# Feeding ecology of franciscana dolphin, *Pontoporia blainvillei* (Cetacea:Pontoporiidae), and oceanographic processes on the Southern Brazilian coast.

PhD Dissertation

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I hereby declare that no part of this thesis has been submitted for a degree to the University of Southampton, or any other University, at any time previously. The material included is the work of the author, except where expressly stated.

Manuela Bassoi
Southampton, December 2005

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## Abstract

Doctor of Philosophy

### Feeding ecology of franciscana dolphin, *Pontoporia blainvillei* (Cetacea:Pontoporiidae), and oceanographic processes on the Southern Brazilian coast.

by Manuela Bassoi

The feeding regime of the franciscana dolphin was investigated from stomach contents of incidentally caught animals in gillnets along the southern Brazilian coast, from 1994 to 2000. The analyses were based mainly on Linear and Generalised Linear Models (LM and GLM). There were some diet differences within the population, as juveniles had eaten more small teleosts and shrimps, and adults consumed larger fish prey and more cephalopods. Adult females had similar diet to juveniles, possibly related to parental guidance. Feeding regimes from northern and southern areas also revealed significant differences, where the most important fish prey from the northern area only occurred once in the diet of the southern animals. More detailed analysis dividing the region into 7 smaller latitudinal zones confirmed many differences, with higher occurrence of warm water species in the diet of northern zones, and cold water species in the southern zones. Additionally, the prey frequency and size do not change gradually along the coast, and different zones revealed a diverse diet composition between northern and southern. This raised the question whether variations in environmental conditions along the coast may affect the distribution of franciscana prey, and consequently its feeding regime.

To investigate the spatial and temporal patterns of environmental conditions off the study area, Sea Surface Temperature (SST) images from *Advanced Very High Resolution Radiometer*, and chlorophyll-$a$ (chl $a$) images from *Sea-viewing Wide Field-of-view* were extracted. The analysis (MANOVA, PCA, and time series) revealed a marked temporal influence of warm temperatures from the Brazil Current (BC) in the northern zones, and cold temperatures related to Malvinas/Falkland Current (MC) in the southern zones. The central zones showed a dynamic-edge region in terms of temperature behaviour probably caused by the mixing of BC and MC. Northern zones showed low values of chl $a$ concentration and southern zones high values, whereas central zones revealed intermediate values and less clear seasonal variation. The characteristics of the franciscana habitat had shown potential factors affecting the distribution and abundance of its prey, thus the prey species and size were treated as a function of the variables SST, chl $a$, latitude, depth, and season, using GLM and LM.

Models suggested that habitat parameters influence the franciscana prey species and size. As expected, warm water species are more likely to occur in the diet for longer periods at lower latitudes, and cold water prey at higher latitudes. The SST effect on prey specimens size shows that bigger cephalopods and fish were most frequent in warmer temperatures. The chl $a$ only influenced Engraulidae species. The latitude was the most important spatial predictor for many species, and bigger cephalopods were consumed in large quantities in central latitudes. The depth had great influence in the abundance of some prey species, with smaller fish and cephalopods being in higher numbers in shallower. The influence of the predictors on the franciscana prey is very similar to that found in the habitat by research cruises. Because some structures analysed may remain longer in the stomachs, the findings not only suggest a fairly opportunistic behaviour but it is likely that franciscana may occupy, possibly for long periods, small spatial ranges. This behaviour might be a strategy of minimizing energetic costs, ensuring low maintenance and thermoregulatory costs, and these include limiting excursions to distant areas.

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*This work is dedicated to*

*Eduardo Secchi and Alexandre Zerbini,*

*who have the true feeling of conservation.*

# Contents

## Appendices

# List of Figures

# List of Tables

# Chapter 1

# Introduction

## 1.1 Preface

The franciscana, *Pontoporia blainvillei*, is a small dolphin endemic in the coastal waters of the southwestern Atlantic Ocean (figure 1.1). The preference for coastal waters makes the franciscana especially vulnerable to anthropogenic activities (*e.g.* habitat degradation due to pollutants, boat traffic, fishing operations). In this sense, incidental catches in gillnets and trammel nets during commercial fishing have been reported throughout the species distribution area making the franciscana the most endangered small cetacean of the southwestern Atlantic Ocean (Ott et al., 2002; Secchi et al., 2003).

Figure 1.1: The franciscana dolphin, an endemic species of the southwestern Atlantic coast. Source: Oceanographic Museum of Rio Grande, Brazil.

In the study area, along the Rio Grande do Sul (RS) state coast - southern Brazil, this species has been experiencing an intense by-catch in gillnets for at least three decades (Secchi et al., 1997; Moreno et al., 1997; Ott et al., 2002). The annual mortality of franciscanas in this region (figure 1.2) has been estimated to range from several hundreds up to around a thousand individuals (Secchi et al., 1997; Ott, 1998; Ott et al., 2002), and it has been estimated that there is a 99% probability that the population is decreasing (Kinas, 2002). The estimated by-catch rates exceed the potential rate of population increase, leading Secchi (1999) to suggest that the persistent and unsustainable levels of by-catch are likely to cause a population collapse. Because of this, the franciscana from the Rio Grande do Sul/Uruguay population has been recently classified as "Vulnerable" by the IUCN Red List of Threatened Species (Secchi and Wang, 2003).

Additionally, recent studies of franciscanas from Rio Grande do Sul report probable habitat preference by latitude (Danilewicz et al., 2004), which could imply a need for different management procedures throughout its distribution on the southern Brazilian coast.

U.S. National Research Council (1996) and Iverson et al. (1997) state that knowledge of the foraging ecology of free-ranging marine mammals is critical in evaluating how they function within the ecosystem, improving the ability to predict influences of marine habitats and prey availability on animals, and supporting advice in conservation issues.

The dynamic hydrography of the study region appears to have a significant influence on the distribution and abundance of many of the franciscana prey (Haimovici et al., 1996), but there are currently no details on how environmental factors influence the franciscana dolphin feeding habits. Therefore, this research study is the first attempt to investigate the interactions of franciscana feeding ecology and the oceanographic parameters in the study region, and the implications of its movements. Moreover, such analyses may help to understand the possible latitude preference of franciscana from southern Brazilian coast reported by Danilewicz et al. (2004).

The effects of oceanographic factors (*e.g.* water currents, fronts, local divergence, upwelling areas) can be used to characterise foraging of marine mammals (Forcada, 2002), and understanding prey availability, mainly fish and cephalopod species, may be done under a variety of marine environmental conditions.

Figure 1.2: Franciscana dolphins accidentally caught in gillnets in southern Brazilian coast. Source: Oceanographic Museum of Rio Grande, Brazil.

Of all environmental factors in the ocean water, temperature is often assumed to have the most important effects on fish and cephalopods, due to its influence on physiological capability and hence spatial distribution (Clarke, 1996). Also, water temperature is likely to be an indicator of other environmental factors, especially water masses and fronts, which in turn determine food availability - prey density and size (Zheng et al., 2002).

For example, Maravelias and Reid (1997) found that the location of ocean fronts influence the distribution of pre-spawning herring. Moreover, Helle (1994) found that the highest abundance of early juvenile cod coincided with the strong inflow of warm Atlantic water in the Barents Sea. In addition, the density and size distribution of many marine species is likely to be influenced by water depth (Zheng et al., 2002).

Another important environmental parameter likely to affect primary predators is the concentration of phytoplankton, the ocean primary production. Abreu (1987) stated that the phytoplankton biomass in the southern Brazilian coast is very important for higher densities of zooplankton, ichthyoplankton, and juvenile fishes, which occurred when higher concentration of phytoplankton were observed. Additionally, some of the pelagic fish species of the southern Brazilian continental shelf, such as Engraulidae species, feed on zooplankton and occasionally on phytoplankton (Castello and Habiaga, 1982). Phytoplankton production can be estimated by relating it directly to satellite-derived pigment concentration, the chlorophyll-$a$. However, turbid coastal waters can exhibits bias of chlorophyll-$a$ measurements because higher concentration of sediments on the water. On the other hand, fresh water discharges on coastal waters can truly increase chlorophyll-$a$ production due to the mixing of the waters (Abreu, 1987).

Previous studies of franciscana diet show that the animal feed on juvenile fishes and some Engraulidae species (*e.g. Engraulis anchoita*, *Anchoa marinii*), thus the phytoplankton environmental parameter (expressed as chlorophyll-$a$) is also investigate in this study.

Recently, there has been a growing interest in the integration of biological and environmental data. This interest, in aquatic systems, raises the question of to what extent oceanographic features and processes influence marine mammal distribution and foraging ecology (Jaquet et al., 2000). There is little empirical evidence of these influences, due to the inherent difficulties of observing and documenting *in situ* marine mammal distribution and predator-prey interactions (Trites, 2002).

Research studies have used many sources of information (*e.g.* Sea Surface Temperature (SST), Sea Bottom Temperature (SBT), bathymetry, tidal data, type of land, salinity, and chlorophyll-$a$) to understand the relationships between the oceanographic conditions and marine animal distribution, foraging and fisheries interactions (Helle, 1994; Bobbitt et al., 1997; Maravelias and Reid, 1997; Shepherd, 1997; Wanless et al., 1997; Ribic et al., 1997; Wadsworth, 1997; Waluda and Pierce, 1998; Gonzalez and Marin, 1998; Watkins, 1998; Xavier et al., 1999; Bruce et al., 2001; Bertrand et al., 2002; Tamura and Fujise, 2002; Bjorge et al., 2002; Zheng et al., 2002; Mendes et al., 2002). Interpreting the relationships between these data is important because it provides some understanding about the resources available to a particular species, and also it should improve our understanding of the factors controlling its habits.

Statistical methods such as Linear Models (LM), Generalized Linear Models (GLM)[1], Generalized Additive Models (GAM), and Geographical Information Systems (GIS) have been used in recent years as more useful means to integrate biological and physical data. However, only recently has grown interest in the use of GLM, GAM, and GIS techniques, and there is as yet no standard methodology in common use.

The classical linear regression model is the most widely employed statistical method in family research. LM are popular because they are simple to construct and interpret, and because they describe the relationship between the expectation of a response (dependent) variable and a set of explanatory (independent) variables very clearly. However, LM are based on the assumption that response variables have conditional normal distributions with constant variance, and that the relationship between the response variable and the explanatory variables is linear. LM are not inappropriate in some circumstances because the response distributions (*e.g.* poisson and binomial) are substantially different from normal distributions with constant variance, and/or violates the linearity assumption. Two solutions to these problems involve using GLM or GAM.

GLM accommodate response variables with nonnormal (conditional) distributions through a transformation called the link function. Having a common theoretical framework, GLM represent a class of statistical models, including classical LM for continuous data, logistic and probit models for binary or binomial data, Poisson and negative binomial models for count data (Graphen and Hails, 2002). These models can be easily formulated by selecting an appropriate response distribution and link function (*e.g.* log link). In this respect, GLM provide a simplified and flexible approach to statistical modeling (Venables and Ripley, 1997). Several commercial statistical software packages now include a routine for standard GLM (*e.g.* SAS, S-PLUS, R).

GAM is a nonparametric regression technique offering advantages over conventional regression techniques because it is not tied to a particular functional relationship (*e.g.* linearity) and because it is less restrictive in assumptions about the underlying statistical distribution of

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[1] Some authors also use GLM to refer to General Linear Models, which is the same as the Linear Models (LM) in this study.

the data. However, in some cases GAM might have the problem of over-fitting the functional relationships (Agenbag et al., 2003). In GAM the covariates are assumed to affect the dependent variable through additive, unspecified (not linear, not parametric) smooth functions (Venables and Ripley, 1997).

LM, GLM, and GAM are used to provide qualitative and quantitative descriptions of the relationships between species abundance and environmental conditions. GIS techniques are used to provide qualitative description of spatial patterns and the visual aspects of results revealed from GLM, or any other statistical analyses (Maravelias and Reid, 1997; Zheng et al., 2002).

Therefore this thesis analyses (a) the franciscana diet, (b) the oceanographic parameters in the study area, and (c) the relationships, mainly through GLM procedures, between the dolphin food habits (mostly fish and cephalopods prey) and environmental (SST, chlorophyll-*a*), spatial (latitude and water depth), and temporal (season) parameters in the southern Brazilian coast.

## 1.2 Objectives

The main objective of this thesis is:

- To understand the effects of environmental conditions in the feeding ecology of the franciscana dolphin along the southern Brazilian coast.

In order to achieve the principal objective above, the specific objectives are:

- To describe the feeding ecology of the franciscana dolphin by analysing stomach contents data, and identify prey species richness and abundance geographically and temporally.
- To characterise the geographic region according to oceanographic parameters, Sea Surface Temperature (SST) and Chlorophyll-*a* (as an indicator of water masses and primary production).
- To determine the parameters that most influence the frequency of different species of prey, and prey specimens sizes, in a dolphin's diet.

## 1.3 Structure of the thesis

The thesis is organised as follows:

- Chapter 1 presents an introduction and the main objectives of the research.
- Chapter 2 presents an overview of the franciscana dolphin biology and reviews its associated feeding ecology studies.
- Chapter 3 explores the study area and its background of important physical processes, and the historical bio-physical studies in the region.

Chapters 4 and 5 are the biological and the physical data analysis, respectively. These chapters have their own methods, results and discussion sections.

- Chapter 4 presents the franciscana feeding ecology in the study area. This Chapter starts with an introduction of feeding studies for marine mammals. Afterwards, the methods and results are divided into two parts.

  In the first part, franciscana and stomach content data are described. Methods and results of the general diet composition is analysed from both source regions of the data, southern and northern areas. To assess the importance of prey in the diet of franciscana two different methods were used: (1) the traditional feeding analysis, the Index of Relative Importance (IRI) (Pinkas et al., 1971); and (2) LM and GLM. The IRI described the data quantitatively and permitted the comparison of the franciscana diet with past studies, since the majority of published studies of this dolphin use this methodology. However, from the IRI it is not possible to test for statistical differences between groups (*e.g.* areas, gender, sexual maturity), hence alternative statistical methods were chosen, i.e. LM and GLM. These models allow one to assess significant differences of the franciscana diet according to biological, (gender and sexual maturity), temporal (season), and spatial (northern and southern areas) parameters. Since the results of the first part showed important differences of the diet between the two areas it was decided to analyse the data in more detailed regions.

  Thus, the second part (Methods II and Results II) consists of refining the study area not only as southern and northern areas, but into 7 latitudinal zones. The analysis compares the franciscana prey between these zones. However, from this point the analysis is focused on the spatial and temporal parameters, which is the main goal of this thesis. In this section Principal Component Analysis (PCA) is used as well as the LM and GLM.

The discussion of Chapter 4 takes into account the franciscana dolphin diet and many aspects of its biology and behaviour, and prey availability (temporally and spatially), which are divided according to the analysis of (I) southern and northern areas and, (II) latitudinal zones. Past feeding studies of franciscana are also discussed.

- Chapter 5 describes the physical oceanographic parameters, Sea Surface Temperature (SST) and chlorophyll-$a$, throughout the study area. The practical aim of Chapter 5 is to assess the environmental dynamics of the study region where the franciscana have been feeding. To achieve this purpose, exploratory analysis, Time Series and PCA were performed for the 7 latitudinal zones, and plus an extra zone (number 8) in the southern portion of the study area.

- Chapter 6 is the synthesis of the results found in chapters 4 and 5, the environmental-biological coupling. The main goal of the Chapter is to analyse the influence of the explanatory variables corresponding to environmental characteristics of the habitat on the franciscana prey. Therefore it analyses the relationships of the franciscana dolphin feeding habits, described in the Chapter 4, and a suite of variables describing the environment, as explored in the Chapter 5, using GLM and LM. These models permit inclusion of more than one explanatory variable, and the combination of categorical and continuous variables, which allows the interactions of the oceanographic parameters (*e.g.* chlorophyll-$a$, SST) with the franciscana diet, and additionally with the spatial and the temporal parameters. Chapter 6 discuss the main objective of this study, which leads to the suggestion of possible habitat preferences, or movements behaviour, of the franciscana dolphin throughout the southern Brazilian coast. As a consequence some suggestions for franciscana management in the study area are included.

- Chapter 7 summarises and presents the main conclusions of this study, as well some suggestions for further investigations.

# Chapter 2

# The franciscana dolphin

## 2.1 The species and its distribution

The franciscana dolphin, *Pontoporia blainvillei*, is one of the smallest cetaceans (odontocete). Although it has been considered by many to be a member of the so-called river dolphins (superfamily Platanistoidea), franciscanas are found mainly in coastal marine waters with occasional occurrences in estuaries (Praderi, 1986).

Females are larger than males, and overall the adult females vary between 137 and 177cm in total length, and adult males between 121 and 158cm. Neonate sizes are between 59 and 80cm. The weight of mature females is between 34 and 53kg, males vary from 29 to 43kg, and neonates around 7.3 to 8.5kg (Brownell, 1984, 1989). In the study area, the lengths of adult individuals vary between 146.4 and 161.9cm for females, and between 129.8 and 136.4cm for males (Danilewicz et al., 2002), and the mean birth length is 73.4cm. Mean length and weight at sexual maturity was estimated at 138.9cm and 32.8kg for females, and 128.2cm and 26.6kg for males (Danilewicz et al., 2000).

Furthermore, like other cetacean species, franciscana has low fecundity rates. Females first reproduce at about 2.7 years of age, the gestation period is between 10.5 and 11.1 months, and the birth intervals vary from 1 to 2 years. Females give birth around November and lactation lasts for around 9 months. However, calves take food from around the third month, and measure between 77 and 83cm (Kasuya and Brownell, 1979; Pinedo, 1982; Pinedo et al., 1989; Danilewicz et al., 2000).

The maximum life span is around 20 years but only a small percentage of the animals survive over 10 years (Kasuya and Brownell, 1979; Pinedo, 1994; Ott et al., 2000; Pinedo and Hohn, 2000; Ramos et al., 2000). Very little is known about their behaviour, but franciscana is thought to form groups of few animals rather than gregarious. Herd size may range from 2 to 15 individuals (Bordino et al., 1999; Crespo, 2002).

The dolphin is endemic in the southwestern Atlantic Ocean and its distribution ranges from Itaúnas (18$^o$25’S-30$^o$42’W), southeastern Brazil (Siciliano, 1994) to Golfo Nuevo (42$^o$35’S-64$^o$48’W), Central Argentina (Crespo et al., 1998) (figure 2.1). The species lives in a narrow strip of coastal waters from the shoreline to an offshore limit coincident with the 30m isobath (Moreno et al., 1997; Secchi et al., 1997). However, franciscanas are not distributed continuously, and the reasons for these hiatuses (absent or low records) are unclear (Bordino et al., 2002) (figure 2.1).

Along the franciscana range, Secchi et al. (2002) propose the following population definitions: (1) Northern: occurring from Geographic Sectors (GS) 1 to 6, and subdivided in (1a) animals

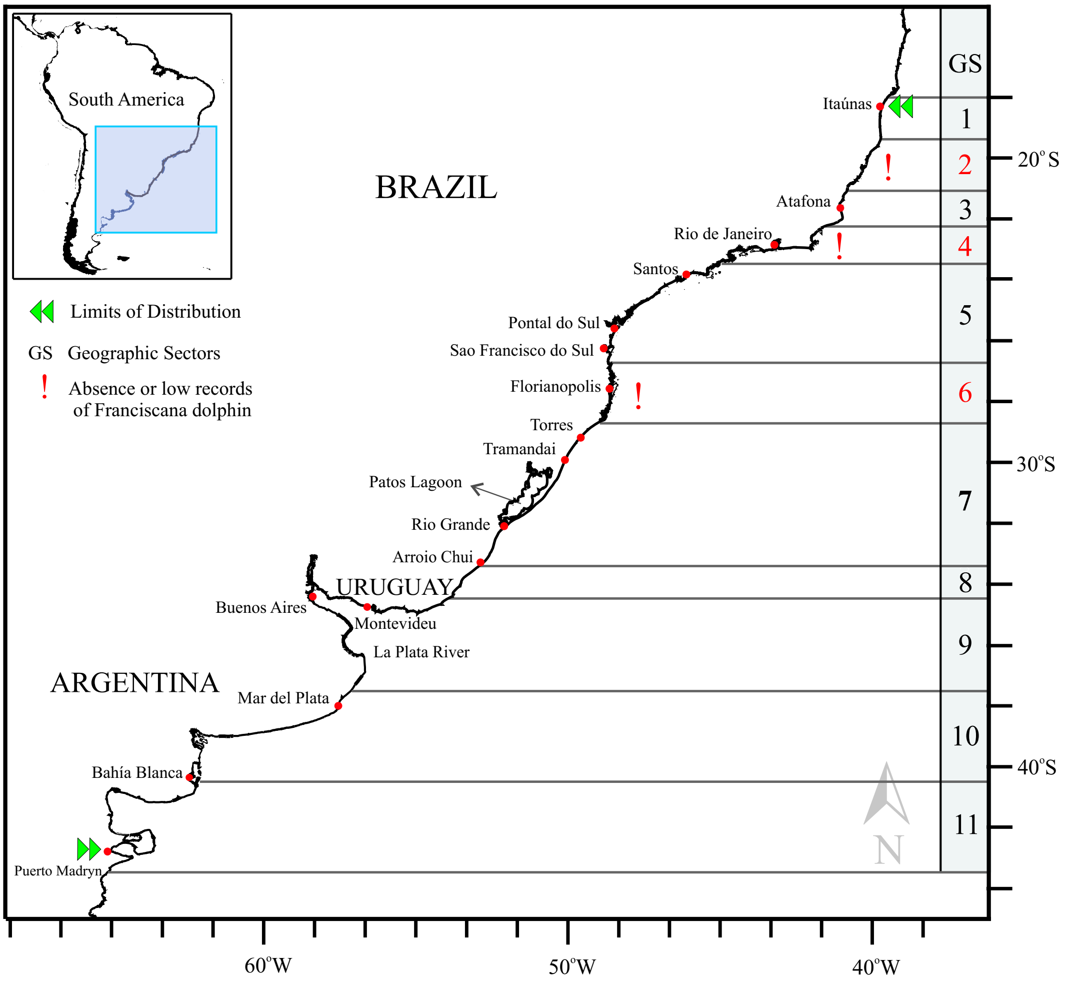

Figure 2.1: Map of franciscana’s range. The area was divided in 11 Geographic Sectors (GS) according to dolphin distribution and proposed population forms during workshops about the species (Secchi et al., 2002).

from GS 1 to 4, and (1b) animals from GS 5 and 6; (2) Southern: occurring from GS 7 to 11, and subdivided into (2a) animals of GS 7 and 8, and (2b) GS 9 to 11. Moreover, franciscanas from southern Brazil (GS 7) and Uruguay (GS 8) should be considered a single stock (Secchi et al., 2002) (figure 2.1).

Furthermore, recent research studies of genetics and habitat use patterns (Danilewicz et al., 2004), suggest a probable latitude preference of franciscanas along the southern Brazilian coast (GS 7, figure 2.1), for northern or southern areas.

## 2.2 Previous studies of feeding ecology

Diet studies conducted throughout Argentina, Uruguay and Brazil indicate that franciscanas' diet is composed of at least 76 food items (Burmeister, 1869; Lahille, 1899; Cabrera and Yepes, 1940; Carvalho, 1961; Brownell and Ness, 1969; Fitch and Brownell, 1971; Brownell, 1975; Brownell and Praderi, 1976; Pinedo, 1982; Praderi, 1986; Perez-Macri, 1987; Brownell, 1989; Schmiegelow, 1990; Bastida et al., 1992; Ott, 1994; Perez et al., 1996, 2000; Bassoi, 1997; Oliveira et al., 1998; Bassoi and Secchi, 1999; Rivero et al., 2000; Di Beneditto, 2000; Rodriguez et al., 2002) (table 2.1).

The majority of prey, from the most significant feeding studies, belonging to three main zoological groups: fish (82.8%), crustaceans (9.2%), and molluscs (7.9%) (Pinedo, 1982; Ott, 1994; Bassoi, 1997; Rivero et al., 2000; Di Beneditto, 2000). Overall, these feeding habit studies indicate that the animal preys predominantly upon bottom-dwelling juvenile teleosts, squids, and crustaceans.

The franciscana is also believed to be an opportunistic feeder, ingesting mainly those prey most frequent in the area. This behaviour can be observed in seasonal fluctuations in the franciscana's diet, which coincide with the pattern of variation observed in the abundance of the prey species through the year (Pinedo, 1982; Perez-Macri, 1987; Ott, 1994; Perez et al., 1996; Bassoi, 1997; Oliveira et al., 1998; Perez et al., 2000; Di Beneditto, 2000; Rivero et al., 2000; Rodriguez et al., 2002).

In addition, Bassoi (1997) and Bassoi and Secchi (1999) noticed that *Micropogonias furnieri*, a very important prey for franciscana more than a decade ago (Pinedo, 1982), presently accounts for a low proportion of the diet as a result of overfishing of the species throughout almost all its geographical distribution (Reis, 1992; Haimovici, 1998). Bassoi and Secchi (1999) also concluded that trends in fish stock abundance seem to dictate trends in prey composition of *Pontoporia blainvillei* and that monitoring the trophic behaviour of this species may help forecast and understand fluctuation patterns in the recruitment of commercial fishes.

The prey species frequently ingested by franciscana (table 2.1) vary along its distribution range, mainly between the southern and northern regions. This can be clearly observed through the studies of Di Beneditto et al. (1998) and Di Beneditto (2000), since the samples were obtained from Rio de Janeiro, a northern sampling area with a different marine coastal ecosystem and a different genetic population of franciscana from southern regions (Secchi et al., 2002).

Table 2.1: General information for prey composition which had been found in feeding studies of franciscana, *Pontoporia blainvillei*, along its geographical distribution (for GS see figure 2.1).

| **Geographic Sector (GS)** | **8** | **7** | **8** | **10** | **8** | **10** | **5** | **7** | **7** | **5** | **9** | **3** | **9** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Region** | **Uruguay** | **South RS** | **Uruguay** | **South BA** | **Uruguay** | **South BA** | **SP / PR** | **North RS** | **South RS** | **PR** | **North BA** | **North RJ** | **North BA** |
| **Authors** | **A** | **B** | **C** | **D** | **E*** | **F** | **G** | **H** | **I** | **J** | **K** | **L** | **M** |
| **Nº of stomachs** | **-** | **277** | **6** | **30** | **-** | **2** | **2** | **36** | **100** | **12** | **60** | **89** | **131** |
| **Year** | **1976** | **1982** | **1984** | **1987** | **1989*** | **1992** | **1990** | **1994** | **1997/2000** | **1998** | **2000/2002** | **2000** | **1996/2000** |
| **Fishes** | | | | | | | | | | | | | |
| Sciaenidae | | | | | | | | | | | | | |
| *Cynoscion guatucupa* | x | x | | x | x | x | | x | x | | x | | x |
| *Cynoscion jamaicensis* | | | | | | | | x | x | | | x | |
| *Cynoscion microlepidotus* | | | | | | | | | | x | | | |
| *Cynoscion virescens* | | | | | | | | | | | | x | |
| *Paralonchurus brasiliensis* | x | x | | | x | | | x | x | x | x | x | |
| *Macrodon ancylodon* | x | x | | x | x | x | | x | x | | x | x | |
| *Micropogonias furnieri* | | x | | x | x | x | | | x | | x | x | |
| *Umbrina canosai* | | x | | | x | | | x | x | | x | | |
| *Menticirrhus sp.* | | x | | | | | | | x | | | | |
| *Menticirrhus americanus* | | | | x | x | x | | | | | | | |
| *Menticirrhus littoralis* | | | | | | | | x | | | | | |
| *Pogonias cromis* | | | | | | | | | | | x | | |
| *Isopisthus parvipinnis* | | | | | | | x | | | x | | x | |
| *Stellifer rastrifer* | | | | | | | x | x | | | | x | |
| *Stellifer brasiliensis* | | | | | | | x | | | | | x | |
| *Stellifer sp.* | | | | | | | x | | | | | x | |
| *Ctenosciaena gracilicirrhus* | | | | | | | | | | | | x | |
| *Larimus breviceps* | | | | | | | | | | | | x | |
| Pomatomidae | | | | | | | | | | | | | |
| *Pomatomus saltatrix* | | x | | | | | | | x | | x | | |
| Mugilidae | | | | | | | | | | | | | |
| *Mugil platanus* | | | | | | | | | | | x | | |
| *Mugil liza* | | | x | | | | | | | | | | |
| *Mugil sp.* | | | | | | | | | x | | | | |
| Phycidae | | | | | | | | | | | | | |
| *Urophycis brasiliensis* | x | x | | x | x | x | | x | x | | x | | |
| Trichiuridae | | | | | | | | | | | | | |
| *Trichiurus lepturus* | x | x | | | x | | | x | x | | | x | |
| Batrachoididae | | | | | | | | | | | | | |
| *Porichtys porosissimus* | x | x | | | x | | | x | x | | | x | |
| Stromateidae | | | | | | | | | | | | | |
| *Peprilus paru* | | x | | x | x | x | | | x | | | x | |
| *Stromateus brasiliensis* | x | | | | x | | | | | | x | | |
| Syngnathidae | | | | | | | | | | | | | |
| *Leptonotus blainvillianus* | | | | | | x | | | | | x | | |

*cont.* Table 2.1

| **Geographic Sector (GS)** | **8** | **7** | **8** | **10** | **8** | **10** | **5** | **7** | **7** | **5** | **9** | **3** | **9** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Region** | **Uruguay** | **South RS** | **Uruguay** | **South BA** | **Uruguay** | **South BA** | **SP / PR** | **North RS** | **South RS** | **PR** | **North BA** | **North RJ** | **North BA** |
| **Authors** | **A** | **B** | **C** | **D** | **E*** | **F** | **G** | **H** | **I** | **J** | **K** | **L** | **M** |
| **N° of stomachs** | **-** | **277** | **6** | **30** | **-** | **2** | **2** | **36** | **100** | **12** | **60** | **89** | **131** |
| **Year** | **1976** | **1982** | **1984** | **1987** | **1989*** | **1992** | **1990** | **1994** | **1997/2000** | **1998** | **2000/2002** | **2000** | **1996/2000** |
| Merlucciidae | | | | | | | | | | | | | |
| *Merluccius hubbsi* | | | | | | | | | x | | | | |
| Engraulidae | | | | | | | x | | | | | | |
| *Anchoa marinii* | x | x | | | x | x | | x | x | | x | | |
| *Anchoa filifera* | | | | | | | | | | x | | x | |
| *Engraulis anchoita* | x | x | | x | x | x | | x | x | | x | | |
| *Cetengraulis edentulus* | | | | | | | | | | x | | | |
| *Anchoviella lepidentostole* | | | | | | | | | | | | x | |
| *Lycengraulis olidus* | | x | | | | | | | | | x | | |
| Ophidiidae | | | | | x | | | | | | | | |
| *Raneya fluminensis* | | | | | | | | | x | | x | | |
| Triglidae | | | | | | | | | | | | | |
| *Prionotus sp.* | | | | | | | | | x | | | | |
| Serraninae | | | | | | | | | | | | | |
| *Dules auriga* | | | | | | x | | | | | | | |
| Congridae | | | | | | | | | | | | | |
| *Conger orbignyanus* | | | | | x | | | x | | | | | |
| *Ariosoma sp.* | | | | | x | | | | | | | | |
| Ophichthyidae | | | | | | | | | | | | | |
| *Ophicthus cf. gomesii* | | | | | | | | x | | | | | |
| Carangidae | | | | | | | | | | | | | |
| *Trachurus lathami* | x | x | | | x | x | | x | x | | x | | x |
| *Trachurus sp.* | | | | x | | | | | | | | | |
| *Parona signata* | | | | | | x | | | | | | | |
| Clupeidae | | | | | | | | | | | | | |
| *Ramnogaster arcuata* | | | | | | | | | | | x | | |
| *Brevoortia aurea* | | | | x | | x | | | | | | | |
| *Ramnogaster melanostoma* | | | x | | | | | | | | | | |
| *Brevoortia pectinata* | | | x | | | | | | | | | | |
| *Sardinella brasiliensis* | | | | | | | | | | | | x | |
| *Odontognathus mucronatus* | | | | | | | | | | | | x | |
| *Chirocentrodon bleekerianus* | | | | | | | | | | | | x | |
| *Pellona harroweri* | | | | | | | | | | | | x | |
| Atherinopsinae | | | | | | | | | | | | | |
| *Odonthestes argentinensis* | | | | | | | | | | | x | | |
| *Odonthestes bonariensis* | | x | x | | | | | | | | | | |
| *Austroatherina incisa* | | | | x | | x | | | | | | | |
| Sparidae | | | | | | | | | | | | | |
| *Spagrus pagrus* | | | | | | | | | | | x | | |
| Percophididae | | | | | | | | | | | | | |
| *Percophis brasiliensis* | | | | | | | | | | | x | | |
| Bothidae | | | | | | | | | | | | | |
| *Syacium papillosum* | | | | | | | | | x | | | | |
| *Paralichtys isosceles* | | | | | | | | | x | | | | |
| Cynoglossidae | | | | | | | | | | | | | |
| *Symphurus sp.* | | | | | x | | | | | | | | |
| Nomeidae | | | | | x | | | | | | | | |
| *Cubiceps sp.* | x | | | | | | | | | | | | |
| Gobiidae | | | | | x | | | | | | | | |

*cont.* Table 2.1

| **Geographic Sector (GS)** | **8** | **7** | **8** | **10** | **8** | **10** | **5** | **7** | **7** | **5** | **9** | **3** | **9** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Region** | **Uruguay** | **South RS** | **Uruguay** | **South BA** | **Uruguay** | **South BA** | **SP / PR** | **North RS** | **South RS** | **PR** | **North BA** | **North RJ** | **North BA** |
| **Authors** | **A** | **B** | **C** | **D** | **E*** | **F** | **G** | **H** | **I** | **J** | **K** | **L** | **M** |
| **N° of stomachs** | **-** | **277** | **6** | **30** | **-** | **2** | **2** | **36** | **100** | **12** | **60** | **89** | **131** |
| **Year** | **1976** | **1982** | **1984** | **1987** | **1989*** | **1992** | **1990** | **1994** | **1997/2000** | **1998** | **2000/2002** | **2000** | **1996/2000** |
| **Cephalopods** | | | | | | | | | | | | | |
| Loliginidae | | | | | | | | | | | | | |
| *Loligo sanpaulensis* | | x | | x | x | x | | x | x | x | x | x | x |
| *Loligo plei* | | | | | | | x | x | x | x | | x | |
| *Lolliguncula brevis* | | | | | | | | | | x | | x | |
| Argonautidae | | | | | | | | | | | | | |
| *Argonauta nodosa* | | | | | | | | x | x | | | | |
| Octopodidade | | | | | | | | | | | | | |
| *Eledone gaucha* | | | | | | | | x | | | | | |
| *Octopus tehuelchus* | | | | | | | | | | | x | | |
| **Crustaceans** | | | | | | | | | | | | | |
| Solenoceridae | | | | | | | | | | | | | |
| *Pleoticus muelleri* | | x | | | x | | | | x | | x | | |
| Penaeidae | | | | | | | | | | | | | |
| *Penaeus paulensis* | | x | | | x | | | | | | | | |
| *Penaeus spp.* | | | | | | | x | | | | | | |
| *Xyphopenaeus kroyeri* | | | | | | | | | | | | x | |
| Palaenomidae | | | | | | | | | | | | | |
| *Artemesia longinaris* | | x | | | x | | | | x | | x | x | |
| Sergestidae | | | | | | | | | | | | | |
| *Peisos petrunkevitchi* | | | | | | | | | | | x | | |
| Mysidacea | | | | | | | | | | | | | |
| *Neomysis americana* | | | | | | | | | | | x | | |
| Calanoid Copepods | | | | | | | | | | | x | | |

References:
Region: (BA) Buenos Aires Province (Argentina); (RS) Rio Grande do Sul State (Brazil); (PR) Paraná State (Brazil); (SP) São Paulo State (Brazil); (RJ) Rio de Janeiro State (Brazil).
Authors: (A) Brownell and Praderi; (B) Pinedo; (C) Praderi; (D) Perez-Macri; (E) Brownell; (F) Bastida *et al.*; (G) Schmiegelow; (H) Ott; (I) Bassoi; (J) Oliveira *et al.*; (K) Rivero *et al.*; (L) Di Beneditto; (M) Perez *et al.*
*Brownell (1989) compiles the results obtained by Brownell and Ness, 1969; Fitch and Brownell, 1971; and Brownell, 1975.

However, the consumption of prey species also can differ between adjacent areas (Danilewicz et al., 2002). According to Rivero et al. (2000), diet components varied between estuarine and marine ecosystems. This was evident from comparison of diets of specimens obtained in the estuarine ecosystem of Bahía Samborombón (northern Buenos Aires Province, Argentina) and the adjacent marine coastal ecosystem. Based on the index of relative importance (IRI) values, *Micropogonias furnieri*, *Odonthestes argentinensis* and *Macrodon ancylodon* were shown to be the main prey species for the estuarine area, whereas *Cynoscion guatucupa*, *Loligo sanpaulensis* and *Urophycis brasiliensis* were the principal prey for the marine coastal ecosystem.

Moreover, it seems that differences also exist between adjacent marine ecosystems; for example, specimens obtained in deeper waters of southern Buenos Aires Province, show *Loligo sanpaulensis* and *Trachurus lathami* as main prey (Perez et al., 1996, 2000). Although these are nearby areas, the diet variation could be explained by different environments between estuarine and marine waters, and inshore and offshore regions.

Many species of the franciscana's diet described on table 2.1 have been studied on the southern Brazilian coast since the late 1970s. Abundance and geographic distribution patterns for demersal and pelagic fishes, and cephalopods, for southern Brazil have been analysed based on fisheries data and research cruises (Castello and Moller, 1977; Castello and Habiaga, 1982; Haimovici, 1982; Haimovici and Andrigueto Jr., 1986; Haimovici and Vieira, 1986; Haimovici, 1988; Andriguetto Jr. and Haimovici, 1991; Haimovici and Perez, 1991b,a; Martins, 1992; Reis, 1992; Haimovici et al., 1993; Lima and Castello, 1995; Haimovici et al., 1996; Castello, 1997; Haimovici, 1997b; Martins and Haimovici, 1997; Santos, 1999).

The majority of these biological research studies describe southern Brazil as a biogeographic transition zone. Consequently, the composition and abundance of species, the pelagic structure, the spatial distribution of communities and their trophic interactions, vary seasonally and it is suggested that these variations may be largely controlled by distinct water masses in the region. However, this remains speculative as there are few studies of the interaction of the biota with oceanographic parameters, as an indicator of water masses. Therefore this thesis attempts to advance our understanding by undertaking such an analysis.

