Early warning indicators of decadal shifts in the planktonic assemblage of the Cabo Frio upwelling ecosystem

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ARTICLE INFO

ABSTRACT

Long-term monitoring of coupled environmental and biological components in upwelling ecosystems is critical for early warning under the global warming context. Temperature, salinity, nutrients, and plankton populations are promising indicators of the ecosystem state that help us to address the current status of the oceans and construct better predictions for the future. The Cabo Frio Upwelling System (CFUS) is a regionally productive wind-driven coastal upwelling ecosystem on the northern boundary of the South Brazilian Shelf sustaining diverse marine life including large stocks of fish and squid. Like other cold marine ecosystems, most of its functioning is likely threatened by ocean warming which emphasizes the need for ecological indicators. This study aimed to analyze the causal relationships between the temporal changes in the physical and chemical properties and the dominant planktonic communities leveraging long-term observations (20 years). The results suggested a link between the temporal changes in the ecosystem conditions and the composition of the plankton assemblage, notably an increasing proportion of dinoflagellates relative to diatoms and cladocerans relative to copepods. This increase in the proportional abundance of dinoflagellates and cladocerans over time suggests a regime shift in the plankton assemblages during the 2000s, highlighting some large phytoplankton and zooplankton groups as early indicators of productivity shifts in upwelling ecosystems.

1. Introduction

The South Atlantic Ocean is surrounded by 24 coastal countries members of the Zone of Peace and Cooperation of the South Atlantic (ZOPACAS) and provides several ecosystem services and goods to nearly 840 million people living in South America and Africa (United Nations, 2021). In its southernmost portion, down to ~20°S (Fig. 1), there are highly productive areas, particularly associated with the upwelling system of the Benguela Current on the east (Hutchings et al., 2009). In the Southwestern Atlantic, the productivity results mainly from major temperate estuarine systems, such as El Rincón, the Río de la Plata plume, and the Patos Lagoon. Secondarily, the Cabo da Santa Marta and

the Cabo Frio Upwelling Systems are regionally significant (Acha et al., 2004), where large stocks of small pelagic fishes, like anchovies (e.g. *Engraulis anchoita* Hubbs & Marini, 1935) and sardines (e.g. *Sardinella brasiliensis* Steindachner, 1879) are exploited (Franco et al., 2020; Gianelli et al., 2023). Some stocks have been overexploited over time as well as vulnerable to hydroclimatic changes and ecosystem degradation (Matsuura, 1996; Bertrand et al., 2018; Verba et al., 2020). Several warnings about the risk of ecosystem change and fishery stock depletion reinforce the need to develop tools to monitor the dynamics of both adults and non-adults (Barange et al., 2018; Franco et al., 2020). Our ability to predict the productivity of fish stocks over time relies on models that claim spawning and larval recruitment as key drivers, both

depending on phytoplankton (mainly diatoms and dinoflagellates) and zooplankton (mainly copepods) as food supply (Beaugrand et al., 2003; Beaugrand, 2005; Lees et al., 2006). Additionally, phytoplankton and zooplankton are key contributors to ecosystem biodiversity, consisting of a wide variety of species in different shapes and sizes, thus being indicators of multiscale oceanic and climatic events (Piontkovski et al., 2006; Lombard et al., 2019).

A better understanding of the planktonic standing stock requires access to consistent, high-quality, near-real-time monitoring data on a series of climate, environmental and biological parameters (Mackas et al., 2004; Miloslavich et al., 2018). Long-term observations on these organisms can help understand the temporal variability in food supply for fish larvae, to better determine trends in the ecosystem productivity (Kléparski et al., 2022), as well as help early detection of global warming effects (Beaugrand and Kirby, 2018; Chust et al., 2023).

The Cabo Frio Upwelling System (CFUS) is a highly dynamic coastal ecosystem characterized by pronounced natural variability across different spatial and temporal scales. Like other seasonal wind-driven coastal upwelling systems that function under variable conditions, the potential resilience of planktonic assemblages to changes resulting from human activities needs to be better addressed (Cury et al., 2011; Coelho-Souza et al., 2012, 2013; Capone and Hutchins, 2013). Nevertheless, some of the reported decadal hydrodynamic changes, like the increasing flow of the Brazilian current (Artana et al., 2019), are thought to cause shifts in plankton biomass, diversity, and composition (Chen et al., 2023). These shifts appear to respond to low-frequency high-amplitude changes in the hydroclimate system that propagate through multiple trophic levels (Lees et al., 2006). However, it is still debated if these shifts are simply part of natural variability generally found in upwelling systems or abrupt and discontinuous (Weidberg et al., 2020). In the Cabo Frio Upwelling System, there exists a natural transition between ecosystem states, from oligotrophic warm to eutrophic cold that ends in a mixed productive state (Rosa et al., 2023). This natural transition is mostly seasonal and drives the plankton phenology in the region (Gonzalez-Rodriguez, 1994; Guenther et al., 2008). Some abrupt changes are known to occur in plankton assemblages between system states, whether caused by global climate change, biological interactions, or local environmental conditions (Bode, 2023), but less evidence exists on whether upwelling populations are threatened by ocean warming. The abrupt changes that could happen in the CFUS upwelling ecosystem are likely to have negative consequences on the zooplankton phenology if populations fail to track these perturbations and, therefore, fail to target the optimal seasonal window of growing and reproduction (Mackas et al., 2012).

Previous studies in the CFUS have shown the temporal variability of phytoplankton and meroplankton associated with ecosystem productivity and recruitment (Fernandes et al., 2017; 2012; Kütter et al., 2014), but it was only recently noted that changes in the copepods can be used as indicators of the CFUS ecosystem state (Rosa et al., 2023). The present study had three main goals: (1) to analyze the inter-annual change in the physical and chemical properties of the environment (namely temperature, salinity, nutrients, dissolved oxygen, and pH), (2) to understand how this variability can explain changes in planktonic assemblage and (3) to address the potential use of phytoplankton and zooplankton populations as indicators of either an abrupt changepoint or gradational interannual changes in upwelling ecosystems like the CFUS.

