Inter-Research Science Publisher
Marine Ecology Progress Series
Volume 756:111–126
Published March 13, 2025
https://doi.org/10.3354/meps14810

Seasonal patterns in the distribution of *Engraulis anchoita* in the North Patagonian Continental Shelf of Southwestern Atlantic Ocean

Manuela Parietti*, Micaela Giorgini, Bruno V. Menna, Paula Orlando, Claudio C. Buratti

National Institute of Fisheries Research and Development, Ministry of Economy, Paseo Victoria Ocampo No. 1, North Breakwater, Mar del Plata, Buenos Aires Province B7602HSA, Argentina

ABSTRACT: The Patagonian stock of the anchovy *Engraulis anchoita* is distributed between 41° and 47° 30′ S over the Argentinian Shelf. This is an underexploited species that plays a key role in the North Patagonian ecosystem (Southwestern Atlantic Ocean) since it constitutes the food of numerous species of fish, birds, and marine mammals. Knowing the spatial and seasonal dynamics of the abundance of this species is a valuable source of information for understanding how it could affect the functioning of this ecosystem. To this end, the effect of oceanographical variables on the presence/absence and relative abundance of the Patagonian anchovy were analyzed in 2 seasons over a 10 yr period. A mixed effect of the oceanographic variables and the relative abundance in warm and cold seasons was found, as well as differences in abundance and presence of this species when comparing consecutive seasons. The spatial evolution of the distribution of the Patagonian anchovy shows a contraction/expansion pattern. It contracts towards the northern area and towards lower latitudes during cold seasons (up to 45° 30′ S) and then disperses to occupy the entire studied area during warm seasons, reaching 47° 30′ S. Knowing the spatial and seasonal dynamics of small pelagic fish is valuable for achieving sustainable management of different resources within the framework of an ecosystem approach.

KEY WORDS: Spatio-temporal distribution · Pelagic ecosystem · Environmental effect · Seasonality · *Engraulis anchoita* · Southwestern Atlantic Ocean

1. INTRODUCTION

The Argentine anchovy *Engraulis anchoita* Hubbs & Marini, 1935 is one of the most important pelagic fishery resources inhabiting the Argentinean Continental Shelf (Southwestern Atlantic Ocean, SWAO). Its area of distribution is wide, ranging from the coastal region to the continental slope zone, from the La Plata river (35° S) to the south of the San Jorge Gulf, in the Northern Patagonian Continental Shelf (NPCS, 47° 30′ S) (Angelescu & Cousseau 1967). This fish species tolerates a wide range of temperatures (8 to 23°C) and salinities (14 to 35 psu), like other species of the genus *Engraulis* (Hansen 1994). Two stocks or fishery management units have been identified off Argentina: a Bonaerensis stock (northern stock) and a Patagonian stock (southern stock), separated at approximately 41° S, based on information from meristic and morphometric characters, parasitology, and population parameters (Ratti 1986, Hansen 1994, Timi 2003). The Patagonian stock is underexploited. Based on the information collected from 10 research surveys carried out by the National Institute for Fisheries Research and Development (INIDEP, Ministry of Economy), during the peak of spawning activity in December, the total biomass of

---

*Corresponding author: manuelaparietti@gmail.com the Patagonian anchovy stock between 2005 and 2014 fluctuated between 1 040 000 and 1 730 000 tonnes (t) (average = 1 260 000 t). The average catch in the period was 2162 t yr^{-1} (Orlando et al. 2023).

Due to its large biomass, foraging habits in the food web, and ecosystem role, the Patagonian anchovy plays an important part in the north Patagonian ecosystem (e.g. Angelescu 1982, Yorio et al. 2017, Koen Alonso et al. 2000, Buratti et al. 2022), as it provides food for numerous species of fish (Sánchez 1995), bird (Marinao & Yorio 2011, Gatto & Yorio 2016, Yorio et al. 2017, Ciancio et al. 2021), and marine mammal (Koen Alonso et al. 1998, 2000, Dans et al. 2003). It is characterized by large interannual fluctuations in its abundance, like other small pelagic fish species (Hilborn et al. 2022). Small pelagic fish (SPF) have a key ecological role, exerting downward control over zooplankton and upward control over pelagic predators, termed 'wasp waist' control (Rice 1995), as seen for *E. anchoita* in the NPCS (Buratti et al. 2022). Thus, large fluctuations in these SPF due to natural factors can have considerable effects on both plankton and predators (Santos et al. 2007), and can greatly modify the structure and function of marine ecosystems (Cury et al. 2000, Costalago et al. 2012).

Moreover, a growing number of studies have shown that key variables commonly used to assess the impacts of climate variation on marine organisms, such as sea temperature variations, chlorophyll *a* concentration, rainfall, and sea level can significantly change the abundance, distribution, and recruitment of SPF (Checkley et al. 2009, Maynou et al. 2014, Brosset et al. 2017). In addition, they could also indirectly affect fish population dynamics by changing food availability (e.g. zooplankton; Pacariz et al. 2016, Nakayama et al. 2018). In the NPCS, where the southern distribution limit of *E. anchoita* has been reported, 2 areas of significant opposite trends in sea surface temperature were observed in the last decade: a warming area between 42° and 45° S, and a cooling area between 49° and 52° S (Risaro et al. 2022). In addition, Risaro et al. (2022) detected a break-point in the area in 2008, with a constant increase in positive temperature anomalies for the region, which could be affecting the Patagonian anchovy. In this scenario, knowing the effect of environmental variables on fish abundance and distribution is essential for assessing the effect of future environmental changes on commercial species and fisheries management.

Previous work has evaluated the effect of abiotic variables over the distribution and abundance of the Patagonian anchovy (Hansen et al. 2001). For instance, the highest fish abundances were related to sharp thermal gradients in the spring, where the formation of sea fronts began (Guerrero & Piola 1997). Although the work of Hansen et al. (2001) increased knowledge about the distribution patterns for this species, in the current context of climate change, coupled with the aforementioned recorded changes, it is important to re-evaluate the existing knowledge. Fortunately, we have a wide time series and a greater spatial coverage to do so. For this purpose, this work aimed to analyze the spatio-temporal distribution (with year-to-year and seasonal comparisons) of the Patagonian anchovy over 10 yr, specifically within a sub-area (43° to 48° S) corresponding to the southern limit of the stock, considering the effects of environmental conditions on the abundance and distribution of this resource. We expected this species to show large seasonal fluctuations in abundance and distribution, like other pelagic species, which may be related to changes in oceanographic conditions.

2. MATERIALS AND METHODS

2.1. Study area (43° to 48° S)

The NPCS (Fig. 1b), located in the SWAO, is characterized by 2 main water masses: Sub Antarctic Shelf Waters (salinities between 33.4 and 34) running in the Malvinas Current, which occupy most of the shelf, and Magellan Strait Waters (salinities < 33.4) present in the inner and mid-shelf as a low-salinity surface tongue, running in the Patagonia Current (Palma et al. 2008; our Fig. 1a). The annual thermal cycle shows well-defined seasons with a sinusoidal pattern typical of Southern Hemisphere middle latitudes, with minimum temperatures in August to September and maximum ones in February to March (Allega et al. 2021). The region is characterized, in the north, by the presence of 3 oceanographic fronts that integrate the Norpatagonic frontal system, and in the south, by 2 frontal systems located south and offshore of the San Jorge Gulf (Glembocki et al. 2015). Over the shelf break (SB), where the maximum depth reaches 4000 m, the SB front is generated by the Malvinas Current, which flows northwards carrying cold and nutrients-rich waters (Matano & Palma 2008). All these fronts influence water flow and result in circulation features that often aggregate and retain zooplankton and poorly swimming organisms, making prey available near the surface for diving predators (Acha et al. 2004).

