

Bottom-up control of common octopus *Octopus vulgaris* in the Galician upwelling system, northeast Atlantic Ocean

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ABSTRACT: This paper investigates the possible underlying causes of the wide interannual fluctuations in catch of the common octopus *Octopus vulgaris* Cuvier, 1797 in one of the main small-scale fisheries off the coast of Galicia (northwest Spain). Galicia is at the northern boundary of the Iberian–Canary current upwelling system in the northeast Atlantic Ocean, where local winds induce seasonal upwelling, largely driving the annual cycles of primary and secondary production. We hypothesize that such dynamics are also fundamental for the survival of the planktonic stages of octopus and set the year class strength. We address this hypothesis by investigating the influence of upwelling on time-series of octopus fishery data. Wind stress structure during the spring–summer (prior to the hatching peak) and autumn–winter (during the planktonic stage) was found to affect the early life phase of this species, and explains up to 85% of the total variance of the year-to-year variability of the adult catch. Despite this bottom-up modulation via environmental conditions, our results also provide evidence for a between-cohort density-dependent interaction, probably caused by cannibalism and competition for habitat.

KEY WORDS: *Octopus vulgaris* · Phytoplankton · Zooplankton · Fisheries · Bottom-up control · Upwelling · NE Atlantic Ocean

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INTRODUCTION

The abundance and productivity of commercial fish stocks varies on annual to decadal time scales as a result of environmental changes (e.g. MacKenzie & Köster 2004), species interactions (e.g. Hjermann et al. 2007) and fishing pressures (e.g. Myers & Worm 2003); however, the relative magnitude of these effects is controversial (see Frank et al. 2007 for review). Nevertheless, the variability of the physical environment will influence early life stages and/or other life phases, both directly and indirectly, through several processes and mechanisms acting at individual, population and community levels (Stenseth et al. 2004, Ware & Thomson 2005).

Most of the commercially important species of cephalopods have a short life cycle (1 to 2 yr), grow rapidly to maturity, spawn once at the end of their life, are ecological opportunists and have labile populations (Guerra 2006). They also show well known year-to-year fluctuations over large spatial and temporal scales. These oscillations are widely believed to be caused, to a greater or lesser extent, by the influence of the environmental conditions on early life phases that have a major effect on recruitment (Agnew et al. 2000) and, later, on the biomass that can be harvested (Rodhouse 2001). Most cephalopod research has focused on large pelagic squid stocks linked to major current systems; however, the direct causative mechanisms affecting fluctuations of these stocks remain

unclear. Nevertheless, some environment–biology links have been found between recruitment or abundance and sea surface temperature (SST) in different areas (*Loligo gahi* in the southwest Atlantic, Agnew et al. 2000; *L. vulgaris* and *L. forbesi* in the English Channel, Robin & Denis 1999). Similarly, catch fluctuations of *Thysanoteuthis rhombus* are closely related with water temperature, salinity and sea level (Miyahara et al. 2005). Dawe et al. (2007) also documented opposite responses to oceanographic variations of 2 sympatric squid species in the northwest Atlantic Ocean. However, in other squid species, relationships with oceanographic processes remain unresolved (e.g. *Martialia hyadesi*, González et al. 1997).

The common octopus *Octopus vulgaris* Cuvier, 1797 is one of the best studied cephalopods worldwide and the subject of an active fishery (see Otero et al. 2005 and references therein); however, little is known about the influence of environmental variability on the dramatic annual fluctuations of octopus catch. Year-to-year changes of this species have been related to coastal retention processes (Faure et al. 2000), water temperature (Balguerías et al. 2002) and rainfall (Sobrino et al. 2002). In Galician waters, the reproductive cycle of *O. vulgaris* appears to be tuned to seasonality in upwelling. There is one peak of spawning in spring time. The embryonic development lasts up to 4 mo, depending on water temperature, and the hatching peak occurs at the end of summer through the beginning of autumn of a given year (Year t) (Otero et al. 2007). Then, depending on water temperature, octopus paralarvae (Young & Harman 1988) stay in the water column up to 4 mo (Katsanevakis & Verriopoulos 2006). In the pelagic realm they are influenced by the frequency and intensity of upwelling episodes (González et al. 2005, Otero 2006) and feed on other zooplankton taxa before settling on the sea-bed (Iglesias et al. 2007). Recruitment (~300 g body weight; i.e. juveniles of Year $t + 1$) is considered to occur during the following summer (Arnáiz 2006), and the bulk of that cohort will be harvested the following year (i.e. adults of Year $t + 2$).

Upwelling areas are among the most productive marine ecosystems and support most of the largest fisheries (Pauly & Christensen 1995). They are 'subsidized' ecosystems, which receive cold and nutrient-rich oceanic waters from 150–200 m depth that replace surface waters through the Ekman transport produced by a combination of coastal winds and the Earth's rotation (Beer 1983). These areas are exposed to rapid spatio-temporal shifts in their physical and chemical characteristics that may alter the entire food web (e.g. Barth et al. 2007). Specifically, these shifts play a major role in controlling population dynamics of near-shore communities, which affect the dispersal and transport of pelagic stages, and, subsequently, the variations in

the supply of settling larval phases that ultimately defines the recruitment success. In spite of these short-term environmental perturbations, environment-related predictive models applied to species inhabiting upwelling ecosystems are useful for managing purposes (e.g. *Dosidicus gigas* in Peru, Waluda & Rodhouse 2006).

Galicia is at the northern boundary of the Iberian–Canary current upwelling system. Coastal winds at these latitudes (42° to 44° 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, more than 70% of the total variability of coastal winds occurs during periods of less than 1 mo, in such a way that the upwelling season appears as a succession of wind stress/relaxation cycles of periods lasting 10 to 20 d (Álvarez-Salgado et al. 2003). The Galician upwelling has been intensively studied from the oceanographic perspective, including physical processes, biogeochemical cycles and plankton ecology and productivity. However, the influence of the oceanographic processes on upper trophic levels has been investigated in just a few studies (see review by Arístegui et al. 2006).

