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2 **The recent population expansion of Boarfish (*Capros aper*): Interactions of**
3 **climate, growth and recruitment**

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14 **Summary**

15 The objectives of this study were to evaluate whether changes in temperature in the
16 Northeast Atlantic influence the growth and recruitment dynamics of boarfish. Two
17 geographically separate areas were examined, “north” at the northern distribution
18 range west of Ireland and “south” on the main fishing grounds south of Ireland. No
19 significant differences in length-at-age were observed between the two areas.
20 Interannual otolith growth patterns were similar between the two areas with distinct
21 years of faster and slower growth. In the “north”, no significant relationship between
22 adult growth and temperature was observed, while growth in the “south” was
23 positively related to temperature up to approximately 16 °C growth rates were
24 suppressed in the years

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26 with temperature above that. Recruitment showed a positive correlation with adult
27 growth the previous year for the Spanish recruitment index only, suggesting spatial
28 connectivity between the Celtic Sea and the Bay of Biscay. The age distributions
29 were similar in both areas and despite the boarfish's longevity of > 30 years, are
30 dominated by the age classes corresponding to the years with high recruitment,
31 suggesting that increased recruitment is responsible for the observed stock
32 expansion.

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34 Keywords: Boarfish, temperature, growth chronology, recruitment, climate

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46 **Introduction**

47 Over the last century, the Northeast Atlantic marine ecosystem has experienced large
48 variation in environmental conditions and biogeographical shifts of marine fauna,
49 driven by climatological changes (Hurrell, 1995; Beaugrand et al., 2002; Hátún et
50 al., 2005). Rapid warming and salinification have been observed since the mid
51 1900's (Hátún et al., 2005) and rising sea temperatures have altered the composition
52 of fish communities in the area (Quéro, 1998; Brander et al., 2003). These changes
53 have been linked to environmental conditions and ecosystem wide trophic
54 interactions (Hátún et al., 2009). The zooplankton community in the area has also
55 shifted since the early 1980's, where a poleward movement of the warm water
56 species *C. helgolandicus* and a northward shift in the southern limit of the coldwater
57 species *C. finmarchicus* distribution range has occurred (Fromentin and Planque
58 1996; Planque and Fromentin, 1996). The northward range expansion of warm water
59 fish species has been well documented in the Northeast Atlantic (Stebbing et al.,
60 2002; Brander et al., 2003; Beare et al., 2004; Kirby et al., 2006) and likewise the
61 disappearance of species in other regions (Alheit and Hagen, 1997; Quéro et al.,
62 1998). These biogeographical shifts have been attributed to a changing climate and
63 the coincident change in water temperatures, ocean currents and other physical
64 mechanisms (Beaugrand et al., 2002). In warm water species for example, the impact
65 of climate change is often reported as a positive correlation between measures of
66 stock abundance or distribution, and rising temperatures (Farina et al., 1997;
67 Blanchard and Vandermeirsch, 2005) and/or food abundance (Reid et al., 2001;
68 Alheit et al., 2005). However the underlying physiological mechanisms are yet to be
69 elucidated.

70

71 The boarfish is a pelagic shoaling species which has historically been considered rare
72 in the Northeast Atlantic except for periodical increases in abundance. Large
73 numbers were captured sporadically between the 1840's and 1880's (Cunningham,
74 1888). In the mid 1900's, Cooper (1952) reported another increase in abundance,
75 which has again been apparent between the 1980's and early 2000's (Farina et al.,
76 1997, Pinnegar et al., 2002, Blanchard & Vandermeirsch, 2005). This trend has
77 developed and has resulted in a population expansion over the last fifteen years
78 (ICES, 2012; O'Donnell et al., 2012). The increase in boarfish abundance in the Bay
79 of Biscay was attributed to increasing water temperatures in that area since the mid
80 1980's (Blanchard and Vandermeirsch, 2005) but the causal mechanisms were not
81 examined.

82 With a maximum age of over 30 years, clear seasonal growth patterns (Hüssy et al.,
83 2012a; 2012b) and strong signals in stock abundance, the boarfish is an ideal species
84 for studying growth dynamics based on dendrochronology methods (Black et al.,
85 2008).

86 The objectives of this study were to evaluate whether changes in temperature in the
87 Northeast Atlantic influence the growth and recruitment dynamics of boarfish and to
88 examine possible mechanisms behind stock expansions at the northern distribution
89 limit of fish. We tested the hypotheses that 1) the observed increase in stock
90 abundance is related to recruitment 2) increasing temperature has a positive effect on
91 growth, particularly at the northern limit of their distribution range, and 3)
92 recruitment is positively related to growth of the adult fish as proxy for fecundity.

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96 **Materials and methods**

97 *Sample selection and preparation*

98 Boarfish samples (n = 1633) were collected between September 2009 and December
99 2010 from commercial fishing vessels and scientific surveys in the Northeast
100 Atlantic (Figure 1). For all samples, total length was measured down to the nearest
101 mm. Samples for ageing (n = 407) were selected per quarter, 10 fish per 0.5 cm
102 length class, with the exception of length classes < 10cm and > 16cm, where all
103 samples were aged.

104 Both sagittal otoliths were removed. The left otolith was cleaned in 95 % ethanol,
105 immersed in undiluted propylene glycol for 6 minutes, placed on a black background
106 under a circular reflected light source and viewed using a Leica MZ12 microscope at
107 a magnification of 0.63 pixels μm^{-1} . Images were digitized using a Leica DFC290
108 camera (8 bits per channel, 2048 \times 1536 pixel frame, 35 ms exposure). The equalize
109 histogram function was set to 4% and image brightness and contrast were adjusted in
110 order to maximize the contrast between growth zones. Ages (A) were estimated by
111 counting the annual growth zones following routine methods (Hüssy et al., 2012a).

112

113 *Growth chronology*

114 A total of 40 fish, > 10 years of age with clearly defined increment patterns and with
115 known geographical positions were selected from those aged in 2010 (Figure 1).
116 Only otoliths with clearly defined transition from opaque to translucent zones and
117 with exact capture positions were chosen. In order to test for latitudinal effects,
118 samples were selected from two separated areas with high boarfish densities, one
119 west of Ireland north of 52°N and one south of 50°N (Figure 1). These areas are

120 henceforth called “north” and “south” (age range “south”: 11 – 28, mean age: 15;
121 age range “north”: 11 – 21, mean age: 15).

122 Otolith measurements were taken along the dorsal anterior axis, from the outer edge
123 towards the nucleus, perpendicular to the growth axis and from the beginning of one
124 annulus to the beginning of the following annulus. One increment width (IW)
125 comprised winter and summer growth from one year (Figure 2). Increment widths
126 were measured using ImageJ (v.1.44p available at <http://rsbweb.nih.gov/ij/>).

