

1 **Reproduction, condition and abundance of the Mediterranean bluefish**

2 *(Pomatomus saltatrix)* in the context of sea warming

3
4 **RUNNING HEAD:** Bluefish and sea warming in NW Mediterranean

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14 **PAPER TYPE:** Research Article

15 **ABSTRACT**

16 This study evaluates the link between sea warming and three important aspects of the population
17 dynamics of bluefish, *Pomatomus saltatrix*, in the NW Mediterranean: condition (health measures),
18 reproduction and abundance (as reflected in catch per unit effort, CPUE). We compared the bluefish
19 populations from two areas with different thermal regimes: the Gulf of Roses and the Ebre Delta.
20 First, in order to compare the condition and reproduction parameters of the two populations,
21 specimens were collected from the commercial catch landed in two ports located in these areas.
22 Several indicators of fish condition and reproduction such as hepatosomatic index, gonadosomatic
23 index, maturation timing, length-at-first maturity, fecundity, egg quality and atresia (ovarian follicle
24 resorption) were analysed and compared between study areas. Secondly, time series analyses of sea
25 surface temperatures (SST) and monthly bluefish CPUEs in the two study areas were assessed using
26 Box-Jenkins transfer function models. Our results indicate that bluefish benefit from sea warming in
27 the NW Mediterranean, particularly in the northernmost zone, as evidenced by increasing fish
28 condition in these waters. Sea warming may favour the changes in spawning phenology and the
29 northward expansion of this species. This study provides evidence that a marine fish species that is
30 able to expand or it is forced to shift its distribution range due to sea warming, may take advantage
31 of other environmental conditions of new habitats, contributing to the enhancement of the
32 population's productivity in these areas.

33

34 **KEYWORDS:** NW Mediterranean, sea surface temperature, *Pomatomus saltatrix*, fish condition,
35 reproductive biology, predator.

36 **INTRODUCTION**

37 The Mediterranean Sea is a semi-enclosed basin where sea warming is likely to be more
38 pronounced and to become apparent sooner than in other more open oceans (Astraldi *et al.*, 1995;
39 Bethoux *et al.*, 1999; Walther *et al.*, 2002; Coll *et al.*, 2010). Climate models predict that the
40 Mediterranean basin will be one of the regions that is most affected by the ongoing warming trend
41 and by an increase in extreme events (Parry, 2000; Lejeusne *et al.*, 2010; Calvo *et al.*, 2011; Durrieu
42 de Madron *et al.*, 2011). Subtropical species are found mainly in the eastern basin and southern
43 Mediterranean, where water temperatures are higher, whereas cold-temperate species inhabit the
44 cooler northern areas (Salat, 1996; Bianchi and Morri, 2000; Coll *et al.*, 2010).

45 A direct consequence of sea warming is a simultaneous increase in the abundance of thermo-
46 tolerant species and the decline or disappearance of 'cold' stenothermal species (Lejeusne *et al.*,
47 2010). In a semi-closed system such as the Mediterranean basin these changes may cause the
48 progressive homogenization of the marine biota, the dislocation of other species, the loss of
49 endemic species coupled with invasion by non-indigenous species and/or cascade effects on food
50 webs (Molinero *et al.*, 2005).

51 Not only could marine biodiversity be seriously affected, but climate change may also affect
52 fisheries directly by influencing fish stocks and the global supply of fish for consumption.
53 Commercial fishing would also be affected by changes to the overall value of fish catches due to
54 changes in the abundance of the species caught. The value of the total catch may decrease as warm
55 water species - which can be of lower commercial value - increase at the expense of other species of
56 greater commercial value, e.g. the increase of the thermophilic, low value *Sardinella aurita*
57 (Sabatés *et al.*, 2006) vs. the decrease of the temperate, high value *Engraulis encrasicolus* and
58 *Sardina pilchardus* (Martín *et al.*, 2011).

59 The bluefish, *Pomatomus saltatrix*, (Linnaeus 1766), is distributed over continental shelves and
60 in estuaries of temperate waters throughout most of the world, with the exception of the northern

61 and mid-Pacific Ocean (Juanes *et al.*, 1996). Relatively little is known about the biology of this
62 species in the Mediterranean. Sabatés and Martín (1993) provided a number of observations
63 regarding its presence in certain areas, and its relative importance in terms of fishing activity as well
64 as the duration of spawning. They proposed the southern Catalan as the northernmost boundary of
65 bluefish distribution in the western Mediterranean Basin. However, more recently, Sabatés *et al.*
66 (2012) found that the bluefish distribution range was expanding northwards due to the increasing
67 water temperatures allowing reproduction to take place in more northern areas, as revealed by the
68 presence of bluefish larvae in plankton. Furthermore, it has been suggested that shifts in the bluefish
69 distribution range could be the result of current climate change and that correct management of fish
70 communities required this issue to be assessed (Goodbred and Graves, 1996; Juanes *et al.*, 1996;
71 Pardiñas *et al.*, 2010). This warm water species appears to be a good candidate for investigating the
72 effects of sea warming.

73 The aim of this study was to evaluate the influence of sea temperature on three important aspects
74 of population dynamics of bluefish in the NW Mediterranean: condition, reproduction and
75 abundance (as reflected in catch per unit effort). The hypothesis behind this study is that the
76 abundance, condition and reproduction of bluefish in coastal waters off the north-western
77 Mediterranean Sea are all being influenced by sea warming, manifested through changes in fish
78 condition and spawning characteristics, which may have resulted in increased catches over time.

79 **METHODS**

80 *Sampling locations*

81 Samples were collected from two areas with different thermal regimes in the Northwest
82 Mediterranean Sea: the more northerly Gulf of Roses and the more southerly Ebre Delta (Fig. 1).
83 The Gulf of Roses and surrounding waters have lower mean water temperatures than the Ebre Delta
84 (Salat *et al.*, 2002).