In this study, we examine the links between atmospheric forcing and trophic levels in the wind driven upwelling system off Galicia. First, we focus on describing the coupling of phytoplankton and zooplankton with the local meteorology. Second, we hypothesize that such dynamics are fundamental for the survival of planktonic stages of the common octopus. We address this hypothesis by using regional wind data as a proxy to the meteorological and hydrographic conditions affecting the paralarval phase. In doing so, we attempt to quantify the extent to which environmental variability results in a bottom-up control of *Octopus vulgaris* and interannual changes in the yield.

MATERIALS AND METHODS

Wind data and offshore Ekman transport calculation. Daily offshore Ekman transport values ($-Q_x$) from 1992 to 2005 were computed from daily geostrophic winds calculated in a 2° × 2° cell centred at 43° N, 11° W (Fig. 1) from the sea surface pressure charts of the Spanish Institute of Meteorology following the method described by Lavín et al. (1991):

$$-Q_x = -\frac{\rho_{\text{air}} \times C_D \times |W| \times W_y}{\rho_{\text{sw}} \times f} \quad (1)$$

where ρ_{air} is the density of air (1.22 kg m⁻³ at 15°C); ρ_{sw} is the density of seawater (1025 kg m⁻³); C_D is an empirical dimensionless drag coefficient (1.4 × 10⁻³);

f is the Coriolis parameter ($9.946 \times 10^{-5} \text{ s}^{-1}$ at 43° latitude); and $|W|$ and W_y are the average daily module and northerly component, respectively, of the geostrophic winds. Positive values of $-Q_X$ ($\text{m}^3 \text{ s}^{-1} \text{ km}^{-1}$) indicate upwelling-favourable offshore Ekman transport. Conversely, negative values of $-Q_X$ indicate downwelling-favourable onshore Ekman transport. These geostrophic winds are representative for local winds blowing off-shore of the northwestern coast of the Iberian Peninsula (Herrera et al. 2005).

Satellite estimates of primary production. Estimation of daily primary production rates (PP) on the continental shelf west of Galicia and the adjacent ocean (Fig. 1) were computed using satellite-derived chlorophyll a (chl a) concentration estimates from the Sea-Viewing Wide Field-of-View Sensor (SeaWiFS) from 1998 to 2004. Estimates of phytoplankton primary production (PP) were computed using the model of Morel (1991) with modifications as described in Groom et al. (2005):

$$PP = 12 a_{\max}^* \phi_{\mu, \max} \int_{\text{sunrise}}^{\text{sunset}} \int_0^{z_{0.1\%}} \int_{400}^{700} C(z) \text{PUR}(z, t, \lambda) f[x(z, t)] d\lambda dz dt \quad (2)$$

where a_{\max}^* ($\text{m}^{-1} [\text{mg chl } a \text{ m}^{-3}]^{-1}$) is the maximum value of the chl a specific phytoplankton absorption spectrum; $\phi_{\mu, \max}$ (mole carbon [mol photons absorbed] $^{-1}$) is the quantum yield for growth; $C(z)$ is the chl a concentration (mg m^{-3}) at depth z ; $\text{PUR}(z, t, \lambda)$ is the photosynthetically usable radiation (spectral photosynthetically active radiation weighted by the spectral phytoplankton absorption, $\text{W m}^{-2} \text{ nm}^{-1}$) at depth z , time t and wavelength λ ; f is a function that relates carbon production to total usable light at depth z and time t expressed as a dimensionless parameter x equal to $\text{PUR}/\text{irradiance}$ scaling factor (KPUR). The KPUR was set to $80 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ at 20°C (Morel et al. 1996) and varied with temperature, T ($^\circ\text{C}$), according to:

$$\text{KPUR}(T) = \text{KPUR}(20) \times 1.065^{(T-20)} \quad (3)$$

Following Morel et al. (1996), $\phi_{\mu, \max}$ and a_{\max}^* were parameterised as a function of chl a . The integration was performed over all daylight hours, for wavelengths 400 to 700 nm and to the productive depth, $z_{0.1\%}$, which is defined here as the 0.1% light level. The model has been parameterised against 24 h *in situ* incubations and, hence, retrieves net primary production.

The model was forced with daily satellite derived estimates of chl a and SST and modelled irradiance computed from Gregg & Carder (1990), with input meteorological variables from National Center for Environmental Prediction (NCEP) reanalysis fields, and cloud

cover from the European Centre for Medium-range Weather Forecasting (ECMWF). SeaWiFS 9 km daily spatial composite data were obtained from the Goddard GES Distributed Active Archive Center and comprise all data that pass the SeaWiFS quality flags (Baith et al. 2001). Chl a was computed using the NASA standard global bio-optical algorithm OC4v4 (O'Reilly et al. 1998). The SST data were obtained from the NASA Pathfinder project (Vázquez et al. 1994) also at 9 km resolution. Where no valid satellite chl a or SST data were available on a given day, the last valid data were used. Vertical profiles of chl a were computed from the near-surface SeaWiFS values (C_{sat}) following the method of Morel & Berthon (1989) modified to ensure that the retrieved C_{sat} value equalled the initial specified C_{sat} value. Where the euphotic depth (0.1% light level) was found to be shallower than the mixed layer given by Levitus (1982), the chl a was assumed to be constant with depth (Bosc et al. 2004). Vertical temperature profiles were constructed following a similar method to Bricaud et al. (2002): surface temperature was extracted from Reynolds SST fields (Reynolds & Smith 1995) and combined with the Levitus (1982) climatological vertical profiles for that location. Where Levitus (1982) gave different surface values, the mixed layer was set equal to the value given by Reynolds & Smith (1995).

