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Growth and survival of the winged oyster *Pteria colymbus* in suspended culture: influence of environmental factors associated to upwelling periods

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Abstract The present study examines the influence that environmental variables exerted on changes in condition index (CI), shell height (SH—dorsal-ventral axis) and soft tissue mass increments (STM) of the winged oyster *Pteria colymbus* in suspended culture during periods of upwelling (December to April) and non-upwelling (August to November) in the Cariaco Gulf, northeastern Venezuela. Environmental variables recorded between April 2012 and May 2013 included seston, water transparency, temperature, dissolved oxygen, chlorophyll *a* (Chl *a*) and the upwelling index (UI). Individuals were cultivated in lantern nets with an overall density of 56 individuals/0.123 m^2. From three randomly chosen baskets, five individuals were sampled each month and changes in CI, STM and SH were related to the environmental variables using Spearman correlation and PCA. Results show that during upwelling, both Chl *a* and UI presented a positive and significant relationship with the oyster condition and growth parameters. During non-upwelling (low UI), this relationship was inverse, demonstrating the important influence of upwelling and non-upwelling periods on the ecophysiology of the species. Furthermore, it was shown that the non-upwelling, characterized by high temperatures and low food availability, is a critical period for *P. colymbus*,

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judging by a decrease in growth and survival rate. Nonetheless, this species reached 50 mm in 5 months, a size considered as commercially viable, suggesting that the study area is favourable to the cultivation of the winged oyster despite a dramatic decrease in upwelling intensity in the last decade.

Keywords Condition index · Growth · Pearl oyster · Suspended culture · Upwelling period

Introduction

Aside from their ecological importance as primary consumers, bivalve mollusc fisheries are of economic importance throughout the South Caribbean. Oysters, pen shell, mussels, scallops and other bivalve species have high market demand there (Lodeiros and Freites 2008; Velasco and Barros 2008). In particular, the Pteriidae family attracts great interest due to their ability to produce pearls naturally or in aquaculture and the quality of the meat of some species (Rodríguez et al. 2005; Saucedo et al. 2005; Lodeiros and Freites 2008; Lodeiros et al. 2011). The winged oyster *Pteria colymbus* (Röding 1798), also commonly known as the black oyster, Atlantic oyster or octocoral oyster, is a bivalve mollusc characterized by a "winged" shell, formed by an extension of the hinge out of the central body of the shell. Shell size of the adult individuals varies between 60 and 80 mm and is normally attached on octocorals in the subtidal zone from North Carolina to southern Brazil at water depths between 3 and 10 m (Díaz and Puyana 1994; Lodeiros et al. 1999a, b).

The world's most productive coastal ocean regions are distributed along eastern boundaries of ocean basins, where wind-induced upwelling drives nutrient influx and phytoplankton productivity in surface waters. The Southern Caribbean, and the NE Venezuelan coast in particular, is under the influence of coastal upwelling (Okuda et al. 1978). High nutrient concentrations in upwelled water can also stimulate phytoplankton productivity, and it has been hypothesized that upwelling and relaxation cycles can also deliver planktonic food to adult benthic filter feeders, which may positively influence their growth in the same region where the upwelling occurs (Menge et al. 1997a, b). The prevailing trade winds blow parallel with the coastline and the shelf topography, and favour year-round wind-induced coastal upwelling of nutrient-rich subtropical underwater in this region, with seasonal intensification between December and April (Richards 1960; Herrera and Febres-Ortega 1975; Muller-Karger and Aparicio-Castro 1994). This helps to maintain a highly productive ecosystem and considerable variability of environmental variables in the water column such as temperature and chlorophyll *a* (Okuda et al. 1978; Muller-Karger et al. 2013).

Analysis of long-term oceanographic observations from the CARIACO Ocean Time-Series program revealed that a secondary upwelling event occurs annually around June-July (Astor et al. 2003; Rueda-Roa and Muller-Karger 2013). Yet, the CARIACO project has further revealed that the upwelling intensity to surface waters decreased dramatically in 2004 due to a northward progression of the Intertropical Convergence Zone (Muller-Karger et al. 2013). Net primary production has declined with a shift in phytoplankton taxon to smaller species with no sign of recovery (Taylor et al. 2012). The implications of this regime shift on the growth and survival of commercially important bivalve molluscs in this increasingly economic-fragile region are poorly understood.

