

# High-frequency coastal upwelling events influence *Octopus vulgaris* larval dynamics on the NW Iberian shelf

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**ABSTRACT:** Planktonic larval dispersal affects the structure, management, and conservation of many fish and coastal invertebrate populations. The dynamics in coastal upwelling areas favour transport of larvae to the open ocean during upwelling episodes, and concentration of larvae in coastal waters under upwelling relaxation or downwelling conditions. Recent work provides evidence that pelagic larval stages in upwelling areas are influenced by specific larval behaviour, biogeography, and life history parameters among others. Nevertheless, very few of these studies have addressed these findings quantitatively. Here, we present a general approach for assessing the influence of high-frequency upwelling events on *Octopus vulgaris* planktonic larvae. Specifically, we analyse the rates of change in abundance and biomass of the *O. vulgaris* early larval phase in the NW Iberian coast, where upwelling events occur with a frequency of 10 to 20 d from April to September. Our analysis indicates that the increase in larval abundance and biomass is significantly correlated with the simultaneous decrease of water column integrated nitrate, ammonium and chlorophyll levels. These conditions occur during the early stage of the relaxation phase of coastal upwelling events, when nutrient salts are consumed to produce biogenic matter, which is retained in the system and transferred through the food web.

**KEY WORDS:** Larvae · Relaxation · Nutrients · Chlorophyll · NW Spain

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## INTRODUCTION

Coastal upwelling areas are fertilised by cold and nutrient-rich oceanic waters from 150 to 200 m depth in response to alongshore winds of variable intensity and persistence, depending on the latitude and the time of the year (Wooster et al. 1976). As a result of upwelled nutrients enhancing phytoplankton growth, coastal upwelling areas are among the most productive marine ecosystems and support most of the large fisheries (Pauly & Christensen 1995). Coastal areas commonly experience shifts in their environmental conditions that may alter the entire food web (e.g. Barth et al. 2007). Specifically, these shifts play a major role in controlling population dynamics in near-shore communities, mainly across taxa with pelagic larval

stages, through effects on (1) the dispersal and transport of these early-life phases and subsequently on (2) the variation in the supply of settling stages that ultimately define recruitment success (see review by Queiroga et al. 2007).

Many studies have examined the influence of coastal oceanography on meroplanktonic organisms with 'complex life cycles' (*sensu* Roughgarden et al. 1988). On the one hand, these studies consider that planktonic phases are transported to the open ocean during upwelling episodes, thus reducing settlement and recruitment (e.g. Connolly et al. 2001). On the other hand, the larvae are transported shoreward during downwelling episodes, thus, favouring recruitment (e.g. Farrell et al. 1991). These studies assume that larval phases behave like passive particles being swept

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offshore (onshore) during upwelling (downwelling) periods, given that swimming speeds are much lower than flow rates in the Ekman layer. However, recent work shows that larval behaviour (e.g. diel vertical migrations) plays an important role in controlling across-shore transport, and suggest that upwelling areas could be retentive rather than dispersive environments for certain species such as *Carcinus maenas* in the Iberian upwelling system (Marta-Almeida et al. 2006) or *Concholepas concholepas* in the Iberian (Marta-Almeida et al. 2006) and Chilean (Poulin et al. 2002) upwelling systems. Thus, transport, supply and settlement of invertebrate larvae will depend on a dynamic interplay between life history attributes, pelagic larval phase behaviour, and environmental conditions (Shanks & Brink 2005, Yannicelli et al. 2006, Bradbury et al. 2008).

Galicia (Fig. 1) is at the northern boundary of the Iberian upwelling system. Coastal winds at these latitudes ( $42^{\circ}$  to  $44^{\circ}$  N) are seasonal; northerly winds prevail from March–April to September–October, promoting coastal upwelling, and southerly winds predominate the rest of the year. However, >70% of the total variability in coastal winds occurs in periods of less than 1 mo, so that the upwelling season appears as a succession of wind-stress episodes separated by calm episodes, with a frequency of 10 to 20 d (Álvarez-Salgado et al. 2003), similar to other coastal upwelling systems at comparable latitudes (Hill et al. 1998). The

Ría de Vigo (Fig. 1) is a large coastal embayment that acts as an extension of the continental shelf during the upwelling season when continental runoff is scarce. The 2D positive residual circulation pattern (ingoing bottom current/outgoing surface current) responds to coastal winds at time scales ranging from a few hours to 2 d (Piedracoba et al. 2005). During the downwelling season, when continental runoff is high, the inner ría circulates as a positive estuary and the circulation of the outer ría reverses (outgoing bottom current/ingoing surface current) in response to the prevailing southerly winds (Álvarez-Salgado et al. 2009). Specific studies on the effects of upwelling and associated residual circulation on larval phases in Galician waters are lacking (but see González et al. 2005). Much more effort has been put into studying upwelling and tidal effects on several species in neighbouring areas, particularly Portugal (e.g. *Sardina pilchardus*: Santos et al. 2004, *Carcinus maenas*: Amaral et al. 2007, cirripede cyprid larvae: dos Santos et al. 2007).

