

Sex ratio variation in an exploited population of common octopus: ontogenic shifts and spatio-temporal dynamics

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Abstract

Sex ratio is a fundamental demographic parameter with major implications for the dynamics, management, and conservation of animal populations. The

objective was to study the main factors affecting the post-settlement population sex ratio (SR) of *Octopus vulgaris* off the NE Atlantic. We investigated the spatio-temporal dynamics in SR using more than 115,000 individual records obtained from onboard observers over a 14-year period. Generalized linear models were used to evaluate the abiotic and biotic factors affecting the variation in SR. The probability of catching a female decreased with size. Seasonal differences in SR resulted in a female-biased ratio in autumn and male dominance in summer. SR also varied along the bathymetric gradient with larger female proportion at deeper waters in winter and spring. The probability of catching a female was lower in hard substrates mainly in summer. Upwelling intensity and sea surface temperature did not show substantial effects on SR. The analysis neither revealed an influence of local density on SR. The spatio-temporal patterns of SR in *O. vulgaris* are likely based on differences in sexual behavior and life history which may affect catchability rates. Understanding the causes in SR patterns will provide valuable knowledge for future assessment and management plans.

Keywords

Sex ratio

Life history

Fisheries

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Electronic supplementary material

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Introduction

Sex ratio is a critical demographic parameter and has been considered as a central concept in studies of population and evolutionary dynamics (Engen et al., 2003). The ratio of males to females may differ from the expected 1:1, as Fisher's principle predicts (Fisher, 1930), and these deviations might be ascribed to multiple dynamic features such as density dependence (Hailey & Willemsen, 2000), resource availability (McKellar et al., 2009), or even the interaction between environmental conditions and density-dependent processes (Manning et al., 2015).

The ratio of males to females can be evaluated at different stages during a species' lifetime, and thus, it is defined differently depending on the moment of the life history when it is estimated. As such, Mayr (1939) established the concept of primary sex ratio as the proportion of male to female eggs (immediately after fertilization), and secondary sex ratio as the proportion of male to female of individuals at hatching. Further, Mayr (1939) defined a tertiary sex ratio as the adult sex ratio (ASR) that is generally measured as the ratio of all independent non juvenile individuals. Apart from those principal concepts, there are other proportions such as the operational sex ratio (OSR), which measures the proportion of ready-to-mate males to ready-to-mate females (Payne et al., 2011) and is usually incorrectly equated to the ASR. In many cases, however, it is difficult to study a specific sex ratio, and authors estimate the sex ratio of the population without focusing on any particular life stage. This fact is common for instance when studying exploited marine species and it allows, among other topics, studying ontogenic changes in sex distribution (e.g., Goñi et al., 2001; Arkhipkin & Middleton, 2002; Farley et al., 2014). While there is a considerable amount of studies focused on understating the drivers of sex determination processes affecting primary and secondary sex ratios in a variety of taxa such as reptiles (Janzen, 1994), marine coastal invertebrates (Lawrence & Soame, 2004), or fish (Ospina-Álvarez & Piferrer, 2008), the factors that affect the frequency and variation in sex ratio during more advanced life stages are still poorly understood (but see Donald, 2007; Manning et al., 2015). This lack of knowledge is even more pervasive for marine organisms.

In closed populations, if primary and secondary sex ratios do not differ from equality, the sex ratio might remain identical when death rates between males and females do not vary during life time (Mayr, 1939). Thus, uneven sex ratio is mainly a result of sex-biased mortality, which in turn may be determined by physiological, ecological, genetic, and/or behavioral differences between sexes (Donald, 2007). By contrast, in open populations, unbalanced sex ratios in adult stages might be caused by additional drivers such as sex-specific emigration and immigration rates (Kokko et al., 2006). Further, the spatio-temporal variation in sex ratio can respond to a number of other factors such as sex-specific foraging migrations (DeMartini et al., 2000) and behavior (Oxenford & Hunte, 1999), sexual segregation in ontogenetic migrations (Arkhipkin & Middleton, 2002), or even size-selective exploitation patterns (Kendall & Quinn, 2013). Much of the existing variation in sex ratio could be ascribed to physiological and/or behavioral traits that would lead to sexual segregation (Wearmouth & Sims, 2008). Apart from this, unbalanced estimates of the sex ratio can be observed even when those differences are not present in the population. For example, sex-dependent behavior and biological cycles can make one sex more vulnerable to a

specific sampling technique, which will therefore overestimate its prevalence and skew the sex ratio estimate (Ziegler et al., 2004).

There is a long tradition in analyzing the mechanisms responsible of skewed sex ratios in terrestrial organisms, including mammals (Bowyer, 2004; Manning et al., 2015; Stewart et al., 2015), birds (Donald, 2007), or reptiles (Hailey & Willemsen, 2000). However, this phenomenon and its ultimate causes are less well analyzed within the marine environment where unbalanced sex ratios are relatively common with a variety of examples among different taxa such as crustaceans (MacDiarmid, 1991), large pelagic elasmobranchs (Mucientes et al., 2009), commercial fin-fishes (Farley et al., 2014), or cephalopods (Westermann, 1969). For the latter group of organisms, characterized for having a short life span, a rapid growth to maturity and typically a unique seasonal spawning period at the end of their life, a balanced sex ratio is basic for the population dynamics especially in exploited stocks (Boyle & Rodhouse, 2005). Despite these facts, the variability in sex ratio in cephalopods is poorly studied. Common octopus, *Octopus vulgaris* Cuvier 1797, is one of the most commercially important cephalopods worldwide (FAO, 2016), and sex ratio for this species is a demographic parameter frequently reported in biological and ecological studies (e.g., Fernández-Rueda & García-Flórez, 2007; Otero et al., 2007). Most of those studies are basically focused on stating, if any, the annual biases from the theoretical balanced sex ratio without providing any further analyses on the potential factor(s) driving the male to female proportion at any time of the life cycle. The main argument used to justify the temporal unbalance would be related to the hiding behavior of the females during the reproductive season (Silva et al., 2002) and an offshore-inshore migration for breeding purposes (Quetglas et al., 1998). However, these postulates have never been formally evaluated, nor addressed the effect(s) of other factor(s) that would affect the ontogenic variations in the proportion of octopus' males to females across space and time.

