


# Influence of environmental conditions on the reproductive success and recruitment of the Argentine hake *Merluccius hubbsi* (southwestern Atlantic Ocean)

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## Abstract

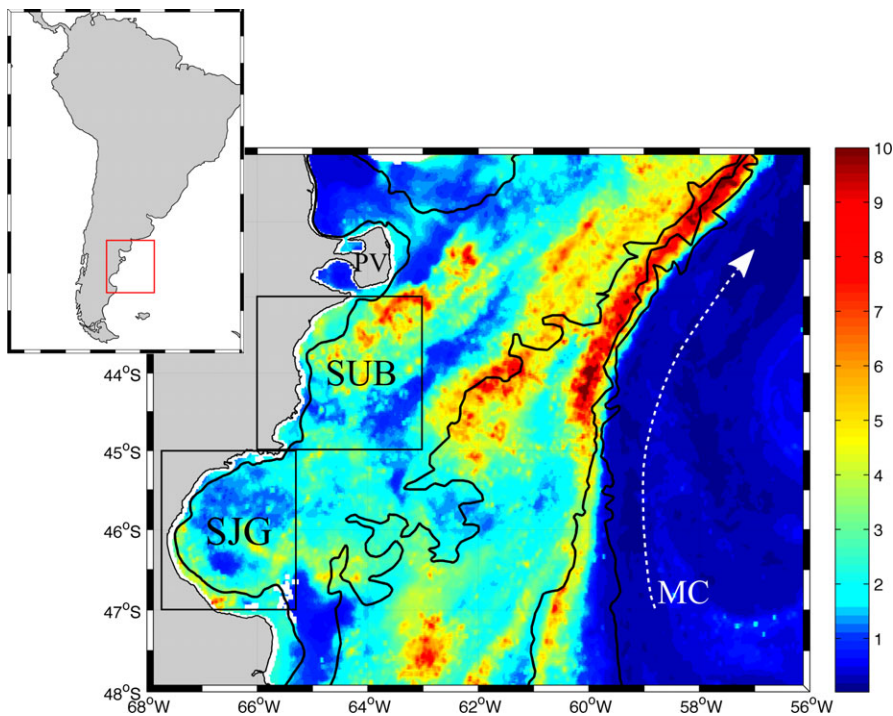
The Argentine hake *Merluccius hubbsi* represents the dominant demersal fish and one of the main fisheries in the Argentine Sea. We analyzed over 17 years (September 1997–February 2015) of satellite surface chlorophyll concentration (CHL) and sea surface temperature anomaly (SSTA) data in the main spawning (SUB) and nursery (SJG) areas of the Patagonian stock of *M. hubbsi*. The variability observed in these environmental conditions was related to interannual differences in the reproductive success of hake. CHL values were maximum during austral spring (October–November) and minimum during winter (June–August). Blooms started in late September and lasted on average 128 and 110 days at SUB and SJG, respectively. At SUB, average CHL at the time of reproduction, the day of occurrence of the maximum chlorophyll concentration, and fall SST anomalies were significantly related to recruitment ( $R_{VPA}$ ) a year later and to two Larval Survival Indices ( $LSI_{SSB}$  and  $LSI_{TEP}$ ) considered. At SJG,  $R_{VPA}$ ,  $LSI_{SSB}$ , and  $LSI_{TEP}$  showed negative correlations with fall (March–May) SSTA. Total egg production was not related to fall SSTA or spring phytoplankton dynamics at SUB or SJG. Significant positive trends were observed in the time series of CHL and SSTA in the study area. The trends observed in CHL represent average increases of 40.7% and 35.7% since 1997 at SUB and SJG, respectively. The potential implications of long-term changes in environmental conditions for hake reproductive success are discussed.

## 1 | INTRODUCTION

The Argentine hake *Merluccius hubbsi* is the dominant demersal fish of the Argentine Sea in terms of biomass and one of the main commercial resources, with a total catch of 282,860 tons reported for 2016 (<http://www.agroindustria.gov.ar>). *Merluccius hubbsi* inhabits waters from southern Brazil (28°S) to the south of Argentina (55°S) between 50 and 500 m depth (Cousseau & Perrota, 1998). In Argentine waters, two main stocks have been identified: a northern stock between 34°S and 41°S, and a southern or Patagonian stock between 41°S and 55°S that is mostly concentrated around 48°S. The Patagonian stock represents the most abundant population,

accounting for about 85% of the fishery. During the 1990s, Argentine hake stocks were overexploited and both the spawning biomass and parent-stock structure were affected (Aubone et al., 2000; Renzi, Santos, & Villarino, 2011).

Hake is a batch spawner with high reproductive activity from December to March and a spawning peak in December–January (Macchi, Pájaro, & Ehrlich, 2004; Pájaro, Macchi, & Martos, 2005). Large concentrations of eggs and larvae are frequently observed in the area of Isla Escondida (SUB, Figure 1), between 43°S and 45°S in coastal and mid-shelf waters, whereas young-of-the-year juveniles are mostly present within the San Jorge Gulf (SJG) where food is abundant (Viñas, Ramirez, Santos, & Perez Seijas, 1992) and



**FIGURE 1** Location of the study area and distribution of monthly mean surface chlorophyll concentration during November 2002 (SeaWiFS,  $\text{mg}/\text{m}^3$ , 2 km/pixel). The subareas SUB and SJG are indicated. MC: Malvinas current; VP: Valdés Peninsula. Black lines represent the 50, 100, 200, and 1,000 m isobaths

circulation is more retentive than in mid-shelf areas (Palma, Matano, & Piola, 2008). The location of the spawning ground is well documented and coincides with a bottom thermal front system located parallel to the coastline between  $43^\circ$  and  $45^\circ 30'$  at  $\sim 80$  m depth (Pájaro et al., 2005; Macchi, Pájaro, & Dato, 2007).

*Merluccius hubbsi* reaches sexual maturity at 2.6 years of age (Simonazzi, 2003). However, the highest mortality occurs during the first year and this stage is critical in determining recruitment (Myers & Cadigan, 1993). One hypothesis for fish in general is that the strength of a year class is mainly controlled by food availability during the larval period (Hjort, 1914; Cushing, 1974). Larvae experiencing favorable feeding conditions will grow faster and attain a larger size, reducing predation mortality during the larval stage (Cushing, 1975). Adult *M. hubbsi* feed primarily on pelagic crustaceans, squid, and fish such as anchovy, whereas young larvae prey on zooplankton, incorporating mainly copepods  $< 2$  mm in length. Young juveniles incorporate larger zooplankton, mostly the euphausiid *Euphausia lucens* and the amphipod *Themisto gaudichaudii* (Viñas & Santos, 2000; Temperoni & Viñas, 2013; Temperoni, Viñas, & Buratti, 2013). Another important factor for fish that are commercially exploited is fishing pressure, which can influence recruitment indirectly by altering the stock reproductive potential and the abundance of spawning individuals, or directly by affecting the abundance of juveniles.

A relationship between chlorophyll concentrations and zooplankton abundance has been suggested for the spawning area of *M. hubbsi* (Temperoni, Viñas, Martos, & Marrari, 2014) and corroborated for other highly productive areas of the continental shelf, such as the main reproductive ground of the Argentine anchovy *Engraulis anchoita* (Marrari et al., 2013). High concentrations of copepodites and adults of *Drepanopus forcipatus*, *Ctenocalanus vanus*, and

*Calanoides carinatus*, which are the preferred prey for hake larvae in the spawning area (Viñas & Santos, 2000; Temperoni & Viñas, 2013), also have been reported associated with high chlorophyll concentrations at the thermocline level (Derisio, 2012). Therefore, we hypothesize that the concentration of chlorophyll in the reproductive area is a good indicator of food availability for larvae and young juveniles and that changes in phytoplankton dynamics may have a strong impact on the reproductive success of *M. hubbsi*. Phytoplankton dynamics, including magnitude, timing, and duration of blooms, have been shown to explain a large percentage of the variability observed in the recruitment of other fish (Platt, Fuentes-Yaco, & Frank, 2003; Marrari et al., 2013) and crustaceans (Fuentes-Yaco, Koeller, Sathyendranath, & Platt, 2007; Marrari, Daly, & Hu, 2008; Ouellet et al., 2011).

The applications of ocean color remote sensing have considerably expanded in the past few decades (IOCCG, 2008; McClain, 2009). Satellite ocean measurements provide unique synoptic and high-resolution information on the global distribution and variability of key parameters. Extended time series of surface chlorophyll concentrations (CHL) and sea surface temperature (SST) measured from satellite allow the analysis of trends and variability in these variables, which have a strong influence on ecosystem dynamics. Considering the high interannual variability observed in the recruitment of *M. hubbsi* and the expected effects of changes in the environmental conditions associated with climate change, the main objectives of this study are to (a) analyze the temporal variability in sea surface temperature anomalies and chlorophyll concentrations in the main spawning and nursery areas of the Patagonian stock of *M. hubbsi*, (b) examine the relationship of these parameters with the reproductive success of hake, (c) determine the optimal environmental conditions for a successful reproduction, and (d) discuss implications of long-

term changes in environmental conditions on stocks of *M. hubbsi*. Results from these analyses will increase our understanding of the variability observed in the recruitment of *M. hubbsi* and will contribute to improved management capabilities.

