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1 **Exploring individual and population eco-evolutionary feedbacks under the coupled effects of**  
2 **fishing and predation**

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19 Running head: Eco-evolutionary feedbacks under fishing and predation

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Abbreviations:

FRII – Holling’s functional response Type II

FRIII – Holling’s functional response Type III

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24 **Abstract**

25 Intensive fishing that selects for large and old individuals can have pervasive effects on traits directly  
26 associated with the fecundity and survival of the target species. The observed reduction in fish body  
27 size can result in earlier sexual maturity at a smaller body size, leading to a lower individual  
28 reproductive output and population productivity in the long term. In addition, increased predation can  
29 induce similar responses in age and size at maturity due to the release of intraspecific competition  
30 and the lower population density. Thus, the combined impact of fisheries and predation is more  
31 difficult to predict due to their competition for fish, ultimately limiting and directing the prey size  
32 selectivity of each competitor. This can lead to various responses of fish on individual and population  
33 levels, depending on how the impacts of fisheries and predation affect each other. To explore this  
34 topic, we used an individual-based model to investigate the responses of the European hake  
35 (*Merluccius merluccius*) to the coupled pressures of the prevailing fishing regime and predation by  
36 bottlenose dolphins (*Tursiops truncatus*) as a study system. By simulating the growth trajectories of  
37 hake with consideration to its pronounced sexual size dimorphism (SSD), we applied Holling's Type  
38 II and III functional responses (FR<sub>II</sub> and FR<sub>III</sub>, respectively) and the Rosenzweig-MacArthur  
39 predator model to describe prey–predator dynamics. Our results demonstrate how the intensity,  
40 duration, and prey sizes selected by predation and fisheries determine the potential for evolutionary  
41 changes in hake life-history traits. Additionally, pronounced SSD in hake as well as the predation  
42 type play a pivotal role in hake resilience and recovery following a period of overexploitation.  
43 Different types of predation reveal the discrepancy in the intensity of competition between predators  
44 and fisheries for fish, as well as predator survival, which is relevant for sustainable fisheries  
45 management and effective predator conservation strategies.

46

47 **Keywords:** Size-selectivity; Fisheries-induced evolution; *Merluccius*; Prey–predator dynamics;

48 **Functional responses**

## 49 **1. Introduction**

50 Fisheries-induced alterations in fish morphology, behavior, and development have been a focus of  
51 research and discussion in fisheries science and management for the past several decades (e.g.,  
52 Hendry et al., 2011; Palkovacs et al., 2012; Heino et al., 2015). A number of researchers have  
53 emphasized the negative, long-term, and potentially irreversible effects of fisheries-induced  
54 evolution (FIE) on fish stock resilience and recovery (Swain et al., 2007; Enberg et al., 2009;  
55 Neubauer et al., 2013), as well as sustainable fisheries yields (Zhou et al., 2010; Garcia et al., 2012).  
56 In particular, the size selectivity of fisheries and removal of larger and older individuals poses a  
57 persistent threat due to its pervasive, damaging effects on individual fecundity and survival (Law,  
58 2000; Palkovacs et al., 2012; Belgrano and Fowler, 2013). Continued high harvest rates and fishing  
59 intensity, selecting for life-history traits with specific heritability, represent the main conditions that  
60 can induce an evolutionary shift in fish species (Hutchings and Kuparinen, 2019). However,  
61 difficulties in distinguishing phenotypic plasticity from evolution (reviewed in Hendry, 2016) and  
62 discerning the direction of ecology-to-evolution or evolution-to-ecology processes are the main  
63 obstacles to proving FIE in harvested fish stocks (see Hendry et al., 2011; Heino et al., 2015).

64 In addition to FIE, predation and other selective pressures of environmental and ecological origin  
65 occurring in marine ecosystems can potentially induce similar responses in the direction or  
66 magnitude of targeted phenotypic traits (see Reznick et al., 1990; Philips et al., 2010; Crozier and  
67 Hutchings, 2014; Ohlberger, 2013; Waples and Audzijonyte, 2016). Predation is, among others, a  
68 size-selective source of natural mortality, removing individuals according to the prey size  
69 selectivity of the predator. Moreover, the size-dependent mortality caused by predation increases  
70 with a decrease in fish body size, especially in those predators limited by gape size (Pettorelli et al.,  
71 2011). Similarly to fisheries, predation directly affects the prey's investment to reproduction  
72 (DeLong and Luhring, 2018) and its reproductive success or resilience (Lowerre-Barbieri et al.,  
73 2017) to other disturbances. This can ultimately lead to shifts in the timing of their sexual

74 maturation and alter their reproductive strategy (e.g., behavioral patterns linked to reproduction)  
75 due to the removal of sexually mature individuals. While such predation-induced changes in prey  
76 have been detected as shifts in size and age at maturity observed under experimental conditions  
77 (Beckerman et al., 2010), changes in predators induced by the changes in prey have also been  
78 observed. For instance, Shuter et al. (2015) predicted that larger size ratios of lake trout (*Salvelinus*  
79 *namaycush*, predator) to cisco (*Coregonus artedii*, prey) lead to earlier maturity at a smaller size in  
80 the predator species. Thus, prey characteristics as well as their adaptations to predation affect predator  
81 development and abundance (Yamamichi and Miner, 2015; Fryxell et al., 2019).

82       Considering that fishing can erode size-dependent interactions, change community compositions,  
83 and weaken the structural integrity of ecosystems (Palkovacs et al., 2012; Bell et al., 2018),  
84 evolutionary changes in individual fish traits can reinforce these shifts and limit or reduce  
85 intraspecific genotypic diversity, which ultimately diminishes fishing yields (Law and Grey, 1989;  
86 Garcia et al., 2012; Belgrano and Fowler, 2013). As a result, concern has been raised regarding the  
87 management of evolving fish stocks and their implications for ecosystem functioning and  
88 sustainable fisheries yields. Recent managerial advice for fish populations has included the  
89 application of balanced harvesting (Law and Plank, 2018), as well as the active monitoring and  
90 accountability of individual trait responses to fishing and other selective pressures (Conover and  
91 Munch, 2002; Palkovacs et al., 2018). Furthermore, particular attention should be given to  
92 exploitation strategies for late and early maturing species (Ernande et al., 2004), as well as to fish  
93 stocks already demographically and genetically altered, which require careful implementation of  
94 different fishing moratoria (de Roos et al., 2006). However, these proposed measures are  
95 accompanied by various operational and logistical difficulties, and they only address fisheries-  
96 induced alterations in individual and population parameters, other threats such as climate change  
97 notwithstanding (Fraser, 2013; Palkovacs et al., 2018).

98 In harvested ecosystems, fisheries and natural predators often compete for the same target fish in  
99 areas of temporal and spatial resource overlap. To account for this, the majority of fish stock  
100 assessments include predation as part of a species-specific fixed value for natural mortality that is  
101 equally applied across all age and size classes of fish (Gislason et al., 2010). However, the risk of  
102 being consumed by a predator decreases as a function of increasing body size, as bigger prey fish  
103 become more elusive due to their size (Abrams and Ginzburg, 2000), as well as their improved  
104 swimming and maneuvering skills (Scharf et al., 2000; DeLong and Luhring, 2018). From the  
105 predator's viewpoint, their prey size selectivity will change and adjust according to prey availability  
106 and the predator's ontogenetic development (Griffiths, 1975). While humans are considered as  
107 predators, their prey selectivity and preference are not governed by the sole need to feed for  
108 survival. As Darimont et al. (2015) concluded, humans are not limited in their exploitation rates or  
109 techniques as natural predators are; thus, humans are considered as "super predators". As a  
110 consequence of intensive harvesting, humans can alter the predation risk through direct impacts on  
111 predators as well as indirectly by affecting the physical environment (see Madin et al., 2016).  
112 Further negative impacts can occur through density-mediated effects (Lankau and Strauss, 2011)  
113 where the removal of large predators has direct implications for the strength of trophic cascades as  
114 well as food web stability (DeLong et al., 2015).

115 The European hake (*Merluccius merluccius*, Linnaeus, 1758) is a gadoid bottom-dweller  
116 inhabiting the seas along the NE and central E Atlantic, the NW African coast, and the  
117 Mediterranean and Black Seas, with a decreasing presence from west to east (Fig. 1; Sion et al.,  
118 2019). Adult hake have a mainly piscivorous diet and exhibit strong sexual size dimorphism (SSD),  
119 with males maturing earlier and having a shorter lifespan than females (Cerviño, 2014; Murua,  
120 2010). Furthermore, the female body size in hake is not just positively correlated with the number  
121 of produced eggs (i.e., individual fecundity), but also with the quality of the produced eggs, which  
122 ensures a higher chances of offspring survival (Mehault et al., 2010). Significant fluctuations in size

123 at maturity have been observed in hake populations of the Bay of Biscay and Galician waters  
124 (Domínguez-Petit et al., 2008). Although these changes have been attributed to phenotypic  
125 plasticity of various strengths (see Hidalgo et al., 2014), these populations have experienced very  
126 high harvest rates since the 1980s and continue to do so (ICES, 2019). Additionally, hake are  
127 preyed upon by the bottlenose dolphin (*Tursiops truncatus*, Montagu, 1821), which has been  
128 confirmed by dietary studies on the Irish, Bay of Biscay, and Galician, as well as the W  
129 Mediterranean bottlenose dolphin populations (Blanco et al., 2001; Fernández et al., 2011;  
130 Hernandez-Milian et al., 2015; Santos et al., 2007, 2014). These opportunistic predators often  
131 interact with fishing activities (i.e., operational interactions; Bearzi et al., 2008), following trawlers  
132 or depredating on coastal nets (e.g., López, 2006; Bearzi et al., 2010; Goetz et al., 2015). While  
133 competing with hake fisheries through direct fish uptake (i.e., ecological interactions), bottlenose  
134 dolphins can notably contribute to the total mortality of hake (Santos et al., 2014). Nevertheless,  
135 only a few studies have attempted to quantify the fish biomass removed by these dolphin species.  
136 For instance, Bearzi et al. (2010) found the annual biomass of fish removed by fisheries to be about  
137 38 times greater than the fish uptake by the bottlenose dolphin population in W Greek waters.  
138 Furthermore, Santos et al. (2014) estimated the predation mortalities of four resident dolphin  
139 species of the NE Atlantic area preying upon European hake, with the bottlenose dolphin population  
140 having the highest uptake of hake (82% of the removed hake biomass).