127 Establishing the growth chronology consists of a two-step process, following the
128 procedure described by Black et al., (2005). First individual growth patterns are
129 established as a proportional deviation from the expected average annual otolith
130 growth resulting in residual growth values for each year. As otolith growth decreases
131 exponentially with fish age this procedure allows the comparison of growth rates
132 between fish of different ages, but also of growth at different ages within the same
133 fish. Secondly, a population growth chronology is calculated by averaging the
134 residual growth values across individuals by year (Black et al., 2005). For each fish a
135 negative exponential regression was fitted to the IW measurements as a function of
136 year when they were formed. The residuals from this regression were divided by the
137 predicted values for each year of formation. To avoid bias of measurements from the
138 inner highly opaque area of the otoliths, the innermost IW corresponding to the first
139 three years of life were excluded. The outermost, incomplete growth zone was also
140 excluded.

141 The resulting individual, de-trended and standardised residuals were tested for a
142 possible bias associated with fish age. The residuals of a good growth year where
143 residuals were generally positive (2004) and a bad growth year where residuals were
144 generally negative (2005) were plotted against fish age and the significance of the

145 slope tested. A slope of 0 means that the chosen approach removed all effects of fish
146 age and warrants using all ages for a combined growth chronology. The individual
147 standardised residual time series were then averaged within each year of formation,
148 resulting in two growth chronologies, one for “north” and one for “south”.

149

150 *Stock data*

151 Abundance estimates were based on the following survey data obtained from ICES
152 (2011): IGFS - Irish Groundfish Survey (ICES Subdivisions VIa, VIIb, VIIc, VIIg
153 and VIIj), EVHOE - French Groundfish Survey in the Celtic Sea and Bay of Biscay
154 (ICES Subdivisions VIIf, VIIg, VIIIh, VIIj, VIIIa and VIIIb) and SPNGFS - Spanish
155 Groundfish Survey on the Northern Spanish Shelf (ICES Subdivisions VIIIc and
156 IXaN). Recruitment was based on the number of 1 year olds caught during the
157 surveys (ICES, 2011). For each area a relative recruitment index was estimated by
158 back shifting the number of recruits by 1 year (as a measure of year class strength)
159 and dividing that number by the annual stock abundance, resulting in a Spanish
160 (R_{SPNGFS}), French (R_{EVHOE}) and Irish (R_{IGFS}) relative recruitment indices, henceforth
161 referred to as “recruitment indices”. Stock abundance and recruitment indices are
162 shown in Figure 3 and 4 respectively.

163

164 *Temperature data*

165 Sea surface temperature (*SST*) data was obtained from ICES at
166 <http://ocean.ices.dk/data/surface/surface.htm> for the Marsden squares corresponding
167 to the boarfish sampling areas “north” and “south”, for the years 1995 - 2009.
168 Measurements were averaged to obtain a single temperature estimate for each month.
169 Missing values were estimated from a fourth order polynomial fitted to the months

170 with data available for each year separately. The resulting monthly values were
171 subsequently used to calculate seasonal average values for: Spring = February,
172 March, April (FMA); Summer = May, June, July (MJJ); Autumn = August,
173 September, October (ASO); Winter = November, December, January (NDJ).
174 Summer average SST is shown in Figure 5.

175

176 *Data analysis*

177 *Length-at-age*: In order to test for latitudinal differences in absolute growth, the
178 length-at-age between “north” and “south” was tested using the sub-sample of the
179 fish with age estimates corresponding to the two area definitions ($n_{\text{north}} = 167$, $n_{\text{south}} =$
180 105). Growth was analysed by fitting the typical parameterization of the von
181 Bertalanffy (1938) growth equation:

$$182 \quad L_A = L_{\text{inf}} \cdot [1 - \exp^{-K \cdot (A - t_0)}] \quad (1)$$

183 where L_A = expected average length at age A , L_{inf} = the asymptotic average length, K
184 = the Brody growth rate coefficient, and t_0 = a parameter representing the age when
185 average length was zero. The growth equation was fitted using a non-linear
186 regression function and parameters estimated by least squares. The difference
187 between the two areas was tested statistically by fitting different von Bertalanffy
188 growth models to the size-at-age data, the most complex being one with area-specific
189 parameters of L_{inf} , K , and t_0 . This model was then tested against all possible
190 combinations of reduced models, with subsequently fewer parameters differing
191 between areas, the most simple being that of a model without differences in
192 parameter estimates between areas (following the procedure described in Hüseyin *et*
193 *al.*, 2012). Model assumptions of normally distributed, homoscedastic residuals were
194 tested for the most complex model, assuming that if model assumptions were met in

195 this model they would also be in all submodels. The submodels were then compared
196 by likelihood ratio tests using the Akaike Information Criterion (AIC), where the
197 models were compared in a hierarchical manner by comparison with the most
198 complex model, following the procedure of Ogle (2011).

199

200 *Growth chronology:* The influence of temperature on residual otolith growth was
201 analysed with multiple linear regression using the model:

$$202 \quad G_y = a + b * SST_{y,FMA} + c * SST_{y,MJJ} + d * SST_{y,ASO} + e * SST_{y,NDJ} + \varepsilon \quad (2)$$

203 Where G_y = residual otolith growth in year y , and SST_y = average seasonal surface
204 temperature in year y . All combinations of the four seasonal average values
205 for sea surface temperature (SST) were used. Sub-models consisting of model (2) but
206 with stepwise elimination of parameters were compared by likelihood ratio tests. As
207 the temperature dependence of growth is known to be parabolic when considering
208 the entire non-lethal temperature range of a species, this relationship was also tested
209 using polynomial models.

210

211 *Recruitment:* The effect of growth on recruitment was tested with linear regression
212 analysis. As copepod abundance is low until the end of April (SAHFOS) boarfish
213 may have to rely on accumulated body reserves for egg production, which from an
214 analytical perspective may introduce a time-lag of one year between offspring
215 production and growth. Each of the three areas recruitment indices (R_{SPNGFS} , R_{EVHOE} ,
216 R_{IGFS}) were therefore analysed not only as a function of residual otolith growth in the
217 same year (G_y) but also as a function of residual growth in the previous year (G_{y-1}).
218 For this analysis the growth data for the years 1997 - 2009 and the corresponding

219 recruitment indices were used for the Spanish (R_{SPNGFS}) and French (R_{EVHOE}) indices,
220 but for the Irish (R_{IGFS}) index only data from 2003 – 2009 was available.