## 2 | MATERIALS AND METHODS

The study area includes coastal and mid-shelf waters of the Argentine Sea between 41°S and 48°S, with emphasis on two subregions of importance for hake reproduction and recruitment. The subregion SUB (Figure 1) between 43°S and 45°S and between 63°W and 66°W in the vicinity of Bahía Camarones/Isla Escondida represents the main spawning area of *M. hubbsi* (Macchi et al., 2007), while the San Jorge Gulf (SJG) region (45°S–47°S, 65.5°W–67.7°W) is the main nursery area, with large concentrations of juveniles (young-of-the-year) often observed (Santos, Dato, Renzi, Buratti, & Reta, 2012; Álvarez Colombo, Dato, Machinandiarena, Castro-Machado, & Betti, 2014). Five-day and monthly composites of surface chlorophyll *a* concentration (CHL, mg/m<sup>3</sup>) were generated from SeaWiFS (SWF) and MODIS/Aqua (AQ) data. All available high-resolution (~1 km/pixel) level 2 data were processed with the standard flags and empirical algorithms (OC4v4 for SeaWiFS and OC3M for MODIS, O'Reilly et al., 2000), binned, and mapped to a 2 km/pixel resolution. Reprocessing versions 2013.0 and 2013.1.1 were used for SWF and AQ, respectively. The spatial resolution of 2 km/pixel was selected to better represent the variability within the subregions analyzed, especially considering the differences that can occur between adjacent pixels in frontal areas. To reduce errors caused by digitization and random noise without losing spatial resolution, a 3 × 3 box around each pixel was selected to compute the mean chlorophyll concentration (Hu, Carder, & Müller-Karger, 2001). Chlorophyll concentrations <0.02 and > 30 mg/m<sup>3</sup> were excluded from all analyses. All data were weighted equally, and monthly composites were generated for the period September 1997–December 2006 for SWF, and July 2002–February 2015 for AQ. Data are distributed by the Ocean Biology Processing Group at NASA's Goddard Space Flight Center (<http://oceancolor.gsfc.nasa.gov>). High-resolution SWF data are available in our study area for the period 1997–2006, while AQ data are available for 2002 to present. Together, both data sets provide almost two decades of chlorophyll concentration measurements, almost 5 years of which temporally overlap (July 2002–December 2006). Composites were generated for the period September 1997–February 2015 using a combination of data from both sensors. Previous analyses of the uncertainty in the retrievals from SeaWiFS and MODIS revealed significant differences between sensors in our study area, particularly for higher CHL values (Marrari, Piola, Valla, & Wilding, 2016; Marrari, Piola, & Valla, 2017). As concentrations increased, the differences between SWF and MODIS also increased, most likely due to differences in the maximum band ratio used in the standard algorithms. OC4v4 (SWF) makes use of a maximum band ratio that incorporates 443, 490, and 510 nm, while OC3M (AQ) only incorporates 443 and 488 nm. As CHL increases, the

selected maximum band migrates from shorter (blue) to longer (green) wavelengths. In the most turbid water, OC4v4 selects 510 nm, while OC3M remains at 488 nm, which results in differences in the functional form of each algorithm leading to large differences in chlorophyll retrievals at higher chlorophyll concentrations (Werdell et al., 2009). Using the available overlapping (2002–2006) data, model II ordinary least squares (OLS) regressions were calculated at each pixel on the log-transformed data and the coefficients were used to adjust the MODIS/Aqua data set (2002–2015). Extended time series of monthly mean CHL were generated for the SUB and SJG areas for the period 1997–2015 using SWF data for 1997–2006 and adjusted AQ data for 2007–2015. A detailed description of this methodology can be found in Marrari et al. (2016). Trend analyses were performed on all pixels following the methods in Saulquin et al. (2013). For the analysis of trends in areal mean SSTA and chlorophyll concentrations at each subregion, the Mann-Kendall test was applied. The significance level for all tests was selected at 0.05.

Five-day, monthly, and summer (average for November–January) climatologies of chlorophyll concentration and their corresponding anomalies were calculated at each subregion for the 1997/1998–2014/2015 seasons. The day of initiation of a phytoplankton bloom was defined as the center day of the 5-day period when the mean chlorophyll concentration at each subregion reached 1.3 mg/m<sup>3</sup>. This value was selected after a preliminary analysis of bloom development in the study area. The duration of the bloom was defined as the number of days during which those conditions were maintained. The magnitude and day of occurrence (center day of the 5-day period) of the maximum chlorophyll concentration were also examined.

Sea surface temperature anomalies (SSTA) for the period January 1982–February 2015 were analyzed from Optimal Interpolation Sea Surface Temperature (OISST) daily data with a resolution of 0.25° (<http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/.OISST/>). Time series of monthly mean SSTA were generated for SUB and SJG and analyzed in relation to trends and variability in chlorophyll concentrations. The OI analysis uses a combination of in situ and satellite SST data from the Advanced Very High Resolution Radiometer (AVHRR; Reynolds, Rayner, Smith, Stokes, & Wang, 2002).

The National Institute for Fisheries Research and Development in Argentina (INIDEP) produces annual estimates of abundance and population structure of *M. hubbsi* from field and model data. Recruitment ( $R_{VPA}$ ) and spawning stock biomass data ( $SSB_{VPA}$ ) for the period 1990–2014 were obtained from virtual population analysis (VPA; Santos & Villarino, 2015). The number of age–1 individuals estimated for each January from VPA was selected as a measure of the reproductive success of *M. hubbsi* during the previous year, as it indicates the abundance of individuals that survived the larval stage, which is the most vulnerable in the life history of fish (Houde, 2009). For example,  $R_{VPA}$  estimated for January 1990 was used as an indication of the reproductive success of the 1988/1989 spring–summer season. In addition, juvenile abundance normalized to spawning biomass provides an index of survival and can ultimately

reveal the size of the incoming year class. A Larval Survival Index ( $LSI_{SSB}$ ) was calculated for each season as the ratio of the abundance of 1-year-old individuals ( $R_{VPA}$ ) during the following season to the spawning biomass ( $SSB_{VPA}$ ) from the given season (Platt et al., 2003; Marrari et al., 2013):

$$LSI_{SSB} = \frac{R_{VPA+1}}{SSB_{VPA}}$$

An alternative index of reproductive output is the total egg production (TEP), which represents an improved index of recruitment potential, because it includes information on parental demographic structure that influences survival of the early life stages (Marshall, Kjesbu, Yaragina, Solemdal, & Ulltang, 1998). Total egg production of the Patagonian Argentine hake stock in a given year was obtained according to Marshall (2009) as:

$$TEP = \sum_a n_a * s_a * m_a * e_a$$

where  $n_a$  is the number of individuals at age obtained from VPA at the beginning of the year (Santos & Villarino, 2015),  $s_a$  is the sex ratio at age,  $m_a$  is the proportion of mature females at age, and  $e_a$  is the number of eggs produced at age. The sex ratios were obtained from data collected during research surveys carried out during January 2001–2013 (Table 1). In the case of age at maturity ogives, we used the models estimated by Macchi, Rodrigues, Diaz, and Militelli (2017) from the same surveys between 2005 and 2013, after including the effect of skipped spawning in females of the Argentine hake Patagonian stock (Table 1). We could not obtain survey data during some years (i.e., before 2001 and in 2002–2003); therefore, reproductive variables during these years were replaced by the mean values estimated for the entire sampling period. During the surveys, ovary samples were collected and preserved for histological analysis to estimate batch fecundity at age by the hydrated oocyte method

and spawning frequency (SF) by the postovulatory follicle proportion, according to Hunter, Lo, and Leong (1985). Batch fecundity–age models were estimated for each sampled year (Table 1), while an average relationship between SF and age (A) was estimated with all data collected from 2001 to 2013 (Macchi, Rodrigues, Leonarduzzi, & Diaz, 2018), described by the following equation:

$$SF = 8.60 - 0.29 * A \quad (r^2 = 0.33, n = 11)$$

These variables were used to obtain the annual number of eggs produced at age by multiplying the batch fecundity by age data with the number of spawning events by age estimated for each year (Mehault, Domínguez-Petit, Cerviño, & Saborido-Rey, 2010). An alternative Larval Survival Index ( $LSI_{TEP}$ ) was calculated for each season as the ratio of the abundance of 1-year-old individuals ( $R_{VPA}$ ) during the following season to the TEP estimated for the current season:

$$LSI_{TEP} = \frac{R_{VPA+1}}{TEP}$$

In order to assess the relationship between environmental variability and the reproductive success of *M. hubbsi*, a correlation matrix was developed relating environmental parameters (chlorophyll dynamics and SSTA) to the response variables ( $R_{VPA}$ , TEP,  $LSI_{SSB}$ ,  $LSI_{TEP}$ ). The Spearman correlation coefficient was used, which is nonparametric and can detect nonlinear relationships between variables. Significance was selected at 95%. To account for multiple comparisons, the Benjamini–Hochberg correction was applied (McDonald, 2014). First, relationships are ranked according to their  $p$  value, which is then compared with the Benjamini–Hochberg critical value:  $(i/m)*Q$ , where  $i$  is the rank,  $m$  is the total number of tests (14 for chlorophyll and 8 for SSTA versus reproductive success relationships), and  $Q$  is the rate of false discovery, selected at 0.25 in this

