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1 **Small pelagic fish dynamics:**
2 **a review of mechanisms in the Gulf of Lions**

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26

27 **Abstract**

28 Around 2008, an ecosystem shift occurred in the Gulf of Lions, highlighted by considerable changes in
29 biomass and fish mean weight of its two main small pelagic fish stocks (European anchovy, *Engraulis*
30 *encrasicolus*; European sardine, *Sardina pilchardus*). Surprisingly these changes did not appear to be
31 mediated by a decrease in fish recruitment rates (which remained high) or by a high fishing pressure
32 (exploitation rates being extremely low). Here, we review the current knowledge on the population's
33 dynamics and its potential causes. We used an integrative ecosystem approach exploring alternative
34 hypotheses, ranging from bottom-up to top-down control, not forgetting epizootic diseases. First, the
35 study of multiple population characteristics highlighted a decrease in body condition for both species
36 as well as an important decrease in size resulting both from a slower growth and a progressive
37 disappearance of older sardines. Interestingly, older sardines were more affected by the decrease in
38 condition than younger ones, another sign of an unbalanced population structure. While top-down

39 control by bluefin tuna or dolphins, emigration and disease were mostly discarded as important
40 drivers, bottom-up control mediated by potential changes in the plankton community appeared to
41 play an important role via a decrease in fish energy income and hence growth, condition and size.
42 Isotopic and stomach content analyses indicated a dietary shift pre- and post-2008 and modeled
43 mesozooplankton abundance was directly linked to fish condition. Despite low energy reserves from
44 2008 onwards, sardines and anchovies maintained if not increased their reproductive investment,
45 likely altering the life-history trade-off between reproduction and survival and resulting in higher
46 natural mortality. The current worrying situation might thus have resulted from changes in plankton
47 availability/diversity, which remains to be thoroughly investigated together with fish phenotypic
48 plasticity.

49 *Keywords:* population dynamics, top-down, disease, zooplankton, exploited species.

50

51

52 *Introduction*

53 Knowledge on population dynamics is key to understanding ecosystem functioning and managing
54 exploited populations. Small pelagic fish are widely known for their rapid and important population
55 fluctuations, rendering their management especially difficult (Bakun, 1997). Indeed, long time series
56 of abundance proxies (i.e., fish scale deposition rates, Baumgartner et al., 1992; McClatchie et al.,
57 2017) demonstrate that large fluctuations are an inherent characteristic of these populations and
58 occur very rapidly, i.e. within a few years. As a consequence, fish landings may drop from thousands
59 or millions of tons to almost nothing in a matter of years (e.g. Lluch-Belda et al., 1989). Such rapid
60 population changes are usually explained by the short lifespan of small pelagic fish and fluctuating,
61 environment-dependent recruitment success (Chambers and Trippel, 2012; Cushing, 1990). In
62 addition, over the last decades, (over-)exploitation has also played a role in those fluctuations as
63 fishing capacity and effort can hardly match such high level variations, generating collapses and
64 longer periods of low abundance in small pelagic fish stocks (Essington et al., 2015; Toresen and
65 Østved, 2000).

66 Sardine and anchovy have a worldwide distribution and are especially known for their prevalence in
67 the five boundary current systems (Benguela, Humboldt, California, Canary, Kuroshio), although their
68 populations are also important in other areas, such as the Northeast Atlantic, south-west Australia
69 and the Mediterranean and Black Seas (Checkley et al., 2009). While the main causes (including
70 environmental and climatic drivers) for population variations as well as the apparent synchrony of
71 the sardine/anchovy alternation have been largely studied in these five major ecosystems (see
72 references within Checkley et al., 2009; Schwartzlose et al., 1999), the question arises on whether
73 results might be transferable to smaller or non-upwelling systems (but see Katara et al., 2011). For
74 those ecosystems, understanding the mechanisms involved in population fluctuations remains a key
75 objective, especially with a view of improving management schemes, benefitting both ecosystem and
76 economy. With a better insight in past and hence future fluctuations, management procedures can
77 be better evaluated and selected, decreasing the probability of overexploitation (Hilborn, 2007).
78 Besides an obvious interest for management, the topic is also interesting from an ecological point of
79 view. To date, most studies have focused on co-variations between climatic or oceanographic
80 parameters and population abundance, biomass or catch. However, those usually lack a
81 comprehensive mechanistic. Using the Gulf of Lions as a pilot area, we attempt to deliver an
82 integrated insight in the population dynamics by tackling the question from several complementary
83 angles.

84 The Gulf of Lions is one of the most productive areas in the Mediterranean Sea, due to a wide (for
85 the Mediterranean Sea) continental shelf and a combination of high discharge by the Rhone river and
86 small-scale upwellings created by strong and transient winds (Millot, 1990; Petrenko et al., 2005).
87 Recently, significant changes have been observed in the pelagic ecosystem of the Gulf of Lions (Fig 1).
88 Since 2008, the prevailing small pelagic species, i.e. sardine (*Sardina pilchardus*) and anchovy
89 (*Engraulis encrasicolus*) have exposed a lasting decrease in individual size and weight, making them
90 far less profitable for fisheries in the absence of a market for fish of such a size. As a result, most
91 pelagic trawlers that used to target sardine and anchovy have now turned towards other more
92 valued species (such as European hake, *Merluccius merluccius*), or halted their activity altogether.
93 Consequently, landings of both species, but especially sardine, have dropped to insignificant levels
94 during the last years (GFCM, 2016; Fig 1). Conversely, the sprat (*Sprattus sprattus*) population which
95 had been scantily present for the last two decades and is of no commercial interest in the region,
96 showed a remarkable upsurge. Nonetheless, its mean size and body condition remained quite low or
97 decreased (Fig 1).

98 Surprisingly, these changes in population dynamics neither appeared mediated by environmentally-
99 driven changes in recruitment or overfishing (as often documented in small pelagic fish; see e.g.
100 Barange et al., 2009; Cushing and Dickson, 1976; Lindegren et al., 2013), as recruitment over this
101 period remained high and the exploitation rate was rather low, even before 2008 (sardine
102 exploitation rate < 15% since 2002; GFCM, 2016).

103 Facing this situation, we launched the EcoPelGol project to understand the underlying causes of
104 recent small pelagic population changes in the Gulf of Lions. As no similar regime shift (in terms of
105 oceanography or other biological compartments) had been observed at that period in the Gulf of
106 Lions, the objective of the project was to provide an integrative assessment of causal mechanisms
107 affecting population dynamics by jointly investigating top-down (predation by tuna or marine
108 mammals) and bottom-up (environmental effects) controls as well as diseases and energy allocation
109 trade-offs (see Fig. 2). Although all studies provide a piece of the puzzle, all need to be combined to
110 provide an in-depth answer to the question. Here, we present a summary and cross-discussion of our
111 findings. First, we present a set of studies investigating changes in size, growth, condition and
112 demographic composition over the last two decades and then assessing whether the present
113 situation really is unusual compared to the last 150 years in terms of fish landings. Then,
114 observations and results from these studies allowed us to build alternative hypotheses regarding the
115 control mechanisms of the populations. Each of these hypotheses will be presented and discussed
116 here: (1) changes in size distribution are due to mortality or emigration; (2) observed decreases in

117 small pelagic fish populations are due to top-down pressure exerted on small pelagics by the recently
118 recovering bluefin tuna (*Thunnus thynnus*) population as well as dolphins (*Tursiops truncatus* and
119 *Stenella coeruleoalba*); (3) changes in demographic composition and biological parameters of sardine
120 and anchovy stocks are due to emigration or disease; (4) changes in population trends are due to
121 bottom-up processes, such as environmental forcing and changes in planktonic preys. In the absence
122 of long-term time series of plankton fields in the Gulf of Lions, we investigated potential changes in
123 fish diet using a combination of stable isotope and stomach content data analyses. Finally, (5) we
124 tested for the hypothesis that changes in fish size and mass should affect life-history trade-off
125 between maintenance, growth and reproduction (Stearns, 1976). To do this, we estimated the
126 reproductive investment of sardine and anchovy along years through different proxies such as the
127 reproductive period duration, the gonado-somatic index or the length at first maturity.

