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Farming-up coastal fish assemblages through a massive aquaculture escape event.

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1 Abstract

We investigated the changes on the mean trophic level of fish assemblages across different spatiotemporal scales, before and after a massive escape event occurred off La Palma (Canary Islands), which resulted in the release of 1.5 million fish (mostly Dicentrarchus labrax) into the wild. The presence of escaped fish altered significantly the mean trophic level of fish assemblages in shallow coastal waters. This alteration was exacerbated by the massive escape. A nearby marine protected area buffered the changes in mean trophic level but exhibited the same temporal patterns as highly fished areas. Moreover, escaped fish exploited natural resources according to their total length and possibly, time since escapement. New concerns arise as a "farming up" process is detected in shallow coastal fish assemblages where marine aquaculture is established. Keywords: escaped fish, aquaculture, trophic level, diet, Dicentrarchus labrax, Sparus aurata.

35 **1. Introduction**

36

37 Aquaculture of high-trophic-level (HTL) fish species is growing, especially in 38 developed countries, as a result of a rising demand on these products and the highest 39 profit obtained from carnivorous species (Deutsch et al., 2007). This process has been 40 named "farming-up" (Pauly et al., 2001; Stergiou et al., 2008), and one of its major 41 concerns is the exploitation of wild fish stocks to fed high trophic level species, called 42 "tigers of the sea" by Naylor and Burke (2005). In addition, culturing non-native or 43 locally absent fish species is already a frequent practice (Casal, 2006; Arismendi et al., 44 2009; Liao et al., 2010) that is predicted to grow in the next years (Shelton and 45 Rothbard, 2006). Thus, as a result of both mentioned trends, in some areas, HTL species 46 that were absent or with low abundances in natural habitats are being released into the 47 wild through escape events. Technical failures and sea storms provoke both recurrent-48 small or punctual-massive escapes across the coasts where open-net cage aquaculture is 49 established (Jensen et al., 2010). This process could be comparable to continuous 50 restocking actions with non-indigenous or locally absent species (Lorenzen et al., 2012), which benefits have been pointed by some authors (Briggs, 2008; Schlaepfer et al., 51 52 2010) but are, in general, not recommended due to the unpredictable negative effects 53 they could have (Courtenay et al., 2009; Ricciardi and Simberloff, 2009).

54

Many studies have pointed out potential and detected consequences due to the release of 55 56 fish (exotic or not): genetic hybridisation (McGinnity et al., 2003); predation on native 57 species (Albins, 2013; Green et al., 2012); competition for trophic resources (Declerck 58 et al., 2002); introduction of parasites and diseases (Arechavala-Lopez et al., 2013); 59 changes in fisheries dynamics (Dimitriou et al., 2007), among others. Recently, it has 60 been demonstrated that marine ecosystems are much more susceptible to large-scale 61 invasion pressures than previously thought (Edelist et al., 2013). But even if escaped 62 fish do not establish self-reproducing populations, they may produce persistent impacts 63 due to the repeated supply of propagules through new escape events (Arismendi et al., 64 2009; Jensen et al., 2010). Given the mobility of escapees (González-Lorenzo et al., 65 2005; Arechavala-Lopez et al, 2011, 2012), they could affect particularly important areas such as marine protected areas (MPAs). However, it has been suggested that 66 67 MPAs could show some resilience (sensu Holling, 1973, "the amount of disturbance 68 that an ecosystem could withstand without changing self-organized processes and

structures", but see Gunderson, 2000 for a review of the concept) to the effects caused
by different impacts, including species introduction, as assemblages within them are
expected to have a better conservation state (Stachowicz et al., 1999).

72

73 In the Canaries, where finfish production in open-net cages during 2009 was 7,910 tons 74 (APROMAR, 2012), European sea bass (*Dicentrarchus labrax*) and gilthead sea bream 75 (Sparus aurata) have been introduced in some of the islands where no natural 76 populations of these species existed (Brito et al., 2002; Toledo-Guedes et al., 2009). 77 That is the case of La Palma Island, where a massive escape event occurred between 78 December 2009 and January 2010. Repeated northwest sea storms generating waves up 79 to 6 meters height resulted in both lack of maintenance operations and increased 80 mechanical stress for aquaculture facilities (Ramírez et al., 2011; Puertos del Estado, 2012). As a result, around 1.5 million fish (90% sea bass and 10% sea bream) were 81 82 released into the wild during that period (Ramírez et al., 2011). A previous study 83 revealed that escaped fish entered a nearby (\sim 15 km) MPA and their abundances within 84 were similar to those found in other areas of the island (Toledo-Guedes et al., 2014). As 85 far as we know, this is the largest sea bass escape event documented to date worldwide.

86

87 We capitalize on this event to examine the potentiality of escaped fish to alter the mean 88 trophic level (mTrL) of fish assemblages in shallow coastal waters and discuss the 89 potential consequences of these changes. In particular we studied i) if fish assemblages 90 mTrL was affected by the massive escape of HTL fish, ii) if the magnitude in mTrL 91 alteration was related to the presence of a MPA and iii) the trophic role of escaped sea 92 bass in coastal waters. For that we analyse the spatiotemporal variation of mTrL before 93 and after the massive escape event, using the estimation of fish abundances and size by 94 visual census in shallow coastal waters, and additionally we studied the diet of fugitive 95 sea bass, in relation to size, through stomach content analysis.

- 96
- 97 2. Material and Methods
- 98

99 2.1. Study site and sampling effort

100

Our study was carried out in La Palma (Fig. 1), one of the westernmost islands of the
Canarian archipelago, situated in the north-eastern part of the Central Atlantic (28°40'N,

103 17°52'W). Aquaculture facilities are in a single location off the western coast. A marine 104 protected area (MPA) is situated 15 kilometres to the south from fish farms. 105 106 A total of 6 localities (Fig. 1), and three sites (n=6) in each locality, were sampled by 107 means of visual census (see next section), at different distances from release point (0.8 108 to 30 km). Three of the localities were situated in La Palma MPA, the other three, 109 outside the MPA, were considered as highly fished areas (HFA) following Sangil et al., 110 2013a. Each locality was sampled four times: March 2009, October 2009, March 2010 111 and October 2010. A total of 432 visual censuses were carried out through the study. 112 113 2.2. Visual censuses 114 115 Based on previous methodology (Toledo-Guedes et al., 2009), snorkelling visual 116 censuses of escapees were performed in transects of 100x5 m, between 1 and 5 m depth.