2. Materials and methods

2.1. Study area

The present study was conducted focusing on a fixed sampling site in Cabo Frio Island (23°S−042.01°W, Fig. 1, black arrow) as part of the Long-term Ecological Research "Cabo Frio Upwelling" (PELD-RECA, https://memoria.cnpq.br/sitios-peld), where the potential decadal oscillation in the upwelling effects upon the planktonic assemblages are
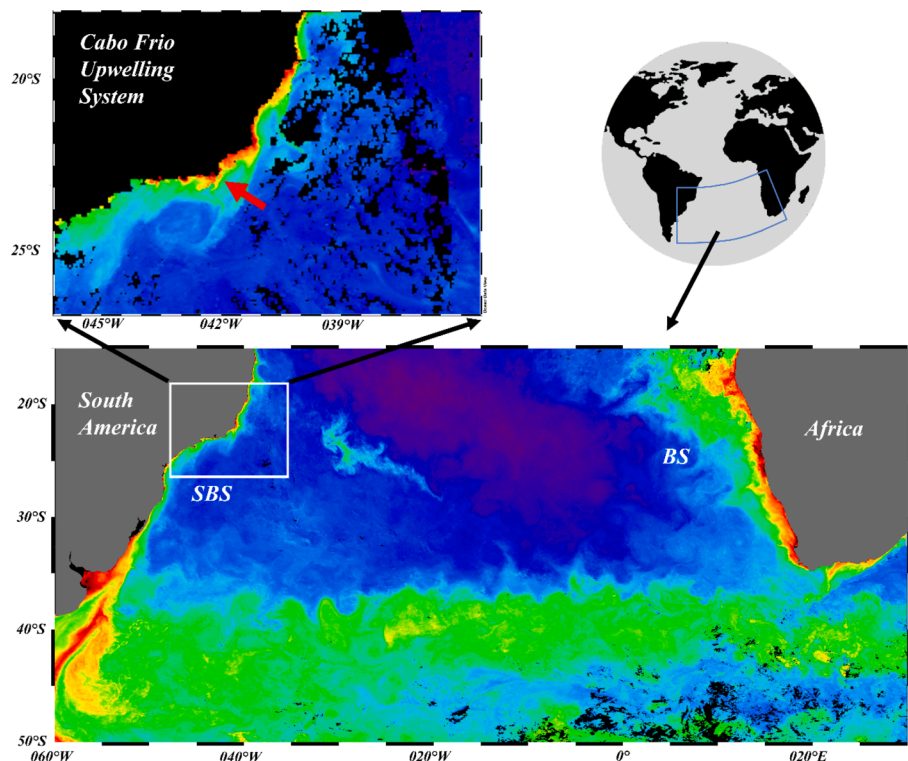
Fig. 1. Monthly composite Chlorophyll concentration (MODIS Aqua L3 4 km resolution) in the South Atlantic Ocean during a strong upwelling (January 2003, Ocean Color, NASA). The Cabo Frio Upwelling System (CFUS, top panel, red arrow) is part of the northern boundary of the South Brazilian Shelf (SBS) and can be highly productive during spring-summer upwellings, contributing to the overall South Atlantic primary production. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

expected to be measurable (Coelho-Souza et al., 2012). This sampling site is located in the cold core of the Cabo Frio Upwelling System (CFUS), a well-known wind-driven coastal upwelling on the southeastern coast of Brazil (Fig. 1), where water temperature range from less than 15 °C in the austral spring-summer (September-January) to more than 28 °C during the autumn (March-April) (Valentin, 2001). Several coastal upwelling ecosystems are marked by strong seasonality, with changes in the ecosystem structure and functioning as those in the depth of the mixed layer and the timing of phytoplankton bloom (Mackas et al., 2012; Lindemann and John, 2014; Peng et al., 2023). The CFUS has also shown seasonal rhythms (Mazzini and Barth, 2013), affecting the copepod size and composition (Rosa et al., 2016; 2023), the bacterial and primary productivity (De Carvalho and Gonzalez-Rodriguez, 2004; Guenther and Valentin, 2008; Cury et al., 2011), and the coupling between larval pool and phytoplankton bloom (Fernandes et al., 2012).

2.2. Biological and environmental data

To resolve the temporal oscillations in the climate and the ecosystem status, this site has been weekly monitored since January 1995 (N=1793). The analysis of the environmental variables, namely water temperature, salinity, dissolved oxygen, and pH, was performed using either an inverted thermometer mounted on a Niskin bottle (1995 – 2012) or a Horiba multiparameter probe (Model U-5000; HGS No. 7JETA790) at ~1-m depth (2012 to date). Additionally, sub-superficial water samples of 2 L were collected with a 3-L Niskin bottle (N=1793) and immediately conducted to the laboratory for spectrophotometric (Agilent UV–Vis Cary 60) estimates of the Chlorophyll-a and nutrient concentration (nitrite, nitrate, ammonia, and phosphate) (Strickland and Parsons, 1972). Chlorophyll-a concentration (µg/l) was estimated from a 0.5 to 1 L subsample filtered in GFF membrane and analyzed in the spectrophotometer following Jeffrey-Humphrey equation (Jeffrey and Welschmeyer, 1997; Ritchie, 2008).

Plankton samples were collected in triplicates every week by sub-superficial horizontal hauls (~1 m) lasting for 2 min with a cylindrical-conical net, 50 cm mouth opening, 100 µm mesh size, and equipped with a calibrated flowmeter (Model 2030R Mechanical Flowmeter, General Oceanics Inc., Miami, FL). Immediately after collection, samples were preserved in a 4 % solution of formaldehyde (final concentration), diluted in seawater and buffered with 20 g/l of Sodium tetraborate. At the laboratory, samples were split with a Folsom Plankton Splitter (Boltovskoy, 1981), one ½ sub-sample was used for seston dry weight in a 0.0001 g precision scale (Shimadzu 82D) and another for organism counting. Even though the most common fraction used for organism counting equals ½, highly concentrated samples were split up to ¼ of the original concentration. The average volume of seawater filtered by the net was 14.6 m^3 (7.6–56.7 m^3).

For organism counting, we used a Benchtop B3 FlowCAM cytometer configured in autoimaging mode with 2x objective, 2000 µm x 2000 µm flow cell. Images were captured at 2400 dpi resolution, with a size of 1024 x 768 pixels, 17 frames per second (efficiency ~40 %), and a flow rate of 10 ml/min. A magnetic stirrer was used to keep the particles in suspension and the subsample concentration homogeneous during the analysis. Sample run interruptions were set on 4,000 particles in total. Each count was converted to density (organisms per cubic meter of seawater, org/m^3) after considering the volume imaged by the Flow-Cam, the subsample dilution (500–1000 ml), the fraction of Folsom (usually ½), and the total volume filtered by the net as estimated by the flowmeter (Álvarez et al., 2011; 2014).Visual Spread-sheet Software (VSP), version 3.4.5 (Yokogawa, Tokyo, JP), was used for prior analysis and measurement of organisms. After the run, the images were pre-treated to split each region of interest by using coupled Python and ImageJ software ('Analyse Particles' function) and uploaded to the Ecotaxa platform (https://ecotaxa.obs-vlfr.fr/prj/6015), where the classification of organisms was performed. In total, 108 categories were generated, including supra-specific taxa and particles (e.g., faeces,

fibres). The density of large (>100 µm) phytoplankton and zooplankton populations were estimated as the density of the four most abundant categories in the CFUS, namely Bacillariophyceae (mostly *Coscinodiscus* spp.), Dinophyceae (mostly *Ceratium* spp. and *Noctiluca* sp.), Copepoda and Diplostraca (*Pseudevadne tergestina*, *Evadne spinifera*, *Podon polyphemoides*, and *Penilia avirostris*), avoiding rare groups and badly annotated images. These categories will be herein referred to as diatoms, dinoflagellates, copepods, and cladocerans for simplicity. Each sub-sample was run into triplicates totalling nearly 50 ml analyzed.

The temporal change in the community structure was addressed using six biotic variables: the density of the four dominant planktonic groups (diatoms, dinoflagellates, cladocerans, and copepods) and two proxies of phytoplankton and zooplankton biomass (Chlorophyll-a and seston dry weight). The full dataset of physical, chemical, and biological variables weekly estimated in the fixed station was averaged to the corresponding month and year from 1995 to 2015 to complete a ~20-year set. Samples from 1995–1997, 2002 and 2003 were missing and, therefore, were replaced by the moving average (subset of 4 data) using the 'impute' function (*Tidyverse* package, v1.3.0, Wickham et al., 2019).