128 **Methods**

129 This paper reviews the main findings of several studies. For clarity, we present here only an overview
130 of the principal data and methods used in this project and refer to specific studies for more details.

131 *Small pelagic data*

132 Data on small pelagics come from two main sources: (i) data collected in July of each year since 1993
133 during scientific PELMED surveys, and (ii) fisheries data. PELMED surveys (Bourdeix and Sarau, 1985)
134 are acoustic and trawl surveys specifically designed to sample and assess small pelagic fish biomasses
135 in the Gulf of Lions. Acoustic sampling is performed along 9 parallel and regularly spaced transects by
136 means of echosounders (Simrad ER60). Discrimination between species is done both by echo trace
137 classification and trawl allocation (Simmons and MacLennan, 2005). Indeed, trawls are conducted
138 each time new fish traces are observed on the echogram. The proportion of each species is then
139 estimated by random sampling of the catch before sorting and weighing per species. Further,
140 measurements such as weight, length, age and fat content are taken for the three main targeted
141 species (anchovy, sardine and sprat) at each trawl. Depending on years, samples (entire fish or
142 tissues) are also conserved (frozen at -20°C or in formol) and brought back to the lab for more
143 complete analyses (e.g. histology, stomach contents, muscle lipid and isotopic analyses). Despite a
144 very rich dataset with a high spatial resolution, these surveys only represent a snapshot of the
145 summer situation and do not inform on potential seasonal patterns. To counteract this problem, a
146 partnership with fishermen has been developed to acquire samples all year round. A few times a
147 month, one crate of the catch is randomly sampled by fishermen on the boat and conserved on ice
148 until they return to the harbour (note that fishing events last a maximum of 24h according to

149 regulation). Individual measurements are then computed in the laboratory in the evening or the next
150 day.

151 These data (~30 years) were complemented by data on sardine and anchovy fish landings spanning
152 1865-2013. This long-term time series was compiled by subregion of the Gulf of Lions by extensive
153 data mining of the Mediterranean French fisheries records (see Van Beveren et al., 2016a for details),
154 and provided us with a historical perspective in this ecosystem.

155 *Environmental data*

156 In a first approach, climatic and environmental variables were used as proxies of habitat quality and
157 prey availability. We also used different global climatic indices including the North Atlantic Oscillation
158 (NAO) or the Western Mediterranean Oscillation (WeMO), that integrate fluctuations of
159 temperature, rainfall and wind mixing over large spatial and temporal scales and may be more
160 relevant in explaining population fluctuations (see Stenseth et al., 2003). In addition, Sea Surface
161 Temperature (SST) and Chlorophyll a concentration (Chla) satellite-derived data were extracted from
162 MODIS aqua data (<http://oceancolor.gsfc.nasa.gov>). Rhone outflow, an indicator of nutrient
163 availability, is measured at the Beaucaire station and data is distributed by the Compagnie Nationale
164 du Rhône.

165 *Biological parameters*

166 Several biological parameters have been studied in this project.

167 *Body condition:* Body condition is commonly defined as the quantity of individual's energetic reserves
168 (Jakob et al., 1996) and reflects the amount of energy extracted from the environment. As such, it
169 may inform on prey availability or foraging efficiency (Lloret et al., 2014). Body condition is also often
170 considered as a good indicator of individual well-being or performance, as it represents the amount
171 of nutrients that can be mobilized for the different vital traits, thus mediating life-history trade-offs
172 (Schulte-Hostedde et al., 2001). We mostly used the LeCren body condition index (Le Cren, 1951)
173 based on morphometrics measurements, as it allowed us to go back in time and investigate changes
174 throughout the years. The Le Cren index is defined as the ratio between the weight of the fish and a
175 theoretical weight for its length derived from measurements over the entire population: $K_n =$
176 $\frac{W}{a L^b}$ where a and b are constants estimated from the length-weight relationships. This parameter has
177 been shown to strongly correlate with bioenergetics measurements of fat contents using a fatmeter,
178 as well as with direct biochemical measurements outside of the breeding period (Brosset et al.,
179 2015a). During breeding, the morphometric index seems to represent a more integrative index of the
180 fish condition (Brosset et al., 2015a).

181 *Reproductive investment:* Two parameters relating to reproduction were used. First, the length at
182 first maturity L_{50} was defined as the length at which half of the population is mature using a sigmoid
183 model. This was estimated each year or through periods of combined years. Second, the
184 gonadosomatic index was used as a proxy of reproductive investment. It was estimated as the ratio
185 between the weight of the gonad and the weight of the eviscerated fish.

186 *Age:* Age was assessed using otolith reading. However, as those were missing in some years, annual
187 age compositions per species were computed using a Bayesian mixture model that uses age-length
188 keys based on otolith readings as priors to slice size distributions (see Van Beveren et al., 2014 for
189 more details).

190 *Estimating predation on small pelagic fish*

191 Predation by bluefin tuna: Top-down control by bluefin tuna was estimated by calculating the total
192 amount of energy needed by bluefin tuna in the Gulf of Lions by combining (i) DEB (Dynamic Energy
193 Budget) modeling to estimate the weight-specific energy requirement of an individual (adapted from
194 Jusup et al., 2014), (ii) population weight structure information from fisheries and (iii) population
195 abundance as estimated from aerial surveys (Bauer et al., 2015). This energy was then partitioned
196 among the different consumed preys using stomach content analyses for 3 years of study and prey
197 energy densities acquired from the literature. This allowed us to estimate the consumption of each
198 prey species. As the PELMED survey delivers estimates of small pelagic fish stock abundances in the
199 Gulf of Lions, we were then able to estimate the percentage of the population predated by bluefin
200 tuna. To account for uncertainty associated with all parameters, calculations were bootstrapped (10
201 000 iterations) using the most appropriate error distributions for each parameter. Furthermore, as
202 the predation pressure might have been more important on specific prey size classes, we also
203 investigated bluefin tuna selectivity. To do so, we estimated the size distribution of consumed prey,
204 based on undigested prey lengths and relationships between otolith and prey lengths for digested
205 prey. Per species, prey size distribution was compared to the population size distribution, obtained
206 from the PELMED survey. All methodological details can be found in Van Beveren et al., 2017.