In the initial 25 m, all the fish species abundances and sizes were recorded, while across the rest of the survey only escaped fish were counted. A second pass of the same transects served to establish habitat heterogeneity and complexity, measuring the cover % of different habitats and habitat features; sandy bottom, rocky platform, cliff and boulders classified by the size of their major length (ML): small boulders-SB (ML \leq 50 cm), medium boulders-MB (50 cm<ML \leq 1 m), and large boulders-LB (ML>1 m) (García-Charton et al., 2004).

124

- 125 2.3. Mean trophic level calculation
- 126

127 Length estimates of fish from surveys were converted to weight by using the allometric128 length-weight conversion:

129 $W = aTL^b$,

where W is weight in grams (i.e. biomass), parameters a and b are constants obtained from the literature (Froese and Pauly, 2012), and TL is total length in cm. When values for a and b were unavailable, the parameters from a congeneric species with similar shape and maximum total length were used.

134

Mean trophic level of the fish assemblage in each transect (mTrL_t) was then calculatedas follows:

137 mTrL_t= $\sum_{t}(TrL_{i-n} \cdot W_{i-n}) / \sum_{t} W_{i-n}$ (Pauly, 1998; CIESM, 2000),

where the summation of trophic level of each species (TrL_{i-n}) recorded in the transect, multiplied by their weight (W_{i-n}) , is divided by the total weight amounted in the same

transect. Trophic levels for each species were recorded from FishBase (Froese and
Pauly, 2012).

142

143 2.4 Statistical analysis

144

145 2.4.1. Overall analysis

146

Possible relations (i.e. direct trophic interactions) between the presence of escaped fish
and the abundance of other species were explored through Spearman's correlation
index.

150

To ascertain whether the mTrL of shallow coastal fish assemblages is altered by the 151 152 presence of escaped fish, we compared untransformed mTrL of transects with no 153 presence of escaped fish against those transects with presence of escapees across the 154 study. Due to the unbalanced nature of the analysis, a PERMANOVA (Anderson, 2001) 155 test was carried out over Euclidean distance matrix and 4999 permutations, using 156 distance to fish farm and arcsinx+1 transformed environmental variables as covariates. 157 The latter allowed detecting differences in mTrL irrespective of the proven 158 environmental influence on fish assemblages (García-Charton et al., 2004).

159

160 Kolmogorov-Smirnov test was used to compare size frequency of both sea bass and sea 161 bream visual counts before and after the massive escape, aiming to test previous 162 hypothesis on the possible alteration of size frequency of escapees in the wild due to 163 punctual massive escape events (Toledo-Guedes et al., 2009).

164

165 2.4.2. Spatiotemporal analysis

166

Univariate PERMANOVA (Anderson, 2001) tests were performed over untransformed
 mTrL to detect spatiotemporal patterns of change. Euclidean distances matrix and 4999
 permutations were used. A five-factor design was constructed as follows:

170

- 171 Year Ye Fixed, two levels (2009, 2010). Test de influence of the massive escape 172 event over the analysed variables.
- *Season Se -* Fixed, two levels (March, October). Test possible cold versus warm
 seasonal changes due to a higher winter release of farmed fish (Toledo-Guedes et al.
 2014).
- 176 Protection Pr Fixed, two levels (marine protected area MPA–, highly fished area –

177 HFA–). Test for differences in mTrL between MPA and HFA.

- 178 *Locality Lo –* Random, nested in *Protection* (three levels).
- 179 *Site Si –* Random, nested in *Locality* (three levels).
- 180

Again, environmental variables (arcsin+1 transformed), and distance to release point in km, were added as covariates to remove their possible effect over mTrL. As the random factor *Locality* remained not significant (p-value=0.657) in the first analysis, it was pooled to gain power of analysis (Underwood, 1997). For the interpretation of the results, significant interaction terms with random factors involved were not taken into consideration, as the higher level fixed factor effect remains relevant regardless of the outcome of the interaction with a random factor (Quinn and Keough, 2002).

188

189 2.4.3. Escapees vs. wild assemblages analysis

190

191 To assess the importance of escaped fish in the study area, their biomass (g $100m^{-2}$) was 192 compared with that of other species with similar trophic level. Biomass of escaped sea 193 bass (trophic level 3.8±0.6; Froese and Pauly, 2012) was compared with the biomass of 194 species whose trophic level is higher than 3.5 (i.e. medium-top predators). This group of 195 species was composed of potential sea bass predators and competitors: Seriola spp., 196 Pomatomus saltatrix, Mycteroperca fusca, Sphyraena viridensis, Aulostomus strigosus, 197 Scorpaena maderensis, Belone belone, Pseudocaranx dentex, Mustelus mustelus, 198 Pomadasys incisus, Epinephelus marginatus and Trachinotus ovatus. This was also 199 done for sea bream (trophic level 3.3 ± 0.5 ; Froese and Pauly, 2012); in this case, we 200 compared against species with a trophic level between 3 and 3.5. This group was 201 composed of sparids: Diplodus cervinus, Diplodus sargus, Oblada melanura and 202 Lithognathus mormyrus and other species whose diet is composed mainly of small 203 crustaceans: Thalassoma pavo, Canthigaster capistrata, Sphoeroides marmoratus and 204 Symphodus trutta. Pair-wise comparisons were made for each area (MPA and HFA) and

time period; U-Mann Whitney test served to assess differences in the mean biomass ofthe groups as normality was not met.