Understanding the causes of sex ratio patterns and how this variation feeds back into the population dynamics are also relevant for providing valuable knowledge for the assessment and management of species of high commercial importance and/or conservation concern. Particularly in the marine environment, sex ratio has been proposed as a useful indicator of a population trend for resource assessment purposes for certain fish species such as the Japanese eel, *Anguilla japonica* Temminck & Schlegel, 1846 (Han & Tzeng, 2006). Sex ratio-at-length patterns are affected by fishing mortality (F), which means that changes over time in sex ratios might help understand changes in F, making these data valuable for assessment purposes (Cerviño, 2014). Indeed, in quantitative

fisheries, the sex ratio is a key demographic parameter in population assessment procedures (Morgan, 2008).

Here we have investigated the variation in sex ratio in a highly exploited population of *O. vulgaris* fished off the Galician coast (Northeastern Atlantic waters). We hypothesized that (i) the population sex ratio varies in time and space due to the life cycle of the species and sex-related differences in growth, mortality and behavior, and (ii) once accounted for the spatio-temporal differences, the proportion of females would be influenced by the prevailing environmental conditions and habitat preferences in the region. Our hypotheses were statistically evaluated by means of using generalized linear models fitted to more than 115,000 records of sexed octopus' individuals obtained from onboard observers enrolled in the small-scale coastal trap fleet. The purpose of the modeling approach was three-fold: (i) to describe the spatio-temporal patterns in sex ratio at the population level, (ii) to relate these patterns to the life history of the species, and (iii) to investigate the effect of extrinsic environmental drivers affecting the sex ratio.

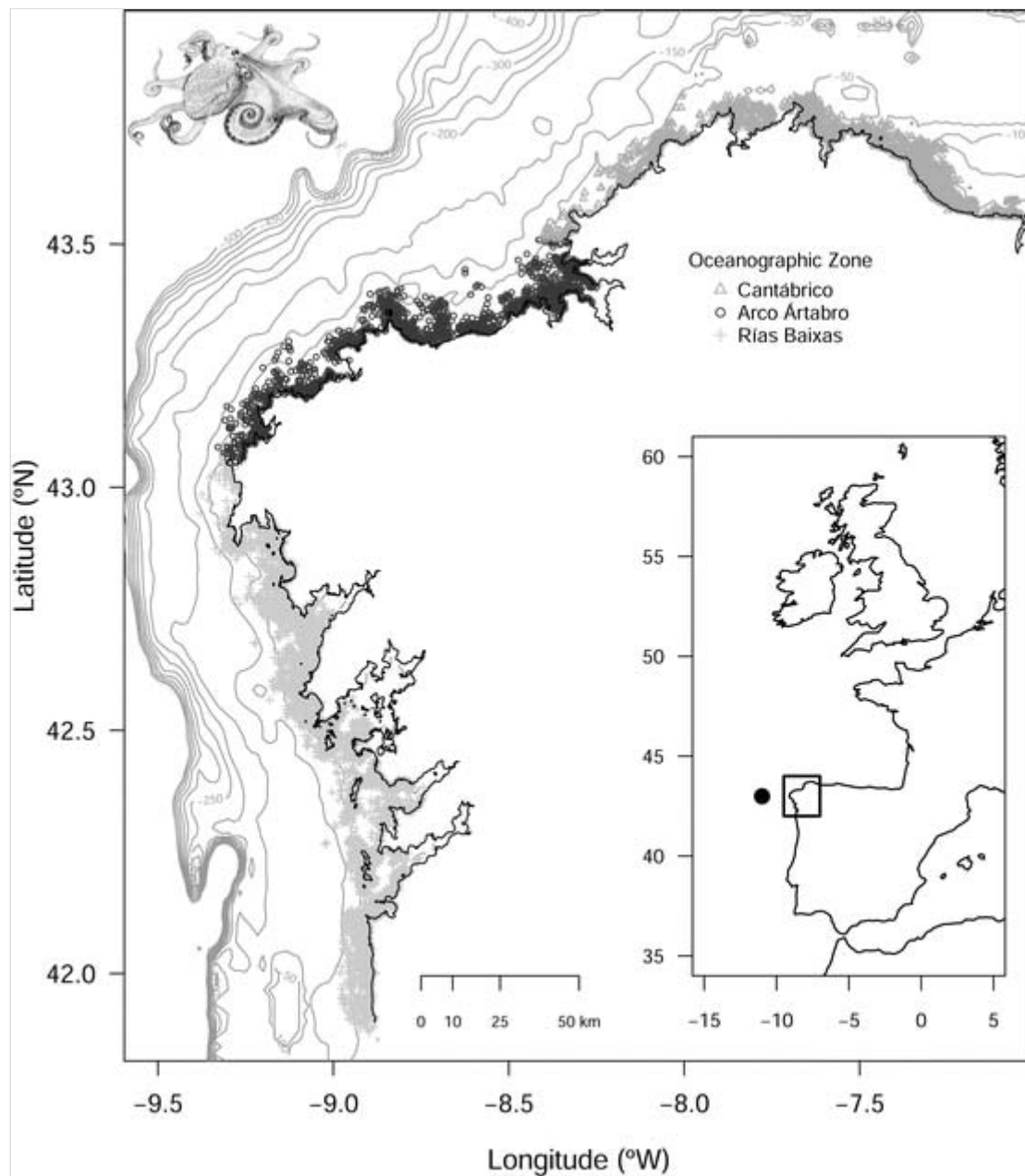
Materials and methods

Study area and species

Galicia (NW Spain, Fig. 1) is one of the main fishing regions in Spain and in Europe (Freire & García-Allut, 2000) counting a fleet of ~4000 small-scale fishing boats that represents ~88% of the total fleet in the region in 2014 (<http://www.pescadegalicia.com>). Galician waters are at the northern boundary of the Iberian-Canary Current upwelling system. Coastal winds at these latitudes (42°–44°N) are seasonal; however, more that 70% of the total variability of coastal winds occurs during periods of less than 1 month (Álvarez-Salgado et al., 2002).

