1 **WIND-DRIVEN UPWELLING EFFECTS ON CEPHALOPOD PARALARVAE: OCTOPUS**
2 **VULGARIS AND LOLIGINIDAE OFF THE GALICIAN COAST (NE ATLANTIC)**

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14 **ABSTRACT**

15 Circulation patterns of coastal upwelling areas may have central consequences for the abundance
16 and cross-shelf transport of the larval stages of many species. Previous studies have provided
17 evidences that larvae distribution results from a combination of subtidal circulation, species-specific
18 behaviour and larval sources. However, most of these works were conducted on organisms
19 characterised by small-sized and abundant early life phases. Here, we studied the influence of the
20 hydrography and circulation of the Ría de Vigo and adjacent shelf (NW Iberian upwelling system)
21 on the paralarval abundance of two contrasting cephalopods, the benthic common octopus (*Octopus*
22 *vulgaris*) and the pelagic squids (Loliginidae). We sampled repeatedly a cross-shore transect during
23 the years 2003 to 2005 and used zero inflated models to accommodate the scarcity and patchy
24 distribution of cephalopod paralarvae. The probability of catching early stages of both cephalopods
25 was higher at night. Octopus paralarvae were more abundant in the surface layer at night whereas
26 loliginids preferred the bottom layer regardless of the sampling time. Abundance of both
27 cephalopods increased when shelf currents flowed polewards, water temperature was high and
28 water column stability was low. The probability of observing an excess of zero catches decreased
29 during the year for octopus and at high current speed for loliginids. In addition, the circulation
30 pattern conditioned the body size distribution of both paralarvae; while the average size of the
31 captured octopuses increased (decreased) with poleward currents at daylight (nighttime), squids
32 were smaller with poleward currents regardless of the sampling time. These results contribute to the
33 understanding of the effects that the hydrography and subtidal circulation of a coastal upwelling
34 have on the fate of cephalopod early life stages.

35 **Keywords**

36 *Octopus vulgaris*; Loliginidae; paralarvae; body size; vertical migration; zero-inflated models;
37 upwelling; NW Spain

38

39 **Highlights**

40 1. Abundance and size of *Octopus vulgaris* and Loliginidae was modelled in an upwelling area.

41 2. Both paralarvae were more abundant with poleward currents, elevated temperatures and low water
42 column stability.

43 3. Subtidal circulation influenced the body size distribution of both paralarvae.

44 4. Probability of capturing these paralarvae increased at nighttime.

45 **1. Introduction**

46 Recruitment and population dynamics of marine organisms are widely influenced by processes
47 that affect larval dispersal and connectivity. Although much effort has been put forward on this topic
48 in recent years (see Cowen and Sponaugle, 2009 for review), understanding the multiple drivers of
49 early life stages is still a challenge for many species. This is particularly true for organisms inhabiting
50 coastal upwelling systems, where the hydrography and circulation patterns might be critical for the
51 spatio-temporal fate of the larvae and their later recruitment (Morgan et al., 2009a).

52 Upwelling regions are characterised by a surface layer under the direct influence of the wind (the
53 Ekman layer), and a compensation counter flow at the bottom. This circulation pattern has been
54 formerly postulated as a plausible mechanism for reducing settlement and recruitment due to the
55 surface offshore advection of larvae during persistent upwelling. Given their low swimming ability,
56 planktonic phases would be transported offshore like passive particles within the Ekman layer during
57 upwelling events. On the contrary, when downwelling takes place larvae would be transported
58 shoreward (e.g. Roughgarden et al., 1988; Farrell et al., 1991; Connolly et al., 2001). However, more
59 detailed studies have revealed that this simple general pattern might result incorrect or incomplete.
60 For instance, intertidal gastropod larvae can stay close to shore (Poulin et al., 2002), bivalve larvae
61 might be transported shoreward by the bottom counter flow (Shanks and Brink, 2005), and decapod
62 larvae perform diel vertical migrations that contribute to their retention on the coast (dos Santos et
63 al., 2008) despite the dominant upwelling conditions in the three cases. Furthermore, Morgan et al.
64 (2009a) concluded that, for a number of near shore crustaceans, wind-driven offshore transport
65 should not limit recruitment; and Shanks and Shearman (2009) have postulated the “lost of the
66 paradigm” showing that neither upwelling nor downwelling affect the cross-shelf distribution of
67 certain invertebrate larvae which tended to avoid the surface Ekman layer. In summary, upwelling
68 effects on larval dynamics are more complex than previously thought; transport in these areas might
69 be species-specific and dependent on the interactions between larval (e.g. vertical behaviour) and

70 adult (e.g. fecundity) traits with the oceanographic conditions (Shanks and Eckert, 2005).

71 Most of the research addressing the effects of upwelling dynamics on larval abundance and
72 transport has been based on the study of species whose early life phases are very small-sized and,
73 usually, with high abundance (e.g. bivalves, decapods, barnacles). However, the effects of the
74 hydrography and dynamics of the coastal ocean in general, and upwelling areas in particular, on the
75 larval stages of other organisms such as cephalopods has been much less investigated. Cephalopods
76 are a key component of marine ecosystems and their economic importance has risen in the recent
77 decades contributing substantially to fisheries in many areas (Hunsicker et al., 2010). Most
78 cephalopod species are semelparous and generally have short life cycles of less than 1–2 years. They
79 are usually ecological opportunists and their populations tend to be very labile with recruitment
80 variability driven, to a greater or lesser extent, by the environment (Boyle and Rodhouse, 2005).

81 Environmental conditions can affect several biological processes such as egg survival, growth and
82 migration, as well as the distribution and abundance of early life stages (Pierce et al., 2008). The
83 abundance of cephalopod larvae (actually termed as “paralarvae” sensu Young and Harman, 1988) is
84 usually scarce compared with other invertebrates and their distribution is patchy (Boletzky, 2003).

85 Consequently, the relationships between the changes in the environment affecting paralarvae
86 abundance and distribution are poorly understood, though an increased research effort has been put
87 forward in recent years. For instance, in the Southern California Bight, the ecology of *Doryteuthis*
88 *opalescens* paralarvae is linked to the California Current system variability and, particularly, their
89 abundance increases after El Niño events (Zeidberg and Hamner, 2002). Sea surface temperature and
90 upwelling intensity are related to paralarval distribution off the western coast of Portugal (Moreno et
91 al., 2009). Furthermore, high planktonic production that promotes suitable conditions for survival and
92 growth during the upwelling season is linked to high densities of various juvenile cephalopod species
93 in southern Brazil (Vidal et al., 2010).

94 Galicia is at the northern boundary of the Iberian upwelling system (Fig. 1). Coastal winds at

95 these latitudes (42° to 44° N) are seasonal; northerly winds prevail from March-April to September-
96 October, promoting coastal upwelling, and downwelling-favourable southerly winds predominate
97 the rest of the year. However, more than 70% of the total variability in coastal winds occurs in
98 periods of less than 1 month, so that the upwelling season appears as a succession of wind-stress
99 episodes separated by calm episodes, with a frequency of 3 to 15 days (Álvarez-Salgado et al.,
100 2003) similar to other coastal upwelling systems at comparable latitude (Hill et al., 1998). The Ría
101 de Vigo (Fig. 1) is a large coastal embayment that acts as an extension of the shelf during the
102 upwelling season, when continental runoff is scarce. The positive residual circulation pattern
103 (ingoing bottom current/outgoing surface current) responds to coastal winds with a delay that
104 ranges from a few hours to two days (Souto et al., 2003; Piedracoba et al., 2005). During the
105 downwelling season, when continental runoff is relatively large, the inner ría circulates as a positive
106 estuary and the circulation of the outer ría reverses (outgoing bottom current/ingoing surface
107 current) in response to the prevailing southerly winds (Piedracoba et al., 2005).