**TABLE 1** Number of trawl stations, individuals sampled for age determination (A) by sex and maturity stage, and number of ovaries collected for histology analyses and batch fecundity (BF) estimations in the main spawning area of the Argentine hake Patagonian stock during January 2001–2013

Year	Trawls (n)	Individuals sampled (n)	Ovaries for histology (n)	Ovaries for fecundity (n)	$P_A = 1/(1 + e(-b*(A-A_{50})))$	$BF = aTL^b$
2001	42	3,362	1,476	102	$A_{50} = 2.93, b = 1.97$	$a = 20,583, b = 1.93$
2004	40	2,273	885	54	$A_{50} = 2.93, b = 1.97$	$a = 24,672, b = 1.88$
2005	32	4,629	1,296	82	$A_{50} = 2.74, b = 2.57$	$a = 21,750, b = 1.99$
2006	32	4,329	1,454	89	$A_{50} = 2.86, b = 1.99$	$a = 26,830, b = 1.83$
2007	32	3,469	1,265	77	$A_{50} = 3.16, b = 1.07$	$a = 30,169, b = 1.87$
2008	32	3,507	1,225	81	$A_{50} = 3.36, b = 1.32$	$a = 19,793, b = 2.09$
2009	32	3,738	1,263	89	$A_{50} = 2.95, b = 2.40$	$a = 21,251, b = 2.04$
2010	31	3,831	1,222	100	$A_{50} = 2.84, b = 1.49$	$a = 22,492, b = 1.91$
2011	29	3,885	741	75	$A_{50} = 2.79, b = 1.87$	$a = 22,422, b = 1.90$
2012	29	6,869	1,277	98	$A_{50} = 2.77, b = 2.81$	$a = 17,326, b = 2.02$
2013	31	6,545	1,146	82	$A_{50} = 2.87, b = 2.21$	$a = 25,350, b = 1.83$

Note. Coefficients of the age at maturity models obtained for females and BF versus A relationships are also included.  $P_A$ , proportion of mature females at age;  $b$ , slope of the curve;  $A_{50}$ , age at which 50% of females are mature. Age at maturity ogives and batch fecundity–age models were obtained from Macchi et al. (2017).

study. The largest  $p$  value that is smaller than the critical value is significant, as well as all smaller  $p$  values, even when not smaller than their critical value. Reproductive success indices were related to chlorophyll parameters from the previous season starting in 1997 (satellite period), while SSTA for the periods 1982–2015 and 1997–2015 were considered.

### 3 | RESULTS

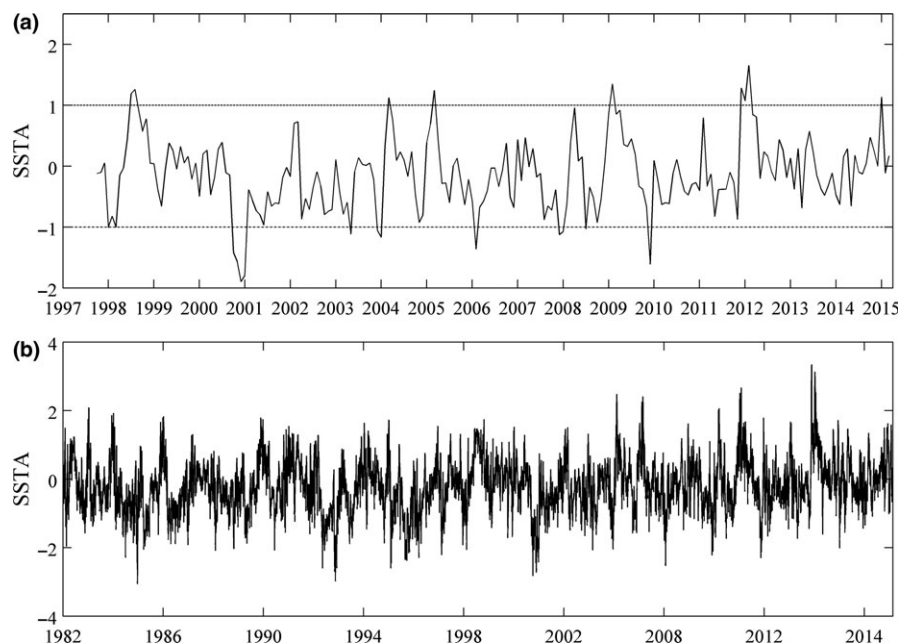
#### 3.1 | Spawning area (SUB)

Monthly sea surface temperature anomalies at SUB indicated large interannual variability during the satellite ocean color period (1997–2015), with average anomalies for the subregion ranging between  $-1.90^{\circ}\text{C}$  and  $1.66^{\circ}\text{C}$  (Figure 2a). Warmer-than-average summers ( $\pm 1^{\circ}\text{C}$  for December–March) occurred during 2003/2004, 2004/2005, 2008/2009, 2011/2012, and 2014/2015, whereas colder-than-average values prevailed in 1997/1998, 2000/2001, 2003/2004, 2005/2006, and 2007/2008. In addition, analysis of daily anomaly data for a longer period of time (January 1982–February 2015) revealed a significant positive trend, with an average increase of  $0.379^{\circ}\text{C}$  since 1982 for this subregion (Mann–Kendall test,  $p < 0.0001$ ,  $n = 12,094$ ; Figure 2b).

Monthly climatology chlorophyll concentrations averaged over the subregion SUB ranged between  $0.92\text{ mg/m}^3$  in August and  $2.40\text{ mg/m}^3$  in November, and showed a clear seasonal pattern: Highest values occurred during spring (October–November), while lowest concentrations were observed in winter months (June–August; Table 2, Figure 3a). A second smaller peak was observed during fall (March–April). The overall mean chlorophyll concentration for summer (November–January) at SUB was  $1.84\text{ mg/m}^3$ . However, there was high interannual variability, with the highest positive

anomalies observed during seasons 2009/2010, 2010/2011, 2011/2012, 2012/2013, and 2014/2015, and the strongest negative anomalies of  $\sim 1\text{ mg/m}^3$  in 1998/1999 and 1999/2000 (Figure 3b). The maximum 5-day areal mean chlorophyll concentration was recorded at the end of October 2014, reaching  $8.64\text{ mg/m}^3$ . The day of the start of the bloom varied between mid-September (day of the year 258) and late October (day of the year 298), with an average during late September (day of the year 273; Table 2). The average duration of the bloom at SUB was 128 days, with minima of 45 and 55 days in seasons 2004/2005 and 2014/2015, respectively, and maxima of 265 and 245 days in seasons 2008/2009 and 2009/2010, respectively. Blooms with a combination of an early start (10 days before average) and long duration (10 days longer than average), which in combination with elevated spring–summer chlorophyll concentrations would represent optimal conditions for hake larvae, only occurred during 2008/2009, 2009/2010, and 2012/2013. The chlorophyll maximum occurred, on average, on November 3. The earliest peaks were observed between October 15 (2012/2013) and October 20 (1997/1998, 1999/2000, and 2004/2005), while the latest occurred on November 24 (2002/2003 and 2013/2014) and December 9 (2009/2010).

A significant increasing trend (slope = 0.0023, intercept = 1.1866) in areal mean chlorophyll concentrations at SUB was observed, with an average increase of  $0.483\text{ mg/m}^3$  since 1997, or 2.33% per year (Mann–Kendall test,  $p = 0.001$ ,  $n = 210$ ). The analysis of individual pixels revealed significant increasing trends in chlorophyll concentrations in 81.29% of the area. In addition, there was a positive trend in the maximum chlorophyll concentration during a season (Mann–Kendall test,  $p = 0.004$ ,  $n = 18$ ), with larger peaks during the last several years in relation to the beginning of the time series. No significant trends were observed in the day of initiation or the duration of the bloom.