85 *Fish condition and reproduction evaluation*

86 In order to compare the condition and reproduction parameters of the bluefish between the two
87 study areas, samples of bluefish were collected monthly from the commercial catch landed at the
88 port of Roses (Gulf of Roses) from July 2010 to August 2012 and at the port of Sant Carles de la
89 Ràpita (Ebre Delta) from May to August 2012, shortly after the small-scale and bottom-trawl
90 fishing vessels had landed their catches. In the laboratory, we recorded the total length (TL) to the
91 nearest 0.5 cm and total weight (TW) to the nearest 1 mg. Subsequently, the bluefish specimens
92 were dissected and eviscerated, and the somatic or eviscerated body weight (SW), the liver weight
93 (LW) and the gonad weight (GW) were obtained to the nearest 1 mg. Finally, the gonads were fixed
94 in buffered formalin (4%) for further histological processing and fecundity estimation.

95 The hepatosomatic (HSI) and gonadosomatic (GSI) indices were calculated for each individual.
96 All indices were calculated based on SW in order to avoid possible variations arising from
97 differences in the contents of the digestive tract. The hepatosomatic index (HSI) was calculated as
98 $HSI = 100 (LW/SW)$, where LW and SW represent liver and somatic wet weights, respectively. The
99 liver is the main energy store of many fishes and therefore the HSI is expected to provide the best
100 estimate of bluefish condition. Finally, the gonadosomatic index (GSI) was estimated using the
101 formula $GSI = 100(GW/SW)$, where GW and SW represent gonad and somatic wet weights,
102 respectively.

103 Although the sex and reproductive status of specimens were first macroscopically determined, a
104 histological analysis was also performed in order to provide a more accurate analysis of the
105 reproductive characteristics and the annual reproductive cycle of bluefish. Thus, a histological study
106 of the gonads of every single individual was carried out in order to determine the stages of
107 development of their germ cells. Central portions (transverse sections) of the fixed gonads were
108 dehydrated and embedded in paraffin, sectioned at between 3-8 μm , depending of their state of
109 maturity, and stained with haematoxylin-eosin and Mallory's trichrome. The latter staining method

110 highlights the *zona radiata* and its continuity and facilitates the detection of atretic oocytes (Muñoz
111 *et al.*, 2010). Maturation stages of the gonads were classified in line with Brown-Peterson *et al.*
112 (2011).

113 In order to define sexual maturation as a function of body length, the L₅₀ (body length at which
114 50% of the individuals were mature) was estimated separately for samples taken from the Gulf of
115 Roses and from the Ebre Delta. To predict the probability that an individual was mature based on its
116 length, binary maturity observations (0=immature, 1=mature) and length (TL; cm) were fitted to
117 binary logistic models to construct maturity ogives based on logistic equations based on 1 cm
118 length-classes. Size at maturity was estimated from 75 and 103 females (length 26-91 cm TL) and
119 from 63 and 84 males (length 26-79 cm TL) sampled at the Gulf of Roses and the Ebre Delta,
120 respectively.

121 The presence of hydrated oocytes and postovulatory follicles (POF) was determined to select
122 suitable specimens for the analysis of fecundity. The oocyte size-frequency distribution for each
123 spawning female was analysed in order to detect the batches of oocytes, since this may demonstrate
124 different maturation patterns and associated fecundities (Kjesbu *et al.*, 1998). Thus, fecundity was
125 estimated for each specimen in 'Spawning Capable' (SC) or 'Actively Spawning' (AS) phases
126 using the Gravimetric Method combined with Image Analysis as explained by Murua *et al.* (2003).
127 With this aim, subsamples of about 150 mg were taken from the central area of the ovary; oocytes
128 were separated from connective tissue using a washing process (Lowerre-Barbieri and Barbieri,
129 1993) and sorted by size through several sieves (from 1000 to 100 µm), which facilitated the next
130 steps of counting and measuring oocytes using a computer-aided image analysis system (Image-Pro
131 Plus 5.1; www.mediacy.com). In order to explore the size distribution for each oocyte
132 developmental stage, the mean diameter of 200 oocytes from each stage were measured from the
133 histological sections as the average of major and minor axes. Due to their irregular shape the mean
134 diameter of the hydrated oocytes was estimated separately after adding glycerine, which facilitates
135 their differentiation.

136 Estimations of fecundity were based on Batch Fecundity (BF) defined as the number of eggs
137 spawned per batch (Murua and Motos, 2006; Domínguez-Petit and Saborido-Rey, 2010). This was
138 estimated as $BF = GW \cdot (O/Sw)$, where GW is the gonad weight after fixation, O is the number of
139 hydrated oocytes in a weighted subsample of ovarian tissue, Sw is the subsample weight. The
140 Relative Batch Fecundity (RBF) was also calculated, as the value of batch fecundity per gram of
141 somatic weight of the fish.

142 The dry mass and diameter of hydrated oocytes were used to estimate the quality of the oocytes,
143 hence an approximation of the reproductive success (Brooks *et al.*, 1997). Thus, mean dry weights
144 were estimated by drying (for 24 h at 110°C) two replicates per sample of the oocytes.

145 The prevalence of atresia, P_a (percentage of sexually mature females that have α -atretic
146 vitellogenic oocytes) and the relative intensity of atresia, R_{Ia} (percentage of α -atretic vitellogenic
147 oocytes in relation to the total number of vitellogenic oocytes) was estimated from observations at
148 three different focal planes of different histological slides of each specimen (Kurita *et al.*, 2003).

149 ***Statistical analyses***

150 Generalized linear models (GLMs) (McCullagh and Nelder, 1989) were used to investigate the
151 variation of fish condition with sex, stage of maturity and size. GLMs were fitted to HSI and GSI as
152 response variables and using as categorical predictor variables the sex (females and males) and
153 maturity (immature, developing, spawning capable, regressing, regenerating) and as continuous
154 predictor variables the size (total length). All predictors and their first order interactions were
155 initially included in the GLM. Analysis of deviance to evaluate the significance (F-test) of the
156 factors in the model was performed by a stepwise procedure, and the most appropriate error models
157 were chosen on the basis of residual plots. GLMs incorporating the sex and maturity as predictor
158 variables accounted significantly for 36.4% of the deviance of HSI and 43.4% of the variability in
159 GSI (Table 1). Size did not significantly accounted for the deviance neither of HSI nor of GSI
160 ($p > 0.05$). Thus, we used the GLM approach to standardize HSI and GSI data only for the effects of

161 sex and maturity by estimating the adjusted means of HSI and GSI as the means after adjusting for
162 the variation of the covariables (sex and maturity).