In this work we attempt to quantify the effects of the wind stress/relaxation cycles induced in coastal upwelling areas on the changes in abundance and biomass of the *Octopus vulgaris* larval phase over a cross-shelf section off the Ría de Vigo (Fig. 1). The reproductive cycle of *O. vulgaris* in Galician waters appears to be tuned to the seasonality of upwelling. Spawning peaks in spring (Otero et al. 2007, Fig. 2a), embryonic development takes up to 4 mo, depending on water

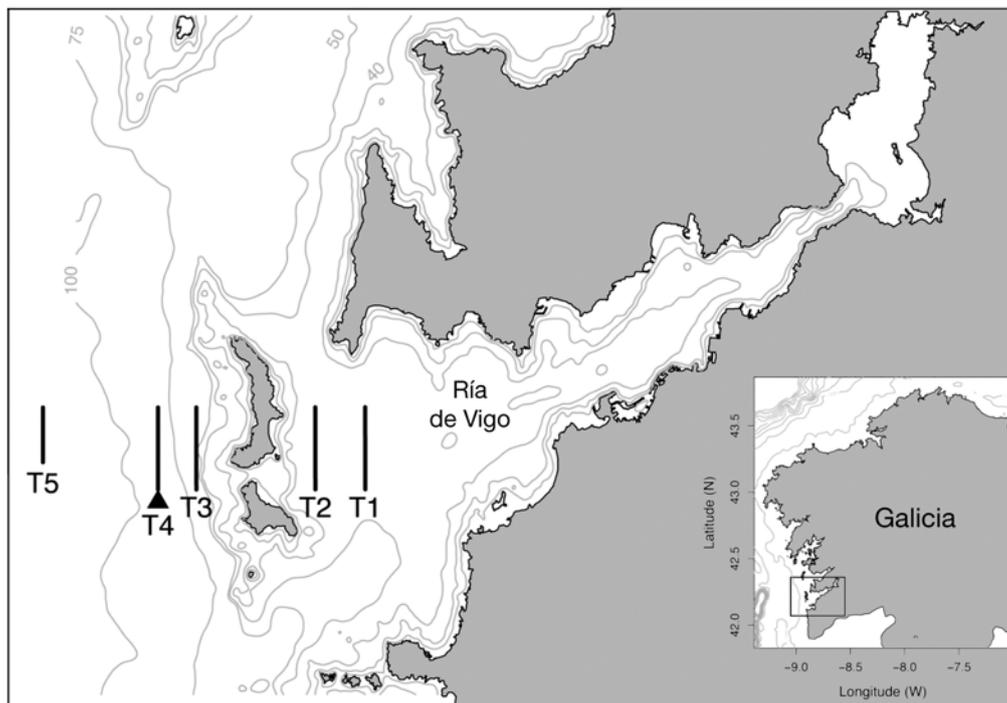


Fig. 1. Galicia, NW Spain. Ría de Vigo showing the sampling points. T1 to T5: plankton transects; (▲) rosette sampler station. Note that T1 was not sampled in 2004 and 2005 and T5 was not sampled in 2003

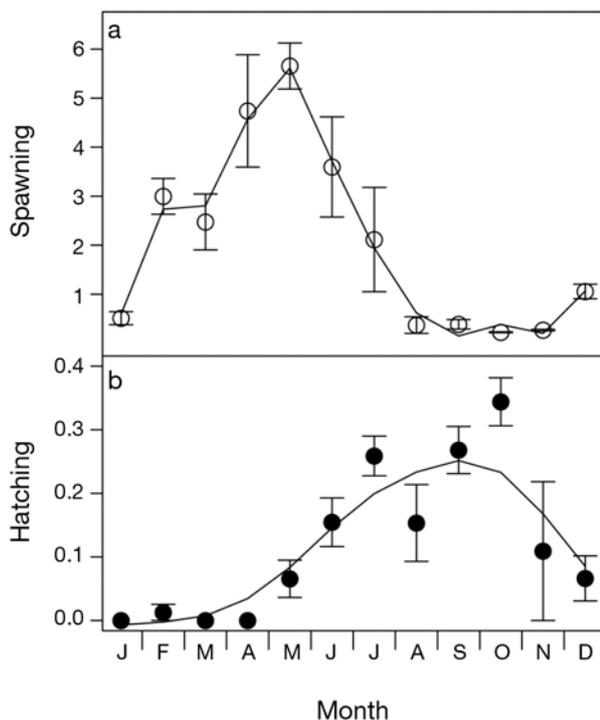


Fig. 2. *Octopus vulgaris*. Average (a) spawning and (b) hatching cycles in Galician waters. Spawning was measured by the gonadosomatic index of females (unitless) using data from Otero et al. (2007). Hatching was measured by the larval abundance ( $x$ ) standardised to the number of larvae per  $10^3 \text{ m}^3$  and  $\log x+1$  transformed using data from González et al. (2005) and this study. The trend is shown with the predicted curve from a generalised additive model. Error bars = SE