108 The oceanographic conditions off the Galician coast affect a broad spectrum of organisms from
109 plankton (e.g. Bode et al., 2009) to fish (e.g. Guisande et al., 2001). Regarding cephalopods, the
110 link between the regional oceanography and the abundance of *Octopus vulgaris* and Loliginidae
111 paralarval stages has been previously suggested (Rocha et al., 1999; González et al., 2005).
112 Furthermore, recent results have outlined the influence of high-frequency upwelling events, and
113 specifically the early stage of a relaxation phase, on the abundance of octopus paralarvae (Otero et
114 al., 2009). These oceanographic features may further lead to important consequences for the
115 artisanal catches of this species (Otero et al., 2008).

116 Biological sampling in the ocean commonly leads to the presence of multiple zero observations
117 of the species of interest, and this is especially apparent when sampling cephalopod early life stages.
118 Thus, counts of paralarvae might result in an excess of zeros and non consideration of the zero-
119 inflation might reduce the ability to detect ecological relationships and make inaccurate inferences

120 (Potts and Elith, 2006 and references therein). The presence of substantially more zeros are generally
121 categorised as false zeros, i.e. those that might be attributable to the absence of a species at a site
122 because is the inappropriate season or to observer fails to detect it; versus true zeros which should
123 arise due to habitat unsuitability or environmental processes (Martin et al., 2005). Therefore, the use
124 of models that explicitly take into account the potential zero inflation, and the ability to deal with the
125 different type of zeros that may be ascribed to different processes, appears to be particularly relevant
126 for the study of cephalopod paralarval abundance. Zero-inflated models have been largely used in a
127 number of fields such as medicine and social science and are recently becoming more popular in
128 terrestrial (e.g. Martin et al., 2005; Potts and Elith, 2006) and marine ecology (e.g. Minami et al.,
129 2007). However, to our knowledge, these techniques have never been used to investigate the changes
130 in abundance of cephalopod paralarvae.

131 The objective of this study is to describe the temporal and spatial distribution of the early life
132 stages of two contrasting cephalopod species, the benthic common octopus (*Octopus vulgaris*) and
133 the pelagic common squids (Loliginidae) that are of great social and economic importance in the
134 North West Iberian peninsula (Pierce et al., 2010). We quantified the short-time scale effects of the
135 hydrography and subtidal circulation patterns in an area characterised by seasonal coastal upwelling
136 using zero-inflated models to accommodate the scarcity and patchy distribution commonly found in
137 cephalopod paralarval sampling, which lead to an excess number of zero counts. Differences in
138 abundance in the water column depending on the sampling time were also examined to infer the
139 potential diel vertical behaviour of the paralarvae. We further assessed the influence that the subtidal
140 circulation had on the distribution of individuals of different body size.

141 2. Material and Methods

142 Forty-three surveys to collect plankton and water samples were conducted onboard R/V *Mytilus*
143 from 2003 to 2005 (Fig. 1, Table S1). The majority of the surveys were carried out during daylight
144 hours, but four of them were undertaken during both day and nighttime (Table S1). In 2003, we
145 sampled monthly from January to December, whereas in 2004 and 2005 sampling was restricted
146 from May to October on a weekly to fortnightly basis (Table S1).

147

148 2.1. Biological sampling

149 Zooplankton samples were collected from four transects parallel to the coast: T1, T2, T3 and T4
150 with average water column depths of 36, 26, 68 and 85 m, respectively (Fig. 1). During the monthly
151 surveys of 2003, few cephalopod paralarvae were captured in T1, thus this transect was replaced by
152 a deeper one (T5, 110 m) in 2004 and 2005 (Fig. 1, Table S1). Following standard procedures,
153 samples were taken, both near-bottom and at the surface, by towing from south to north a 750 mm
154 diameter bongo net of 375 μ m mesh except for the first three surveys where a Tucker net was used.
155 At a ship speed of 2 knots, the bongo net was first lowered and stabilised near the bottom for a
156 period of 15 min and subsequently hauled up at 0.5 m s⁻¹ (hereafter denoted as bottom for
157 simplicity). Then, it was cleaned and towed in the surface layer for another 15 min period. In some
158 instances however, the bongo did not fish at the expected depth (see further discussion on the
159 sampling design in the supplementary material). In total, 356 samples were collected. The bongo
160 net was equipped with a mechanical General Oceanics flow meter to record the water flow, and a
161 depth meter to record the effective sampling depth. Plankton samples were fixed onboard with 4%
162 buffered formalin for 24 hours, and preserved in 70% alcohol. Common octopus (*Octopus vulgaris*)
163 paralarvae were separated and later classified with reference to Sweeney et al. (1992). Despite at
164 least three species from the Loliginidae family are abundant in Galician waters (*Alloteuthis media*,
165 *A. subulata*, and *Loligo vulgaris*), identification guides based on morphology are not accurate (e.g.

166 Sweeney et al., 1992). Therefore, for the purpose of this study we pooled all squids and considered
167 those paralarvae as Loliginidae.

168 Each paralarvae was placed on blotting paper to remove alcohol from the mantle cavity and
169 weighed (BW) in a Sartorius MC-210-P microbalance to the nearest 0.01 mg. The following
170 measurements were also taken according to Roper and Voss (1983): Total length (TL), dorsal
171 mantle length (DML), ventral mantle length (VML), mantle width (MW), eye diameter (ED), and
172 arm length (AL). In addition, tentacle length (TeL) was measured for the loliginid individuals, and
173 in *O. vulgaris* paralarvae it was estimated the Mantle Area Index (i.e. $MAI = DML \times MW$, in
174 mm^2) as proposed by Sakaguchi et al. (2002). All measurements were recorded to the nearest 0.001
175 μm using the software Eclipsenet 1.20 (Laboratory Imaging s.r.o. for Nikon B.V.) running on a PC
176 (Asus) connected to a digital camera (Nikon DXM1200F) installed on a dissecting microscope
177 (Nikon SMZ800). Individuals deformed during collection (e.g. those with damaged or inverted
178 mantles) were not measured.

179

180 2.2. Hydrographic sampling

181 A *Seabird 25* conductivity-temperature-depth (CTD) probe equipped with a *WetLabs ECO FL*
182 fluorometer was deployed at each hydrographic station before and after every plankton transect (Fig.
183 1). Conductivity measurements were converted into practical salinity scale values with the equation
184 of UNESCO (1986). CTD data were used to estimate average values of temperature (T_L), salinity (S),
185 density (ρ) and fluorescence (F) in (i) a 10 m thick layer 5 meters above the bottom in the
186 hydrographic stations at the beginning of each plankton transect; and (ii) in a 5 m thick layer 5 meters
187 below the surface in the hydrographic stations at the end of each plankton transect. These two water
188 layers matched the bottom and surface biological sampling.

