



Reproductive success of the Argentine anchovy, *Engraulis anchoita*, in relation to environmental variability at a mid-shelf front (Southwestern Atlantic Ocean)

MARINA MARRARI,^{1*} SERGIO R. SIGNORINI,²
CHARLES R. MCCLAIN,² MARCELO
PÁJARO,³ PATRICIA MARTOS,^{3,4} MARÍA
DELIA VIÑAS,^{3,5} JORGE HANSEN,³ ROXANA
DIMAURO,⁶ GEORGINA CEPEDA^{3,5} AND
CLAUDIO BURATTI³

¹Departamento de Oceanografía, Servicio de Hidrografía Naval,
Buenos Aires, Argentina

²NASA Goddard Space Flight Center, Greenbelt, MD, U.S.A

³Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina

⁴Universidad Nacional de Mar del Plata, Mar del Plata,
Argentina

⁵Instituto de Investigaciones Marinas y Costeras (IIMyC), Mar
del Plata, Argentina

⁶Louisiana State University, Baton Rouge, LA, U.S.A

ABSTRACT

The mid-shelf front (MSF) of the Buenos Aires province continental shelf in the Southwestern Atlantic Ocean plays a central role in the pelagic ecosystem of the region acting as the main spring reproductive area for the northern population of the Argentine anchovy *Engraulis anchoita* and supporting high concentrations of chlorophyll as well as zooplankton, the main food of anchovy. To investigate the influence of environmental variability on the reproductive success of *E. anchoita*, we analyzed a 13-yr time series (1997–2009) of environmental data at MSF including chlorophyll dynamics, as well as zooplankton composition and abundance, ichthyoplankton distributions, and recruitment of *E. anchoita*. Spring chlorophyll concentrations showed high interannual variability and were mainly influenced by changes in water temperature and vertical stratification, which in turn control nutrient supply to the surface. Chlorophyll dynamics (magnitude, timing, and duration of the spring bloom) explained most of the variability observed in *E. anchoita* recruitment, most likely via fluctuations in the

availability of adequate food for the larvae. Our results suggest that satellite ocean color products can be valuable tools for understanding variability in ecosystem dynamics and its effects on the recruitment of fish.

Key words: *Engraulis anchoita*, frontal systems, ocean color, recruitment, SeaWiFS, South Atlantic Ocean, zooplankton

INTRODUCTION

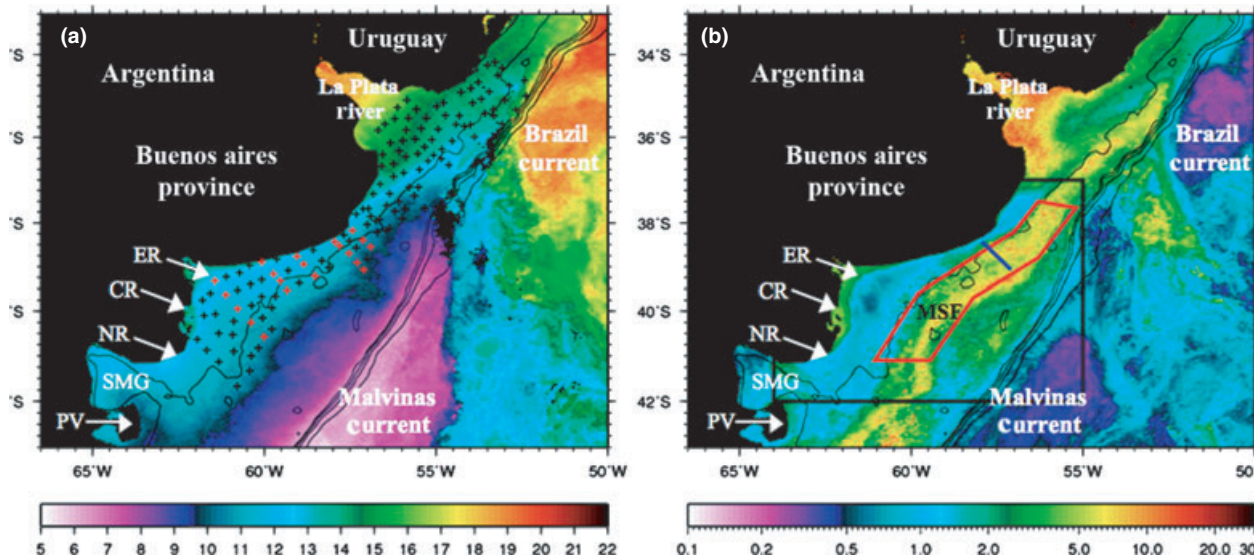
The continental shelf of the southwestern Atlantic Ocean (SWA) (Fig. 1) is a dynamic area influenced by water masses of sub-Antarctic origin modified by significant freshwater input, as well as mixing from winds and tides. The main circulation feature is the Malvinas Current, a branch of the Antarctic Circumpolar Current that flows northward along the shelf break, transporting cold nutrient-rich waters which can ultimately be advected onto the shelf through intrusions at the shelf break (Guerrero and Piola, 1997; Piola *et al.*, 2010). Between 35°S and 37°S, the La Plata River discharges at an annual mean flow rate of 22 000 m³ s⁻¹ onto the shelf, supplying nutrients and high concentrations of dissolved and suspended materials (Framiñan and Brown, 1996; Acha *et al.*, 2004). Further south, the area of El Rincón (39–41°30' S) is characterized by relatively fresh waters near the coast due to the discharge of the Colorado and Negro rivers and a salinity maximum generated by the northward advection of waters from the San Matías Gulf (Fig. 1) (Martos and Piccolo, 1988; Guerrero and Piola, 1997; Lucas *et al.*, 2005). Coastal waters shallower than 50 m are vertically homogeneous throughout the year due to wind-induced mixing and are characterized by nitrate limitation and generally low phytoplankton abundance (Martos and Piccolo, 1988; Carreto *et al.*, 1995). The mid-shelf presents seasonal vertical stratification, with a thermocline established during spring and summer overlying colder nutrient-rich waters. Maximum phytoplankton concentrations occur in spring, followed by a smaller peak during fall after the breakdown of the thermocline (Carreto *et al.*, 1995).

*Correspondence. e-mail: marinam_ar@yahoo.com

Received 5 March 2012

Revised version accepted 29 November 2012

Figure 1. Location of the study area and geographic references over example of distribution of (a) sea surface temperature (SST, °C) (MODIS Aqua) and (b) SeaWiFS chlorophyll *a* concentration (CHL, mg m⁻³) during October 2003. Crosses in (a) indicate the locations of the plankton samples collected for analyses of distribution of eggs/larvae of *Engraulis anchoita* (red and black) and zooplankton (red). The red polygon in (b) represents the Mid-Shelf Front (MSF) subregion, the blue line is the cross-shelf transect examined in Figs 5 and 6, and the black box represents the area considered for the wind speed and direction calculations. Thin black lines indicate the 50-, 200-, 300-, 500- and 1000-m isobaths. CR, Colorado River; NR, Negro River; ER, El Rincón; SMG, San Matías Gulf; PV, Peninsula Valdés.



Frontal systems are areas of sharp density discontinuities characterized by the aggregation of particles, elevated rates of primary production, and high concentrations of higher trophic level organisms (Mann and Lazier, 1996). Fronts play an important role in the ecosystem of the SWA, with many species of ecological and commercial importance relying on them as feeding and reproductive grounds, including the squid *Illex argentinus* (Brunetti *et al.*, 2000), the Argentine anchovy *Engraulis anchoita* (Sánchez and Martos, 1989; Padovani *et al.*, 2011), the chub mackerel *Scomber japonicus* (Perrotta and Christiansen, 1993) and the Argentine hake *Merluccius hubbsi* (Ehrlich and de Ciechomski, 1994; Bezzi *et al.*, 2004). A Mid Shelf Front (MSF) is established during spring and summer close to the 50 m isobath along the shelf of the Buenos Aires province, separating vertically homogeneous coastal waters from stratified mid-shelf waters (Martos and Piccolo, 1988; Lucas *et al.*, 2005; Romero *et al.*, 2006). MSF has a moderate expression at the surface ($\sim 0.02^\circ\text{C km}^{-1}$) but presents a stronger gradient at depth, detected from both model and observational data (e.g., Auad and Martos, 2012). Frontal systems of similar physical structure associated with elevated primary and secondary production have been described for other regions of the world's ocean, including the Bering Sea, where an inner front develops from spring

to fall in the proximity of the 50-m isobath separating mixed coastal waters from a two-layer system on the middle shelf (Schumacher and Stabeno, 1998). This system presents elevated nutrient concentrations on the stratified side and is characterized by enhanced phytoplankton growth and the aggregation of zooplankton and upper trophic level predators (Coyle and Cooney, 1993; Hunt *et al.*, 1996; Kachel *et al.*, 2002; Sambrotto *et al.*, 2008). In Georges Bank, shallow well-mixed waters on the central bank are separated from stratified waters off the bank by a dynamic thermal front, where a high proportion of the total and new production in the area occurs (Franks and Chen, 1996).

Engraulis anchoita is the most important pelagic fish in the Argentine Sea and plays a critical role in the pelagic ecosystem, acting as the link between zooplankton and higher trophic levels. In addition, it represents a potentially important commercial resource, with annual landings north of 41°S of 27 000 tons in 2010 (Subsecretaría de Pesca y Acuicultura, Argentina). Two main populations occur south of 34°S: a northern or Buenos Aires population, and a southern or Patagonian population, separated at approximately 41°S (Hansen *et al.*, 1984; Sánchez and Ciechomski, 1995). Spawning for the northern stock is extensive and takes place throughout the year but maximum reproductive activity occurs during spring (October

and November) in coastal waters in proximity of MSF (Pájaro, 1998). Despite the importance of the MSF area as a spawning and nursery ground for *E. anchoita*, it remains one of the least studied frontal systems in the Argentine Sea, with only a few recent studies examining its physical and biological characteristics (Marrari *et al.*, 2004; Lucas *et al.*, 2005; Romero *et al.*, 2006; Auad and Martos, 2012; Cepeda *et al.*, 2012).