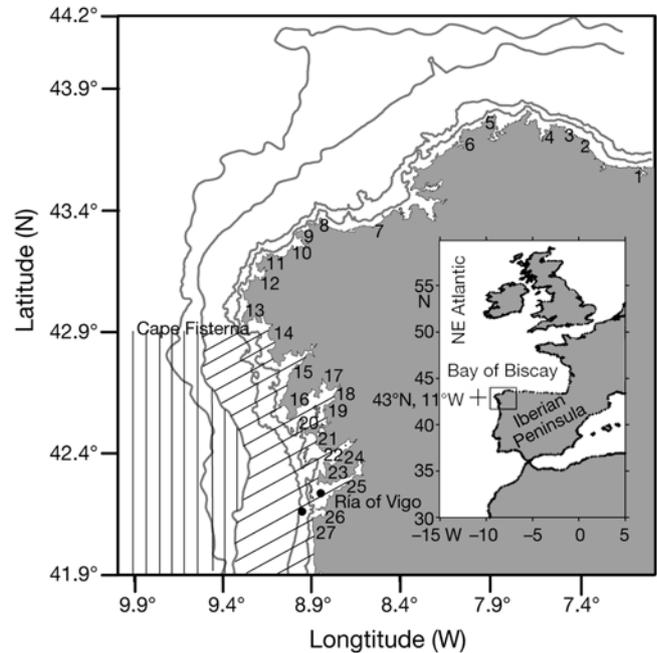


Fig. 1. Study area showing the position of the 27 selected ports, the $2^\circ \times 2^\circ$ geostrophic cell centred at 43° N , 11° W (+) used to compute the daily offshore Ekman transport, the zones (hatched areas) where satellite primary production (PP) was estimated, and the (●) zooplankton stations. Vertically and diagonally-hatched areas were used to calculate PP in the ocean and on the shelf, respectively

Net PP rates, i.e. the gross phytoplankton production minus the microbial (bacteria, phytoplankton and microzooplankton) respiration, were computed for the shelf (PP_{shelf}) and the ocean (PP_{ocean}). The excess PP of the shelf compared with the ocean is considered to be due to the entry of new nutrients onto the shelf by coastal upwelling (Joint et al. 2002) and can be considered a proxy to the 'new production' (NP) of the shelf. The NP is a key variable in any exploitable marine ecosystem because it indicates the threshold for extraction without affecting the long term integrity of the ecosystem (Quiñones & Platt 1991).

Zooplankton data. Zooplankton samples were collected monthly from January 1994 to December 2005 by towing a 40 cm diameter bongo net of 200 μ m mesh at 2 stations, one in the Ría of Vigo and the other one the adjacent shelf (Fig. 1). The bongo net was lowered and stabilized near the bottom for performing oblique hauls at a ship speed of 1.5 knots. The bongo net was equipped with depth and flow meters. Zooplankton samples were fixed onboard with 5% buffered formalin–seawater solution for identification of taxa. In the laboratory, the mesozooplankton (individuals from 200 μ m to 2 mm) were identified (to the species level in most cases) and

counted under a stereomicroscope. However, for this study, we only used total abundance expressed as log transformed no. individuals m^{-3} .

Octopus fishery data. For administrative purposes, the Galician coast is divided into 9 geographical areas from south to north. For the present study, the area was split into 2 regions: Region I to the north and Region II to the south of Cape Fisterra (ICES Divisions VIIIc and IXa, respectively), the boundary between the western and northern coasts (Fig. 1). Each region includes numerous ports each with a different number of multi-species and multi-gear vessels constituting the diverse Galician small-scale fishing sector. Official data are provided by the Galician government, which is responsible for maintaining catch data. Although catch data are incomplete, these can be used as a proxy for the variations in species abundance (Otero et al. 2005). Annual catch data between 1994 and 2006 (in metric tonnes) of *Octopus vulgaris* from the artisanal sector were obtained from the former fisheries information service (Servicio de Información Pesquera), and the current official fisheries service (Plataforma Tecnológica de la Pesca, www.pescadegalicia.com). A group of 27 ports that provided uninterrupted catch statistics over the whole study period were selected (Fig. 1;

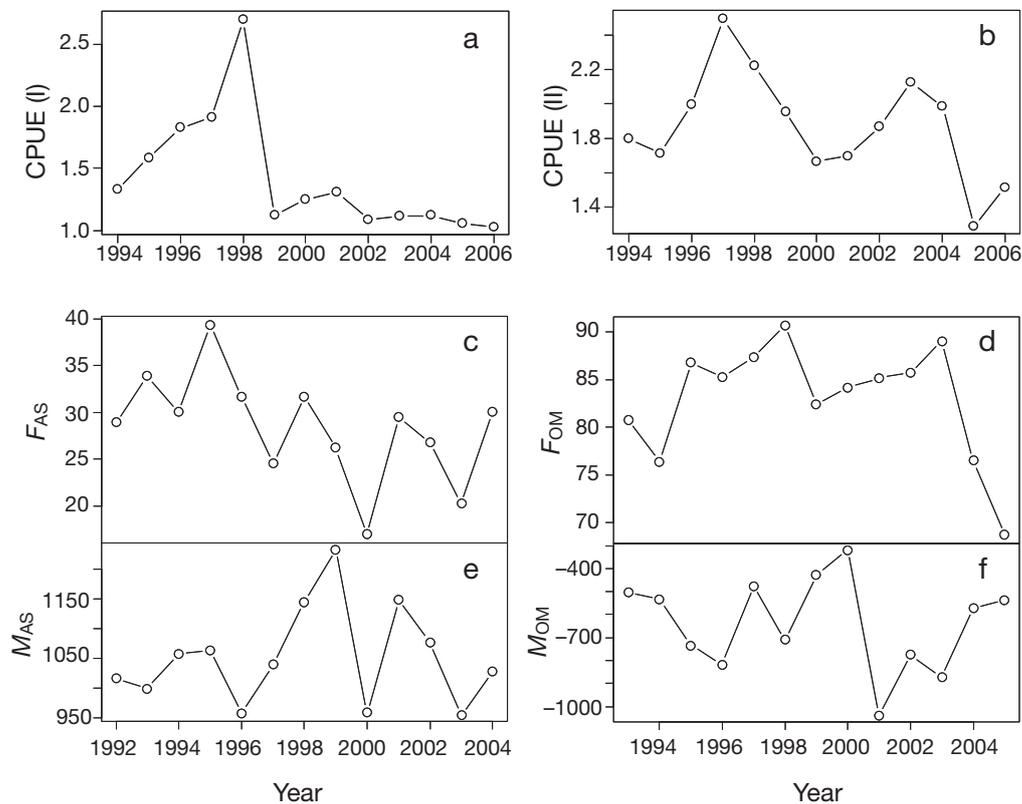


Fig. 2. *Octopus vulgaris*. Trends in $\ln(\text{CPUE})$ ($t d^{-1}$) from 1994 to 2006 in (a) Region I (northern) and (b) Region II (southern) off the Galician coast. (c–f) Meteorological indices (see 'Materials and methods', 'Meteorological indices') calculated from the geostrophic cell (see Fig. 1)

Table A1, available as MEPS Supplementary Material at: www.int-res.com/articles/suppl/m362p181_app.pdf), giving a representative picture of the interannual variability of this resource along the Galician coast (Fig. 2a,b). These 27 ports represent 71 to 84% of the total catch depending on the year.