# Chapter 3

# The study area

## 3.1 Physical oceanographic processes

### 3.1.1 South-western Atlantic coast

The southwestern region of the Atlantic Ocean comprises a high dynamically active region, namely the Brazil-Malvinas (Falkland) Confluence (BMC) region. The BMC region includes territorial waters of Brazil, Uruguay and Argentina, and is an oceanographic frontal zone between the Brazil Current (BC) and the Malvinas (Falkland) Current (MC), where cold waters of subantarctic origin carried by the MC meet warms waters of tropical origin carried by the BC (Souza, 2000).

An important feature of the BMC region is that the position of the confluence oscillates seasonally, with the BC reaching its southernmost limit in the austral summer, and the MC achieving its northernmost limit in wintertime.

Legeckis and Gordon (1982) found the variable limit of 38$^o$S to 46$^o$S as the maximum latitude of warm water related to the BC, and Souza (2000) reported 42$^o$S. In relation to the MC, Souza (2000) suggests that in wintertime the northern limit is around 32$^o$S offshore, but extends up to 24$^o$S throughout coastal waters (figure 3.1).

### 3.1.2 Southern Brazilian continental shelf

Within the BMC there is a region described as the Southern Brazilian Continental Shelf (SBCS), from Arroio Chui (33$^o$48'S) to Santa Marta Cape (28$^o$40'S) (Castro and Miranda, 1998), which coincides exactly with one GS area of this study (GS 7, figure 2.1). For the

SBCS it is important to take into consideration the presence of coastal waters formed by the BMC, because it has a considerable influence on shallower waters in the area (Souza, 2000).

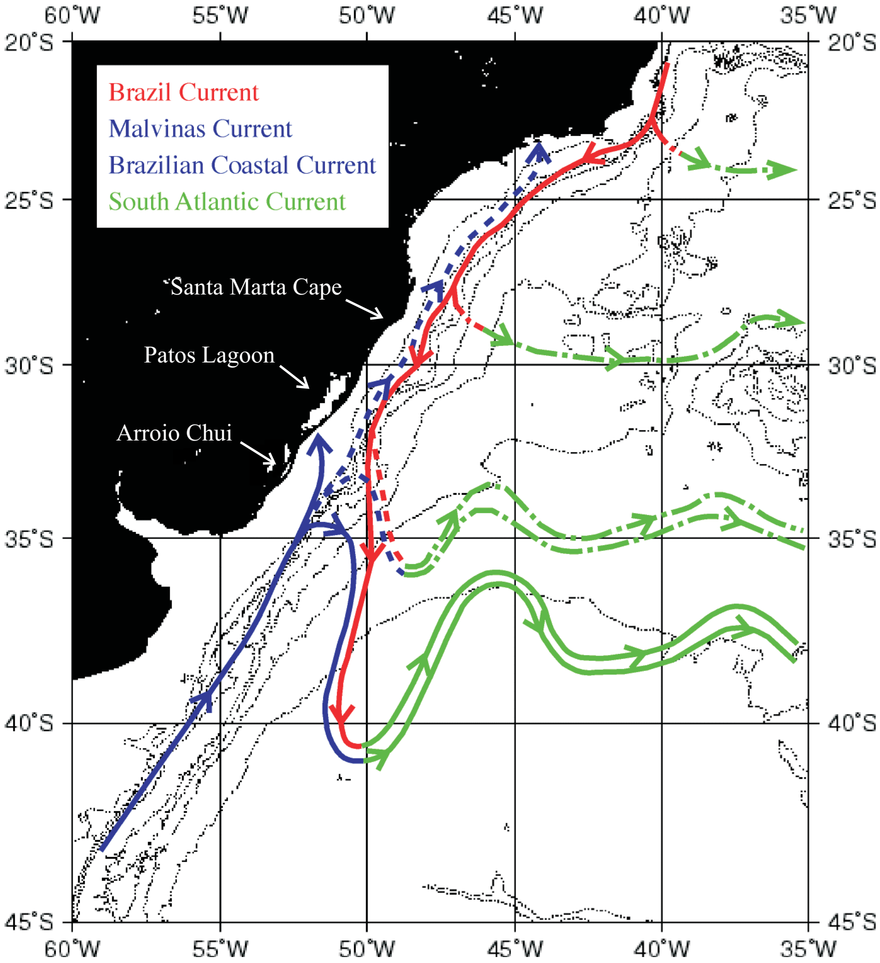

Figure 3.1: Schematic illustration of the surface currents in Brazil-Malvinas (Falkland) Confluence (BMC) region. Isobaths ranging from 100 to 2000m. Source: Souza (2000).

Souza (2000) describes the Brazilian Coastal Current (BCC) as a relatively slow but highly energetic coastal current, flowing in the opposite direction to the BC. This current is actually an extension of the MC carrying cool coastal waters to latitudes lower than 32$^o$S (dashed blue line, figure 3.1). The current occurs within the SBCS during spring to wintertime, showing the seasonal oscillation of the BMC along the southern Brazilian coast. Figure 3.2 presents a schematic illustration of the mean BCC and BC distributions through summer (left map) and winter (right map) seasons at the SBCS.

The BCC/BC front lies parallel to the continental shelf above the 100m isobath off Uruguay and Brazil, starting in winter time. The front extends to the north of Santa Marta Cape (28$^o$40'S), the limit in the SBCS for the penetration of waters with subantarctic influences (figure 3.2).

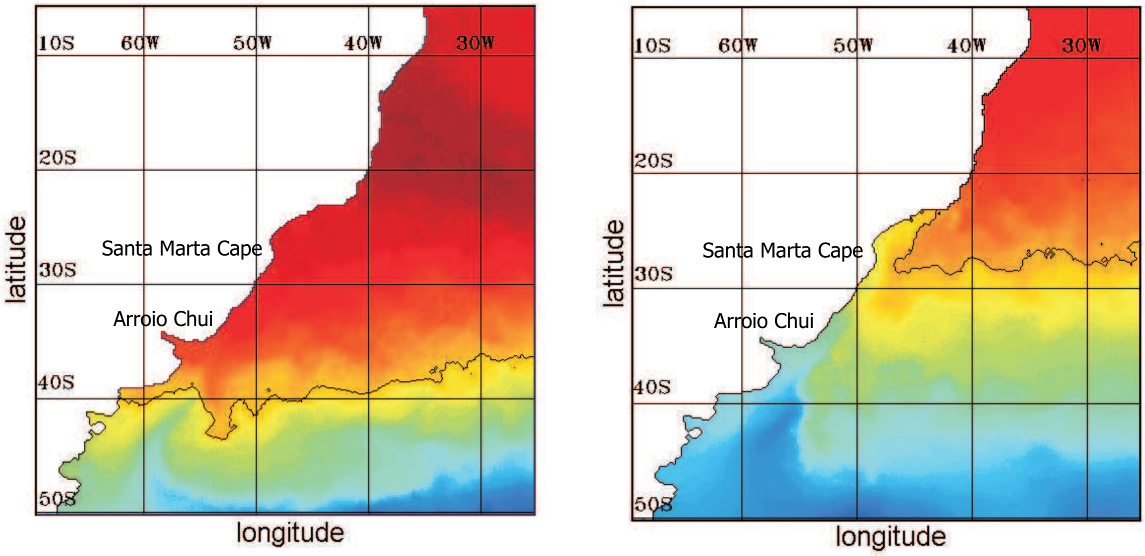

Figure 3.2: Images (MCSST) for February 1984 and August 1983 indicating the minimum (left) and maximum (right) latitudinal position of the BCC for the period of 1984 to 1995. This is indicated by the black line representing the 20$^o$C isotherm. Source: Souza (2000).

Additionally, Garfield (1990) studying the BC in latitudes from 20$^o$S to 33$^o$S, verified that the region close to Santa Marta Cape shows greater variability of this current. To the south of Santa Marta Cape, the author suggests that the change in the bathymetry would be enough to increase the variability in the front between the BC and coastal waters. Abreu and Castello (1997) also discuss that the topography of the SBCS, and suggest that the discharge of Patos Lagoon waters controls the transport of coastal water masses.

Moreover, higher precipitation in southern Brazil as a consequence of the El Niño Southern Oscillation (ENSO) events substantially increase the freshwater outflow from Patos Lagoon. This large freshwater outflow promotes the stability of the water column in coastal shelf regions, and consequently may change the behaviour of the BCC during ENSO events (Abreu and Castello, 1997).

According to Garcia (1997), upwelling is common in the SBCS region. This upwelling can be divided into two types, one occurring at the coast and another attached to the shelf break. The first case, in our study area, is more likely to happen in the spring and summertime, and may occur between 28$^o$S and 32$^o$S, according to Miranda (1972) and Hubold (1980).

Souza (2000) suggests that the BMC and SBCS regions exhibit important seasonal behaviour and penetration limits that should be better investigated. Besides, the BC/BCC front is equally important because the present delimitation of biogeographical regions is apparently dependent on the extension and behaviour of these currents, mainly in the wintertime when domination of the SBCS by waters with coastal origins is significant (figure 3.2).

To conclude, the study area (SBCS) is a complex region affected by the BMC and its water masses, variability in freshwater discharges from Patos Lagoon as a consequence of ENSO, and upwelling phenomenon. The SBCS also presents particular oceanographic features due to rapid changes of topography throughout the coastal region.

More about the oceanic processes in the study region will be discussed in the Chapter 5 (The physical data: oceanographic parameters).

## 3.2 Previous bio-physical studies

Some evidence that frontal systems of the BMC and southern Brazil shelf are regions of concentration of biota, specifically fish and cephalopods, are reviewed and discussed by Castello et al. (1997) and Haimovici (1997b). Many other studies (discussed below) also suggest empirically that the BMC influences the biota, but only a few of them analysed physical conditions as well as biological data.

Abreu (1987) analysed temporal fluctuations of chlorophyll-*a* and abiotic factors near the mouth of Patos Lagoon estuary, on the southern Brazilian coast. Highest values of chlorophyll-*a* are exported from the estuary to adjacent coastal waters of the SBCS, mainly in winter and autumn, and probably due to mixing with the MC from the south. Abreu (1987) considers that water temperature is a limitation for chlorophyll-*a* development in temperate zones.

Moreover, Ciotti et al. (1995) discuss the even higher spring chlorophyll-*a* concentrations, related with ENSO events, because of the increase of Patos Lagoon outflow.

Ciotti et al. (1995) also pointed out that the southern part of the Brazilian continental shelf is the most important fishery area of the Brazilian coast according to primary production, nutrients and SST analyses. High phytoplankton biomass is related to nutrients made available from the intrusion of the MC into coastal waters of the shelf.

Lima and Castello (1995) related the occurrence of anchovy *Engraulis anchoita* to discharges from Patos Lagoon and found large concentrations of this fish in years of large water outflow. They concluded that the stability of the water column in coastal waters, because of the outflow, inhibit the dispersal of eggs and larvae and thus increase their chances of survival. In addition Lima and Castello (1995) mention the influence of the MC during spring and wintertime, leading to low temperatures in coastal waters.

Podesta (1990) studied the migratory patterns of Argentine hake *Merluccius hubbsi* in the southwestern Atlantic and its association with environmental conditions. The author found that the extension of the hake feeding migration, reached during June-August, is associated with the BMC (see figure 3.2), and the confluence appears to be an effective barrier for adult hake of commercial size.

Odebrecht and Garcia (1997) indicate that the distinct water masses of the SBCS have different chlorophyll-$a$ patterns. Since a coastal current (BCC) flowing northwards would carry eutrophic waters throughout the SBCS, they strongly recommend more physical investigations along with biological data collection, for assessing more realistic scenarios for the area.

Sunye and Servain (1998) investigated the effects of hydrographical data, specifically temperature fields on the sardine, *Sardinella brasiliensis*, fisheries in the region between Santa Marta Cape and Cabo Frio (23$^o$S and 28$^o$S). Their results show very clearly that there is a coincidence between the latitudinal extreme positions of the BCC and the sardine catch in São Paulo and Santa Catarina states, Brazil. When the BCC northern limits are to the south of SBCS (during summer), the sardine catches are higher in Santa Catarina. On the other hand, when the BCC is displaced to the north in winter, the catches of sardine are higher in São Paulo.

The vertical distribution of chlorophyll in the upper layers of the southern Atlantic, and its interpretation in relation to frontal systems and the general hydrographic features were studied by Brandini et al. (2000). Their results showed a rather consistent oceanographic structure, with similar patterns of chlorophyll-$a$ distributions with latitude. The results indicate greater phytoplankton production throughout the colder seasons in the upper euphotic zone of the BMC.

Further investigation of eddy-like surface structures with the Advanced Very High-Resolution Radiometer (AVHRR) thermal infrared and TOPEX/POSEIDON altimeter data has unveiled interesting eddy-like surface structures in the BMC region. These multiple eddies are clearly visible on both thermal and colour imagery off southern Brazil (Mata and Garcia, 1996). Furthermore, a decrease in chlorophyll-$a$ concentration was found as those eddies propagate northward, due to mixing with chlorophyll-poor tropical waters carried southward by the Brazil Current (Garcia et al., 2004).

A connection between the 1982/83 and 1997/98 ENSO events and pigment distribution, using monthly composites of chlorophyll-$a$ concentration, over southern and southeastern Brazil was clearly demonstrated in temporal pigment distributions (Gonzales-Silvera et al., 2004).

Summing up, the environmental aspects throughout the SBCS are of considerable significance. These environmental changes through the year, and between years, may strongly influence the occurrence and abundance of several species, such as franciscana dolphin prey, which will be discussed in this research study.

# Chapter 4

# The biological data: foraging ecology

## 4.1 Introduction of marine mammal feeding studies

Marine mammals feeding habits have been reported from analyses of scat, stomach contents, direct observations, or inferred by indirect methods such as isotope ratios, fatty acids and molecular identification (Barros and Clarke, 2002). The most common methods, stomach contents and scat, rely on the finding and identification of tissue remains and structures representing a typical meal, *e.g.* fish bones and the jaws of cephalopods, or "beaks".

In particular fish ear stones, or "otoliths" (figure 4.1), and cephalopods beaks (figure 4.2) are diagnostic structures in the identification of prey because their size and shape vary considerably from species to species. Figure 4.3 presents an example of the variety of fish otoliths, and highlights the importance of reference collections of such structures for feeding studies. Furthermore, the dimensions of these structures correlate well with the length and weight of the species from which they originate, and yield reliable regressions between them. This allows good reconstruction of the original prey size, and estimates can then be made of weight and size classes of particular prey species for a single mammal and, sometimes, their populations (Fitch and Brownell, 1968, 1971; Lagler et al., 1977; Treacy, 1981; Härkönen, 1986; Jobling and Breiby, 1986; Clarke, 1986a,b; Murie, 1987; Pierce et al., 1991a,b; Barros, 1993; Latja and Michener, 1994; Pauly et al., 1998).

The advantages of these methods are (1) knowledge of prey composition and size classes allows the relationships with the spatial and temporal distribution of predators to be investigated;

(2) studies of predator-prey dynamics are made possible; (3) prey species may be very poorly sampled by humans using other methods, and predator diets can give considerable information about them in undersampled areas; (4) changes in diet can be monitored; and (5) samples can be collected from carcasses in an advanced stage of decomposition, which in several cases is the main source of data of marine mammals, mainly cetaceans.

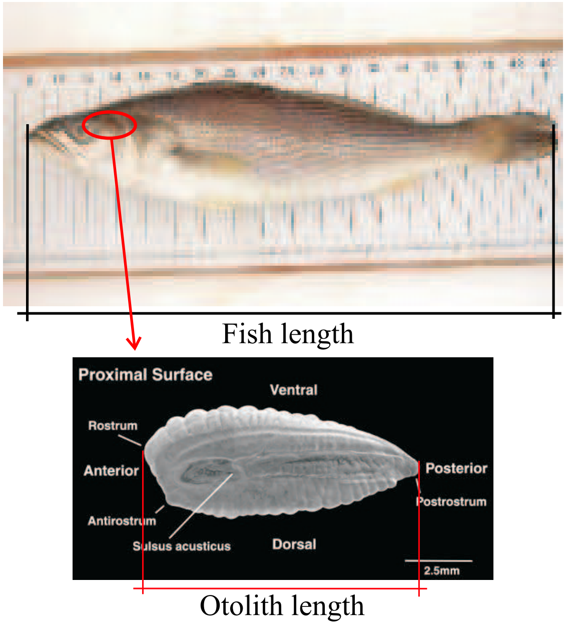

Figure 4.1: Fish ear stone, the otolith, and the fish lengths. The otolith dimension correlates with the length and weight of the fish, allowing the calculation of regression formulas. Sources: www.fishbase.org and www.marinebiodiversity.ca.

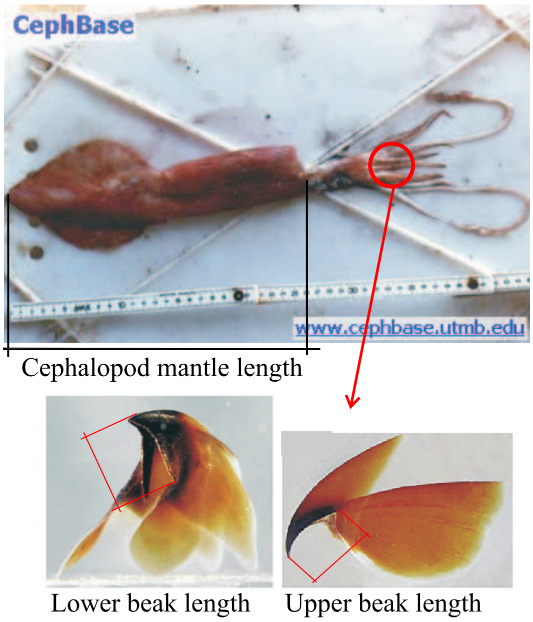

Figure 4.2: Cephalopod beak and cephalopod mantle lengths. The beak dimension correlates with the mantle length and weight of the cephalopod species, allowing the calculation of regression formulas. Sources: www.cephbase.utmb.edu and www.tolweb.org.

The disadvantages of the methods are: (1) fish otoliths can last for only a few days in the gastrointestinal tracts of marine mammals, whereas cephalopod beaks may accumulate for several days or months, leading to a complicated calculation of reconstructed meal sizes; (2) prey lacking hard parts (*e.g.* invertebrates) will be underrepresented; and (3) a comprehensive reference collection of fish otoliths and cephalopod beaks from a particular area is needed for precise identification of prey, and accurate estimation of size and weight.

The majority of diet analyses addressing the importance of prey consider: (1) percentage frequency of occurrence (%FO) of a specific prey in each animal; (2) the percentage by number of a particular prey (%N); (3) regressions used to estimate weight (g) and size (mm) and; (4) the Index of Relative Importance (IRI) (Pinkas et al., 1971; Cortes, 1997; Koen Alonso et al., 2001); and (5) Cluster analyses.

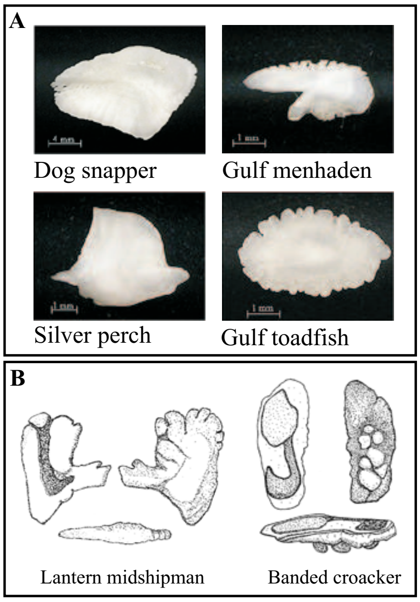

Figure 4.3: Illustration of otoliths. Photos (A) and drawing (B) examples of reference collections. Source: www.sefscpanamalab.noaa.gov.

The relationships of (1) prey and predator sizes; (2) prey and predator weights; (3) predator sex / age class / sexual maturity *vs.* prey occurrence / number / size and weight; and (4) seasonal variations; are generally evaluate of using analysis of variance (ANOVA) and multiple analysis of variance (MANOVA). However, the use and combination of these analyses varies among the feeding studies (Perrin et al., 1973; Murie and Lavigne, 1986; Murie, 1987; Hanna and Hohn, 1989; Recchia and Read, 1989; Thompson et al., 1991; Pierce and Boyle, 1991; Pierce et al., 1991b; Sekiguchi et al., 1992; Young and Cockcroft, 1994; Walker, 1996; Gould et al., 1997; Gannon et al., 1997; Pauly et al., 1998; Lunneryd, 2001; Santos et al., 2001; Santos and Haimovici, 2001).

## 4.2 Methods

### 4.2.1 Franciscana dolphin data

The samples analysed in this study consisted of franciscanas incidentally caught in gillnets by the coastal commercial fleet sited in Rio Grande/Barra (32°08'S, 52°05'W) (N= 172), and Tramandai/Imbé (29°58'S, 50°07'W) (N= 98), from 1994 to 2000 (figure 4.4). The division of the study region into the northern and southern coast areas was based on the fishing areas utilised by the fishing vessels of (1) Rio Grande/Barra and (2) Tramandai/Imbé (figure 4.4).

In Rio Grande/Barra, the commercial fleet operates from the lighthouse of Albardao (33°05'S) to the lighthouse of Mostardas (31°13'S). On the other hand, the vessels from Tramandai operate from the lighthouse of Mostardas to Torres (29°11'S). Additionally, some stranded animals (N= 29) in the northern area were also sampled. Data of location, date of capture event (or stranding), sex, length, and weight were recorded, and sexual maturity and age were obtained from parallel studies (Danilewicz, 2000; Danilewicz et al., 2000).

Adults and juveniles were categorised for sexual maturity from gonad analysis, or when this was not possible by total lengths (female adult >138.9cm, and male adult >128.2cm) (Danilewicz, 2000). For this study the length-weight curve was estimated from regression analysis (N= 185). Differences in sizes and weights between the areas were investigated using

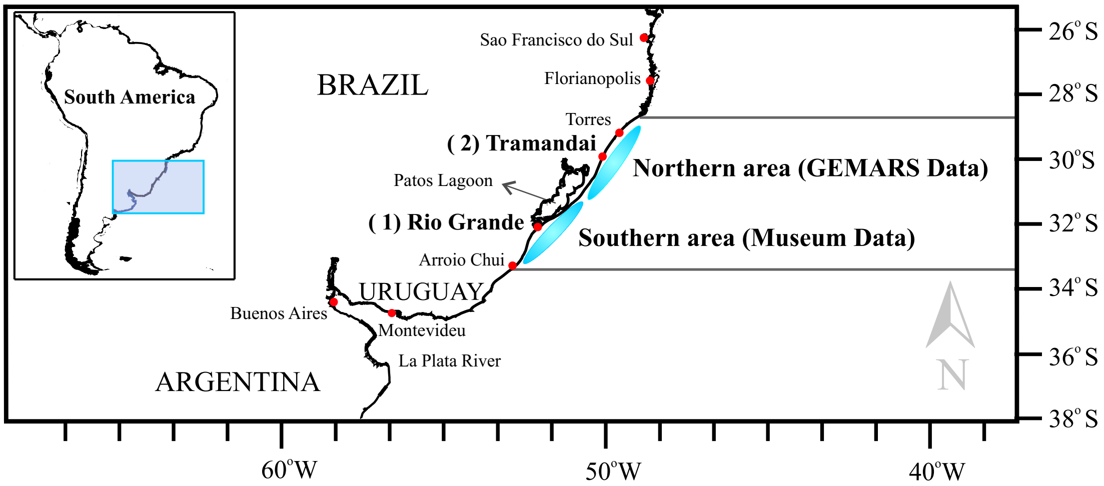

Figure 4.4: Areas of franciscana dolphin data sampled. The division of the study region into the northern and southern coast areas was based on the fishing areas utilised by the fishing vessels of (1) Rio Grande/Barra and (2) Tramandai/Imbé.

One-way ANOVA. In addition, missing weights from 84 dolphins were calculated (predicted values) from the regression formula. The number of franciscanas sampled in northern and southern areas, categorised by sex, sexual maturity, and seasons, were analysed using Chi-square contingency tables to test the hypothesis of homogeneity of groups.

### 4.2.2 Stomach contents data

The stomachs (including all the chambers) were excised (A) and opened (B) for the contents analysis (C) (figure 4.5). The principal contents analysed were otoliths (N= 13,354) for fish, beaks (N= 12,248) for cephalopods, and remains of crustaceans (mainly cephalothorax, N= 182).

Crustaceans from the southern area were identified by specialists in the Decapoda Laboratory (University of Rio Grande, Brazil), and in the northern they were identified in the Crustacea Laboratory (Catholic University of Rio Grande do Sul, Brazil). The taxa used are presented

Figure 4.5: Illustrations of franciscana dolphin stomach and contents processing: (A) stomach; (B) opening in current water with a 600$\mu$m net and; (C) stomach contents cleaned. Photos: M. Bassoi

in table 4.1. Unfortunately, it was not possible to obtain suitable lengths and weight data for crustacean specimens.

**Crustaceans Classification**

**Source:** T. E. Bowman and L. G. Abele. 1982. The Biology of Crustacea. *In:* Systematics, the fossil record and biogeography. Ed. Abele, L. G. New York Academic Press. Vol. 1: 1-27pp.

| Phylum Crustacea (Pennant, 1777) | Table Code |
|---|---|
| Order Isopoda (Latreille, 1817) | Ki = "bugs" (benthic fauna) |
| Order Decapoda (Latreille, 1803) | Ks = "shrimps" (benthic fauna) |
| Suborder Dendrobranchiata (Bate, 1888) | |
| Superfamily Penaeoidea (Rafinesque, 1815) | |
| Family Penaeidae (Rafinesque, 1815) | |
| *Artemesia longinaris* | |
| Family Solenaceridae (Wood-Mason and Alcock, 1891) | |
| *Pleoticus muelleri* | |
| Suborder Pleocyemata (Burkenroad, 1963) | Kc = "crabs" (benthic fauna) |
| Infraorder Anomura (H. Milne Edwards, 1832) | |
| Superfamily Coenobitoidea (Dana, 1851) | |
| Family Diogenidae (Ortamann, 1892) | |
| *Loxopagurus loxocheles* | |
| *Dardanus insignis* | |
| Infraorder Brachiura (Latreille, 1803) | |

Table 4.1: Taxa classifications of the species of crustaceans found in franciscana dolphin's stomach contents.

| **Species** | **ML**<br>URL and LRL/UHL and LHL | **R$^2$** | **TW**<br>URL and LRL/UHL and LHL | **R$^2$** |
|---|---|---|---|---|
| *Semirrosia tenera* | 19.318URL + 0.4763 | 0.6689 | $3.489\mathrm{URL}^{2.421}$ | 0.6770 |
| | 17.179LRL + 0.757 | 0.8415 | $6.609\mathrm{LRL}^{2.334}$ | 0.8110 |
| *Octopus tehuelchus* | $17.339\mathrm{UHL}^{1.2954}$ | 0.8206 | $1.8517\mathrm{UHL}^{3.5947}$ | 0.8646 |
| | $26.866\mathrm{LHL}^{1.1755}$ | 0.8739 | $6.315\mathrm{LHL}^{3.2365}$ | 0.9106 |
| *Argonauta nodosa* | $4.923\mathrm{UHL}^{1.2933}$ | 0.9481 | $0.0377\mathrm{UHL}^{3.4949}$ | 0.9457 |
| | $9.5338\mathrm{LHL}^{1.2314}$ | 0.9507 | $0.2593\mathrm{LHL}^{3.1856}$ | 0.9353 |
| *Loligo plei* | $67.431\mathrm{URL}^{1.2908}$ | 0.9608 | $8.8096\mathrm{URL}^{2.8564}$ | 0.9799 |
| | $64.303\mathrm{LRL}^{1.3143}$ | 0.9532 | $7.9418\mathrm{LRL}^{2.908}$ | 0.9734 |
| *Loligo sanpaulensis* | $14.408e^{1.1418\mathrm{URL}}$ | 0.9294 | $0.3804e^{2.6451\mathrm{URL}}$ | 0.9286 |
| | $13.497e^{1.0836\mathrm{LRL}}$ | 0.9441 | $0.2947e^{2.5972\mathrm{LRL}}$ | 0.9388 |
| *Eledone* sp (*E. gaucha*) | $13.805\mathrm{UHL}^{1.2966}$ | 0.8041 | | |

Source: Demersal Fishes and Cephalopods Laboratory, University of Rio Grande, Brazil. * Rostral and hood length definitions follow Clarke (1986).
ML = mantle lenght (mm), WT = squid or octopus weight (g), URL = upper rostral* length beak (squids and sepiolids),
LRL = lower rostral length beak (squids and sepiolids), UHL = upper hood* length beak (octopuses), LHL = lower hood length beak (octopuses).

Table 4.2: Regressions of cephalopod beak and mantle lengths (mm), and wet mass (g), for southern and northern areas.

Reference collections of fish otoliths (Lucato) and cephalopod beaks (Santos, 1999) for the study area were available in the Demersal Fishes and Cephalopods Laboratory, University of Rio Grande, Rio Grande, Brazil. Otoliths and beak lengths were measured with a microscope equipped with an ocular micrometer (0.1mm scale). The collections allowed correct prey identification and reliable regressions to estimate lengths and weights of the prey species (tables 4.2 and 4.3). Prey items were identified to the lowest possible taxon with the aid of the laboratory reference collections.

| **Species** | **TL** | **$R^2$** | **N** | **WT** | **$R^2$** | **N** |
|---|---|---|---|---|---|---|
| *Cynoscion guatucupa* | $13.799*LO^{1.2007}$ | 0.9894 | 78 | $0.0186*LO^{3.7392}$ | 0.9959 | 78 |
| *Trichiurus lepturus* | $84.378*LO^{1.3022}$ | 0.9785 | 49 | $0.1093*LO^{4.5265}$ | 0.9807 | 49 |
| *Paralonchurus brasiliensis* | $26.005*LO^{-21.709}$ | 0.9847 | 80 | $0.0103*LO^{4.1717}$ | 0.9790 | 80 |
| *Urophycis brasiliensis* | $41.793*E^{0.1714*LO}$ | 0.9732 | 86 | $0.2611*E^{0.5795*LO}$ | 0.9624 | 86 |
| *Porichthys porosissimus* | $24.263*LO^{1.0254}$ | 0.9941 | 54 | $0.0809*LO^{3.3225}$ | 0.9908 | 54 |
| *Peprilus paru* | $0.75*LO^2+22.515*LO^{-8.4221}$ | 0.9878 | 63 | $0.1126*LO^{3.569}$ | 0.9801 | 63 |
| *Merluccius hubbsi* | $26.266*LO^{-46.715}$ | 0.9786 | 58 | $0.0217*LO^{3.4658}$ | 0.9759 | 58 |
| *Anchoa marinii* | $25.593*LO^{1.0656}$ | 0.9599 | 45 | $0.069*E^{1.2033*LO}$ | 0.8718 | 45 |
| *Umbrina canosai* | $12.517*LO^{1.3266}$ | 0.9620 | 77 | $0.0196*LO^{4.1369}$ | 0.9600 | 77 |
| *Raneya fluminensis* | $82.241*E^{0.1386*LO}$ | 0.9515 | 35 | $1.4751*E^{0.5108*LO}$ | 0.9370 | 35 |
| *Cynoscion jamaicensis* | $13.515*LO^{1.1462}$ | 0.9820 | 38 | $0.0166*LO^{3.6616}$ | 0.9690 | 38 |
| *Pomatomus saltator* | $18.828*LO^{1.2357}$ | 0.9927 | 41 | $0.0487*LO^{3.8106}$ | 0.9940 | 41 |
| *Prionotus* spp. | $22.374*LO^{1.2462}$ (*P. punctatus* ) | 0.9902 | 56 | $0.0903*LO^{3.9397}$ (*P. punctatus* ) | 0.9896 | 55 |
| *Menticirrhus* spp. | $15.141*LO^{1.318}$ (*M. americanus* ) | 0.9950 | 30 | $0.0131*LO4^{.4341}$ (*M. americanus* ) | 0.9940 | 30 |
|  | $18.901*LO^{1.2455}$ (*M. littoralis* ) | 0.9870 | 42 | $0.0401*LO^{3.9463}$ (*M. littoralis* ) | 0.9850 | 42 |
| *Macrodon ancylodon* | $1.725*LO^2+1.9196*LO^{31.348}$ | 0.9860 | 61 | $0.1988*E^{0.5878*LO}$ | 0.9870 | 61 |
| *Micropogonias furnieri* | $18.343*LO^{1.0987}$ | 0.9935 | 149 | $0.0359*LO^{3.6081}$ | 0.9875 | 149 |
| *Engraulis anchoita* | $32.803*LO^{1.088}$ | 0.9757 | 39 | $0.1748*LO^{3.4088}$ | 0.9736 | 39 |
| *Trachurus lathami* | $20.417*LO^{1.1571}$ | 0.8248 | 45 | $0.0548*LO^{3.5828}$ | 0.8149 | 45 |
| *Mugil* spp. | $63.786*LO^{-163.69}$ | 0.8627 | 27 | $63.48*LO^{-249.34}$ | 0.5880 | 14 |
| *Syacium papillosum* | $30.608*LO^{1.0528}$ | 0.9355 | 23 | $1.8824*E^{0.6416*LO}$ | 0.9485 | 23 |
| *Paralichtys isoceles* | $39.965*LO^{1.056}$ | 0.9795 | 42 | $0.2377*LO^{3.6309}$ | 0.9750 | 42 |
| *Stellifer rastrifer* | $14.621*LO^{1.4317}$ | 0.8930 | 32 | $0.0187*LO4^{.7695}$ | 0.8810 | 32 |
| *Stromateus brasiliensis* | $38.653*LO^{-14.341}$ | 0.9806 | 12 | $0.2496*LO^{3.3996}$ | 0.9850 | 12 |
| *Pagrus pagrus* | $16.272*LO^{1.2296}$ | 0.9893 | 27 | $0.0669*LO^{3.6755}$ | 0.9857 | 27 |
| *Ctenosciena gracilicirrhus* | $20.591*LO^{1.0043}$ | 0.9793 | 49 | $0.0819*LO^{3.2482}$ | 0.9810 | 49 |

Source: Demersal Fishes and Cephalopods Laboratory, University of Rio Grande, Rio Grande, Brazil.
TL = total fish lenght (mm), WT = fish weight (g), LO = total otolith lenght (mm), R= regression coeficient, and N = sample number.

Table 4.3: Regressions of fish and otoliths lengths (mm), and wet mass (g), for southern and northern areas.

### 4.2.3 Prey assessment through the traditional method: Index of Relative Importance (IRI)

To access the importance of prey in the diet of franciscana, the majority of the published studies calculate the Index of Relative Importance (IRI) (Pinkas et al., 1971):

- IRI = (%N + %W) * %O.

Where, (%N) is the numerical abundance of prey; (%W) is the percentage of prey reconstituted mass; and (%O) the percentage of stomach contents in which a prey taxon occurred. The reconstituted mass is calculated from linear regressions (see tables 4.2 and 4.3).

In order to compare this study with previous feeding results, the prey importance was analysed according to the IRI. This is relevant in order to identify whether the franciscana diet had changed through the time. Previous analyses (N= 36) were made from 1992 to 1994 (Ott, 1994) for the northern area. In addition, there is a good source of feeding information (N= 277) for this region 20 years ago (Pinedo, 1982).

For a general overview, IRI values considering all the prey ingested were calculated for the southern and the northern areas. However, IRI values for cephalopod species are highest, probably because the cephalopod beaks digestion time is larger than otolith digestion time (see section 4.1). Therefore, the % of number of prey, occurrence in the stomachs, estimated mass (g), and IRI values, were only compared within the prey groups (*e.g.* fish species just with fish species) and not between fish species and cephalopod species. The categorical groups sex, sexual maturity, and seasons (for each area) values were also calculated separately for each prey group (fish, cephalopod, and crustacean).

Nevertheless, from the IRI results, it is not possible to estimate the statistical significance of differences between the groups. Hence alternative statistical analyses such as LM and GLM were also used.

### 4.2.4 Prey assessment through statistical methods: Linear Models (LM) and Generalized Linear Models (GLM)

Linear Models (LM) form the core of classical statistics, and many modern modelling and analytical techniques build on its methodology. LM are simply a combination of elements from analysis of variance and regression, using a similar method for the partitioning of variance between explanatory variables, which can be either continuous or categorical. Using the statistical software S-PLUS (6.1 for Windows, Math-Soft Inc., Seattle, Washington), the structure of the model can be specified in the model formula in a word equation:

- response variable $\sim$ explanatory variable(s);

where the dependent variable is on the left, and the variables we suspect of influencing the data are on the right hand side of the formula. The tilde symbols reads "is modelled as function of" (Venables and Ripley, 1997).

Following standard procedures for linear models, the relationships between prey lengths and estimated mass according to franciscana dolphin sex and sexual maturity, temporal variation (season), and spatial variation (northern and southern areas) were analysed. Log-transformations were performed when the residuals contravened the assumption of normality. Accordingly, the models can be written as:

- LM (log(prey length) $\sim$ area);
- LM (log(prey estimated mass) $\sim$ season).

From the models, analysis of variance tables were used to obtain the values of degrees of freedom, residuals, F, and $p$, to identify significant relationships.

The estimated lengths (mm) and mass (g) of the prey species (n=31) used for the LM analysis, were calculated from the regression analyses previously cited (tables 4.3 and 4.2).

For LM it is assumed that the variance is constant and the errors are normally distributed. However, in count data, where the response variable is an integer and there are often lot of zeros in the data frame, the variance may increase linearly with the mean. Additionally, the response variable is expected to follow a Poisson distribution. Thus, LM is not a good choice to handle this kind of data (Crawley, 2002).

In this case, we are looking at estimates of fish abundance in terms of fish numbers (count data), and the data may be assumed to come from a Poisson distribution. The way to deal with these problems, in a single theoretical framework, is the technique of GLM.

GLM is used in the same way as the model-fitting procedure of LM, but we also need to specify a family of error structures, in our case the Poisson for count data, and a particular link function. The method for categorical data, such as our variable "area" with two-level factor (northern and southern), uses the log-link function, and a linear variance-mean relationship, and this way the GLM suitable for categorical data is called the log-linear model (Graphen and Hails, 2002). Another advantage of GLM is that it works reasonably well with unbalanced data, as is the case for the categorical variable *season* (see the Chi-square test for hypothesis of homogeneity of groups in the section 4.3.1).