temperature (Katsanevakis & Verriopoulos 2006), and hatching peaks at the end of summer or the beginning of autumn (Fig. 2b). *Octopus* larvae (actually termed paralarvae, following Young & Harman 1988, but we use 'larvae' for simplicity) are estimated to stay in the water column up to 4 mo (dependent on water temperature; Katsanevakis & Verriopoulos 2006). Previous studies suggest a link between octopus pelagic larval abundance and upwelling in Galician waters (Rocha et al. 1999, González et al. 2005, Moreno et al. 2009); and Otero (2006) provides evidence that early stages are mostly present near the sea bottom during the day and near the surface during the night, as has also been described in Japanese waters (Takeda 1990, Sakaguchi et al. 1999). Recruitment is considered to occur during the following summer (Arnáiz 2006), and the bulk of that cohort will be harvested the following year. Based on this framework, Otero et al. (2008) hypothesise that in Galician waters, environmental factors related to upwelling have a major effect on the survival of the planktonic stages of *O. vulgaris*, setting the year class strength and largely driving interannual changes in yield.

The objective of this study was to examine the influence of high-frequency coastal upwelling events on dynamics in octopus hatchlings in near shore waters. Most of the previous quantitative studies relating larval abundance and oceanography have been conducted using organisms which possess a small-sized and abundant planktonic phase (e.g. barnacles and crabs), attempting to correlate abundance with, for instance, temperature, salinity and wind-stress; or comparing abundances among contrasting previously defined oceanographic conditions. In this work, we relate the rates of change in larval abundance between surveys with the rates of change in the hydrographic and chemical conditions of the water column. Our unique purpose in using this approach was to test the possibility to assess the increase (or decrease) of larval abundance and biomass associated with a specific oceanographic situation (spin-up or spin-down phases of upwelling or downwelling episodes) defined from the shifts in the hydrography of the water column, associated with the wind stress/relaxation cycles.

## MATERIAL AND METHODS

**Sampling regime.** Surveys ( $n = 47$ ; daytime = 43, nighttime = 4) to collect plankton and hydrographic samples were conducted onboard RV 'Mytilus' from 2003 to 2005 (Fig. 1). In 2003, we sampled from February to December, whereas in 2004 and 2005 sampling was restricted to May to October (Table 1).

**Plankton samples.** Zooplankton samples were collected from 4 transects parallel to the coast: T1, T2, T3 and T4 with average bottom depths of 36, 26, 68 and 85 m, respectively (Fig. 1). During the monthly surveys of 2003, larvae were not captured in T1, thus a deeper transect (T5, 110 m depth) was substituted for T1 in 2004 and 2005 (Fig. 1). Samples were taken by towing near-bottom and at the surface a 750 mm diameter bongo net of 375  $\mu\text{m}$  mesh. At a ship speed of 2 knots, the bongo net was lowered and stabilised near the bottom for 15 min and subsequently hauled up at  $0.5 \text{ m s}^{-1}$ . Then, it was cleaned and towed in the surface layer for another 15 min. The bongo net was equipped with a mechanical meter to record the water flow. Plankton samples were fixed onboard with 4% buffered formalin for 24 h, and preserved in 70% alcohol. Larvae were separated and later classified with reference to Sweeney et al. (1992) and to a larvae reference collection previously obtained from laboratory-reared specimens. The data were standardised to the number of larvae per  $10^3 \text{ m}^3$  and log-transformed before further analyses. A constant (+1) was added to include zero data.

Each octopus larva was placed on blotting paper to remove alcohol from the mantle cavity and body

Table 1. Values in each survey of the selected environmental covariates that entered the optimal model. See 'Results—Environmental variables' for abbreviations. Surveys 2 (27/03/03) and 5 (05/05/03) were not used due to problems with the rosette sampler; Surveys 24 (15/09/04), 30 (21/10/04), 34 (18/07/05) and 41 (26/09/05) were performed during the night and are not included in this study

Survey	Date (dd/mm/yy)	NO <sub>3i</sub> ( $\mu\text{mol kg}^{-1}$ )	NH <sub>4i</sub> ( $\mu\text{mol kg}^{-1}$ )	Chl <sub>i</sub> ( $\mu\text{g l}^{-1}$ )
1	13/02/03	7.21	0.48	0.75
3	10/04/03	3.25	0.09	2.15
4	21/04/03	2.19	0.97	1.07
6	26/05/03	7.82	0.33	1.21
7	05/06/03	5.34	0.81	2.30
8	02/07/03	5.40	1.05	1.38
9	21/07/03	8.32	0.36	3.99
10	19/08/03	7.30	0.28	1.10
11	04/09/03	6.63	0.72	1.08
12	25/09/03	7.22	0.46	0.57
13	08/10/03	8.44	0.54	0.27
14	23/10/03	5.73	0.36	1.61
15	11/12/03	5.73	0.25	0.50
16	27/05/04	5.40	0.52	2.52
17	10/06/04	6.56	0.65	2.12
18	17/06/04	5.98	0.37	0.78
19	23/06/04	4.41	0.34	2.12
20	02/07/04	5.02	0.38	1.73
21	09/07/04	9.60	0.21	1.31
22	16/07/04	9.81	0.24	2.05
23	08/09/04	7.71	1.25	3.50
25	15/09/04	9.43	0.81	0.77
26	22/09/04	10.38	0.22	1.37
27	08/10/04	9.43	0.10	0.89
28	15/10/04	4.98	1.00	0.45
29	21/10/04	2.58	1.22	1.31
31	12/07/05	5.44	0.25	9.45
32	14/07/05	9.35	0.21	4.76
33	18/07/05	6.48	0.26	1.76
35	21/07/05	7.88	0.31	3.32
36	26/07/05	6.49	0.75	1.86
37	28/07/05	3.89	1.68	2.31
38	20/09/05	8.50	0.30	3.38
39	22/09/05	8.62	0.66	2.63
40	26/09/05	6.89	0.44	2.19
42	29/09/05	9.03	0.51	1.11
43	04/10/05	10.06	0.61	2.02
44	06/10/05	11.77	0.30	0.54
45	11/10/05	11.21	0.43	1.88
46	13/10/05	5.95	0.69	1.97