Accurate data on effort were not available, but it was assumed that there were no substantial changes in the fishing effort during the study period. This is supported by the fact that, since the government of Galicia permits a maximum of 5 gears per artisanal vessel, the fishing power or 'virtual vessels' (parameter B, sensu Otero et al. 2005) exclusively targeting octopus in Galicia (i.e. vessels licensed to use octopus creels) can be estimated by taking into account the number of gear types that can be used by each vessel (number of gears registered). Assuming that a vessel expends equal fishing effort with each gear type, (i.e. a vessel with 2 different registered gears has a value of 0.5), the parameter B can be estimated by summing the number of virtual octopus fishing vessels in each port. Accordingly, we compared the number of vessels registered to target *Octopus vulgaris* (N) and their fishing power (B) in each of the 27 selected ports between 2 periods, up to 2000 (Otero et al. 2005) and from 2001 to 2005 (www.pescadegalicia.com, accessed in January 2006, Table A1). Single-factor ANOVA resulted in no significant differences among fishing effort during the 2 selected periods ($p > 0.05$). In addition, Galician laws force fishers to update their logbooks and provide them to the authorities. However, these data were not available for the present study. Instead of the logbook data, the official web site provides the total days fishing from each port. We do not know if these data correspond to the number of days that the boats are exclusively fishing common octopus, the number of days that octopus were sold in the auctions, or even whether fishers include those days that octopus was a bycatch of a particular boat when other species, e.g. *Necora puber*, were being fished. Nevertheless, we used those data to calculate a proxy of catch per unit of effort (CPUE in $t d^{-1}$) and finally used this variable as a response in the model. Total catch and CPUE were correlated ($r = 0.89$, $p < 0.00001$).

Meteorological indices. We have assumed that the offshore Ekman transport must exceed a threshold to produce a significant impact over the entire water column. The threshold was fixed at $500 m^3 s^{-1} km^{-1}$, a value that represents about twice the long-term average for the upwelling favourable period, $230 m^3 s^{-1} km^{-1}$ off NW Spain (Álvarez-Salgado et al. 2003). Four indices were defined from the daily time series of $-Q_X$ to account for the structure and intensity of the wind field: (1) the percentage of days with $-Q_X > 500 m^3 s^{-1} km^{-1}$ from April to September, F_{AS} ; (2) the average $-Q_X$

for the days with $-Q_X > 500 m^3 s^{-1} km^{-1}$ from April to September, M_{AS} ; (3) the percentage of days with $-Q_X < 500 m^3 s^{-1} km^{-1}$ from October to March, F_{OM} ; and (4) the average $-Q_X$ for the days with $-Q_X < 500 m^3 s^{-1} km^{-1}$ from October to March, M_{OM} . The 2 periods, April to September and October to March, were not chosen arbitrarily. First, these periods represent the upwelling and downwelling seasons, respectively, for the NW Iberian Peninsula (Álvarez-Salgado et al. 2003) and, second, it has been hypothesized that the selected periods may influence the planktonic stage of octopus. The succession of stress ($-Q_X > 500$) and relaxation ($-Q_X < 500$) wind pulses will allow an optimum balance between nutrient supply for phytoplankton, plankton growth and retention of primary production on the shelf. We hypothesize that the dominant upwelling conditions from April to September will indirectly affect the summer/autumn hatched pelagic paralarvae through the feeding pattern, i.e. upwelling influence on plankton productivity (indices F_{AS} and M_{AS}). We also hypothesize that the relaxation and moderate downwelling conditions from October to March will mainly exert a direct effect through the physical conditions that the paralarvae might face during the planktonic stage (indices F_{OM} and M_{OM}). The time evolution of the meteorological indices is shown in Fig. 2c–f.

Statistical analyses. Average seasonal cycles (SC) of $-Q_X$, PP_{shelf} , PP_{ocean} , NP, and mesozooplankton abundance were obtained by adjusting, sensu minimum squares, the corresponding time series to the first (period 365 d) and second (period 182.5 d) harmonics of the Fourier analysis:

$$SC = A_0 + A_1 \times \sin(2 \times \pi \times t / 365 + \phi_1) + A_2 \times \sin(4 \times \pi \times t / 365 + \phi_2) \quad (4)$$

where A_0 is the annual mean; A_1 and A_2 are the amplitudes and ϕ_1 and ϕ_2 the phases of the first and second harmonics; t is the day of the year (from 1 to 365).

Bottom-up control should result in a positive correlation between the wind field and any trophic level. To identify general patterns, the correlation coefficients between daily PP_{shelf} and daily $-Q_X$ from April to September during years 1998 to 2004 were studied using a random-effects (i.e. year) meta-analysis (Lipsey & Wilson 2001, Worm & Myers 2003) after removing temporal autocorrelation adjusting the degrees of freedom using the modified Chelton method (Pyper & Peterman 1998). Although the relationship between primary production and upwelling could be consistent throughout the time series, its strength can change due to the wide variation of upwelling intensity from year to year (Álvarez-Salgado et al. 2002). To investigate this heterogeneity, the strength of the correlation of daily primary production (PP_{shelf}) versus upwelling ($-Q_X$) was compared with the