2.3. Time series analysis

To extend the time series to previous decades (before 1995) and also to a larger area in the north boundary of the South Brazilian Shelf, all data available in the National Oceanographic Database (BNDO, Brazilian Navy, https://www.marinha.mil.br/chm/bndo) between 20°S–24°S and 040°W–044°W (0 to 20 m depth) was included in the dataset and used to build a decadal grid (1′ x 1′, radius = 50, kriging method). Sea surface temperature (N = 9568) and salinity (N = 2939) data were obtained through distinct methods over the years (1960–2019) in many oceanographic cruises, including inverted thermometers mounted on Nansen bottles, bathythermographs, and CTD profiles. We thus standardized all data (z transformation) before analysis to reduce the bias effect due to the distinct devices used. To our knowledge, there is no available data on pH, dissolved oxygen, or nutrient concentration for the whole area and before 1995 that could be included in the time series analysis. The monthly average of temperature and salinity were pooled every 10 years to address the coherence and constancy of the seasonal cycle in the CFUS over decades. Due to the scarcity of data from the 1950s, the matrix of seasonality was built exclusively with the monthly averages of temperature and salinity (12 months) estimated between 1960 and 2019 (the last 6 decades). Potential changes in the frequency of inter-annual oscillation in temperature and salinity were checked by the univariate Morlet wavelet value (Torrence and Compo, 1998), calculated as:

$$\varphi(t) = \exp\left(-t^2/2\right) * \cos(5t)$$

using the 'wt' function (*biwavelet* package, v0.20.19, Gouhier et al., 2019). We addressed coincident shifts in both series by calculating the coherence wavelet index ('wtc' function) and then highlighting significant correlations between temperature and salinity oscillations.

Considering only the CFUS region, the most relevant variables among the eight abiotic variables measured since 1995 (water temperature, salinity, dissolved oxygen, pH, nitrite, nitrate, ammonia, and phosphate) were selected using a Principal Component Analysis (PCA) calculated over the 8 x 21 matrix of year anomaly using the 'pca' function (*stats* package, R Core Team, 2020). The data was previously standardized (z-transformed) by the 'decostand' function (*vegan* package, v2.6–4, Oksanen et al., 2022). Potential collinearity between variables was verified through Pearson's Product Moment correlation by the 'pairs.panels' function (*psych* package, v2.4.1, Revelle 2024) and also through the Variance Inflation Factor (VIF) using 'vif' function (*car* package, Fox and Weisberg, 2019) (Zuur et al., 2010). Variables with a correlation higher than ±50 % and VIF > 3 were excluded from the analysis. Potential covariance between the abiotic parameters and the

community structure was addressed by the contingency table (8 physical–chemical variables x 6 biological variables). We used the contingency table to check for potential linear or unimodal relationships between the organisms' composition and the environmental variables through Redundancy Analysis ('rda' function) and Canonical Correspondence Analysis ('cca' function) respectively and thus selected the best-fit model as suggested by the resulting inertia (Legendre and Legendre, 2012). The best model was detailed based on the forward selection of significant variables using the 'ordiR2step' function. We assessed potential significant deviation from stability over the years through the linear regression breakpoint analysis (function 'breakpoints', *structchange* package, Zeileis et al., 2002), and highlighted through the traffic light plot (function 'trafficlight', *IEAtools* package, Otto, 2024).

3. Results

3.1. Indicators of decadal changes in the marine environment

The CFUS has a major spatial gradient of temperature and salinity (Fig. 2), ranging from warm and salty Tropical Water (T > 20 °C, S > 36 psu, Fig. 2 red and dark green symbols) off the shelf break on the east to seasonally mixed waters near the coast. During upwelling seasons, the cold and less saline water (T < 20 °C, S ≈ 35-36 psu, Fig. 2 blue and pink symbols) observed off Arraial do Cabo result from the mixing at the surface of the deep South Atlantic Central Water (SACW) with coastal waters (Valentin, 2001; Castro-Filho et al., 2015; Piola et al., 2018).

Relatively to the 1960–2019 average, there was an increase (>1 Standard Deviation, SST_{SD}=1.8 °C) in the sea surface temperature in the cold core and near the coast in the northeast region after the 90 s (Fig. 3, reddish areas). In contrast, the most prominent variation in salinity occurred in the south coastal region (Fig. 4, reddish areas) and over the shelf on the east (Fig. 4, blueish areas), coincident in time with that in temperature after the 90 s. This variation in salinity represents a weakening in the gradient, since less saline coastal waters turn into more saline, including that in the cold core, while those over the shelf became less saline after the 90 s.

Internally in each decade, most of the stronger oscillations followed a 12-month rhythm in temperature (Fig. 5a-c) representing the seasonal cycle common in upwelling regions. During the late 70 s and early 80 s, high-frequency disturbances (~3 months) weakened the annual seasonal oscillation (~12 months) of temperature and salinity. By combining both temperature and salinity time series (Fig. 5c), it seems that the coherence between oscillations is concentrated in cycles of 12 months before the 80 s and 3 ~ 4 months after the 00 s (Fig. 5c, reddish areas). Hence, the seasonality in the thermohaline regime has also weakened since the 80 s and is likely disturbed by high-frequency (every 3 ~ 4 months) oscillations from the early 2000s up to the present day. This temporal shift in the frequency coincided with the largest spatial increase in SST and SSS near the coast that was registered in 2000–09 (Figs. 3 and 4).

Zooming in the CFUS region, most of the environmental variables in the cold core oscillate cyclically (Fig. 6a-h) and have no significant linear trend, except for temperature, salinity, and Dissolved Oxygen (Table 1). The overall (1995–2015) average, standard deviation, slope of regression, and significance level are presented in Table 1. The sea surface temperature on the coast has decreased 0.06 °C year^{-1}, while salinity and dissolved Oxygen have increased respectively 0.04 psu and 0.02 ml.L^{-1} year^{-1} over the last 25 years (Fig. 6b). The sea surface