weight (BW) determined on a Sartorius MC-210-P microbalance to the nearest 0.01 mg. The dorsal mantle length (DML) and mantle width (MW) of each larva was recorded to the nearest 0.001  $\mu\text{m}$  using the software Eclipsenet 1.20 (Laboratory Imaging s.r.o. for Nikon B.V.) on a PC (Asus) connected to a digital camera (Nikon DXM1200F) on a dissecting microscope (Nikon SMZ800). Individuals deformed during collection (e.g. those with damaged or inverted mantles) were not measured.

**Hydrographic samples.** A rosette sampler with twelve 10 l Niskin bottles was deployed at the southern

end of Transect T4 (85 m depth; Fig. 1). Salinity and temperature were recorded with a Seabird 9/11 CTD probe attached to the sampler, also equipped with a WetLabs ECO FL fluorometer and a Seatech transmissometer. Conductivity measurements were converted into practical salinity scale values with the equation of UNESCO (1986). Seawater samples for the analysis of dissolved oxygen, nutrient salts, and chlorophyll were taken from 5, 15, 30, 50, 70 and 80 m.

To analyse dissolved oxygen ( $\text{O}_2$ ) water was collected in calibrated 110 ml glass flasks. After fixation, they were kept in the dark until analysis in the laboratory 24 h later.  $\text{O}_2$  was determined by Winkler potentiometric endpoint titration using a Titrimo 720 analyser (Metrohm) with a precision of  $\pm 0.5 \mu\text{mol kg}^{-1}$ . The apparent oxygen utilisation,  $\text{AOU} = \text{O}_{2\text{sat}} - \text{O}_2$ , was calculated using the algorithm proposed by Benson & Krause (UNESCO 1986) for oxygen saturation ( $\text{O}_{2\text{sat}}$ ).

Water samples for nutrient salt analysis were collected in 50 ml polyethylene bottles. They were frozen ( $-20^\circ\text{C}$ ) until segmented flow analysis in the laboratory. The precision is  $\pm 0.02 \mu\text{mol kg}^{-1}$  for nitrite ( $\text{NO}_2^-$ ),  $\pm 0.1 \mu\text{mol kg}^{-1}$  for nitrate ( $\text{NO}_3^-$ ),  $\pm 0.05 \mu\text{mol kg}^{-1}$  for ammonium ( $\text{NH}_4^+$ ),  $\pm 0.02 \mu\text{mol kg}^{-1}$  for phosphate ( $\text{HPO}_4^{2-}$ ) and  $\pm 0.05 \mu\text{mol kg}^{-1}$  for silicate ( $\text{SiO}_4\text{H}_4$ ) (Álvarez-Salgado et al. 2006).

The chlorophyll-a (chl a) of 100 to 200 ml of each water sample was retained on a GF/F filter that was immediately frozen ( $-20^\circ\text{C}$ ) until analysis in the laboratory. Chl a concentration was determined with a Turner Designs 10000R fluorometer after 90% acetone extraction (Yentsch & Menzel 1963). The precision is  $\pm 0.05 \mu\text{g l}^{-1}$ .

**Statistical analysis.** The purpose of this study was to evaluate the changes in larval abundance and biomass arising from shifts in the hydrography of the water column. We tested different generalised linear models built up considering the pairs of surveys separated  $\leq 20$  d, given that upwelling episodes, separated by wind calms, occur with a frequency of 10 to 20 d in this area (see 'Introduction'). Therefore, we computed the rate of change in average larval abundance ( $A$ ) and biomass ( $B$ ) between surveys separated by up to 20 d as response variables. The same rates of change between surveys were computed for the independent selected hydrographic and chemical covariates as follows:

(1) The rate of change in average larval abundance was computed gathering all stations and strata sampled during daylight surveys, i.e.  $\Delta A/\Delta t$ . The same approach was used to compute the rate of change in average larval biomass,  $B$ , i.e.  $\Delta B/\Delta t$ . Two biomass variables were estimated,  $B_1 = A_i \times \text{BW}_i$ , where  $A_i$  and  $\text{BW}_i$  are the average larval abundance and average body weight in each station and strata sampled, respectively; and  $B_2 = A_i \times \text{MAI}_i$ , where  $\text{MAI}_i$  is the

average mantle area index (i.e. MAI = DML × MW [mm<sup>2</sup>]) according to Sakaguchi et al. (2002), in each station and strata sampled.