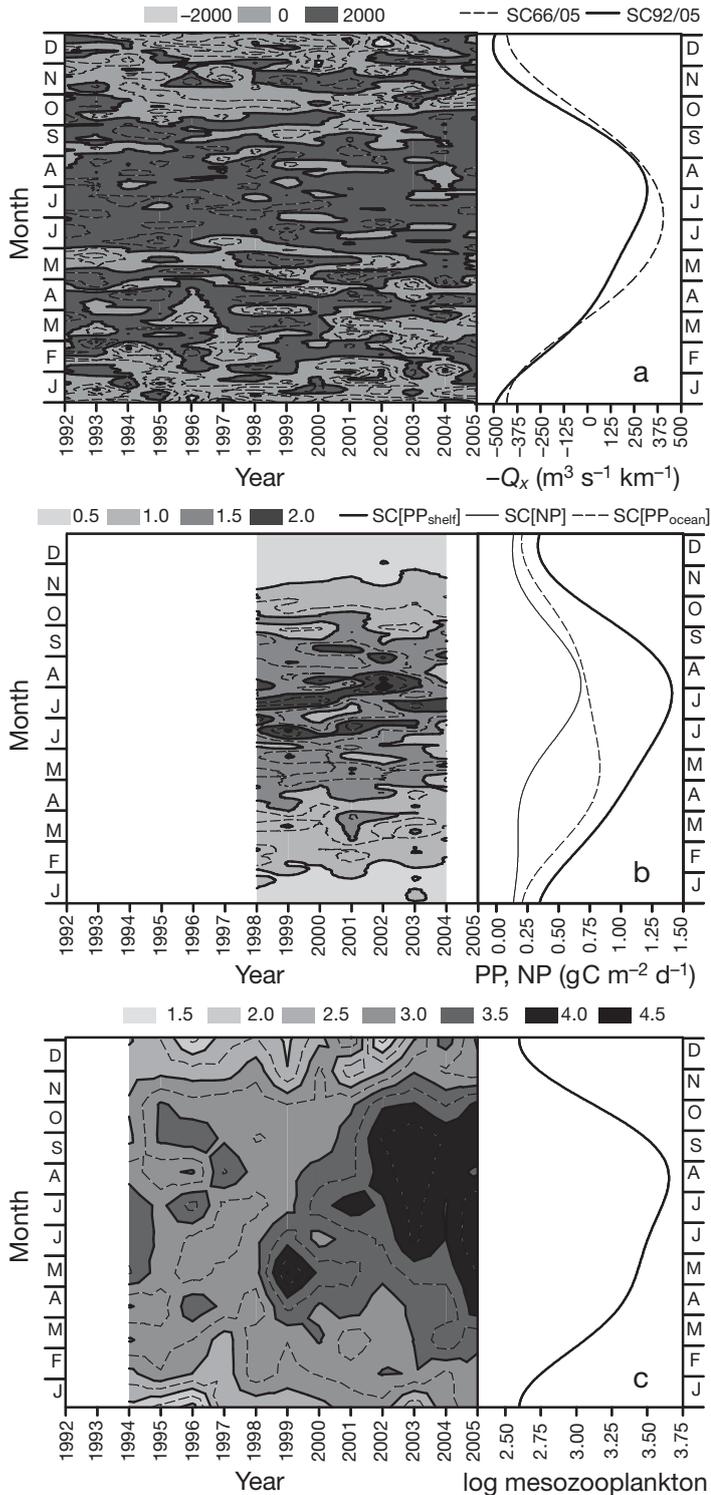


Fig. 3. (a) Average 1992 to 2005 seasonal cycle and interannual changes of the 7 d running mean of $-Q_x$. Positive and negative values indicate upwelling and downwelling favourable winds, respectively. (b) Average 1998 to 2004 seasonal cycle and interannual changes of the 7 d running mean of primary production on the shelf (PP_{shelf}) and ocean (PP_{ocean}) and new production (NP). (c) Average 1994 to 2005 seasonal cycle and interannual changes of the monthly \log_{10} (mesozooplankton abundance). SC: seasonal cycle

average value of $-Q_x$ from April to September each year. Finally, mesozooplankton monthly data were correlated with PP_{shelf} , adjusting the degrees of freedom according to Pyper & Peterman (1998).

To test the importance of the potential forcing factors (meteorological indices) on *Octopus vulgaris* catch (natural logarithm of annual CPUE), we used generalized additive models (GAMs, Hastie & Tibshirani 1990) as implemented in the mgcv library of R (www.R-project.org). In line with our hypothesis that major effects should occur during the pelagic stage, we expect a temporally lagged response. Thus, the meteorological indices were time-lagged when the model was fitted to the data (e.g. the CPUE in a Year t were forced with F_{AS} in a Year $t-2$ and F_{OM} in a Year $t-1$). We also tested for density dependence (DD) by adding the previous year's catch as an additional predictor. Thus, we effectively fitted an additive model of the form:

$$Y_t = a + b + g(Y_{t-1}) + \sum_j f_j(E^j) + \varepsilon_t \quad (5)$$

where Y_t is the $\ln(\text{CPUE})$ in Year t ; a is the intercept; b is a categorical variable (1 and 2) distinguishing between the 2 different regions; Y_{t-1} is the density dependent variable (i.e. previous year's catch); E^j is a vector of environmental variables, where the superscript j identifies each environmental variable time-lagged accordingly; g and f_j are non-parametric smoothing functions, specifying the effect of the density dependence and environmental forcing on the octopus CPUE; and ε_t is the error term assumed to be normally distributed. The smoothness of the functions was estimated by minimizing the generalized cross validation (GCV) criterion. Predictors were tested for multicollinearity (Variance Inflation Factors: 1.8–3.9), and model validation consisted of verifying the underlying assumptions of homogeneity, normality and independence.

RESULTS

Coastal upwelling and its impact on low trophic levels

The offshore Ekman transport ($-Q_x$) over the period from 1992 to 2005 exhibited a seasonal cycle that explains 16.4% of the variability of the daily time series (Fig. 3a). It is characterized by 186 d of upwelling favourable northerly winds from Day 91 (April) to Day 276 (September), with an average intensity of $194 \pm 95 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ and 179 d of downwelling favourable southerly winds, with an average intensity of $-300 \pm 160 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$. Therefore, on an annual basis, wind-driven downwelling is the dominant forcing mechanism in this coastal upwelling system. These

numbers are in close agreement with previous studies about the intensity and extension of the upwelling and downwelling seasons off northwest Spain (Álvarez-Salgado et al. 2003).