207

208 2.5. Stomach content analysis

209

Individuals of *D. labrax* (n=144) were caught by spearfishing. A total of 112 escaped fish were captured during surveys in Tenerife and La Palma in 2008 and 2009. These were not associated to any known massive escape event; therefore, this group of fish was assigned to recurrent leaking escapees (leak group). On the other hand, 32 fish were caught in June 2010 in La Palma Marine Protected Area and, thus, due to the recent massive escape and their schooling behaviour, were assigned to that event (massive group).

217

All fish were measured (total length TL) to the nearest mm and weighted (accuracy of 218 219 0.01 g). The stomach intestine was separated from the body and its contents removed. 220 Prey items were counted by number, fresh weighted and identified to the lowest 221 possible taxonomical level. Thus, for each prey, percentage by number (N%) and 222 weight (W%), frequency of occurrence (O%) and the alimentary coefficient (Q = N% x223 W%) were calculated (Hureau, 1970). The importance of prey groups was assessed 224 using the following categories (based on values of Q and O%; Rosecchi and Nouaze, 225 1987): main preferred prey (Q>100, O%>30%); main occasional prey (Q>100, 226 O%<30%); secondary common prey (10<Q<100, O%>10%); secondary additional prey 227 (10<Q<100, O%<10%); accidental prey (Q<10). The index of relative importance (IRI) 228 (Pinkas et al., 1971) was also estimated, $IRI = (N\% + W\%) \times O\%$. Trophic level of both 229 groups of escaped sea bass were calculated as the mean weighted trophic level of the 230 food items plus one (Froese and Pauly, 2012).

231

With the aim of detecting possible differences in the diet of recent escapees, non-metric Multidimensional Scaling (MDS) was performed over Bray Curtis similarity matrix of the weights of the three main prey groups found in stomach contents (i.e. insects, crustaceans and fish). Moreover, PERMANOVA test was carried out comparing the diet of the two groups using total length (TL) as a covariate, given that the diet of sea bass changes during its life cycle in the wild (Kelley, 1987; Rogdakis et al., 2010). For the statistical analyses, SPSS 15.0 and PRIMER6 & PERMANOVA+ were used.

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239	
240	3. Results
241	
242	3.1. Overall results
243	
244	None of the pair-wise Spearman's correlations between abundances of escapees and the
245	rest of wild fish species resulted significant.
246	
247	Mean trophic level of shallow coastal fish assemblages was significantly increased
248	(p<0.001) in those surveys where the presence of escaped fish was recorded
249	(mTrL±SE=3.16±0.55) in comparison to those transects with no escaped fish
250	(mTrL±SE=2.78±0.41; Table 1 and Fig. 2).
251	
252	Size frequency distributions in visual counts showed significant differences for sea bass
253	(Z=15.110; p<0.001) and sea bream (Z=6.948; p<0.001) before and after the massive
254	escape event. Mean TL of escaped sea bass (28.01±5.51 cm) and sea bream (28.39±8.08
255	cm) were clearly increased after the massive escape: sea bass and sea bream mean TL
256	was 40.35±9.3 cm and 43.73±3.52 cm, respectively (Fig 3a and b).
257	
258	3.2. Spatiotemporal patterns
259	
260	As the random factor <i>Locality</i> remained not significant (p-value=0.657), it was pooled
261	to gain power of analysis. In this way, PERMANOVA detected spatiotemporal patterns
262	of mTrL, these patterns consisted in higher mTrL in 2010, during March and at HFA
263	localities when they are compared to 2009, October and MPA localities respectively
264	(Table 2; Fig. 4).
265	
266	3.3. Escapees vs. wild assemblages
267	
268	Pair-wise comparisons showed that biomass of escaped sea bass at the two sampled
269	areas was equal or higher than the sum of the other medium-high trophic level species
270	for all the sampled periods with the exception of October 2010 (Fig. 5a). Conversely,

- biomass of escaped sea bream resulted always significantly lower than the biomass of
- 272 other species with similar trophic level (Fig. 5b).

273

274 *3.4. Use of trophic resources*

275

276 Table 3 shows the diet composition and importance of each prey for the two groups of 277 sea bass analysed. For the leak group (Table 3a), fish was the main prey group, 278 followed by crustaceans, being the rest of the prey groups classified as accidental. It is 279 remarkable that only one individual was found with pellets in the stomach. Lower prey 280 diversity is observed in sea bass associated with massive escape (Table 3b). In this case, 281 the main prey group was crustaceans; the most preferred being the decapod *Percnon* 282 gibessi. Regarding the vacuity index, leak group had a 33.9% of empty stomachs, while 283 the massive group showed a 12.5%. Trophic level of the massive escape group was 284 lower (3.2) than that of the leaking group (4.2).

285

MDS indicated that sea bass associated with massive escape in La Palma had a different diet in comparison to the leak group (Fig. 6a.). The ordination responds to the importance of the three prey groups in the diet of each individual (Fig 6bcd). The group denoted as massive is situated in the area where crustaceans are the main item by weight in the stomachs. PERMANOVA test confirms that sea bass of the leak and massive groups had differing diets (p<0.001), irrespective of their sizes (TL), but size resulted in an important variable when explaining the diet of escaped sea bass (p<0.001; Table 4).

293

294 **4. Discussion**

295

The input of HTL fish by aquaculture through escapes events generates a "farming up" process over shallow wild fish assemblages, rising their mTrL. This alteration was exacerbated by the massive escape that also changed the size frequency distribution of escaped individuals in the wild. Although temporal patterns of mTrL were the same in both HFA and MPA, the latter showed certain degree of resilience to alterations on mTrL. Moreover, escaped fish exploited natural resources according to their total length and, possibly, depending on the time at liberty.

