68:580–
538   591

539   Froese F, Pauly D (2012) FishBase. www.fishbase.org (accessed Mar 2017)

540   Gadgil M, Solbrig OT (1972) The concept of r-and K-selection: evidence from wild flowers and
541   some theoretical considerations. Am Nat 106:14–31

542   Gohin F (2011) Annual cycles of chlorophyll-a, non-algal suspended particulate matter, and
543   turbidity observed from space and in-situ in coastal waters. Ocean Sci 7:705

544   Gross N, Le Bagousse-Pinguet Y, Liancourt P, Berdugo M, Gotelli NJ, Maestre FT (2017)
545   Functional trait diversity maximizes ecosystem multifunctionality. Nat Ecol Evol 1:0132

546 Hoffmann AA, Sgro CM (2011) Climate change and evolutionary adaptation. Nature 470:479–
547   485

548 Hooper DU, Chapin III FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM,
549   Loreau M, Naeem S, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of
550   biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr
551   75:3–35

552 Jiguet F, GADOT A, Julliard R, Newson SE, Couvet D (2007) Climate envelope, life history
553   traits and the resilience of birds facing global change. Glob Change Biol 13:1672–1684

554 Kremen C (2005) Managing ecosystem services: what do we need to know about their ecology?
555   Ecol Lett 8:468–479

556 Kristiansen T, Drinkwater KF, Lough RG, Sundby S (2011) Recruitment variability in North
557   Atlantic cod and match-mismatch dynamics. PLoS One 6:e17456

558 Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem
559   functioning from plant traits: revisiting the Holy Grail. Funct Ecol 16:545–556

560 Lindegren M, Checkley DM, Rouyer T, MacCall AD, Stenseth NC (2013) Climate, fishing, and
561   fluctuations of sardine and anchovy in the California Current. Proc Natl Acad Sci
562   110:13672

563 Leps J, De Bello F, Lavorel S, Berman S (2006) Quantifying and interpreting functional diversity
564   of natural communities: practical considerations matter. Preslia 78:481–501

565 Mcgill B, Enquist B, Weiher E, Westoby M (2006) Rebuilding community ecology from
566   functional traits. Trends Ecol Evol 21:178–185

567 McLean M, Mouillot D, Lindegren M, Engelhard G, Villéger S, Marchal P, Brind'Amour A,
568   Auber A (In press) A climate-driven functional inversion of connected marine
569   ecosystems. Curr Biol

570 McQueen K, Marshall CT (2017) Shifts in spawning phenology of cod linked to rising sea
571   temperatures. ICES J Mar Sci 74:1561–1573

572 Molfese C, Beare D, Hall-Spencer JM (2014) Overfishing and the Replacement of Demersal
573   Finfish by Shellfish: An Example from the English Channel. PLoS One 9:e101506

574 Moore GWK, Halfar J, Majeed H, Adey W, Kronz A (2017) Amplification of the Atlantic
575   Multidecadal Oscillation associated with the onset of the industrial-era warming. Sci Rep
576   7:40861

577 Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach
578   reveals community responses to disturbances. Trends Ecol Evol 28:167–177

579   Pakeman RJ (2011) Multivariate identification of plant functional response and effect traits in an
580   agricultural landscape. Ecology 92:1353–1365

581   Pauly D, Christensen V, Guénette S, Pitcher TJ, Sumaila UR, Walters CJ, Watson R, Zeller D
582   (2002) Towards sustainability in world fisheries. Nature 418:689–695

583   Pearson RG, Stanton JC, Shoemaker KT, Aiello-Lammens ME, Ersts PJ, Horning N, Fordham
584   DA, Raxworthy CJ, Ryu HY, McNees J (2014) Life history and spatial traits predict
585   extinction risk due to climate change. Nat Clim Change 4:217–221

586   Pecuchet L, Lindegren M, Hidalgo M, Delgado M, Esteban A, Fock HO, Gil de Sola L, Punzón
587   A, Sólmundsson J, Payne MR (2017) From traits to life-history strategies: Deconstructing
588   fish community composition across European seas. Glob Ecol Biogeogr 26:812–822

589   Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine
590   fishes. Science 308:1912–1915

591   Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecol
592   Lett 9:741–758

593   Pianka ER (1970) On r- and K-Selection. Am Nat 104:592–597

594   Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA (2013) Marine taxa track local
595   climate velocities. Science 341:1239–1242

596   Rayner N, Parker DE, Horton E, Folland C, Alexander L, Rowell D, Kent E, Kaplan A (2003)
597   Global analyses of sea surface temperature, sea ice, and night marine air temperature
598   since the late nineteenth century. J Geophys Res Atmospheres 108

599   Reid PC, Fatima Borges M de, Svendsen E (2001) A regime shift in the North Sea circa 1988
600   linked to changes in the North Sea horse mackerel fishery. Fish Res 50:163–171

601   Rijnsdorp AD, Peck MA, Engelhard GH, Möllmann C, Pinnegar JK (2009) Resolving the effect
602   of climate change on fish populations. ICES J Mar Sci 66:1570–1583

603   Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to
604   observation. Trends Ecol Evol 18:648–656

605   Simpson SD, Jennings S, Johnson MP, Blanchard JL, Schön P-J, Sims DW, Genner MJ (2011)
606   Continental Shelf-Wide Response of a Fish Assemblage to Rapid Warming of the Sea.
607   Curr Biol 21:1565–1570

608   Sir Alister Hardy Foundation for Ocean Science (SAHFOS). Continuous Plankton Recorder
609   Dataset. www.cprsurvey.org (accessed Sep 2017).