The PP rates also followed a marked seasonal cycle (Fig. 3b) explaining 76 % of PP_{ocean} , 78 % of PP_{shelf} and 53 % of NP daily variability from 1998 to 2005. The average annual PP_{ocean} was $0.57 \pm 0.22 \text{ g C m}^{-2} \text{ d}^{-1}$, with maximum values ($0.83 \text{ g C m}^{-2} \text{ d}^{-1}$) occurring in April, the time of the spring bloom in the oceanic waters adjacent to the northwest Iberian upwelling system. In contrast with the expected behaviour in temperate open ocean waters, the average PP_{ocean} from June to September was $0.72 \pm 0.10 \text{ g C m}^{-2} \text{ d}^{-1}$. This less dramatic decrease during the summer is probably due to the beneficial effect of the export of materials, including healthy plankton assemblages, from the adjacent coast via cold upwelling filaments (Joint et al. 2001). The average annual PP_{shelf} was $0.90 \pm 0.27 \text{ g C m}^{-2} \text{ d}^{-1}$, with a peak of $1.38 \pm 0.03 \text{ g C m}^{-2} \text{ d}^{-1}$ in July, the middle of the upwelling season. Finally, the average annual NP was $0.33 \pm 0.20 \text{ g C m}^{-2} \text{ d}^{-1}$, with a peak of $0.65 \pm 0.03 \text{ g C m}^{-2} \text{ d}^{-1}$ in July. Therefore, on average, about 37 % of PP_{shelf} ($= NP/PP_{\text{shelf}} \times 100$) can be assigned to new nutrients upwelled from the adjacent ocean (Joint et al. 2002); in July, up to 47 % of PP_{shelf} is new production.

Total mesozooplankton abundance (individuals from 200 μm to 2 mm) in shelf waters off Galicia also exhibited a marked seasonal cycle that explains 67 % of the total variability of the 1994 to 2005 monthly time series (Fig. 3c). Abundance increases abruptly from January to April, the time when the spring bloom occurs (Fig. 3b) and peaks in July through August, coinciding with the NP maximum over the shelf (Fig. 3b).

In addition to the tight coupling of the seasonal cycles, a meta-analysis of the correlation coefficients between daily PP_{shelf} and upwelling from April to September was conducted. The strength of this correlation was then compared against the mean upwelling index for the same period (i.e. the average value of $-Q_X$ from April to September each year). The meta-analysis indicated that the overall relationship between daily PP_{shelf} and $(-Q_X)_{\text{AS}}$ is positive and significant ($\bar{r} = 0.22$; $z = 6.77$; $p < 0.00001$). If the data are aggregated on a weekly basis, the strength of the relationship increases ($\bar{r} = 0.30$; $z = 5.71$; $p < 0.00001$). Furthermore, a negative and significant relationship was found when the correlation coefficients for daily PP_{shelf} and $(-Q_X)_{\text{AS}}$ from 1998 to 2004 were plotted against average $(-Q_X)_{\text{AS}}$ ($r = -0.77$, $p < 0.05$; Fig. 4). This result implies that the higher the $-Q_X$ is in weaker upwelling seasons, the higher PP_{shelf} is. As expected in bottom-up controlled ecosystems, mesozooplankton was positively correlated with PP_{shelf} on a monthly basis ($r = 0.61$, $p < 0.05$). These results also indicate that factors other than wind-induced upwelling are important for

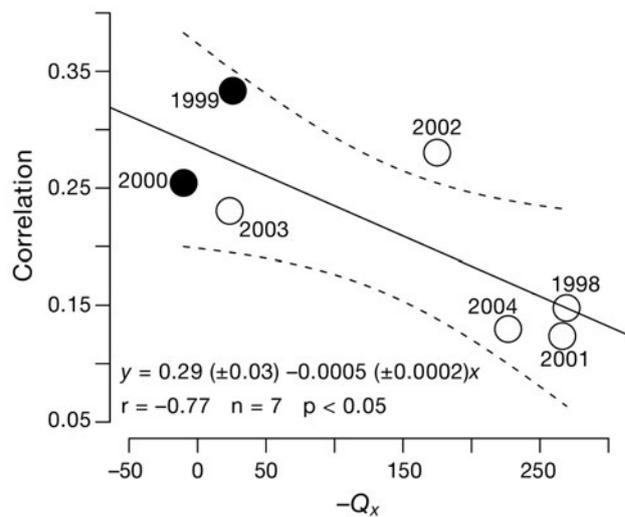


Fig. 4. Relationship between the Pearson product moment (r) of the correlation between daily primary production in the shelf (PP_{shelf}) versus upwelling ($-Q_X$, $\text{m}^3 \text{ s}^{-1} \text{ km}^{-1}$) from April to September during years 1998 to 2004 and the average value of $-Q_X$ from April to September of each year. The solid line represents the model and dashed lines represent 95 % confidence intervals. Black circles (●) identify those correlation coefficients that remained significant after correcting for autocorrelation

plankton productivity; however, these are beyond the scope of the present study (e.g. abiotic factors: other oceanographic processes such as water column stability; biotic factors: density dependence, predation).

Octopus catch and meteorological indices

The wind structure from October to March of the previous year (i.e. F_{OM}) and from April to September 2 yr before (i.e. F_{AS}) had positive effects on common octopus catch in Galicia, while the intensity of wind stress from April to September 2 yr before (i.e. M_{AS}) showed a negative nonlinear effect (Table 1, Fig. 5). The 1-yr-lagged octopus catch had a dome-shaped effect with an optimum in the middle section of the previous year's catch range (Table 1, Fig. 5), and the intensity of wind stress from October to March (i.e. M_{OM}) did not have a significant effect. In addition, in Region II, 0.28 more CPUE (t d^{-1}) is expected compared with Region I (Table 1). The model accounts for 85 % of the variance and it appears to capture the catch trends in both regions I and II (Fig. 6a,b). The variance and normality are well behaved, independence was not violated, non-serious influential observations were detected, and residuals do not show any remaining structure (see Fig. A1, available as MEPS Supplementary Material at: www.int-res.com/articles/suppl/m362p181_app.pdf).

