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PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

LUIS CARLOS PINTO DE MACEDO SOARES

**O PAPEL DAS MASSAS DE ÁGUA E DO CLIMA NA
VARIAÇÃO ESPACIAL E TEMPORAL EM GRANDE ESCALA
DO ICTIOPLÂNCTON NO OCEANO ATLÂNTICO SUDOESTE
(21º - 41ºS)**

Florianópolis/SC
2015

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Tese de Doutorado apresentada ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina, como parte dos requisitos necessários à obtenção do título de Doutor em Ecologia.

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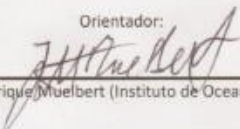
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2015

"O papel das massas de água e do clima na variação espacial e temporal em grande escala do ictioplâncton no Oceano Atlântico Sudoeste (21º - 41ºS)"

Por
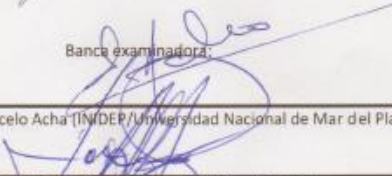
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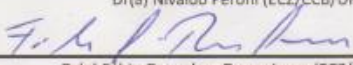
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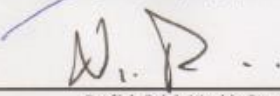
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Dedico esta Tese à minha amada filha Bibi.

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"Viver é desenhar sem borracha"

Yana Novi

RESUMO

A estrutura de comunidades é determinada por processos que agem em múltiplas escalas espaciais e temporais, como variações climáticas que podem provocar alterações nos ecossistemas. Sendo assim, a distribuição e composição do ictioplâncton são influenciadas por fatores ambientais que atuam nas características da história de vida das espécies. Além das mudanças climáticas, os ecossistemas marinhos estão sujeitos à pesca, o que afeta a produção de pequenos peixes pelágicos como a *Engraulis anchoita*. O objetivo desta Tese foi investigar o papel das massas de água e do clima nas variações em grande escala espacial e temporal na distribuição e estrutura do ictioplâncton no sudoeste do Atlântico Sul. Para este fim, foi utilizada uma ampla base de dados de ovos e larvas de peixes, adquirida em 21 cruzeiros realizados entre 1977 e 2010. Além disso, foram utilizados índices climáticos e dados de temperatura superficial do mar, salinidade, descarga do estuário do Rio da Prata e intensidade de vento para investigar possíveis relações e impactos sobre as variações interanuais da população Bonaerense da anchoita, utilizando dados de desembarques e ainda 20 anos de dados de sucesso de recrutamento. Os resultados demonstraram que a composição e distribuição do ictioplâncton em grande escala espacial está associada às massas de água, considerando simultaneamente o gradiente latitudinal e costa-oceano. Táxons dominantes são preferencialmente associados a massas de água distintas, independente da sazonalidade e do ano, que determinam a abundância e influenciam a dominância da comunidade. Enquanto isso, táxons raros e pouco frequentes são selecionados por uma determinada massa de água, como é o caso da enchova *Pomatomus saltatrix* exclusivamente associada à Água Subtropical de Plataforma. Além disso, o ambiente de desova e ocorrência larval da população Bonaerense da anchoita foi definida nos limites termohalinos da Água da Pluma do Prata, massa de água influenciada pela drenagem do estuário do Rio da Prata e pela dinâmica de ventos Sul e Nordeste. Os resultados nos levam a hipótese de que eventos como a Oscilação Sul do El Niño, que modificam o balanço entre o aporte de água do estuário do Rio da Prata na plataforma continental adjacente e o espalhamento da frente estuarina, afetam negativamente o ambiente de desova e ocorrência larval da anchoita, seu sucesso de recrutamento e produção pesqueira. A Tese demonstra que os estágios iniciais de peixes do sudoeste do Atlântico Sul são influenciados em grande escala espacial e temporal pela dinâmica das massas de água, bem como pelo clima que

pode afetar o recrutamento das espécies, resultando em flutuações nas populações de peixes e na produção pesqueira.

Palavras-chave: espécies indicadoras, gradiente latitudinal e costa-oceano, *Engraulis anchoita* Bonaerense, Oscilação Sul do El Niño, mudanças climáticas.

ABSTRACT

Community structure is determined by processes that act in multiple spatial and temporal scales, such as climatic variability, which affect community assembly through changes in the ecosystem. Therefore, ichthyoplankton distribution and composition are influenced by environmental factors that regulate life history traits. Beside climate change, marine ecosystems are also influenced by fisheries, which can affect production of small pelagic fish such as the anchovy *Engraulis anchoita*. This Thesis aimed to investigate the role of water masses and climate on the large-scale spatial and temporal variability in the distribution and structure of ichthyoplankton in the western South Atlantic. Ichthyoplankton data were acquired from the most comprehensive dataset from southern Brazilian waters based on 21 surveys conducted between 1977 and 2010. In addition to climatic indices, data on sea surface temperature, salinity, Rio de La Plata estuary outflow and winds were used to investigate the relation and impact of these variables on the interannual variability of the Bonaerense anchovy population, using landings and also 20 years of data of recruitment success. Results showed that ichthyoplankton composition and large-scale spatial distribution are associated with water masses, and latitudinal and cross-shelf gradients. Dominant taxa were preferentially associated with particular water mass, regardless of season and year, which determine taxa abundance and influencing dominance in ichthyoplankton community. Rare-low frequent taxa were exclusively associated with particular water mass, like the bluefish *Pomatomus saltatrix* that was associated with Subtropical Shelf Water. Furthermore, spawning and larva habitats of the Bonaerense anchovy population were defined in the thermohaline conditions of the cool and low salinity Plata Plume Water, that is influenced by the Rio de La Plata estuary outflow and by the seasonal variability of southerly and northeasterly winds. Our findings lead to hypothesized that climate variability such as the El Niño Southern Oscillation impact negatively Bonaerense anchovy habitat, recruitment success and thus its fisheries, by modifying the balance between Rio de La Plata estuary outflow and oceanward and northward displacement of the estuarine front. The Thesis demonstrated that early life history stages of fishes from the western South Atlantic are influenced in large spatial and temporal scales by water masses dynamics, as well as by climate that can affect recruitment, and drive fluctuations in fish population and its fisheries.

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1 INTRODUÇÃO

A ecologia de comunidades objetiva entender os padrões de distribuição, abundância e composição das espécies nas comunidades, bem como os processos subjacentes a existência desses padrões (Vellend, 2010). Estes processos agem em múltiplas escalas no espaço e no tempo, moldando as comunidades biológicas regionais e locais (Menge & Olson, 1990). Os ecossistemas marinhos mudam de acordo com diferentes escalas temporais, da sazonal até centenas de anos, decorrentes de processos influenciados por fenômenos atmosféricos e climáticos (Lehodey et al., 2006), e estão sujeitos a uma ampla variedade de impactos antropogênicos, como as mudanças climáticas e a pesca (Frederiksen et al., 2006). A importância de se obter séries temporais para a avaliação da dinâmica de um ecossistema é conhecida (Bograd et al., 2003; Greve et al., 2004; Batten & Welch, 2004; Mackas et al., 2012a), bem como o uso de organismos zooplanctônicos, incluindo o ictioplâncton, para o diagnóstico dos impactos de mudanças climáticas nos ecossistemas marinhos (Hsieh et al., 2009; Auth et al., 2011; Mackas et al., 2012b). Organismos do zooplâncton são bons sinalizadores de mudanças climáticas por uma série de razões (Richardson, 2008): seus processos fisiológicos são altamente suscetíveis a mudanças na temperatura; alguns não são comercialmente explorados e por isso tendências de longo prazo em resposta a mudanças ambientais não são confundidas com mudanças devido à sobrepesca; sua distribuição pode refletir com precisão a temperatura e as correntes oceânicas porque flutuam livremente na coluna de água.

1.1 Grandes escalas espaciais: gradientes latitudinal e costa-oceano

A distribuição do ictioplâncton sofre influência de fatores ambientais que regulam as características da história de vida das espécies, determinando sua amplitude geográfica (Sabatés et al., 2007; Olivar, et al., 2010; Muhling et al., 2013). Estudos que contemplam grandes escalas espaciais tem relacionado o gradiente latitudinal com variações na diversidade e composição de espécies no ambiente marinho devido à relação direta com a variação na temperatura superficial do mar (Woodd-Walker et al., 2002; Floeter et al., 2004; Fuhrman et al., 2008; Vinagre et al., 2009). Sendo assim, uma importante relação pode ser estabelecida entre a variação latitudinal e a distribuição em grande escala das comunidades ictioplanctônicas, uma vez que o desenvolvimento das larvas de peixes é dependente da temperatura e do

fotoperíodo (Vinagre et al., 2009). Relações entre o gradiente latitudinal e variações na composição das associações de larvas de peixes forma relatadas para o Oceano Pacífico Norte (Moser & Smith, 1993). Na costa do Chile, diferenças no tamanho dos ovos e comprimento das larvas recém-eclodidas da anchoveta *Engraulis ringens* obtidos em um gradiente latitudinal (20º – 36ºS) foram decorrentes de variações em condições ambientais em uma maior escala espacial associada com a latitude (Llanos-Rivera & Castro, 2004). Em estuários localizados em diferentes latitudes em Portugal, a taxa de crescimento de larvas do badejo *Dicentrarchus labrax* e época de desova apresentaram variações ao longo do gradiente de latitude em função de diferenças no fotoperíodo e temperatura, sendo a temperatura o fator determinante nos estuários localizados em maiores latitudes (Vinagre et al., 2009).

Associações de larvas de peixes são formações temporárias, uma vez que são restritas as fases larvais (Mafalda Jr. & Rúbin, 2006) e são resultantes dos padrões e estratégias de desova dos adultos, bem como de influências do ambiente (Boehlert & Mundy, 1993; Sabatés et al., 2007; Franco-Gordo et al., 2008). Em um gradiente costa-oceano, i.e., da plataforma continental ao talude, a composição do ictioplâncton é fortemente influenciada pelas correntes oceânicas e massas de água (Lopes et al., 2006; Muhling et al., 2008), esta última é também relacionada com a variação da latitude (Nonaka et al., 2000; Franco et al., 2006). Massas de água são porções de água com propriedades físicas e químicas distintas, como temperatura e salinidade, que resultam na circulação termohalina dos oceanos (Thurman & Burton, 2001). Em regiões costeiras, processos oceanográficos como a drenagem continental e a ressurgência induzida pelo vento, desempenham um papel importante na composição das associações ictioplanctônicas (Lopes et al., 2006; Franco-Gordo et al., 2008). Estudos sobre a distribuição das espécies e composição das associações de larvas de peixes no gradiente costa-oceano tem sido desenvolvidos em diferentes regiões do mundo (Sanvicente-Añorve et al. 1998; Hernández-Miranda et al., 2003; Mafalda Jr. & Rúbin, 2006; Mafalda Jr. et al., 2006; Muhling et al., 2008), no entanto, a maioria dos desenhos amostrais não permite a análise simultânea de gradientes latitudinal e costa-oceano.

1.2 Grandes escalas temporais: processos oceanográficos e clima

A composição das associações ictioplanctônicas também pode variar ao longo do tempo em virtude da sazonalidade nos fatores ambientais que delimitam a distribuição das espécies (Sanvicente-

Añorve et al., 1998; Nonaka et al., 2000; Katsuragawa et al., 2014), e que determinan mudanças nas espécies que ocorrem em uma determinada localidade e que podem ser selecionadas do conjunto total de espécies de uma região (Menge & Olson, 1990; Keddy et al., 1992). No Golfo do México, variações sazonais nas associações larvais (costeira, nerítica, oceânica) foram decorrentes da desova dos adultos e de fatores ambientais como a drenagem continental, que também variam sazonalmente (Sanvicente-Añorve et al., 1998). Na região do Banco de Abrolhos também foram econtradas variações sazonais nas associações larvais como a formação de um subgrupo no outono (p.ex., associação costeira do Banco de Abrolhos) ou redução da área ocupada por associações neríticas e oceânicas no verão. Estas variações foram relacionadas com diferentes condições oceanográficas locais como formação de vórtices e ressurgências costeiras (Nonaka et al., 2000). Além disso, na Plataforma Continental Sudeste (PCSE) do Brasil, mudanças na composição de espécies dominantes das associações larvais foram relacionadas com a sazonalidade na distribuição das massas de água (Katsuragawa et al., 2014).

Organismos planctônicos estão sujeitos a uma variedade de processos estocásticos como fluxos turbulentos que podem desagregar os agrupamentos de larvas reduzindo as chances de encontro com suas presas, ou transporte de Ekman induzido pelo vento no sentido da costa que pode agregar larvas e mantê-las em ambientes mais favoráveis ao seu desenvolvimento (Lima & Castello, 1995; Houde, 2008). Algumas massas de água estão relacionadas com processos de enriquecimento da coluna de água, retenção larval induzida pela estabilidade vertical e concentração de organismos zooplanctônicos, características ambientais essenciais para a sobrevivência e desenvolvimento larval (Bakun, 2010). Essas características ambientais são fatores chave para um recrutamento bem sucedido, pois favorecem a disponibilidade de alimento em tamanho adequado e quantidade suficiente durante a primeira alimentação de uma larva, no chamado "Período Crítico" (Hjort, 1914), e a sobreposição entre a disponibilidade de alimento e a produção de larvas (Lasker, 1975).

Nos ecossistemas marinhos, além da influência das forçantes físicas oceanográficas, variações no clima podem influenciar alterações em diferentes processos ecológicos, afetando a abundância e distribuição das espécies (Stenseth et al., 2003; Hsieh et al., 2009). No Oceano Pacífico Norte, por exemplo, índices climáticos como a Oscilação Decadal do Pacífico (*Pacific Decadal Oscillation*) explicaram melhor as oscilações decadais na diversidade e abundância de larvas de

peixes do que fatores oceanográficos de mesoescala como o transporte de Ekman ou ressurgências costeiras (Auth et al., 2011). No Hemisferio Sul, o principal modo de variabilidade na circulação atmosférica é o Modo Anular Sul (*Southern Annular Mode*, SAM), também conhecido como Oscilação da Antártica (*Antarctic Oscillation*, AAO), porém com sinal oposto. O SAM é associado a diferenças nas anomalias de pressão do nível do mar entre a Antártica e latitudes médias (Marshall, 2003; Jones et al., 2009), e estudos demonstraram relações positivas e impactos não estacionários (p.ex., que variam ao longo do tempo) em relação à precipitação sobre a região sul da América do Sul durante a primavera (Silvestri & Vera, 2003; Silvestri & Vera, 2009). Entretanto, estudos sobre a influência do SAM nas comunidades marinhas ou estoques pesqueiros no sudoeste do Atlântico Sul não foram publicados até o momento.

A Oscilação Sul do El Niño (*El Niño Southern Oscillation*, ENSO), que consiste no deslocamento para o leste das águas quentes do oeste do Pacífico Equatorial e mudanças na circulação atmosférica (Stenseth et al., 2003; Lehodey et al., 2006), é outro fenômeno climático com efeitos importantes no Hemisfério Sul. Apesar do sinal principal dessa interação oceano-atmosfera ocorrer no Oceano Pacífico tropical, seus efeitos afetam os ecossistemas no âmbito global (Lehodey et al., 2006). Eventos extremos de El Niño são associados a anomalias positivas na precipitação sobre a América do Sul (Aceituno, 1988; Ropelewski & Halpert, 1989), e anomalias positivas na drenagem continental na bacia do Rio da Prata (Mechoso & Iribarren, 1992). No sudoeste do Atlântico Sul, o El Niño foi associado à ocorrência de águas anormalmente quentes na Corrente do Brasil, e águas anormalmente frias na Corrente das Malvinas e na região da Confluência Brasil-Malvinas (Severov et al., 2004). O baixo recrutamento de espécies alvo da pesca com o camarão rosa *Farfantepenaeus paulensis* no estuário da Lagoa dos Patos e da corvina *Micropogonias furnieri* no estuário do Rio da Prata foi associado à alta drenagem continental decorrente do El Niño (Möller Jr. et al., 2009; Acha et al., 2012).

As variações interanuais na estrutura das comunidades podem estar relacionadas com mudanças no padrão sazonal do ambiente (Menge & Olson, 1990; Tonn, 1990). No ambiente pelágico, o ictioplâncton pode ser influenciado por uma variedade de fatores oceanográficos e climáticos, como por exemplo, a drenagem continental e a Oscilação Sul do El Niño, que induzem a variações na distribuição e abundância das espécies desde escalas sazonais (Nonaka et al., 2000; Muelbert et al., 2008; Katsuragawa et al., 2014), interanuais (Franco-

Gordo et al., 2008; Muhling et al., 2013), até decadais (Auth et al., 2011). No entanto, poucos estudos englobam simultaneamente grandes escalas temporais e espaciais (Hsieh et al., 2009), especialmente aqueles conduzidos no sudoeste do Oceano Atlântico Sul (Sánchez & Ciechomski, 1995), devido a dificuldade da manutenção de programas de longo prazo. Sendo assim, a utilização de dados pretéritos devidamente padronizados pode auxiliar no preenchimento de lacunas no conhecimento, ampliando o entendimento dos padrões de distribuição das espécies em grandes escalas temporais e espaciais.

1.3 Ambiente de desova e de ocorrência larval de pequenos peixes pelágicos

Ecossistemas marinhos altamente produtivos sujeitos a ressurgências ou influência de drenagem continental são dominados por grandes cardumes de pequenos peixes pelágicos como as anchoitas (*Engraulis*) e as sardinhas (*Sardinops*, *Sardina* e *Sardinella*) (Checkley et al., 2009). Os pequenos peixes pelágicos ocupam níveis tróficos intermediários na teia trófica pelágica conduzindo energia e nutrientes a partir da produção primária e secundária planctônica até os predadores de topo (Frederiksen et al., 2006). São responsáveis por em média 33% da produção pesqueira mundial (Herrick et al., 2009), e suas populações estão sujeitas às mudanças climáticas por responderem rapidamente às variações ambientais, devido a características biológicas como: alta mobilidade, ciclo de vida de curta duração, alta fecundidade, por alimentarem-se diretamente do plâncton, e em alguns casos, desovarem durante o ano todo (Alheit et al., 2009).

No sudoeste do Oceano Atlântico Sul, o gênero *Engraulis* é representado pela espécie *Engraulis anchoita* Hubbs & Marini, 1935, conhecida localmente por anchoita. A distribuição da espécie inclui a região entre o Golfo de San Jorge, Argentina (48ºS), até o Cabo de São Tomé no Brasil (20ºS) (Bakun & Parrish, 1991). Existem três estoques reconhecidos de anchoita: o estoque Patagônico localizado entre 48ºS e 41ºS; o estoque Bonaerense entre 41ºS e 28ºS; e, o estoque da Plataforma Continental Sudeste (PCSE) do Brasil localizado entre 28ºS e 20ºS (Sánchez & Ciechomski, 1995; Carvalho & Castello, 2013). O estoque Bonaerense é considerado o principal em relação à pesca, com uma biomassa estimada entre 1,6 e 5,4 milhões de toneladas, contra uma biomassa estimada de 0,4 a 2,0 milhões de toneladas para o estoque Patagônico e 0,2 a 0,4 milhões de toneladas para o estoque da PCSE que não é explorado comercialmente (Castello, 1989; Hansen et al., 2010;

Madirolas et al., 2013). A anchoita é ainda uma importante presa para outras espécies exploradas comercialmente como a merluza, a cavalinha e as lulas, bem como para aves e mamíferos marinhos (Angelescu, 1982).

A população Bonaerense da anchoita, que se concentra principalmente na plataforma continental da Argentina, realiza duas migrações sazonais: a primeira entre a região nerítica e águas costeiras com profundidade menor do que 50 metros, e a segunda entre a região da plataforma continental Argentina e do Uruguai, e as águas da plataforma continental sul do Brasil (Sánchez & Ciechomski, 1995; Castello, 2007). Na primeira migração, o estoque desovante da anchoita deixa as águas ricas em nutrientes (especialmente os nitratos) de origem subantártica localizadas na região mais externa da plataforma continental, onde se alimentam intensamente de zooplâncton (Carreto et al., 1986; Pájaro et al., 2002), para iniciar uma atividade massiva de desova, durante outubro e novembro, em águas costeiras sob influência do estuário do Rio da Prata (Sánchez & Ciechomski, 1995). Apesar da desova massiva durante a primavera, ovos e larvas de anchoita podem ser encontrados sobre a plataforma continental durante todo o ano (Sánchez & Ciechomski, 1995), onde a frente estuarina de águas frias e de baixa salinidade conhecida como Água da Pluma do Prata (APP) proporciona estabilidade vertical na coluna de água e concentração de zooplâncton, garantindo um ambiente adequado para a alimentação e crescimento larval (Guerrero et al., 1997; Viñas et al., 2002; Piola et al., 2008).

A segunda migração ocorre durante o final do outono e inverno seguindo o deslocamento para o norte da APP, que é impulsionada pela intensificação do vento sul encontrando o reforço da pluma do estuário da Lagoa dos Patos na plataforma continental sul do Brasil. Durante essa migração que atinge aproximadamente os 31ºS, próximo ao farol da Conceição, o estoque desovante da anchoita libera ovos em águas brasileiras até a primavera, quando retorna para a plataforma continental Argentina e Uruguaia com o recúo da APP para o sul, devido à intensificação do vento nordeste (Lima & Castello, 1995; Castello, 2007; Piola et al., 2008). Ao retornarem para a plataforma continental Argentina, o estoque desovante da anchoita recompõe o estoque remanescente, que não realizou a migração para águas brasileiras, para realizar a massiva atividade de desova da primavera (Sánchez & Ciechomski, 1995).

Pequenos peixes pelágicos, como as anchoitas, apresentam flutuações naturais na abundância de suas populações (Lluch-Belda et

al., 1989; Baumgartner et al., 1992), que podem estar relacionadas à variações climáticas (Lloret et al., 2001; Borja et al., 2008). Flutuações na abundância das populações são resultantes do efeito do clima nos ecossistemas marinhos e de diversos processos ecológicos que ocorrem em diferentes escalas temporais (Stenseth et al., 2003; Lehodey et al., 2006), bem como na localização do ambiente de desova adequado (Hunter & Alheit, 1995). Locais onde podem ser encontrados ovos e larvas de uma determinada espécie podem ser caracterizados como um ambiente de desova e ocorrência larval, uma vez que oferecem um conjunto de condições ambientais apropriadas para a desova e desenvolvimento dos estágios iniciais dos peixes (Castro et al., 2005). A análise da abundância e distribuição de ovos e larvas de peixes ao longo de séries temporais tem sido utilizada para investigar a localização espacial e temporal do ambiente de desova e ocorrência larval de pequenos peixes pelágicos, em virtude da facilidade de amostragem dos estágios iniciais em relação aos adultos sexualmente maduros (van der Lingen et al., 2001). O ambiente de desova e ocorrência larval de pequenos peixes pelágicos tem sido estudado em relação a diferentes fatores ambientais como temperatura superficial do mar, salinidade e biomassa do fitoplâncton (Lluch-Belda et al., 1991; van der Lingen et al., 2001; Palomera et al., 2007; Twatwa et al., 2005).

1.4 Hipóteses

Diante do exposto, as seguintes hipóteses orientaram esta Tese:

1) A distribuição e a composição das associações de larvas de peixes em grande escala espacial estão relacionadas à composição e distribuição das massas de água (capítulo 1);

2) A composição das associações de larvas de peixes é determinada pela variação sazonal na distribuição das massas de água (capítulo 2);

3) Os efeitos não-estacionários do clima e de processos oceanográficos afetam negativamente as populações de pequenos peixes pelágicos (capítulo 3).

1.5 Objetivo geral

Investigar o papel das massas de água e do clima nas variações em grande escala espacial e temporal na distribuição e estrutura do ictioplâncton no sudoeste do Oceano Atlântico Sul.

1.6 Objetivos específicos

1) Investigar simultaneamente os gradientes latitudinal e costa-oceano na abundância e estrutura do ictioplâncton na Plataforma Continental Sul do Brasil (capítulo 1);

2) Investigar o papel das massas de água na variabilidade sazonal e interanual da distribuição em grande escala das associações ictioplanctônicas (capítulo 2);

3) Verificar os efeitos não-estacionários do clima e processos oceanográficos na variabilidade interanual da população Bonaerense da anchoita *Engraulis anchoita*, e em seu ambiente de desova e ocorrência larval, para responder as seguintes questões: Qual a relação do Modo Anular Sul (SAM) e da Oscilação Sul do El Niño (ENSO) com a variabilidade interanual da população adulta do estoque Bonaerense da anchoita *Engraulis anchoita*? Qual a principal forçante ambiental que afeta o ambiente de desova e ocorrência larval da população Bonaerense da anchoita? De que forma a variabilidade climática em grande escala afeta o ambiente de desova e ocorrência larval da população Bonaerense da anchoita *Engraulis anchoita*? (capítulo 3).

2 MATERIAIS E MÉTODOS

2.1 Área de estudo

O estudo foi realizado no sudoeste do Oceano Atlântico Sul na região que compreende dois grandes ecossistemas marinhos (Duda & Sherman, 2002), a Plataforma Sul do Brasil (South Brazil Shelf) e a Plataforma Patagônica (Patagonian Shelf) (Figura 1). A Plataforma Sul do Brasil (PSB) se estende desde o Cabo de São Tomé (22º02'S) ao Chuí (33º41'S), e pode ser dividida em três grandes regiões de acordo com suas características oceanográficas, do norte para o sul: região do Cabo de São Tomé-Cabo Frio (CSTF), Plataforma Continental Sudeste (PCSE) e a Plataforma Continental Sul (PCS). Ao sul do Chuí, o estudo na Plataforma Patagônica extendeu-se até ao sul de Mar del Plata (41ºS) (Figura 1A). Ao longo do talude na PSB, a Corrente do Brasil (CB) transporta em direção ao sul a Água Tropical (AT), quente e salina, na camada superior até 200 m de profundidade, e logo abaixo a Água Central do Atlântico Sul (ACAS), fria e rica em nutrientes, entre 200 e 500 m de profundidade (Silveira et al., 2000). Águas de origem subantártica, frias e ricas em nutrientes, são carregadas para o norte pela Corrente das Malvinas (CM), originada a partir de um ramo da Corrente Circumpolar Antártica (Sánchez & Ciechomski, 1995). Aproximadamente em 38ºS, CB e CM se encontram em uma frente denominada Confluência Brasil-Malvinas (CBM) (Garcia et al., 2004), onde ambas são deflectidas para leste como parte do giro subtropical do Atlântico Sul (Figura 1B).

Ressurgência costeira induzida pelo vento e topografia ocorre na parte norte da área de estudo (CSTF), especialmente durante a primavera e o verão, resultante da predominância do vento nordeste (Valentin, 1984; Rodrigues & Lorenzzetti, 2001). A ressurgência da ACAS promove condições adequadas para um aumento da produção primária ao longo da costa. A proximidade entre o fluxo no sentido sul da CB e a região costeira induz a uma intensa atividade de fenômenos de mesoescala, como a ocorrência de ressurgência induzida por vórtices decorrentes de meandros instáveis quase estacionários (Campos et al., 2000; Calado et al., 2010). A plataforma continental é caracterizada pela presença da Água de Plataforma (AP) resultante da mistura de águas da drenagem continental com águas sob a influência da CB. Na região entre Cabo Frio (22º52'S) e Cabo de Santa Marta (28º36'S) (PCSE) a AP ocorre na sua porção norte e a Água Subtropical de Plataforma (ASTP) na porção sul, espalhando-se também pela região nerítica da PCS. A

ASTP é uma massa de água resultante da mistura entre a Água da Pluma do Prata (APP), de menor salinidade e relativamente fria, com a AT (Möller Jr. et al., 2008). Durante o inverno, com a intensificação do vento sul, o transporte da APP para o norte torna-se mais intenso por toda a PCS, podendo atingir a parte sul da PCSE. A ação conjunta dos intensos ventos do sul e Corrente Patagônica aumenta o espalhamento para o norte da Água Subantártica de Plataforma (ASAP) que atinge a porção sul da PCS (Möller Jr. et al., 2008; Piola et al., 2008). No sul da área, os estuários do Rio da Prata e da Lagoa dos Patos possuem uma descarga média entre 20.000 e 25.000 m^3 s^{-1} e 700 a 3.000 m^3 s^{-1}, respectivamente. O primeiro drena a segunda maior bacia hidrográfica da América do Sul, enquanto que o segundo é a maior laguna costeira estrangulada do mundo (Ciotti et al., 1995; Guerrero et al., 1997; Seelinger & Odebrecht, 2010).

Diferentes processos oceanográficos promovem o enriquecimento das águas superficiais e aumento da produção primária na região ao sul de Cabo Frio, associando-a ao maior estoque pesqueiro do Brasil como, por exemplo, em Santa Catarina e Rio Grande do Sul (Castello et al., 2009). No Cabo de Santa Marta, a Água Central do Atlântico Sul (ACAS) contribui com o aumento da concentração de nitrato nas camadas superiores da coluna de água (Braga et al., 2008) devido a uma ressurgência resultante de vento nordeste moderado durante a primavera e verão (Acha et al., 2004; Campos et al., 2013). A ressurgência afeta a produção pelágica principalmente ao sul do cabo, onde o transporte de Ekman ao longo da costa, no sentido do oceano, torna-se mais intenso (Odebrecht & Djurfelt, 1996; Campos et al., 2013).

No estuário do Rio da Prata o padrão de distribuição de salinidade pode ser dividido em dois períodos: o primeiro durante o outono e inverno com alta descarga continental, baixa frequência de ventos de leste (no sentido da costa) e velocidade média alta do vento de oeste (no sentido do oceano); o segundo na primavera e verão, quando a descarga continental tende a ser mínima e os ventos de leste tornam-se mais intensos e frequentes (Guerrero et al., 1997). A água marinha penetra no estuário próximo ao fundo equanto que as águas do Rio da Prata avançam em direção ao oceano pela superfície, gerando uma forte estratificação salina nas águas da frente estuarina que se espalham pela plataforma continental (Sánchez & Ciechomski, 1995; Acha et al., 2008). Os efeitos combinados da condição de outono-inverno da frente estuarina do Rio da Prata, pluma estuarina da Lagoa dos Patos e intensificação do vento sul, resultam no espalhamento para o norte da Água da Pluma do Prata (APP), que gera uma estabilidade vertical

moderada na coluna de água ao longo da plataforma. Além disso, a predominância do vento sul resulta em transporte de Ekman em direção a costa durante todo o inverno (Lima & Castello, 1995; Möller Jr. et al., 2008). A alta concentração de silicato ao longo da costa e plataforma está associada às águas de origem continental da APP (Carreto et al., 1986; Braga et al., 2008).
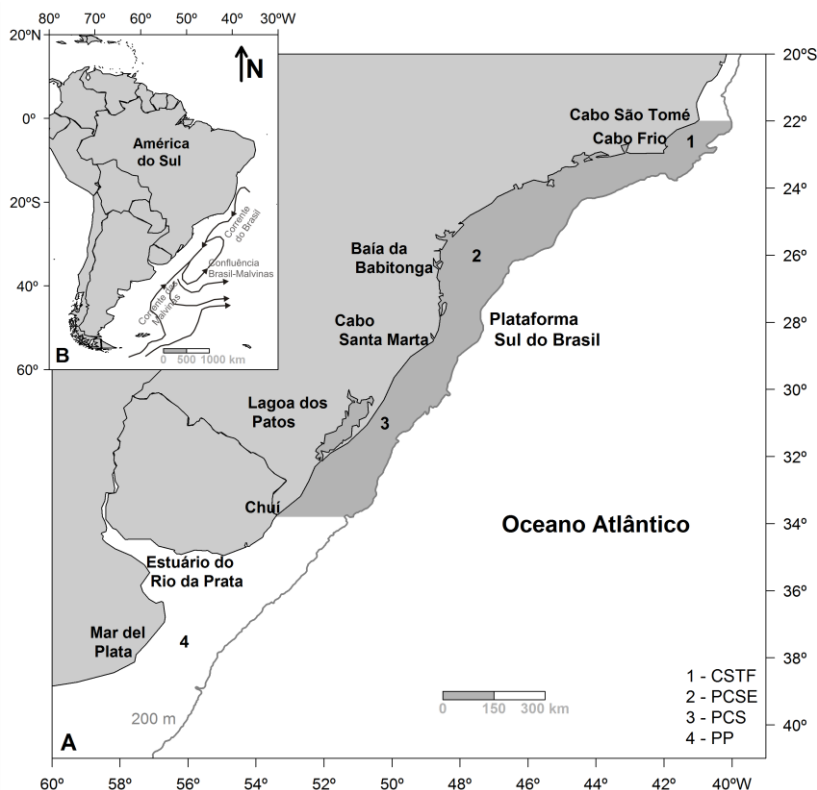
Figura 1. Localização da área de estudo no sudoeste do Oceano Atlântico Sul (A), compreendendo os grandes ecossistemas marinhos da Plataforma Sul do Brasil (sombreado cinza) e a Plataforma Patagônica (branco), no detalhe a circulação das principais correntes (B) segundo Acha et al. (2004). 1 - CSTF, Cabo de São Tomé-Cabo Frio; 2 - PCSE, Plataforma Continental Sudeste; 3 - PCS, Plataforma Continental Sul; 4 - PP, Plataforma Patagônica.

Na plataforma continental Argentina a mistura da Água Subantártica de Plataforma (ASAP) com águas frias e salinas da

Corrente das Malvinas (CM) resulta em uma frente termohalina que se estende por toda a região da quebra da plataforma (Acha et al., 2004). A porção norte está sob a influência da Confluência Brasil-Malvinas (CBM), uma relevante zona de captura de carbono atmosférico devido à alta atividade fotossintetizante estimulada pelas águas de origem subantártica ricas em nutriente (Garcia et al., 2004). A alta concentração de fosfato está associada à ASAP (Braga et al., 2008), enquanto que a principal fonte de nitrato está localizada próximo a quebra da plataforma associada as águas subantárticas trazidas pela CM, atingindo valores maiores do que 10 µM (Carreto et al., 1986). O nitrato originado da bacia do Rio da Prata é consumido no estuário, e por isso torna-se o nutriente limitante para a produção primária nas águas costeiras (Acha et al., 2008). Como uma extensão da CBM, a Frente Subtropical da Plataforma (FSTP) é um sistema frontal termohalino entre a Água Subtropical de Plataforma (ASTP) e a ASAP ao longo da isóbata de 50 m em 33ºS (Piola et al., 2008), que aumenta a disponibilidade de nutrientes na zona eufótica, produção primária e abudância do zooplâncton (Muelbert et al., 2008).

2.2 Base de dados de ictioplâncton

Os dados utilizados foram adquiridos a partir de coletas realizadas em 21 cruzeiros oceanográficos conduzidos entre 1977 e 2010, organizados em um banco de dados compilado para o sudoeste do Oceano Atlântico Sul, com maior concentração das amostragens na Plataforma Continental Sul, entre o Cabo de Santa Marta e o Chuí (Tabela 1). As amostragens e processamento das amostras de ictioplâncton foram realizados pelo Laboratório de Ecologia do Ictioplâncton da Universidade Federal do Rio Grande. No cruzeiro MCT-II o trabalho foi realizado pelo Laboratório de Crustáceos e Plâncton da Universidade Federal de Santa Catarina.

Esta base de dados conta com 335.073 ovos e 111.562 larvas, coletados em 1.527 estações oceanográficas, nas diferentes estações do ano. As estações oceanográficas foram distribuídas em transectos perpendiculares a linha de costa cobrindo toda a extensão da plataforma continental, e o talude em alguns cruzeiros (Figura 2). Nos cruzeiros Conversut, Arepe, Sueste e Ecopel (1-3), a temperatura foi medida em todas as estações na superfície e em profundidades padronizadas, utilizando termômetros invertidos acoplados ao conjunto de garrafas Niskin ou Nansen, enquanto que a salinidade foi medida com um salinômetro KAHLSICO (Grundy 6230N no cruzeiro Sueste) a partir

das amostras de água. Posteriormente, perfis verticais de temperatura e salinidade foram medidos utilizando um perfilador CTD (*conductivity-temperature-depth*) Sensordata no cruzeiro Ecopel 4, Sea Bird Electronics modelo 911 nos cruzeiros La Plata e MCT-II, e Sea Bird Electronics modelo 19 no cruzeiro Pronex. As amostras de ictioplâncton foram realizadas com diferentes tipos de redes de plâncton: Hensen, Bongo, Motoda, MultiNet e WP-2 (detalhes sobre as redes em Calazans et al., 2011). A principal estratégia de amostragem e características das redes para cada cruzeiro são apresentadas na Tabela 1.