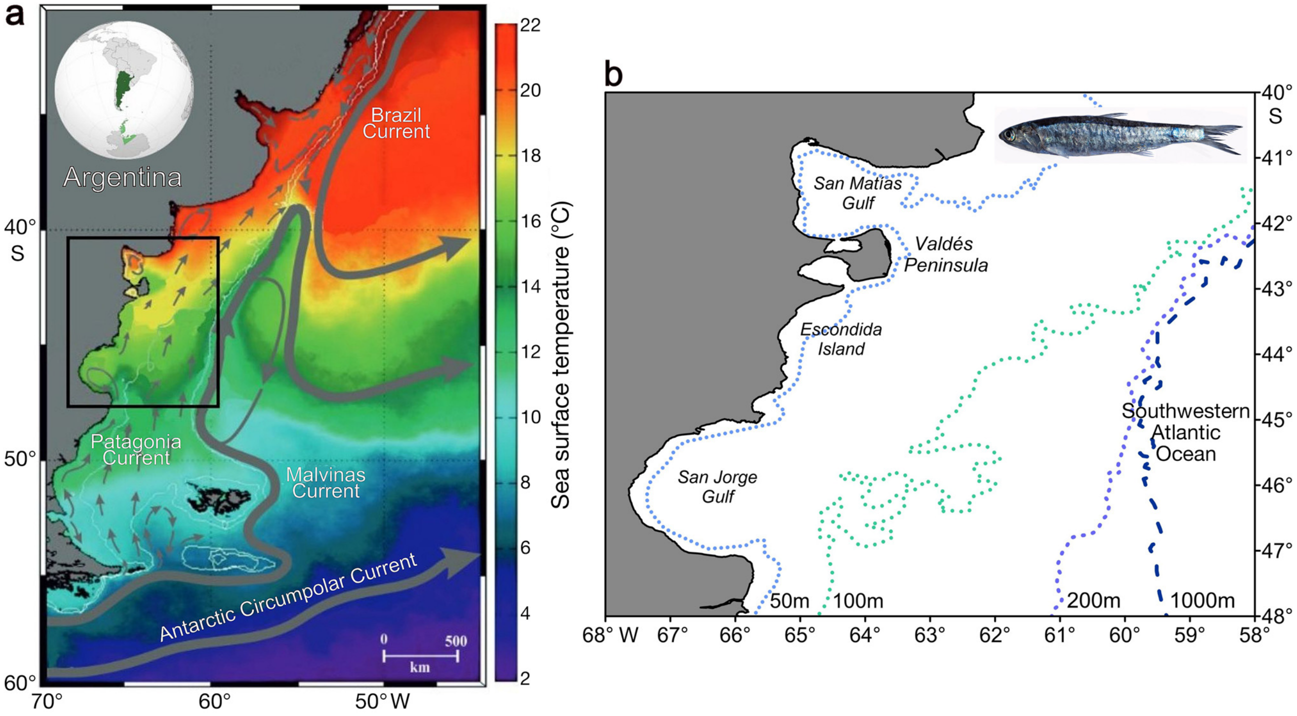

Fig. 1. Argentine Continental Shelf (Southwestern Atlantic Ocean). (a) General circulation scheme over the region and climatological sea surface temperature (1985–2015) redrawn from Allega et al. (2021). Thick arrows: schematic circulation of the Antarctic Circumpolar Current, Malvinas Current and Brazil Current; thin arrows: Patagonia Current. (b) Study area on the north Patagonian Shelf, indicating bathymetry (50, 100, 200 and 1000 m isobaths)

2.2. Acquisition and processing of acoustic and oceanographic data

To analyze the distribution patterns of the Patagonian anchovy, acoustic data collected during the surveys conducted by INIDEP in the study of the southern stock of Argentine hake *Merluccius hubbsi* were used. Acoustic methods have been widely used in fisheries research for pelagic fish biomass estimation, lately including very sophisticated techniques, such as multi-frequency, wide band, multibeam, vertical, and horizontal echosounding (Georgakarakos et al. 2011). There is a spatial coincidence of Patagonian anchovy schools with Argentine hake. This bony fish preys on Patagonian anchovy, feeding mainly on the pre-adult and adult fractions of the Patagonian population (Belleggia et al. 2017). One of the advantages of the acoustic methods used in research surveys is the possibility of studying the spatial distribution of resources from research carried out on surveys targeting other species of fishery interest (Simard et al. 1993). We analyzed the 2005 to 2014 warm season surveys, carried out to assess the abundance of juvenile and spawning Argentine hake during austral summers (January and February), and the global cold surveys of 2005, 2006, 2011, and 2013, carried out from August to October (Table 1). The warm season surveys covered the area between 43° and 47° S from 50 to 180 m depth, while the winter surveys covered an area between 41° and 48° S and depth between 40 and 230 m. It is worth mentioning that the spatial extent of the survey paths in the warm and cold seasons is not the same, since they have different specific objectives. Moreover, the path covered within cold season surveys is not the same throughout the studied period, due to changes in prospection in the years 2005 and 2006 with respect to the rest (2011 and 2013). However, the winters of 2005 and 2006 cover the area beyond the southern limit of the species distribution, so we consider them suitable for analysis. This was taken into account in the statistical analysis and subsequent discussion. While other surveys evaluating the Patagonian anchovy exist, they were excluded from our analyses because they were carried out in late spring, and did not cover the southern end of their distribution; thus, they were not appropriate to investigate the warm–cold patterns in the distribution of this species.

A SIMRAD EK500 echosounder operating with 38, 120, and 200 kHz split-beam transducers was em-

Table 1. Summary of year, season, beginning and end dates, sea surface temperature (SST), sea surface salinity (SSS), total number of acoustic data, number of Patagonian anchovy records (N), and percentage representation of Patagonian anchovy presence ($N_{\text{not null}}$). EH and OB refer to oceanographic fishery research vessels 'Eduardo Holmberg' and 'Oca Balda', respectively. Dates are given as mo/d/yr

Survey code	Survey year	Season	Beginning date	Ending date	Fishing hauls	SST (°C) Mean (min.–max.)	SSS (psu) Mean (min.–max.)	Acoustic data	
								N	$N_{\text{not null}}$ (%)
EH-2005/01	2005	warm	1/11/2005	1/31/2005	75	15.96 (13.29–17.49)	33.55 (33.12–34.17)	1583	510 (32.2)
EH-2005/06	2005	cold	7/27/2005	8/20/2005	68	7.33 (5.96–8.69)	33.35 (32.85–33.90)	2928	174 (5.9)
EH-2006/01	2006	warm	1/11/2006	2/5/2006	93	14.61 (11.6–17.16)	33.29 (32.87–33.61)	1612	580 (36)
EH-2006/05	2006	cold	9/1/2006	9/23/2006	60	8.11 (6.97–9.48)	33.29 (32.97–33.58)	2058	275 (13.4)
EH-2007/01	2007	warm	1/10/2007	2/4/2007	91	15.43 (11.42–18.67)	33.46 (33.02–34.16)	2930	1530 (52.2)
EH-2008/01	2008	warm	1/21/2008	2/17/2008	81	16.11 (11.64–17.81)	33.34 (33.01–33.53)	3559	2070 (58.2)
EH-2009/01	2009	warm	1/7/2009	1/31/2009	96	16.38 (11.57–19.07)	33.13 (33.04–33.76)	3668	2808 (76.6)
EH-2010/01	2010	warm	1/13/2010	2/6/2010	83	15.98 (11.23–19.18)	33.33 (32.85–33.64)	3509	1938 (55.3)
OB-2011/01	2011	warm	1/14/2011	2/12/2011	72	16.06 (11.91–18.37)	33.34 (33.10–33.67)	3801	2613 (68.8)
EH-2011/03	2011	cold	8/4/2011	10/4/2011	151	7.60 (5.33–9.38)	33.50 (33.11–33.98)	5015	360 (7.2)
EH-2012/01	2012	warm	1/7/2012	1/31/2012	86	16.20 (12.05–19.18)	33.51 (33.00–33.82)	2784	1439 (51.7)
EH-2013/01	2013	warm	1/12/2013	2/7/2013	86	16.06 (12.05–18.42)	33.46 (33.03–33.83)	2787	816 (29.3)
EH-2013/04	2013	cold	8/9/2013	10/15/2013	150	7.87 (5.63–10.49)	33.45 (32.92–34.02)	4715	443 (9.4)
EH-2014/01	2014	warm	1/16/2014	2/9/2014	83	15.33 (12.21–17.56)	33.39 (33.07–33.62)	2880	1547 (53.7)
Total								55697	

ployed from 2005 to 2014. Acoustic data were stored continuously, during night and day, without interruption. Data interpretation was performed during surveys with Bergen Echo Integrator (BEI) software. Species identifications were done by taking into account the species composition of trawl samples, and catch proportions by species and sub-samples were obtained to determine length and weight distributions. An average of 85 fishing hauls per year were done in warm seasons and 107 in cold seasons (range: 72–96 and 60–151 fishing hauls, respectively; Table 1). In the interpretation of the acoustic data, the proportions of each acoustic category were assigned according to the proportion of the catch of each haul and the knowledge about the schooling behavior of anchovy (Madirolas et al. 2017). The interpreted acoustic data in the 38 kHz frequency were then echointegrated and the nautical area scattering coefficient values (s_A, expressed in units of m^2 nm^{-2}) were obtained for every nautical mile of the survey. This variable (s_A) can be converted to density of individuals by means of target strength (TS) relations applicable to each species. In this way, it is possible to make abundance estimates by combining duly processed acoustic data with the proportions of catch and biological sampling in fishing sets (Georgakarakos et al. 2011). This is why s_A values are commonly used as a proxy for the relative abundance of pelagic species (Boyd et al. 2015). The original interpreted acoustic data were migrated to the more recent MAREC LSSS (Large Scale Survey System) acoustic data processing software, which provides tools to improve acoustic data by smoothing and denoising (Menna et al. 2022a). Original interpretations were revised and data from anchovy schools were exported for frequency response analysis, in terms of the volume backscattering coefficient, using a clustering algorithm (Menna et al. 2022b). After revision, echointegration values were obtained.

Precise acoustic characterization of Patagonian anchovy distribution could be made as (1) the echo signals of anchovy were identified using multifrequency responses (Menna et al. 2023), (2) there was no-overlap between the distribution of this species and that of other SPF in the 43° to 48° S study area, (3) Patagonian anchovy was the only small pelagic species caught as by-catch in bottom fishing hauls over the last 3 decades, and (4) 28 surveys assessing the biomass of this species using mid-water trawls nets further support the accuracy of our data.

Conductivity, temperature, depth (CTD) profiles were obtained at all stations and for all surveys with a Seabird SBE-19 CTD profiler (warm, n = 1086; cold, n = 198). These data were obtained from the 'Regional Oceanographic Data Base' of INIDEP (BARDO 2022). The horizontal distributions of sea surface temperature (SST) and salinity (SSS) taken at 1 m depth (to avoid the mixed layer caused by winds and thus acquire better quality data) were processed and mapped through Ocean Data View software (Schlitzer 2018). The *in situ* measured SST and SSS data were horizontally interpolated using Data Interpolating Variational Analysis (DIVA, Ocean Data View software) to regular 1 nm grids for the areas covered in the different surveys (Troupin et al. 2012) to spatially associate the values of the oceanographic variables with the Patagonian anchovy acoustic data (relative abundance). The DIVA method interpolates irregularly spaced, noisy data onto regular grids. The function penalizes the misfit between the observations and the reconstructed field, as well as the regularity or smoothness of the field, taking into account topographic and dynamic constraints (e.g. coasts and advection), providing gridded fields in 2 dimensions (Troupin et al. 2012).