610   Skogen MD, Svendsen E, Berntsen J, Aksnes D, Ulvestad KB (1995) Modelling the primary
611   production in the North Sea using a coupled three-dimensional physical-chemical-
612   biological ocean model. Estuar Coast Shelf Sci 41:545–565

613   Southwood TRE, May RM, Hassell MP, Conway GR (1974) Ecological Strategies and
614   Population Parameters. Am Nat 108:791–804

615   Stearns SC (1989) Trade-offs in life-history evolution. Funct Ecol 3:259–268

616   Thuiller W, Richardson DM, Rouget M, Procheş Ş, Wilson JRU (2006) Interactions between
617   environment, species traits, and human uses describe patterns of plant invasions. Ecology
618   87:1755–1769

619   Thurstan RH, Brockington S, Roberts CM (2010) The effects of 118 years of industrial fishing on
620   UK bottom trawl fisheries. Nat Commun 1:15

621   Ting M, Kushnir Y, Seager R, Li C (2009) Forced and internal twentieth-century SST trends in
622   the North Atlantic. J Clim 22:1469–1481

623   Van den Brink PJ, Ter Braak CJ (1999) Principal response curves: Analysis of time-dependent
624   multivariate responses of biological community to stress. Environ Toxicol Chem 18:138–
625   148

626   Verges A, Steinberg PD, Hay ME, Poore AGB, Campbell AH, Ballesteros E, Heck KL, Booth
627   DJ, Coleman MA, Feary DA, Figueira W, Langlois T, Marzinelli EM, Mizerek T,
628   Mumby PJ, Nakamura Y, Roughan M, Sebille E van, Gupta AS, Smale DA, Tomas F,
629   Wernberg T, Wilson SK (2014) The tropicalization of temperate marine ecosystems:
630   climate-mediated changes in herbivory and community phase shifts. Proc R Soc B Biol
631   Sci 281:20140846–20140846

632   Villéger S, Miranda JR, Hernández DF, Mouillot D (2010) Contrasting changes in taxonomic vs.
633   functional diversity of tropical fish communities after habitat degradation. Ecol Appl
634   20:1512–1522

635   Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the
636   concept of trait be functional! Oikos 116:882–892

637   Wagner HH, Dray S (2015) Generating spatially constrained null models for irregularly spaced
638   data using Moran spectral randomization methods. Methods Ecol Evol 6:1169–1178

639   Wernberg T, Bennett S, Babcock RC, Bettignies T de, Cure K, Depczynski M, Dufois F,
640   Fromont J, Fulton CJ, Hovey RK (2016) Climate-driven regime shift of a temperate
641   marine ecosystem. Science 353:169–172

642   Winemiller KO, Fitzgerald DB, Bower LM, Pianka ER (2015) Functional traits, convergent
643   evolution, and periodic tables of niches. Ecol Lett 18:737–751