141 Since little is known about how fishing and predation in combination affect the ecology and  
142 evolution of individual traits and, in return, alter predator abundance and fishing yields, here we  
143 investigate the responses of individual traits and population parameters of the European hake under  
144 the prevailing fishing selectivity and predation by the bottlenose dolphin. Gårdmark et al. (2003)  
145 theoretically explored the evolutionary responses of the age at first reproduction to density-  
146 independent and density-dependent predation and harvesting with regards to the number of species  
147 involved and predation type (i.e., Holling's Type I and II). Other studies investigating the effects of

148 fishing and predation have explored these from the perspectives of fisheries assessment and eco-  
149 evolutionary feedbacks independently, using approaches that range from individual-based to  
150 ecosystem models (e.g., Melián et al., 2011; Allhoff et al., 2015; Kindsvater and Palkovacs, 2017;  
151 Wood et al., 2018; Govaert et al., 2019). In this paper, we use an individual-based model to  
152 examine how the competitive interactions of natural predators and fisheries affect individual fish  
153 traits as well as population resilience and recovery. Similarly to ecosystem resilience (Holling,  
154 1973), we observe the population resilience as the capacity of the population dynamics and  
155 structure to withstand and absorb a disturbance whilst maintaining its main ecological and structural  
156 characteristics, while recovery is reflected in the speed of recovery of observed parameters after the  
157 disturbance has ceased. While the methodological approach allows us to account for the ecological  
158 characteristics of the prey and the co-evolved prey–predator dynamics, we firstly focus our  
159 investigation on the potential for FIE under the coupled effects of the size-selective pressures. Then  
160 we observe the impact of predation on hake population and fisheries. Lastly, we attempt to  
161 understand the dynamics between the predator and fisheries with consideration to the eco-  
162 evolutionary feedbacks and disruptive fishing regime.

163

## 164 **2. Material and methods**

165

### 166 **2.1 Individual-based model**

167 In the attempt to address the current research questions, we used an individual based model (IBM),  
168 which is an eco-genetic model encompassing quantitative genetics, evolutionary processes, and the  
169 ecological characteristics of the fish species. The IBM approach provides an insight into fish  
170 individual variability of life history traits, whilst aiding to overcome the lack of information about  
171 the exact gene responsible for shaping the response to size-selective removals in hake growth.  
172 Furthermore, it also allows us to observe an evolutionary change in fish life history traits in “fast  
173 forward mode”. To identify the coupled impact of fishing and predation, we expanded an IBM



174 initially developed for the Atlantic cod (*Gadus morhua*; see Kuparinen et al. 2012, 2014; Kuparinen  
175 and Hutchings, 2012 for details) and later parameterized for the European hake (see Jusufovski and  
176 Kuparinen, 2014). While the baseline model and parameterization for hake are described  
177 extensively elsewhere (see Jusufovski and Kuparinen, 2014), in the following text we provide a  
178 brief overview of the main model characteristics with a focus on the novel elements: (i) size-  
179 selective mortality caused by predation and (ii) SSD in hake accounted for through sex-specific  
180 differences in asymptotic lengths with an individual-based prediction of the length at which a fish  
181 becomes sexually mature.

182

## 183 **2.2 Data collection and model parameterization**

184

### 185 **2.2.1 Hake growth and ecological characteristics**

186 The model simulates fish growth trajectories described by the von Bertalanffy (1938) equation,  
187 which calculates an individual's length at age or time step  $t$  ( $L_t$ ) as:  $L_t = L_\infty - (L_\infty - L_0) e^{-Kt}$ .  $L_\infty$  is the  
188 asymptotic length of an individual,  $K$  is the individual intrinsic growth rate (i.e., the rate at which an  
189 individual approaches its  $L_\infty$ ), and  $L_0$  is the fish body length at  $t = 0$ .  $L_0$  is the same value for all  
190 individuals and calculated from obtained data, while the length–weight relationship applied  
191 corresponds to values used for the southern hake stock (ICES, 2019). We attained the final model of  
192 the growth equation through the log-transformation of  $K$  and linear regression as:  $\log(K) = -0.511 -$   
193  $0.0041L_\infty$ . For this purpose, we used hake growth parameters through the introduction of 64  
194 unsexed data points, available as published data from Mediterranean study cases (see Jusufovski  
195 and Kuparinen, 2014). Information on the biological characteristics and fishing regime of European  
196 hake reflects the current state of the southern hake stock of the Bay of Biscay and Iberian waters  
197 ICES ecoregion (ICES, 2019). Overall, we did not focus on geographical or stock-specific

198 characteristics, but rather prioritized reliability and quality in the choice of data and information that  
199 is representative for the fish species in general.

200 Assuming that quantitative traits are defined by a large number of loci with a small additive  
201 effect (Roff, 2002), we describe the genotype of each individual with 20 loci, assigning a value of 1  
202 or 0 to each locus. Therefore, summing the values for the loci gives the genotypic value of an  
203 individual, ranging from 0 (minimum value) up to 20 (the maximum value). The genetic diversity  
204 then corresponds to the range of genotypic values observed with respect to the set conditions and  
205 parameters (see further explanation of the tested scenarios in the section *Simulation design*).  
206 Through sexual reproduction, parental genotypic information is transferred to the offspring in  
207 accordance with the basic Mendelian laws of inheritance. The phenotype is then based on the  
208 individual's genotype, to which phenotypic variation (i.e., normally distributed random noise with  
209 mean zero) is added to account for phenotypic plasticity, whilst remaining within the realistic  
210 values of heritability (0.2–0.3 for fish species; Mousseau and Roff, 1987). After the genotype is  
211 transferred to the phenotype (i.e.,  $L_{\infty}$ ),  $K$  is then predicted through the strong negative correlation  
212 between  $K$  and  $L_{\infty}$ . The maximum hake age is set according to Murua (2010), so that all individuals  
213 above 12 years of age have a 100% probability of dying.

214 Each individual goes through basic ecological processes depicted in Figure 2. To account for  
215 SSD among hake males and females,  $L_{\infty}$  is increased by 41% for female hake, a value representing  
216 the discrepancy between the female and male  $L_{\infty}$  and calculated using the  $RL$  ratio =  $L_{mat} / L_{\infty}$ . As  
217 male and female hake sexually mature at different lengths or  $L_{mat}$  (i.e., length at maturity),  $L_{\infty}$  was  
218 calculated separately for each sex, applying the average value of  $RL$  (0.51) obtained from the hake  
219 dataset. The male and female  $L_{mat}$  applied for the calculation of the percentage difference in  $L_{\infty}$  was  
220 32 and 45 cm, respectively (Cerviño, 2014). Apart from the average  $RL$  value used as an initial  
221 individual value in all simulations (see Table 1), with each time step and for each individual, the  $RL$   
222 is attained based on the individual's  $L_{mat}$  and  $L_{\infty}$  values. During each reproduction event, sexually

223 mature male and female hake are randomly selected and mated, with the sex of the offspring being  
224 assigned by a Bernoulli trial ( $p = 0.5$ ). Egg production depends directly on female weight, which is  
225 derived from the length–weight relationship, and the average recruit-per-spawner value attained  
226 through available information on recruitment and the spawning stock biomass (Jusufovski and  
227 Kuparinen, 2014). Juvenile survival is determined by a baseline juvenile mortality rate with a  
228 probability of survival set to 10%, which also takes into account the known cannibalism in hake  
229 (Murua, 2010). Each juvenile is then assigned its own density-dependent growth (for further details,  
230 see Jusufovski and Kuparinen, 2014).

231 Other ecological processes included in the model are density-dependent growth and three  
232 sources of natural mortality (Fig. 2). The density-dependent growth of each individual diminishes  
233 the growth by 50% each time the fish population exceeds 90% of its carrying capacity (see  
234 Jusufovski and Kuparinen, 2014 for a detailed description and logistic equation). Instantaneous  
235 natural mortality or  $M$  (for individuals older than two years) and mortality due to the cost of  
236 reproduction or  $M_{rc}$  (only for sexually mature individuals) are estimated through parameterization  
237 and both are applied equally to male and female hake (Table 1). The fate of each individual is then  
238 decided using a Bernoulli trial at each time step.

239 Fishing is described through a logistic selectivity curve with  $L_{50}$  (the length at which 50% of the  
240 population is retained) set at 26.4 cm based on the prevailing fishing regime (ICES, 2019; Table 1).  
241 Only individuals older than three are fished, since at this age, hake have reached or are well over  
242 their permitted minimum landing size (MLS).

243

### 244 **2.2.2 Introduction of predation**

245 The predator population is calculated on a population level using a modification of the  
246 Rosenzweig–MacArthur prey–predator model (Rosenzweig and MacArthur, 1963). Depending on

247 the Holling's functional response (Holling, 1959) used in the prey equations, the predator equations  
 248 yield the value of the predator density ( $p$ ) at each time step  $t$  as:

$$249 \quad p_t = p_i e^{e_p a_p n_t / (1 + h_p a_p n_t) - d_p} \quad (1)$$

250 in the case of FRII, while in FRIII,  $p_t$  depends on:

$$251 \quad p_t = p_i e^{(e_p a_p n_t)^2 / (1 + (h_p a_p n_t)^2) - d_p} \quad (2)$$

252 where  $p_i$  is the predator's initial density set for the first time step (see Table 1), after which it  
 253 becomes the value of  $p_{t-1}$  for all subsequent time steps.  $p_t$  depends on  $n_t$  or the prey population  
 254 density attained as a quotient of the number of prey at time  $t$  ( $N_t$ ) and the prey's carrying capacity  
 255 (CC) at each time step.  $e_p$ , or the predator's assimilation efficiency, the attack rate ( $a_p$ ), and handling  
 256 time ( $h_p$ ) are fixed values estimated through parameterization. In turn, the quantity of fish eaten or,  
 257 more precisely, the probability of an individual being eaten ( $p_{eat}$ ) is introduced at an individual level  
 258 and given as:

$$259 \quad p_{eat} = a_p p_t / (1 + h_p a_p n_t) \quad (3)$$

260 when FRII is applied and

$$261 \quad p_{eat} = a_p p_t n_t^{(2-1)} / (1 + (h_p a_p n_t)^2) \quad (4)$$

262 in the case of FRIII.  $p_t$  in both equations denotes the predator population density calculated by  
 263 equations (1) and (2) for FRII and FRIII, respectively. The functional responses are used here as the  
 264 probability of a prey fish being eaten in order to account for any uncertainty brought about by intra-  
 265 and interspecific competition of the predator.

266 Predation is applied across the hake size range from 21 to 51 cm, set according to the average  
 267 size of hake (36 cm) and the hake size range consumed by the bottlenose dolphin populations of the  
 268 Ibero-Atlantic waters (Saavedra, 2017). The predator parameters  $a_p$ ,  $h_p$ , and  $d_p$  were estimated  
 269 (Table 1) and compared to species-specific information on the generation time and dietary  
 270 requirements from published research on wild and captive bottlenose dolphins (Kastelein et al.,  
 271 2003; Lockyer, 2007; Santos et al., 2014; Saavedra, 2017; Spitz et al., 2018). Since the diet

272 composition of the bottlenose dolphin is catholic (Santos et al., 2007; 2014) and its feeding is  
273 opportunistic, this is accounted for in the estimation of  $h_p$ . The applied value of the predator's  
274 assimilation efficiency ( $e_p$ ) is in accordance with the observed range of values for toothed whales,  
275 i.e. 0.90–0.95 (Lockyer, 2007). Prey and predator population parameters ( $p_i$ ,  $N_i$  and  $C$ ) are  
276 estimated through parameterizations (see Table 1) and set in such a manner that they allow for  
277 stable prey–predator dynamics throughout the simulation.