189 In addition, CTD data were used to estimate average water column-integrated temperature (T_C),
190 and stability (N^2 , in min^{-2}). N^2 is the squared Brunt-Väisälä frequency, calculated as Millard et al.

191 (1990):

$$192 \quad N^2 = -\frac{g}{\rho} \frac{d\rho}{dz} \quad (1)$$

193 where g is the gravity acceleration, ρ is the density (kg m^{-3}) and z is the depth (m). Average water
194 column-integrated stability due to temperature (N_T^2 , in min^{-2}) and salinity (N_S^2 , in min^{-2}) were
195 also estimated:

$$196 \quad N_T^2 = -\frac{g}{\rho} \left(\frac{\partial \rho}{\partial t} \right) \frac{dt}{dz} \quad (2)$$

$$197 \quad N_S^2 = -\frac{g}{\rho} \left(\frac{\partial \rho}{\partial s} \right) \frac{ds}{dz} \quad (3)$$

198 where t is the temperature ($^{\circ}\text{C}$) and s is the salinity.

199

200 2.3. Circulation model

201 Residual current speed and direction were simulated for each sampling transect using a C++
202 version of the HAMBURG Shelf Ocean Model (HAMSOM), developed by the Group of Physical
203 Oceanography of the University of Vigo (GOFUVI) from the core code of the Institut für
204 Meereskunde (Hamburg). Briefly, HAMSOM is a 3D, z -coordinate (Arakawa-C grid), baroclinic,
205 semi-implicit finite-difference numerical prediction model. It allows the introduction of salinity and
206 temperature at any point of the model, as well as the heat exchange with the atmosphere and the
207 evaporation/rainfall. The HAMSOM model has been adapted for the domain of our study area and
208 validated with moored current meters for various zones of the Ría de Vigo (Souto et al., 2001;
209 2003). From the outputs of the model we estimated the residual current speed (CU_s , in cm s^{-1}) near
210 the bottom and at the surface layer for each plankton transect during the sampling day and up to five
211 days preceding the sampling day. Current direction (CU_D) was also estimated for each water layer
212 and computed on anticlockwise east degrees, that is, positive (negative) values indicate poleward
213 (southward) currents.

214

215 2.4. Statistical analyses

216 2.4.1. Modelling paralarvae abundance

217 Cephalopod paralarvae are scarce and have a patchy distribution. This leads to the presence of
218 many null samples during the collection process meaning that the count data might be zero-inflated
219 (Fig. S1). Therefore, to take into account that the response variable may contain more zeros than
220 expected, based on a Poisson or negative binomial distribution, we used zero-inflated models (ZI;
221 Cameron and Trivedi, 1998) to deal with potential excess of zero counts.

222 The ZI model is a mixture model where a binomial generalised linear model (GLM) is used to
223 model the probability of measuring a zero, and the count process is modelled by a Poisson (ZIP) or
224 negative binomial GLM (ZINB). The detailed description of the mathematics can be found elsewhere
225 (Cameron and Trivedi, 1998; Zuur et al., 2009). Briefly, the ZI model would have a first component
226 that contains only the zeros (the false zeros, $Y_i = 0$), and the second component would contain the
227 count data, which may produce zeros (true zeros, $Y_i = y_i = 0$) as well as values greater than zero ($Y_i =$
228 $y_i \mid y_i > 0$). Thus the probability Y of catching a paralarvae at a site i can be summarised as follows:

$$229 \Pr(Y_i = 0) = \Pr(\text{False zeros}) + (1 - \Pr(\text{False zeros})) \times \Pr(\text{Count process gives a zero}) \quad (4)$$

230 where it is assumed that the probability that Y_i is a false zero is binomially distributed with
231 probability π_i , and that the counts follow a Poisson (or negative binomial) distribution with
232 expectation μ_i :

$$233 \Pr(y_i = 0) = \pi_i + (1 - \pi_i) \times e^{-\mu_i} \quad (5)$$

234 The probability π_i of having a false zero could be then modelled using logistic regression:

$$235 \pi_i = \frac{e^{v + \gamma_l X_{i,l} + \gamma_n X_{i,n}}}{1 + e^{v + \gamma_l X_{i,l} + \gamma_n X_{i,n}}} \quad (6)$$

236 and the mean μ_i of positive count data can be modelled just as in Poisson GLM:

$$237 \mu_i = e^{\alpha + \beta_l X_{i,l} + \beta_n X_{i,n}} \quad (7)$$

238 In both parts of the model X_s are covariates (that may be different), v and α are the intercepts, and γ

239 and β are regression coefficients to be estimated. To model the paralarval abundance of *O. vulgaris*
240 and Loliginidae we used as covariates the variables recorded at the surface and bottom layers in each
241 sampling transect as obtained from the CTD profiles and the simulated currents (see Table 1 for a
242 summary of covariates).

243 Before model fitting, it was explored the potential collinearity among covariates computing
244 variance inflation factors (Table S2) and using pair plots (Zuur et al., 2010). For both *O. vulgaris* and
245 Loliginidae model selection was performed on a hypothesis-basis regarding the false zeros, and then
246 deleting non-significant covariates in the count part of the model. In general, there are multiple
247 sources of zeros in ecological observations (Martin et al., 2005). On the one hand, we here
248 hypothesised that the false zeros might be caused by failing to record the paralarvae at: (i) the time of
249 the sampling (DoY), (ii) the sampled layer (Layer), and (iii) the simulated subtidal currents (CU_s and
250 CU_D). On the other hand, the count process was modelled as a function of the sampling time (DoY),
251 the sampled layer (Layer), the subtidal current (CU_s and CU_D), and the thermohaline conditions
252 derived from the CTD profiles. In addition, the volume of the bongo-filtered water (in m³) was ln-
253 transformed and used as an offset in the count part of the ZI models. Models were compared using
254 the Bayesian Information Criterion (BIC), and the optimal ZI models were further contrasted with the
255 corresponding models using different distributions such as Poisson and negative binomial. Finally,
256 the residuals of the optimal models were used for validation and to assess potential spatial correlation
257 by computing the Spearman's correlation coefficient for each pair of stations within each depth and
258 year. Moreover, we assumed that temporal autocorrelation was not worrisome due to the ample
259 separation between sampling dates.