(2) The thermohaline and chemical variables in the study area, as in other coastal upwelling systems, are not mutually independent: the cold and salty upwelled waters are relatively nutrient rich and oxygen poor (Álvarez-Salgado et al. 2002). This could lead to models that are redundant and difficult to interpret. To identify candidate variables to introduce into the models, a principal component analysis (PCA) based on the correlation matrix was applied to the hydrographic data: temperature (Temp), salinity (Sal), apparent oxygen utilisation (AOU), nitrate (NO<sub>3</sub>), nitrite (NO<sub>2</sub>), phosphate (PO<sub>4</sub>), silicate (SiO<sub>4</sub>), ammonium (NH<sub>4</sub>) and chlorophyll *a* (chl *a*). Three principal components (PCs) interpretable from the environmental point of view were selected. Based on this result, the 3 hydrographic variables highly related with each PC were extracted to compute candidate covariates and their rates of change (see 'Results — Environmental variables').

Akaike's information criterion (AIC) was used to select the optimal model. Large variability in the increase or decrease in abundance and biomass could be more plausible within surveys separated by few days (explained by for example, a high hatching rate in a given day or larval sweeping due to rapid water movement) leading to models with heterogeneity of variance. To take 'time' into account, data were grouped according to the number of days between 2 considered surveys as follows: surveys separated by ≤7 d (Group 1); surveys separated by 7 to 14 d (Group 2); and surveys separated by >14 d (Group 3). Models were then fitted using Generalised Least Squares (GLS) that allow errors to have unequal variances for each group. Analyses were performed using R version 2.6.2 software (R Development Core Team 2008).

## RESULTS

### Distribution of the larvae

In general, octopus larvae were more abundant in the bottom layer and the outer transects (Fig. 3). However, for the purposes of this work we gathered the abundances of all stations and strata sampled during each survey. A detailed spatially explicit analysis will be presented in a separate paper.

### Environmental variables

Three straightforwardly interpretable PCs were extracted by the PCA (Fig. 4). AOU, silicate, phosphate

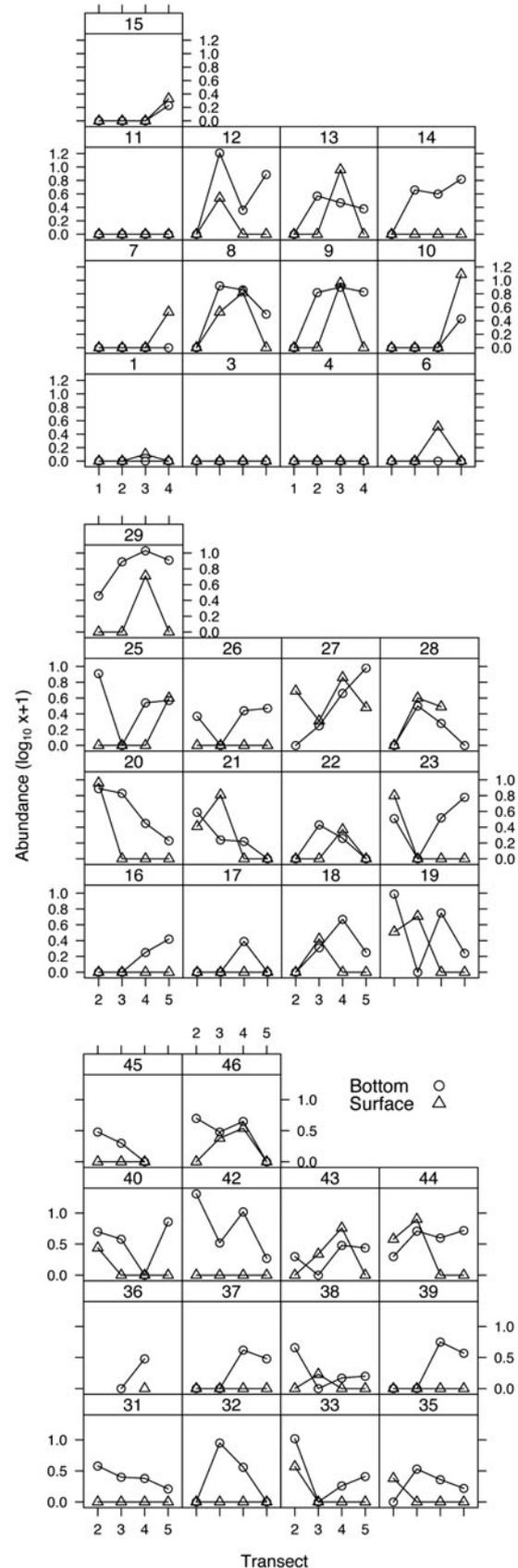


Fig. 3. *Octopus vulgaris*. Larval abundance (x, ind. per 10<sup>3</sup> m<sup>3</sup>) at surface and bottom in each plankton transect for each survey, grouped by year, as numbered in Table 1