Furthermore, the log-link is frequently used for count data, where negative values are prohibited. For our data we performed the analysis of deviance for a categorical explanatory variable with count data, using chi-square test at the 0.05 confidence level (Crawley, 2002). Besides, to compensate for overdispersion (where the residual deviance is greater than the residual degrees of freedom), remedial measures when using the $F$ test were taken. The $F$ test uses the residual deviance and residual degrees of freedom ratio parameter as an estimate equivalent to the error variance, and performs a test much harsher than the chi-square test. From the models, analysis of deviance was performed to obtain the values of degrees of freedom, residuals, and $p$, to identify significant relationships.

In short, the GLM has three important properties:

- (1) The error structure - a GLM allows the specification of a variety of different error distributions (*e.g.* binomial errors, useful with data on proportions; poisson errors, useful with count data, etc). The error structure is defined by means of the family directive, used as part of the model formula (see number 3).
- (2) The linear predictor - the right hand side of the model equations are of exactly the same form in GLM as in LM. This has categorical terms, continuous terms, and all kinds of interaction. But instead of making this model equal to the fitted value directly, the expression is called the linear predictor, and related to it by a link function. The identity link, in which we just make linear predictor equal to the fitted value, is the link function for an ordinary LM.
- (3) The link function - the link function relates the mean value of y to its linear predictor. An important criterion in the choice of link function is to ensure that the fitted values stay within reasonable bounds. We would want to ensure, for example, that counts are all greater than or equal to 0 (negative count data are not feasible values). In this case, a log link is appropriate because the fitted values are antilogs of the linear predictor, and all antilogs are greater than or equal to 0. Moreover, the most appropriate link function may be the one which produces the minimum residual deviance. The use of link function replaces transformation of variables without corrupting the error structure.

Thus, for example, the GLM formula can be written as:

- GLM (prey species $\sim$ area, family = poisson (link = log)).

Log-linear models were fitted using the GLM procedure in S-plus to analyse differences between franciscana sex and sexual maturity, season, and sites (northern and southern), in franciscana prey frequencies. The values of degrees of freedom, residuals, F, and $p$, are demonstrated in the variance (LM) and deviance (GLM) tables.

The results from GLM analysis are used not only to identify significant results but also to determine if the prey importance is similar to the results obtained using the traditional method (IRI). Beyond that, the LM and GLM methods were chosen because the analysis can be widely explored. These models allow inclusion of more than one explanatory variable, and combination of categorical and continuous variables, which permits exploring interactions between them as well as adding and analysing "oceanographic parameters" variables (*e.g.* sea surface temperature, chlorophyll-$a$). It is here that the flexibility of these models will become apparent for further analysis, mainly in Chapter 6. Therefore identification of the significant parameters for the variety of franciscana prey through LM and GLM in this Chapter is the first step for more complex models in Chapter 6.

## 4.3 Results

### 4.3.1 Franciscana dolphin data

The length of franciscanas studied ranged from 76 to 170cm (mean= 128.4, N= 265), and the weight ranged from 5.4kg to 51.5kg (mean= 26.5, N= 186). The most representative size classes for both areas are 120-140cm in length (figure 4.6). No significant differences in lengths were detected between the sites (F= 0.71, df= 263, $p$= 0.402).

The representative weight class was 20-30kg in weight for southern area, and 10-20kg for northern area. However this difference in weights may have occurred because there were few animals (N= 28) with weight measurements for the northern area, whereas 158 animals were measured according to weight for the southern area.

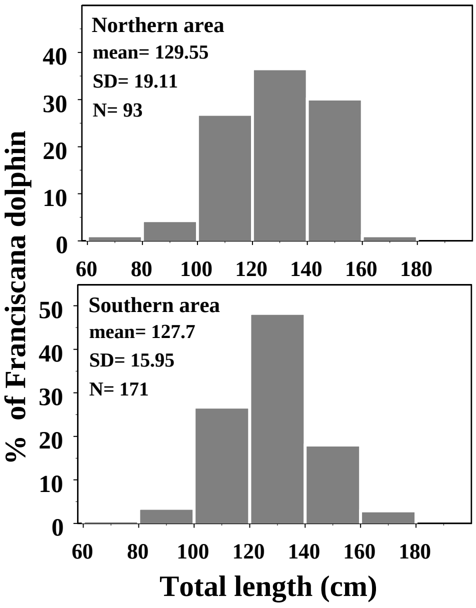

Figure 4.6: Franciscana dolphin total length (cm) frequencies for northern and southern areas off southern Brazilian coast (mean, SD= standard variation of the mean, and N= number of franciscana sampled).

The length-weight relationship was estimated as: Body weight(g) = 0.012×Total length(cm)$^3$ (R$^2$= 0.981, SD= 3840, N= 185) (figure 4.7).

Chi-square contingency tables show homogeneity of males and females ($\chi^2$= 0.08, df= 1, $p$= 0.774), juveniles and adults ($\chi^2$= 0.91, df= 1, $p$= 0.339), between the areas. However, for seasons the groups are not homogeneous ($\chi^2$= 26.57, df= 3, $p$< 0.001)) (figure 4.8).

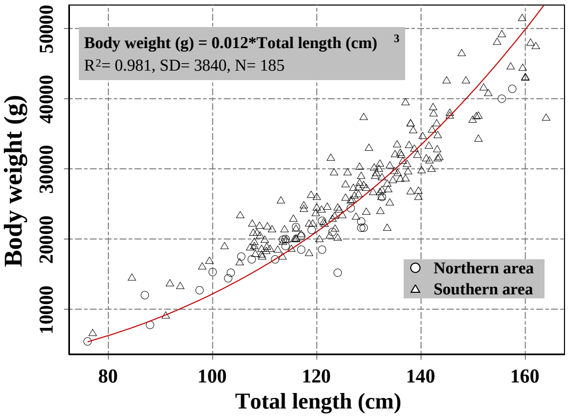

Figure 4.7: Length-weight relationship of franciscana dolphin from southern Brazilian coast.

| **Southern area** | summer | autumn | winter | spring | **total** |
|---|---|---|---|---|---|
| male | 12 | 28 | 33 | 27 | 100 |
| female | 12 | 20 | 23 | 17 | 72 |
| juvenile | 14 | 22 | 35 | 29 | 100 |
| adult | 10 | 26 | 21 | 15 | 72 |
| **total** | 24 | 48 | 56 | 44 | |

| **Northern area** | summer | autumn | winter | spring | **total** |
|---|---|---|---|---|---|
| male | 10 | 2 | 12 | 20 | 44 |
| female | 9 | 3 | 7 | 9 | 28 |
| juvenile | 12 | 2 | 16 | 16 | 46 |
| adult | 9 | 4 | 4 | 27 | 44 |
| **total** | 25 | 7 | 22 | 43 | |

Figure 4.8: Numbers of franciscana dolphin analysed in this study.

## 4.3.2 Diet composition

Fish and cephalopod prey are found to be the most important groups in the diet of franciscana dolphin. From variety of combinations of different taxon groups, "fish+cephalopod" was the most representative in the diet of the animals (44.8%)(figure 4.9).

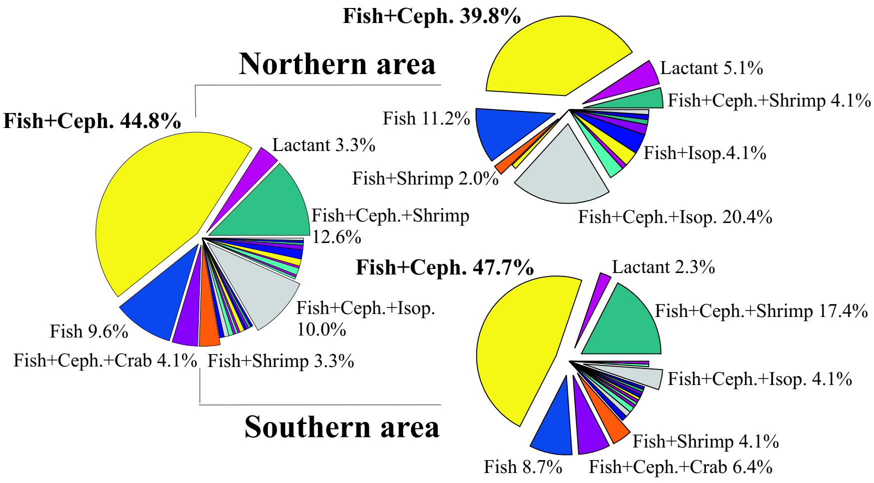

Figure 4.9: Principal groups of prey combinations from stomach contents of franciscana dolphin of Southern Brazilian coast, and its northern and southern areas. Abbreviations: Ceph.= Cephalopod and Isop.= Isopoda.

Among the fish species (26 in total) the greatest number corresponds to bottom-dwelling teleosts. Cephalopod species belong mainly to shelf-demersal squids and shelf-benthic octopuses. Crustacean species are mainly marine shrimps and crabs (table 4.4).

Unfortunately, the shrimp species *Artemesia longinaris*, *Pleoticus muelleri*, and the family Penaidae identified for southern area, could not be identified at these taxon levels for the northern area. For these area the shrimps were identified as the superfamily Penaeoidea.

| Species/Family | Common name | Habitat and Region | Depth ranges* |
|---|---|---|---|
| **Fish** | | | |
| *Cynoscion guatucupa* | striped weakfish | shelf-demersal/pelagic as juveniles | 0-180m (0-60m) |
| *Cynoscion jamaicensis* | Jamaica weakfish | shelf-demersal | 0-180m (40-80m) |
| *Paralonchurus brasiliensis* | banded croacker | shelf-demersal | 0-80m (0-60m) |
| *Macrodon ancylodon* | king weakfish | shelf-demersal | 0-120m (0-40m) |
| *Micropogonias furnieri* | white croaker | shelf-demersal | 0-180m (0-80m) |
| *Umbrina canosai* | Argentine croaker | shelf-demersal | 0-180m (>40m) |
| *Menticirrhus* spp. | southern kingcroacker | shelf-demersal | 0-60m (0-20m) |
| *Stellifer rastrifer* | rake stardrum | shelf-demersal | 0-40m |
| *Ctenosciena gracilicirrhus* | barbel drum | shelf-demersal, muddy and sandy bottoms | 10-130m |
| *Pomatomus saltatrix* | bluefish | estuary/shelf-pelagic | 0-200m (0-30m) |
| *Mugil* spp. | mullet | estuary/shelf-pelagic | 0-200m (0-20m) |
| *Urophycis brasiliensis* | squirrel codling | shelf-demersal | 0-250m (0-180m) |
| *Trichiurus lepturus* | cutlassfish | shelf-demersal/pelagic as juveniles | 0-350m (0-250m) |
| *Porichthys porosissimus* | lantern midshipman | shelf-demersal | 0-250m (20-120m) |
| *Peprilus paru* | American harvestfish | shelf-pelagic | 0-200m (25-70m) |
| *Stromateus brasiliensis* | butterfish | shelf-pelagic | 0-200m (>20m) |
| *Merluccius hubbsi* | Argentine hake | shelf-demersal/pelagic as juveniles | 20-600m (40-180m) |
| *Anchoa marinii* | anchoita | shelf-pelagic | 0-200m (0-40m) |
| *Engraulis anchoita* | anchoita | shelf-pelagic | 0-200m (>30m) |
| *Raneya fluminensis* | cusk-eels | shelf-demersal | 20-150m |
| *Prionotus* spp. | searobins | shelf-demersal | 0-180m (0-120m) |
| *Trachurus lathami* | rough scad | shelf-pelagic/demersal | 0-350m (20-180m) |
| *Syacium papillosum* | dusky flounder | shelf-demersal | 10-140m |
| *Paralichtys isosceles* | flounder | shelf-demersal | 20-250m (60-250m) |
| *Licengraulis grossidens* | Atlantic sabretooth anchovy | estuary/shelf-pelagic | 0-60m (0-20m) |
| *Pagrus pagrus* | red porgy | shelf-demersal | 0-250m (80-180m) |
| **Cephalopods** | | | |
| *Loligo sanpaulensis* | common long-finned squid | shelf-demersal/pelagic | 0-250m (0-60m) |
| *Loligo plei* | slender inshore squid | shelf-demersal/pelagic | 15-280m |
| *Argonauta nodosa* | Knobby argonaut | shelf-epipelagic | 20m-500m |
| *Octopus tehuelchus* | tehuelche octopus | shelf-benthic, muddy and rocky bottoms | 0-90m (0-30m) |
| *Eledone* spp. | octopus | shelf-benthic, muddy and rocky bottoms | 40-600m (40-120m) |
| *Semirrosia tenera* | lesser bobtail squid* | shelf-demersal, muddy and sandy bottoms | 50-200m |
| **Crustaceans** | | | |
| *Pleoticus muelleri* | marine shrimp | estuary/shelf-pelagic | 0-70m |
| *Artemesia longinaris* | marine shrimp | estuary/shelf-pelagic | 0-70m (0-15m) |
| *Loxopagurus loxocheles* | marine crab | estuary/shelf-benthic | 0-30m (15-25m) |
| *Dardanus insignis* | marine crab | estuary/shelf-benthic | 0-500m (>25m) |

* The range in which the animals are most abundant is given in parenthesis.

Source: a) Seeliger, U., Odebrecht, C. and Castello, J. P. (Eds.) 1997. Subtropical Convergence Environmemts. Springer Editora, Berlin, Germany. 308pp.
b) Santos, R. A. 1999. Cephalopods and them food web importance in South Brasil. PhD Thesis. University of Rio Grande. Rio Grande, Brasil. 150pp.
c) Haimovici, M. 1998. Present state and perspectives for the southern Brasil shelf demersal fisheries. Fisheries Management and Ecology. 5, 277-289p.
d) http://www.fishbase.org

Table 4.4: General information for prey species, for the southern Brazilian coast, which had been found in stomachs contents of franciscana dolphin, *Pontoporia blainvillei*.

The crab species *Loxopagurus loxocheles* and *Dardanus insignis*, the infraorder Brachiura, and the suborder Pleocyemata, were only identified for the diet of the southern franciscanas due to problems of identification in the northern area and not their absence in this region.

Analysis of lengths, discriminated by species, show that the values vary among them (table 4.5), and some fishes ingested can be considerably larger (*e.g. Trichiurus lepturus*) than the mean fish length (figure 4.10). Furthermore, the minimum lengths for some prey species have to be looked at carefully, since the regression equations used for these estimations may not be very appropriate for the smallest fish otoliths or cephalopod beaks, and also the effect of digestive erosion. Therefore, some values of lengths and weights probably are underestimated.

| | **Lengths (mm)** | | | | | **Weights (g)** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **Mean** | **Min.** | **Max.** | **SE** | **SD** | **Mean** | **Min.** | **Max.** | **SE** | **SD** | **n** |
| **Fishes** | | | | | | | | | | | |
| *Anchoa marinii* | 69.66 | 31.08 | 112.12 | 0.78 | 13.85 | 1.75 | 0.29 | 8.50 | 0.05 | 1.03 | 317 |
| *Ctenosciena gracilicirrhus* | 67.58 | 49.97 | 86.35 | 5.96 | 14.60 | 4.37 | 1.44 | 8.45 | 1.16 | 2.85 | 6 |
| *Cynoscion guatucupa* | 55.22 | 12.16 | 356.44 | 0.72 | 29.99 | 3.53 | 0.01 | 464.68 | 0.39 | 16.50 | 1753 |
| *Cynoscion jamaicensis* | 73.69 | 18.80 | 312.73 | 8.61 | 66.10 | 22.67 | 0.05 | 378.98 | 9.25 | 71.05 | 59 |
| *Engraulis anchoita* | 108.07 | 54.70 | 151.65 | 3.44 | 23.60 | 8.46 | 0.87 | 21.18 | 0.76 | 5.23 | 47 |
| *Macrodon ancylodon* | 200.15 | 60.61 | 359.63 | 12.39 | 66.71 | 78.17 | 1.65 | 479.57 | 17.67 | 95.14 | 29 |
| *Menticirrhus* spp. | 148.93 | 64.42 | 342.56 | 11.70 | 69.20 | 60.13 | 1.71 | 472.55 | 19.07 | 112.84 | 35 |
| *Merluccius hubbsi* | 25.46 | 5.82 | 95.12 | 6.63 | 30.39 | 1.40 | 0.24 | 7.50 | 0.49 | 2.22 | 21 |
| *Micropogonias furnieri* | 103.96 | 26.90 | 240.37 | 9.25 | 62.77 | 28.25 | 0.13 | 167.74 | 6.67 | 45.30 | 46 |
| *Mugil* spp. | 207.40 | 100.00 | 314.70 | | | 118.40 | 10.00 | 226.80 | | | 2 |
| *Pagrus pagrus* | 49.22 | 27.01 | 80.22 | 4.87 | 18.86 | 2.62 | 0.30 | 7.88 | 0.70 | 2.73 | 15 |
| *Paralichtys isosceles* | 96.31 | | | | | 4.89 | | | | | 1 |
| *Paralonchurus brasiliensis* | 102.43 | 6.47 | 228.72 | 2.78 | 53.82 | 17.18 | 0.01 | 130.69 | 1.28 | 24.85 | 376 |
| *Peprilus paru* | 36.88 | 12.45 | 86.59 | 2.20 | 15.23 | 1.61 | 0.08 | 12.61 | 0.29 | 2.04 | 48 |
| *Pomatomus saltator* | 119.17 | 44.34 | 290.93 | 16.81 | 60.61 | 29.01 | 0.68 | 225.98 | 16.69 | 60.20 | 13 |
| *Porichthys porosissimus* | 92.77 | 19.30 | 270.44 | 5.02 | 60.19 | 19.05 | 0.04 | 199.92 | 3.07 | 36.89 | 144 |
| *Prionotus* spp. | 54.58 | 19.62 | 248.38 | 12.69 | 52.31 | 11.71 | 0.06 | 182.18 | 10.65 | 43.95 | 17 |
| *Raneya fluminensis* | 63.07 | 28.66 | 119.77 | 1.60 | 3.57 | 11.90 | 9.85 | 14.57 | 0.32 | 8.19 | 5 |
| *Stellifer rastrifer* | 53.37 | 3.62 | 206.71 | 1.19 | 27.86 | 3.36 | 0.01 | 127.06 | 0.37 | 8.62 | 551 |
| *Stromateus brasiliensis* | 128.70 | 117.08 | 140.32 | | | 21.91 | 16.00 | 27.83 | 5.92 | 8.37 | 2 |
| *Syacium papillosum* | 104.49 | 63.50 | 177.16 | 6.19 | 27.67 | 17.03 | 6.79 | 56.43 | 2.56 | 11.45 | 20 |
| *Trachurus lathami* | 64.94 | 28.49 | 129.33 | 6.99 | 33.51 | 3.86 | 0.15 | 16.64 | 1.12 | 5.35 | 23 |
| *Trichiurus lepturus* | 402.05 | 84.38 | 888.97 | 10.31 | 194.81 | 51.22 | 0.11 | 392.12 | 3.31 | 62.67 | 357 |
| *Umbrina canosai* | 67.02 | 12.52 | 193.57 | 3.17 | 48.76 | 11.38 | 0.02 | 100.25 | 1.22 | 18.79 | 236 |
| *Urophycis brasiliensis* | 103.70 | 52.31 | 454.24 | 3.86 | 69.04 | 23.97 | 0.56 | 831.93 | 4.50 | 80.60 | 320 |
| **Cephalopods** | | | | | | | | | | | |
| *Argonauta nodosa* | 20.62 | 4.30 | 71.14 | 1.23 | 12.09 | 3.00 | 0.03 | 15.84 | 0.34 | 3.39 | 96 |
| *Eledone* spp. | 31.72 | | | | | 18.60 | | | | | 1 |
| *Loligo plei* | 155.72 | 50.56 | 256.64 | 6.00 | 44.06 | 61.91 | 4.66 | 166.81 | 4.85 | 35.67 | 54 |
| *Loligo sanpaulensis* | 106.47 | 22.75 | 250.21 | 0.47 | 36.36 | 48.64 | 1.10 | 283.21 | 0.46 | 36.03 | 6034 |
| *Octopus tehuelchus* | 32.08 | 19.62 | 62.78 | 7.82 | 17.47 | 17.18 | 2.60 | 65.95 | 12.22 | 27.31 | 5 |
| *Semirrosia tenera* | 16.90 | 13.99 | 19.79 | | | 2.48 | 1.47 | 3.49 | | | 2 |

Table 4.5: Analysis of prey species lengths (mm) and weights (g) ingested by franciscana dolphins off the southern Brazilian coast (SE= standard error of the mean, SD= standard variation).

The mean and median fish total length are 96.37 and 59.98mm, respectively (n= 4443)[2], which represents juvenile fish (Haimovici, 1997a) (figure 4.10). The range of lengths were similar for both areas, and northern fish mean length was 107.95mm (median= 60.94, n= 1522) and southern fish mean was 90.34mm (median= 59.11, n= 2921). On the other hand, the cephalopods mantle lengths represent adult individuals in the population (Santos, 1999) (mean= 105.48, median= 105.77, n= 6192) (figure 4.11). The mean lengths for the northern area was 101.65mm (median= 105.77, n= 1135), and for the southern it was 106.33mm (me-

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[2] The letter "n" refers to the number of prey, whereas the capital letter "N" to the number of franciscana.

dian= 105.80, n= 5057). The mantle lengths were mostly from the species *Loligo sanpaulensis* (97.44%).

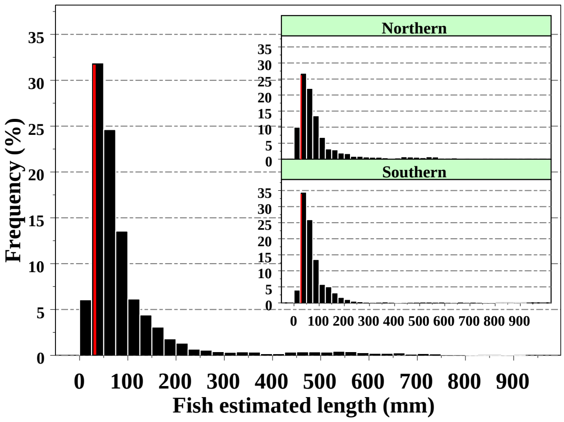


Figure 4.10: Length frequency distribution of fish specimens (26 species) in the diet of franciscana. The red line shows the median (valuable value for skewed distribution).

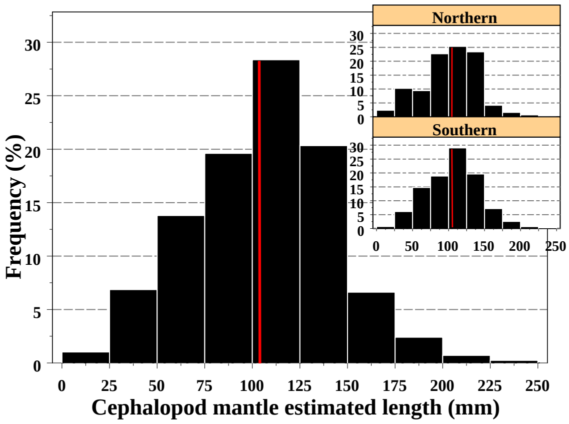


Figure 4.11: Mantle length frequency distribution of cephalopod specimens (6 species) in the diet of franciscana.

Mean fish body weight was 12.58g (median= 1.33, n= 4443) (figure 4.12); with similar mean values for northern (13.99g, median= 1.33, n= 1522) and southern (11.84g, median= 1.44, n= 2922). Cephalopod mean weight was 48.01g (median= 40.97, n= 6192) (figure 4.13), also with similar means for both areas (southern with 48.85g, median= 40.97, n= 5058); northern with 44.25g, median= 40.97, n= 1134).

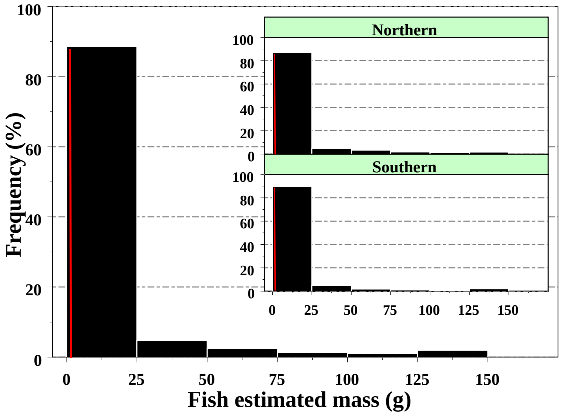


Figure 4.12: Estimated mass frequency distribution of fish specimens (26 species) in the diet of franciscana. The red line is the median.

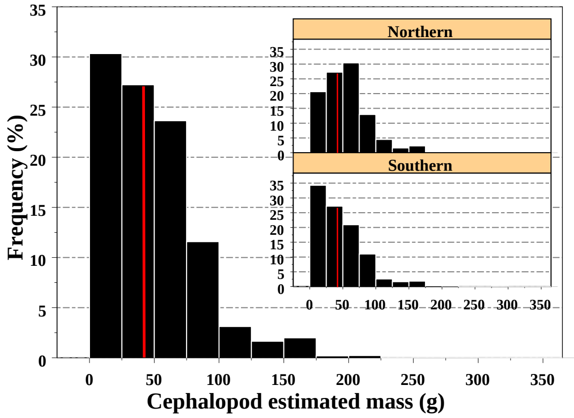


Figure 4.13: Estimated mass frequency distribution of cephalopod specimens (6 species) in the diet of franciscana. The red line is the median.

### 4.3.3 Prey assessment through the Index of Relative Importance

A general description of the most important prey and the main differences between areas, sex, sexual maturity, and season, is given here. For more details about the IRI values, see tables A.1 to A.10 in Appendix "A".

- **Northern and Southern areas**

The IRI values for both areas are given in appendices A.1 and A.2. In the franciscana diet of southern area there were higher number of species for all groups (fish, cephalopod and crustacean), 34 in total, whereas in northern the number decreased to 26 species. However, the crustacean identifications were made in different laboratories, and for southern area they were identified at higher taxonomic levels than for the northern (see section 4.3.2), which it increases the number of species. Furthermore, more stomach contents were analysed in the southern area.

IRI values for the cephalopod *Loligo sanpaulensis* were the highest, because cephalopod beaks can remain longer in the stomachs (see section 4.2.3). Therefore, the percentage of number of prey, occurrence in the stomachs, estimated mass (g), and IRI values, will be compared within the prey groups and not between them (fish species will be compared with fish species and so on).

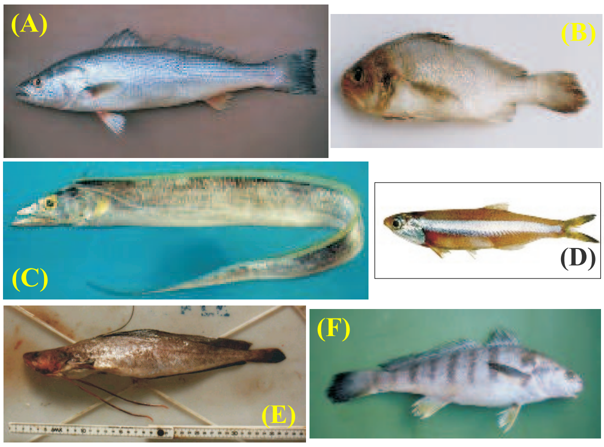


Figure 4.14: Illustrations of the fishes (A) *Cynoscion guatucupa*, (B) *Stellifer rastrifer*, (C) *Trichiurus lepturus*, (D) *Anchoa marinii*, (E) *Urophycis brasiliensis*, and (F) *Paralonchurus brasiliensis*. Sources: www.fishbase.org and www.viarural.com.ar.

The most important teleost fish species for the southern area were: *Cynoscion guatucupa*, *Trichiurus lepturus*, *Paralonchurus brasiliensis*, *Anchoa marinii*, and *Urophycis brasiliensis*, whilst for the northern they were: *Stellifer rastrifer*, *Trichiurus lepturus*, *Urophycis brasiliensis*, *Paralonchurus brasiliensis*, and *Cynoscion guatucupa* (see figure 4.14).

Both areas share 7 from the 10 teleosts of main importance. Nevertheless, the principal prey for the southern area, *Cynoscion guatucupa* (IRI= 16433.7), is far more important than the second *Trichiurus lepturus* (IRI= 225.6), whilst in the northern the main species are close in values of importance (*Stellifer rastrifer* with IRI= 968.2 and *Trichiurus lepturus* with 869.7).

Notably, only one occurrence of *Stellifer rastrifer* was found in the diet of southern franciscana (N= 172 stomachs), while this teleost occurred in 44.9% of the stomachs from the northern area and was its main prey.

The most important fish prey according to the number found in the stomachs (n%) were *Cynoscion guatucupa*, *Anchoa marinii*, and *Paralonchurus brasiliensis*, and *Trichiurus lepturus* (southern area); and *Stellifer rastrifer*, *Urophycis brasiliensis*, *Paralonchurus brasiliensis*, and *Trichiurus lepturus* (northern area). In general, *Trichiurus lepturus*, *Paralonchurus brasiliensis*, and *Urophycis brasiliensis* are important prey in numbers for both areas.

The prey species that most contributed to the diet in terms of biomass (W%), for both areas, was *Trichiurus lepturus* followed by *Cynoscion guatucupa* and *Urophycis brasiliensis* in southern, and *Urophycis brasiliensis* and *Paralonchurus brasiliensis* in northern. Generally, the teleosts that most added in terms of biomass were *Trichiurus lepturus* and *Urophycis brasiliensis*.

Figure 4.15: Illustrations of the squid *Loligo sanpaulensis* (above) and the argonaut *Argonauta nodosa*. Source: www.cephbase.utmb.edu and www.tolweb.org.

The squid *Loligo sanpaulensis* is by far the most important cephalopod species for the whole study area (figure 4.15). *Loligo plei* is the second species in IRI value for the northern area and the third for the southern, although the occurrences in both diets are very similar (8.7 and 8.2%, respectively). The argonaut *Argonauta nodosa* has less different indexes for southern (IRI= 8.9), and northern (IRI= 7.7) areas.

According to the total number of fish and cephalopod prey ingested, northern franciscanas appeared to have consumed more fish (64.4%) than southern animals (46.9%), whereas cephalopods were more consumed in the southern (51.6%) than in the northern (34.1%).

Figure 4.16: Illustration of the shrimp *Pleoticus muelleri*. Source: www.ecomarina.com.ar.

For crustacean species, *Artemesia longinaris* and *Pleoticus muelleri* (figure 4.16), and the family Penaidae were identified as the superfamily Penaeoidea by the northern area analyses. They are marine shrimps. The occurrence of this superfamily is very similar to that of both species together from southern area, as well as the IRI values.

The order Isopoda occurred more in the diet of franciscanas from the northern (32.7% and IRI= 31.3), than from southern (5.8% and IRI= 1.9). However, counting all the crustacean specimens, there seems to be no difference in terms of number and occurrence.

- **Male and Female**

The IRI values for male and female franciscanas are given in appendices tables A.3 and A.4. In the southern area, there are just a few differences of prey preference between males and females, whereas within northern the area these differences on the diet appear slightly more evident.

The *Stellifer rastrifer* has higher IRI for males than females, whereas Engraulidae species are more consumed for females. The cephalopods *Loligo plei* and *Argonauta nodosa* occurred more for males in the northern area.

The abundance of cephalopod and crustacean species is higher for females in the southern area, but cephalopod occurrences and abundance do not differ between sexs. Females in the whole area had eaten more crustacean species than males.

- **Adult and Juvenile**

The IRI values for adult and juvenile franciscanas are given in appendices tables A.5 and A.6. Cephalopod species are more frequent ingested by adults in both areas. For teleosts in the southern area, the results revealed no strong differences. Comparing the main fish prey, *Trichiurus lepturus* is more frequent for adults in both areas, and *Cynoscion guatucupa* and *Stellifer rastrifer* for the juveniles for southern and northern areas, respectively. The shrimp species and families had high IRI for juveniles in whole study area.

- **Seasonality**

The IRI values for season are given in appendices tables (see tables A.7, A.8, A.9, and A.10).

The Engraulidae family and species, *Anchoa marinii* and *Engraulis anchoita*, clearly have higher IRI in the winter for both areas, although in autumn they are also frequent in the southern area.

The main fish species *Stellifer rastrifer* of northern area appeared during the whole year in the franciscana diet, mainly in the wintertime. Similar to the main species of southern area, the *Cynoscion guatucupa*, which also occurs all year even though it is more abundant and frequent during winter.

For the southern area, *Trichiurus lepturus* has its highest values in summer and autumn, decreasing considerably in the winter. *Trichiurus lepturus* is important in the summer and spring for the northern franciscanas, though still not decreasing so much in the wintertime as for the southern area. Hence, *Trichiurus lepturus* is an important species for summer in both areas.

Furthermore during summer, the fish species *Porichthys porosissimus*, *Umbrina canosai*, and *Cynoscion jamaicensis* had higher occurrences for both areas; and the *Paralonchurus brasiliensis* during the winter season. The *Merluccius hubbsi* only occurred in the diet of the southern animals, with higher IRI in the winter.

Cephalopod species, mainly *Loligo plei* and *Argonauta nodosa*, occur more during summer and autumn through the coast, and *Loligo sanpaulensis* in the winter and spring seasons. Marine shrimps are more likely to be found in summer in the northern, and during spring in the southern area.

Autumn revealed more variability in species for the southern locality, and summer for the northern area. However, this should be treated with caution, as for the northern area there is an unbalanced sampling (*i.e.* the number of franciscanas analysed is lower for autumn and winter seasons).

### 4.3.4 Prey assessment through Linear and Generalized Linear Models

From the previous analyses it was only possible to give a general description of the diet, and the importance of prey according to the percentage of their number, occurrence, and body mass ingested. However, statistical methods are needed to identify if the differences found are significant, and the GLM was chosen. Additionally, the LM was the statistical method selected to interpret the prey specimens body length and weight in the franciscana diet.

The results of LM and GLM comparing similar groups between the areas (*i.e.* males of the southern area *vs.* males of the northern area) showed similar differences as when all animals were included (Northern *vs.* Southern area franciscanas). Therefore these results just reflect the differences caused by the areas, hence the comparisons of groups (sex, sexual maturity and season) were made only within each area. Furthermore, pairwise comparisons were used to reveal which season(s) are different (4 levels variable).

Furthermore, as explained in the results of ”Diet composition” (section 4.3.2), the shrimp specimens were identified at species and family levels for the southern area, and only at superfamily level for the northern. For this reason they were grouped as ”shrimp specimens” in order to compare this group between the areas in further analyses.

- **Overview**

The linear models for prey estimated lengths and mass between the areas, sex, maturity, and seasons, showed significant differences for 86% of the analyses (table 4.6). Only for four linear models (rows 9, 10, 19, and 20), significant differences were not found. As expected, the highest $F$ values are from prey size comparison between adult and juvenile franciscanas of both areas (rows 13 to 18).