Fig. 1

Map of the study area showing the distribution of the hauls during the whole study period separated according to the three different oceanographic zones. The *dot* in the inset locates the 43°N, 11°W cell from where upwelling intensity was calculated



The common octopus is a species of great social and economic importance in the artisanal fishery context of SW Europe (Pierce et al., 2010). At present, in Galicia, octopus is basically exploited by a small-scale trap fishery of around 800 boats authorized to fish with traps that landed an average of ~2400 tons over the last 5 years (<http://www.pescadegalicia.com/>). As for most cephalopods, it has a short life cycle of less than two years; it grows rapidly to maturity, spawns once, often seasonally, at the end of its life and is an ecological opportunist with labile populations (Jereb et al., 2015). In Galician waters, the reproductive cycle appears to be seasonal with only one peak of spawning in spring time and a size at maturity estimated at 1.5 kg (Sieiro et al., 2014), though both females and males can reach maturity at much smaller sizes (Otero et al., 2007). The embryonic development lasts up to 4 months, depending on water temperature (Garci et al., 2016), and the hatching peak occurs at the end of summer, beginning of autumn of the same year (González et al., 2005). Then, depending on water temperature, octopus planktonic paralarvae stay in the water column

less than 3 months (Katsanevakis & Verriopoulos, 2006). In the pelagic realm, they are influenced by the frequency and intensity of upwelling episodes (Otero et al., 2008, 2016), and they feed on other zooplankton taxa before settling on the sea-bed (Roura et al., 2012). One of the most characteristic features for this species is that females during the reproductive period look for a shelter for spawning and care the eggs inside the refuge during all embryonic development until hatching occurs (Garci et al., 2016). Mark-recapture experiments suggest a sedentary behavior for this species in both the Atlantic (Fuentes & Iglesias, 2010) and the central Western Mediterranean Sea (Mereu et al., 2015a). However, several authors have suggested that, before spawning, this species performs an offshore-inshore migratory process for breeding in shallower waters (Quetglas et al., 1998) given the decrease in density and differences in the adult sex ratio along the depth gradient (Belcari et al., 2002).

Biological data

Sampling was undertaken off the Galician coast, between the river Eo mouth (43°32'N to 7°01'W) and the river Miño estuary (41°50'N to 9°40'W) (Fig. 1). Data were obtained from the historical (2000–2013) artisanal fishing sampling program run by the Unidade Técnica de Pesca de Baixura (UTPB, Technical Unit of Artisanal Fisheries) of the Xunta de Galicia (Galician Autonomous Government). UTPB observers are enrolled in fishing vessels randomly selected from the trap artisanal fishing fleet. In a single trip, each vessel usually performs numerous hauls, and thus at each haul, observers record all basic operational data such as date, geographical position, depth, and number of traps deployed in each haul. Apart from the operational data, the following information was recorded in each haul: total catch of both retained and discarded (i.e., individuals below 750 g and 1 kg which were the legal fishing size before and after year 2006, respectively) specimens, and total weight (± 10 g) and sex for each individual. Sex of each specimen was determined macroscopically by visually examining the presence of the hectocotylus, a modified third right arm of the male octopus. All specimens <200 g were excluded from analysis in order to avoid misidentification issues. In total, 115,780 individuals, sampled from 11,357 hauls performed during 1697 trips by 509 fishing vessels, were sexed during the period January 2000 to December 2013.

The Galician small-scale fishery is characterized for its intrinsic complexity in terms of the number of targeted species and gears used (Freire & García-Allut, 2000); however, the common octopus is a specific resource exploited almost exclusively by traps. Boats from the Galician artisanal fleet can license up to 5 different gears which can interchange along the year once they have notified the shift to the authorities. An average of 790 boats had a license to fish with traps

per fishing season since 2005. Each individual vessel would have a specific catchability given the intrinsic vessel characteristics. Therefore, if observers would have sampled the same vessels or just a small sample of the whole fleet, then catchability could be an important source of bias in the analysis. However, observers have sampled at least 10% of the total fleet, covering the complete boat size range, which can be considered as a representative sample of the total number of boats involved in such a fishery (Fig. S1 in Electronic Supplementary Material). Thus, despite the intrinsic complexity of the fishery, and the fishery-dependence nature of the data, we believe that this sampling design is appropriate for our purposes and has two main advantages: (i) it might reduce the likely bias in the aggregate catch of each fishing vessel due to differences in catchability and (ii) it provides a wider spatio-temporal coverage than a fishery-independent survey. Summarizing, we can assume that this monitoring provides a suitable and well-balanced set of data among years, seasons, and spatial coverage within the main fishing grounds of the study area.

Environmental data

Seafloor type information based on traditional fishers' knowledge was used in the modeling approach. Fishers characterize the sea floor in multiple categories; however, all these categories were reduced to three in order to harmonize all the information gathered in the surveys: hard (rocky bottoms), mixed (mixture of rocky and soft bottoms), and soft (sand, mud, etc.) bottom types which appear along the line of traps in a single haul.

To evaluate the role of environmental conditions as an indicator of habitat preference, we compiled data on sea surface temperature (SST, in °C) and upwelling intensity (UI, in $\text{m}^3 \text{s}^{-1} \text{km}^{-1}$). On the one hand, optimum interpolation SST data available at daily 0.25° latitude \times 0.25° longitude grid resolution from a combination of satellite and in situ measurements (Reynolds et al., 2007) were obtained from the NOAA Earth System Research Laboratory (<http://www.esrl.noaa.gov/psd/>) for the period 1999 to 2013. Each haul was assigned the SST data from the grid cell in which the given haul falls in. On the other hand, the upwelling intensity was computed in a $2^\circ \times 2^\circ$ cell centered at 43°N , 11°W (Fig. 1) from geostrophic winds calculated from the surface atmospheric pressure fields analyzed every 6 h by the Fleet Numerical Meteorology and Oceanography Center (<http://www.usno.navy.mil>) and following the method described by Bakun (1973). Data were obtained for the period 1999 to 2013 and downloaded from: http://www.indicedeafloramiento.ieo.es/index_en.html. Positive values of UI indicate upwelling-favorable conditions. Conversely, negative values indicate downwelling-favorable conditions.

At the latitude of our study site, temperature and upwelling show marked seasonality. Therefore, in order to avoid confounding relationships and interpretations, both environmental variables were deseasonalized and detrended using generalized additive models [see Alonso-Fernández et al. (2014) for details] before including that variable as a predictor in the GLMs (see below). For the upwelling time series, values outside the lower and upper extreme boundary were rejected before analysis of the time series (Álvarez-Salgado et al., 2002). The obtained environmental anomalies were averaged over a period of 18 and 6 days preceding the catch for UI and SST, respectively. Upwelling events at our latitude appear as a succession of wind stress/relaxation cycles with a wide variety of frequencies ranging from 3 to 15 days (Álvarez-Salgado et al., 2002). Therefore, we decided to average upwelling conditions over the three weeks preceding the catch to account for such variability. Temperature conditions are more stable along the season, and thus, a smaller time lag such as a week was considered good enough to depict the general thermal conditions preceding the catch.

