1 **Life strategies of cephalopod paralarvae in a coastal upwelling system**
2 **(NW Iberian Peninsula): insights from zooplankton community and**
3 **spatio-temporal analyses**

4 **ÁLVARO ROURA^{12*}, X. ANTÓN ÁLVAREZ-SALGADO², ÁNGEL F.**
5 **GONZÁLEZ², MARÍA GREGORI², GABRIEL ROSÓN³, JAIME OTERO²,**
6 **ÁNGEL GUERRA²**

7 ¹ *Department of Ecology, Environment and Evolution, School of Life Sciences, La Trobe*
8 *University, 3086 Melbourne, Australia*

9 ² *Instituto de Investigaciones Marinas (IIM-CSIC), 36208, Vigo, Spain*

10 ³ *GOFUVI, Facultad de Ciencias del Mar, Universidad de Vigo, 36200 Vigo, Spain*

11 * Corresponding author: a.rouralabiaga@latrobe.edu.au

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13 **Running title:** Life strategies of planktonic cephalopod larvae

ABSTRACT

Early life stages of cephalopods -octopods, squids, sepiolids and ommastrephids- are uncommon in zooplankton samples and little is known about their life strategies. Accordingly, cephalopod paralarvae were examined in the upwelling ecosystem of the Ría de Vigo (NW Spain) at night from 2008-2010. Multivariate analyses and generalized linear models (GLMs) were used to explore relationships between cephalopod paralarvae and the zooplankton communities that they inhabited in 2008. In addition, the foraging strategy and prey preferences of *Octopus vulgaris* paralarvae within these communities were determined. Multivariate and GLM results showed a strong association of cephalopod paralarvae with coastal and frontal zooplankton communities. *Octopus* paralarvae were shown to be specialist predators with a strong preference for decapod zoeae in each of the communities examined. Using the three years of sampling, GLM analyses of paralarval spatio-temporal variations in relation with the upwelling strength showed a positive relationship with upwelling intensity for *O. vulgaris* and sepiolids, as well as contrasting temporal, horizontal and vertical distributions for the different paralarvae analysed. Under strong upwelling events *Octopus* paralarvae were more abundant in surface waters, whereas abundance of loliginids and sepiolids was higher in the water column. This vertical behaviour in conjunction with the physical conditions of the Western Iberian Upwelling ecosystem suggest the coexistence of two different life strategies: a coastal strategy displayed by loliginid and sepiolid paralarvae that are retained over the shelf, and an oceanic strategy displayed by *O. vulgaris* paralarvae that are dispersed far from the shelf.

KEY WORDS: cephalopod paralarvae, zooplankton communities, trophic ecology, early life strategies, vertical behaviour, NW Iberian upwelling.

40 INTRODUCTION

41 Early life history stages of cephalopods are scarce in plankton samples due to their high
42 growth rates, patchy distributions and seasonal life cycles. Their scarcity combined with
43 a short-life span and the absence of overlap between successive generations brings
44 about drastic inter-annual fluctuations in recruitment, mostly driven by environmental
45 variability (Boyle and Boletzky, 1996; Boyle and Rodhouse, 2005). The NW coast of
46 the Iberian Peninsula has been surveyed since the mid 1990s to understand the
47 variability of early life stages of cephalopods in relation to the coastal oceanographic
48 conditions (e.g. Rocha *et al.*, 1999; González *et al.*, 2005; Moreno *et al.*, 2009; Otero *et*
49 *al.*, 2009). In this region, northerly winds promote seasonal coastal upwelling from
50 March-April to September-October, however the upwelling season appears as a
51 succession of wind stress/relaxation cycles of periods lasting 10 to 20 days (Álvarez-
52 Salgado *et al.*, 2003). Early hatchlings of *Octopus vulgaris* Cuvier, 1797 have been
53 studied in daylight hours, revealing that changes in abundance were linked to the
54 hydrographic conditions (Otero *et al.*, 2009), and that the environmental forcing
55 affecting the paralarval stage was related to the variability found in later adult catches
56 (Otero *et al.*, 2008). Furthermore, Moreno *et al.* (2009) studied the distribution patterns
57 of several neritic and oceanic paralarvae along the western Iberia upwelling system,
58 showing that temperature and upwelling were the most important variables affecting the
59 spatio-temporal distribution of neritic cephalopod paralarvae.

60 All the studies previously mentioned investigated abiotic influences on paralarvae
61 abundance. Few studies have addressed the interactions between cephalopod paralarvae
62 and zooplankton communities, likely due to the inherent difficulties in obtaining
63 zooplankton data. The studies that did address these interactions revealed relevant
64 ecological traits: like coastal community preferences in the long fin inshore squid -
65 *Doryteuthis pealei*- paralarvae (Vecchione and Grant, 1983), changes in diet during the

development of oceanic cephalopod paralarvae (Passarella and Hopkins, 1991), migration patterns in the Chokka squid hatchlings -*Loligo reynaudii*- towards areas of copepod concentration on the eastern Agulhas Bank (Roberts, 2005), or retention at seamounts that favours local recruitment (Dickmann *et al.*, 2006). The only study carried out in the waters off NW Iberian Peninsula addressed the diet of wild *Octopus vulgaris* hatchlings in the zooplankton of the Ría de Vigo in 2008, revealing that octopus paralarvae were mainly feeding on crustaceans (Roura *et al.*, 2012). The authors suggested that *O. vulgaris* hatchlings were specialist predators and detected this by comparing the prey detected within hatchlings against the averaged abundances of zooplankton organisms in the Ría de Vigo.

The mesozooplankton communities present at night in the Ría de Vigo in 2008 were recently described by Roura *et al.* (2013). Three mesozooplankton communities - named as coastal, frontal and oceanic- were identified depicting a coastal-oceanic gradient, according to the following ecological descriptors: holoplankton-meroplankton ratio, species richness and total abundance. These communities changed qualitatively and quantitatively from summer to autumn and, consequently, six mesozooplankton communities were identified in the Ría de Vigo. These findings provide a unique opportunity to explore the relationships of the cephalopod paralarvae with the zooplankton communities they inhabit. Moreover, knowing the composition of the different zooplankton communities permits testing of the hypothesis that *O. vulgaris* hatchlings are specialist predators on each community from which they were collected. This will enable testing of whether *O. vulgaris* hatchlings were selective in their feeding preferences and whether their foraging tactics differed on each community. The need of studies linking development at the planktonic stage and ecology in cephalopods is advocated, since it helps to deepen our comprehension of the different life strategies displayed by the paralarvae (Robin *et al.*, 2014).

Specifically, the aims of this work are 1) to understand the short-term spatio-temporal distributions of the cephalopod paralarvae found at night in the Ría de Vigo in 2008 and their relationships with the mesozooplankton community; 2) to study the trophic ecology of *O. vulgaris* hatchlings within the zooplankton communities; and 3) to examine the inter-annual spatio-temporal variability of cephalopod paralarvae collected in the Ría de Vigo from 2008 to 2010 at night in relation to the upwelling index. These three aims explore different aspects of the ecology of cephalopod paralarvae during their planktonic stage and will increase our understanding of their life strategies in this productive coastal upwelling ecosystem.