GLM revealed most of the highly significant differences of prey species number (table 4.7)

| | Linear Model Formula | df | res. df | F | *p* | Means (log) | Estimated effects |
|---|---|---|---|---|---|---|---|
| | **Northern and Southern areas = explanatory** | | | | | | |
| 1 | log (Fish estimated length) | 1 | 4441 | 6.6 | 0.010 | N= 4.3 S= 4.2 | N= 0.1 S= 0.0 |
| 2 | log (Fish estimated mass) | 1 | 4441 | 6.3 | 0.012 | N= 1.4 S= 1.3 | N= 0.1 S= 0.0 |
| 3 | log (Cephalopod estimated length) | 1 | 6190 | 32.8 | <0.001 | N= 4.5 S= 4.6 | N= -0.1 S= 0.0 |
| 4 | log (Cephalopod estimated mass) | 1 | 6190 | 37.2 | <0.001 | N= 3.3 S= 3.5 | N= -0.2 S= 0.0 |
| | **Male and female of northern area = explanatory** | | | | | | |
| 5 | log (Fish estimated length) | 1 | 1272 | 51.0 | <0.001 | F= 4.6 M= 4.1 | F= 0.4 M= -0.1 |
| 6 | log (Fish estimated mass) | 1 | 1272 | 48.7 | <0.001 | F= 2.0 M= 1.2 | F= 0.7 M= -0.2 |
| 7 | log (Cephalopod estimated length) | 1 | 932 | 14.1 | <0.001 | F= 4.6 M= 4.4 | F= 0.1 M= -0.1 |
| 8 | log (Cephalopod estimated mass) | 1 | 932 | 14.3 | <0.001 | F= 3.4 M= 3.1 | F= 0.2 M= -0.2 |
| | **Male and female of southern area = explanatory** | | | | | | |
| 9 | log (Fish estimated length) | 1 | 2920 | 2.8 | 0.094 | F= 4.2 M= 4.2 | F= 0.0 M= 0.0 |
| 10 | log (Fish estimated mass) | 1 | 2920 | 0.0 | 0.878 | F= 1.3 M= 1.3 | F= 0.0 M= 0.0 |
| 11 | log (Cephalopod estimated length) | 1 | 5056 | 28.2 | <0.001 | F= 4.5 M= 4.6 | F= -0.1 M= 0.0 |
| 12 | log (Cephalopod estimated mass) | 1 | 5056 | 52.6 | <0.001 | F= 3.3 M= 3.6 | F= -0.2 M= 0.1 |
| | **Adult and juvenile of northern area = explanatory** | | | | | | |
| 13 | log (Fish estimated length) | 1 | 1472 | 93.4 | <0.001 | A= 4.8 J= 4.0 | A= 0.5 J= -0.2 |
| 14 | log (Fish estimated mass) | 1 | 1472 | 97.2 | <0.001 | A= 2.4 J= 1.1 | A= 1.0 J= -0.3 |
| 15 | log (Cephalopod estimated length) | 1 | 1038 | 8.8 | 0.003 | A= 4.5 J= 4.4 | A= 0.1 J= -0.1 |
| 16 | log (Cephalopod estimated mass) | 1 | 1038 | 9.4 | 0.002 | A= 3.4 J= 3.1 | A= 0.1 J= -0.1 |
| | **Adult and juvenile of southern area = explanatory** | | | | | | |
| 17 | log (Fish estimated length) | 1 | 2920 | 54.4 | <0.001 | A= 4.5 J= 4.0 | A= 0.3 J= -0.1 |
| 18 | log (Fish estimated mass) | 1 | 2920 | 55.5 | <0.001 | A= 1.8 J= 1.1 | A= 0.5 J= -0.2 |
| 19 | log (Cephalopod estimated length) | 1 | 5056 | 0.0 | 0.925 | A= 4.6 J= 4.6 | A= 0.0 J= 0.0 |
| 20 | log (Cephalopod estimated mass) | 1 | 5056 | 0.5 | 0.489 | A= 3.5 J= 3.5 | A= 0.0 J= 0.0 |
| | **Seasonality of northern area = explanatory** | | | | | **Sum \| Aut \| Win \| Spr** | **Sum \| Aut \| Win \| Spr** |
| 21 | log (Fish estimated length) | 3 | 1517 | 24.1 | <0.001 | 4.0 \| 4.7 \| 4.2 \| 4.5 | -0.2 \| 0.4 \| 0.0 \| 0.2 |
| 22 | log (Fish estimated mass) | 3 | 1517 | 16.1 | <0.001 | 1.1 \| 2.0 \| 1.5 \| 1.7 | -0.3 \| 0.5 \| 0.0 \| 0.2 |
| 23 | log (Cephalopod estimated length) | 3 | 1130 | 9.0 | <0.001 | 4.5 \| 4.3 \| 4.5 \| 4.5 | 0.0 \| -0.2 \| -0.1 \| 0.0 |
| 24 | log (Cephalopod estimated mass) | 3 | 1130 | 3.3 | 0.020 | 3.4 \| 2.8 \| 3.2 \| 3.4 | 0.1 \| -0.6 \| -0.2 \| 0.1 |
| | **Seasonality of southern area = explanatory** | | | | | | |
| 25 | log (Fish estimated length) | 3 | 2918 | 56.7 | <0.001 | 4.5 \| 4.4 \| 4.0 \| 4.2 | 0.3 \| 0.2 \| -0.1 \| 0.0 |
| 26 | log (Fish estimated mass) | 3 | 2918 | 46.4 | <0.001 | 2.1 \| 1.5 \| 1.1 \| 1.5 | 0.7 \| 0.1 \| -0.2 \| 0.2 |
| 27 | log (Cephalopod estimated length) | 3 | 5054 | 57.2 | <0.001 | 4.5 \| 4.4 \| 4.5 \| 4.7 | -0.1 \| -0.2 \| -0.1 \| 0.1 |
| 28 | log (Cephalopod estimated mass) | 3 | 5054 | 46.2 | <0.001 | 3.4 \| 3.0 \| 3.4 \| 3.8 | -0.2 \| -0.5 \| -0.1 \| 0.3 |

Table 4.6: List of LM and the analysis of variance according to areas, sex, maturity, and season for fish and cephalopod lengths (mm) and weights (g). The estimated effects are average responses due to the given treatment combinations, having adjusted for all model terms. For instance, the interaction effects are changes in response after adjusting for the grand mean and both main effects.

for areas (rows 1 to 11) and seasons (rows 18 to 36), with few significant differences for adult and juvenile franciscanas (rows 12 to 17), and no significant differences for male and female

| | **Generalised Linear Model Formula (family= Poisson, link =log)** | **df** | **res. df** | ***p*** | **Means (log)** | | | | **Estimated effects** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Northern and Southern areas = explanatory** | | | | | | | | | | | |
| 1 | *Anchoa marinii* | 1 | 259 | 0.002 | N= 0.2 S= 0.5 | | | | N= -0.2 S= 0.1 | | | |
| 2 | *Cynoscion guatucupa* | 1 | 259 | <0.001 | N= 0.4 S= 1.5 | | | | N= -0.7 S= 0.4 | | | |
| 3 | *Cynoscion jamaicensis* | 1 | 259 | 0.006 | N= 0.2 S= 0.0 | | | | N= 0.1 S= -0.1 | | | |
| 4 | *Menticirrhus sp.* | 1 | 259 | 0.015 | N= 0.1 S= 0.0 | | | | N= 0.1 S= 0.0 | | | |
| 5 | *Merluccius hubbsi* | 1 | 259 | 0.025 | N= 0.0 S= 0.1 | | | | N= -0.1 S= 0.0 | | | |
| 6 | *Peprilus paru* | 1 | 259 | 0.049 | N= 0.0 S= 0.1 | | | | N= -0.1 S= 0.0 | | | |
| 7 | *Stellifer rastrifer* | 1 | 259 | <0.001 | N= 0.8 S= 0.0 | | | | N= 0.5 S= -0.3 | | | |
| 8 | *Trachurus lathami* | 1 | 259 | 0.004 | N= 0.1 S= 0.0 | | | | N= 0.1 S= 0.0 | | | |
| 9 | *Urophycis brasiliensis* | 1 | 259 | 0.018 | N= 0.6 S= 0.4 | | | | N= 0.2 S= -0.1 | | | |
| 10 | *Loligo sanpaulensis* | 1 | 259 | <0.001 | N= 1.7 S= 2.3 | | | | N= -0.4 S= 0.2 | | | |
| 11 | Total shrimp specimens | 1 | 259 | 0.013 | N= 0.1 S= 0.2 | | | | N= -0.1 S= 0.1 | | | |
| | **Male and female of northern area = explanatory** | **NS** | | | | | | | | | | |
| | **Male and female of southern area = explanatory** | **NS** | | | | | | | | | | |
| | **Adult and juvenile of northern area = explanatory** | | | | | | | | | | | |
| 12 | *Stellifer rastrifer* | 1 | 91 | 0.024 | A= 0.2 J= 1.4 | | | | A= -0.6 J= 0.6 | | | |
| 13 | Total fish specimens | 1 | 91 | 0.003 | A= 2.1 J= 2.9 | | | | A= -0.4 J= 0.4 | | | |
| 14 | Total shrimp specimens | 1 | 91 | <0.001 | A= 0.0 J= 0.2 | | | | A= -0.1 J= 0.1 | | | |
| | **Adult and juvenile of southern area = explanatory** | | | | | | | | | | | |
| 15 | *Cynoscion guatucupa* | 1 | 167 | 0.043 | A= 1.2 J= 1.6 | | | | A = -0.2 J= 0.2 | | | |
| 16 | Total fish specimens | 1 | 167 | 0.023 | A= 2.6 J= 2.8 | | | | A= -0.1 J= 0.1 | | | |
| 17 | Total shrimp specimens | 1 | 167 | 0.003 | A= 0.1 J= 0.3 | | | | A= -0.1 J= 0.1 | | | |
| | **Seasonality of northern area = explanatory** | | | | **Sum** | **Aut** | **Win** | **Spr** | **Sum** | **Aut** | **Win** | **Spr** |
| 18 | *Anchoa marinii* | 3 | 91 | <0.001 | 0.0 | 0.3 | 0.7 | 0.1 | -0.2 | 0.1 | 0.4 | -0.1 |
| 19 | *Stellifer rastrifer* | 3 | 91 | 0.036 | 1.0 | 0.7 | 1.5 | 0.4 | 0.1 | -0.1 | 0.7 | -0.4 |
| 20 | *Trichiurus lepturus* | 3 | 91 | <0.001 | 1.1 | 0.5 | 0.2 | 0.9 | 0.3 | -0.3 | -0.6 | 0.1 |
| 21 | family Engraulidae | 3 | 91 | 0.020 | 0.0 | 0.0 | 0.4 | 0.1 | -0.1 | -0.1 | 0.2 | -0.1 |
| 22 | *Loligo plei* | 3 | 91 | <0.001 | 0.3 | 0.5 | 0.0 | 0.0 | 0.2 | 0.4 | -0.1 | -0.1 |
| 23 | *Argonauta nodosa* | 3 | 91 | 0.009 | 0.3 | 0.2 | 0.0 | 0.1 | 0.2 | 0.1 | -0.1 | -0.1 |
| | **Seasonality of southern area = explanatory** | | | | | | | | | | | |
| 24 | *Anchoa marinii* | 3 | 167 | <0.001 | 0.1 | 0.6 | 1.0 | 0.2 | -0.5 | 0.0 | 0.5 | -0.4 |
| 25 | *Cynoscion guatucupa* | 3 | 167 | <0.001 | 0.5 | 1.1 | 2.5 | 1.0 | -1.0 | -0.4 | 1.0 | -0.5 |
| 26 | *Macrodon ancylodon* | 3 | 167 | 0.008 | 0.0 | 0.0 | 0.2 | 0.0 | -0.1 | 0.0 | 0.1 | 0.0 |
| 27 | *Paralonchurus brasiliensis* | 3 | 167 | <0.001 | 0.3 | 0.2 | 0.7 | 0.8 | -0.2 | -0.4 | 0.2 | 0.3 |
| 28 | *Peprilus paru* | 3 | 167 | <0.001 | 0.3 | 0.2 | 0.0 | 0.0 | 0.2 | 0.1 | -0.1 | -0.1 |
| 29 | *Porichthys porosissimus* | 3 | 167 | 0.001 | 0.4 | 0.6 | 0.1 | 0.1 | 0.1 | 0.3 | -0.2 | -0.2 |
| 30 | *Trichiurus lepturus* | 3 | 167 | <0.001 | 0.8 | 0.9 | 0.1 | 0.5 | 0.3 | 0.4 | -0.4 | 0.0 |
| 31 | *Umbrina canosai* | 3 | 167 | <0.001 | 0.4 | 0.2 | 0.1 | 0.4 | 0.2 | 0.0 | -0.2 | 0.2 |
| 32 | family Engraulidae | 3 | 167 | 0.001 | 0.0 | 0.1 | 0.3 | 0.1 | -0.1 | -0.1 | 0.1 | 0.0 |
| 33 | Total fish specimens | 3 | 167 | <0.001 | 2.2 | 2.6 | 3.2 | 2.4 | -0.5 | -0.1 | 0.5 | -0.3 |
| 34 | *Loligo sanpaulensis* | 3 | 167 | <0.001 | 1.8 | 1.5 | 2.6 | 3.1 | -0.5 | -0.8 | 0.3 | 0.8 |
| 35 | *Argonauta nodosa* | 3 | 167 | <0.001 | 0.4 | 0.2 | 0.0 | 0.0 | 0.3 | 0.1 | -0.1 | -0.1 |
| 36 | Total shrimp specimens | 3 | 167 | 0.012 | 0.2 | 0.3 | 0.1 | 0.4 | 0.0 | 0.0 | -0.1 | 0.1 |

Table 4.7: List of GLM and the analysis of deviance according to areas, sex, maturity, and season for the franciscana prey species.

franciscanas in both areas. Furthermore, southern area had shown twice as many significantly different prey species frequency through seasons than the northern area (rows 24 to 36). A more detailed description of the significant results according to each explanatory variable (*e.g.* areas, sex, sexual maturity, and season) is presented next.

- **Northern and Southern areas**

The fish species *Cynoscion guatucupa* and *Stellifer rastrifer*, and the cephalopod *Loligo sanpaulensis*, had shown the most significant differences between southern and northern areas in the franciscana's diet (rows 2, 7, 10 table 4.7 and figure 4.17). They were also the most representative species in IRI values (see tables A.1 and A.2).

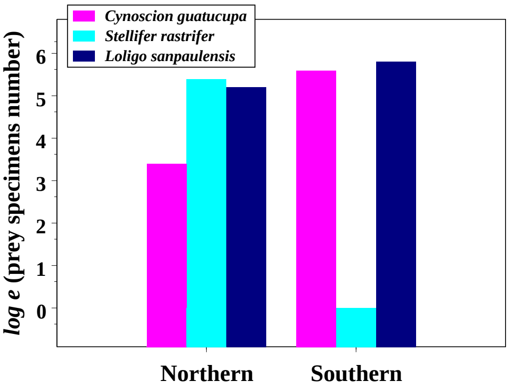


Figure 4.17: The fish species *Cynoscion guatucupa* and *Stellifer rastrifer*, and the cephalopod *Loligo sanpaulensis*, discriminated by southern and northern areas.

The fishes *Anchoa marinii*, *Merluccius hubbsi*, and *Peprilus paru* were more frequently consumed by franciscanas in the southern area. The fish species *Cynoscion jamaicensis*, *Menticirrhus* sp., *Urophycis brasiliensis*, and *Trachurus lathami*, were more frequent in the northern area. However, *Menticirrhus* sp. and *Trachurus lathami* are fishes with low occurrence in the franciscana diet. The shrimps are significantly more abundant for the southern area.

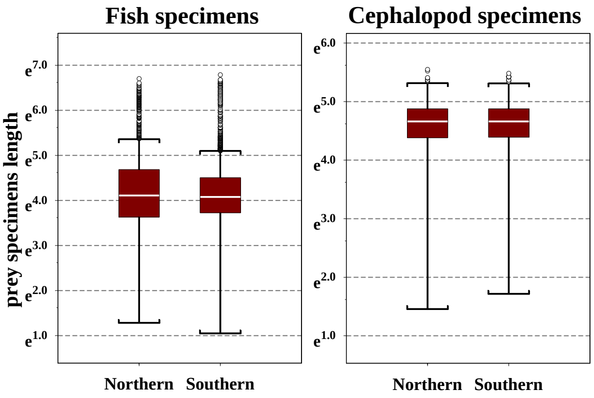


Figure 4.18: Fish and cephalopod specimens estimated length (n= 10,635), for the southern and northern areas. The horizontal line in the interior of the box is located at the median of the data. The height of the box is equal to the interquartile range, and the outliers are drawn individually, indicated as circles. All the points more than 1.5*(Inter-Quartile Range) are considered outliers.

The length and weight of the fishes also differed, with bigger sizes found in the northern area than in the southern (figure 4.18). Nonetheless, the differences are not high (rows 1 and 2, table 4.6).

The lengths and weights of cephalopods were both bigger for the southern and northern areas, and significantly different between them (rows 3 and 4 table4.6). However, the actual differences are small (figure 4.18).

Adding fish and cephalopod groups, franciscanas from the southern area have significantly higher stomach contents biomass (df= 1, F= 82.47, $p<0.001$).

- **Male and Female**

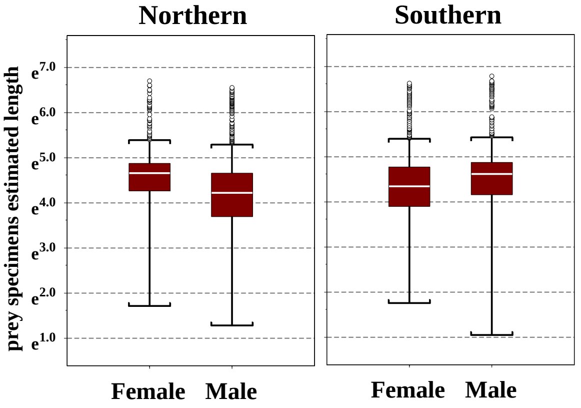


Figure 4.19: General prey specimens estimated length (n= 10,635) for female and male franciscanas, for the southern and northern areas.

Analyses revealed that there were no prey species preferences between male and female individuals for both areas ($p>0.05$). However, there are differences of lengths and weights of cephalopod and fish specimens (table 4.6). Females ate larger cephalopods in the northern area (rows 7 and 8), while the males had ingested bigger cephalopods in the southern area (rows 11 and 12). The females in the northern area also ingested bigger fish specimens (rows 5 and 6), while in the southern coast the fish sizes eaten did not differ between males and females (rows 9 and 10). Overall, it seems that females are ingesting bigger prey in the northern area, and males in the southern (figure 4.19). However, considering all male and female for the whole area, there were no significant differences of the estimated mass of prey ingested (df= 1, F= 1.22, $p<0.269$).

- **Adult and Juvenile**

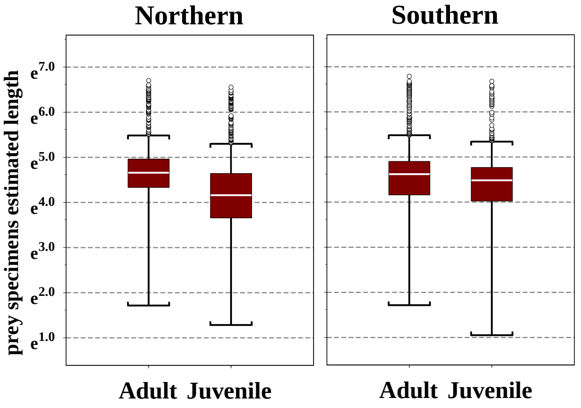


Figure 4.20: General prey specimens estimated length (n= 10,635) for adult and juvenile franciscanas, for the southern and northern areas.

For fish prey, the principal species in each area and the total numbers consumed differed significantly between adults and juveniles (table 4.7). Juveniles had consumed greater numbers of *Cynoscion guatucupa*, *Stellifer rastrifer*, total fish specimens, and the shrimps (rows 12 to 17). Nevertheless, adult franciscanas ingested lower numbers of prey, but with greater sizes (figure 4.20) and biomass (all prey, df= 4394, F= 457.9, $p<0.001$ ). For fish prey, adults from both southern and northern areas had eaten bigger specimens than juveniles (rows 13, 14, 17 and

18 table 4.6). For cephalopod specimens there were size differences between adult and juvenile for the northern area (rows 15 and 16), where adults had also ingested bigger specimens, but no differences were found for the southern area (rows 19 and 20).

- **Seasonality**

For the number of prey consumed for different seasons, *Trichiurus lepturus* was consumed in significantly higher numbers (rows 20 and 30 table 4.7), during summer, spring, and autumn, than winter for both areas (figure 4.21). *Anchoa marinii* were significantly more important (rows 18 and 24) during the winter in the northern area, and during winter and autumn in the southern (figure 4.21). In addition, specimens from the family Engraulidae also were significantly more consumed during the wintertime in the southern area (row 32). The argonaut *Argonauta nodosa* was more consumed during summer for both areas (rows 23 and 35). Pairwise comparisons were used to reveal the different season(s).

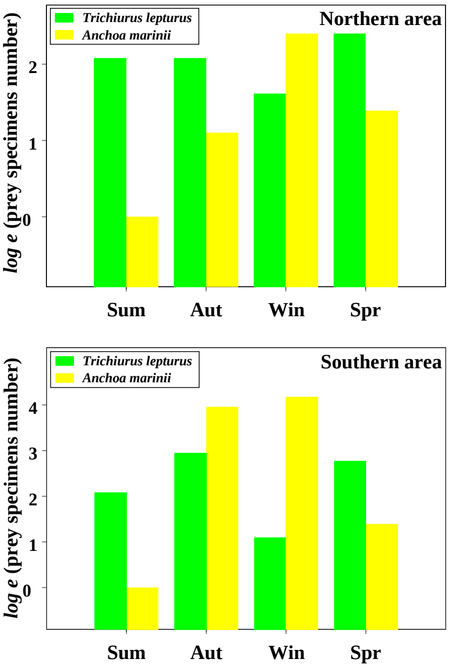


Figure 4.21: The seasonal variability of the fish *Anchoa marinii* and *Trichiurus lepturus*, discriminated by southern and northern areas.

The *Trichiurus lepturus*, *Anchoa marinii*, and *Argonauta nodosa*, are the only species which differ significantly according to season for both areas, even though *Argonauta nodosa* is not as important prey for franciscana as the *Trichiurus lepturus* and *Anchoa marinii* (see tables A.1 and A.2).

For the northern area, *Stellifer rastrifer* is more often consumed during the winter season (row 19), despite one noticeable ingestion (outlier) in the summer (figure 4.22), hence the prey seemed present in the area throughout all year. *Loligo plei* were eaten more by franciscanas through summer and autumn (row 22, figure 4.22).

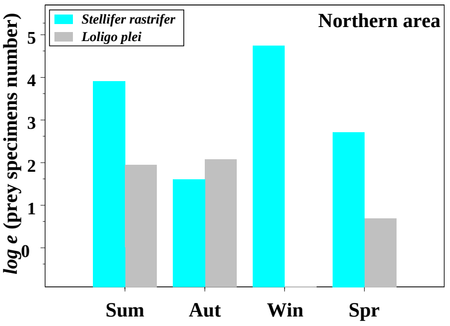


Figure 4.22: The seasonal variability of the fish *Stellifer rastrifer* and the squid *Loligo plei* off the northern area.

In the southern area, consumption of *Cynoscion guatucupa* (figure 4.23), *Macrodon ancylodon*, and the total fish specimens are higher in the winter and autumn seasons (rows 25, 26 and

33). However, as the *Cynoscion guatucupa* is the most frequent fish species, the result for the total fish specimens is probably dominated by this species. *Paralonchurus brasiliensis* also is significantly more frequent during winter, followed by the spring (row 27). In the summer, *Umbrina canosai* and *Peprilus paru* were present in significant numbers (rows 28 and 31), whereas during autumn it was the fish *Porichthys porosissimus* (row 29, figure 4.23). Nonetheless, the teleosts *Macrodon ancylodon* and *Peprilus paru* are not very important prey for franciscanas in general (see tables A.1 and A.2).

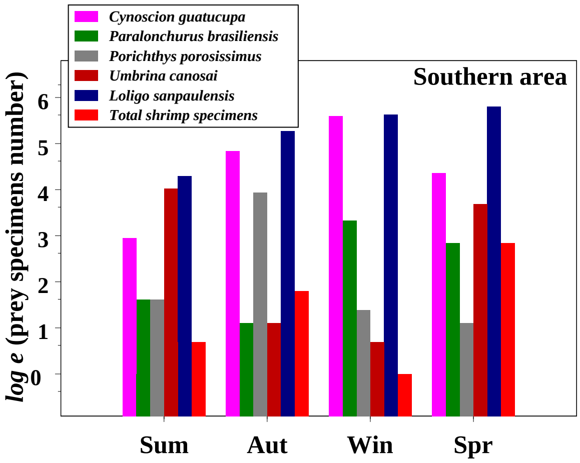


Figure 4.23: The seasonal variability of the fish species *Cynoscion guatucupa*, *Paralonchurus brasiliensis*, *Porichthys porosissimus*, *Umbrina canosai*, the squid *Loligo plei*, and the shrimp specimens off the southern area.

Continuing in the southern area, the cephalopod *Loligo sanpaulensis* shows significant seasonal variation (row 34) starting in the spring and higher number through winter (figure 4.23). Total shrimp specimens were significantly more abundant (row 36) in the spring, autumn, and summer, with few occurrences in the winter (figure 4.23). The biggest fish lengths and weights ingested were found in the summer and autumn, and the smaller fish were found in the winter (rows 25 and 26 in table 4.6, and figure 4.24), in the southern area.

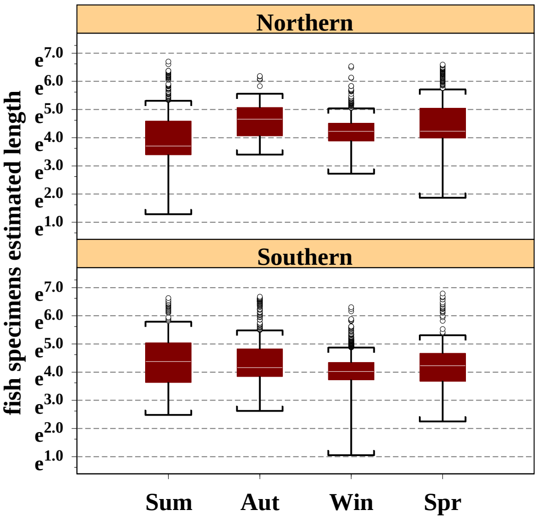


Figure 4.24: Fish specimens estimated length (n= 4,443) discriminated by seasons, in the northern and southern areas.

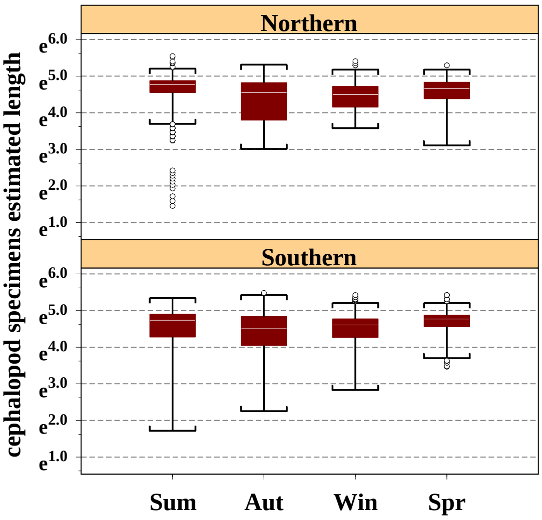


Figure 4.25: Cephalopod specimens estimated mantle length (n= 6,192) discriminated by seasons, in the northern and southern areas.

In the northern area, summer and spring had the larger fishes whereas winter shows the smallest prey (rows 21 and 22). Hence seasonal results for both areas are similar. Fish body mass for the seasons is not illustrated since the figure for fish lengths is very similar.

The biggest cephalopods were consumed during spring and summer for both areas (rows 23, 24, 27 and 28), and the smallest cephalopods were eaten through autumn and winter (figure 4.25), but the differences are small. Cephalopod body mass for the seasons is not illustrated either since the figure for cephalopod mantle lengths are similar.

Overall, there are evident differences between the diets of both areas.

What follows in this Chapter is to analyse the franciscana diet in more detailed spatial subdivisions of the southern Brazilian coast. The diet will be reanalysed dividing the study area into 7 smaller "latitudinal zones" to understand how the franciscana feeding is changing along the coast (i.e. abrupt changes, smooth changes).

However, from the following analysis we will focus only in the spatial and temporal diet variation of franciscana, and differences within the population (*e.g.* sex) are not considered.

## 4.4 Methods II

In the following sections the data are reanalysed through LM and GLM for a new spatial subdivisions - 7 latitudinal zones - and an exploratory statistical technique, the PCA, was also used to visualise the trends in franciscana diet with respect to spatial location.

### 4.4.1 Refining the study area: the latitudinal zones

The variation in the franciscana diet between the two major areas, northern and southern, of the study region was analysed in the previous sections. The northern and southern areas were defined according to the fishing areas utilised by the fishing vessels of Tramandai/Imbé and Rio Grande/Barra, respectively (see section 4.2.1). However, the location of franciscanas within each area is expected to vary continuously along the coast (capture events), and it is possible to divide the study region into more detailed zones.

According to the fishing vessels, the information on captures were given according to cities and light house references, and occurred in depths less than 50m. Hence in the midst of the limit of the 50m isobath, and according to the distances of the cities and light houses, the study area was further subdivided into 7 latitudinal zones (figure 4.26) as follows:

- Zone 1 = $29^o$ 11' to $30^o$ 01' S (Torres city to Tramandai city);
- Zone 2 = $30^o$ 01' to $30^o$ 41' S (Tramandai city to Solidao lighthouse);
- Zone 3 = $30^o$ 41' to $31^o$ 09' S (Solidao lighthouse to Mostardas lighthouse);
- Zone 4 = $31^o$ 09' to $31^o$ 40' S (Mostardas lighthouse to Conceicao lighthouse);
- Zone 5 = $31^o$ 40' to $32^o$ 07' S (Conceicao lighthouse to Barra);
- Zone 6 = $32^o$ 07' to $32^o$ 35' S (Barra to southern Sarita lighthouse);
- Zone 7 = $32^o$ 35' to $33^o$ 05' S (southern Sarita lighthouse to Albardao lighthouse).

In the previous analysis, the northern area dolphins belonged to the zones 1, 2, and 3, whereas for the southern franciscanas were from the zones 4, 5, 6, and 7. Except for one animal from the northern coast which belonged to the zone 4. The franciscana specimens sampled, which contained stomach contents, for each zone were: N= 30 (zone 1), N= 34 (zone 2), N= 26 (zone 3), N= 12 (zone 4), N= 52 (zone 5), N= 72 (zone 6), and N= 18 (zone 7).

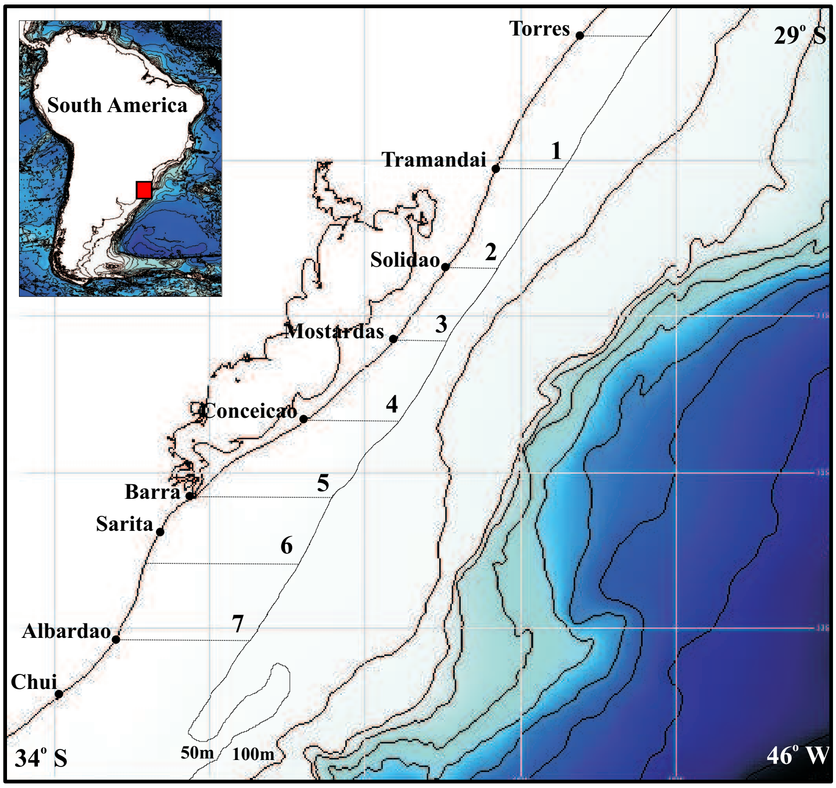


Figure 4.26: Map corresponding to the new subdivisions - 7 latitudinal zones - for further analysis of franciscana diet along the study area.

### 4.4.2 Linear and Generalized Linear Models and the latitudinal zones

Following the methodology described on section 4.2.4, the relationships between franciscana prey species frequency (GLM), prey lengths and weights (LM), were analysed according to the latitudinal zones. Temporal variation (season) was considered as well. The values of degrees of freedom, residuals, F, *p*, and the estimated effects, are demonstrated in the variance/deviance tables.

According to the results of sections 4.3.3 and 4.3.4, for further analysis of LM and GLM the prey species with low numbers or occurrences were discarded. They are: the fishes *Ctenosciena gracilicirrhus*, *Pomatomus saltatrix*, *Mugil* sp., *Stromateus brasiliensis*, *Licengraulis grossidens*, *Raneya fluminensis*, *Prionotus* sp., *Syacium papillosum*, *Paralichtys isosceles*, and *Pagrus pagrus*; and the cephalopods *Octopus tehuelchus*, *Eledone* sp., and *Semirrosia tenera*.

For the prey taxa, the crab species *Loxopagurus loxocheles* and *Dardanus insignis*, the infraorder Brachiura, and the suborder Pleocyemata were not included because the correct identification was only possible for the southern franciscanas (see section 4.3.2). Similarly, the shrimp species (*Artemesia longinaris*, *Pleoticus muelleri*, *Loxopagurus loxocheles*, *Dardanus insignis*), the family Penaidae, superfamily Penaeoidea, and the suborder Dendrobranchiata were not considered. However, they are again treated as the "shrimp specimens" group.

### 4.4.3 Principal Component Analysis (PCA) and the latitudinal zones

Principal component analysis (PCA) is a well-known technique which reduces the information of many variables into fewer, orthogonal dimensions. PCA finds a set of standardized linear combinations (SLCs), called the principal components, which are orthogonal and taken together can explain all the variance of the original data. The first principal component explains the largest variance among all SLCs of x. Similarly, the second principal component explains the largest variance among all SLCs of x uncorrelated with the first principal component, and so on. In general, there are as many principal components as variables. However, because of the way they are calculated, it is usually possible to consider only a few of the principal components, which together explain "most" of the original variation. An important aspect of PCA, as opposed to discriminant analysis, is that it does not use any information on group membership and, thus, only accounts for the variation observed in the data (Venables and Ripley, 1997).

We used PCA to analyse the 7 latitudinal zones (figure 4.26) according to the franciscana diet. The variables were standardised to their means prior to conducting the PCA. The variables entered were: (a) "prey numbers" (numerical abundance of prey species ingested in the area/total number of franciscanas analysed in the area)(n= 39 prey species), and (b) "prey occurrence" (number of franciscanas in which a prey taxon occurred/total number of franciscanas analysed in the area)(n= 39 prey species). Furthermore, the means of (c) "estimated prey lengths" and "estimated prey mass" of the prey species for each zone were also investigated within PCA. The last two data are physical measurements, so the strategy was to work on a log scale (as in section 4.3.4). The prey species (n= 31) used for the analysis are listed in the tables 4.2 and 4.3. The covariance estimation function was chosen to perform the principal components analysis, when the original observations were on a equal measure, as in the case of prey numbers and prey occurrence, and were unscaled data. The correlation estimation function was used for the prey lengths and mass because they are observations of different types, and also because they are scaled data.

The percent of variance in each data set explained by each principal component (PC) is reported (*e.g.* PC1 (89%)). Furthermore, the principal component loadings were calculated. The principal component loadings are the coefficients of the principal components transformation. They provide a convenient summary of the influence of the original variables on the principal components, and thus a useful basis for interpretation. A graphic plotted of the loadings allows one to see at a glance which variables are best explained by each component (*S-PLUS 6 for Windows Guide to Statistics, Volume 2,* Insightful Corporation, Seattle, WA).

To finish this section analyses, another graphical representation of the loadings was explored. The biplot (Gabriel, 1971) is a method to represent both the cases and variables. It allows representation of both the original variables and the transformed observations on the major principal components axes. By showing the transformed observations, one can easily interpret the original data in terms of the principal components. By showing the original variables, one can view graphically the relationships between those variables and the principal components (PC1 and PC2). In short, the biplot gives a comprehensive view of both the principal components and the original data.

## 4.5 Results II

### 4.5.1 Linear and Generalized Linear Models and the latitudinal zones

With the data subdivided into 7 zones, GLM revealed significant differences for the fish species *Cynoscion guatucupa*, *Stellifer rastrifer*, *Anchoa marinii*, *Merluccius hubbsi*, *Peprilus paru*, and the cephalopod *Loligo sanpaulensis* (table 4.8 and figure 4.27). However, the fishes *Merluccius hubbsi* and *Peprilus paru* are not highly frequent in numbers in the franciscana diet as the other prey species (figure 4.27).

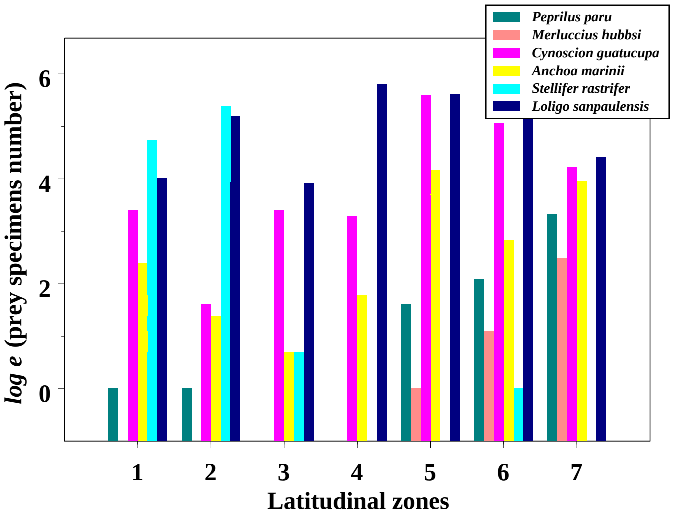


Figure 4.27: The prey species which differed significantly in numbers through the latitudinal zones.

Figure 4.27 shows the total number of prey consumed using bar plots (natural log scale), which is practical for comparisons between the zones, and also minimizes the number of figures plotted if using the partial residuals of GLM for each prey species. Comparing such results with the previous analysis of northern and southern areas, the same prey species generally show significant differences (tables 4.7 and 4.8), although 4 species and the total shrimp specimens lost their significance comparing the latitudinal zones. From the GLM, the significant species *Cynoscion guatucupa*, *Stellifer rastrifer*, *Loligo sanpaulensis*, and *Anchoa marinii* are important prey in the diet of franciscana through the study area (see tables A.1 and A.2). Additionally, the temporal variation within the latitudinal zones was investigated, and the significant differences of prey numbers and occurrences are shown in the table 4.9.

| | **Generalised Linear Model Formula (family= Poisson, link =log)** | **df** | **res.df** | ***p*** | **Means (log)** | | | | | | | **Estimated effects** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Latitudinal zones = explanatory** | | | | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **1** | **2** | **3** | **4** | **5** | **6** | **7** |
| 1 | *Anchoa marinii* | 6 | 259 | <0.001 | 0.5 | 0.1 | 0.1 | 0.3 | 0.7 | 0.3 | 1.1 | 0.0 | -0.3 | -0.3 | -0.1 | 0.3 | -0.1 | 0.7 |
| 2 | *Cynoscion guatucupa* | 6 | 259 | 0.008 | 0.6 | 0.3 | 0.4 | 0.8 | 1.9 | 1.4 | 1.2 | -0.5 | -0.8 | -0.7 | -0.3 | 0.8 | 0.3 | 0.1 |
| 3 | *Merluccius hubbsi* | 6 | 259 | <0.001 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 |
| 4 | *Peprilus paru* | 6 | 259 | 0.006 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 | 0.2 | 0.0 | -0.1 | -0.1 | -0.1 | 0.0 | 0.0 | 0.1 |
| 5 | *Stellifer rastrifer* | 6 | 259 | <0.001 | 1.6 | 0.5 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 1.3 | 0.2 | 0.0 | -0.3 | -0.3 | -0.3 | -0.3 |
| 6 | *Loligo sanpaulensis* | 6 | 259 | <0.001 | 1.6 | 1.7 | 1.7 | 3.6 | 2.9 | 1.9 | 1.7 | -0.5 | -0.4 | -0.4 | 1.5 | 0.8 | -0.2 | -0.4 |

Table 4.8: GLM and the analysis of deviance of franciscana prey species according to the zones.