Data analysis

Traditionally, sex ratio is calculated as the proportion of adult males to females. However, due to sex-related behavior and life history in octopus, we considered females the key component of the variation in sex ratio of the species. Therefore, in order to facilitate the interpretation, we modeled the probability of catching a female in each haul by means of fitting generalized linear models (GLMs; McCullagh & Nelder, 1989). In doing so, we assumed that the response variable, Sex_i was binomial distributed with probability π_i , $\text{Sex}_i \sim B(1, \pi_i)$, and expected mean and variance of Sex_i given by: $E(\text{Sex}_i) = \pi_i$, and $\text{var}(\text{Sex}_i) = \pi_i \times (1 - \pi_i)$. We let Sex be 1 if a specimen i was a female and 0 if male, and a logit link function was further used. The full model was then formulated as follows. The first term "logit" in the equation below should not be written in italics, just normal text. :

$$\text{logit}(\pi_i) = \alpha + \beta_1(\text{YR} \times \text{ZN})_i + \beta_2(\text{DP} \times \text{SS} \times \text{WT})_i + \beta_3(\text{SF} \times \text{SS})_i + \beta_4\text{SST}_i$$

where α is the intercept; β_n 's are the linear coefficients; and ε is the error term. Nine explanatory variables were included in the model: YR, year of operation; SS, season of operation; ZN, Galician zone; DP, depth of operation; SF, type of seafloor; SST, sea surface temperature; UI, upwelling Index; WT, total weight of each individual caught; and CPUE, catch per unit effort of the haul in which each individual i was caught. Year was a factor, and SS was also a factor with four levels comprising winter (SS1: December–February), spring (SS2: March–May), summer (SS3: June–August), and autumn (SS4: September–November).

ZN was included as a categorical variable dividing the Galician coast in three oceanographic zones (ZN1: Rías Baixas, ZN2: Arco Ártabro, and ZN3: Cantábrico, Fig. 1) in agreement with the well-known differences in the environmental conditions that occur along the coast (Álvarez-Salgado et al., 2011; ~~Álvarez et al.~~, 2008). DP was a categorical variable with four levels (DP1: [0–25) m, DP2: [25–50) m, DP3: [50–75) m, and DP4: >75 m), and SF was also a categorical variable with three levels (SF1: Hard, SF2: Mixed, and SF3: soft), and jointly with SST and UI were meant to account for habitat preferences. CPUE, estimated as the number of octopus per trap caught in each haul, was further included in the model to account for potential local density-dependent effects on SR. Three reasonable interactions were further included in the model. First, YR by ZN interaction, which may capture different temporal trends for each of the oceanographic zones defined in our study area; second, WT by DP by SS interaction, which would account for the ontogenic-related seasonal migration along the depth gradient; and third, SF by SS, which may capture seasonal changes in habitat use. A summary of all variables considered in the full model and corresponding distribution of the data are available in Table S1 and Fig. S2.

Prior to model run all explanatory covariates were inspected for collinearity using variance inflation factors (VIFs; Zuur et al., 2010), and WT and CPUE were natural log-transformed. The GLM was built on the open-source AD Model Builder nonlinear fitting engine (Fournier et al., 2012). AD Model Builder has the capability to run post hoc Markov chains (MCMC) to assess the variability for the fixed effects assuming flat priors. Thus, to evaluate the uncertainty of each explanatory variable, we report 95% credible intervals calculated as the highest posterior density (HPD) interval using 100,000 MCMC iterations.

All analyses and treatment of data were performed on R-3.2.4 (R Development Core Team, 2014) and using packages “glmmADMB_3.1.1” (Skaug et al., 2014), “coda_0.18-1” (Plummer et al., 2006), and “ggplot2_2.1.0” (Wickham, 2009).

Results

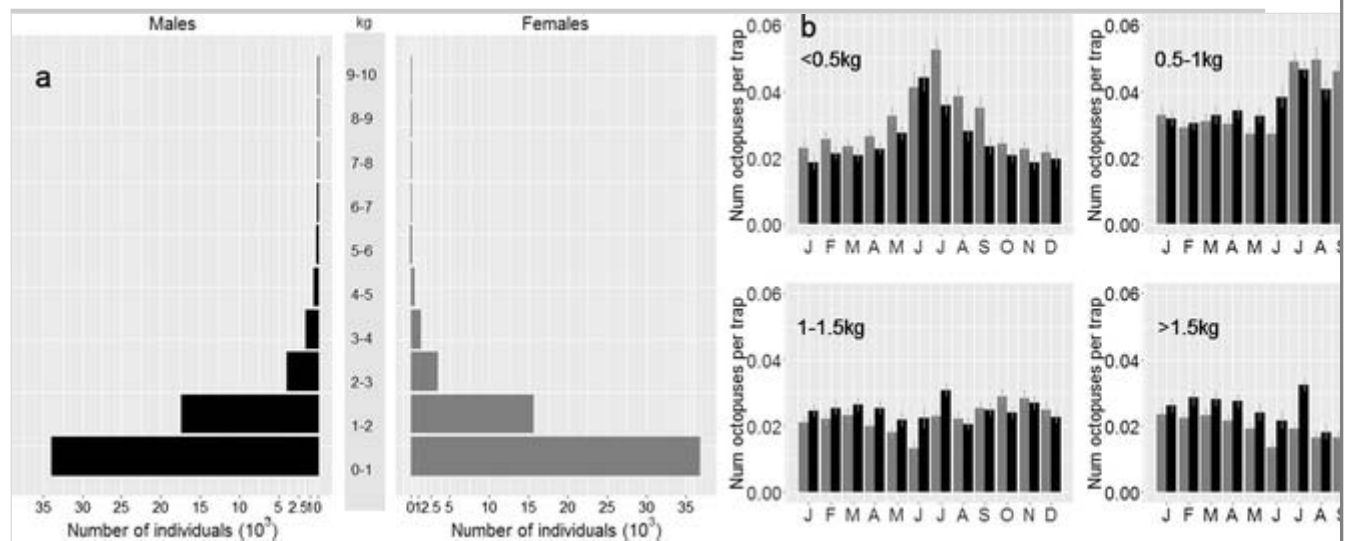
Descriptive statistics

Out of a total of 115,780 octopus sexed during the study period, 58,216 were males (50.28%) and 57,564 were females (49.72%); however, this proportion was not constant neither in time nor in space (see below). Sexed females ranged from 200 g to 8300 g and averaged 1019.53 ± 745.35 g, while males ranged from 200 to 9700 g and averaged 1130.55 ± 845.41 g with different proportions between size groups. SR was biased to females at smaller size classes; however,

larger size classes were dominated by males (Fig. 2 a, b). Size classes also depicted differing seasonal patterns, while the number of individuals below 500 g per trap (as a proxy for recruitment) peaked in summer months, the bulk of the adult cohort maximized over the autumn–winter period (Fig. 2b).