MATERIAL AND METHODS

Mesozooplankton sampling and cephalopod paralarvae sorting

Thirty surveys to collect zooplankton and hydrographic data were undertaken at night in the Ría de Vigo (NW Spain, 42°12.80'N, 09°00'W) onboard RV “Mytilus” from 2008 to 2010 (Fig. 1). Ten surveys per year were performed in early summer (four in July) and early autumn (six in September-October), coinciding with the peaks of mesozooplankton and *O. vulgaris* paralarvae hatchlings (Otero *et al.*, 2009; Moreno *et al.*, 2009). Four stations (T2, T3, T4 and T5, Fig. 1) parallel to the coast were sampled in each survey following an onshore-offshore depth gradient (26, 68, 85 and 110 m, respectively), and two samples were collected on each station. The samplings carried out in 2008 and 2009 employed a 75 cm diameter bongo net of 375 μm mesh. At a ship speed of 2 knots, the bongo net was first lowered and stabilised close to the bottom for a period of 5-15 min depending on the amount of salps present and subsequently hauled up at 0.5 m s^{-1} . We considered this sample as “column” since the zooplankton was captured throughout the water column. Then, the net was cleaned on board and a second sample was taken from the surface to 5 meters depth and named “surface sample”. The volume of filtered water was determined from a calibrated flow meter attached to the mouth of the bongo. Zooplankton samplings carried out in 2010 employed a Multinet type maxi (Hydro-Bios) with a mouth opening of 70 x 70 cm and 200 μm mesh. Samples were collected at the same stations, collecting two samples per station: one at the surface (0 to 5 m) and other close to the bottom (mean depths 25, 30, 60 and 90 m, in stations T2 to T5 respectively). The water filtered for each sample was approximately 200 m^3 (average = 202.8 m^3).

Samples were fixed with 96% ethanol and stored at -20°C, to allow DNA preservation for genetic analyses. All cephalopod paralarvae were sorted and identified

127 to the lowest taxon according to Sweeney *et al.* (1992) and our own reference
128 collections. The dorsal mantle length (DML) of each paralarvae collected in 2008 was
129 recorded to the nearest 0.001 mm using an image analysis system NIS-Elements 3.0
130 connected to a digital camera (Nikon DXM1200F) under a binocular microscope
131 (Nikon SMZ800).

132 *Oceanographic and meteorological data*

133 Wind (10 m above sea level) and surface current velocities (3 m depth) were provided
134 by the Seawatch buoy of Puertos del Estado (www.puertos.es) located off Cape Silleiro
135 (42°7.8'N, 9°23.4'W, Fig. 1). Due to the lack of data from this buoy in 2009, we also
136 obtained wind data from Ons Islands meteorological station (42°22.8'N, 8°55.8'W, Fig.
137 1). Continuous records of water temperature at 4 m depth at the Rande bridge (inner part
138 of the Ría de Vigo, 42°17.4'N, 8°39.6'W; Fig. 1) were provided also by Meteogalicia
139 (www.meteogalicia.es). The sampling area was situated between these three
140 observatories, thus providing valuable information of the environmental conditions
141 before, during and after the mesozooplankton surveys. Daily upwelling index ($-Qx$, in
142 $m^3 s^{-1} km^{-1}$) was calculated using the wind data obtained from Cape Silleiro buoy and
143 the Ons Islands station following methods described in Bakun (1973).

144 *Cephalopod paralarvae and zooplankton communities*

145 The mesozooplankton communities present off the Ría de Vigo in 2008 were
146 characterized with multivariate techniques using PRIMER6 and PERMANOVA+
147 software (Anderson *et al.*, 2008), as detailed in Roura *et al.* (2013). Briefly, prior to
148 analysis the database was screened to select those taxa that appeared at least in 10% of
149 the stations and then transformed using the natural logarithm (a constant of 1 was added
150 before taking the log) (Legendre and Legendre 1998). The Bray–Curtis similarity matrix
151 was used to calculate the resemblance matrix among samples, and principal coordinate

analysis (PCO) ordination was then used to visualise the natural groupings of the samples. The communities emerging from the PCO plot were first analysed with PERMDISP, based on distances to centroids, to examine the dispersion among groups. Subsequently, a non-parametric permutational ANOVA (PERMANOVA) analysis was used to test for statistical differences in the communities found in the multidimensional space. Overall, six mesozooplankton communities identified in the Ría de Vigo in 2008 (Roura *et al.*, 2013) were used to analyse the short-term spatio temporal interactions of cephalopod paralarvae on them: summer coastal (SC), summer frontal (SF), summer oceanic (SO), autumn coastal (AC), autumn frontal (AF) and autumn oceanic (AO).

In order to study the association between cephalopod paralarvae and the zooplankton communities identified off the Ría de Vigo, the abundance of ommastrephid paralarvae had to be added to the matrix since they were present in less than 10% of the samples and were excluded from the original zooplankton analysis. Then, the scores of PCO1 and 2 for the different cephalopod paralarvae were used to plot the vectors that define the strength and direction of the association between the paralarvae and the different mesozooplankton communities. RELATE analysis was carried out to test if the spatial pattern of the cephalopod paralarvae assemblage matched with the spatial pattern of the mesozooplankton communities, by correlating the matching entries of their resemblance matrices based on the Spearman rank correlation. PERMANOVA analysis was carried out with the different cephalopod paralarvae to test differences in abundance among zooplankton communities. PERMANOVA was run for 999 permutations using the “unrestricted permutation of raw data” and type III sum of squares, which yields an exact test for one-way design (Anderson *et al.*, 2008).

Cephalopod paralarvae abundance was further related with the main descriptors of the mesozooplankton communities (summarized in Table 1) by means of fitting

180 generalized linear models (GLMs) to the cephalopod counts. The paralarvae data was
181 overdispersed, i.e., variances were greater than the mean (not shown), thus we assumed
182 that cephalopod counts for a given sample i (Y_i) were negative binomial distributed with
183 mean μ_i and shape parameter k . The variance was parameterised as $\mu_i + \mu_i^2 / k$ (Venables
184 and Ripley 2002). The ln-transformed water volume filtered was used as an offset and
185 the following variables were used as potential explanatory variables:
186 holoplankton/meroplankton ratio (H/M), species richness (S), species diversity (H'),
187 zooplankton total abundance (ind 1000 m⁻³), Simpson's index (λ), and evenness (J'). In
188 order to account for short-term spatio-temporal effects, the strata (two categories:
189 surface and water column) and month of sampling (three categories: July, September
190 and October) were added to the models. Collinearity among mesozooplankton
191 descriptors was assessed by means of calculating variance inflation factors and
192 subsequently dropping those above a cut-off value of 3 (Zuur *et al.*, 2007). Model fitting
193 was performed with R 3.0.1 language (R Development Core Team, 2013) and using the
194 "MASS 7.3-26" package (Venables and Ripley, 2002).