207 *Predation by dolphins:* A similar approach was used to estimate predation by the two main dolphin
208 species inhabiting the Gulf of Lions (*Tursiops truncatus* and *Stenella coeruleoalba*). Plane and boat
209 surveys were used to estimate dolphin abundance and population structure, while allometric
210 energetic models were used to estimate individual energy requirement and stomach contents of
211 stranded dolphins were used to determine prey composition in the diet. Uncertainty was estimated
212 using a simulation approach (more details in Queiros et al., subm.).

213 *Pathogen and disease analyses*

214 To assess whether pathogens might be an additional source of mortality for sardine in the Gulf of
215 Lions, monthly sampling was performed for one year in 2014-2015 (see details in Van Beveren et al.,
216 2016b). Nine sampling events of 150 sardines each were used to perform a large-band search for
217 bacteria, parasites (micro and macro) and viruses. Fresh samples were obtained from fishermen or
218 the PELMED survey and were analysed within 24h. All fish were first measured, weighed and their fat
219 content was assessed using a fatmeter (Brosset et al., 2015a), so that we could investigate the link
220 between fish morphological characteristics and pathogen prevalence and intensity. Regarding
221 viruses, we used both broad-spectrum cell cultures and specific PCR analyses targeting the pilchard
222 herpes virus known to decimate sardine populations (see Whittington et al., 2008) and the
223 betanodavirus (the most common fish virus in the Mediterranean Sea). To check whether detected
224 infectious agents could be harmful pathogens, we also ran tissue analyses through autopsy and
225 histology.

226 *Planktonic data analyses*

227 The study of bottom-up processes requires detailed information on prey (plankton) availability.
228 Unfortunately, surveys of phyto- and zooplankton are scarce in the Gulf of Lions and no historical
229 datasets are available. Therefore, we used modeled plankton concentration estimates extracted
230 from a coupled physical-biogeochemical model called SYMPHONIE – Eco3m-S (Auger et al., 2011;
231 Baklouti et al., 2006; Marsaleix et al., 2012). This model includes 6 groups of plankton:
232 picophytoplankton, nanophytoplankton, microphytoplankton (mainly diatoms), nanozoopankton
233 (small ciliates and flagellates), microzooplankton (large ciliates and flagellates) and mesozooplankton
234 (mainly copepods).

235 We investigated whether fish diet had changed across time and tested whether this could be related
236 to changes in small pelagic fish populations. We compared the diet of small pelagics before and after
237 2008 (i.e. when most of the changes occurred). We used a combination of complementary
238 approaches, i.e. stomach content and stable isotope analyses (Caut et al., 2006) on fish sampled from
239 PELMED surveys. This ensured all samples were collected at a similar time of year and avoided any
240 potential bias due to seasonal variation.

241

242 ***Results and Discussion***

243 **1. State of the population**

244 As often in fisheries studies, the first alarming sign was observed from fish landings with a sudden
245 crash in sardine landings around 2008, while anchovy landings had been decreasing at a slower rate
246 over a longer time period. Looking at it from a historical perspective (Fig. 3) highlighted an even more
247 alarming trend. Indeed, a first study describing the historical landings of sardine and anchovy in the
248 Gulf of Lions showed that their present total landings are similar to those before the 1960s, when
249 fishing was still non-industrial since sonars and large-scale trawlers had not yet appeared (Van
250 Beveren et al., 2016a). Focusing on sardine, the recent situation (after 2008) is highly unusual, as
251 recent landings are the lowest recorded over the past 150 years. Biomass and abundance estimates
252 resulting from recent PELMED surveys did not reveal such drastic changes. Especially, fish abundance
253 has been maintained if not increased lately contrary to the landings (Fig.1). The contradiction
254 between the crash in landings and an increase in abundance suggests a decrease in fishing effort.
255 One reason for this might be fish size. Indeed, the low price and quasi-absence of a market for small
256 fish and the increase in fishing marginal costs (e.g. fuel) would lead to a halt in fishing effort. To test
257 this hypothesis and obtain a better awareness of the current situation and population dynamics, we
258 investigated changes in fish size, condition, age and length composition using PELMED survey data
259 (Van Beveren et al., 2014). Sardine and anchovy size decreased around 2008 and fish remained small
260 thereafter (Fig. 4). Annual anchovy size distributions are usually unimodal, so that the decrease in
261 mean size corresponds to a shift of the entire mode towards small individuals due to a rather slow
262 growth, as confirmed by von Bertalanffy growth curves (Van Beveren et al., 2014). Conversely,
263 sardine distributions are bimodal and the decrease in size translated in the disappearance of the
264 second mode containing large sardines. For sardine, which displayed the most significant size
265 truncation, the shift towards smaller fish was explained by a combination of slower growth and the
266 disappearance of older individuals (ages 2+, see Van Beveren et al., 2014).

267 Large old individuals might have disappeared because they emigrated towards different areas and/or
268 they experienced a higher than usual mortality rate. If fish emigrated, they most likely did so towards
269 Spanish waters, because of the main current direction and the presence of continental shelf in this
270 area. However, a comparison between French and Spanish size distributions of the landings from
271 2002 to 2013 (Fig 5) reveals that size distributions are similar between both regions. In particular,
272 when large fish disappeared from French landings, the same happened with Spanish landings. This
273 not only suggests that large fish did not migrate to Spain, but also that the recent changes observed
274 in the Gulf of Lions might take place at a larger scale in the North-Western Mediterranean Sea
275 (although sardine exploitation has always been much more important in Spain; Palomera et al.,
276 2007). As a consequence, it is more likely that large individuals experienced higher mortality rates.
277 Higher mortality is expected to occur if fish are in a lower condition (Millar and Hickling, 1990).

278 Accordingly, since 2008 both sardine and anchovy populations have been characterized by a
279 continuous trough of low body condition, compared to short, transient troughs in the past (Van
280 Beveren et al., 2014, Fig 4). Thus, the current situation is the first to occur over such a long period.
281 Interestingly, the decrease was most pronounced for sardine, for which the largest decline in size and
282 age was observed. Moreover older sardines were more affected by the decrease in condition than
283 younger ones, supporting the hypothesis that natural mortality rates primarily increased for larger
284 size classes (Brosset et al., 2015b).

285 As expected when fish populations decline (e.g. Ballon et al., 2008), sardines and anchovies matured
286 earlier (length at maturity for sardine was about 12.1 cm prior to 2009, but about 9.6 cm after 2009
287 for sardines). Further, despite poor energy reserves, they maintained, or in some cases even
288 increased, their reproductive investment (as expressed by the reproductive period duration as well
289 as their gonadosomatic index, see Brosset et al., 2016b). These findings might explain why
290 abundance and recruitment remained surprisingly high throughout the last decade (Fig. 1). However,
291 such changes might also come at a cost and explain the disappearance of older sardines through a
292 change in the life-history trade-off between reproduction and maintenance. This is especially true for
293 sardines, which act as capital breeders reproducing in winter when feeding conditions are poorer. An
294 especially low condition at the start of winter (Albo-Puigserver et al., 2017) and reproduction
295 associated with an important reproductive effort may thus result in increased adult mortality. The
296 change in the reproduction/maintenance trade-off might incur costs in terms of immunity for
297 instance, so that fish might be more susceptible to disease (Krams et al., 2017). Such a change may
298 also affect the amount of energy a fish can mobilize for muscle activity and as such decrease its
299 swimming efficiency, so that weaker individuals might be more prone to predation (Herting and Witt,
300 1967). Ultimately, fish might reach a critical condition for their survival and die from starvation, if
301 they are not able to find large quantity of prey especially at the end of winter.