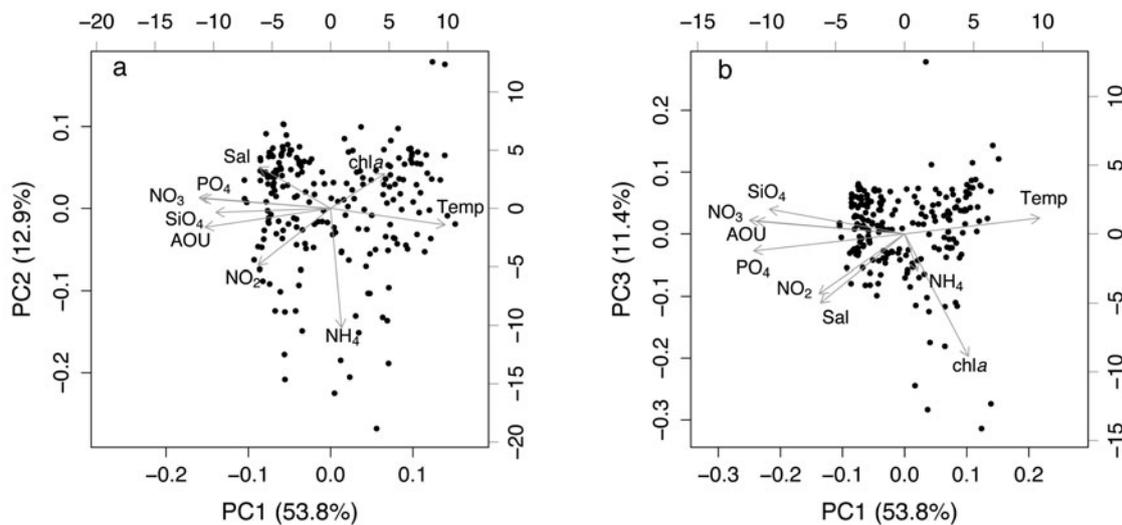


Fig. 4. PCA correlation biplots showing the loadings of each environmental variable (arrows) on the first 3 axes of variability. Points represent the scores of each individual observation. (a) PC1 versus PC2, and (b) PC1 versus PC3. See 'Materials and methods—Statistical analysis' for abbreviations

and, mainly, nitrate have strong negative loadings on PC1, and explain 53.8% of the variability. These variables are likely to be highly and positively correlated with each other, but negatively correlated with temperature, which has strong positive loading on this PC (Fig. 4a). Therefore, a negative (positive) score of an individual observation on PC1 can be used as an internal upwelling (downwelling) index (Rosón et al. 1995). PC2, which explains 12.9% of the variability, is highly represented by ammonium, the reduced form of nitrogen involved in fast recycling processes (Eppley & Peterson 1979). A negative PC2 score indicates *in situ* regeneration and a positive PC2 score *in situ* assimilation of nutrient salts (Fig. 4a). Finally, chlorophyll represents PC3, which explains 11.4% of the variability, pointing to the loss (positive scores) or accumulation (negative scores) of phytoplanktonic biomass (Fig. 4b). Since PC1, PC2, and PC3 show high correlations with nitrate, ammonium and chlorophyll, respectively, we decided to use these 3 hydrographic variables to characterise upwelling/ downwelling, nutrient regeneration/ consumption, and phytoplankton biomass loss/accumulation, respectively.

Since nitrate, ammonium and chlorophyll were measured at several depths, derived covariates were introduced into the models. For nitrate, 2 covariates were defined: bottom nitrate concentration ( $\text{NO}_{3b}$ ), and average nitrate concentration in the water column

( $\text{NO}_{3i}$ ); that can be used as an indicator of new production (i.e. the production supported by the nutrients transported by upwelling; Eppley & Peterson 1979, Álvarez-Salgado et al. 1996). For ammonium, the same covariates were chosen: bottom ammonium concentration ( $\text{NH}_{4b}$ ); and average ammonium concentration in the water column ( $\text{NH}_{4i}$ ); that can be used as an indicator of regenerated production (i.e. the production supported by autochthonous nutrients; Eppley & Peterson 1979). For chlorophyll, the average chlorophyll concentration in the water column ( $\text{chl}_i$ ) was chosen, which can be used as an indicator of the retention/loss of phytoplanktonic biomass. Values of the covariates (Table 1) are within the ranges normally found in this area (Álvarez-Salgado et al. 2009), however, some covariates were highly skewed due to the presence of

Table 2. Estimated parameters for the optimal abundance model fitted by generalised least squares (GLS). Dependent variable is the rate of change in abundance (see 'Materials and methods—Statistical analysis'); and covariates are the rates of change in  $\text{NO}_{3i}$ ,  $\text{NH}_{4i}$  and  $\text{Chl}_i$  (water-column averaged nitrate [ $\mu\text{mol kg}^{-1}$ ], ammonium, [ $\mu\text{mol kg}^{-1}$ ] and  $\text{chl a}$  [ $\mu\text{g l}^{-1}$ ], respectively). Model AIC is included, and AICs of  $B_1$  and biomass models  $B_2$ , respectively are also shown in parenthesis.