193 *Trophic ecology of O. vulgaris hatchlings within the zooplankton communities*

194 The diet of 18 *O. vulgaris* hatchlings collected in 2008 was determined with molecular
195 techniques and up to 20 different prey were identified (Roura *et al.*, 2012). In order to
196 test whether octopus prey preferences remain the same with changing prey fields –i.e.
197 within different zooplankton communities- we analysed the linear index of food
198 selection (L). This food selection index avoids the bias observed for other indices like
199 Ivlev's Electivity index and the forage ratio when the sizes of the prey samples in the
200 gut and in the environment are unequal (Strauss, 1979). This index is obtained for every
201 prey detected with the formula:

202
$$L = r_i - p_i$$

203 resulting from the unweighted difference in relative proportions of prey item i in the gut
 204 (r_i) and in the community (p_i). L ranges from -1 to +1, with positive values indicating
 205 preference, negative values indicating avoidance or inaccessibility, and zero values
 206 showing random feeding. Accordingly, we calculated L for all the prey detected in *O.*
 207 *vulgaris* hatchlings, which allowed assessment of prey preferences of each octopus
 208 paralarvae within the different communities where they were collected: 4 in the SC, 3 in
 209 SF, 4 in AC and 7 in AF.
 210 Furthermore, we examined the trophic niche breadth for every octopus paralarvae using
 211 the Czekanowski's Index (CI) also called Proportional Similarity Index (Feinsinger *et*
 212 *al.*, 1981). Trophic niche breadth was calculated with the formula:
 213
$$CI = 1 - 0.5 \sum_i |p_i - q_i|$$

 214 where p_i and q_i are the relative abundance of resource item i eaten by the paralarvae (p_i)
 215 and in the zooplankton (q_i). Values of CI range from 1 for the broadest possible niche (a
 216 population uses resources in proportion to their availability) to $[\min q_i]$ for the
 217 narrowest possible niche (a population is specialized exclusively on the rarest resource).
 218 CI relies on how objectively the available resources for the predator are defined.
 219 Accordingly, all the zooplankton organisms not likely to be consumed by the octopuses
 220 according to their ecology were removed (reviewed in Villanueva and Norman, 2008).
 221 These included salps, cnidarians, siphonophores and appendicularians, as well as small-
 222 sized organisms like platyhelminthes or harpacticoids. When the available resources are
 223 objectively chosen, CI index is appropriate not only for measuring niche breadths but
 224 also for quantifying foraging patterns on individual animals (Feinsinger *et al.*, 1981).
 225 Therefore, individual values of CI for each paralarvae were compared among the
 226 mesozooplankton communities, in order to test whether the foraging tactics of *O.*
 227 *vulgaris* changed in summer and autumn communities (t-test).

228 *Cephalopod paralarvae variability and its relationship with the upwelling between*
229 *2008-2010*

230 Finally, the spatio-temporal variability of cephalopod paralarvae collected in the Ría de
231 Vigo from 2008 to 2010 was evaluated using as input predictors into the GLMs, the
232 strata (two categories: surface and water column), the station (four categories: T2, T3,
233 T4 and T5), the month sampled (three categories: July, September and October), and the
234 upwelling index during the day preceding the surveys. The upwelling index was chosen
235 because it is one of the most important forcing factors in this region (e.g. Piedracoba *et*
236 *al.*, 2005). Model fitting was performed as outlined above.

237

238 RESULTS

239 *Hydrography and dynamics off the Ría de Vigo*

240 Coastal wind speed (W_x , W_y , Fig. 2a), upwelling index ($-Q_x$, Fig. 2b), and sea surface
241 temperature recorded at Rande observatory (Fig. 2c) showed that in summer 2008,
242 surveys 1 to 4 (from July 2–11) were conducted under downwelling conditions,
243 characterised by weak coastal winds of variable direction and a progressive increase of
244 sea surface temperature, with the exception of the strong downwelling-favourable winds
245 recorded on July 4 (Fig. 2a). Conversely, surveys 5 to 10 (conducted from September 26
246 to October 14) were characterised by upwelling-favourable winds (Fig. 2a), which
247 cooled the surface layer sharply (Fig. 2c). The only exception occurred in October 14,
248 with the presence of weak southerly winds. In summer 2009 (surveys 11–14, conducted
249 from July 15–24) all samples were collected under downwelling conditions, although an
250 upwelling event occurred in between surveys 12 and 13, producing a transient decrease
251 in temperature that was appreciable up to the innermost side of the Ría (Fig. 2c).
252 Autumn samples (surveys 15–20, from September 23 to October 10), were first
253 collected under weak upwelling conditions (surveys 15–16) produced by northerly
254 winds of $<4 \text{ m s}^{-1}$ that provoked a steep decrease of surface water temperature up to
255 September 27 and a subsequent increase accompanying wind relaxation (surveys 17–
256 18). The last two surveys (19–20) were carried out after a strong downwelling event that
257 pushed warm oceanic waters inshore. In summer 2010 (surveys 21–24, from July 13–
258 22) the first two surveys were carried out under weak downwelling conditions, while
259 the last two surveys (23 and 24) were carried out under upwelling conditions. Autumn
260 samplings (surveys 25–30, from September 22 to October 15) took place under
261 upwelling-relaxation conditions (surveys 25, 26 and 28), while upwelling conditions
262 forced by moderate to strong northerly winds dominated surveys 27, 29 and 30 (Fig. 2).

263 *Short-term spatio-temporal interactions between cephalopod paralarvae and*
264 *mesozooplankton communities*

265 The main characteristics of the six mesozooplankton communities described in the Ría
266 de Vigo in 2008 are summarized in Table 1. Briefly, the summer coastal community
267 (SC) showed the greatest abundance and diversity as a result of the great contribution of
268 the meroplankton fraction (Fig. 3). The main groups were copepods, larval stages
269 (calytopis and furcilia) of the euphausiid *Nyctiphanes couchii*, larval stages of
270 echinoderms and salps. The meroplankton fraction was less important in the summer
271 frontal community (SF), which was dominated by larval stages of *N. couchii*, copepods
272 and salps. The summer oceanic community (SO) was dominated by the holoplankton
273 fraction (salps and copepods) with the lowest values of homogeneity and biodiversity.
274 The autumn coastal community (AC) showed the highest abundance, with echinoderm
275 larval stages (echinopluteus and ofiopluteus) contributing the most to the overall
276 abundance, followed by larval stages of *N. couchii*, salps, copepods and cirriped larvae.
277 The autumn frontal community (AF) was dominated by larval stages of *N. couchii*
278 followed by copepods and salps. Finally, the autumn oceanic community (AO) had the
279 lowest abundance values, with an equitable contribution of both copepods and salps,
280 and followed by larval stages of *N. couchii*.

281 Regarding cephalopod paralarvae, a total of 2039 individuals were captured from
282 2008 to 2010 off the Ría de Vigo (Table 2). *Octopus vulgaris* was the most abundant
283 species (64.4, 61.5, and 70.4%, collected from 2008 to 2010 respectively), followed by
284 loliginids (22.7, 29.4, and 23.9%), sepiolids (12.3, 8.7 and 5.1%) and ommastrephids
285 (0.6, 0.4 and 0.6%). With the exception of *O. vulgaris*, cephalopod paralarvae were
286 classified at the family level due to the lack of accurate descriptions for loliginid,
287 sepiolids and ommastrephid paralarvae below this level of classification. All
288 ommastrephid paralarvae (n=11) were found in the column sample, mainly in autumn

(only two were collected in summer). With the exception of three ommastrephids that remained inside the egg covered with chromatophores, all other ommastrephid individuals were considered as “rhynchoteuthions” because of the fusion of the tentacles into a proboscis. All *O. vulgaris* captured had three suckers per arm, with DML ranging from 1.04 to 2.18 mm that was not significantly different among the mesozooplankton communities. Regarding loliginids and sepiolids, the DML of these groups of species was more variable ranging from 1.12 to 7.91 and from 1.24 to 3.82 mm, respectively, though their average DML neither varied significantly among communities, sampling periods or strata.

Cephalopod paralarvae were unevenly distributed among the mesozooplankton communities (Fig. 3), which was confirmed with the PERMANOVA results (Table 3). A decreasing gradient from coastal to oceanic communities was observed, with the exception of the autumn frontal community. *Octopus vulgaris* showed higher abundances in the frontal and coastal communities throughout the sampled period, with a maximum of 395 ind / 1000 m³ in the autumn frontal community at the surface (Fig. 3). Loliginids and sepiolids were more abundant in the coastal and frontal communities in both sampling periods, being almost absent in the oceanic samples. Finally, all the ommastrephid paralarvae were found in the water column samples collected in autumn, three belonging to the coastal and one to the oceanic community.