163 In order to carry out the comparative analyses between sampling areas, a sub-dataset of the
164 samples from Gulf of Roses was created matching the temporal scale of the Ebre Delta (from May
165 to August 2012) so that the spatial variation could be evaluated. This analysis indicated that there
166 were significant differences between sampling areas in the condition and reproduction variables,
167 e.g. in GSI (ANOVA, $F_{1,238}=4.67$, $p=0.032$) or HSI (ANOVA, $F_{1,238}=4.91$, $p=0.028$). Furthermore,
168 there was an insignificant interannual difference (2010, 2011 and 2012) in the Gulf of Roses, e.g.
169 GSI (ANOVA, $F_{2,137}=2.05$, $p=0.133$) or HSI (ANOVA, $F_{2,137}=2.37$, $p=0.097$). All these analyses
170 support the grouping of all three reproductive annual cycles of the Gulf of Roses in order to
171 compare each variable to those of the Ebre Delta.

172 Subsequently, for all aforementioned variables the Shapiro-Wilk test was used to test the
173 assumptions of normality and Levene's test was used to test the homogeneity of variances (Zar,
174 1996). Once assumptions were checked and met, ANOVA models were used to compare all indices
175 between sampling areas. A p-value of $\alpha=0.05$ or less was considered to be statistically significant.
176 Moreover, if the ANOVA indicated significant differences Bonferroni's multiple tests were applied
177 for post hoc comparisons of significant effects (Sokal and Rohlf, 1995). Conversely, if the
178 assumptions were not met, the data were analysed with a non-parametric Mann-Whitney U test
179 (Sokal and Rohlf, 1995). A p-value of $\alpha = 0.05$ or less was considered to be statistically significant.

180 Finally, the relationship between batch fecundity (BF) and the total length (TL) was estimated by
181 fitting power functions. Then, ANOVAs (for relative batch fecundity), ANCOVAs (for batch
182 fecundity using TL as covariate) and paired Student's tests (for oocyte quality and relative intensity
183 of atresia) were also used to find out whether, on average, differences between sampling areas in the
184 aforementioned variables were statistically significant (Zar, 1996).

185

187 Trends in sea surface temperatures (SSTs) and bluefish landings in Catalan waters have already
188 been explored by Sabatés *et al.* (2012), who found that both parameters showed a tendency to
189 increase from 1997 to 2010 (particularly during spring months). They also explored the seasonality
190 of bluefish landings and observed a seasonal pattern, closely matching that of the SSTs, in the
191 monthly landings over the year in which landings were almost nil during the colder months but
192 began increasing at the time SSTs also began to increase; subsequently, landings decreased as SSTs
193 decreased. Thus, our analyses focuses on determining and quantifying the possible relationships
194 between the monthly time series of bluefish catch per unit effort (CPUE) and SST using bivariate
195 ARIMA (autoregressive-integrated-moving-average) transfer functions (Box and Jenkins, 1976).

196 First, the data on sea surface temperature (SST, in °C) from both areas (the Gulf of Roses and the
197 Ebre Delta) was retrieved from the International Comprehensive Ocean-Atmosphere Data Set
198 (ICOADS) for the period 2000-2011 (ds540.0-Release 2.5) (Woodruff *et al.*, 2011). The data
199 comprised individual daily mean sea surface temperature observations for 1° latitude x 1° longitude
200 units. In this study, we used the time series from two 1° squares in the north-western
201 Mediterranean: the Gulf of Roses (42.0 to 43.0°N and 3.0 to 4.0° E) and the Ebre Delta (40.0 to
202 41.0°N and 0.0 to 1.0° E). The mean monthly and seasonal values of SST in both areas were
203 calculated by averaging daily temperatures retrieved from the ICOADS data. The seasons were
204 defined as follows: winter (January, February, and March), spring (April, May, and June), summer
205 (July, August, and September) and autumn (October, November, and December).

206 Secondly, data was collected - on total monthly bluefish landings (recorded in kg) and nominal
207 fishing effort (number of vessels), from the fishing ports along the Catalan coast (Fig. 1) - from the
208 fishery statistics of the Department of Agriculture and Fisheries of the Government of Catalonia
209 (2000-2011) (www20.gencat.cat/portal/site/DAR). It should be noticed that bluefish landings
210 included only those catches landed by the small-scale fleets (devoted to artisanal fishing and whose

211 fishing grounds are located in the vicinity of the base port) because it is the more prevalent vessel
212 type that catches most of the bluefish landings (from 90 to 95%) in all ports. The occasional
213 landings recorded by the bottom trawler and purse-seine fleets were not included, which have been
214 suggested previously and used by Sabatés *et al.* (2012). Since there has been a considerable
215 reduction in the fishing effort in Catalan waters in recent years (Martín *et al.*, 2011; Catalonia
216 Fisheries Statistics, 2012; Sabatés *et al.*, 2012), the monthly number of active vessels at each port
217 was used as a proxy of fishing effort at each port. In this way, the time series of the monthly catches
218 per unit effort (CPUE), expressed as kg per vessels, were estimated for different periods (2000-
219 2011) at two fishing ports from the Gulf of Roses (Roses and L'Escala) and three from the Ebre
220 Delta area (L'Ametlla de Mar, L'Ampolla, and Sant Carles de la Ràpita).

221 Finally, in order to determine and quantify the possible relationships between the time series of
222 bluefish CPUEs and SST, bivariate ARIMA transfer function models were constructed using the
223 statistical package ForeTESS (Prat *et al.*, 2010). These models describe the time-lagged relationship
224 between the dependent (CPUE) and the independent (SST) variables while taking into account the
225 autocorrelation of the disturbance of the data (Box and Jenkins, 1976).

226 In order to look at the temperature thresholds related to the timing of the arrival of bluefish in
227 both study areas as environmental conditions become favourable to this species, we repeated the
228 transfer function models but this time using only the values of those months when SST increased by
229 a factor of 1°C, from 13°C (minimum SST observed) to 27°C (maximum SST observed): $SST_{13} +$
230 $SST_{14} + \dots + SST_{27}$, and only physical values from months when SST was higher than 13°C were
231 included in the transfer function models and the rest of the months when temperature was lower
232 than 13°C were replaced by zeroes, which meant 'no influence on CPUE' in our models. In this
233 way, several transfer function models were explored and applied to the 13-27°C SST range so that a
234 minimum SST threshold could be found for each time series. Models were compared using
235 Akaike's information criterion (AIC) to determine which model offered the best fit for SST
236 thresholds at each time series.