Table 1. Structure of the generalized additive model. edf is the estimated degree of freedom of each examined covariate. An edf = 1 implies a linear effect and values > 1 indicate a progressively stronger nonlinear effect. See 'Materials and methods' for abbreviations

Parameter	Estimate	SE	t-value	edf	F	p
Intercept	<i>a</i>	1.51	0.07	21.32		1.01×10^{-12}
Region II	<i>b</i>	0.28	0.12	2.35		0.033
F_{OM}	E^1			1.93	12.33	0.0006
F_{AS}	E^2			1.00	38.40	1.63×10^{-5}
M_{AS}	E^3			1.95	10.60	0.001
DD	Y_{t-1}			1.95	8.64	0.003
$r^2_{adj} = 0.85$, deviance explained = 89.8%, n = 24						

DISCUSSION

The octopus artisanal fishery in Galicia comprises almost 1500 vessels. The legislation imposed on this sector requires all fishery data to be provided to the government; however, this is not totally fulfilled, leading to an underestimation by hundreds of metric tonnes in the official catch statistics (Otero et al. 2005). Although this fact has been demonstrated, we assumed that

the underestimation remained constant. Therefore, common octopus catch would be increased proportionally to the registered vessels in each port, having no effects on either the interannual trend reported here or in the model investigated. Moreover, we did not identify major changes in the number of vessels registered during the study period.

Correlation analysis is essential for understanding causative mechanisms in systems difficult to manipulate; thus, although the identified effects do not mean causality, the environmental variables retained in the model should be important factors

regulating the year class strength of common octopus. In this sense, we hypothesize that abundance is determined very early in the life cycle of this species as has been proposed for other Cephalopoda species (e.g. Chen et al. 2007, Dawe et al. 2007).

Theoretically, 3 major processes must combine to yield favourable reproductive habitats: (1) nutrient fertilization, (2) food concentration and (3) larval re-

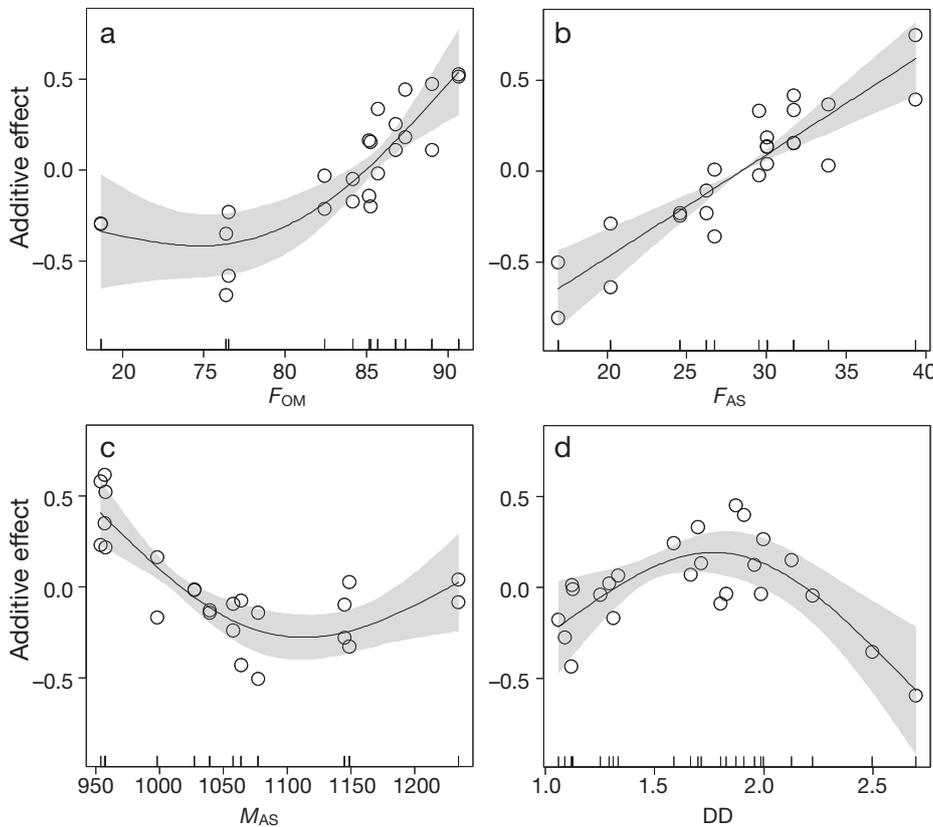


Fig. 5. *Octopus vulgaris*. Results of generalized additive modelling (GAM) of effects on CPUE: (a) the F_{OM} effect, (b) the F_{AS} effect, (c) the M_{AS} effect, and (d) the DD effect. Shaded areas represent 95% point-wise confidence intervals. Open circles (O) are the partial residuals around the significant covariate effects, and tick marks along the x-axis below each curve represent the values of the effect where the observations occurred. See 'Materials and methods', 'Meteorological indices' for F_{OM} , F_{AS} and M_{AS} ; DD: Density dependence

tention (Bakun 1996). Within this conceptual framework, simple wind-based upwelling indices were constructed to investigate the hypothesis of major impact during the pelagic stage.

Common octopus larvae hatch at the end of summer through the beginning of autumn, at the end of the strong upwelling and productive season. The frequency of upwelling episodes with $-Q_X > 500 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ (i.e. F_{AS}) had a positive effect on the CPUE. These conditions may induce a significant impact on the whole ecosystem during the upwelling season, suggesting that fertilization of the system with nutrients from subsurface adjacent ocean waters is of vital importance for enhancing biological productivity from phytoplankton upwards throughout the food web (see Fig. 3). We propose that this process contributes indirectly to larval survival through food quantity and quality. However, the effect of the average offshore Ekman transport during the upwelling season (i.e. M_{AS}) was almost negative (Fig. 5c). This response may indicate that very intense northerly winds might have a detrimental effect on the primary production of the ecosystem (see Fig. 4). This behaviour is related to the well-known lag time that the recently upwelled phytoplankton cells need to adapt to the new light conditions of the surface layer before starting to photosynthesize at optimal rates (Zimmerman et al. 1987). Strong upwelling is characterized by extremely high flushing rates that do not allow phytoplankton adaptation and concentration of food particles; this behaviour could presumably affect higher trophic levels of the food web. Furthermore, we can not exclude the possibility that strong upwelling and its associated low water temperatures increase the embryonic development time leading to a mismatch between early hatched paralarvae and their prey.