302 Regardless of the exogenous pressures, one hypothesis is that the observed changes in life-history
303 traits (slower growth, decreased size at first maturity) and associated trade-offs might result from
304 population adaptation. For instance, fish facing an important selective exploitation on large
305 individuals have been shown to react towards slower growth and earlier maturation (Audzijonyte et
306 al., 2013; Devine et al., 2012; Kuparinen et al., 2016; Mollet et al., 2016). Yet, whether such changes
307 derive from phenotypic plasticity or genetic changes remains mostly unknown. We recently aimed at
308 experimentally disentangling those effects by capturing wild sardines in October 2015, which we
309 placed in 4.5 cubic meter tanks for three months. Our results highlighted phenotypic plasticity rather
310 than genetic adaptation. Despite the winter period over which the experiment was conducted and
311 low water temperature at that time, sardines fed daily to 1.5% of their body mass (as often

312 recommended in aquaculture) immediately exhibited compensatory growth ($13.0 \pm 0.1\text{cm}$ after 40
313 days vs. $11.2 \pm 0.1\text{cm}$ at t_0) and an important upsurge in their body condition (Le Cren index: $1.43 \pm$
314 0.02 at t_{40} vs. 0.93 ± 0.01 at t_0). Such an increase would take 6 months up to one year to occur in the
315 wild according to the von Bertalanffy curves estimated between 1993 and 2012 confirming that
316 observed changes are a direct consequence of a dietary restriction in the wild.

317

318 **2. Factors affecting small pelagic populations**

319 Although previously cited studies contributed to our general understanding of the core population
320 dynamics, the underlying factors affecting population dynamics still needed to be determined. Given
321 the exceptionality of the situation (high mortality of older fish rather than low recruitment), a large
322 scope of potential mechanisms were scrutinised, including some which are commonly neglected in
323 small pelagic fish research (e.g., predation and disease; Fig 2).

324 **2.1 Top-down Control**

325 First and foremost, fishing pressure was examined as overexploitation is a likely candidate when
326 investigating decrease in fish size and condition. Due to differential catchability, fishing can cause or
327 magnify a shift towards young, small and early-maturing individuals (Audzijonyte et al., 2013; Devine
328 et al., 2012; Kuparinen et al., 2016; Mollet et al., 2016). Over the past 25 years, harvest rates
329 (landings/population biomass) have generally been low (mean of 13% for anchovy and 10% for
330 sardine) but varied significantly around these means (Fig. 6). A safe level of medium term
331 exploitation for small pelagic fish is considered to be 0.4 (Patterson et al., 1992), a threshold that has
332 only been crossed once in 1997 for sardine. This occurred right before sardine biomass peaked,
333 indicating that there had been little effect on the population. Finally, since 2010 the sardine harvest
334 rate has been reduced to 1% or less, but no signs of recovery in terms of growth, survival or
335 condition have yet been recorded despite the high turnover rate of the species. These results suggest
336 that fishery is not the main cause for high sardine and anchovy mortality. Further, stock assessments
337 for sardines in this area based on a 2-stage biomass model, estimated an extremely low exploitation
338 rate, confirming this vision (GFCM, 2016). As such, the General Fisheries Commission for the
339 Mediterranean Sea judged the sardine stock ecologically unbalanced due to its lack of old individuals
340 and problems of growth and body condition (GFCM, 2016).

341 Similarly to the fishery hypothesis, another top-down regulating mechanism could be the effect of
342 predators removing an important part of the adult population. However, despite sardine and
343 anchovy being the two main prey species of bluefin tuna (accounting for more than 80% of the diet in

344 terms of mass and abundance), top-down control by tuna has been estimated to be extremely
345 limited, the percentages of each population consumed being lower than 2% (Van Beveren et al.,
346 2017). Further, bluefin tuna seemed to be opportunistic in terms of prey size, as no consistent size-
347 selective feeding was observed. Similarly, the fraction of the sardine and anchovy population
348 ingested by dolphins was even lower (<0.1%, Queiros et al., submitted). The current situation of small
349 pelagics in the Gulf of Lions is thus unlikely to be due to top-down processes.

350 **2.2 Disease**

351 A general veterinary study focusing at sardine was conducted, aiming to detect a wide range of
352 potential pathogens, including parasites, viruses and bacteria (Van Beveren et al., 2016b). However,
353 our analyses did not reveal any trace of macro-parasites or viruses (whether on culture or by specific
354 PCRs) and detected only few bacteria, all of which with little prevalence (Van Beveren et al., 2016b).
355 Only micro-parasites were observed in 77% of the fish (Van Beveren et al., 2016b). Those
356 microparasites observed in the liver were coccidies, a hepatic parasite, whose effect is mostly
357 unknown. However, no clear damage to tissues and no link between pathogen presence and host
358 size or condition were highlighted (Van Beveren et al., 2016b). This study therefore suggested that
359 the probability of pathogens acting as a key mechanism affecting the sardine population is fairly low,
360 although further research on the prevalence and harmfulness of coccidies as well as occurrence in
361 different waters needs to be conducted for this hypothesis to be entirely refuted.

362 **2.3. Bottom-up control**

363 Rather, changes in growth, size and condition, and hence possibly increased mortality, might reflect
364 bottom-up controls mediated by changes in plankton composition and/or concentrations. Indeed, we
365 showed that the concentration in mesozooplankton (from biogeochemical models) was the only
366 variable significantly affecting body condition of both sardines and anchovies, while river runoff, sea
367 surface temperature (SST) or microphytoplankton (i.e. diatom concentration) affected condition in
368 only one of the two species (Brosset et al., 2015b). Following up on this analysis and suggestions in a
369 previous review (Palomera et al., 2007), we compared pre- and post- 2008 diets for fish of similar
370 size. Those exhibited important changes in carbon isotopic values as well as in consumed plankton
371 composition and size for both sardines and anchovies (Brosset et al., 2016a). A principal component
372 analysis on the diet composition of all sampled fish clearly showed segregation between the years
373 prior to (2007 for sardines and 1994 for anchovies) and posterior to the changes (2011-2012) with a
374 shift towards smaller prey species in both sardines and anchovies in recent years (Brosset et al.,
375 2016a). Despite previous associations between small pelagic abundance and basic environmental
376 parameters such as temperature (Palomera et al., 2007), a study on climatic (large-scale indices such