Arrastos oblíquos e verticais integrados foram conduzidos nos cruzeiros Conversut 1 e 2, utilizando a mesma rede Hensen, a partir dos 200 m de profundidade (Hubold, 1980a, 1980b). Nos cruzeiros Arepe e Ecopel, arrastos oblíquos com rede Bongo de 300 μm de tamanho de malha e 0,6 m de diâmetro de boca, foram realizados a partir dos 5 m do fundo até a superfície em águas rasas, e a partir dos 200 m de profundidade nas estações profundas (Vasconcellos et al., 1998). Arrastos horizontais superficiais foram realizados nas amostragens do cruzeiro Sueste nas estações rasas (profundidade < 50 m), enquanto que arrastos oblíquos foram conduzidos a partir de 5 m do fundo até a superfície em profundidades intermediárias (> 50 m e < 200 m), e a partir de 200 m de profundidade nas estações profundas. MultiNets foram equipadas com duas redes de 200 μm e três redes de 330 μm de tamanho de malha no cruzeiro Pronex. As redes foram descidas até a máxima profundidade de amostragem com a primeira rede de 330 μm aberta realizando um arrasto oblíquo. Na sequência, a MultiNet foi arrastada de volta a superfície conduzindo arrastos horizontais estratificados em quatro diferentes intervalos de profundidade. O ictioplâncton foi selecionado das amostras coletadas com a rede de 330 μm (Torquato & Muelbert, 2014). Arrastos verticais integrados foram realizados no cruzeiro MCT-II com rede WP-2 entre a superfície e 10 m do fundo nas estações com águas rasas (até 20 m) ou com a coluna de água homogênea, e a partir da profundidade do pico de fluorescência até a superfície nas estações profundas (Macedo-Soares et al., 2014).

Tabela 1. Informações sobre os cruzeiros realizados no sudoeste do Oceano Atlântico Sul, região compreendida entre 21ºS a 41ºS, durante o período de 1977 a 2010.

Cruzeiro	Ano/Estação do ano	Intervalo de latitude	Número total de estações	Estações c/ coleta plâncton	Nº total de ovos coletados	Nº total de larvas coletadas	Principal estratégia de coleta (arrasto)	Malha e diâmetro da rede
Conversut 1	1977/pri	25°12'S a 40°34'S	200	196	40.214	24.164	oblíquo	250/0,8
Conversut 2	1978/out	28°00'S a 40°34'S	179	172	9.201	17.746	oblíquo	250/0,8
Conversut 3	1981/ver	29°22'S a 40°34'S	137	105	7.630	4.674	oblíquo	250/0,8
Arepe 1	1980/out	28°36'S a 34°40'S	102	102	2.163	5.338	oblíquo	300/0,6
Arepe 2	1980/inv	28°36'S a 34°40'S	86	86	16.541	2.910	oblíquo	300/0,6
Arepe 3	1980/pri	28°36'S a 34°40'S	90	90	92.094	4.147	oblíquo	300/0,6
Arepe 4	1981/pri	32°07'S a 34°40'S	62	62	28.198	7.503	oblíquo	300/0,6
Arepe 5	1982/pri	28°36'S a 34°40'S	108	102	59.120	6.693	oblíquo	300/0,6
Sueste 1	1982/inv	24°06'S a 29°36'S	91	91	10.181	7.051	oblíquo	300/0,6
Sueste 2	1983/out	25°45'S a 27°55'S	91	45	3.533	1.244	oblíquo	300/0,6
Sueste 3	1984/ver	24°26'S a 28°38'S	92	47	4.318	3.352	oblíquo	300/0,6
Sueste 4	1985/pri	24°06'S a 27°37'S	90	18	2.316	1.146	oblíquo	300/0,6
Ecopel 1	1987/pri	28°39'S a 34°39'S	57	53	18.083	3.291	oblíquo	300/0,6
Ecopel 2	1988/inv	31°52'S a 34°39'S	50	50	33.582	11.759	oblíquo	300/0,6
Ecopel 3	1990/ver	31°52'S a 34°39'S	51	51	2.258	2.365	oblíquo	300/0,6
Ecopel 4	1991/out	31°52'S a 34°39'S	54	39	739	1.963	oblíquo	300/0,6
La Plata 1	2003/inv	27°01'S a 39°18'S	83	30	900	2.607	vertical	300/0,6
La Plata 2	2004/ver	27°01'S a 39°18'S	102	34	219	280	vertical	300/0,6
Pronex 1	2005/inv	28°23'S a 34°09'S	33	32	1.225	1.209	oblíquo	330/0,25[*]
Pronex 2	2007/ver	28°23'S a 34°09'S	33	33	628	673	oblíquo	330/0,25[*]
MCT-II	2010/pri	21°36'S a 34°51'S	113	89	1.930	1.447	vertical	200/0,5

Malha da rede de plâncton em μm e diâmetro da boca da rede em m, [*] área da boca da rede MultiNet em m².
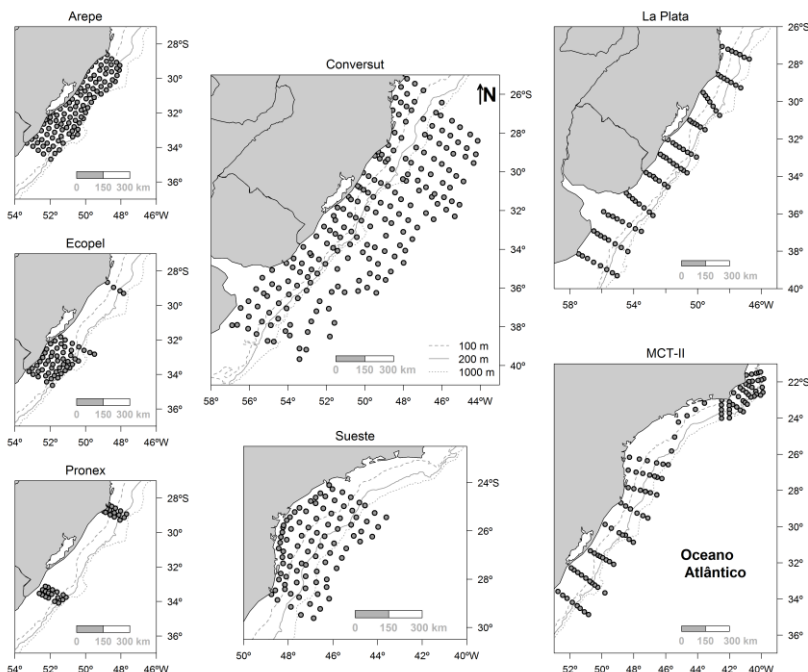
Figura 2. Disposição das estações oceanográficas para cada conjunto de cruzeiros (nome indicado na parte superior) realizados no sudoeste do Oceano Atlântico Sul, região compreendida entre 21ºS a 41ºS, durante o período de 1977 a 2010.

Foram aplicadas três estratégias de amostragem no cruzeiro La Plata. Arrastos verticais integrados foram conduzidos nas estações localizadas próximas as isóbatas de 50 m e 200 m com uma rede Motoda com 300 μm de malha e 0,6 m de diâmetro. Durante o cruzeiro La Plata 2, uma rede WP-2 com 140 μm de malha (danificada e substituída por uma malha de 500 μm posteriormente) e 0,6 m de diâmetro foi utilizada nos arrastos verticais integrados. A segunda estratégia consistiu em arrastos verticais estratificados em duas profundidades utilizando uma rede WP-2 acoplada com um mecanismo de fechamento. Os arrastos foram realizados nas estações próximas a isóbata de 100 m. Esta rede foi substituída posteriormente durante o cruzeiro La Plata 2 por uma rede cônica com 200 μm de malha e 0,6 m de diâmetro. A última estratégia foi conduzida no transecto do Albardão (entre 33ºS e 34ºS) utilizando a rede Motoda, arrastada horizontalmente em duas profundidades, por 10 minutos. Todas as amostras

estratificadas foram tomadas abaixo e acima da haloclina. Foram obtidas duas subamostras com um subamostrador de Folson e compartilhadas entre a Universidade Federal do Rio Grande (FURG) e Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP). Os dados compilados no banco de dados são resultantes das análises das subamostras da FURG.

As amostras foram fixadas e preservadas em uma solução de água do mar com 4% de formaldeído. Ovos e larvas foram separados, contados e identificados sob esteriomicroscópio até o menor nível taxonômico possível utilizando as cataterísticas morfológicas e merísticas dos estágios de desenvolvimento descritos por Ahlstrom & Moser (1980), Fahay (1983), Olivar & Fortuño (1991), Moser (1996), Olivar & Beckley (1995), Olivar et al. (1999), Richards (2005), Bonecker & Castro (2006). Literatura adicional foi utilizada: Ciechomski (1965), Matsuura (1975), Olney & Grant (1976), Moser et al. (1984), Matsuura & Suzuki (1997), Olivar & Beckley (1997), Sassa et al. (2003), e Derisio et al. (2012). A classificação taxonômica seguiu Nelson (2006).

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3 CAPÍTULO 1 – Large-Scale Ichthyoplankton and Water Mass Distribution along the South Brazil Shelf

Large-Scale Ichthyoplankton and Water Mass Distribution along the South Brazil Shelf

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Abstract

Ichthyoplankton is an essential component of pelagic ecosystems, and environmental factors play an important role in determining its distribution. We have investigated simultaneous latitudinal and cross-shelf gradients in ichthyoplankton abundance to test the hypothesis that the large-scale distribution of fish larvae in the South Brazil Shelf is associated with water mass composition. Vertical plankton tows were collected between 21º27' and 34º51'S at 107 stations, in austral late spring and early summer seasons. Samples were taken with a conical-cylindrical plankton net from the depth of chlorophyll maxima to the surface in deep stations, or from 10 m from the bottom to the surface in shallow waters. Salinity and temperature were obtained with a CTD/rosette system, which provided seawater for chlorophyll-a and nutrient concentrations. The influence of water mass on larval fish species was studied using Indicator Species Analysis, whereas environmental effects on the distribution of larval fish species were analyzed by Distance-based Redundancy Analysis. Larval fish species were associated with specific water masses: in the north, *Sardinella brasiliensis* was found in Shelf Water; whereas in the south, *Engraulis anchoita* inhabited the Plata Plume Water. At the slope, Tropical Water was characterized by the bristlemouth *Cyclothone acclinidens*. The concurrent analysis showed the importance of both cross-shelf and latitudinal gradients on the large-scale distribution of larval fish species. Our findings reveal that ichthyoplankton composition and large-scale

spatial distribution are determined by water mass composition in both latitudinal and cross-shelf gradients.

Introduction

Ichthyoplankton distribution is under the influence of environmental factors that regulate life history traits and determine its geographical range [1–3]. At large-scales, latitudinal gradients influence species diversity and composition in the marine realm (e.g., [4–6]) and most studies relate latitudinal influences directly with sea surface temperature (e.g., [4,7]). In addition, latitudinal influences are also associated with oceanographic features such as water mass distribution (e.g., [8,9]). Latitudinal influence is important in determining large-scale distribution, since fish larvae are dependent on temperature as well as long photoperiods for their development [7]. A latitudinal gradient is reported to be related to differences in larval assemblage composition in the North Pacific Ocean [10], to variability in egg size and newly hatched larval length of the anchovy *Engraulis ringens* in the Chilean coast [11], and to influence the growth rate and spawning season of the sea bass *Dicentrarchus labrax* in estuaries in Portugal [7].

It is known that larval fish assemblages result from adult spawning strategies and environmental influences [12,3]. In the continental shelf and slope, ichthyoplankton species composition is strongly influenced by ocean currents and water masses [8,13,14]. Closer to the coast, continental runoff and coastal wind-induced upwelling play an important role in ichthyoplankton species composition [15,13]. Therefore, the study of cross-shelf gradients in larval fish assemblages might help to understand the factors that influence larval species distribution and abundance.

The South Brazil Shelf (SBS), in the Southwest Atlantic Ocean (SWAO), is a region associated with the largest Brazilian fish stocks [15,16], due to several coastal water enrichment processes. Continental runoff from La Plata estuary and Patos Lagoon [17–19] and both coastal and along shelf break upwelling [17,20,15] of the South Atlantic Central Water (SACW) are the main processes that influence nutrient availability in the euphotic zone [21]. In the Cape Frio and Cape Santa Marta region, coastal upwelling results in short duration and low intensity blooms, which increase phytoplankton and zooplankton

biomass in this tropical region [17]. Submarine groundwater discharge might also provide an important flux of nutrients to the coastal waters due to the permeable sediments in the barriers of coastal lagoons along the southern Brazilian coast [22,23]. These processes result in an increase in biological production that supports fisheries in this tropical/subtropical continental shelf.

Ichthyoplankton has been studied in the region over 30 years [24], focusing on larval recruitment of species of interest to fisheries (e.g., [25,15]), the relationship between the distribution and composition of fish larvae and physical-chemical factors [8,26], interactions between ichthyoplankton and zooplankton biovolume [27], and larval fish assemblages across a cross-shelf gradient [13,28]. The patterns found are the result of adult distribution and reproductive strategies, water mass distribution, and zooplankton distribution, i.e., food availability [8,13,14]. Although cross-shelf gradients in larval fish assemblages have been studied in different oceans (e.g., [28,14,29,30]), most experimental designs do not allow for concurrent cross-shelf and latitudinal gradient analysis. Therefore, the aim of this study was to investigate latitudinal and cross-shelf gradients in ichthyoplankton abundance to test the hypothesis that the large-scale distribution of fish larvae in the South Brazil Shelf is associated with water mass composition.

Materials and methods

Study area

The South Brazil Shelf (SBS), located at the Southwest Atlantic Ocean (SWAO) stretches from Cape São Tomé (21ºS) to Chuí (33ºS). The shelf waters of the SBS can be divided into three major latitudinal regions according to their oceanographic characteristics, from north to south: the Cape São Tomé-Cape Frio region (CSTF), the Southern Brazilian Bight (SBB) and the Southern Subtropical Shelf (SSS) (Figure 3.1A). Along the entire slope, warm and salty oligotrophic Tropical Water (TW) is transported southwards by the Brazil Current (BC) in the upper layer of the water column down to 200 m depth, whereas cold and nutrient-rich South Atlantic Central Water (SACW) occupies depths between 200 and 500 m [13,31].

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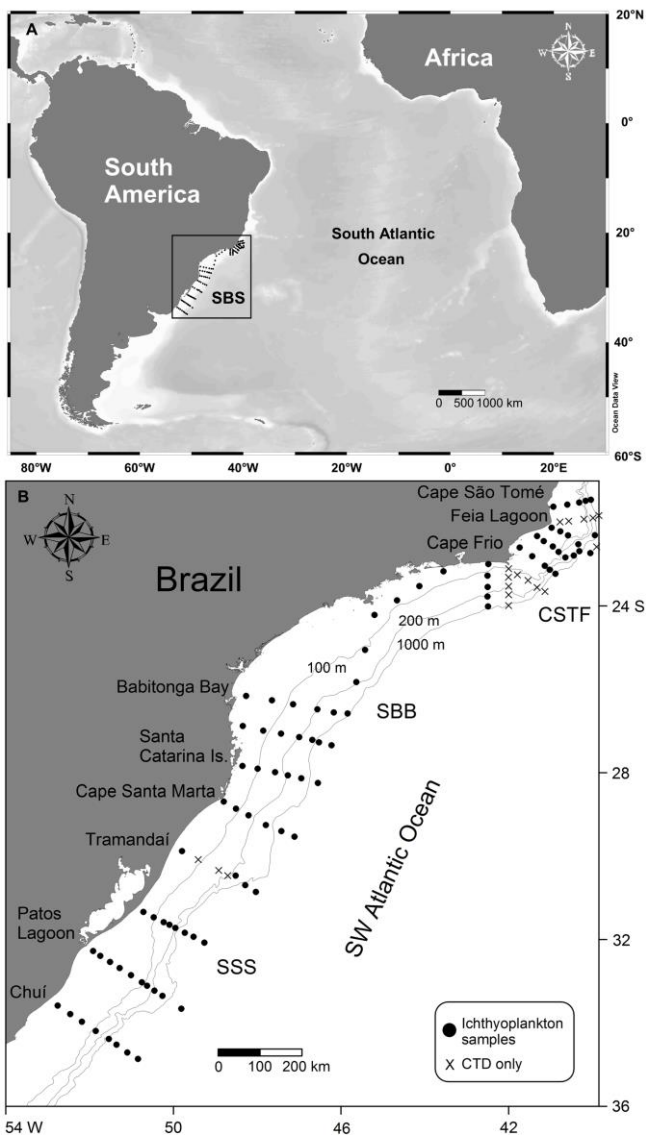
Figure 3.1. Map of the study region. A: Location of the study region on the South Atlantic Ocean (SBS, South Brazil Shelf inside the black square); B: Distribution of sampled stations in the South Brazil Shelf from Cape São Tomé (21ºS) to Chuí (33ºS) during the period of the cruise. CSTF, Cape São Tomé-Cape Frio region; SBB, Southern Brazilian Bight; SSS, Southern Subtropical Shelf.

Coastal upwelling due to wind and topographic effects, occurs in the northern portion of the study area (CSTF) [32,33], especially during austral spring and summer, due to prevalent northeasterly winds. The cold and nutrient-rich SACW is upwelled and provides special conditions for high primary production levels along the coastline. The region is also characterized by intense mesoscale activity [20] due to the proximity of the BC to the coast. The possibility of background eddy-induced upwelling is also suggested to exist, as the southward-flowing BC and its quasi-stationary unstable meanders approach the coast in the vicinity of Cape São Tomé [34]. The continental shelf is characterized by Shelf Water (SW) that results from the mixing of continental runoff with shelf waters influenced by the BC.

The Southern Brazilian Bight (SBB) is located between Cape Frio (22º52'S) and Cape Santa Marta (28º36'S), and is characterized by the presence of SW in its northern portion, and by Subtropical Shelf Water (STSW) in its southern area. The STSW is the result from a mixture of Plata Plume Waters (PPW) and TW, and spreads throughout the neritic region of the SBB and SSS [19]. In the SBB region, SACW contributes to high nitrate concentration mainly near Cape Frio and Cape Santa Marta [21,35]. The SBB is also a biogeographic limit for the occurrence of reef fishes, since it is a transition area between tropical and temperate fauna [36]. Between Cape Santa Marta and the La Plata estuary (~35ºS), the SSS is characterized by the northwards spreading of the relatively cold and fresh Plata Plume Water (PPW). This transport is most intense during austral winter [19], when Subantarctic Shelf Water (SASW) is also transported northwards by the Patagonian Current (PC), which results in a wedge of cold water between PPW and STSW [19,37]. A high silicate and phosphate concentration was associated with the terrestrial input from PPW and austral waters from SASW [21]. A sharp thermohaline frontal system exists between STSW and SASW around 33ºS, named the Subtropical Shelf Front (STSF) [37], which increases local nutrient availability in the euphotic zone, primary production and zooplankton abundance [26].

Data sampling and processing

Cruises were carried out between 21º27'S and 34º51'S during late austral spring (December 2010) and early austral summer (January 2011). Temperature, salinity, fluorescence and oxygen were measured vertically with a conductivity-temperature-depth (CTD) profiler Sea Bird Electronics model 911 at 107 stations distributed at 17 cross-shelf

transects (Figure 3.1B). Additionally, water samples were collected with 5-L Niskin bottles to determine nutrients (ammonium, nitrite, nitrate, phosphate and silicate) and chlorophyll-a (chl-a) at selected depths (at 3 m or 5 m, the chlorophyll maximum depth and at the base of the mixture layer). Nutrients were determined using the methods described by Grasshoff et al. [38] and Strickland and Parsons [39], and chl-a according to Welschmeyer [40]. Vertical plankton tows were taken from the chlorophyll maximum depth to the surface at deep stations, and from 10 m from the bottom to the surface at homogeneous and shallow water stations (up to 20 m). Zooplankton samples were taken using a conical-cylindrical plankton net with a 200 μm mesh and 0.5 m mouth diameter, equipped with a digital flowmeter (General Oceanics) and towed behind the ship. The depth of the deep chlorophyll maximum ranged from 7 to 125 m and the depth of plankton samples ranged from 12 to 130 m. The mean ($\pm$ SE) volume of water filtered by the net of all samples was 29.4 $\pm$ 2.3 m^3 and the values for each sample are displayed in Table S3.1. All necessary permits for the described field study were issued by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/MMA), permit #13509-1 to ASF. All locations were not privately-owned or protected in any way, and the field study did not involve endangered or protected species.

Plankton samples (89, black circles in Figure 3.1B) were fixed and preserved in 4% buffered seawater-formaldehyde solution, since they are fragile and easily damaged and should be preserved immediately [41]. Ichthyoplankton was sorted and counted from the whole sample under a stereomicroscope. Fish eggs and larvae were identified to the lowest possible taxonomic level according to morphometric and meristic characteristics, using the larval development stages described by Ahlstrom and Moser [42], Bonecker and Castro [43], Fahay [44], Moser [45], Olivar and Beckley [46], Olivar and Fortuño [47], Olivar et al. [48] and Richards [49]. Additional literature was also used: Ciechomski [50], Derisio et al. [51], Matsuura [52], Matsuura and Suzuki [53], Moser et al. [54], Olivar and Beckley [55], Olney and Grant [56], and Sassa et al. [57]. Taxonomic classification was according to Nelson [58].

Sea surface temperature (SST) images were used to evaluate ichthyoplankton distribution in relation to surface thermal mesoscale features in the Brazilian shelf and slope waters, such as meanders, eddies and upwelling. We used monthly SST composition images for December 2010 and January 2011 with a 4 km spatial resolution from the Moderate Resolution Imaging Spectroradiometer (MODIS)/Aqua

sensor. These images were obtained from the Ocean Color web site (http://oceancolor.gsfc.nasa.gov).

Data analysis

Ichthyoplankton abundance was standardized to the number of individuals per 100 m^3 filtered water. To select the most important species, a combination between the frequency of occurrence and relative abundance was obtained by multiplying these two values. The fish larvae species composition across the shelf was evaluated using samples classified according to a coast, inner shelf, outer shelf, inner slope or outer slope position. Between Cape São Tomé and Cape Frio, due to the narrow continental shelf, samples were classified as shelf. Chl-a and nutrients used in the analyses were integrated, whereas temperature and salinity were expressed as the mean value in the water column, from the depth of chl-a maxima to the surface (10 m depth). Oxygen stratification was used to characterize the relationship between ichthyoplankton abundance and oxygen distribution in the water column. This was calculated using the surface oxygen value and the value for the bottom of the oxycline, and respective depths.

Samples were also classified as being located within specific water masses (PPW, STSW, SW and TW) [19,37] by their surface (10 m depth) temperature and salinity, since the majority of the samples were collected within these water mass depth ranges. South Atlantic Central Water was not used because its presence was not detected at the surface (10 m depth) in the region during the study. In addition, the physical control of ichthyoplankton species distribution was identified using Indicator Species Analysis (ISA) [59], according to groups formed by water mass classification. Multivariate Analysis of Variance with permutations (PERMANOVA) confirmed the validity of these groups formed a priori [60], using the Bray-Curtis index for similarity between samples. Species abundances were fourth-root transformed to reduce the weight of abundant species [61]. Prior to the analysis, the assumption of independence and homogeneity of multivariate dispersions within groups was tested using the PERMDISP routine. Once this assumption was confirmed (F = 2.527, p(perm) = 0.115), a one-way PERMANOVA design was used and whenever significant differences between groups were detected via PERMANOVA, they were tested using a pairwise test for comparisons among all pairs of groups [62]. PERMANOVA and additional tests were performed in PRIMER 6 with the PERMANOVA+ package [62,63].

Distance-based Redundancy Analysis (db-RDA) was used to investigate the variability in ichthyoplankton composition constrained by centered environmental explanatory variables (latitude, distance from shore, temperature, salinity, oxygen stratification, ammonium, nitrite, nitrate, phosphate, silicate and chl-a), using the Bray-Curtis index for similarity between samples [64]. Prior to the analysis, ichthyoplankton abundance was Hellinger-transformed [65] to reduce the wide disparity in magnitude between species abundances. Only taxa that occurred in more than 4% of the samples were considered. The Cailliez correction was applied to the db-RDA function to avoid negative eigenvalues. The Variance Inflation Factor (VIF) was used to test and remove (VIF > 20) collinearity between explanatory variables [66]. All explanatory variables were kept in the analysis according to the VIF. A Monte Carlo permutation test was used to test the null hypothesis of independence among species data and explanatory variables, and the significance of each canonical axis. Triplot was displayed using scaling = 2 and sample scores were plotted using the weighted sums of species scores [66]. Samples were also displayed according to specific water masses, using the same classification as Indicator Species Analysis. Distance-based Redundancy Analysis and additional tests were performed in R [67] with the Vegan and HH packages [68,69].

Results

Oceanographic conditions

Six water masses were identified in the study area down to the maximum zooplankton sampling depth (130 m): Subtropical Shelf Water (STSW), Shelf Water (SW), Tropical Water (TW), Plata Plume Water (PPW), Subantarctic Shelf Water (SASW) and South Atlantic Central Water (SACW) (Figure 3.2). Among these, three water masses were present in the shelf area (SW, STSW and PPW), except at stations near the coast in the Cape Frio-Cape São Tomé and Cape Santa Marta regions, where SACW was also found closer to the surface, and at stations located in the southern part of the study area (Chuí), where SASW was also present. At the slope, TW occupies the surface layer in the water column, whereas SACW is present at depths between 100 m and 500 m.
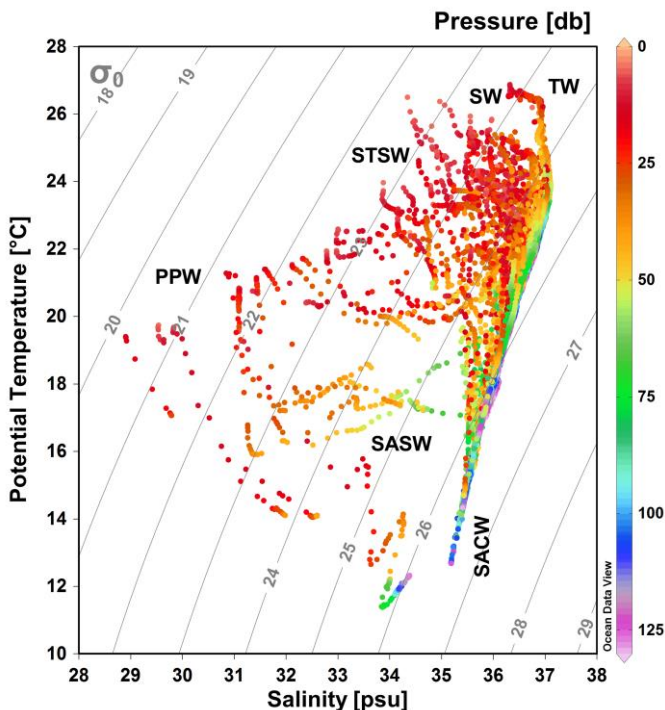
Figure 3.2. Temperature-salinity diagram from Cape São Tomé to Chuí for late austral spring and summer seasons. The water masses are as follows: Plata Plume Water (PPW), Subtropical Shelf Water (STSW), Shelf Water (SW), Tropical Water (TW), Subantarctic Shelf Water (SASW) and South Atlantic Central Water (SACW). Only stations to 130 m depth (maximum zooplankton sampling depth) are displayed.

Over the shelf, a latitudinal pattern in the distribution of the water masses can be observed (Figure 3.3). Cold and fresh PPW spreads from Chuí to Tramandaí (~ 30ºS), mainly at 10 m depth. Due to its low density, PPW does not reach depths under 50 m, where it is replaced at its southern limit by SASW and at the northern limit by STSW. The area between Cape São Tomé and Cape Frio was occupied by warmer and salty SW, whereas STSW was the dominant water mass at the surface between Babitonga Bay and Tramandaí (25ºS to 30ºS). Salty-warm TW was present in the whole slope area from the surface to a depth of 100 m. Intrusion of SACW was evident from Cape São Tomé (21ºS) to Cape Santa Marta (28ºS) at 50 m and 100 m depth, reaching lower depths (~20–30 m) in the vicinity of Cape Frio and Cape Santa Marta.
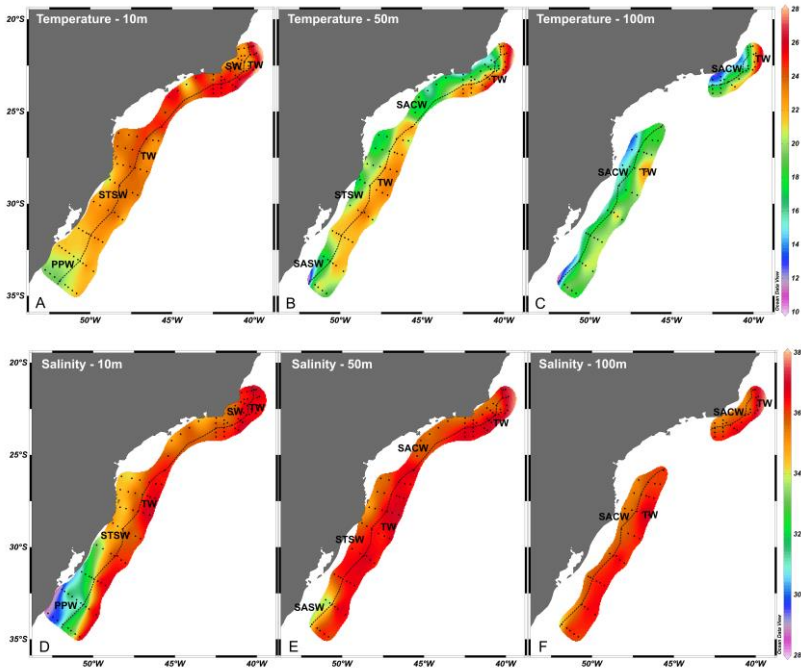
Figure 3.3. Temperarure and salinity horizontal distribution from Cape São Tomé to Chuí. A–C: Temperature at 10 m depth (A), 50 m depth (B) and 100 m depth (C); D–F: Salinity at 10 m depth (D), 50 m depth (E) and 100 m depth (F). The dashed black line represents approximately the shelf break position (~ 200 m depth).

Ichthyoplankton composition and distribution

A total of 1,447 fish larvae and 1,930 fish eggs were caught during the cruise. Larval identification resulted in 115 taxa that belonged to 40 families (Table S3.2), and 52 of these taxa were caught in only one sample. Ninety-six taxa were representative of an individual species. Identification occurred at the species level for 58 of these 96 taxa, and 38 were identified to the family or genus level (e.g., Bythitidae sp. and *Auxis* sp.). The 19 remaining taxa might be members of two or more species (e.g., Macrouridae spp.). The most specious family in the samples was Myctophidae (21), followed by Serranidae (5), Paralepididae (4), Scorpaenidae (4), Carangidae (4), Sciaenidae (4) and Scombridae (4) (Table S3.2). Fish egg identification resulted in three taxa. Engraulidae eggs were the most abundant and represented 21% of

the total eggs caught. However, 75% off eggs remained unidentified (Table S3.2).

Fish egg distribution showed spawning activity in the whole area, mostly at coastal and shelf stations (Figure 3.4A). Peaks in fish egg abundance were found in front of Patos Lagoon (4,116 ind. 100 m^{-3}), on the coast of Tramandaí (631 ind. 100 m^{-3}) and on Cape Frio (1,174 ind. 100 m^{-3}) and Cape São Tomé (1,184 ind. 100 m^{-3}) shelves. The abundance of Engraulidae eggs was higher near Patos Lagoon (1,403 ind. 100 m^{-3}) and Anguilliformes eggs showed a low abundance and were mostly present in the SBB area. The abundance of *Maurolicus muelleri* eggs peaked at the slope near to the Feia lagoon area (374 ind. 100 m^{-3}) and occurred along the slope in the southerly direction (Figure 3.4B).

Fish larvae abundance was higher at SSS (Figure 3.5), mainly near Chuí (168 to 445 ind. 100 m^{-3}) and the Patos Lagoon area (119 to 479 ind. 100 m^{-3}), the slope near Feia Lagoon (215 ind. 100 m^{-3}) and the shelf at Cape Frio (131 to 246 ind. 100 m^{-3}). Low abundances were observed mostly at the slope, nevertheless, two peaks of high abundance were registered in the northern area at stations 83 and 91 (Figure 3.5). In station 91, situated on the outer shelf (103 ind. 100 m^{-3}), there was a mixture of yolk sac larvae (29%), larvae of Scorpaenidae sp. 1 (14%) and larvae of pelagic fishes such as Myctophidae (29%), Phosichthyidae (14%) and Paralepididae (7%). Station 83, located at the slope (215 ind. 100 m^{-3}), the same stations where *M. muelleri* eggs peaked (Figure 3.4B), mainly contained yolk sac larvae (204 ind. 100 m^{-3}). The SST image showed the formation of BC meanders at the boundary between TW at the slope and SW over the continental shelf in the northern area (Figure 3.5), and this is coincident with the position of stations 83 and 91 in the area.

Engraulidae larvae were the most abundant (35%) followed by those of Myctophidae (24%), Clupeidae (9%), Bregmacerotidae (3%), Scombridae (3%) and Gobiidae (3%). The highest abundance was for the anchovy *Engraulis anchoita* at 17.3 ± 7.1 ind. 100 m^{-3} and occurred in 18% of all samples. The second most abundant was the lanternfish *Diaphus brachycephalus* (6.3 ± 2.5 ind. 100 m^{-3}) with a 22% frequency of occurrence, followed by the Brazilian sardine *Sardinella brasiliensis* (4.7 ± 2.9 ind. 100 m^{-3}). Some species had a low abundance but were frequently found in samples, for example, larvae of the pelagic fishes such as the lanternfishes *Diaphus mollis* (26%) and *Ceratoscopelus townsendi* (13%); the bristlemouth *Cyclothone acclinidens* (16%); the codlet *Bregmaceros cantori* (10%); and others from coastal origins such

as the lizardfish *Synodus foetens* (10%) and the largehead hairtail *Trichiurus lepturus* (10%) (Table S3.2).
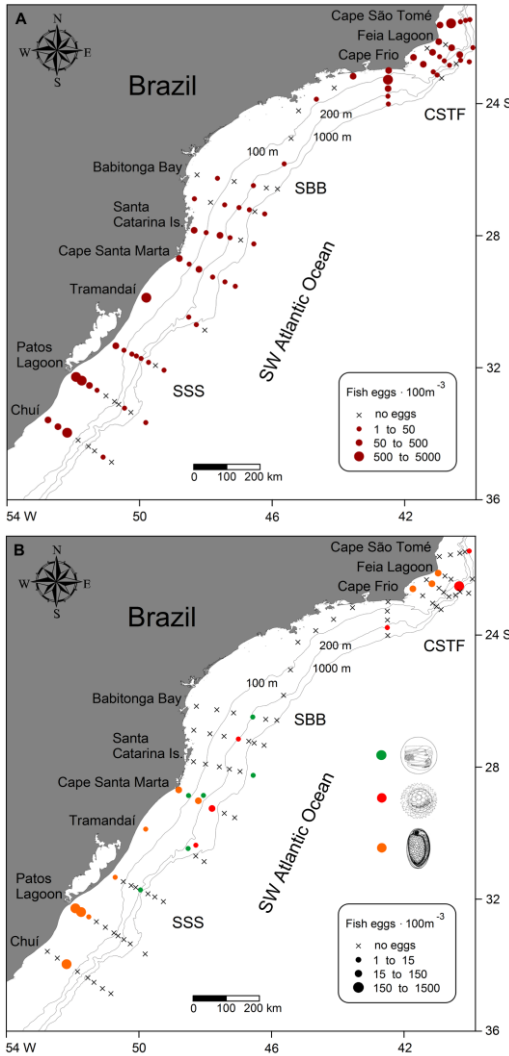
Figure 3.4. Fish egg abundance distribution at the South Brazil Shelf. A: Distribution of total fish egg abundance; B: Distribution of Anguilliformes eggs (green circles), Maurolicus muelleri eggs (red circles) and Engraulidae eggs (orange circles) abundances. CSTF, Cape São Tomé-Cape Frio region; SBB, Southern Brazilian Bight; SSS, Southern Subtropical Shelf.
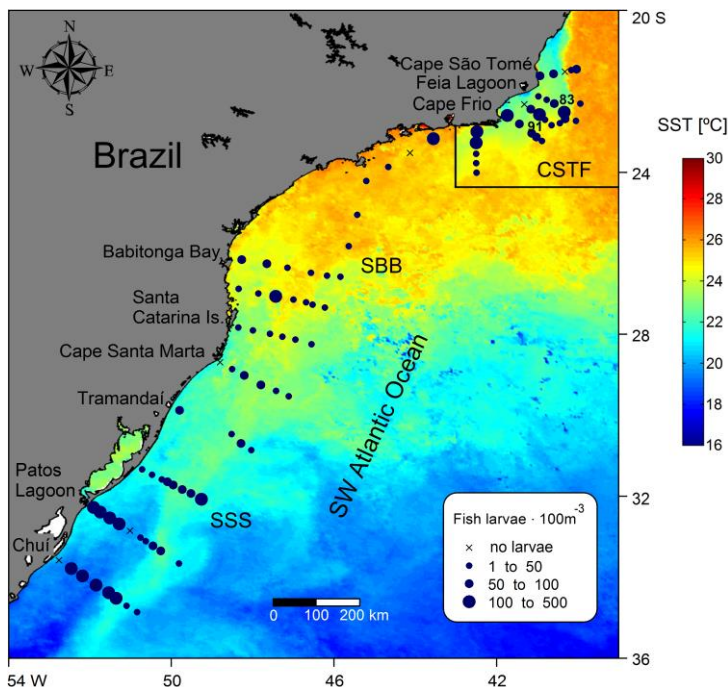
Figure 3.5. Fish larvae abundance distribution at the South Brazil Shelf.
Fish larvae abundance (blue circles) superimposed onto a SST satellite image
monthly composition, from December 2010. Inside the square, the monthly SST
image from January 2011 is shown. CSTF, Cape São Tomé-Cape Frio region;
SBB, Southern Brazilian Bight; SSS, Southern Subtropical Shelf.