The direction of the vectors shown in Fig. 4 show that loliginids and sepiolids were mainly associated with the coastal-frontal communities (represented by positive values of PCO1 axis) found in summer (as shown by the positive values of PCO2 axis). *Octopus vulgaris* was associated with the coastal community (positive value of PCO1 axis) found in autumn (negative value of PCO2). Ommastrephids were associated with autumn frontal communities. The length of the vectors displayed in Fig. 4 evidenced that the contribution of cephalopod paralarvae to the discrimination of the zooplankton

communities identified in the Ría de Vigo in 2008 was very low, owed to their low abundance in the zooplankton. RELATE analysis showed that the spatial pattern of the cephalopod assemblage, did not match the spatial pattern of the mesozooplankton resemblance matrix (Spearman rank correlation, $S_r = 0.171$, $N = 79$, $P > 0.2$), thus evidencing the uneven distribution of the cephalopod paralarvae among the mesozooplankton communities.

The relationships found between cephalopod paralarvae abundance and the descriptors of the mesozooplankton communities complete the above description and are summarized in Table 4. Ommastrephids were excluded from the analysis due to their low abundance. It can be drawn that all cephalopods were inversely correlated with the holoplankton-meroplankton ratio and the evenness, especially *O. vulgaris* and loliginids. This implied that there were more chances of finding cephalopod paralarvae mainly in the coastal communities where the meroplankton fraction was higher and the community was evenly distributed (Table 1). The short-term spatio-temporal analysis showed that *O. vulgaris* was more abundant in September > October > July, preferentially at the surface though this was not significant. Loliginids were more abundant in September, preferentially in the water column though this was not significant. Concerning sepiolids, they were more abundant in the water column than at the surface, with no statistical differences in the month sampled.

Octopus vulgaris trophic interactions

The eighteen *O. vulgaris* hatchlings analysed in the work of Roura *et al.* (2012) were collected from four different mesozooplankton communities identified off the Ría de Vigo in 2008 (Table 5). At least one decapod species was found within the digestive tract of every single paralarvae, a diverse taxonomic group that is found in very low abundance within the different communities (Table 1). Linear food selection indices (L)

calculated for the different decapods (Brachyura, Processidae, Alpheidae, Paguridae, Crangonidae, Thalassinidae and Porcellanidae) were positive and even 1, thus showing a clear preference for these organisms in all the communities analysed (Table 5). In the case of krill, octopus showed preference for this item in the AC community (positive value), but not in the AF community (negative), since krill abundance greatly increased in the latter (Table1). Octopus also showed preference for fish larvae or eggs (positive), since they consumed them despite their low abundance in the AF community (Table1).

The trophic niche breadth (CI) estimated for each paralarva ranged from 0.042 to 0.374. These low values show that *O. vulgaris* foraging tactics are prey-specific and do not depend on the prey available in the different communities. In summer, octopuses feeding on the coastal community showed significantly higher CI mean values 0.11 ± 0.019 than those of the frontal community 0.056 ± 0.008 (t-test, $p\text{-value} = 0.033$, $n = 7$). However, this change did not reflect a change in prey niche but rather it reflected the decrease of decapods in the frontal community compared to the coastal community (Table 1). CI values were on average lower in summer 0.087 ± 0.032 than those obtained in autumn 0.13 ± 0.12 , although not significantly (t-test, $p\text{-value} = 0.617$, $n = 18$) showing that paralarvae display similar foraging strategies in both seasons. Mean CI values for autumn were 0.144 ± 0.096 and 0.10 ± 0.142 for the coastal and frontal communities respectively, showing no statistical differences (t-test, $p\text{-value} = 0.214$, $n = 11$). The increase found for CI values in autumn was due to the fact that three octopuses (one from AC and two from AF communities, Table 5) feed on krill, which was evenly distributed in those communities (specially in AF community, Table 1).

Spatio-temporal distribution of cephalopod paralarvae from 2008-2010

The abundance of all the paralarvae collected between 2008 and 2010 at the different strata sampled is shown in Fig. 5. This figure show the different vertical distribution of

the cephalopod paralarvae, which is more evident in 2010 when the Multinet was used to sample the bottom layer. GLMs showed inverse spatio-temporal relationships for *O. vulgaris* compared to those found for loliginids and sepiolids, except for the upwelling index (Table 6). *Octopus vulgaris* abundance increased under upwelling-favourable conditions the day preceding the survey, and it was significantly higher in September, at the surface layer and East of the Cies Islands (Fig. 6a). The modelling of loliginid and sepiolid paralarvae revealed the same trend for both groups, indicating that abundance of loliginids (Fig. 6b) and sepiolids (Fig. 6c) was higher in July and decreased in autumn, mainly in October. Moreover, both paralarvae were mostly found in the water column/bottom layer and West of Cíes Islands (T3, Fig. 1), with loliginids almost absent in the westernmost station (T5, Fig. 1). Abundance of these two paralarvae increased during upwelling-favourable conditions, though this was not significant for loliginids.

DISCUSSION

With the exception of *Octopus vulgaris*, the identification of the cephalopod paralarvae was restricted to family level due to the lack of accurate descriptions for ommastrephid, loliginid and sepiolid paralarvae. Currently, the only reliable method to identify these groups is genetic barcoding. Indeed, the cephalopod paralarvae collected during a cruise in shelf waters off NW Iberian Peninsula –including the outer part of the Ría de Vigo– were identified to species level using the cytochrome oxidase subunit I gene, COI (Roura 2013, CEPAR project on iBOLD). The paralarval assemblage was comprised by *O. vulgaris*, three loliginid species (*Alloteuthis media*, *A. subulata* and *Loligo vulgaris*), two sepiolids (*Sepiola atlantica* and *S. tridens*), and three ommastrephids (*Illex coindetii*, *Todaropsis eblanae* and *Todarodes sagittatus*). Accordingly, the conclusions drawn herein about the planktonic ecology of cephalopod paralarvae in the Ría de Vigo are accurate for *O. vulgaris*, but are generalisations for loliginids and sepiolids due to the fact that our data on these taxa might be comprised of multiple species in both cases.

Mesozooplankton communities and cephalopod paralarvae

Cephalopod paralarvae were unevenly distributed in the mesozooplankton communities found in the Ría de Vigo, and suggests that the cephalopod paralarvae actively choose the communities they inhabit as observed in other ecosystems (Vecchione *et al.*, 1986; Roberts, 2005). Multivariate analysis suggests different associations of the cephalopod paralarvae with the zooplankton communities despite their low abundance: loliginids and sepiolids were associated with the coastal-frontal summer community, whilst *O. vulgaris* was lightly associated with the coastal community during autumn, and ommastrephids with the autumn frontal community (Fig. 4). Common octopus and loliginid paralarvae were negatively related to the holoplankton/meroplankton ratio (H/M). This variable was the best descriptor of the mesozooplankton communities

accounting for 40% of the variability present in the zooplankton similarity matrix (Roura *et al.*, 2013). H/M ratio summarizes both the spatial variability (from coast to ocean, with more meroplankton close to the coast and more holoplankton in the ocean) as well as the differences in the zooplankton assemblage. Accordingly, smaller values of the H/M ratio would indicate a greater contribution of the meroplankton in the samples, an inherent characteristic of coastal communities (e.g. Blanco-Bercial *et al.*, 2006). The observed lack of relationship between sepiolid abundance and the zooplankton descriptors might be due to the presence of different species present in the Ría de Vigo, as suggested by Moreno *et al.* (2009) and indicated above.