278

### 279 **2.2.3 Simulation design**

280 In order to observe and detect the independent and coupled effects of fishing and predation, as  
281 well as the eco-evolutionary feedbacks under these effects, we formed eight different scenarios  
282 (Figure 3). Among the tested scenarios, those without predation and a sex-specific difference in  $L_\infty$   
283 were simulated as reference scenarios. The scenarios used for the comparative approach are chosen  
284 with the focus on the independent and joint impacts of predation and fisheries, rather than the effect  
285 of the ecological characteristics of the prey. As the stabilization of prey–predator dynamics is time-  
286 consuming (a total of 3000 time steps), to minimize the computation time, we recorded *a priori* the  
287 adapted hake populations for each scenario. The adapted populations were recorded during the last  
288 150 time steps of a 3000 time step simulation based on the confirmation of stabilization gained  
289 through preliminary simulations (output and visual confirmation using graphs). Then, to test the  
290 scenario, we used the recorded populations to run simulations for 600 time steps in total and  
291 simulated 30 runs for each scenario in order to obtain the representative outcomes of the individual  
292 and population parameters. During these simulations in all predation scenarios, predation was  
293 applied continuously, while in all eight scenarios, fishing was introduced at the 400<sup>th</sup> time step. In  
294 this manner, we could effectively distinguish the impact of predation, fishing, and evolutionary  
295 processes. After the fishing period, we observed effects of the given pressures during the recovery

296 time until the end of the simulation. All simulations were performed in R Program v3.6.1 (R Core  
297 Team, 2019).

298 During the simulation testing stage, the introduction of fishing with an intensity of 0.15 and the  
299 duration of 100 time steps revealed that each scenario had a different threshold for the fishing  
300 duration (Figs S1–S3 in the Supplementary material). In other words, prey and predator population  
301 resilience as well as post-fishing recovery were affected by the total mortality applied to hake. The  
302 scenarios without predation demonstrated the highest resilience, enduring 100 time steps of fishing,  
303 followed by a successful recovery. The reference scenarios had a lower resilience of 75 time steps  
304 for the fishing duration, while the FRII scenarios endured 35 time steps of fishing. The FRIII  
305 predation scenarios were the least resilient and could only endure 30 time steps of fishing. There  
306 was no difference between non-evolutionary and evolutionary scenarios in the maximum sustained  
307 duration of the fishing period. For a balanced scenario design, we further applied exactly 30 time  
308 steps of fishing to investigate the ecological and evolutionary feedbacks under the coupled effects  
309 of fishing and predation. All outputs (incl. Supplement) represent average values of extracted  
310 parameters pulled across all 30 simulations for each scenario. In the results, we observe different  
311 aspects of predation, fisheries, evolution, and SSD on hake growth, maturity, genotypic diversity  
312 and demographic parameters with the regards to their implication for hake recovery and resilience.  
313 Firstly, we explore the coupled effects of predation and fishing with respect to FIE alone focusing  
314 on the differences between the evolutionary and non-evolutionary scenarios. Secondly, we explore  
315 the impact of predation on hake survival as well as how predation affects the fish size availability to  
316 fisheries. Lastly, we observe the interactions between the predator and hake fisheries with respect to  
317 evolutionary processes, and their implications for predator survival and fishing catches.

318

### 319 3. Results

#### 320 3.1 Potential for FIE under the coupled effect of predation and fishing

321 Overall results between the evolutionary scenarios and their non-evolutionary versions (e.g., the  
322 evolutionary and non-evolutionary scenarios without predation and with SSD, and so on) indicate  
323 mainly minor discrepancies for the stage of initial introduction of fisheries (presented in the  
324 Supplement). In the individual parameters for hake such as asymptotic length ( $L_{\infty}$ ) and intrinsic  
325 growth rate ( $K$ ), all non-evolutionary scenarios reach higher and lower scale values, respectively,  
326 than the same scenarios with evolution (Figs S1a and c). Similar responses in  $L_{\infty}$  and  $K$  are observed  
327 in simulations where an identical duration of fishing was applied (Figs 4a and b). More precisely,  
328 the impact of evolutionary processes in achieving the maximum length and its effect on growth rate  
329 work in favor of a higher growth rate per time step (age). Furthermore, in simulations with different  
330 and identical fishing durations, the evolutionary scenarios demonstrate continuously increasing and  
331 decreasing trends in all evolutionary scenarios of  $L_{\infty}$  and  $K$ , respectively (Figs S1a, c and Figs 4a,  
332 b). Compared to non-evolutionary scenarios, trends observed in the evolutionary scenarios of  $L_{\infty}$   
333 and  $K$  indicate that the ecological characteristics of hake (SSD, lifespan, and reproduction) in  
334 combination with evolutionary processes notably delay the stabilization of these individual  
335 parameters, despite the hake populations applied for each scenario being fully adapted to the  
336 respective scenario settings.

337 The FRIII scenarios demonstrate differences with evolution absent and present in age at maturity  
338 (Fig. 5a), affecting the speed of recovery. In the absence of evolution and with FRIII predation  
339 present, hake displays a slower recovery to the respective pre-fishing level, while evolutionary  
340 processes provide quicker recovery after fishing cessation. In addition, in the absence of evolution,  
341 hake displays a tendency for maturity at a younger age in the FRIII scenarios, although no similar  
342 effects of evolutionary processes on size at maturity (Fig. 5b) are observed under FRIII predation.  
343 In contrast, with only 30 time steps for the fishing period, size at maturity drops slightly (by  $\approx 1\%$ )

344 in the FRII scenarios, while under FRII predation, a similar reduction in age at maturity gradually  
345 levels out at its pre-fishing level by the end of the simulation time. However, longer fishing periods  
346 applied during the introduction of fishing induce an increase and decrease in the age and size at  
347 maturity, respectively, in the FRII scenario, whereas during the reference and no-predation  
348 scenarios (Figs S1b and d), age and size at maturity do not return to their pre-fishing values within  
349 the 170 time steps of the recovery period. The reference scenarios, as well as the scenarios without  
350 predation, endure the longest fishing periods (75 and 100 time steps in the reference and no-  
351 predation scenario, respectively); this indicates that longer fishing periods have a higher potential to  
352 induce persistent phenotypic changes (e.g., a long-term decrease or increase in the age and size at  
353 maturity) when hake SSD is unaccounted for.

354 The observed cumulative number of juveniles compared to the present genotypes suggests  
355 different genotypic range values among all scenarios (Figs S2 and 5c). Regardless of the applied  
356 fishing duration, a wider genotypic range is present in all evolutionary scenarios, as opposed to their  
357 respective non-evolutionary versions, which indicates a lower genotypic range due to the absence of  
358 sexual reproduction. When a longer fishing period is applied during the introduction fishing (Fig.  
359 S2), the range of genotypic values widens in the no-predation scenarios without evolution, while all  
360 FRII scenarios, as well as the evolutionary FRIII scenario, exhibit higher numbers of hake juveniles  
361 among lower genotypic values when compared to the same scenarios with a fishing period having  
362 30 time steps. While the genotypic values of the current approach translate directly to phenotype, or  
363 more precisely to body size, the genotypic trends observed are not reflected in the age–size  
364 distribution among evolutionary and non-evolutionary scenarios, meaning that the higher age–size  
365 ranges are not present in the evolutionary scenarios, as would be expected (Fig. 6). However, one  
366 exception exists where, under the conditions of absent evolutionary processes, the range of the  
367 average size at age is slightly higher in the non-evolutionary FRIII scenario than its evolutionary  
368 version (S7 and S8, respectively, in Fig. 6).



369 Among population parameters, recruitment, and biomass with respect to the carrying capacity  
370 (BM to CC) show a discrepancy between the FRIII scenarios in which evolutionary processes are  
371 present and absent (Figs 7a–b). The FRIII evolutionary scenario exhibits higher scale values for  
372 these parameters than the non-evolutionary scenario, which suggests higher hake survival due to the  
373 survival of favorable genotypes (i.e., evolutionary rescue). A similar discrepancy between  
374 evolutionary and non-evolutionary FRIII scenarios is observed in recruitment when a longer fishing  
375 period is applied (S3a), where no-predation and reference scenarios indicate delayed or impeded  
376 recovery to their respective pre-fishing levels. Although not presented in the Supplement, other  
377 population parameters such as prey abundance and BM to CC exhibit the same trend in reference  
378 scenarios and scenarios without predation in the presence of evolutionary processes and a longer  
379 fishing period. Hake population level parameters (i.e., BM to CC, recruitment) in the FRIII  
380 scenarios show a reciprocal relationship between hake numbers and predator density (Figs S3d and  
381 8c), where higher hake biomass do not increase FRIII predator density in the presence of evolution,  
382 although there are no differences in recovery among evolutionary and non-evolutionary FRIII  
383 scenarios. While evolutionary rescue supports a higher hake biomass, this occurs through the  
384 survival of prey sizes that are elusive to an FRIII predator, which otherwise thrives in the absence of  
385 an evolving prey. These trends in hake abundance with evolution present support higher fishing  
386 catches in the evolutionary FRIII scenario. While the presence or absence of evolutionary processes  
387 does not affect the prey–predator density ratio among FRII and FRII scenarios (Figs S3c and 8b),  
388 the female–male ratio of hake captures shows some discrepancies between non-evolutionary and  
389 evolutionary scenarios of no-predation and reference scenarios. FRII and FRIII scenarios show  
390 similar responses to the fishing period with respect to the absence and presence of evolution,  
391 although there is a slight delay in response to fishing in the case of FRIII predation.  
392

### 393 **3.2 Impact of predation mortality on hake survival and fisheries**

394 The discrepancy in population resilience observed in the simulation testing stage is most evident  
395 among scenarios with and without predation, where hake is more susceptible to demographic  
396 collapse under predation, especially in the FRIII scenario due to the lowest resilience of only 30  
397 time steps (Figs S1 and S3). Independent of fishing duration, most individual and population  
398 parameters of hake demonstrate different scale values due to the trait-mediated effects of predation  
399 (Figs S1 and S3, as well as Figs 4–5 and 7–8). Contrary to all scenarios without predation,  $L_{\infty}$   
400 shows distinctly higher values under the effect of predation (Figs S1a and 4a), which is reflected as  
401 a higher  $K$  in the absence of predation (Figs S1c and 4b). As the increasing trend in  $L_{\infty}$  and the  
402 decreasing trend in  $K$  are also present in all scenarios without predation, this suggests that the  
403 density-dependent parameters applied in all the scenarios contribute to the slow adaptation of these  
404 parameters (in addition to evolutionary processes and hake ecological characteristics). The reduced  
405 somatic growth rate under predation is further reflected in the lower age at maturity due to  
406 potentially higher allocation to reproduction under predation pressure, whereas reference and no-  
407 predation scenarios demonstrate maturity at an older age (Figs S1b and 5a). While all predation  
408 scenarios indicate lower somatic growth, size at maturity is unaffected by the presence of predation,  
409 with a slightly higher size at maturity in the FRII scenarios than the FRIII scenarios during the pre-  
410 fishing period (Figs S1d and 5b).

411 Both predation types exhibit strong overcompensation in age and size at maturity with fishing  
412 cessation, due to the release of fishing pressure (Figs 5a and b). For both age and size at maturity,  
413 the recovery is faster in all scenarios without predation but with SSD accounted for. In age at  
414 maturity, recovery under the reference and FRIII scenarios occurs within a narrow time period,  
415 whereas FRII scenarios prolong the recovery the most. Size at maturity more distinctly  
416 demonstrates the differences in recovery among scenarios, where the no-predation scenarios are  
417 followed by the FRIII, FRII, and reference scenarios. However, with a longer fishing period in the

418 reference and the no-predation scenarios (Figs S1b and d), these individual parameters exhibit a  
419 strong phenotypic shift in the absence of predation. Comparing the two predation types, the FRIII  
420 scenarios allow for quicker recovery, indicating a lesser negative impact than FRII predation,  
421 although this could be partly implied by the slightly longer fishing period applied in the FRII  
422 scenarios.