377 as NAO, AMO and WeMO) and oceanographic parameters (SST and river runoff) did not show any
378 significant change in 2008, suggesting that the mechanisms behind small pelagic changes might be
379 more complex (Van Beveren et al., 2016a). Also, a study at a larger scale including most of the
380 northern side of the Mediterranean Sea showed that fish size and body condition decreased in
381 almost all areas but not concomitantly and suggests that the causes of these declines might be
382 different and occurring at subregional scales (Brosset et al., 2017). Nonetheless, smaller plankton
383 species are known to be less energetic (Zarubin et al., 2014), which might explain why small pelagics
384 have experienced a trough of low body condition. Still, this result might be surprising as a regime
385 shift towards smaller plankton size is thought to be favourable for sardines (Van der Lingen et al.,
386 2006). Indeed, sardines are known to feed on smaller plankton than anchovies probably because
387 they are more efficient filter-foragers (Van der Lingen et al., 2002). Why then would sardines be the
388 ones most affected by a change in plankton communities towards smaller sizes? This observation
389 might reflect an important difference in sardine feeding strategies between upwelling systems and
390 other areas. Sardines from upwelling areas might have developed adaptations increasing their
391 filtering efficiency because of high plankton densities. In the Mediterranean Sea, which is known to
392 be rather productive in spring but mostly oligotrophic otherwise, sardines seem to have developed
393 both feeding modes, i.e. filter and particulate feeding (Nikolioudakis et al., 2012). Therefore,
394 adaptations to filter-feeding might not have evolved so strongly in the Mediterranean Sea. Gill rakers
395 for instance have a higher density in the upwelling area off the Iberian coast than in the North-
396 Western Mediterranean Sea (Costalago et al., 2015). Also, traditional differences in diet between
397 sardines and anchovies (Van der Lingen et al., 2002) are not clearly observed in the Mediterranean
398 Sea (e.g. LeBourg et al., 2015). Therefore, a change towards smaller prey might thus not have been
399 beneficial for Mediterranean sardines, in contrast to what would have been expected in other
400 systems.

401 **3. Further research**

402 While bottom-up control seems the most likely explanation to recent declines in small pelagic fish
403 populations in the Gulf of Lions, the detailed mechanisms underlying the effect of plankton size and
404 composition on fish life-history traits remain to be tested. In particular, the use of an experimental
405 approach (wild fish maintained in tanks) where food size, quantity and quality may be manipulated
406 for might help refine the understanding of individual and combined effects of food on fish foraging
407 behavior, energy expenditure and gain, growth and reproduction. Further, the reconstruction of
408 high-resolution zooplankton fields as well as a better understanding of the energy density of
409 different plankton species or size-classes is urgently needed. If this indeed confirms a change in
410 plankton, then oceanographic, atmospheric and hydrological parameters would need to be further

411 analysed to better identify a potential regime shift of the ecosystem. In particular, we need to further
412 examine the main factors affecting ocean productivity: nutrient input (through the Rhone river
413 discharge) and water mixing (winds, local upwellings, and deep water convection). Additionally,
414 density-dependence and competition might be important synergistic factors contributing to the
415 dynamics of these populations, especially if resource partitioning is lower due to greater similarities
416 in feeding behavior and prey preference. The total abundance of small pelagics in the Gulf of Lions
417 has somewhat increased, in particular after the upsurge of sprats (Fig. 1). Further, these three
418 species strongly co-occur in the Gulf of Lions (Saraux et al., 2014) and there has been an increase in
419 the isotopic niche overlap of sardine and anchovy with sprat (Brosset et al., 2016a). A study of intra-
420 and inter-specific competition within and among these three species would be of high interest.
421 Finally, few ecotoxicological studies have been performed so far on small pelagic fish in the Gulf of
422 Lions (but see COSTAS project; Tronczynski et al., 2013). Yet, pollution or a decreased water quality
423 could elicit a decrease in fish condition with direct or indirect mortality. Given that the Gulf of Lions
424 contains considerable concentrations of pollutants (Harmelin et al., 2012) and is the most polluted
425 Mediterranean area in terms of PCBs (Bodiguel et al., 2008; Gomez-Gutierrez et al., 2007), this
426 hypothesis would be worth a detailed examination. Pollutants might change fish physiology after
427 ingestion (Heath, 1995), whether or not after bioaccumulation or biomagnification of the
428 contaminants along the trophic web. However, for the few pollutants (PCB, PBDE, Hg and ¹³⁷Cs)
429 looked at so far in anchovy and sardine of the Gulf of Lions (see Harmelin et al., 2012), no
430 exceptionally high levels were found when compared to other European regions (Bocio et al., 2007;
431 Martí-Cid et al., 2007; Naso et al., 2005). This indicates that it might be necessary to look at a mixture
432 of pollutants, as the combined effect of numerous weakly present ones might become an influential
433 cocktail. Further, pollutants might have an indirect effect on fish through the food web. In particular,
434 planktonic species could be impacted (Tiano et al., 2014), potentially resulting in a community and/or
435 abundance change (Arfi et al., 1981; Uriarte and Villate, 2005). However, a study on the aspects of
436 PCBs (including multiple congeners) in the Gulf of Lions indicated that PCB biomagnification in
437 plankton is relatively low, and concentrations are not correlated to the plankton biomass in the
438 system (although such a relation might have been masked; Tiano et al., 2014). While first results,
439 mostly on PCB, were not particularly significant, ecotoxicology of fish and plankton is an important
440 research venue to consider in order to further understand dynamics of small pelagics.

441 **4. Conclusions**

442 In conclusion, the important decrease in small pelagic landings in the Gulf of Lions resulted from a
443 decrease in fish size and condition rather than from a decrease in abundance. Changes in size
444 resulted from a decrease in growth (anchovy and sardine) and disappearance of old individuals

445 (sardines). The EcoPelGol project enabled us to test for different control mechanisms that we
446 discussed here. Namely, our results provide little evidence of top-down control by predators of those
447 populations and suggested a very low probability of a control by disease and fisheries. Rather, our
448 results suggest changes in diet of these species supporting a bottom-up control. Nonetheless, despite
449 low energy reserves, the investment in reproduction does not appear to be impaired but might occur
450 at a cost to adult maintenance. Future research should further explore the bottom-up control
451 hypothesis to (1) confirm whether plankton communities have changed drastically in recent years
452 and if so (2) examine which factors might explain such changes; and (3) investigate the
453 ecophysiological mechanisms relating changes in diet to fish phenotypes.

454

455

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Figure legends

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Fig. 1. Biomass, abundance, landings and mean weight of anchovies (in green), sardines (in blue) and sprats (in black) in the Gulf of Lions.