Costal upwelling has the potential to influence the structure of intertidal invertebrate populations and communities by enhancing productivity and thereby food supply and by influencing the transport and abundance of propagules (Xavier et al. 2007). In this way, the variability of temperature and other factors, particularly food availability (phytoplanktonic biomass), affects the physiological condition of many aquatic invertebrates (Lodeiros and Himmelman 1994). For instance, the growth and reproduction of organisms under cultivation have been shown to be significantly influenced by upwelling (Lodeiros and Himmelman 1999). Freites et al. (2003) showed that the non-upwelling period in NE Venezuelan, characterized by scarce availability of chlorophyll *a* and high temperature (≈27 °C), is a critical period for the growth and survival of the tropical scallop *Nodipecten nodosus*. However, Lodeiros et al. (2002) observed a slow but steady growth in young pearl oyster *Pinctada imbricata*, grown in the Cariaco Gulf (NE Venezuela), with little correlation between growth rates, food availability (phytoplankton abundance and seston) and temperature. They concluded that growth was independent of environmental factors.

The present study has extended a similar ecophysiological analysis to the bivalve mollusc *P. colymbus* under suspended culture in the Cariaco Gulf. We examine and report the influence of environmental variables generated by upwelling and non-upwelling periods on shell size, soft tissue mass and condition index increments. We find that, in agreement with *N. nodosus*, upwelling has a significant effect on the growth and survival of this species, despite the wider regional decline in upwelling intensity in recent years.

Materials and methods

Oyster culture experiment

This study was conducted from April 2012 to May 2013 at the Turpialito (Cariaco Gulf, NE Venezuela, 10° 27′ 30″ N, 64° 01′ 52″ W). The *P. colymbus* seeds were obtained from artificial collectors (sardine nets) in nearby Charagato Bay, Cubagua Island (10° 49′ 17″ N; 64° 09′ 40.42″ O). The oysters were transferred to Turpialito in insulated containers packed with moistened foam layers to maintain a cool environment and limit stress.

At the beginning of the experimental period, a pre-selection of the initial size of juveniles based on shell axis length was made to exclude very large or small specimens. The chosen individuals showed an initial size of the dorsal-ventral axis of 3.5 ± 0.2 cm. The juveniles were placed in five basket lantern nets, with mesh of Ø 0.5 cm and base area of 0.123 m^2, consisting of five levels within each basket. Initially, 56 oysters were placed in each level with an areal coverage of the bottom basket by each individual of 9.53 cm^2 and with a total coverage of the bottom basket of 40%.

The baskets were suspended on a 50-m-long line placed on the inner side of the bay at a maximum water depth of 2 m. Monthly, five individuals were sampled randomly from three of the five replicate baskets and transported to the laboratory of the Fisheries Biology Department, Oceanographic Institute of Venezuela, to be processed. The three baskets subsampled on each chosen were also chosen randomly. The number of live oysters in each basket was also recorded to determine the survival rate. Selected individuals were carefully cleaned of fouling fixed on the shells, and the fouling was then dried (60 °C for 48 h) and weighed. Size measurement of the shell height axis (SH) (maximum perpendicular distance from the umbo to the ventral edge) was made with a digital calliper. Soft tissues were then carefully dissected from each individual to obtain the mass of shell and soft tissues. All components were dehydrated in an oven (60 °C for 48 h) to obtain dry mass values with an uncertainty of 0.001 g. The dimensionless condition index (CI) of the oysters was then calculated as the ratio of dry meat weight to dry shell weight (Beninger and Lucas 1984). In accordance with standard practice, following each sampling occasion, all remaining individuals from each net were removed, cleaned and replaced randomly so that the coverage remained at 40% to prevent competition for space.

The degree of gonadal development was observed visually (qualitatively) taking into account the five stages of gonadal development previously established by O'Connor et al. (2003): inactive, pale gonad without white colour; developing I, gonad with whitish spots; developing II, gonad with more generalized whitish colour; ripe, gonad with dense and more turgid whitish colour; and spawned, flaccid gonad of dark colour. We calculated the gonadic index by adopting the system described by Heffernan et al. (1989). For each individual, we assigned a rank for gonadal development based on the visual inspection. Then, a gonad index was calculated for each date as the average rank for the individuals collected. A rank of 1 was assigned to the stage "developing I", 2 for "developing II", 3 for "ripe" and 0 for "spawned".