423 Predation mortality and the prey size selectivity shape the genotypic diversity (Fig. 5c) and  
424 demographic structure of the hake population (Fig. 6). Reference scenarios demonstrate a very  
425 narrow range of genotypes in comparison to the genotypic range values driven by the sex-specific  
426 difference in  $L_{\infty}$  and predation size selectivity. This strengthens the importance of the size  
427 discrepancy among hake females and males, and also suggests that predation drives genotypic  
428 diversity in hake, which in return reflects the wider range of the age–size distribution (Fig. 6) in all  
429 the predation scenarios. In comparison to the reference scenarios (S1–S2 in Fig. 6), the scenarios  
430 without predation (S3–S4 in Fig. 6) show an age–size distribution skewed towards larger females.  
431 However, the average size of hake is clearly higher in the FRII and FRIII scenarios (S5–S8 in Fig.  
432 6) than in all the scenarios without predation (S1–S4 in Fig. 5). While the size at age 0 (i.e.,  $L_0$ ) is  
433 the same for all the scenarios, the discrepancies are firstly observed in 1- to 2-year-old hake, which  
434 are larger in size for S4–S8 than for S2–S3.

435 Population parameters (BM to CC and recruitment) exhibit strong overcompensation after  
436 fishing cessation in all the predation scenarios (Figs 7a and b), where hake is clearly low in biomass  
437 and other abundance-correlated parameters in the presence of predation. The strong fish removal,  
438 however, is more pronounced under FRII than FRIII predation, which can be explained by the  
439 higher efficiency of an FRII predator in consuming prey at a lower prey density than an FRIII  
440 predator, particularly as prey density in the current IBM is solely dependent on prey abundance.  
441 While biomass levels are lower in the reference and all the predation scenarios, in the no-predation  
442 scenarios, biomass exceeds the carrying capacity during the pre-fishing and recovery periods. Such

443 levels of biomass suggest weaker density-dependent processes in the conditions of the scenarios  
444 without predation, which with the absence of top-down control allow the hake population to  
445 outgrow its own carrying capacity. During the pre-fishing period, FRII additionally induces greater  
446 fluctuation in all population parameters, regardless of fishing duration (Figs S3a and 7a–b).  
447 However, during the recovery period, all the presented population parameters demonstrate the same  
448 trend of recovery among scenarios as the size at maturity, where the no-predation scenarios allow  
449 for the fastest recovery, followed by the FRIII and FRII scenarios, and lastly the reference  
450 scenarios. The order of scenarios showing the fastest to the slowest recovery changes as the  
451 duration of the fishing period is increased, as FRIII scenarios now enable faster recovery in  
452 recruitment, followed by FRII scenarios, which show a delayed reduction in numbers towards the  
453 end of simulation time (Fig. S3a). Furthermore, all scenarios without predation notably slow down  
454 the recovery in recruitment, while in the absence of hake, SSD and predation recovery (i.e.,  
455 reference scenarios) is completely disabled.

456 The ratio of female to male hake exhibits different responses to fishing depending on the  
457 presence or absence of predation, particularly when observed within the overlapping time frame of  
458 fishing and predation (Fig. 7c). Reference scenarios as well as scenarios without predation exhibit a  
459 similar trend of a delayed response to fishing, where the proportion of hake males removed by  
460 fisheries increases by the end of the fishing period. Contrary to this, FRII and FRIII predators  
461 demonstrate different sex (size) selectivity during the fishing period, where an FRII predator  
462 increasingly selects hake females towards the middle of the fishing period and then shifts to male  
463 hake as fishing ends. An FRIII predator consumes more males as fishing starts, but this ratio of  
464 hake sexes gradually shifts towards hake females and then fluctuates around the middle towards the  
465 cessation of fishing. Furthermore, the predation types, with their respective targeted prey size,  
466 reveal the dynamics of predation and fisheries, suggesting a higher intensity of competition between  
467 fisheries and FRII predators. Particularly in case of the FRIII evolutionary scenario, the prey size

468 selectivity of predation is reciprocal to the size selectivity of the fisheries. When comparing Figure  
469 7c with the same graph for a longer fishing period (S3b), the comparison of hake sexes targeted by  
470 fisheries and predation is only possible among the scenarios with the two longest durations of the  
471 fishing period, meaning the reference scenarios and the scenarios without predation. The reference  
472 scenarios with a longer fishing period continue the trend observed in the reference scenarios under a  
473 short fishing period, where the proportion of female and male hake continues to fluctuate, with  
474 increasingly greater oscillations following each shift from one sex to the other (Fig. S3b). When  
475 comparing no-predation scenarios with short and long fishing periods, the proportions of hake  
476 males and females removed by the fisheries show a similar trend as in the reference scenarios, but  
477 with much lower oscillations.

478

### 479 **3.3 Predator–fisheries interactions: bottlenose dolphin survival and fishing catches**

480 The dynamic interactions between bottlenose dolphins and fisheries are mainly steered by the  
481 availability of hake to each competitor. While the absence of a natural competitor provides a higher  
482 gain for fisheries, the fishing catches decrease as the fishing period progresses, with catch slopes  
483 becoming steeper in all scenarios (Fig. 8a). The steepest decrease in catches is observed in the  
484 reference scenarios, which fall under the catches achieved in the conditions of the evolutionary  
485 FRIII scenario by the end of the fishing period. This demonstrates that incorporating key ecological  
486 parameters associated with the trait selected by fisheries (i.e., size), as well as predation mortality,  
487 slows down the potential depletion of fish. As observed in the hake population parameters (Figs 7a–  
488 b), as well as in the female–male ratio of hake (Fig. 7c), the most intensive fish removal when  
489 comparing the two types of predation is noted in FRII predation, which also reduces fishing catches  
490 the most. However, even though predation decreases fishing catches, the smoother catch slope  
491 observed in the evolutionary FRIII scenario (Fig. 8a) suggests a lower level of unsustainable  
492 fisheries removals in the long term.

493 Considering the competitive interaction between predators and fisheries, the prevailing fishing  
494 regime exerts a negative indirect effect on predator density through prey–predator interactions (Figs  
495 8b and c). More precisely, fishing reduces the predator density in both predation scenarios, which is  
496 also reflected in the overcompensation of the prey–predator density ratio after the cessation of  
497 fishing (Fig. 8b), particularly in the FRII scenarios with a longer fishing period (Fig. S3c). While an  
498 FRII predator achieves a higher density level through the co-evolved prey–predator interaction and  
499 more efficient consumption of prey, FRIII predator density benefits less from such interaction,  
500 particularly if evolutionary processes are accounted for (Fig. 8c). Interestingly enough, the prey–  
501 predator density ratio and particularly, the predator density of the evolutionary FRIII scenario  
502 demonstrates micro-oscillations between the time steps. In comparison to predation, the removal of  
503 hake by fisheries is significantly higher in intensity (observed in hake population parameters) than  
504 hake removal by bottlenose dolphins, which impacts on predator survival more profoundly than  
505 predators affect the fisheries gain due the absence of other target and prey species (Fig. 8c).  
506 Moreover, with a slightly longer fishing period applied in the FRII scenarios (Fig. S3d), predator  
507 density does not fully recover to its pre-fishing levels, with or without evolutionary processes in the  
508 prey.

509

## 510 **4. Discussion**

### 511 **4.1 Specific conditions dictate the potential for FIE under coupled size-selective pressures**

512 The coupled effects of predation and fishing have diverse implications for a range of fish life-  
513 history traits (e.g.,  $K$ , size and age at maturity), with one trait being more susceptible to  
514 evolutionary change than another under specific conditions: this dictates the resilience and stability  
515 of observed hake parameters, as well as affecting the speed and pattern of recovery in the  
516 parameters. These specific conditions are identified here as the presence or the absence of SSD in  
517 hake, the duration and intensity of both size-selective pressures, as well as the predation type.  
518 Among the individual hake parameters,  $L_{\infty}$  and  $K$  show resistance towards an evolutionary shift, as

519 the ecological characteristics of hake and the density-dependent processes slow down the  
520 stabilization of these parameters during the evolutionary scenarios. This can be explained by the  
521 formulation of SSD incorporated directly in hake  $L_{\infty}$ , which, in the presence of all other mentioned  
522 conditions, prolongs the time needed for the stabilization of  $L_{\infty}$  and, consequently,  $K$ . Furthermore,  
523 as  $L_{\infty}$  is the only evolving trait, the evolution in other life-history traits is not as affected by SSD  
524 due to the phenotypic rather than genetic correlations among  $L_{\infty}$  and other traits. As SSD in fish  
525 species is reflected in higher growth rate in males, which reach maturity earlier than females, an  
526 improved approach to the description of SSD would be to introduce additional and more reliable  
527 sex-specific data on hake growth parameters.

528 The length of the fishing period, removal intensity, and predation type appear crucial in inducing  
529 very persistent alterations in size and age at maturity. While age at maturity shows some resilience  
530 to the phenotypic shift in the FRII predation scenarios, size at maturity slightly drops after the  
531 cessation of fishing in the same scenarios. With a longer fishing period, the evolutionary change for  
532 both individual parameters becomes obvious in all scenarios without predation and SSD accounted  
533 for, while age at maturity under the FRII scenarios also shows a lack of recovery to its pre-fishing  
534 level. A longer fishing period applied in the reference and no-predation scenarios, as well as FRII  
535 scenarios, indicates that fishing duration is pivotal to inducing more pronounced shifts in these  
536 individual parameters. This is corroborated by studies on exploited stocks that demonstrate a  
537 delayed evolutionary response to fishing after a longer period of exploitation (Devine et al., 2012).  
538 Fish species naturally prone to early maturation schedules have demonstrated a higher potential for  
539 reduced size at maturity under fishing pressure (Landi et al., 2015). This can only partly explain the  
540 decrease in size at maturity of hake in the FRII scenarios after fishing cessation, since the expected  
541 decrease in age at maturity did not occur within the same scenario settings. Fishing duration might  
542 not be enough to explain the observed alterations in size and age at maturity, as the overall intensity  
543 of size-selective removal caused by predation and fishing ultimately contributes to the direction and

544 magnitude of their responses. For predation pressure, the predation type is associated with the  
545 predation intensity owing to the differences in consumption patterns between the two predation  
546 types. The difference in the intensity of size-selective removal between the two predation types  
547 supports the higher potential for FIE in the mentioned parameters when the FRII predation type is  
548 applied. However, while the currently prevailing fishing size selectivity in synergy with predation  
549 removal does not impoverish the genotypic diversity of hake, as observed in other fish species  
550 experiencing size-selective removals (see Marty et al., 2015), the ensured phenotypic diversity  
551 (owing to the phenotypic variation added to the genotypic values) could mask the potential  
552 evolutionary shifts in individual life-history traits. In this case, the potential for adaptive phenotypic  
553 plasticity in hake has minimized the impact of evolutionary feedbacks, which is consistent with  
554 other studies addressing the phenotypic adaptations of hake to evolutionary processes under  
555 harvesting pressure (Hidalgo et al., 2014). Consequently, intraspecific phenotypic diversity further  
556 facilitates population demographic stability (i.e., a wide range of age–size classes) and minimizes  
557 the impact of size-selective fishing.