Understanding the influence of variability in chlorophyll dynamics on higher trophic levels including zooplankton and fish is critical for improving management capabilities and providing a better predictive capacity of fish recruitment. Here, we use satellite data from a variety of sensors to investigate the factors controlling interannual variability in concentrations of chlorophyll *a* and zooplankton abundance at MSF in relation to interannual variability in the reproductive success of *E. anchoita*.

METHODS

The study area included continental shelf waters of the Argentine Sea in the southwestern Atlantic Ocean between 33–43°S and 50–67°W (Fig. 1). High resolution (twice-daily, ~1 km pixel⁻¹) SeaWiFS level 2 ocean color data were processed with the standard algorithm (OC4v4) and flags for the period September 1997 to December 2006. Due to frequent cloud cover, the spatial coverage was poor in the daily data and 5-day and monthly composites were generated with a spatial resolution of 2 km pixel⁻¹. These high resolution data are used to examine interannual differences in the timing and duration of the spring bloom. A longer time series of Level 3 SeaWiFS data (monthly composites, 9 km pixel⁻¹) are available between September 1997 and December 2009 and is used for all other analyses. Monthly mean chlorophyll *a* concentrations at both spatial resolutions were not significantly different ($r^2 = 0.92$, $P < 0.001$, $n = 106$).

A preliminary analysis of the distribution of chlorophyll concentration revealed that the spring bloom frequently occurred offshore of the 50 m isobath following the bathymetry south of 35°S; however, sediment and high concentrations of terrigenous material present in estuarine waters of the La Plata River (35–37°S) cause significant overestimation of chlorophyll concentration from ocean color (Garcia *et al.*, 2005). In consequence, even though *in situ* data indicate that the La Plata estuary can support high chlorophyll concentrations, particularly at the estuarine front (Carreto *et al.*, 1986), the subregion selected to represent MSF was defined between 37°30' °S and 41°S (MSF, red polygon in Fig. 1b) and is assumed to be a good

indicator of the conditions for the northern area. Time series of median chlorophyll concentrations and monthly anomalies at MSF were generated for the period September 1997 to December 2009.

Sea surface temperature (SST) data for the period September 1997 to December 2009 were analyzed from Optimal Interpolation Sea Surface Temperature (OISST) daily data with a spatial resolution of 0.25° (<http://www.esrl.noaa.gov/psd/>). Time series of monthly mean SST and monthly anomalies were generated for the MSF subregion. The OI analysis uses a combination of *in situ* and satellite SST data from the Advanced Very High Resolution Radiometer (AVHRR) (Reynolds *et al.*, 2002).

Daily wind speed and direction data from Quikscat (<http://podaac.jpl.nasa.gov>) were obtained for the study area for the period August 1999 to November 2009 (ascending pass, spatial resolution of 0.25° pixel⁻¹). Daily median wind speed and direction were calculated for a subregion between 37–42°S and 55–62°W (black box in Fig. 1b) and monthly medians were calculated. Only days with at least 30% valid pixels were included. To investigate the persistence of upwelling-favorable winds, the *v* component of the wind was rotated 45° (*Vrot*) to align with the approximate orientation of the 50 m isobath. Winds blowing predominantly from the NNE favor offshore Ekman transport, thus large negative monthly *Vrot* values are indicative of upwelling-favorable winds. The rotation was done according to: $Vrot = u \cdot \sin(45) + v \cdot \cos(45)$.

Mixed layer depth (MLD) data from the OCCAM model (Ocean Circulation and Climate Advanced Modelling) were obtained for the period 1997–2004 (<http://www.noc.soton.ac.uk/JRD/OCCAM/>). Monthly data were extracted for the study area (1/12° resolution) and mapped. In addition, monthly mean MLD and monthly anomalies (MLDA) were estimated for the MSF subregion.

The National Institute for Fisheries Research and Development (INIDEP) of Argentina carries out stock assessment cruises to evaluate stock size, population structure, and reproductive activity of *E. anchoita*. For the northern stock of *E. anchoita*, cruises occupy shelf waters of the Argentine Sea between 34°S and 41°S during October, and include waters from the coast to approximately 140 m depth. Data are available for the period 1990–2008; however, during the SeaWiFS period, cruises only occurred in 1999, 2001, 2002, 2003, 2004, 2006 and 2008. Stock size was estimated from high-frequency acoustic data collected at 38 kHz along 40–42 parallel transects perpendicular to the isobaths and separated by approximately 20 km. Trawl samples were collected at several locations along the cruise

track and data were used to estimate length frequency, sex ratio, and reproductive condition, among other parameters. Estimations of spawning stock biomass and recruitment were obtained for the period 1997–2009 by fitting the model of Mertz and Myers (1996) to commercial catch-at-age data. Survey results (total biomass, age structure) were used to calibrate the model fitting (Hansen *et al.*, 2010). A Larval Survival Index was estimated for each year following:

$$\text{Larval Survival Index} = R/\text{SSB}$$

where R is recruitment (millions of 1-yr-old individuals, 1-yr lag) and SSB is spawning biomass (tons) (Platt *et al.*, 2003).

Plankton samples were obtained with a 220- μm -mesh CalVET net towed vertically from 70 m to the surface (Table 1, Fig. 1a) at stations located along the acoustic transects. Samples were preserved in 5% formaldehyde and stored for later analysis. During 2001 no samples were obtained south of 39°30'S. In the laboratory, the abundance of eggs and larvae of *E. anchoita* was estimated for each station. During each year, between 10 and 21 samples were analyzed for zooplankton abundance (Table 1). Subsamples were obtained in order to include at least 100 individuals of the most abundant taxon. Subsamples were scanned on polystyrene plates using a commercial scanner (Epson Perfection Photo 4490) and the resulting images were analyzed using the ZOOIMAGE software (www.sciviews.org/zooimage). Individuals were classified into a number of taxonomic groups and counted. The categories considered were: small copepods (<2 mm total length, TL), large copepods (>2 mm TL), appendicularians, chaetognaths, cladocerans and cnidarians. More details on this methodology can be found in DiMauro *et al.* (2011). Because small copepods (small calanoids + cyclopoids) are one of the main prey of *E. anchoita* larvae (Viñas and Ramírez, 1996), we used their abundance as an indication of availability of adequate food.

Table 1. Number of samples analyzed for abundance of zooplankton and eggs and larvae of *Engraulis anchoita* during stock assessment cruises between 1999 and 2008.

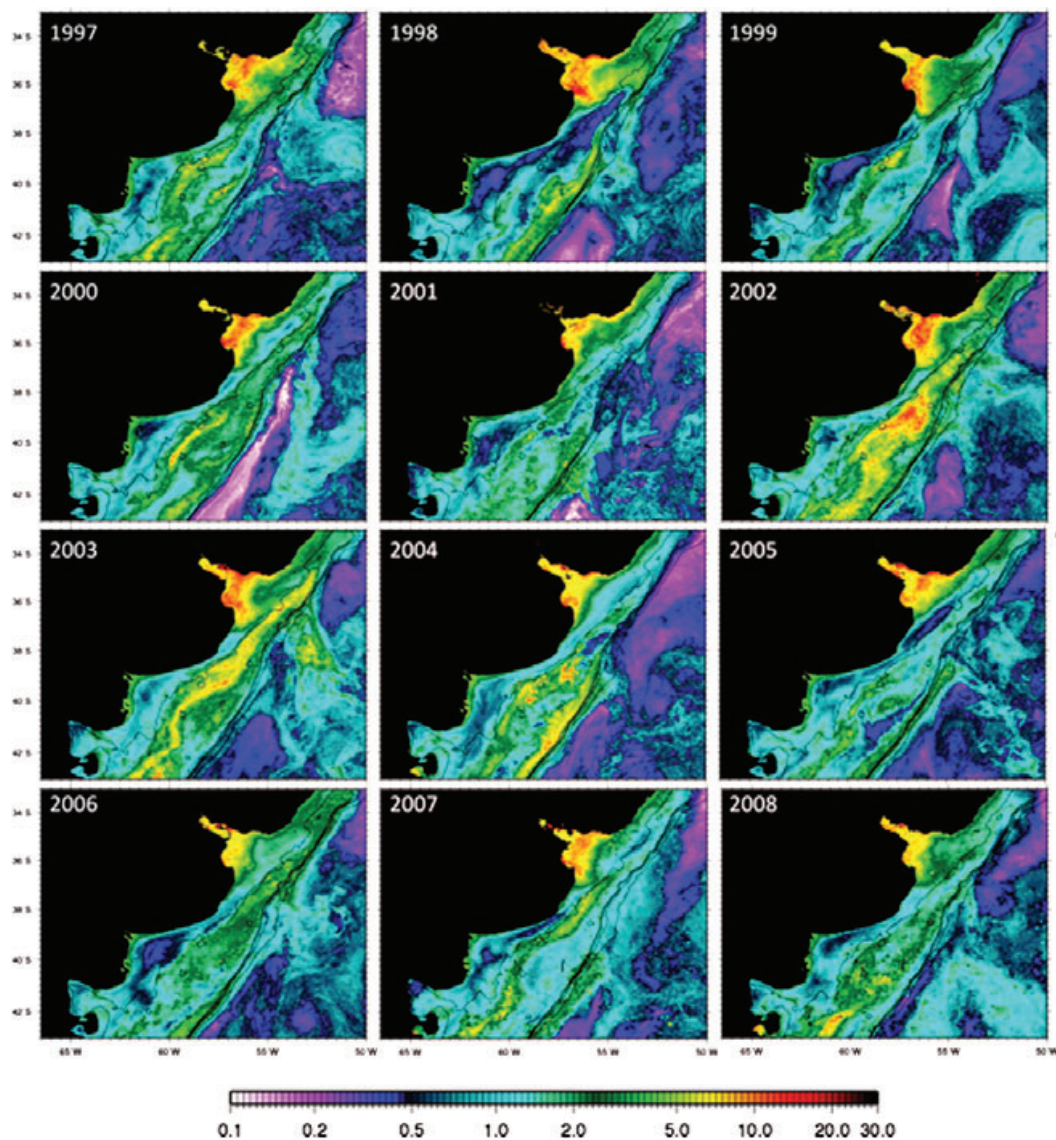
Year	Zooplankton	<i>E. anchoita</i>
1999	17	152
2001	10	84
2002	20	131
2003	18	121
2004	20	137
2006	–	133
2008	21	141

Data from CTD (Conductivity – Temperature – Density) profiles also were obtained at all stations with a Seabird 19 CTD. Simpson's Stability Index, ϕ (J m^{-3} ; Simpson, 1981), was calculated at each station, as a measure of the work required to mix the water column. A value of $\phi = 40 \text{ J m}^{-3}$ was selected as the limit between vertically homogeneous and stratified waters (Martos and Sánchez, 1997), with higher values indicating stronger vertical stratification.