2.3. Statistical analysis

Trends in the spatiotemporal variation in the presence/absence and relative abundance (s_A) of Patagonian anchovy (1) in the cold seasons of 2005, 2006, 2011, and 2013, (2) in the warm seasons corresponding to the years from 2005 to 2014, and (3) between consecutive seasons in the periods 2005–2007, 2011–2012, and 2013–2014 were analyzed.

Generalized additive mixed models (GAMMs) were used to investigate presence/absence trends, as a function of environmental conditions. SST and SSS were used as smoothed fixed predictors, year was used as a parametric fixed predictor and bottom depth as a smoothed random factor, accounting for variations in the paths taken by the vessels across different years and seasons. Due to differences in the path and areas, the variable depth was classified into 4 categories (<50, 50–100, 101–200, and >200 m). In addition, in Comparison 3, season was added as a second smoothed random factor, accounting for the intrinsic season variations, and year_season (i.e. the corresponding warm/cold season of each year, e.g. 2005_cold, 2005_warm) was used as a parametric fixed predictor (instead of year). Models were fitted using the 'mgcv' package in R (Wood 2015), with 'bam' function due to the large N in all comparisons (i.e. 1, 2, 3) following a binomial error distribution. Different models were fitted for each comparison, testing different arrangements of predictor variables, and the best model was determined using a selection approach by comparing AIC values. Achievement of normality of residuals and homoscedasticity assumptions were inspected using the 'DHARMa' package (Hartig 2021). Model diagnostics were run using the 'mgcViz' package in R (Fasiolo et al. 2020) and the effect among year levels was calculated using the *a posteriori* Tukey test whenever necessary, using the 'emmeans' package in R (Lenth 2021).

Optimal model structures:

(1) Cold seasons: presence/absence ~ intercept + ti(SST × SSS) + year + s(depth, bs = 're')

(2) Warm seasons: presence/absence ~ intercept + ti(SST × SSS) + year + s(depth, bs = 're')

(3) Consecutive seasons: presence absence ~ intercept + ti(SST × SSS) + s(SSS) + s(SST) + year + s(depth, bs = 're') + s(season, bs = 're')

where ti() and s() represent the smoothing functions, and the term bs = 're' is used to specify that this variable is to be modelled as a random effect.

In the analysis of Patagonian anchovy abundance spatiotemporal trends in (1), (2), and (3), models did not achieve a non-linear fitting; thus we proceeded to fit linear models, using generalized linear mixed models (GLMMs). Models were fitted following a negative binomial error distribution with quadratic parametrization. Similarly to presence/absence models, GLMMs were fitted as a function of environmental conditions, where SST, SSS and year (year_season in Comparison 3) were used as fixed predictors and depth as a random factor (1 | depth). In the case of Comparison 3, season was used as a second random factor (1 | season). Models were fitted using the package 'glmmTMB' in R (Bolker 2020). Different models were fitted for each comparison, testing different arrangements of predictor variables, and the best model was determined using a selection approach by comparing Akaike's information criterion (AIC) values. Given that DHARMa showed zero-inflation in all cases (i.e. 1, 2, and 3), a zero-inflation parameter was added to all models, through the zi-formula; and heteroscedasticity was accounted for by adding a dispersion parameter (dispformula) to the models (Brooks et al. 2017). The significance of the fixed predictors was tested using the ANOVA function (Zuur et al. 2009), and the effect among year_season levels was calculated using the *a posteriori* Tukey test whenever necessary.

Optimal model structures:

(1) Cold seasons: relative abundance ~ intercept + SST + SSS + year + + (1 | depth)

(2) Warm seasons: relative abundance ~ intercept + SST × SSS + year + (1 | depth)

(3) Consecutive seasons: relative abundance ~ intercept + SST + SSS + year_season + (1 | depth) + (1 | season)

Graphs to visualize the results were made with the 'ggplot2' package (Wickham & Chang 2016). All the analyses were performed with R software (v.4.4.2, R Core Team 2024).

3. RESULTS

3.1. Distribution of Patagonian anchovy in cold seasons

The SST recorded during the 4 cold seasons ranged between 5.33 and 10.49°C and the SSS values varied from 32.11 to 34.02. Across these seasons, the proportion of total acoustic data attributed to Patagonian anchovy ranged from 5.9 to 13.4% (Table 1). In 2005 and 2006, fish schools were registered north of 46° S, whereas in 2011, they were also observed in the southern coastal sectors of the San Jorge Gulf. Schools were registered up to 108 m depth, even when the research surveys covered an area that exceeded 48° S and extended over 200 m deep. In 2013, the presence of anchovy was recorded exclusively north of 45° S. Importantly, no schools were recorded below 6.52°C in any cold seasons sampled, indicating this as the lower thermal limit for the species in the cold seasons (Fig. 2).

Best model selection included SST and SSS interaction plus year, and the χ^2 test showed an extremely significant relationship between these factors and Patagonian anchovy presence (Table 2). The model explained 59.8% of total deviance. Across most of the SST and SSS range, no significant non-linear relationships were observed between these oceanographic variables and the presence of Patagonian anchovy, but a boundary effect was detected. A positive relationship was found at SST below 6°C for SSS between 33.25 and 33.75. Conversely, a negative relationship with presence occurred at SST above 10°C for SSS of ~33.25, and also at SSTs of 8.5 to 9.5°C for SSS above 33.75 (Fig. 3a, cold panel). Patagonian anchovy presence was similar during the cold seasons of 2005 and 2006, but significant differences were found among the remaining comparisons (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m756p111_supp.pdf).

Patagonian anchovy relative abundance was positively influenced by SST and by SSS, and differences between years were detected (Table 2). Relative abundance increased with increasing SST and, to a lesser extent, with increasing SSS (Fig. 3b, cold panel). The cold seasons in 2005 and 2006 showed similar values that differed from those in 2011 and 2013, which were also different from each other. The cold season in 2013 presented the lowest relative abundance values from the studied period (see Table S1).

3.2. Distribution of Patagonian anchovy in warm seasons

During these seasons, the species distribution was relatively uniform across the surveyed areas, with fish schools detected as far south as 47° S, which corresponds to the southernmost limit of the research surveys. Schools were also recorded at depths reaching up to 176 m (Fig. 4). The SST ranged from 11.23 to 19.18°C and the SSS from 32.85 to 34.17. The proportion of acoustic data associated with Patagonian anchovy records varied from 29.3 to 76.6% (Table 1).

As in the cold seasons, best model selection included the SST and SSS interaction plus year, and the χ^2 test showed an extremely significant relationship between these factors and Patagonian anchovy presence (Table 2). The model explained 18.6% of the total deviance. Across most of the SST and SSS range, no significant non-linear relationships were identified between these oceanographic variables and the presence of Patagonian anchovy, but a boundary effect was detected. A positive correlation was identified at SSTs between 12.5 and 16.5°C, coupled with SSS values below 33 (Fig. 3c, warm panel). Differences in presence/absence among years were observed, except for 2007–2012–2014, 2008–2010–2014, and 2006–2013 (see Table S1).

Relative abundance was influenced by the SST and SSS interaction, and differences among years were found (Table 2). Patagonian anchovy relative abun-