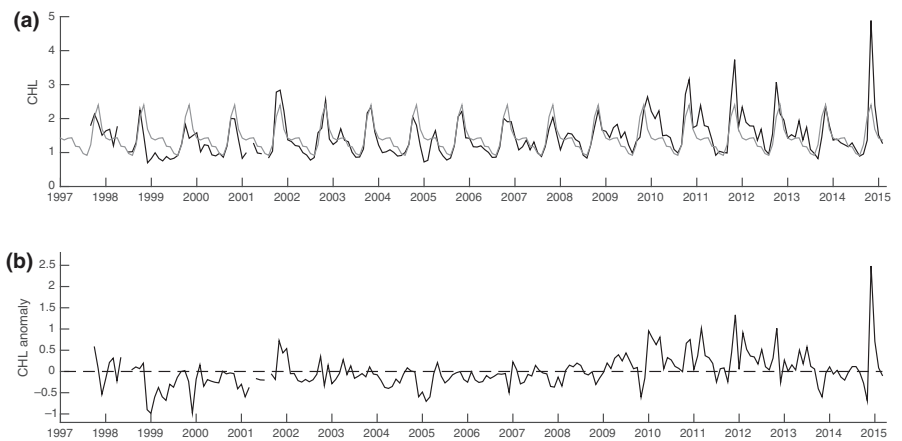


**FIGURE 2** (a) Monthly sea surface temperature anomaly (SSTA,  $^{\circ}\text{C}$ ) at SUB for the period September 1997–February 2015. The black dotted lines indicate an anomaly of  $\pm 1^{\circ}\text{C}$ . (b) Daily SSTA at SUB since 1982

**TABLE 2** Monthly mean chlorophyll concentrations (CHL) during the period September 1997–February 2015 and overall mean during the peak of reproductive activity (November–January: CHL<sub>NJ</sub>, mg/m<sup>3</sup>) at SUB

Season	CHL July	CHL August	CHL September	CHL October	CHL November	CHL December	CHL January	CHL February	CHL March	CHL April	CHL May	CHL June	CHL <sub>NJ</sub>	Bloom start	Bloom duration	Max day	
1997/1998	1.81	1.02	1.30	2.13	1.86	1.51	1.64	1.69	1.20	1.76			1.67	278	120	2.92	293
1998/1999	1.02	1.02	1.30	2.25	1.50	0.70	0.82	0.99	0.82	0.75	0.88	0.80	1.01	263	60	2.51	288
1999/2000	0.83	0.92	1.25	1.82	1.42	1.51	1.58	1.02	1.23	1.21	0.93	0.90	1.50	268	135	2.38	293
2000/2001	0.98	0.86	1.20	2.01	1.99	1.39	0.83	0.98	1.21	1.27	0.99	0.97	1.40	283	65	2.72	308
2001/2002	0.78	0.85	1.04	2.78	2.84	2.22	1.38	1.32	1.70	1.19	1.00	0.93	2.15	283	105	3.36	303
2002/2003	0.86	0.85	1.58	1.72	2.55	1.40	1.24	1.33	1.02	1.36	1.32	1.01	1.73	263	85	3.44	328
2003/2004	0.91	0.87	1.10	2.16	2.34	1.61	1.22	1.00	1.37	1.08	1.00	0.90	1.72	268	100	3.54	308
2004/2005	0.78	1.00	1.24	2.05	1.81	1.20	0.72	0.77	1.16	1.64	1.08	0.90	1.24	288	45	2.52	293
2005/2006	0.86	0.84	1.20	2.05	2.21	1.43	1.42	1.17	1.17	1.20	1.09	1.01	1.69	268	85	3.46	313
2006/2007	1.00	0.86	1.16	2.01	1.91	1.91	1.47	1.08	1.57	1.37	1.08	1.31	1.76	263	130	2.46	298
2007/2008	0.92	0.88	1.17	1.70	2.03	1.55	1.08	1.40	1.73	1.55	1.38	1.31	1.56	273	80	2.45	298
2008/2009	1.22	0.84	1.22	1.75	2.25	1.66	1.63	1.44	2.23	1.83	1.43	1.61	1.84	258	265	3.52	313
2009/2010	1.09	0.98	1.32	1.45	2.25	2.64	2.21	2.00	1.79	1.50	1.51	1.44	2.37	258	245	3.44	343
2010/2011	1.04	0.99	1.22	2.72	3.15	1.73	1.79	2.39	1.78	1.76	1.38	0.92	2.23	278	235	5.37	318
2011/2012	1.08	1.00	0.99	2.50	3.73	1.74	2.34	1.89	1.46	1.78	1.36	1.69	2.60	298	180	5.03	313
2012/2013	1.09	0.96	1.54	3.07	2.14	1.95	1.43	1.53	1.29	1.94	1.36	1.75	1.84	258	235	4.67	288
2013/2014	1.09	0.98	0.82	1.46	2.36	1.80	1.37	1.40		1.23	1.17	1.28	1.84	283	75	3.75	328
2014/2015		0.89	0.96	1.36	4.89	2.39	1.51	1.28					2.93	288	55	8.64	303
Climatology	0.97	0.92	1.23	2.06	2.40	1.69	1.43	1.37	1.42	1.44	1.19	1.17	1.84	273	128	3.68	307

Note. The day of the year when the bloom started, the bloom duration (days), the maximum chlorophyll concentration observed (mg/m<sup>3</sup>), and its day of occurrence are also indicated.



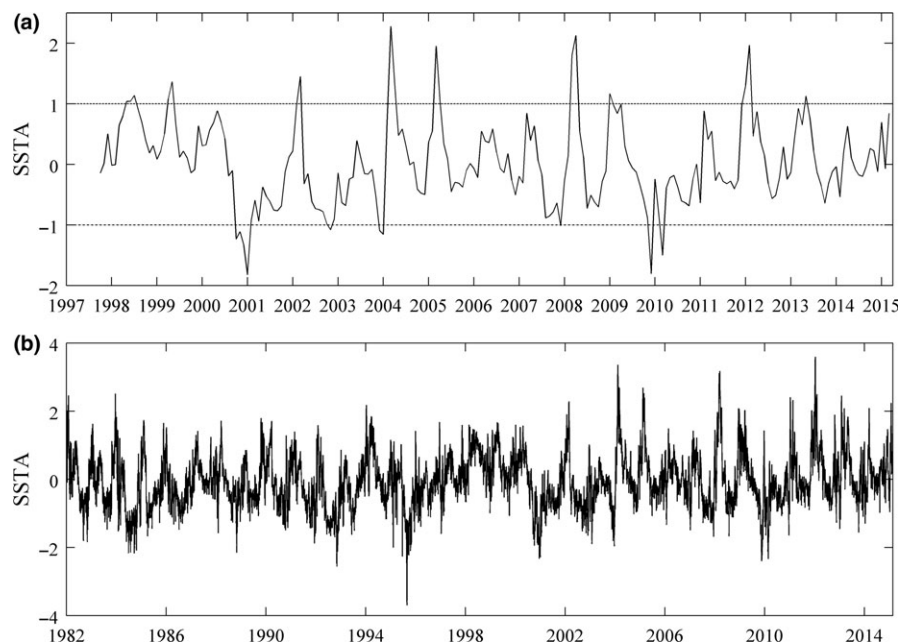
**FIGURE 3** Time series of (a) monthly mean chlorophyll concentrations (CHL, black) and monthly climatology (gray), and (b) monthly chlorophyll concentration anomalies (black) at SUB. Data correspond to SeaWiFS for 1997–2006 and corrected MODIS for 2007–2015 (2 km/pixel)

### 3.2 | Nursery area (SJG)

The time series of monthly SST anomalies at SJG between 1997 and 2015 showed warmer-than-normal summer months ( $\pm 1^\circ\text{C}$  for December–March) in 2001/2002, 2003/2004, 2004/2005, 2007/2008, 2008/2009, and 2011/2012, and colder-than-average conditions in 2000/2001, 2003/2004, and 2009/2010 (Figure 4a). Analysis of a longer time series of daily anomalies also showed a significant positive trend at SJG, with an average increase of  $0.337^\circ\text{C}$  since 1982 (Mann–Kendall test,  $p < 0.0001$ ,  $n = 12,094$ ; Figure 4b).

The SJG subarea showed a similar chlorophyll concentration pattern to that observed at SUB between 1997 and 2015, although maximum values occurred on average a month earlier, in October ( $2.66 \text{ mg/m}^3$ ) followed by November ( $2.19 \text{ mg/m}^3$ ; Table 3, Figure 5a). Minima occurred in June–July–August, with monthly climatology values ranging between  $1.16$  and  $1.19 \text{ mg/m}^3$ . The maximum 5-day mean value of the time series was recorded during late November 2014 and reached  $13.91 \text{ mg/m}^3$ . Anomalies showed

larger amplitudes than at SUB, with maximum values of up to  $5.46 \text{ mg/m}^3$  for October 2011 (Figure 5b). Above-average spring–summer values occurred during seasons 1997/1998, 2006/2007, 2008/2009, 2009/2010, and 2014/2015, while lower-than-normal values were observed in 1998/1999, 1999/2000, 2001/2002, 2002/2003, 2004/2005, 2007/2008, and 2012/2013. The start of the phytoplankton bloom varied between Days 238 (late August) and 288 (mid-October), with a mean value of 268, which corresponds to late September. At SJG, blooms lasted 110 days on average, with minima of 30 and 35 days during 2004/2005 and 2005/2006, and maxima of 255 and 245 days during 2006/2007 and 2009/2010, respectively. The combination of early and long-lasting blooms occurred during 2001/2002 and 2006/2007 (Table 3). In this subregion, chlorophyll concentrations peaked on November 10, on average, with the earliest peaks between September 15 (1999/2000) and September 25 (2007/2008), and the latest observed on April 28 (2009/2010) as well as on January 18 (1997/1998) and January 13 (2006/2007).