A turnover was observed in both dominant species according to
the latitude in the shelf and in species composition according to a cross-
shelf direction (Figure 3.6, 3.7). At high latitudes and over the shelf *E.
anchoita* was the dominant species. Between 25ºS and 30ºS, anchovy
shared dominance with *T. lepturus*, *S. foetens* and *B. cantori* in the coast
and inner shelf. *Trichiurus lepturus* and *S. foetens* also occurred
between Cape São Tomé and Cape Frio, but *S. brasiliensis* and the goby
Ctenogobius boleosoma were the most abundant species on the shelf
(Figure 3.6). Larvae of pelagic species such as the tuna *Euthynnus
alletteratus* and the lanternfishes *D. mollis* and *C. townsendi* occurred
on the outer shelf and inner slope area at all latitudes (Figure 3.6, 3.7).
At the slope, *E. alletteratus* remained abundant between Cape São Tomé
and Cape Frio, and the lanternfishes including *D. brachycephalus*,

together along with the bristlemouth *C. acclinidens*, dominated the slope area between 26ºS and 35ºS (Figure 3.7).
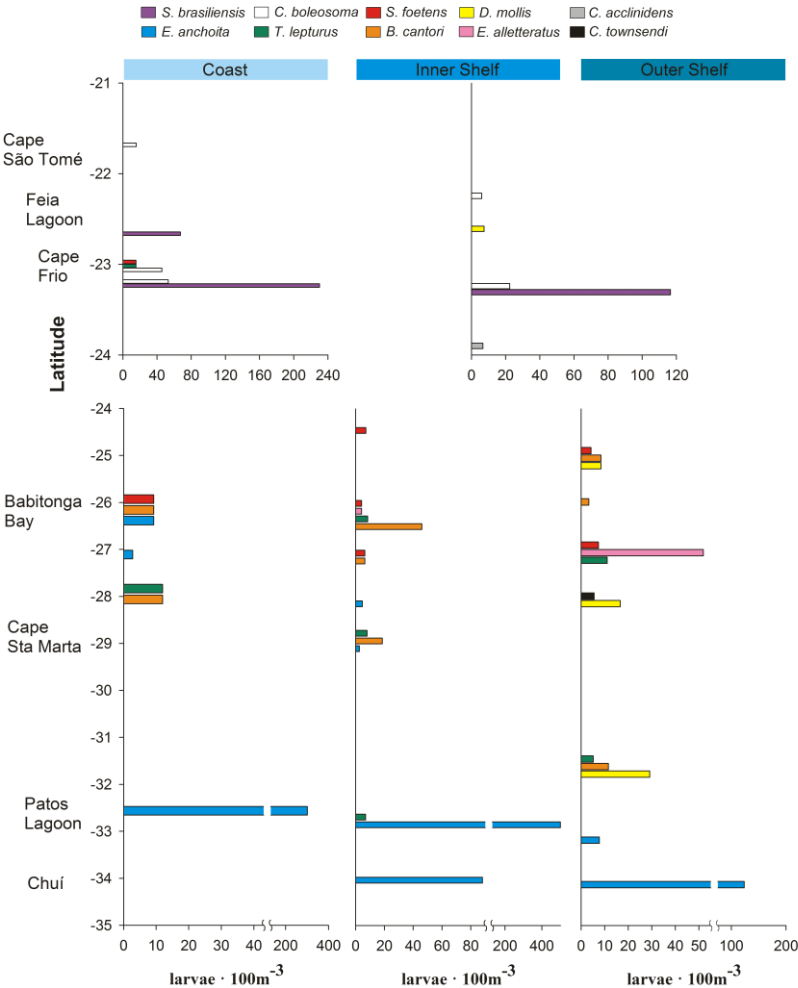
Figure 3.6. Latitudinal and cross-shelf distribution of ichthyoplankton composition at the shelf of the South Brazil Shelf. Fish larvae composition of the 10 most important species according to the combination of relative abundance and frequency are shown for the coast and the inner and outer shelf. Stations between 21ºS and 24ºS latitude were classified only as shelf because of the narrow continental shelf. Note the difference of scales on the X axes. Full species names are given in Table S3.2.
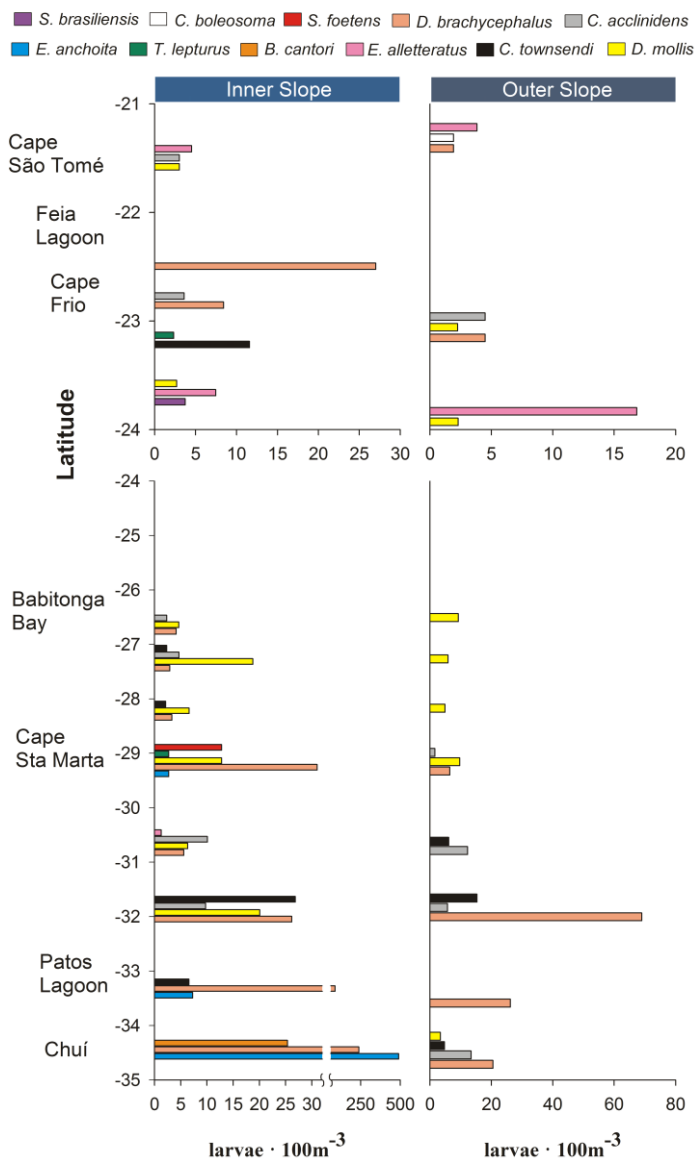
Figure 3.7. Latitudinal and cross-shelf distribution of ichthyoplankton composition at the slope of the South Brazil Shelf. Fish larvae composition of the 11 most important species according to the combination of relative abundance and frequency are shown for the inner and outer slope. Note the difference of scales on the X axes. Full species names are given in Table S3.2.

Fish larvae assemblages and water masses

According to Indicator Species Analysis (ISA), the group formed by SW samples was characterized by larvae of the Brazilian sardine *S. brasilliensis*, the goby *C. boleosoma*, and the blenny *Parablennius* sp., which resulted in an assemblage with a mix of reef-associated/benthic species (blennies and gobies) and pelagic species (sardines), considering adult habitat (Table 3.1). In the STSW group, the larvae of two fishes of coastal provenance; the largehead hairtail *T. lepturus* and the lizardfish *S. foetens*, and larvae of the codlet *B. cantori* were the indicator species. Furthermore, larvae of the anchovy *E. anchoita* and Engraulidae eggs characterized the group from the PPW. The TW group was characterized by the bristlemouth *C. acclinidens*. All groups formed by the four water masses are valid according to PERMANOVA (Pseudo-F = 4.095, p(perm) = 0.0001, Residual d.f. = 77), when all mean similarities within groups were higher than similarities between groups (Table 3.2).

Table 3.1. Results of indicator species analysis (ISA), indicating groups according to the water mass in which the sample was collected in the South Brazil Shelf.

Indicator species	Indicator value (%)	Monte Carlo p value[1]	Water mass[2]
Sardinella brasiliensis	23.5	0.007	SW
Ctenogobius boleosoma	29.2	0.004	SW
Parablennius sp.	11.8	0.040	SW
Bregmaceros cantori	35.7	0.002	STSW
Trichiurus lepturus	32.0	0.002	STSW
Synodus foetens	30.5	0.002	STSW
Engraulis anchoita	56.5	0.001	PPW
Engraulidae eggs	27.9	0.017	PPW
Cyclothone acclinidens	27.6	0.011	TW

[1]Only species with significant results ($p < 0.05$) according to the Monte Carlo test are shown.
[2]Water masses: SW, Shelf Water; STSW, Subtropical Shelf Water; PPW, Plata Plume Water; TW, Tropical Water.

Table 3.2. Results of PERMANOVA pairwise tests indicating differences between groups formed by water mass classification in the South Brazil Shelf.

PERMANOVA pairwise tests		
Groups[1]	Similarity[2]	P(perm)
SW-STSW	4.813	0.0009
SW-PPW	3.645	0.0001
SW-TW	4.012	0.0001
STSW-PPW	10.987	0.0116
STSW-TW	4.399	0.0001
PPW-TW	4.744	0.0001

[1]Water masses: SW, Shelf Water; STSW, Subtropical Shelf Water; PPW, Plata Plume Water; TW, Tropical Water.
[2]Similarity between groups. Similarity within groups: SW = 4.935, STSW = 15.978, PPW = 15.472, TW = 14.990.

Environmental effects on the distribution of larval fish assemblages

Distance-based Redundancy analysis (db-RDA) constrained 24% of ichthyoplankton variance in relation to the explanatory variables (Figure 3.8). The Monte Carlo permutation test was significant for all canonical axes together (F = 1.926, p = 0.001) and rejected the null hypothesis of independency between ichthyoplankton and environmental variables. In addition, the first and second canonical axes were significant and accounted together for 61.7% of the constrained variance. The first axis (db-RDA 1, F = 7.808, p = 0.001), accounted for 36.9% of the variance, represented the cross-shelf gradient, and was positively correlated with distance from shore (0.784) and salinity (0.459); and was negatively correlated with chl-a (-0.511). However, the second axis (db-RDA 2, F = 5.264, p = 0.001), which accounted for 24.8%, represented the latitudinal gradient (Figure 3.8), was positively correlated with salinity (0.716) and temperature (0.669); and was negatively correlated with latitude (-0.569), oxygen stratification (-0.545), phosphate (-0.539) and silicate (-0.488).

According to the species distribution (Figure 3.8), larvae of the anchovy *E. anchoita* were positively correlated with latitude, oxygen stratification, silicate and phosphate concentration and low temperatures from PPW. At mid-latitudes and in inshore waters, under the influence of STSW, larvae of the codlet *B. cantori*, the largehead hairtail *T. lepturus* and the lizardfish *S. foetens* were also positively correlated with high chl-a concentration. The abundance of Engraulidae eggs and other

fish eggs was highest mostly in inshore waters, with a high chl-a concentration. In addition, a high abundance of *S. brasiliensis* and *C. boleosoma* larvae and *M. muelleri* eggs was influenced by the high-temperature SW. Larvae of oceanic species, such as the bristlemouth *C. acclinidens* and the lanternfishes *D. mollis*, *D. brachycephalus*, *L. guentheri* and *C. townsendi* were associated with TW, low nutrients and chl-a concentration, and high salinity.
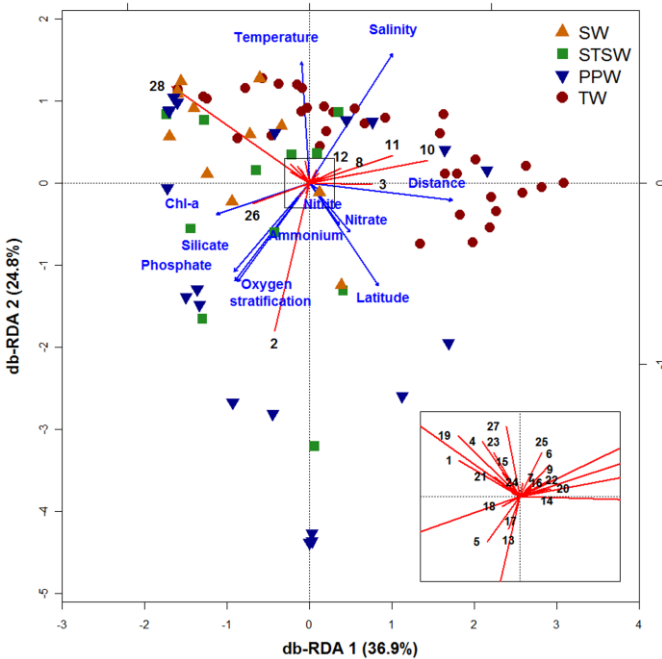
Figure 3.8. Distance-based Redundancy Analysis ordination for ichthyoplankton composition constrained by environmental variables. Triplot with explanatory variables, species and samples. Numbers represents species/taxa names: 1. *Sardinella brasiliensis*; 2. *Engraulis anchoita*; 3. *Cyclothone acclinidens*; 4. *Pollichthys mauli*; 5. *Synodus foetens*; 6. *Lestrolepsis intermedia*; 7. *Myctophum nitidulum*; 8. *Ceratoscopelus townsendi*; 9. *Diaphus garmani*; 10. *Diaphus brachycephalus*; 11. *Diaphus mollis*; 12. *Lepidophanes guentheri*; 13. *Bregmaceros cantori*; 14. *Urophycis mystacea*; 15. Scorpaenidae sp. 1; 16. *Prionotus* sp.; 17. *Bairdiella* sp.; 18. *Micropogonias furnieri*; 19. *Ctenogobius boleosoma*; 20. *Sphyraena barracuda*; 21. *Trichiurus lepturus*; 22. *Auxis* sp.; 23. *Euthynnus alletteratus*; 24. *Scomber colias*; 25. Anguilliformes eggs; 26. Engraulidae eggs; 27. *Maurolicus muelleri* eggs; 28. Other fish eggs.

Discussion

Our findings provide information on ichthyoplankton distribution and its relationship with the oceanographic environment within a wide latitudinal range in the South Brazil Shelf. Four surface water masses were present in the whole study area, and over the shelf, three were positioned in a latitudinal gradient. Larval fish species were associated with specific water masses: in the north *Sardinella brasiliensis* characterized Shelf Water (SW); in the south *Engraulis anchoita* was found in Plata Plume Water (PPW); and, in Subtropical Shelf Water (STSW) species from both coastal and shelf origins were found. At the slope, Tropical Water (TW) was characterized only by the bristlemouth *Cyclothone acclinidens*, although a high abundance and occurrence of lanternfishes were also found. Ichthyoplankton composition was influenced by the cross-shelf gradient and by the latitude in continental shelf waters.

A maximum ichthyoplankton abundance and the presence of coastal- and estuarine-related species, such as *Parona singnata*, Gerreidae, *Cynoscion* sp., *Micropogonias furnieri*, *Mugil* sp., *Symphurus* spp. and Engraulidae eggs, are expected near or in front of large estuaries because of the contribution of estuarine spawners and estuarine-dependent fishes that use these environments for reproduction and/or as nursery areas [70–72]. Even small coastal lagoons can contribute to high quantities of fish eggs and larvae and increase ichthyoplankton abundance in coastal waters [73]. Continental runoff and tidal cycles associated with wind stress transport fish eggs and larvae to coastal waters [74] and increase their abundance in adjacent regions. Another process that might increase ichthyoplankton abundance in the continental shelf is the wind induced coastal upwelling (e.g., [15,3]). In Brazilian shelf waters, areas under the influence of coastal upwelling, such as Cape São Tomé and Cape Frio [35], showed a high abundance of eggs (> 1000 ind. 100 m^{-3}) and larvae (> 100 ind. 100 m-3), once the enhancement of the primary and secondary production ensure the availability of food for the future larvae [27,33]. This is especially required during the critical period [75].

Ichthyoplankton abundance distribution in shelf waters was comparable to that of previous studies in the region between Cape Frio and Chui [8,27]. In addition, a high abundance of fish larvae in the southernmost of the study area is due to freshwater influences by PPW [26], and is comparable to other temperate and oligotrophic areas in the

south-western Australian coast [14], where a maximum larval abundance of 414 ind. 100 m^{-3} in late austral spring was found. Fish egg abundance was similar, and sometimes higher, than that described for the Northern Brazilian coast [76]. The abundance of eggs and larvae in oceanic waters was lower (< 50 ind. 100 m^{-3}) than in coastal and shelf waters, and fish eggs were absent in some offshore stations. This is probably an effect of the nutrient-poor TW that is driven by the Brazil Current (BC) throughout the entire slope [19,31]. In most of the slope stations, the abundance of fish larvae followed the trend described for oceanic regions [77,78].

A high larval abundance occurred between Cape São Tomé and Cape Frio, at the outer shelf and slope. This pattern might be related to the eddy-induced upwelling [34] that contributes to the enrichment of the euphotic layer by intrusion of the South Atlantic Central Water (SACW) and consequently to shelf brake upwelling [20]. In addition, peaks in fish larvae abundance at the slope are possibly due to larval retention by meanders or eddies from BC [35,8]. This mechanism of larval retention was described in the Mediterranean Sea, when a high concentration of tuna larvae inside anti-cyclonic eddies induced by topography was indicative that these structures act as retention areas for these larvae [3].

Fish larvae species composition reflected the spawning area of adult fish populations and was similar to that previously registered for the area [8,24]. Coastal and shelf waters showed a dominance of larvae from coastal species such as Trichiuridae and/or of larvae from demersal eggs such as those of Gobiidae, Blenniidae, and Synodontidae. This region also contained species from the continental shelf and slope with pelagic eggs such as those of Clupeidae, Engraulidae, Bregmacerotidae and Scombridae. Some oceanic species spawn near land masses, such as tuna larvae *Auxis* sp., *Thunnus* spp. and *Katsuwonus pelamis*, and release their eggs in areas with a higher primary production than in the open ocean, where waters are more suitable for the early larvae [79]. However, our results showed that these species were distributed in different parts of the shelf in a latitudinal gradient according to their specific water mass. Alternatively, larvae of oceanic fish such as the Myctophidae and Gonostomatidae occupied mostly the inner and outer slope in the entire study area, as previously shown [8,24]. Since most of these species have a circumglobal distribution, this pattern has been recorded in different oceanic areas around the world (e.g., [77,80,78,14,81]).

Water mass composition is an important controlling factor that

conditions larval fish distribution [80,14,81]. The water mass composition in the southern part (SSS) of the study area was very similar to that demonstrated previously for the area [19,37] and influenced fish larvae species distribution. The SW group was influenced by a mixture of larvae from demersal eggs, such as those of the goby *C. boleosoma* and the blenny *Parablennius* sp., with larvae from pelagic eggs such as from the sardine *S. brasiliensis*. In a region in southwestern Australia, inshore stations were also dominated by larvae from demersal eggs such as those from Tripterygiidae, Gobiidae and Blenniidae, and larvae of neritic species such as Clupeidae [14].

The spawning area of the Brazilian sardine *S. brasiliensis* is located on the Southern Brazilian Bight (SBB) between Cape Frio (~23ºS) and Cape Santa Marta (~28ºS) [25,82]. Sardine spawning is strongly dependent on and influenced by SACW intrusion and the stability of the water column due to vertical stratification [83], which is a key ingredient for larval survival [84], since it helps larval retention and nutrient enrichment of the euphotic layer [83,25]. In this study, the intrusion of the SACW over the inner shelf occurred in the vicinity of Cape Santa Marta and Cape Frio due to local coastal wind-induced upwelling [85,32]. A close inspection of the isotherms in cross-shelf sections showed a more pronounce intrusion of SACW in Cape Frio (~ 20–30 m depth), which increased the stratification of the water column, favoring the occurrence of *S. brasiliensis* in the continental shelf area around Cape Frio.

The STSW group comprised mainly stations from the SBB area, and was associated with larvae of fish that spawn in inshore waters, such as the lizardfish *S. foetens* and the largehead hairtail *T. lepturus*, which shared dominance with larvae of oceanic origin such as the codlet *B. cantori*. Due to the lack of intrusion of SACW in the SBB area, the STSW group did not contain any *S. brasiliensis* larvae in its composition. This same larval association was registered in the Subtropical Shelf Front (STSF), the transition between the STSW and Subantartic Shelf Water (SASW) located near the 50 m isobaths, around 33ºS [26,37]. This frontal assemblage was studied in the summer and was characterized by the occurrence of species of both coastal or oceanic origin, such as *T. lepturus* and other codlet *B. atlanticus*, respectively [26].

In the area under the influence of PPW, larvae of the anchovy *E. anchoita* and its pelagic eggs were dominant. Anchovy has a wide distribution range from Cape Frio (23ºS) to the Gulf of San Jorge (47ºS) [86], and unlike other anchovy species that form large schools in areas

under the influence of intense upwelling [82], the distribution of *E. anchoita* is associated with a lower intensity upwelling, cold water from the south and continental runoff from La Plata and Patos Lagoon [87,88,19]. It is the only species that occurred in both winter and summer assemblages, and in inshore, frontal and offshore assemblages at the STSF [26]. Its wide range distribution and capacity to survive in different oceanographic conditions make *E. anchoita* larvae an important component of the pelagic ecosystem in the Southwest Atlantic Ocean (SWAO).

Regarding the TW group, characterized by a high abundance and occurrence of the bristlemouth *C. acclinidens*, Myctophidae species such as *D. mollis*, *D. brachycephalus* and *C. townsendi* were also overwhelmingly abundant in the slope waters. Larvae from Myctophidae and Gonostomatidae are good indicators of the presence of oceanic waters such as TW [80], which partly explained the occurrence of oceanic species over the shelf, which can result from the intrusion of TW through the continental shelf. Water masses were good predictors of larval species associations that resulted in significantly different assemblages from each other, as in this study. In fact, species associations from water masses can be stronger than those that are only considered a spatial or a temporal association [14].

The main role of water mass influence can be attributed to the ordination of larval species distribution in space. Cross-shelf and latitudinal environmental effects were the two main components that accounted for the composition of fish larval assemblages, and reflect the influence of water masses (e.g., [8,14,9]). The latitudinal gradient shows an inverse relationship with sea surface temperature (e.g., [4,7]), whereas cross-shelf variability is related to salty ocean waters and coastal productive waters (e.g., [13]). In the oligotrophic Brazil Current domain, upwelling of SACW is the main input of nitrates over the continental shelf, whereas phosphates and silicates might derive from terrestrial origin and be associated with the PPW contribution [21]. This is the main characteristic observed in our cruises (Figure 3.8), where phosphorous and silicate are present at high latitudes and indicate the influence of continental runoff.

Our results revealed a high unexplained source of variation, and we suggest that other sources of variability should be investigated. Large-scale ichthyoplankton composition and distribution are also influenced by food availability and geostrophic circulation [75,84,2], and we were not able to assess these. Coupling between physical–chemical and biological effects are an important mechanism in larval

fish growth and survival. For example, SBB restricted the *S. brasiliensis* population and its spawning is influenced by SACW intrusion [15]. Studies from Matsuura [15] showed that the failures in recruitment of two year-classes (1975 and 1987) was probably because the lack of intrusion of SACW in the SBB inner shelf, which caused a high mortality of sardine larvae [15,82]. In the Mediterranean Sea, shelf species are mainly influenced by trophic resources, whereas oceanic species are controlled by current-mediated transport [2].

In conclusion, our study supports the hypothesis that in the South Brazil Shelf, the large-scale distribution of the ichthyoplankton is mainly controlled by water mass composition. In addition, larval fish assemblages are influenced by the cross-shelf gradient and by the latitude of continental shelf waters. Species are more abundant and frequent at different areas under the influence of specific thermohaline characteristics in the water column. Further studies should be performed to assess the role of food availability in the control of fish larvae abundance.

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Author Contributions

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Supporting Information

Table S3.1. Plankton data for the stations visited at the South Brazil Shelf.
Depth of plankton sample (m) and water volume (m3) filtered for each of the 89 stations between Cape São Tomé (21ºS) and Chuí (33ºS) from December 2010 to January 2011.

Station	Plankton sample depth (m)	Water volume (m^3)
1	23	5.52
2	22	2.27
3	25	11.33
4	30	7.87
5	40	8.39
6	30	3.94
7	85	63.25
8	87	29.30
9	120	80.17
10	115	50.90
11	95	38.21
12	25	13.72
13	30	38.80
14	31	17.82
15	32	14.29
16	30	29.65
17	17	14.53
18	13	7.43
19	39	20.76
20	40	14.74
21	80	77.34
22	70	35.58
23	100	23.91
24	100	33.04
25	105	29.82
26	110	52.15
27	120	65.26
28	105	79.07
29	40	35.84
34	25	9.50
35	14	5.09
36	58	37.60
37	68	37.19
38	70	42.07
39	85	61.95
40	100	34.80
45	22	8.36
46	50	21.36
47	38	18.02
48	45	46.70

Table S3.1. (Continued)

Station	Plankton sample depth (m)	Water volume (m^3)
49	82	30.21
50	107	40.38
51	89	51.16
52	92	42.65
53	75	42.60
54	61	34.61
55	30	26.99
56	48	15.49
57	31	36.21
58	25	10.83
59	37	23.90
60	49	19.72
61	66	24.24
62	85	43.11
63	85	21.59
64	86	30.11
65	39	23.58
66	36	13.98
67	37	14.97
68	30	10.14
69	32	11.30
70	12	6.37
71	22	7.35
72	13	7.10
73	60	66.29
74	66	52.11
80	14	4.27
81	32	16.58
82	29	11.11
83	21	8.83
84	121	61.46
86	130	48.68
87	25	8.98
88	50	28.79
89	75	55.30
90	39	23.76
91	46	13.54
92	22	11.17
93	22	10.76
94	20	25.23
95	35	13.82
96	55	24.58
97	90	43.10
98	89	44.44
108	78	130.58

Table S3.1. (Continued)

Station	Plankton sample depth (m)	Water volume (m^3)
109	98	37.07
110	60	26.81
111	40	22.31
112	22	6.56

Table S3.2. Taxonomic list of the ichthyoplankton from the South Brazil Shelf. Total catch of fish larvae and eggs, abundance (mean ± SE) and frequency (%) for the 89 stations visited between Cape São Tomé (21ºS) and Chuí (33ºS) from December 2010 to January 2011. *Species/taxa caught in only one sample.

Family	Species	Total catch (nº. larvae)	Abundance ± SE (nº. · 100m^{-3})	Frequency (%)
Congridae	*Ariosoma balearicum* (Delaroche, 1809)	2	0.16±0.14	2.25
Ophichthidae	*Ophichthus gomesii* (Castelnau, 1855)	1	0.03±0.03	1.12*
Clupeidae	*Sardinella brasiliensis* (Steindachner, 1879)	70	4.69±2.97	4.49
Engraulidae	*Engraulis anchoita* Hubbs and Marini, 1935	240	17.33±7.15	17.98
Gonostomatidae	*Cyclothone acclinidens* Garman, 1899	38	0.87±0.25	15.73
Gonostomatidae	*Cyclothone alba* Brauer, 1906	7	0.12±0.08	3.37
Gonostomatidae	*Cyclothone pseudopallida* Mukhacheva, 1964	3	0.09±0.08	2.25
Gonostomatidae	*Cyclothone* spp.	14	0.26±0.1	8.99
Sternoptychidae	*Maurolicus muelleri* (Gmelin, 1789)	1	0.15±0.15	1.12*
Phosichthyidae	*Pollichthys mauli* (Poll, 1953)	9	0.45±0.22	6.74
Phosichthyidae	*Vinciguerria attenuata* (Cocco, 1838)	1	0.02±0.02	1.12*
Phosichthyidae	*Vinciguerria nimbaria* (Jordan & Williams, 1895)	3	0.07±0.04	3.37
Stomiidae	*Stomias boa ferox* Reinhardt, 1842	3	0.1±0.07	2.25
Synodontidae	*Synodus foetens* (Linnaeus, 1766)	13	0.75±0.26	10.11
Synodontidae	*Synodus synodus* (Linnaeus, 1758)	1	0.1±0.1	1.12*
Synodontidae	*Trachinocephalus myops* (Forster, 1801)	2	0.08±0.08	1.12*
Synodontidae	Synodontidae spp.	1	0.08±0.08	1.12*
Paralepididae	*Lestidium atlanticum* Borodin, 1928	4	0.11±0.07	3.37
Paralepididae	*Lestrolepis intermedia* (Poey, 1868)	8	0.27±0.12	6.74
Paralepididae	*Sudis* sp.	1	0.02±0.02	1.12*
Paralepididae	*Uncisudis* sp.	1	0.02±0.02	1.12*
Paralepididae	Paralepididae spp.	3	0.07±0.06	2.25
Evermannellidae	*Evermannella melanoderma* Parr, 1928	1	0.03±0.03	1.12*
Myctophidae	*Hygophum hygomii* (Lütken, 1892)	2	0.04±0.03	2.25

Table S3.2. (Continued)

Family	Species	Total catch (nº. larvae)	Abundance ± SE (nº. · 100m^{-3})	Frequency (%)
Myctophidae	*Hygophum reinhardtii* (Lütken, 1892)	1	0.03±0.03	1.12*
Myctophidae	*Hygophum* sp.	1	0.04±0.04	1.12*
Myctophidae	*Myctophum affine* (Lütken, 1892)	1	0.04±0.04	1.12*
Myctophidae	*Myctophum nitidulum* Garman, 1899	7	0.44±0.28	5.62
Myctophidae	*Myctophum* spp.	5	0.12±0.05	5.62
Myctophidae	*Ceratoscopelus warmingii* (Lütken, 1892)	2	0.07±0.05	2.25
Myctophidae	*Ceratoscopelus townsendi* (Eigenmann & Eigenmann, 1889)	34	0.91±0.31	13.48
Myctophidae	*Ceratoscopelus* spp.	2	0.15±0.13	2.25
Myctophidae	*Diaphus garmani* Gilbert, 1906	11	0.37±0.21	4.49
Myctophidae	*Diaphus brachycephalus* Tåning, 1928	156	6.34±2.55	22.47
Myctophidae	*Diaphus mollis* Tåning, 1928	66	1.96±0.46	25.84
Myctophidae	*Diaphus metopoclampus* (Cocco, 1829)	5	0.47±0.32	3.37
Myctophidae	*Diaphus* spp.	4	0.16±0.11	3.37
Myctophidae	*Lampadena luminosa* (Garman, 1899)	11	0.19±0.14	2.25
Myctophidae	*Lampanyctus lepidolychnus* Becker, 1967	3	0.08±0.05	3.37
Myctophidae	*Lampanyctus* sp. 1	1	0.02±0.02	1.12*
Myctophidae	*Lampanyctus* sp. 2	1	0.02±0.02	1.12*
Myctophidae	*Lampanyctus* spp.	1	0.05±0.05	1.12*
Myctophidae	*Lepidophanes guentheri* (Goode & Bean, 1896)	20	0.54±0.23	8.99
Myctophidae	*Lepidophanes* spp.	5	0.11±0.11	1.12*
Myctophidae	*Lobianchia gemellarii* (Cocco, 1838)	1	0.05±0.05	1.12*
Myctophidae	*Lobianchia* sp.	2	0.1±0.1	1.12*
Myctophidae	*Notolychnus valdiviae* (Brauer, 1904)	1	0.02±0.02	1.12*
Myctophidae	*Notoscopelus resplendens* (Richardson, 1845)	4	0.11±0.07	3.37
Myctophidae	*Taaningichthys minimus* (Tåning, 1928)	1	0.04±0.04	1.12*

Table S3.2. (Continued)

Family	Species	Total catch (nº. larvae)	Abundance ± SE (nº. · 100m^{-3})	Frequency (%)
Myctophidae	Myctophidae spp.	8	0.39±0.21	7.87
Bregmacerotidae	*Bregmaceros atlanticus* Goode & Bean, 1886	3	0.05±0.04	2.25
Bregmacerotidae	*Bregmaceros cantori* Milliken & Houde, 1984	34	1.59±0.66	10.11
Bregmacerotidae	*Bregmaceros* spp.	7	0.17±0.13	2.25
Phycidae	*Urophycis mystacea* Miranda Ribeiro, 1903	11	0.59±0.3	7.87
Merlucciidae	*Merluccius* sp.	1	0.01±0.01	1.12*
Macrouridae	Macrouridae spp.	5	0.26±0.18	4.49
Ophidiidae	*Lepophidium* sp.	2	0.11±0.09	2.25
Ophidiidae	*Ophidion* sp.	1	0.02±0.02	1.12*
Ophidiidae	Ophidiidae sp.	1	0.05±0.05	1.12*
Bythitidae	Bythitidae sp.	3	0.43±0.43	1.12*
Lophiidae	Lophiidae sp.	1	0.08±0.08	1.12*
Melamphaidae	*Poromitra* sp.	1	0.05±0.05	1.12*
Fistulariidae	*Fistularia petimba* Lacepède, 1803	1	0.13±0.13	1.12*
Scorpaenidae	*Pontinus rathbuni* Goode & Bean, 1896	2	0.08±0.06	2.25
Scorpaenidae	Scorpaenidae sp. 1	6	0.52±0.29	4.49
Scorpaenidae	Scorpaenidae sp. 2	1	0.03±0.03	1.12*
Scorpaenidae	Scorpaenidae sp. 3	1	0.02±0.02	1.12*
Triglidae	*Prionotus* sp.	7	0.21±0.11	5.62
Bramidae	*Brama caribbea* Mead, 1972	1	0.04±0.04	1.12*
Serranidae	*Centropristis* sp. 1	2	0.1±0.1	1.12*
Serranidae	*Centropristis* sp. 2	1	0.05±0.05	1.12*
Serranidae	*Mycteroperca* sp.	1	0.05±0.05	1.12*
Serranidae	*Rypticus* sp.	1	0.05±0.05	1.12*
Serranidae	Serranidae sp.	3	0.11±0.11	1.12*

Table S3.2. (Continued)

Family	Species	Total catch (nº. of larvae)	Abundance ± SE (nº. · 100m^{-3})	Frequency (%)
Carangidae	*Parona signata* (Jenyns, 1841)	2	0.08±0.08	1.12*
Carangidae	*Trachinotus* sp.	1	0.04±0.04	1.12*
Carangidae	*Trachurus* sp.	9	0.42±0.4	2.25
Carangidae	*Selene* sp.	1	0.04±0.04	1.12*
Carangidae	Carangidae spp.	9	0.25±0.14	4.49
Gerreidae	Gerreidae sp.	2	0.18±0.13	2.25
Sciaenidae	*Bairdiella* sp.	5	0.19±0.1	4.49
Sciaenidae	*Cynoscion* sp.	3	0.27±0.17	3.37
Sciaenidae	*Larimus* sp.	1	0.04±0.04	1.12*
Sciaenidae	*Micropogonias furnieri* (Desmarest, 1823)	5	0.32±0.18	4.49
Sparidae	Sparidae sp.	1	0.07±0.07	1.12*
Mugilidae	*Mugil* sp.	2	0.09±0.08	2.25
Scaridae	*Sparisoma* sp.	1	0.03±0.03	1.12*
Blenniidae	*Parablennius* sp.	2	0.2±0.14	2.25
Blenniidae	*Hypleurochilus fissicornis* (Quoy & Gaimard, 1824)	2	0.14±0.11	2.25
Blenniidae	Blenniidae sp. 1	2	0.11±0.09	2.25
Blenniidae	Blenniidae spp.	1	0.15±0.15	1.12*
Gobiidae	*Bathygobius soporator* (Cuvier & Valenciennes, 1837)	1	0.02±0.02	1.12*
Gobiidae	*Ctenogobius boleosoma* (Jordan & Gilbert, 1882)	17	1.63±0.84	6.74
Gobiidae	Gobiidae spp.	11	0.97±0.37	10.11
Sphyraenidae	*Sphyraena barracuda* (Edwards, 1771)	6	0.3±0.19	5.62
Sphyraenidae	*Sphyraena tome* Fowler, 1903	1	0.1±0.1	1.12*
Sphyraenidae	*Sphyraena* spp.	7	0.2±0.1	4.49
Gempylidae	*Nealotus tripes* Johnson, 1865	1	0.01±0.01	1.12*

Table S3.2. (Continued)

Family	Species	Total catch (nº. of larvae)	Abundance ± SE (nº. · 100m^{-3})	Frequency (%)
Trichiuridae	*Trichiurus lepturus* Linnaeus, 1758	17	0.81±0.29	10.11
Scombridae	*Auxis* sp.	11	0.3±0.14	5.62
Scombridae	*Euthynnus alletteratus* (Rafinesque, 1810)	45	1.01±0.62	7.87
Scombridae	*Katsuwonus pelamis* (Linnaeus, 1758)	1	0.03±0.03	1.12*
Scombridae	*Scomber colias* Gmelin, 1789	5	0.27±0.16	5.62
Scombridae	*Thunnus* spp.	14	0.69±0.39	5.62
Scombridae	Scombridae spp.	3	0.07±0.05	2.25
Bothidae	*Bothus* sp.	1	0.05±0.05	1.12*
Bothidae	*Monolene antillarum* Norman, 1933	1	0.05±0.05	1.12*
Bothidae	Bothidae sp.	1	0.08±0.08	1.12*
Paralichthyidae	*Citharichthys* sp.	3	0.25±0.18	3.37
Paralichthyidae	*Etropus longimanus* Norman, 1933	1	0.1±0.1	1.12*
Cynoglossidae	*Symphurus plagiusa* (Linnaeus, 1766)	6	0.25±0.22	2.25
Cynoglossidae	*Symphurus trewavasae* Chabanaud, 1948	1	0.03±0.03	1.12*
Cynoglossidae	*Symphurus kyaropterygium* Menezes & Benvegnú, 1976	4	0.27±0.23	2.25
Cynoglossidae	*Symphurus* spp.	6	0.28±0.19	3.37
Molidae	*Mola mola* (Linnaeus, 1758)	1	0.02±0.02	1.12*
Yolk sac larvae	Unidentified	175	12.07±3.31	40.45
Yolk sac larvae	Leptocephalus	2	0.07±0.05	2.25
Unidentified	Unidentified larvae	176	8.66±1.87	61.80
Anguilliformes	Unidentified eggs	13	0.44±0.2	6.74
Engraulidae	Unidentified eggs	408	39.54±22.14	12.36
Sternoptychidae	*Maurolicus muelleri* (Gmelin, 1789)	57	4.87±4.21	6.74
Unidentified	Unidentified eggs	1452	116.71±39.76	71.91

4 CAPÍTULO 2 – The role of water masses driving the distribution and composition of larval fish assemblages at the South Brazil Shelf

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The role of water masses driving the distribution and composition of larval fish assemblages at the South Brazil Shelf

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Abstract: Physical factors and climate constrain species distribution and abundance in marine ecosystems. Besides specific physical and chemical properties, water masses are associated with enrichment processes, retention and concentration processes that are favorable features to larval fish survival. This study aims to investigate the role of water masses on the seasonal and interannual variability of ichthyoplankton assemblages large scale distribution. Data were acquired from 9 oceanographic surveys conducted in the 1980s and 2000s, on the southern Brazilian continental shelf between 26ºS and 34ºS. Surveys design accounted for seasonal and interannual variability in larval assemblages. Results showed a clear seasonal pattern in the distribution of water masses and most abundant and frequent larval taxa, with high occurrence and abundance associated with particular water mass: *Engraulis anchoita* in Plata Plume Water, *Bregmaceros* sp. and *Trichiurus lepturus* in Subtropical Shelf Water, and Myctophidae in Tropical Water. Interannual variability in environmental conditions, such as salinity below 26.0 in the 1980s, affected larval community decreasing abundance of species like *E. anchoita*. Concurrent use of multivariate analysis (ISA, CAP) and statistical modeling (GAM) confirmed the hypothesis that water masses select species of fish larvae and influenced larval fish community assembly in two ways: determining abundance of dominant taxa, which influenced dominance in larval community; selecting rare taxa with low frequency that were exclusively associated with particular water mass (e.g. *Pomatomus saltatrix* associated with Subtropical Shelf Water). We hypothesized that

climate events, such as the El Niño, could change environmental conditions such as freshwater input and sea surface temperature, which will affect water masses characteristics and thus ichthyoplankton community assembly.