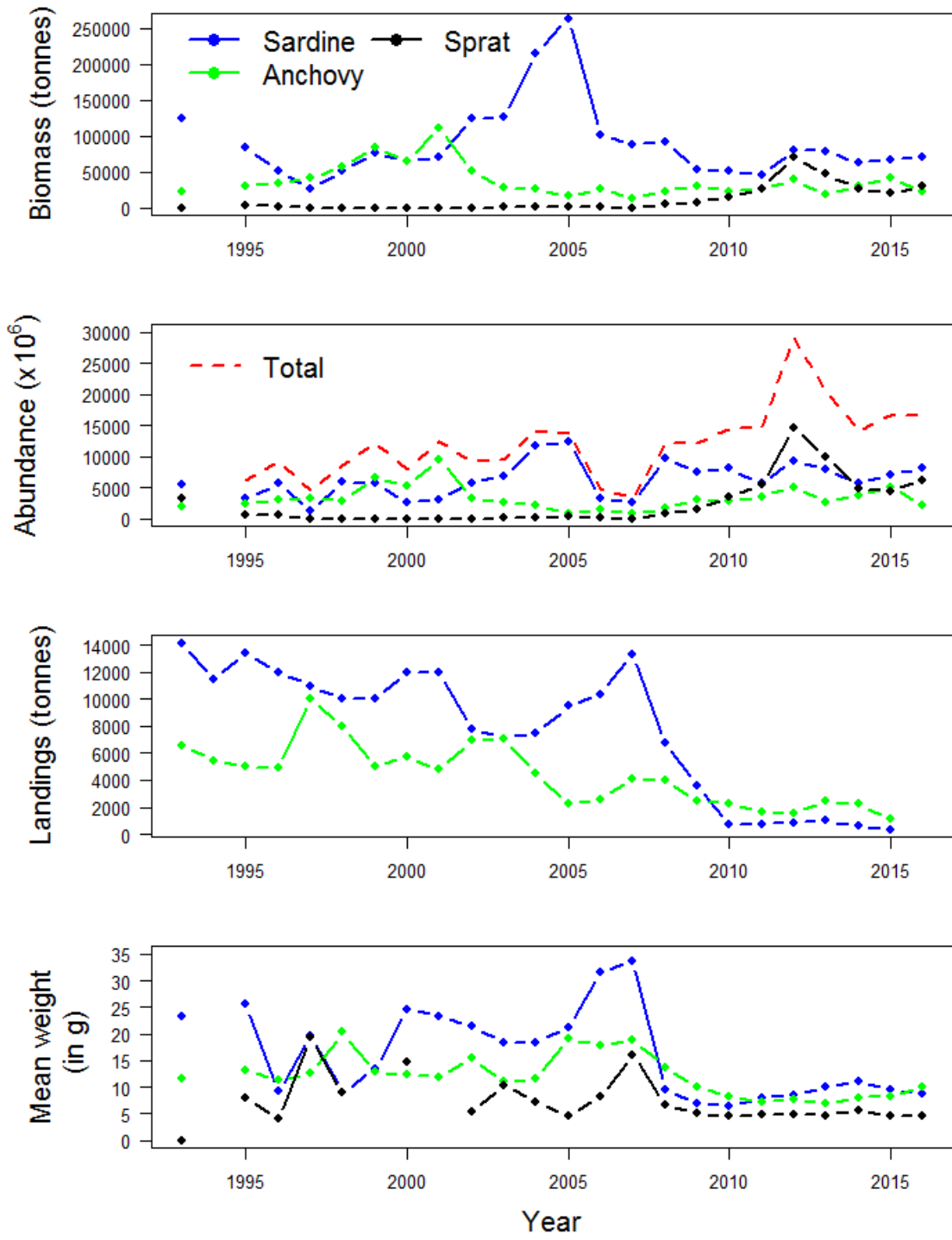
Fig 2: Schematics on the main drivers of small pelagics population dynamics. Significant drivers appear in bold, while less important ones appear in grey and in italics. Green items are perspectives for future work.

Fig 3: Historical landings of sardines and anchovies adapted from Van Beveren et al., 2016a

Fig 4: Size distribution and mean body condition (\pm SE) of sardines and anchovies in 1984 and 85 and from 1992 to 2015, adapted and updated from Van Beveren et al., 2014. N and n represent the number of trawls and the number of measured fish respectively.

Fig 5: Comparison of the annual size distributions of sardine and anchovy landed in Spain (blue) and France (red). Vertical lines indicate the median size of each distribution.

Fig 6: Harvest rates of sardine and anchovy as estimated by the total landings divided by the biomass of the stock assessed by acoustics. Dashed line indicates the reference point of Patterson (1996)



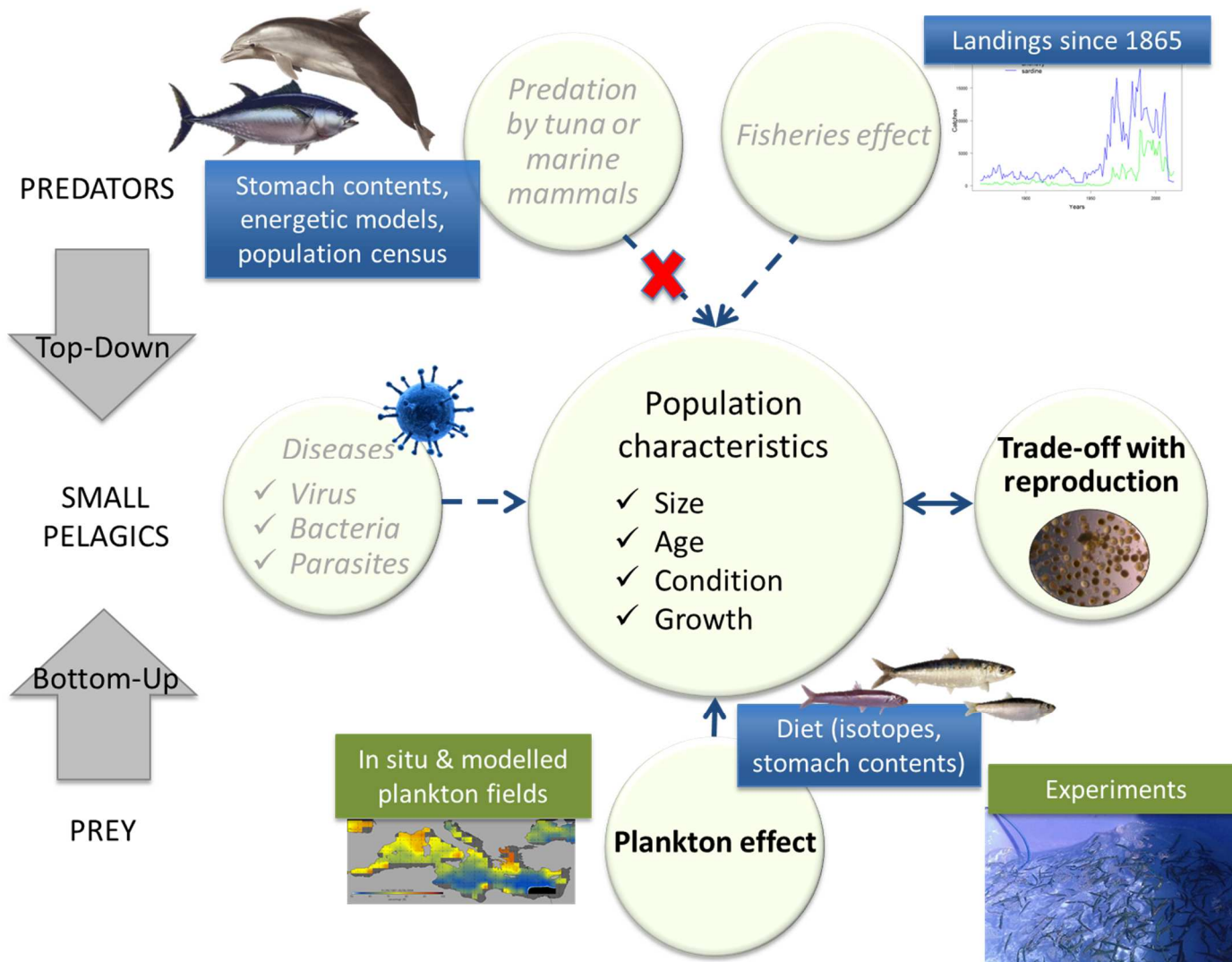
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Fig. 1