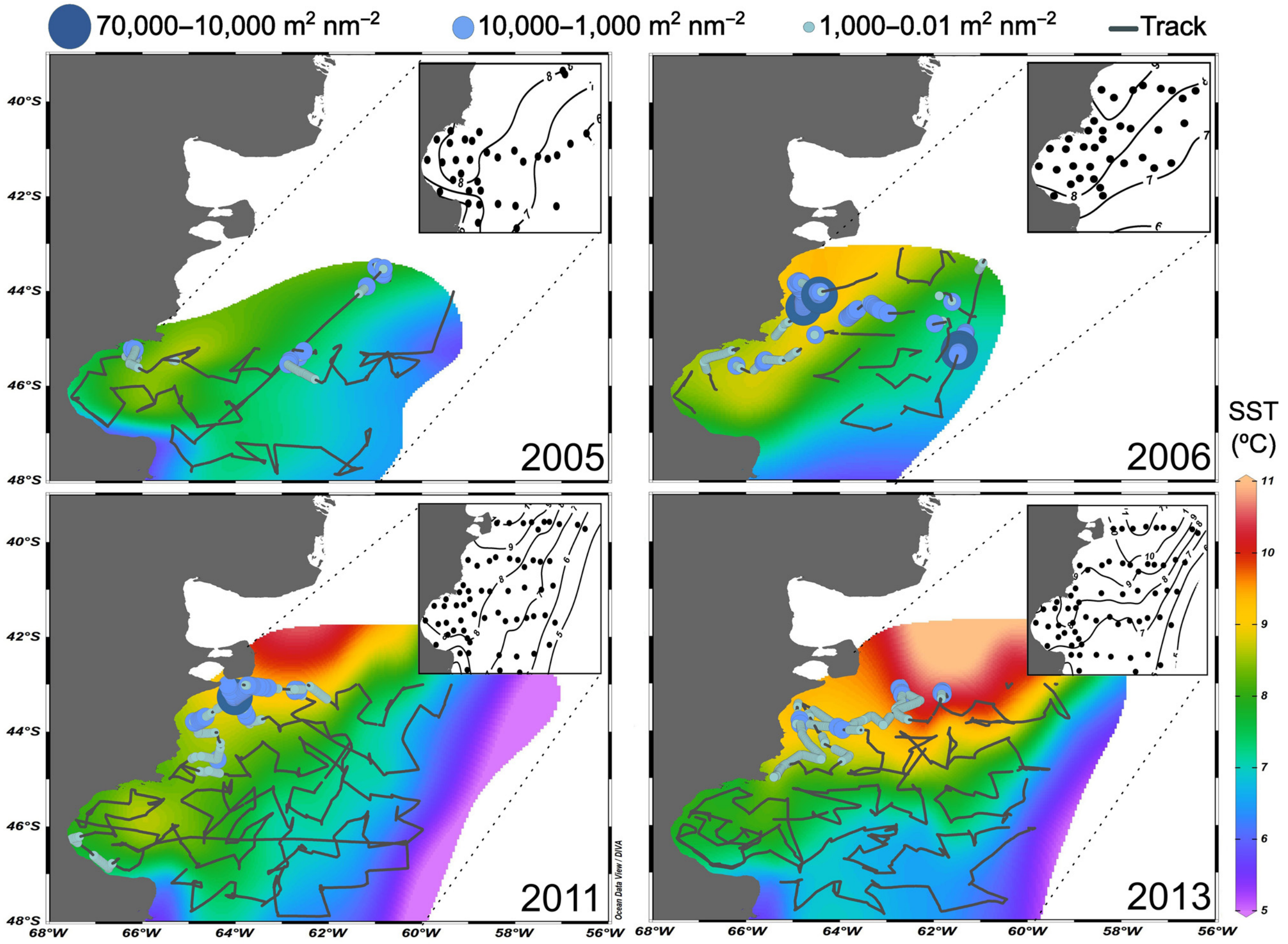

Fig. 2. Spatial distribution of Patagonian anchovy (s_A) and SST (°C) in the cold season. Dots indicate the relative abundances of Patagonian anchovy, and the background color corresponds to the SST recorded for the area. Inset: (black dots) oceanographical stations where conductivity, temperature, depth (CTD) profiles were obtained; (black lines) isotherm contours

dance significantly increased with increasing SST at maximum SSS values (>33.82) and no effect was detected at minimum SSS values (Fig. 3d, warm panel). Differences among years were observed, except for 2005–2006–2009, 2007–2011–2012–2014, and 2008–2010 (see Table S1).

3.3. Comparative distribution of Patagonian anchovy between consecutive seasons in the 2005–2007, 2011–2012, and 2013–2014 periods

Best model selection for presence/absence included both the interaction between SST and SSS, the individual effect of each one, and also year_season (the seasons from each year). The χ^2 test showed an extremely significant relationship between these factors and Patagonian anchovy presence in cold and warm seaso and the model explained 31.4% of the total deviance (Table 2). Across most of the SST and SSS range, no significant non-linear relationships were identified between these oceanographic variables and presence/absence, but boundary effects were detected. There was a positive effect on presence/absence at SSTs between 10 and 13°C for SSS lower than 33, and a negative one at SSTs between 8 and 10°C for SSS higher than 33.6 (Fig. 3e, warm vs. cold panel). In the analysis of the individual effect of these oceanographic variables, no variation in species presence was evidenced at SSS between 33.25 and 33.75, but above and below that range, the presence was lower (Fig. 3f, warm vs. cold panel); and Patagonian anchovy presence increased when water temperature reached 6 to 10°C. At SSTs beyond 12°C, no variation in presence was detected (Fig. 3f, warm vs. cold panel). The comparison between consecutive seasons indicated differences between all of them, in all periods (see Table S1).

Table 2. Model selection results of GAMM for Patagonian anchovy presence/absence and of GLMM for Patagonian anchovy relative abundance (s_A) for cold, warm and warm vs. cold seasons. Significant values are given in **bold**

	Models	Response variable	Optimal model terms	df	χ^2	p	AIC
Cold	Non-linear (GAMM)	Presence / absence	SST × SSS	265	1384.51	**<0.001**	3809.21
			Year	3	159.27	**<0.001**	
	Linear (GLMM)	Relative abundance (s_A)	SST	1	310.63	**<0.001**	22708.72
			SSS	1	8.60	**0.003**	
			Year	3	241	**<0.001**	
Warm	Non-linear (GAMM)	Presence / absence	SST × SSS	393	3350.61	**<0.001**	33373.74
			Year	9	1359.52	**<0.001**	
	Linear (GLMM)	Relative abundance (s_A)	SST × SSS	1	26.87	**<0.001**	243701.8
			Year	9	2314.45	**<0.001**	
Warm vs. Cold	Non-linear (GAMM)	Presence / absence	SST × SSS	41.28	859.72	**<0.001**	28216.74
			SSS	6.22	44.36	**<0.001**	
			SST	9.69	234.16	**<0.001**	
			Year_season	10	1242.86	**<0.001**	
	Linear (GLMM)	Relative abundance (s_A)	SST	1	30.07	**<0.001**	159456.5
			SSS	1	198	**<0.001**	
			Year_season	10	971.50	**<0.001**	

Relative abundance was influenced by the individual effects of SST and SSS, and differences between consecutive seasons in each period were also found (Table 2). A slight increase in relative abundance was observed with SSS, and a similar but weaker relation was observed with SST (Fig. 3g, warm vs. cold panel). Regarding differences among periods, *a posteriori* analysis indicated that relative abundance was only equal in warm and cold seasons in the year 2006. Differences were registered between the other consecutive seasons from the subset periods (see Table S1).

4. DISCUSSION

Patagonian anchovy distribution showed a marked seasonality with differences between cold and warm seasons. During warm seasons, Patagonian anchovy was distributed throughout the area covered by the research surveys. However, during the cold seasons, a northward contraction was observed, with the fish schools shifting up to 1.5° farther north compared to their distribution in the warm seasons. In summary, the spatial evolution of the distribution of Patagonian anchovy shows a seasonal contraction/expansion pattern or shifting to the north of the analyzed area. These patterns were also observed in other SPF. *Engraulis encrasicolus* expands its distribution during summer in association with oceanographic processes and food availability in the Mediterranean Sea (Giannoulaki et al. 2013). Similarly, in the Gulf of Viscaya, the geographic range of this anchovy contracts during the peak of reproductive activity in response to optimal thermal ranges and expands at its end (Motos et al. 1996).

Patagonian anchovy acoustic data were collected during bottom trawl surveys aimed at evaluating the abundance of Argentine hake, and cruise design responded to this objective. However, the distribution of Patagonian anchovy analyzed using this acoustic data aligns with what has been previously described in the literature for Argentina. We consider that demersal trawl surveys are not ideal, but acceptable to use for the presented purposes, as reported in other similar studies (e.g. Barange et al. 1998, Jansen et al. 2012, Post et al. 2019).

Patagonian anchovy breeding activity takes place between 41° and 45° S in coastal waters (Pájaro 2002), in the latter austral spring, and is associated with the 3 oceanographic fronts that integrate the Norpatagonic frontal system (Sánchez 1995, Hansen et al. 2001). In the Patagonian sea fronts, several mechanisms promote retention of larvae and lead to positive conditions for Patagonian anchovy reproduction in late spring (Do Souto et al. 2018). Once the spawning period is over in early summer, a southward dispersion of the schools begins (41° to 47° S), reaching the interior and south of the San Jorge Gulf. These movements are possibly associated with an intense feeding phase after reproductive activity, since adults have been found in spring with empty or almost empty stomachs, despite the high availability of zooplankton prey in the environment (Pájaro 2002). In late summer, anchovy distribution on the NPCS, although still patchy, was found to be more dispersed. During