260 2.4.2. Modelling paralarvae body size

261 We postulate that the time of sampling, the water layer and sampling site, and the residual
262 circulation should influence the distribution of individuals of different body size. To test for this,
263 paralarval body size patterns were modelled using linear mixed-effects models (LME, Pinheiro and

264 Bates, 2000) of the form:

$$265 \quad Y_{i,t} = \alpha + a_i + \beta_1 X_{1,i,t} + \beta_n X_{n,i,t} + \epsilon_{i,t} \quad (8)$$

266 where Y is the body size (MAI and DML were used in *O. vulgaris* and Loliginidae, respectively)
267 measured at a survey *i* and time *t*. α is an intercept, a_i is a random effect allowing for variation in the
268 intercept between surveys and assumed to be normally distributed with mean 0 and variance σ_a^2 .
269 X_s are covariates and β_s are regression coefficients to be estimated. The residuals $\epsilon_{i,t}$ are a normally
270 distributed random error with mean 0 representing the within-survey variation. Residuals were used
271 for model validation and, if present, heterogeneity was handled by means of modelling the variance
272 (σ^2) in residual size, for instance:

$$273 \quad \text{var}(\epsilon_{i,t}) = \sigma^2 \exp(2\delta X_{1,i,t}) \quad (9)$$

274 where δ is a parameter to be estimated that describes the estimated change in variance with $X_{1,i,t}$.
275 This model of the residual variance was compared with other variance structures through selection
276 criteria (Pinheiro and Bates, 2000). For any body size equation, model selection was performed
277 iteratively. First, with all fixed effects included in the model the appropriateness of a random
278 intercept was evaluated using likelihood ratio tests. Model parameters were estimated by means of
279 restricted maximum likelihood (REML). Second, the variance models were selected. Third, the
280 optimal fixed effects were determined by means of maximum likelihood (ML) parameter estimation.
281 Finally, with the optimal fixed structure in place the random effects were reassessed and model
282 parameters presented were estimated by REML (Zuur et al., 2009).

283 All analyses and treatment of data were performed with R 3.0.1 language (R Development Core
284 Team, 2013) and using the “mgcv 1.7-22” (Wood, 2006), “nlme 3.1-109” (Pinheiro and Bates,
285 2000), “MASS 7.3-26” (Venables and Ripley, 2002), “pscl 1.04.4” (Zeileis et al., 2008), and
286 “effects 2.2-4” (Fox, 2003) packages.

287 3. Results

288 In total, 627 (daytime = 378, nighttime = 249) individuals of *O. vulgaris* and 397 (daytime = 306,
289 nighttime = 91) Loliginidae were caught in the 356 plankton samples (average filtered water was
290 $925 \pm 634 \text{ m}^3$) collected from 2003 to 2005 in the mouth of the Ría de Vigo (Fig. 1). These catches
291 resulted in an *O. vulgaris* average abundance of 1.4 ± 2.6 and 13.3 ± 26.2 individuals per 10^3 m^3 at
292 daytime and nighttime, respectively. Regarding Loliginidae, the average abundances were 1.1 ± 3.7
293 and 4.1 ± 7.2 individuals per 10^3 m^3 at daytime and nighttime, respectively. This scarcity, common to
294 paralarval sampling of multiple cephalopod species using the current sampling methods, lead to the
295 presence of many null samples during the collection process for both *O. vulgaris* (60% and 25% of
296 zeroes at daytime and nighttime, respectively) and Loliginidae (70% and 34% of zeroes at daytime
297 and nighttime, respectively) (Table S1; Fig. S1a, b).

298 In general, the plankton samples were undertaken during a broad spectrum of environmental
299 conditions over the three years of sampling (Fig. 2), though resulting in different effects in
300 abundance on the two cephalopods (see below).

301 3.1. Daytime abundance models

302 3.1.1. *Octopus vulgaris*

303 Table 2 and Table S3 show the results of the final ZINB model fitted to *O. vulgaris* paralarval
304 abundance and the model selection process, respectively. The probability of false zeros was higher in
305 the surface layer than in the bottom layer, and decreased when surveys approached the autumn (Fig.
306 3a). In other words, at daytime it was more probable to catch common octopus paralarvae close to the
307 bottom and in autumn months. In addition, the expected counts of *O. vulgaris* paralarvae increased
308 when the average residual current over the five days preceding the sampling date flowed northwards
309 (Fig. 3b), at elevated temperature values in the corresponding water layer (Fig. 3c), and at low values
310 of water column stability (Fig. 3d). Moreover, it was also apparent a positive relationship with water
311 column stability due to temperature (Fig. 3e). The final model was not overdispersed (dispersion

parameter = 0.97), and corresponding models with other distributions were not more optimal than the ZINB (Table S4). There were not detected patterns in the residuals (Fig. S2) or any sign of residual spatial correlation (Table S5).

3.1.2. *Loliginidae*

Table 3 and Table S6 show the results of the final ZINB model fitted to *Loliginidae* paralarval abundance and the model selection process, respectively. The probability of false zeros was higher in the surface layer compared to the bottom layer, and decreased when the subtidal current speed averaged over the five days preceding the sampling date was strong (Fig. 4a). That is, at daytime it was more probable to catch loliginid paralarvae close to the bottom and at higher residual currents. In addition, the expected counts of *Loliginidae* paralarvae slightly decreased with the day of the year (Fig. 4b) and at elevated values of the water column stability (Fig. 4e). Additionally, the expected counts increased with higher poleward subtidal currents averaged over the five days preceding the sampling date (Fig. 4c) and at elevated values of the water column temperature (Fig. 4d). The final model was not overdispersed (dispersion parameter = 1.07), and corresponding models with other distributions were not more optimal than the ZINB (Table S7). Again, there were not detected patterns in the residuals (Fig. S3) or any sign of residual spatial correlation (Table S8).

3.2. *Diel vertical distribution*

Using data from the four surveys when daytime and nighttime samples were collected we found that *O. vulgaris* paralarvae was not abundant in the surface layer at daytime. However, octopus paralarvae concentrated in the surface during nighttime sampling (Table 4, Fig. 5a). Abundance in the bottom layer at daytime was not significantly different from abundance in the bottom layer at nighttime. Regarding *Loliginidae* paralarvae, abundance was higher during the night sampling time and at the bottom layer (Table 4, Fig. 5b). The general pattern in vertical distribution did not varied if size of individuals was taken into account. However, slight differences were detected. Abundance of

337 Loliginidae with a DML smaller than 2.5 mm was higher at the bottom layer regardless of the
338 sampling time, whereas, abundance of Loliginidae with a DML larger than 2.5 mm was higher during
339 nighttime regardless of the sampled layer (Fig. 5b).

340

341 3.3. Body size models

342 3.3.1. *Octopus vulgaris*

343 The MAI was measured in a total of 584 individuals (349 and 235 during daylight and nighttime,
344 respectively) and all octopus paralarvae were recently hatched individuals as everyone counted three
345 suckers per arm. Despite this fact, the different morphological measurements of size were also highly
346 heterogeneous for this species (Table S9, Fig. S4). Pooling all MAI data together, the LME revealed
347 spatial differences as larger individuals were caught at T2 and T5 during daylight hours and at T3
348 and T5 during nighttime (Table 5). In addition, size was related to the subtidal current direction
349 depending on the sampling time. At daytime, octopus size increased with poleward currents, whereas
350 the relationship switched to negative during nighttime (Table 5, Fig. 6a). Furthermore, a seasonal
351 cycle in early hatchlings' size was also apparent with larger individuals occurring at the end of
352 summer (Table 5, Fig. 6b). However, it should be noted that this annual pattern was influenced by the
353 few number of samples at the beginning and end of the year. For instance, if removed the paralarvae
354 sampled in February (Fig. S5a) the seasonal trend was no longer significant while the other
355 covariates remained the same. Finally, the LME also showed a high correlation (~ 0.85) among the
356 size of the individuals sampled within the same survey, and an increase in variance at larger sizes
357 (Table 5). Residuals and random effects did not show any patterns (Fig. S5).