The association found with the cephalopod paralarvae and the coastal and frontal communities may be driven by optimal trophic conditions present within these environments. Several reasons might support this hypothesis. Coastal communities showed the greatest zooplankton abundances increasing the chances for successful feeding even for recently hatched paralarvae, as it was observed for *Loligo pealei* (Vecchione, 1981) or for capelin larvae (Fossheim *et al.*, 2006). Moreover, besides abundance, the taxonomic composition of the coastal and frontal communities would meet the diet requirements of the different cephalopod paralarvae. Regarding loliginids and ommastrephids, these are generalist paralarvae known to primarily feed on copepods (Passarella and Hopkins 1991; Vecchione, 1991; Vidal and Haimovici, 1998; Venter *et al.*, 1999, Hoving *et al.*, 2005) whose abundances peaked on coastal and frontal communities in the Ría de Vigo (Table 1), thus providing an optimal prey environment. These communities would also be appropriate rearing environments even for the selective early hatchlings of *O. vulgaris*, since decapod zoeae are most abundant in coastal communities (Table 1). Therefore, coastal and frontal communities off the Ría de Vigo potentially satisfy the quantitative and qualitative zooplankton requirements for the optimal development of cephalopod paralarvae. Indirect evidence of this is finding

the wide range of sizes for loliginids and sepiolids, since these paralarvae are optimally growing in the Ría de Vigo and their surroundings. However, all the *O. vulgaris* collected in this study ($n = 1297$), as well as in previous works ($n = 95$ González *et al.*, 2005; $n = 584$ Otero *et al.*, 2009), had only three suckers per arm, meaning that all of them were early hatchlings less than ten days old (Villanueva and Norman, 2008). This fact suggests that the Ría de Vigo is optimal for the hatchlings of *O. vulgaris*, but sub-optimal for further development as evidenced by the absence of older stages.

The specialist trophic ecology of *O. vulgaris* heavily contrasts with the generalist diet of paralarvae of other cephalopod species (Passarella and Hopkins, 1991; Vecchione, 1991; Vidal and Haimovici, 1998; Venter *et al.*, 1999; Hoving *et al.*, 2005). Prey selection was consistent in four different mesozooplankton communities analysed (Table 5), thus showing that *Octopus* paralarvae actively chose the prey, even though they were very rare in the samples. This strategy suggests that the groups that were targeted (mainly decapods) may meet the nutritional requirements of the paralarvae. This suggestion is supported by captive studies where increased survival rates were obtained when *Artemia* diets were complemented with decapod zoeae (reviewed in Villanueva and Norman, 2008). The results observed for the planktonic paralarvae contrasts with the diet of adult *O. vulgaris* that prey upon a wide range of items when the whole population is considered, but where individual choices are markedly specific (Anderson *et al.*, 2008; Mather *et al.*, 2012; Hernandez-Urcera *et al.*, 2014).

Spatio-temporal changes on paralarval abundance

Our analysis showed that *O. vulgaris* paralarvae displayed contrasting spatio-temporal patterns compared to those of sepiolids and loliginids. Considering the month sampled, common octopus were more abundant in September and October, as observed earlier in this area (Otero *et al.*, 2009) and for the whole western Iberian coast (Moreno *et al.*, 2009). A different pattern occurred with loliginids and sepiolids whose abundance

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2 456 peaked in July concurring with previous results (González *et al.*, 2005; Moreno *et al.*,
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4 457 2009; Rodrigues *et al.*, 2011). This temporal change in abundance is likely to be due to
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6 458 their different reproductive cycles. On one hand, loliginid spawning peaks occur in
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8 459 December–January and, to a lesser extent, in June–July (Moreno *et al.*, 2002). Given
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10 460 that the embryonic development lasts for 40–47 days on average (Villanueva *et al.*,
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12 461 2003), two peaks of hatchlings are expected around March and August. Regarding
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14 462 sepiolids, spawning occurs between March and July (Rodrigues *et al.*, 2011a) with an
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16 463 early development lasting for around 62–23 days at 13–18°C (Rodrigues *et al.*, 2011b)
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18 464 and hatching occurring between May and September (Rodrigues *et al.*, 2012). In
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20 465 contrast, *O. vulgaris* has an extended embryonic development of up to 4 months
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22 466 (Mangold and Boletzky, 1973). Taking into account that spawning occurs between
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24 467 March and June (Sieiro *et al.*, 2014) the main hatching peak would occur at the end of
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26 468 summer (July) and early autumn (September–October, Otero *et al.*, 2009).

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30 469 Clear differences were evident in the vertical position of the paralarvae. *Octopus*
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32 470 *vulgaris* were more abundant in surface waters, while loliginids and sepiolids were
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34 471 more abundant in the water column layer (Table 6, Fig. 6). These results indicate
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36 472 contrasting vertical distributions at night-time with common octopus reaching the
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38 473 surface layer (0–5 m) and the other cephalopod paralarvae presenting a clear affinity for
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40 474 water column/bottom layers. This vertical pattern can be observed straightforward in the
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42 475 cephalopods collected in 2010 with the Multinet (Fig. 5). Previous results in diel
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44 476 vertical distribution of loliginid paralarvae showed a widespread distribution between 5
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46 477 and 40 m at night (Moreno *et al.*, 2009) agreeing with our observation that loliginids are
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48 478 spread throughout the water column. Horizontal distribution was also slightly different
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50 479 among the different cephalopods. Recently hatched *O. vulgaris* mainly appeared East of
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52 480 the Cíes Islands and displayed a coastal–ocean gradient decreasing towards station 5;
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481 whereas sepiolids and loliginids were more abundant West of the Cíes Islands also
482 decreasing towards the ocean.

483 The abundance of all cephalopods increased with the upwelling strength the day
484 preceding the sampling, which is a reasonable lag for the Ría de Vigo whose subtidal
485 circulation responds immediately to the shelf winds forcing (Piedracoba *et al.*, 2005).
486 The probability of positive captures of cephalopod paralarvae with higher upwelling
487 strength has been previously described for the Western Iberian coast (Moreno *et al.*,
488 2009) and other upwelling areas (e.g. California Current: Zeidberg and Hamner, 2002;
489 and South African waters: Roberts, 2005). Most benthic organisms with planktotrophic
490 larvae found in the coastal area of the Atlantic Iberian Peninsula match their
491 reproductive cycle with the upwelling season, which is the main forcing factor of the
492 region (Queiroga *et al.*, 2007). This oceanographic feature increases primary production
493 due to the cold nutrient-rich upwelled waters that sustains the high zooplankton
494 production observed from early spring to late autumn (Santos *et al.*, 2007).

495 *Cephalopod paralarval life strategies in the Ría de Vigo*

496 The intermittency of upwelling/downwelling events coupled with the vertical migration
497 patterns is an important mechanism for larvae retention in inshore waters (Santos *et al.*,
498 2004; Shanks and Brink, 2005; Marta-Almeida *et al.*, 2006; Queiroga *et al.*, 2007; dos
499 Santos *et al.*, 2008). However, this pattern is species-specific. For instance, inshore
500 crustacean larvae (e.g. *Necora puber* or *Carcinus maenas*) experience larger along-
501 shore rather than cross-shelf transport, retaining the larvae within 10 km off the
502 Portuguese coastal shelf (dos Santos *et al.*, 2008), while shelf species (*Atelecyclus*
503 *rotundatus*, *Liocarcinus* spp. or *Anapagurus* spp.) appear widely distributed over the
504 shelf (10–20 km) suggesting a more active cross-shelf rather than along-shore transport
505 (dos Santos *et al.*, 2008). Accordingly, the underlying mechanism of the observed

506 cephalopod paralarvae distribution might result from the interaction between their
507 vertical behaviour and the residual circulation in the Ría de Vigo. During upwelling
508 (downwelling) conditions a coastal surface jet enters (leaves) the Ría through the
509 northern mouth and leaves (enters) through the southern mouth (Gilcoto *et al.*, 2007).