RESULTS

Spring chlorophyll concentrations varied widely throughout the study area and showed high interannual variability between 1997 and 2009. The highest concentrations occurred in frontal areas such as the shelf-break front, MSF in the vicinity of the 50 m isobath, the La Plata River estuarine front, and coastal waters of El Rincón (Fig. 2). Minimum values were generally observed in oceanic waters of the Malvinas and Brazil currents and in coastal areas shallower than 50 m between 37°S and 41°S. At MSF, spring chlorophyll concentrations showed high interannual variability with maxima during 2002 and 2003, when extensive phytoplankton blooms occupied most of the shelf between 50 and 200 m. Dense blooms were also observed during 1997, 1999, 2000 and 2004, and generally weak or spatially limited chlorophyll accumulations occurred in 1998, 2001, 2005, 2006, 2007 and 2008. In addition, chlorophyll concentrations at MSF showed strong seasonality. Phytoplankton blooms generally developed during early spring, with maximum chlorophyll concentrations during September and November. The overall monthly median value indicated that MSF supported $1.92 \text{ mg Chl m}^{-3}$ during October (Table 2, Fig. 3a), with the lowest value in October 1998 (0.66 mg m^{-3}) and maxima in October 2002 and 2003 (4.46 and 4.59 mg m^{-3} , respectively). SeaWiFS data are not available for September–October 2009 due to an interruption in data collection; however, November 2009 data showed high chlorophyll concentrations at MSF (5.52 mg m^{-3}) (Fig. 3a) suggesting a dense and long-lived but perhaps delayed spring bloom, which is confirmed from analysis of concurrent MODIS chlorophyll data (not shown). A second smaller peak often occurred in June. Minimum chlorophyll concentrations were observed during summer, with lowest values in February and March (Table 2, Fig 3a). Positive chlorophyll concentration anomalies ($\text{Chl-}a > 0.3 \text{ mg m}^{-3}$) prevailed during October 1997, 2000, 2002, 2003 and 2004, whereas mostly negative anomalies ($\text{Chl-}a < -0.3 \text{ mg m}^{-3}$) were observed in 1998, 2001, 2005 and 2008

Figure 2. Distribution of monthly SeaWiFS chlorophyll *a* concentration (CHL, mg m^{-3}) during October 1997–2008. Spatial resolution is 2 km pixel^{-1} for 1997–2006 and 9 km pixel^{-1} for 2007–2008. No data were available for October 2009.



(Fig. 3b). Sea surface temperature (SST) also showed high seasonal variability at MSF, with monthly average values (1997–2009) ranging from 9.52°C in August to 18.91°C in February (Table 2, Fig. 3c). In addition, there was high interannual variability with colder than average temperatures during October 1999, 2000 and 2004 (Fig. 3d). Positive October SST anomalies were predominant during 1998, 2001, 2007 and 2008. The average depth of the mixed layer at MSF varied between 8.4 m in January and 43.6 m in August when the water column is well mixed. Average spring values ranged between 14.4 m in October and 9.0 m in December (Table 2).

There was a positive relationship between monthly anomalies in Vrot and anomalies in mixed layer depth (MLDA) ($r = 0.41$, $P = 0.002$, $n = 53$) (Fig. 4a), with shallower mixed layers (negative MLDA) during years of stronger than average winds from the NNE (negative Vrot anomalies). The highest chlorophyll concentrations occurred at average or close to average (± 2 m) mixed layer depths, with both deeper and shallower mixed layers associated with lower chlorophyll concentrations (Fig. 4b).

CTD data collected along a cross-shelf transect at 38–39°S (blue line in Fig. 1b) during stock assessment cruises showed a surface layer of relatively warm

(12–15°C) water and a thermocline of varying strength at ~20–40 m (Fig. 5). A tongue of colder water

(6–10°C) of variable extent was present below the thermocline and along the bottom. The water column was vertically homogeneous in terms of salinity (data not shown), indicating that the temperature field mostly determined the pycnocline structure. An exception occurred in 2001, when a layer of fresher water ($S < 33$) was detected at the surface and a halocline was established at ~10–20 m. Analysis of the distribution of Simpson's Stability Index, ϕ , indicated

Table 2. Monthly values (1997–2009) for chlorophyll concentrations and environmental variables in the study area. Median chlorophyll concentration (CHL, mg m^{-3}), mean SST ($^{\circ}\text{C}$), and mean mixed layer depth (MLD, m) at MSF, as well as median wind speed (Wspeed, m s^{-1}) and Vrot for the region delimited by the black box in Figure 1b.

Month	CHL	SST	MLD	Wspeed	Vrot
January	0.53	18.44	8.44	6.79	-1.15
February	0.48	18.91	11.16	6.64	-0.87
March	0.41	18.42	12.86	6.85	-0.20
April	0.61	16.16	20.05	7.94	2.26
May	0.77	13.65	28.46	7.28	1.71
June	1.02	11.62	42.29	7.40	2.09
July	0.82	10.18	43.56	7.86	2.17
August	1.01	9.52	34.09	7.08	1.70
September	1.97	9.63	22.14	6.24	0.54
October	1.92	11.10	14.40	6.53	0.29
November	1.48	13.20	9.63	6.6	0.47
December	0.87	15.90	9.02	6.78	0.22

that in the study area, the water column was vertically stratified ($\phi > 40 \text{ J m}^{-3}$) offshore of the 50 m isobath during all years analyzed; however, the strength of the stratification varied interannually. A weak thermocline was present in the vicinity of MSF in 2004 ($\phi = 41 \text{ J m}^{-3}$), whereas very strong stratification occurred in 2001 ($\phi = 362 \text{ J m}^{-3}$), in coincidence with lowest chlorophyll concentrations. Intermediate values between 80 and 140 J m^{-3} were observed during the remaining years. October SeaWiFS chlorophyll concentrations along the same transect showed the development of blooms in stratified waters offshore of the 50 m isobath and extending onto the mid-shelf, and coastal waters with generally lower chlorophyll concentrations (Fig. 6). The magnitude and spatial extent of blooms in 2002 and 2003 are evident. Other years with considerable phytoplankton aggregations include 1999 and 2004, whereas spatially limited or absent blooms were predominant during 2001, 2006 and 2008. Maximum chlorophyll concentrations at MSF occurred during years of moderate stratification in the vicinity of the 50 m isobath ($\phi = 139$ and 140 J m^{-3} for 2002 and 2003, respectively) (Fig. 5).

Bloom dynamics

The day of the start of the spring bloom, defined as the center day of the 5-day period when 70% of pixels at MSF had chlorophyll concentrations $> 1 \text{ mg m}^{-3}$, varied widely between 1998 and 2006 (Fig. 7a). The earliest phytoplankton blooms started during late August (2001, 2002 and 2003), whereas other years first presented blooms in September (1998, 1999, 2000 and 2006). The most delayed spring blooms occurred in

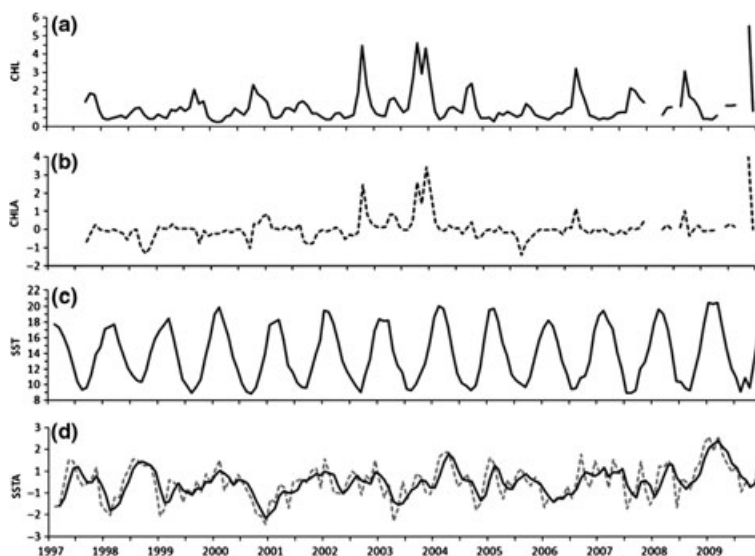
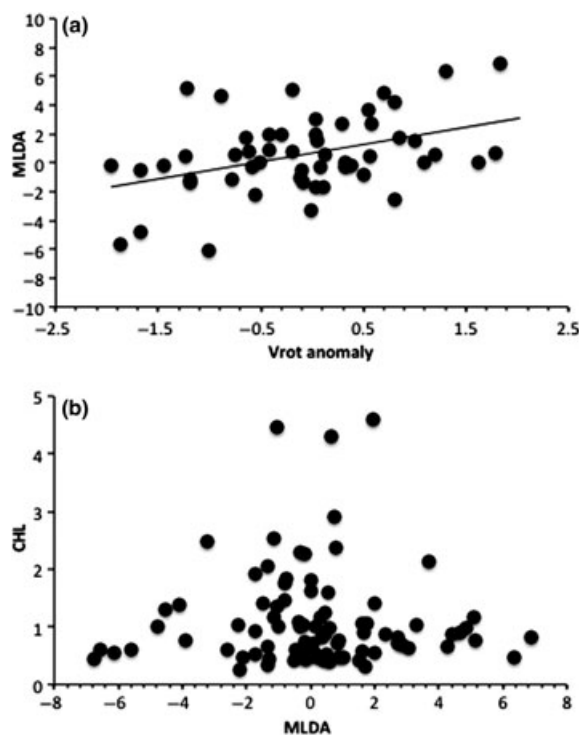


Figure 3. Time series of monthly (a) median chlorophyll *a* concentration (CHL, mg m^{-3}); (b) chlorophyll *a* concentration anomaly (CHLA, mg m^{-3}), (c) mean sea surface temperature (SST, $^{\circ}\text{C}$), and (d) sea surface temperature anomaly (SSTA, $^{\circ}\text{C}$) at MSF (red polygon in Fig. 1a) during September 1997 to December 2009. Solid line in (d) represents the 3-month moving average.