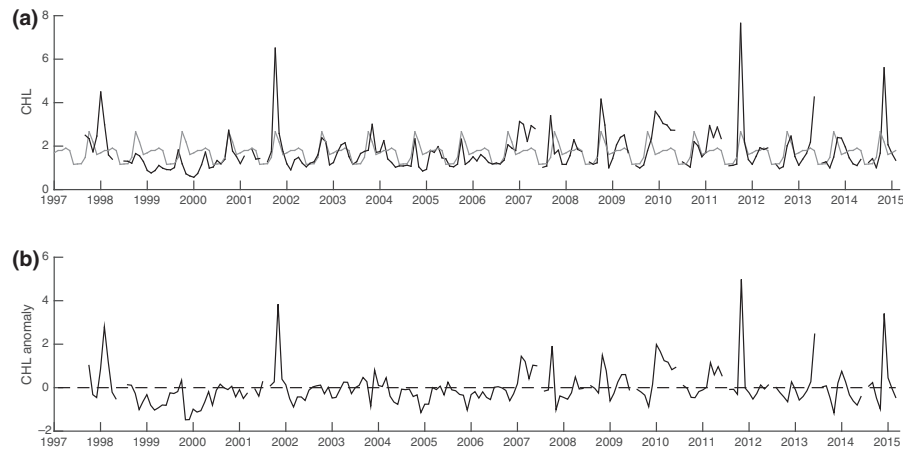
**FIGURE 4** (a) Monthly sea surface temperature anomaly (SSTA,  $^\circ\text{C}$ ) at SJG for the period September 1997–February 2015. The black lines indicate an anomaly of  $\pm 1^\circ\text{C}$ . (b) Daily SSTA at SJG since 1982

**TABLE 3** Monthly mean chlorophyll concentrations (CHL) during the period September 1977–February 2015 and overall mean during the peak of reproductive activity (November–January): CHL<sub>NJ</sub>, mg/m<sup>3</sup> at SJG

Season	CHL Jul	CHL Aug	CHL Sept	CHL Oct	CHL Nov	CHL Dec	CHL Jan	CHL Feb	CHL Mar	CHL Apr	CHL May	CHL June	CHL <sub>NJ</sub>	Bloom start	Bloom duration	Max day	
1977/1998	2.50	2.34	1.74	2.46	4.49	2.99	1.59	1.40	0.98	0.92	1.24	278	2.90	278	5.38	018	
1998/1999	1.31	1.30	1.21	1.66	1.55	1.29	0.88	0.77	0.88	1.11	0.98	0.92	1.24	278	65	2.01	278
1999/2000	0.91	1.01	1.82	1.19	0.72	0.63	0.57	0.74	1.14	1.72	0.99	1.04	0.64	253	65	2.02	258
2000/2001	1.34	1.19	1.39	2.73	1.77	1.52	1.19	1.54	1.37	1.85	1.40	1.43	1.50	278	95	2.75	288
2001/2002	1.21	1.28	1.75	6.51	2.58	1.75	1.18	0.91	2.06	1.48	1.21	1.05	1.84	248	130	6.99	278
2002/2003	1.28	1.28	1.60	2.38	2.21	1.14	1.24	1.70	1.41	2.15	1.52	1.16	1.53	268	70	4.31	303
2003/2004	1.09	1.66	1.76	1.81	3.00	1.71	1.74	2.25	1.71	1.25	1.03	1.09	2.15	288	175	4.28	308
2004/2005	1.08	1.12	1.07	2.33	1.05	0.85	0.93	1.80	1.61	1.98	1.46	1.41	0.94	278	30	3.32	293
2005/2006	1.22	1.05	1.17	2.32	1.16	1.30	1.51	1.32	2.22	1.46	1.25	1.18	1.32	268	35	3.88	288
2006/2007	1.02	1.18	1.35	2.06	1.91	1.79	3.13	3.00	2.29	2.94	2.80	2.80	2.28	258	255	4.61	013
2007/2008	1.27	1.08	3.40	1.65	1.81	1.16	1.16	1.56	2.40	1.85	1.76	1.76	1.38	258	95	5.16	268
2008/2009	1.10	1.17	1.23	4.16	2.97	1.00	1.43	2.06	2.97	2.51	1.70	1.70	1.80	258	65	7.06	313
2009/2010	1.27	0.99	1.13	1.79	2.34	3.60	3.35	3.04	2.39	2.74	2.73	2.73	3.10	273	245	7.29	118
2010/2011	1.10	1.16	1.03	2.20	2.01	1.51	1.71	2.95	1.93	2.88	2.35	2.35	1.74	278	80	3.25	298
2011/2012	1.19	1.12	1.17	7.65	2.18	1.38	1.16	1.53	1.66	1.85	1.92	1.92	1.57	238	115	7.92	298
2012/2013	1.21	0.96	1.06	2.01	2.46	1.52	1.12	1.39	1.18	2.18	4.26	4.26	1.70	273	110	3.83	328
2013/2014	1.25	1.28	1.00	1.49	2.40	2.37	1.96	1.46	1.11	1.39	1.39	1.39	2.24	288	135	6.79	303
2014/2015	1.43	1.00	1.00	1.68	5.60	2.06	1.66	1.35	1.80	1.80	1.80	1.16	1.83	268	110	13.91	323
Climatology	1.18	1.19	1.48	2.66	2.19	1.61	1.69	1.80	1.80	1.91	1.80	1.16	1.83	268	110	4.76	314

Note. The day of the year when the bloom started, the bloom duration (days), the maximum chlorophyll concentration observed (mg/m<sup>3</sup>), and its day of occurrence are also indicated.





**FIGURE 5** Time series of (a) monthly mean chlorophyll concentrations (CHL, black) and monthly climatology (gray), and (b) monthly chlorophyll concentration anomalies (black) at SJG. Data correspond to SeaWiFS for 1997–2006 and corrected MODIS for 2007–2015 (2 km/pixel)

A significant increasing trend (slope = 0.0025, intercept = 1.459) in chlorophyll concentrations was also recorded for this subregion, with a slope representing an increase of  $0.525 \text{ mg/m}^3$  in mean chlorophyll concentration since 1997, or 2.06% per year (Mann–Kendall test,  $p = 0.005$ ,  $n = 210$ ). The analysis of the spatial patterns of the trends revealed that 43.4% of the pixels showed increases in chlorophyll concentrations, with the remaining 56.6% of the area showing no trend. No significant trends were observed in the day of initiation or the duration of the bloom, the maximum chlorophyll concentration, or its day of occurrence.

### 3.3 | SUB versus SJG

Sea surface temperature anomalies were correlated at SUB and SJG ( $R^2 = 0.554$ ,  $p < 0.0001$ ,  $n = 12,094$ ), suggesting that the same environmental processes influence physical conditions in both areas. Overall, summer and fall anomalies showed larger amplitudes at SJG, likely due to the more enclosed and retentive characteristics of this region.

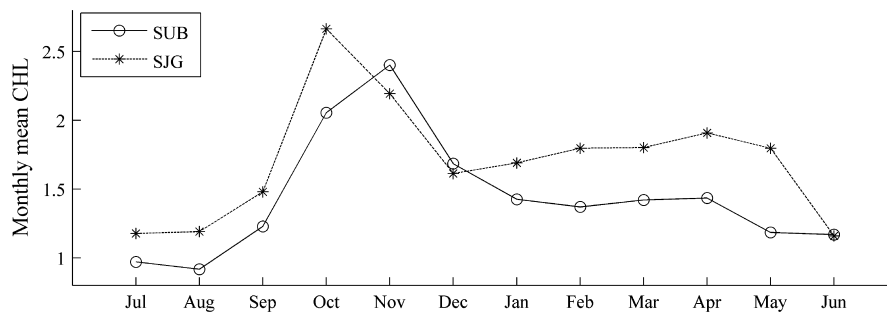
Monthly climatology chlorophyll concentration data showed that seasonal patterns were similar at both subregions, with spring maxima and winter minima (Figure 6). The monthly mean maximum chlorophyll concentration occurred in November at SUB and a month earlier during October at SJG. In general, SJG had higher chlorophyll concentrations than SUB during the summer, fall, and

winter months, and somewhat lower values during late spring (November–December). However, climatology mean CHL for the summer months (November–January) when maximum reproductive activity occurs was  $1.84 \text{ mg/m}^3$  for SUB and  $1.83 \text{ mg/m}^3$  for SJG. In addition, phytoplankton blooms started an average of 5 days later at SUB and lasted for 18 days longer than at SJG.