237 **RESULTS**

238 A total of 138 bluefish (75 females and 63 males) were sampled in the Gulf of Roses, and 187
239 (103 females and 84 males) in the Ebre Delta. The fish length ranged from 26.0 to 91.0 cm TL.

240 *Fish condition and reproductive biology*

241 Since bluefish specimens were not significantly different between sampling areas in size
242 (ANOVA, $F_{1,324}=2.86$, $p=0.092$) or sexes (ANOVA, $F_{1,324}=3.24$, $p=0.073$), data were pooled
243 (grouped into a single dataset per sampling area).

244 HSI (standardized based on GLMs for sex and maturity) were significantly (ANOVA,
245 $F_{1,324}=4.56$, $p=0.034$) higher in the Gulf of Roses (1.56 ± 0.48) than in the Ebre Delta (1.26 ± 0.31)
246 indicating better fish conditioning in the northern population (Fig. 2). Significant differences were
247 also found in GSI (ANOVA, $F_{1,324}=5.97$, $p=0.015$), in which case specimens sampled at the Gulf of
248 Roses showed higher GSI (3.64 ± 2.54) compared to specimens from the Ebre Delta (1.86 ± 1.39)
249 indicating that the reproductive investment was much higher in the northern population (Fig. 2). In
250 terms of the time of the year, in both sampling areas, the GSI was low during spring and then
251 increased sharply, peaking in the summer before declining again in autumn (Fig. 3).

252 Differences in the timing of gonadal development were also observed between sampling areas
253 (Fig. 3). In females from the Gulf of Roses, the early stages of development were observed mainly
254 during the spring (April to June); then, during the summer (July to September), spawning activity
255 occurred; and subsequently, the rate of spawning activity declined in late summer (September) and
256 autumn (October to December) when all the females were in the regeneration stage (Fig. 3a).
257 Similarly, the spawning season of females from the Ebre Delta is mainly during the summer,
258 although 'Spawning Capable' females were also observed earlier during the spring (which was not
259 the case in the Gulf of Roses) (Fig. 3b). In addition, later on in the summer, the proportion of
260 'Regressing' females from the Ebre Delta (28.9%) was higher than it was in the Gulf of Roses in

261 the same season (4.4%), indicating that not only did spawning activity begin earlier in the Ebre
262 Delta but also that the rate of spawning activity there declined earlier than it did in the Gulf of
263 Roses. Similar differences between the two sampling areas were observed in the timing of gonadal
264 development of bluefish males (Fig. 3). In the Gulf of Roses the early stages of development and
265 'Spawning Capable' males were observed in the spring, but spawning activity did not peak until the
266 summer, as revealed by the presence of specimens in the samples that were in 'Actively Spawning'
267 and 'Regressing' stages. However, in the Ebre Delta, although the spawning season of males also
268 takes place mainly in summer, some 'Actively Spawning' males were already observed in spring
269 (Fig. 3d), suggesting that the spawning activity of males, as was the case with females, began earlier
270 in the Ebre Delta than it did in the Gulf of Roses.

271 The mean length at which 50% specimens were mature (L_{50}) was, for females, 37.5 cm TL in the
272 Gulf of Roses and 37.7 cm TL in the Ebre Delta. For males, the L_{50} in the Gulf of Roses was 36.5
273 cm TL while in the Ebre Delta it was 36.2 cm TL. In both sampling areas all females and males
274 were mature at about 40 cm TL.

275 The oocyte size-frequency distribution in bluefish females showed a continuous size-frequency
276 development of oocytes except for ovaries in the 'Actively Spawning' phase, which had a separate
277 mode of very large ($>600\ \mu\text{m}$) hydrated oocytes (Fig. 4). Only when hydration occurred just before
278 ovulation, did hydrating oocytes outgrow the standing stock of vitellogenic oocytes and a separate
279 mode of mature hydrated oocytes developed. The presence of hydrated oocytes alongside the
280 standing stock of developing oocytes in individual ovaries, as well as the presence of post-ovulatory
281 follicles (POFs) in ovaries with advanced vitellogenic oocytes, indicates that asynchronic multiple
282 batch spawning occurs in this species.

283 The specific size ranges for each stage of secondary oocyte development are shown in Table 2.
284 Significant differences (Mann-Whitney U test) in the median diameter of oocytes from the two
285 sampling areas were found at nearly all stages of development: at CA ($U=4331.5$, $p<0.05$), at Vtg-1

286 (U=8459.5, $p<0.05$), at Vtg-2 (U=4488.5, $p<0.05$), at Vtg-3 (U=4224.5, $p<0.05$), and at GVM
287 (U=4738.0, $p<0.05$), with Gulf of Roses oocytes being always slightly larger than Ebre Delta
288 oocytes. However no significant differences were observed in the median diameters of hydrated
289 oocytes (U=808.5, $p=0.48$).

290 Only 13 females (5 from the Gulf of Roses and 8 from the Ebre Delta) met the histological
291 criteria (actively spawning with hydrated oocytes and without POFs) for fecundity analysis. The
292 batch fecundity (BF) of bluefish ranged from 84009 to 259636 eggs per spawning batch in fish
293 ranging from 41.0 to 76.5 cm TL. The relationship between BF and TL was fitted to the following
294 exponential regression model: $BF=832.45 \cdot TL^{1.275}$ ($r^2=0.652$, $n=13$). Among sampling areas, the
295 mean batch fecundities were estimated at 166559(± 62062) and 153653(± 42613) eggs per spawning
296 batch for the Gulf of Roses and the Ebre Delta, respectively; and the mean relative batch fecundities
297 (RBF) were estimated at 102.1(± 32.5) and 92.6(± 37.7) oocytes per gram of body mass for each
298 area, respectively. No significant differences were found between the Gulf of Roses and the Ebre
299 Delta either in BF (ANCOVA, $F_{1,12}=0.86$, $p=0.377$) or in RBF (ANOVA, $F_{1,12}=0.22$, $p=0.649$).