Figure 4. Relationship between (a) Vrot anomalies and mixed layer depth anomalies (MLDA, m) ($r = 0.41$, $P = 0.002$, $n = 53$), and (b) MLDA (m) and median chlorophyll concentrations (CHL, mg m^{-3}) ($n = 88$) at MSF during September 1997 to December 2009.



2004 and 2005, and were first established in October. The duration of the spring bloom also varied extensively and ranged between 5 days in 1998 and 135 days in 2003. A combination of early and long-lived blooms, which would be favorable for secondary production and higher trophic levels, occurred in 2002 and 2003. There was a strong relationship between the duration of the spring bloom and chlorophyll concentrations at MSF (Fig. 7b), indicating that the densest blooms are also the longest-lived.

Zooplankton

The abundance of small copepods (<2 mm total length) between 38 and 41°S showed high variability, with values up to 18 397 ind m^{-3} in 2002, at a station located in the proximity of the highest chlorophyll concentrations at MSF (Fig. 8). In general, the highest abundances occurred in the vicinity of the spring bloom, with lower concentrations in more coastal areas onshore of the 50 m isobath. Overall mean copepod abundance was highest during 2002 and 2003 (2407.3 and 2235.5 ind m^{-3} , respectively), in coincidence with highest chlorophyll concentrations and long-lived widespread blooms. On the other hand, the

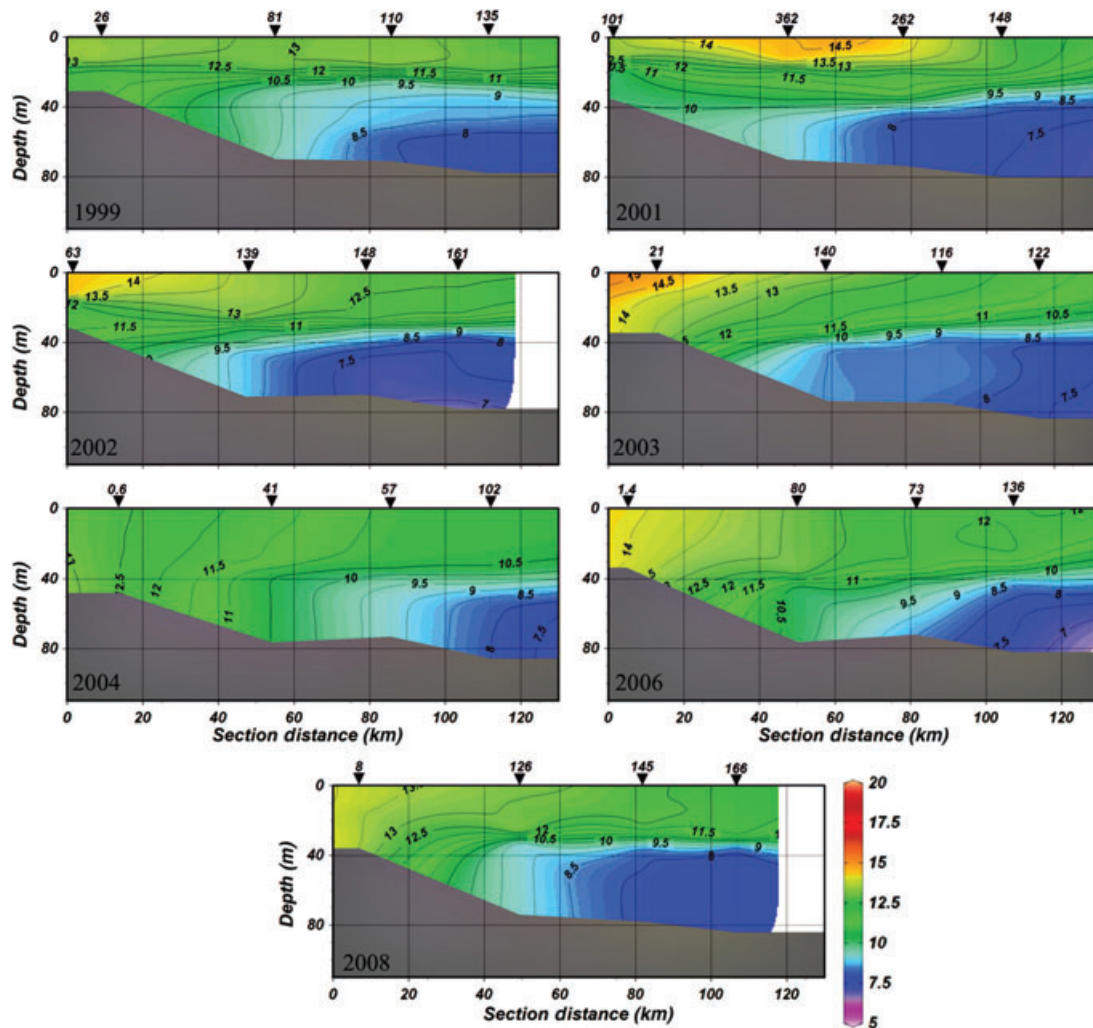
lowest average copepod abundances were observed during 2001 (490 ind m^{-3}) and 2008 (1091.9 ind m^{-3}), when October chlorophyll concentrations at the MSF were lowest. The strong relationship between chlorophyll concentrations at the MSF and abundance of small copepods ($r = 0.92$, $P = 0.009$, $n = 6$) suggests that phytoplankton dynamics at the front may control zooplankton production in the area (Fig. 9a). The mean abundance of other zooplankton taxa also showed positive relationships with chlorophyll concentrations at MSF, including cladocerans ($r = 0.71$) and appendicularians ($r = 0.69$). For carnivorous groups such as chaetognaths ($r = 0.42$) and cnidarians ($r = 0.42$) relationships were weaker (Fig. 9b).

Engraulis anchoita

Spawning of *E. anchoita* was concentrated along a narrow band located slightly onshore of the 50 m isobath (Fig. 10). Eggs were also present in shallower areas, although in lower abundances, except for coastal waters of El Rincón, where high abundances were observed in 2003 and 2004. No eggs were present in the samples collected in the high chlorophyll concentration area offshore of the 50 m isobath. Mean abundance of eggs for the entire study area was highest during 2004 (12 949 ind 10^{-1}m^{-2}), 2002 (12 354 ind 10^{-1}m^{-2}) and 1999 (11 336 ind 10^{-1}m^{-2}), and lowest in 2008 (5065 ind 10^{-1}m^{-2}) and 2006 (5725 ind 10^{-1}m^{-2}). The distribution of larvae of *E. anchoita* was similar to that of eggs although slightly more widespread, with the highest densities in coastal waters shallower than 50 m (Fig. 11). It is notable that larvae were very scarce at MSF in the areas of highest chlorophyll concentrations offshore of the 50 m isobath. The mean abundance of larvae for the study area reached a maximum in 2002 (6775 ind 10^{-1}m^{-2}) and a minimum in 2001 (750 ind 10^{-1}m^{-2}). There was no relationship between chlorophyll concentrations at MSF during September or October and mean abundance of eggs ($n = 7$, $r = -0.643$, $P = 0.12$ for September; $r = 0.344$, $P = 0.45$ for October) or larvae ($n = 7$, $r = 0.201$, $P = 0.67$ for September; $r = 0.487$, $P = 0.27$ for October) of *E. anchoita*.

Larval survival, as a measure of the success of a year class, showed high interannual variability for *E. anchoita* north of 41°S. Survival was highest during 2003 and 2007 and lowest during 2004 and 2005 (Fig. 12a). Variability in spring bloom dynamics at MSF explained most of the interannual variability in larval survival. Larval survival was significantly related to spring–summer chlorophyll concentrations

Figure 5. October distribution of temperature ($^{\circ}\text{C}$) from CTD data along a cross-shelf transect at $\sim 38\text{--}39^{\circ}\text{S}$ (blue line in Fig. 1b). The value of Simpson's Stability Index (J m^{-3}) at each station (black triangles) is indicated.