558

#### 559 **4.2 The importance of accounting for size-related ecological characteristics**

560 Hake population parameters demonstrate different responses to predation and fishing depending  
561 on the presence or absence of SSD and evolutionary processes, as well as the predation type and  
562 fishing period. The impact of predation and fishing is most intensive in the FRII scenarios (with  
563 SSD in hake accounted for), while the most negative ecological impact of fishing is noted in  
564 conditions where predation and SSD are not accounted for. Evolutionary processes, however, have  
565 crucial implications for hake abundance and recruitment in the case of the FRIII predation type,  
566 where hake survival increases, despite fishing and predation pressures, through evolutionary rescue.  
567 This demonstrates that true adaptive changes in hake life-history traits have the potential to  
568 counteract the negative effects of size-selective pressures (see Hendry et al., 2011). At the



569 individual and population levels, a short fishing duration and accounting for SSD without predation  
570 allows hake to recover faster from fishing than under conditions with predation, which supports the  
571 cases arguing for slow or even disabled recovery in some overexploited fish stocks due to high  
572 predation mortality (Hutchings and Kuparinen, 2019). With an increase in fishing duration, the  
573 implications of accounting for SSD, the presence of predation, and the predation type become more  
574 crucial to the speed of recovery in hake population parameters. Without SSD accounted for and  
575 predation, recovery is impeded or disabled, although the FRIII predation type enables faster  
576 recovery than FRII predation. Here, SSD forms the basis for recovery, which is not surprising  
577 considering the important implications of SSD for growth parameters, size and age at maturity, size-  
578 selective mortality, and ultimately, the demographic structure of many fish species (Carroll and  
579 Lowerre-Barbieri, 2019; Cerviño, 2014; Keyl et al., 2015). Furthermore, the life-history traits of  
580 shared fish prey targeted by predators and fisheries is pivotal in determining to what degree the  
581 coexistence of predators and fisheries is possible (Huss et al., 2014).

582

#### 583 **4.3 Predator individual variability: implications for fish stock assessments**

584 Under the condition of a two-species prey–predator interaction, it is not surprising that the  
585 predation tested here profoundly impacts on fish biomass and population resilience. The current  
586 results, however, should be considered alongside the assumptions of this approach, which does not  
587 account for the individual variability, ontogenetic development stage, or catholic diet of the  
588 bottlenose dolphin. According to Navarrete and Manzur (2008), individual predator parameters  
589 (e.g., body size, diet composition, and *per capita* prey consumption) are more responsive to changes  
590 in prey for a generalist predator. However, with regards to the wide range of prey species,  
591 bottlenose dolphins have been known to demonstrate prey species preference when offered a choice  
592 (Corkeron et al., 1990). Furthermore, under low availability of other prey species, in small food  
593 webs as well as in the case of predator specialization to feed on specific prey species (Pettorelli et

594 al., 2011), the factors associated with opportunistic feeding in bottlenose dolphins can be less  
595 relevant in the presence of high intra- or interspecific competition. In the absence of individual  
596 variability, predation types provide a source of ecological complexity directing the response of  
597 predator parameters to fishing. Thus, with the increased level of ecological complexity from FRII to  
598 FRIII, the competition between predators and fisheries decreases. Here the consumption pattern of  
599 predators is of high importance in fish stock assessments, not just for the quantification of predation  
600 but also to avoid negative indirect effects of fisheries on marine trophic links and the environment.  
601 Moreover, as the evolving prey can facilitate the survival of a non-evolving predator (termed as  
602 “indirect evolutionary rescue” by Yamamichi and Miner [2015]), this coincides with the predator  
603 population dynamics observed in the FRII predator, but not for the FRIII. In contrast, the reciprocal  
604 size selectivity of the prey noted between fisheries and FRIII predation is similar to the fishing  
605 strategies targeting all individuals regardless of maturation status, thus reducing the potential for  
606 FIE (Ernande et al., 2004). Studies addressing the competitive interactions between marine  
607 mammals and fisheries, as well as the impact of high fishing mortality, have revealed that  
608 overexploitation is more detrimental to the sustainability of long-term fisheries yields than marine  
609 mammals (Garcia et al., 2012; Morissette et al., 2012) or the potential FIE (Hutchings and  
610 Kuparinen, 2019). Furthermore, even without a multi-species aspect, the current results predict  
611 potential long-term unsustainable outcomes for hake abundance and, consequently, for fisheries in  
612 the absence of predation, which is consistent with ecosystem-based studies that predict a decline in  
613 fisheries yields due to the lower ecosystem productivity caused by the removal of top predators  
614 (Morissette et al., 2010; Roman et al., 2014).

615

## 616 **5. Conclusions**

617 In this study, we demonstrated how two sources of size-selective mortality in combination with  
618 the interplay between ecological and evolutionary processes shape the responses of prey parameters

619 at individual and population levels. With respect to this, the duration, intensity, and selected fish  
620 size range of both predation pressures have the most prominent implications for the heritability of  
621 shifts observed in hake life-history traits, which need to be accounted for when aiming to avoid FIE.  
622 As different factors can determine the duration, intensity, and size selectivity of predation and  
623 fisheries, the future direction in understanding the prerequisites driving the evolution of individual  
624 life-history traits is to investigate which combinations, as well as thresholds of these conditions,  
625 have the potential to trigger heritable changes. Since in our study the predation type was found to  
626 determine the intensity and size selectivity of predation pressure, future research should address the  
627 potential for evolutionary changes with an increase in ecological complexity (i.e., predation type,  
628 multi-species, or even ecosystem aspect). According to the outputs of the initial introduction of  
629 fisheries, incorporating more than one type of predation in fish stock assessments can aid in setting  
630 more reliable limits for harvest yields and rates, weighted against the risks associated with predation  
631 intensity as well as potential heritable phenotypic changes. Ultimately, understanding of how  
632 predation affects fish availability for fisheries will consequently provide insights into the conditions  
633 under which predators indirectly support fisheries or render fishing yields low.

634 While conservative, the current approach applies key prey ecological characteristics and  
635 evolutionary processes providing insights into pivotal, baseline mechanisms in the prey–predator  
636 dynamics, as well as the ecological interactions between bottlenose dolphins and hake fisheries.  
637 With consideration of the implications of SSD for hake fecundity and size-selective mortality, SSD  
638 combined with the predation type provides additional insights into the species-specific resilience to  
639 and recovery potential under one or multiple size-selective pressures. Such prey–predator dynamics  
640 has direct implications for setting sustainable reference points and successful conservation measures  
641 to ensure fish survival and the gain of future fisheries. Furthermore, while SSD and FRIII predation  
642 selectivity in the presence of evolutionary processes enrich the prey’s phenotypic and consequently

643 genotypic diversity, this can ensure a higher resilience to potential shifts in size at maturity, as it  
644 disperses the intensity of size-selective removals by fisheries.

645 The fishing mortality and selectivity applied here resulted in a profoundly negative ecological  
646 impact on hake survival, exceeding the removals and selectivity of predation mortality. Moreover,  
647 indirect fishing effects extend to predator survival, as hake consumption by the bottlenose dolphin,  
648 and more precisely its prey size selectivity, will depend on the age–size classes available to the  
649 predator in the presence of an intensive fishing regime. The dynamics of the fishing regime and  
650 predation types of the current study demonstrate how predators adapt their prey size selectivity  
651 according to the size selectivity of fishing. The question is whether these predator adjustments to  
652 fishing size selectivity will be sufficient to counteract the effects of overexploitation. To answer  
653 this, further research is required to address the role of predation from a wider perspective of  
654 complex trophic interactions or the ecosystem level. Such aspects are comprehensively included  
655 within dynamic ecosystem and individual-based models, which could also explore indirect or even  
656 “food-web competition” between bottlenose dolphins and hake fisheries (see ICES, 2015; Wood et  
657 al., 2018). However, incorporating individual variability in both prey and predators with the  
658 integration of eco-evolutionary feedbacks in a more complex trophic structure is an ambitious step  
659 forward to improving the ecosystem approach to fisheries, as well as conservation efforts for natural  
660 predators. While similar approaches to the current one do exist, they have not generally accounted  
661 for one of the features or processes included in our model. Thus, addressing such a multilayered  
662 research question requires a basic approach, where underlying mechanisms can be tested and  
663 brought to light. On the other side, holistic approaches to fisheries management demand models that  
664 can encapsulate such complexity whilst maintaining the applicability of their outputs to managerial  
665 decision-making processes. In line with this, the management of wild fish stocks still remains a  
666 multidisciplinary agenda with a strong need for a transdisciplinary approach.

667

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674

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936 **Tables**

937 **Table 1.** Set values of model parameters ( $M$  = natural mortality;  $M_{rc}$  = natural mortality due to cost  
938 of reproduction;  $N_i$  = prey initial population size;  $CC$  = prey carrying capacity;  $p_i$  = predator initial  
939 population density;  $a$  = predator attack rate;  $e$  = assimilation efficiency;  $d$  = predator death rate;  $h$  =  
940 predator handling time;  $F$  = fishing intensity;  $a, b$  = fishing selectivity parameters;  $L_{50}$  = length at  
941 50% retention).

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<i>Set model parameters</i>	<i>Prey initial values</i>	<i>Parameters</i>	<i>Values</i>	<i>Sources</i>	<i>Predation</i>	<i>Parameters</i>	<i>Values</i>	<i>Sources</i>
		<i>M</i>	0.1	Estimated through model parameterization		<i>Predation</i>	<i>e</i>	0.90
<i>M<sub>rc</sub></i>	0.1	<i>d</i>	0.06		Estimated through model parameterization			
<i>N<sub>i</sub></i>	4000	<i>h</i>	0.5					
<i>CC</i>	6000	<i>F</i>	0.15					
<i>Predation</i>	<i>p<sub>i</sub></i>	0.3	<i>Fishing</i>		<i>a, b</i>		-10.85; 0.411	Estimated through model parameterization
	<i>a</i>	0.07		<i>L<sub>50</sub></i>	24.6 cm	ICES, 2019		

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954 **Figure captions**

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956 **Figure 1.** The European hake and its native distribution range in European, African, and Asian seas

957 (Wikipedia Commons, user Misigon; ec.europe.eu).

958

959 **Figure 2.** Visual presentation of an individual growth trajectory and density-dependent growth (plot

960 A) as well as a stepwise introduction of the size-selective removals by predation (plot B) and

961 fisheries (plot C). In all plots fish body length is plotted against the simulation time steps (T) with



962 the curved line depicting the asymptotic growth trajectory (full line denoting the trajectory with  
963 evolution and dashed without evolution). In plot A), each individual trajectory is defined by length  
964 at maturity ( $L_{mat}$ ) and maximum theoretical length ( $L_{\infty}$ ). If the hake population density is high, the  
965 time left for the individual to grow (i.e., the interval between  $T$  and  $T+1$ ) is reduced by 50%  
966 (adapted from Kuparinen et al., 2012). Plot B) demonstrates the introduction of predation, which is  
967 present throughout the entire simulation time (denoted by the green background), selecting only  
968 individuals between 21 and 51 cm of length (denoted by dotted horizontal lines). In plot C), with  
969 predation present, fishing is introduced through a narrower time period in the simulation (denoted  
970 by the red background), but targeting a range of hake length with a 50% retention at the length of  
971 26.4 cm ( $L_{50}$ ; red dot-dashed horizontal line). The lower limit for the hake size range is set by the  
972 age of the individual ( $> 2$ ) denoted in the red dotted horizontal line, which approximately  
973 corresponds to 22–23 cm of length. However, it is important to note that the actual retention by the  
974 fishing gear is described by logistic, asymptotic curve.