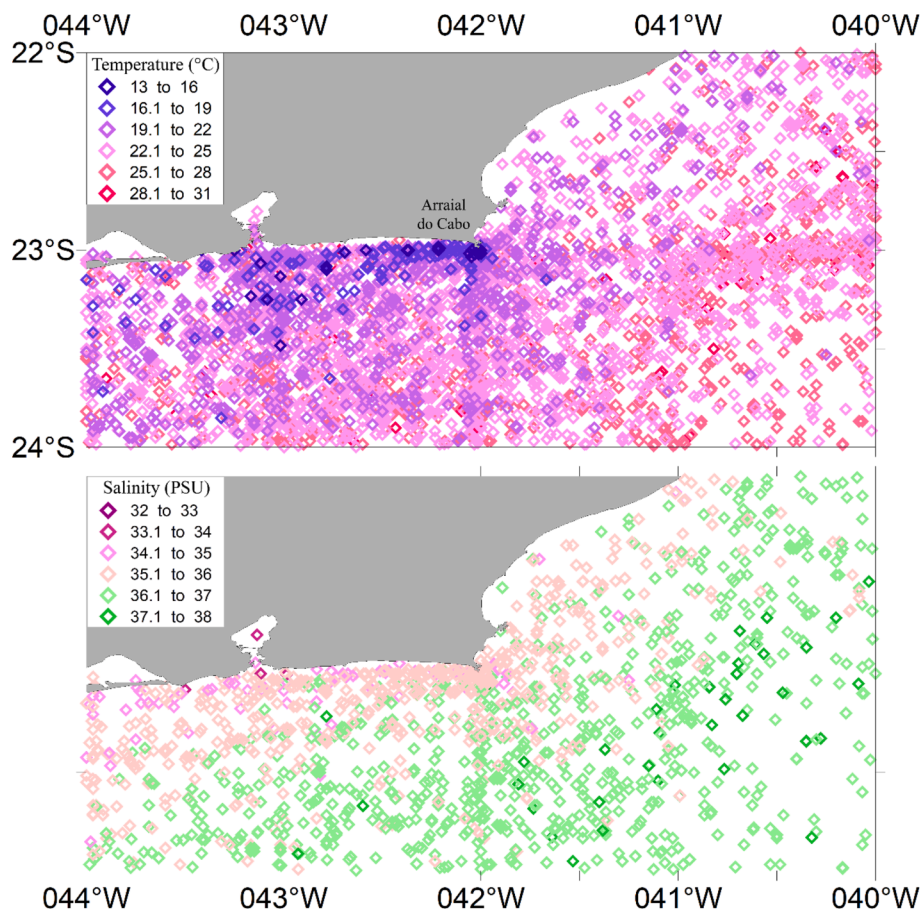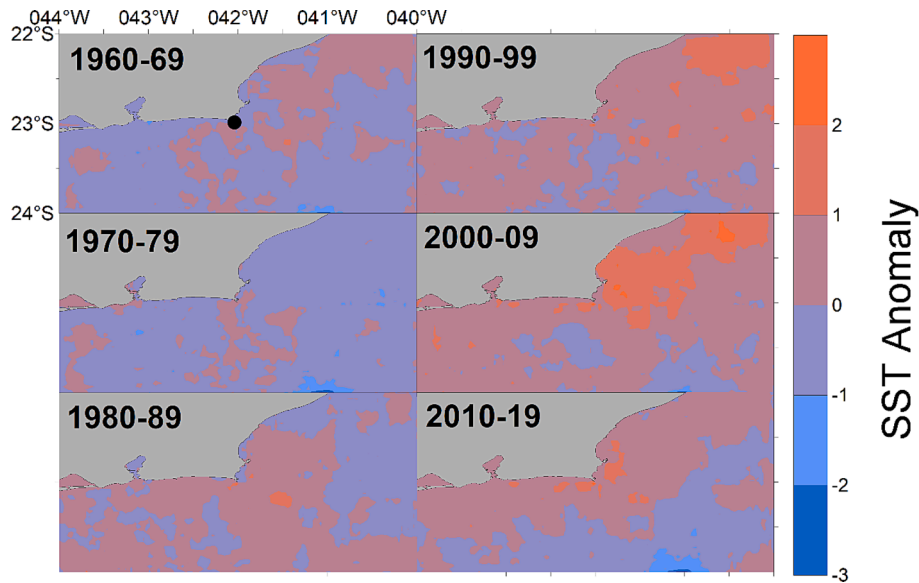**Fig. 2.** Spatial coverage of raw data in the CFUS measured from 1960 to 2019: (top) Sea surface temperature (N = 9568) and (bottom) salinity (N = 2939). Data set extracted from BNDO.

Fig. 3. Decadal (1960–2019) changes in the sea surface temperature (SST anomaly) in the CFUS. Positive/negative anomalies represent an increase/decrease in temperature relative to the overall average (1960–2019). The black dot locates the sampling site.
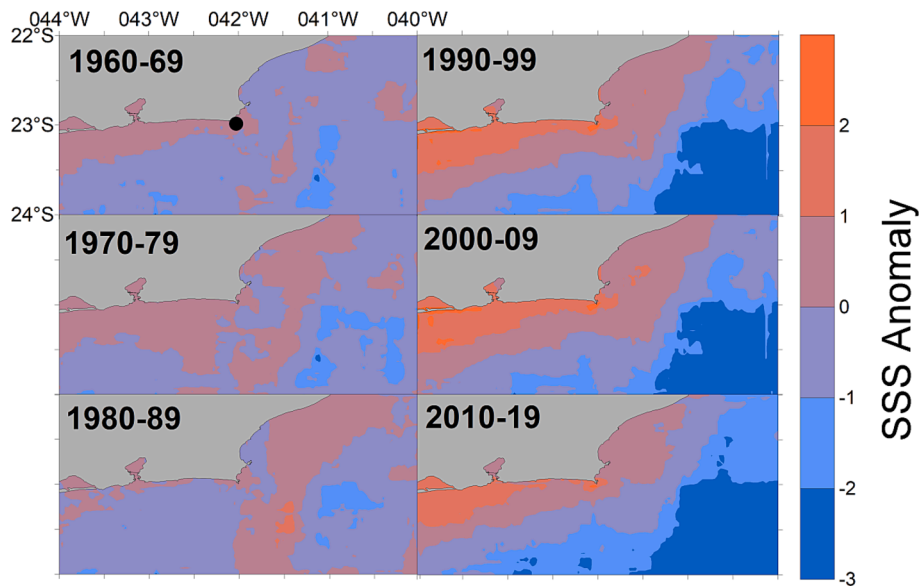
Fig. 4. Decadal (1960–2019) changes in the sea surface salinity (SSS anomaly) in the CFUS. Positive/negative anomalies represent an increase/decrease in salinity relative to the overall average (1960–2019). The black dot locates the sampling site.

temperature differed from the increasing trend observed in the whole CFUS and slightly decreased over the years, reaching the lowest average in 2015. Several environmental variables displayed high intra-annual (Fig. 6, vertical bars) and interannual variability (Fig. 6, annual averages), mainly pH, phosphate, and ammonia.

In general, more than 56.5 % of the environmental variability in the cold core region can be summarized in two principal orthogonal components (Fig. 7). The analysis places sea surface temperature, salinity, and concentration of dissolved oxygen, the variables with a significative trend (Table 1), as the most relevant drivers in the ecosystem, being the largest contributors of the first principal component that explains 34.2 % of the inter-annual variability in the CFUS. This component highlights years with warm waters (1998, 2003, and 2006) associated with high concentrations of ammonia. The period of the time series marked by the most intense upwellings, with high salinity and dissolved oxygen – 2012 to 2015 (Fig. 6a) – was entirely concentrated on the negative side of the

first principal component. The second axis (22.3 %) describes the nutrient-driven bottom-up effect in the ecosystem, placing years with high input of new nutrients ($PO_4 + NO_3 + NO_2$) that happened in 2001/02 and 2011/12 against oligotrophic years like 2004, 2013/14.