300 As a measure of egg quality, the mean dry mass of hydrated oocytes was estimated at
301 0.032(± 0.011) and 0.036(± 0.014) mg per egg for the Gulf of Roses and the Ebre Delta, respectively,
302 which meant there was no significant difference between the two areas ($t=-0.8089$, $p=0.426$, $n=40$).

303 The prevalence of atresia (P_a) increased in both areas from the 'Spawning Capable' phase to the
304 'Regressing' phase of the ovaries. No sign of α -atresia was observed in other development stages,
305 such as the 'Developing' or 'Regenerating' phases (Table 3). The P_a also varied and differed
306 seasonally between sampling areas, i.e. from spring to summer in the Ebre Delta, the P_a decreased
307 while in the Gulf of Roses it increased. On the other hand, the mean relative intensity of atresia
308 (R_{Ia}) increased in relation to the season and the stage of ovarian development as the spawning
309 period advanced.

310

311 ***Relationship between SST and bluefish CPUE***

312 The transfer function models fitted to the CPUEs with SSTs as an independent variable
313 explained a considerable amount of the variability in CPUEs (Table 4). The amount of variability
314 explained by these models ranged from 71% for the time series of Sant Carles de la Ràpita to 81%
315 for the time series from Roses. Fig. 5 compares the expected CPUE values (from the transfer
316 function models) with the observed (actual) bluefish CPUE for each time series.

317 The transfer functions models showed that CPUE correlated positively with SSTs with a time lag
318 of between 0 and 1 months (significant at $t\text{-value} > |2| = p < 0.05$) in almost all time series (Table 4).
319 For example, the transfer function model fitted to bluefish CPUE in Roses (Y_t ; output; kg vessel⁻¹)
320 and the corresponding SST (X_t ; input; °C) at lags of 0 and 1 month (time lag 0: $t\text{-value} = 2.31$, time
321 lag 1: $t\text{-value} = 3.65$) is represented by the equation $Y_t = f(X_t) = 0.42 \cdot X_{t-0} + 0.34 \cdot X_{t-1} + a_t$. Thus, the model
322 estimates that an additional 1°C of SST leads to 0.42(± 0.06) kg vessel⁻¹ added to CPUE of this
323 species during the same month, and 0.34(±0.08) kg vessel⁻¹ added to CPUE during the following
324 month, giving a total gain of 0.76 kg vessel⁻¹ for both months. The R² value of the transfer function
325 model was 0.81 (residual standard error of 0.94 kg vessel⁻¹). Similar patterns were found in the
326 transfer functions of L'Escala, L'Ametlla de Mar, L'Ampolla and St. Carles de la Ràpita (Table 4).

327 Finally, the temperature thresholds analysis applied to the transfer function models indicated that
328 the minimum SST that needs to be reached within each study area in order to enhance bluefish
329 CPUE significantly was around 17-18°C since significant $t\text{-values} (> |2|, p < 0.05)$ were only
330 observed from this threshold to higher SSTs at each fishing port (Table 5). The AIC value (for each
331 time series) decreased as the SST threshold increased, thereby indicating that the most parsimonious
332 models were those obtained at higher SSTs (Table 5), which in turn supports the idea that bluefish
333 CPUE have been closely linked to the sea surface temperatures.

334

335 **DISCUSSION**

336 Our analysis of different reproductive and condition indices shows that it is not only in terms of
337 reproduction that bluefish seem to benefit from actual environmental conditions in the north, but
338 they also appear to be in better condition. Moreover, oocytes of the females from the Gulf of Roses
339 were significantly larger than those of females from the Ebre Delta, suggesting they have higher
340 quality eggs. Apparently, despite the warmer environment that prevails in the Ebre Delta, bluefish
341 were in significantly better condition in the northern study area where the waters are colder. This
342 later may be due to ecological differences between northern and southern areas of the NW
343 Mediterranean. The Gulf of Lions is known to be affected by a permanent cyclonic circulation of
344 surface waters and intense vertical convections which promote intense algal blooms and elevated
345 primary production (Bosc *et al.*, 2004). These later authors estimated a 4-year average annual
346 primary production relatively higher for the Gulf of Lions basin (including the Gulf of Roses) from
347 180 to 204 gC m⁻² y⁻¹ than estimates for the Balearic basin (including the Ebre Delta area) from
348 153 to 175 gC m⁻² y⁻¹. Regarding the trophic structure and functioning of these two marine
349 ecosystems, the total biomass (excluding detritus) has been estimated for the Gulf of Lions at 68.9 t
350 km⁻² (Bănaru *et al.*, 2013) and for the Ebre Delta at 58.99 t km⁻² (Coll *et al.*, 2006). It is
351 noteworthy the total net primary production that differed noticeable between these areas, being
352 considerably higher in the Gulf of Lions, 1042.4 t km⁻² y⁻¹ (Bănaru *et al.*, 2013), than that
353 estimated for the Ebre Delta, 386.68 t km⁻² y⁻¹ (Coll *et al.*, 2006). Thus, bluefish inhabiting the
354 more northern area appear to be taking advantage of the environmental conditions found there.

355 The results concerning the reproductive biology, such as the oocyte size-frequency distribution
356 and the seasonal relative intensity of atresia, provide evidence that bluefish are multiple batch
357 spawners with asynchronous oocyte development and indeterminate fecundity which is in
358 accordance with previous studies (Conand, 1975; Robillard *et al.*, 2008). Our estimates of batch
359 fecundities for bluefish in the two Mediterranean areas we sampled were very similar to each other,
360 but smaller than those estimated for the bluefish in U.S. East Coast (Robillard *et al.*, 2008) or the

361 West African Coast (Conand, 1975), which ranged 0.2-1.4 and 0.6-1.6 million oocytes,
362 respectively. To date, this study represents the first published work that estimates not only the
363 fecundity, but also the size at maturity of this species in the Mediterranean Sea. It should be noticed
364 that the L_{50} values we obtained for females 37.6 cm TL are much lower than those reported for areas
365 in the Atlantic: 48.0 cm TL in the East Coast of the U.S (Robillard *et al.*, 2008) and 43.0 cm TL in
366 the West African Atlantic Coast (Conand, 1975). It is worth to mention that size at maturity was
367 estimated from relatively similar size ranges (TL): 23.0-97.5 cm (Robillard *et al.*, 2008) and 26.0-
368 91.1 cm (this study). It has been suggested that maturation in fish populations usually might be
369 closely related to total population abundance over the life of a cohort, with cohorts maturing at an
370 earlier age and smaller size when population size is low (Morgan and Colbourne, 1999). Besides the
371 fact that bluefish mature at smaller sizes in the Mediterranean and also that better fish conditioning
372 was observed in the north would somehow facilitate its capacity for expansion since some studies
373 have shown that fish in better condition may have more surplus energy to devote to reproduction
374 (i.e. an increase number and quality of eggs) which can have a direct impact on spawning biomass
375 and growth of a population (Kjesbu *et al.*, 1991; Rideout *et al.*, 2000; Morgan, 2004).