358 3.3.2. *Loliginidae*

359 The DML was measured in a total of 378 individuals (288 and 90 during daylight and nighttime,
360 respectively). Compared to octopus, Loliginidae paralarvae varied largely in size (Table S10, Fig.
361 S6). Pooling all DML data together, the LME revealed that DML was slightly larger at the bottom

362 layer, and considerably larger at night. In addition, Loliginidae size decreased with poleward currents
363 (Table 6, Fig. 7a). Furthermore, body size slightly increased during the year (Fig. 7b). Finally, the
364 LME also showed a moderate correlation (~ 0.40) among the size of the individuals sampled within
365 the same survey, and an increase in variance at larger sizes (Table 6). Residuals and random effects
366 did not show any patterns (Fig. S8).

367 4. Discussion

368 4.1. Sampling method

369 Samples taken with a bongo net are not ideal to depict accurate variation in zooplankton
370 abundance across the water column (see further explanations on the sampling design in the
371 supplementary material). We are aware of this flaw, thus, to test for vertical differences we decided
372 to keep it simple and be conservative, therefore the water column was factorized in two strata to be
373 further included in the models. That said, we believe that for non-abundant organisms such as
374 cephalopod early stages the sampling design performed here suffices to provide insights about their
375 ecology and behaviour and derive valid inferences. A discussion on each of the specific findings
376 shown in this study follows.

377 4.2. Daytime paralarvae abundance

378 There is a large body of evidence of the environmental impacts on cephalopod populations and
379 commercial stocks. This research is largely based on analysing catch trends in relation to a suite of
380 environmental factors, for example, catches of *Illex argentinus* and *Ommastrephes bartramii* are
381 related to changes in subsurface temperature and chlorophyll fronts, respectively (Chen et al., 2007;
382 Ichii et al., 2011). Furthermore, other analyses rely on assessing indirectly the effects of
383 oceanographic conditions on the variability in recruitment, for instance, the changes in size of the
384 spawning areas affect the dynamics of *Todarodes pacificus* (Rosa et al., 2011). However, specific
385 studies focused on disentangling the environmental influence on the fate of early life phases are less
386 abundant. This is in part due to the low concentration of the paralarvae and their patchy distribution
387 (Boletzky, 2003). Despite these difficulties several works have related the variability in paralarval
388 abundance with oceanographic features such as upwelling conditions (e.g. Moreno et al., 2009; Otero
389 et al., 2009), or climatic phenomena such as El Niño (e.g. Zeidberg and Hamner, 2002). Typically,
390 paralarval research is largely descriptive (e.g. Vecchione et al., 2001). In some instances though, it
391 presents comparisons of abundances, for example, among water masses or seasons (e.g. Bower et al.,

1999; Crespi-Abril et al., 2014), or develops two-steps GLMs in order to deal with the high proportion of null samples (e.g. Moreno et al., 2009; Staaf et al., 2013).

Several approaches have been used to model zero-inflated ecological data (Martin et al., 2005), though these type of models are less frequent in marine ecology as compared to terrestrial ecology (but see Maunder and Punt, 2004; Minami et al., 2007 and references therein). In particular, abundance data of marine larvae has been commonly modelled using two-step models treating the presence/absence of larvae separately from positive larvae (e.g. Fox et al., 2000 for fish larvae; and Moreno et al., 2009 for cephalopod paralarvae). This assumes a distinction between the processes associated with the absence of larvae and those associated with positive catches. By contrast, zero-inflated models assume that the positive event might include zero and non-zero values, and this is conceptually more appropriate when the causes resulting in the presence of larvae are poorly understood and there is an interest in ascribing a process leading to the zero-valued observations (Martin et al., 2005; Minami et al., 2007). To this end, we focused here on determining the processes that causes the excess zero counts in cephalopod paralarvae from a benthic (*O. vulgaris*) and pelagic (Loliginidae) species.

In particular, we hypothesised that the probability of measuring a zero at daylight hours (i.e. binomial part of the ZI model) would be generated by spatio-temporal and subtidal water circulation related causes. On the one hand, in *O. vulgaris* the probability of false zeros decreased with increasing the day of the year. This result agrees with the well-known seasonality in spawning (Otero et al., 2007) and hatching (Otero et al., 2009) for the species in this region with a peak of paralarval abundance occurring at the end of the summer and autumn months. The higher probability of finding octopus paralarvae in fall was also common both in near (Portugal, Moreno et al., 2009) and distant (Japan, Sakaguchi et al., 1999) waters. On the other hand, we were more likely to catch loliginid paralarvae at elevated subtidal currents, meaning that (slower) water circulation might be responsible to catch failure of squids paralarvae. This could indicate that higher current speed would favour the

417 concentration of squid paralarvae in the Ría de Vigo and adjacent waters transported from close areas
418 along the coast. The importance and role of currents in paralarvae distribution have been illustrated in
419 detail for other squid species such as *Loligo reynaudii* in the South Africa's Agulhas Bank (Roberts
420 and Mullon, 2010). Common to both octopus and loliginid paralarvae we found that the probability
421 of false zeros during daytime was lower at the bottom layer as compared to the surface layer. This
422 would indicate that paralarval abundance of these species was higher at the bottom at least at daylight
423 hours and taking into account the sampling technique. If the water-column were to be properly
424 sampled using an opening/closing net the proportion of false zeros below the surface layer would be
425 presumably even lower.

426 A NB distribution instead of Poisson might be considered for the count part of the ZI model when
427 data are highly skewed with a heavy right tail (Minami et al., 2007) as was the case here (Fig. S1).
428 Model comparison for our data resulted in finding that the ZINB model provided a better fit for both
429 cephalopods than ZIP, or the corresponding NB and Poisson models, and even a two-step model
430 (Tables S4 and S7). Subtidal current direction exerted a positive effect on the expected counts of both
431 *O. vulgaris* and Loliginidae suggesting that catches of cephalopod paralarvae increased in the area
432 when the current flowed polewards. In addition, both paralarvae were also positively affected by
433 water temperature. These two conditions, warmer water flowing polewards, tend to occur during
434 relaxation and downwelling conditions (Herrera et al., 2008), suggesting that such a scenario would
435 favour the coastal concentration of the paralarvae, which concurs with earlier analyses (González et
436 al., 2005; Otero et al., 2009). The cross-shelf distribution of the larvae of multiple species in
437 upwelling areas depend on the water circulation patterns with most species remaining nearshore by
438 concentrating below the seaward flowing surface waters as shown for several crustaceans in northern
439 California (Morgan et al., 2009a). Similarly, the shelf-slope circulation in Portuguese waters is
440 determinant for the coastal retention of sardine eggs and larvae during the spawning period (Santos et
441 al., 2004). Regarding cephalopods, few analyses have assessed the effects of current patterns on the

442 fate of paralarvae distribution. Nonetheless, Roberts and Mullan (2010) illustrated the influence that
443 the water circulation has for the drift of chokka squid paralarvae off the South Africa's Agulhas
444 Bank.