Introduction

One of the major concerns in community ecology is related to understand patterns in distribution, abundance, and composition of species in communities, and their underlying processes such as biotic interactions and environmental influences (Vellend 2010). These processes act at multiple scales in space and time, shaping local and regional communities (Menge and Olson 1990). The importance of physical factors in delimiting distribution range of species in marine ecosystems is well understood (e.g. Checkley et al. 2000, Macedo-Soares et al. 2014). Physical factors are also involved in seasonal variability of the environmental conditions, which affect the composition of larval fish assemblages through time (Muelbert et al. 2008, Franco-Gordo et al. 2008).

Temperature is an important environmental condition controlling the rates of growth and metabolism in the early stages of fishes (Pepin 1991). Spawning habitat of small pelagic fish, for instance, have been accessed in terms of physical factors such as temperature and salinity (e.g. Checkley et al. 2000), showing that early stages of fishes are associated with ranges throughout environmental gradients. Climate also influences several ecological processes affecting abundance and distribution of species (Stenseth et al. 2003, Hsieh et al. 2009, Auth et al. 2011). Decadal oscillations in larval fish abundance and diversity in the Northeast Pacific were best explained by climate indices such as the Pacific Decadal Oscillation than local physical factors such as Ekman transport or upwelling (Auth et al. 2011). In the California Current System, regime shift in climate conditions (from cold to warm period, 1976/1977) extended shoreward distribution of larvae of oceanic fish, while distribution of coastal-neritic fish larvae retreated shoreward (Hsieh et al. 2009).

In a *stricto sensu*, water masses are portions of water with specific physical and chemical properties that results in the thermohaline

circulation of the oceans. Furthermore, water masses are associated with enrichment processes, retention of larval stages, and concentration of food that are favorable features to larval survival and development (Bakun 2010). This ocean triad (Bakun 2010) is related to the availability of food in suitable size and quantity at first feeding by a larva, and the overlap between zooplankton and larval production, which are key factors for a recruitment success (Hjort 1914, Lasker 1975). The relationship of water masses and ichthyoplankton comunities have been studied in different oceans (e.g. Marancik et al. 2003, Muhling et al. 2008, Macedo-Soares et al. 2014) as well as in relation to climate variability (e.g. Franco-Gordo et a. 2008). In the South Brazil Shelf, recent findings demonstrate the influence of water masses large-scale distribution in the composition of ichthyoplankton assemblages, showing that in a given season and year early life stages of fishes have preferences for particular water mass (Macedo-Soares et al. 2014).

The South Brazil Shelf (western South Atlantic Ocean) that lies between Babitonga Bay (~26ºS) and Chuí (~34ºS, Uruguay/Brazil border), are associated with the largest Brazilian fish stocks (Castello et al. 2009) due to several coastal water enrichment processes. Continental discharge of Rio de La Plata (Plata hereafter) and Lagoa dos Patos (Patos hereafter) estuaries associated with nutrient rich subantarctic waters from Brazil-Malvinas Confluence (BMC) and Patagonian Current contributes to enhanced primary production over southern coastal and shelf waters (Carreto et al. 1986, Acha et al. 2004, Möller Jr. et al. 2008). During autumn/winter, the high Plata estuary discharge, the low frequency of onshore winds and the high average offshore wind speed result in the northeastward spread of the cool and brackish Plata Plume Water (PPW). The outflow from Patos estuary and the intensification of southerly winds combined with the PPW facilitate the water enrichment process (Acha et al. 2004, Möller Jr. et al. 2008). Further north, the intensification of northeasterly winds during the summer drive the upwelling of the nutrient rich South Atlantic Central Water (SACW), which result in a temporary increase of plankton biomass mostly around Cape Santa Marta (Acha et al. 2004, Campos et al. 2013). The warm and salty oligotrophic Tropical Water (TW) is transported southward by the Brazil Current along the slope (Silveira et al. 2000).

Larval fish community in the neritic pelagial zone is under the influence of climatic and oceanographic events (e.g. El Niño Southern Oscillation, continental runoff) that regulate life history traits and determine its geographical range in seasonal (Nonaka et al. 2000,

Marancik et al. 2003, Muelbert et al. 2008, Katsuragawa et al. 2014), interannual (Franco-Gordo et al. 2008, Muhling et al. 2013), and decadal time scales (Auth et al. 2011), as well as at large spatial scales (Macedo-Soares et al. 2014). However, few studies encompass concurrent large spatial and temporal scales (Hsieh et al. 2009), in special regarding those conducted in the western South Atlantic (Sánchez and Ciechomski 1995). This study aims to investigate the role of water masses on the seasonal and interannual variability of ichthyoplankton assemblages large scale distribution to test the hypothesis that seasonal variability on water masses distribution determines larval fish assemblages composition in the South Brazil Shelf.

Materials and methods

Fish larvae and environmental dataset

Fish larvae data were acquired from the most comprehensive dataset on southern Brazilian waters collected during 9 oceanographic surveys conducted from the early 1980s and to late 2000s (Fig. 4.1). Samples were taken at stations distributed at cross-shelf transects on the continental shelf between Babitonga Bay (~26ºS) and Chuí (~34ºS; Brazil/Uruguay border). In the 1980s, three surveys were performed between Cape Santa Marta (~28ºS) and Chuí (~34ºS), during austral winter and spring 1980 (Arepe 2, 3) and summer 1981 (Conversut 3). The northern area, between Babitonga bay and Cape Santa Marta, was sampled during winter 1982, summer 1984 and spring 1985 (Sueste 1, 3, 4). These surveys were combined to represent each season in the entire area in the 1980s. During the 2000s, the entire area was sampled in winter 2003, summer 2004 (La Plata 1, 2) and spring 2010 (MCT-II). The 9 surveys were initially designed to address different goals, as a consequence, fish larvae were sampled using different gears and methods, and at different spatial resolutions. Therefore, all grids were standardized to minimize artifacts due to differences in sample effort (Fig. 4.1). In the 1980s surveys, ichthyoplankton samples were obtained from transects performed in similar positions to that in the 2000s surveys. For all surveys, offshore stations were considered up to the 1000 m isobath.

For surveys conducted in the early 1980s, temperature at 10 m depth was measured using reversing thermometers attached to Niskin or Nansen bottles, and salinity was measured with a salinometer from

water in those samples. During the 2000s, vertical profiles were measured with a conductivity-temperature-depth (CTD) profiler (Sea Bird Electronics model 911). Ichthyoplankton collections were made with Bongo, Motoda, and WP-2 samplers with digital flowmeters, mostly with oblique and vertical hauls (details in Appendix A and Table S4.1). Sample processing and larval identification, with the specific literature, followed the procedures described in Macedo-Soares et al. (2014).
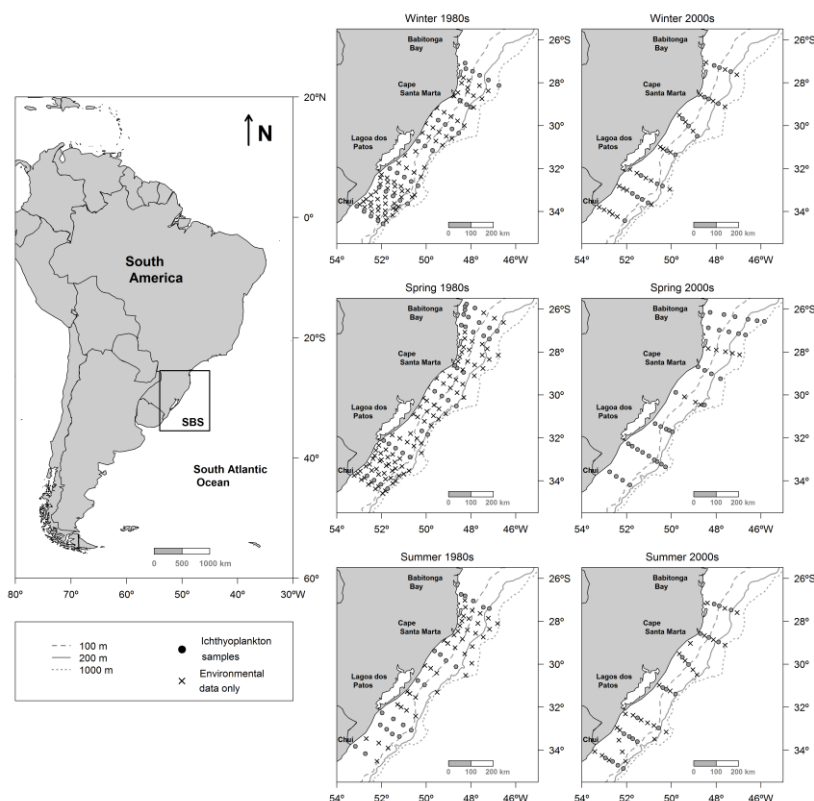
Fig. 4.1. The South Brazil Shelf (SBS) in the western South Atlantic Ocean, from Babitonga Bay (26ºS) to Chuí (34ºS, Uruguay/Brazil border). Also shown is the distributions of sampled stations from the ichthyoplankton surveys performed at the different seasons in the 1980s and 2000s.

Taxonomic standardization

Throughout almost 30 years, knowledge regarding larval fish identification has improved, and some species that were combined in upper taxonomic level (e.g. family) were later resolved to the species level. To avoid taxonomic inconsistency through time during data analyses, species without continuous records in one taxonomic level were aggregated back to genus or family level using a modified version of the procedures described by Muhling et al. (2013). Larvae from a particular family were classified to the species level only if more than 75% of these larvae were identified at species level in ≥75% of the 6 seasons sampled. For larvae of a particular family that >75% were identified at genus level in 75% or more of the 6 seasons, analysis were performed to the genus level, and larvae identified until at family level were excluded. Larvae of a particular family that did not achieve both criteria were included in the analysis at family level (Table S4.2). Species aggregated at ordinal level were not considered.

The use of higher taxonomic levels approach (e.g. genus, family) as surrogates of species-level assemblage structure have been shown consistent for different biological groups (e.g. macroinvertebrates, zooplankton) in freshwater ecosystems (Heino and Soininen 2007, Machado et al. 2015). Regarding reef fish and its larvae, which shown species-specific spatial preferences when small scales are considered (10–100 m), the use of higher taxonomic level approach was consistent at large (> 1 km) spatial scales (Carrassou et al. 2012).

Data analysis

Fish larvae abundance was standardized to the number of individuals per 100 m^3 filtered water, except larvae collected between Babitonga Bay and Cape Santa Marta in the 1980s (Sueste surveys) due to lack of information to apply standardized procedures. Data of the Sueste surveys were used only as presence/absence. Hypothesis that seasonal variability in water masses distribution determines composition of larval fish assemblages was investigated using exploratory techniques and tested through multivariate community analyses and statistical modeling. Temperature-salinity (T-S) diagrams were combined to fish larvae data to assess if particular water mass shows more abundance and/or occurrence of a specific taxa (Checkley et al. 2000). T-S analysis was performed only for most relevant taxa, which were selected

according to combination of abundance and occurrence in each survey (Table S4.3).

In the second approach, samples from each survey (seasons in the 1980s and 2000s) were classified as being located within particular water mass (PPW, STSW and TW) (Möller Jr et al. 2008) by their temperature and salinity at 10 m depth, and was subjected to an indicator species analysis (ISA) (Dufrene and Legendre 1997). ISA was used to identify if one taxa or group of taxa were consistently an indicator of particular water mass throughout all seasons and years, showing preference for a specific thermohaline range. ISA is based on the combination of species relative abundance and frequency among different *a priori* defined groups (e.g. water masses). Indicator value (IndVal) varies between 0 (no indication) to 100 (perfect indication), and its statistical significance was evaluated by a Monte Carlo randomization procedure (Dufrene and Legendre 1997). From the 1980s surveys, only samples located between Cape Santa Marta and Chuí were considered, since in the northern samples (Sueste surveys) only fish larvae taxa occurrence was determined.

Presence/absence matrix of larval fish taxa for combined surveys was used to calculate similarities between pairs of samples using Jaccard's coefficient. Similarity matrix was submitted to a Canonical Analysis of Principal Coordinates (CAP) to discriminate significant groups of samples according to particular water masses, using the same classification as ISA (Anderson and Willis 2003). A leave-one-out procedure was used to define the number of orthogonal principal coordinate axes (m) that minimize probabilities of misclassification of a particular water mass sample in a wrong group. Distinctiveness among groups of water masses was evaluated by cross-validation (Anderson et al. 2008). Spearman Rank correlations between each larval fish taxa and CAP axes were used to investigate which taxa tended to distinguish between water mass groups. Taxa with Spearman Rank correlation greater than 0.35 and lower than -0.35 were associated to group formation. The canonical correlations (δ) were used to assess significance in relation to groups' separation though the trace statistics (i.e. sum of all canonical eigenvalues) and the first canonical squared correlation, using permutational procedures. CAP was performed in PRIMER 6 with the PERMANOVA+ package (Anderson et al. 2008, Clarke and Warwick 2005).

Significant relations between larval fish community (CAP axes) and particular water masses, represented by temperature, salinity and potential density (Sigma-T), were assessed using Generalized Additive

Models (GAM) (Wood 2006). Larval fish community was modeled using Gaussian distribution and GAM function was set to estimate the optimal dispersion parameter k. The degree of smoothness of model terms was estimated by penalized cubic regression splines and effective degree of freedom (edf > 1 indicates a nonlinear relationship) was tested to access approximate significance of smooth terms (Wood 2006). Prior the analysis outliers (Sigma-T < 19.0 kg m-3) were removed. All analyses and graphics were performed in R (v3.1.1; R Core Team 2014), unless otherwise indicated.

Results

Ichthyoplankton community was dominated by larvae of the anchovy *Engraulis anchoita* in spring and winter, with high occurrence in 1980s (> 60% of samples) and abundance in 2000s (mean > 40 ind. 100 m^{-3}). Larvae of oceanic fish such as the lanterfish Myctophidae and the silvery lightfish *Maurolicus muelleri* were abundant and frequent in almost all seasons and both decades (Table S4.3). During summer, larvae of the largehead hairtail *Trichiurus lepturus* is the dominant (60 ± 39 ind. 100 m^{-3}), followed by the codlet *Bregmaceros* sp., mainly in the 1980s. Changes in community among seasons highlighted: winter/spring species such as the codling *Urophycis mystacea*, the bristlemouth Gonostomatidae and the bathypelagic *Bathylagus* sp.; and summer/spring species such as the lizardfish Synodontidae, the searobin *Prionotus* sp. and the harvestfish Stromateidae. Extremely rare taxa (i.e. one catch) or those which were occasionally caught (i.e. one occurrence) included the sabretooth anchovy *Lycengraulis* sp., the mullet *Mugil* sp., the silver scabbardfish *Lepidopus caudatus* and the lightfish *Vinciguerria* sp. (Table S4.3).

T-S diagrams (Fig. 4.2) and temperature and salinity fields (Fig. S4.1, S4.2) indicated that water masses at 10 m depth varied among seasons and decades, with an increasing in temperature in all water masses throughout each year cycle (e.g. PPW from ~11 to 25ºC). Most remarkable differences between 1980s and 2000s were related to salinity during winter surveys and temperature during spring. Salinity reached values bellow 26.0 (which was the lower limit in the 2000s) during winter of the 1980s (Fig. 4.2, S4.2), while temperature was higher during late austral spring (December) of the 2000s, than in early spring (October/November) of the 1980s (Fig. 4.2, S4.1). Northeastward spread of the PPW reached south of Santa Catarina Island (28ºS) during winter of the 2000s (Fig. S4.1, S4.2). Upwelling of the SACW only reached

surface waters in one station during summer of the 2000s (Fig. S4.1, S4.2).
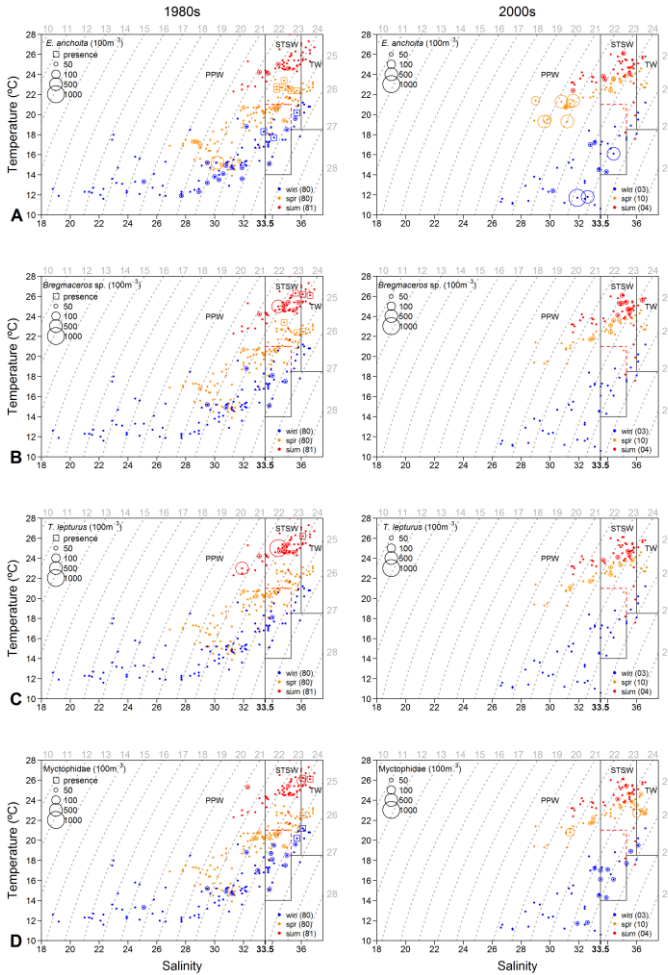
Fig. 4.2. T-S diagrams (10 m depth) with abundance (circle) and presence (square) of larve of *Engraulis anchoita* (A), *Bregmaceros* sp. (B), *Trichiurus lepturus* (C) and Myctophidae (D), for each season (winter = blue, spring = orange, summer = red) in the 1980s and 2000s. Water masses: Plata Plume Water (PPW), Subtropical Shelf Water (STSW), Tropical Water (TW). Dashed red line indicated temperature thresholds for STSW during summer.

Abundance and occurrence of *E. anchoita* larvae were associated with PPW (Fig. 4.2A, S4.3), higher in the 2000s (> 500 ind. 100 m-3) than in the 1980s, when salinity reached low values (< 26.0). *E. anchoita* larvae were also associated with STSW mostly at stations located at the northern area (beyond Cape Santa Marta, Fig. S4.3). Larvae of *Bregmaceros* sp. and *T. lepturus* were abundant in warm and intermediate salinity waters of STSW (Fig. 4.2B, C). *Bregmaceros* sp. also occurred in warm and salty waters of TW and PPW, however it was mainly associated with STSW in the 2000s (Fig. 4.2B). *T. lepturus* abundance was higher in the 1980s (> 500 ind. 100 m-3) at the southern portion of the continental shelf (~33–34ºS), than in the 2000s (≤ 50 ind. 100 m-3) (Fig. S4.4). Myctophidae larvae occurred in all water masses, with high abundance associated with TW (Fig. 4.2D, S4.5).

Indicator species analysis resulted in seven groups of taxa of fish larvae to be exclusively or preferentially associated to particular water mass (Table 4.1). Groups of exclusively associated taxa were mainly composed by extremely rare taxa or those which were occasionally caught, such as *Lycengraulis* sp. and *Mugil* sp. associated with PPW; *L. caudatus* and *Vinciguerria* sp. exclusively associated to TW. Whereas taxa exclusively associated to STSW included rare larvae caught in more than one sample such as the Brazilian codling *Urophycis brasiliensis* and the bluefish *Pomatomus saltatrix*, and groups like the bathypelagic Stomiidae and Macrouridae. Remaining groups were composed by taxa preferentially associated to particular water mass due to high abundance and occurrence (high IndVal). Larvae of *E. anchoita* were preferentially associated with PPW showing high IndVal in almost all surveys (except summer 1980s). Larvae of *T. lepturus* were associated with STSW, mainly during spring and summer, and *Bregmaceros* sp. showed high IndVal in almost all seasons and years. Synodontidae larvae were seasonally associated to particular water masses, shifting from STSW in spring to TW in summer, while Paralepididae larvae were associated to STSW in winter, shifting to TW in spring (Table 4.1). Larvae of oceanic taxa such as Myctophidae*, M. muelleri* and the snaketooth fish Chiasmodontidae shifted their preferences between STSW and TW, but without apparent seasonal pattern.

Table 4.1. Results of indicator species analysis (ISA), showing groups of taxa exclusively or preferentially associated to particular water mass. Significant (p < 0.05) indicator values (IndVal %) are in bold.

Fish larvae taxa	Plata Plume Water						Subtropical Shelf Water						Tropical Water			
	win 80	spr 80	sum 80	win 00	spr 00	sum 00	win 80	spr 80	sum 80	win 00	spr 00	sum 00	sum 80	win 00	spr 00	sum 00
Lycengraulis sp.	6															
Mugil sp.					14											
Bythitidae					7											
Merluccius hubbsi	11			27	7					5						
Engraulis anchoita	67	58	8	75	**63**	82	6	12	18	4	1	6				
Stromateidae			57					1				17				
Prionotus sp.			40		10						4	8				
Serranidae					7				10			17				
Blenniidae					1						10					
Gerreidae					2						9					
Anchoa marinii	6								10							
Gobiidae	6		13						7							
Clupeidae		10							10							
Carangidae					14						5					
Bothidae					7							25				
Scorpaenidae					14							33				
Urophycis mystacea	2			17	8		**64**				16					
Sciaenidae				17	33		14	25	20		1					
Trichiurus lepturus		< 1	21		3		14	36	33		**41**	33				
Muraenidae							14									
Macrouridae							14			25		8				
U.brasiliensis							14	12								
Macroramphosus scolopax							14									

Table 4.1. (Continued)

Fish larvae taxa	Plata Plume Water						Subtropical Shelf Water						Tropical Water			
	win 80	spr 80	sum 80	win 00	spr 00	sum 00	win 80	spr 80	sum 80	win 00	spr 00	sum 00	sum 80	win 00	spr 00	sum 00
Stomiidae							**43**				25					
Pomatomus saltatrix								20				8				
Bathylagus sp.										12						
Ophichthus sp.											12	17				
Ophidiidae											12					
Citharichthys sp.											12	8				
Etropus sp.											12					
Balistidae												17				
Bregmaceros sp.	2	2	1		2		32	20	58		**42**	50				25
Synodontidae		2			1			19	8		**49**	3	73		2	82
Myctophidae	8	6	< 1	16	8		**77**	54		59	7	17	99	8	**53**	
Cynoglossidae					26		14		2		1	33	76			
Maurolicus muelleri	6	11					**56**	21		25		8	100			
Scombridae		2	3		1			10	9		44	1				88
Gonostomatidae				7	3					8	2				29	
Sphyraenidae					3						8				3	100
Paralepididae							14			25					11	
Chiasmodontidae							**57**					17	100			
Lepidopus caudatus													100			
Congridae															14	
Vinciguerria sp.															14	

Surveys: wi80, winter 1980s; sp80, spring 1980s; su80, summer 1980s; wi00, winter 2000s; sp00, spring 2000s; su00, summer 2000s.

Canonical Analysis of Principal Coordinates (CAP) ordination among water mass groups showed a clear separation of larval fish assemblages (Fig 4.3), with an overall classification success of 62% (trace statistic = 0.36, p = 0.0001), and an allocation success for each group higher than 60% (Table S4.4). The first canonical axis (CAP 1) separated assemblages of PPW from that of TW ($\delta1 = 0.60$), being larvae of *E. anchoita* highly negative correlated to CAP 1, while larvae of the oceanic taxa such as the Gonostomatidae and Myctophidae positively correlated. Furthermore, second canonical axis (CAP 2) separated assemblages of PPW and TW from that of STSW ($\delta2 = 0.48$), showing negative correlation with larvae of *Bregmaceros* sp., *T. lepturus* and Synodontidae. Results of CAP also highlighted larval fish taxa that were associated (high correlation) to separation among water masses groups: *E. anchoita* (-0.75) associated with PPW; *T. lepturus* (-0.48), *Bregmaceros* sp. (-0.56) and Synodontidae (-0.38) with STSW; Gonostomatidae (0.45) and Myctophidae (0.49) with TW.

GAM showed for CAP 1 significantly nonlinear relationships with temperature, salinity and potential density (Sigma-T), with high deviance explained by temperature and salinity, respectively (Table S4.5). Positive CAP 1 that represents larvae of oceanic taxa was associated with warm-salty waters of TW (Fig. 4.4), while negative values were related to cool and brackish waters of PPW, indicating relationship with shelf-related taxa such as *E. anchoita* and *U. mystecea* (Fig. 4.3, 4.4). CAP 2 showed a nonlinear relation only with Sigma-T (Table S4.5, Fig. 4.4). Negative CAP 2, which represented taxa of shelf provenance such as *T. lepturus* and *Bregmaceros* sp. (Fig. 4.3), and associated with warm and intermediate salinity waters of STSW (Fig. 4.2B, C), were related with Sigma-T between 22 and 23 kg m^{-3} and of 24-25 kg m^{-3}, values that can be representative of the STSW influence (Fig. 4.2). Analysis of residuals indicated no evidence of spatial autocorrelation and/or heterogeneity among residuals of any of the models.
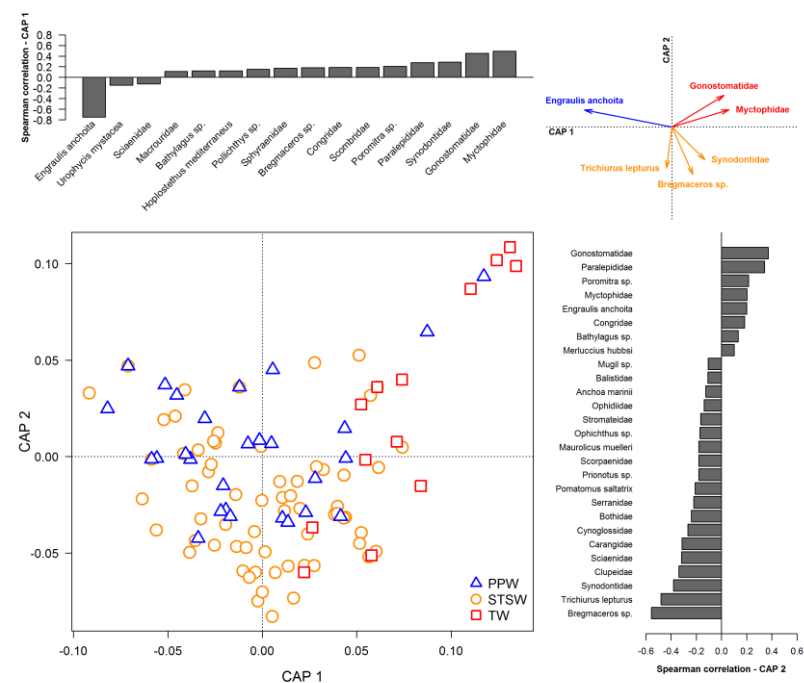
Fig. 4.3. Canonical Analysis of Principal Coordinates (CAP) ordination discriminating groups formed by water masses classification (PPW, Plata Plume Water; STSW, Subtropical Shelf Water; TW, Tropical Water), using Jaccard similarities between sites based on presence/absence of 48 fish larvae taxa (main panel). Vertical and horizontal bars showed Spearman Rank correlation between fish larvae taxa and canonical axes. Ordination of fish larvae taxa on CAP axes showed most relevant taxa associated to discrimination of water masses groups (small upper panel).

Discussion

South Brazil Shelf larval fish assemblages showed consistent association with particular waters masses in spatial and temporal large-scales. Taxa such as *Urophycis brasiliensis* and *Pomatomus saltatrix* were exclusively associated with the characteristic environmental conditions of STSW. However, species exclusively associated to PPW and TW were extremely rare or occasionally caught, being difficult to confirm such association. For dominant taxa, like *Engraulis anchoita*, *Bregmaceros* sp. and *Trichiurus lepturus*, particular water mass influenced their abundances, and then dominance in larval community.

In addition, interannual changes in the abundance of dominant species were related with variability in salinity and temperature between the 1980s and 2000s.
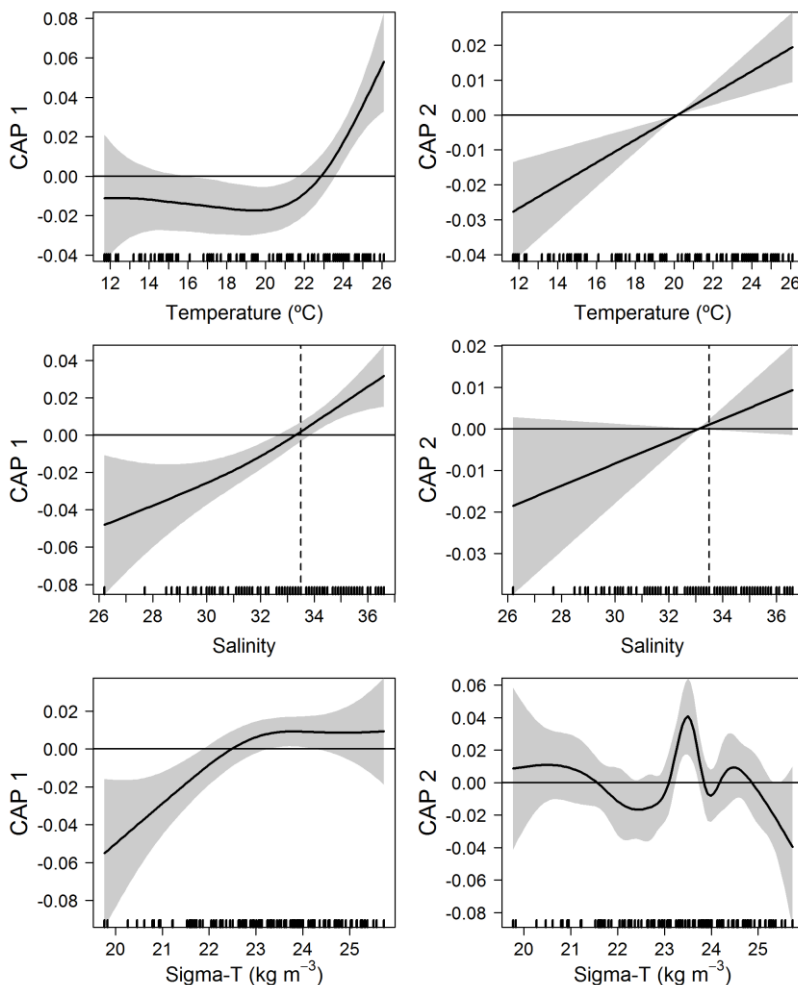
Fig. 4.4. GAM fits for CAP axes showing estimated smooth functions (solid lines) with 95% confidence intervals (gray shading) in relation to temperature (°C), salinity and potential density (Sigma-T, kg m^{-3}) at 10 m depth. Vertical dashed line in salinity plots indicate Plata Plume Water upper limit of 33.5 and horizontal lines indicate zero level.

Overall larval community structure showed similar pattern to the ones found in previous studies conducted at the South Brazil Shelf during spring and autumn. Dominant larvae were the Brazilian sardine *Sardinella brasiliensis* and *E. anchoita*, followed by oceanic lanternfishes species of *Diaphus*, *Ceratoscopelus* and *Myctophum*. Coastal and shelf water species such as *Bregmaceros cantori*, *Synodus foetens* and *T. lepturus* were also abundant and frequent (Katsuragawa et al. 2014, Macedo-Soares et al. 2014). The structure of larval fish assemblages at continental shelf and slope areas in different regions around the world followed this same pattern, with dominance of larvae of small pelagic fish (e.g. Engraulidae, Clupeidae), meso- and bathypelagic species (e.g. Myctophidae) and larvae from species of shelf waters provenance (e.g. Bregmaceros) (Marancik et al. 2003, Franco-Gordo et al. 2008, Muhling et al. 2008, Muhling et al. 2013).

Studies have shown that larval taxa association related to water mass can be stronger than those that are only considered a spatial or a temporal association (Marancik et al. 2003, Muhling et al. 2008, Katsuragawa et al. 2014, Macedo-Soares et al. 2014). In the continental shelf off Georgia (US, 31ºN to 32ºN), larval assemblages were related to concurrent cross-shelf gradient and water masses distribution influenced by seasonality. Larvae of the shouthern kingcroaker *Menticirrhus americanus*, for instance, were the dominant species of the inner-shelf (inshore of the 20 m isobath) group, with high abundance associated with the inner-shelf-mid-shelf mixed water mass and mid-shelf water mass during summer (Marancik et al. 2003). Seasonal changes in assemblages compostition from Southeastern Brazilian Bight (23ºS to 29ºS) were related to seasonality of water masses distribution. During spring wind driven upwelling of SACW leads to a shelf assemblage dominated by larvae of small pelagic fish as *S. brasiliensis*, *E. anchoita* and *Trachurus lathami*, while during autumn SACW retreats and the presence of low salinity (S < 34) Coastal Water (CW) shifts the dominant species to *B. cantori* and *E. anchoita*. Transitional and oceanic assemblages that comprised larvae of mesopelagic fish such as Myctophidae and hatchetfishes Sternopthychidae were influenced by TW with less pronounced seasonal variability (Katsuragawa et al. 2014). On the other hand, in the southwestern Australia, larval assemblages associated to particular water masses differed in relation to the cross-shelf position, for example, Leeuwin Current assemblages taken in shelf waters and in offshore waters were distinct (Muhling et al. 2008). The authors attributed these differences to spawning location of adult fish and suggested that water depth and/or distance from shore had some role

in structuring local larval assemblages.

Spatial and seasonal patterns in larval fish assemblages are the result of processes related to spawning distribution and larval transport, combined with oceanographic features such as water mass and oceanic fronts that promote suitable conditions to development and growth of early stages of fishes (Sánchez and Ciechomski 1995, Franco et al. 2006, Muelbert et al. 2008, Bakun 2010, Macedo-Soares et al. 2014). In the South Brazil Shelf, large-scale spatial patterns in larval fish assemblages were associated with water masses distribution during austral spring. Species from continental shelf such as *S. brasiliensis* and *E. anchoita* were associated with particular water masses (Shelf Water and PPW, respectively) in a latitudinal gradient, while larvae of oceanic species (e.g. Myctophidae, Gonostomatidae) were associated with oceanic waters of TW (Macedo-Soares et al. 2014). In the Argentine shelf, larvae of *E. anchoita* can be found throughout the year with maximum abundance in austral spring (October and November), as a result of spawning migration of adult schools from deeper shelf waters to coastal (< 50 m depth) waters associated with the presence of PPW (Sánchez and Ciechomski 1995). In the Abrolhos Bank region (17ºS to 23ºS, western South Atlantic Ocean), variations between and within assemblages among seasons were resulted from seasonal variability in species distribution and oceanographic conditions, such as the wind induced coastal upwelling of the SACW during austral spring and summer in the southern portion of Abrolhos Bank region (~22º to 23ºS) (Nonaka et al. 2000).