975

976 **Figure 3.** Scheme of eight tested scenarios denoted by S1–S8, as follows: S1) non-evolutionary  
977 scenario without predation, a sex-specific difference in asymptotic length ( $L_{\infty}$ ), as well as without  
978 evolution (reference scenarios); S2) evolutionary scenario without predation and a sex-specific  
979 difference in  $L_{\infty}$ ; S3) non-evolutionary scenario without predation; S4) evolutionary scenario  
980 without predation; S5) non-evolutionary scenario with FRII predation; S6) evolutionary scenario  
981 with FRII predation; S7) non-evolutionary scenario with FRIII predation; and S8) evolutionary  
982 scenario with FRIII predation.

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984 **Figure 4.** Graphs showing the average values of individual hake growth parameters, asymptotic  
985 length (a) and the intrinsic growth rate (b). The parameters are plotted against the simulation time  
986 on the x-axis, where vertical dashed lines delineate the fishing period of 30 time steps from the pre-  
987 fishing period (up to 399 time steps) and recovery period (431–600). Non-evolutionary and

988 evolutionary scenarios are denoted by dotted and bold lines, respectively. Scenarios without  
989 predation are depicted in grey, FRII in green, and FRIII in red. Scenarios without predation and a  
990 sex-specific difference in  $L_{\infty}$  (reference scenarios) are presented in black.

991

992 **Figure 5.** Average values of hake individual parameters showing the age (a) and size at maturity  
993 (b), and genotypic diversity (c) with respect to each scenario. Plots a) and b) are plotted against  
994 simulation time steps where the fishing period is denoted with vertical, dashed lines (400–430). In  
995 plot c), the cumulative number (N) of juveniles is plotted against the genotype values. In all plots,  
996 the dotted lines denote the non-evolutionary scenarios, whereas the bold lines denote the  
997 evolutionary scenarios. All reference scenarios are depicted in black color, while no-predation, FRII  
998 and FRIII scenarios are depicted in grey, green and red colors, respectively.

999

1000 **Figure 6.** Hake demographic structure based on each scenario. The x-axis denotes the scenarios as:  
1001 S1) non-evolutionary scenario without predation and a sex-specific difference in  $L_{\infty}$  (reference  
1002 scenario without evolution); S2) evolutionary scenario without predation and a sex-specific  
1003 difference in  $L_{\infty}$  (reference scenario with evolution); S3) non-evolutionary scenario without  
1004 predation; S4) evolutionary scenario without predation; S5) non-evolutionary scenario with FRII  
1005 predation; S6) evolutionary scenario with FRII predation; S7) non-evolutionary scenario with FRIII  
1006 predation, and S8) evolutionary scenario with FRIII predation. Each bar per scenario depicts the  
1007 average size at age as well as each age category ranging from 0–12 years. Size at  $L_0$  (first size bar)  
1008 is the same for all scenarios and set to 3.9 cm.

1009

1010 **Figure 7.** Graphs presenting the average values of hake demographic parameters for each scenario,  
1011 as follows: a) recruitment; b) population biomass with respect to carrying capacity (BM to CC); and  
1012 c) hake female to male density ratio. Simulation time steps on the x-axis are divided into pre-fishing

1013 (0–399), fishing (400–430), and recovery periods (431–600) by vertical dashed lines. Scenarios  
1014 differ according to the presence or absence of evolution as bold or dotted lines, while a black color  
1015 depicts reference scenarios, a grey color depicts scenarios without predation, green with FRII, and  
1016 red with FRIII predation scenarios.

1017

1018 **Figure 8.** Hake and bottlenose dolphin population dynamics under fishing pressure with respect to  
1019 each scenario. Average values of the following population parameters are presented: a) caught hake  
1020 biomass; b) hake and bottlenose dolphin density ratio; and c) bottlenose dolphin density. Simulation  
1021 time steps (x-axis) are divided by vertical dashed lines into pre-fishing (0–399), fishing (400–430),  
1022 and recovery periods (431–600), although plot a) only shows the fishing period. Dotted and bold  
1023 lines depict non-evolutionary and evolutionary scenarios, respectively, where a grey color denotes  
1024 scenarios without predation, green FRII, and red FRIII predation scenarios. Reference scenarios are  
1025 denoted in black only in plot a).

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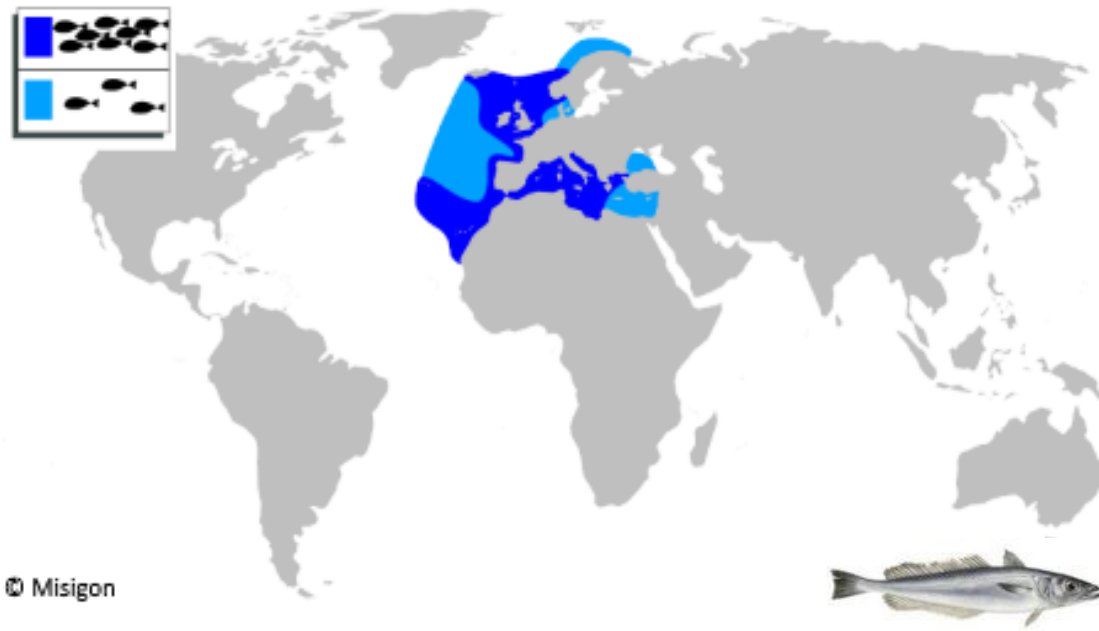
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1031 **Figures**

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1034 **Figure 1.** The European hake and its native distribution range in European, African, and Asian seas  
1035 (Wikipedia Commons, user Misigon; ec.europe.eu).

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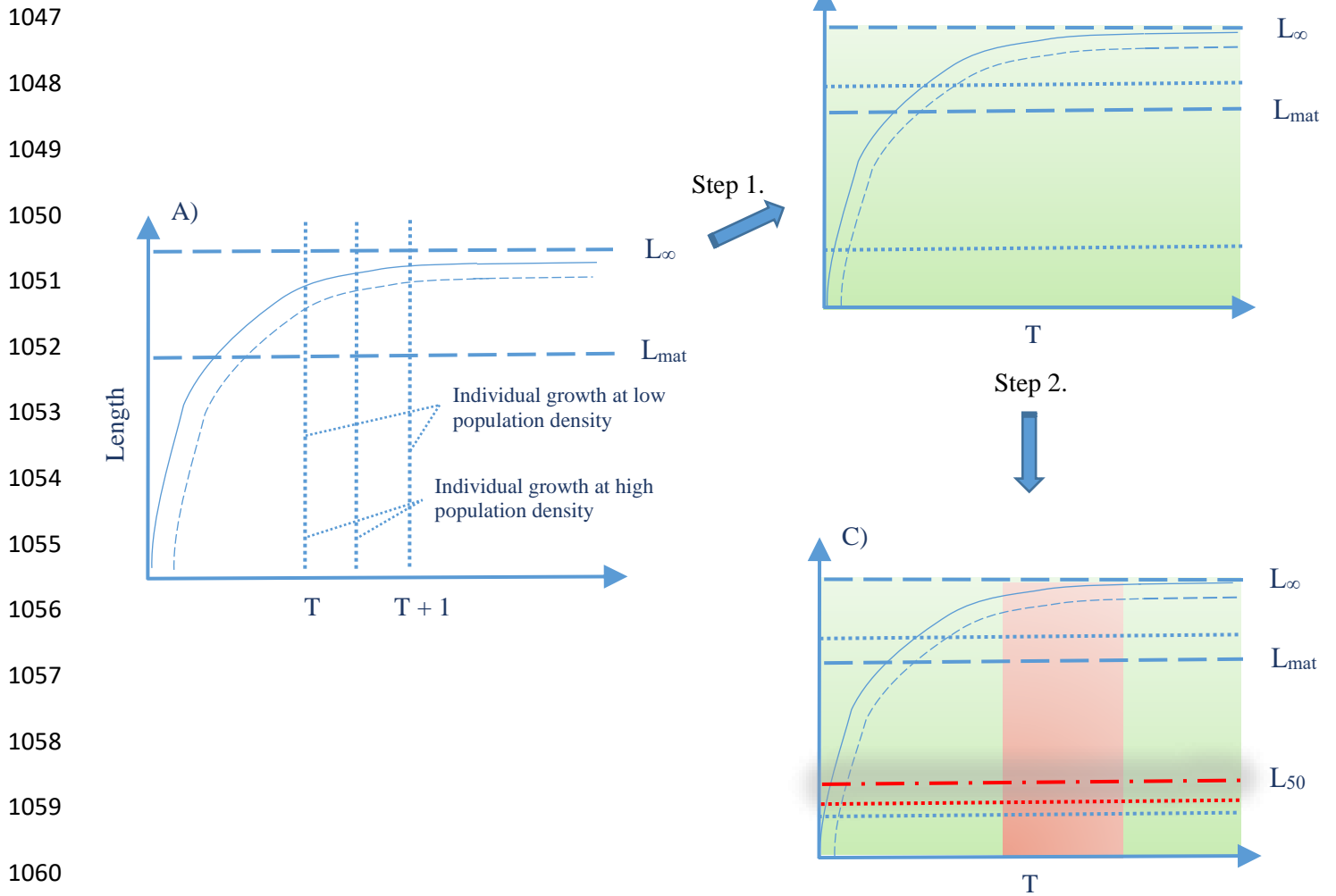
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1061 **Figure 2.** Visual presentation of an individual growth trajectory and density-dependent growth (plot  
 1062 A) as well as a stepwise introduction of the size-selective removals by predation (plot B) and  
 1063 fisheries (plot C). In all plots fish body length is plotted against the simulation time steps (T) with  
 1064 the curved line depicting the asymptotic growth trajectory (full line denoting the trajectory with  
 1065 evolution and dashed without evolution). In plot A), each individual trajectory is defined by length  
 1066 at maturity ( $L_{mat}$ ) and maximum theoretical length ( $L_{\infty}$ ). If the hake population density is high, the  
 1067 time left for the individual to grow (i.e., the interval between T and T+1) is reduced by 50%  
 1068 (adapted from Kuparinen et al., 2012). Plot B) demonstrates the introduction of predation, which is  
 1069 present throughout the entire simulation time (denoted by the green background), selecting only  
 1070 individuals between 21 and 51 cm of length (denoted by dotted horizontal lines). In plot C), with  
 1071 predation present, fishing is introduced through a narrower time period in the simulation (denoted