221

222 *Statistics*

223 All statistical analyses were carried out in R ver. 2.12.2 ([R Development Core Team,](#)
224 [2009](#)). Model residuals were tested for normality and homogeneity of variances
225 using a Shapiro–Wilk’s normality test and the Bartlett test of homogeneity of
226 variances. Effects of environmental condition on growth were tested in a multiple
227 linear analysis approach, while age distributions were compared with Wilcoxon
228 ranks sum test for equality of means.

229

230 **Results**

231 *Age distribution:* The age distribution showed a prominent peak in abundance of 4 -
232 6 year old fish and a lower peak of 20 to 24 year old fish ($n = 406$) (Figure 6). On
233 average, fish in the “north” and “south” had the same age (Wilcoxon signed rank
234 test, $p = 0.85$). However, geographical differences were evident in the age
235 distribution pattern, in that fish from the “south” show strong age classes 3 and 4
236 (corresponding to year classes 2006 and 2007), while the abundance of these age
237 classes in the “north” is lower with peaks in abundance at age 6 (corresponding to
238 year class 2004) and higher abundance in the youngest age classes.

239

240 *Length - at - age:* The residuals of the fitted von Bertalanffy growth equation were
241 normally distributed and homoscedastic, with increasing fitted values without
242 outliers. The growth model with the lowest AIC was the general growth model (1),
243 without any area-specific effects ($L_{inf} = 15.768$ (0.293), $K = 0.167$ (0.013), $t_0 = -$

244 2.814 (0.389), with standard errors in brackets). This shows that boarfish follow the
245 same general growth trajectories in the two different areas (Figure 7).

246

247 *Growth chronology*: The slope of the standardised residuals against fish age
248 regression was not significantly different from 0 for both 2004 and 2005 ($n = 40$,
249 both $p > 0.05$). The residuals from all individuals were therefore averaged within
250 each year of formation to obtain two growth chronologies, one for the “north” $>$
251 52°N and one for the “south” $< 50^{\circ}\text{N}$ (Figure 8). Residual values > 0 indicate years
252 of good growth, while values < 0 indicating years of poor growth. Henceforth, these
253 residuals are referred to as “growth”.

254 “South”: For this analysis, only the years 1997 – 2009 were used in order to avoid
255 bias introduced by low sample numbers, as growth estimates of years before that
256 consisted of subsequently fewer individuals. Only summer temperatures (MJJ)
257 showed a consistent pattern with growth. Growth was not linearly related to
258 temperature ($df = 11$, $r^2 = 0.004$, $p > 0.05$). However, a second order polynomial
259 relationship between temperature and growth, with a temperature optimum at
260 approximately 16°C ., explained 63% of the inter-annual variability in growth: $G = -$
261 $1.8992 + 0.2405 \cdot SST - 0.0076 \cdot SST^2$ ($df = 11$, $r^2 = 0.63$), suggesting that boarfish
262 growth may be limited in years with high summer temperatures (Figure 9). All other
263 seasonal temperatures explained less than 10% of the variability in growth (all $p >$
264 0.05).

265 “North”: The relationship of between growth and sea surface temperatures (*SST*)
266 was positive, but none of the seasonal averages had a significant effect on boarfish
267 growth.

268

269 *Recruitment:* Before 2004, recruitment of boarfish from the Bay of Biscay to the
270 Celtic Sea has been very low. Since then, recruitment has increased significantly
271 with peaks in 2005 - 2007 and 2009 and a somewhat lower level in 2008 (Figure 4).
272 Even though the three recruitment indices follow the same general pattern, regional
273 differences are evident, in that the Spanish index (R_{SPNGFS}) consistently shows a
274 higher level than the French index (R_{EVHOE}), while the Irish index (R_{IGFS}) is less
275 variable and at a much lower level.

276 The effect of residual growth in the same year as well as in the previous year was
277 analysed with multiple linear regression analysis for each area and recruitment index
278 separately. In all analyses, only growth the previous year (G_{y-1}) explained a certain
279 degree of the variability in recruitment while growth in the same year (G_y) had no
280 effect. “South”: Growth the previous year explained 25 % of the interannual
281 variation in relative recruitment of the Spanish recruitment index R_{SPNGFS} ($R_{SPNGFS} =$
282 $14.942 + 690.4 \cdot G_{y-1}$, $df = 11$, $r^2 = 0.25$, $p = 0.11$), where only one year-class (2002)
283 prevented the relationship to be strongly significant ($R_{SPNGFS} = 19.206 + 1308.2 \cdot G_{y-1}$,
284 $df = 10$, $r^2 = 0.57$, $p < 0.005$), indicating that in most years growth alone may
285 explain $> 50\%$ of the variation in recruitment. No significant relationship between
286 growth and recruitment was found for the French ($R_{EVHOE} = 44.102 + 421.59 \cdot G_{y-1}$,
287 $r^2 = 0.0298$, $p > 0.05$) and Irish ($R_{IGFS} = 1.925 - 23.15 \cdot G_{y-1}$, $r^2 = 0.065$, $p > 0.05$)
288 indices.

289 “North”: Growth had no significant effect on either the Spanish ($R_{SPNGFS} = 18.81 +$
290 $335.87 \cdot G_{y-1}$, $r^2 = 0.1484$, $p > 0.05$), the French ($R_{EVHOE} = 47.41 + 472.99 \cdot G_{y-1}$, r^2
291 $= 0.05$) or the Irish ($R_{IGFS} = 1.89 + 14.47 \cdot G_{y-1}$, $r^2 = 0.0384$, $p > 0.05$) recruitment
292 indices.

293 **Discussion**

294 Expansions in a species' distribution range are generally associated with changes in
295 stock size and depend on a suite of processes, from shifts in adult fish's migration
296 and spawning patterns in response to changes in hydrographic conditions
297 (Drinkwater, 2006; Hátun et al., 2009; Valdimarsson et al., 2012) to changes in early
298 life stage survival (Drinkwater, 2006; Kirby et al., 2006; Rijnsdorp, 2009;
299 Solmundsson et al., 2010). We tested the hypotheses that adult boarfish's growth
300 potential has improved at the northern boundary of their distribution range, with a
301 subsequent impact on the production of offspring.

302 The three recruitment indices and the area-specific age distributions show that the
303 stock expansion is not the result of migration dynamics but linked to recruitment.

304 The presence of 20 – 30 year old fish in both areas shows that boarfish have been
305 present in the Celtic Sea for many years, albeit in limited numbers. The high
306 frequency of age 4 - 6 year old fish on the other hand corresponds to the years when
307 all recruitment indices were strongest. The results of this study suggest that
308 variability in water temperatures may have contributed to the recent population
309 expansion of boarfish in the Northeast Atlantic by affecting adult growth with a
310 subsequent impact on the production of recruits. However, the results are somewhat
311 unclear, so in the following they are discussed individually to resolve their respective
312 significance.