Interannual variability in communities may be related to changes in the environmental seasonal pattern that may affect community assembly (Tonn 1990). El Niño Southern Oscillation (ENSO) is one of the most important sources of interannual variability in the tropical Pacific, which spreads its effects globally (Lehodey et al. 2006). In the Mexican Pacific coast, the El Niño is an important source of variability in ichthyoplankton community by decreasing abundance and changing assemblage structure (Franco-Gordo et al. 2008). Tropicalization of communities associated with El Niño is the main cause of ichthyoplankton assemblage change due to intrusion of warm water mass. In the northern coast of Chile, 1997 winter El Niño induced tropicalization of the larval fish community due to coastward advection of warm and salty Subtropical Surface Waters, which favor species associated to tropical water masses (Rodríguez-Graña and Castro 2003). In the western South Atlantic, Plata estuary discharge varies interannually with El Niño-associated rainfall over Southeastern South

America (Aceituno 1988, Mechoso and Iribarren 1992). This explains, for example, the anomalous northward penetration of cool and low salinity PPW in the Southern Brazilian Bight (~24º–25ºS) one year after the large river outflow associated with the 1992 El Niño (Pimenta et al. 2005). Our findings showed interannual changes in the abundance of dominant species such as *E. anchoita* and *T. lepturus* (Table S4.2, Fig. S4.3, S4.4). However, these changes did not impacted ichthyoplankton assemblies, probably because our sampling did not include atypical El Niño years. El Niño changes mechanisms that ensure larval fish survival, including spawning patterns, food availability and transport (Franco-Gordo et al. 2008). We hypothesized that El Niño could change the community assembly rules at the South Brazil Shelf, through changes in environmental factors such as freshwater input and sea surface temperature, which will affect water masses characteristics and thus ichthyoplankton community.

In the southern portion of the South Brazil Shelf the Subtropical Shelf Front (STSF) is a sharp thermohaline frontal system between STSW and Subantarctic Shelf Water around the 50 m isobath at 33ºS (Piola et al. 2008). STSF changes composition of copepod and larval fish community during austral winter and summer, selecting species from frontal copepod (e.g. *Acartia tonsa*, *Ctenocalanus vanus*) and larval fish (e.g. *Urophycis mystacea*, *Pomatomus saltatrix*) assemblages (Muelbert et al. 2008). Transitional environments like fronts supports communities dominated by stress-tolerant species (Sommer at al. 2014). Species with high tolerance to the sharp water mass change (e.g. *Calanoides carinatus*, *E. anchoita*) were common in all assemblages, but showed low abundance in a specific condition such as *E. anchoita* in summer (Muelbert et al. 2008). Regarding water mass as an environmental factor, rare taxa (e.g. *P. saltatrix*) probably less tolerant to different environmental conditions, were exclusively associated with particular water mass (e.g. STSW). While dominant taxa (e.g. *E. anchoita*), which tolerate a wide range of environmental conditions, occurred in different water mass but were preferentially associated to a particular water mass (e.g. PPW), where they had high abundance.

In summary the present study provides insights about the relative role of mesoscale oceanographic features, such as water masses, selecting species of fish larvae and influencing in the structure of larval fish assemblages. Our findings confirm the hypothesis, once fish larvae taxa show different responses to environmental forcing (Auth et al. 2011). Water masses influenced larval fish community in two ways: first, abundance of dominant taxa was determined by particular water

mass, which influenced species dominance in larval community; second rare-low frequent taxa were selected by particular water mass, however some associations were difficult do confirm due to rarity and/or occasionality of the selected taxa.

Acknowledgements

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Supporting Informaton

Appendix A. Description of sampled strategies applied during ichthyoplankton samples.

The 9 surveys used to obtain ichthyoplankton samples (Table S4.1) were initially designed to address different goals, then fish larvae were sampled using different gears and methods. Oblique hauls with a Bongo net, 300 µm mesh size and 0.6 m mouth diameter, were performed in Arepe and Conversut surveys from 5 m from the bottom to the surface at shallow water, and from 200 m depth at deep stations (Vasconcellos et al. 1998). During the Sueste surveys, horizontal subsurface hauls were performed in shallow stations (< 50 m depth), while oblique hauls were conducted from 5 m from the bottom to the surface at stations at intermediate depth (> 50 m and < 200 m depth), and from 200 m depth at stations deeper than 200 m. Vertically integrated samples conducted in the MCT-II were taken with WP-2 net between the surface and 10 m from the bottom at homogeneous water column and shallow water stations (up to 20 m), and from the chlorophyll maximum depth to the surface at deeper ones (Macedo-Soares et al. 2014).

Three sample strategies were used in La Plata surveys. First a vertically integrated tow performed at stations close to the 50 m and 200 m isobaths with a Motoda net, 300 µm mesh size and 0.6 m mouth diameter. In La Plata 2 survey, a WP-2 net with 140 µm mesh size (later replaced by a mesh of 500 µm) and 0.6 m mouth diameter was used in vertically integrated tows. The second strategy consisted in a two level vertical tow using a WP-2 net mounted on a closing mechanism structure, conducted at stations close to the 100 m isobaths. This net was further replaced in La Plata 2 survey by a conical net with 200 µm mesh size and 0.6 m mouth diameter. Finally, a horizontal two level tow, lasted 10 min., was performed at the Albardão transect (between 33ºS and 34ºS) with the Motoda net. All stratified samples were taken below and above the halocline. Two sub-samples were obtained with a Folson splitter and shared between University of Rio Grande (FURG-Brazil), used in this study, and National Institute for Fisheries Research and Development (INIDEP-Argentina).

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Supplementary Tables

Table S4.1. Oceanographic surveys performed in the South Brazil Shelf between Babitonga Bay (~26ºS) and Chuí (~34ºS, Brazil/Uruguay border) in the early 1980s and late 2000s.

Survey	Year/Season	Latitudinal range	Number of stations	Stations plankton sampling	Total catch of fish eggs	Total catch of fish larvae	Main sampled strategy	Net mesh and diameter
Arepe 2	1980/win	28º36'S to 34º40'S	86	25	9,562	751	oblique	300/0.6
Arepe 3	1980/spr	28º36'S to 34º40'S	90	18	23,388	729	oblique	300/0.6
Conversut 3	1981/sum	29º22'S to 40º34'S	37	16	427	370	oblique	250/0.8
Sueste 1	1982/win	24º06'S to 29º36'S	19	6	462	423	oblique	300/0.6
Sueste 3	1984/sum	24º26'S to 28º38'S	24	5	158	146	oblique	300/0.6
Sueste 4	1985/spr	24º06'S to 27º37'S	36	14	2,315	1,083	oblique	300/0.6
La Plata 1	2003/win	27º01'S to 39º18'S	45	19	863	2,359	vertical	300/0.6
La Plata 2	2004/sum	27º01'S to 39º18'S	49	21	142	167	vertical	300/0.6
MCT-II	2010/spr	21º36'S to 34º51'S	43	35	994	615	vertical	200/0.5

Mesh size in µm and net mouth diameter in m.

Table S4.2. Identification level of all families for each survey, results of taxonomic level selection and selected taxa for further data analysis. Full species names are given in Table S4.3.

Family	Identified to species level (%)						Identified to genus or species level (%)						Identified to species ≥ 75% of surveys (%)	Identified to genus ≥ 75% of surveys (%)	Taxonomic level For analysis	Selected taxa
	winter 80	spring 80	summer 80	winter 00	spring 00	summer 00	winter 80	spring 80	summer 80	winter 00	spring 00	summer 00				
Muraenidae	0	—	—	—	—	—	0	—	—	—	—	—	0	0	Family	Muraenidae
Ophichthidae	0	—	0	—	100	100	0	—	100	—	100	100	60	80	Genus	*Ophichthus* sp.
Congridae	—	—	—	—	100	—	—	—	—	—	100	—	50	50	Family	Congridae
Engraulidae	89	94	37	100	100	100	89	94	37	100	100	100	86	86	Species	*A. marinii*, *E. anchoita*, *Lycengraulis* sp.
Clupeidae	—	0	100	—	—	—	—	0	100	—	—	—	67	67	Family	Clupeidae
Microstomatidae	—	—	—	0	—	—	—	100	—	100	—	—	0	100	Genus	*Bathylagus* sp.
Gonostomatidae	0	—	—	0	25	—	0	50	—	83	75	—	0	50	Family	Gonostomatidae
Sternoptychidae	85	100	100	100	—	100	85	100	100	100	—	100	100	100	Species	*Maurolicus muelleri*
Phosichthyidae	—	100	50	—	100	—	—	100	100	—	100	—	67	100	Genus	*Pollichthys* sp., *Vinciguerria* sp.
Stomiidae	0	0	—	0	—	—	70	0	—	100	—	—	0	25	Family	Stomiidae
Synodontidae	—	33	0	—	90	0	—	33	0	—	91	25	40	40	Family	Synodontidae
Paralepididae	0	—	—	0	33	—	0	—	—	0	33	—	0	0	Family	Paralepididae
Myctophidae	0	0	0	21	91	0	0	6	0	71	98	11	14	14	Family	Myctophidae
Bregmacerotidae	63	21	75	—	80	0	97	100	100	—	81	100	50	100	Genus	*Bregmaceros* sp.
Macrouridae	0	—	—	0	—	0	0	—	—	50	—	0	0	0	Family	Macrouridae
Merlucciidae	100	—	100	100	0	—	100	—	100	100	100	—	75	100	Species	*M. hubbsi*

Table S4.2. (Continued)

Family	Identified to species level (%)						Identified to genus or species level (%)						Identified to species ≥ 75% of surveys (%)	Identified to genus ≥ 75% of surveys (%)	Taxonomic level For analysis	Selected taxa
	winter 80	spring 80	summer 80	winter 00	spring 00	summer 00	winter 80	spring 80	summer 80	winter 00	spring 00	summer 00				
Phycidae	100	100	—	100	100	—	100	100	—	100	100	—	80	80	Species	*U. brasiliensis, U. mystacea*
Ophidiidae	—	0	0	—	0	—	—	100	0	—	100	—	0	67	Family	Ophidiidae
Bythitidae	—	—	—	—	0	—	—	—	—	—	0	—	0	0	Family	Bythitidae
Mugilidae	—	—	—	—	0	—	—	—	—	—	100	—	0	100	Genus	*Mugil* sp.
Melamphaidae	0	—	—	—	—	—	100	—	—	—	—	—	0	100	Genus	*Poromitra* sp.
Trachichthyidae	—	100	—	—	—	—	—	100	—	—	—	—	100	100	Species	*H. mediterraneus*
Centriscidae	100	—	—	—	—	—	100	—	—	—	—	—	100	100	Species	*M. scolopax*
Scorpaenidae	0	—	—	—	100	0	0	—	—	—	100	0	25	25	Family	Scorpaenidae
Triglidae	—	0	0	—	0	0	—	100	100	—	100	100	0	100	Genus	*Prionotus* sp.
Serranidae	—	0	33	—	0	0	—	0	67	—	0	100	0	40	Family	Serranidae
Pomatomidae	—	100	100	—	—	100	—	100	100	—	—	100	100	100	Species	*Pomatomus saltatrix*
Carangidae	—	0	—	—	16	—	—	53	—	—	25	—	33	33	Family	Carangidae
Gerreidae	—	0	—	—	0	—	—	0	—	—	0	—	0	0	Family	Gerreidae
Sciaenidae	0	0	0	0	22	89	0	3	0	0	100	100	14	29	Family	Sciaenidae
Chiasmodontidae	0	—	0	—	—	—	100	—	0	—	—	—	0	50	Family	Chiasmodontidae
Blenniidae	0	—	0	—	100	—	0	—	0	—	100	—	25	25	Family	Blenniidae
Gobiidae	0	—	0	—	—	—	0	—	0	—	—	—	0	0	Family	Gobiidae
Sphyraenidae	—	—	—	—	50	0	—	—	—	—	75	0	0	33	Family	Sphyraenidae
Trichiuridae	33	100	99	—	100	100	33	100	99	—	100	100	83	83	Species	*L. caudatus, T. lepturus*

Family	Identified to species level (%)						Identified to genus or species level (%)						Identified to species ≥ 75% of surveys (%)	Identified to genus ≥ 75% of surveys (%)	Taxonomic level For analysis	Selected taxa
	winter 80	spring 08	summer 80	winter 00	spring 00	summer 00	winter 80	spring 80	summer 80	winter 00	spring 00	summer 00				
Scombridae	—	0	—	—	77	0	—	33	0	—	96	75	25	50	Family	Scombridae
Stromateidae	—	—	—	—	—	100	—	—	0	—	—	100	67	67	Family	Stromateidae
Caproidae	—	—	100	—	—	—	—	—	100	—	—	—	100	100	Species	*Antigonia capros*
Paralichthyidae	—	—	—	—	50	0	—	—	—	—	100	100	0	100	Genus	*Citharichthys* sp., *Etropus* sp.
Bothidae	—	0	0	—	0	33	—	0	0	—	0	33	0	20	Family	Bothidae
Cynoglossidae	0	—	0	—	50	12	0	—	0	—	100	88	0	50	Family	Cynoglossidae
Balistidae	—	—	—	—	—	0	—	—	—	—	—	0	0	0	Family	Balistidae

Table S4.3. Taxonomic list of fish larvae from the South Brazil Shelf, including total catch for the stations visited between Babitonga Bay (26ºS) and Chuí (34ºS), abundance (mean ± SE) and frequency (%) for each season (winter, spring and summer) in the 1980s and 2000s. *Species/taxa caught in only one sample. NA, not available.

Taxa	Total catch (n° of larvae)	Abundance ± SE (n°. · 100 m^{-3})						Frequency (%)					
		wi80	sp80	su80	wi00	sp00	su00	wi80	sp80	su80	wi00	sp00	su00
Muraenidae													
Muraenidae spp.	3	0.04±0.04	—	—	—	—	—	3.2*	—	—	—	—	—
Congridae													
Ariosoma balearicum (Delaroche, 1809)	1	—	—	—	—	0.07±0.07	—	—	—	—	—	2.9*	—
Ophichthidae													
Ophichthus gomesii (Castelnau, 1855)	3	—	—	—	—	0.08±0.08	0.05±0.04	—	—	—	—	2.9*	9.5*
Ophichthus sp.	1	—	—	NA	—	—	—	—	—	4.8*	—	—	—
Ophichthidae spp.	1	NA	—	—	—	—	—	3.2*	—	—	—	—	—
Clupeidae													
Sardinella brasiliensis (Steindachner, 1879)	2	—	—	0.16±0.15	—	—	—	—	—	4.8*	—	—	—
Clupeidae spp.	65	—	0.03±0.03	—	—	—	—	—	25	—	—	—	—
Engraulidae													
Anchoa marinii Hildebrand, 1943	15	0.28±0.28	—	0.07±0.07	—	—	—	3.2*	—	9.5	—	—	—
Engraulis anchoita Hubbs and Marini, 1935	3732	6.45±2.46	13.74±6.47	3.97±2.75	54.97±37.69	40.83±17.43	0.58±0.25	67.7	62.5	19	42.1	37.1	23.8
Lycengraulis sp.	1	0.09±0.09	—	—	—	—	—	3.2*	—	—	—	—	—
Engraulidae spp.	157	1.53±0.67	NA	NA	—	—	—	29	12.5	19	—	—	—
Microstomadidae													
Bathylagus sp.	27	—	NA	—	0.99±0.99	—	—	—	3.1*	—	5.3*	—	—
Gonostomatidae													
Cyclothone acclinidens Garman, 1899	1	—	—	—	—	0.07±0.07	—	—	—	—	—	2.9*	—
Cyclothone alba Brauer, 1906	1	—	—	—	—	0.08±0.08	—	—	—	—	—	2.9*	—
Cyclothone sp.	8	—	NA	—	0.27±0.27	—	—	—	3.1*	—	5.3*	—	—
Cyclothone spp.	6	—	—	—	—	0.38±0.20	—	—	—	—	—	11.4	—
Gonostoma sp.	1	—	—	—	0.02±0.02	—	—	—	—	—	5.3*	—	—
Gonostomatidae spp.	31	NA	NA	—	0.14±0.14	—	—	3.2*	3.1*	—	5.3*	—	—
Sternoptychidae													
Maurolicus muelleri (Gmelin, 1789)	112	0.52±0.20	0.17±0.09	0.06±0.05	0.07±0.05	—	0.21±0.21	35.5	21.9	9.5	10.5	—	4.8*
Sternoptychidae spp.	12	0.08±0.08	—	—	—	—	—	3.2*	—	—	—	—	—
Phosichthyidae													
Pollichthys mauli (Poll, 1953)	4	—	NA	NA	—	—	—	—	3.1*	4.8*	—	—	—

Surveys: wi80, winter 1980s; sp80, spring 1980s; su80, summer 1980s; wi00, winter 2000s; sp00, spring 2000s; su00, summer 2000s.

Table S4.3. (Continued)

Taxa	Total catch (n° of larvae)	Abundance ± SE (n°. · 100 m^{-3})						Frequency (%)					
		wi80	sp80	su80	wi00	sp00	su00	wi80	sp80	su80	wi00	sp00	su00
Vinciguerria nimbaria (Jordan & Williams, 1895)	1	—	—	—	—	0.06±0.05	—	—	—	—	—	2.9*	—
Vinciguerria sp.	1	—	—	NA	—	—	—	—	—	4.8*	—	—	—
Stomiidae													
Melanostomiinae sp.	1	—	—	—	0.02±0.02	—	—	—	—	—	5.3*	—	—
Stomiinae sp.	1	—	—	—	0.04±0.04	—	—	—	—	—	5.3*	—	—
Idiacanthus sp.	7	0.07±0.05	—	—	—	—	—	9.7	—	—	—	—	—
Stomiidae spp.	4	0.02±0.02	NA	—	—	—	—	3.2*	3.1*	—	—	—	—
Synodontidae													
Synodus foetens (Linnaeus, 1766)	18	—	0.15±0.09	—	—	1.15±0.46	—	—	9.4	—	—	17.1	—
Synodus sp.	1	—	—	—	—	—	0.16±0.16	—	—	—	—	—	4.8*
Synodontidae spp.	35	—	NA	0.53±0.3	—	0.20±0.20	0.20±0.14	—	12.5	28.6	—	2.9*	9.5
Paralepididae													
Lestrolepis intermedia (Poey, 1868)	1	—	—	—	—	0.07±0.07	—	—	—	—	—	2.9*	—
Paralepididae spp.	11	0.02±0.02	—	—	0.09±0.06	0.13±0.13	—	6.5	—	—	10.5	2.9*	—
Myctophidae													
Benthosema sp.	1	—	—	—	—	—	0.04±0.04	—	—	—	—	—	4.8*
Hygophum reinhardtii (Lütken, 1892)	22	—	—	—	0.71±0.31	—	—	—	—	—	31.6	—	—
Myctophum sp.	3	—	—	—	0.05±0.05	—	—	—	—	—	5.3*	—	—
Myctophum spp.	2	—	—	—	—	0.14±0.10	—	—	—	—	—	5.7	—
Symbolophorus sp.	20	—	—	—	0.45±0.33	—	—	—	—	—	10.5	—	—
Ceratoscopelus warmingii (Lütken, 1892)	2	—	—	—	—	0.17±0.14	—	—	—	—	—	5.7	—
Ceratoscopelus townsendi (Eigenmann & Eigenmann, 1889)	6	—	—	—	—	0.49±0.27	—	—	—	—	—	11.4	—
Ceratoscopelus sp.	19	—	NA	—	0.66±0.53	—	—	—	3.1*	—	21.1	—	—
Diaphus garmani Gilbert, 1906	8	—	—	—	—	0.07 ±0.51	—	—	—	—	—	5.7	—
Diaphus brachycephalus Tåning, 1928	54	—	—	—	—	3.77±1.89	—	—	—	—	—	20.0	—
Diaphus mollis Tåning, 1928	30	—	—	—	—	2.41 ±0.95	—	—	—	—	—	22.9	—
Diaphus sp.	4	—	—	—	0.15±0.15	—	—	—	—	—	5.3*	—	—
Diaphus spp.	1	—	—	—	—	0.06±0.05	—	—	—	—	—	2.9*	—
Lampadena luminosa (Garman, 1899)	5	—	—	—	—	0.28±0.29	—	—	—	—	—	2.9*	—
Lampadena sp.	4	—	—	—	0.25±0.19	—	—	—	—	—	10.5	—	—
Lampanyctus lepidolychnus Becker, 1967	1	—	—	—	—	0.07±0.07	—	—	—	—	—	2.9*	—
Lampanyctus sp.	12	—	NA	—	0.34±0.18	—	—	—	3.1*	—	21.1	—	—
Lepidophanes guentheri (Goode & Bean, 1896)	2	—	—	—	—	0.16±0.12	—	—	—	—	—	5.7	—
Lepidophanes sp.	5	—	—	—	—	0.28±0.29	—	—	—	—	—	2.9*	—
Lobianchia gemellarii (Cocco, 1838)	1	—	—	—	—	0.12±0.12	—	—	—	—	—	2.9*	—

Surveys: wi80, winter 1980s; sp80, spring 1980s; su80, summer 1980s; wi00, winter 2000s; sp00, spring 2000s; su00, summer 2000s.

Table S4.3. (Continued)

Taxa	Total catch (n° of larvae)	Abundance ± SE (n°. · 100 m⁻³)						Frequency (%)					
		wi80	sp80	su80	wi00	sp00	su00	wi80	sp80	su80	wi00	sp00	su00
Notoscopelus sp.	2	—	—	—	0.04±0.04	—	—	—	—	—	5.3*	—	—
Myctophidae spp.	813	1.68±0.48	3.3±1.23	4.87±4.58	0.88±0.27	0.19±0.14	0.32±0.32	48.4	31.2	28.6	47.4	5.7	4.8*
Bregmacerotidae													
Bregmaceros cantori Milliken & Houde, 1984	74	0.34±0.2	0.13±0.08	11.58±10.57	—	2.63±1.44	—	19.4	9.4	33.3	—	14.3	—
Bregmaceros sp.	83	—	NA	NA	—	—	1.72±0.64	—	9.4	14.3	—	—	42.9
Bregmacerotidae spp.	8	<0.01	—	—	—	0.43±0.34	—	3.2*	—	—	—	5.7	—
Macrouridae													
Coryphoenoides sp.	1	—	—	—	0.02±0.02	—	—	—	—	—	5.3*	—	—
Macrouridae spp.	5	0.03±0.03	—	—	0.09±0.09	—	0.03±0.03	3.2*	—	—	5.3*	—	4.8*
Merlucciidae													
Merluccius hubbsi Marini, 1933	19	0.08±0.06	—	NA	0.41±0.26	—	—	6.5	—	4.8*	21.1	—	—
Merluccius sp.	1	—	—	—	—	0.04±0.03	—	—	—	—	—	2.9*	—
Phycidae													
Urophycis brasiliensis (Kaup, 1858)	3	0.01±0.01	<0.01	—	—	—	—	3.2*	3.1*	—	—	—	—
Urophycis mystacea Miranda Ribeiro, 1903	20	0.23±0.08	—	—	0.16±0.16	0.72±0.35	—	29	—	—	5.3*	14.3	—
Ophidiidae													
Ophidion sp.	2	—	NA	—	—	—	—	—	3.1*	—	—	—	—
Lepophidium sp.	1	—	—	—	—	0.08±0.08	—	—	—	—	—	2.9*	—
Ophidiidae spp.	3	—	—	NA	—	—	—	—	—	4.8*	—	—	—
Bythitidae													
Bythitidae sp.	3	—	—	—	—	1.09±1.08	—	—	—	—	—	2.9*	—
Mugilidae													
Mugil sp.	2	—	—	—	—	0.24±0.20	—	—	—	—	—	5.7	—
Melamphaidae													
Poromitra sp.	1	NA	—	—	—	—	—	3.2*	—	—	—	—	—
Trachichthyidae													
Hoplostethus mediterraneus mediterraneus Cuvier, 1829	1	—	NA	—	—	—	—	—	3.1*	—	—	—	—
Centriscidae													
Macroramphosus scolopax (Linnaeus, 1758)	1	0.02±0.02	—	—	—	—	—	3.2*	—	—	—	—	—
Scorpaenidae													
Pontinus rathbuni Goode & Bean, 1896	2	—	—	—	—	0.20±0.14	—	—	—	—	—	5.7	—
Scorpaenidae spp.	6	NA	—	—	—	—	0.29±0.17	3.2*	—	—	—	—	19.0
Triglidae													
Prionotus sp.	12	—	NA	0.33±0.22	—	0.39±0.25	0.02±0.02	—	6.2	14.3	—	8.6	4.8*

Surveys: wi80, winter 1980s; sp80, spring 1980s; su80, summer 1980s; wi00, winter 2000s; sp00, spring 2000s; su00, summer 2000s.

Table S4.3. (Continued)

Taxa	Total catch (n° of larvae)	Abundance ± SE (n°. · 100 m⁻³)						Frequency (%)					
		wi80	sp80	su80	wi00	sp00	su00	wi80	sp80	su80	wi00	sp00	su00
Serranidae													
Anthias sp.	1	—	—	NA	—	—	—	—	—	4.8*	—	—	—
Epinephelus niveatus (Valenciennes, 1828)	1	—	—	0.04±0.02	—	—	—	—	—	4.8*	—	—	—
Centropristis sp.	2	—	—	—	—	—	0.26±0.18	—	—	—	—	—	9.5
Serranidae spp.	57	—	NA	NA	—	0.29±0.29	—	—	3.1*	4.8*	—	2.9*	—
Pomatomidae													
Pomatomus saltatrix (Linnaeus, 1766)	3	—	NA	0.11±0.07	—	—	0.05±0.05	—	3.1*	9.5	—	—	4.8*
Carangidae													
Parona signata (Jenyns, 1841)	2	—	—	—	—	0.19±0.19	—	—	—	—	—	2.9*	—
Trachinotus sp.	36	—	NA	—	—	0.10±0.10	—	—	15.6	—	—	2.9*	—
Carangidae spp.	40	—	NA	—	—	0.64±0.34	—	—	12.5	—	—	11.4	—
Gerreidae													
Gerreidae spp.	63	—	NA	—	—	0.46±0.32	—	—	3.1*	—	—	5.7	—
Sciaenidae													
Menticirrhus sp.	1	—	NA	—	—	—	—	—	3.1*	—	—	—	—
Bairdiella sp.	4	—	—	—	—	0.37±0.24	—	—	—	—	—	8.6	—
Cynoscion sp.	2	—	—	—	—	0.58±0.42	—	—	—	—	—	5.7	—
Larimus sp.	1	—	—	—	—	0.10±0.10	—	—	—	—	—	2.9*	—
Micropogonias furnieri (Desmarest, 1823)	7	—	—	—	—	0.47±0.39	0.15±0.13	—	—	—	—	5.7	9.5
Paralonchurus brasiliensis (Steindachner, 1875)	3	—	—	—	—	—	0.08±0.08	—	—	—	—	—	4.8*
Paralonchurus sp.	1	—	—	—	—	—	0.04±0.04	—	—	—	—	—	4.8*
Sciaenidae spp.	69	0.07±0.07	1.17±1.09	2.07±1.73	0.13±0.13	—	—	9.7	15.6	9.5	5.3*	—	—
Chiasmodontidae													
Chiasmodon sp.	17	—	—	0.06±0.05	—	—	—	—	—	4.8*	—	—	—
Chiasmodontidae spp.	1	0.33±0.28	—	—	—	—	—	12.9	—	—	—	—	—
Blenniidae													
Hypleurochilus fissicornis (Quoy & Gaimard, 1824)	2	—	—	—	—	0.36±0.27	—	—	—	—	—	5.7	—
Blenniidae spp.	3	NA	—	NA	—	—	—	3.2*	—	4.8*	—	—	—
Gobiidae													
Gobiidae spp.	4	0.02±0.02	—	0.43±0.25	—	—	—	3.2*	—	14.3	—	—	—
Sphyraenidae													
Sphyraena barracuda (Edwards, 1771)	1	—	—	—	—	0.04±0.03	—	—	—	—	—	2.9*	—
Sphyraena tome Fowler, 1903	1	—	—	—	—	0.19±0.14	—	—	—	—	—	5.7	—
Sphyraena spp.	2	—	—	—	—	0.26±0.27	—	—	—	—	—	2.9*	—
Sphyraenidae spp.	1	—	—	—	—	—	0.05±0.05	—	—	—	—	—	4.8*

Surveys: wi80, winter 1980s; sp80, spring 1980s; su80, summer 1980s; wi00, winter 2000s; sp00, spring 2000s; su00, summer 2000s.

Table S4.3. (Continued)

Taxa	Total catch (n° of larvae)	Abundance ± SE (n°. · 100 m^{-3})						Frequency (%)					
		wi80	sp80	su80	wi00	sp00	su00	wi80	sp80	su80	wi00	sp00	su00
Trichiuridae													
Lepidopus caudatus (Euphrasen, 1788)	1	—	—	0.06±0.05	—	—	—	—	—	4.8*	—	—	—
Trichiurus lepturus Linnaeus, 1758	149	0.02±0.02	0.38±0.22	60.07±39.35	—	1.21 ±0.49	0.75±0.46	3.2*	12.5	47.6	—	17.1	19.0
Trichiuridae spp.	3	0.01±0.01	—	NA	—	—	—	3.2*	—	4.8*	—	—	—
Scombridae													
Auxis sp.	4	—	0.01±0.01	—	—	—	0.08±0.08	—	3.1*	—	—	—	4.8*
Euthynnus alletteratus (Rafinesque, 1810)	15	—	—	—	—	1.60±1.49	—	—	—	—	—	5.7	—
Katsuwonus pelamis (Linnaeus, 1758)	1	—	—	—	—	0.08±0.08	—	—	—	—	—	2.9*	—
Scomber colias Gmelin, 1789	1	—	—	—	—	0.36±0.35	—	—	—	—	—	2.9*	—
Thunnus spp.	4	—	—	—	—	0.87±0.79	—	—	—	—	—	5.7	—
Scombridae spp.	6	—	0.05±0.04	1.43±1.32	—	0.10±0.10	0.05±0.05	—	3.1*	9.5	—	2.9*	4.8*
Stromateidae													
Peprilus paru (Linnaeus, 1758)	2	—	—	—	—	—	0.06±0.04	—	—	—	—	—	9.5
Stromateidae spp.	22	—	—	5.77±3.48	—	—	—	—	—	23.8	—	—	—
Caproidae													
Antigonia capros Lowe, 1843	1	—	—	NA	—	—	—	—	—	4.8*	—	—	—
Paralichthyidae													
Citharichthys sp.	3	—	—	—	—	0.08±0.08	—	—	—	—	—	2.9*	—
Etropus longimanus Norman, 1933	1	—	—	—	—	0.26±0.27	—	—	—	—	—	2.9*	—
Bothidae													
Bothus ocellatus (Spix & Agassiz, 1831)	1	—	—	—	—	—	0.10±0.10	—	—	—	—	—	4.8*
Bothidae spp.	13	—	NA	NA	—	0.20±0.20	0.20±0.17	—	6.2	9.5	—	2.9*	9.5
Cynoglossidae													
Symphurus ginsburgi Menezes & Benvegnú, 1976	1	—	—	—	—	—	0.03±0.03	—	—	—	—	—	4.8*
Symphurus plagiusa (Linnaeus, 1766)	1	—	—	—	—	0.08±0.08	—	—	—	—	—	2.9*	—
Symphurus trewavasae Chabanaud, 1948	1	—	—	—	—	0.08±0.08	—	—	—	—	—	2.9*	—
Symphurus kyaropterygium Menezes & Benvegnú, 1976	4	—	—	—	—	0.69±0.59	—	—	—	—	—	5.7	—
Symphurus sp.	6	—	—	—	—	—	0.27±0.19	—	—	—	—	—	9.5
Symphurus spp.	6	—	—	—	—	0.72±0.47	—	—	—	—	—	8.6	—
Cynoglossidae spp.	13	0.01±0.01	—	0.24±0.17	—	—	0.02±0.02	3.2*	—	14.3	—	—	4.8*
Balistidae													
Balistidae spp.	2	—	—	—	—	—	0.07±0.05	—	—	—	—	—	9.5
Unidentified Anguilliformes	15	0.1±0.05	0.07±0.06	0.04±0.02	—	0.19±0.14	0.04±0.04	12.9	6.2	4.8*	—	5.7	4.8*
Unidentified Pleuronectiformes	66	—	0.37±0.30	3.56±2.62	—	—	0.50±0.27	—	25	42.9	—	—	19.0
Unidentified larvae	389	0.8±0.36	1.99±1.16	12.85±7.65	0.53±0.22	21.94±9.69	0.60±0.31	35.5	53.1	81.0	31.6	62.9	33.3

Surveys: wi80, winter 1980s; sp80, spring 1980s; su80, summer 1980s; wi00, winter 2000s; sp00, spring 2000s; su00, summer 2000s.

Table S4.4. Results of cross-validation for Canonical Analysis of Principal Coordinates (CAP) showing allocations derived from leave-one-out procedure of observations to classified groups.

Original group	Classified group			Total	% correct
	PPW	**STSW**	**TW**		
PPW	30	16	3	49	60.0
STSW	20	42	8	70	61.2
TW	0	5	10	15	66.7

Water masses groups: PPW, Plata Plume Water; STSW, Subtropical Shelf Water; TW, Tropical Water.

Table S4.5. Single explanatory variables GAM fits for CAP axes showing the effective degrees of freedom (edf) with significance and percentage of deviance explained.

Models	n	CAP 1		CAP 2	
		edf	% deviance	edf	% deviance
s(Temperature)	132	**3.07**	19.2	**1.00**	10.4
s(Salinity)	132	**1.43**	14.5	1.00^{ns}	2.3
s(Sigma-T)	132	**2.18**	9.7	8.50^{*}	15.0

All terms (edf) in bold were significant with $p<0.01$, * $p<0.05$, ^{ns} non-significant. Smooth functions = s().