376 Our results support the idea previously presented by Sabatés *et al.* (2012) that in the northern
377 areas of the NW Mediterranean the temperature conditions are gradually becoming more favourable
378 to the bluefish reproduction. Although, the spawning of occurs mainly during the summer season in
379 both of our sampling areas the presence of 'Spawning Capable' females and 'Actively Spawning'
380 males during spring in the Ebre Delta (but not in the Gulf of Roses) and a higher proportion of
381 'Regressing' females during the summer in the Ebre Delta further supported the thesis that
382 spawning activity starts and declines earlier in the more southern Ebre Delta. In addition, a higher
383 prevalence of atresia was found in females from the Ebre Delta earlier during spring and this was
384 also found to decrease earlier in summer. This indicates that active oocyte resorption takes place
385 earlier in the Ebre Delta than it does in the Gulf of Roses.

386 Sea temperature may influence the timing of various life processes such as the spawning date
387 (Kjesbu *et al.*, 2010; Morgan *et al.*, 2013). Reproductively active fish from the Ebre Delta were
388 caught when SSTs were between 18.2 and 27.3°C from May to August, while in the Gulf of Roses
389 they were caught when SSTs were between 17.7 and 23.8°C from July to September. Spawning
390 activity started earlier in the Ebre Delta as SSTs rose over 18.0°C in May, in contrast to the Gulf of
391 Roses where spawning individuals were not landed until early summer (July) when SSTs attained
392 similar temperatures, in this case over 17.7°C. However, despite this two-month lag (from May to
393 July), spawning activity was found to begin in both areas at similar temperature thresholds
394 ($\approx 18.0^\circ\text{C}$). This indicates that, for both areas, temperature may trigger the initiation of spawning
395 activity. In contrast, Sabatés *et al.* (2012) reported that the threshold temperature for spawning was
396 21°C. The discrepancies with our study may be related to differences in the approaches used to
397 estimate the timing of spawning. In our study, the timing of spawning was estimated by means of a
398 histological study of the gonads, whereas Sabatés *et al.* (2012) used larvae sampling surveys. Other
399 studies have reported that spawning of bluefish in the mid-Atlantic region occurs at temperatures
400 between 17-24°C (Norcross *et al.*, 1974; Kendall and Walford, 1979), while in the Marmara Sea
401 (Turkey) it occurs from early spring until August at SSTs between 20-26°C (Ceyhan *et al.*, 2007).

402 The difference in the timing of spawning activity in the NW Mediterranean coast may be the
403 result of the seasonal migratory behaviour usually exhibited by this species. Although, to date, no
404 information is available regarding the migration of bluefish in the Mediterranean, this species is
405 known to have large distributions and show seasonal migratory behaviour, spending the colder
406 months in warm-water areas and, when the surface temperature reaches a certain value, migrating
407 towards cooler waters where the species spawns once a threshold temperature has been attained
408 (Juanes *et al.*, 1996; Shepherd *et al.*, 2006). We suspect the bluefish from the north move towards
409 the south, where the waters are warmer, but we do not have any clear evidence of this at present.
410 Sabatés *et al.* (2012) suggest that the actual sea warming trends and the changes in the seasonality
411 of the sea water temperature - particularly during spring months - may be causing changes in

412 spawning phenology and the timing of the seasonal arrival of bluefish into more northern areas
413 favouring the northward temperature-dependent expansion of this species. Similarly, the round
414 sardinella (*Sardinella aurita*) has expanded its northernmost limit of distribution in the NW
415 Mediterranean (Sabatés *et al.*, 2006).

416 The influence of water temperature on bluefish fisheries is revealed in this study using CPUE
417 and transfer functions, and our findings support the results found by Sabatés *et al.* (2012) who used
418 data on landings and sequential *t*-test analysis to detect regime shifts (STARS method). The use of
419 transfer functions in the present study showed that CPUE correlated positively with SST indicating
420 that an increase of temperature in a particular month is followed by an increase of CPUE in that
421 month and in the following month. Therefore, it seems that higher SSTs contribute to increasing
422 bluefish availability in the NW Mediterranean. Fluctuations in fish availability may be related to
423 environmental factors (Smith and Page, 1996), i.e. increased or reduced availability may reflect the
424 temperatures that appear to be avoided or preferred by certain fish species (Swain *et al.*, 2000;
425 Colbourne and Bowering, 2001).

426 Bluefish show behavioural thermoregulation, that is to say they are able to avoid or select the
427 right environmental temperature (Olla and Studholme, 1985). However, within certain thermal
428 limits, their distribution may be based on other ecological factors such as food availability (small
429 pelagic fish) (Juanes and Conover, 1994). In this sense, both the Gulf of Roses and the Ebre Delta
430 have been recognized as important spawning grounds for small pelagic fish (García and Palomera,
431 1996; Olivar *et al.*, 2001; Palomera *et al.*, 2007); however higher densities of anchovy has been
432 observed in the southern Gulf of Lyon than in the Ebre Delta (Bellido *et al.*, 2008). Furthermore,
433 bluefish have also been found in and around sea-cages used in the aquaculture of the seabass
434 (*Dicentrarchus labrax*; Sanchez-Jerez *et al.* 2008). This interaction has been observed in the Gulf of
435 Roses, where bluefish tend to congregate during spring-summer time around the existing sea-cages
436 or even break into the cages to prey on the cultured seabass (sea-cage farm technician, *pers.*
437 *comm.*). Although, the existence of seabass cages in the Gulf of Roses and the Ebre Delta area may

438 thus enhance the bluefish's food supply, it is not quite clear if the increase in bluefish is related to
439 the culture of seabass in the Gulf of Roses because the farm has been active since 20 years ago.