445 Both paralarvae increased their abundances at low values of water column stability, and at high
446 thermal stability in the case of common octopus. Moreover, the expected catches of Loliginidae
447 decreased during the year as found in adjacent Portuguese waters (Moreno et al., 2009) and agreeing
448 with the intensive spawning season that occurs in winter and spring (Guerra and Rocha, 1994). It
449 should be noted that water-column stability patterns in this region tend to be seasonal with average
450 values decreasing during the year but with thermal stability peaking during summer and autumn
451 months. Thus, this might imply that stability and day of the year effects could be confounded.
452 However, comparison between paralarvae, that have roughly opposite cycles of abundance though a
453 similar response to water-column stability, may indicate that the effects on expected catches could be
454 distinguishable. At a shorter time scale, stability increases during relaxations and decreases during
455 strong upwelling or downwelling episodes (Pérez et al., 2000). Therefore, the expected elevated
456 catches at low values of N^2 but relatively high values of N_T^2 could be attributed to a relaxation or
457 weak to moderate downwelling scenario agreeing with the warmer temperature and subtidal current
458 direction effects. A less stable water-column was also found to positively influence plankton
459 dynamics in other areas such as larval richness in Chilean waters (Bustos et al., 2011).

460

461 4.3. *Diel vertical distribution*

462 Nocturnal ascent and diurnal descent in the water column is a common behaviour across
463 zooplankton species (Hays, 2003), and this diel vertical migration (DVM) has been attributed to more
464 efficiency in resource use or to avoidance of visual predators (Gliwicz, 1986). Moreover, the diel
465 cycle might be a mechanism that would favour the coastal retention in advective systems such as
466 upwelling regions as shown both in field observations (e.g. Morgan and Fisher, 2010) and through

467 biophysical modelling experiments (e.g. Marta-Almeida et al., 2006). Few information, however, is
468 available regarding cephalopod paralarvae (but see for instance Salman et al., 2003). Analyses of the
469 24h surveys showed here that *O. vulgaris* paralarvae concentrated in the surface at night being almost
470 absent from that layer during daylight hours. This fact suggests that this species moved up at night
471 and down during the day. However, due to the sampling protocol, we cannot accurately quantify the
472 differences in abundance across the water column (below the surface layer) at daylight sampling thus
473 we might be cautious when interpreting this result. In any case, these differences in abundance
474 between layers are consistent with those reported previously for the species in Japanese waters
475 (Takeda, 1990; Sakaguchi et al., 1999) and the Mediterranean Sea (Zaragoza et al., 2015). In contrast
476 to common octopus, the diel cycle was not evident for loliginids whose paralarvae were more
477 abundant in the bottom layer regardless of the sampling time. In addition, as they increased in size
478 the higher abundance in the bottom layer at night was more apparent. This result contrast with that
479 from Moreno et al. (2009) who reported a consistent DVM for loliginids in Portuguese waters. One
480 explanation could be the differences in sampling design and the non identification at the species level
481 in both studies that might lead to wrong conclusions.

482 Overall, the vertical behaviour of cephalopod paralarvae pretty much differs among species. On
483 the one hand, species of the benthic family Octopodidae can exhibit a broad suite of early life modes,
484 from a planktonic phase in *O. vulgaris* (this work) and *Macroctopus maorum* (Higgins et al., 2013),
485 to a holobenthic in *O. pallidus* (Higgins et al., 2013) or suprabenthic in *Enteroctopus megalocyathus*
486 (Ortiz et al., 2006). On the other hand, paralarvae of pelagic species of cephalopods also show
487 different distributions in the water column. For instance, DVM is not evident for several taxa of
488 gonatid squids (Bower and Takagi, 2004). Moreover, abundance varies with depth in *Doryteuthis*
489 *opalescens* (Zeidberg and Hamner, 2002) and *Todarodes pacificus* (Yamamoto et al., 2007)
490 paralarvae, however, differences between daytime and nighttime are not strongly apparent for both
491 species remaining in shallower waters regardless of the sampling period. *T. pacificus* paralarvae

gradually descend in the water column as they increase in size, though (Yamamoto et al., 2007). Therefore, DVM patterns in newly hatched cephalopods seem to be species-specific and related to ontogenic changes and ecological transformations (Shea and Vecchione, 2010). Notwithstanding, the vertical position of cephalopod paralarvae could be important for cross-shelf and along-shore transport. For instance, Martins et al. (2010) showed that –modelled– vertical distribution of chokka squid (*Loligo reynaudii*) paralarvae had strong implications for horizontal dispersal on the Agulhas Bank, South Africa.

4.4. Body size models

Developmental modes and reproductive strategies influence offspring body size, which in turn is a central trait for dispersal ability and distribution in marine invertebrates (Rundle et al., 2007). Whilst inhabiting the pelagic realm, organisms with planktonic stages (both planktotrophic and lecithotrophic) are subjected to active (e.g. response to settlement cues) and passive (e.g. current movements) factors that may determine their range size. Thus body size at hatching and larval duration would be linked to distribution determined in turn by the early life dispersion patterns. Environmental variability (O'Connor et al., 2007) and water circulation (Largier, 2003) would be the factors ultimately affecting dispersion.

Regarding cephalopods in particular, size at hatching is very variable and strongly depends on water temperature as shown for both *O. vulgaris* (Sakaguchi et al., 2002) and *L. vulgaris* (Moreno et al., 2012). However, the influence of circulation patterns on size distribution has been rarely addressed in field work. Despite all *O. vulgaris* individuals found here were recent hatchlings (every specimen counting 3 suckers per arm; Villanueva and Norman, 2008), the influence of the subtidal currents on the cross-shelf distribution of individuals of different body size was apparent. On average, larger individuals were found close to shore as transported by poleward currents during daylight, however, this pattern reversed at night finding larger individuals in the outer station. This,

517 combined with the inferred diel vertical migration displayed by the species, might suggest that
518 recently hatched octopus paralarvae would be maintained in a circulatory cell following the water
519 movements as hypothesised earlier (Rocha et al., 1999). By contrast, the squids sampled here varied
520 largely in age (see González et al., 2010) and consequently in size with a slight apparent trend
521 towards larger individuals during the year concurrent with the spawning period (Guerra and Rocha,
522 1994) and hatching peak (González et al., 2010). Despite the heterogeneous size distribution, it was
523 also detected a significant effect of the subtidal currents on the cross-shelf distribution of body size.
524 On average, larger individuals were found in the bottom layer at night and inversely related to the
525 poleward subtidal current, suggesting that younger squid paralarvae would be transported close to
526 shore. Notwithstanding, these conclusions should be taken with caution due to the sampling design,
527 the narrow spatial coverage, and the non-identification to the species level for loliginids that could
528 influence and bias the later results.

529 Compared to cephalopods, spatial trends in larval size have been commonly studied in several
530 other taxa. For instance, Santos et al. (2004) showed a cross-shelf and along-shore gradient in mean
531 length of sardine larvae with implications for coastal retention during a winter upwelling event in
532 Portuguese waters. Furthermore, multiple crustacean species in northern California typically remain
533 close to shore throughout development (Morgan et al., 2009a) with later effects for recruitment and
534 settlement (Morgan et al., 2009b,c).