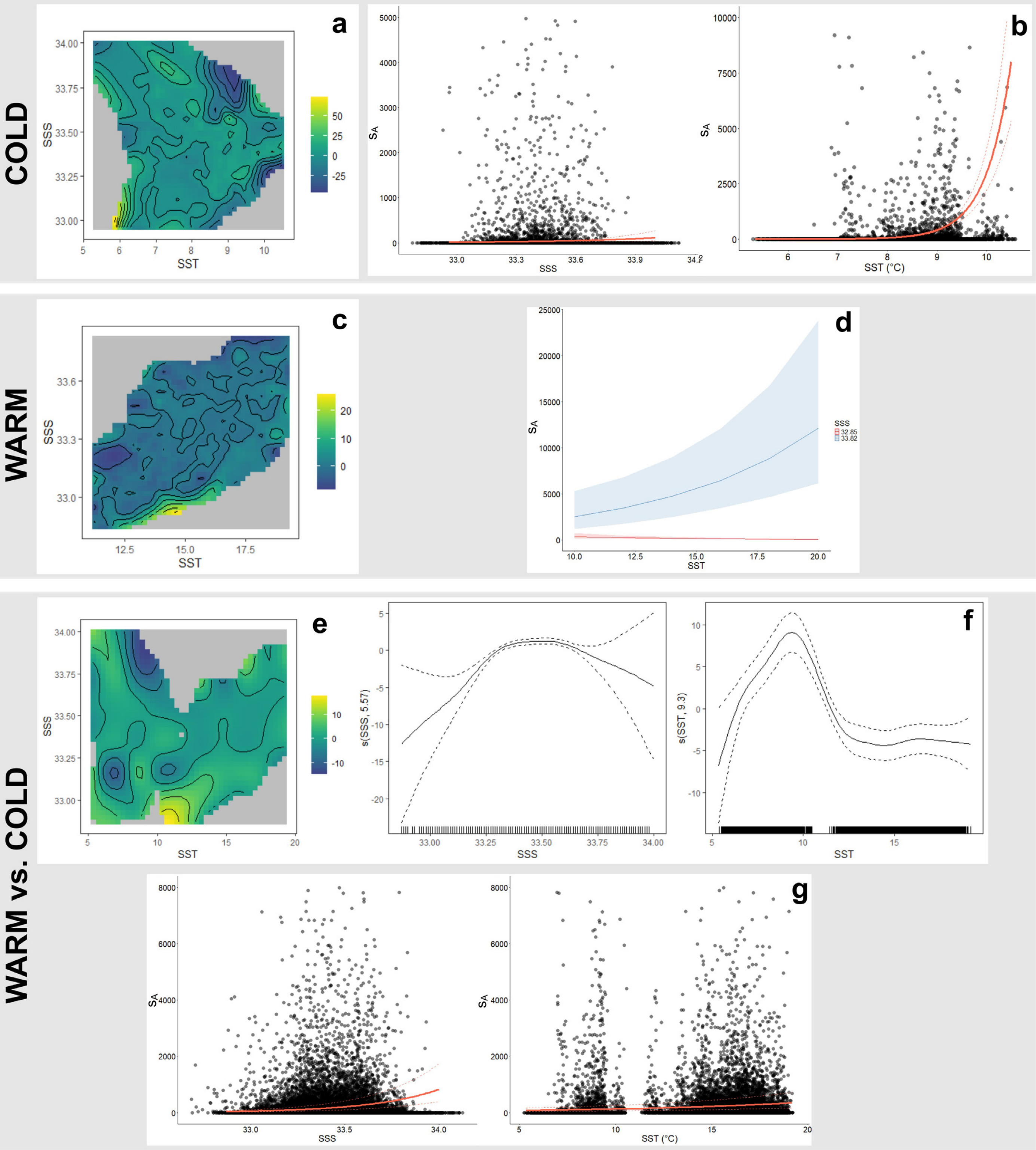

Fig. 3. GAMM smoothed term outputs for the effects of SST and SSS on Patagonian anchovy presence in the (a) cold, (c) warm, and (e) warm vs. cold seasons. Response curves for significant variables derived from GLM models for (b) the effect of SST and SSS on Patagonian anchovy relative abundance (s_A) for the cold seasons, (d) the interaction SST × SSS for the warm seasons (blue and red buffered lines: maximum and minimum values of the SSS range, respectively), and (g) the SST and SSS for warm vs. cold seasons. In the warm vs. cold output, (f) response curves for significant individual variable effects of GAMM are also shown (SSS and SST); dashed lines: 95% confidence intervals

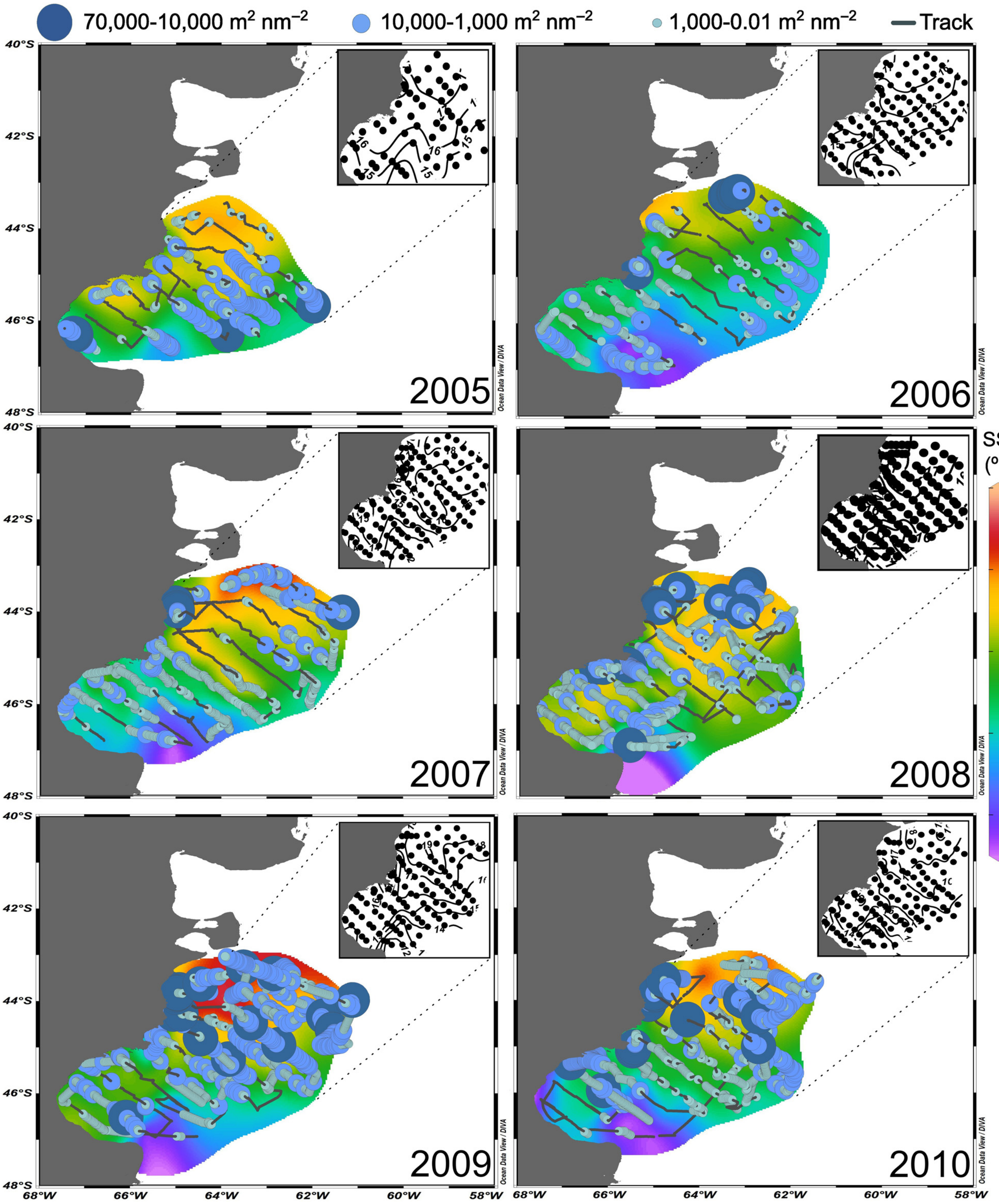

Fig. 4. Spatial distribution of Patagonian anchovy (s_A) and SST (°C) in the warm season. See Fig. 2 for definition of symbols

Fig. 4. (continued on next page)

austral winter, adult schools are once again concentrated off Valdés Peninsula and even at lower latitudes, up to 45° S, and near the coast or in the mid-shelf (Angelescu & Anganuzzi 1986). This pattern coincides with the observations made in the warm and cold seasons in this study.