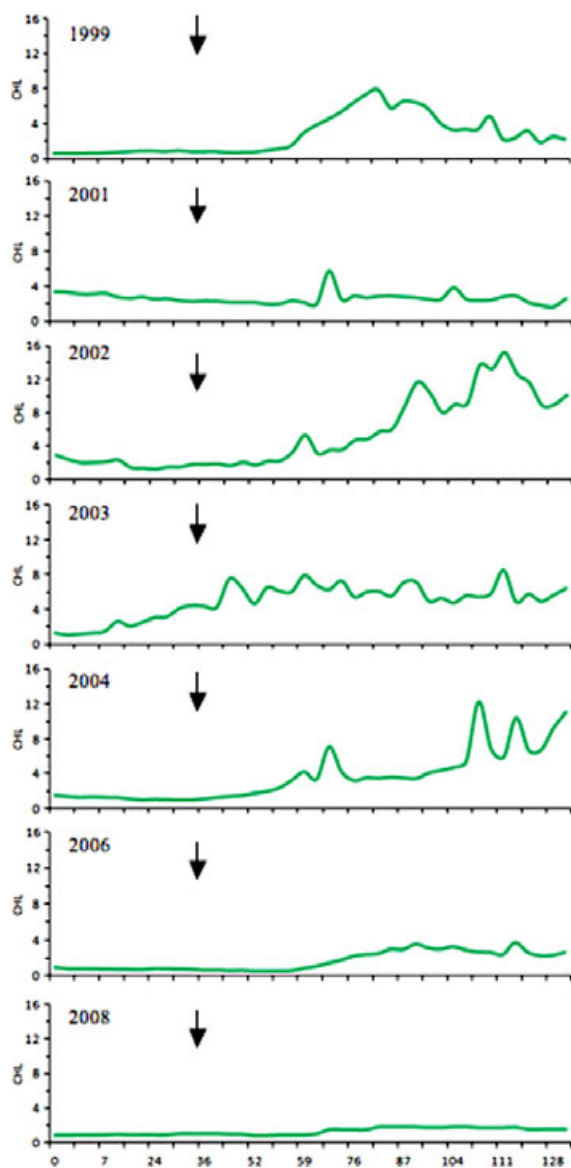
($r = 0.80$, $n = 11$, $P = 0.003$) (Fig. 12a), as well as with the timing ($r = -0.68$, $n = 9$, $P = 0.042$) (Fig. 12b) and duration ($r = 0.81$, $n = 9$, $P = 0.008$) (Fig. 12c) of the spring bloom. Highest larval survival of *E. anchoita* was associated to strong, early and long-lived phytoplankton blooms.

DISCUSSION

The mid-shelf front area plays an important role as the main spring spawning and nursery area for the northern population of *E. anchoita*, yet it is one of the least studied frontal systems in the Argentine Sea and many aspects of its dynamics remain unclear. Previous studies examined chlorophyll concentrations at MSF from *in situ* (Carreto *et al.*, 1995) and satellite (Saraceno *et al.*, 2005; Romero *et al.*, 2006; Signorini *et al.*,

2009) data and described the presence of an $\sim 80\text{-km}$ band of high chlorophyll concentration offshore of the 50 m isobath during spring, associated with a moderate temperature front at the surface that separates vertically mixed nitrate-poor coastal waters from seasonally stratified-shelf waters (Martos and Piccolo, 1988; Carreto *et al.*, 1995). The bottom layer of the mid- and outer shelf is occupied by cold, high salinity, nutrient-rich water resulting from mixing with oceanic waters of the Malvinas Current (Guerrero and Piola, 1997). These nutrient-rich waters are mixed with surface waters after the breakup of the thermocline in winter. Years of moderate stratification combined with widespread extension of deep nutrient-rich waters present the most favorable conditions for phytoplankton growth. Strong stratification would prevent nutrients from being supplied to the surface, whereas a

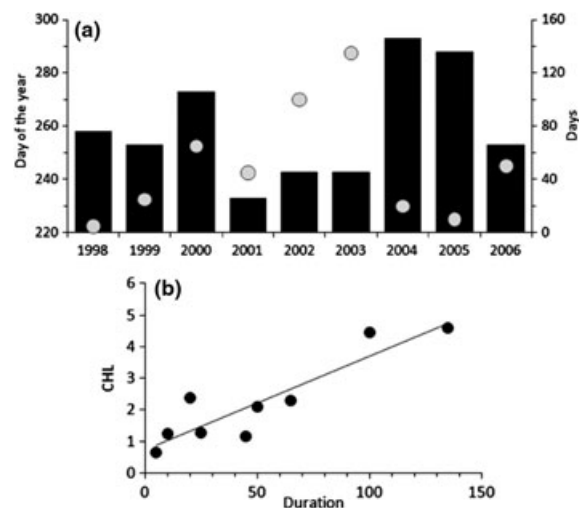
Figure 6. October distribution of surface chlorophyll *a* concentration (CHL, mg m^{-3}) along a cross-shelf transect at $\sim 38\text{--}39^\circ\text{S}$ (blue line in Fig. 1b) for years with available concurrent CTD data (presented in Fig. 5). The *x*-axis represents distance (km) along the transect. Black arrow indicates the location of the 50-m isobath.



weak thermocline would facilitate mixing of phytoplankton cells into deeper light-limited waters.

Northerly winds, which are predominant in the region during spring–summer, favor offshore Ekman transport, leading to shallower and warmer mixed layers, and thus a stronger gradient between surface and bottom waters, resulting in decreased nutrient input to the surface and reduced chlorophyll concentrations. This is in line with the recent analysis of Auaud and

Figure 7. (a) Interannual variability in timing (day of the year when 70% of pixels at MSF reached $>1 \text{ mg m}^{-3}$) (black bars) and duration (days) (gray circles) of the spring bloom at MSF ($r = 0.53$, $n = 9$, $P = 0.14$). (b) Relationship between duration of the spring bloom (days) and median chlorophyll concentration at MSF during October (mg m^{-3}) ($r = 0.91$, $n = 9$, $P = 0.001$).



Martos (2012) who confirmed the dominant role of the local wind forcing on the circulation, and identified two statistically coupled modes of wind stress–surface velocity. During summer, wind accelerations (decelerations) would accelerate (decelerate) alongshore shelf currents, in synchrony with a strengthening (weakening) of the alongshore temperature front, particularly of its near-bottom expression. Saraceno *et al.* (2005) reported high chlorophyll concentrations in the vicinity of the shelf break in 2002 and 2003 and attributed them to increased northerly winds relative to other years and the interleaving of water masses at the shelf break that enhanced vertical stability. In contrast to the shelf break area where mixing is intense and light is limiting, phytoplankton growth at MSF is mainly constrained by nutrient availability via changes in SST and vertical stratification and thus the effect of Ekman-favorable winds is expected to be different to that at the shelf break. Signorini *et al.* (2009) examined in detail the conditions that led to the anomalously intense spring bloom in 2003 and reported negative SST anomalies and stronger than average northerly winds over the shelf and shelf-break areas. Signorini *et al.* (2009) also proposed that increased phytoplankton biomass might be stimulated by the input of soluble iron from a variety of potential sources, including groundwater discharge, sediment resuspension, terrigenous and oceanic sources.

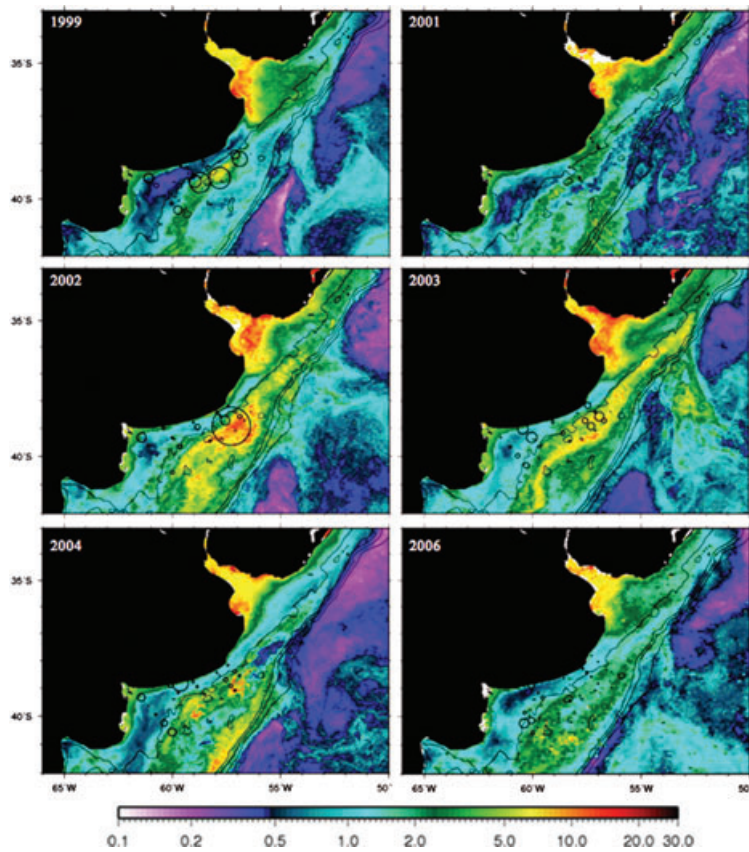


Figure 8. Abundance of small copepods (<2 mm TL) (black circles, ind m⁻³) over distribution of chlorophyll concentration (mg m⁻³) during October. The size of the circles is proportional to abundance, with the largest circle (in 2002) representing 18 397 ind m⁻³.

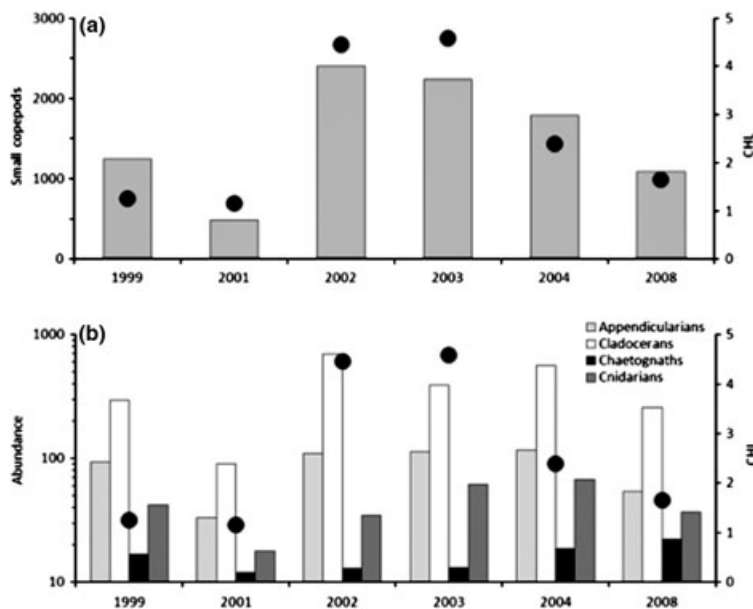


Figure 9. Mean abundance of (a) small copepods and (b) other zooplankton (ind m⁻³) between 38–41°S (red stations in Fig. 1a) (bars) and median chlorophyll a concentration (mg m⁻³) at MSF during October (black circles).