535

536 4.5. *Cephalopod paralarvae within the context of marine larval ecology*

537 Population dynamics of marine organisms mostly depend on the fate of their early life stages.
538 Distribution, dispersal, and connectivity use to be a function of species-specific life history traits and
539 are capital for evolutionary stability and the persistence of species and communities (Cowen et al.,
540 2007; Bradbury et al., 2008). This also occurs for the molluscan class Cephalopoda which is a
541 diverse taxa with multiple developmental modes and reproductive strategies even within the same

542 family (e.g. Octopodidae, Villanueva and Norman, 2008). Upwelling regions tend to support some
543 of the largest fisheries worldwide. Early viewed as dispersive environments for the larval stages,
544 these systems are now considered more retentive areas than previously thought where the larvae are
545 capable to regulate their transport by exploiting the circulation patterns and later recruit close to their
546 natal habitats. This capacity of 'controlling' transport and dispersion is species-specific and depends
547 on multiple traits such as the vertical behaviour (Queiroga et al., 2007). Migration in the water
548 column is a key mechanism that contributes to the maintenance of the larvae close to shore despite
549 the strong circulation patterns during upwelling/downwelling. For instance, several crustacean larvae
550 in the Iberian (dos Santos et al., 2008) and Californian (Morgan et al., 2009a) upwelling systems
551 perform classic DVMs concentrating close to the bottom during daylight and thus facilitating onshore
552 transport by the undercurrent shoreward flow. Other species undertake reverse vertical migrations
553 that again favour coastal retention despite the two-layer upwelling dynamics (e.g. *Concholepas*
554 *concholepas* in Central Chile, Poulin et al., 2002). Furthermore, biophysical modelling experiments
555 also tend to point to DVMs as a mechanism for coastal retention (Marta-Almeida et al., 2006;
556 Martins et al., 2014; but see Carr et al., 2008). Besides early distinct distribution in the water column,
557 ontogenic vertical migratory behaviour could also serve as a mechanism contributing to cross-shore
558 distribution throughout development and later recruitment in upwelling areas (Carr et al., 2008;
559 Morgan et al., 2009a).

560 Although taken cautiously, we postulate here that common octopus paralarvae perform DVMs
561 and would be concentrated in the sampled area as transported by the bottom-layer poleward onshore
562 current during daytime. This mechanism would contribute to ameliorate *O. vulgaris* paralarvae
563 dispersal, at least during early development, despite the upwelling dynamics as suggested for the crab
564 *Carcinus maenas* in neighbouring waters (Queiroga et al., 2007), and other crustaceans elsewhere
565 (Morgan et al., 2009a). Note that for the dorsal mantle length range obtained here average swimming
566 speeds do not exceed 2.9 cm s^{-1} (Villanueva et al., 1996). By contrast, current velocity is higher than

that value (Souto et al., 2003). Therefore, in order to avoid going with the flow, paralarvae might perform DVMs to remain close to the coast. In support of the abundance pattern, it was also apparent an opposite diel cross-shore body size gradient. This circulation pattern would not exclude however the offshore advection of a certain number of individuals from the coastal pool throughout development as found by Moreno et al. (2009), or perhaps transported by upwelling filaments as shown for other organisms (Joint et al., 2001). Regarding Loliginidae we found that these paralarvae, in common with other studies (e.g. Moreno et al., 2009), spanned a wide size range with larger individuals occurring in the bottom layer during nighttime. Moreover, they were more abundant in the bottom layer regardless of the sampling time, and expected catches increased with the bottom layer poleward onshore current that transported small-sized individuals. These facts, may suggest that squids' paralarvae could perform ontogenic vertical migrations and would be subjected to seaward (landward) transport during prevailing downwelling (upwelling) conditions throughout development resembling the distribution patterns of certain crustaceans (Morgan et al., 2009a).

In summary our study provides an improvement on the knowledge of the oceanographic effects on the fate of cephalopod paralarvae in upwelling areas using appropriate modelling techniques to accommodate the sampling limitations. The approach, however, must serve as a framework to further develop the hypotheses suggested here mainly by means of improving the sampling design. It is crucial to increase the cross- and along-shore spatial coverage which would facilitate for testing the influence of specific upwelling-related mesoscale and sub-mesoscale structures such as the convergence front, that uses to move during relaxations (Castro et al., 1994), and other oceanographic features such as the lateral circulation (Souto et al., 2003) or the upwelling filaments (Joint et al., 2001). Moreover, the sampling methodology must change in order to effectively decompose the vertical distribution of the paralarvae into multiple strata during full day cycles. These two facts may lead, for instance, to find large octopus individuals strikingly not common in the area though frequently found in coastal waters elsewhere (Takeda, 1990; Sakaguchi et al., 1999).

592 Furthermore, the use of genetic techniques, that will facilitate the identification of loliginid species
593 and help to analyse the degree of self-recruitment, so as the development of biophysical models,
594 hardly used for studying early life stages of cephalopods (but see Martins et al., 2014), are urgently
595 needed in our region.

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860 **FIGURE CAPTIONS**

861 **Fig. 1.** Detailed map of the Ría de Vigo (Galicia, NE Atlantic) showing the sampling stations. T1 to
862 T5 show the plankton transects and the black dots indicate the CTD stations. Note that T1 was not
863 sampled in 2004 and 2005 and T5 was not sampled in 2003.

864

865 **Fig. 2.** Pooled environmental conditions during the plankton sampling during the years 2003 to 2005
866 at transect T4. (a) Values of the water column stability and stability due to temperature, (b)
867 temperature and (c) direction of the subtidal current in the surface and bottom layer. The rugs in
868 panel (c) indicate the sampling dates over the three years.

869

870 **Fig. 3.** *O. vulgaris* optimal model results. (a) Predicted probabilities of false zeros in the surface
871 (dotted line) and the bottom layer (solid line) as a function of the day of the year based on the
872 binomial part of the ZINB model. Predicted values based on the count part of the ZINB model as a
873 function of current direction (b), water layer temperature (c), water column stability (d), and water
874 column stability due to temperature (e). The count part panels depict the effect of each covariate
875 given the average values of the other covariates. Expected counts are standardised at 1000 m³ of
876 filtered water. Blue and red colours indicate water-layer and water-column covariates, respectively.
877 The rugs in panel (a) indicate the sampling dates. Note the scarcity of samples at the beginning and
878 end of the year that presumably prevents a resultant more cyclic pattern of the day of the year
879 covariate.

880

881 **Fig. 4.** Loliginidae optimal model results. Predicted probabilities of false zeros in the surface (dotted
882 line) and the bottom layer (solid line) as a function of current speed based on the binomial part of the
883 ZINB model (a). Predicted values based on the count part of the ZINB model as a function of the day
884 of the year (b), current direction (c), water column temperature (d), and water column stability (e).

885 The count part panels depict the effect of each covariate given the average values of the other
886 covariates. Expected counts are standardised at 1000 m³ of filtered water. Blue and red colours
887 indicate water-layer and water-column covariates, respectively. The rugs in panel (b) indicate the
888 sampling dates. As already noted, the scarcity of samples at the beginning and end of the year
889 presumably prevents a resultant more cyclic pattern of the day of the year covariate.

890

891 **Fig. 5.** Diel vertical behaviour. Predicted values ($\pm$ 95% CI) from models depicted in Table 4 in the
892 surface and bottom layers at daytime (open circles) and nighttime (filled circles) for *O. vulgaris* (a)
893 and Loliginidae (b) paralarvae sampled during the four day/night surveys. The insets in panel (b)
894 show the vertical behaviour for Loliginidae in two groups of body size, that is, below and above 2.5
895 mm of DML (see Fig. S7).