Environmental factors

Water temperature was monitored every 30 min in the experiment locality, using an electronic thermograph, with a precision of 0.01 °C (Sealog-Vemco). Water samples were taken using a Niskin bottle. One aliquot of each sample was carefully taken to avoid air bubbles for the determination of dissolved oxygen using the Winkler method within 6 h of sampling (detection limit 0.07 mg L^{-1}). Salinity was determined with an Atago refractometer, and water transparency (m) was estimated using a Secchi disc. Samples for phytoplankton biomass, determined as chlorophyll *a*, and total seston were transferred on board to an opaque plastic bottle. All samples were transported to the laboratory in isothermal containers. Thereafter, two 1 L replicates were pre-filtered (153 μm) to remove large particulate matter and zooplankton and then used to determine chlorophyll *a* and total particulate matter for each water depth. These samples were filtered on pre-combusted (450 °C for 4 h) and weighed GF/F 0.7-μm filters and rinsed with isotonic ammonium formate (0.5 M). Total dry matter was established as the weight measured after drying the filters to constant weight at 80 °C for 48 h. Particulate organic seston (Oses) corresponded to the weight loss after ignition at 450 °C for 4 h in a muffle furnace. Inorganic seston was determined by weight difference between total and organic seston. Phytoplankton abundance was estimated as chlorophyll *a* using the spectrophotometric method following Strickland and Parsons (1972).

On the northern coast of Venezuela, where the coastline is approximately parallel to the equator, the cross shore component of the Ekman transport can be described using the upwelling index (UI; $m^3\ s^{-1}\ km^{-1}$ of coastline). UI was calculated applying the formula described in Bowden (1983) and Lavin et al. (1991)

$$\mathrm{UI} = \frac{\tau}{f \cdot \rho_w} \cdot 10^3$$
$$\tau = \rho_a \cdot C_d \cdot \omega^2$$

where τ ($N\ m^{-2}$) is the along shore stress at 10 m above the sea surface calculated using the mean air density, ρ_a (1.22 kg m^{-3}), and wind velocity (ω, m s^{-1}) from a nearby weather station at Cumana airport, C_d is a dimensionless empirical drag coefficient (0.0014), ρ_w (1025 kg m^{-3}) is the mean water density and f (s^{-1}) is the Coriolis frequency, equal to $2\Omega\sin(\theta)$ where Ω is the angular velocity of Earth ($7.3 \times 10^{-5}\ s^{-1}$).

Statistical analysis

To evaluate the effect of environmental factors on oyster growth, CI, shell height and mass of soft tissues were compared to the mean for each environmental factor corresponding to the same period.

Principal component analysis (PCA) was performed as an exploratory method of graphic ordination (Chatfield and Collins 1980; Clarke and Warwick 2001). In order to determine whether association among variables changed during upwelling and non-upwelling, PCAs were done separately on data corresponding to $UI/10^3 \geq 1$ and $UI/10^3 < 1$ (hereafter $UI \geq 1$ and $UI < 1$). Analyses were performed using the statistical software R (R Core Team 2015).

Results

Environmental variables

Temperature showed notable temporal variability, with highest values of 27.4 ± 0.6 to 28.3 ± 0.8 °C recorded between mid-August to October 2012 and lowest temperatures of 23.9 ± 0.5 °C in April 2012 and 22.9 ± 0.4 °C in February 2013(Fig. 1a). Temperature showed an inverse relation with the UI (Fig. 1b), which presented low values (22.9 ± 0.3 °C) between January and April (upwelling season) and high values (>27.4 ± 0.6 °C) between August and October (low upwelling) when the water column was stratified.