Wind-induced turbulence can also affect larval fish directly through changes in the distribution of zooplankton and predator–prey encounter rates (e.g., Bakun and Parrish, 1982; Incze *et al.*, 2001; Maar *et al.*, 2006). Studies have shown that the probability of

feeding by larval fish is a dome-shaped function of turbulent velocity with maximum feeding success at an optimal level, and detrimental effects at lower or higher turbulence levels (MacKenzie *et al.*, 1994; Dixon *et al.*, 1999). Starvation and predation are the

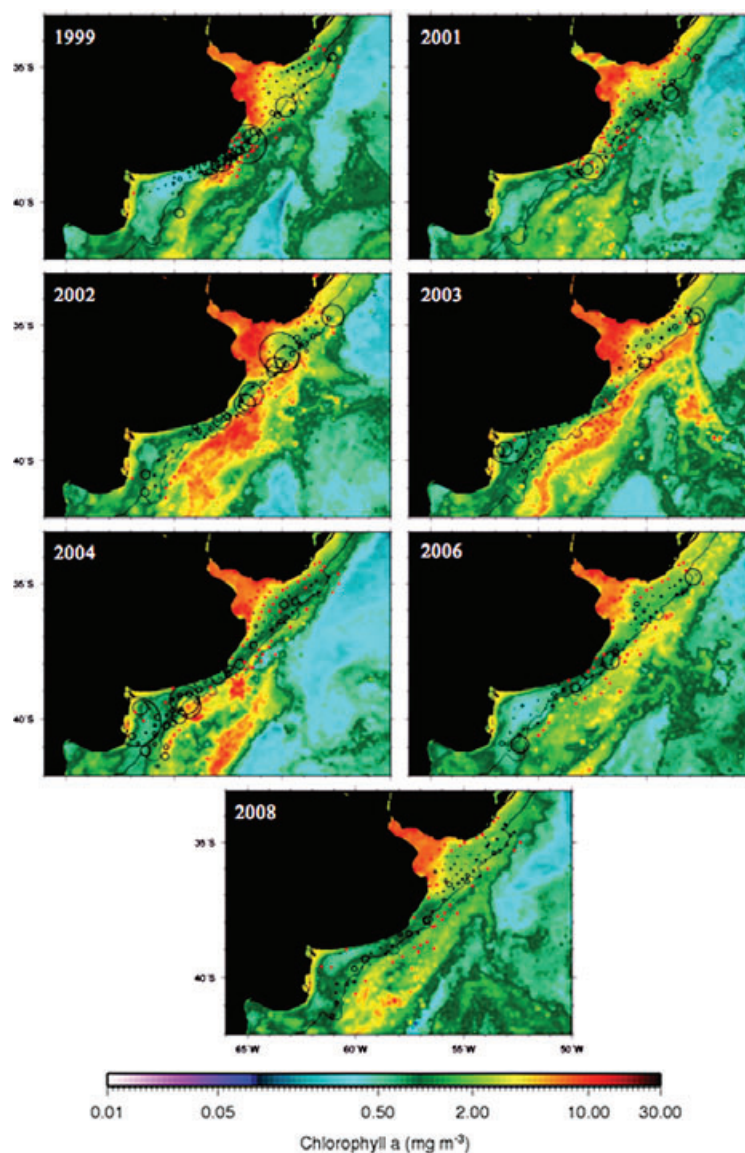


Figure 10. Abundance of eggs of *Engraulis anchoita* (ind 10^{-1} m^{-2} , black circles) over distribution of October chlorophyll concentration (mg m^{-3}). The size of the circles is proportional to the abundance of eggs, with the largest circle (2004) representing $235\,148 \text{ eggs } 10^{-1} \text{ m}^{-2}$. Red crosses indicate no eggs were present in the sample. Black solid line represents the 50-m isobath.

two main processes influencing survival of fish larvae. First-feeding larvae of northern anchovy *E. mordax* require at least $1 \text{ nauplii mL}^{-1}$ to survive (i.e., $1 \text{ million nauplii m}^{-3}$), indicating that average zooplankton concentrations in the ocean are too low to support larval anchovy, and that larvae need to exploit patches of concentrated prey (reviewed in Hunter, 1977). It is noteworthy that eggs and larvae of *E. anchoita* were virtually absent in the areas with the highest chlorophyll and zooplankton concentrations, which may be interpreted as either a predator avoidance strategy by spawners or the result of differential predation on eggs and larvae in the core of the bloom relative to adjacent areas. By avoiding the most productive areas for spawning, *E. anchoita* would provide the larvae with access to sufficient food while reducing exposure to

predators that aggregate where production is maximum. In addition, frontal areas where particles tend to aggregate and dense phytoplankton blooms commonly develop, are characterized by reduced visibility. Fish larvae are visual predators and the shading effect of high phytoplankton concentrations may reduce predation rates substantially (Fiksen *et al.*, 2002) making areas of intermediate production more favorable for prey encountering. It is also possible that spawning would indeed occur over a more widespread area including the core of the bloom and that the absence of eggs and larvae where chlorophyll is most concentrated is the result of increased predation relative to neighboring waters.

The Hjort–Cushing hypothesis (Hjort, 1914; Cushing, 1974) promotes the idea that the strength of a fish

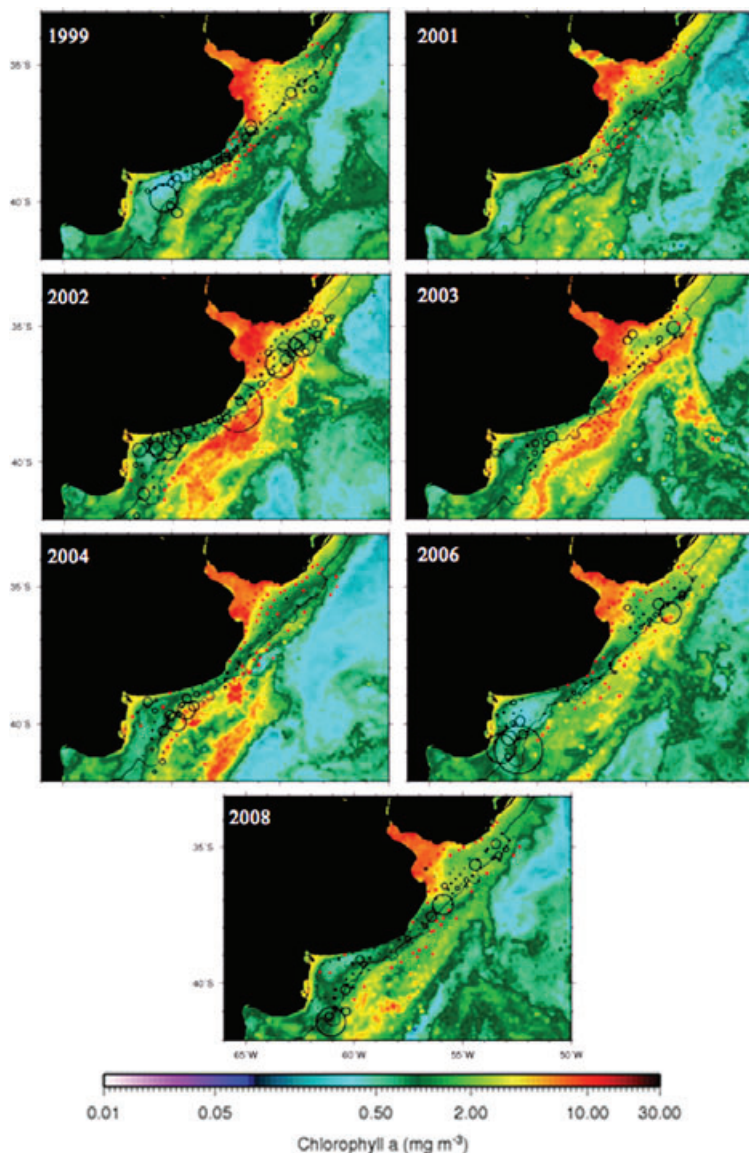


Figure 11. Abundance of larvae of *Engraulis anchoita* ($\text{ind } 10^{-1} \text{ m}^{-2}$, black circles) over distribution of October chlorophyll *a* concentration (mg m^{-3}). The size of the circles is proportional to the abundance, with the largest circle (2002) representing $93\,089 \text{ larvae } 10^{-1} \text{ m}^{-2}$. Red crosses indicate no eggs were present in the sample. Black solid line represents the 50-m isobath.

year class is primarily determined by food availability during the critical period of larval development. The differences between the timing of a phytoplankton bloom and the timing of fish spawning may be important to account for later variations in the abundance of juveniles and adults. Interannual differences in the reproductive success of a variety of fish have been linked to variability in the timing of phytoplankton blooms (Platt *et al.*, 2003) and rates of primary production (Bonhommeau *et al.*, 2008; Chassot *et al.*, 2010). Platt *et al.* (2003) combined remote sensing satellite data with haddock recruitment data and showed that larval survival, and consequently the abundance of haddock year-classes, depended on the timing of the local spring bloom. They concluded that an early spring bloom might not be sufficient to ensure

high fish survival but it could be a necessary condition. At MSF, larval survival for *E. anchoita* was significantly related to the timing of initiation, duration and magnitude of the spring bloom, suggesting that phytoplankton dynamics strongly influence recruitment. Although larval survival showed strong relationships with phytoplankton conditions, the abundance of anchovy eggs and larvae was not correlated to spring chlorophyll concentrations, which suggests that reproductive output is not controlled by concurrent spring conditions and is possibly determined by processes influencing the females earlier in the year. Environmental modulation on recruitment success seems to occur at a later developmental stage than measured during the stock assessment cruises, with an observed decoupling of the reproductive activity from the spring