Fig. 2

Distribution of male and female individuals of *Octopus vulgaris* across size classes (a). b shows the average number of octopus per trap by month for the time period 2000–2013 and separated by four representative size classes. Black bars are for males and gray bars for females. Error bars show 95% confidence intervals



Sex ratio modeling

Calculation of VIFs for all explanatory variables revealed no signs of collinearity, with all values below a cut-off level of 3, and the inspection of the trace plots and posterior distribution of the coefficients showed no major model convergence or performance issues (Fig. S3 and S4, respectively). Table 1 shows the Type I analysis of deviance for the SR model, and the coefficient estimates and HDP credible intervals for all variables included in the full GLM are provided in Table S2 and Fig. S5. We found that SR was negatively related to the size of the individuals and that this relationship was likely to vary among seasons (Table 1). More specifically, the probability of catching a female decreased with body size and the steepest decline occurred during summer months (Fig. 3 a). The SR was female-biased in smaller sizes, whereas males dominated in larger size classes being this fact especially apparent in summer when males started to dominate from ~0.6 kg onward as compared to autumn when the shift occurred around ~1.5 kg (Fig. 3 a). Additionally, the model results showed that this decline in female probability with body size was similar in all depth strata, although the negative relationship was less pronounced in shallower waters (Fig. 3 b). Furthermore, we also found

a substantial variation in how depth distribution affects SR depending on the season of the year. During autumn, the proportion of sexes remained relatively stable along the depth range of fishing activity with females dominating in all depth strata. By contrast, in summer, males dominated along the full depth range. In the other two seasons, sex-dominance shifted slightly from males in shallower waters to females in deeper waters being this change more apparent in spring months (Fig. 3c).

Table 1

Analysis of deviance (Type I) of the SR model (see text)

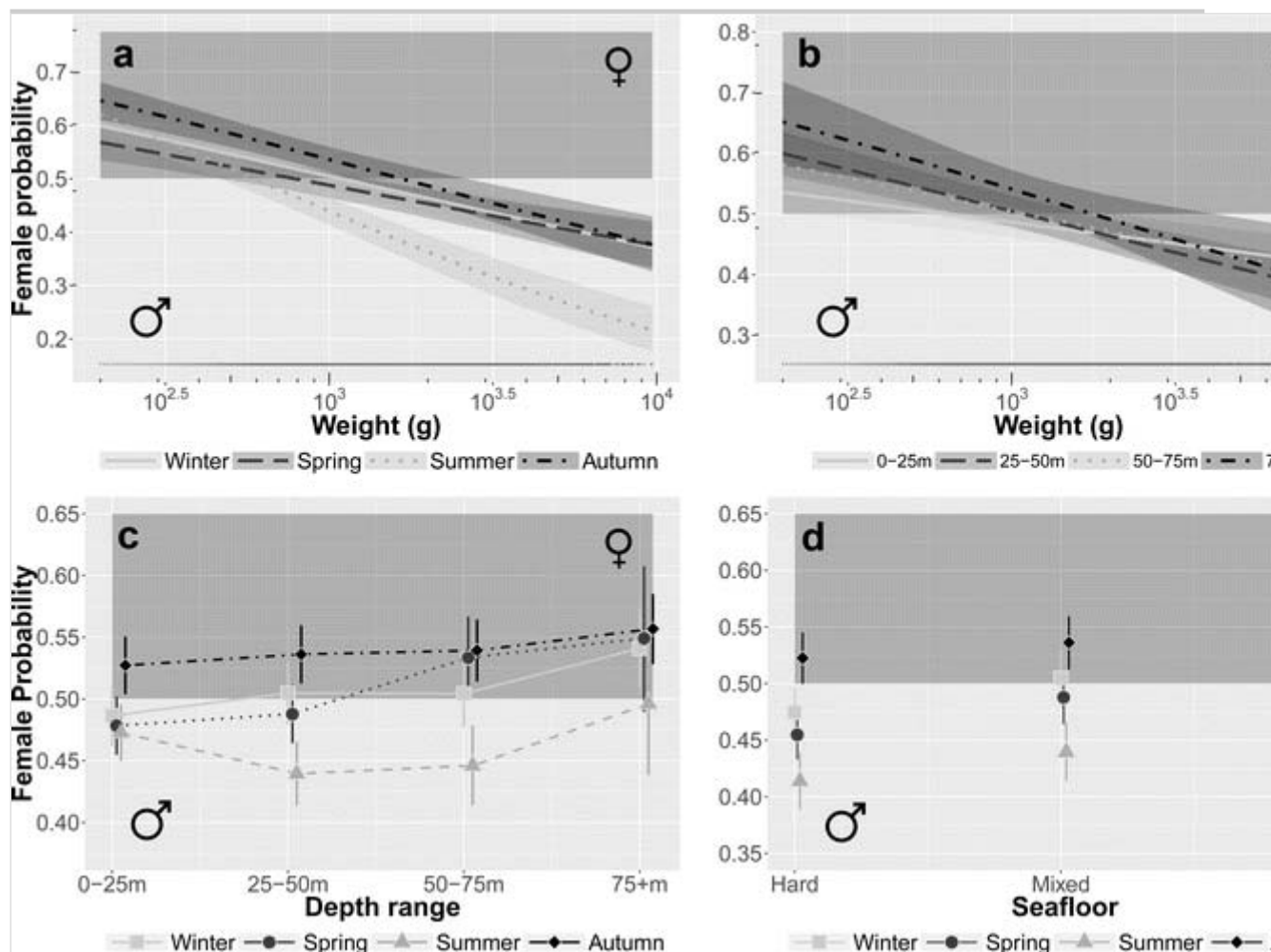
	df	Deviance	Resid. df	Resid. dev	P value
NULL			115,019	159,448	
YR	13	456.56	115,006	158,992	<2.2e−16
ZN	2	110.16	115,004	158,881	<2.2e−16
WT	1	690.77	115,003	158,191	<2.2e−16
DP	3	142.16	115,000	158,048	<2.2e−16
SS	3	232.82	114,997	157,816	<2.2e−16
SF	2	57.58	114,995	157,758	<0.0001
SST	1	1.03	114,994	157,757	0.3106
UI	1	0.29	114,993	157,757	0.5889
CPUE	1	2.67	114,992	157,754	0.1024
YR:ZN	26	319.68	114,966	157,434	<2.2e−16
WT:DP	3	2.39	114,963	157,432	0.4955
WT:SS	3	134.99	114,960	157,297	<2.2e−16
DP:SS	9	34.45	114,951	157,263	0.0001
SF:SS	6	22.47	114,945	157,240	0.0010
WT:SS:DP	9	6.76	114,936	157,233	0.6624

df degrees of freedom, *Resid. df* residual degrees of freedom, *Resid. dev* residual deviance. See the main text and Table S1 for abbreviations