The upwelling period was further characterized by changes in other variables (Fig. 1c–f). Chlorophyll *a* showed maximum values of 6.9 ± 1.1 and 8.5 ± 0.3 μg/L during the peak upwelling periods of April 2012 and May 2013, respectively. Low concentrations down to 0.7 ± 0.2 μg/L were observed in September 2012, including a sharp decrease in the last sampling month from 9.5 ± 0.3 μg/L (late April) to 3.2 ± 1.5 μg/L (mid-May). Total seston was dominated by the organic fraction. Higher values were observed during the first months of the study with a maximum of 23.5 ± 0.5 mg/L in July 2012, of which 18.2 ± 0.9 mg/L was organic. Organic seston remained stable from August 2012 at around 6 mg/L until the end of the study. Dissolved O_2 also showed large seasonal variation from minimum values of 4.9 ± 0.2 mg/L in September 2012 to maximum values 8.1 ± 0.5 mg/L in December 2012 (Fig. 1d). Oxygen remained elevated until completion of the study. As expected, the lowest water transparency corresponded to those periods of higher chlorophyll *a* and total seston (Fig. 1d), whilst highest transparency was associated with the lowest values of these variables.

Growth

Shell size in the dorsal-ventral (height) dimension showed almost a sustained increase throughout the study period (Fig. 2a). The dorsal-ventral axis increased from 35.2 ± 0.3 mm and culminated in a maximum length of 73.6 ± 1.8 mm. Shell mass (Fig. 2b) showed a similar steady growth during over the study period, from 1.66 g in April 2012 to 13.31 g in May 2013.

Soft tissue dry mass showed marked increases and decreases (Fig. 2c), with lowest values in the months of May 2012 (0.20 g), December 2012 (0.55 g) and May 2013 (1.11 g). Increases were observed in the periods of May to August 2012 and December 2012 to April 2013, achieving values of 1.25 and 2.30 g, respectively. The CI showed the same trends with the exception of the initial value. Highest CI was 16–18 in mid-July to August 2012 and