440 On the whole, we hypothesize that the expansion of bluefish in the NW Mediterranean may have
441 been facilitated by the physical conditions (nowadays favourable water temperatures) and also the
442 productivity, so that this new habitat therefore may become a more advantageous ecological niche
443 for this species to exploit.

444 The increasing abundance of bluefish in the northernmost parts of the western Mediterranean
445 may have important consequences for other coastal species that may be ecologically affected by
446 predation or competition. Bluefish is a top predator that feeds on small pelagic species such as, the
447 anchovy, the sardine, the round sardinella, the gilthead seabream or the Mediterranean horse
448 mackerel (Juanes and Conover, 1994; Juanes *et al.*, 1996; Sánchez-Jerez *et al.*, 2008). Therefore,
449 bearing in mind the trophic level of bluefish and the fact that sea warming is impinging favourably
450 on its biology, the status of bluefish populations needs to be studied and monitored.

451 Sea temperatures can actually act as an oceanic barrier between fish populations by creating
452 temperature boundaries in their geographic ranges (Crow *et al.*, 2007). Although the distribution of
453 bluefish coincides with sea surface temperatures of 18–27°C along the subtropical continental
454 shelves of the world (Juanes *et al.*, 1996), it has been suggested by Goodbred and Graves (1996)
455 that shifts in the distribution ranges of bluefish and contact between isolated populations have
456 resulted from historical changes in water temperature. However, although no genetic studies have
457 been carried out yet on the bluefish within our study area, Pardiñas *et al.* (2010) did report
458 insignificant genetic differentiation between eastern Atlantic Ocean (Cadiz and Canary Islands) and
459 Mediterranean Sea (Alicante) populations of this species. We can therefore hypothesize that there is
460 a homogenous bluefish population within the NW Mediterranean, where seasonal migrations take
461 place along a latitudinal gradient in response to changes in water temperature and food supply.

462 In summary, this study provides evidence that a marine fish species such as bluefish, which is
463 able to expand or it is forced to shift its distribution range due to sea warming, may take advantage
464 of other environmental conditions - such as better food availability – in new habitats which will
465 contribute to increasing its energy reserves and reproductive potential and therefore contribute to
466 enhancing the population's productivity in these areas.

467 **ACKNOWLEDGEMENTS**

468 The authors would like to thank the Abertis Foundation for the financial support given to this
469 research (Ref. 1018-100305-00) and the University of Girona for further financial support (R+D
470 ASING2011, Ref. SING11/10). Our sincere thanks to the IRTA research centre (particularly to
471 Guiomar Rotllant and Rosa Trobajo), to Toni Font and Xavier Corrales for their assistance during
472 sampling, to the Catalan Fishing Statistics Department for providing the landings and vessels data,
473 and especially to Ignasi Solé for his advises regarding the ForeTESS statistical analyses. We also
474 thank the comments from two reviewers who contributed to improve an early version of the
475 manuscript. Finally, Harold Villegas-Hernandez would like to thank the Consejo Nacional de
476 Ciencia y Tecnología (CONACYT) in Mexico for the scholarship (Ref. 215050) that has enabled
477 him to pursue his PhD studies at the University of Girona.

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- 630

632 **Fig. 1** Map of the north-western Mediterranean basin showing the two study areas (Gulf of Roses
633 and Ebre Delta) and the location of fishing ports along the Catalan coast where sampling of
634 *Pomatomus saltatrix* was carried out during the 2010-2011-2012 period. The upper panel shows the
635 mean (\pm std. dev.) monthly variation of sea surface temperatures (SST, °C) during the study period
636 (2010-2012) at the Gulf of Roses and the Ebre Delta.

637 **Fig. 2** Box-whisker plots of the adjusted means of HSI and GSI (standardized based on GLMs for
638 sex and maturity) per sampling area. Interquartile box range (25-75%), mean (+), median (\square),
639 whiskers (represented as Q1 and Q3 deviations from the smallest and largest observation,
640 respectively) are also given.

641 **Fig. 3** Seasonal ovarian and testis development stages frequency (percent abundance) and mean (\pm
642 std. dev.) seasonal variation in the GSI of bluefish during the 2010-2012 reproductive cycles in the
643 Gulf of Roses (all years pooled) and the Ebre Delta (2012). Development stages: early developing
644 (EDEV), developing (DEV), spawning capable (SC), actively spawning (AS), regressing (RGS) and
645 regenerating (RGN). Sample number per season (n) is also given in parentheses, n/s denotes periods
646 in which none sample was caught.

647 **Fig. 4** Oocyte size-frequency distribution (per cent abundance per 20 μ m diameter classes) in an
648 actively spawning bluefish female (with hydrated oocytes).

649 **Fig. 5** Comparisons between the observed (actual) and the expected bluefish CPUE in two fishing
650 ports in the Gulf of Roses: (a) Roses and (b) L'Escala, and three fishing ports in the Ebre Delta: (c)
651 L'Ametlla de Mar, (d) L'Ampolla and (e) Sant Carles de la Ràpita. The expected CPUE values
652 represent the contribution of the sea surface temperature (SST) to the bluefish CPUE (kg vessel⁻¹).

LIST OF TABLES

654 **Table 1** Analysis of deviance tables for generalized linear models fitted to HSI and GSI using as
 655 categorical predictors the stage of maturity and sex. Significance are shown as *** for $p < 0.001$ and
 656 ** for $p < 0.05$; d.f. = degrees of freedom.

Variable	Source	d.f.	Residual deviance	Explained deviance (%)	p-value
HSI	Null		94.088		
	Sex	1	4.334	6.9	***
	Maturity	4	7.162	11.0	***
	Sex*Maturity	4	10.539	15.3	***
	Model	324		36.4	
GSI	Null		2005.451		
	Sex	1	73.046	6.2	***
	Maturity	4	771.885	41.2	***
	Sex*Maturity	4	36.573	3.2	**
	Model	324		43.4	

657

658 **Table 2** Summary of oocyte size distributions for each developmental stage in bluefish ovaries. Size
 659 ranges are given for each stage. For CA, Vgt-1, Vgt-2, Vgt-3 and GVM oocyte developmental
 660 stages, measurements were obtained directly from histological sections, and for hydrated oocytes,
 661 previously selected by applying glycerin, image analysis was used.