Our results also show that the frequency of upwelling episodes with $-Q_X < 500 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ from October to March (i.e. F_{OM}) also had a positive effect on the octopus CPUE. However, wind intensity during this period (i.e. M_{OM}) does not have a significant effect on common octopus catch ($p > 0.05$). The conditions in this period will favour the succession of wind-stress and subsequent relaxation events suggesting a contribution to larval survival through retention processes (Otero 2006), enhancing potential prey encounter rates and precluding offshore dispersion. In addition to the local wind pattern, from October to March the Iberian Poleward Current (IPC) flows along the slope of the northwest Iberian Peninsula and the French coast, from Lisbon to the American Shelf (Álvarez-Salgado et al. 2003). The IPC is generated to compensate for the difference in dynamic height between the warm subtropical and the cold sub-polar waters of the northeast Atlantic, and only one fifth of the intensity of the IPC

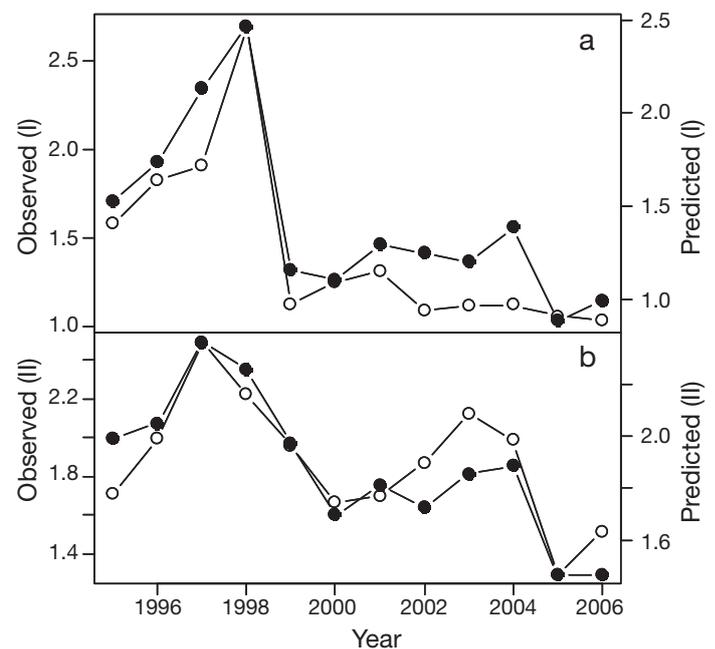


Fig. 6. *Octopus vulgaris*. Observed (O) and predicted (●) values of common octopus CPUE in (a) Region I and (b) Region II

off Galicia is due to the dominant local southerly winds (Frouin et al. 1990). Nutrients to support primary production during the downwelling season are provided by continental waters via the Western Iberian Buoyant Plume (Peliz et al. 2005). These conditions have already been identified as a prerequisite for coastal retention of planktonic organisms over the shelf (Álvarez-Salgado et al. 2003, Santos et al. 2004, Peliz et al. 2005). Furthermore, sardine *Sardina pilchardus* recruitment success off the northwest coast of the Iberian Peninsula has been attributed to moderate upwelling intensity prior to spawning, enough input of nutrients during the upwelling season and reduced offshore larval transport (Guisande et al. 2001).

In addition to the oceanographic processes, we also identified a dome-shaped relationship with 1-yr-lagged octopus catch (Fig. 5d). This suggests negative density dependence at high octopus densities. After settlement, octopuses do not move large distances (Fuentes 2004), and the availability of shelters is a limiting factor for octopus distribution (Katsanevakis & Verriopoulos 2004). Thus, competition for habitat between adults and new recruits becomes possible, leading to an increased mortality of the new recruits by predators. Moreover, large octopuses can feed on conspecifics (Guerra 1978, Smith 2003). Therefore, cannibalism of adults of any particular cohort on the recruits of the following cohort could also contribute to density-dependent mortality. Although predatory and competitive interactions between species (e.g. Arkhip-

kin & Middleton 2002), and negative density-dependent effects in stock–recruit relationships (e.g. Agnew et al. 2000) have been suggested as factors regulating annual squid abundance levels, to our knowledge, this is the first description of an intraspecific density-dependent effect in benthic cephalopods. By contrast, inter-cohort density-dependent mortality attributed to competition and cannibalism is well known and studied in fishes (e.g. Fromentin et al. 2001).

Finally, it appears that south of Cape Fisterra (i.e. Region II) higher CPUE is expected compared with the northern region, as the average CPUE increased about 18% in that area. This could be explained by the latitudinal differences in the upwelling characteristics (Castro et al. 2000) and intrinsic variability of the fishery patterns throughout the Galician coast (see Otero et al. 2005, Arnáiz 2006).

It is realized that the model fits the data quite well given that so many biological processes are integrated (e.g. embryonic development, planktonic stage and subsequent settlement) and it is based on a limited time series. This could be because Galicia constitutes the northern boundary of the Iberian–Canary current upwelling system, and almost the northern limit of the species distribution. Moreover, low upwelling-related water temperatures during the embryonic development of octopuses (Sakaguchi et al. 2002) and the mother's reproductive investment (Otero et al. 2007) favour the increase of paralarvae size, which could improve survival, as has been described in laboratory experiments (Steer et al. 2003). In addition, survival also increases with sea temperature during the planktonic larval stage (O'Connor et al. 2007). Finally, possible overexploitation of finfish in this fishing ground could lead to a release of predation pressure thereby increasing the relationship between upwelling and *Octopus vulgaris* as has been suggested in other areas (Faure et al. 2000).

Nevertheless, it appears that our results are in agreement with those of Faure et al. (2000) for the octopus spring spawning cohort in the Arguin Bank (northwest Africa), highlighting the importance of environmental control of this species, with major effects on early life stages, leading to fluctuations in recruitment and, consequently, the yield. This fragile balance between enrichment and retention processes could even induce large changes in catch arising from relatively small wind variations and might be of major importance if upwelling changes in response to climate change (Diffenbaugh et al. 2004). Although the time series needs to be augmented with past and future data, models possibly updated (e.g. using survey-based data and/or recruitment indices) and other dynamics (e.g. non-additivity) and methods tested, our results contribute to understanding the

effects that underlie the fluctuations of one of the most important harvested cephalopods worldwide. The results highlight the importance of local winds in a productive and bottom-up controlled ecosystem and show a between-cohorts effect, and might be used to improve future octopus management strategies.

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