The latitudinal zones 3, 4, and 7 have fewer prey species differing significantly between the seasons (table 4.9 and figure 4.28), also have the lower numbers of franciscana sampled (26, 12, and 18, respectively). The highest numbers of significant values are from the zones with the larger samples, the zones 6 (N= 72) and 5 (N= 52). Thus it is not reliable to compare these numbers between the areas because the number of prey species identified vary because of the sample size. However, within the areas, it seems that some prey species are considerably influenced by the seasons (figure 4.28).

| | **Generalised Linear Model Formula** | **df** | **res.df** | ***p*** | **Means (log)** | | | | **Estimated effects** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Seasonality of zone 1 = explanatory** | | | | **Sum** | **Aut** | **Win** | **Spr** | **Sum** | **Aut** | **Win** | **Spr** |
| 1 | *Anchoa marinii* | 3 | 26 | 0.024 | 0.0 | 0.7 | 0.9 | 0.2 | -0.5 | 0.2 | 0.4 | -0.3 |
| 2 | *Cynoscion jamaicensis* | 3 | 26 | 0.033 | 0.3 | 0.3 | 0.0 | 0.7 | 0.0 | 0.1 | -0.3 | 0.4 |
| 3 | *Micropogonias furnieri* | 3 | 26 | <0.001 | 0.1 | 0.9 | 0.1 | 0.0 | 0.0 | 0.8 | -0.1 | -0.1 |
| 4 | *Paralonchurus brasiliensis* | 3 | 26 | 0.001 | 0.1 | 0.3 | 1.1 | 0.2 | -0.5 | -0.2 | 0.6 | -0.4 |
| 5 | *Stellifer rastrifer* | 3 | 26 | 0.016 | 0.9 | 1.7 | 2.4 | 1.0 | -0.7 | 0.1 | 0.8 | -0.7 |
| 6 | *Trichiurus lepturus* | 3 | 26 | 0.021 | 1.3 | 1.4 | 0.3 | 1.3 | 0.4 | 0.6 | -0.6 | 0.5 |
| 7 | Total fish specimens | 3 | 26 | 0.035 | 2.1 | 3.0 | 3.7 | 2.7 | -0.1 | 0.0 | 0.7 | -0.3 |
| 8 | *Loligo plei* | 3 | 26 | <0.001 | 0.6 | 1.1 | 0.0 | 0.0 | 0.4 | 0.9 | -0.2 | -0.2 |
| 9 | *Argonauta nodosa* | 3 | 26 | 0.009 | 0.5 | 0.0 | 0.0 | 0.0 | 0.4 | -0.1 | -0.1 | -0.1 |
| | **Seasonality of zone 2 = explanatory** | | | | | | | | | | | |
| 10 | *Cynoscion jamaicensis* | 3 | 30 | 0.009 | 1.0 | 0.0 | 0.0 | 0.0 | 0.6 | -0.3 | -0.3 | -0.3 |
| 11 | *Trichiurus lepturus* | 3 | 30 | 0.009 | 1.1 | 0.0 | 0.0 | 0.7 | 0.4 | -0.7 | -0.7 | 0.0 |
| 12 | *Umbrina canosai* | 3 | 30 | 0.004 | 0.8 | 0.0 | 0.0 | 0.0 | 0.5 | -0.3 | -0.3 | -0.3 |
| 13 | *Argonauta nodosa* | 3 | 30 | 0.037 | 0.2 | 1.4 | 0.0 | 0.1 | 0.1 | 1.2 | -0.2 | -0.1 |
| | **Seasonality of zone 3 = explanatory** | | | | | | | | | | | |
| 14 | *Porichthys porosissimus* | 3 | 22 | 0.001 | 1.0 | 0.0 | 0.0 | 0.2 | 0.8 | -0.3 | -0.3 | -0.1 |
| 15 | *Trichiurus lepturus* | 3 | 22 | 0.002 | 1.7 | 0.0 | 0.2 | 0.9 | 0.8 | -0.8 | -0.6 | 0.1 |
| | **Seasonality of zone 4 = explanatory** | | | | | | | | | | | |
| 16 | *Anchoa marinii* | 3 | 9 | 0.002 | 0.0 | - | 2.0 | 0.2 | -0.3 | - | 1.7 | -0.1 |
| 17 | *Cynoscion guatucupa* | 3 | 9 | 0.007 | 0.0 | - | 3.3 | 0.7 | -0.8 | - | 2.5 | -0.1 |
| 18 | *Argonauta nodosa* | 3 | 9 | <0.001 | 2.7 | - | 0.0 | 0.1 | 2.2 | - | -0.5 | -0.4 |
| | **Seasonality of zone 5 = explanatory** | | | | | | | | | | | |
| 19 | *Anchoa marinii* | 3 | 48 | 0.002 | 0.0 | 0.2 | 1.4 | 0.2 | -0.7 | -0.5 | 0.6 | -0.6 |
| 20 | *Cynoscion guatucupa* | 3 | 48 | 0.047 | 1.5 | 1.6 | 2.5 | 1.0 | -0.4 | -0.2 | 0.6 | -0.8 |
| 21 | *Peprilus paru* ~ season | 3 | 48 | 0.030 | 0.0 | 0.4 | 0.0 | 0.1 | -0.1 | 0.3 | -0.1 | -0.1 |
| 22 | *Porichthys porosissimus* | 3 | 48 | <0.001 | 0.7 | 1.5 | 0.1 | 0.1 | 0.3 | 1.2 | -0.3 | -0.3 |
| 23 | *Trichiurus lepturus* | 3 | 48 | 0.002 | 0.2 | 0.7 | 0.1 | 0.4 | -0.1 | 0.5 | -0.2 | -0.1 |
| 24 | *Umbrina canosai* | 3 | 48 | <0.001 | 1.3 | 0.4 | 0.1 | 0.1 | 1.1 | 0.2 | -0.1 | -0.1 |
| 25 | Total fish specimens | 3 | 48 | 0.016 | 2.4 | 2.9 | 3.4 | 2.0 | -0.4 | 0.1 | 0.5 | -0.1 |
| 26 | *Loligo plei* | 3 | 48 | <0.001 | 0.4 | 0.3 | 0.0 | 0.0 | 0.3 | 0.2 | -0.1 | -0.1 |
| 27 | *Argonauta nodosa* | 3 | 48 | 0.008 | 0.0 | 0.2 | 0.0 | 0.0 | -0.1 | 0.2 | 0.0 | -0.1 |
| | **Seasonality of zone 6 = explanatory** | | | | | | | | | | | |
| 28 | *Anchoa marinii* | 3 | 68 | 0.013 | 0.1 | 0.1 | 0.6 | 0.3 | -0.2 | -0.2 | 0.3 | -0.1 |
| 29 | *Cynoscion guatucupa* | 3 | 68 | <0.001 | 0.4 | 0.7 | 2.6 | 1.2 | -1.0 | -0.7 | 1.2 | -0.2 |
| 30 | *Engraulis anchoita* | 3 | 68 | 0.008 | 0.0 | 0.0 | 0.3 | 0.0 | -0.1 | -0.1 | 0.2 | -0.1 |
| 31 | *Paralonchurus brasiliensis* | 3 | 68 | 0.002 | 0.3 | 0.1 | 0.8 | 1.1 | -0.2 | -0.4 | 0.2 | 0.6 |
| 32 | *Peprilus paru* | 3 | 68 | 0.045 | 0.1 | 0.2 | 0.0 | 0.0 | 0.1 | 0.1 | -0.1 | -0.1 |
| 33 | *Trichiurus lepturus* | 3 | 68 | <0.001 | 0.8 | 0.9 | 0.1 | 0.7 | 0.3 | 0.4 | -0.5 | 0.1 |
| 34 | *Umbrina canosai* | 3 | 68 | 0.002 | 0.3 | 0.2 | 0.0 | 0.4 | 0.1 | 0.0 | -0.1 | 0.2 |
| 35 | Total fish specimens | 3 | 68 | <0.001 | 2.0 | 2.2 | 3.2 | 2.9 | -0.6 | -0.4 | 0.6 | 0.3 |
| 36 | *Loligo sanpaulensis* | 3 | 68 | 0.015 | 1.5 | 1.4 | 2.1 | 3.1 | -0.4 | -0.5 | 0.2 | 1.2 |
| 37 | *Argonauta nodosa* | 3 | 68 | 0.021 | 0.2 | 0.4 | 0.1 | 0.0 | 0.0 | 0.2 | -0.1 | -0.2 |
| 38 | order Isopoda | 3 | 68 | <0.001 | 0.0 | 0.1 | 0.0 | 0.2 | -0.1 | 0.0 | -0.1 | 0.2 |
| 39 | Total shrimp specimens | 3 | 68 | 0.004 | 0.2 | 0.2 | 0.0 | 0.5 | 0.0 | 0.0 | -0.1 | 0.3 |
| | **Seasonality of zone 7 = explanatory** | | | | | | | | | | | |
| 40 | *Merluccius hubbsi* | 3 | 16 | 0.024 | 0.0 | 0.1 | 1.0 | - | -0.3 | -0.2 | 0.8 | - |
| 41 | *Paralonchurus brasiliensis* | 3 | 16 | 0.038 | 0.0 | 0.1 | 0.6 | - | -0.2 | -0.1 | 0.4 | - |
| 42 | *Peprilus paru* | 3 | 16 | <0.001 | 1.7 | 0.0 | 0.0 | - | 1.5 | -0.2 | -0.2 | - |
| 43 | *Loligo sanpaulensis* | 3 | 16 | 0.006 | 3.4 | 1.2 | 2.5 | - | 1.7 | -0.5 | 0.8 | - |

Table 4.9: GLM (family poisson, log link) and the analysis of deviance of franciscana prey species according to the seasons, for the 7 latitudinal zones.

Figure 4.28 illustrates the prey species variation between the seasons for each latitudinal zone. The prey *Trichiurus lepturus*, *Anchoa marinii*, and *Argonauta nodosa*, are the species that frequently differ seasonally for the latitudinal zones, as in the previous analysis (table 4.7).

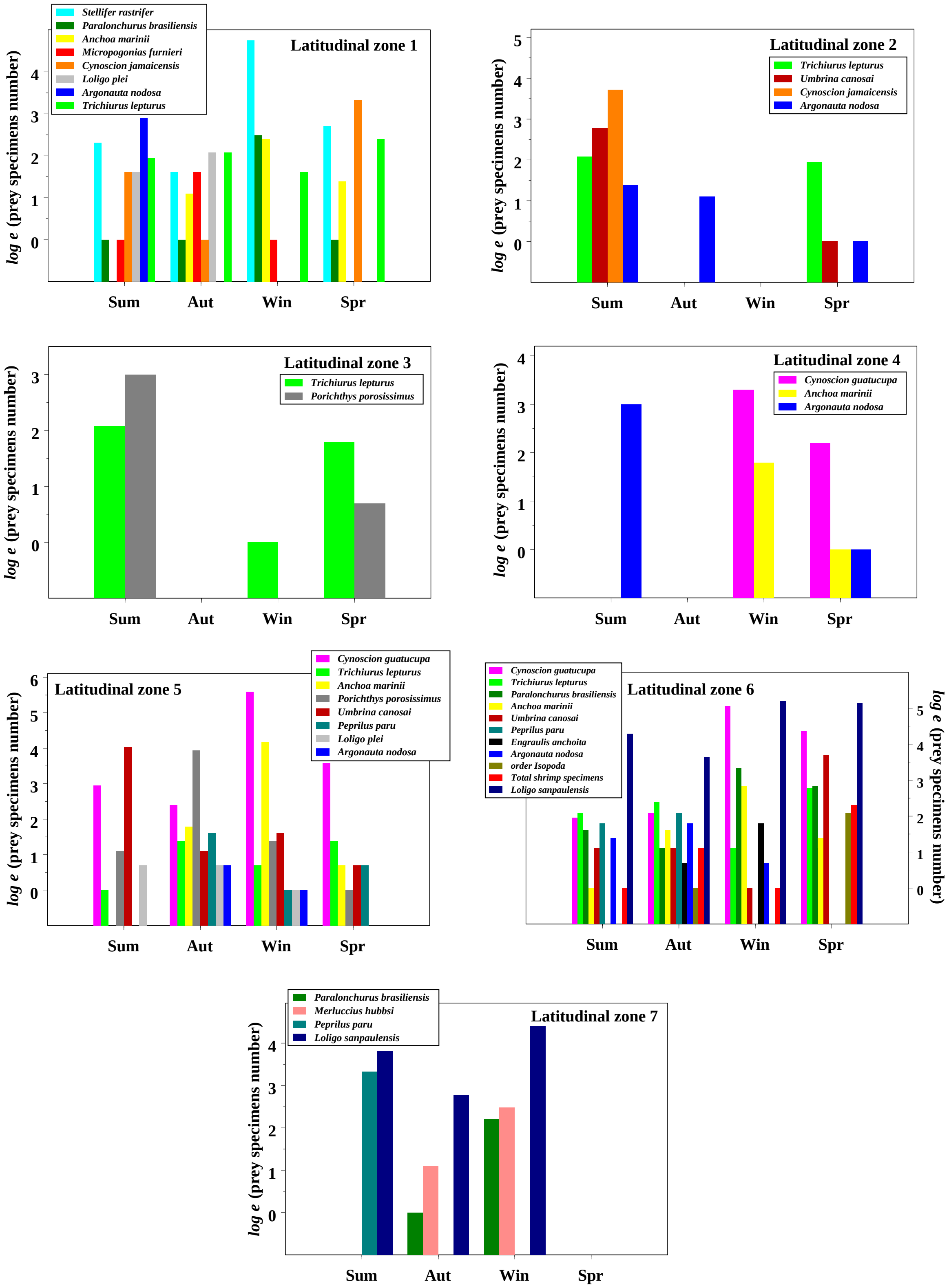


Figure 4.28: Prey species numbers variability through the seasons for the latitudinal zones.

Beyond that, other prey species also fluctuate according to seasons for at least 3 latitudinal zones (*e.g. Cynoscion guatucupa*, *Paralonchurus brasiliensis*, and *Umbrina canosai*). Clearly, the main species of the northern area, the *Stellifer rastrifer*, is also very important during wintertime in the latitudinal zone 1, as is the main species of the southern area, the *Cynoscion guatucupa*, for the zones 4, 5 and 6.

From the graphs it is apparent that some prey species prefer specific seasons. This is the case for *Trichiurus lepturus*, *Umbrina canosai*, *Cynoscion jamaicensis*, *Loligo plei*, and *Argonauta nodosa*, which prefer warmer seasons; while *Cynoscion guatucupa*, *Anchoa marinii*, and *Paralonchurus brasiliensis*, were frequent during colder seasons. *Loligo sanpaulensis* were again more frequent in winter and spring.

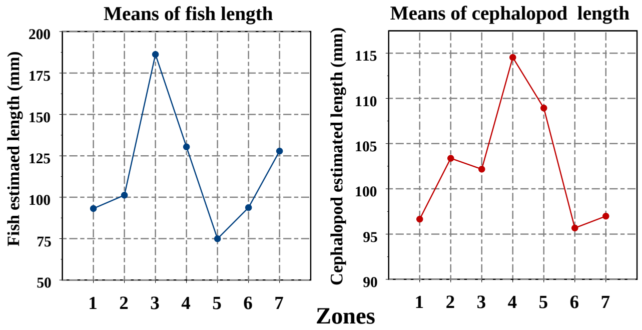


Figure 4.29: Means of fish and cephalopod estimated lengths (mm) plotted for each latitudinal zone.

For fish and cephalopod specimens lengths (mm) and weights (g), there are also significant differences between the latitudinal zones (table 4.10). However, these differences are not related simply to the variation of latitude.

Large fish specimens may be found in all zones (see the outliers of figure 4.30), although the length average is higher for the zones 3 and 4 (figure 4.29). Likewise the cephalopod specimens (4.30), with the larger length mean are found in the latitudinal zones 4 and 5 (see figure 4.29). This shows that the size of prey exhibits a complex variation through the study area. Fish and cephalopod body mass are not illustrated since the figures for fish and cephalopod lengths present the same information.

A graphical presentation of prey estimated lengths contrasting the seasons for each latitudinal zone (see also table 4.11) are showed in the figures 4.31 and 4.32 (the plots of prey body mass are not shown since the prey lengths graphics present essentially the same information).

The variability of fish lengths is high through the seasons (figure 4.31). However, this may happen because different fish species occur in different seasons (figure 4.28), and the sizes among the species vary (see table 4.5). In general, the wintertime shows smaller mean lengths for fish specimens, whereas summer had the larger fish mean sizes for 4 latitudinal zones.

|  | **Linear Model Formula** | **df** | **res.df** | **F** | ***p*** | **Means (log)** |  |  |  |  |  |  | **Estimated effects** |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | **Latitudinal zones = explanatory** |  |  |  |  | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **1** | **2** | **3** | **4** | **5** | **6** | **7** |
| 1 | log (Fish estimated length) | 6 | 4142 | 22.4 | <0.001 | 4.3 | 4.1 | 4.7 | 4.6 | 4.1 | 4.2 | 4.3 | 0.1 | -0.1 | 0.5 | 0.4 | -0.1 | 0.0 | -0.1 |
| 2 | log (Fish estimated mass) | 6 | 4142 | 22.1 | <0.001 | 1.4 | 1.2 | 2.2 | 2.0 | 1.2 | 1.3 | 1.5 | 0.0 | -0.1 | 0.8 | 0.7 | -0.2 | 0.0 | 0.2 |
| 3 | log (Cephalopod estimated length) | 6 | 5858 | 41.1 | <0.001 | 4.4 | 4.5 | 4.5 | 4.7 | 4.6 | 4.5 | 4.5 | -0.2 | 0.0 | 0.0 | 0.1 | 0.1 | -0.1 | 0.0 |
| 4 | log (Cephalopod estimated mass) | 6 | 5858 | 48.1 | <0.001 | 3.0 | 3.4 | 3.4 | 3.8 | 3.6 | 3.2 | 3.4 | -0.5 | -0.1 | -0.1 | 0.3 | 0.1 | -0.3 | -0.1 |

Table 4.10: Linear Models associations according to the latitudinal zones and the franciscana prey estimated lengths (mm) and mass (g).

|  | **Linear Model Formula** | **df** | **res.df** | **F** | ***p*** | **Means (log)** |  |  |  | **Estimated effects** |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | **Seasonality of zone 1 = explanatory** |  |  |  |  | **Sum** | **Aut** | **Win** | **Spr** | **Sum** | **Aut** | **Win** | **Spr** |
| 1 | log (Fish estimated length) | 3 | 766 | 19.7 | <0.001 | 4.7 | 4.8 | 4.2 | 4.3 | 0.5 | 0.6 | -0.1 | 0.0 |
| 2 | log (Fish estimated mass) | 3 | 766 | 13.3 | <0.001 | 2.0 | 2.2 | 1.3 | 1.2 | 0.6 | 0.8 | -0.1 | -0.2 |
| 3 | log (Cephalopod estimated length) | 3 | 298 | 0.6 | 0.612 | 4.4 | 4.6 | 4.4 | 4.4 | 0.0 | 0.2 | 0.0 | 0.0 |
| 4 | log (Cephalopod estimated mass) | 3 | 298 | 0.2 | 0.883 | 3.0 | 3.3 | 3.0 | 3.0 | 0.0 | 0.3 | 0.0 | 0.0 |
|  | **Seasonality of zone 2 = explanatory** |  |  |  |  |  |  |  |  |  |  |  |  |
| 5 | log (Fish estimated length) | 3 | 544 | 59.1 | <0.001 | 3.8 | - | 4.6 | 4.7 | -0.3 | - | 0.5 | 0.6 |
| 6 | log (Fish estimated mass) | 3 | 544 | 56.7 | <0.001 | 0.8 | - | 2.2 | 2.1 | -0.4 | - | 0.9 | 0.9 |
| 7 | log (Cephalopod estimated length) | 3 | 532 | 8.4 | <0.001 | 4.6 | 3.8 | 4.5 | 4.5 | 0.1 | -0.8 | 0.0 | 0.0 |
| 8 | log (Cephalopod estimated mass) | 3 | 532 | 7.5 | <0.001 | 3.5 | 1.9 | 3.3 | 3.3 | 0.1 | -1.5 | -0.2 | -0.1 |
|  | **Seasonality of zone 3 = explanatory** |  |  |  |  |  |  |  |  |  |  |  |  |
| 9 | log (Fish estimated length) | 3 | 188 | 5.8 | <0.001 | 5.2 | 4.4 | 5.1 | 4.5 | 0.5 | -0.3 | 0.5 | -0.2 |
| 10 | log (Fish estimated mass) | 3 | 188 | 8.7 | <0.001 | 2.6 | 1.7 | 3.6 | 1.9 | 0.4 | -0.5 | 1.4 | -0.3 |
| 11 | log (Cephalopod estimated length) | 3 | 245 | 7.9 | <0.001 | 4.4 | 3.5 | 4.5 | 4.6 | -0.2 | -1.0 | -0.1 | 0.1 |
| 12 | log (Cephalopod estimated mass) | 3 | 245 | 7.8 | <0.001 | 3.1 | 1.0 | 3.2 | 3.6 | -0.3 | -2.5 | -0.2 | 0.2 |
|  | **Seasonality of zone 4 = explanatory** |  |  |  |  |  |  |  |  |  |  |  |  |
| 13 | log (Fish estimated length) | 3 | 63 | 31.3 | <0.001 | 6.1 | - | 4.0 | 4.7 | 1.5 | - | -0.6 | 0.2 |
| 14 | log (Fish estimated mass) | 3 | 63 | 32.6 | <0.001 | 4.3 | - | 0.7 | 2.5 | 2.3 | - | -1.4 | 0.5 |
| 15 | log (Cephalopod estimated length) | 2 | 1249 | 59.5 | <0.001 | 3.7 | - | 4.4 | 4.7 | -1.0 | - | -0.3 | 0.1 |
| 16 | log (Cephalopod estimated mass) | 2 | 1249 | 86.1 | <0.001 | 1.8 | - | 3.0 | 3.9 | -2.0 | - | -1.0 | 0.1 |
|  | **Seasonality of zone 5 = explanatory** |  |  |  |  |  |  |  |  |  |  |  |  |
| 17 | log (Fish estimated length) | 3 | 1131 | 29.4 | <0.001 | 4.2 | 4.3 | 4.0 | 4.5 | 0.1 | 0.2 | -0.1 | 0.4 |
| 18 | log (Fish estimated mass) | 3 | 1131 | 24.8 | <0.001 | 1.6 | 1.5 | 1.0 | 1.8 | 0.4 | 0.3 | -0.2 | 0.6 |
| 19 | log (Cephalopod estimated length) | 3 | 1916 | 6.8 | <0.001 | 4.6 | 4.5 | 4.6 | 4.7 | 0.0 | -0.1 | 0.0 | 0.0 |
| 20 | log (Cephalopod estimated mass) | 3 | 1916 | 5.9 | <0.001 | 3.6 | 3.4 | 3.6 | 3.7 | 0.0 | -0.2 | 0.0 | 0.1 |
|  | **Seasonality of zone 6 = explanatory** |  |  |  |  |  |  |  |  |  |  |  |  |
| 21 | log (Fish estimated length) | 3 | 1180 | 56.8 | <0.001 | 4.6 | 4.8 | 4.1 | 4.0 | 0.4 | 0.6 | -0.1 | -0.2 |
| 22 | log (Fish estimated mass) | 3 | 1180 | 40.2 | <0.001 | 2.3 | 2.0 | 1.2 | 1.1 | 0.9 | 0.7 | -0.1 | -0.4 |
| 23 | log (Cephalopod estimated length) | 3 | 1362 | 81.4 | <0.001 | 4.6 | 4.1 | 4.4 | 4.7 | 0.1 | -0.3 | -0.1 | 0.2 |
| 24 | log (Cephalopod estimated mass) | 3 | 1362 | 85.3 | <0.001 | 3.6 | 2.5 | 3.0 | 3.7 | 0.4 | -0.7 | -0.2 | 0.4 |
|  | **Seasonality of zone 7 = explanatory** |  |  |  |  |  |  |  |  |  |  |  |  |
| 25 | log (Fish estimated length) | 3 | 252 | 16.9 | <0.001 | 4.5 | 4.4 | 3.7 | - | 0.2 | 0.2 | -0.8 | - |
| 26 | log (Fish estimated mass) | 3 | 252 | 4.2 | 0.016 | 2.2 | 1.4 | 1.7 | - | 0.6 | -0.2 | 0.2 | - |
| 27 | log (Cephalopod estimated length) | 2 | 237 | 27.3 | <0.001 | 4.8 | 4.2 | 4.5 | - | 0.3 | -0.3 | 0.0 | - |
| 28 | log (Cephalopod estimated mass) | 2 | 237 | 29.6 | <0.001 | 4.0 | 2.7 | 3.4 | - | 0.6 | -0.7 | 0.0 | - |

Table 4.11: Linear Models and the analysis of variance according to seasons for each latitudinal zone, and the franciscana prey estimated lengths (mm) and mass (g).

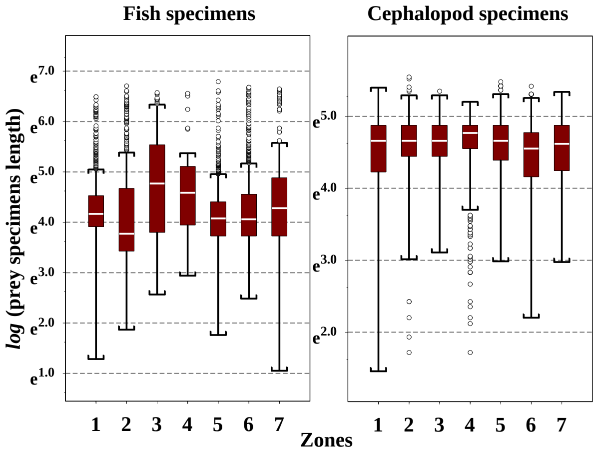


Figure 4.30: Fish and cephalopod estimated lengths (n= 10,635) plotted for the latitudinal zones.

For cephalopods, summer or spring generally exhibit the largest prey, although there were a few variations. In the previous analysis for cephalopods lengths and seasons between the northern and southern areas, either summer or spring also had showed the largest cephalopods.

In the graphics (figures 4.31 and 4.32), the prey length differences shown were significant (contrasting the seasons for all latitudinal zones), except for the cephalopod length of the zone 1 (table 4.11). Cephalopod mass of zone 1 and fish mass of zone 7 didn't vary significantly through seasons. Cephalopod lengths exhibit a better pattern as the variety of cephalopod species is lower than the fish species, and it represents practically one species, the *Loligo sanpaulensis* (see section 4.3.2).

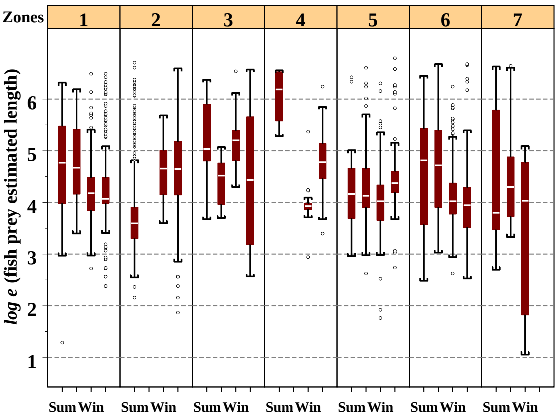


Figure 4.31: Fish estimated lengths (n= 4,443) plotted through the seasons for the seven latitudinal zones.

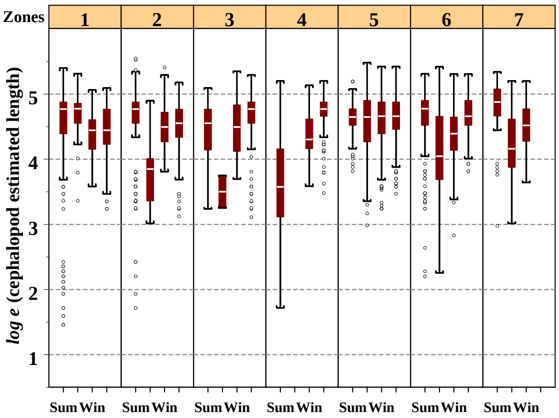


Figure 4.32: Cephalopod estimated mantle lengths (n= 6,192) plotted through the seasons for the seven latitudinal zones.

### 4.5.2 Principal Component Analysis and the latitudinal zones

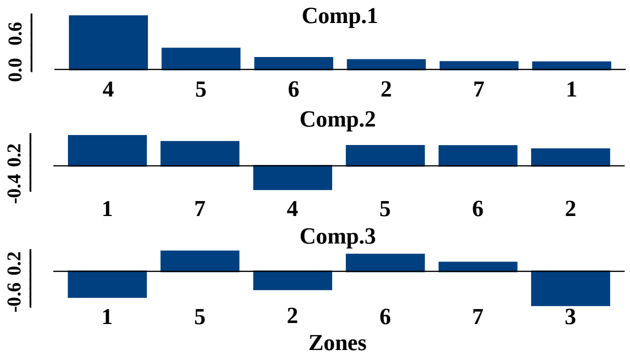
The main use of PCA is to reduce the dimensionality of a data set while retaining as much information as is possible. It computes a compact and optimal description of the data set, and was chosen to analyse the franciscana diet according to its geographic variation in the study area, because previous analyses using LM and GLM had shown spatial differences in the diet regime of franciscana. Hence the main purpose is to find how the prey of franciscana vary in terms of numbers, diversity, and sizes, for the latitudinal zones.

For the numerical mean abundance of prey species, the first principal component explains 87.6% of the variance, and the first two principal components together explain 98.6% of the variance (table 4.12).

| | Comp.1 | Comp.2 | Comp.3 | Comp.4 | Comp.5 | Comp.6 | Comp.7 |
|---|---|---|---|---|---|---|---|
| Standard deviation | 5.285 | 8.969 | 2.846 | 1.152 | 0.624 | 0.306 | 0.206 |
| Proportion of Variance | 0.876 | 0.110 | 0.011 | 0.001 | 0.001 | 0.0001 | 0.00005 |
| Cumulative Proportion | 0.876 | 0.986 | 0.997 | 0.999 | 0.999 | 0.999 | 1.000 |

Table 4.12: Principal component values for the numerical mean abundance of prey species and the latitudinal zones.

The loadings of the numerical mean abundance of prey species are shown in the figure 4.33. Loadings suppresses small values to emphasise the more important ones. Eigenvector 1 is positively correlated with all zones, while the eigenvector 2 is negatively associated with the latitudinal zone 4. Eigenvector 3 is a north/south zones contrast, and now the zone 4 has the smallest value. The loadings plot helps to visualise those values (figure 4.33).



| Zones | Comp.1 | Comp.2 | Comp.3 |
|---|---|---|---|
| 1 | 0.119 | 0.534 | -0.608 |
| 2 | 0.156 | 0.295 | -0.425 |
| 3 | | 0.150 | -0.835 |
| 4 | 0.884 | -0.415 | -0.140 |
| 5 | 0.346 | 0.355 | 0.474 |
| 6 | 0.191 | 0.353 | 0.399 |
| 7 | 0.124 | 0.427 | 0.211 |

Figure 4.33: Principal component loadings for the numerical mean abundance of prey species and the latitudinal zones (n= 39 prey species).

The loadings for the first principal component, which represents essentially an average of prey numbers consumed by franciscana for the latitudinal zones, are all of the same sign although the zone 4 has a larger size and zone 3 lower (figure 4.33). The second component contrasts the zone 4 against the northern (1, 2) and southern (5, 6, 7) zones, where the first (1) and last (7) zones weighted most heavily. The third component basically contrast the northern zones (1, 2, 3) against the southern zones (5, 6, 7), according to the number of prey ingested by franciscana.

The next plot represents both the original variables and the transformed observations on the principal components axes (figure 4.34). It is also a loading representation. The zone 4 has the largest loadings in absolute value for the first component, and the loading on the second component has a negative sign. Thus the zone 4 is represented by a longish, downward sloping arrow (figure 4.34). This zone appears distinctly from the others in relation to the number of prey consumed by franciscana.

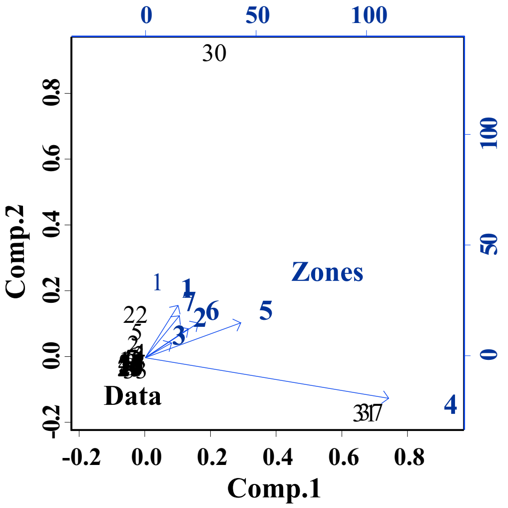
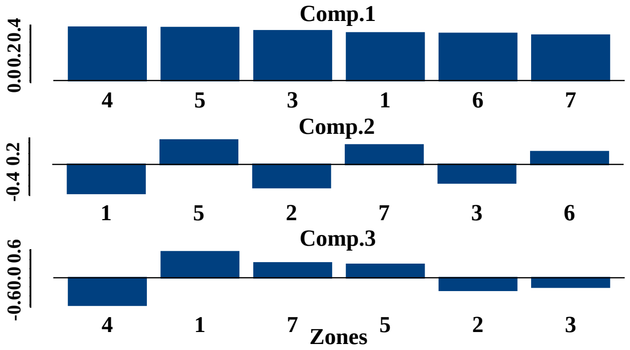


Figure 4.34: Biplot loadings of the numerical abundance of the prey species (n= 39 prey species). The x-axis represents the scores for the first principal component, the y-axis the scores for the second principal component. The original variables are represented by arrows which graphically indicate the proportion of the original variance explained by the first two principal components. The direction of the arrows indicates the relative loadings on the first and second principal components. The zones are in blue and the data of each prey species in black.

The PCA of the prey diversity (species mean occurrence) shows the first principal component explaining 90.1% of the variance, with the first two principal components together explaining 95.7% of the variance (table 4.13).

| | Comp.1 | Comp.2 | Comp.3 | Comp.4 | Comp.5 | Comp.6 | Comp.7 |
|---|---|---|---|---|---|---|---|
| Standard deviation | 64.299 | 16.083 | 10.339 | 7.117 | 4.549 | 3.872 | 1.840 |
| Proportion of Variance | 0.900 | 0.056 | 0.023 | 0.011 | 0.004 | 0.003 | 0.001 |
| Cumulative Proportion | 0.901 | 0.957 | 0.980 | 0.991 | 0.995 | 0.999 | 1.000 |

Table 4.13: Principal component values for the numerical mean occurrence of prey species and the latitudinal zones.



| Zones | Comp.1 | Comp.2 | Comp.3 |
|---|---|---|---|
| 1 | 0.371 | -0.535 | 0.571 |
| 2 | 0.332 | -0.427 | -0.274 |
| 3 | 0.388 | -0.341 | -0.204 |
| 4 | 0.416 | 0.185 | -0.601 |
| 5 | 0.412 | 0.449 | 0.292 |
| 6 | 0.367 | 0.232 | |
| 7 | 0.353 | 0.356 | 0.325 |

Figure 4.35: Principal component loadings for the numerical mean occurrence of prey species and the latitudinal zones (n= 39 prey species).

The first component loadings again represents an average of the prey species occurrence for all zones (figure 4.35). The second component contrast again the northern zones (1, 2, 3) against the southern zones (5, 6, 7); and the central latitudinal zone 4 has the smallest PC loading. Thus in terms of prey diversity in the franciscana feeding, there are clear geographic differences.

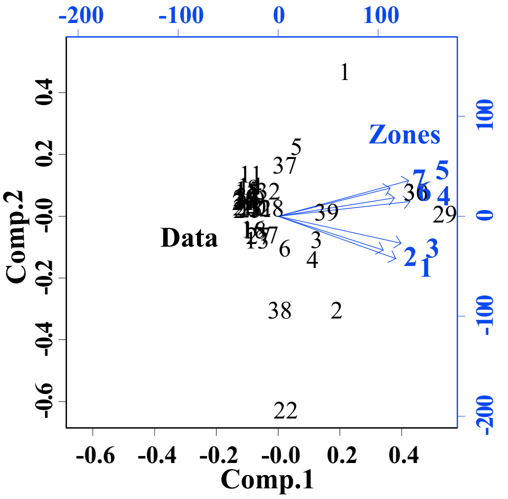


Figure 4.36: Biplot loadings of the prey species occurrence (n= 39 prey species).

The biplot (figure 4.36) represents the latitudinal zones 1, 2, and 3 a group with similar loadings signs, and the zones 4, 5, 6, and 7 a different group from them. This provide further support for the broad division into northern and southern areas discussed previously.

The previous PCA, means of prey species number and occurrence, had pointed some peculiar differences of the zones in the middle region from the most southern and northern zones. Hence, we re-analysed the data grouping the central zones 3 and 4, the most southern 5 to 7, and the most northern 1 and 2. The figure 4.37 confirmed such differences between the zones.

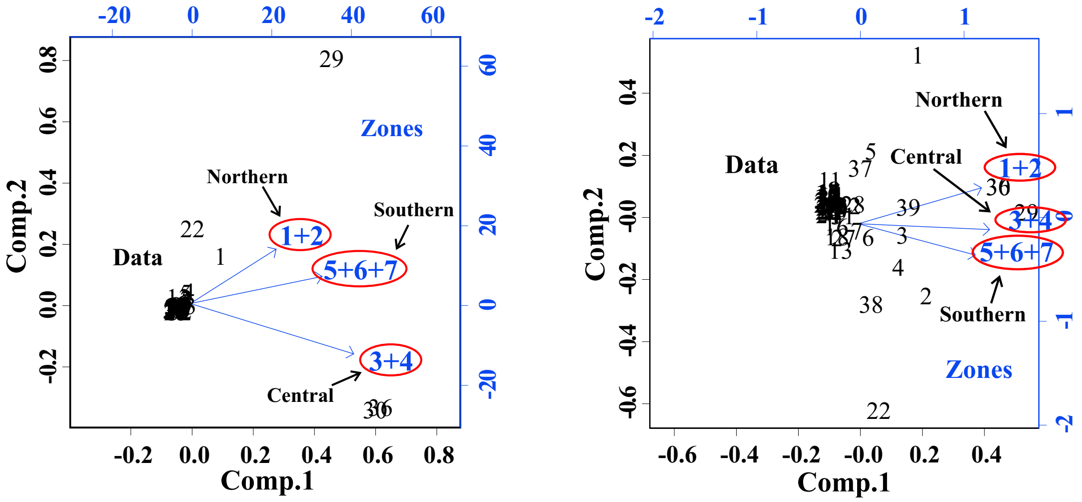


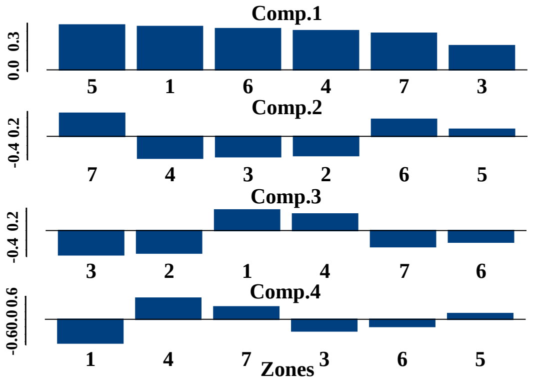
Figure 4.37: Biplot loadings of the numerical abundance (left), and occurrence (right) of prey species, grouping the zones into 3 main groups: 1+2 (Northern), 3+4 (Central), and 5+6+7 (Southern).