Fig. 3

Predicted model results for the main sources of variation in octopus SR. **a** Seasonal variation in the relationship between SR and body size; **b** relationship between SR and body size by depth range; **c** seasonal variation in the relationship between SR and depth of trap deployment; and **d** seasonal variation in the

relationship between SR and seafloor type. Predictions for **a–d** were obtained for the oceanographic zone Rías Baixas in year 2000 and continuous variables were held at $SST = 0^{\circ}\text{C}$, $UI = 0 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$, and $CPUE = 0.2$ octopuses per trap. We used Mixed seafloor as reference level for **a–c**. In **a** and **d**, depth stratum was held at (25–50] m, and in **c** and **d**, individual size was held at the natural log of 1000 g. *Shaded areas* in **a** and **b**, and *error bars* in **c** and **d** show 95% confidence intervals for the predictions



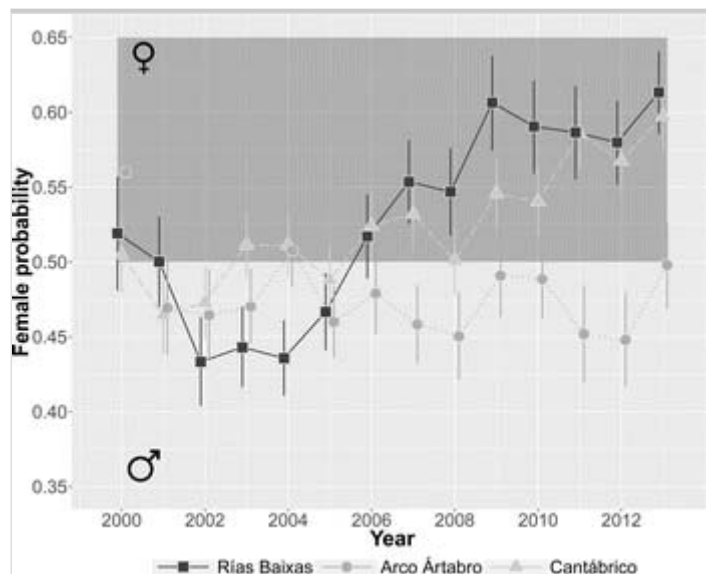
The inclusion of environmental variables in the model revealed distinct results (Table 1). First, SR was likely to be affected by seafloor type. Female octopuses showed higher prevalence in mixed and soft bottoms as compared to hard seafloor substrates, mainly during summer (Table 1; Fig. 3 d). Second, neither SST nor UI were found to be likely influential factors in driving variations in SR (Table 1). Furthermore, local density of octopus, roughly measured by means of CPUE estimates, was not related with female proportion (Table 1).

Finally, at a broader geographical and temporal scale, the model revealed differing inter-annual trends in female proportion among the three oceanographic zones. On the one hand, both the northern (Cantábrico) and southern (Rías Baixas) areas experienced a steady increase in the proportion of females during

the study period. On the other hand, the female-to-male ratio remained relatively constant in the central part of the Galician coast (Arco Ártabro) (Fig. 4). These contrasting trends started to diverge basically from 2006 onward and showed the highest differences at the end of the time series.

Fig. 4

Predicted inter-annual (2000–2013) variation in SR by oceanographic zone. Predictions were obtained for the Winter season in a Mixed seafloor and at the (25–50] m depth stratum. Continuous variables were held at SST = 0°C, UI = 0 m³ s⁻¹ km⁻¹ and CPUE = 0.2 octopuses per trap. *Error bars* show 95% confidence intervals for the predictions



Discussion

Significant deviations from an equal sex ratio at any stage of an organism's lifetime are a common feature in nature (e.g., Weimerskirch et al., 2005; Sinclair et al., 2012). Multiple processes can produce skews in sex ratios, from a number of sex-related physiological and/or behavioral traits in specific life stages to environmental conditions and adaptive adjustments of the progeny's sex ratio to maximize the parents' fitness (Hardy, 2002). Most studies on sex ratio variation have been focused on understanding the mechanisms causing primary, secondary, or tertiary sex biases in terrestrial vertebrates and invertebrates so as in plants (Hardy, 2002). However, much less is known regarding marine species for which direct observations of individual behavior are not usually available, and thus, it is hard to disentangle between real patterns and sampling bias. This is even more problematic for exploited species. For instance, in fished stocks, it is relatively common to observe changes in sex distribution due to seasonal variation in male and female catchability, which is usually ascribed to contrasting annual biological cycles and the differing sex-

susceptibility to the environmental conditions that might constrain their specific physiological requirements (Solmundsson et al., 2003; Ziegler et al., 2004). Our approach tried to overcome these difficulties by means of analyzing sexed individuals by onboard observers with a wide spatio-temporal coverage and sampling the broad spectrum of octopus's size classes. In this regard, common octopus in the studied waters can reach maturity at small sizes (Otero et al., 2007). This implies that we, somehow, have dealt with tertiary sex ratio sensu Myers (1939); however, a large proportion of the individuals included in the study can be considered juveniles though. Unfortunately, information on maturation was not available. Therefore, we can speak of sex ratio at the population level. In populations subjected to intensive exploitation, the spatio-temporal variation in sex ratio could result in disproportionate harvesting of a specific sex with unknown consequences for the populations and fished stocks (Morgan & Trippel, 1996; Wearmouth & Sims, 2008). Therefore, it is timely to understand the factors that drive SR variability in coastal populations of commercial interest.