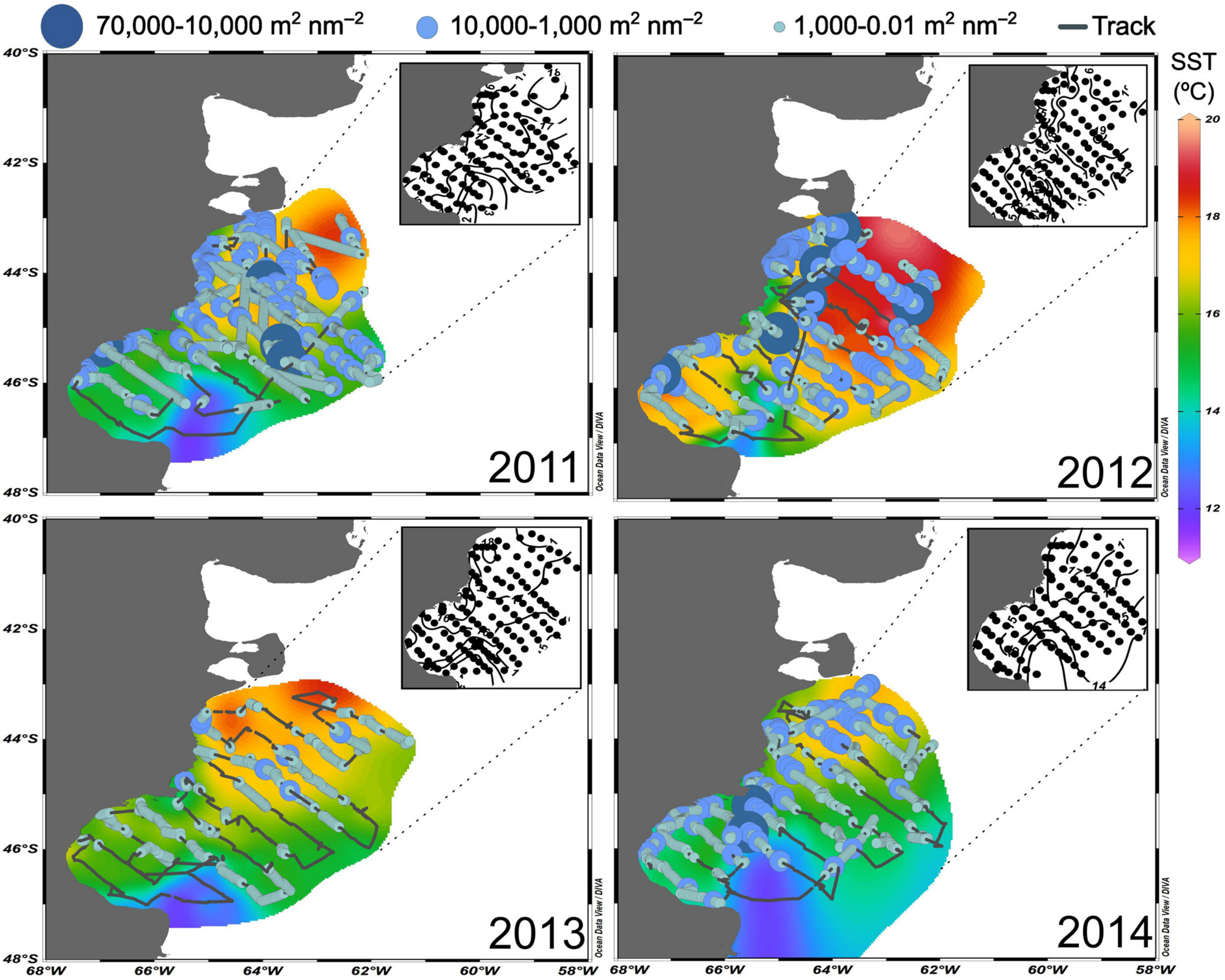

Fig. 4. (continued)

Patagonian anchovy is a euryhaline and eurythermal species (Hansen 2004). Its lower thermal limit has been identified as 8°C (Angelescu 1982), with a suitable thermal range of 12 to 17°C in spring on the NPCS (Hansen et al. 2001). This SST thermal range was extended in our work, with schools recorded at 6.52°C in cold seasons and between 11 and 19.5°C in warm ones. In any case, Hansen et al. (2001) clarified in their work that the higher abundances of Patagonian anchovy in thermal fronts may be due to spawning activity and retention mechanisms, rather than to temperatures per se. Regarding SSS, the ranges registered in both seasons were within the values tolerated (33 to 34.3) (Pájaro 2002). In a wide range of SST and SSS values, no relationships between these variables and the presence of Patagonian anchovy were recorded, which aligns with expectations for eurythermal and euryhaline species. A similar pattern emerged when comparing consecutive warm and cold seasons, with the only notable effects being a positive impact on presence when SST increased up to 10°C, and a negative impact when SSS was either relatively high (>33.75) or low (<33.25). In addition, the relative abundance of Patagonian anchovy showed a linear weak relationship with both SST and SSS, increasing slightly as temperature and salinity rose. Other biological factors probably also influence Patagonian anchovy presence and abundance (e.g. food availability). Effects of SST and SSS on *Engraulis* distributions are widely reported in the literature and, in general, turn out to be context-dependent. Mixed and significant effects of both variables resulting in positive, negative, dome-shaped and u-shaped relationships have been reported for the juvenile and adult stages of *E. encrasicolus*; and the type of predominant effect depended on the analyzed area of the Mediterranean Sea (Fernández-Corredor et al. 2021). In the case of the Japanese anchovy *E. japonicus*, the seasonal analysis indicated a 73.7% contribution with a dome-shape effect of SSS and SST on presence in the summer and winter seasons (Bang et al. 2022). For *E. ringens* in north Chile, the increase in SST in the context of climate change could reduce the size of fish by up to 15%, which will reduce fecundity, affecting anchovy population dynamics (Hernández-Santoro et al. 2019).

The typical annual thermal cycle of Southern Hemisphere mid-latitudes significantly influences Patagonian anchovy distribution patterns, as demonstrated by the comparison between consecutive warm and cold seasons. However, inter-annual SST anomalies (as well as atmospheric pressure, winds, and extent of sea ice) in the large ocean basins (such as the SWAO) are affected by a northward shift of the Antarctic Circumpolar Current, which follows a 4 to 5 yr cycle (Marrari et al. 2019). This may be related with the differences recorded between the same seasons over the years. In this context, some particularities were detected. Unexpected similarities in the relative abundance of Patagonian anchovy were observed in the warm and cold seasons of 2006. Its presence during the 2006 warm season was one of the lowest over the studied period, similar to that recorded in 2013. The summer of 2006 was notably colder than average, and within the San Jorge Gulf, the typical chlorophyll blooms that usually occur in late spring and persist for an average of 110 d, had their shortest duration that year, lasting only 35 d (Marrari et al. 2019). This change in bloom persistence is relevant, considering that high chlorophyll concentrations in spring and summer generally support production, presumably leading to the high abundance of zooplankton described in the San Jorge Gulf (e.g. Derisio 2012, Temperoni et al. 2014), which constitutes the main food of Patagonian anchovy (Angelescu 1982). Thus, a low availability of food caused by a short phytoplankton bloom in 2006 may explain the low presence and relative abundance of Patagonian anchovy during the 2006 warm season.

Given that the summer expansion of the Patagonian anchovy is typically related to its feeding phase (Pájaro 2002), the reduced presence of the prey species in the San Jorge Gulf and the denser aggregation of schools in the northern part of the study area seem logical. Essentially, why expand if there is relatively little food available? This hypothesis is supported by the abundance estimate made for this species in the spring of 2006, which recorded a biomass value of 1 600 000 t of fish located mainly north of 44° S, particularly within the San Matías Gulf, which is unusual (Hansen 2006). This estimate represents the highest abundance value of the 6 surveys conducted in the last 20 yr (Orlando et al. 2023). Thus, these findings may explain the lack of differences between the warm and cold seasons of 2006, and also shed light in part on the complex interactions between the abiotic and biotic factors that shape Patagonian anchovy seasonal distribution and abundance patterns.

Notably, it is also crucial to highlight that the relative abundance and presence during the warm season of 2013 marked the lowest recorded values throughout the entire study period. Regrettably, due to the lack of acoustic information from the cold season of 2012, we face limitations in assessing the reasons for this observed decline in 2013. However, we ruled out the hypothesis that it could be attributed to a fishing impact. This assertion is reinforced by the consistently low fishing levels and consequently minimal impact of fishing activities on the Patagonian anchovy stock, accounting for less than 4% of the acceptable biological catch and a fishing mortality in the period calculated at 0.005 (Orlando et al. 2023). We also rejected the hypothesis of a negative effect on recruitment in 2013. If that had been the case, a low abundance would have been expected in the summer of 2014; but on the contrary, Patagonian anchovy abundance again reached high values (similar to those of previous summers).

The low presence and relative abundance of Patagonian anchovy in the summer of 2013 cannot be explained by a colder-than-usual season, since temperature in 2013 was within the average range (Marrari et al. 2019). Instead, it is more likely due to oceanographic forces affecting the region. The interaction between the NPCS and the shelf break (SB: 200 to 1000 m), where the Malvinas Current flows, may be linked to the process described by Palma et al. (2008). Their study showed that north of 50° S, the cross-shelf barotropic pressure gradient created by the Malvinas Current strongly influences shelf circulation. Related to this process, Allega et al. (2021) detected contrasting SST anomalies between the middle of the NPCS and the SB in 2013 (positive vs. negative, respectively). These contrasting anomalies were attributed to the inter-annual variability of the Malvinas Current and remote forcing by the El Niño-Southern Oscillation (ENSO) (Artana et al. 2018), generating a strengthening of northward transport of cold water. We suggest that this intensified cooling at the SB, and its impact on the NPCS may have pushed the schools northward during the summer of 2013, potentially beyond 42° S (outside our study area and beyond our detection). In 2014, these oceanographic forces were attenuated, and therefore, Patagonian anchovy relative abundance presented values within the ranges previously observed. Further data and analysis are necessary to substantiate this hypothesis.

The findings of this study of Patagonian anchovy seasonal distribution patterns are also relevant for the North Patagonian trophic web dynamics, where this species plays a key ecological role. In this sense, its inter-annual abundance fluctuations appear to have a greater impact on the behavior of its main predators than on Patagonian anchovy spatial distribution (presence/absence), which is often emphasized (Hilborn et al. 2017), and many studies support this hypothesis. For instance, Patagonian anchovy constitutes the main food of dusky dolphins *Lagenorhynchus obscurus* between 43° and 46° 30′ S, contributing up to 50% by weight of their diet (Koen Alonso et al. 1998), and there is a spatial overlap between dusky dolphin groups and zones of high abundance of Patagonian anchovy (Garaffo et al. 2011). The Magellanic penguin *Spheniscus magellanicus* mainly feeds on Patagonian anchovy (Wilson et al. 2005, Yorio et al. 2017, Ciancio et al. 2021). Moreover, the size of its isotopic niche was negatively correlated with Patagonian anchovy abundance in the 2013 warm season (Ciancio et al. 2021) when the lowest fish abundance was recorded in our study. During years of low forage fish abundance, the penguins change their strategy, incorporating a wider range of prey, and niche size tends to increase (Ciancio et al. 2021). The South American sea lion *Otaria byronia* (previously *Otaria flavescens*), which feeds primarily on demersal and benthic species, also feeds on Patagonian anchovy when it is abundant in the region (Koen Alonso et al. 2000). Regarding species of great fishing interest in Argentina, the Argentine hake *Merluccius hubbsi* preys mainly on zooplankton in north Patagonia (Belleggia et al. 2019), but presents opportunistic habits, feeding on Patagonian anchovy according to its seasonal changes in abundance, with high consumption in warm seasons and low in cold ones (Belleggia et al. 2014).