303

A clear increase in mTrL is observed due to the escaped fish. However, these alterations seem to be related to the direct presence of escapees. The cultured (and escaped) species have a TrL well above the mTrL of native fish assemblages found in shallow coastal

307 waters in the area, thus, the presence of escapees in the wild inevitably provokes a rise 308 in this indicator. Consistent temporal trends revealed that mTrL was higher in 2010, 309 after the massive escape event, but also in March sampling period when compared to 310 October in both years. This is in concordance with previous studies that found the same 311 temporal trends for the abundance of escaped sea bass in the wild (Toledo-Guedes et al., 312 2014). This would correspond to a higher release of farmed fish during winter storms, 313 reflected in March sampling (Toledo-Guedes et al., 2014). Our results show that, 314 although mTrL inside the MPA is altered, the magnitude of this alteration is not as large 315 as in HFA. In other words, MPA seems to exhibit certain resilience to changes in mTrL 316 if compared to HFA. The ability of MPA to buffer the rise in mTrL could be based on a 317 higher abundance of herbivorous (i.e. low trophic level) species. Owing to the 318 protection against fishing, an increment of predators of the barren-ground founder sea 319 urchin Diadema africana (Rodríguez et al., 2013) have been observed; subsequent 320 depletion of the latter and further recovery of erect algae together with herbivorous fish 321 species represents an already well-studied trophic cascade effect (Sangil et al., 2012). 322 Thus herbivorous biomass 'pulls down' the mTrL maintaining it at relative low levels despite the MPA is equally affected by the presence of escaped fish (Toledo-Guedes et 323 324 al., 2014).

325

326 Although this study failed at detecting negative or positive correlations between number of escapees and abundance of other fish species, direct or indirect effects (e.g. trophic 327 328 cascades) cannot be discarded in the mid and long term. Other studies have revealed 329 that the input of predators in a semi-closed systems can cause an alteration of trophic 330 interactions and cascade effects (Ojaveer et al., 2004; Casini et al., 2012). The same 331 scenario of relative isolation occurs in La Palma island as the absence of coastal shelf 332 (Acosta et al., 2003) promotes the concentration of shallow bentho-demersal fish 333 assemblages (including escapees) near the coast, limiting connectivity and dilution of 334 potential impacts among the islands (Sangil et al., 2013b).

335

336 Sea bass have become the most abundant predator in shallow coastal waters (between 1 337 and 5 m depth) in La Palma (this study) and probably in those islands where sea bass is 338 cultured (pers. obs.). Even in areas such as the MPA, where fish assemblages are 339 supposed to be best preserved and abundances of top predators reach maximum 340 (Newman et al., 2006), escaped sea bass outnumbers in biomass the rest of medium-

341 high trophic level species. Actually, similar results have been indicated in other areas 342 where top predators have been introduced; as Cephalopholis argus and Lutjanus 343 kasmira in Hawaii (Friedlander et al., 2002; Dierking, 2007) or the red lionfish (Pterois 344 spp.) that is now established and in rapid expansion in the western North Atlantic 345 (Whitfield et al., 2002; Schofield, 2009). Nonetheless, the success of these invaders is 346 based upon their ability to close their life-cycle in natural habitats, while populations of 347 escaped fish are strongly dependant on new escapees in the Canaries (Toledo-Guedes et 348 al., 2009, 2012). It is necessary to remark that our results are valid in the depth strata we 349 have studied (i. e. very shallow coastal waters), where a big proportion of escaped fish 350 are found (Toledo-Guedes et al., 2009) and top predators are uncommon. In the case of 351 escaped sea bream, their abundances in the surveyed areas are not as high, and fish 352 species of their "trophic surroundings" are well represented by several species, mainly 353 sparids.

354

Functional diversity (sensu lato) has been proven to be an indicator of ecosystem health 355 356 and function (Clemente et al., 2010). It has been also suggested that it could prevent the 357 insertion of non-indigenous species in recipient ecosystems (Stachowicz et al., 1999). 358 Thus, the lack of top predators in the surveyed areas could favour escaped sea bass 359 (avoiding competition and predation), while abundance of sparids could avert the 360 success of escaped sea bream in the wild. Nonetheless, other reasons for a lower 361 prevalence of the latter seems to be the result of lower intensity of release, together with 362 a naive behaviour that could increase natural and fishing mortality in comparison to sea 363 bass (Arechavala-Lopez et al., 2012; Toledo-Guedes et al., 2014).

364

365 Our data on the diet of escaped sea bass supplement those previously published 366 (Toledo-Guedes et al., 2009). The results obtained for the individuals not associated to 367 any known massive escape (leak group) are in line with the mentioned study. On the 368 other hand, the diet of sea bass associated with the massive escape markedly differs to 369 the leak group in several aspects (e.g. lower percentage of vacuity, lower prey diversity 370 and lower trophic level). Even though the number of studied stomachs is limited, 371 vacuity percentage was very low for the massive group. This indicates that six months 372 after the massive escape event, surviving escapees were able to actively exploit 373 available resources in natural habitats as the MPA. Many studies have pointed to the 374 ontogenetic changes in diet suffered by sea bass in their natural range of distribution

375 (Kelley, 1987; Rogdakis et al., 2010 and references therein). In extensive cases, we can 376 say that trophic level of wild sea bass is positively related with the size (Rogdakis et al., 377 2010). Our results support the importance of fish's total length in its diet, and highlight 378 that trophic interactions posed by escaped sea bass could largely depend on the size of 379 the fish that escape. Nonetheless, time at liberty seems to be another factor explaining 380 the observed diet, actually a "hunting learning" period has been already suggested for 381 escaped sea bream in the Mediterranean (Arechavala-Lopez et al., 2012). This 382 adaptation period would also account for the lower trophic level showed by recent 383 escapees (i.e. massive group), as they predated mainly over crustaceans that are less 384 mobile and thus, easier to catch than fish.

385

386 4.1. Conclusions and final recommendations

387

With this study we propose a further dimension of the concept 'farming up' related not only to a rise in the trophic level of cultured species (as presented by Stergiou et al., 2009) but also a rise of mTrL of wild fish assemblages in the coasts where aquaculture facilities are present, due to the release of those farmed fish. If we scale up the issue, the need for studies at wider spatial scales (e.g. Mediterranean) arises.