313 Environmental temperatures differed between the two areas examined in this study,
314 where the “south” was consistently 2 degrees higher than the “north” during winter.
315 Also during summer the “south” was warmer - but subject to much higher inter-
316 annual variability where temperatures ranged between $< 14^{\circ}\text{C}$ to $> 18^{\circ}\text{C}$.

317 Temperature differences between “north” and “south” have diminished from ca. 5 °C
318 in the 1990’s to < 1 °C since 2005.

319 Residual otolith growth of boarfish was only related to summer/autumn temperatures
320 and none of the other seasons. This is not surprising as the main growth season of
321 boarfish lasts from May to July/August (Hüssy et al., 2012a) while feeding seems
322 virtually suspended during winter as suggested by observations on stomach contents
323 (K. Hüssy, pers. obs.). In the “south” the growth was positively related to
324 temperature up to approximately 16 °C, while growth rates were suppressed in the
325 years with temperature above that (1997 – 1999, 2003). Such a parabolic temperature
326 response of growth is a well-known phenomenon when considering the entire non-
327 lethal temperature range of a species (Jobling, 2003) and suggests that the 16 °C
328 correspond to boarfish’s optimal temperature for growth. In the “north”, where
329 temperatures were consistently below this optimal of 16 °C and boarfish at the
330 northern limit of their distribution area, one would expect an even stronger
331 temperature signal. The expected positive temperature - growth relationship was not
332 significant in the “north”. The general interannual pattern in residual otolith growth
333 is nevertheless similar in the two areas except for the warm 2003, where growth in
334 the “south” was suppressed compared to the “north”, and 2001, where growth was
335 above average in the “south” but low in the “north”. The use of *SST* as measure for
336 the environmental temperature experienced by boarfish may not be ideal as this
337 species is generally distributed over a wide depth range (O’Donnell et al., 2012).
338 However, no data covering that depth range is currently available for all areas.

339 The recent increase in this species’ abundance has previously been correlated with
340 rising water temperatures (Farina et al., 1997; Blanchard and Vandermeirsch, 2005).
341 The results from the present study indicate that adult growth response to increasing

342 temperatures to some degree may be one of the underlying physiological
343 mechanisms for this relationship. However, increasing temperatures can only support
344 faster growth if sufficient prey is available (Buckley et al., 2004). Large copepods,
345 specifically *C. helgolandicus*, dominate the diet of boarfish which also consists of
346 euphausiids, their larvae, mysid shrimp and gastropods (MacPherson, 1979; Fock et
347 al., 2002; Lopes et al., 2006). These prey items are observed in areas where *C.*
348 *helgolandicus* are abundant and given that daily and seasonal prey switching has
349 been observed, boarfish may have an adaptable prey preference depending on prey
350 availability (MacPherson, 1979; Fock et al., 2002; Lopes et al., 2006). The fact that
351 length-at-age did not differ between “north” and “south”, showing that growth is
352 similar in the two areas despite the differences in environmental temperature
353 regimes, suggests that other drivers are impacting on boarfish growth as well. Prey
354 availability and utilisation may well contribute to the similar growth rates in the two
355 areas.

356 A positive influence of temperature on boarfish growth alone is not necessarily
357 enough to cause a stock expansion, therefore we test the hypothesis that faster
358 growth rates will subsequently lead to higher offspring production. With the
359 exception of an apparent link between growth in the “south” and the Spanish
360 recruitment index none of the recruitment indices were significantly related to
361 growth conditions in the two areas. The fecundity of fish is generally positively
362 correlated with somatic condition before spawning in both experimental fish (Ma et
363 al., 1998) and wild fish (Hutchings et al., 1998; Lambert and Dutil, 2000). Adult
364 growth in the year prior to recruitment (and not the corresponding year) explained a
365 higher degree of variability in all recruitment indices, indicating that energy
366 accumulation in the year before is essential for the boarfish’s egg production. The

367 reproductive cycle of boarfish begins as early as February and spawning commences
368 in early June (Farrell et al., 2012) and nutritional condition (or growth as a proxy
369 thereof) built up during the previous summer/autumn can be expected to have a
370 direct impact on gonad maturation, oocyte viability, egg production and spawning
371 the following year. This is not unheard of as reduced recruitment in the South
372 African anchovy (*Engraulis capensis*) also has been linked to poor adult condition
373 (Hutchings et al., 1998) and low production in the year prior to recruitment (Waldron
374 et al., 1997).

375 From the age distribution it is evident that recruitment is the driving force behind
376 boarfish's stock expansion in the Northeast Atlantic and improved conditions for
377 adults seems to some degree to contribute to increased recruitment. The causal
378 mechanisms for boarfish's stock expansion are not resolved with this study, but the
379 results suggest the existence of a complex source - sink type of link between the
380 main spawning areas in the Celtic Sea and juvenile nursery areas in the Bay of
381 Biscay (Coad and Hüsey, 2012). Boarfish spawn along the continental shelf edge;
382 the main spawning locations are to the west of Ireland and in the southern Celtic Sea,
383 in the same areas as mackerel (*Scomber scombrus*) (O' Donnell et al., 2012).
384 Mackerel eggs and larvae are known to drift from the spawning grounds towards the
385 south-east (Bartsch and Coombs, 2004) as a result of the counter flow along the
386 Celtic shelf-break (Pingree and LeCann, 1989). West of Ireland, a circulation pattern
387 over the Porcupine Bank (Mohn et al., 2002; Mohn and White, 2007) is known to
388 retain mackerel eggs (Bartsch and Coombs, 2004). These drift patterns indicate that
389 boarfish eggs spawned in the southern Celtic Sea may be transported southward
390 towards the Bay of Biscay while those spawned west of Ireland are retained in the
391 area (Coad and Hüsey, 2012). The age distribution of our sample indicates a higher

392 number of 0 and 1 year olds in the north compared to the south. It is possible that
393 this could be a sampling effect however, these age distributions fit with the drift-
394 retention hypothesis in that the presence of the youngest age classes in the north
395 suggest they were retained in that area. In the south on the other hand, they may have
396 been transported out of the area sampled and thus not present in the age distribution
397 in this area. Length frequency distribution data from the IBTS surveys shows an
398 increase in mean total length with latitude (ICES, 2012) with significantly smaller
399 size in the southern Bay of Biscay than in the Celtic Sea. The poleward flow of the
400 Shelf Edge Current (Pingree and LeCann, 1989; 1990) may subsequently promote
401 drift and/or migration of adult fish northward and support the hypothesis of spatial
402 connectivity between these areas. Due to its reproductive strategy, especially its
403 indeterminate fecundity, boarfish are capable of reproducing as long as
404 environmental conditions are favourable (Farrell et al., 2012). This suggests that
405 such an observed increase in stock size and possible northward distribution
406 expansion is not only the result of climatic conditions, but also a function of the
407 species' physiological capabilities.