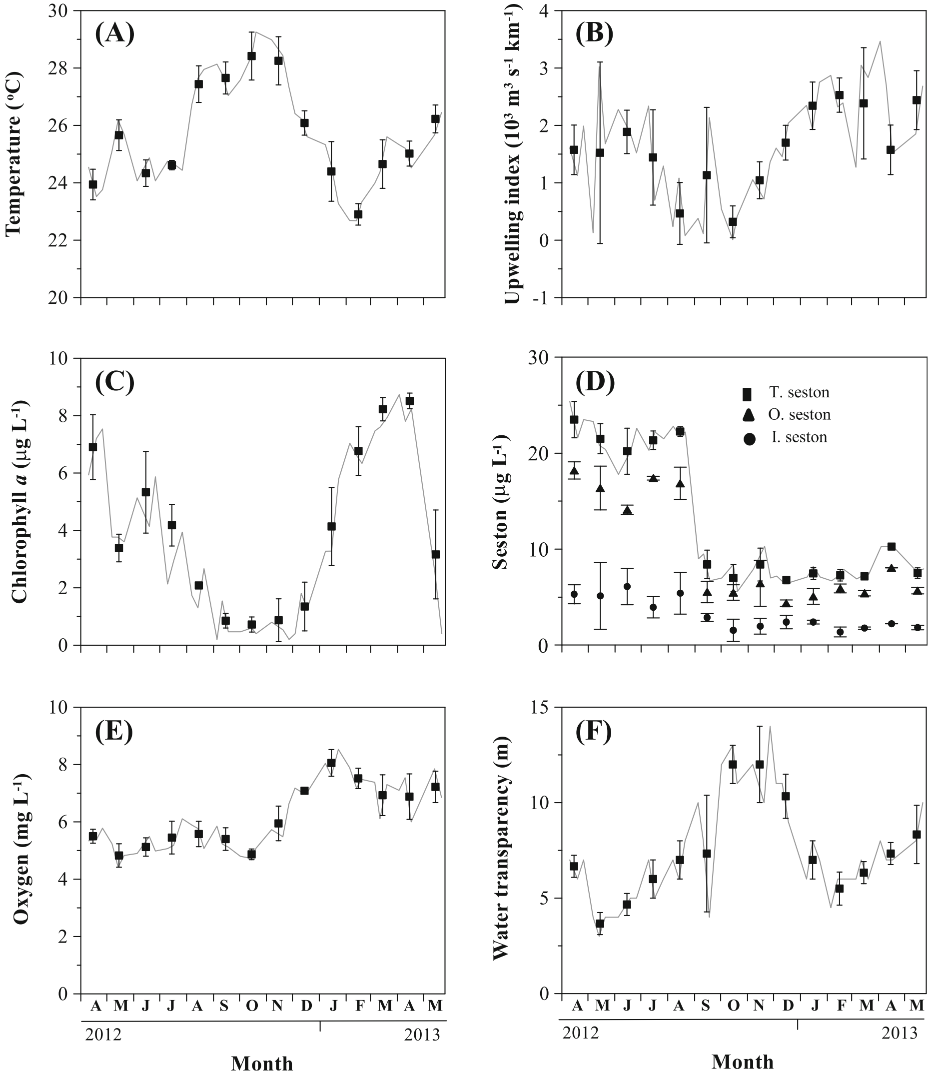

Fig. 1 Variation of environmental variables. **a** Temperature. **b** Upwelling index. **c** Chlorophyll *a*. **d** Seston (*squares*: total, *triangles*: organic; *circles*, inorganic). **e** Oxygen. **f** Water transparency during the experimental period. *Symbols* and *error bars* represent mean monthly values plus the standard deviation, respectively. The *grey lines* denote the measured data

mid-December 2012 to January 2013. Lowest CI was around 10–11 in mid-March to June 2013 and was >8 in the period from mid-November 2012 to mid-January 2013.

Gametogenic cycle and survival

The reproductive stages of *P. colymbus* reflected 4 months with a high percentage of spawning in May (2012) 80%, September 100%, December 100% and May (2013) 90%, all preceded by sexual maturity stages greater than 60% (Fig. 3).

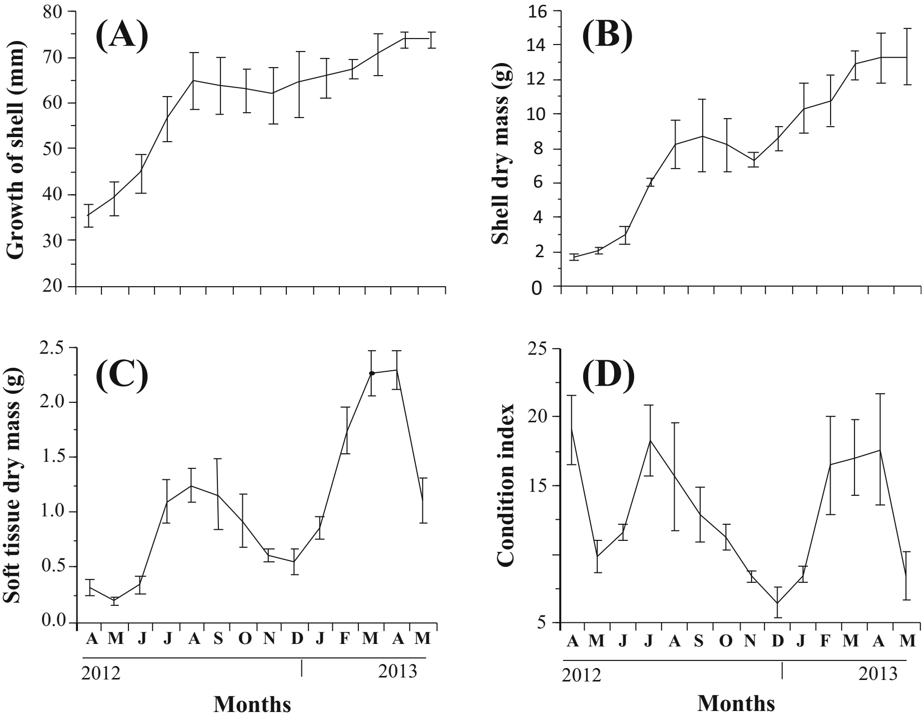

Fig. 2 Variation of different biometric variables of *Pteria colymbus*. **a** Growth of shell axis. **b** Shell dry mass. **c** Soft tissues dry mass. **d** Condition index, observed during the experimental period. *Symbols* and *error bars* represent mean monthly values plus the standard deviation, respectively

Oyster survival remained at 100% between April and August (Fig. 4), followed by a decrease from September to 94% in January 2013. This value was maintained until the end of the study period.