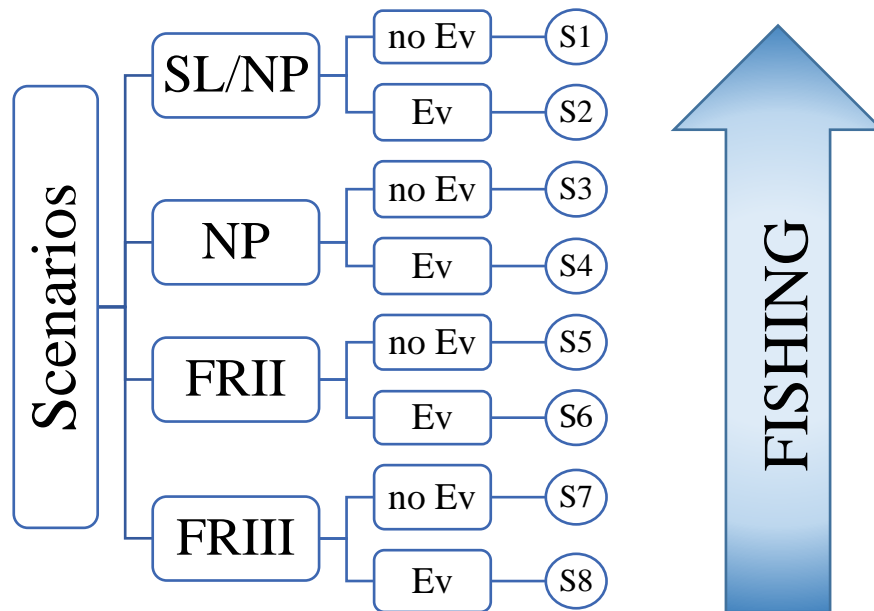
1072 by the red background), but targeting a range of hake length with a 50% retention at the length of  
 1073 26.4 cm ( $L_{50}$ ; red dot-dashed horizontal line). The lower limit for the hake size range is set by the  
 1074 age of the individual ( $> 2$ ) denoted in the red dotted horizontal line, which approximately  
 1075 corresponds to 22–23 cm of length. However, it is important to note that the actual retention by the  
 1076 fishing gear is described by logistic, asymptotic curve.

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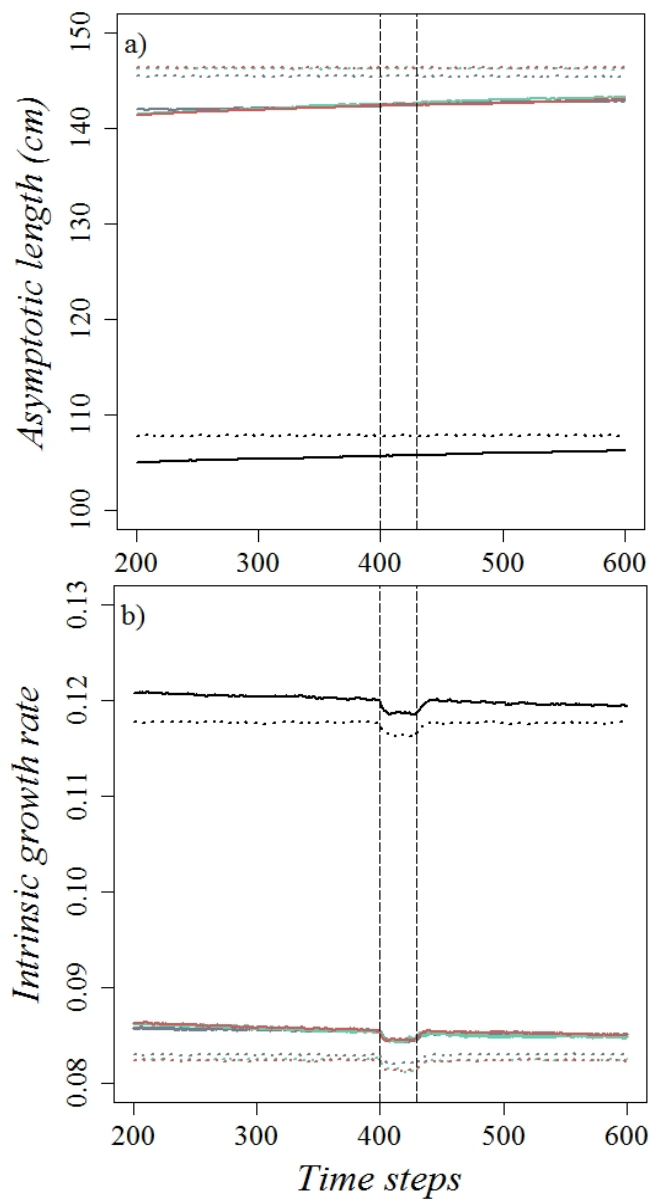
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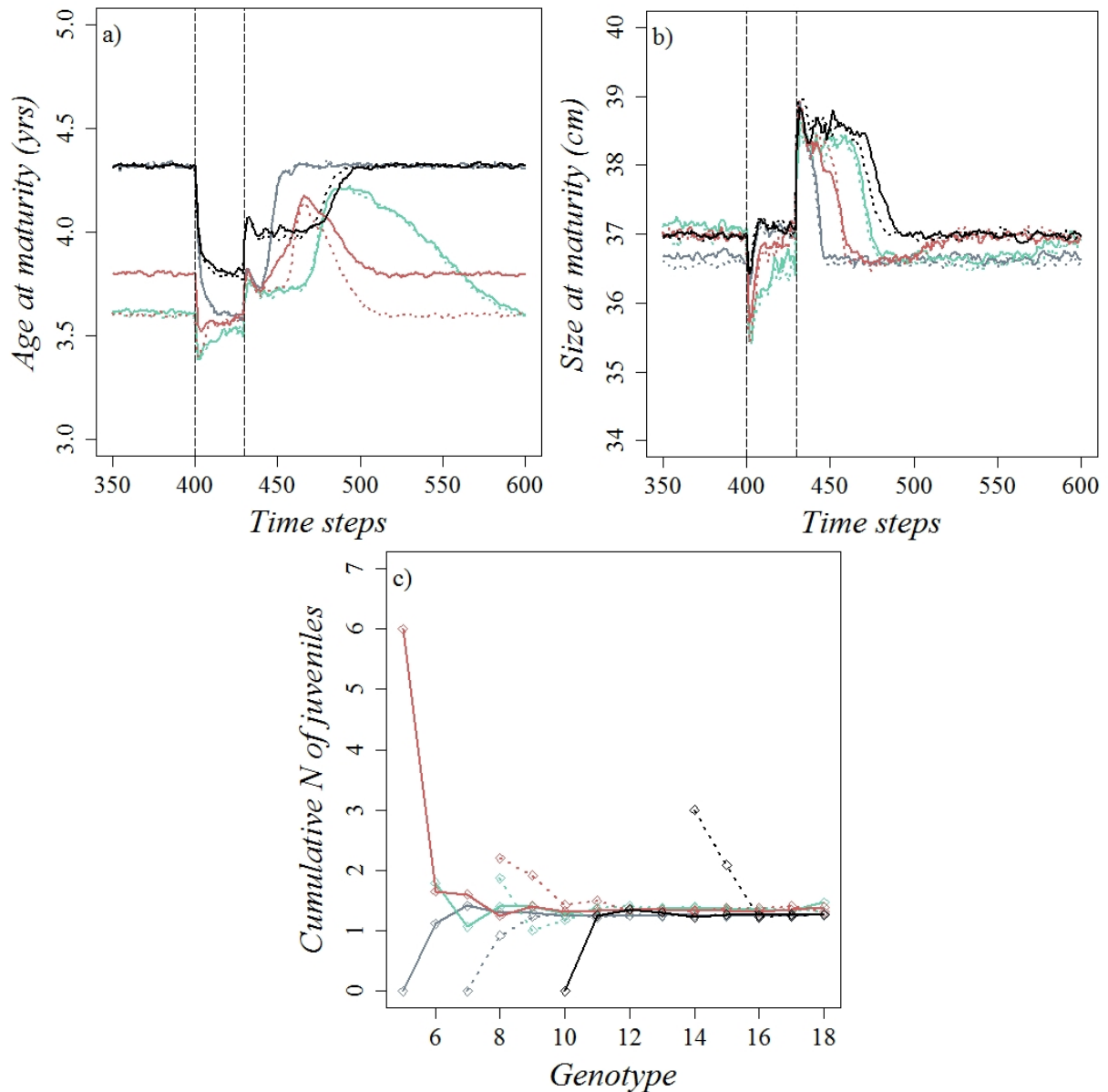
1081 **Figure 3.** Scheme of eight tested scenarios denoted by S1–S8, as follows: S1) non-evolutionary  
 1082 scenario without predation, a sex-specific difference in asymptotic length ( $L_{\infty}$ ), as well as without  
 1083 evolution (reference scenarios); S2) evolutionary scenario without predation and a sex-specific  
 1084 difference in  $L_{\infty}$ ; S3) non-evolutionary scenario without predation; S4) evolutionary scenario  
 1085 without predation; S5) non-evolutionary scenario with FRII predation; S6) evolutionary scenario  
 1086 with FRII predation; S7) non-evolutionary scenario with FRIII predation; and S8) evolutionary  
 1087 scenario with FRIII predation.