3.2. Indicators of decadal changes in the plankton assemblage

The interannual variability in the average abundance (Table 1 Suppl.) of some phytoplankton and zooplankton groups is significantly cross-correlated (Fig. 1 Suppl.). Copepods (Fig. 8f), for instance, are highly inversely correlated with dinoflagellates (Fig. 8b, R = −0.83) and Chlorophyll-a (Fig. 8a, R = −0.56), and were removed from the model to avoid collinearity. Most of the biological indicators analyzed herein have a sinusoidal rather than linear trend, even though the relationship between the physical–chemical variables and the spatial representation of biological variables follows a linear model (inertia = 2.96) rather than
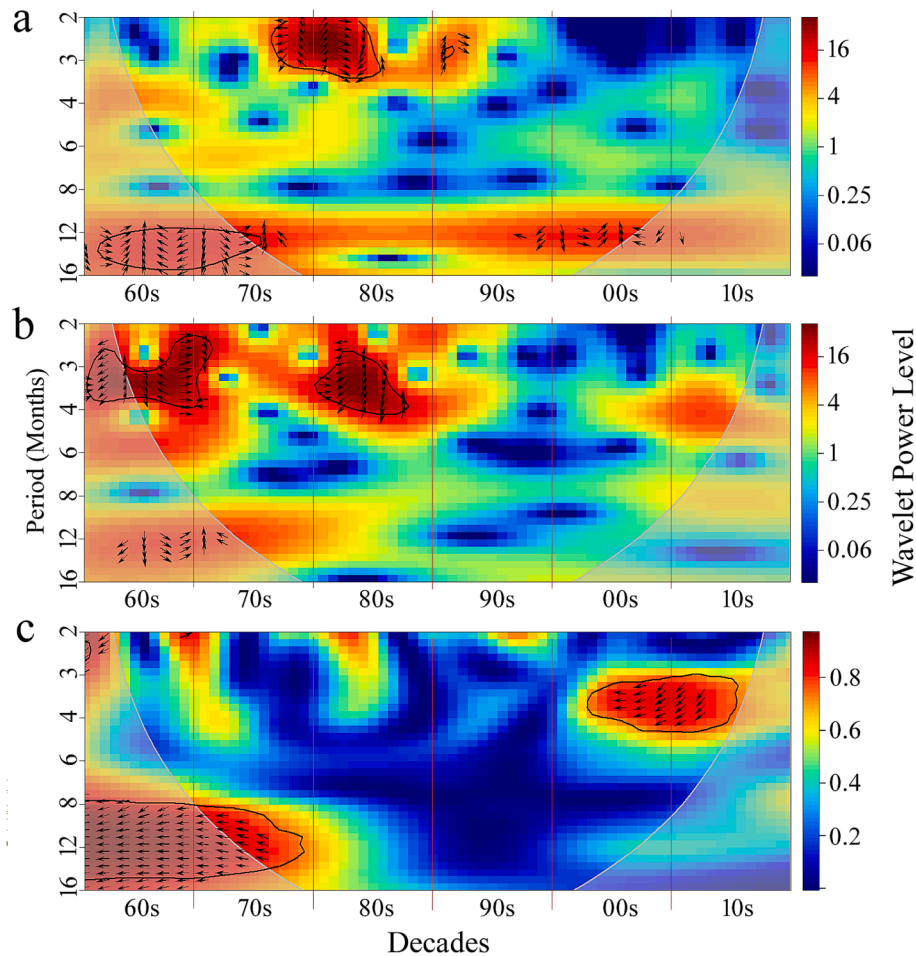
Fig. 5. Strength (wavelet power) of monthly to annual (period) oscillation in the CFUS over the decades: (a) temperature; (b) salinity; (c) coherence between temperature and salinity. The shadow areas indicate the outer limits of the 90% confidence level.

a Gaussian one (inertia = 0.07). The forward selection steps lead to the inclusion of all variables in the model, except for Copepoda due to its collinearity ($R^2_{adjusted} = 0.23$), and the linear model produced by the redundancy analysis (RDA) explained the majority (69 %) of the temporal variance of the 5 biotic variables selected in the round 2 (Table 2 Suppl.).

For diatoms and copepods, there were coincident peaks in abundance during 2004 followed by a decreasing trend thereafter (Fig. 8c and f). There was a coincident peak of Chlorophyll-a in 2004, followed by the same general linear trend of decreasing after, showing a punctual association that did not lead to a significant correlation (Fig. 1 Suppl.). Dinoflagellates, in contrast, do not peak at the beginning of the series nor in 2004 and seem to be increasing yearly instead. Cladocerans peaked in 2004 coincident with diatoms and copepods, but differently from them, they have an increasing trend in most recent years. The seston biomass exhibited highly interannual variability, but an increasing trend in more recent years that is positively correlated with dinoflagellates (R = 0.64, p < 0.1, Fig. 1 Suppl.).

According to the distribution of monthly average abundances over the years (Fig. 9), the peaks of diatoms and copepods were frequent up until 2004, while after that the majority of the abundances fell below the 60 % quintile. In contrast, high abundances of dinoflagellates and cladocerans and high concentrations of plankton biomass (both Chlorophyll-a and Seston dry weight) started to be more frequent in 2004. This difference was also evidenced by the breakpoint analysis as significant. The combined lowest value of the Residual Sum of Squares (RSS) and the Bayesian Information Criterion (BIC) correspond to m = 2 (Fig. 10), thus suggesting the existence of up to two breaking dates

(2002 and 2004, Table 3 Suppl.). The superposition of year scores in the first RDA dimension on top of the yearly distribution (Fig. 9, blue line) illustrates the shift between regimes that was suggested by the 2004 breakpoint (Fig. 10). From 2004 to 2007, the scores of years in the first dimension of the RDA turned into negative values illustrating the apparent regime shift after 2004.