Many marine organisms may be distributed differently with respect to body size in response to differing nutritional requirements, predation risk, or activity budgets which are the basic postulated mechanisms underlying the hypotheses for explaining sexual segregation (Wearmouth & Sims, 2008). Regarding common octopus, we found a clear pattern: the proportion of females decreased as body size increased, and the strength of this decline varied among seasons. It is well known that this species presents a hiding behavior for spawning. Once mating has occurred, and females are ready to spawn, they search for a refuge in shelters to lay the egg strings and care the offspring for up to four months until hatching happens (Garci et al., 2016). After this period, females die. This strategy implies that females would not be available for the fishery over the spawning and breeding months. Changes in activity patterns due to spawning and parental care are common in many marine organisms. For instance, in Galician waters, the life history strategy and behavior of the sedentary ballan wrasse shape the catchability of passive fishing gears like gillnets (Villegas-Ríos et al., 2014). In marine invertebrates, such as *Palinurus elephas* (Fabricius, 1787) and *Jasus edwardsii* (Hutton, 1875), mating behavior and seasonal molting are also good predictors of changes in catchability (Goñi et al., 2001; Ziegler et al., 2004). In the study region, octopus spawning tends to occur all year round, although there is a marked peak of sexual maturation in spring months (Sieiro et al., 2014). Thus, this fact would explain the disappearance of females from the catches at larger sizes and why this effect would be more pronounced in summer months during the period of parental care. By contrast, the SR was female-biased at smaller size classes in all seasons. This fact might be explained as a result of higher daily growth rates in females (Domain et al.,

2000; Mereu et al., 2015b) which would make females available for the fishery much earlier than males of the same age. A rapid decrease in female proportion with the increase of body size seems to be a general pattern as indicated by results found in different locations (e.g., Northwest coast of Africa, Hatanaka, 1979; and Japanese waters, Sakaguchi et al., 2000). However, in those areas, the ratios were ca. 1 in smaller size classes contrasting with our results.

Sex-dependent distribution patterns along a depth gradient are frequent in many marine organisms in response to differing foraging strategies or social behavior (Wearmouth & Sims, 2008). We found that SR was related to the depth of fishing operation (ranging from 1 to 150 m), and this relationship varied seasonally. The female proportion tended to increase toward deeper waters basically during winter and spring. However, two different patterns occurred in summer and autumn. While males dominated in all depth strata during summer months, basically the breeding period, in autumn, when new recruits are growing, females dominated along the bathymetric gradient. Additionally, the decrease in SR with body size was fairly similar in all depth strata. Differing ratios among seasons is a common feature for this species as found in South African waters (Smith & Griffiths, 2002), Northeastern Atlantic waters (Otero et al., 2007), or the Canary Islands (Hernández-García et al., 2002). Other authors, however, did not find monthly differences (Silva et al., 2002). Apart from the seasonality, bathymetric gradients are also frequently studied providing contrasting results. While Oosthuizen & Smale (2003), working on the southeastern coast of South Africa up to 20 m, found significant deviances from the 1:1 ratio by depth with a female dominance in intertidal waters and no significant difference in the subtidal sex ratio, others did not show any variability in SR by bathymetric stratum as shown in the Gulf of Cádiz up to 500 m depth (Silva et al., 2002). These disparities in bathymetric trends among studies may well be the result of using different sampling methodologies that might target contrasting fractions of the population, or even different species within the species complex (Amor et al., 2016). Therefore, comparisons may be taken with caution. Notwithstanding, common octopus is a coastal species constrained by the outer edge of the continental shelf that could undertake limited seasonal migrations (Jereb et al., 2015). For an animal to be considered migratory, they have to perform “persistent and straightened-out movements effected by the animal’s own locomotory exertions [...]” (Kennedy, 1985), a definition well-suited for squids and other cephalopods (Hanlon & Messenger, 1996). Regarding common octopus several authors have postulated the occurrence of an inshore migratory displacement for spawning based on a distinct distribution pattern for recruits and adults. This would also differ among regions. In particular, in the Mediterranean Sea and Canary Islands, mature females would move to shallower waters looking for shelters to spawn, and

recruits would be distributed over an extensive large area. By contrast, in Northwestern African waters, recruitment would be exclusively coastal, and spawning would occur over the whole continental shelf once juveniles have dispersed toward deeper waters, i.e., ontogenic migration (see Faraj & Bez, 2007, for more details). However, recent mark-recapture experiments carried out in Northeastern Atlantic waters (Fuentes & Iglesias, 2010) and the central Western Mediterranean Sea (Mereu et al., 2015a) suggested a sedentary behavior for this species providing no significant evidences for any long distance seasonal migrations; octopuses would rather “make limited horizontal movements probably linked to the availability of food partners and/or shelters” (Mereu et al., 2015a). Therefore, whether common octopus performs well-marked seasonal reproductive migrations, or just limited horizontal movements, or both, seems to be a question not fully resolved.

Regarding our NE Atlantic area, in light of the results presented in this study and taking into account the above explanations, we could suggest the following scheme: in summer, during the spawning and parental care period, larger females would not be available for the fishery in any sampled strata due to the hiding behavior for breeding and massive post-spawning mortality; however, in autumn, when new recruits have been incorporated to the system, the ratio would be female dominated in all the bathymetric gradient, with a slight increase toward deeper waters, presumably as a result of higher growth rates. In winter and spring, females would dominate seawards, though and apparent displacement toward the coast for spawning would be also evident given the lower ratios in the shallower strata. The new cohort of paralarvae would hatch mostly at the end of summer beginning of autumn (González et al., 2005), and oceanographic processes would favor their retention in the area (Otero et al., 2007, 2016) resulting in coastal recruitment (Moreno et al., 2014). Thus, we hypothesize that *O. vulgaris* in NE Atlantic waters would disperse toward deeper waters as juveniles following an ontogenic displacement and females presumably would move back to the coast for spawning and significantly contributing to the skewed sex ratios. Notwithstanding, these movements would be by no means large displacements, and they would rather be limited movements that need further confirmatory studies on spatial distribution of body size and abundance, and probably extensive tagging experiments. Moreover, considering standard definitions and concepts of fish migration (see Morais & Daverat, 2016, and references therein), we would classify this behavioral pattern as a sexual segregation rather than a true migratory behavior. This would broadly concur with the predation-risk hypothesis (reproductive strategy hypothesis) postulated by Wearmouth & Sims (2008) which states that female habitat choice is primarily driven by a necessity to reduce predation risk and maximizing offspring security even at the cost of sub-optimal foraging conditions. The latter would not apply to octopus as they

stop feeding during the breeding period. Regarding other cephalopod species, there have been described complex spatial behavioral patterns that differ among sexes like habitat range expansion in *Sepia officinalis* Linnaeus, 1758 (Bloor et al., 2013), ontogenic vertical migrations in deep-sea cephalopods (Villanueva, 1992), or the residence time in breeding areas of a giant Australian cuttlefish, *Sepia apama* Gray, 1849 (Payne et al., 2011). However, few examples have reported sex-related changes in migratory processes. For instance, Arkhipkin & Middleton (2002) illustrated about the seasonal shifts in the variation of SR by depth linked to vertical and spatial migrations in *Doryteuthis (Amerigo) gahi* (d'Orbigny, 1835).