408 This study contributes towards understanding the relationships between temperature,
409 growth and recruitment of Boarfish. Observations in the two areas suggest complex
410 climate related mechanisms are responsible for the boarfish's stock expansion in the
411 Northeast Atlantic. To improve our understanding of these mechanisms and their
412 impact on boarfish stock dynamics inter-disciplinary research to establish stock
413 structure, feeding and predation dynamics as well as drift and migration patterns is
414 essential.

415

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605 **Figure 1** Map of the study area with position of aged and chronology samples. Aged
606 samples represented by the black circles, in ascending order of size the smallest
607 circle represents <25 samples followed by 26-50 samples, 51-75 samples and >75
608 samples respectively. Chronology samples represented by grey circles and legend
609 numbers.

610

611 **Figure 2** Left sagittal otolith of *C. aper*. The diagonal white line represents the
612 optimal measuring axis and the perpendicular lines indicate where measurements
613 were taken from the
614 beginning of one annulus to the beginning of the next.

615 **Figure 3** Stock size of *C. aper* (represented as number of boarfish per 30 minute
616 haul per ICES rectangle in ICES Subareas VI, VII, VIII from IBTS surveys 1985 to
617 2010 (data from ICES, 2011).

618

619 **Figure 4** Relative recruitment (R) of *C. aper* in the Northeast Atlantic. Grey =
620 Spanish index (R_{SPNGFS}), open symbols and broken line = French index (R_{EVHOE}), and
621 black = Irish index (R_{IGFS}) survey areas from 1997 to 2009.

622

623 **Figure 5** Average summer SST for the study area (black=north; grey=south). For the
624 “south” no data was available for 2008.

625

626 **Figure 6** Age frequency distribution of *C. aper*. in the Northeast Atlantic
627 (black=north; grey=south). Asterisks denote years with exceptionally strong
628 recruitment.

629

630

631 **Figure 7** Size at age of *C. aper* in the Northeast Atlantic (black=north; grey=south).

632 Lines are fitted von Bertalanffy growth curves for the two areas.

633

634 **Figure 8** Growth chronologies for *C. aper* sampled in the Northeast Atlantic

635 ((black=north; grey=south). The horizontal dashed line represents a residual value of

636 zero, positive values above the line indicate good growth and negative values below

637 the line represent poor growth.

638

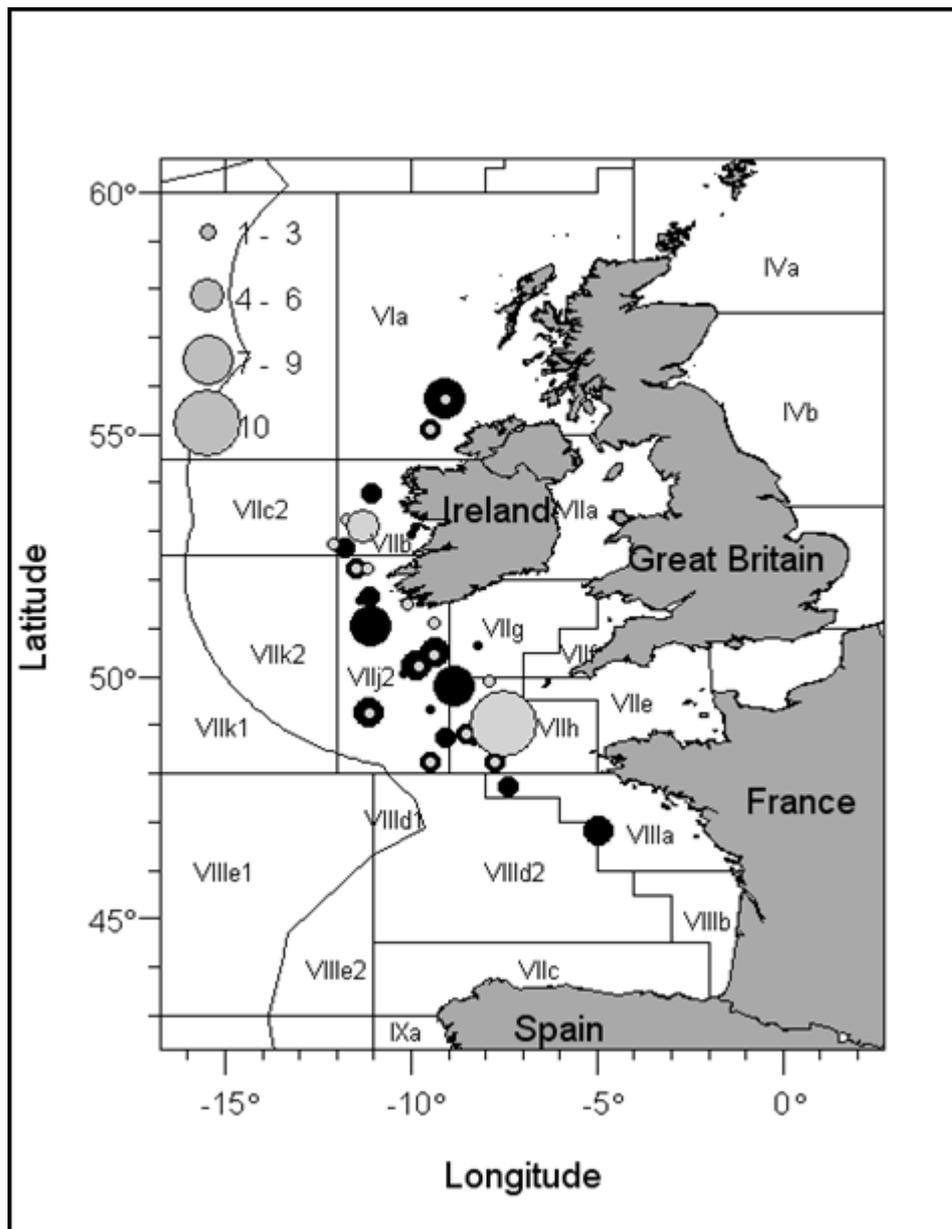
639 **Figure 9** Relationship between residual otolith growth and summer *SST* for two

640 areas in the Northeast Atlantic ((black=north; grey=south). The line is the

641 polynomial model fitted to the “south” data.