Oocyte Development Stage	Samples (n)	Sampling Area	Mean Diameter ($\mu\text{m} \pm \text{Std. Dev.}$)	Diameter Range (μm)
<i>Pre-vitellogenic</i>				
Cortical alveolar (CA)	200	Ebre Delta	144.1 (± 25.3)	100 - 200
	200	Gulf of Roses	152.9 (± 20.8)	
<i>Vitellogenic (yolked)</i>				
Early Vitellogenesis (Vtg-1)	200	Ebre Delta	228.9 (± 24.2)	200 - 300
	200	Gulf of Roses	248.6 (± 25.8)	
Mid Vitellogenesis (Vtg-2)	200	Ebre Delta	334.5 (± 27.6)	300 - 400
	200	Gulf of Roses	345.6 (± 29.2)	
Advanced Vitellogenesis (Vtg-3)	200	Ebre Delta	427.9 (± 30.3)	400 - 500
	200	Gulf of Roses	438.6 (± 24.0)	
<i>Maturation</i>				
Germinal Vesicle Migration (GVM)	200	Ebre Delta	529.2 (± 24.4)	500-600
	200	Gulf of Roses	539.9 (± 26.7)	
Hydration	200	Ebre Delta	757.1 (± 56.9)	600-1000
	200	Gulf of Roses	763.5 (± 50.7)	

662

663 **Table 3** Prevalence of atresia (P_a) and mean relative intensity of atresia (R_{Ia}) for each stage of
 664 ovarian development for each season at each study area (NA denotes that no sign of α -atresia was
 665 observed).

Variation source	P_a (%)		Mean R_{Ia} (% \pm std. dev.)	
	Gulf of Roses	Ebre Delta	Gulf of Roses	Ebre Delta
<i>Maturity stage</i>				
Developing	NA	NA	NA	NA
Spawning Capable	23.7	17.2	9.9(\pm 5.9)	4.4(\pm 1.1)
Regressing	100.0	23.1	96.3(\pm 2.0)	29.9(\pm 10.3)
Regenerating	NA	NA	NA	NA
<i>Season</i>				
Spring	14.3	50.0	14.3(\pm 0.1)	4.8(\pm 0.1)
Summer	27.0	15.4	26.7(\pm 37.1)	17.0(\pm 15.5)
Autumn	NA	NA	NA	NA
Winter	NA	NA	NA	NA

666

667

668 **Table 4** Results of the ARIMA transfer functions between CPUE and SST. Arithmetic mean and
 669 standard deviations of the CPUE are given; RSEU is the residual standard error of each transfer
 670 function; RSE is the residual standard error of each coefficient; R^2 is the variance explained.
 671 Significant coefficients at a t-value $>|2|$ ($p < 0.05$) are shown in bold.

Port	CPUE (kg vessel ⁻¹)		RSEU (kg vessel ⁻¹)	R^2	Time lag (months)	Coeff. (kg vessel ⁻¹)	RSE (kg vessel ⁻¹)	t-value
	Mean	Std. Dev.						
Roses	1.21	2.15	0.94	0.81	0	0.42	0.06	2.31
					1	0.34	0.08	3.65
					2	0.03	0.06	0.59
L'Escala	1.79	2.74	1.21	0.80	0	0.38	0.08	2.34
					1	0.41	0.08	3.80
					2	0.05	0.08	0.60
L'Ametlla de Mar	28.92	34.76	15.68	0.80	0	1.93	0.97	2.36
					1	2.27	0.96	2.19
					2	0.16	0.94	0.17
L'Ampolla	3.29	4.20	1.93	0.79	0	2.23	0.19	2.32
					1	3.42	0.23	3.54
					2	0.02	0.14	0.02
St. Carles de la Ràpita	63.71	53.05	28.62	0.71	0	7.97	1.85	2.30
					1	3.84	1.95	2.85
					2	1.16	1.48	0.78

672

673 **Table 5** Results of the SST threshold analyses using the ARIMA transfer functions between
674 bluefish CPUEs and SSTs at different thresholds ($SST_{13} + \dots + SST_{27}$). Significant coefficients
675 from the time lag of ‘0 months’ at a t-value $> |2|$ ($p < 0.05$) are shown in bold. The Akaike’s
676 Information Criterion (AIC) is also shown in parentheses.

Threshold	Port				
	Roses	L’Escala	L’Ametlla de Mar	L’Ampolla	St. Carles de la Ràpita
T_{13}	0.28 (2492)	0.78 (2580)	0.52 (2635)	0.85 (2503)	0.61 (2751)
T_{14}	0.39 (1971)	1.01 (1543)	0.68 (1321)	0.91 (1450)	1.64 (2630)
T_{15}	0.68 (1053)	1.13 (1413)	1.08 (1310)	0.87 (1398)	1.58 (1497)
T_{16}	1.21 (845)	1.14 (1424)	1.32 (1003)	1.69 (928)	1.36 (1399)
T_{17}	2.45 (721)	2.09 (1387)	1.95 (991)	1.83 (812)	2.09 (967)
T_{18}	2.68 (760)	2.21 (1326)	2.13 (945)	3.56 (820)	2.07 (841)
T_{19}	2.97 (612)	2.62 (955)	2.31 (819)	4.45 (736)	2.16 (804)
T_{20}	3.34 (694)	2.54 (838)	3.33 (809)	4.84 (735)	3.91 (629)
T_{21}	3.28 (657)	2.93 (705)	2.41 (795)	3.96 (601)	3.93 (612)
T_{22}	3.56 (535)	3.12 (645)	3.01 (663)	3.01 (647)	3.75 (506)
T_{23}	3.68 (501)	3.55 (537)	3.93 (661)	3.23 (473)	3.83 (494)
T_{24}	3.34 (589)	3.11 (525)	3.84 (607)	3.72 (414)	3.09 (337)
T_{25}	4.45 (423)	3.17 (424)	3.05 (541)	3.31 (415)	3.25 (345)
T_{26}	4.98 (425)	4.33 (416)	3.64 (552)	3.48 (311)	3.22 (234)
T_{27}	4.51 (422)	4.19 (313)	3.99 (501)	3.94 (398)	3.77 (293)

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