In conclusion, our results suggest that while the Patagonian anchovy is a euryhaline and eurythermal species, there are some thermal and salinity ranges in which its distribution and abundance are influenced by environmental conditions, potentially impacting the broader trophic web, probably along with other biotic factors. Moreover, certain extreme oceanographic conditions registered at the study site may be related to some infrequent low values of Patagonian anchovy relative abundance and presence. Taking this into account, the significant warming trend between 1982 and 2015, with an average increase of 0.379°C on the NPCS (Marrari et al. 2019), becomes relevant. Under a climate change scenario, in which extreme weather events and other interannual oscillations may be exacerbated (Cai et al. 2020), regular monitoring before major weather events occur is crucial to identify unexpected changes in this fish population and determine if such shifts persist over time. This study is the first to provide essential insights into the seasonal distribution patterns of the Patagonian anchovy in the NPCS but, unfortunately, there have been no studies with temporal continuity after 2014. Thus, it is urgent to carry out evaluations of the current stock, both in summer and winter. This will allow construction of better models that will allow us to make predictions for all IPCC climate change scenarios. Also, these assessments would not only support sustainable fisheries management in the face of climate change, but would also offer valuable insights into the seasonal dynamics of the fish, birds, and mammals that rely on this small pelagic species as a food source.

Data availability. Data will be made available on request.

Acknowledgements. We express our gratitude to PhD Clara Díaz de Astarloa for revising the English. We thank the crew and scientific staff on board the scientific and oceanographic research vessels for their assistance and sample collection during surveys. This is a National Institute for Fisheries Research and Development (Instituto Nacional de Investigacion y Desarrollo Pesquero — INIDEP) Contribution No. 2423.

LITERATURE CITED

Acha EM, Mianzan HW, Guerrero RA, Favero M, Bava J (2004) Marine fronts at the continental shelves of austral South America: physical and ecological processes. J Mar Syst 44:83–105

Allega L, Pisoni JP, Cozzolino E, Maenza RA, Piccolo MC (2021) The variability of sea surface temperature in the Patagonian Shelf Argentina, from 35 years of satellite information. Int J Remote Sens 42:6090–6106

Angelescu V (1982) Ecología trófica de la anchoíta del Mar Argentino (Engraulidae, *Engraulis anchoita*). Parte II. Alimentación, comportamiento y relaciones tróficas en el ecosistema. Ser Contrib Inst Nac Invest Dessaro Pesq No. 409. Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, p 1–83

Angelescu VA, Anganuzzi A (1986) Ecología trófica de la anchoíta (Engraulidae, *Engraulis anchoita*) del Mar Argentino. Parte III. Requerimiento trófico individual en relación con el crecimiento, ciclo sexual y las migraciones estacionales. Rev Invest Dessaro Pesq 9:194–223 (in Spanish with English Abstract)

Angelescu V, Cousseau MB (1967) Distribución espacial y cronológica de la anchoíta en el Mar Epicontinental Argentino. CARPAS/FAO Doc Téc No. 9. Oficina Regional de Pesca para America Latina, Río de Janeiro, p 1–48

Artana C, Ferrari R, Koenig Z, Sennéchael N, Saraceno M, Piola AR, Provost C (2018) Malvinas current volume transport at 41° S: a 24 yearlong time series consistent with mooring data from 3 decades and satellite altimetry. J Geophys Res Oceans 123:378–398

Bang M, Sohn D, Kim JJ, Choi W, Jang CJ, Kim C (2022) Future changes in the seasonal habitat suitability for anchovy (*Engraulis japonicus*) in Korean waters projected by a maximum entropy model. Front Mar Sci 9: 922020

Barange M, Pillar SC, Hampton I (1998) Distribution patterns, stock size, and life history strategies of Cape horse mackerel *Trachurus trachurus* capensis, based on bottom trawl and acoustic surveys. S Afr J Mar Sci 19:433–447

BARDO (Base Regional de Datos Oceanográficos) (1984–2024) National Institute of Fisheries Research and Development (Instituto Nacional de Investigación y Desarrollo Pesquero; INIDEP) database. Gabinete de Oceanografía Física, Ministry of Agriculture, Livestock and Fisheries. https://catalogo.inidep.edu.ar/geonetwork/srv/spa/catalog.search#/home (accessed 6 Jun 2022)

Belleggia M, Figueroa DE, Irusta G, Bremec C (2014) Spatio-temporal and ontogenetic changes in the diet of the Argentine hake *Merluccius hubbsi.* J Mar Biol Assoc UK 94:1701–1710

Belleggia M, Giberto D, Bremec C (2017) Adaptation of diet in a changed environment: increased consumption of lobster krill *Munida gregaria* (Fabricius, 1793) by Argentine hake. Mar Ecol 38:e12445

Belleggia M, Alves NM, Leyton MM, Álvarez-Colombo G, Temperoni B, Giberto D, Bremec C (2019) Are hakes truly opportunistic feeders? A case of prey selection by the Argentine hake *Merluccius hubbsi* off southwestern Atlantic. Fish Res 214:166–174

Bolker B (2020) Getting started with the glmmTMB package. https://cran.r-project.org/web/packages/glmmTMB/vignettes/glmmTMB.pdf

Boyd C, Castillo R, Hunt GL, Punt AE, Van Blaricom GR, Weimerskirch H, Bertrand S (2015) Predictive modelling of habitat selection by marine predators with respect to the abundance and depth distribution of pelagic prey. J Anim Ecol 84:1575–1588

Brooks ME, Kristensen K, Van Benthem KJ, Magnusson A and others (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Brosset P, Fromentin JM, Van Beveren E, Lloret J and others (2017) Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas. Prog Oceanogr 151:149–162

Buratti CC, Cortés F, Acha EM, Allega L and others (2022) Cambios biológicos en el Océano Atlántico Sudoccidental. In: Buratti CC, Chidichimo MP, Cortés F, Gaviola S and others (eds) Estado del conocimiento de los efectos del cambio climático en el Océano Atlántico Sudoccidental sobre los recursos pesqueros y sus implicancias para el manejo sostenible. Ministerio de Agricultura, Ganadería y Pesca, Buenos Aires, p 83–159

Cai W, McPhaden MJ, Grimm AM, Rodrigues RR and others (2020) Climate impacts of the El Niño–Southern Oscillation on South America. Nat Rev Earth Environ 1:215–231

Checkley D, Alheit J, Oozeki Y, Roy C (eds) (2009) Climate change and small pelagic fish. Cambridge University Press, Cambridge

Ciancio JE, Yorio P, Buratti CC, Colombo GA, Frere E (2021) Isotopic niche plasticity in a marine top predator as indicator of a large marine ecosystem food web status. Ecol Indic 126:107687

Costalago D, Navarro J, Álvarez-Calleja I, Palomera I (2012) Ontogenetic and seasonal changes in the feeding habits and trophic levels of two small pelagic fish species. Mar Ecol Prog Ser 460:169–181

Cury P, Bakun A, Crawford RJ, Jarre A, Quinones RA, Shannon LJ, Verheye HM (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in ‘wasp-waist’ ecosystems. ICES J Mar Sci 57:603–618

Dans SL, Koen Alonso M, Pedraza SN, Crespo EA (2003) Incidental catch of dolphins in trawling fisheries off Patagonia, Argentina: Can populations persist? Ecol Appl 13: 754–762

Derisio C (2012) El rol del frente de mareas de Península Valdés en el control de la comunidad zooplanctónica. PhD thesis, Universidad Nacional de Mar del Plata

Do Souto M, Spinelli M, Brown R, Pájaro M, Diaz M, Capitanio F (2018) Benefits of frontal waters for the growth of *Engraulis anchoita* larvae: the influence of food availability. Fish Res 204:181–188

Fasiolo M, Nedellec R, Goude Y, Capezza C, Wood SN (2020) mgcViz: visualisations for generalized additive models. R package version 0.1.6. https://CRAN.R-project.org/package=mgcViz

Fernández-Corredor E, Albo-Puigserver M, Pennino MG, Bellido JM, Coll M (2021) Influence of environmental factors on different life stages of European anchovy (*Engraulis encrasicolus*) and European sardine (*Sardina pilchardus*) from the Mediterranean Sea: a literature review. Reg Stud Mar Sci 41:101606

Garaffo GV, Dans SL, Pedraza SN, Degrati M, Schiavini A, González R, Crespo EA (2011) Modeling habitat use for dusky dolphin and Commerson's dolphin in Patagonia. Mar Ecol Prog Ser 421:217–227

Gatto AJ, Yorio PM (2016) Assessing the trophic niche of South American terns integrating conventional and isotopie method. Emu 116:230–240

Georgakarakos S, Trygonis V, Haralabous J (2011) Accuracy of acoustic methods in fish stock assessment surveys. In: Kolev N (ed) Sonar Systems. IntechOpen, London

Giannoulaki M, Iglesias M, Tugores MP, Bonanno A and others (2013) Characterizing the potential habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages. Fish Oceanogr 22: 69–89

Glembocki NG, Williams GN, Góngora ME, Gagliardini DA, Orensanz JML (2015) Synoptic oceanography of San Jorge Gulf (Argentina): a template for Patagonian red shrimp (*Pleoticus muelleri*) spatial dynamics. J Sea Res 95:22–35