Parameter	Estimate	95% CI	<i>t</i>	<i>p</i>
Intercept	0.0018	-0.0018, 0.0054	1.0034	0.3198
$\text{NO}_{3i}$	-0.0796	-0.1066, -0.0527	-5.9104	<0.0001
$\text{NH}_{4i}$	-0.0654	-0.093, -0.0377	-4.7281	<0.0001
$\text{Chl}_i$	-0.0818	-0.1089, -0.0547	-6.0479	<0.0001
Variance function (different SD per group): 2.1233 (1); 1 (2); 0.7702 (3)				
N = 63; Residual SE = 0.0112				
AIC = -308.55 (-291.99); -274.75 (-260.81); -296.29 (-283.17)				

extreme outliers, thus, they were transformed accordingly. All covariates were standardised to  $N(0,1)$  before computing rates of change.

### Parametric models

The AIC criterion used to choose an optimal formulation suggested selecting a model having different variances for each group fitted by GLS. Table 2 summarises the selected model for the larval abundance; and the observed vs. predicted scatter plot derived from the GLS model is presented in Fig. 5. Three covariates should be retained to model both larval abundance and biomass. According to the model, abundance and biomass increases when the concentrations of water column average nitrate ( $\text{NO}_{3i}$ ), ammonium ( $\text{NH}_{4i}$ ) and chlorophyll ( $\text{Chl } a_i$ ) decrease. In addition, as expected, largest residual variance was at Group 1 (i.e. surveys separated by  $\leq 7$  d). It is worth noting, for example, that within 9 d (Surveys 43 to 46, Fig. 3) 2 major increases and 1 decrease in abundance took place. Nevertheless, removing these surveys from the analyses lead to the same results (Fig. 5). Finally, major departures from normality or differences in variability in each group were not observed on any plot of the standardized residuals.

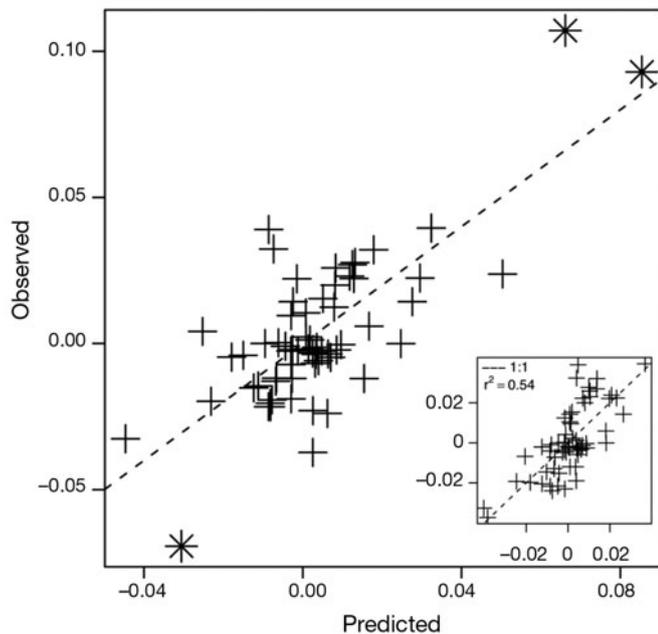


Fig. 5. Observed vs. fitted values for the optimal abundance GLS model summarised in Table 2 ( $\text{obs} = -0.0005 + 1.001 \text{ pred}$ ;  $r^2 = 0.57$ ;  $p = 9.75e - 13$ ). The 1:1 line is also shown. The inset shows the observed vs. predicted values for a model (fitted with GLS using the same predictors and different variances for each group, and including 2 interactions,  $\text{NO}_{3i} \times \text{NH}_{4i}$  and  $\text{NO}_{3i} \times \text{Chl}_i$ ) omitting the points indicated with asterisks in the main plot (see 'Results—Models')

## DISCUSSION

Pelagic egg and/or larval phases of many coastal marine organisms undergo dispersal from a spawning source, facing numerous oceanographic features and high mortality before settlement in a different site. Transport of early life stages over a given distance is considered a key factor for population dynamics and their connectivity, genetic structure, and biogeography (Cowen et al. 2007). Mesoscale physical processes, such as upwelling and downwelling, have long been recognised as a cause of variation in larval supply. However, the premise of offshore transport by upwelling cannot be invoked without a specific sampling program (Shanks & Brink 2005). In this sense, recent studies have suggested different mechanisms that larvae may use to avoid offshore sweeping, including vertical migration (e.g. Ma et al. 2006) or the possession of sensory systems (e.g. smell, Gerlach et al. 2007).