### 3.4 | Egg production, larval survival, and recruitment

Total egg production (TEP) ranged between 1921 and 4,425 billions of eggs between 1989/1990 and 2013/2014 (Figure 7a). The first period between 1989/1990 and 2003/2004 showed a clear declining trend, which reversed to an increasing trend after 2004/2005. Maximum values for the entire time series were observed between 1989/1990 and 1997/1998 and then again during seasons 2005/2006, 2006/2007, 2012/2013, and 2013/2014. Minima were recorded between 1999/2000 and 2004/2005.

Recruitment of 1-year-old individuals of *M. hubbsi* estimated from VPA ( $R_{VPA}$ ) showed large interannual variability with 4- to 5-year cycles of lower and higher values and a general declining trend since 1990 that represents an average decrease of 39.71% (slope =  $-48,926$ , intercept =  $3,080,408$ ,  $n = 25$ ; Figure 7b). Maximum values were recorded during a four-season period from 1992/1994 to 1995/1996, and during January 2001/2002 and 2002/2003.



**FIGURE 6** (1997–2015) Monthly climatology of mean chlorophyll concentrations at SUB (circles) and SJG (stars; CHL,  $\text{mg/m}^3$ )

Even though the spawning biomass also showed an average declining trend of 36.45% since 1989/1990 (slope =  $-8887$ , intercept =  $594,014$ ,  $n = 25$ ; Figure 7c), the Larval Survival Index (LSI<sub>SSB</sub>) showed no significant trend (Mann–Kendall test,  $p = 0.835$ ,  $n = 24$ ; Figure 7d). LSI<sub>TEP</sub> showed an almost identical pattern as LSI<sub>SSB</sub>. These indices provide an indication of the proportion of larvae that survived during the first year.

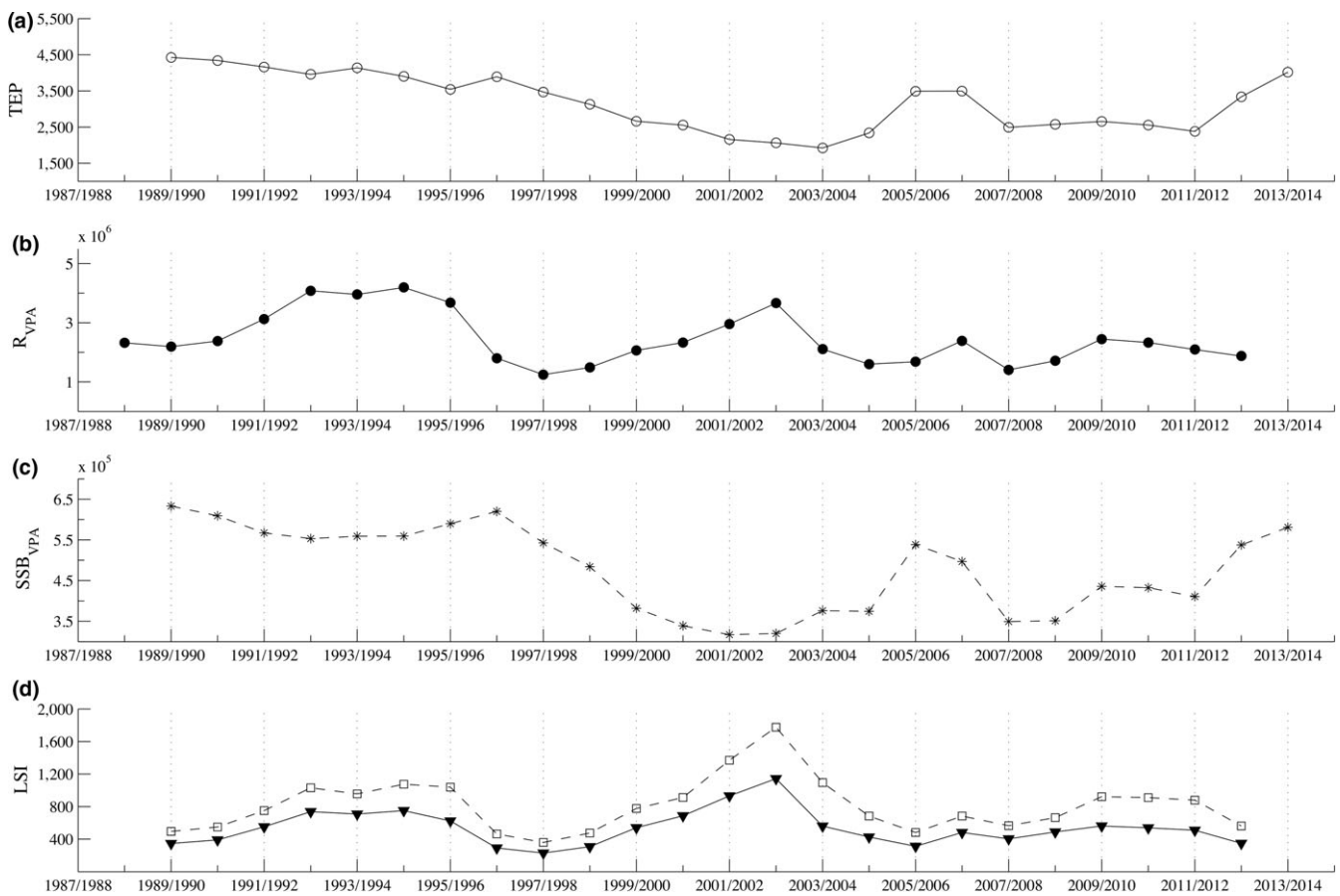
Several significant relationships (after applying the Benjamini–Hochberg correction) were observed between environmental (SSTA and CHL dynamics) and reproductive success parameters, including  $R_{VPA}$ , TEP, LSI<sub>SSB</sub>, and LSI<sub>TEP</sub> (Table 4). In general, relationships were consistent with the different measures of reproductive success. At SUB, recruitment ( $R_{VPA}$ ) showed significant positive relationships with November and spring (November–January) chlorophyll concentrations and the day of occurrence of the chlorophyll maximum, and negative relationships with SST anomalies during March, April, and May. At SJG, no relationships were observed with chlorophyll, but  $R_{VPA}$  was related to SSTA during all months from November through May, except for December and January, as well as to the average anomaly for January–March.

LSI<sub>SSB</sub> and LSI<sub>TEP</sub> were positively related to the day of maximum chlorophyll concentration and also showed negative relationships with April and May SSTA at SUB. In addition, LSI<sub>TEP</sub> was related to November chlorophyll in this subregion. At SJG, no relationships were observed with chlorophyll, while LSI<sub>SSB</sub> showed negative correlations with SSTA in March, April, and May, and LSI<sub>TEP</sub> only for March. No significant relationships between TEP and chlorophyll or SSTA were observed at SUB or SJG.

There was no correlation between recruitment ( $R_{VPA}$ ) and total egg production ( $p = 0.188$ ,  $n = 16$ ) or spawning biomass at the time of reproduction ( $p = 0.119$ ,  $n = 16$ ).

## 4 | DISCUSSION

Chlorophyll dynamics in the main reproductive area of the Patagonian stock of *M. hubbsi* showed large spatial and temporal variability with maximum chlorophyll concentrations during October and November, one or 2 months prior to the peak in hake spawning (December–January). In the main spawning area (SUB) bloom



**FIGURE 7** Time series of: (a) total egg production (TEP, billions of eggs), (b) recruitment estimated from the VPA model ( $R_{VPA}$ , thousands of individuals), (c) spawning biomass ( $SSB_{VPA}$ , tons) estimated from VPA, and (d) Larval Survival Index (LSI) calculated from  $SSB_{VPA}$  ( $LSI_{SSB} = R_{VPA} + 1/SSB_{VPA} \times 100$ ; black triangles) and from TEP data ( $LSI_{TEP} = R_{VPA} + 1/TEP$ ; white squares) for the Patagonian stock of *M. hubbsi*. TEP and  $SSB_{VPA}$  for a given season represent the values measured during that season.  $R_{VPA}$  corresponds to the season when the larvae originated and indicates the abundance 1-year-old individuals estimated for the following season. LSI values for a given season include the  $SSB_{VPA}$  or TEP value for that season and the  $R_{VPA}$  value for the following season

**TABLE 4** Spearman's correlation indices for the relationships between environmental and reproductive output variables, including the recruitment index, larval survival indices, and total egg production