In general, nearly 70 % of the total variance observed in the ecosystem is described by the two most significant dimensions (Fig. 11). The first dimension summarized 38.9 % of the variance and pointed to a transition from a diatom-dominant up to 2004 to a relatively dinoflagellate-dominant regime after. This apparent regime shift is coincident with the peak of cladocerans and copepods (Fig. 8e and f), the highly oligotrophic 2004 year (Fig. 7, PCA), the largest spatial warming in SST registered in the 2000–09 decade (Fig. 3), and the high-frequency oscillations that started in the early 2000s (Fig. 5c). As observed in the PCA, the temperature defined the positive side in the first dimension, mainly grouping years before 2004/05, featuring as the most nutrient-poor period in the PCA and RDA, while nutrients like phosphate and oxygen spread on the negative bottom quadrant. The nutrients and the dissolved oxygen that increase during cold upwelled waters positively correlated with the dinoflagellates and the seston dry weight, particularly during recent years. The salinity was the strongest vector on the second dimension, separating salty and nutrient-depleted waters with diatoms (2004) from some years when nitrogen sources ($NO_3 + NH_4$) point towards newly-upwelled eutrophic waters.
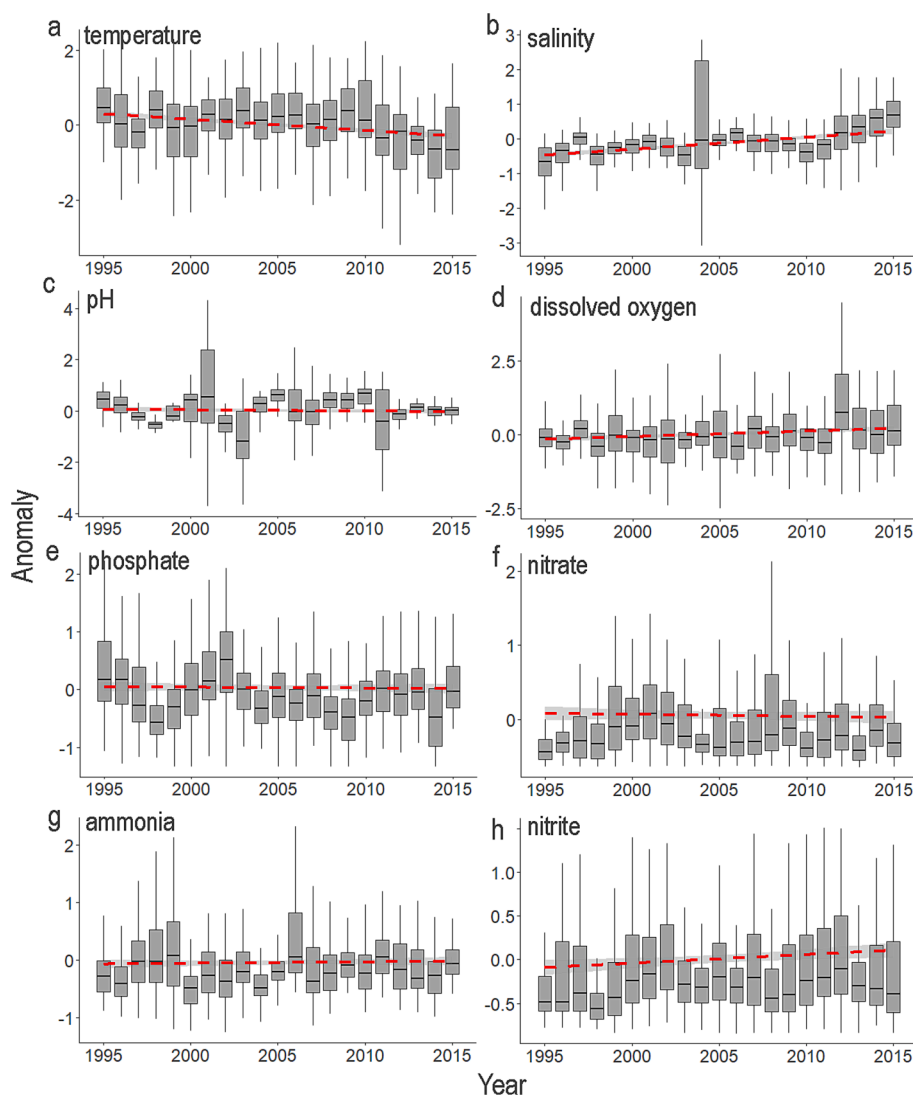
Fig. 6. Intra-annual and Interannual variability (1995–2015) of the major environmental variables in the main core of the upwelling in the CFUS near the coast showed as anomalies in (a) temperature; (b) salinity; (c) pH; (d) dissolved oxygen; (e) phosphate; (f) nitrate; (g) ammonia; and (h) nitrite. The boxplots represent the intra-annual variability from the annual average (black horizontal line), ±1 SD (grey box), ±2 SD (black vertical line), and the linear trend (red dotted line) ±95 % confidence interval (grey line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Overall average, standard deviation, slope (Linear Fit), and significance level of slope (p) of Temperature (SST), Salinity (SSS), Dissolved Oxygen (DO), pH, and nutrients (PO4, NO2, NO3, and NH4).

	SST (°C)	SSS (psu)	DO (ml/l)	pH	PO4 (µM)	NO2 (µM)	NO3 (µM)	NH4 (µM)
Average	22.16	35.74	5.65	8.16	0.27	0.09	0.75	1.38
SD	2.10	1.08	1.03	0.38	0.20	0.10	1.14	0.95
Slope	−0.06	0.04	0.02	0	0	0	0	0
p (slope)	0.01	0.01	0.01	0.22	0.68	0.72	0.48	0.43

4. Discussion

The CFUS is located in a subtropical-temperate transient ecosystem in the South Brazilian Bight (23–28.5°S, Nogueira-Júnior and Brandini, 2018) and marks the limits between the South Brazilian Shelf and the East Brazilian Shelf. As a transient ecosystem in the southwestern South Atlantic Ocean (SWAO), it is likely to have a high intra-annual natural variability in the environment that masks inter-annual temporal trends. The weakening registered in the seasonal rhythm (12 months) of thermohaline coherence after the 80 s suggests the permanence of warm and salty Tropical Water at the surface for long periods, which could have had some significant temporary effect on the CFUS ecosystem functioning and the plankton dynamics. There is additional evidence derived from a coincident increasing trend in the rainfall, air temperature, and sea surface temperature after the 90 s-00 s on the southern Brazilian coast that supports the enhancement of the thermohaline circulation (Penereiro and Meschiatti, 2018; Vasconcellos et al., 2023). Temperature and salinity are two of the most powerful physiological constraints for marine life (Walker et al., 2020) and drivers of phytoplankton and zooplankton phenology (Mackas et al., 2012). The CFUS is a hot spot of diatoms (Brandini, 2018), mainly at seasons of intense upwelling regimes, as observed when the increased nutrient availability in the euphotic mixed layer fuels primary productivity (Gonzalez-Rodriguez et al., 1992; De Carvalho and Gonzalez-Rodriguez, 2004; Guenther and Valentin, 2008; Guenther et al., 2008). Our results revealed a high abundance of diatoms coincident with low nutrient conditions in 2004, suggesting that growing is likely favoured by the relaxing of grazing by the consumers rather than through bottom-up stimulus. The relaxing in the top-down control is currently explained by the occurrence of multiple biological and physical controls
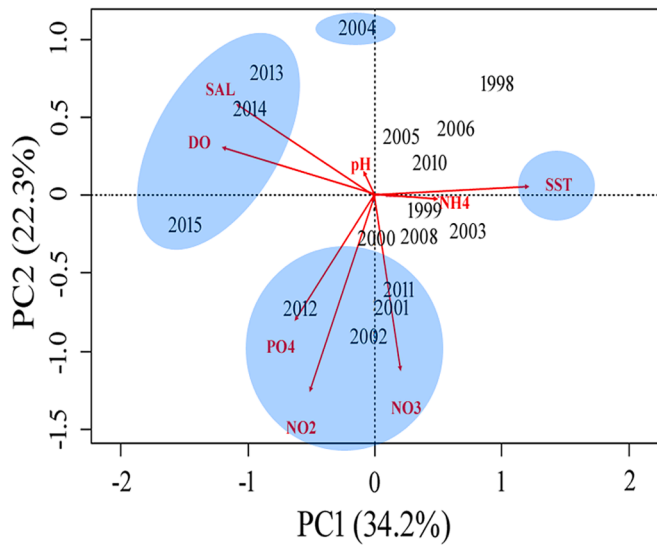
Fig. 7. Scatterplot of the first two components resulting from the Principal Component Analysis (PCA) on the monthly average abiotic parameters. The blue circles group correlated key environmental drivers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

decoupling phytoplankton from grazers, mainly the temporal variation of the depth of the mixed layer (Lindemann and John, 2014). Hence, the decadal increase in the sea temperature in the northern and salinity in the southern coastal zone of the CFUS, accompanied by the weakening in the seasonality of upwelling over the years is expected to temporarily

disturb the depth of the mixed layer and thus the ecosystem functioning. Particularly in upwelling ecosystems, disturbs in the mixed layer affect the input of deep nutrients, dilute planktonic populations, and determine the plankton phenology (Piontkovski and Castellani, 2009; Lindemann and John, 2014). The disturbance in the mixed layer can be seen in the high inter-annual variability of nutrients in CFUS, which in turn hid significant temporal trends over the 1995–2015 period.