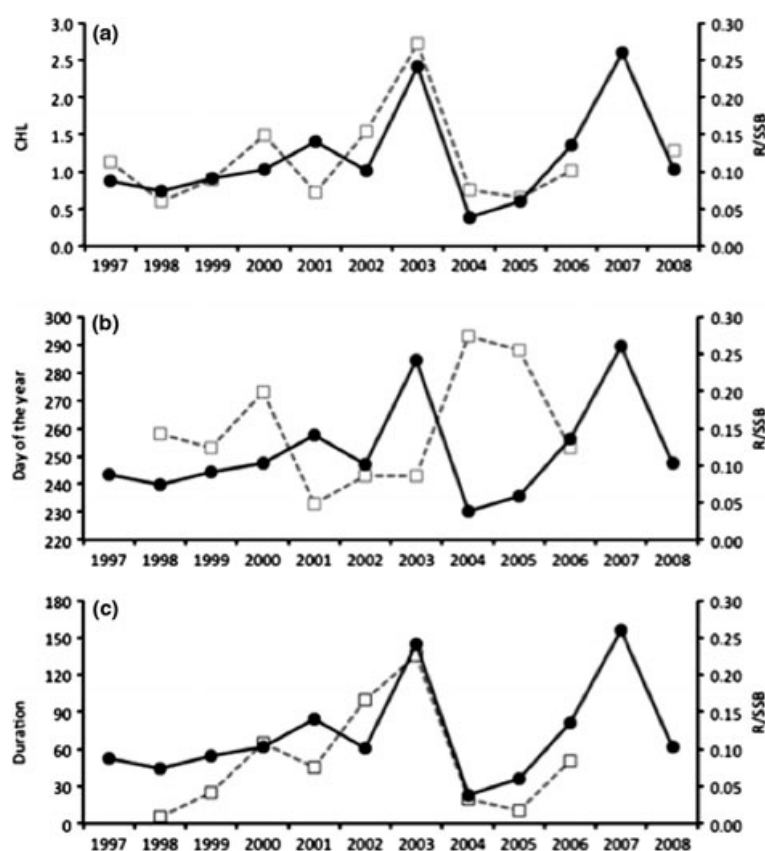


Figure 12. Time series of Larval Survival Index, R/SSB, for *Engraulis anchoita* north of 41°S (black circles): (a) median spring-summer (September–February) chlorophyll *a* concentration (CHL, mg m^{-3}) at MSF (gray squares) ($r = 0.80$, $n = 11$, $P = 0.003$), (b) day of the start of the bloom (day of the year when 70% of pixels at MSF reached $>1 \text{ mg m}^{-3}$) ($r = -0.68$, $n = 9$, $P = 0.042$), and (c) duration of the bloom (days) ($r = 0.81$, $n = 9$, $P = 0.008$). SSB is the spawning biomass (tons) and R is recruitment (millions of 1-yr-old individuals).

conditions but a strong link with the survival of early stages.

Reproductive success in fish has been linked more directly to the abundance of adequate zooplanktonic prey for the larvae. Beaugrand *et al.* (2003) observed that long-term changes in cod recruitment in the North Sea covaried positively with changes in plankton a year earlier, and showed that survival of larval cod depends on the mean size of prey, the timing and the abundance. *Engraulis anchoita* larvae were mainly distributed in coastal waters where zooplankton biomass is low but the abundance of small copepods, which are their main prey (Viñas and Ramírez, 1996), is elevated throughout the year (Viñas *et al.*, 2002; Marrari *et al.*, 2004). Production of these small copepods does not depend on phytoplankton concentrations as they can feed on a variety of prey (Turner, 2004). Juvenile anchovy inhabit coastal waters as well as mid-shelf areas (Angelescu, 1982), where biomass is higher and larger zooplankton more abundant (Marrari *et al.*, 2004). Juveniles incorporate larger zooplankton including calanoid copepods and the amphipod *Themisto gaudichaudii* (Pájaro *et al.*, 2007; Padovani *et al.*, 2012), whose abundance is directly or indirectly dependent on phytoplanktonic production. The

availability of adequate food accelerates growth, reducing the period during which larvae are vulnerable to predation (Bailey and Houde, 1989; Leggett and DeBlois, 1994). Buckley and Durbin (2006) observed strong correlations between copepod biomass and growth rates of cod and haddock in Georges Bank, and concluded that rapid larval growth may be a necessary but not sufficient requirement for a strong year class. Maximum growth rates for *E. anchoita* larvae occur during spring (0.51 mm day^{-1}) rather than summer or fall (0.4 and 0.42 mm day^{-1} , respectively) (Leonarduzzi *et al.*, 2010), in coincidence with the highest phytoplankton and zooplankton abundances. The tight coupling between chlorophyll concentration at MSF and small copepods abundance suggest that satellite-retrieved chlorophyll data, which are easily accessible, may be a good predictor of food availability for larval *E. anchoita* on the Buenos Aires province shelf. Our results demonstrate that satellite ocean color products can be valuable tools for studies of ecosystem dynamics and fisheries research in particular. A better understanding of the links between primary production and fish populations will contribute to improved resource management capabilities and a better predictive capacity of fish reproductive success.

ACKNOWLEDGEMENTS

We thank John Wilding, Bryan Franz, Jeremy Werdell and Sean Bailey for their help with data processing and analysis. Oak Ridge Associated Universities and Fundación Bunge y Born provided financial support. G. Auad provided a critical reading of the manuscript. We are grateful to the captain and crew of the R/V *Eduardo Holmberg* and *Capitan Oca Balda* for their assistance with sample collection. This is INIDEP contribution No. 1773.

REFERENCES

- Acha, E.M., Mianzán, H.W., Guerrero, R.A., 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.
- Angelescu, V. (1982) Ecología trófica de la anchoíta del Mar Argentino (*Engraulidae*, *Engraulis anchoíta*). Parte II. Alimentación, comportamiento y relaciones tróficas en el ecosistema. Serie Contribuciones INIDEP 409, p 83.
- Auad, G., Martos, P. (2012) Climate variability of the northern Argentinean shelf circulation: impact on *Engraulis anchoíta*. *Int. J. Ocean Clim. Syst.* **3**:17–44.
- Bailey, K.M., Houde, E.D. (1989) Predation on eggs and larvae of marine fishes and the recruitment problem. *Adv. Mar. Biol.* **25**:1–83.
- Bakun, A., Parrish, R.H. (1982) Turbulence, transport, and pelagic fish in the California and Peru Current systems. *Calif. Coop. Oceanic Fish. Invest.* **23**:99–112.
- Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S., Reid, P.C. (2003) Plankton effect on cod recruitment in the North Sea. *Nature* **426**:661–664.
- Bezzi, S.I., Renzi, M., Irusta, G. et al. (2004) Caracterización biológica y pesquera de la merluza (*Merluccius hubbsi*). In: El Mar Argentino y sus Recursos Pesqueros. Tomo 4. Los peces marinos de interés pesquero. R.P. Sánchez & S.I. Bezzi (Eds). Mar del Plata: Publicación Especial INIDEP, pp. 157–205.
- Bonhommeau, S., Chassot, E., Rivot, E. (2008) Fluctuations in European eel (*Anguilla anguilla*) recruitment resulting from environmental changes in the Sargasso Sea. *Fish. Oceanogr.* **17**:32–44.
- Brunetti, N., Ivanovich, M., Aubone, A. and Rossi, G. (2000) Calamar (*Illex argentinu*). In: Síntesis del estado de las pesquerías marítimas argentinas y de la Cuenca del Plata. S.I. Bezzi, R. Akselman & E.E. Boschi (eds) Mar del Plata: Contribución INIDEP 1129, pp. 103–116.
- Buckley, L.J., Durbin, E.G. (2006) Seasonal and interannual trends in the zooplankton prey and growth rate of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae on Georges Bank. *Deep-Sea Res. II* **53**:2758–2770.
- Carreto, J.I., Negri, R.M. and Benavides, H.R. (1986) Algunas características del florecimiento del fitoplancton en el frente del Río de la Plata. Parte I: Los sistemas nutritivos. Revista Investigación y Desarrollo Pesquero, Vol. 5: Mar del Plata: INIDEP. pp. 7–29.
- Carreto, J.I., Lutz, V.A., Carignan, M.O., Cuchi Colleoni, A.D., De Marco, S.G. (1995) Hydrography and chlorophyll *a* in a transect from the coast to the shelf-break in the Argentinian Sea. *Cont. Shelf Res.* **15**:315–336.
- Cepeda, G.D., Di Mauro, R., Martos, P. and Viñas, M.D. (2012) A section-sampling design to assess zooplankton distribution in a highly complex hydrographic region (SW Atlantic Ocean, 34–41°S): insights for a new time series? *Brazil. J. Oceanogr.* **60**:381–390.
- Chassot, E., Bonhommeau, S., Dulvy, N.K. et al. (2010) Global marine primary production constrains fisheries catches. *Ecol. Lett.* **13**:495–505.
- Coyle, K.O., Cooney, R.T. (1993) Water column sound scattering and hydrography around the Pribilof Islands, Bering Sea. *Cont. Shelf Res.* **13**:803–808.
- Cushing, D.H. (1974) The natural regulation of fish populations. In: Sea Fisheries Research. F.R. Harden Jones (ed.) London: Elek Science, pp. 399–412.
- Di Mauro, R., Cepeda, G., Capitano, F., Viñas, M.D. (2011) Using Zoolmage automated system for the estimation of biovolume of copepods from the northern Argentine Sea. *J. Sea Res.* **66**:69–75.
- Dixon, P.A., Milicich, M.J., Sugihara, J. (1999) Episodic fluctuations in larval supply. *Science* **283**:1528–1530.
- Ehrlich, M.D., de Ciechowski, J.D. (1994) Reseña sobre la distribución de huevos y larvas de merluza (*Merluccius hubbsi*) basada en veinte años de investigaciones. *Frente Marit.* **15**:37–50.
- Fiksen, Ø., Aksnes, D.L., Flyum, M.H., Giske, J. (2002) The influence of turbidity on growth and survival of fish larvae: a numerical analysis. *Hydrobiologia* **484**:49–59.
- Frañan, M., Brown, O. (1996) Study of the Río de la Plata turbidity front, part 1: spatial and temporal distribution. *Cont. Shelf Res.* **16**:1259–1282.
- Franks, P.J.S., Chen, C. (1996) Plankton production in tidal fronts: a model of Georges Bank in summer. *J. Mar. Res.* **54**:631–651.
- García, C.A.E., García, V.M.T., McClain, C.R. (2005) Evaluation of SeaWiFS chlorophyll algorithms in the Southwestern Atlantic and Southern Oceans. *Remote Sens. Environ.* **95**:125–137.
- Guerrero, R.A., Piola, A.R. (1997) Masas de agua en la plataforma continental. In El Mar Argentino y sus recursos pesqueros, vol 1, E. Boschi (ed) **Mar del Plata**: INIDEP, pp. 107–118.
- Hansen, J.E., Cousseau, M.B., Gru, D.L. (1984) Características poblacionales de la anchoíta (*Engraulis anchoíta*). Parte I. El largo medio al primer año de vida, crecimiento y mortalidad. *Rev. Invest. Desarr. Pesq.* **5**:49–68.
- Hansen, J.E., Garcarena, A.D. and Buratti, C.C. (2010) Recomendación de capturas biológicamente aceptables de anchoíta bonaerense durante el año 2010, a partir de estimaciones de la estructura y abundancia de la población en el período 1990–2009. INIDEP Technical Report 05/10, Mar del Plata. p 23.
- Hjort, J. (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer* **20**:1–228.
- Hunt, J.L. Jr, Coyle, K.O., Hoffman, S., Decker, M.B., Flint, E.N. (1996) Foraging ecology of short-tailed shearwaters near the Pribilof Islands, Bering Sea. *Mar. Ecol. Prog. Ser.* **141**:1–11.
- Hunter, J.R. (1977) Behavior and survival of northern anchovy *Engraulis mordax* larvae. *Calif. Coop. Oceanic Fish. Invest.* **19**:138–146.