	SUB				SJG			
	$R_{VPA}$	$LSI_{SSB}$	$LSI_{TEP}$	TEP	$R_{VPA}$	$LSI_{SSB}$	$LSI_{TEP}$	TEP
SSTA (November)	-0.310	-0.354	-0.395	0.283	<u>-0.350</u>	-0.369	-0.389	0.239
SSTA (December)	0.150	-0.047	-0.018	0.012	-0.309	-0.256	-0.300	0.071
SSTA (January)	0.284	0.353	0.390	<b>-0.482*</b>	-0.159	-0.044	0.009	-0.373
SSTA (February)	0.028	0.146	0.212	-0.414	<u>-0.390</u>	-0.299	-0.230	-0.224
SSTA (March)	<u>-0.494</u>	-0.368	-0.297	-0.087	<b>-0.712*</b>	<b>-0.524*</b>	<u>-0.456</u>	-0.142
SSTA (April)	<b>-0.547*</b>	<b>-0.615*</b>	<b>-0.612*</b>	0.243	<b>-0.615*</b>	<b>-0.718*</b>	<b>-0.690*</b>	0.375
SSTA (May)	<b>-0.576*</b>	<b>-0.550*</b>	<b>-0.588*</b>	0.356	<b>-0.597*</b>	<b>-0.600*</b>	<b>-0.591*</b>	0.221
SSTA (January–March)	-0.047	0.112	0.174	-0.458	<u>-0.382</u>	-0.182	-0.091	-0.478
CHL (September)	-0.206	-0.231	-0.297	0.104	-0.103	0.118	0.060	-0.311
CHL (October)	-0.068	-0.215	-0.118	-0.152	0.262	0.262	0.247	-0.404
CHL (November)	<b>0.539*</b>	<b>0.502*</b>	<b>0.584*</b>	-0.374	0.488	0.441	0.491	-0.270
CHL (December)	0.429	0.229	0.282	0.157	0.328	0.071	0.153	0.319
CHL (January)	0.185	0.047	0.044	0.262	0.260	0.085	0.152	0.288
CHL (February)	0.097	-0.018	0.009	0.158	0.171	0.062	0.150	-0.069
CHL (March)	0.262	0.262	0.256	-0.059	0.100	0.062	0.097	-0.026
CHL (April)	-0.212	-0.252	-0.259	0.056	0.425	0.242	0.239	-0.073
CHL (May)	0.023	-0.032	-0.007	0.022	0.200	-0.082	-0.025	0.150
CHL (November–January)	<b>0.531*</b>	0.347	0.409	-0.029	0.368	0.174	0.244	0.199
Start	-0.094	0.086	0.242	-0.265	-0.204	-0.177	-0.133	0.125
Duration	0.258	-0.131	0.103	0.113	<b>0.588*</b>	0.378	0.475	0.046
Max CHL	0.229	0.141	0.221	-0.071	0.179	0.141	0.179	-0.059
Max day	<b>0.560*</b>	<b>0.587*</b>	<b>0.600*</b>	-0.138	0.190	-0.052	0.016	0.252

Note. Recruitment index,  $R_{VPA}$ ; larval survival indices,  $LSI_{SSB}$  and  $LSI_{TEP}$ ; total egg production, TEP. Values in bold and next to an asterisk (\*) indicate significant at 95%. Underlined values are significant after applying the Benjamini–Hochberg correction, with a false discovery rate of 0.25.

conditions generally developed during late September and lasted for an average of 4 months, whereas in the main nursery area (SJG), blooms started 5 days earlier but were 18 days shorter than at SUB. The seasonal patterns observed at SUB and SJG coincide with the seasonal cycle typical of temperate seas previously described for the Patagonian shelf, with spring and summer temperature and chlorophyll maxima associated with a stratified water column in the mid- and outer shelf regions, a second smaller chlorophyll peak during fall, and winter minima associated with a vertically homogeneous water column after the breakdown of the thermocline (Rivas & Piola, 2002).

The location of the main spawning area at SUB and the primary nursery ground at SJG is well established for *M. hubbsi* (Otero, Gianjogbe, & Renzi, 1986; Pérez Comas, 1990; Macchi et al., 2004; Pájaro et al., 2005; Álvarez Colombo et al., 2014). Nonetheless, the conditions that make these particular areas suitable for reproduction are not yet fully understood. Reproductive areas should provide the following: (a) adequate environmental conditions, including temperature and salinity ranges, as well as processes leading to water column stability; (b) retention mechanisms to maintain the early life stages within the favorable area; and (c) nutrient enrichment

resulting in adequate production of appropriate prey for larvae and young juveniles (e.g., Bakun & Parrish, 1991; Bakun, 1996). The circulation at SUB follows the general patterns described for the Patagonian continental shelf, with a general north–northeast flow. However, a cross-shelf section through SUB in summer showed a two-layer flow, with the intense offshore flow in the upper layers, decreasing in intensity with depth and inverting direction toward the coast in the bottom boundary layer (Álvarez Colombo et al., 2011). Numerical model results from the same study showed an almost continuous bottom layer flow toward the southwest, from the spawning area to the northern San Jorge Gulf, combined with a gradual increase in the size of hake larvae estimated from concurrent net samples. The analysis of 10 years of high-frequency acoustic data showed that the bulk of hake larvae was located in the SUB area and that larger larvae with functional swim bladders performed daily vertical migrations from near the bottom, where a weak inshore flow dominates, to the level immediately below the thermocline where water moves offshore at different speeds. The authors concluded that this positioning behavior constitutes the main retention mechanism for hake larvae in this region (Álvarez Colombo et al., 2011). In the San Jorge Gulf area, modeling studies revealed the

presence of one or two gyres, depending on the direction of the forcing winds, which in either case result in retentive circulation patterns within the gulf (Tonini, Palma, & Rivas, 2006). Our results indicated that bloom conditions both at SUB and SJG start early in the spring and last for an average of 128 days, which is considerably longer than bloom periods reported for other areas of the Patagonia Shelf (e.g., Romero, Piola, Charo, & García, 2006; Marrari et al., 2013). Our analyses of satellite data revealed high chlorophyll concentrations at the surface during spring and summer, favoring secondary production and presumably leading to abundant zooplanktonic prey for the new larvae at the time of their appearance in December–January. In addition, previous studies reported high concentrations of zooplankton throughout the water column and at the thermocline level in this region (e.g., Derisio, 2012). In particular, mesozooplankton concentrations including mainly the calanoid copepods *C. vanus*, *D. forcipatus*, *C. carinatus*, and *Acartia tonsa* have been reported to be highest at SUB relative to SGJ, while maximum densities of adult euphausiids and amphipods, the main prey for juvenile hake, were observed at SJG (e.g., Temperoni, 2015; Derisio, Martos, Berghoff, & Dato, 2017). Analysis of larval hake gut content from the SUB area indicated 87% feeding incidence in this region during January and confirmed a clear preference for calanoid copepodites <2 mm in size (Temperoni & Viñas, 2013), which are lipid-rich and of high nutritional quality relative to other zooplankton (Nelson, Mooney, Nichols, & Phleger, 2001; Gigliotti, Davenport, Beamer, Tou, & Jaczynski, 2010). On the other hand, age-0+ juvenile *M. hubbsi* (60–150 mm TL) from SJG had an almost exclusively pelagic diet of larger zooplankton that consisted mainly of the euphausiid *E. lucens* and the hyperiid amphipod *T. gaudichaudii*, which combined accounted for 99% of the total prey consumed (Temperoni et al., 2013). This almost exclusively pelagic diet suggests that final settling might occur at larger sizes than the 20 mm previously reported. It was recently shown that age-0+ year juveniles school during daytime in layers 10–20 m in height at ~10–15 m from the bottom, but are dispersed in the water column at night (Álvarez Colombo et al., 2014), possibly following the migration patterns of their prey (Williams & Robins, 1981; Gibbons, Barange, & Pillar, 1991).

The retentive physical processes described, combined with elevated phytoplankton abundances and the observed abundant zooplankton in the area, contribute to making SUB and SJG favorable spawning and nursery areas for *M. hubbsi*. The relationships observed between recruitment ( $R_{VP}$ ) and larval survival index (LSI) of *M. hubbsi*, and November chlorophyll concentrations at SUB support this conclusion. The higher dependency of larval survival on chlorophyll concentrations in the spawning area relative to the nursery area agrees with the presence in this area of the bulk of the young larvae, which feed on small herbivorous zooplankton that in turn depend more directly on phytoplankton concentrations. On the other hand, hake juveniles, mostly present at SJG, feed on larger zooplankton that are either omnivorous (*E. lucens*; Stuart, 1986; Stuart & Huggett, 1992) or carnivorous (*T. gaudichaudii*; Boltovskoy, 1999), and whose abundance is likely not so strongly dependent on phytoplankton concentrations.

This is also supported by larval condition index determined by the RNA/DNA ratio, which showed that SUB is a favorable area for larval growth and survival (Díaz, Pilar Olivar, & Macchi, 2014).