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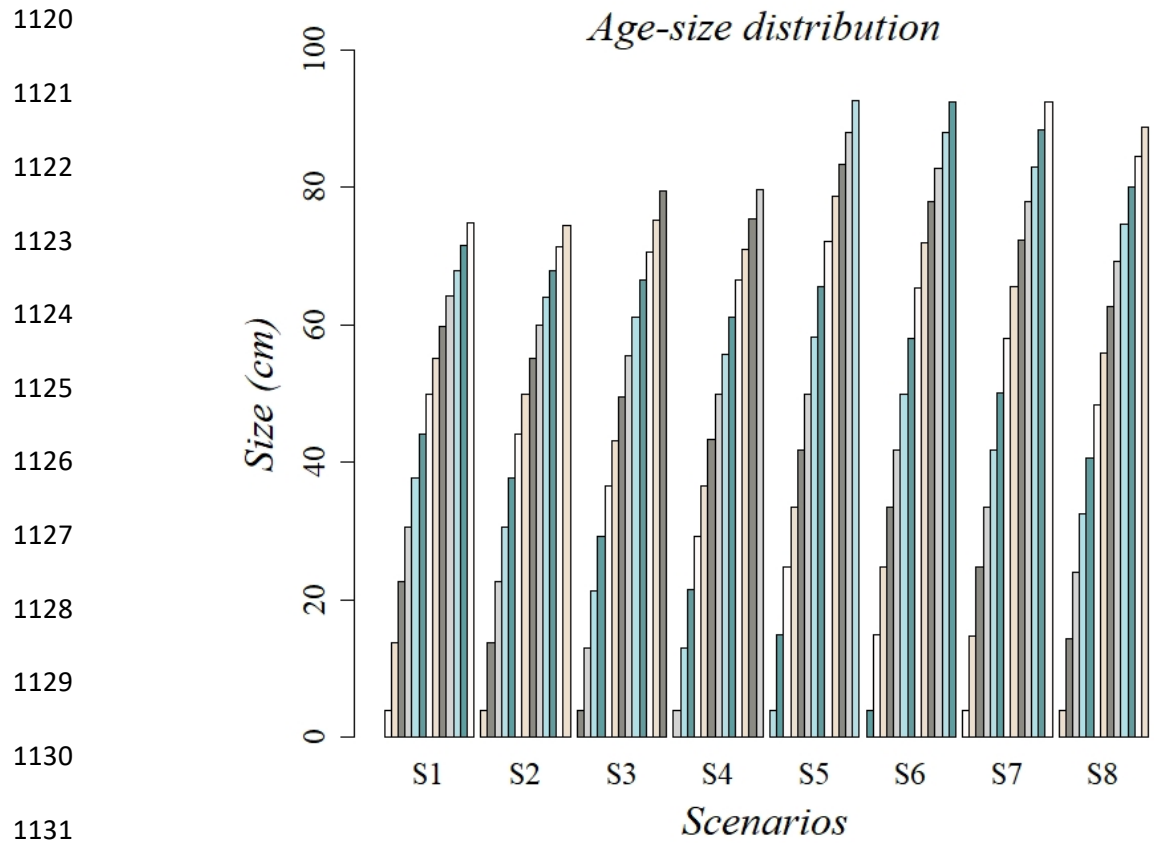
**Figure 4.** Graphs showing the average values of individual hake growth parameters, asymptotic length (a) and the intrinsic growth rate (b). The parameters are plotted against the simulation time on the x-axis, where vertical dashed lines delineate the fishing period of 30 time steps from the pre-fishing period (up to 399 time steps) and recovery period (431–600). Non-evolutionary and evolutionary scenarios are denoted by dotted and bold lines, respectively. Scenarios without predation are depicted in grey, FR II in green, and FR III in red. Scenarios without predation and a sex-specific difference in  $L_{\infty}$  (reference scenarios) are presented in black.

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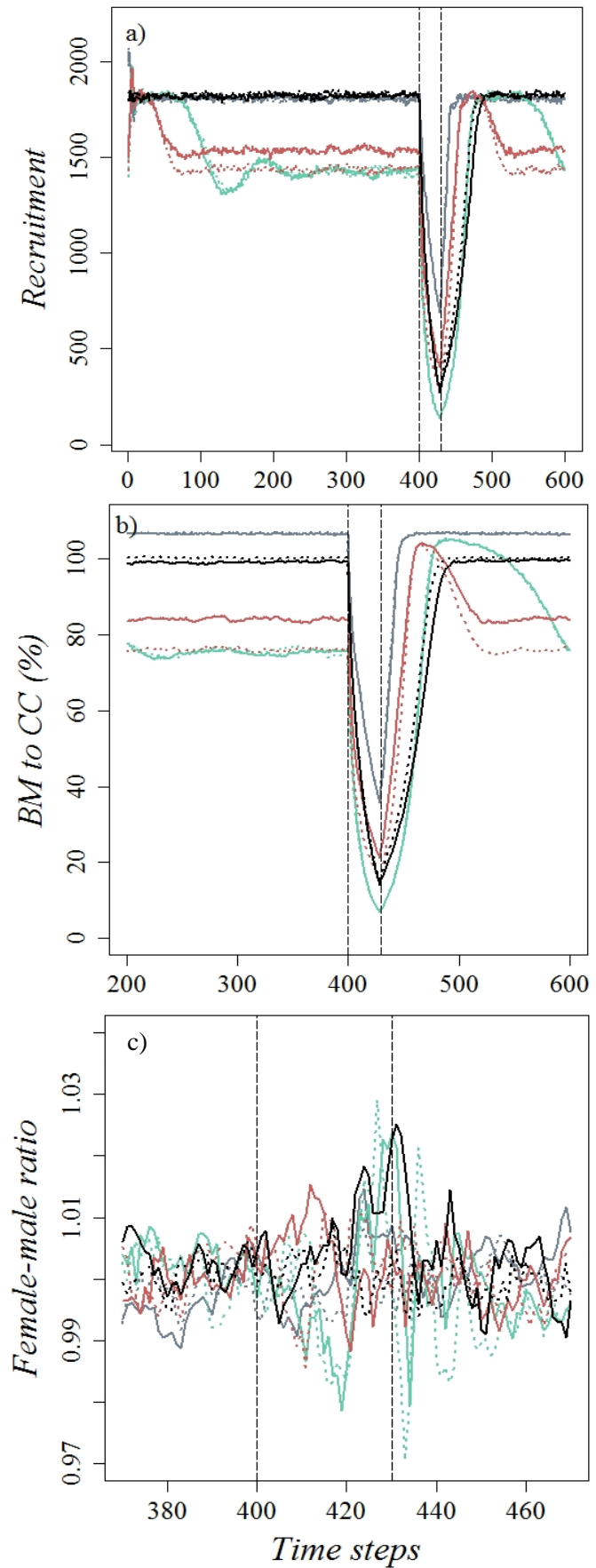
1113 **Figure 5.** Average values of hake individual parameters showing the age (a) and size at maturity  
 1114 (b), and genotypic diversity (c) with respect to each scenario. Plots a) and b) are plotted against  
 1115 simulation time steps where the fishing period is denoted with vertical, dashed lines (400–430). In  
 1116 plot c), the cumulative number (N) of juveniles is plotted against the genotype values. In all plots,  
 1117 the dotted lines denote the non-evolutionary scenarios, whereas the bold lines denote the  
 1118 evolutionary scenarios. All reference scenarios are depicted in black color, while no-predation, FRII  
 1119 and FRIII scenarios are depicted in grey, green and red colors, respectively.



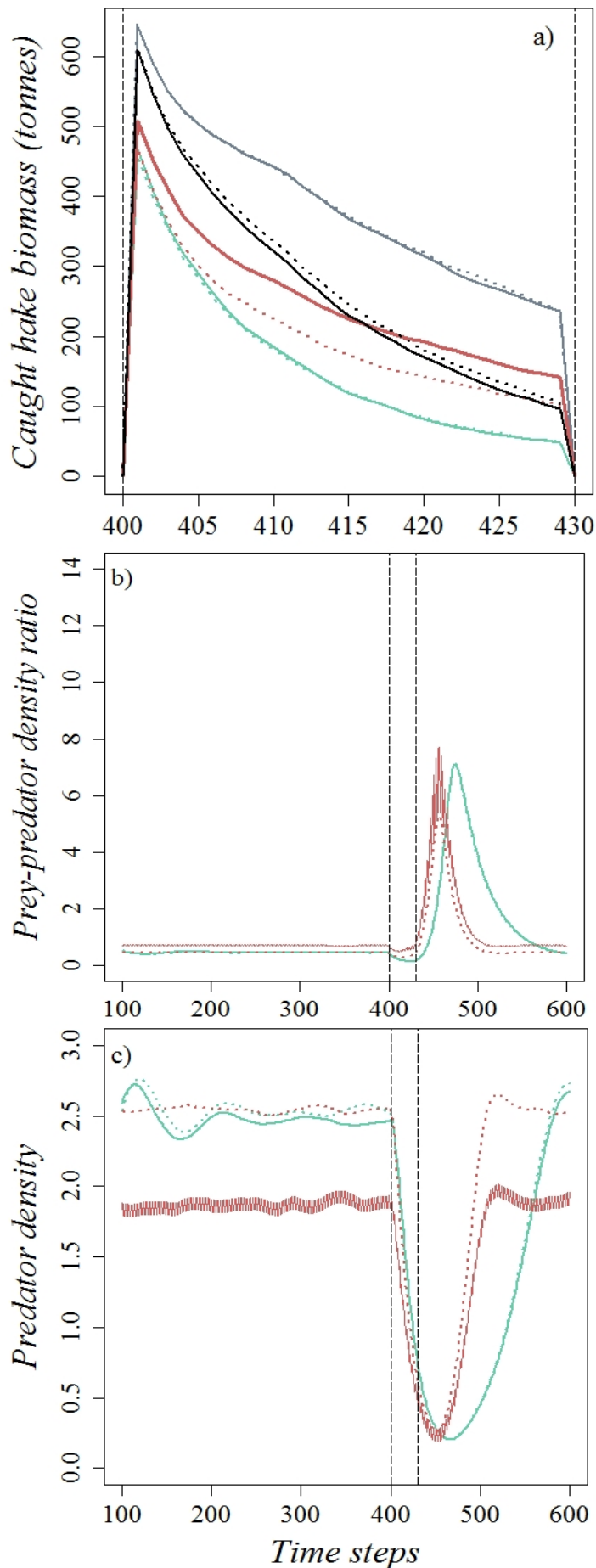


**Figure 6.** Hake demographic structure based on each scenario. The x-axis denotes the scenarios as: S1) non-evolutionary scenario without predation and a sex-specific difference in  $L_{\infty}$  (reference scenario without evolution); S2) evolutionary scenario without predation and a sex-specific difference in  $L_{\infty}$  (reference scenario with evolution); S3) non-evolutionary scenario without predation; S4) evolutionary scenario without predation; S5) non-evolutionary scenario with FRII predation; S6) evolutionary scenario with FRII predation; S7) non-evolutionary scenario with FRIII predation, and S8) evolutionary scenario with FRIII predation. Each bar per scenario depicts the average size at age as well as each age category ranging from 0–12 years. Size at  $L_0$  (first size bar) is the same for all scenarios and set to 3.9 cm.

1145 **Figure 7.** Graphs presenting the average  
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 1147 each scenario, as follows: a) recruitment;  
 1148 b) population biomass with respect to  
 1149 carrying capacity (BM to CC); and c) hake  
 1150 female to male density ratio. Simulation  
 1151 time steps on the x-axis are divided into  
 1152 pre-fishing (0–399), fishing (400–430),  
 1153 and recovery periods (431–600) by vertical  
 1154 dashed lines. Scenarios differ according to  
 1155 the presence or absence of evolution as  
 1156 bold or dotted lines, while a black color  
 1157 depicts reference scenarios, a grey color  
 1158 depicts scenarios without predation, green  
 1159 with FRII, and red with FRIII predation  
 1160 scenarios.



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**Figure 8.** Hake and bottlenose dolphin population dynamics under fishing pressure with respect to each scenario. Average values of the following population parameters are presented: a) caught hake biomass; b) hake and bottlenose dolphin density ratio; and c) bottlenose dolphin density. Simulation time steps (x-axis) are divided by vertical dashed lines into pre-fishing (0–399), fishing (400–430), and recovery periods (431–600), although plot a) only shows the fishing period. Dotted and bold lines depict non-evolutionary and evolutionary scenarios, respectively, where a grey color denotes scenarios without predation, green FRII, and red FRIII predation scenarios. Reference scenarios are denoted in black only in plot a).