Guerrero RA, Piola AR (1997) Masas de agua en la plataforma continental. El Mar Argentino y sus Recursos Pesqueros 1:107–18 (in Spanish with English Abstract)

Hansen JE (1994) Diferencias entre parámetros vitales de las poblaciones bonaerense y patagónica de anchoíta Argentina. Rev Invest Desarro Pesq 9:11–24 (in Spanish with English Abstract)

Hansen JE (2004) Anchoíta (*Engraulis anchoita*). In: Sánchez RP, Bezzi SI (eds) El Mar Argentino y sus recursos pesqueros, tomo 4. Los peces marinos de interés pesquero. Caracterización biológica y evaluación del estado de explotación. INIDEP, Mar del Plata, p 101–115

Hansen JE (2006) Evaluación de anchoíta patagónica (41° –45° 20′ S) e investigación del Golfo San Matías en la primavera de 2006. Informe Final de Campaña 'EH-09/06'. INIDEP, Mar del Plata

Hansen JE, Martos P, Madirolas A (2001) Relationship between spatial distribution of the Patagonian stock of Argentine anchovy, *Engraulis anchoita*, and sea temperatures during late spring to early summer. Fish Oceanogr 10:193–206

Hartig F (2021) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.4. https://CRAN.R-project.org/web/packages/DHARMa/index.html

Hernández-Santoro C, Contreras-Reyes JE, Landaeta MF (2019) Intra-seasonal variability of sea surface temperature influences phenological decoupling in anchovy (*Engraulis ringens*). J Sea Res 152:101765

Hilborn R, Amoroso RO, Bogazzi E, Jensen OP, Parma AM, Szuwalski C, Walters CJ (2017) When does fishing forage species affect their predators? Fish Res 191:211–221

Hilborn R, Buratti CC, Díaz Acuña E, Hively D and others (2022) Recent trends in abundance and fishing pressure of agency-assessed small pelagic fish stocks. Fish Fish 23: 1313–1331

Jansen T, Campbell A, Kelly C, Hátún H, Payne MR (2012) Migration and fisheries of North East Atlantic mackerel (*Scomber scombrus*) in autumn and winter. PLOS ONE 7: e51541

Koen Alonso M, Crespo EA, García NA, Pedraza SN, Coscarella MA (1998) Diet of dusky dolphins, *Lagenorhynchus obscurus*, in waters off Patagonia, Argentina. Fish Bull 96: 366–374

Koen Alonso M, Crespo EA, Pedraza SN, Garcia NA, Coscarella MA (2000) Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina. Fish Bull 98:250–263

Lenth RV (2021) emmeans: estimated marginal means, aka least-squares means. R package version 1.5.4. https://CRAN.R-project.org/package=emmeans

Madirolas A, Membiela F, Gonzalez JD, Cabreira AG, dell'Erba M, Prario IS, Blanc S (2017) Acoustic target strength (TS) of Argentine anchovy (*Engraulis anchoita*): the nighttime scattering layer. ICES J Mar Sci 74: 1408–1420

Marinao CJ, Yorio P (2011) Fishery discards and incidental mortality of seabirds attending coastal shrimp trawlers at Isla Escondida, Patagonia, Argentina. Wilson J Ornithol 123:709–719

Marrari M, Macchi GJ, Santos B, Leonarduzzi E (2019) Influence of environmental conditions on the reproductive success and recruitment of the Argentine hake *Merluccius hubbsi* (southwestern Atlantic Ocean). Fish Oceanogr 28:66–81

Matano RP, Palma ED (2008) On the upwelling of downwelling currents. J Phys Oceanogr 38:2482–2500

Maynou F, Sabatés A, Salat J (2014) Clues from the recent past to assess recruitment of Mediterranean small pelagic fishes under sea warming scenarios. Clim Change 126:175–188

Menna BV, Cassanelli M, Madirolas A, Cabreira AG (2022a) BI500 y BEI a LSSS: Migración de datos de la información acústica de las campañas de investigación. Informe de Asesoramiento y Transferencia No. 080-22. INIDEP, Mar del Plata, p 1–26

Menna BV, Derisio CM, Temperoni B, Castro Machado F, Cabreira AG, Álvarez Colombo GL (2022b) Caracterización de las fuentes de retrodispersión acústica en el área de cría del efectivo patagónico de merluza común (*Merluccius hubbsi*). Informe de Investigación No. 102-22. INIDEP, Mar del Plata, p 1–25

Menna BV, Rossi GE, Cascallares G, Castro Machado F and others (2023) Caracterización acústica en múltiples frecuencias de las principales especies pelágicas de la plataforma continental argentina. Informe de Investigación No. 099-23. INIDEP, Mar del Plata, p 1–16

Motos L, Uriarte A, Valencia V (1996) The spawning environment of the Bay of Biscay anchovy (*Engraulis encrasicolus L.*). Sci Mar 60:117–140

Nakayama S, Takasuka A, Ichinokawa M, Okamura H (2018) Climate change and interspecific interactions drive species alternations between anchovy and sardine in the western North Pacific: detection of causality by convergent cross mapping. Fish Oceanogr 27:312–322

Orlando P, Buratti CC, Garciarena AD, Buratti G, Parietti M (2023) Estado de la población de anchoíta (*Engraulis anchoita*) al sur de 41° S y determinación de la captura biológicamente aceptable del año 2023. Informe Técnico Oficial No. 030. INIDEP, Mar del Plata, p 1–19

Pacariz SV, Hátún H, Jacobsen JA, Johnson C, Eliasen S, Rey F (2016) Nutrient-driven poleward expansion of the Northeast Atlantic mackerel (*Scomber scombrus*) stock: a new hypothesis. Elementa 4: 000105

Pájaro M (2002) Alimentación de la anchoíta argentina (*Engraulis anchoita* Hubbs y Marini, 1935) (Pisces: Clupeiformes) durante la época reproductiva. Rev Invest Desarro Pesq 15:111–125 (in Spanish with English Abstract)

Palma ED, Matano RP, Piola AR (2008) A numerical study of the Southwestern Atlantic Shelf circulation: stratified ocean response to local and offshore forcing. J Geophys Res 113:C11010

Post S, Heino OF, Teunis J (2019) Blue whiting distribution and migration in Greenland waters. Fish Res 212: 123–135

R Core Team (2024) R: a language and environment for statistical computing. R foundation for Statistical Computing, Vienna

Ratti MM (1986) Estudio comparativo de caracteres merísticos y morfométricos de la anchoíta (*Engraulis anchoita*). Rev Invest Desarro Pesq 5:169–182 (in Spanish with English Abstract)

Rice J (1995) Food web theory, marine food webs, and what climate change may do to northern marine fish populations. Can Spec Publ Fish Aquat Sci 121:561–568

Risaro DB, Chidichimo MP, Piola AR (2022) Interannual variability and trends of sea surface temperature around southern South America. Front Mar Sci 9:829144

Sánchez RP (1995) Patrones de distribución espacio-temporal de los estadíos embrionarios y larvales de la anchoíta (*Engraulis anchoita* Hubbs & Marini) a micro y macroescala. Su relación con la supervivencia y el reclutamiento. PhD thesis, Buenos Aires University

Santos AMP, Chícharo A, Dos Santos A, Moita T, Oliveira PB, Peliz A, Ré P (2007) Physical–biological interactions in the life history of small pelagic fish in the Western Iberia Upwelling Ecosystem. Prog Oceanogr 74: 192–209

Schlitzer R (2018) Ocean Data View, version 5.7.2. http://odv.awi.de

Simard Y, Marcotte D, Bourgault G (1993) Exploration of geostatistical methods for mapping and estimating acoustic biomass of pelagic fish in the Gulf of St. Lawrence: size of echo-integration unit and auxiliary environmental variables. Aquat Living Resour 6:185–199

Temperoni B, Viñas MD, Martos P, Marrari M (2014) Spatial patterns of copepod biodiversity in relation to a tidal front system in the main spawning and nursery area of the Argentine hake *Merluccius hubbsi.* J Mar Syst 139:433–445

Timi JT (2003) Parasites of Argentine anchovy in the southwest Atlantic: latitudinal patterns and their use for discrimination of host populations. J Fish Biol 63:90–107

Troupin C, Barth A, Sirjacobs D, Ouberdous M and others (2012) Generation of analysis and consistent error fields using the Data Interpolating Variational Analysis (DIVA). Ocean Modell 52–53:90–101

Wickham H, Chang W (2016) ggplot2: create elegant data visualisations using the grammar of graphics. R package version 2.2.1. https://ggplot2.tidyverse.org/

Wilson RP, Scolaro JA, Grémillet D, Kierspel MAM and others (2005) How do Magellanic penguins cope with variability in their access to prey? Ecol Monogr 75: 379–401

Wood SN (2015) mgcv: mixed GAM computation vehicle with automatic smoothness estimation. R package version 1.8-10. https://CRAN.R-project.org/web/packages/mgcv/index.html

Yorio PM, González-Zevallos D, Gatto A, Biagioni O, Castillo J (2017) Relevance of forage fish in the diet of Magellanic penguins breeding in northern Patagonia, Argentina. Mar Biol Res 13:603–617

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY

Editorial responsibility: Elliott Hazen,
Pacific Grove, California, USA
Reviewed by: J. Ciancio, A. R. Thompson and 1 anonymous referee

Submitted: April 18, 2024
Accepted: December 5, 2024
Proofs received from author(s): March 5, 2025