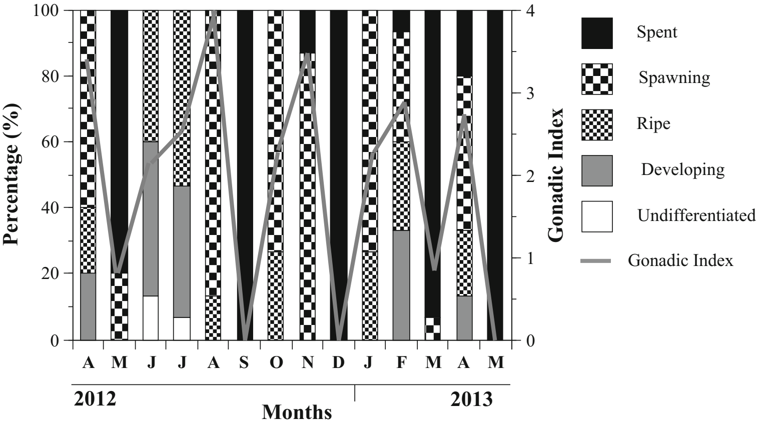

Fig. 3 Frequency of different reproductive stages of *Pteria colymbus*, observed during the experimental period

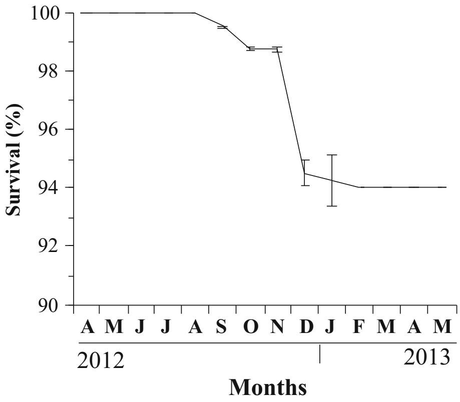

Fig. 4 Survival of *Pteria colymbus* observed during the experimental period. The *vertical bars* represent the standard deviations of the values

Influence of environmental variables on biometric variables

For the PCA during the period of low UI (UI ≤ 1), the first two components explained 73% of the variance (Table 1**)**. Further, chl *a*, organic seston, shell height, CI and soft tissue mass were more correlated with the first component, whilst showing an inverse relation with the UI and temperature (Fig. 5a). In contrast, for the data set associated with UI > 1, the first two components explained 74% of variance (Table 2). The bi-plot revealed possible associations between CI, soft tissue mass, UI and chl *a*, whilst showing an inverse relation with temperature (Fig. 5b).

Discussion

Few studies have demonstrated the influence of environmental variables generated by periods of upwelling and water column stratification (non-upwelling) on biometric variables of marine bivalves. Those available are mostly related to the impact on diversity, vertical distribution or abundance of various invertebrates, such as brachiopods (Kowalewski et al. 2002), octopus paralarvae (Vidal et al. 2010), bivalve larvae (Ma et al. 2006) and crab larvae (Marta-Almeida et al. 2006). Notably, Xavier et al. (2007) showed that upwelling influences the growth rate and maximum size of *Mytilus galloprovincialis* on the west coast of South Africa. In that

Table 1 Eigenvalues, variance percentage and accumulated variance percentage for each component of PCA analysis for the first data set (UI ≤ 1)

Component	Eigenvalue	Variance (%)	Cumulative (%)
1	3.73	53.25	53.25
2	1.38	19.75	73.00
3	0.86	12.33	85.33
4	0.57	8.10	93.42
5	0.39	5.57	98.99
6	0.07	0.92	99.91
7	0.01	0.09	100.00