642

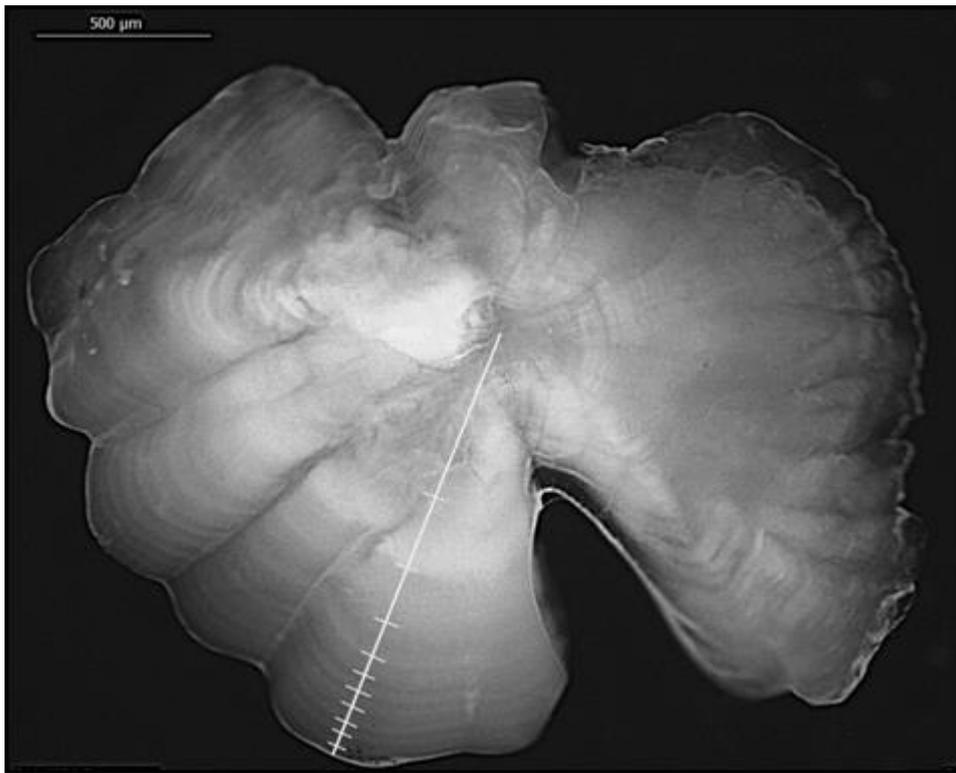
643 **Figure 1**



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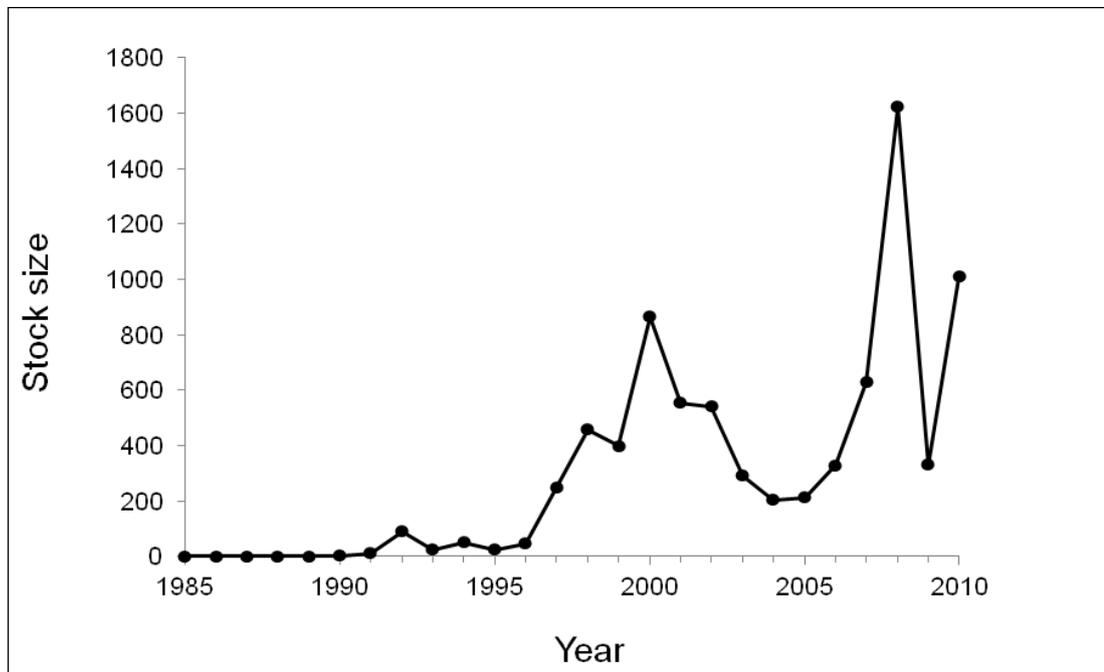
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646 **Figure 2**



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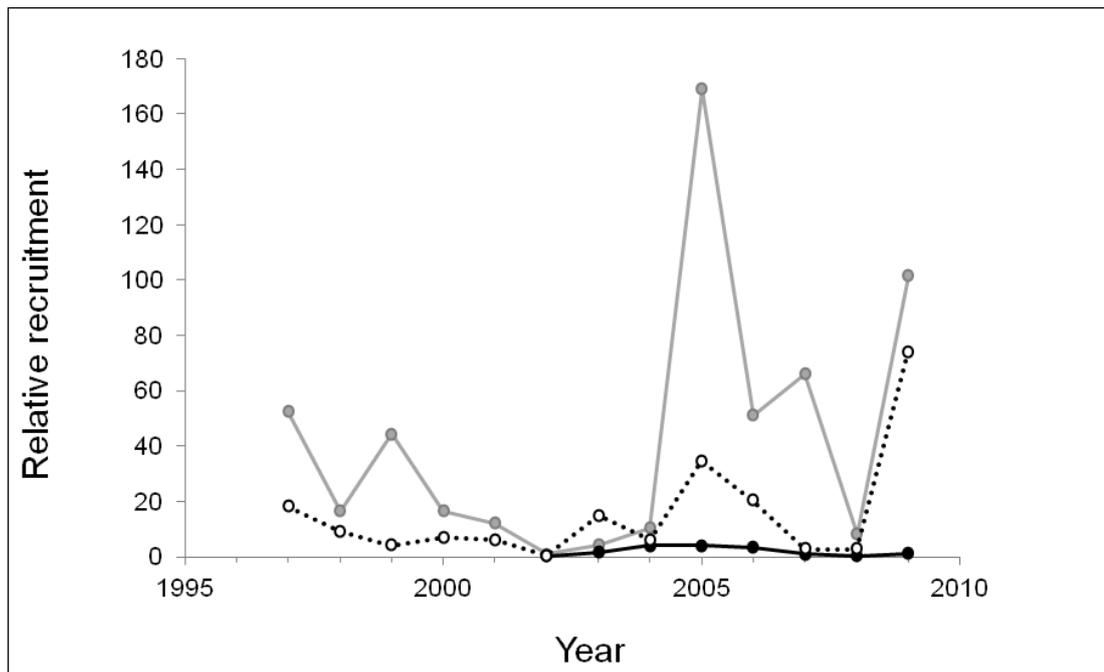
648 **Figure 3**