393

Taking into account the high mobility of the escapees, remediation through regular 394 395 eradication actions with highly selective fishing techniques (e.g. spearfishing) seems 396 unaffordable in terms of costs. However, as natural and fishing mortality apparently 397 control abundances of escaped fish (Toledo-Guedes et al., 2014), eradication efforts 398 should be centred in valuable areas where fishing pressure is low or absent as MPAs. 399 Adaptive management of these areas would prevent potential negative effects caused by 400 escaped fish. In any case, this would not be applicable to other regions (e.g. 401 Mediterranean), where wild counterparts cohabit with escapees because in most of the 402 cases, wild and escaped fish can only be differentiated after being caught (Arechavala-403 Lopez et al., 2012).

404

A likely grow in aquaculture production worldwide, together with a concentration on a
few proven species (several of which would be exotic or locally absent; Shelton and
Rothbard, 2006) could lead to ethical and environmental issues. Thus, for a correct
development of aquaculture industry, the necessity of risk assessment plans grounded

409 on empirical data is clear. The implementation of mitigation, contingency and
410 restoration plans, has special relevance when aquaculture facilities are situated near
411 sensible areas (e.g. MPAs) and/or imply species introductions.

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	ACCEPTED MANUSCRIPT
631	Captions
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633	Figure 1. Study area. Black circle: aquaculture facilities / release point. White circles:
634	localities sampled outside La Palma MPA. White triangles: localities sampled at MPA.
635	Black line: limits of La Palma MPA.
636	R'
637	Figure 2. Box plot comparing mean trophic level of visual censuses with absence (grey)
638	and presence (black) of escaped fish.
639	
640	Figure 3. Size frequency of escaped sea bass (a) and sea bream (b), before (grey) and
641	after (black) the massive escape event.
642	
643	Figure 4. 3-dimensional plot of $mTrL_0$, $\Delta Troph$ and $mTrL$ at locality level through
644	sampling periods.
645	
646	Figure 5. Mean biomass (\pm SE) of both escaped (a)sea bass and (b) sea bream (black
647	bars) and other fish species with similar trophic level (grey bars) at MPA and HFA
648	through sampling periods: n.s.: not significant, *: p<0.05, **: p<0.01, ***: p<0.001.
649	Note the logarithmic scale in "y" axis.
650	
651	Figure 6. MDS plot showing the ordination of sea bass individuals by diet according to
652	their (a) origin, and by weight of each group of preys: (b) insects, (c) crustaceans and
653	(d) fish.

Appendix. Mean biomass (grams 100 m⁻² \pm SE) for each species recorded in the studied localities. Localities are numbered from North to South.