The PCs of the prey specimens mean measurement (estimated lengths and mass of fish and cephalopods), are presented in table 4.14, with the first four principal components together explaining more than 90.0% of the variance.

For the first component the average with lower weights are from the zones 2 and 3 (figure 4.38). The second component contrasts the neighborhood zones 2, 3, and 4, against the southern zones 5, 6, and 7. The third component groups the zones 2 and 3 with the same sign and weight, followed by 6 and 7 latitudinal zones. Neighboring zones are likely to have prey specimens with similar sizes.

| | Comp.1 | Comp.2 | Comp.3 | Comp.4 | Comp.5 | Comp.6 | Comp.7 |
|---|---|---|---|---|---|---|---|
| Standard deviation | 3.828 | 1.986 | 1.498 | 1.021 | 0.894 | 0.871 | 0.679 |
| Proportion of Variance | 0.612 | 0.165 | 0.093 | 0.043 | 0.033 | 0.031 | 0.019 |
| Cumulative Proportion | 0.613 | 0.778 | 0.872 | 0.916 | 0.949 | 0.981 | 1.000 |

Table 4.14: Principal component values for the numerical mean measurement of prey species and the latitudinal zones.



| Zones | Comp.1 | Comp.2 | Comp.3 | Comp.4 |
|---|---|---|---|---|
| 1 | 0.448 | | 0.428 | -0.636 |
| 2 | 0.180 | -0.416 | -0.468 | 0.103 |
| 3 | 0.250 | -0.440 | -0.505 | -0.311 |
| 4 | 0.405 | -0.472 | 0.342 | 0.565 |
| 5 | 0.465 | 0.151 | 0.235 | 0.151 |
| 6 | 0.425 | 0.365 | -0.241 | -0.190 |
| 7 | 0.379 | 0.497 | -0.335 | 0.332 |

Figure 4.38: Principal component loadings for the prey species mean measurements and the latitudinal zones (n= 31 prey species).

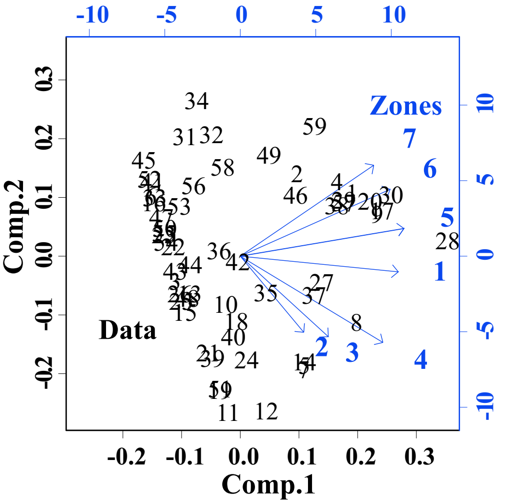


Figure 4.39: Biplot loadings of the prey species mean measurement (n= 31 prey species).

The southern geographic zones (5, 6, 7) and the northern zones (2, 3, 4) look distinct in terms of prey specimens lengths and weights (see figure 4.39), whereas zone 1 seems to be diverging from the other zones.

Overall, the PCA results showed basically that the franciscana diet seems geographically distinct mainly between the southern and northern zones. Additionally, closer zones are likely to illustrate similar franciscana diet, whereas geographic distant zones are more likely to point up different food habits of franciscana dolphin.

## 4.6 Discussion

### 4.6.1 General

The general diet composition of franciscana from previous studies is similar to the results presented in this research, and the majority of prey species are bottom-dwelling teleosts (table 4.4) and the squid *Loligo sanpaulensis*. However, this study revealed differences in prey composition for two areas of the southern Brazilian coast, which was not expected, and also revealed a probable prey size selection by franciscana dolphin.

It is still not clear whether the franciscana dolphin is selective according to the prey size. In the same area of this study, Pinedo (1982) concluded that the preference of this dolphin is for fish prey under 50mm in total length (80% of fish consumed). However, these fish were basically all one species, the *Cynoscion guatucupa*. Ott (1994) found an average of 33.4mm for *Cynoscion guatucupa*, which also was the main fish prey of franciscana. In this study, the mean total length for *Cynoscion guatucupa*, the most predated fish of southern area, and *Stellifer rastrifer*, of northern area, were 56.3 and 53.3mm, respectively. The most highly represented length class for the fish species from northern Argentina (GS 9) (Rivero et al., 2000), was from 40 to 60mm, and these were mostly *Cynoscion guatucupa* in the area sampled. The shallow coastal waters of the southern Brazilian shelf and Uruguay represent an important spawning area for many demersal teleosts, with dense schools of recruits (<50mm) (Menezes and Figueiredo, 1980; Haimovici and Vieira, 1986), and *Cynoscion guatucupa* is the most abundant teleost (Haimovici et al., 1996; Haimovici, 1997b). Furthermore, clear evidence for higher predation on more abundant prey was presented by Bassoi and Secchi (1999), with the reduction in occurrence of *Micropogonias furnieri* and *Macrodon ancylodon* in the diet of franciscanas from southern Brazil through a period of 15 years, as a probable consequence of stock depletion for those species.

Nevertheless, all these studies also demonstrated franciscana predation on a variety of other teleost species with mean total length greater than 150mm (table 4.5 and figure 4.10), representing the fish subadult sizes for many of them. An example is *Trichiurus lepturus*, which had a mean length of over 400mm (subadults), and various specimens greater than 700mm, categorized as adult size (Martins, 1992).

Overall, it seems likely that franciscana just eats more of the most available prey in the area, in many cases recruit teleosts (<50mm) (Haimovici et al., 1996), while juveniles and subadults with larger length bodies (>100mm, *e.g. Urophycis brasiliensis*, *Macrodon ancy-*

*lodon*, *Umbrina canosai*) are less common but also important in the diet in terms of biomass (energy) ingested.

At present there is therefore no evidence to reject the hypothesis that feeding is non-selective according to fish specimens size.

On the other hand, franciscana does appear to select larger squids, because the average size of squid preyed on by this dolphin (106.1mm, figure 4.11) was higher than those found during research surveys in this area, especially in summer, where the mantle length average was 58.4mm (Andriguetto Jr. and Haimovici, 1991; Santos, 1999). Clarke (1996) suggests that some cetaceans feed on the larger individuals on the spawning grounds, so the predator takes the protein at its maximum production and concentration.

Therefore, it seems that franciscana feeding behaviour is selective by size of prey, however the dolphin prefers bigger specimens, which differs from Pinedo (1982) studies.

### 4.6.2 The northern and southern areas

In the first part of methods and results it was analysed the franciscana diet between northern and southern areas through IRI, LM, and GLM.

The results from the IRI, a traditional method in many diet studies, provide an essential overview of the distinct importance in number, occurrence, and biomass, of different prey species in the franciscana diet.

Moreover, the feeding was also analysed through IRI in order to compare this data with past feeding studies of franciscana off the southern Brazilian coast, which had used such methodology (see the last section 4.6.4).

GLM analysis confirmed many of the results and tendencies found in the examination of the IRI (numbers and occurrences of prey species), and they are indeed statistically significant. This is important because such models validate the results of traditional methods, and show an appropriate methodology for further analysis where environmental factors will be included (Chapter 6).

Moreover, it was possible to analyse the significant differences of prey lengths and body mass between all groups, as well as spatial and temporal analysis using LM.

The results from the IRI are firstly discussed, and further considerations of GLM and LM results, mainly regardless of specimens size, are following.

- **Northern and Southern areas (IRI)**

The most common Lolignidae squid in southern Brazil is *Loligo sanpaulensis* (Haimovici and Andrigueto Jr., 1986), which occurs in the shelf from 20$^o$S to 42$^o$S, associated with the Subtropical Convergence Zone (Roper et al., 1984; Haimovici and Perez, 1991b; Santos, 1999). In the diet regime of franciscana through its range this squid was an important prey, but the abundance seems to have been greater for southern areas, decreasing in the northern regions of distribution (Perez et al., 1996; Bastida et al., 1992; Brownell, 1975, 1989; Pinedo, 1982; Ott, 1994; Bassoi, 1997; Oliveira et al., 1998; Di Beneditto, 2000). In this study, the diet of franciscana dolphins seem to follow this same pattern, with this prey being more important in the southern area (tables A.1 and A.1).

Overall, the abundant teleost fishes throughout the southern Brazilian coast (Haimovici et al., 1996; Haimovici, 1998; Garcia, 1999) are well represented in the diet of franciscana dolphins from northern and southern areas. Although overlapping areas from southern and northern animals are very likely to occur, since Secchi et al. (2002) suggested that the franciscanas from Uruguay and southern Brazil correspond to a single stock, the diets between those areas of the southern Brazilian coast demonstrate some diverse and peculiar features. This could indicate some differences of franciscana's distribution through the southern Brazilian coast. The main evidence was the absence of *Stellifer rastrifer* in the stomachs of southern animals, while it was the principal prey of northern area franciscanas (tables A.1 and A.1). According to Tropical Data Base Program, sponsored by the Brazilian Government (source: www.bdt.fat.org.br), the southern range limit of this species is around 29$^o$S, which could be associated with warmer waters of the Brazil Current (Menezes and Figueiredo, 1980) (see section 3.1.1). Thus, it could be suggested that the northern limit of the feeding range is not higher than 31$^o$S for specimens from southern area (see figure 2.1).

On the other hand, northern franciscanas also could have southern limits not so far from the central area ($\sim$31$^o$S). An indication of this is a lower consumption of Engraulidae species in this location. The distribution of this fish follows the coastal branch of the Malvinas (Falkland) Current, as it is more abundant in the southern area and less abundant in the limits of the warmer front ($\sim$28$^o$S) of the Brazil Current (Castello et al., 1990; Castello, 1997). This evidence will be discussed later in the "Seasonality" paragraph.

In addition, the franciscana diet in the southern area is very similar to that reported for Uruguay (Brownell and Praderi, 1976; Praderi, 1986; Brownell, 1989) and northern Argentina (Rodriguez et al., 2002). Our results suggest that franciscanas from southern area of the study region and Uruguay are more likely to occupy similar habitat than the animals from northern area, according to feeding regimes. The diets indicate some differences in franciscana distribution, though it is not yet clear that foraging is the cause of such possible distributions. However, the foraging of marine mammals is influenced by different oceanographic factors (Bradshaw et al., 2004; Laidre et al., 2004; Hastie et al., 2005; Jimenez, 2005), and these factors can be used to characterise the foraging behaviour (Forcada, 2002), and possibly the movements and distribution of the predators.

Therefore, the following chapters will analyse the oceanographic process (Chapter 5) in the study area, and its association with the franciscana food habits (Chapter 6), to better understand possible geographical movements, or habitat preferences, of franciscana through the southern Brazilian coast.

- **Northern and Southern areas (LM and GLM)**

For the northern and southern areas, the most important species were clearly significantly different (table 4.7 and figure 4.17), and the species related to warm and cold waters (*e.g. Cynoscion jamaicensis*, *Anchoa marinii*) also differed. As with the IRI values, *Loligo sanpaulensis* was significantly more important for the southern area. It seems that cephalopods play an important role for the animals in the southern area, as the sizes also were significantly higher than the northern coast prey cephalopods.

On the other hand, animals from northern area ingested bigger fishes on average (figure 4.18). The major contributor to the greater fish lengths in the northern area was *Trichiurus lepturus* (see table 4.5). Nevertheless, the estimated mass of fish species did not differ significantly between the areas (row 2 table 4.6), possibly because the animals from southern area consume more fish in terms of numbers comparing with the northern area.

- **Male and Female (IRI)**

The prey species are basically the same regardless of the sex of the dolphins, despite some particular tendencies that were noted in the prey composition of males and females, mainly in the northern area.

Males from the northern area are likely to consume more of species related to warm water masses from the northern Brazilian coast, such as *Stellifer rastrifer* and the cephalopods *Loligo plei* and *Argonauta nodosa* (tables A.3 and A.4). In addition, females from the same location consumed more Engraulidae fishes, which are more abundant in southern areas. Thus, males from northern coast could be occupying a more northern range than females.

Females throughout the study area also eat more shrimp species, in agreement with other franciscana studies (Pinedo, 1982; Ott, 1994; Perez et al., 1996; Bassoi, 1997), possibly related to the parental guidance of juveniles, as these show a high importance of shrimps in the diet (Smith and Read, 1992; Bastida et al., 1992; Danilewicz et al., 2002). Furthermore, females consumed more crabs (*e.g. Loxopagurus loxocheles*, *Dardanus insignis*, Pleocyemata), benthic specimens abundant in shallow waters (Capítoli, 1997). Additionally, in terms of numerical abundance females consumed more fish than males, however small fish specimens (recruits), as well the juveniles of franciscana.

In short, adult females may be distributed closer to the coast than adult males, at least in some periods, as result of juvenile guidance. Prey biomass(g) ingestion by males and females is discussed in the following paragraphs.

- **Male and Female (LM and GLM)**

Females from northern area and males from the southern area had ingested bigger cephalopods (figure 4.19). These observations could suggest a geographic differential use of habitat by those animals in different areas of the coast, as bigger cephalopods are concentrated in deeper coastal waters (Haimovici and Perez, 1991a; Santos, 1999).

Danilewicz et al. (2004) compared the sex ratio of franciscanas accidentally captured in the northern and southern coast of the southern Brazilian coast, and the analyses regarding the northern area showed that the sex ratio was biased towards males. The fishery effort of the surveyed fishery vessels was near the coast, with the maximum bottom depth at capture being 35m. Thus two of the hypothesis were that the females from the northern coast may occupy more distant/deeper coastal waters, or more northern areas.

Because the sex ratio from southern area was similar, the hypothesis that the female dolphins from northern area may travel to the southern coast was discarded. Bordino et al. (2002) also discussed segregation by sex for franciscana, suggesting latitudinal differences along the study area for adult and juvenile males, although more investigation on this subject was recommended. However, it still not clear why the male and female from northern and southern areas have some different patterns in their diet.

For all prey together, analysis of the estimated mass ingested by males and females for the whole area showed no significant differences. Female franciscanas have greater body lengths and extra demands for energy during pregnancy and lactation, but notably adult males had similar values of total prey biomass. Therefore this suggests that males are consuming more prey biomass even though they are smaller than the females. This finding is consistent with total lipid concentration on blubber composition for males and females in southern Brazil, which males have higher concentrations (369.3mg/g) than females (296.9mg/g) (Caon and Kucharski, 2000).

- **Adult and Juvenile (IRI)**

The numerical abundances of the smallest teleosts are higher for juveniles than for adults (tables 4.5, A.5 and A.6). The teleost species sizes which were more ingested by juveniles than by adults are typical of dense schools of demersal teleost recruits distributed throughout coastal continental shelf (Haimovici et al., 1996), and it seems that juveniles are not very selective ingesting the most abundant and available resource in the area.

Furthermore, juveniles eat more marine shrimps, which may be an easier prey than fishes and cephalopods due to their limited mobility. Adults seem to be more selective, consuming larger fish prey with superior biomass, and more cephalopods (occurrence and abundance), which suggest an active behaviour and high mobility (Clarke, 1996; Santos, 1999). Energy requirement is higher for larger individuals, but also the variations on feeding regimes between sexual maturity categories could indicate a degree of adaptation to minimise prey competition within the population (Nikolsky, 1963).

- **Adult and Juvenile (LM and GLM)**

The significant differences for prey occurrence and number between adult and juvenile franciscanas (table 4.7) corroborate the analysis and discussion of the IRI method. Adult and juvenile dolphins both had greater predation on juvenile fishes. However, the differences of fish prey sizes between juveniles and adults is explained by young animals consuming more juvenile fishes, and mature franciscanas eating more the subadult and adult sizes (figures 4.40 and 4.41). According to all prey specimens size, adults from both areas had eaten larger prey (figure 4.20), as expected.

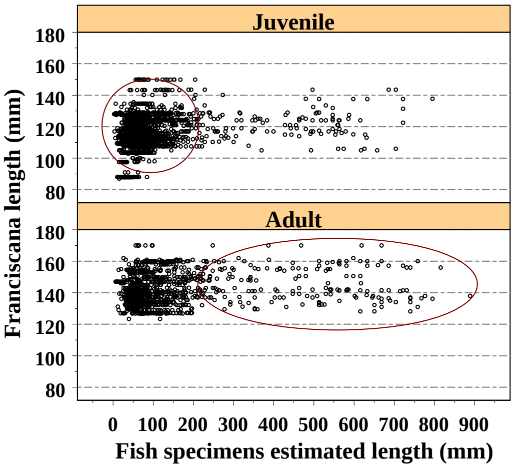


Figure 4.40: Franciscana dolphin lengths and fish estimated lengths relationship, discriminated by sexual maturity.

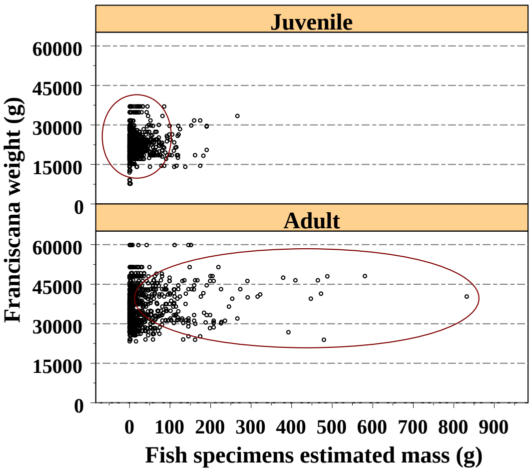


Figure 4.41: Franciscana dolphin weights and fish estimated mass relationship, discriminated by sexual maturity.

- **Seasonality (IRI)**

The demersal ichthyofauna of the southern Brazilian shelf is transitional between tropical and temperate zones, and extends between 22$^o$S and 42$^o$S (Figueiredo, 1981). The seasonal variations of species richness and relative abundance follow seasonal temperature variations in coastal waters ($>10^o$C) (Haimovici et al., 1996).

The higher diversity of species in summer/autumn could be associated with warm waters of tropical origin, carried by the Brazil Current, which increases the species diversity in southern Brazil (Haimovici et al., 1996). Characteristic species from this tropical water mass, *e.g.* fishes *Trichiurus lepturus*, *Porichthys porosissimus*, *Cynoscion jamaicensis*, *Menticirrhus* sp., and the octopus *Argonauta nodosa*, were highly represented in the summer diet of both areas (tables A.7 and A.9). However, for the northern coast some of those species are also important for spring and/or autumn. This might be explained because the southern Brazilian continental shelf (SBCS) is the southern limit of this tropical current (Souza, 2000; Castro and Miranda, 1998), and the northern area might be exposed for a longer period to its influence than the southern coast. Moreover, *Trichiurus lepturus* which showed higher values of IRI for summer, mainly in the northern area, is especially abundant near thermal fronts (Martins and Haimovici, 1997).

On the other hand, during winter, the waters of subantarctic origin carried by the Malvinas/Falkland Current reach their northern limit on the SBCS. Engraulidae species (such as *Anchoa marinii* and *Engraulis anchoita*) carried by this current (Lima and Castello, 1995) are more strongly represented in the diet of southern franciscanas (tables A.8 and A.10).

The squid *Loligo sanpaulensis*, which was more frequent for winter and spring, also demonstrated the same pattern during research cruises in the study area (Santos, 1999). The squid *Loligo plei* is a warm water species relatively abundant in the southern Brazilian coast, mainly in summer and autumn seasons (Costa and Haimovici, 1990), in agreement with findings of the present study. In the main, the franciscana dolphin seems to consume this prey according to its availability in the area.

The marine shrimps *Pleoticus muelleri* and *Artemesia longinaris* are commercially important in the study area, and have been fished mainly from spring to summer (Boshi, 1969; Haimovici, 1997b). This season coincides with the higher IRI values of these marine shrimps, also of related families, in northern and southern areas.

- **Seasonality (LM and GLM)**

There are clear seasonal variation of prey species in the franciscana feeding habit from the GLM significant results (table 4.7). As discussed in the IRI section (4.4.1), the importance of some prey in specific seasons is apparent, as the case of *Anchoa marinii* during wintertime and *Trichiurus lepturus* during summer (figure 4.21).

The southern area may exhibit more temporal variation in terms of fish species (table 4.7, figures 4.21 and 4.23). From the significant species for the northern area (table 4.7, figures 4.21 and 4.22), only the fish *Anchoa marinii* and the family Engraulidae are related to cold waters, whereas in the southern area there are many significant species characteristic of cold waters (*e.g. Anchoa marinii*, *Cynoscion guatucupa*) as well as many from warm currents (*e.g. Umbrina canosai*, *Argonauta nodosa*, *Trichiurus lepturus*, *Peprilus paru*).

It is possible that the southern region could be more spatially, or temporally, influenced by warmer currents than the northern area by colder water masses. In Chapter 5 we will analyse the SST data and discuss the impact of cold and warm waters in the study area, so that this suggestion can be investigated.

Warmer seasons are essential for franciscanas in terms of biomass consumed, and *Trichiurus lepturus* and cephalopods were clearly the prey that had contributed most in these periods (figures 4.24 and 4.25). The greater ingestion of prey biomass in warmer seasons could be explained by the needs to increase fat reserves (blubber), as energy storage for colder seasons. These diet results corroborate with studies on the concentration of total lipid in the blubber, being higher for summer/spring, 357.4mg/g, than in autumn/winter, 318.6mg/g (Caon and Kucharski, 2000). The high consumption of smaller fish in warmer seasons could also be associated with the abundance of small juvenile fishes (<100mm), from many teleost species (*e.g. Cynoscion guatucupa*, *Prionotus* sp.), in shallow coastal waters for this area (Haimovici, 1997b).

The feeding regime of the franciscana dolphin and its biological aspects within the population were discussed in the first part of this section. Temporal and spatial differences of the franciscana diet between the northern and southern sectors of the study region are clear.

What follows in this section is to discuss the franciscana diet from the more detailed spatial subdivisions of the southern Brazilian coast, which were analysed in the second part of the methods and results.

### 4.6.3 The latitudinal zones

Many of the results concerning the diversity and abundance of prey species (temporal and spatial) in the latitudinal zones are very similar to those previously discussed. Indeed, overall this more detailed analysis in the second part supports the validity of the differences of the franciscana diet through the study area.

All the significant results for species numerical abundance and occurrence, and specimens sizes, for the new spatial division and seasons analysis still show that the presence of the prey in the franciscana diet is certainly associated with spatial and temporal factors.

Therefore, we here discuss mainly the temporal and spatial significant differences of species in the diet of franciscana, in preparation for the further analysis of interactions with oceanographic parameters in Chapter 6.

- **LM and GLM analysis**

The mean sizes of both fishes and cephalopods are significantly higher for the zones 3 and 4, respectively (see figure 4.29). Looking at the map of the study region (figure 4.26), the zones 3 and 4 are associated with a subtle decrease in bottom depths, mainly for the 100m isobath. Thus, the closer coastal areas seems to be more influenced by deep waters, mainly when compared to the southern region. Haimovici and Perez (1991b) found bigger teleost specimens in deep coastal waters during research cruises on the study area continental shelf. Santos (1999) also had presented similar results for larger cephalopod specimens, mainly

*Loligo sanpaulensis*, in deeper coastal waters. Furthermore, the larger cephalopods in the diet of franciscana from southern zones also corroborates results in the literature (Andriguetto Jr. and Haimovici, 1991). Thus, the fish and cephalopod prey sizes also suggest a significant variation of prey size in the franciscana feeding through these latitudinal zones.

Additionally, differences of prey frequency do not change gradually between the latitudinal zones. The *Cynoscion guatucupa* and *Stellifer rastrifer* showed abrupt changes for the zones 4 and 3, respectively. Remembering that those species are the most important fish prey for the southern *Cynoscion guatucupa* and northern *Stellifer rastrifer* areas. Furthermore, other fish species also decreased significantly (numerical abundance and occurrence) in such areas (*e.g. Peprilus paru* and *Merluccius hubbsi*). The squid *Loligo sanpaulensis* also had showed a rapid increase of frequency in the franciscana diet in the zone 4.

In the main, all those results appear to indicate that northern and southern zones of the study area represent different environments in terms of available prey to franciscana. Additionally, the findings of central latitudinal zones (3 and 4) may represent another diverse environment from the southern and northern zones regarding to prey species.

Clearly, some species such as *Cynoscion guatucupa*, *Stellifer rastrifer*, *Anchoa marinii*, and *Loligo sanpaulensis*, are important prey associated to spatial variation in the diet of franciscana dolphin along the Southern Brazilian coast.

There were some prey species that differed seasonally in all the latitudinal zones, and they are good indicators of the temporal variation in the feeding of franciscana throughout the coast. Consequently, significant prey may indicate both the behaviour of the water masses in the study area and their distribution. The species strongly influenced by warm seasons were *Trichiurus lepturus*, *Umbrina canosai*, the octopus *Argonauta nodosa*, and shrimp specimens; whereas *Anchoa marinii*, *Cynoscion guatucupa*, *Stellifer rastrifer* and *Paralonchurus brasiliensis* were influenced by cooler seasons.

Nonetheless, *Stellifer rastrifer* is also a species associated with warm water masses but its ingestion by the franciscanas was higher for the colder season. This species occurred in the northern area throughout the year, but it is more abundant in the winter months. However, the larger fish species *Trichiurus lepturus* has its higher occurrence in warmer months, which probably is preferred by franciscana due to its greater size to the smallest *Stellifer rastrifer*. During cooler months when the *Trichiurus lepturus* decrease in abundance and occurrence, franciscanas probably eat more easily available fish species, like the *Stellifer rastrifer*.

There were other relevant prey species which also vary temporally, such as *Merluccius hubbsi* and *Porichthys porosissimus* in the colder months; and *Cynoscion jamaicensis*, *Peprilus paru*, and the squid *Loligo plei* in the warm months. However, they are not so important in terms of abundance. On the other hand, the squid *Loligo sanpaulensis* is an abundant prey of franciscana and is not only temporally significant for the southern zones in the winter and spring seasons, but also an important prey through all the year.

The temporal variation of prey species in the diet of franciscana also differed between the zones. The northern zones were mostly influenced by warm waters related species. Moreover, some species only occurred in the northern latitudinal zones (*e.g. Stellifer rastrifer*). Garfield (1990) verified that the regions close to Cabo Frio (Rio de Janeiro) and southern of Santa Marta Cape (northern latitudinal zones) were the regions most strongly influenced by the warm Brazil Current (BC).

Some prey associated with colder water masses also occurred in the diet of the dolphins in the northern zones (*e.g. Anchoa marinii*, *Cynoscion guatucupa*, *Engraulis anchoita*, *Micropogonias furnieri*. Those species could be related to the presence of the Brazilian Coastal Current (BCC), which was studied by Souza (2000). The BCC only penetrates the Southern Brazilian Continental Shelf (SBCS) during the winter and spring months, and is restricted to isobaths shallower than 200m (Souza, 2000) (see Chapter 3 for more information).

The temporal variation of prey in the southern zones were significantly related to colder water species (*e.g. Cynoscion guatucupa*, *Anchoa marinii*, *Engraulis anchoita*, *Loligo sanpaulensis*), despite warm waters species also occurring (*e.g. Trichiurus lepturus*, *Argonauta nodosa*). The southern zones are more temporally influenced by the BCC (Souza, 2000), which reasonably explains these prey occurrences. Moreover, these zones also are influenced by the BC during the warmer months (Castro and Miranda, 1998; Souza, 2000).

Notably, warm water related species occurred in the diet of franciscana in the southern zones, but the tropical species *Stellifer rastrifer* does not occur at all. It may be that this species is strongly associated with higher temperatures, or is not tolerant to changes in water temperatures. However, this remains unclear. Thus, the further interaction analysis of the diet and the parameter of sea surface temperature may help to elucidate this question.

As previously discussed, the higher abundance and occurrence of *Stellifer rastrifer* in the franciscana diet in the northern area, and its practically absence in the stomach contents of southern animals may also suggest some latitude differentiation in the use of habitat by franciscana in the study area. From all the stomachs analysed of the southern animals (N=

270), only a single otolith pair of *Stellifer rastrifer* was found. If the animals are similarly distributed along the coast, more *Stellifer rastrifer* otoliths should be found in the stomachs. According to Tropical data Base Program (cited in the section 4.4), the southern range limit of *Stellifer rastrifer* is about 29°S.

Possibly the animals could eat the *Stellifer rastrifer* in the northern zones and than travel to the southern coast, and by this time the otolith structures in the stomachs could be completely dissolved, and consequently not be found. This would imply no difference in the use of habitats. However, this hypothesis can be questioned. Firstly, many authors suggest the otolith dissolution times are near or more than 24 hours (Prime and Hammond, 1979; Murie and Lavigne, 1986; Sekiguchi and Best, 1997; Tollit et al., 1997)); and Bassoi et al. propose an digestion time of otoliths (fish lengths of 15cm) of not less than 48 hours, from a captive franciscana experiment. The distances between the northern and southern areas are relatively short, and franciscana dolphin could realistically swim those distances in periods less than 24 hours, and the otoliths could be easily found. Secondly, the *Stellifer rastrifer* otolith is not as thin and fragile as other species (*e.g.* Engraulidae). Indeed, it is more robust, and thus probably slowly digested. In fact, the species *Stellifer rastrifer* is probably a good indicator of some habitat variation by franciscanas off the southern Brazilian coast.

In addition to these observations, suggesting some habitat variation by franciscana, so too do other results concerning its diet. There were also differences in the cephalopod data, and the beaks could remain for longer periods in the stomachs, and so not be affected by fast dissolution. Additionally, differences in both fish and cephalopod sizes between the latitudinal zones also existed.

For fish size, summer was the frequent season for the larger prey. On the other hand, the winter is represented by the smallest means of fish prey. As discussed before, these results are due to the presence of the larger species *Trichiurus lepturus* in the summer, and the smaller fish *Cynoscion guatucupa*, and also *Stellifer rastrifer*, in the winter seasons. The cephalopod lengths through the seasons also vary between the latitudinal zones, with the higher frequency of larger prey found in the spring months, which corroborate with the findings of Santos (1999) with the bigger specimens in the spring probably associated with squid groups about to reproduce.

To conclude, many differences of prey abundance, occurrence, and sizes were found for the spatial and temporal analysis throughout the coast. Possibly these significant results may associated with the environmental characteristics in the study area (see Chapter 3), and this is the next topic of this thesis.

Nevertheless, not all prey species are appropriate for further models of interactions with the oceanographic parameters because of their small contribution, or lack of significant variation. The relevant species of the dolphin diet and are selected for further interaction model analyses are the fishes *Cynoscion guatucupa*, *Stellifer rastrifer*, *Trichiurus lepturus*, *Anchoa marinii*, *Paralonchurus brasiliensis*, *Porichthys porosissimus*, *Umbrina canosai*, *Urophycis brasiliensis*, *Cynoscion jamaicensis*, *Peprilus paru*, *Merluccius hubbsi*; the cephalopods *Loligo sanpaulensis*, *Loligo plei*, and *Argonauta nodosa*; the crustaceans ”shrimp” specimens; and the prey group of total ”fish” specimens. The cephalopod group is practically represented by the single species *Loligo sanpaulensis*, which is 99% of the cephalopods ingested. The fish and cephalopod sizes also will be included in the further models of interactions.

- **PCA analysis**

Our particular interest in PCA analysis was in finding an alternative description of the franciscana diet data and its spatial distribution at higher resolution. The spatial analysis of the 7 latitudinal zones took into account the means of prey abundance, occurrence, and size (lengths and weights).

The PCA confirms that the diversity and abundance of species differed among the zones. The prey occurrence seems very well distinct between the southern and northern zones (see figure 4.36), which may be possibly related to the differences of warm and cold water species that vary significantly between the zones according to the GLM results (see discussion above). Additionally, for the mean of prey species size the results had shown that distant geographic zones are more likely to differ in terms of prey size in the franciscana diet, and neighboring geographic zones are likely to be similar, with exception of zone 1 (figure 4.39). The numerical mean analysis of prey had shown that the prey numbers in the franciscana diet are likely to distinguish the latitudinal zone 4 from the other zones. For the prey species size the zone 4 together with zones 3 and 2 also look like diverging from the other zones.

Overall, the spatial behaviour of the PCs confirm that the data separate into northern and southern zones, with the most central zones possibly diverging (see figure 4.37). From the LM and GLM results, similar divergences regarding the diet were discussed for the intermediate zones (see previous section 4.7.1).

The central region comprises the latitudes $31^o$ 09’ to $31^o$ 40’ S, and is associated with a considerable change in the bathymetry along the coast. This coastal area presents some peculiar environmental features. Owing to the influence of the Antarctic gyre, the southward flowing BC becomes deeper and wider between $24^o$ and $31^o$ S (Souza, 2000). The change of the bathymetry and the topography of the shelf under $29^o$ S cause instability of the flow and oscillations of the front towards $31^o$ S (Garfield, 1990). Moreover, during the winter the BMC confluence is strong in the SBCS, and this results in a strong horizontal current, and the change in the bathymetry ($\sim 31^o$ 30' S) would be enough to cause upwelling at the front between the two water masses in the shelf break (Lima and Castello, 1995) (see Chapter 3).

Therefore, such variations in the physical circulation along the coast may affect the distribution of franciscana prey of the northern and southern zones, and middle geographic zones may exhibit an intermediate area of influence from both cold and warm currents.

Summarizing, the franciscana diet spatial variations are substantial in the study area, which may be influenced spatial and temporally by divergent water masses (BC and BCC), but also by considerable changes in the topography and bathymetry. Furthermore, the outflow of Patos Lagoon estuary ($\sim 32^o$ S) also affects the coastal waters of southern zones (*e.g.* physical circulation, chlorophyll-*a* concentration) (Garcia, 1997).

### 4.6.4 Past feeding studies in the study area

Comparisons with previous studies carried out during the late 70's in the southern coast (Pinedo, 1982) and early 90's (Bassoi, 1997) showed similar trends in the diet composition of franciscana and the relative abundance of catches of target species (Bassoi and Secchi, 1999). Historical catch records demonstrated a decline in yearly landings of *Micropogonias furnieri* and *Macrodon ancylodon* (Reis, 1992) and a drastic decrease in the density of juveniles in coastal waters (Ruffino and Castello, 1992). The results from this study confirm this tendency. The incidence of *Macrodon ancylodon* decreased drastically from 40% (Pinedo, 1982), to 11% (Bassoi, 1997), and 4.7% (this study) of occurrence in the diet composition, and *Micropogonias furnieri* from 26.9% to 5.6%, and 5.2%, respectively. On the other hand, the frequency of *Trichiurus lepturus* increased from about 5% in the past to 36.6% in this study.

Recent comparisons for northern area (Ott, 1994) revealed a decrease in the occurrence of *Cynoscion guatucupa*, from 71.4% to 26.5% in the present study. However, *Cynoscion guatucupa* has not been extensively exploited (Haimovici, 1998). There was a sudden significant increase in the occurrence of *Stellifer rastrifer*, from 9.1% to 44.9%. There is still no satisfactory hypothesis for this major change in the diet of northern area franciscanas. As the fishes *Stellifer rastrifer* and *Trichiurus lepturus* are species associated with warm currents in summer months, their increase in the franciscana diet with time may be associated with changes of such currents in recent years in this region. This assumption could be investigated by analysing the sea surface temperature in the study area through these years (Chapter 5). However, a natural fluctuation of the stocks sizes is another possible explanation.

Natural subdivisions of the ocean are delineated by the presence, size, and depth of the continental shelf, current systems and their boundaries, and regimes of temperatures (Bax and Laevastu, 1989). The northern and southern coast areas present distinct features related to continental shelf extent and current systems and boundaries. In other words, the differences in the diets of both areas could be due to natural subdivisions off the coast and distinct influence of oceanographic processes, which should be investigated.

The following Chapter will therefore analyse the spatial and temporal variability of sea surface temperature (SST) and chlorophyll-$a$ towards the latitudinal zones, the southern Brazilian coast.

# Chapter 5

# The physical data: oceanographic parameters

As previously summarized in Chapter 3, the study area is a complex region affected by different water masses, variability in freshwater discharges from an important estuary, eddies, and upwelling phenomenon. Moreover, the area is also associated with particular oceanographic features due to rapid changes of topography throughout the coastal region.

Nonetheless, the research studies carried out on different oceanographic aspects (*e.g.* sea temperature, surface oceanic topography, chlorophyll-*a* concentration) of the BMC Confluence and the southern Brazilian waters were mainly conducted considering large spatial scales (*e.g.* range of more than $10^o$ of latitude, offshore limits of about 2000m depth). Hence, physical aspects of small range areas, such as the coastal region of the present study (less than $5^o$ of latitude and maximum of 100m isobath, see figure 5.1), might not be accurately represented.

Therefore, this Chapter addresses temporal and spatial variability of sea surface temperature (SST), and chlorophyll-*a*, along the very coastal region of the southern Brazilian waters.

The main purpose of this analysis is to explore the behaviour of these oceanographic parameters through the study region, from an ecological view point, and verify if such small range zone exhibits patterns or cycles of SST and chlorophyll-*a*.

This Chapter address relevant information prior to using the oceanographic parameters as explanatory variables in analysis of franciscana feeding data (Chapter 6).

## 5.1 Methods

### 5.1.1 The latitudinal zones

The latitudinal zones defined for the biological data analysis, were also used for analysis of the oceanographic parameters SST and chlorophyll-$a$. The area numbers correspond with those from the previous analyses, with the inclusion of zone 8, the southern portion of the southern Brazilian coast (figure 5.1).