510 Previous works carried out mostly during day-time suggested that early
511 cephalopod paralarvae of neritic species might be retained in a cell over the shelf
512 avoiding offshore transport through a combination of behavioural and physical
513 processes (Rocha *et al.*, 1999; Zeidberg and Hamner, 2002; González *et al.*, 2005;
514 Roberts, 2005; Otero *et al.*, 2009; Moreno *et al.*, 2009). However, this hypothesis
515 assumes similar vertical behaviours for the different cephalopod paralarvae within these
516 cells. Notwithstanding, we found two different vertical behaviours in the cephalopod
517 paralarvae at night (Table 6): recently hatched *O. vulgaris* were mostly present in the
518 surface under upwelling conditions, while loliginids and sepiolids of variable sizes were
519 associated to the water column. Consequently, it might be plausible to suggest two
520 different life strategies in the coastal waters of the Iberian Peninsula, driven by changes
521 in the vertical distribution of the paralarvae: 1) we postulate that loliginids and sepiolids
522 display a coastal retention strategy through the avoidance of surface offshore currents,
523 which is in agreement with the shelf-cell retention hypothesis; 2) we postulate an
524 oceanic strategy for *O. vulgaris*, hatching near the coast and then selecting offshore
525 superficial currents under upwelling conditions to be transported far from the shelf for
526 later development.

527 We suggest that the separation between both life strategies would be the
528 continental shelf (~200 m depth), which greatly modulates the circulation patterns in the
529 Western Iberian Upwelling System by complex mesoscale processes (Relvas *et al.*,
530 2007). One of the most important mesoscale features is originated by the blocking effect
531 of the Iberian Poleward Current that acts as a barrier for the shelf-ocean exchange of

upwelled waters (Castro *et al.*, 1997; Álvarez-Salgado *et al.*, 2003; Santos *et al.*, 2007). Indeed, this feature has been recognised as an important retention mechanism for fish and crustacean larvae over the shelf (Santos *et al.*, 2004; dos Santos *et al.*, 2008).

The occurrence of loliginid and sepiolid paralarvae with different sizes and their presence in the water column under upwelling conditions off the Ría de Vigo, supports their coastal distribution favoring an alongshore dispersion rather than a cross-shelf transport, as observed in an larger study through the Western Iberian Peninsula (Moreno *et al.*, 2009) and other upwelling areas such as in California (Zeidberg and Hamner, 2002) or South Africa (Roberts, 2005). Our data support the hypothesis suggested by Bello and Biagi (1995) that sepiolids of the subfamily Sepiolinae display a merobenthic -i.e. distributed in the water column and close to the bottom-, instead of a holobenthic -i.e. real benthic- life cycle (sensu Boletzky, 2003). The alongshore transport during the juvenile stage would also help to explain why sepiolids, a group with limited displacement capability, is able to maintain genetic connectivity across a wide area of distribution (Reid and Jereb 2005; Groenenberg *et al.*, 2009; Roura, 2013).

It has been assumed that a circulatory cell would retain *O. vulgaris* paralarvae close to the coast (Rocha *et al.*, 1999; Faure *et al.*, 2000; González *et al.*, 2005; Otero *et al.*, 2009). Alternatively, Moreno *et al.* (2009) suggested that *O. vulgaris* paralarvae could be retained within the double frontal system present in the wide NW continental shelf of the Iberian Peninsula (Peliz *et al.*, 2002) as shown for other organisms (Castro *et al.*, 1997; Santos *et al.*, 2004). However, if octopus paralarvae were retained over the shelf, then one would expect to find octopus paralarvae of different sizes, but to date, not a single *O. vulgaris* with more than three suckers has ever been found over the Iberian shelf in 4673 zooplankton samples analysed (Rocha *et al.*, 1999; González *et al.*, 2005; Otero *et al.*, 2009; Moreno *et al.* 2009). Larger octopus paralarvae have been caught in other areas though. Rees and Lumby (1954) found some individuals in the

English Channel, the northernmost limit of distribution of the species, and other specimens counting more than three suckers per arm occurred in Japanese waters (Takeda 1990; Sakaguchi *et al.*, 1999). It is important to note that the octopus that occurs in Japan is genetically distinct from *O. vulgaris* (Guerra *et al.*, 2010; Amor *et al.*, 2014) and may represent a sibling species within the *O. vulgaris* complex, with a different life strategy.

Therefore, the affinity of early stages of *O. vulgaris* for surface waters at night under upwelling conditions suggests an offshore displacement far from the continental shelf into the ocean, offering an explanation for the absence of large individuals in the coastal region. To this end the occurrence of upwelling filaments (Barton *et al.*, 1993) would be a plausible mechanism for such offshore transport. Indeed, during a drifter experiment following the offshore displacement of upwelled waters within a filament, *O. vulgaris* paralarvae were found far from the shelf and increasing in size towards oceanic waters (Roura, 2013). In particular, up to 30 *O. vulgaris* paralarvae with more than three suckers per arm (from 4 to 12) were found over the continental slopes of both the Iberian Peninsula and Morocco (from 600 to 3100 m water depth).

In conclusion, our study suggests that the spatio-temporal distributions of cephalopod paralarvae observed herein might be driven by two contrasting early life strategies: a coastal-shelf strategy in loliginids and sepiolids, and an oceanic strategy in *O. vulgaris*. Nevertheless, more detailed sampling combined with biophysical models is needed to accurately resolve the vertical, along-shore and cross-shelf distribution of the cephalopod paralarvae in order to confirm the contrasting life strategies proposed. Furthermore, molecular analyses are also needed to clarify the diversity of loliginid, sepiolids and ommastrephid larvae found in coastal environments to elucidate their different life history strategies.

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Table 1. Ecological descriptors and taxonomic composition (ind.1000m⁻³) of the mesozooplankton communities characterized off the Ría de Vigo in 2008, expressed as mean values. Asterisks show prey detected in *O. vulgaris* paralarvae. The abundances of the different decapod groups detected in the gut of *O. vulgaris* paralarvae are detailed below.