			March 2	2009					October	2009		
Species	1	2	3	4	5	6	1	2	3	4	5	6
Dicentrarchus labrax	289.8 ± 247.7	421.1 ± 403.3	42.9 ± 27.8	9.3 ± 8.9	1 ± 1.7	95.4 ± 78.2	88.4 ± 158.8	$215{,}273.3 \pm 152{,}105.3$	$5,\!483 \pm 4,\!239.3$	$3,\!117.3\pm3,\!166.8$	$4{,}716 \pm 3{,}040$	721 ± 502.7
Sparus aurata	9.3 ± 9.6	-	-	268.1 ± 319.6	1.3 ± 2.3	41.8 ± 60.6	32.1 ± 105.5	$5,\!808.2\pm10,\!060.1$	-	-	489.4 ± 796.7	10.6 ± 18.3
Abudefduf luridus	58 ± 44.7	101.9 ± 89.3	192.4 ± 129.6	24 ± 14	189.4 ± 103.2	177.4 ± 74.1	167.4 ± 93.8	68.1 ± 78.5	104.7 ± 65.3	109.8 ± 83.9	7.6 ± 7.8	93.4 ± 71.2
Atherina presbyter	0.4 ± 0.3	0.1 ± 0.1	0.6 ± 0.7	0.1 ± 0.1	0.1 ± 0.2	-	0.5 ± 1.4	96.3 ± 166.9	5.1 ± 8.3	1.5 ± 2.5	-	1.4 ± 2.5
Aulostomus strigosus	-	-	-	-	-	-	3 ± 12.2	- 6	· ·	-	-	-
Belone belone	-	-	-	-	-	-	0.4 ± 2.1	-	-	-	-	-
Boops boops	-	-	-	-	-	-	-		-	-	-	-
Canthigaster capistrata	-	0.4 ± 0.7	-	-	-	-	0.1 ± 0.4		-	-	-	-
Diplodus cervinus	-	-	-	1.8 ± 3.1	-	-	0.2 ± 1	(-) ^y	-	-	77.8 ± 119.5	-
Diplodus puntazzo	-	-	-	-	-	-	-		-	-	96.8 ± 167.7	-
Diplodus sargus	$1,024.5 \pm 741.7$	236.4 ± 314.4	$1,\!875.7 \pm 1,\!470.5$	527.4 ± 279	384.2 ± 598	55.4 ± 51	556.5 ± 613.1	906.2 ± 497.1	$5,848.4 \pm 9,242.1$	619.9 ± 342	$2,\!401.6 \pm 1,\!667.7$	529.3 ± 546.7
Epinephelus marginatus	-	-	-	-	-	-	-	-	-	-	100.4 ± 130.7	-
Gymnothorax unicolor	-	-	-	-	-	-		-	-	-	-	-
Kyphosus saltatrix	-	-	-	11.4 ± 19.7	-	-	15.3 ± 36.3	4 ± 7	34.2 ± 59.2	11.4 ± 19.7	23.3 ± 36.8	164.7 ± 285.2
Liza aurata	$723.3 \pm 1{,}120.6$	-	600.4 ± 997	$2,\!878.5 \pm 2,\!350.1$	$2,\!304.8\pm3,\!598.1$	-	$841.1 \pm 1,571.9$	$7,\!052 \pm 7,\!421.3$	-	$2{,}544.4 \pm 4{,}407.1$	$4,\!316.1\pm4,\!104.9$	$3,\!757.5 \pm 3,\!989.4$
Lythognathus mormyrus	-	-	-	-	-	-	<u> </u>	-	-	-	-	-
Mugil cephalus	-	-	-	-	-	-	-	-	-	-	-	-
Mustelus mustelus	-	-	-	-	-	-	-	-	-	-	-	-
Mycteroperca fusca	-	-	-	-	-		-	-	-	-	28.7 ± 49.6	-
Oblada melanura	1.4 ± 2.4	-	7.2 ± 8.6	-	- /		1.3 ± 3.5	92.1 ± 159.5	-	-	6.9 ± 11.9	-
Ophioblennius atlanticus	240.7 ± 135.1	122 ± 79.4	275.5 ± 95.1	49.8 ± 42.1	201.1 ± 101.9	101.7 ± 42.3	321 ± 202.8	124.4 ± 105.8	123.1 ± 99.6	329.9 ± 162.2	23.5 ± 19.1	289.2 ± 181.1
Pomadasys incisus	-	-	-	-		·	32.6 ± 178.8	-	-	-	-	-
Pomatomus saltatrix	-	-	-	-	<u> </u>	-	-	-	-	-	-	-
Pseudocaranx dentex	-	2.6 ± 4.5	3 ± 5.2	-		-	1.1 ± 3.6	-	28.8 ± 49.9	-	-	-
Sardinella aurita	-	-	-	-	$\sum_{i=1}^{n}$	-	-	-	-	-	-	-
Sardinella maderensis	-	-	-		Y -	-	-	-	-	-	-	-
Sarpa salpa	13,944 ± 5,692.6	$7{,}695.2 \pm 3{,}141.6$	$13,\!269.6\pm5,\!417.3$	$17,\!968.9\pm7,\!335.8$	2,247.8 ± 917.7	-	$10,\!438.1\pm4,\!261.3$	$3,\!765.2 \pm 1,\!537.1$	$1,\!624.9\pm 663.4$	$11,\!221.3\pm4,\!581.1$	$9,\!295.8 \pm 3,\!795$	$16,\!404.2\pm6,\!697$
Scorpaena maderensis	-	-	-	(-)	-	-	-	-	-	-	-	-
Seriola spp.	-	-	-		-	-	-	-		-	-	-
Sparisoma cretense	29.6 ± 51.4	16.4 ± 25.9	403 ± 266.8	$3,781.9 \pm 1,946.1$	178.9 ± 101.1	176.3 ± 127.6	525.3 ± 761.1	138.9 ± 110.9	48.1 ± 48.8	311.5 ± 195.1	$3{,}900.9 \pm 2{,}143.9$	857.8 ± 736.7
Sphoeroides marmoratus	-	-	-	¥ -	-	-	-	-	-	-	-	-
Sphyraena viridensis	-	0.6 ± 1	-	-	0.3 ± 0.5	-	2.1 ± 7.2	46.8 ± 81.1	-	-	0.1 ± 0.1	-
Symphodus trutta	-	-	-	-	-	-	-	-	-	-	1.2 ± 2	-
Thalassoma pavo	72 ± 19.7	92.5 ± 56.5	107.8 ± 35.3	281.8 ± 122.2	224.6 ± 97	227.1 ± 99.6	214.6 ± 104.2	14.3 ± 13.2	324.7 ± 230.9	293.9 ± 127.1	155.8 ± 88.9	552.1 ± 495
Trachinotus ovatus	0.5 ± 0.9	-	59.6 ± 103.2	12.3 ± 21.3	-	-	10.6 ± 34.5	4 ± 6.9	11.4 ± 19.7	55.9 ± 72.7	83.3 ± 131	-
Unidentified larvae	-	1 ± 1.6	1.3 ± 1.7	-	-	-	0.5 ± 1	-	0.4 ± 0.4	0.3 ± 0.5	0.1 ± 0.2	0.1 ± 0.2