The main causes of larval mortality are starvation and predation, as well as environmental factors that have determinant effects on recruitment (discussed in Cury & Roy, 1989). The match–mismatch hypothesis (Cushing, 1975) emphasizes that the annual production of larvae is matched or mismatched to the production of their food. A second hypothesis is based on the suggestion that first feeding for larvae is the most vulnerable stage in the life history of fish (Hjort, 1914, 1926). Maximum larval survival occurred during years of (a) average or above-average spring chlorophyll concentrations, and (b) late or average chlorophyll maxima at SUB, suggesting that if the phytoplankton peak occurs too early or chlorophyll concentrations show negative anomalies, fewer larvae will survive. Although there was a positive correlation between LSI and spring chlorophyll, some years of favorable conditions had average or low larval survival, which implies that adequate timing of abundant chlorophyll, which presumably translates into abundant zooplanktonic prey, is a necessary but not exclusive condition for hake larval survival, and that other factors such as predation and mortality contribute to determining recruitment success (Houde, 2009).

Although total egg production (TEP) and spawning stock biomass of *M. hubbsi* showed a general declining trend since 1990, larval survival indices have remained steady. TEP was independent of chlorophyll dynamics or recruitment. The fact that no relationship was observed between years with high egg production and the abundance of juveniles 1 year later could be related to density-dependent mechanisms (Cowan, Rose, & Devries, 2000; Rose, Cowan, Wine-miller, Myers, & Hilborn, 2001). That is, a high concentration of eggs and larvae may produce more competition for prey and therefore higher starving mortality and/or cannibalism.

The analysis of the variability in chlorophyll dynamics presented in this study included the longest time series of chlorophyll concentrations in the region to date, with the highest spatial and temporal resolutions reported for the region, which allowed the identification of patterns and trends that had gone unnoticed. Previous studies have observed either decreasing or increasing trends in regional chlorophyll concentrations, including positive trends offshore of the Patagonian shelf (e.g., Boyce, Lewis, & Worm, 2010; Gregg & Rousseaux, 2014; Marrari et al., 2017). Boyce et al. (2010) also noted that most declining trends occurred in oceanic areas, while in shelf regions, trends were positive since 1980, consistent with reported intensified coastal eutrophication and land runoff (Gregg, Casey, & McClain, 2005). Saulquin et al. (2013) used SeaWiFS and MERIS data (1998–2011) to examine global trends in chlorophyll concentrations with regionally varying results, although they observed the maximum positive trends for the entire global ocean ( $0.009 \text{ mg m}^{-3} \text{ year}^{-1}$ ) on the Patagonian shelf.

The increases in chlorophyll concentrations observed in the SWA coincide with warmer SST, which is opposite to observations for other regions of the global ocean where warmer temperatures are associated with decreasing chlorophyll concentrations (e.g., Boyce et al.,

2010). In general, warmer surface waters result in a more intense stratification, limiting nutrient supply to the surface and inhibiting production (Behrenfeld et al., 2006). Although there are no long-term analyses of sea surface temperature trends for our study area in particular, a 6-year (1995–2000) analysis of January temperatures in the San Jorge Gulf and adjacent areas indicated a significant increase (Louge, Reta, Santos, & Hernández, 2004). In addition, global mean increases of  $0.71^{\circ}\text{C}/\text{century}$  since 1900 (Wu et al., 2012) and between  $0.09^{\circ} \pm 0.03^{\circ}$  and  $0.18^{\circ} \pm 0.04^{\circ}\text{C}/\text{decade}$  since the 1980s have been reported, with moderate increases for the SWA region (Lawrence, Llewellyn-Jones, & Smith, 2004; Good, Corlett, Remedios, Noyes, & Llewellyn-Jones, 2007; Belkin, 2009; Wu et al., 2012). For the reproductive area of *M. hubbsi*, where seasonal stratification provides phytoplankton with an illuminated environment, the observed increase in chlorophyll concentrations is likely related to an enhanced nutrient supply, possibly as a result of eutrophication of coastal areas.

Studies have shown varying effects of temperature on fish recruitment (Houde, 2009). In the case of cod, increasing temperature was associated with either negative or positive trends in recruitment over the broad geographical range of distribution of the species. Recruitment was positively related to temperature in the northern part of its range distribution, while the opposite was observed in the southern part. In agreement with our results for hake, Planque and Fox (1998) observed an inverse relationship between recruitment of Atlantic cod in the Irish Sea and sea surface temperature during the egg and larval stages, with recruitment values varying fourfold over the range of temperature anomalies. For *M. hubbsi*, all reproductive success measurements analyzed were negatively related to fall temperature anomalies, which is at the late larval or early juvenile phase. It is possible that the higher survival associated with colder fall seasons is the result of less competition for food between hake larvae and other plankton predators. It has been suggested that the presence of large concentrations of gelatinous zooplankton can have an impact on young hake populations via competition for food. In the tidal front area of Peninsula Valdés, just north of our study area, Mianzán and Guerrero (2000) observed that *Mnemiopsis leidy*, which has been shown to feed primarily on copepods (Costello, Loftus, & Wagget, 1999; Waggett & Costello, 1999), dominated the zooplankton biomass representing ~60% of total organic carbon. Sabatini and Martos (2002) examined the mesozooplankton community in the northern Patagonian shelf area during spring 1995 and 1998 and observed warmer temperatures during the second year in coincidence with large concentrations of gelatinous zooplankton and depressed copepod populations. In addition, there are previous reports of earlier maximum abundances of the lobate ctenophore *M. leidy* during spring in Narragansett Bay associated with a warming trend (Sullivan, Van Keuren, & Clancy, 2001). Thus, during colder years when the abundance of gelatinous zooplankton is reduced, zooplankton abundances are likely high, supplying adequate food for hake larvae and favoring survival.

The trends observed in the environmental conditions analyzed in the reproductive area of *M. hubbsi* can have important implications for the ecology of the species, as well as for the fishery. Increasing

chlorophyll concentrations in the spawning and nursery areas are expected to result in higher abundances of herbivorous zooplankton and greater availability of adequate small zooplanktonic prey for the hake larvae, as well as larger concentrations of macrozooplankton for juveniles. These higher overall food abundances would translate into higher larval survival and recruitment of hake. Although the trends in sea surface temperature and chlorophyll concentrations are significant, the Larval Survival Indices estimated in this study remained steady over time with no detectable trend. It is most likely that other mechanisms that have not been analyzed here are also influencing larval survival, including, but not limited to, advection out of favorable areas or density-dependent processes such as competition for food or cannibalism (Cowan et al., 2000; Rose et al., 2001).

It is also possible that the relationship between bloom dynamics and hake larval survival is not as strong as that observed for other fish (e.g., Platt et al., 2003; Marrari et al., 2013) because average chlorophyll concentrations in this region are sufficiently high to support unlimiting food for larvae throughout the reproductive season. The average chlorophyll concentration at SUB for the period November–January was  $1.84\text{ mg}/\text{m}^3$ , which is relatively high compared to other regions of the world's ocean. In addition, the main assumption of this analysis is that the increased phytoplankton abundances observed at SUB and SJG directly translate into higher zooplankton concentrations. This has been previously documented north of our study area in waters of the Buenos Aires Province continental shelf ( $38^{\circ}\text{S}$ – $41^{\circ}\text{S}$ ), with a strong positive relationship between median chlorophyll concentrations in the spawning area of the Argentine anchovy *E. anchoita*, and the abundance of small copepods (Marrari et al., 2013). However, for our study area, the relationship between chlorophyll dynamics and zooplanktonic prey abundance will be examined in the future using zooplankton data collected during hake stock assessment cruises between 2004 and 2014.

Future studies of the mechanisms controlling the reproductive success of *M. hubbsi* in the Argentine Sea should include information on the abundance, composition, and dynamics of the zooplankton community to further contribute to our predictive capacity of recruitment and improved management of this important fishery.

## 5 | CONCLUSIONS

Reproductive success of the Patagonian stock of *M. hubbsi* between 1989/1990 and 2013/2014 was related to fall SST anomalies and spring–summer chlorophyll conditions in the main reproductive area. Colder-than-average fall sea surface temperatures in combination with high spring chlorophyll concentrations and a late chlorophyll maximum in the spawning area represent the most favorable conditions for recruitment and larval survival. However, a large fraction of the variability observed in reproductive success of hake remains unaccounted for; thus, other factors such as mortality and advection should be considered in future studies. In addition, the relationship between chlorophyll dynamics and zooplankton dynamics should be measured directly in the spawning area of *M. hubbsi*. Although variability in chlorophyll

dynamics could not fully explain the differences observed in hake larval survival since 1997, satellite data proved to be a useful tool in assessing spatial and temporal variability, as well as longer term trends in environmental conditions in the reproductive area.

The analysis of time series of satellite surface chlorophyll concentrations and SST anomalies in the reproductive area of *M. hubbsi* revealed increasing trends in both variables, with potentially important implications for hake. As climate change is predicted to continue, the effects of environmental change on fish reproductive success and population structure are yet to be determined.

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