Supplementary Figures
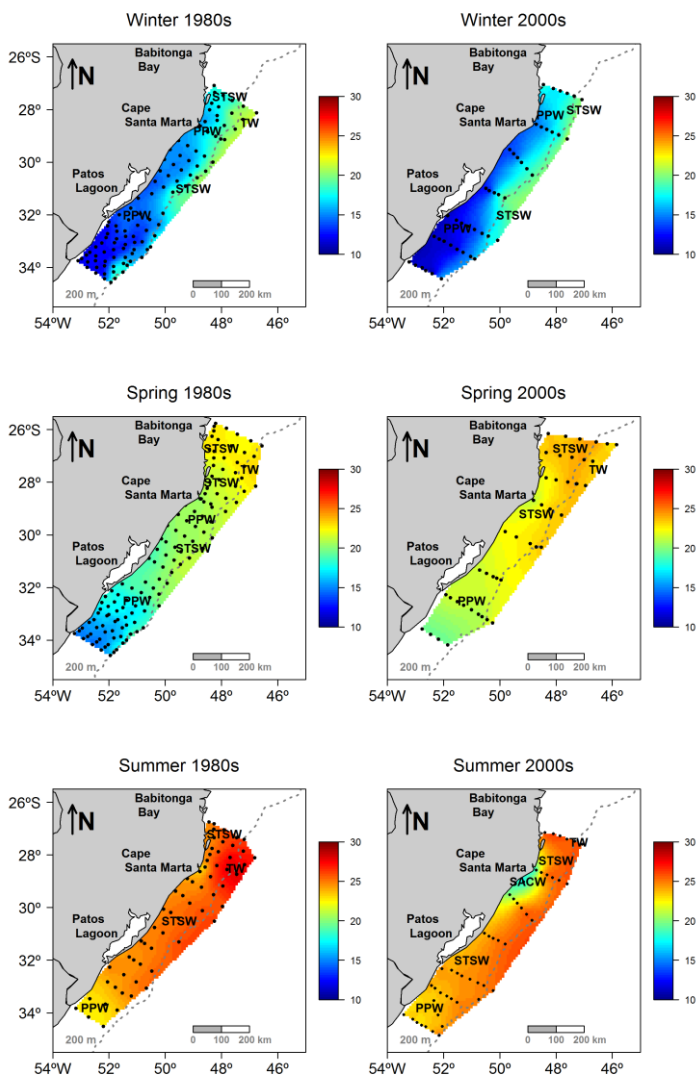
Fig. S4.1. Interannual and seasonal temperature (ºC) horizontal distribution at 10 m depth. Water masses: Plata Plume Water (PPW), Subtropical Shelf Water (STSW), Tropical Water (TW), South Atlantic Central Water (SACW).
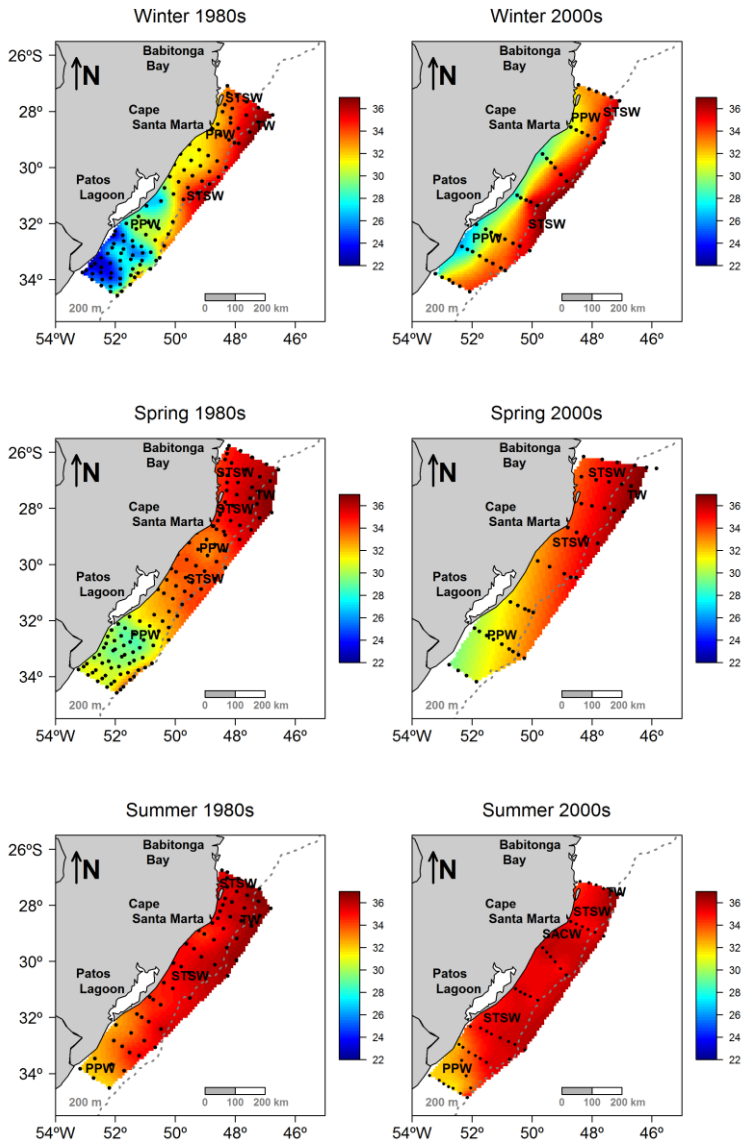
Fig. S4.2. Interannual and seasonal salinity horizontal distribution at 10 m depth. Water masses: Plata Plume Water (PPW), Subtropical Shelf Water (STSW), Tropical Water (TW), South Atlantic Central Water (SACW).
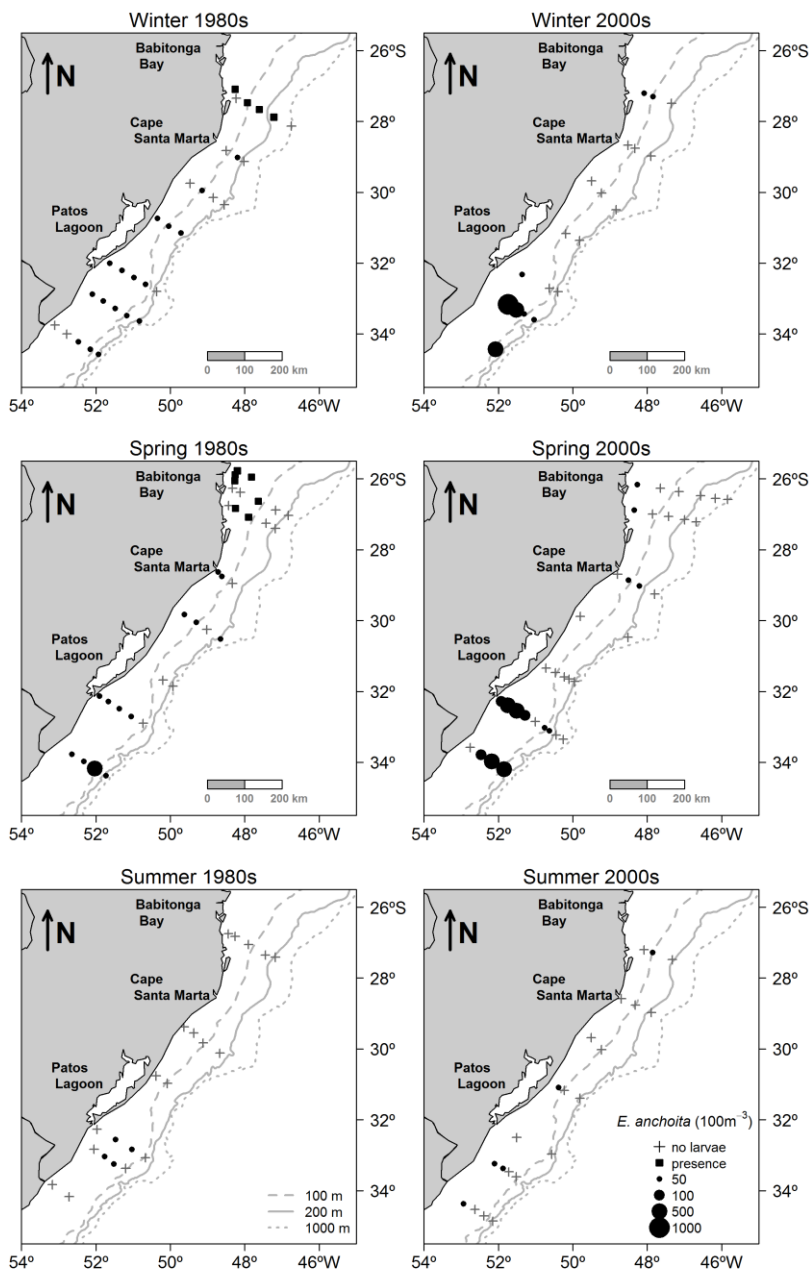
Fig. S4.3. Interannual and seasonal distribution of *Engraulis anchoita* larvae.
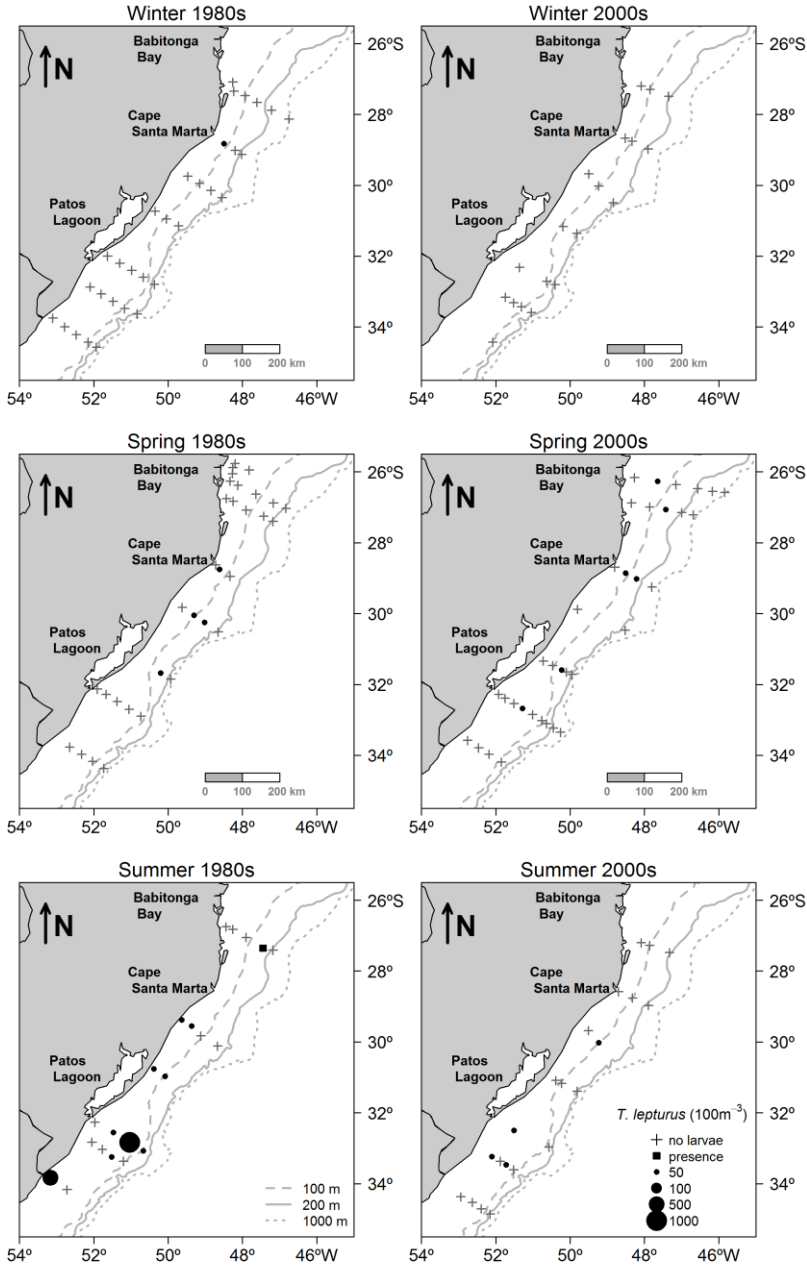
Fig. S4.4. Interannual and seasonal distribution of *Trichiurus lepturus* larvae.
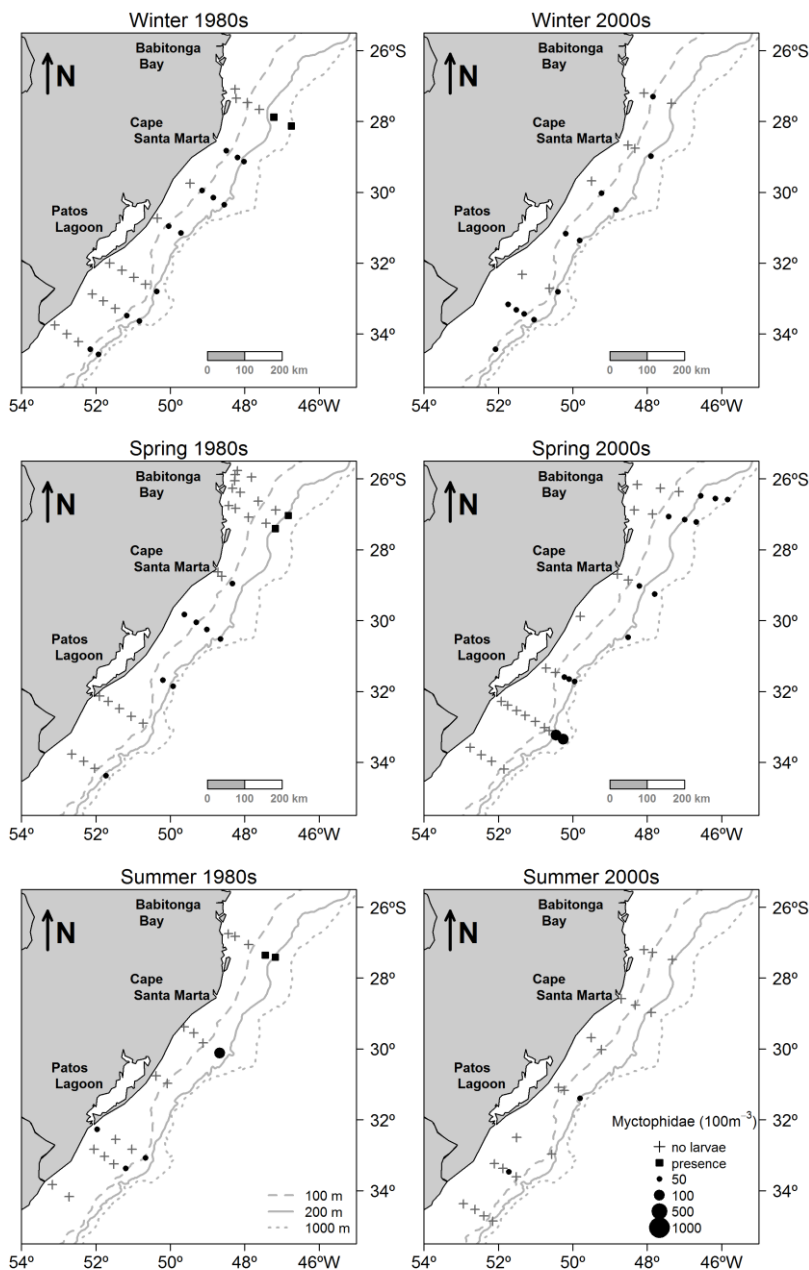
Fig. S4.5. Interannual and seasonal distribution of Myctophidae larvae.

5 CAPÍTULO 3 – Nonstationary effects of climate and oceanography on interannual variability of the Bonaerense population of the anchovy *Engraulis anchoita*

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Highlights

- Climate and oceanography affects ecosystem and productivity of Bonaerense anchovy.

- Anchovy spawning habitat is cool, low-salinity Plata Plume Water.

- Plata Plume Water distribution influenced by Rio de La Plata outflow and winds.

- Climate change hypothesized to negatively affect Bonaerense anchovy and fishery.

Nonstationary effects of climate and oceanography on interannual variability of the Bonaerense population of the anchovy *Engraulis anchoita*

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Abstract: The Bonaerense population of the anchovy *Engraulis anchoita* is important for both fisheries and trophic relations in the pelagic ecosystem in the western South Atlantic Ocean. It is well known that climate and oceanography affect the productivity of small pelagic fish, including anchovies, and the spawning habitat. This study investigates nonstationary effects of climate and oceanography on the interannual variability of the anchovy *Engraulis anchoita* Bonaerense population and its spawning and larva habitats. Two datasets were used, one with 50 years of data on the environment and anchovy population and other with 30 years of data from ichthyoplankton surveys. Results showed that climate (*e.g.*, the Southern Annular Mode, SAM) affects anchovy landings negatively through increased river flow and wind from the northeast. Spawning and larva habitats were defined using thermohaline limits of the cool and low salinity Plata Plume Water, whose distribution is influenced by the Rio de La Plata outflow and wind dynamics. Climate acts on the spawning and larva habitats through changes in the balance between river flow discharge and northward displacement of the estuarine front over the continental shelf, which modifies enrichment, concentration and retention and, thus, suitable habitat for anchovy. We hypothesize that climate change, manifest by increased SAM and frequency and intensity of extreme ENSO events,

will negatively affect the Bonaerense anchovy population and its fisheries.

Key Words: small pelagic fish, Southern Annular Mode, El Niño Southern Oscillation, western South Atlantic Ocean, ocean triads, climate change

Introduction

Small pelagic fish such as those belonging to the genus *Engraulis* are abundant in different productive coastal ecosystems around the globe (Checkley et al., 2009). In the western South Atlantic Ocean, *Engraulis anchoita* Hubbs & Marini, 1935, known locally as anchoita, is distributed from Gulf San Jorge (Argentina, 48ºS) to Cape São Tomé (Brazil, 20ºS) (Bakun and Parrish, 1991) (Fig. 5.1). There are three stocks of *E. anchoita*, the Patagonic between 48ºS and 41ºS, the Bonaerense between 41ºS and 28ºS, and the Southeastern Brazilian Bight (SBB) stock between 28ºS and 20ºS (Sánchez and Ciechomski, 1995; Carvalho and Castello, 2013). Regarding fisheries, the Bonaerense is considered the main stock with an estimated biomass of 1.6 to 5.4 MMT, in contrast to 0.4 to 2 MMT for the Patagonian stock and 0.2 to 0.4 MMT for the unexploited SBB stock (Castello, 1989; Hansen et al., 2010; Madirolas et al., 2013). Besides its importance to fisheries, the anchovy *E. anchoita* is an important prey for other commercially exploited species like hake, mackerel and squid, and also for species of marine mammals and birds (Angelescu, 1982).

Bonaerense anchovy performs two seasonal migrations: between coastal (< 50 m depth) and deeper shelf waters and between Argentine/Uruguay and southern Brazilian waters (Sánchez and Ciechomski, 1995; Castello, 2007). In the first migration, anchovy spawners move from nutrient (nitrate) rich waters of subantarctic origin over the shelf, where they feed intensively on large zooplankton (Carreto et al., 1986; Pájaro, 2002), to coastal waters under influence of Rio de La Plata (Plata hereafter) estuary, where the main spawning activity occurs in October and November (Sánchez and Ciechomski, 1995). However, eggs and larvae are present throughout the year over the continental shelf where relatively cold and low salinity Plata Plume Water (PPW) provides vertical stability and allows zooplankton to aggregate, ensuring a suitable environment for larva feeding and growth (Sánchez and Ciechomski, 1995; Guerrero et al., 1997; Viñas et al., 2002; Piola et al., 2008). A second migration occurs in late austral fall

and winter, with the northward displacement of PPW caused by strong southerly (*i.e.*, from the south) winds (Lima and Castello, 1995; Piola et al., 2008). In southern Brazilian waters, PPW is enhanced by Lagoa dos Patos (Patos hereafter) runoff. During a migration that can reach as far north as 31ºS, anchovy spawn in Brazilian waters until early austral spring, when they return to Argentine waters with the retreat of PPW to the south associated with the intensification of the northeasterly winds (Lima and Castello, 1995; Castello, 2007). Upon their return to the Argentine shelf, Bonaerense anchovy join the remaining stock for the austral spring spawning peak (Sánchez and Ciechomski, 1995).

Along the slope waters of the Bonaerense anchovy habitat, two water masses are transported southward by the Brazil Current (BC), warm and salty oligotrophic Tropical Water (TW) in the upper layer, and cold, nitrate-rich South Atlantic Central Water (SACW) between 200 and 500 m (Silveira et al., 2000; Braga et al., 2008). Subantarctic waters of the Malvinas (Falklands) Current (MC) flow northeastward (Fig. 5.1), originating as a branch of the Antarctic Circumpolar Current (Sánchez and Ciechomski, 1995). Around 38ºS, BC and MC converge in the Brazil-Malvinas Confluence (BMC), a zone of high primary production (Garcia et al., 2004). The area is also influenced by the Subtropical Shelf Water (STSW) in the north, a mixture between the Plata Plume Water (PPW) and TW, and in the south by the Subantarctic Shelf Water (SASW) with high phosphate concentration (Braga et al., 2008; Möller Jr. et al., 2008). Different oceanographic processes promote enrichment and enhance primary production in the Bonaerense anchovy habitat. Near Cape Santa Marta, SACW is upwelled by dominant northeasterly winds during spring and summer (Acha et al., 2004), affecting local pelagic production mostly south of the cape, where cross-shore Ekman transport along the coast turns more intense and upwelling driven by topography and wind stress curl is more significant (Odebrecht and Djurfelt, 1996; Campos et al., 2013; Mazzini and Barth, 2013). Plata and Patos estuaries (Fig. 5.1) combined discharge on average about 25,000 m^3 s^{-1} freshwater (Möller Jr. et al., 2008) and contribute to the high silicate concentration over coastal and shelf waters (Ciotti et al., 1995; Braga et al., 2008). Surface salinity in the Plata estuary is controlled by wind and river discharge, and is characterized by strong vertical salinity stratification (Guerrero et al., 1997; Acha et al., 2008), whereas salinity distribution in the Patos estuary are mainly affected by regional precipitation and winds (Acha et al., 2004). The Argentine shelf brake front, resulting from a mixture of SASW and waters of MC, is the main source of nitrate in the southern

portion of the Bonaerense anchovy habitat, reaching values higher then 10 μM (Carreto et al., 1986). Around the 50 m isobath at 33ºS, the Subtropical Shelf Front, a sharp thermohaline frontal system between STSW and SASW (Piola et al., 2008), increases local nutrient flux to the euphotic zone, primary production and zooplankton abundance (Muelbert et al., 2008).
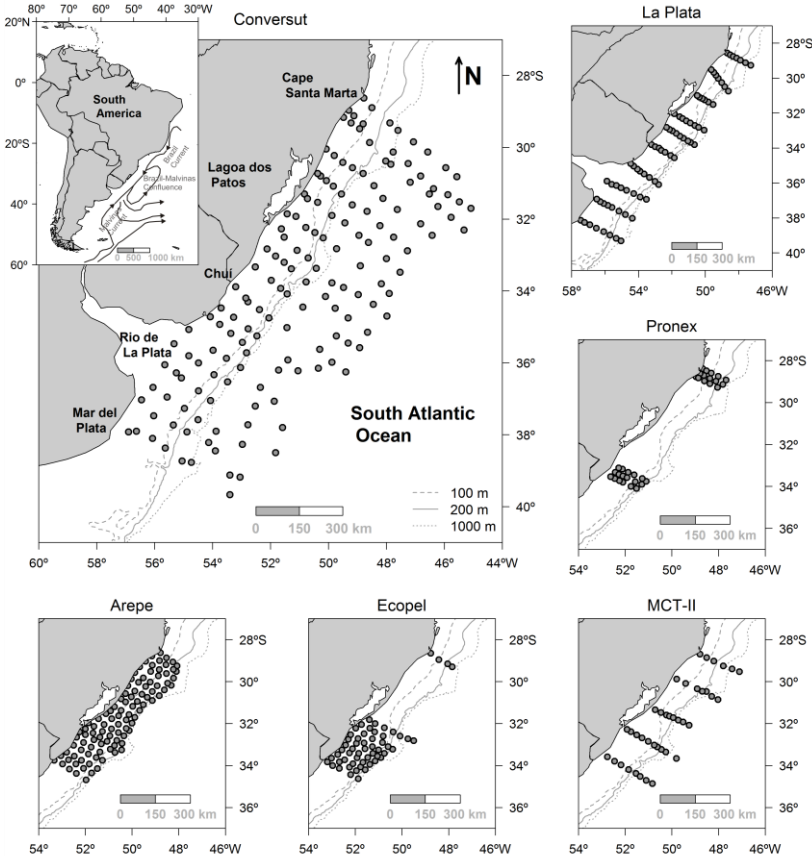
Fig. 5.1. Location of the Bonaerense anchovy (*Engraulis anchoita*) in the western South Atlantic Ocean, from Cape Santa Marta (28ºS) to Mar del Plata (40ºS). Also shown are the distributions of sampled stations from the ichthyoplankton surveys performed between 1977 and 2010. Details of the main circulation (small panel) according to Acha et al. (2004). Names in the top of each panel indicate each respectively survey (see Table A5.1).

Climate affects marine ecosystems and ecological processes on a variety of time scales, from seasonal to centennial (Stenseth et al., 2002; Lehodey et al., 2006). Climate variability is a strong driver of changes in the productivity of small pelagic fish (e.g., Lloret et al., 2001; Lloret et al., 2004; Borja et al., 2008), and it has been hypothesized to affect the spatial and temporal location of suitable spawning habitat (Hunter and Alheit, 1995). *Engraulis* species are affected by changes in climate, mediated by their habitat, and react to environmental change rapidly due to their biological characteristics: high mobility, short life span, high fecundity, feeding on plankton and, in some cases, spawning all year (Alheit et al., 2009). Predicting changes in the abundance of small pelagic fish associated with climate change is still considered a challenge, while predicting changes in spawning and larva habitats may be more feasible (Castro et al., 2005; Fréon et al., 2009).

Spawning habitat can be separated into three components: (1) potential spawning habitat, where environmental conditions are suitable for spawning; (2) realized spawning habitat, where spawning actually occurs and eggs and/or larvae are found; and, (3) successful spawning habitat, where spawning results in successful recruits (Castro et al., 2005). Analysis of egg and larva abundance and distribution is generally used to assess spawning and larva habitats, for these stages are more easily sampled than adults and indicate active spawing and larva occurrence (van der Lingen et al., 2001). Such data identify the realized spawning habitat and can be used to delineate potential spawning habitat (Castro el al., 2005). Habitat can be identified in relation to a variety of environmental variables, including sea surface temperature (*e.g.*, Lluch-Belda et al., 1991; Checkley et al., 2000; van der Lingen et al., 2001), salinity (*e.g.*, Palomera et al., 2007; Planque et al., 2007; Basilone et al., 2013), phytoplankton biomass (*e.g.*, Twatwa et al., 2005; Claramunt et al., 2012), dynamic height (Asch and Checkley, 2013) and remotely sensed sea surface temperature and chlorophyll (Reiss et al., 2008).

In the Southern Hemisphere the dominant mode of climate variability is the Southern Annular Mode (SAM), also known as the Antarctic Oscillation (AAO) but opposite in sign, which is associated with differences in sea level pressure anomalies between Antarctica and mid latitudes (Marshall, 2003; Jones et al., 2009). SAM covaries with climate over the Southeastern South America (SESA), including a positive relationship and nonstationary impacts (*i.e.*, varying over time) on precipitation during austral spring (Silvestri and Vera, 2003; Silvestri and Vera, 2009). However, there are no studies on the influence of SAM

on fisheries stocks in the western South Atlantic Ocean. Precipitation over SESA is also influenced by the El Niño Southern Oscillation (ENSO), where a high negative Southern Oscillation Index (SOI) value (El Niño) is related to positive precipitation anomalies over the region (Aceituno, 1988, Ropelewski and Halpert, 1989) and positive river flow anomalies in the Plata basin (Mechoso and Iribarren, 1992). In addition, El Niño events are related to anomalously cold waters in both the Malvinas Current and Brazil-Malvinas Confluence region, and warm waters of the Brazil Current (Severov et al., 2004). Recruitment of whitemouth croaker, an important fishery at the Plata estuary, and pink-shrimp in the Patos estuary, are negatively related to extreme river discharges during El Niño (Möller Jr. et al., 2009; Acha et al., 2012).

Oceanography also plays a central role in small pelagic fish production (*e.g.*, Lima and Castello, 1995; Checkley et al., 2000; Borja et al., 2008). Temperature, for example, is an important environmental condition controlling the rates of growth and metabolism in the early stages of fishes (Pepin, 1991). The availability of food of suitable size and quantity at first feeding by a larva, and the overlap between zooplankton and larval production, are key factors for recruitment success (Hjort, 1914; Cushing, 1974; Lasker, 1975). Furthermore, suitable environmental conditions occur in optimal ranges, since there are physical constraints that shape non-linear relationships between a desirable environmental condition and fish recruitment (*e.g.*, optimal window of Cury and Roy, 1989). Anchovy from the Patagonian stock, for instance, showed a preferred temperature range between 12.5 and 16ºC (Hansen et al., 2001). Bonaerense anchovy were most abundant at salinity fronts at temperatures higher than 12.5ºC (Martos et al., 2005). The triad of concurrent enrichment, retention of early stages, and concentration have been hypothesized to be necessary for a successful spawning habitat (Bakun, 2010).

We asked the following questions: What is the relation of SAM and ENSO to the interannual variability of the Bonaerense anchovy population? What is the main environmental process affecting the spawning and larva habitats of the Bonaerense anchovy? How does large-scale climate variability affect spawning and larva habitats? We also investigate nonstationary effects of climate and oceanography on the interannual variability on the Bonaerense population of the anchovy *Engraulis anchoita* and its spawning and larva habitats. Two data sets were used: First, 50 years data on the environment (*e.g.*, SAM, SST) and the Bonaerense anchovy population. Second, 30 years data from ichthyoplankton surveys. We investigate relationships between the

environment and Bonaerense anchovy, including possible spatial and temporal variations of the spawning and larva habitats.

Material and Methods

Environmental Data

Two types of variables were used to represent environmental conditions that influence the Bonaerense anchovy stock: climate indices represented by the Southern Oscillation Index (SOI) and the Southern Annular Mode (SAM), and physical variables, represented by sea surface temperature (SST; ºC), winds (m s^{-1}) and Rio de La Plata outflow (RF; m^3 s^{-1}). Data were acquired as annual time series (climate indices) or were averaged by year (physical variables) from 1960 to 2010. The Southern Oscillation Index (SOI) was obtained from http://www.cru.uea.ac.uk/cru/data/soi (Ropelewski and Jones, 1987) and the Southern Annular Mode (SAM) from http://www.antarctica.ac.uk/met/gjma/sam.html (Marshall, 2003).

Monthly time series of sea surface temperature (SST) and meridional (v; from the N/S) and zonal (u; from the E/W) wind components were derived from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS Release 2.5), with a 1º x 1º resolution spatial grid for the area between 28ºS to 40ºS and 58ºW to 44ºW (http://rda.ucar.edu/datasets/ds540.1). ICOADS is an analysis of data from ships, moored and drifting buoys, and interpolation is not used to fill temporal or spatial data gaps (Woodruff et al., 2011). Wind speed (WS) and wind direction (WD) were calculated from u and v components of the wind. Wind direction was used to select values to create two variables from WS: southerly wind speed (SWS) with WD between 135º and 225º, and northeasterly wind speed (NeWS), with WD between 0º and 90º. Meridional sea surface wind stress (τ_m; N m^{-2}) was estimated by multiplying the meridional component of the wind (v; m s^{-1}) by |v|, the density of the air (1.22 kg m^{-3}) and the drag coefficient of the water (0.0013; dimensionless) (Bakun and Parrish, 1991). Rio de La Plata outflow (RF) time series was provided by National Institute of Water and Environment, Argentina (Borús et al., 2013).

Bonaerense Anchovy Stock Data

Landings of the Bonaerense anchovy stock were available for 1960 to 2010 (Sánchez et al., 2012, Garciarena and Buratti, 2013).

Recruitment at age 3 (R_3) and spawning stock biomass (SSB) of the Bonaerense anchovy stock were acquired from the stock assessment conducted by National Institute for Fisheries Research and Development (INIDEP-Argentina) for 1990 to 2010 (Hansen et al., 2014). Annual values of SSB were estimated by statistical models based on the Daily Egg Production Method, and were computed for austral spring, the season when spawning activity of the Bonaerense anchovy stock is greatest (Sánchez and Ciechomski, 1995; Hansen et al., 2014). Recruitment success (R_3/SSB) was also used to investigate the influence of the environment on the anchovy population.

Anchovy Egg and Larva Data

A total of 1691 samples, collected at 1215 oceanographic stations during 17 surveys from 1977 to 2010 in the western South Atlantic, were compiled in a database to assess spatial, seasonal and interannual variability in the Bonaerense anchovy spawning and larva habitats (Fig. 5.1, Table A5.1). Samples were taken at stations distributed on cross-shelf transects in the area between Cape Santa Marta (~28ºS) and Mar del Plata (~40ºS), covering the continental shelf and slope. Temperature and salinity at 10 m depth were measured at the same stations where ichthyoplankton samples were taken and at an additional 164 stations where only physical variables were measured. In the Conversut, Arepe and Ecopel (1-3) surveys, temperature was measured with reversing thermometers attached to Niskin and Nansen bottles, and salinity was measured with a salinometer from water in those samples. In addition, a conductivity-temperature-depth (CTD) profiler was used in the Ecopel 4 (Sensordata), La Plata and MCT-II (Sea Bird Electronics model 911), and in the Pronex (Sea Bird Electronics model 19).

Ichthyoplankton collections were made with Hensen, Bongo, Motoda, MultiNet and WP-2 samplers with digital flowmeters, mainly in oblique and vertical hauls (details in Appendix A and Table A5.1). Samples were fixed and preserved in 4% buffered seawater-Formalin solution. Bonaerense anchovy eggs and larvae were sorted and counted under a stereomicroscope, and identification was conducted using the development stages described by Ciechomski (1965), considering morphometric and meristic characteristics. Flowmeter data were used to compute the volume of water filtered and, with the number of individuals per sample, ichthyoplankton abundance (ind. 100 m^{-3}). Data

from stratified samples were combined to compute the abundance of anchovy eggs and larvae over multiple depth strata.

Data analysis

Standardized time series or anomalies were calculated by subtracting the mean and dividing by the standard deviation of the entire series. Before analysis, linear trend was removed from time series by linear regression, due to our interest in the periodic component. Detrended (*i.e.*, residuals from linear regression) time series were analyzed for autocorrelation (Fig. A5.1) (Legendre and Legendre, 1998).

Given the nonstationary relationship between climate and local physical factors (*e.g.*, Silvestri and Vera, 2009), the sequential *t*-test analysis of regime shifts (STARS) was applied to detect significant changes between stable mean states (Rodionov, 2004) for both environmental and Bonaerense anchovy landings time series. Significant changes between stable mean states were assessed by the regime shift index (RSI), which represents a cumulative sum of the normalized anomalies. For STARS analysis, length of the change between stable mean states was set to $L = 10$ years, with $\alpha = 0.05$ and the Huber weight parameter, $H = 6$ SD (Rodionov, 2004). Due to small size of the time series, the IP4 (Inverse Proportionality with 4 corrections) method was used for an accurate estimation of the autoregressive parameter (ρ), derived from the first order autoregressive (AR1) model, and to account for temporal autocorrelation (Fig. A5.1). IP4 was based on 4-year ([L + 1]/3) subsampling time series, to estimate ρ based on the median value among the estimates for all subsamples. Although IP4 was used and low values of ρ were estimated ($\rho < 1$), a prewhitening routine was not used due to a high chance of increasing in Type-II error rates (Rodionov, 2006). STARS analysis was run using the procedures described by Rodionov (2004, 2006) and codes provided in http://www.beringclimate.noaa.gov/regimes.

Periods defined based on STARS results for standardized landings were used to test correlations between the environment and the Bonaerense anchovy stock. This approach was applied because analysis of different periods in time series results in different relationships due to nonstationary effects (Silvestri and Vera, 2009). Cross-correlation analysis was used to identify the time lag that maximizes the correlation between explanatory (climate indices and physical variables) and response (standardized landings) time series (Legendre and Legendre, 1998). Relationships between large-scale indices and physical variables

were also investigated. In addition, cross-correlation analysis was used to assess relationship between environment and recruitment success (R_3/SSB), using the entire time series (1990 to 2010).

Spawning and larva habitats were assessed by means of both T-S and quotient curve analyses. T-S analysis provides insight about spawning and larva habitats by investigating the association of eggs and larvae of a population with specific water masses (Checkley et al., 2000). Quotient curve analysis describes the relationship between the percent frequency distribution for eggs or larvae with that for a single environmental or biological variable such as temperature or chlorophyll (Lluch-Belda et al., 1991). Quotient curves were obtained for surveys grouped by decade (1980s, 1990s and 2000s), taking the total number of eggs or larvae binned into 0.5 unit temperature or salinity intervals, and expressed as a percentage of the total number of eggs or larvae collected in surveys during each interval. This value was divided by the percent frequency distribution for all stations in the particular temperature or salinity bin (van der Lingen et al., 2001). A 3-point running mean was applied to quotient curves to prevent artifact due to sites with very high abundance of anchovy early stages (Drapeau, 2005). Quotient values > 1 indicate positive habitat electivity within a temperature or salinity interval, or increased eggs or larval survival, whereas quotient values < 1 suggest avoidance by spawners, mortality of eggs or larvae, or advection (van der Lingen et al., 2001; Asch and Checkley, 2013).

Nonlinear relationships between egg and larva abundance (ind. m^{-3}) and physical variables (temperature and salinity) were assessed using Generalized Additive Models (GAM) (Wood, 2006). Relationships were investigated for surveys grouped by decade, as used in T-S and quotient curve analyses, and for data from all surveys. Single and multiple predictor approaches were used to assess individual and combined effects of temperature and salinity. Anchovy early stages data were modeled using a negative binomial (NB) distribution. Water volume (log transformed) was included as an offset, so that egg and larva abundance could be modeled as count data. GAMs were used to estimate the optimal dispersion parameter k of NB distribution (Zuur et al., 2009). Smoothness of model terms was estimated by penalized cubic regression splines and parameters selected by the unbiased risk estimator (UBRE) score (residuals variance > 0). To avoid overfitting while smoothing, gamma was set to 1.4, putting a heavier penalty on each effective degree of freedom (edf > 1 indicates a nonlinear relationship) in the UBRE score (Wood, 2006). Models were evaluated by means of deviance explained (0–100%) and UBRE score. High

explained deviance and low UBRE score are goals. GAMs were run using the mgcv package (Wood, 2011). The NB distribution also required the MASS package (Venables and Ripley, 2002). All analyses and graphics were performed in R (v3.1.1; R Core Team, 2014), unless otherwise indicated.

Results

Climate, Oceanography and Long-Term Variability of Anchovy Population

Environmental conditions showed high variability between 1960 and 2010, manifest as both climate indices and physical variables (Fig. 5.2). STARS analysis of the SST anomaly time series showed three different mean states: a weak warm period from 1960 to 1982, a cool phase between 1983 and 1999 and a warm phase from 2000 to 2010 (Fig. 5.3). SAM showed a negative phase between 1960 and 1996, followed by a positive phase until 2010 (Fig. 5.2A), with a significant shift in the stable mean state (RSI = 0.196, p = 0.0029) in 1997 (Fig. 5.3). The main pattern of SOI indicated a La Niña dominant phase from 1960 to 1976 (cold SOI), changing to a warm El Niño dominant phase until 2000. This period was marked by four strong El Niño events: 1982-83, 1987, 1992 and 1997-98. From 2000, SOI showed weak El Niño conditions (2003-05) and a La Niña in the end of the time series. The Plata outflow (RF) anomaly showed mostly negative values during the La Niña dominant phase and positive anomalies during the El Niño dominant phase (Fig. 5.2B). No significant shifts of the stable mean state for both SOI and RF anomaly were detected by STARS.