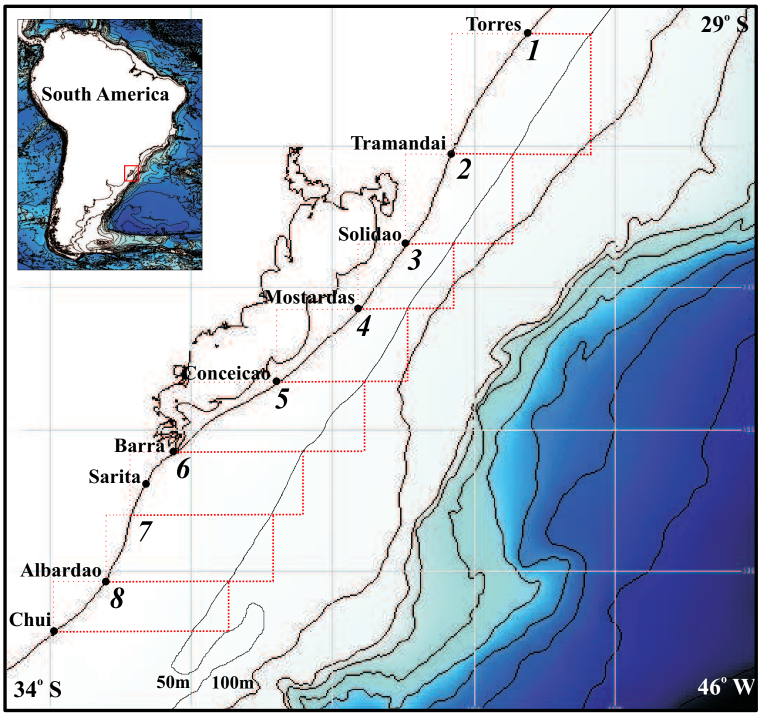


Figure 5.1: Map of the study area subdivisions for the analysis of the physical parameters. The sectors are similar to the latitudinal zones of the biological analysis, with the inclusion of the southern sector off the southern Brazilian coast (zone 8).

The map shows the zones as rectangular, which means that the physical latitudinal zones analysed are slightly greater than those described in Chapter 4 (limited by the 50m isobath). This is a result of working with the values of the oceanographic parameters in pixels, and it is done in order to facilitate the analysis of the physical data. The land portion (null values) is automatically discarded from the analysis, and all of the oceanic region is considered for each zone. The 50m isobath is the limit range of our data due to franciscana capture events and its distribution.

- Zone 1 = 29$^o$ 11’ to 30$^o$ 01’ S (Torres city to Tramandai city);
- Zone 2 = 30$^o$ 01’ to 30$^o$ 41’ S (Tramandai city to Solidao lighthouse);
- Zone 3 = 30$^o$ 41’ to 31$^o$ 09’ S (Solidao lighthouse to Mostardas lighthouse);
- Zone 4 = 31$^o$ 09’ to 31$^o$ 40’ S (Mostardas lighthouse to Conceicao lighthouse);
- Zone 5 = 31$^o$ 40’ to 32$^o$ 07’ S (Conceicao lighthouse to Barra);
- Zone 6 = 32$^o$ 07’ to 32$^o$ 35’ S (Barra to southern Sarita lighthouse);

- Zone 7 = 32$^o$ 35' to 33$^o$ 05' S (southern Sarita lighthouse to Albardao lighthouse);
- Zone 8 = 33$^o$ 05' to 33$^o$ 26' S (Albardao lighthouse to Chui city).

### 5.1.2 Sea Surface Temperature (SST) data

With the aim of providing data for climate studies and large to mesoscale oceanography, the MCSST (Multi-Channel Sea Surface Temperature) Program - long term data set derived from the AVHRR (Advanced Very High Resolution Radiometers) - was established by NASA in the 1980s. Each MCSST image in this global data set is on a regular grid which consists of 2048 pixels from east to west (180$^o$E to 180$^o$W) and 1024 pixels from north to south (90$^o$N to 90$^o$S). The height and width of each grid cell is the same in degrees, i.e. 360/2048 or 0.1757812 degrees. This represents 18km X 18km at the Equator, considered to be the nominal spatial resolution of the data set. Weekly and monthly average data for both the ascending pass (daytime) and descending pass (nighttime) exist since October 1981 (Smith, 1992).

In order to investigate the spatial and temporal patterns of the SST off the southern Brazilian coast, a series of 20 years of weekly-averaged MCSST images was extracted to cover the study area, from 27$^o$ S to 34$^o$ S and 47$^o$ W to 53$^o$ W, an example is given in figure 5.2. The data was kindly obtained by the staff of the SOC Laboratory for Satellite Oceanography (LSO) which has access to the MCSST program from NASA (National Aeronautics and Space Administration), USA.

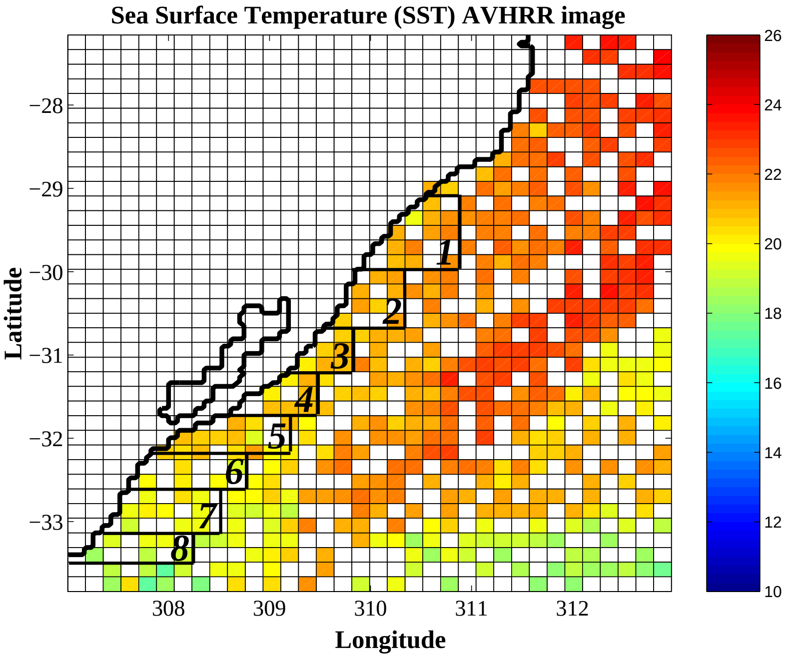


Figure 5.2: Weekly-averaged Sea Surface Temperature (SST) AVHRR image, with the study area and location of zones where the data were extracted. The image corresponds to the third week of December 1997, from a total of 982 images (nighttime). The legend bar at right represents the values in $^o$C.

The data set covers the period between November 1981 and February 2001 and consists of weekly-averaged MCSST images, totalling 993 images for daytime SST data, and 982 for nighttime SST data. Probably because of the effects of cloud coverage in the daytime SST, it was preferable to work with the nighttime SST as the final averaged values were more complete spatially. The spatial resolution is nominally 18km x 18km (as explained above), and the claimed accuracy of the MCSST estimate is 0.5$^o$C. The data were manipulated using the software MatLab (*version 6.5*, MathWorks Inc.). From the 982 images for the descending pass (nighttime), the weekly-averaged SST ($^o$C) of each latitudinal zone was extracted (figure 5.2 is an example), and the monthly-averaged SST was calculated. The monthly-averaged values instead of the weekly-averaged were chosen with the purpose of working with the same temporal scale as that for the chlorophyll-$a$ data, and also to minimise missing values. According to the pixel coordinates of each zone, the monthly-averaged values were calculated considering these pixel values for each week (N= 4) of a respective month, with a total of 232 month-averaged values for each one of the 8 latitudinal zones. Figure 5.3 is an example of the weekly-averaged images for the month of April 2000, from which the monthly-averaged values were calculated.

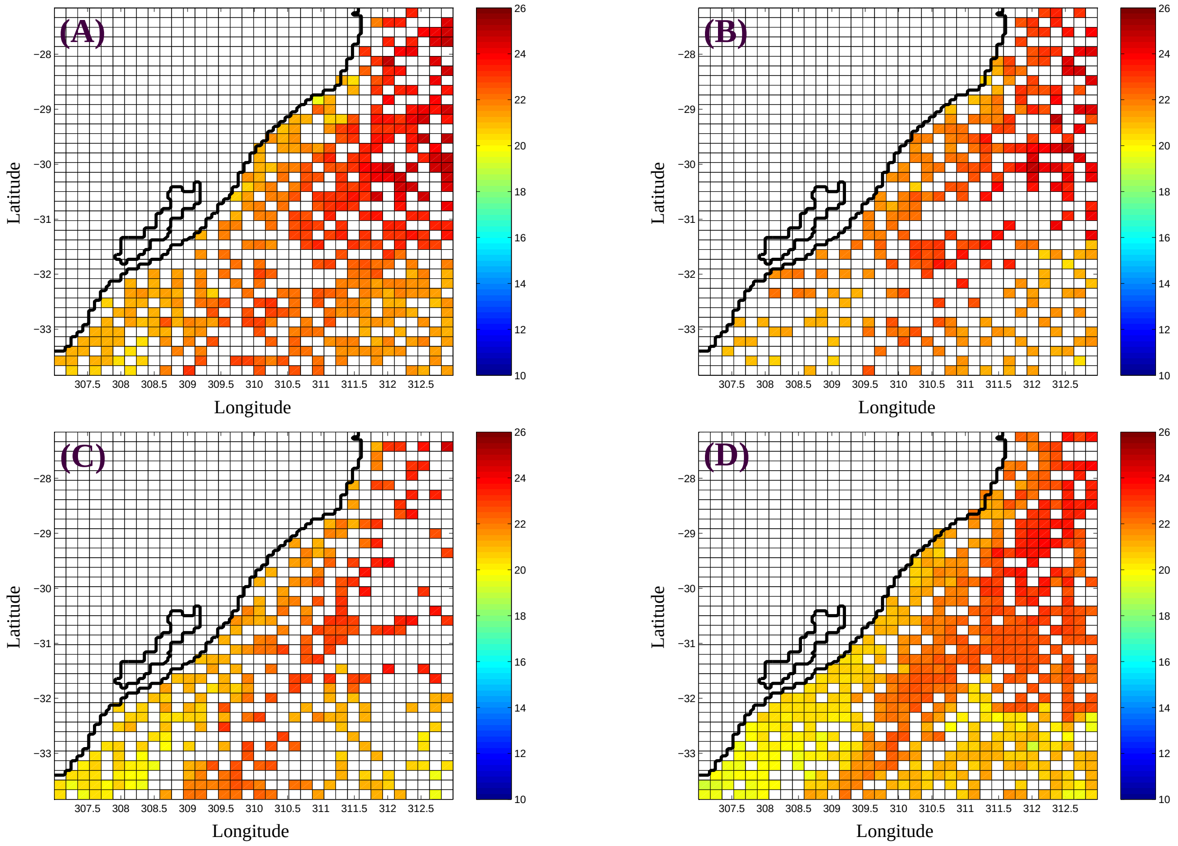


Figure 5.3: Weekly-averaged Sea Surface Temperature (SST) AVHRR images for the month of April 2000, where (A) week 1, (B) week 2, (C) week 3, and (D) week 4. The legend bars at right show the values of temperatures in $^o$C.

- **Statistical analysis**

In order to characterise each one of the 8 zones, and identify any significant differences in temperature and patterns behaviour between them, several analyses were made.

To examine SST spatial patterns across the study area, analysis of means (two sample t-Test) and analysis of variance were applied. After an ANOVA model has been fitted, it is often of interest to determine whether any significant differences exist between the temperatures for the various latitudinal zones and, if so, to estimate the size of the differences. MCA (multiple comparisons) computes simultaneous confidence intervals or bounds for the specified estimable linear combinations of the parameters in a fixed effects model (Hsu, 1996). In our analysis, MCA has resulted in the calculation of simultaneous 95% confidence intervals for all pairwise differences between SST means, based on the levels of latitudinal zones. The critical point is the Tukey studentized-range quantile scaled by square root (Tukey's method), and validity of the Tukey's method is checked using the method of Hayter (1989) (*S-PLUS 6 for Windows Guide to Statistics, Volume 1,* Insightful Corporation). This method identifies statistically significant comparisons, that correspond to pairs of means which can be declared "different" by Tukey's HSD (honestly significant difference) method.

Following the methodology described in section 4.5.2, the spatial behaviour of temperatures in the study area was also investigated through PCA. A correlation estimation function was used to perform the principal components analyses as the SST values are a scaled data set.

For temporal analysis, ANOVA analyses were conducted to determine the differences in the temperatures through time (years and months) for each latitudinal zone. Additionally, two-way ANOVA was chosen for year and month effects, and its interaction, to investigate seasonal and inter-annual SST variation for the whole study region.

Furthermore, Time Series analyses were applied to examine more complex behaviour of the temperatures over time, such as possible cyclic behaviours and patterns. As for many data collected over time, like monthly temperature means, there may be correlation between successive observations, this is known as autocorrelation or serial correlation.

Firstly, the basic time series plot shows each observation plotted against time to investigate cyclic behaviours. Then, the autocorrelation function (ACF) plots, which are important tools for describing the serial (or temporal) dependence structure of a time series. It describes how one month's temperature is related to the previous month temperature: this is the autocorrelation at lag 1. Then it calculates how that month's temperature is related to the temperature in the one before last: this is the autocorrelation at lag 2, and so on. The ACF plot provides an estimate of the correlation between observations separated by a lag of zero, one, or more time units - in our case "months". The autocorrelation estimate at each lag is given by the height of the vertical lines in the ACF plot. The value of the autocorrelation function at lag 0 is always 1. Note that approximate 95% confidence limits are shown for the ACF plots. If no autocorrelation estimate falls outside the strip defined by the two dotted lines and the data contain no outliers, it is assumed that there is no serial correlation. Otherwise, we should be concerned about the presence of serial correlation.

Another basic diagnostic technique is to examine the residuals of the time series for a more complete analysis of the adequacy of the models, and they are important as a basis for diagnostic analysis of the autocorrelations as a whole. ACF plots of the time series residuals were analysed.

Finally, the same autocorrelation function (ACF) method was used for the yearly means to investigate possible cyclic behaviour across years.

### 5.1.3 Chlorophyll-$a$ data

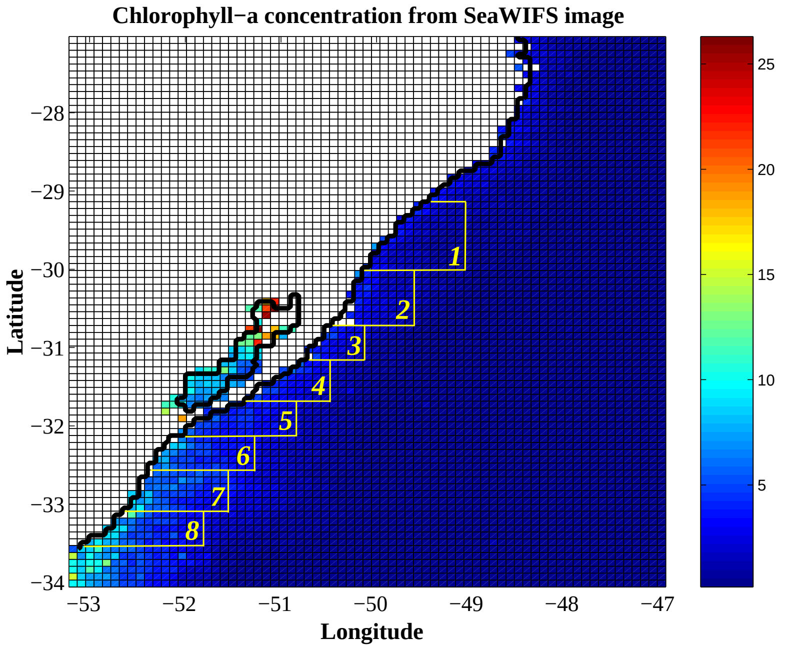


Figure 5.4: Monthly-averaged chlorophyll-$a$ concentration from SeaWIFS image off the southern Brazilian coast, for June 2001. Limits of latitudinal zones are superimposed on the images (yellow lines). The legend bar at right shows the values of chlorophyll-$a$ concentration in mg/m$^3$.

The concentration of phytoplankton, chlorophyll-$a$ as a measure of ocean primary production, can be derived from satellite observation and quantification of ocean colour. This is due to the fact that the colour in most of the world's oceans in the visible light region, (wavelengths of 400-700nm) varies with the concentration of chlorophyll and other plant pigments present in the water, i.e., the more phytoplankton present, the greater the concentration of chlorophyll-$a$ and the greener the water.

The chlorophyll-$a$ concentration is here measured as mg/m$^3$ (also cited as mg m$^{-3}$), and the typical range (monthly average) is 0.05mg/m$^3$ for tropical and non-coastal waters, to 30mg/m$^3$ for coastal waters, North Pacific and North Atlantic (source:oceancolor.gsfc.nasa.gov).

The SeaWIFS (Sea-viewing Wide Field-of-view Sensor) Project provides quantitative data on global ocean bio-optical properties. The project develops and operates a research data system that processes, calibrates, validates, and distributes data received from an Earth orbiting ocean colour sensor. The chlorophyll-$a$ data were kindly obtained by the staff of the SOC Laboratory for Satellite Oceanography (LSO) which has access to the SeaWIFS from NASA (National Aeronautics and Space Administration), USA. The data used are Level 3 SMI monthly and 9km resolution chlorophyll-$a$ from SeaWIFS. Unfortunately, the data set covers only the period between September 1997 and December 2001 with monthly-averaged images, totalling a number of 52 images, from 27$^o$ S to 34$^o$ S and 47$^o$ W to 53$^o$ W. From all the images, the monthly-averaged chlorophyll-$a$ of each latitudinal zone was extracted (figure 5.4) and calculated. The data were manipulated using the software MatLab (*version 6.5*, MathWorks Inc.). Figure 5.5 is an example of monthly composites of chlorophyll-$a$ concentration from SeaWIFS images for July of 2000 and 2001, in the study area.

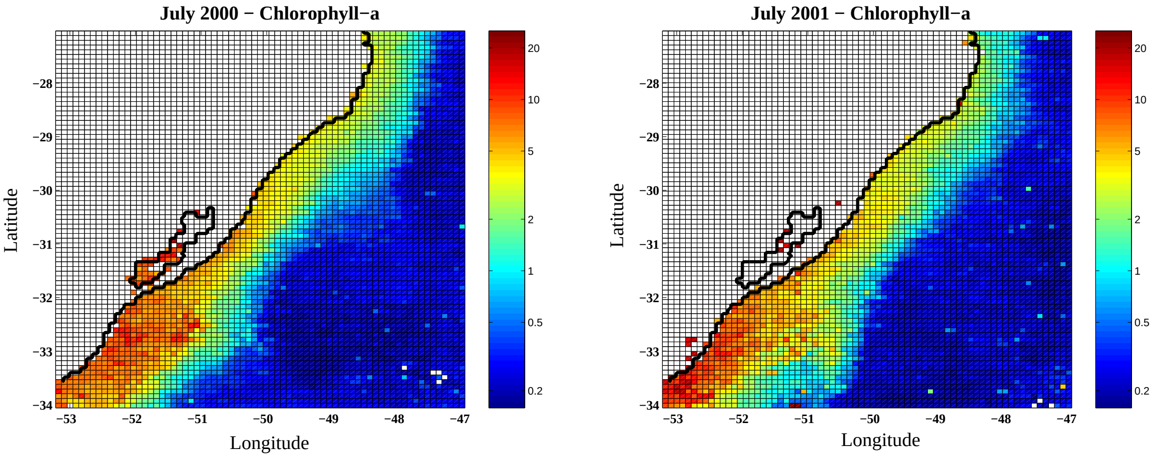


Figure 5.5: Monthly averaged of chlorophyll-$a$ concentration from SeaWIFS images plotted in a log scale, for July of 2000 and 2001. The legend bar at right shows the values of chlorophyll-$a$ concentration in mg/m$^3$.

- **Statistical analysis**

Following the same methodology used for SST, similar analyses were made to characterise each one of the 8 zones, and identify if there are any significant differences of chlorophyll-$a$ and patterns of behaviour between them.

Spatial and temporal analyses similarly included explanatory statistics, analysis of means (two sample t-test, plot design of the treatments means), ANOVA, MCA (Multiple Comparisons), PCA, and Time Series. Furthermore, the relationship of chlorophyll-$a$ and temperature were also analysed through LM.

## 5.2 Results

### 5.2.1 Sea Surface Temperature Spatial Variability

From all data analysed, the monthly-averaged temperatures ($^o$C) vary considerably between 10.08 and 26.10$^o$C, with a mean of 19.35 (SE= 0.08, SD= 3.38, Variance= 11.44, N= 1840). The mean values of the monthly-averaged temperatures across the latitudinal zones - for the 20 years data set - vary from 20.44 to 17.58$^o$C, decreasing from the northern to the southern zones (see table 5.1 and figure 5.6).

| Zones | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| Min. | 12.99 | 13.06 | 12.97 | 12.37 | 11.38 | 10.55 | 10.56 | 10.08 |
| Mean | 20.44 | 20.46 | 20.33 | 20.46 | 19.00 | 18.35 | 18.17 | 17.58 |
| Max. | 25.55 | 25.57 | 25.73 | 26.10 | 24.83 | 24.28 | 24.13 | 23.68 |
| SE | 0.19 | 0.19 | 0.20 | 0.29 | 0.22 | 0.23 | 0.24 | 0.25 |
| SD | 2.85 | 2.80 | 2.90 | 2.87 | 3.27 | 3.47 | 3.56 | 3.71 |
| Variance | 8.14 | 7.86 | 8.40 | 8.23 | 10.71 | 12.04 | 12.70 | 13.80 |

Table 5.1: Monthly-averaged temperatures, in $^o$C, for each latitudinal zone.

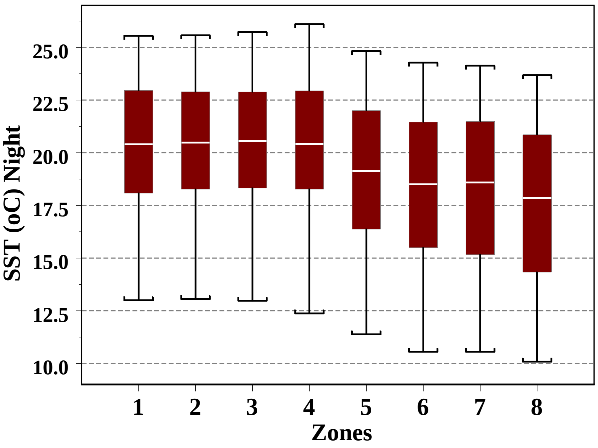


Figure 5.6: Monthly-averaged temperatures ($^o$C) range for each latitudinal zone, from November 1981 to February 2001.

Pairwise analysis of differences among the means between the northern zones (1 to 4) presented no significant differences. However, from the zone 4 to 5 the null hypothesis is rejected (table 5.2). On the other hand, the southern zones (5 to 8) are not only significantly different from the northern zones, they also present significant differences of means between them, confirming the visual effect evident in figure 5.6.

Figure 5.7, illustrates the value of the mean for each level of the factor ”zone”, showing the differences between the latitudinal zones.

| t($p$) | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| 1 | | 0.07(0.95) | 0.40(0.69) | 0.06(0.94) | 5.01(<0.01) | 6.94(<0.01) | 7.42(<0.01) | 9.13(<0.01) |
| 2 | | | 0.47(0.64) | 0.002(0.99) | 5.08(<0.01) | 7.02(<0.01) | 7.49(<0.01) | 9.19(<0.01) |
| 3 | | | | 0.46(0.65) | 4.53(<0.01) | 6.43(<0.01) | 6.91(<0.01) | 8.58(<0.01) |
| 4 | | | | | 4.94(<0.01) | 6.82(<0.01) | 7.28(<0.01) | 8.93(<0.01) |
| 5 | | | | | | 2.03(0.04) | 2.55(0.01) | 4.28(<0.01) |
| 6 | | | | | | | 0.55(0.59) | 2.27(0.02) |
| 7 | | | | | | | | 1.70(0.09) |

Table 5.2: Two-Sample t-Test for the SST data between the latitudinal zones, with the values of t and $p$ (in parenthesis).

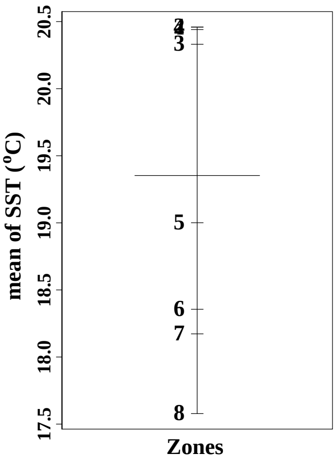


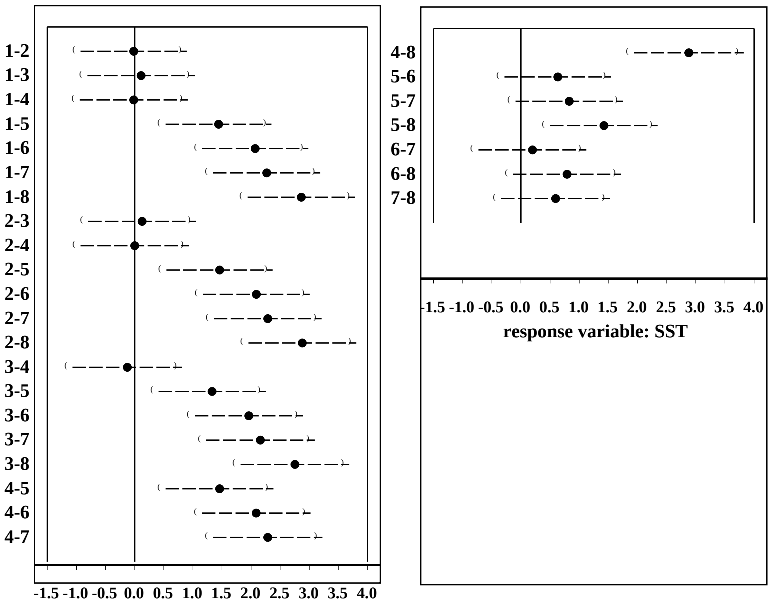
Figure 5.7: Plot design of the SST treatment means for the factor "zone".

Not surprisingly, the analysis of variance shows that the SST values also differed significantly between latitudinal zones (df= 7, F= 31.23, $p$<0.001). However, more detailed results are offered by an analysis of all pairwise differences in SST for the ANOVA model between the zones, referred to as MCA. In our analysis, MCA has resulted in the calculation of simultaneous 95% confidence intervals for all pairwise SST means, and identifies significant differences between several combinations. The graphic and printed results are shown in the figure 5.8.

The printed results indicate via asterisks the confidence intervals which exclude zero; in the figure 5.8, these can be identified by noting intervals that do not intersect the vertical reference line at zero. These statistically significant differences correspond to pairs of (long run) means, in our case the temperatures. This again confirms the previous analysis.

The PCA of the monthly-averaged temperatures confirms the findings from the treatment means analysis and the MCA illustrate above. The first principal component explains 96.0% of the variance, and the first two principal components together explain 98.0% (table 5.3).

According to the loadings (figure 5.9), for the first component all zones have similar values (first PC is essentially a mean). The second component contrasts the three latitudinal zones 8, 7, and 6, with three most northern zones 4, 3, and 2, with the 4 and 8 weighted most heavily. The third component groups the zones 1, 2, and 3 with the same sign, contrasting the zone 4. Loadings suppresses small values to emphasize the more important ones.

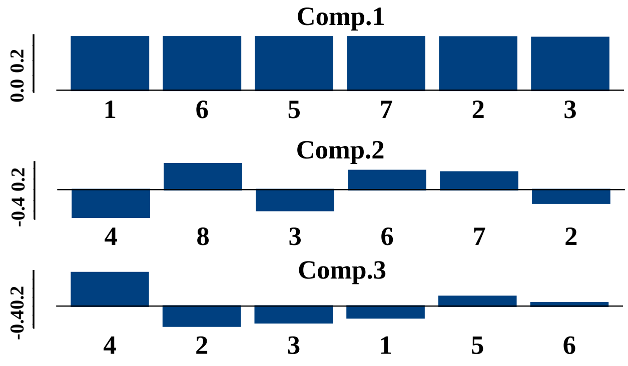


| Zones | | Estimate | SE | Lower Bound | Upper Bound |
|---|---|---|---|---|---|
| 1 | 2 | -0.017 | 0.301 | -0.93 | 0.895 |
| 1 | 3 | 0.11 | 0.304 | -0.811 | 1.030 |
| 1 | 4 | -0.017 | 0.306 | -0.945 | 0.91 |
| 1 | 5 | 1.440 | 0.299 | 0.532 | 2.350 **** |
| 1 | 6 | 2.070 | 0.301 | 1.160 | 2.980 **** |
| 1 | 7 | 2.270 | 0.304 | 1.350 | 3.190 **** |
| 1 | 8 | 2.860 | 0.304 | 1.940 | 3.790 **** |
| 2 | 3 | 0.128 | 0.305 | -0.797 | 1.050 |
| 2 | 4 | 0.001 | 0.307 | -0.931 | 0.932 |
| 2 | 5 | 1.460 | 0.301 | 0.546 | 2.370 **** |
| 2 | 6 | 2.090 | 0.302 | 1.170 | 3.010 **** |
| 2 | 7 | 22.900 | 0.305 | 1.360 | 3.210 **** |
| 2 | 8 | 2.880 | 0.305 | 1.950 | 3.810 **** |
| 3 | 4 | -0.127 | 0.31 | -1.070 | 0.813 |
| 3 | 5 | 1.330 | 0.304 | 0.409 | 2.250 **** |
| 3 | 6 | 1.960 | 0.305 | 1.040 | 2.890 **** |
| 3 | 7 | 2.160 | 0.308 | 1.220 | 3.090 **** |
| 3 | 8 | 2.750 | 0.308 | 1.820 | 3.690 **** |
| 4 | 5 | 1.460 | 0.306 | 0.53 | 2.390 **** |
| 4 | 6 | 2.090 | 0.307 | 1.160 | 3.020 **** |
| 4 | 7 | 2.290 | 0.31 | 1.350 | 3.230 **** |
| 4 | 8 | 2.880 | 0.31 | 1.940 | 3.820 **** |
| 5 | 6 | 0.631 | 0.301 | -0.282 | 1.540 |
| 5 | 7 | 0.828 | 0.304 | -0.093 | 1.750 |
| 5 | 8 | 1.420 | 0.304 | 0.501 | 2.340 **** |
| 6 | 7 | 0.197 | 0.305 | -0.729 | 1.120 |
| 6 | 8 | 0.792 | 0.306 | -0.135 | 1.720 |
| 7 | 8 | 0.595 | 0.308 | -0.34 | 1.530 |

Figure 5.8: Temperature ANOVA for all pairwise means and the levels ”zone”, with 95% simultaneous confidence intervals for specified linear combinations, by the Tukey’s method.

| | Comp.1 | Comp.2 | Comp.3 | Comp.4 | Comp.5 | Comp.6 | Comp.7 | Comp.8 |
|---|---|---|---|---|---|---|---|---|
| Standard deviation | 2.771 | 0.401 | 0.242 | 0.205 | 0.154 | 0.128 | 0.114 | 0.090 |
| Proportion of Variance | 0.956 | 0.020 | 0.007 | 0.005 | 0.003 | 0.002 | 0.002 | 0.001 |
| Cumulative Proportion | 0.960 | 0.980 | 0.987 | 0.992 | 0.995 | 0.997 | 0.999 | 1.000 |

Table 5.3: Principal components variance for the latitudinal zones’ monthly-averaged temperatures.



| Zones | Comp.1 | Comp.2 | Comp.3 |
|---|---|---|---|
| 1 | 0.356 | -0.176 | -0.257 |
| 2 | 0.355 | -0.251 | -0.441 |
| 3 | 0.352 | -0.387 | -0.367 |
| 4 | 0.347 | -0.515 | 0.742 |
| 5 | 0.356 | 0.149 | 0.214 |
| 6 | 0.356 | 0.356 | |
| 7 | 0.356 | 0.328 | |
| 8 | 0.351 | 0.484 | |

Figure 5.9: Principal components loadings for the latitudinal zones’ monthly-averaged temperatures.

From the biplot loadings (figure 5.10) it seems that the latitudinal zones 1, 2, 3, and 4 represent a group with similar loading signs, and 5, 6, 7, and 8 are a different group from them. So, these zones could be divided into 2 groups of similarities according to the monthly averaged temperatures: the northern (1 to 4) and the southern (5 to 8) latitudinal zones.

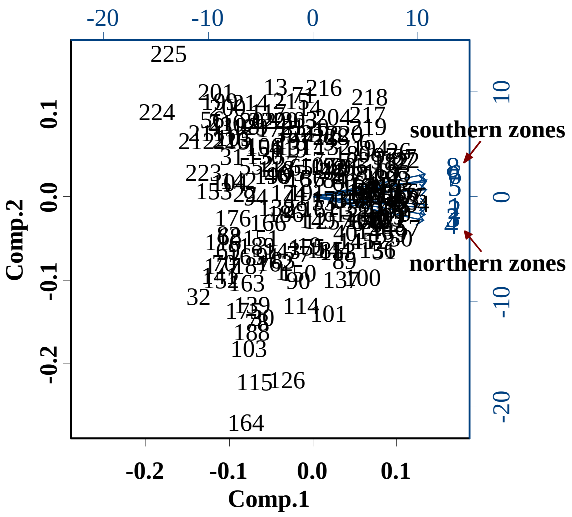


Figure 5.10: Biplot loadings of the monthly averaged temperatures. The zones are plotted in blue and the SST data are plotted in black.

Summarizing, all the analyses chosen for the spatial investigation of the temperatures in the study area showed significant differences between the northern zones and the southern zones (see figures 5.7, 5.8, and 5.10).

We have 8 zones measured over the same period, thus the question naturally arises as to whether or not the ups and downs of temperatures from these different zones are correlated. The strong positive correlations are clear enough (table 5.4). The temperatures indicate strong correlations between all the latitudinal zones (>90%), which means that for of all zones the temperatures vary together. These variations of temperatures over time are better investigated in the follow section.

| Zones | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| 1 | 1.000 | 0.985 | 0.966 | 0.951 | 0.969 | 0.960 | 0.958 | 0.945 |
| 2 | | 1.000 | 0.973 | 0.947 | 0.960 | 0.952 | 0.954 | 0.936 |
| 3 | | | 1.000 | 0.952 | 0.940 | 0.938 | 0.945 | 0.920 |
| 4 | | | | 1.000 | 0.938 | 0.920 | 0.921 | 0.901 |
| 5 | | | | | 1.000 | 0.979 | 0.971 | 0.962 |
| 6 | | | | | | 1.000 | 0.990 | 0.981 |
| 7 | | | | | | | 1.000 | 0.981 |
| 8 | | | | | | | | 1.000 |

Table 5.4: Correlation matrix of SST monthly values for the latitudinal zones over 20 years data set.

### 5.2.2 Sea Surface Temperature Temporal Variability

The results presented so far were related to the spatial variation of temperatures throughout the study area. We now focus on the temporal variability of SST.

The colour maps (B.1 to B.3) in the appendix B show an example of the SST temporal variation along the southern Brazilian coast. Shallow coastal water pixels are the main source of the SST data (see figure 5.2 in methodology section for the extracted pixels used in the study area).

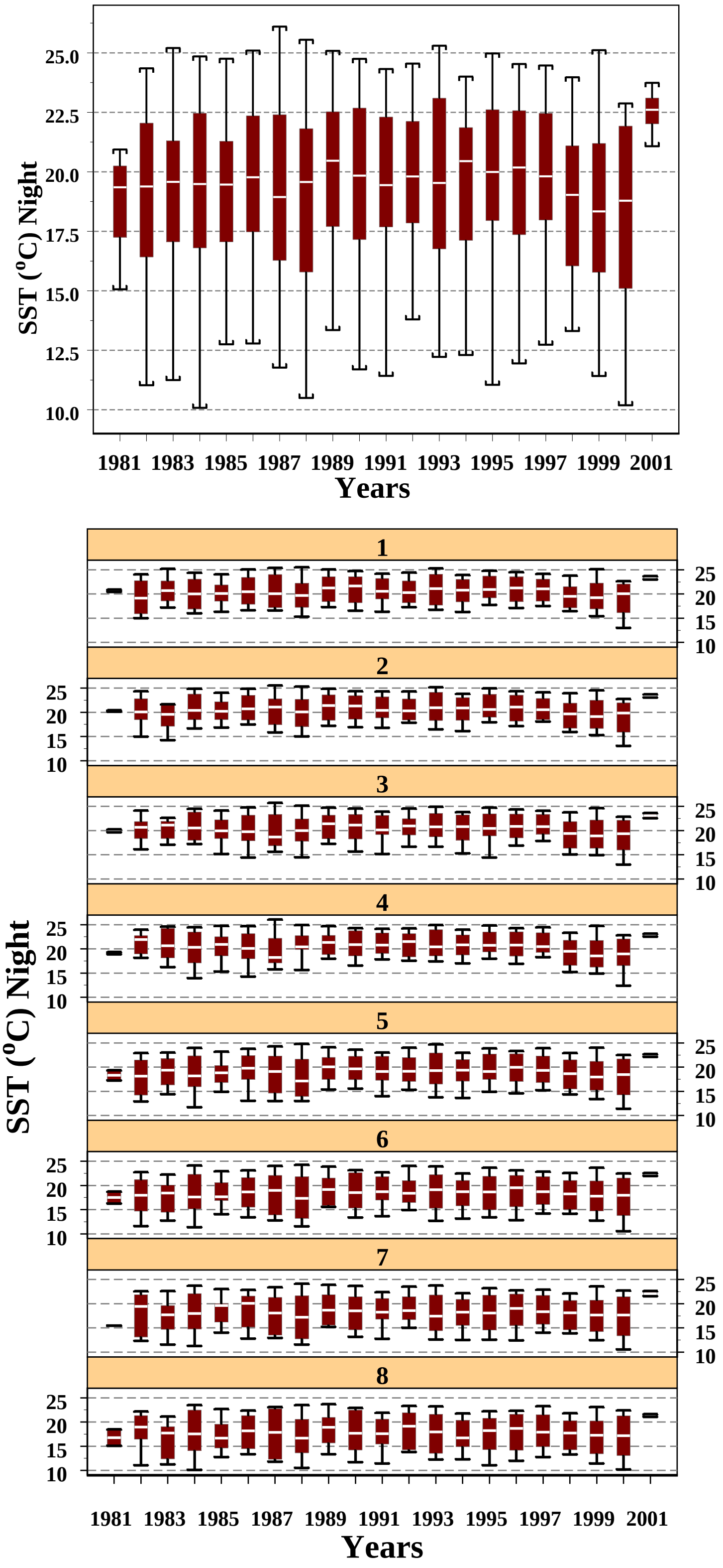


Figure 5.11: Annual-averaged SST (°C) between November 1981 and February 2001, for the whole study area (top) and discriminated by the latitudinal zones (bottom) over years (1981 and 2001 are incomplete years).