The physical forces behind this circulation and the upwelling are largely derived from the dynamics of the Brazilian Current (BC) (Silva et al., 2023), a major component of the Atlantic Meridional Overturning Circulation in the region that exhibits a warming trend and a shift in the meandering behavior over the past decades (Castro et al., 2006; Vasconcellos et al., 2023). Together, the flow of the Brazilian Current, wind regime, and local bathymetry result in the upwelling of the nutrient-rich cold South Atlantic Central Water (SACW) in the vicinity of Cabo Frio Island (namely the upwelling cold core) (Valentin, 2001; Piola et al., 2018). This upwelling is characterized by temperatures lower than 20 °C and, according to our results, its cold core intensified between 2010 and 2018, contrasting with the broad warming trend observed in the coastal zone of the CFUS. These results, therefore, revealed contrasting trends between a decreasing temperature in the CFUS cold core and increasing SST on a broad scale that reinforces the need for regional-scale studies.

In the main upwelling zone, the natural seasonal oscillations of temperature, salinity, and nutrient concentration are well-known to drive the plankton phenology, particularly the spring bloom of phytoplankton (Fernandes et al., 2017; 2012). The coincidence between the weakening of seasonal oscillation in more recent years and the increasing trend for dinoflagellates and seston biomass over the years are potential intrinsic impacts on organisms' physiology that can propagate across the trophic interconnections (Ji et al., 2010). The shift between a diatom-dominant regime towards a dinoflagellate one
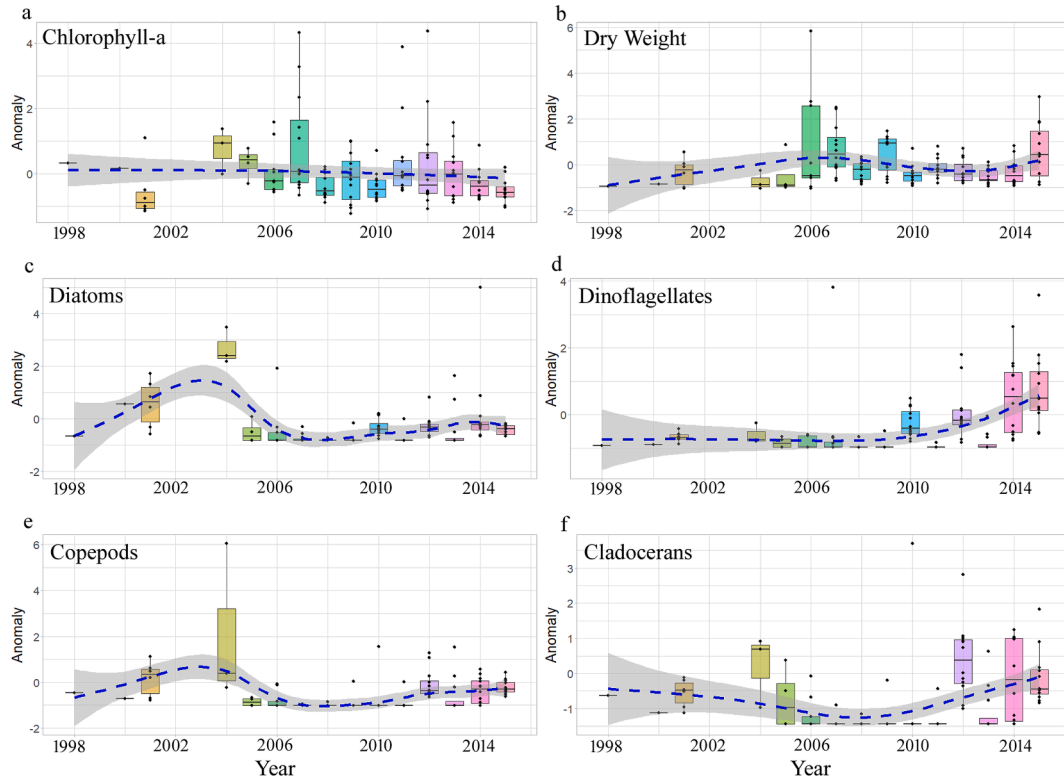

Fig. 8. Interannual variability in the normalized Chlorophyll-a concentration, Seston Dry Weight, and abundance of phytoplankton and zooplankton. (a) Chlorophyll-a; (b) Seston Dry Weight; (c) Diatoms; (d) Dinoflagellates; (e) Copepods; and (f) Cladocerans. Boxplots represent the annual median (black horizontal line), 25th and 75th percentiles (lower and upper hinges respectively), ±1.5* inter-quartile range (lower and upper whiskers respectively), raw data (black dots), and the 'GAM' model (dashed blue line). Years are represented in a gradient of colors for comparison purposes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
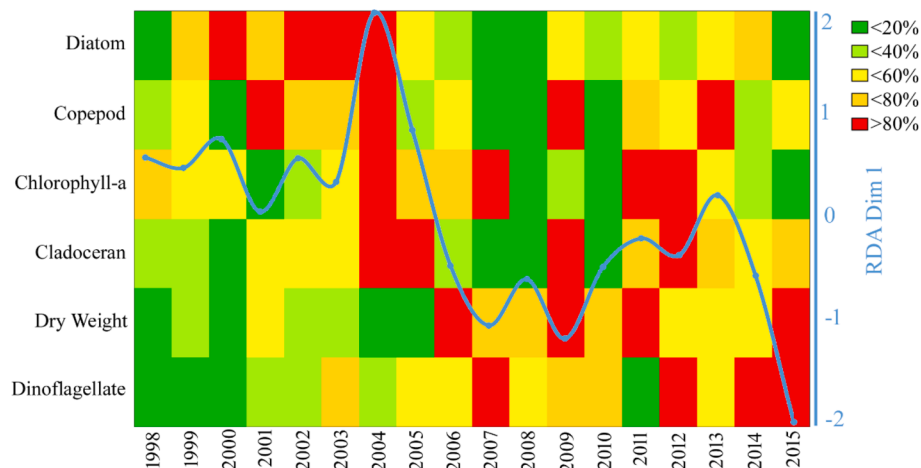
Fig. 9. Key indicators of temporal ecosystem shift in the CFUS. Ranked yearly distribution of quintiles (20 %) of phytoplankton, zooplankton, and seston (coloured scale) with superimposed scores of years in the first dimension of Redundancy Discriminant Analysis (RDA) (blue line, scales on the right). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
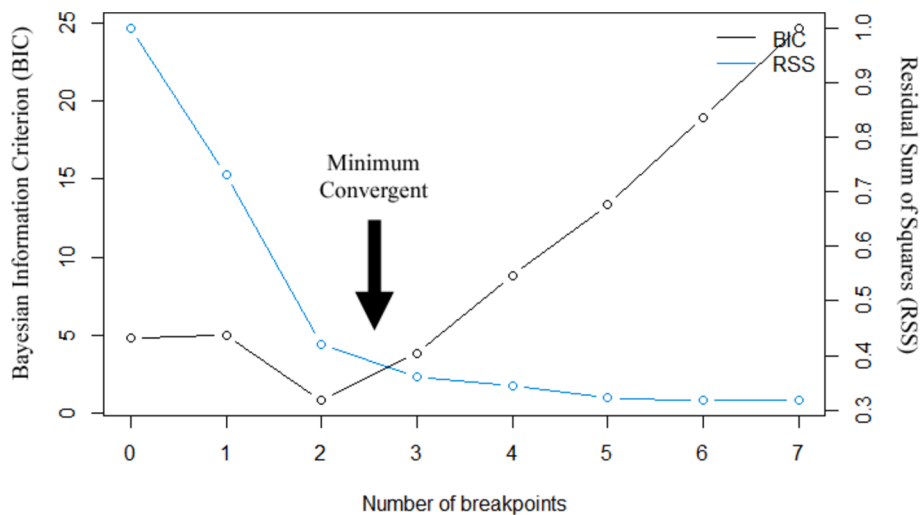