644   Young EF., Tysklind Niklas, Meredith Michael P., Bruyn Mark, Belchier Mark, Murphy Eugene
645   J., Carvalho Gary R. (2018) Stepping stones to isolation: Impacts of a changing climate
646   on the connectivity of fragmented fish populations. Evol Appl 11:978–994
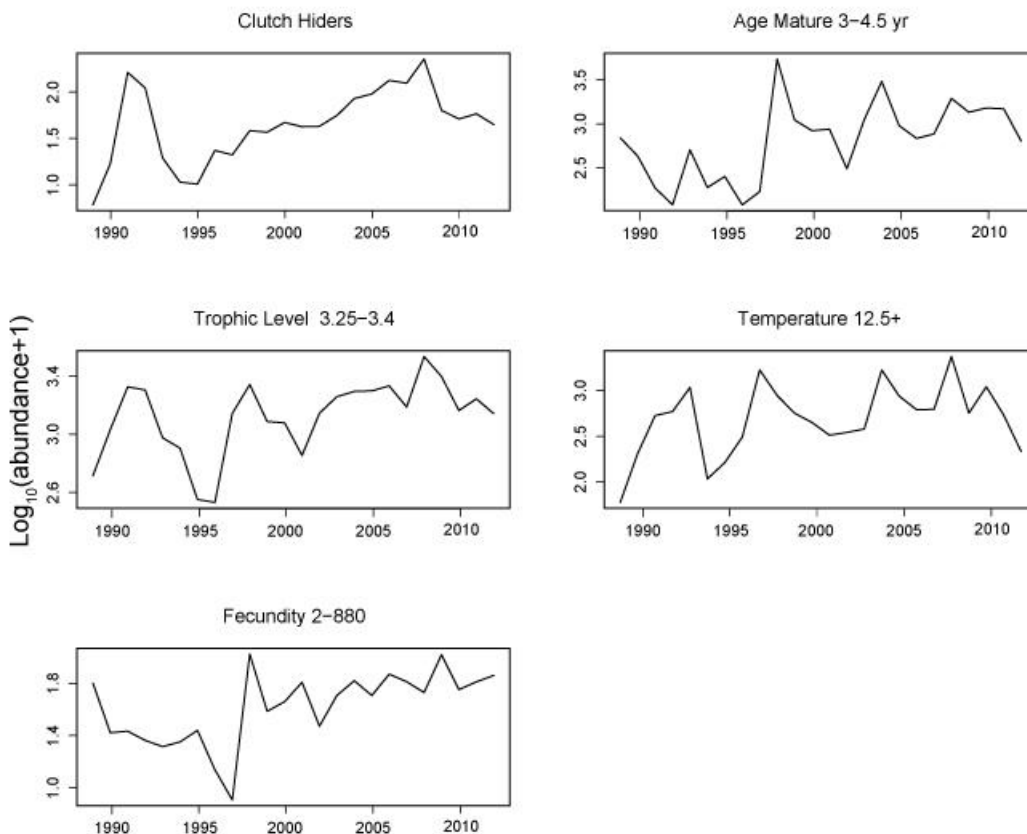
647

648 **Supplemental Material**

649
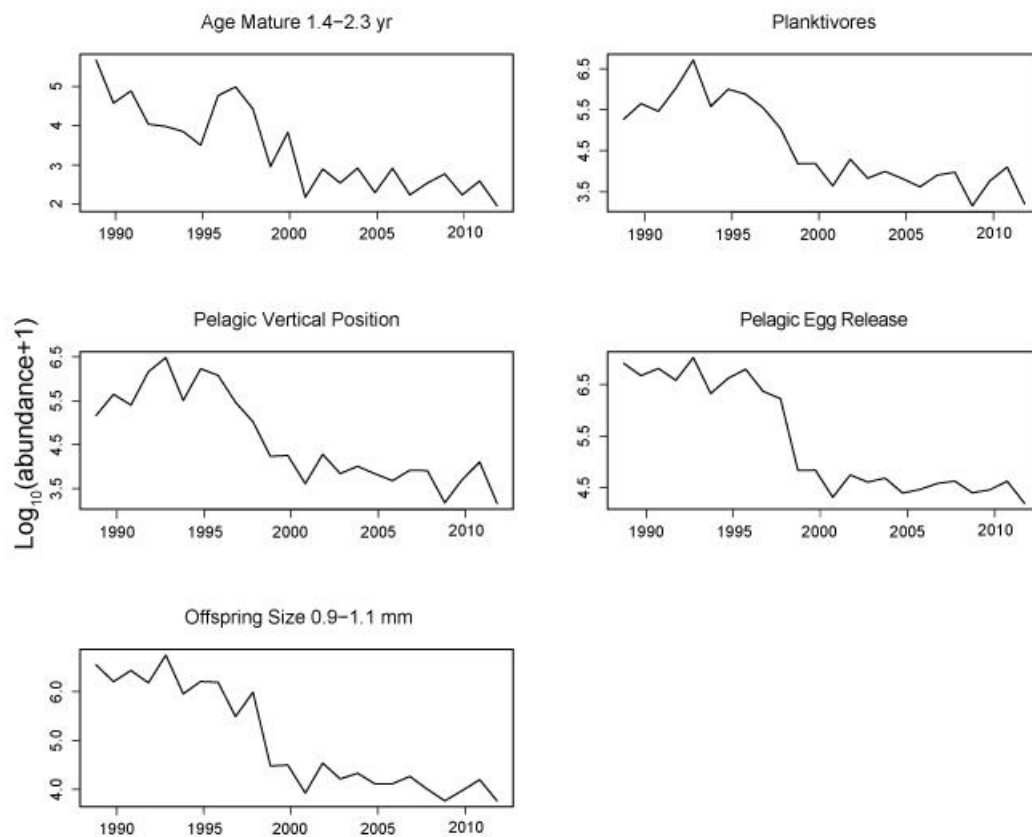
650

651 **Supplemental Figure 1**. Temporal dynamics of the most contributive functional groups that
652 decreased in abundance before and after the shift in functional structure

653

654

655 **Supplemental Figure 2**. Temporal dynamics of the most contributive functional groups that
656 increased in abundance before and after the shift in functional structure

657

658

659

660

661

662

663

664

665

666

667