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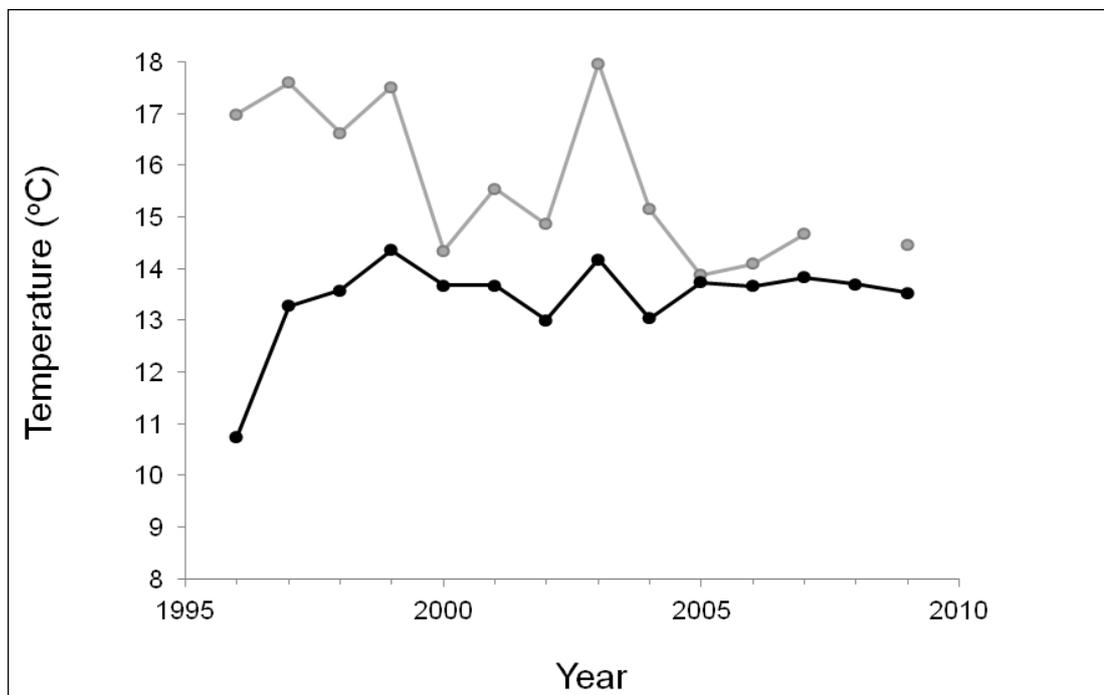
651 **Figure 4**



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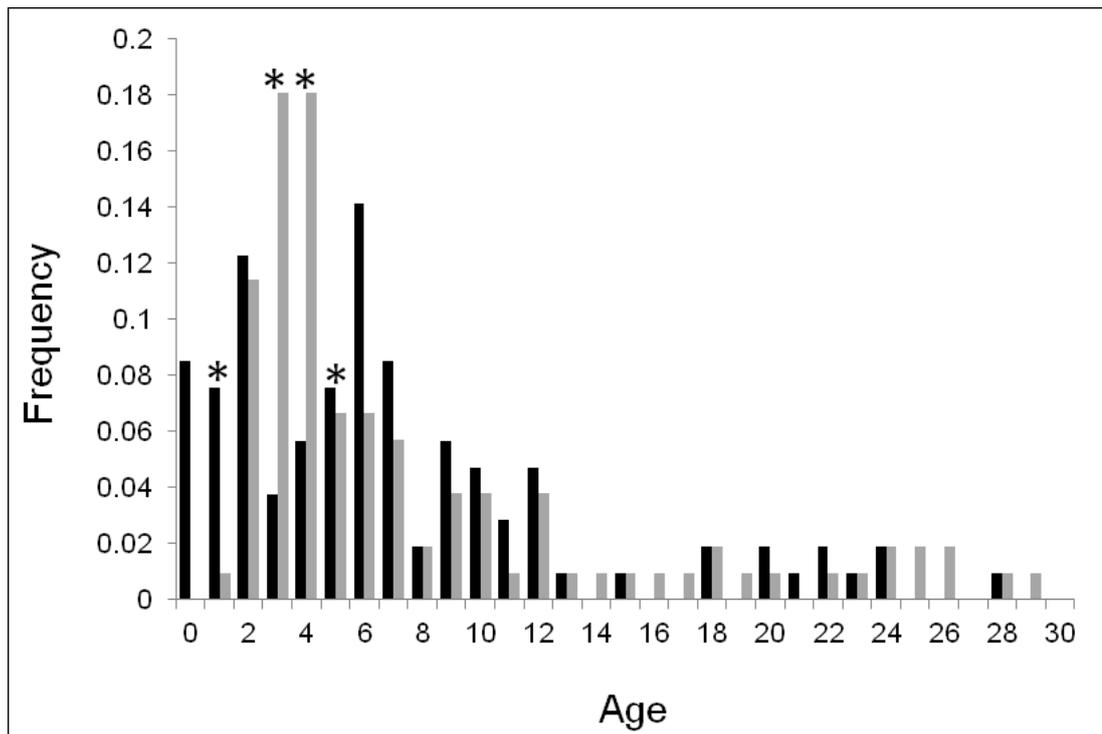
654 **Figure 5**