Fig. 10. Estimated number of breakpoints in the time series based on the BIC and RSS values.

indicates the distinct responses these organisms have to the observed environmental changes. Dinoflagellate species, in contrast to diatoms, are specialists in ecosystems with higher salinity and low nutrient concentrations (Irwin et al., 2012; Cael et al., 2021).

Differently from most of the South Brazilian Shelf, where the seasonal variability in plankton assemblage is mostly driven by the amount of riverine runoff through the rainy season (Brandini, 2018), there is less continental and more atmospheric (e.g. evaporation) interference in the CFUS. The region is alternatively influenced by intrusions of the warm Tropical Water (TW) and the rise of the cold South Atlantic Central Water (SACW) (Castro et al., 2006; Marcolin et al., 2014). The suggested predominance of TW at the surface in the CFUS, as revealed by the persistent salty waters after 2004, coincides with the vertical stratification and permanent thermocline usually observed in the CFUS (Silva et al., 2023). Under this stratified and oligotrophic regime, the plankton assemblage does not maintain highly dense populations nor high biomass for a long time, even though it is highly diverse and size-dominated by small organisms that quickly regenerate the nitrogen (Bode et al., 2004). The 2004 breakpoint thus reflected a potential regime shift towards the salty oligotrophic mixed layer that fueled the growth of dinoflagellates and thermophilic taxa, while constraining diatoms and copepods. Most cladocerans are also well-adapted to consume

small phytoplankton cells (Agasild and Nõges, 2005) and may thrive under this oligotrophic scenario.

In the CFUS, decadal shifts in salinity combined with changes in the plankton composition, biomass, and abundance are expected to propagate through the food web since the small pelagic fishes, mainly sardines, and fish larvae regulate the plankton growth (Coelho-Souza et al., 2012). In the Baltic, the cascading effects of decreasing copepods involved increasing sprat and cod declines (Möllmann et al., 2008). In the Benguela upwelling system, the low biomass of fish stocks after the 80 s was associated with a less efficient energy flow and an indicative of a regime shift (Cury and Shannon, 2004). The spawning of sardines in the CFUS varies annually but is mostly concentrated in waters with 22 to 26 °C and 34.5 to 36 PSU (Matsuura, 1996; 1998). The water temperature influences the larval survival and the inter-annual variability of the spawning of the Brazilian sardine, particularly in the CFUS due to the upwelling (Dias et al., 2014). Sardine and anchovy larvae exert a major top-down control on large copepods and must represent an additional pressure towards a cladoceran-dominated assemblage. Our analysis demonstrates a general trend of increase in salinity with a coincident threshold level in 2004 that propagated in phytoplankton and zooplankton, and perhaps up to the higher trophic levels. This threshold may suggest an abrupt and reversible regime shift instead of a
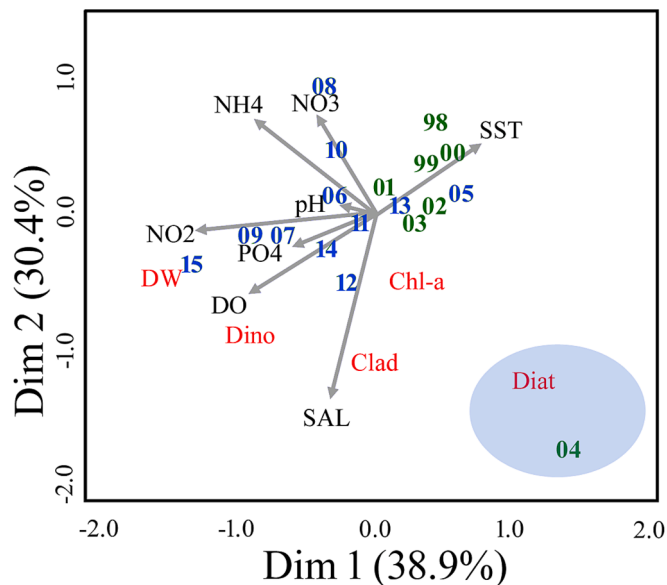
Fig. 11. Scatterplot of dimensions 1 and 2 resulting from the Redundancy Discriminant Analysis (RDA) in the main core of the upwelling. Explanatory (abiotic) and response variables (Seston Dry Weight, DW; Chlorophyll-a, Chl-a; Diatoms, Diat; Dinoflagellates, Dino; Cladocerans, Clad) are respectively shown in black and red. Years were split into ≤2004 (green) and >2004 (blue) to reflect the breakpoint analysis. Copepods were removed from the RDA due to collinearity. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

discontinuous one since no second critical threshold that justifies hysteresis (Collie et al., 2004) was found. In summary, the temporal changes in the water salinity, temperature, and planktonic assemblage are indicators of a potential cascade effect that propagates through the food web in the South Brazilian Shelf.

5. Conclusions

The phytoplankton and zooplankton assemblages in the Cabo Frio Upwelling System, the northern limit of the South Brazilian Shelf are responding to inter-annual changes in temperature, salinity, and nutrient conditions. Large spatial and temporal scale analyses demonstrated the influence of these drivers, but mainly the potential effect of a decadal change in salinity on the planktonic composition. Copepods and diatoms still dominate the plankton assemblage, although cladocerans and dinoflagellates have increased their proportional abundance over time. The observed increasing proportion of cladocerans and dinoflagellates in the plankton assemblage is likely linked to both the thermohaline circulation and the increased seston dry weight. Therefore, these assemblage changes are supposed indicators of an abrupt cascade effect that can have propagated through the food web up to several planktivorous clades. Based on these potential early warning indicators of a regime shift in the CFUS ecosystem, we thus recommend an increase in future efforts to monitor the responses of the populations of planktivorous fishes, such as sardines, to these observed decadal changes.

Funding

CRediT authorship contribution statement

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.112674.

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