- Incze, L.S., Hebert, D., Wolff, N., Oakey, N., Dye, D. (2001) Changes in copepod distributions associated with increased turbulence from wind stress. *Mar. Ecol. Prog. Ser.* **213**:229–240.
- Kachel, L.B., Hunt, G.L. Jr, Salo, S.A., Schumacher, J.D., Stabeno, P.J., Whitledge, T.E. (2002) Characteristics and variability of the inner front of the southeastern Bering Sea. *Deep-Sea Res. II* **49**:5889–5909.
- Leggett, W.C., DeBlois, E. (1994) Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Neth. J. Sea Res.* **32**:119–134.
- Leonarduzzi, E., Brown, D.R., Sánchez, R.P. (2010) Seasonal variations in the growth of anchovy larvae (*Engraulis anchoita*) on the Argentine coastal shelf. *Sci. Mar.* **74**:267–274.
- Lucas, A.J., Guerrero, R.A., Mianzán, H.W., Acha, M.E., Lasta, C.A. (2005) Coastal oceanographic regimes of the Northern Argentine Continental Shelf (34–43°S). *Estuar. Coast. Shelf Sci.* **65**:405–420.
- Maar, M., Visser, A.W., Nielsen, T.G., Stips, A., Saito, H. (2006) Turbulence and feeding behavior affect the vertical distributions of *Oithona similis* and *Microsetella norvegica*. *Mar. Ecol. Prog. Ser.* **313**:157–172.
- MacKenzie, B.R., Miller, T.J., Cyr, S., Leggett, W.C. (1994) Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. *Limnol. Oceanogr.* **39**:1790–1799.
- Mann, K.H., Lazier, J.R.N. (1996) Dynamics of Marine Ecosystems: Biological–Physical Interactions in the Oceans. Boston: Blackwell Science, p 394.
- Marrari, M., Viñas, M.D., Martos, P., Hernández, D. (2004) Spatial patterns of mesozooplankton distribution in the Southwestern Atlantic Ocean (34–41°S) during austral spring: relationship with the hydrographic conditions. *ICES J. Mar. Sci.* **61**:667–679.
- Martos, P., Piccolo, M.C. (1988) Hydrography of the Argentine continental shelf between 38° and 42°S. *Cont. Shelf Res.* **8**:1043–1056.
- Martos, P. and Sánchez, R.P. (1997) Caracterización oceanográfica de regiones frontales en la plataforma patagónica en relación con áreas de desove y cría de anchoíta (*Engraulis anchoita*). In: Abstracts Coloquio Argentino de Oceanografía, IAPSO-IA-DO (Conicet), Bahía Blanca, Argentina, 4–5 September 1997, p 30.
- Mertz, G., Myers, R.A. (1996) An extended cohort analysis: incorporating the effect of seasonal catches. *Can. J. Fish. Aquat. Sci.* **53**:159–163.
- Padovani, L.N., Viñas, M.D., Pájaro, M. (2011) Importance of the Río de la Plata estuarine front (Southwest Atlantic Ocean) in the feeding ecology of Argentine anchovy, *Engraulis anchoita* (Clupeiformes, Clupeidae). *Latinoam. J. Ecol.* **32**:205–213.
- Padovani, L., Viñas, M.D., Sánchez, F., Mianzan, H. (2012) Amphipod-supported food web: *Themisto gaudichaudii*, a key food resource for fishes in the southern Patagonian Shelf. *J. Sea Res.* **67**:85–90.
- Pájaro, M. (1998) El canibalismo como mecanismo regulador denso-dependiente de mortalidad natural en la anchoíta argentina *Engraulis anchoita*. Su relación con las estrategias reproductivas de la especie. Dissertation. Universidad Nacional de Mar del Plata: Mar del Plata, Argentina. p 187.
- Pájaro, M., Curelovich, J., Macchi, G.J. (2007) Egg cannibalism in the northern population of the Argentine anchovy, *Engraulis anchoita* (Clupeidae). *Fish. Res.* **83**:253–262.
- Perrotta, R.G., Christiansen, H.E. (1993) Estimación de la frecuencia reproductiva y algunas consideraciones acerca de la pesca de la caballa (*Scomber japonicus*) en relación con el comportamiento de los cardúmenes. *Physis* (Buenos Aires). *Secc. A* **48**:1–14.
- Piola, A.R., Martínez Avellaneda, N., Guerrero, R.A., Jardón, F.P., Palma, E.D., Romero, S.I. (2010) Malvinas-slope water intrusions on the northern Patagonia continental shelf. *Ocean Sci.* **6**:345–359.
- Platt, T., Fuentes-Yaco, C., Frank, K.T. (2003) Spring algal bloom and larval fish survival. *Nature* **423**:398–399.
- Reynolds, R.W., Rayner, N.A., Smith, T.M., Stokes, D.C., Wang, W. (2002) An improved in situ and satellite SST analysis for climate. *J. Clim.* **15**:1609–1625.
- Romero, S.I., Piola, A.R., Charo, M., García, C.A.E. (2006) Chlorophyll-*a* variability off Patagonia based on SeaWiFS data. *J. Geophys. Res.* **111**:C05021.
- Sambrotto, R.N., Mordy, C., Zeeman, S.I., Stabeno, P.J., Macklin, S.A. (2008) Physical forcing and nutrient conditions associated with patterns of Chl *a* and phytoplankton productivity in the southeastern Bering Sea during summer. *Deep-Sea Res. II* **55**:1745–1760.
- Sánchez, R.P., Ciechowski, J.D. (1995) Spawning and nursery grounds of pelagic fish species in the sea-shelf off Argentina and adjacent areas. *Sci. Mar.* **59**:455–478.
- Sánchez, R.P. and Martos, P. (1989) Synopsis on the reproductive biology and early life history of *Engraulis anchoita*, and related environmental conditions in Argentine waters. In: Second IOC Workshop on Sardine/Anchovy Recruitment Project (SARP) in the Southwest Atlantic, Montevideo, Uruguay, 65, p 7.
- Saraceno, M., Provost, C., Piola, A.R. (2005) On the relationship between satellite-retrieved surface temperature fronts and chlorophyll *a* in the Western South Atlantic. *J. Geophys. Res.* **110**:C11016.
- Schumacher, J.D., Stabeno, P.J. (1998) The continental shelf of the Bering Sea. In *The Sea: The Global Coastal Ocean: Regional Studies and Synthesis*, vol 11, **A.R. Robinson, K.H. Brink (eds)** New York: Wiley, pp. 789–822.
- Signorini, S.R., García, V.M.T., Piola, A.R. *et al.* (2009) Further studies on the physical and biological causes for large interannual changes in the Patagonian Shelf spring-summer phytoplankton bloom biomass. NASA/TM-2009-214176.
- Simpson, J.H. (1981) The shelf-sea fronts: implications of their existence and behaviour. *Philos. Trans. R. Soc. Lond. A* **302**:531–546.
- Turner, J.T. (2004) The importance of small planktonic copepods and their roles in pelagic marine food webs. *Zool. Stud.* **43**:255–266.
- Viñas, M.D., Ramírez, F.C. (1996) Gut analysis of first-feeding anchovy larvae from Patagonian spawning area in relation to food availability. *Arch. Fish. Mar. Res.* **43**:231–256.
- Viñas, M.D., Negri, R.M., Ramírez, F.C., Hernández, D. (2002) Zooplankton and hydrography in the spawning area of anchovy (*Engraulis anchoita*) off Río de la Plata estuary (Argentine-Uruguay). *Mar. Freshw. Res.* **53**:1–13.