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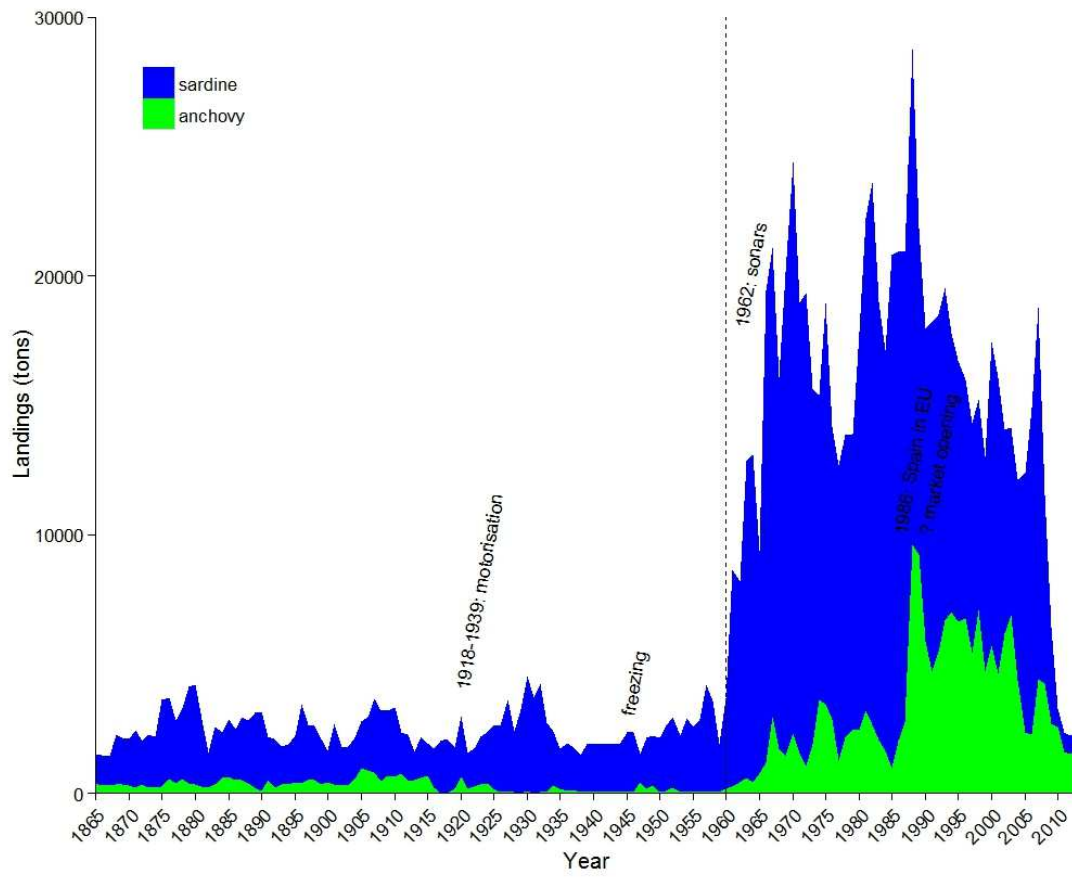


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695 Fig 2

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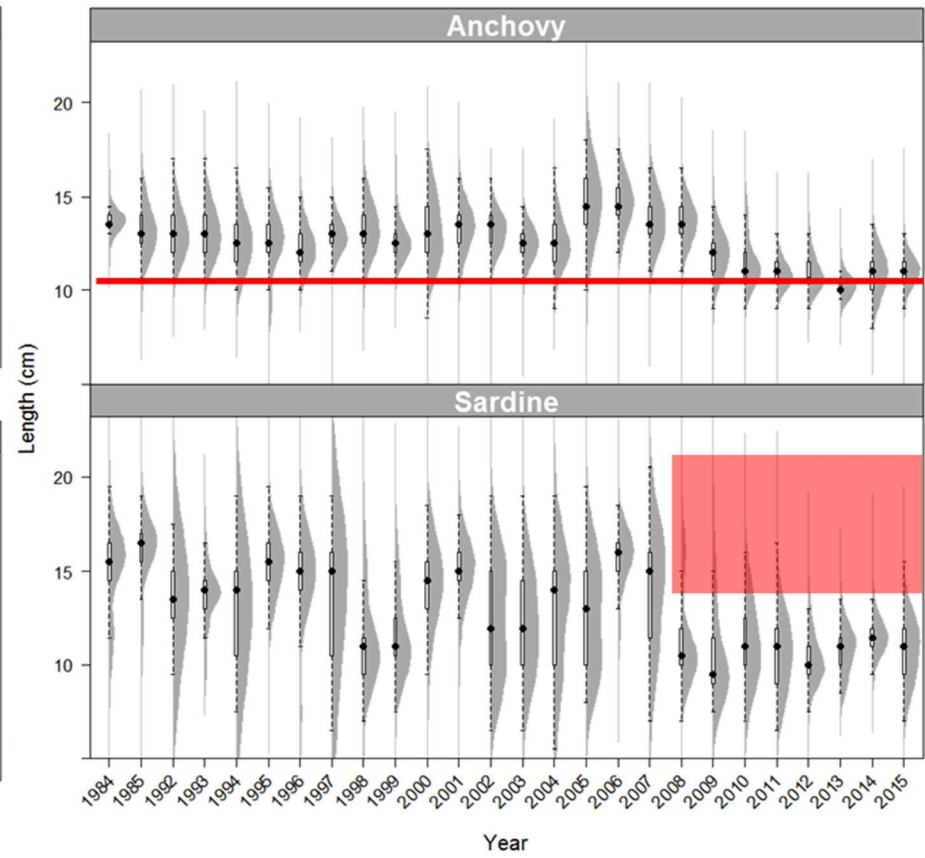
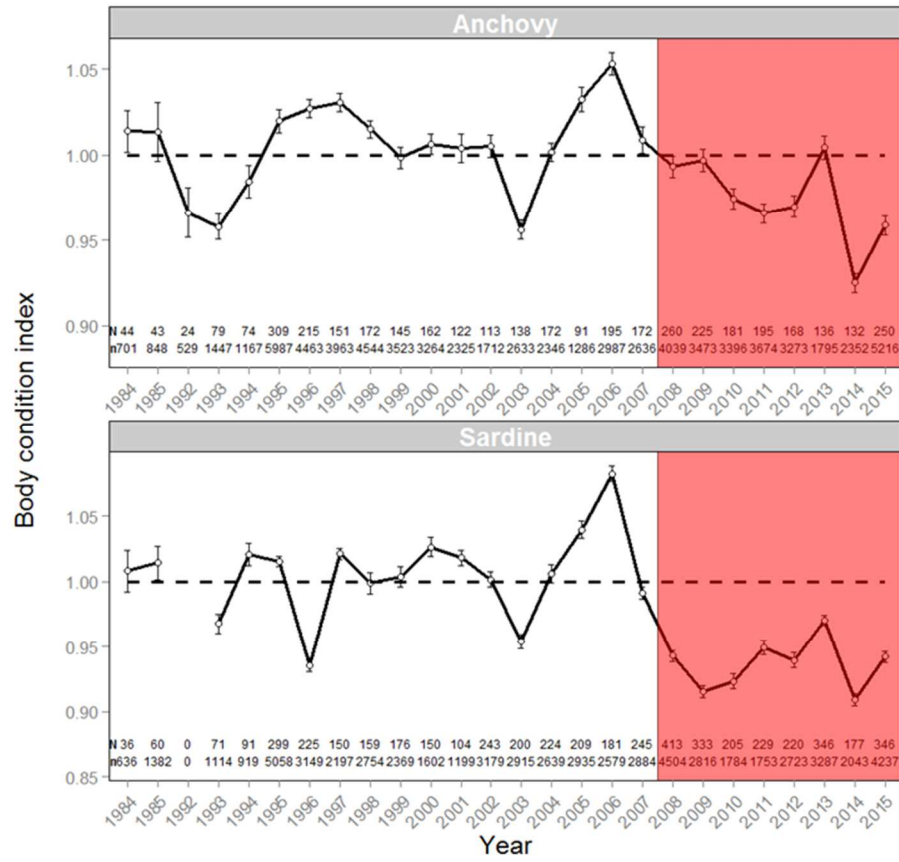
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Fig 3