Descriptors	Summer						Autumn					
	Coastal (n = 12)		Frontal (n = 12)		Oceanic (n = 8)		Coastal (n = 27)		Frontal (n = 11)		Oceanic (n = 9)	
Richness (S)	42		26		21		36		30		21	
Diversity (H')	2.25		1.61		1.31		1.98		1.85		1.70	
Uniformity (J)	0.42		0.34		0.30		0.38		0.38		0.39	
Simpson Index (λ)	0.19		0.33		0.44		0.25		0.29		0.28	
Total Abundance	1665502		1314714		387248		1952373		538493		168932	
Holo/Meroplankton	4.27		51.71		557.31		2.74		47.4		418.66	
Taxa	Abundance	%	Abundance	%	Abundance	%	Abundance	%	Abundance	%	Abundance	%
Copepoda	399617.1	24.000	443349.7	33.723	146886.9	37.906	205950.9	10.549	112934.4	20.972	53745.0	31.800
Euphausiacea *	381745.8	22.927	707947.7	53.849	18593.8	4.798	408420.2	20.919	326348.8	60.603	31617.9	18.708
Echinodermata	369368.7	22.184	103.9	0.008	-	-	656140.8	33.607	6725.6	1.249	-	-
Urochordata	230985.8	13.873	120264.7	9.148	213801.5	55.174	247044.7	12.654	40856.9	7.587	61478.5	36.375
Decapoda *	107870.2	6.479	22291.4	1.696	1546.4	0.399	100729.6	5.159	5422.2	1.007	396.7	0.235
Cladocera	96835.0	5.816	3890.9	0.296	574.6	0.148	39702.0	2.034	616.3	0.114	-	-
Cirripedia	25626.2	1.539	1332.8	0.101	-	-	135228.6	6.926	5161.1	0.958	59.2	0.035
Gasteropoda	19886.8	1.194	3711.1	0.282	247.3	0.064	21447.4	1.099	1440.9	0.268	12.5	0.007
Chaetognatha	11020.9	0.662	4384.5	0.333	2838.0	0.732	76317.7	3.909	32060.3	5.954	16780.6	9.929
Cnidaria	9933.4	0.597	1427.3	0.109	117.9	0.030	51543.1	2.640	3029.5	0.563	698.9	0.414
Chordata *	4949.5	0.297	1982.7	0.151	231.0	0.060	6296.5	0.323	370.5	0.069	76.5	0.045
Misidacea	4284.9	0.257	3189.0	0.243	2190.3	0.565	1400.6	0.072	2668.6	0.496	3691.8	2.184
Bivalvia	867.5	0.052	-	-	-	-	161.4	0.008	-	-	-	-
Platemintha	860.4	0.052	115.0	0.009	-	-	363.0	0.019	32.3	0.006	25.5	0.015
Polychaeta	495.6	0.030	2.8	0.000	25.3	0.007	368.6	0.019	341.4	0.063	106.7	0.063
Amphipoda	321.9	0.019	228.6	0.017	255.2	0.066	596.0	0.031	308.2	0.057	292.5	0.173
Cumacea	205.2	0.012	89.3	0.007	46.4	0.012	110.6	0.006	88.7	0.016	8.1	0.005
Cephalochordata	76.5	0.005	-	-	-	-	-	-	-	-	-	-
Ostracoda	56.1	0.003	-	-	-	-	-	-	-	-	-	-
Isopoda	21.4	0.001	1.6	0.000	1.4	0.000	41.6	0.002	28.2	0.005	10.5	0.006
Stomatopoda	0.4	0.000	357.9	0.027	147.8	0.038	-	-	-	-	5.2	0.003

Briozoa	-	-	-	-	-	-	478.5	0.025	-	-	-	-
<i>Octopus vulgaris</i>	8.650	0.000	4.191	0.000	1.940	0.000	19.201	0.000	59.490	0.000	3.596	0.000
Loliginidae	5.302	0.000	15.304	0.000	-	-	7.164	0.000	4.532	0.000	2.008	0.000
Sepiolidae	5.207	0.000	3.674	0.000	0.151	0.000	1.748	0.000	3.511	0.000	-	-
Ommastrephidae	-	-	-	-	-	-	0.236	0.000	-	-	-	-
Decapoda												
Brachyura *	63520.0	3.814	17732.3	1.349	918.3	0.237	31089.2	1.592	2252.4	0.418	113.6	0.067
Porcellanidae *	28471.8	1.710	1047.4	0.080	310.5	0.080	56116.2	2.874	184.2	0.034	-	-
Paguridae *	8681.0	0.521	1632.1	0.124	-	-	5983.4	0.306	1375.2	0.255	60.4	0.036
Alpheidae *	1792.4	0.108	1273.0	0.097	79.0	0.020	525.6	0.027	173.3	0.032	52.3	0.031
Processidae *	1445.6	0.087	318.9	0.024	121.6	0.031	3973.8	0.204	370.8	0.069	51.2	0.030
Thalassinidae *	571.3	0.034	-	-	-	-	64.7	0.003	-	-	-	-
Crangonidae *	375.4	0.023	85.3	0.006	-	-	714.2	0.037	76.9	0.014	-	-

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Table 2. Number of cephalopod paralarvae caught in the Ría de Vigo (NW Spain) at night from 2008 to 2010.

Species	Station	2008		2009		2010		Total
		Surface	Column	Surface	Column	Surface	Bottom	
<i>O. vulgaris</i>	T2	69	58	215	114	44	4	504
	T3	139	44	67	28	18	15	311
	T4	40	36	113	63	80	0	332
	T5	9	11	46	36	48	0	150
Loliginids	T2	12	25	2	54	6	19	118
	T3	24	51	29	107	3	26	240
	T4	7	19	26	79	11	6	148
	T5	1	5	7	22	1	0	36
Sepiolid	T2	2	9	1	13	1	3	29
	T3	9	26	2	44	3	2	86
	T4	6	16	0	18	1	5	46
	T5	1	8	1	17	0	1	28
Ommastrephids	T2	0	0	0	2	0	0	2
	T3	0	2	0	0	0	1	3
	T4	0	1	0	1	0	1	3
	T5	0	1	0	2	0	0	3
Total		319	312	509	600	216	83	2039
		631		1109		299		

Table 3. PERMANOVA results after 999 permutations to test differences in the abundance of *O. vulgaris*, loliginid and sepiolid paralarvae among the zooplankton communities (Abbreviated as: SC, summer coast; SF, summer front; SO, summer ocean; AC, autumn coast; AF, autumn front; AO, autumn ocean). • $p < 0.1$ marginally significant, values in bold are significant at $p < 0.05$.

Tests	Level	Cephalopod paralarvae	<i>Octopus vulgaris</i>	Loliginidae	Sepiolidae
Main test	Community	0.001	0.027	0.037	0.04
pair-wise	SC-SF	0.206	0.112	0.981	0.951
	SC-SO	0.001	0.091 •	0.002	0.068 •
	SC-AC	0.182	0.273	0.63	0.239
	SC-AF	0.089 •	0.585	0.293	0.692
	SC-AO	0.003	0.088 •	0.019	0.038
	SF-SO	0.003	0.672	0.01	0.022
	SF-AC	0.014	0.008	0.659	0.135
	SF-AF	0.16	0.127	0.439	0.588
	SF-AO	0.002	0.664	0.07 •	0.003
	SO-AC	0.007	0.021	0.016	0.139
	SO-AF	0.112	0.163	0.087 •	0.165
	SO-AO	0.734	1	0.494	0.418
	AC-AF	0.322	0.803	0.529	0.548
	AC-AO	0.002	0.011	0.056 •	0.067 •
	AF-AO	0.116	0.133	0.256	0.102

Table 4. Results of the generalized linear methods (GLMs) fitted to the abundance of *O. vulgaris*, loliginids and sepiolids using the descriptors of the mesozooplankton communities found in the Ría de Vigo in 2008 as explanatory variables. The GLMs assumed a negative binomial distribution and used the ln-transformed water volume filtered as an offset. Shown is the estimate ($\pm$ S.E.) for each parameter. Note that the reference values were the water column and July for the categorical factors strata and month, respectively. ns: non-significant, * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

Parameter	<i>O. vulgaris</i>	Loliginids	Sepiolids
Intercept	-2.77 (0.85)***	-2.63 (0.75)***	-4.52 (1.18)*
Surface	0.47 (0.29) ^{ns}	-0.44 (0.27) ^{ns}	-0.85 (0.41)*
September	2.03 (0.49)***	0.90 (0.43)*	0.06 (0.70) ^{ns}
October	0.85 (0.33)**	-0.12 (0.30) ^{ns}	-0.64 (0.45) ^{ns}
Ln (H/M)	-0.22 (0.08)**	-0.19 (0.08)*	-0.08 (0.11) ^{ns}
Evenness	-5.27 (1.85)**	-5.46 (1.62)***	-1.39 (2.57) ^{ns}

Table 5 Prey preferences of eighteen *O. vulgaris* paralarvae (Oc 1 - Oc 18) in the different mesozooplankton communities calculated with the linear food selection index for each zooplankton group. Czekanowski's index (CI) is shown for each paralarvae to elucidate changes on foraging tactics depending on the community.