896

897 **Fig. 6.** *O. vulgaris* body size model results. (a) Relationship between the mantle area index (MAI)
898 and the subtidal current direction (CU_D) depending on the day and night sampling hours. (b) Seasonal
899 cycle of the mantle area index. Rugs in panel (b) show the sampling dates where it is apparent the
900 isolation of a data point in February. Plots represent the estimated effect and 95% pointwise
901 confidence interval while holding the other factors constant (Fox, 2003).

902

903 **Fig. 7.** Loliginidae body size model results. (a) Relationship between the ln-transformed dorsal
904 mantle length (DML) and the subtidal current direction (CU_D). (b) Time trend of the dorsal mantle
905 length. Rugs in panel (b) show the sampling dates. Plots represent the estimated effect and 95%
906 pointwise confidence interval while holding the other factors constant (Fox, 2003).

907 **Table 1** Summary of the different variables used in this study.

Variable	Abbreviation (units)	Description
CTD sampler		
Temperature	T (°C)	Average water column-integrated temperature (T_c), or average temperature of the surface and bottom layers (T_L)
Salinity	S	Average salinity of the surface and bottom layers
Density	ρ (kg m ⁻¹)	Average density of the surface and bottom layers
Fluorescence	F (mV)	Average fluorescence of the surface and bottom layers
Stability	N ² (min ⁻²)	Average water-column stability
Stability (temperature)	N _T ² (min ⁻²)	Average water-column stability due to temperature
Stability (salinity)	N _S ² (min ⁻²)	Average water-column stability due to salinity
Circulation model		
Direction	CU _D (°S–°N)	Modelled current direction of the surface and bottom layers
Speed	CU _S (cm s ⁻¹)	Modelled current speed of the surface and bottom layers
Other data		
Day of the Year	DoY (1 is the 1 st of January)	Day of the year when the sampling took place
Water-column layer	Layer	Categorical variable splitting surface (S) and bottom (B) sampling
Sampling time	Time	Categorical variable splitting daytime (D) and nighttime (N) sampling
Sampling transect	T	Categorical variable splitting sampling transects 1 to 5

908

909

910 **Table 2** Summary of the optimal Zero Inflated Negative Binomial (ZINB) model fitted to paralarval
 911 catches of *O. vulgaris*. Note that water volume was used as an offset in the count model. S.E.:
 912 Standard Error. Model selection is shown in Table S3.

Parameter	Estimate	S.E.	z-value	P-value
Count model coefficients				
Intercept	0.540	0.160	3.373	0.0007
CU_D	0.006	0.002	3.538	0.0004
T_L	0.260	0.077	3.393	0.0007
N^2	-0.893	0.214	-4.175	<0.0001
N_T^2	1.454	0.440	3.307	0.0009
Logistic model coefficients				
Intercept	3.369	0.789	4.271	<0.0001
$Layer_B$	-2.249	0.442	-5.086	<0.0001
DoY	-0.012	0.003	-3.572	0.0004

913

914 **Table 3** Summary of the optimal Zero Inflated Negative Binomial (ZINB) model fitted to paralarval
 915 catches of Loliginidae Note that water volume was used as an offset in the count model. S.E.:
 916 Standard Error. Model selection is shown in Table S6.

Parameter	Estimate	S.E.	z-value	P-value
Count model coefficients				
Intercept	1.305	0.401	3.256	0.0011
DoY	-0.005	0.002	-2.495	0.0126
CU _D	0.012	0.002	5.036	<0.0001
T _c	0.387	0.147	2.637	0.0084
N ²	-0.373	0.186	-2.005	0.0449
Logistic model coefficients				
Intercept	3.952	1.095	3.610	0.0003
Layer _B	-6.925	1.936	-3.578	0.0003
CU _s	-2.338	0.743	-3.145	0.0017

917

918 **Table 4** Results of a negative binomial GLM fitted to *O. vulgaris* and Loliginidae paralarval catches
 919 during the four day/night sampling days. Note that ln-transformed water volume was used as an
 920 offset in both models. S.E.: Standard Error.

Parameter	Estimate	S.E.	z-value	P-value
<i>O. vulgaris</i>				
Intercept	−0.432	0.472	−0.915	0.3603
Layer _B	1.760	0.576	3.059	0.0022
Time _N	3.616	0.561	6.445	<0.0001
Layer _B × Time _N	−4.157	0.739	−5.622	<0.0001
Loliginidae				
Intercept	−0.963	0.546	−1.765	0.0775
Layer _B	1.513	0.558	2.709	0.0067
Time _N	1.722	0.558	3.087	0.0020

921

922 **Table 5** Summary of the optimal linear mixed-effects model (LME) fitted to all MAI records of *O.*
923 *vulgaris* ($n = 584$ observations). See parameter abbreviations in Table 1. C.I. = Confidence Interval;
924 S.D. = Standard Deviation. Note that DoY was introduced in the model as an orthogonal polynomial
925 of degree 2. Residual analyses of this model are shown in Fig. S5.

Parameter	Estimate	95% C.I.	t-value	P-value
Fixed effects				
Intercept	2.368	2.263; 2.472	44.652	<0.0001
T3	-0.261	-0.362; -0.161	-5.125	<0.0001
T4	-0.193	-0.286; -0.100	-4.076	0.0001
T5	-0.097	-0.207; 0.013	-1.737	0.0829
Time _N	-0.231	-0.479; 0.017	-1.884	0.0672
DoY	-1.021	-2.535; 0.493	-1.365	0.1803
DoY ²	-1.760	-2.511; -1.009	-4.742	<0.0001
CU _D	0.001	0.0001; 0.002	2.309	0.0213
T3 × Time _N	0.462	0.293; 0.631	5.375	<0.0001
T4 × Time _N	0.114	-0.068; 0.295	1.233	0.2181
T5 × Time _N	0.214	0.031; 0.398	2.290	0.0224
CU _D × Time _N	-0.002	-0.004; -0.001	-2.593	0.0098
Random effects (S.D.)				
σ_a	0.199	0.147; 0.270		
σ	0.085	0.044; 0.166		
Variance function				
δ	0.550	0.254; 0.847		

926

927 **Table 6** Summary of the optimal linear mixed-effects model (LME) fitted to all ln-DML records of
 928 Loliginidae ($n = 378$ observations). See parameter abbreviations in Table 1. C.I. = Confidence
 929 Interval; S.D. = Standard Deviation. Residual analyses of this model are shown in Fig. S8.

Parameter	Estimate	95% C.I.	t-value	P-value
Fixed effects				
Intercept	0.667	0.517; 0.817	8.736	<0.0001
Layer _B	0.106	0.006; 0.206	2.079	0.0384
Time _N	0.190	0.070; 0.309	3.205	0.0027
DoY	0.001	-0.00002; 0.001	1.933	0.0603
CU _D	-0.001	-0.002; -0.0005	-3.542	0.0005
Random effects (S.D.)				
σ_a	0.073	0.037; 0.145		
σ	0.096	0.057; 0.162		
Variance function				
δ	1.164	0.600; 1.729		

930