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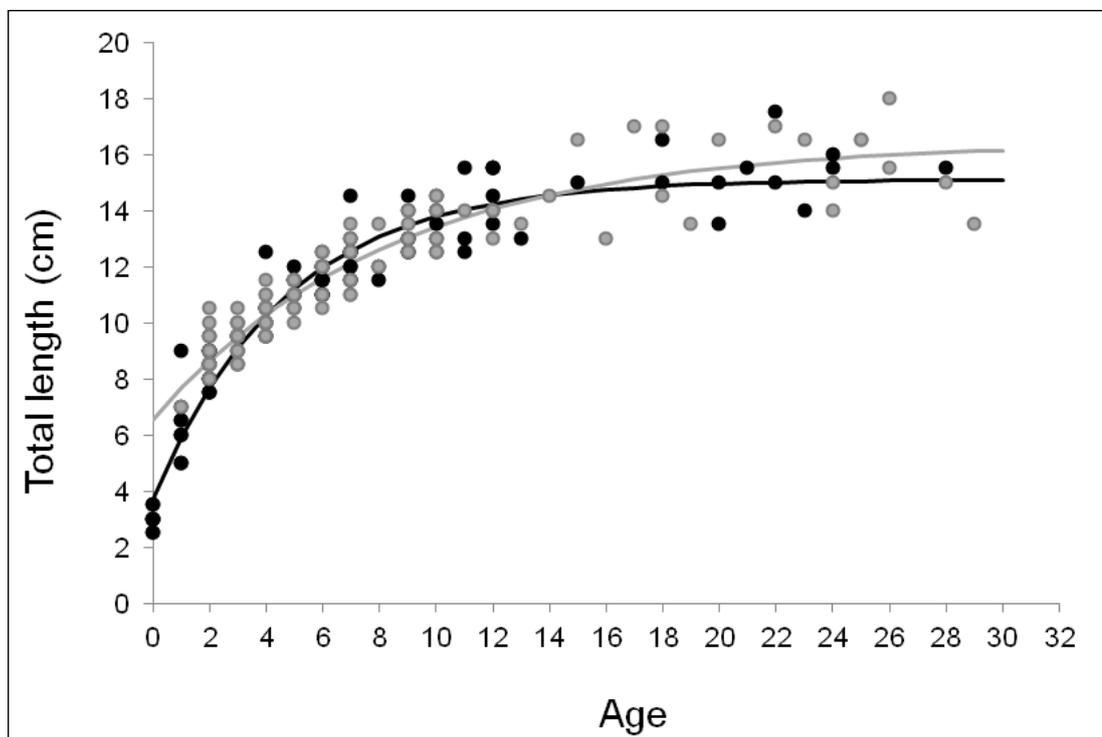
657 **Figure 6**



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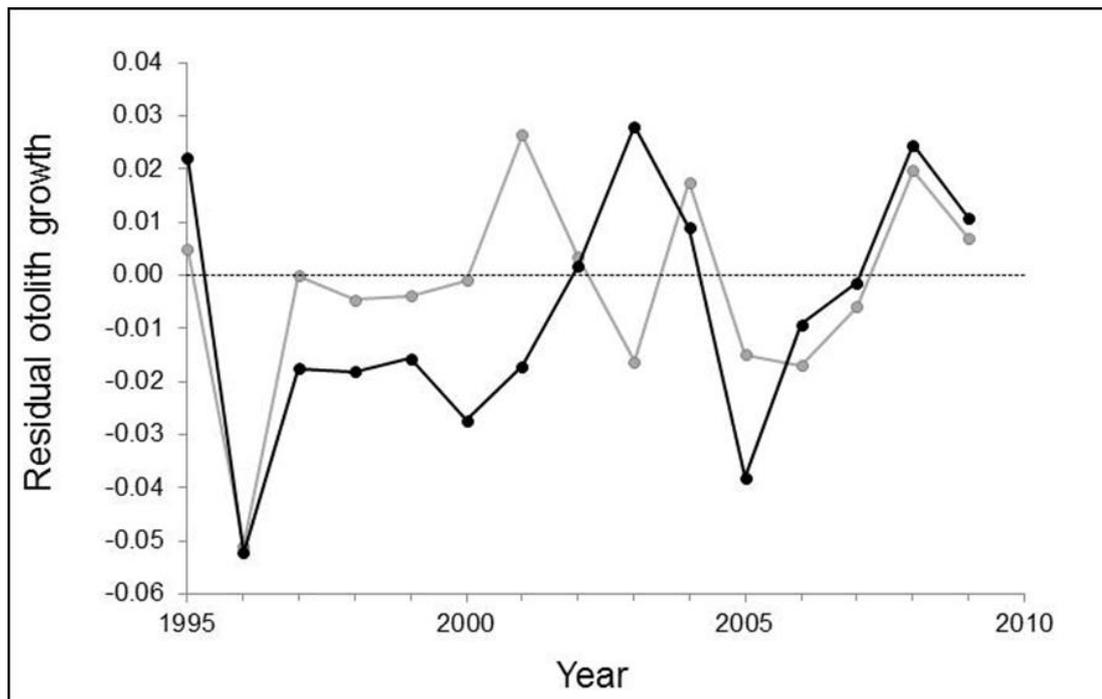
660 **Figure 7**



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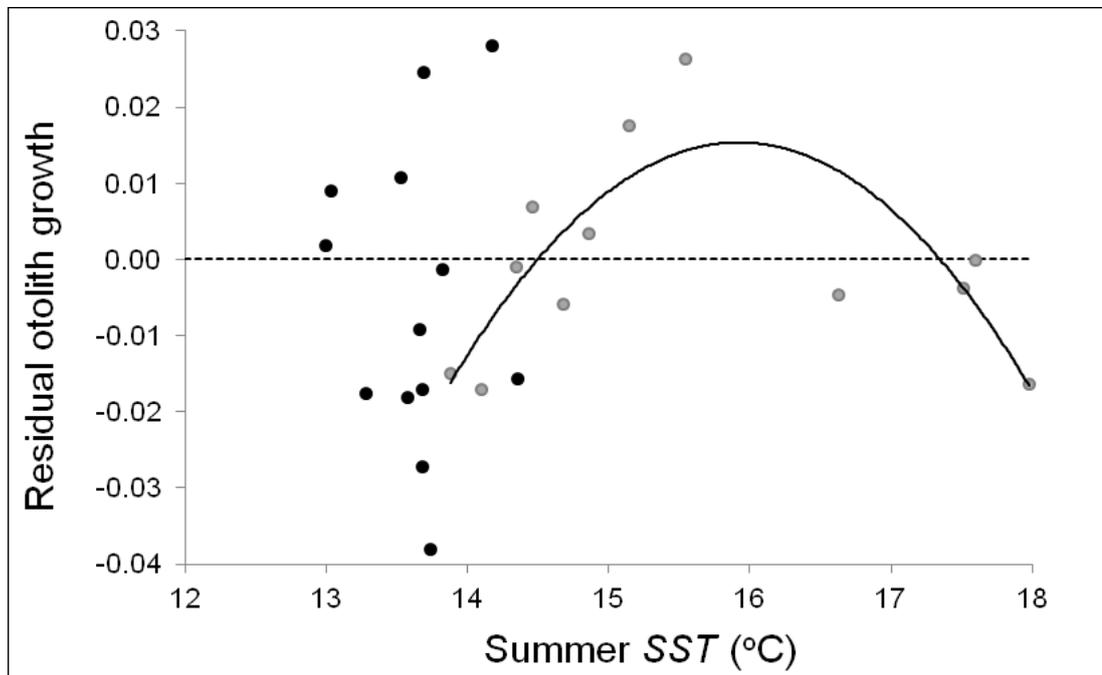
663 **Figure 8**



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666 **Figure 9**



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