Community		Brachyura	Processidae	Alpheidae	Paguridae	Crangonidae	Thalassinidae	Porcellanidae	Krill larvae	CI
SC	Oc 1	0.46		0.50						0.118
	Oc 2	0.30		0.33	0.33					0.123
	Oc 3		0.33	0.33			0.33			0.081
	Oc 4	0.96								0.117
SF	Oc 5	0.32		0.33		0.33				0.061
	Oc 6		1.00							0.047
	Oc 7	1.00								0.060
AC	Oc 8	0.32		0.67						0.093
	Oc 9	0.38	0.40	0.20						0.095
	Oc 10	0.23	0.25	0.25	0.25					0.098
	Oc 11		0.50						0.29	0.288
AF	Oc 12		0.50						-0.11	0.288
	Oc 13		0.50						0.50	0.042
	Oc 14	0.33		0.67						0.045
	Oc 15			0.67					-0.27	0.374
	Oc 16	0.50						0.50		0.045
	Oc 17	0.33	0.33						0.33	0.046
	Oc 18	0.50							0.50	0.045

Table 6. GLM results fitted to the abundance of *O. vulgaris*, loliginids and sepiolids using the spatio-temporal variables and the upwelling strength the day preceding the sampling date from 2008 to 2010 as explanatory variables. The GLMs assumed a negative binomial distribution and used the ln-transformed water volume filtered as an offset. Shown is the estimate ($\pm$ S.E.) for each parameter. Note that the reference values are July, water column and T2 for month, strata and station, respectively. ns: non-significant, * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

Parameter	<i>O. vulgaris</i>	Loliginids	Sepiolids
Intercept	-5.06 (0.25)***	-4.73 (0.21)***	-5.95 (0.29)***
September	0.68 (0.24)**	-0.03 (0.22) ^{ns}	-0.29 (0.28) ^{ns}
October	0.46 (0.24) ^{ns}	-0.74 (0.23)**	-0.93 (0.31)**
Surface	1.12 (0.19)***	-0.82 (0.18)***	-1.46 (0.26)***
T3	-0.52 (0.27) ^{ns}	0.59 (0.23)*	0.98 (0.32)**
T4	-0.51 (0.27) ^{ns}	0.02 (0.24) ^{ns}	0.31 (0.34) ^{ns}
T5	-1.11 (0.28)***	-1.51 (0.30)***	-0.36 (0.37) ^{ns}
- <i>Q_x</i>	1.08 (0.27)***	0.46 (0.26) ^{ns}	0.79 (0.34)*

Fig. 1. Sampling area showing the four stations (T2–T5) where mesozooplankton samples and cephalopod paralarvae were collected off the Ría de Vigo (NW Iberian Peninsula). Hydrographical data was obtained from Rande bridge and meteorological data was obtained from Silheiro buoy and from Ons Island meteorological station.

Fig. 2 Meteorological conditions recorded around the sampled area. a Wind speed and direction (W_x , W_y , m s^{-1}), b upwelling index ($-Q_x$, $\text{m}^3 \text{s}^{-1} \text{km}^{-1}$), and c sea surface temperature ($^{\circ}\text{C}$) obtained from Rande observatory for 2008–2010 samplings. Vertical bars indicate the sampling days, which are numerated sequentially.

Fig. 3 PCO plot showing the distribution and abundance (ind. 1000 m^3) of *Octopus vulgaris* (a,b), loliginid (c,d) and sepiolid (e,f) paralarvae at the surface and in the integrated water column samples within the different mesozooplankton communities identified off the Ría de Vigo in 2008. Abbreviations: SC, summer coast; SF, summer front; SO, summer ocean; AC, autumn coast; AF, autumn front; AO, autumn ocean.

Fig. 4 PCO plot showing the strength and direction of the associations between the cephalopod paralarvae collected in 2008 and the mesozooplankton communities found off the Ría de Vigo. The blue circle represents the maximum correlation with PCO axis. Abbreviations: lol, loliginidae; oct, *Octopus vulgaris*; oma, ommastrephidae; sep, sepiolidae.

Fig. 5 Mean cephalopod paralarval abundance (ind 1000 m^3) collected at the different strata during the 30 samplings carried out in the Ría de Vigo between 2008 and 2010. Samples were collected with a bongo net in 2008 and 2009 (column samples) and with a Multinet in 2010 (bottom sample).

Fig. 6 Predicted number of (a) *O. vulgaris* at station 2, and (b) loliginids and (c) sepiolids at station 3 as a function of the upwelling index the previous day of the capture, the strata and month sampled. The expected values are the result of a negative

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860 binomial GLM fitted to the abundance of cephalopod paralarvae collected from 2008 to
861 2010 (see Table 6). Values were standardized to 1000 m³.

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Sampling area showing the four transects (T2–T5) where mesozooplankton samples and cephalopod paralarvae were collected off the Ría de Vigo (NW Iberian Peninsula). Hydrographical data was obtained from Rande bridge and meteorological data was obtained from Silheiro buoy and from Ons Island meteorological station.

142x93mm (300 x 300 DPI)

Fig. 2 Meteorological conditions recorded around the sampled area. a Wind speed and direction (W_x , W_y , $m\ s^{-1}$), b upwelling index ($-Q_x$, $m^3\ s^{-1}\ km^{-1}$), and c sea surface temperature ($^{\circ}C$) obtained from Rande observatory for 2008–2010 samplings. Vertical bars indicate the sampling days, which are numerated sequentially.

210x148mm (300 x 300 DPI)

PCO plot showing the distribution and abundance (ind. 1000 m³) of *Octopus vulgaris* (a,b), loliginid (c,d) and sepiolid (e,f) paralarvae at the surface and in the integrated water column samples within the different mesozooplankton communities identified off the Ría de Vigo in 2008. Abbreviations: SC, summer coast; SF, summer front; SO, summer ocean; AC, autumn coast; AF, autumn front; AO, autumn ocean.
158x204mm (300 x 300 DPI)

PCO plot showing the strength and direction of the associations between the cephalopod paralarvae collected in 2008 and the mesozooplankton communities found off the Ría de Vigo. The blue circle represents the maximum correlation with PCO axis. Abbreviations: lol, loliginidae; oct, Octopus vulgaris; oma, omastrephidae; sep, sepiolidae.
104x81mm (300 x 300 DPI)

Mean cephalopod paralarval abundance (ind 1000 m³) collected at the different strata during the 30 samplings carried out in the Ría de Vigo between 2008 and 2010. Samples were collected with a bongo net in 2008 and 2009 (column samples) and with a Multinet in 2010 (bottom sample).
212x94mm (300 x 300 DPI)

Fig. 6 Predicted number of (a) *O. vulgaris* at station 2, and (b) loliginids and (c) sepiolids at station 3 as a function of the upwelling index the previous day of the capture, the strata and month sampled. The expected values are the result of a negative binomial GLM fitted to the abundance of cephalopod paralarvae collected from 2008 to 2010 (see Table 6). Values were standardized to 1000 m³.
190x59mm (300 x 300 DPI)