Wind speed showed high variability (Fig. 5.2C), with a predominantly positive phase of the northeasterly winds between 1960 and 1983, followed by a negative phase until 1994 (Fig. 5.3). Southerly winds were more variable than northeasterly winds (Fig. 5.2C), and no significant discontinuities in the series were detected by STARS. Recruitment success (R_3/SSB) of the Bonaerense anchovy stock started with high values between 1990 and 1994, decreasing to its lowest value in 2000, then increasing to a new maximum in 2005 (Fig. 5.2D). This is associated with decreased in recruitment (R_3) in 1998-99, after the 1997-98 El Niño, and also the increase in SSB between 1994 and 1998 that affects the relationship R_3/SSB (Fig. A5.2). Anchovy landings were highest in the late 1960s and early 1970s, reaching almost 40 thousand tons, and again in 2000s with catches between 25 and 35 thousand tons

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(Fig. 5.2D). STARS detected discontinuities in standardized landings time series, with two significant shifts on the stable mean states (Fig. 5.3), first in 1980 (RSI = -0.359, p = 0.0024) and a second in 2003 (RSI = 0.655, p = 0.0001).
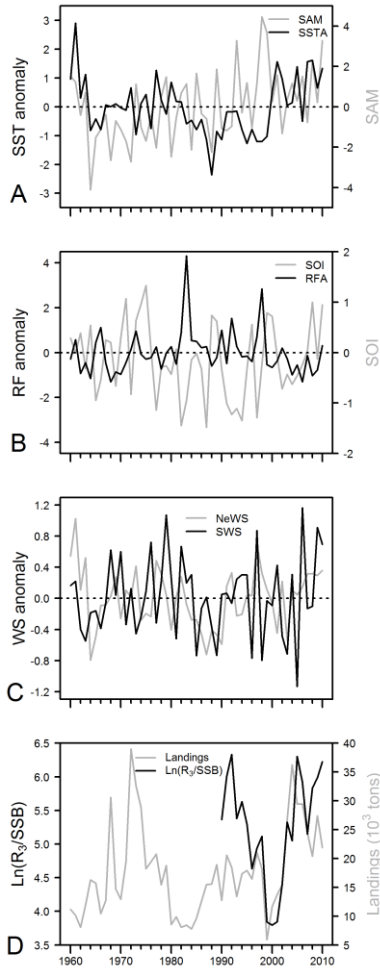
Fig. 5.2. (A) Sea Surface Temperature anomaly (SSTA; black) and Southern Annular Mode (SAM; gray), (B) Rio de La Plata outflow anomaly (RFA; black) and Southern Oscillation Index (SOI; gray), (C) northeasterly (NeWS) and southerly (SWS) wind speed anomaly (NeWS; gray, SWS; black), (D) recruitment success (Ln(R/SSB) at age 3) (black) and annual landings (gray) of Bonaerense anchovy (*Engraulis anchoita*) stock. All values are annual means.
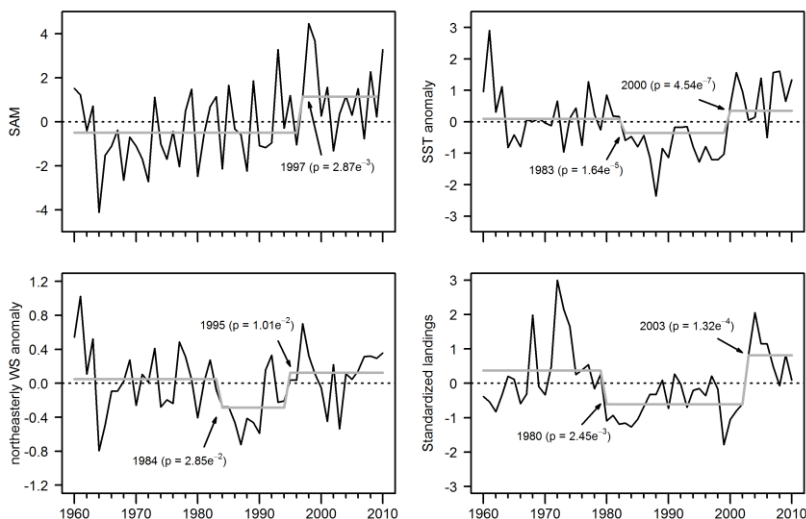
Fig. 5.3. Significant discontinuities detected by STARS in Southern Annular Mode (SAM), SST anomaly, northeasterly wind speed (WS) anomaly and standardized landings of Bonaerense anchovy (*Engraulis anchoita*) stock. Significant shift points (year and significance level) in the stable mean state were indicated.

The following results include only significant correlations. Relationships between climate indices, physical variables and Bonaerense anchovy landings showed two main pathways of influence over the last 50 years (Fig. 5.4, A5.3, Table 5.1). Warm SOI (El Niño) is positively correlated with negative anomalies in SST lagged by 1 year, with high correlation from 1960 to 2002 (Fig. A5.3), but also significant for the entire period (0.33 lagged by 1 year, 1960 to 2010). The RF anomaly showed negative relationship (no lag) with SOI, indicating that warm SOI (El Niño) is correlated with high Plata discharge. Furthermore, negative correlation (no lag) was detected between SOI and southerly WS for 22 years within 1980-2002 (Fig. A5.3). Landings were positively cross correlated with SST (2-y lag) and negatively cross correlated with RF anomaly (1-y lag). No direct effect of SOI on landings was observed (Table 5.1). These findings support the following pathways: El Niño through RF and SST negatively influencing landings (Fig. 5.4A).
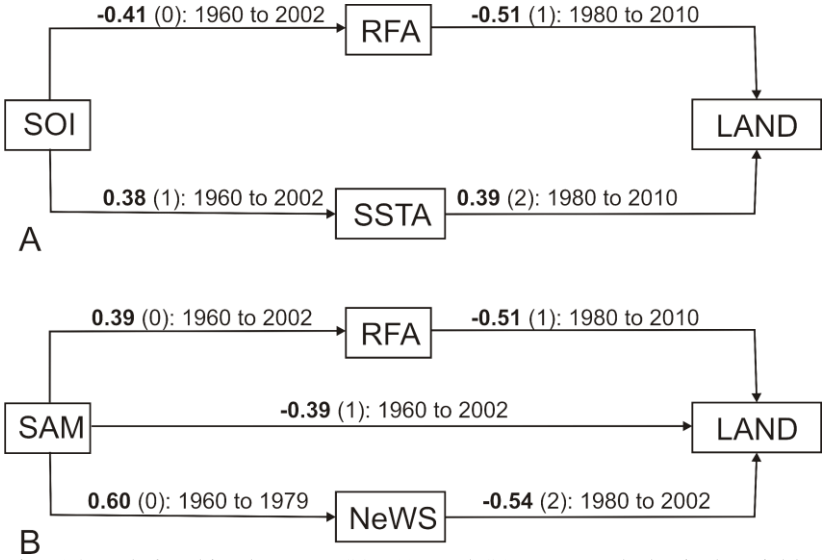
Fig. 5.4. Relationships between SOI (A) and SAM (B) and physical variables (RFA, Rio de La Plata outflow anomaly; SSTA, sea surface temperature anomaly; NeWS, northeasterly wind speed) showing the two main pathways of influence on the Bonaerense anchovy (*Engraulis anchoita*) landings (LAND) between 1960 and 2010. Periods with high correlation (in bold) and lag (in parentheses) are shown.

Correlations between SAM and RF anomaly were positive from 1960 to 2002 (Fig. 5.4B). Southerly WS showed negative correlation (4-y lag) from 1960-1979, while northeasterly WS showed high positive correlation (no lag) with SAM from 1960 to 1979 (Fig. A5.3). In contrast to SOI, SAM showed a direct relationship with landings, with a negative sign, from 1960 to 2002, whereas northeasterly WS anomaly was also negatively related with landings between 1980 and 2002 (Table 5.1). The second pathway with direct negative effect of SAM on landings: SAM through RF and northeasterly WS affecting landings negatively (Fig. 5.4B). Recruitment success (Ln(R$_3$/SSB)) for 1990 to 2010 was cross correlated with SAM (negative) and SST anomaly (positive) (Fig. 5.5).

Table 5.1. Cross correlation of standardized landings of Bonaerense anchovy (*Engraulis anchoita*) with SOI, SAM, southerly and northeasterly WS anomaly, SST anomaly and RF anomaly. For each variable, periods resulting from the STARS analysis for standardized landings start in years indicated in rows and finish in years indicated in columns. Significant correlations are in bold. Lags (in parentheses) are in years.

Subperiods start\finish	1979	2002	2010
SOI			
1960	0.31 (1)	0.28 (1)	0.20 (1)
1980	—	–0.29 (0)	–0.28 (11)
SAM			
1960	–0.39 (4)	**–0.39 (1)**	–0.26 (1)
1980	—	–0.39 (1)	0.33 (5)
SWSA			
1960	–0.36 (4)	-0.22 (6)	-0.22 (6)
1980	—	–0.32 (2)	-0.24 (2)
NeWSA			
1960	–0.36 (8)	**0.35 (12)**	**0.37 (12)**
1980	—	**–0.54 (2)**	0.27 (0)
SSTA			
1960	–0.30 (6)	**0.47 (11)**	**0.29 (11)**
1980	—	–0.31 (0)	**0.39 (2)**
RFA			
1960	**–0.52 (4)**	**–0.32 (1)**	**–0.36 (1)**
1980	—	**–0.46 (1)**	**–0.51 (1)**

Spatial and Interannual Variability in the Spawning and Larva Habitats

Surface temperature and salinity from selected surveys between Cape Santa Marta (~28ºS) and Mar del Plata (~40ºS) varied seasonally (Fig. 5.6). In late austral autumn, high intensity of southeasterly winds pushed cold and fresh PPW to the north resulting in a strong thermohaline gradient close to the coast and in a cross-shelf direction. Over the shelf, PPW reached Cape Santa Marta in the winter, pushing STSW to the north and offshore, which remained blocked by warm, salty TW that extended along the entire slope. Furthermore, northward displacement of PPW, allowed the spread of SASW along the Argentine shelf. With the intensification of northeasterly winds in spring, PPW retreated southward to Patos (~32ºS, 1978) and was replaced by STSW, reaching its southernmost position in the summer near Brazil and Uruguay border (~34ºS, 1981 and 2004). In addition, upwelling of the

SACW reaching the surface was observed only in the summer of 2004 in the vicinity of Cape Santa Marta.

Eggs and larvae were restricted to the continental shelf in Brazilian waters, mainly shoreward of the 200 m isobath. In front of the Plata estuary, however, they reached beyond the continental shelf (Fig. 5.6, A5.4, A5.5). Eggs and larvae viewed in temperature and salinity space (Fig. 5.6) showed that *E. anchoita* early stages occurred in PPW during autumn, winter and early spring, when eggs and larvae reached northward to Cape Santa Marta (~28ºS). High abundances of eggs occurred mainly between Plata estuary and Conceição lighthouse (31º30'S), north of Patos (Fig. 5.6, A5.4). On the other hand, larval abundances were also high north of Conceição lighthouse (Fig. 5.6, A5.5). When PPW retreated, high abundances of eggs and larvae occurred in front of Patos estuary and the southernmost stations (spring 2010; Fig. A5.4, A5.5). Finally, during the austral summer, eggs were absent or occurred in low abundances on the Brazilian shelf, with highest abundances in the vicinities of Plata estuary.

Temperature-salinity diagrams of all surveys grouped by decade indicated that water masses described above varied among seasons and decades (Fig. 5.7). Warming of PPW was evident during the year, with low temperatures in winter (10 to 20ºC) and warm in summer (20 to 26ºC). Salinity range was higher in 1980s than in other decades, with low values around 18.8. In the 1990s, PPW was cool and salty, ranging between 10 and 14ºC for temperature, and 29.3 and 33.5 for salinity. Upwelling of SACW was observed only in summer of 2004, despite occurrence of stations in SACW thermohaline range in the 1980s. T-S diagrams showed high occurrence and abundance of eggs and larvae in PPW in all seasons and decades, but mostly in winter and spring. Eggs and larvae also were found in high occurrence in STSW at low abundance and with low occurrence and abundance in SASW and TW.
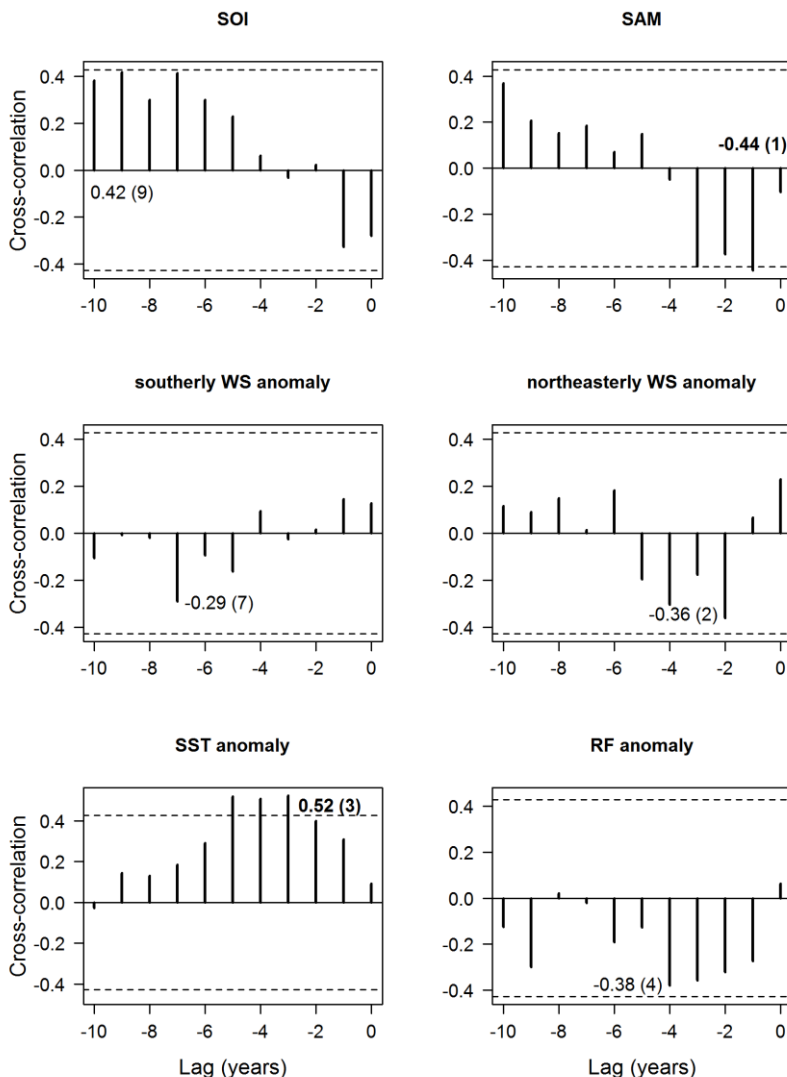
Fig. 5.5. Cross-correlation analysis of recruitment success (Ln(R/SSB) at age 3) of anchovy (*Engraulis anchoita*) Bonaerense with: SOI, SAM, southerly and northeasterly WS anomaly, SST anomaly and RF anomaly. Negative lag indicates environmental variable leads recruitment success. Bars extending beyond dashed black lines (confidence intervals) mean significant correlation (p < 0.05). Maximum correlation lag (in parentheses) were indicated with significant relationships in bold.
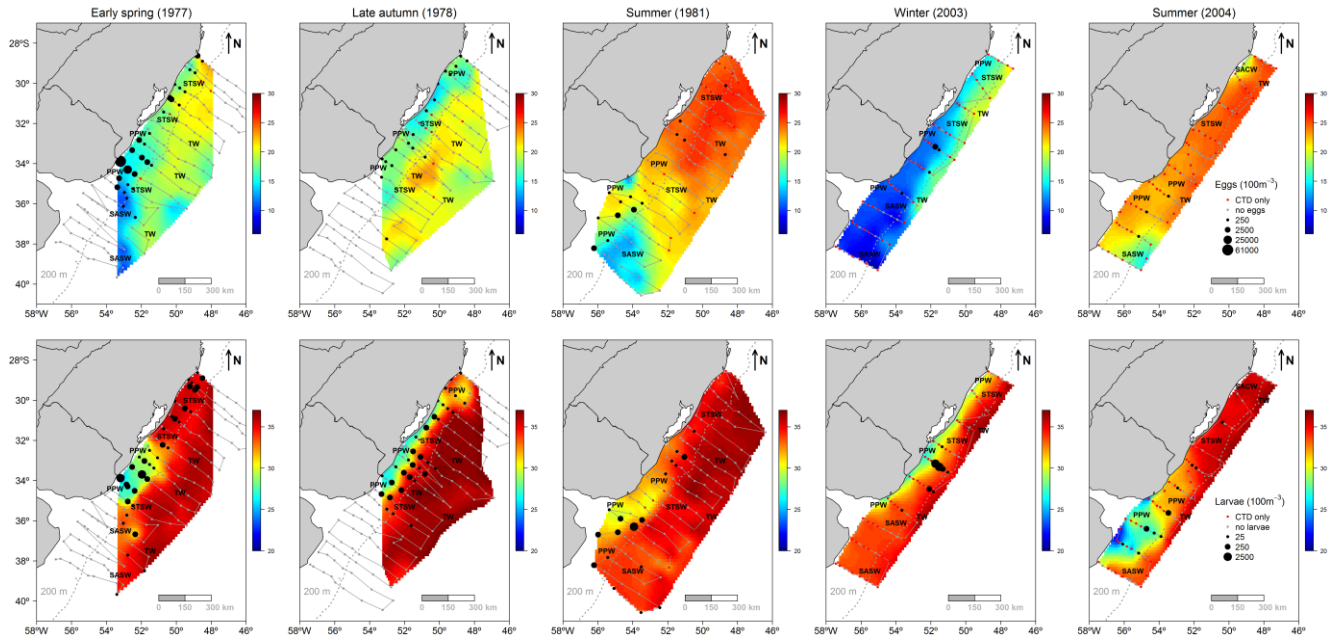
Fig. 5.6. Selected surveys showing Bonaerense anchovy (*Engraulis anchoita*) eggs abundance overlaid on temperature (ºC) (upper), and larval abundance overlaid on salinity (bottom). Tropical Water (TW), Plata Plume Water (PPW), Subtropical Shelf Water (STSW), Subantarctic Shelf Water (SASW), South Atlantic Central Water (SACW).
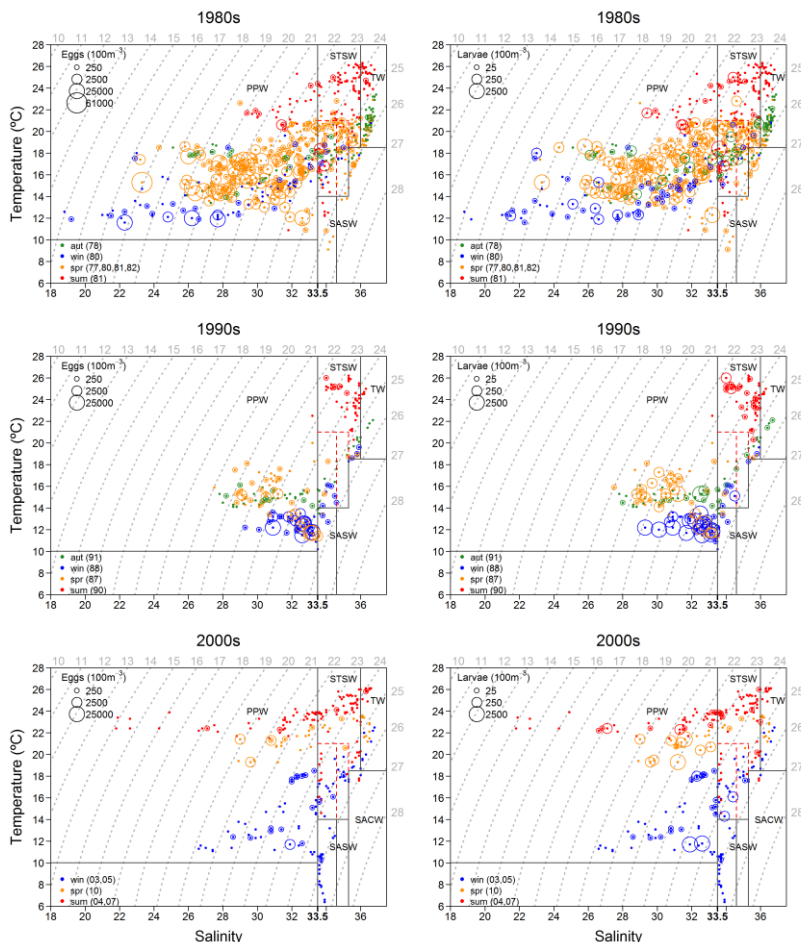
Fig. 5.7. T-S diagrams (10 m depth) with Bonaerense anchovy (*Engraulis anchoita*) eggs (left) and larvae (right) abundances for each season (autumn = green, winter = blue, spring = orange, summer = red) grouped by decade (1980s upper, 1990s middle, 2000s bottom). Tropical Water (TW), Plata Plume Water (PPW), Subtropical Shelf Water (STSW), Subantarctic Shelf Water (SASW), South Atlantic Central Water (SACW). Dashed red line indicated temperature thresholds for STSW and SASW during summer according to Möller Jr. et al. (2008).

Quotient analysis (Fig. 5.8) showed high electivity for salinities lower than 33.5 and temperatures between 11ºC and 16ºC, the

thermohaline range of PPW. In the 1990s, there was a slight shift in the peak of electivity for salinity close to PPW upper limit (33.5) and a return to lower salinities in the 2000s, whereas temperature electivity remained the same for all decades. Quotient curves also showed a high degree of overlap between eggs and larvae, indicating the importance of PPW for spawning, eggs, and larvae of Bonaerense anchovy.

GAMs results from all surveys combined showed that temperature explains more of the variability in the abundance of anchovy eggs and larvae than does salinity, with high percentage of deviance explained and low UBRE score (Table A5.2). However, in models using data by decade, the best fits were obtained between salinity and egg abundance for the 1980s and with salinity and larva abundance in all decades. Models that considered the combined effect of temperature and salinity explained more variability in anchovy egg and larva abundance. Smoothed functions for temperature and salinity showed the link between anchovy early stages and low temperatures (11–14ºC) and salinities (23–27 and 31–33), inside the thermohaline range of PPW (Fig. 5.9). This pattern was consistent in almost all decades except during 2000s, which there was no clear maximum value of eggs in relation to temperature. Anchovy eggs showed a bimodal response in relation to salinity for all models, whereas larvae bimodal response in relation to temperature and salinity were not evident in the 2000s model. Despite most of the models indicated spatial autocorrelation and heterogeneity in the residuals, results were consistent with T-S plots and quotient analysis showing high degree of electivity of Bonaerense anchovy early stages on PPW.

Interannual variability in salinity distribution was related to a combined effect between variations on wind stress and positive RF anomaly (Fig. 5.10). In the 1980s, high abundance of eggs (winter) and larvae (spring) occurred in waters with low salinity (< 30.0), spread northward by high southerly wind stress and positive RF anomalies in the period before the surveys. Low intensity of wind speed and river flow in the second half of the 1980s (Fig. 5.2) reduced northward spread of low salinity waters of PPW and influence of estuarine waters (S < 30.0), with only estuarine front waters (30.0 < S < 33.5) over the Brazilian continental shelf. Even with high positive anomalies in RF during several months before the survey (spring 1987), low intensity of southerly wind stress acts as a limiting factor in PPW northward spread. Anchovy eggs (winter) and larvae (spring) continued to show high abundances related in PPW. The same pattern can be observed in 2000s, with abundance in low salinity in spring.
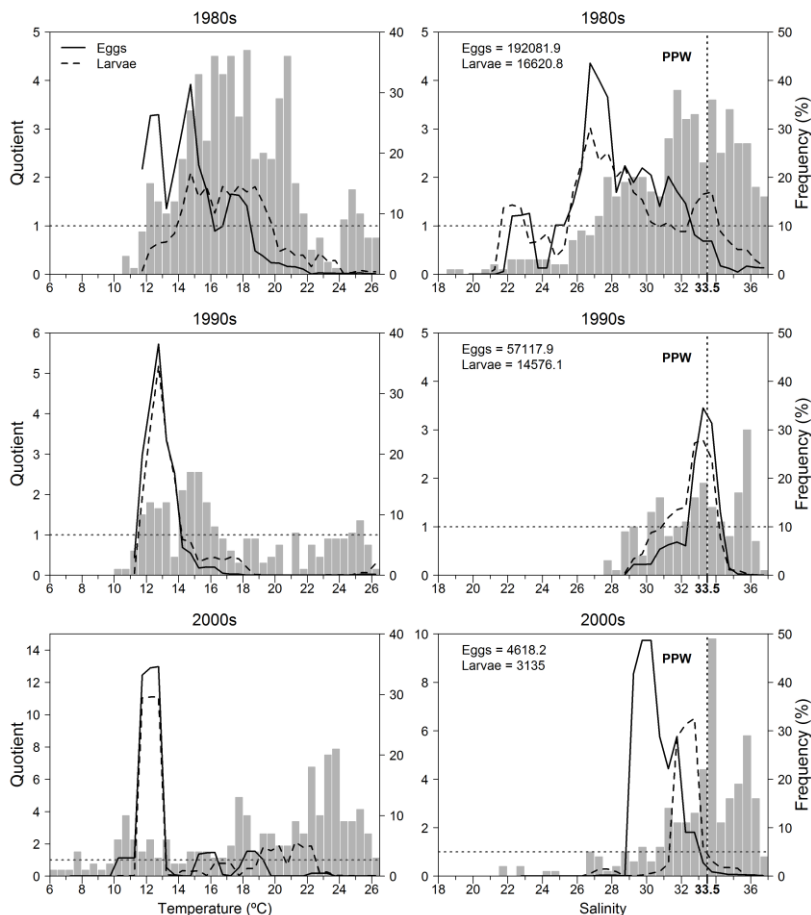
Fig. 5.8. Quotient curves showing the ranges of temperature (left) and salinity (right) with high occurrence of Bonaerense anchovy (*Engraulis anchoita*) eggs (continuous line) and larvae (dashed line) for surveys grouped by decade. Curves were superimposed on the frequency distribution of temperature and salinity (gray bars). The horizontal gray dotted line denoted a quotient of 1. Vertical dotted black line in salinity plots denotes PPW upper limit (salinity = 33.5). Bin widths were 0.5 units for temperature and salinity and a three-point mean was used to smooth quotient curves. The total abundance (ind. 100 m^{-3}) of eggs and larvae are indicated for each decade.
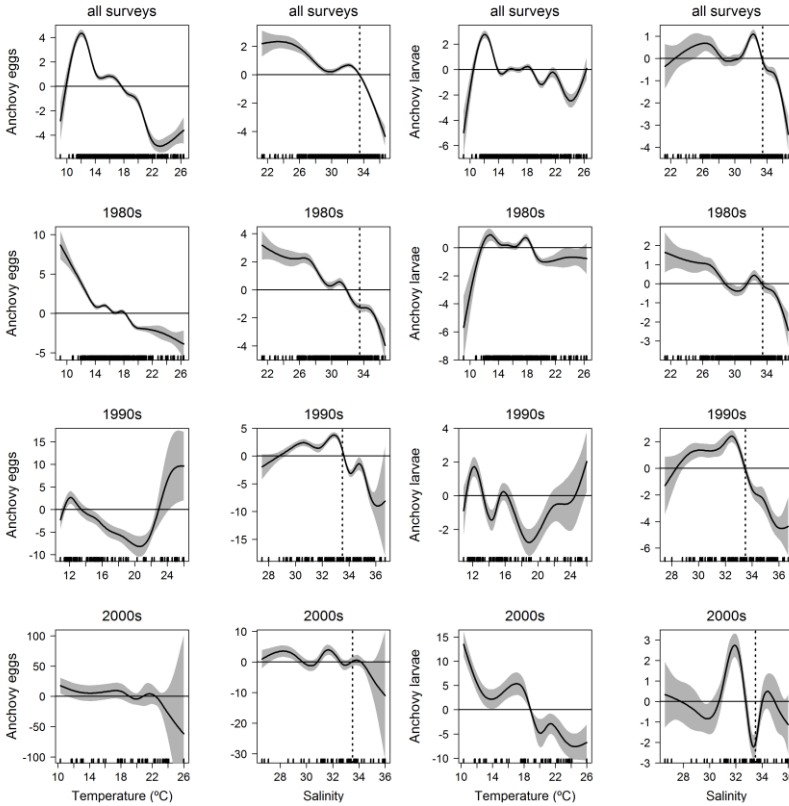
Fig. 5.9. GAM model fits for Bonaerense anchovy (*Engraulis anchoita*) eggs (left columns) and larvae (right columns) abundance with respect to temperature and salinity at 10 m. Estimated smooth functions (solid lines) with 95% confidence intervals (gray shading) are displayed for all surveys together and by decade. The partial effects for the factor variable season are suppressed. Vertical dotted line in salinity model fits indicate Plata Plume Water upper limit of 33.5 and horizontal lines indicate zero level.
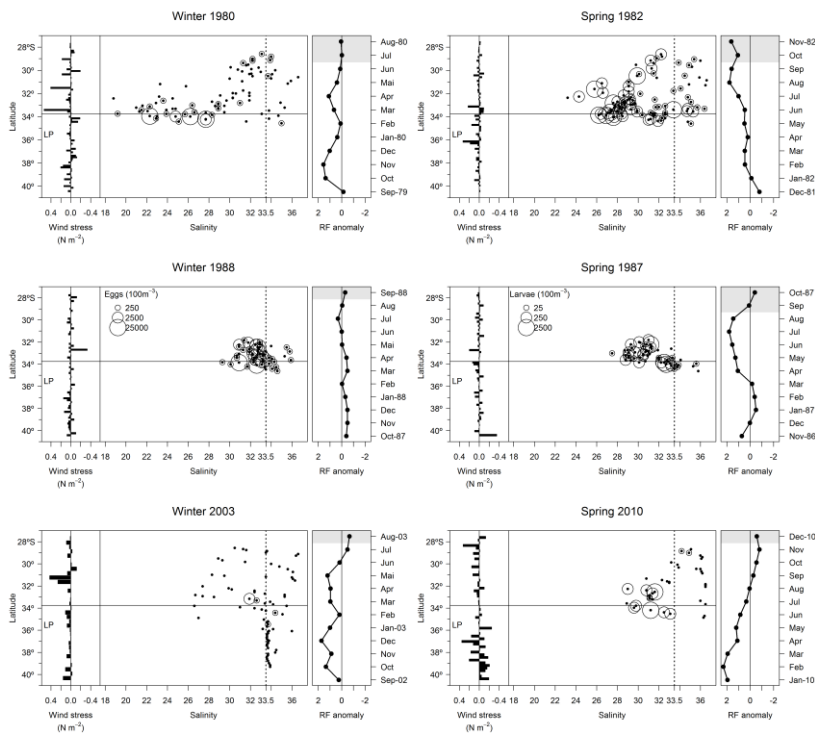
Fig. 5.10. Distribution of Bonaerense anchovy (*Engraulis anchoita*) eggs abundance in winter (left) and larvae abundance in spring (right), in the salinity gradient (x axis) across latitude (y axis). On the left side of each plot is meridional wind stress (N m^{-2}) averaged by latitude, and on the right side Plata outflow anomaly (RF anomaly) for the year before each survey. Gray shading in RF anomaly plots indicates the period of sampling. Vertical dotted lines indicate PPW upper limit and continuous horizontal line in wind stress and salinity plots indicate Brazil/Uruguay border. LP indicates Plata estuary position.

Discussion

This study investigated nonstationary effects of climate and oceanography on the interannual variability of the Bonaerense anchovy *Engraulis anchoita* population and its spawning and larva habitats. Relationships between long-term changes in climate (*e.g.*, SAM), physical variables (*e.g.*, Plata outflow) and Bonaerense anchovy relative abundance represented by fisheries catch data were investigated for the first time. In addition, the study used the large amount of data from

ichthyoplankton surveys in southern Brazilian waters in an effort to highlight major patterns in distribution and abundance of Bonaerense anchovy early stages and the principal oceanographic features that control these patterns. Two main pathways resulted from relationships between Bonaerense anchovy landings and the environment: first, changes in abundance induced by SOI (ENSO) through Plata outflow (RF) and SST; second, the Bonaerense anchovy population is negatively affected by SAM through RF and northeasterly WS. Spawning occurred primarily in cool and low salinity Plata Plume Water (PPW), the distribution of which affected mainly by RF and wind. Landings approximated abundance and varied with the environment like recruitment success.

Nonstationary Effects of Climate and Oceanography on Anchovy Populations

The populations of small pelagic fish, such as anchovies, fluctuate in their productivity and show long-term natural fluctuations in their abundance (Lluch-Belda et al., 1989). Their biological characteristics make them sensitive to climatic fluctuations (Alheit et al., 2009). The SOI (ENSO) pathway showed a relative stability in its negative indirect influence through RF on the landings of Bonaerense anchovy, with the same pattern independent of the period analyzed (*e.g.*, 1960–2002, 1980–2010) and for the entire time series (1960–2010). Plata discharge varied interannually with El Niño-associated rainfall over Southeastern South America (SESA). The relatively stable relationship between ENSO, precipitation and river flow is well known (Aceituno, 1988; Ropelewski and Halpert, 1989; Mechoso and Iribarren, 1992). This explains the anomalous northward penetration of cool and low salinity waters in the Southern Brazilian Bight (~24º–25ºS) one year after the large river outflow associated with the 1992–93 El Niño (Pimenta et al., 2005). Recruitment success of the Bonaerense anchovy decreased after the 1992-93 El Niño and even more after the 1997 El Niño, reaching its lowest value in 2000 (Fig. 5.2A, D). Although summer rainfall and river flow increase significantly during a strong El Niño, northeasterly wind stress causes the low salinity water move offshore in front of the estuary, and rather than leading to a significant northward penetration of the PPW (Piola et al., 2005). This affects negatively Bonaerense anchovy eggs and larvae survival and thus recruitment success (Fig. 5.2D) by increasing transport offshore, far from the area suitable for their development in coastal and shelf waters

(Sanchéz and Ciechomski, 1995). This is also consistent with the seminal hypothesis of Hjort (1914) on one of the major cause of recruitment variation, *i.e.*, transport away from nursery areas. ENSO impacts reach not only discharge of Plata estuary but also formation, separation, location and displacement of its turbidity and estuarine fronts (Nagy et al., 2008). During low river discharges associated with La Niña, zonal winds control the displacement and distances between fronts. However, during El Niño river flow is the dominant forcing factor.

The second branch of influence of SOI on Bonaerense anchovy landings was through SST (Fig. 5.4A), *i.e.*, in an El Niño phase SST is cooler than average and landings lower. In the western South Atlantic, waters at the BMC region are characterized by negative SST anomalies during El Niño. Conversely, waters from the Brazil Current (BC) are abnormally warm (Severov et al., 2004). Although, Bonarense anchovy northern habitat is influenced by the BC and the typical position of BMC is around 38ºS, in the southernmost part of the Bonaerense anchovy habitat (Silveira et al., 2000; Garcia et al., 2004), our data showed the same relationship for ENSO and SST anomalies as described by Severov et al. (2004) for the BMC region. This is because they considered the BMC region as the entire habitat for the Bonaerense anchovy. Warm waters can accelerate larval growth by increasing metabolic and survival rates in early stages by reducing time spent in more vulnerable stages (Pepin, 1991). El Niño-induced water cooling can affect these processes for the Bonaerense and Patagonian populations (Hansen et al., 2001; Martos et al., 2005), slowing larval development and reducing survival and recruitment. We have observed the same relationship between SOI, SST anomalies and recruitment success of the Bonaerense anchovy.

Nonstationary impacts of the SAM on oceanography and Bonaerense anchovy landings are evident, with the period from 1960 to 2002 accounting for most of this relationship. SAM appears to influence Bonaerense anchovy on a 20-y cycle with an opposite sign, with a direct significant relationship with landings and recruitment success, contrary to the relationship with SOI (Fig. 5.4, 5.5). The Antarctic Oscillation (AAO) has shown a decreasing trend and a periodicity of 4–5 years since 1960 (Stenseth et al., 2003) and SAM has an opposite sign and an increasing trend. These trends might be related to the state transitions in the SST anomaly and standardized landings, lagged 3 and 6 years respectively, during late 1990s and early 2000s, when SST changed from a cool to a warm, followed by landings increasing from a lower to

a higher state (Fig. 5.3). One of the most abrupt transitions occurred in 1976–77 in the North Pacific, including atmospheric patterns, SST, stratification of the water column, strength of coastal upwelling, and local abundance and community structure in pelagic ecosystems of the southern California Current ecosystem (Mantua et al., 1997; Bograd and Lynn, 2003; McGowan et al., 2003). This abrupt state transition also was inversely related to the Pacific Decadal Oscillation and Pacific salmon production (Gargett, 1997). Thus, the state transitions observed here, albeit with fewer data, have precedent elsewhere.

       The nonstationary relationship between SAM and the Bonaerense anchovy population mediated by RF are complementary to the El Niño effects. Silvestri and Vera (2003) showed an effect of SAM and ENSO on precipitation anomalies over northeastern Argentina, eastern Paraguay and southern Brazil, which influence Plata discharge. Precipitation anomalies over northwestern and eastern Argentina and Uruguay are more dependent on ENSO and independent of SAM. Nonstationary impacts of SAM are largest during austral spring, when negative relationships with ENSO and precipitation over SESA were observed. Thus positive SAM, related to positive pressure anomalies at SESA, modulates the ENSO relation to SESA precipitation (Silvestri and Vera, 2009).