Our results show that *Octopus vulgaris* average larval abundance and biomass is higher when the nitrate, ammonium and chlorophyll in shelf waters off the Ría Vigo (NW Iberian upwelling system) decrease. A decrease of nitrate is associated with the relaxation, or spin-down phase, of an upwelling episode. It indicates that the nitrate-rich and ammonium-poor Eastern North Atlantic Central Water (ENACW) upwelled from 150 to 200 m depth to fertilise the rías of the NW Iberian shelf during the spin-up phase of upwelling episodes returns to its original depth (Rosón et al. 1995). A decrease in the water-column ammonium concentration occurs at the early stage of an upwelling relaxation, when the net ecosystem metabolism is favourable to nutrient assimilation rather than regeneration (Álvarez-Salgado et al. 1996). As a result, a net increase of biomass susceptible to be transferred to higher trophic levels occurs. On the other hand, nutrient regeneration is the dominant process during the late phase of upwelling relaxations (Álvarez-Salgado et al. 1996). A decrease in the water-column chlorophyll concentration in the early stage of an upwelling relaxation should be interpreted in this context as an evidence of the transference of phytoplankton biomass to higher trophic levels mediated by zooplankton grazing (Slaughter et al. 2006). Finally, variability appears to be higher when considering short time-periods. All the processes invoked above are driven by the prevailing wind-forcing in the area, but direct relationships with measured upwelling are not immediate, often weak and complex, involving time-lags (e.g. Pérez et al. 2000) and other factors such as topography and materials coming from the coast (e.g. Herrera et al. 2008).

Upwelling relaxation is thought to have 2 effects on larval dynamics: (1) it allows phytoplankton growth and increased concentration at the expense of the nutrients

upwelled during the dispersive spin-up phase (Zimmerman et al. 1987, Álvarez-Salgado et al. 1996), subsequently allowing zooplankton growth, on which octopus larvae feed; and (2) it reduces larval transport to the adjacent ocean (e.g. Peterman & Bradford 1987). Therefore, as has been described elsewhere, upwelling does not necessarily lead to offshore transport of larvae. Mechanisms involved in the maintenance of larvae in coastal waters should then be related to the vertical distribution of the larvae in the water column and the surface- and deeper-layer flows. Consistent with these processes we suggest that octopus larvae take advantage of the landward flow of the deeper layer during upwelling events (Souto et al. 2003) in combination with their capacity for performing diel vertical migrations (Otero 2006). In neighbouring Portuguese waters, subjected to similar upwelling regimes, 3D numerical modelling showed that near-shore larval retention is enhanced when simulated *Carcinus maenas* larvae perform vertical migrations synchronised with the diel cycle (Marta-Almeida et al. 2006). Slow-swimming bivalve larvae can, as well, remain near the coast despite upwelling and downwelling episodes (Shanks & Brink 2005); and Poulin et al. (2002) demonstrated the non-offshore transport during upwelling of competent migratory larvae of the gastropod *Concholepas concholepas* in Chilean coastal waters.

The variability not accounted for by the model may be attributable to other abiotic factors such as water circulation; biotic features, e.g. predation, other interactions or variations in the spawning biomass between and within a year; and/or under sampling of the water column (however, it should be noted that models using only data from the bottom layer gave the same result). On the other hand, part of the variation in the cross-shelf abundance is possibly due to along-shore larval drift as a result of the lateral circulation (Souto et al. 2003). However, this effect should be balanced between the southward and northward flows associated with upwelling, downwelling and the topography of the ría, thus, being the abundances consistent in the cross-shore direction. Unfortunately, along-shore information on larval abundance is non-existent. Spatial analysis of larvae and the investigation of their origin and hatching dates are beyond the scope of this work and do need complementary approaches such as genetic analysis and/or the use of Individual Based Models (IBMs).

The same model result was obtained when considering the size of the larvae, suggesting that size does not have a significant influence on dispersal, at least at the measured ranges—we assumed that all specimens captured were early hatchlings ( $\leq 10$  day old) according to measured sizes (range 2.48 to 0.96 mm DML) and that each had 3 suckers per arm (Villanueva 1995). Low sample abundances, patchy distribution, and absence

of large individuals are common features of cephalopod larval studies (e.g. Zeidberg & Hamner 2002). These suggest the possible existence of a threshold size determining high movement capacity and/or the ability to avoid the plankton nets by larger specimens.

On a seasonal time-scale, the reproductive cycle of *Octopus vulgaris* is coupled with the seasonality of wind-driven upwelling in this area (Otero et al. 2007; Fig. 2). The same hatching peak has been observed for a broader area of the western Iberia (Moreno et al. 2009), and even in Japanese waters (Sakaguchi et al. 1999). Apart from the coupling with seasonality, our analysis suggests that high frequency variability in environmental abiotic factors may play an important role in the dynamics of the early life stage of *O. vulgaris* and we believe that this bottom-up effect would affect the population structure of *O. vulgaris* in the NW Iberian upwelling system.

We conclude, therefore, that *Octopus vulgaris* larvae in Galician waters are more abundant during the relaxation phase of an upwelling event, and that the residual circulation pattern of the ría (dependent on coastal winds), and the migratory behaviour of the larvae, could be responsible for the retention of the larvae near the coast. *O. vulgaris* is a coastal species whose populations tend to be abundant in the waters of the studied area, thus, a non-offshore-swept planktonic phase makes sense. This could point, to some extent, to the occurrence of self-recruitment, a phenomenon more common than previously thought, surprisingly even at relatively small spatial scales (Pineda et al. 2007).

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