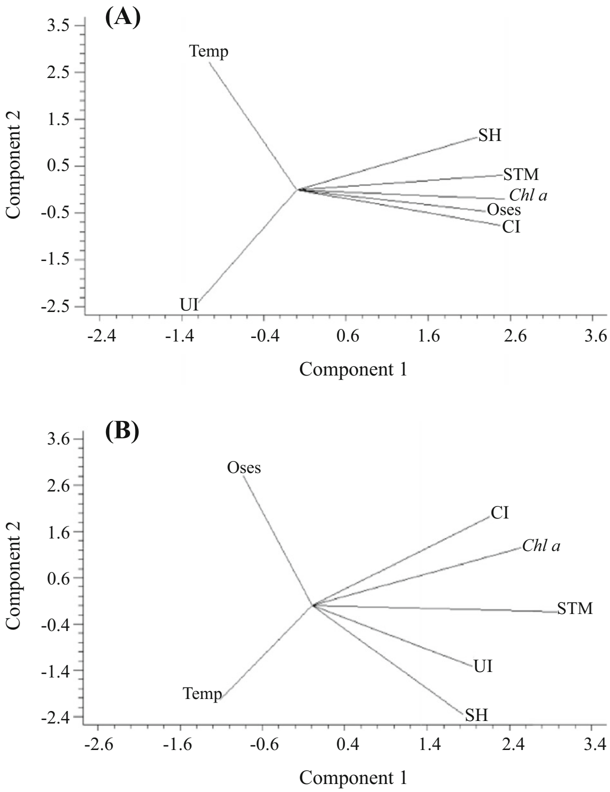

Fig. 5 **a** Bi-dimensional plot of the first two components of the PCA for the first data set (upwelling index ≤1). **b** Bi-dimensional plot of the first two components of the PCA for the second data set (UI > 1). *CI* condition index, *STM* soft tissue mass, *SH* shell height, *UI* upwelling index, *Chl a* chlorophyll *a*, *Oses* organic seston

study, upwelling was determined indirectly by differences between surface temperatures, whereas in the present study, upwelling was calculated based on the well-recognized upwelling index. The UI has previously been related to phytoplankton growth and assemblages as well as mussel cultivation in the Galician Rias (Figueiras et al. 2002; Miguez et al. 2001), whereas Phillips (2005) suggests that some factors as temperature in conjunction with the planktonic productivity may drive large-scale differences in mussel *Mytilus californianus* growth rates, in a region with variable upwelling intensity (north and south of Point Conception, California, USA). Here, we directly relate the UI with the growth index of the winged oyster *P. colymbus*.

Table 2 Eigenvalues, variance percentage and accumulated variance percentage for each component of PCA analysis for the second data set (UI > 1)

Component	Eigenvalue	Variance (%)	Accumulated (%)
1	3.02	43.16	43.16
2	2.18	31.12	74.28
3	0.80	11.49	85.77
4	0.56	8.05	93.83
5	0.30	4.23	98.06
6	0.12	1.78	99.84
7	0.01	0.16	100.00

Upwelling can be envisaged as a master variable that has impacts upon other environmental factors such as temperature and Chl *a*. In this way, the condition index (CI) and soft tissues mass (STM) were positively correlated with Chl *a* and UI, suggesting a direct influence of upwelling on the growth of *P. colymbus* presumably due to the increase in food availability of phytoplanktonic origin (Hawkins et al. 1986; Dupuy et al. 2000; Pernet et al. 2012; Kang et al. 2006). These results contrast with those obtained by Lodeiros et al. (1999a, b) who observed that *P. colymbus* was little affected by marked changes in environmental conditions in the same locality of the present study. Nonetheless, these workers began their study in December 1993, thus comprising the complete upwelling and high productivity period (January to July) when *P. colymbus* displays rapid increase in shell and somatic tissue growth. Accordingly, they had reached sizes of 60 mm by the non-upwelling period (August-October). In contrast with the results obtained in this study, this may have masked the influence of the environmental variables during the non-upwelling period (low and high phytoplankton food source temperatures). However, we cannot rule out that the possibility that the abrupt decline in upwelling intensity and primary productivity in 2004 and persisting until today, due to a northward progression of the Intertropical Convergence Zone (Muller-Karger et al. 2013), may confound any comparisons in growth of *P. colymbus* before and after this event.