       Negative impacts of SAM associated with northeasterly winds might be related to the southward displacement of PPW (*e.g.*, Piola et al., 2008) during SAM-induced high RF, resulting in oceanward displacement of anchovy early stages far from suitable habitats, as described for El Niño-induced high RF during austral summer (Piola et al., 2005). In the Plata estuary zonal (westerly and easterly) winds influence seaward discharge and estuarine front displacement (Guerrero et al., 1997; Acha et al., 2008; Nagy et al., 2008). Part of the interannual variability in zonal winds are related to ENSO (Meccia et al., 2009), where easterly winds contribute to retention of early stages of fishes and are linked to El Niño, while westerly winds contribute to advection offshore of early stages and are linked to La Niña (Acha et al., 2012). According to Acha et al. (2012), the combined effect of El Niño-related easterly winds with high Plata discharge might reduce seaward dispersion of whitemouth croaker early life stages, ensuring a suitable environment for spawning and development of this and other species that use Plata estuarine front, including the Bonaerense anchovy.

       Most relationships between recruitment success (R_3/SSB) and environment variables were not significant. This result may be due to the brevity of the time series, their inherent variability and to dome

shaped relationships between maximum recruitment and physical forces, including wind mixing (Cury and Roy, 1989). These authors posed the "optimal environmental window" hypothesis whereby optimal environmental conditions (*e.g.*, upwelling intensity) occur at an intermediate value (*e.g.*, wind speed around 5–6 m s^{-1}). Although lack of relationship between R_3/SSB and southerly and northeasterly winds, R_3/SSB may depend on westerly and easterly winds associated with Plata estuary discharge (Guerrero et al., 1997) and estuarine front displacement (Nagy et al., 2008), both affected by El Niño- and SAM-induced high precipitation (Aceituno, 1988; Ropelewski and Halpert, 1989; Mechoso and Iribarren, 1992; Silvestri and Vera, 2003) and ENSO-induced changes in zonal wind dynamics (Meccia et al., 2009; Acha et al., 2012). Landings of *E. encrasicolus* in the Mediterranean Sea are positively affected by Ebre river flow (Lloret et al., 2004), and a positive North Atlantic Oscillation is associated with reduced precipitation and river flow, leading to a negative impact on anchovy recruitment (Lloret et al., 2001). Low recruitment of the *E. encrasicolus* population from Bay of Biscay is caused by downwelling influenced by intensification of winds from southwest, driven by positive phases in the East Atlantic pattern (Borja et al., 2008). Seasonality existis for ENSO-related variability in precipitation and Plata outflow (*e.g.*, Mechoso and Iribarren, 1992; Silvestri and Vera, 2003) and SAM-related variability in precipitation (Silvestri and Vera, 2003, 2009). While we focused on time scales longer than seasonal, the mechanisms observed for *E. anchoita* are consistent with those of *E. encrasicolus*.

Climate-Driven Changes in Spawning Habitat Mediated by Oceanography

Our findings are consistent with relationships between the early stages of Bonaerense anchovy and PPW observed by Bakun and Parrish (1991), Sánchez and Ciechomski (1995), Castello (2007) and Torquato and Muelbert (2014). Macedo–Soares et al. (2014) used community multivariate data analysis to show that high abundance of Bonaerense anchovy larvae is associated with PPW. Despite low biomass between 31ºS and Cape Santa Marta (Lima and Castello, 1995), eggs and larvae are distributed across the entire continental shelf from northern Argentina and Uruguay up to Cape Santa Marta, moving northward in PPW and reaching Santa Catarina Island (~27ºS) in normal winter conditions (Piola et al., 2008). Anchovy spawning is associated with river discharge in other areas around the globe, including the European

anchovy *E. encrasicolus* in the Mediterranean Sea associated with the Ebro and Rhone rivers (Palomera et al., 2007), eggs of *E. encrasicolus* in Bay of Biscay in coastal waters influenced by the Adour, Gironde and Loire estuaries (Planque et al., 2007), and the Northern anchovy *E. mordax* associated with the Columbia River plume (Checkley et al., 2009).

Egg and larva distributions varied seasonally as described for the Bonaerense anchovy spawners, migrating from Argentine/Uruguay to southern Brazilian waters to spawn in austral winter and early spring (Lima and Castello, 1995; Castello, 2007). During winter, the main processes that affect eggs and larvae in southern Brazilian waters are increased primary production associated with cold subantarctic waters and continental runoff (Carreto et al., 1986; Ciotti et al., 1995; Braga et al., 2008), vertical stability due to continental runoff and cool bottom water, and onshore Ekman transport (strong south of Patos, ~32º) induced by southerly wind stress (Bakun and Parrish, 1991; Lima and Castello, 1995). Vertical stability reinforces primary production by reducing depth of the mixed layer (Lima and Castello, 1995) and permits aggregation of food (Lasker, 1975), while distribution of eggs and larvae supports observations from Lima and Castello (1995) that onshore Ekman transport provides retention of early stages over the shelf. During spring, the "ocean triad" (Bakun, 2010) conditions favorable to the Bonaerense anchovy population move south with the PPW, supporting spawning south of Patos, and reaching a maximum during late austral spring and summer (Sánchez and Ciechomski, 1995). The spawning and larva habitats, independent of seasonality, were characterized by the temperature and salinity characteristics of the PPW.

There is no apparent general pattern in relation to temperature and salinity electivity for *Engraulis* in different habitats (Checkley et al., 2009). Quotient analysis shows similar ranges in temperature (11–16ºC) and salinity electivity for *E. anchoita* eggs and larvae, indicating that there is no environmental distinction between spawning and larva habitats. A similar pattern was observed for *E. mordax* in the California Current System, with the same quotient curves of eggs and larvae (Lluch-Belda et al., 1991). GAM models show a unimodal response for temperature (12.5ºC) and a bimodal for salinity (23–30.5 and 31.5–33) for both early stages of *E. anchoita*. Unimodal response for temperature was also observed for *E. encrasicolus* in the southern Benguela upwelling system (van der Lingen et al., 2001; Twatwa et al., 2005), *E. mordax* in the California Current System (Lluch-Belda et al., 1991) and *E. encrasicolus* at the Mediterranean Sea (Palomera et al., 2007). A

bimodal response for salinity (32–36 and 37.5) was also found for eggs of *E. encrasicolus* at the Mediterranean Sea, where they are associated with waters of continental origin (Palomera et al., 2007), but was not observed for *E. encrasicolus* in the southern Benguela upwelling system (Twatwa et al., 2005). The two main mechanisms that are related to small pelagic fish abundance around the world, salty oceanic waters associated with upwelling or brackish waters associated with fresh water, may be related to anchovy's tolerance to wide range in salinity and thus bimodal response to salinity.

Interannual variability in the spawning and larva habitats of the Bonaerense anchovy is related to variations in Plata ouflow (RF) and wind mainly associated with ENSO and SAM. Major changes in maximum salinity in quotient curves (Fig. 5.8) between 1980s (low), 1990s (high) and 2000s (intermediate) were related to the combined effects of ENSO-associated high RF and PPW displacement over the continental shelf due to southerly wind stress (*e.g.*, Mechoso and Iribarren, 1992; Piola et al., 2005). Low salinity (< 27.0) associated with anchovy larvae occurred in moderate southerly wind stress and high RF during the 1982 El Niño (Fig. 5.10). However, in a neutral ENSO condition (1980) with strong southerly wind stress and positive RF, low salinity values were also found in southern Brazilian waters and associated with high egg abundance. Although high RF occurred during the 1987 moderate El Niño, due to high precipitation over SESA (Ciotti et al., 1995; Lima and Castello, 1995), weak southerly wind stress precluded high dispersal of low salinity waters (Piola et al., 2005), as well as during the 1988 La Niña. Both conditions were associated with high larva and egg abundance.

Local and mesoscale oceanographic processes are also important to the interannual variation of the small pelagic fish spawning habitat (*e.g.*, Planque et al., 2007; Claramunt et al., 2012; Basilone et al., 2013; Asch and Checkley, 2013). Analyses of 10 years of data of *E. encrasicolus* eggs at the Strait of Sicily showed interannual variability in egg abundance and in spatial expansion of the spawning habitat (Basilone et al., 2013). Years with low egg abundance were associated with warm, stratified waters with low primary productivity, whereas high egg abundance occurred in waters with moderate current speeds. The distribution of *E. encrasicolus* eggs in Bay of Biscay varies among years, from being widespread and patchy over the shelf to concentrated narrowly along the coast and near estuaries in both coastal well-mixed waters and highly stratified river plumes (Planque et al., 2007). Similarly, the distribution of eggs of *E. ringens* in northern Chile varies

interannually from being coastal to more oceanic, moving latitudinally between north of 20ºS and south of 21ºS (Claramunt et al., 2012). Part of this variability may be related to changes in temperature induced by ENSO, since quotient analyses showed significant shifts in electivity for temperature during warm El Niño, intermediate neutral ENSO and cool La Niña phases. ENSO also affects spatial extention of *E. mordax* spawning habitat, which contracted shoreward during 1998 El Niño phase (Asch and Checkley, 2013).

The shape of the quotient curves and GAMs suggest that suitable environmental conditions for Bonaerense anchovy spawning and larval development occur in optimal ranges, consistent with physical and climate constraints. Plata outflow (RF) plays the main role due to its influence on PPW formation, which affects enrichment and vertical stability. Extreme phases of ENSO and/or SAM modulated RF affecting Bonaerense anchovy spawning and larva habitats in two ways: (1) El Niño and/or positive SAM induces high RF, increases oceanward advection of eggs and larvae over the Argentine shelf and we hypothesize low recruitment due to high mortality of early stages; (2) low RF during La Niña and/or negative SAM reduces suitability of conditions in the spawning and larva habitats, including lower RF and vertical stability. Wind-induced northward displacement of the estuarine front may leads to retention of early stages within suitable habitat of PPW and thus to enrichment due to northward displacement of nitrate-rich subantarctic waters. Temperature seems to play a secondary role being abnormally cold in El Niño and abnormally warm in La Niña (Severov et al., 2004).

Future impacts of climate change, such as changes in annual river runoff, frequency and intensity of extreme ENSO and in sea surface temperature (IPCC, 2014), on Bonaerense anchovy population and its fisheries will depend on relations like those presented here. Decadal trends in small pelagic fish abundance driven by climatic variability may be useful to detect changes caused by long-term global climate change (Hunter and Alheit, 1995). However, these models require an understanding of the relation of fish to the environment that comes only from long time series of data, an example being sardines and anchovies from the California Current System shown to fluctuate with 60 years over two millennia before the development of modern fisheries (Baumgartner et al., 1992).

Conclusions

We have shown two pathways by which climate influences negatively the Bonaerense anchovy *Engraulis anchoita* population: first by El Niño increasing Plata outflow (RF) and decreasing sea surface temperature; second by the Southern Annular Mode (SAM) increasing RF and northeasterly winds. SAM also showed a direct negative influence on anchovy catch and recruitment success. In addition, spawning and larva habitats were defined using temperature and salinity as the cool and low salinity Plata Plume Water, whose distribution is influenced by RF and seasonal variability of southerly/northeasterly winds. ENSO and SAM impacts Bonaerense anchovy spawning and larva habitats modifying the balance between Plata outflow and oceanward and northward displacement of the estuarine front. In conclusion, we hypothesize that changes in climate, such as increase in the frequeny and/or intensity of El Niño combined with increased trend in SAM, will affect recruitment success and hence the productivity of Bonaerense anchovy and thus its fisheries.

Acknowledgements

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Supporting Information

Appendix A. Description of sampled strategies applied during ichthyoplankton samples.

The 17 surveys used to obtain ichthyoplankton samples (Table A5.1) were initially designed to address different goals, as a consequence, early stages of Bonaerense anchovy were sampled using different gears and methods, and at different spatial resolutions. Oblique and vertically integrated hauls were performed in the Conversut 1 and 2 surveys. At each station, one oblique and one vertical haul were conducted with the Hensen net through the upper 200 m (Hubold, 1980a, 1980b). Oblique hauls with a Bongo net, 300 μm mesh size and 0.6 m mouth diameter, were performed in Arepe and Ecopel surveys from 5 m from the bottom to the surface at shallow water stations, and from 200 m depth at deep stations (Vasconcellos et al., 1998). Additionally, MultiNet samples were collected during the Pronex surveys. MultiNets were equipped with two 200 μm and three 330 μm mesh-nets, and towed at 2 knots. It was deployed with the first 330 μm mesh-net open in an oblique haul, when was lowered to the maximum sampling depth. Then, MultiNet was hauled back performing stratified horizontal samples in four different depth intervals. Anchovy eggs and larvae were sorted only from the 330 μm mesh-nets samples (Torquato and Muelbert, 2014). Vertically integrated samples conducted in the MCT-II survey were taken with WP-2 net between the surface and 10 m from the bottom at homogeneous water column and shallow water stations (up to 20 m), and from the chlorophyll maximum depth to the surface at deeper ones (Macedo-Soares et al., 2014).

Three sample strategies were used in La Plata surveys. First a vertically integrated tow performed at stations close to the 50 m and 200 m isobaths with a Motoda net, 300 μm mesh size and 0.6 m mouth diameter. In La Plata 2 survey, a WP-2 net with 140 μm mesh size (later replaced by a mesh of 500 μm) and 0.6 m mouth diameter was used in vertically integrated tows. The second strategy consisted in a two level vertical tow using a WP-2 net mounted on a closing mechanism structure, conducted at stations close to the 100 m isobaths. This net was further replaced in La Plata 2 survey by a conical net with 200 μm mesh size and 0.6 m mouth diameter. Finally, a horizontal two level tow, lasted 10 min., was performed at the Albardão transect (between 33ºS and 34ºS) with the Motoda net. All stratified samples were taken below and above the halocline. Two sub-samples were obtained with a Folson

splitter and shared between University of Rio Grande (FURG) and INIDEP. Data used in this study results from FURG sub-samples analysis.

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Supplementary Tables

Table A5.1. Information about surveys used in the Bonaerense anchovy (*Engraulis anchoita*) egg and larva database for sampling between Cape Santa Marta (~28ºS) and Mar del Plata (~40ºS) from 1977 to 2010 in the western South Atlantic Ocean.

Survey	Year/Season	Latitudinal range	Nt. stat	Np. stat	M. eggs	M. larvae	Haul type	Mesh/Net
Conversut 1	1977/spr	28º32'S to 40º34'S	157	153	2,482.0	65.0	oblique[1]	250/0.8
Conversut 2	1978/aut	28º32'S to 40º34'S	170	163	26.5	31.1	oblique[1]	250/0.8
Conversut 3	1981/sum	28º32'S to 40º34'S	129	105	19.2	12.4	oblique[1]	250/0.8
Arepe 1	1980/aut	28º36'S to 34º40'S	102	102	838.2	24.8	oblique	300/0.6
Arepe 2	1980/win	28º36'S to 34º40'S	86	86	783.4	15.0	oblique	300/0.6
Arepe 3	1980/spr	28º36'S to 34º40'S	90	90	683.9	172.0	oblique	300/0.6
Arepe 4	1981/spr	32º07'S to 34º40'S	62	62	379.6	76.3	oblique	300/0.6
Arepe 5	1982/spr	28º36'S to 34º40'S	106	102	895.5	79.1	oblique	300/0.6
Ecopel 1	1987/spr	28º39'S to 34º39'S	57	53	636.6	68.7	oblique	300/0.6
Ecopel 2	1988/win	31º52'S to 34º39'S	50	50	823.7	274.4	oblique	300/0.6
Ecopel 3	1990/sum	31º52'S to 34º39'S	51	51	29.9	9.1	oblique	300/0.6
Ecopel 4	1991/aut	31º52'S to 34º39'S	54	39	9.4	28.5	oblique	300/0.6
La Plata 1	2003/win	28º34'S to 39º18'S	76	27	227.2	322.4	vertical[2]	300/0.6
La Plata 2	2004/sum	28º34'S to 39º18'S	84	31	20.8	23.4	vertical[2]	300/0.6
Pronex 1	2005/win	28º23'S to 34º09'S	33	32	25.8	17.1	oblique[3]	330/0.25*
Pronex 2	2007/sum	28º23'S to 34º09'S	33	33	2.0	3.7	oblique[3]	330/0.25*
MCT-II	2010/spr	28º41'S to 34º51'S	39	36	403.8	117.4	vertical	200/0.5

Nt. stat is the total number of stations and Np. stat is the total number of stations with plankton collections. M. eggs and M. larvae are the mean abundance (ind. 100 m^{-3}) of anchovy eggs and larvae, respectively. [1] vertical hauls were also performed, [2] at stations close to 50 and 200 m isobaths, [3] just the first haul/net. All sample strategies description are in the text. Mesh/Net is mesh size (μm) and net mouth diameter (m) (* net mouth area for MultiNet in m^{2}).

Table A5.2. Single and multiple explanatory variables GAM fits for Bonaerense anchovy (*Engraulis anchoita*) eggs and larvae for all surveys and by decade. Results showed the effective degrees of freedom (edf) with significance, percentage of deviance and the Unbiased Risk Estimator (UBRE) score. Explanatory variables are smooth functions (s) or factors (f).

| Models	n	Eggs edf	Eggs % deviance	Eggs UBRE score	Larvae edf	Larvae % deviance	Larvae UBRE score
all surveys							
s(TEM) + f(SEAS)	560	**8.75**	32.7	4.810	**8.91**	23.6	1.642
s(SAL) + f(SEAS)	541	**5.83**	26.0	5.337	**8.56**	18.3	1.837
s(TEM) + s(SAL) + f(SEAS)	539	**8.91**, **8.89**	41.6	4.081	**8.84**, **8.65**	31.3	1.442
1980s							
s(TEM) + f(SEAS)	360	**8.68**	31.3	4.750	**8.49**	20.6	1.265
s(SAL) + f(SEAS)	345	**7.90**	32.6	4.581	**7.87**	21.6	1.239
s(TEM) + s(SAL) + f(SEAS)	343	**8.94**, **8.77**	39.0	4.153	**7.54**, **8.15**	27.4	1.147
1990s							
s(TEM) + f(SEAS)	123	**8.61**	54.9	3.294	**8.13**	45.7	1.556
s(SAL) + f(SEAS)	119	**8.69**	51.2	3.614	**7.84**	59.1	0.994
s(TEM) + s(SAL) + f(SEAS)	119	**7.88**, **8.21**	61.7	2.866	**7.96**, **6.09**	67.2	0.820
2000s							
s(TEM) + f(SEAS)	77	**6.84**	67.9	0.783	**8.65**	57.8	1.131
s(SAL) + f(SEAS)	77	**7.23**	59.1	1.186	**8.11**	58.2	1.098
s(TEM) + s(SAL) + f(SEAS)	77	**7.27**, 5.97[*]	82.8	0.354	**5.23**, **7.60**	68.7	0.842

SEAS (season), TEM (temperature), SAL (salinity). All terms (edf) in bold were significant with p<0.001, [*] p<0.01.

Supplementary Figures
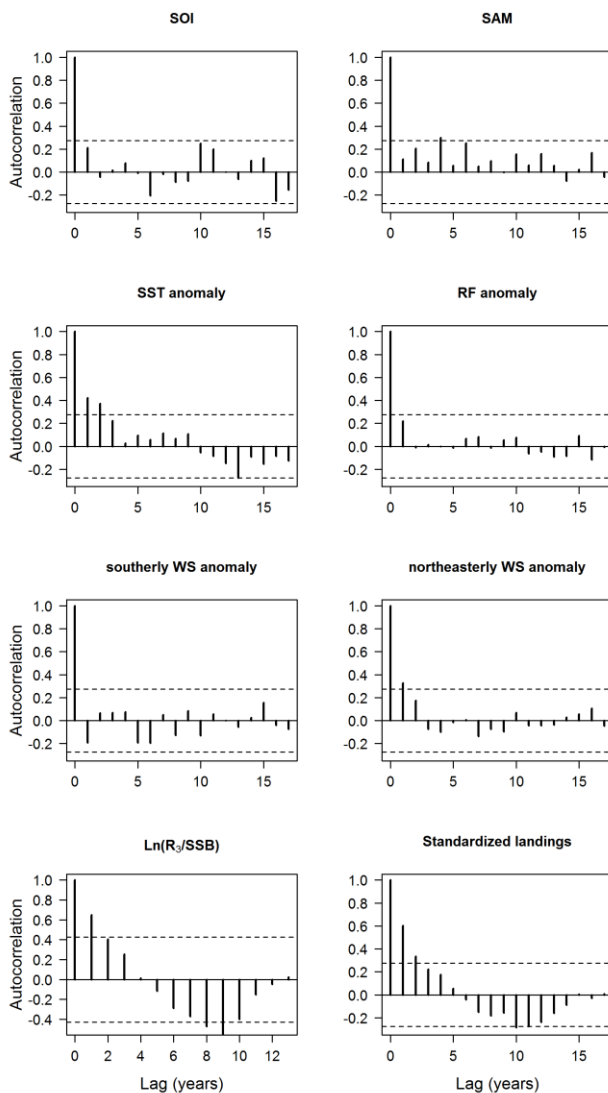
Fig. A5.1. Autocorrelation of the large-scale indices (SOI and SAM), physical variables (SST anomaly, RF anomaly, southerly WS anomaly and northeasterly WS anomaly) and Bonaerense anchovy stock (Landings anomaly and Ln(R/SBB) at age 3). Bars extending beyond dashed black lines mean significant correlation ($p < 0.05$). Time series were detrended before analysis.
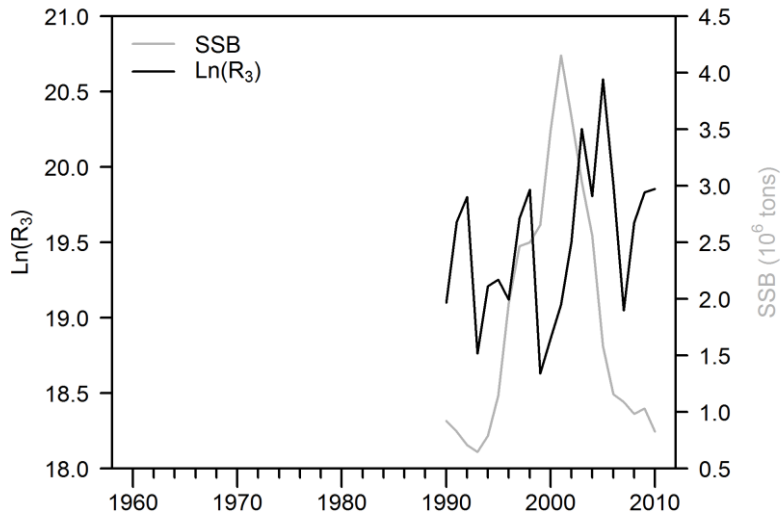
Fig. A5.2. Recruitment at age 3 (R_3; black) and spawning stock biomass (SSB; gray) annual values.
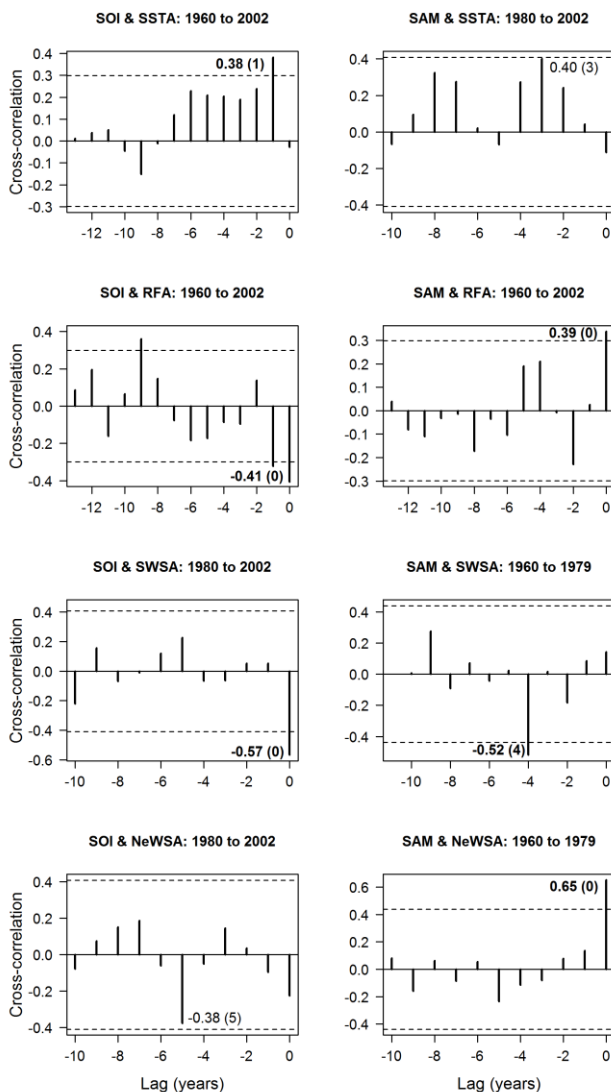
Fig. A5.3. Selected relationships between climatic indices (SOI left, SAM right) and physical variables: (from upper to bottom) SST anomaly, RF anomaly, southerly and northeasterly WS anomaly. Negative lag indicates that climatic forcing leads physical variables. Bars extending beyond dashed black lines (confidence intervals) mean significant correlation (p < 0.05). Maximum correlations (lag) were also indicated with significant relationships in bold.
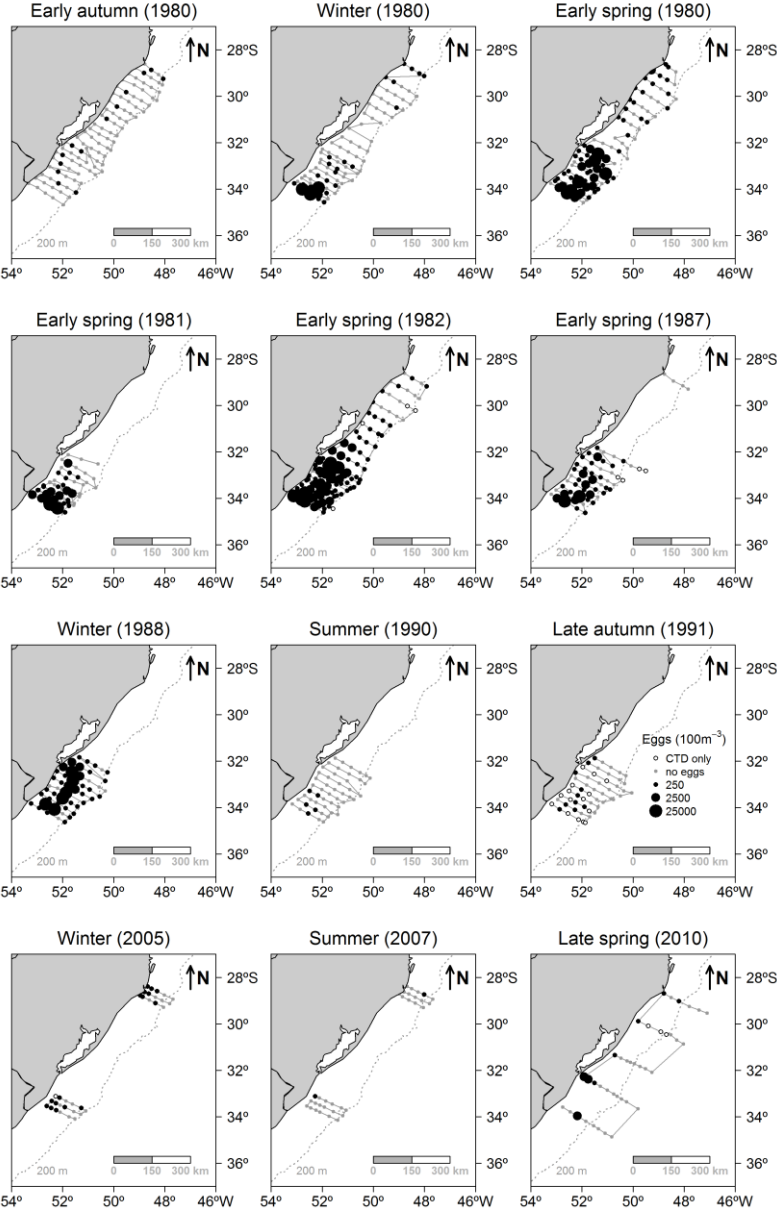
Fig. A5.4. Bonaerense anchovy (*Engraulis anchoita*) eggs distribution for surveys not displayed in Fig. 5.6.
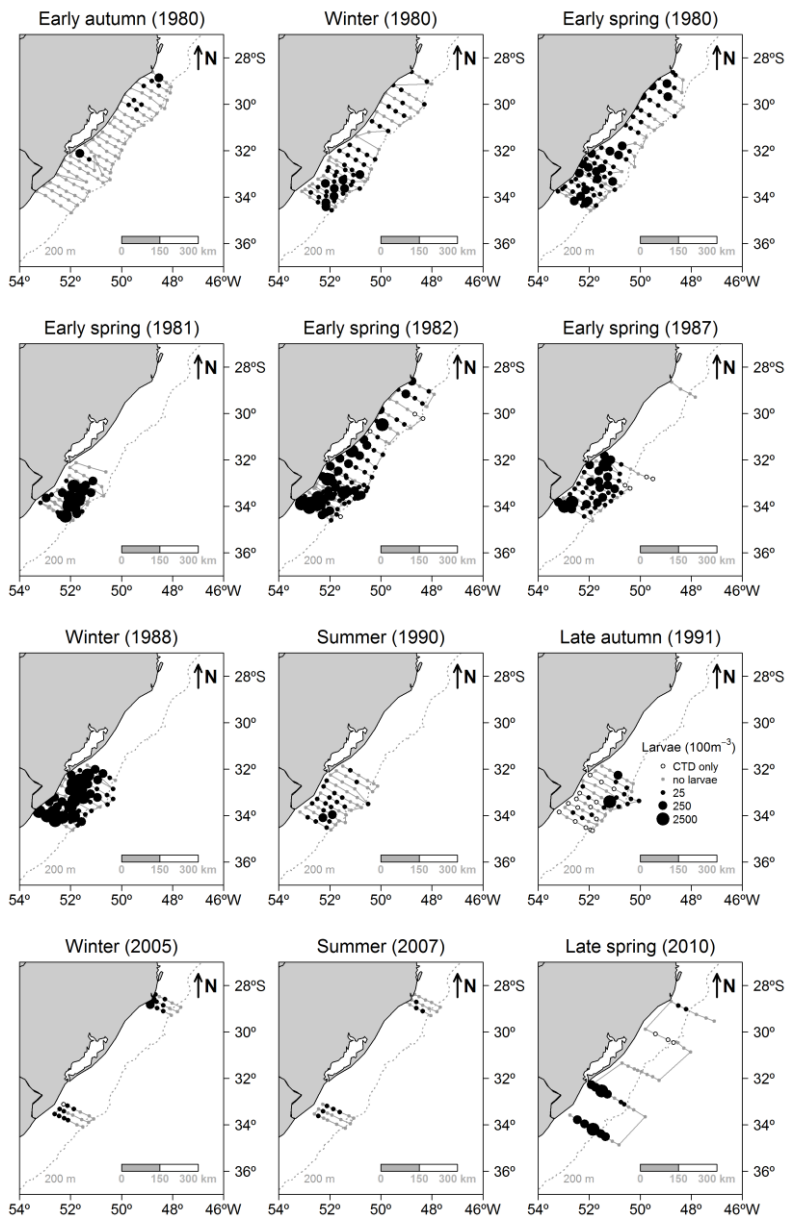
Fig. A5.5. Bonaerense anchovy (*Engraulis anchoita*) larvae distribution for surveys not displayed in Fig. 5.6.

6 CONSIDERAÇÕES FINAIS

Os resultados possibilitaram um melhor entendimento dos padrões de distribuição do ictioplâncton e da estrutura das associações de larvas de peixes em grandes escalas espacial e temporal no sudoeste do Oceano Atlântico Sul, em especial no grande ecossistema marinho da Plataforma Sul do Brasil. Foram investigados o papel dos eventos climáticos e processos oceanográficos direcionadores desses padrões, como a Oscilação Sul do El Niño (*El Niño Southern Oscillation*, ENSO) e o Modo Anular Sul (*Southern Annular Mode*, SAM), drenagem continental dos estuários do Rio da Prata e Lagoa dos Patos, ventos e distribuição das massas de água.

A distribuição de ovos e larvas de peixes está associada a quatro massas de água presentes na plataforma continental e talude da área estudada. A estrutura das associações ictioplanctônicas é influenciada pelas massas de água ao longo do gradiente latitudinal sobre a plataforma continental e também pelo gradiente costa-oceano. Ao norte de Cabo Frio, larvas da sardinha brasileira *Sardinella brasiliensis* foram características da Água de Plataforma, enquanto que ao sul do Farol da Conceição (31º30'S), ovos e larvas da anchoita *Engraulis anchoita* foram associadas à Água da Pluma do Prata. Na Água Subtropical de Plataforma as larvas do peixe espada *Trichiurus lepturus* foram dominantes e frequentes, e sobre todo o talude larvas de peixes meso- e batipelágicos são característicos da Água Tropical.

Quando esse padrão foi analisado ao longo do tempo, a relação entre as espécies dominantes das associações larvais com determinadas massas de água foi consistente independente da estação do ano (inverno, primavera, verão) e da década (1980 e 2000). As massas de água influenciam as espécies de larvas de peixes de duas formas: na primeira, a abundância de táxons dominantes foi determinada por massas de água distintas, que influenciam a dominância da comunidade larval; na segunda, os táxons raros e pouco frequentes são selecionados por uma determinada massa de água, como o caso da enchova *Pomatomus saltatrix* associada exclusivamente à Água Subtropical de Plataforma. Algumas associações de espécies com determinadas massas de água foram difíceis de serem confirmadas devido às larvas serem muito raras e ocasionais, i.e., um espécime capturado uma única vez.

A Água da Pluma do Prata, que se estende por toda a Plataforma Continental Sul, entre o Chuí e o Cabo Santa Marta, durante o inverno, foi associada ao ambiente de desova e ocorrência larval da população Bonaerense da anchoita *Engraulis anchoita*. Os resultados

demonstraram uma preferência por desova e pelo desenvolvimento larval na região ocupada pela massa de água, uma vez que essas águas apresentam condições propícias para o desenvolvimento dos estágios iniciais dos peixes, como estabilidade vertical da coluna de água e concentração de plâncton. O transporte de Ekman no sentido da costa durante o inverno contribui para a retenção de ovos e larvas no domínio da Água da Pluma do Prata, tornando-a um hábitat favorável ao desenvolvimento dos estágio iniciais de algumas espécies de peixes.

Os efeitos não estacionários do clima e dos processos oceanográficos na variação interanual da população Bonaerense da anchoita resultaram em dois caminhos principais: o primeiro efeito negativo do El Niño através da drenagem do estuário do Rio da Prata e temperatura superficial do mar; e o segundo efeito negativo associado ao SAM através da drenagem do Rio da Prata e intensidade do vento nordeste. Esses resultados demonstram que o ambiente de desova e ocorrência larval da população Bonaerense da anchoita pode ser impactado por eventos climáticos como o El Niño, modificando o balanço entre a quantidade de água drenada pela bacia do Rio da Prata e o deslocamento para o norte da frente estuarina, ou pela temperatura superficial do mar que sofre um resfriamento anormal na região da Confluência Brasil-Malvinas ou um aquecimento anormal nas águas da Corrente do Brasil. Sendo assim, o clima pode afetar direcionadores ambientais como as massas de água, quando são alteradas as suas características termohalinas, e consequentemente influenciar na composição e estrutura das associações de larvas de peixes.

Estudos ecológicos de longa duração que abrangem simultaneamente grandes escalas temporais e espaciais ainda são escassos, em particular aqueles conduzidos no ambiente marinho no sudoeste do Oceano Atlântico Sul, devido à dificuldade da manutenção de programas de pesquisa de longo prazo. Sendo assim, a reunião de dados obtidos em programas de pesquisa pretéritos realizados em grandes escalas espaciais na mesma região geográfica, devidamente padronizados, demonstrou-se uma importante ferramenta para ampliar o entendimento dos padrões de distribuição e estrutura das associações ictioplanctônicas ao longo do tempo, e as relações com os direcionadores ambientais, tanto climáticos como oceanográficos.

A Tese apoia a hipótese de que a distribuição em grande escala do ictioplâncton na Plataforma Sul do Brasil é associada à composição das massas de água, e que as associações ictioplanctônicas são influenciadas pelo gradiente costa-oceano e pela latitude nas águas da plataforma continental. Os resultados ainda confirmam a hipótese de que

as massas de água determinam a composição das associações de larvas de peixes na Plataforma Sul do Brasil, uma vez que independente da escala de tempo (sazonal ou interanual) as espécies estão associadas a uma determinada massa de água. Sendo assim, enquanto algumas espécies são selecionadas por fatores ambientais como as massas de água, outras sofrem influência na sua abundância, e consequentemente na dominância da comunidade. Os resultados nos levam a hipótese de que mudanças climáticas, como o aumento na frequência e/ou intensidade de eventos de El Niño combinado com tendência de aumento do SAM, modificam o a ação do ambiente na comunidade ictioplanctônica, afetando o sucesso de recrutamento e consequentemente a abundância e produção pesqueira de peixes, como por exemplo, a população Bonaerense da anchoita *Engraulis anchoita*.

Concluindo, os estágios iniciais da fauna de peixes do sudoeste do Oceano Atlântico Sul, em especial da Plataforma Sul do Brasil, são influenciadas pela dinâmica das massas de água em grande escala espacial e temporal, bem como por eventos climáticos que podem afetar o recrutamento das espécies, resultando em flutuações nas populações de peixes e na produção pesqueira.