The mechanisms affecting the deviations from equal sex ratios can depend on environmental conditions. For instance, winter rainfall affects nutritional stress during red deer pregnancy influencing the sex ratio at birth (Kruuk et al., 1999), and low levels of salinity increase the proportion of females at hatching in marine Polychaeta (Prevedelli & Simonini, 2000). However, comparatively fewer studies have focused on studying this influence on tertiary sex ratios. Manning et al. (2015) provided evidence that climate interacts with local demography and resources to determine asymmetrical adult sex ratios in feral horses, and resource levels may drive the adult sex ratio variation in freshwater Trinidadian guppies (McKellar et al., 2009). Regarding the marine realm, in ectotherms, sex differences in thermal habitat selection is probably the most common environmental driver for unbalanced sex ratios (Wearmouth & Sims, 2008). Environmental conditions can also act as triggering factors of specific life history events like upwelling and temperature conditions affecting the deposition of egg strands by squids, thus, driving the presence of females in spawning areas (Downey et al., 2010). However, SR in *O. vulgaris* was not likely to be affected by changes in SST. Additionally, we also included in the model the upwelling intensity as an indirect parameter of system productivity (Álvarez-Salgado et al., 2002). However, SR was not likely to be affected by this factor either. Apart from these two environmental parameters, we further included the fishers' knowledge on seafloor type to ascertain sex-related habitat preferences. As such, we found a substantial prevalence of females in mixed and soft bottoms over a hard seafloor mainly during summer. A likely explanation could rely on changes in sex-related vulnerability and habitat use. In general, *O. vulgaris* females use hard complex structures such as rocky outcrop and hard bottom substrates for making their spawning nests (Garci et al., 2016). Consequently, females reduced their vulnerability to fishing due to breeding behavior that occurs preferentially in hard bottoms substrates as it was observed during summer.

Besides the abiotic factors that may drive variations in sex ratios, there is also substantial evidence regarding the influence of demographic traits, such as population density, in operating as a mechanism affecting sex proportion at birth (Kruuk et al., 1999) and also at the adult level (Donald, 2007). This demographic influence can be even more complex through interactions with the weather fluctuations (Manning et al., 2015). Regarding marine organisms, population density has been negatively related to the proportion of females in Japanese eel (Han & Tzeng, 2006). In our model, we included the CPUE as a rough index of local octopus' density in order to account for density-dependent effects. However, octopus SR was not likely affected by changes in local density, which may be explained by the solitary behavior of this species. Additionally, our index of octopus' density could not accurately capture the changes in abundance over an appropriate and influential spatial scale.

We found inter-annual fluctuations in octopus SR, though the pattern varied depending on the oceanographic zone. While the southern (Rías Baixas) and northern (Cantábrico) areas showed a steadily increase in the proportion of females in the catch, the central part of the Galician coast (Arco Ártabro) remained relatively stable. Annual variations in SR for this species were also found in neighboring areas. For instance, (Fernández-Rueda & García-Flórez, 2007) using data from the coast of Asturias (Northern Spain) showed an overall predominance of males in the artisanal catches with a maximum in 2002 over the period 2002–2005. However, apart from this example, long-term analyses of sex ratio for this species are limited. Our two distinct trends are difficult to explain and could be influenced by a combination of different factors that might be attributed to changes in the legislation passed by the Galician authorities in 2006 and the implementation of differing specific exploitation plans along the coast. Some of these measures include: an increase in the minimum legal landing size from 750 g to 1 kg; the establishment of no-catch periods during the end of spring and early summer (generally in July; though the specific dates have changed along the coast among years); and the general restriction of fishing operations, i.e., gear deployment and retrieval, to daylight hours. Given these facts, a change in the size limit could have affected the sex balance as a result of sexual differences in growth rates and mortality rates which would have influenced the catchability of both sexes. Indeed, in exploited fish populations with significant body size differences depending on sex, it has been documented that gear selectivity can induce sex-selective fishing ultimately affecting sex ratios (Kendall & Quinn, 2013). Additionally, the inclusion of specific periods of fishing closures may have interacted with the life cycle of the species influencing the population estimates due to sampling bias or even affecting directly the population composition. Finally, restricting the fishing operations to

daylight hours could have changed the daily patterns of fishing effort. Thus, sex ratio may have been affected by this fact if there were apparent any sex-related differences in octopus' circadian rhythms that would ultimately affect their vulnerability to the fishing gear. However, studies on common octopus' activity patterns are scarce and have arisen conflicting results (Meisel et al., 2003). Nevertheless, the ultimate causes of these broad spatio-temporal patterns remain unclear and further research might be conducted to investigate the relationship of SR with population status.

We can conclude that data obtained from onboard observers have been revealed as a useful source of information to better understand the factors that drive the spatio-temporal patterns in SR for a highly exploited marine coastal species. As such, we found that variations in SR of common octopus at the population level were driven by a set of temporal, spatial, and environmental factors. The SR was biased toward males during spring and summer, basically within the mature fraction of the population. We suggest that this pattern is highly associated with differences in mortality and behavioral patterns related to the reproductive cycle and hiding strategy of females for breeding. Certain sexual segregation due to ontogenic and reproductive processes would be apparent, though further detailed studies on spatial distribution of body size and abundance, so as acoustic telemetry experiments would be needed to confirm the hypothesis anticipated here. Octopus SR was likely affected by habitat type with male-biased distribution associated to hard bottoms substrates mainly in summer. This fact would be also likely driven by the behavior of females during the breeding period. However, other environmental factors, namely, thermal conditions and upwelling intensity did not show any influence on the variation in SR. Furthermore, octopus SR was not affected by local density. Finally, annual trends in SR varied geographically along the Galician coast in the three different oceanographic areas, which may be partially related to changes in the exploitation regimes conditioned by the legislation. In summary, all these factors may affect the catch composition of common octopus in Galician waters and ultimately have significant influences on the population estimates that might be further consider when implementing future monitoring, assessment and management plans. To this respect, the current management rules, such as the no-fishing periods, should be thoroughly revised.

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest and consent was obtained from all participants of the study.

Ethical Approval All the animals have been sampled from regular operations of the artisanal fishery under the regional monitoring program of the fishing activity.

Electronic supplementary material

Below is the link to the electronic supplementary material.

Supplementary material 1 (PDF 393 kb)

Supplementary material 2 (PDF 5 kb)

Supplementary material 3 (PDF 33 kb)

Supplementary material 4 (PDF 610 kb)

Supplementary material 5 (PDF 412 kb)

Supplementary material 6 (PDF 9 kb)

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