The trends of the growth curves of the soft tissue and shell dry mass were similar. Periods of growth stagnation and/or decline between September and December 2012 were attributed to the limited food availability (Chl *a* and organic seston) in the environment. In this sense, the mass of soft tissue was most affected by the availability of food rather than the variability of the shell since shell growth is mostly independent of food availability, as observed in the scallop in culture (Lodeiros and Himmelman 1994) and the natural environment (Thompson and MacDonald 1991). This suggests that the binding of calcium carbonate in the shell does not require the same large amounts of energy as required for the production of other compartments of the soma such as reproductive tissue (Sudent and Vahl 1981). Besides, the tissue mass curve showed sharp decreases in May 2012 and 2013 attributed to spawning. The slow shell growth observed during the last months of the study, where the availability of nutrients of phytoplankton origin was high, is attributed to the fact that the species was reaching to near maximum size (70–80 mm).

Periods of sharp increase in the mass of soft tissue observed in June-August 2012 and January to April 2013 were associated with food availability (Chl *a* and organic seston). This behaviour is related to the increase in soft tissue mass during the months of high food availability. Significant decreases during the spawning months suggests that prior periods of accumulation of reserves are then redirected to gametogenesis and consequently spawning of the species, as has been described for *Lima scabra* in the same study area (Lodeiros and Himmelman 1999). On the other hand, is it clear that the stronger decrease observed in the CI in May (2012, 2013) and December (2012) was affected by parallel spawning events. These results are consistent with those shown by Díaz and Buckle-Ramírez (1996) who observed that the gonads of *Pteria sterna* in August in spawn and regression stages contained little gametogenic matter (intense spawn), thus decreasing the CI.

The reproductive strategies of *P. colymbus* were developed under different environmental conditions during the study. Most of the individuals developed gonads between June and August during the second peak of reactivation of coastal upwelling (see Fig. 1b). At this time, phytoplankton food availability was elevated (2 to 6 mg/L) and temperatures were between 24 and 27 °C. Gonadal development culminated with a spawning in September. The next reproductive cycle took place between the months of October and December in an unfavourable period from the point of view of the energy availability for gametogenic development. Phytoplanktonic food availability (Chl *a*) was minimal (~1.0 μg/L) in this period, and maximum temperatures were above 27–28 °C. The cycle developed further between January and May 2013 during the period of coastal upwelling, with maximum phytoplankton availability (4–8 mg/L chlorophyll *a*) and low temperatures (23–25 °C). Together, this suggests that *P. colymbus* is able to develop opportunist and conservative reproductive strategies, whereby reproduction and gametogenesis is dependent on the energy supplied by the environment. In conservative species, in contrast, this energy is provided by the energy stored in tissues (Bayne 1976). More recently, it has been shown that these categories are not exclusive, particularly in tropical and subtropical species, which can adopt a combination of both tactics to ensure reproductive function (Racotta et al. 1998, 2003; Kang et al. 2000; Luna-González et al. 2000; Arellano-Martínez et al. 2004; Vite-García and Saucedo 2008; Gómez-Robles and Saucedo 2009; Freites et al. 2010a, b). This combination of reproductive strategies throughout the year occurs mainly as a response to changes in water temperature and food availability in a specific location (Saucedo et al. 2005).

A low mortality was observed, equal to only ~6% (29 individuals) for the entire study period. Mortality was probably attributed to two factors. The first is low nutrient availability, especially for the months of September to December 2012, when dead individuals were observed. The second is the presence of the predator *Linatella caudata* in the culture baskets, which is a member of the Ranellidae (Cymatidae) family. Semidey et al. (2010), in an experiment using ropes and baskets as in Japanese culture for *P. imbricata* at the same study site, also observed the presence of the gastropod *Cymatium poulsenii* (=*L. caudata*). This gastropod is considered as a severe problem to cultivation of bivalve molluscs in the Cariaco Gulf (Freites et al. 1999; Malavé et al. 2012).

The association of variables that displayed an increase and decrease in size, tissue mass and CI of *P. colymbus* with contrasting environmental variables (temperature, upwelling index, Chl *a* and organic seston) suggests a strong influence on the ecophysiology of *P. colymbus*. For example, the period of non-upwelling (August to November), characterized by high temperature and low food availability, can be considered as a critical period for the species, judging by the decrease in growth parameters and survival. Nonetheless, *P. colymbus* reached 50 mm in 5 months, a size considered as commercially viable. The area study is thus propitious to the cultivation of the winged oyster, despite a dramatic decrease in upwelling intensity in the last decade.

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