5 Appendix. Continued.

			March	2010					Octob	er 2010		
Species	1	2	3	4	5	6	1	2	3	4	5	6
Dicentrarchus labrax	$5{,}676.7 \pm 8{,}348.6$	$23,\!845\pm53,\!765.9$	$11,\!966.7\pm38,\!274.7$	95.9 ± 76.1	117.5 ± 122.6	34.5 ± 35.4	12.7 ± 21.9	34.2 ± 50.3	17.8 ± 19.8	47.9 ± 59.8	$1,\!262.8 \pm 1,\!987.7$	343.4 ± 390.2
Sparus aurata	-	$641.9 \pm 3{,}189.6$	$337 \pm 2,256.9$	7.7 ± 8	9 ± 11.7	-	-	-	-	3.3 ± 8.9	-	-
Abudefduf luridus	354.6 ± 104.8	141.3 ± 88.5	154.4 ± 91.2	95.2 ± 80.8	682.7 ± 388.4	786.5 ± 261.4	277.6 ± 120.3	253.3 ± 132.2	$1,225.9 \pm 417.4$	471 ± 270.8	131.9 ± 56.2	499.7 ± 301.4
Atherina presbyter	3.6 ± 4.3	10.8 ± 52.8	5.7 ± 37.4	-	4.5 ± 4.7	4 ± 6.7	1 ± 1.7	9.1 ± 10.3	6.3 ± 6.2	3.4 ± 5.2	5.3 ± 8.3	0.1 ± 0.2
Aulostomus strigosus	-	3 ± 12.2	3 ± 12.1	-	-	19.7 ± 34.1	4.7 ± 8.2	-		2.4 ± 11.1	267 ± 308.3	40.4 ± 54.1
Belone belone	3.9 ± 6.8	0.4 ± 2.1	0.4 ± 2.1	-	-	-	-	- /		-	-	78.1 ± 135.2
Boops boops	-	-	-	-	-	78.6 ± 94.1	17.2 ± 29.8	-	-	9.6 ± 31.9	$987.2 \pm 1{,}581.2$	-
Canthigaster capistrata	-	0.1 ± 0.3	0.1 ± 0.3	-	2 ± 3.4	7 ± 11.3	-		-	1 ± 3.8	-	1.7 ± 2.3
Diplodus cervinus	-	7.8 ± 38	4 ± 26.9	0.9 ± 1.6	5.9 ± 7.4	-	2 ± 3.5	6.7 ± 11.6	-	1.6 ± 4.5	-	4.1 ± 4.8
Diplodus puntazzo	-	9.7 ± 53	4.8 ± 37.5	-	-	-	7.3 ± 12.6	24.1 ± 41.7	-	3.1 ± 13.8	-	-
Diplodus sargus	382 ± 235.2	$1,\!180.6 \pm 2,\!989.2$	$868.6 \pm 2{,}158.4$	941.9 ± 319.6	424.6 ± 252	428.5 ± 259.4	814.2 ± 603.3	217.7 ± 142.2	780 ± 589.2	682.2 ± 560.7	947.2 ± 720.7	315 ± 181.3
Epinephelus marginatus	-	10 ± 42.1	5 ± 29.8	-	-	-		-	-	-	-	-
Gymnothorax unicolor	-	-	-	-	-	-	<u> </u>	-	-	-	-	-
Kyphosus saltatrix	48.3 ± 62.7	37.9 ± 98.9	26.6 ± 74.5	-	4.9 ± 7.1	17.2 ± 29.8		-	79.7 ± 138.1	15.9 ± 51.3	22 ± 38	4.1 ± 7
Liza aurata	$1,\!169.8 \pm 1,\!800.6$	$1,\!957.4 \pm 3,\!378.6$	$1,\!399.3 \pm 2,\!641.1$	-	3.6 ± 6.2	290.2 ± 441.4	307.8 ± 295.7	657.6 ± 637.8	835.4 ± 796.4	$1,\!000.1\pm2,\!036.3$	$4{,}509.8 \pm 7{,}202.8$	-
Lythognathus mormyrus	-	-	-	-	-		-	-	-	-	-	-
Mugil cephalus	-	-	-	-	-	-	ζ΄-	-	-	-	-	-
Mustelus mustelus	-	-	-	-	-		-	-	-	-	-	-
Mycteroperca fusca	-	2.9 ± 15.7	1.4 ± 11.1	-	-	-	-	-	-	2.2 ± 12.2	-	28.7 ± 49.6
Oblada melanura	-	10.4 ± 50.6	5.9 ± 35.8	6.9 ± 8	16 ± 19.1		4 ± 4.9	0.1 ± 0.2	-	9.2 ± 33.6	28.4 ± 48.5	40.3 ± 53.5
Ophioblennius atlanticus	394.1 ± 176.6	316.6 ± 213	318.8 ± 207.7	536 ± 223.9	448.2 ± 235.1	726.7 ± 179.1	550.9 ± 284.2	742.4 ± 311.7	472.8 ± 236	440.2 ± 214.8	213.4 ± 93.4	231.4 ± 153.9
Pomadasys incisus	-	32.6 ± 178.8	32.6 ± 178.6	-	-	· · ·	97.9 ± 169.6	-	-	9.8 ± 53.6	-	-
Pomatomus saltatrix	-	-	-	525.2 ± 667.3	-	-	-	-	-	52.5 ± 215.5	168.7 ± 292.3	-
Pseudocaranx dentex	-	3.4 ± 16	2.2 ± 11.6	-	18.2 ± 31.3	-	-	-	5.5 ± 9.4	3.5 ± 11	1.5 ± 2.6	5.2 ± 9
Sardinella aurita	-	-	-	-	-	-	11.4 ± 19.7	-	-	1.1 ± 6.2	-	-
Sardinella maderensis	-	-	-	- /	1.3 ± 2.3	-	-	-	-	6.5 ± 34.6	-	2.7 ± 4.6
Sarpa salpa	$8,\!208.3 \pm 3,\!351$	$10{,}310.9 \pm 4{,}209.4$	$10,\!366.6\pm4,\!232.1$	7,352.2 ± 3,001.5	17274.8 ± 7052.4	$11,\!664.7\pm4,\!762.1$	$2{,}554.5 \pm 1{,}042.9$	$5,366.9 \pm 2,191$	$11{,}546.2 \pm 4{,}713.7$	$11,\!654.1\pm\!4,\!757.8$	$6{,}410.5 \pm 2{,}617.1$	$4,\!113.9\pm1,\!679.5$
Scorpaena maderensis	-	-	-) -	-	-	-	-	-	-	-
Seriola spp.	-	-	-	C	-	-	-	-	-	-	-	-
Sparisoma cretense	158 ± 165.5	595 ± 846.1	560.1 ± 803.7	153.5 ± 126.6	123.1 ± 131.2	978.1 ± 440.1	198.3 ± 93	248.5 ± 315.4	499.9 ± 289.7	600.3 ± 610.3	142.1 ± 116.9	204.6 ± 165.5
Sphoeroides marmoratus	-	-	-		0.6 ± 1.1	-	-	-	-	0.5 ± 2.3	-	-
Sphyraena viridensis	18.6 ± 22.1	6.7 ± 26.6	4.4 ± 19.5	66.6 ± 75.1	-	142 ± 245.9	185.8 ± 321.8	-	8 ± 10.6	41 ± 129.8	-	-
Symphodus trutta	-	0.1 ± 0.7	0.1 ± 0.4	-	-	-	-	-	-	0.8 ± 3.9	-	-
Thalassoma pavo	243.3 ± 105.1	259.7 ± 199.9	237.1 ± 159.4	182.3 ± 74.1	298.3 ± 118.1	326.4 ± 112.7	339.1 ± 155.6	117.9 ± 49.5	249 ± 122	246.6 ± 106.9	132.9 ± 62.6	168.7 ± 77.5
Trachinotus ovatus	10.8 ± 10.9	20.8 ± 48.9	15.7 ± 42.3	-	32.2 ± 51	-	-	-	-	13.5 ± 37.4	0.5 ± 0.9	2.5 ± 2.1
Unidentified larvae	0.9 ± 1.5	0.3 ± 0.7	0.4 ± 0.9	-	-	-	-	-	-	0 ± 0.1	-	-