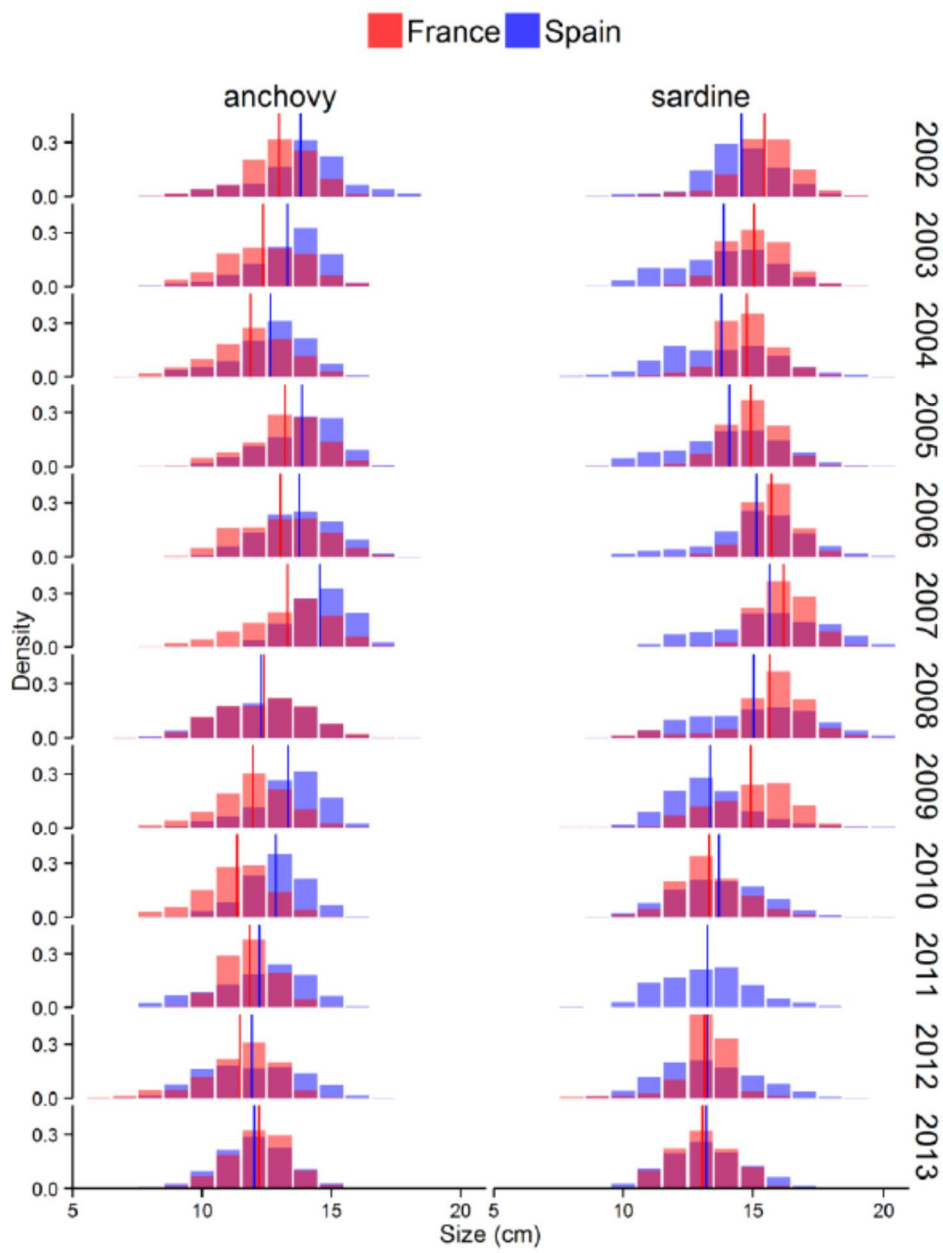


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701 Fig. 4

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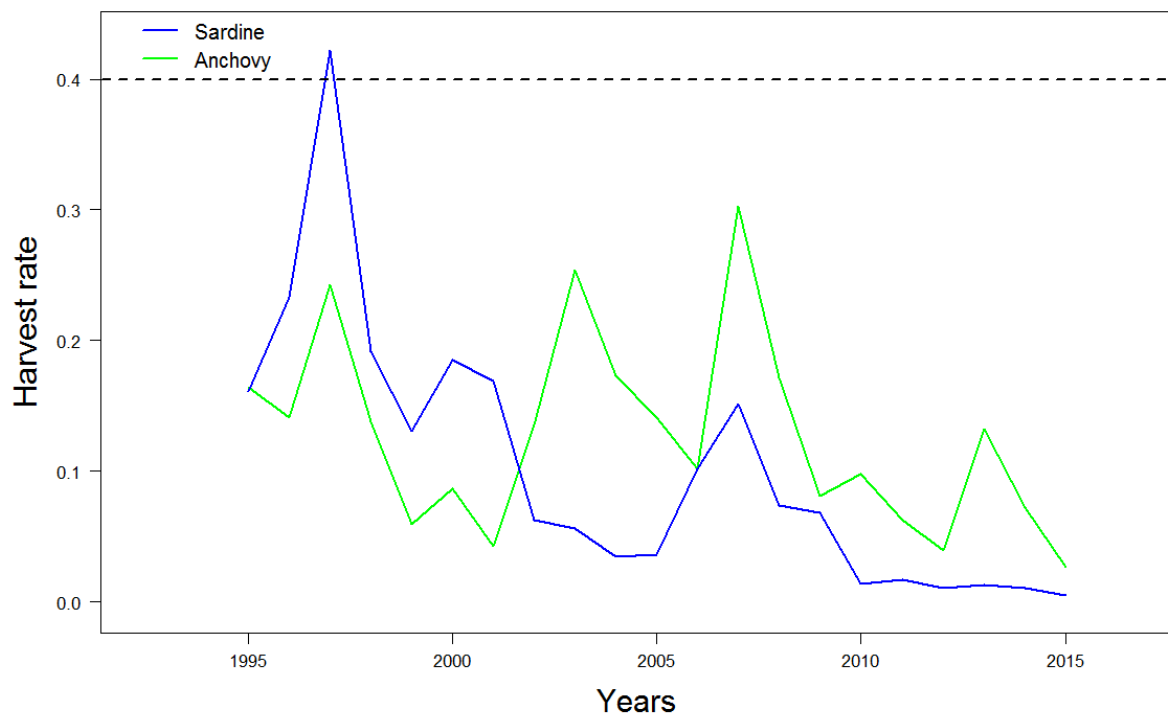
705 Figure 5.

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711 Fig 6

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