Table 1. Univariate PERMANOVA, comparing mean trophic level of fish assemblages with presence of escaped fish versus those with no escaped fish. In bold those p-values<0.05.

sence vs. Absence 1 8.8648 39.33 0.0002 Res 423 0.2254 Total 431	esence vs. Absence 1 8.8648 39.33 0.0002 Res 423 0.2254 Total 431	Presence vs. Absence 1 8.8648 39.33 0.0002 Res 423 0.2254 Total 431	Presence vs. Absence 1 8.8648 39.33 0.0002 Res 423 0.2254 Total 431	resence vs. Absence 1 8.8648 39.33 0.000 Res 423 0.2254 Total 431	Source	df	MS	Pseudo-F	P(perm)
Res 423 0.2254 Total 431	Res 423 0.2254 Total 431	Res 423 0.2254 Total 431	Res 423 0.2254 Total 431	Res 423 0.2254 Total 431	resence vs. Absence	1	8.8648	39.33	0.0002
Total 431	Total 431			Total 431	Res	423	0.2254		
S		ALLAN ALLAND	AND MARINE	ALA ALA	Total	431			
		ALL ALL	CER HIN	CER HIN	lotal	431		S	8

Table 2. Univariate PERMANOVA, exploring spatiotemporal patterns of mTrL. In bold those p-values<0.05 for fixed factors and their relevant interactions. Ye: Year, Pe: Period, Pr: Protection, Si: Site.

Source	df	MS	Pseudo-F	P(perm)
Year	1	6.5392	14.131	0.002
Period	1	3.6593	16.625	<0.001
Protection	1	5.1611	13.981	0.002
Site(Pr)	16	0.36111	2.0037	0.014
YexPe	1	0.81318	2.127	0.162
YexPr	1	1.1631	2.5015	0.132
PexPr	1	0.49561	2.2613	0.146
YexSi(Pr)	16	0.46161	2.5613	0.002
PexSi(Pr)	16	0.21772	1.2081	0.267
YexPexPr	1	6.1848E-2	0.16501	0.686
YexPexSi(Pr)	16	0.37805	2.0977	0.008
Res	353	0.18022		
Total	431			\mathbf{D}

Table 3. Diet composition of the "leak" and "massive" escaped *Dicentrarchus labrax*.

Leak group Vacuity=33.9%						9
n=112 Trophic Level=4.2						u
Prey	N%	W%	0%	Q	IRI	Prey preferences
Fish	62.9	76.4	54.1	4803.2	7528	Main preferred prey
Atherina presbyter	2.4	0.4	4.1	1.0	11	
Sparisoma cretense	1.0	7.0	2.7	6.6	21	
Thalassoma pavo	1.4	10.3	2.7	14.7	32	
Scorpaena sp.	0.5	4.7	1.4	2.2	7	
Trachinus draco	0.5	5.7	1.4	2.7	8	
Sardinella aurita	33.3	23.9	5.4	795.7	309	
Unidentified fish	23.8	24.5	36.5	582.6	1762	
Crustaceans	14.3	5.1	32.4	73.4	630	Secondary common prey
Percnon gibbesi	1.0	2.9	2.7	2.7	10	
Plagusia depressa	0.5	< 0.01	1.4	< 0.01	1	
Pachygrapsus sp.	2.9	0.2	2.7	0.6	8	
Xantho sp.	0.5	0.1	1.4	< 0.01	1	
Unidentified crustaceans	9.5	1.9	27.0	18.5	310	
Mollusks	2.4	0.8	4.1	1.9	13	Accidental prey
Cephalopoda	1.9	0.8	2.7	1.5	7	
Gastropoda	0.5	< 0.01	1.4	< 0.01	1	
Insects	10.5	0.7	28.4	7.4	317	Accidental prey
Blattaria	0.5	0.3	1.4	0.2	1	
Hymenoptera	1.9	< 0.01	5.4	<0.01	10	
Coleoptera	0.5	< 0.01	1.4	< 0.01	1	
Unidentified insects	7.6	0.4	21.6	2.7	173	
Plants						
Cymodocea nodosa	1.9	1.3	5.4	2.4	17	Accidental prey
Mammals						
Rattus norvegicus	0.5	1.4	1.4	0.6	2	Accidental prey
Pellets	1.0	10.3	2.7	9.8	30	Accidental prey
Other Items	6.7	4.1	17.6	27.1	189	Secondary common prey

Massive group n=32	Vacuity=12.5% Trophic Level=3.2						b
Prey		N%	W%	0%	Q	IRI	
Fish		2.7	0.1	3.6	0.4	10	Accidental prey
Unidentified fish		2.7	0.1	3.6	0.4	10	
Crustaceans	X	89.2	80.1	100.0	7142.7	16927	Main preferred prey
Percnon gibbesi	7	45.9	57.3	42.9	2634.0	4426	
Eriphia verrucosa		2.7	10.0	3.6	27.0	45	
Unidentified crusta	aceans	40.5	12.8	53.6	518.1	2856	
Other Items		5.4	1.2	7.1	6.5	47	Accidental prey

Table 4. PERMANOVA results comparing the diet of sea bass escaped in leak and massive events, including total length as a covariable. In bold those p-values<0.05.

Source	df	MS	Pseudo-F	P(perm)
Total Length	1	16215	3.7611	0.0002
Leak vs. Massive	1	19094	4.429	0.0002
Total Length x Leak vs. Massive	1	6301.8	1.4618	0.0734
Res	94	4311.1		
Total	97			4



CR R













A CRIME

Highlights:

- An aquaculture massive escape released 1.5 million fish into the wild in the Canaries.
- Mean trophic level of marine fish assemblages was investigated through visual census.
- Diet of escaped sea bass was studied regarding size and time in the wild.
- Mean trophic level was raised but a nearby marine protected area showed resilience.
- Escaped sea bass exploited natural resources according to size and time at liberty.

A ALANCE