These data are the monthly-averaged SST images throughout the years of 1998, 1999 and 2000. From the 20 years data set (total of 982 colour images), we chose these periods to illustrate since they are years relevant to the data on the diet of franciscana, and in addition that there is chlorophyll-*a* data for the same period of time. The maps of chlorophyll-*a* are illustrated in appendix B.

It is clear that there are strong monthly fluctuations in this region, with the waters being cooled (<17°C) from southern towards northern region around May, and about June/July the whole coastal area is influenced by these waters (figures B.1 to B.3). From October/November the waters start being heated (∼20°C) from northern towards southern coast, and about December the whole southern Brazilian coast is characterised by water temperatures >20°C. From all the colour maps (figures B.1 to B.3) the lower temperatures in the coastal area are about August and September (austral winter), and the higher values about February and March (austral summer).

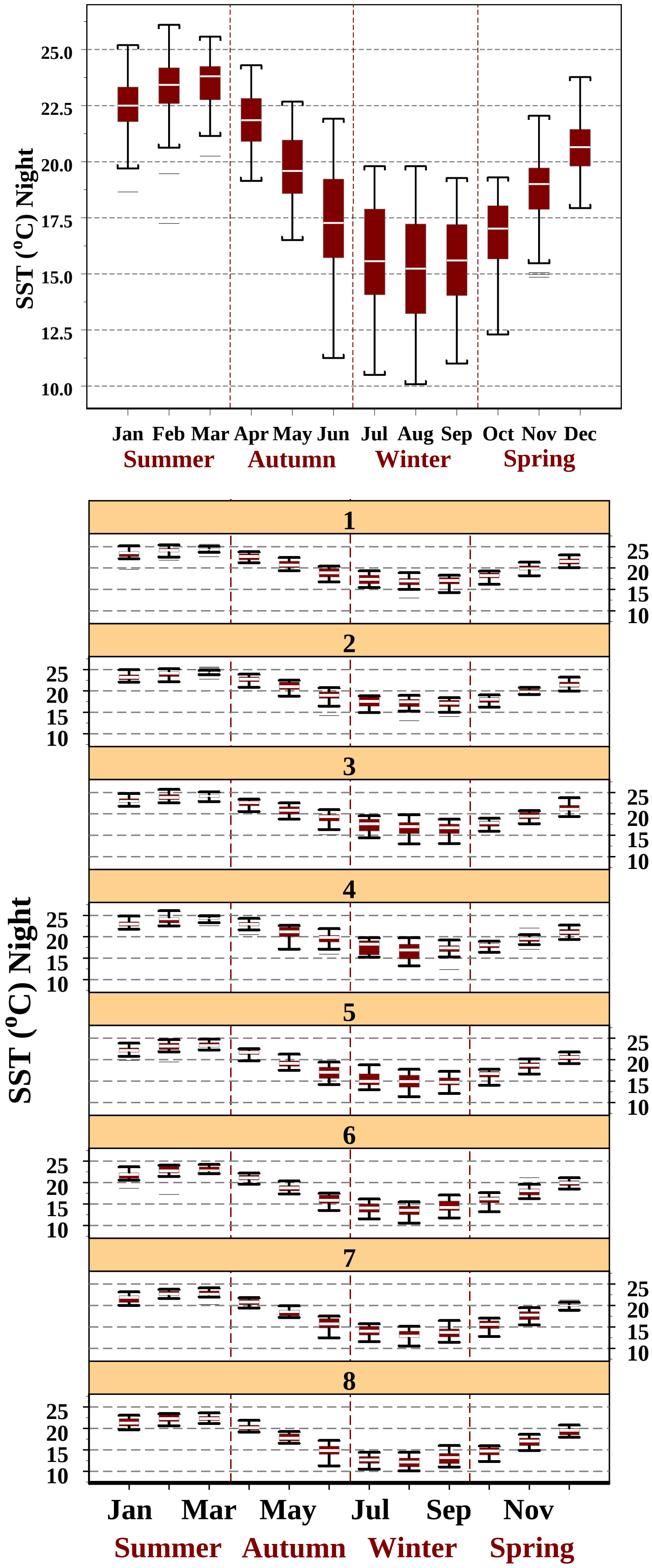


Figure 5.12: Monthly-averaged SST (°C) for the whole study area (top) and discriminated by the latitudinal zones (bottom) over months.

The influence of cold waters from the south throughout inshore areas during winter time, and the presence of warmer waters for most of the months are apparent.

The following analyses investigate those temporal variability of temperature observed from the colour maps, however for the whole data set period (20 years). They are based on monthly-averaged values, which were calculated from the individual weekly-averaged images of each particular month, as previously described. The analyses are expressed firstly for the entire study area, afterwards splitting into latitudinal zones.

The results revealed no significant inter-annual differences in the temperature (df= 18, F= 0.98, $p$= 0.456, see top graphic of figure 5.11). The seasonal variation however revealed significant differences throughout months (df= 11, F= 508.10, $p$<0.001, see top graphic of figure 5.12)). Additionally, the interaction of month and year effects (Two-way ANOVA to look at seasonal cycle differences from year to year) showed no significant differences for the whole area (df= 11, F= 0.94, $p$= 0.438), similarly when discriminated by the zones (table 5.5, right side).

| **SST Month analysis** | | | | | | | | | | | | | | | | **Interaction effect** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | **Estimated means ($^{o}$C)** | | | | | | | | | | | | **Month : Year** | | | |
| **Zone** | **df** | **F** | ***p*** | **Jan** | **Feb** | **Mar** | **Apr** | **May** | **Jun** | **Jul** | **Aug** | **Sep** | **Oct** | **Nov** | **Dec** | **Zone** | **df** | **F** | ***p*** |
| **1** | 11 | 148.92 | <0.001 | 23.3 | 24.1 | 24.3 | 22.7 | 20.9 | 18.8 | 17.3 | 16.7 | 16.9 | 18.1 | 20.0 | 21.5 | **1** | 11 | 0.69 | 0.746 |
| **2** | 11 | 131.15 | <0.001 | 23.3 | 24.0 | 24.3 | 22.6 | 21.0 | 18.8 | 17.4 | 17.2 | 16.9 | 17.9 | 19.9 | 21.5 | **2** | 11 | 1.58 | 0.107 |
| **3** | 11 | 101.87 | <0.001 | 23.1 | 24.0 | 24.1 | 22.5 | 20.8 | 18.9 | 17.4 | 16.8 | 16.6 | 17.8 | 19.5 | 21.3 | **3** | 11 | 0.45 | 0.926 |
| **4** | 11 | 80.13 | <0.001 | 23.1 | 24.0 | 24.2 | 22.8 | 20.9 | 19.4 | 17.6 | 16.7 | 17.0 | 18.0 | 19.5 | 21.1 | **4** | 11 | 1.77 | 0.062 |
| **5** | 11 | 128.49 | <0.001 | 22.1 | 23.0 | 23.4 | 21.6 | 19.2 | 16.9 | 15.3 | 14.8 | 15.0 | 16.4 | 18.6 | 20.5 | **5** | 11 | 0.42 | 0.945 |
| **6** | 11 | 140.97 | <0.001 | 21.7 | 22.6 | 23.0 | 21.1 | 18.7 | 15.9 | 14.0 | 13.4 | 14.5 | 15.8 | 18.1 | 19.9 | **6** | 11 | 0.90 | 0.538 |
| **7** | 11 | 201.66 | <0.001 | 21.6 | 22.7 | 22.7 | 20.8 | 18.4 | 15.7 | 13.9 | 13.1 | 13.7 | 15.3 | 17.7 | 19.9 | **7** | 11 | 0.41 | 0.952 |
| **8** | 11 | 212.17 | <0.001 | 21.3 | 22.3 | 22.4 | 20.3 | 17.9 | 14.8 | 12.8 | 12.1 | 13.1 | 14.7 | 16.9 | 19.3 | **8** | 11 | 0.82 | 0.616 |

Table 5.5: The results of the ANOVA analysis of the temperatures ($^{o}$C) over months (left side), and the two-way ANOVA of the interaction between month and year (right side) to investigate the monthly cycle (seasonal) over years. The analyses are discriminated by the latitudinal zones.

The water temperatures were also compared over years for each one of the latitudinal zones (ANOVA) and no significant differences were found (table 5.6, see bottom graphic of figure 5.11). Additionally, the temperatures according to month are again significantly different when analysed separately for each zone (table 5.5), confirming similar seasonal cycles among the zones (see bottom graphic of figure 5.12). As expected, the northern zones presented higher temperatures, whereas towards the southern zones the cycles exhibit lower temperatures.

| **SST Year analysis** | | | | **Estimated means ($^{o}$C)** | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Zone** | **df** | **F** | ***p*** | **82** | **83** | **84** | **85** | **86** | **87** | **88** | **89** | **90** | **91** | **92** | **93** | **94** | **95** | **96** | **97** | **98** | **99** | **00** |
| **1** | 18 | 0.63 | 0.885 | 19.3 | 20.8 | 20.0 | 20.3 | 20.7 | 20.5 | 19.8 | 21.1 | 20.9 | 20.8 | 20.6 | 21.0 | 20.6 | 21.3 | 21.0 | 20.8 | 19.7 | 19.6 | 19.1 |
| **2** | 18 | 0.67 | 0.848 | 20.3 | 18.9 | 20.6 | 20.4 | 21.0 | 20.5 | 20.0 | 21.1 | 20.1 | 20.8 | 20.7 | 21.0 | 20.6 | 21.2 | 20.9 | 20.7 | 19.6 | 19.5 | 18.9 |
| **3** | 18 | 0.59 | 0.917 | 20.4 | 20.4 | 20.6 | 19.9 | 20.1 | 20.0 | 20.0 | 20.9 | 20.7 | 20.6 | 20.7 | 20.9 | 20.5 | 20.8 | 20.8 | 21.1 | 19.3 | 19.2 | 18.8 |
| **4** | 18 | 0.82 | 0.683 | 20.6 | 20.7 | 20.0 | 20.5 | 20.2 | 19.7 | 20.5 | 21.1 | 21.0 | 21.0 | 20.9 | 21.0 | 20.9 | 21.3 | 20.8 | 21.2 | 19.2 | 19.0 | 18.7 |
| **5** | 18 | 0.52 | 0.952 | 18.0 | 19.1 | 18.6 | 18.7 | 19.4 | 18.6 | 17.9 | 19.9 | 19.7 | 19.2 | 19.4 | 19.4 | 19.1 | 19.7 | 19.7 | 19.4 | 18.6 | 18.3 | 17.9 |
| **6** | 18 | 0.31 | 0.998 | 17.8 | 17.6 | 18.2 | 18.3 | 18.4 | 18.2 | 17.6 | 19.2 | 18.7 | 18.7 | 18.9 | 18.6 | 18.3 | 18.5 | 18.9 | 18.8 | 18.2 | 17.9 | 17.5 |
| **7** | 18 | 0.34 | 0.996 | 18.2 | 17.2 | 18.3 | 18.8 | 18.8 | 17.7 | 17.5 | 19.0 | 18.2 | 18.5 | 19.0 | 17.9 | 18.0 | 18.0 | 18.5 | 18.5 | 17.8 | 17.7 | 17.4 |
| **8** | 18 | 0.27 | 0.999 | 17.8 | 16.3 | 17.5 | 17.3 | 17.8 | 17.4 | 16.9 | 18.7 | 17.5 | 17.6 | 18.5 | 17.8 | 17.2 | 17.5 | 18.0 | 17.9 | 17.4 | 17.1 | 17.0 |

Table 5.6: The results of the ANOVA analysis of the temperatures ($^{o}$C) over years, discriminated by the latitudinal zones. The years 1981 and 2001 were discarded as they are incompletes.

Time series analyses were used to look for cyclic patterns and trends. The monthly time series (from November 1981 to April 2001, N= 232) exhibits regular cycles for all the latitudinal zones (figure 5.13). Furthermore, these figures also show that the seasonal pattern is fairly stable over time for all zones.

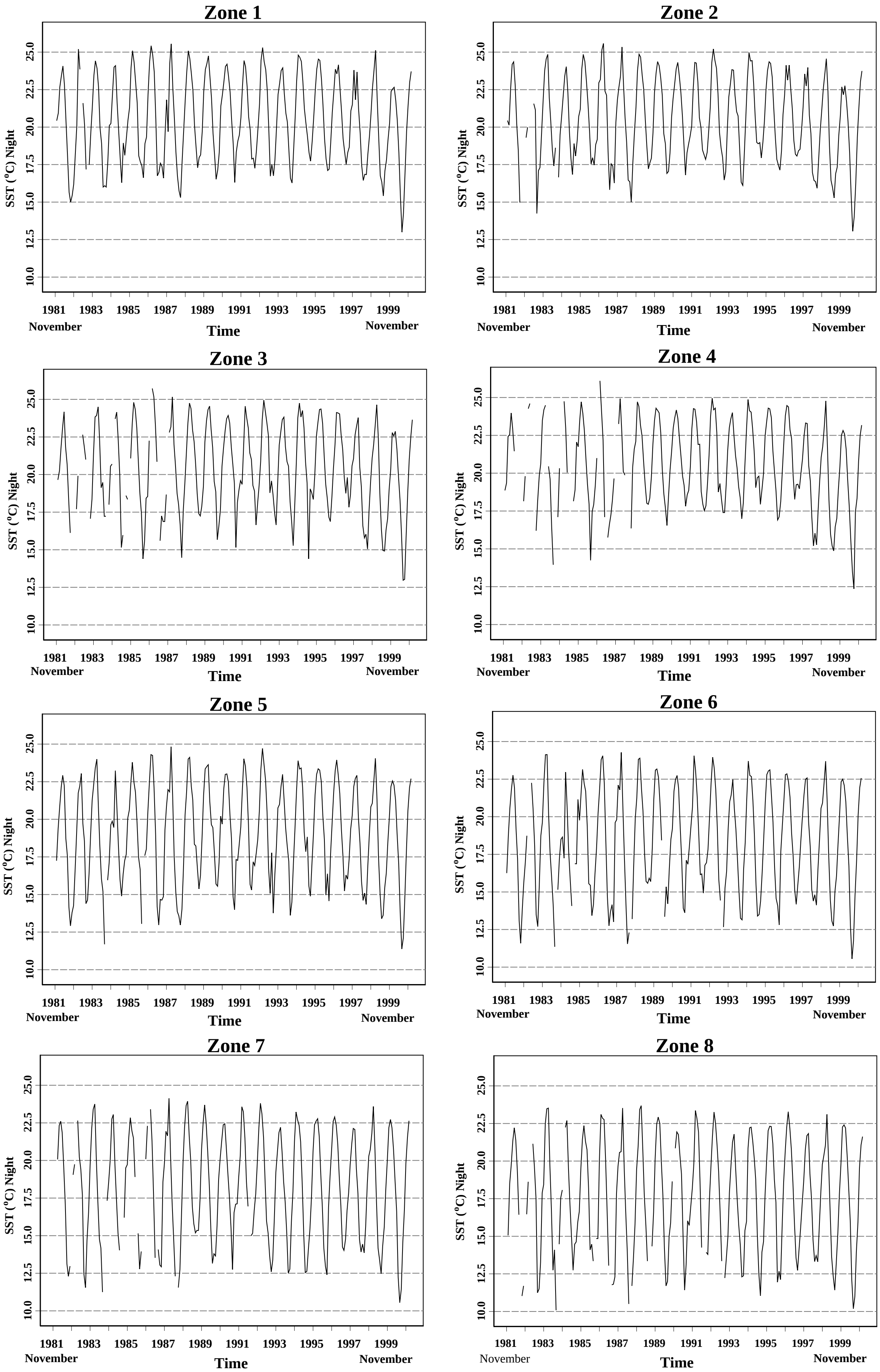


Figure 5.13: Monthly time series of SST ($^o$C), from November 1981 to April 2001 (N= 232 months).

The data are clearly cyclic, but we test for the existence of significant cyclic behaviour. There is one important element to this: the autocorrelation plot (figure 5.14). The plot shows clear cycles, with a period of roughly 12 months (as expected). What the $y$ axis shows is the correlation between temperatures taken different values of months apart (lag). There is obviously a perfect correlation between temperature values and themselves (so ACF= 1.0 for lag= 0). There is a strong negative correlation between the temperature in the month 12 and the temperature 6 months previous, and a strong and significant correlation between this temperature and 11-12 months previous. The horizontal dotted lines show correlations that would be significant at the 5% level. So we conclude that there are indeed significant strong cycles and with a period of 1 year.

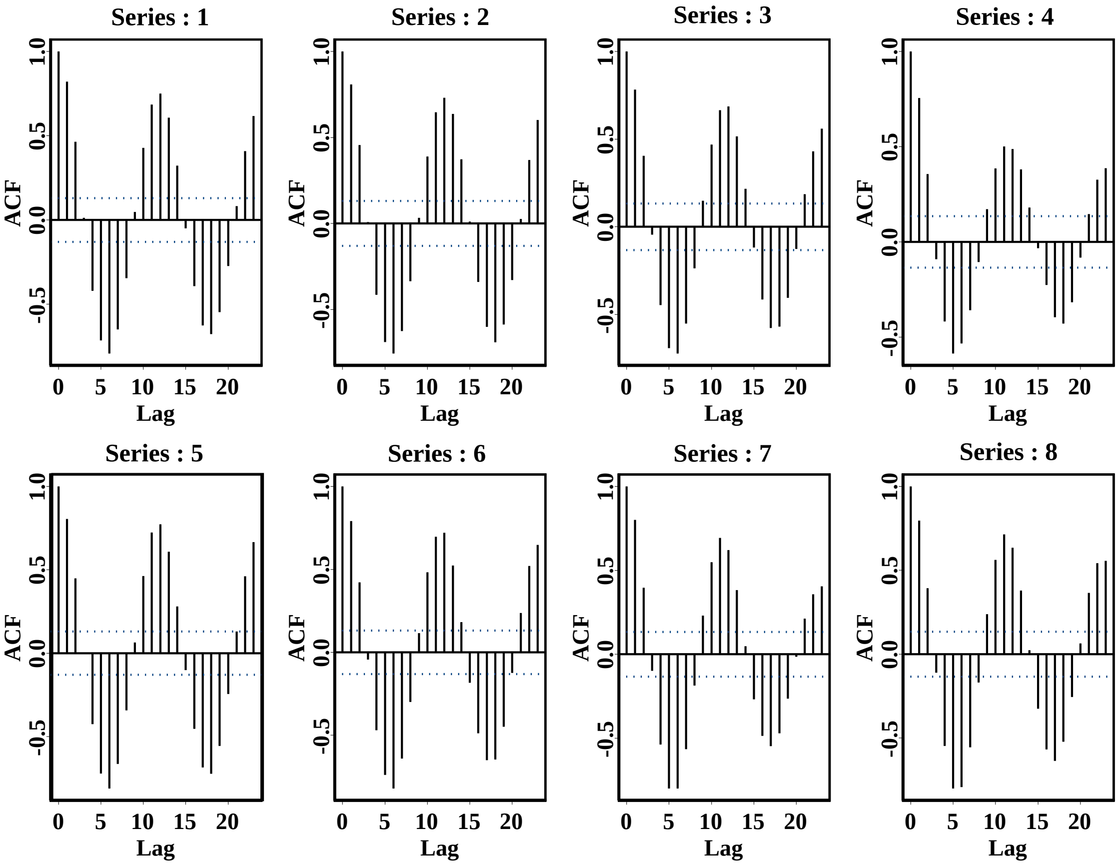


Figure 5.14: Autocorrelation plots of the multiple SST time series to look for evidence of cyclic behaviour (seasonal pattern).

It is a useful diagnostic to decompose a time series into the component of residuals. Residuals are the important tool for verifying different patterns from the time series models, or relevant differences. For the ACF plots of the residuals from the overall seasonal cycle, it appears that there are similar cyclic behaviours to the time series models (figure 5.15). Nevertheless, the zones 3 to 8 show stronger cyclic patterns than the very northern zones 1 and 2. However it may be expected as at higher latitudes there are stronger seasonal regimes.

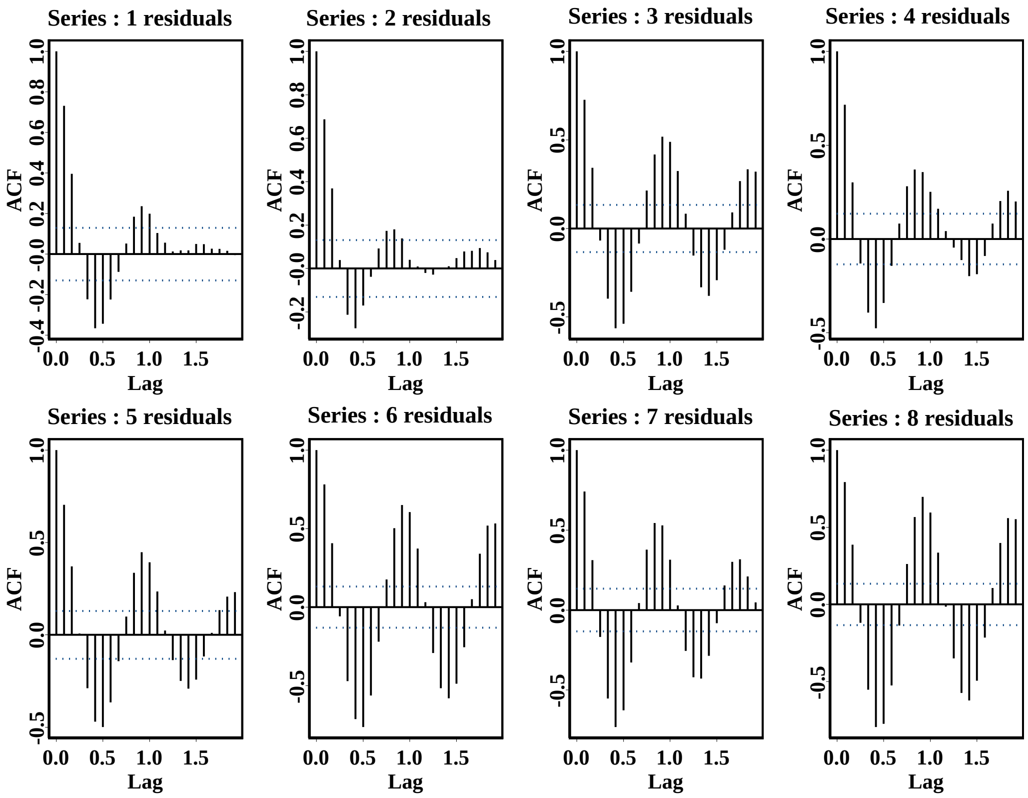


Figure 5.15: Autocorrelation plots of the residuals component from the SST time series models to examine cyclic patterns.

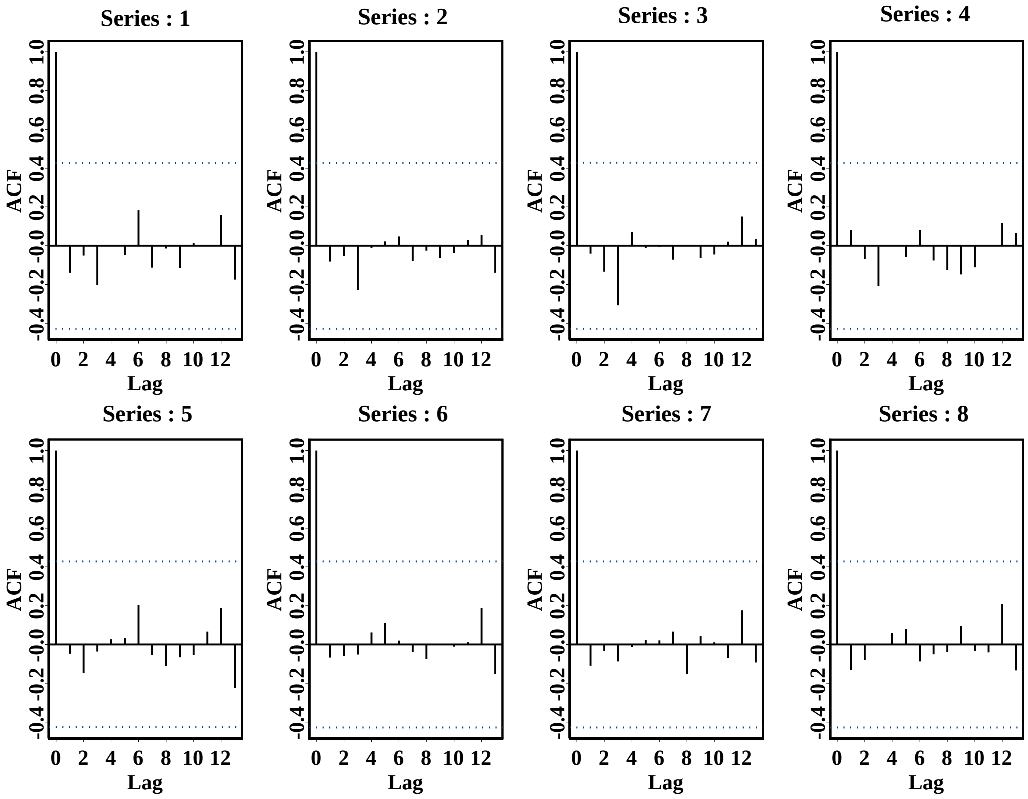


Figure 5.16: Autocorrelation plots of the multiple SST time series to look for patterns across years.

There is a near perfect cycle with the period= 12 (figure 5.14, on top of the previous page). However, what about patterns across years? We use the same autocorrelation function, but now considering the yearly means (figure 5.16, on bottom of the previous page), and there is no patterns across years. There are no significant cycles, as no ACF line reaches the dotted lines (correlations that would be significant at 5%). There is strong pattern from month to month within years (January is warm, July is cold). But there is no periodic pattern at all from year to year. Overall, there is no inter-annual cyclic pattern of the water temperature in the study area through the 20 years period analysed.

### 5.2.3 Chlorophyll-*a* Spatial Variability

From the whole study area, the monthly-averaged chlorophyll-*a* (mg/m$^3$) varies between 0.46 and 9.12, with a mean of 3.38 (SE= 0.08, SD= 1.61, Variance= 2.59, N= 416).

The overall mean values of the chlorophyll-*a* through the latitudinal zones - for the 52 months data set - vary from 1.86 to 4.01 mg/m$^3$, generally increasing from the northern to the southern zones (see table 5.7 and figure 5.17).

| Zones | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| Min. | 0.46 | 0.58 | 0.76 | 0.73 | 1.42 | 1.26 | 1.36 | 1.50 |
| Mean | 1.86 | 2.23 | 3.23 | 3.79 | 4.05 | 3.85 | 4.00 | 4.01 |
| Max. | 5.39 | 5.72 | 6.52 | 8.35 | 9.12 | 8.09 | 8.37 | 8.47 |
| SE | 0.14 | 0.14 | 0.18 | 0.19 | 0.20 | 0.22 | 0.23 | 0.22 |
| SD | 1.04 | 1.02 | 1.30 | 1.40 | 1.47 | 1.57 | 1.67 | 1.58 |
| Variance | 1.08 | 1.04 | 1.69 | 1.95 | 2.15 | 2.46 | 2.80 | 2.51 |

Table 5.7: Monthly-averaged chlorophyll-*a*, in mg/m$^3$, for each latitudinal zone.

The analysis of means between the areas demonstrated no significant differences for the northern zones 1 and 2, or any of the combinations from the zones 4 to 8 (table 5.8). Nevertheless, for the neighbouring zones 2 and 3; 3 and 4 the null hypothesis is rejected. The central zone 3 seems mostly differing from the other latitudinal zones, and figure 5.18 illustrates clearly such divergences. The chlorophyll-*a* values also differed significantly between the zones according to the analysis of variance (df= 7, F= 19.98, $p$<0.001).

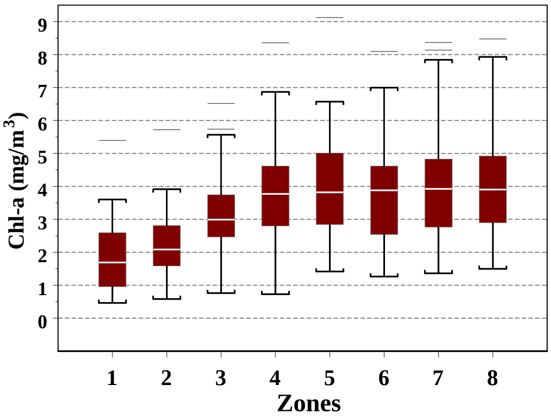


Figure 5.17: Monthly-averaged chlorophyll-*a* (mg/m$^3$) ranges for each latitudinal zone, from September 1997 to December 2001.

| t($p$) | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| 1 | | 1.83(0.07) | 5.92(<0.01) | 7.99(<0.01) | 8.78(<0.01) | 7.62(<0.01) | 7.84(<0.01) | 8.19(<0.01) |
| 2 | | | 4.35(<0.01) | 6.50(<0.01) | 7.35(<0.01) | 6.24(<0.01) | 6.52(<0.01) | 6.82(<0.01) |
| 3 | | | | 2.13(0.04) | 3.03(<0.01) | 2.20(0.03) | 2.63(0.01) | 2.76(<0.01) |
| 4 | | | | | 0.93(0.35) | 0.20(0.84) | 0.70(0.49) | 0.76(0.45) |
| 5 | | | | | | 0.68(0.50) | 0.16(0.87) | 0.13(0.90) |
| 6 | | | | | | | 0.48(0.63) | 0.53(0.60) |
| 7 | | | | | | | | 0.04(0.97) |

Table 5.8: Two-Sample t-Test for the chlorophyll-$a$ concentration between the latitudinal zones, with the values of t and $p$ (in parenthesis).

MCA offers more comprehensive results of the ANOVA model of all pairwise differences in chlorophyll-$a$ mean between the zones. Printed values of figure 5.19 indicate via asterisks the confidence intervals which exclude zero; these can also be identified by noting intervals that do not intersect the vertical reference line at zero. These identified comparisons corresponding to pairs of the chlorophyll-$a$ means which can be stated as different. Summing up, the zones 1 and 2 are not significantly different, but both are significantly different in terms of chlorophyll-$a$ compared with all the other zones.

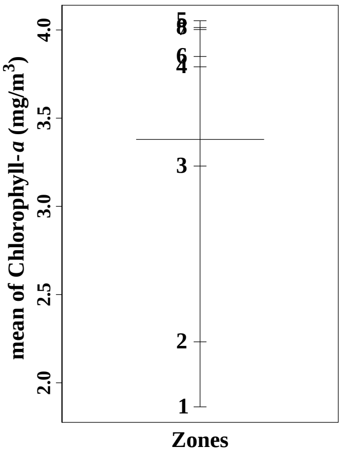
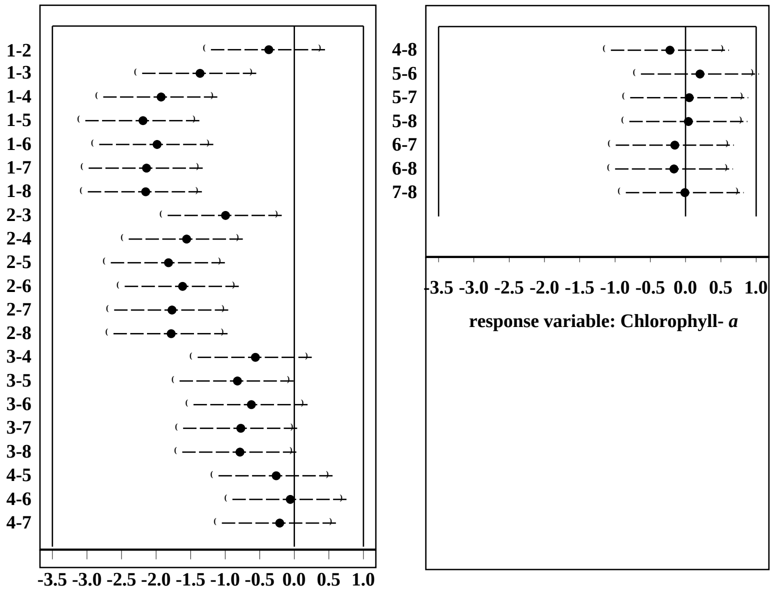


Figure 5.18: Plot design of the treatment means of the chl-$a$ for the factor "latitudinal zone".



| Zones | | Estimate | SE | Lower Bound | Upper Bound |
|---|---|---|---|---|---|
| **1** | **2** | -0.369 | 0.275 | -1.210 | 0.467 |
| **1** | **3** | -1.370 | 0.275 | -2.200 | -0.529**** |
| **1** | **4** | -1.930 | 0.275 | -2.760 | -1.090**** |
| **1** | **5** | -2.190 | 0.275 | -3.030 | -1.350**** |
| **1** | **6** | -1.990 | 0.275 | -2.820 | -1.150**** |
| **1** | **7** | -2.140 | 0.275 | -2.980 | -1.300**** |
| **1** | **8** | -2.150 | 0.275 | -2.990 | -1.310**** |
| **2** | **3** | -0.996 | 0.275 | -1.830 | -0.159**** |
| **2** | **4** | -1.560 | 0.275 | -2.390 | -0.722**** |
| **2** | **5** | -1.820 | 0.275 | -2.660 | -0.983**** |
| **2** | **6** | -1.620 | 0.275 | -2.450 | -0.781**** |
| **2** | **7** | -1.770 | 0.275 | -2.610 | -0.933**** |
| **2** | **8** | -1.780 | 0.275 | -2.620 | -0.945**** |
| **3** | **4** | -0.563 | 0.275 | -1.400 | 0.274 |
| **3** | **5** | -0.824 | 0.275 | -1.660 | 0.012 |
| **3** | **6** | -0.622 | 0.275 | -1.460 | 0.215 |
| **3** | **7** | -0.774 | 0.275 | -1.610 | 0.063 |
| **3** | **8** | -0.786 | 0.275 | -1.620 | 0.051 |
| **4** | **5** | -0.261 | 0.275 | -1.100 | 0.575 |
| **4** | **6** | -0.059 | 0.275 | -0.895 | 0.777 |
| **4** | **7** | -0.211 | 0.275 | -1.050 | 0.625 |
| **4** | **8** | -0.223 | 0.275 | -1.060 | 0.613 |
| **5** | **6** | 0.202 | 0.275 | -0.634 | 1.040 |
| **5** | **7** | 0.05 | 0.275 | -0.786 | 0.887 |
| **5** | **8** | 0.038 | 0.275 | -0.798 | 0.875 |
| **6** | **7** | -0.152 | 0.275 | -0.989 | 0.684 |
| **6** | **8** | -0.164 | 0.275 | -1.000 | 0.672 |
| **7** | **8** | -0.012 | 0.275 | -0.848 | 0.825 |

Figure 5.19: Chlorophyll-$a$ ANOVA for all pairwise means and the levels "zone", with 95% simultaneous confidence intervals for specified linear combinations, by the Tukey's method.

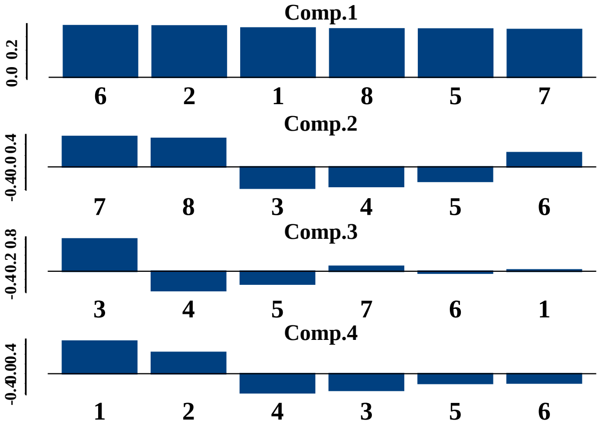
The mean and variance analyses confirm the spatial differences of chlorophyll-$a$ between the northern-most zones 1 and 2, against the southern zones 4 to 8, with the central zone 3 most likely a transitional zone.

The following analysis investigate the chlorophyll-$a$ concentration spatial distribution at higher resolution, using the PCA. For the monthly-averaged chlorophyll-$a$, the first principal component (PC) explains 77.6% of the variance, the first two principal components together explain 86.0%, and the first three PCs explain 92.1% (table 5.9).

| | Comp.1 | Comp.2 | Comp.3 | Comp.4 | Comp.5 | Comp.6 | Comp.7 | Comp.8 |
|---|---|---|---|---|---|---|---|---|
| Standard deviation | 2.492 | 0.817 | 0.703 | 0.533 | 0.444 | 0.241 | 0.229 | 0.192 |
| Proportion of Variance | 0.776 | 0.084 | 0.062 | 0.035 | 0.025 | 0.007 | 0.007 | 0.005 |
| Cumulative Proportion | 0.776 | 0.860 | 0.921 | 0.957 | 0.982 | 0.989 | 0.995 | 1.000 |

Table 5.9: Principal components variance for the latitudinal zones' monthly-averaged chlorophyll-$a$.

The loadings values of chlorophyll-$a$ are shown in the figure 5.20. The loadings for the first principal component (representing the overall mean), have coefficients of about 0.3 to 0.4. The second component is negatively associated with the zones 1 to 5, and positively with the zones 6 to 8 - northern and southern zones contrast. The third component presents the zone 3 weighting heavily and contrasted with zones 4 and 5 (figure 5.20). Remember that the loadings suppress very small values to emphasize the more important ones.



| Zones | Comp.1 | Comp.2 | Comp.3 | Comp.4 |
|---|---|---|---|---|
| 1 | 0.364 | -0.221 | | 0.667 |
| 2 | 0.379 | -0.169 | | 0.433 |
| 3 | 0.298 | -0.374 | 0.807 | -0.340 |
| 4 | 0.333 | -0.345 | -0.480 | -0.390 |
| 5 | 0.356 | -0.254 | -0.317 | -0.198 |
| 6 | 0.381 | 0.248 | | -0.189 |
| 7 | 0.352 | 0.535 | 0.123 | |
| 8 | 0.357 | 0.501 | | -0.145 |

Figure 5.20: Principal components loadings for the latitudinal zones' monthly-averaged chlorophyll-$a$.

From the biplot (figure 5.21) it seems that the latitudinal zones could represent different groups, with similar loadings signs the zones 6, 7, and 8, and the zones 1 to 5 diverging from them. From those, zone 3 followed by zone 4 look spaced out from the other zones.

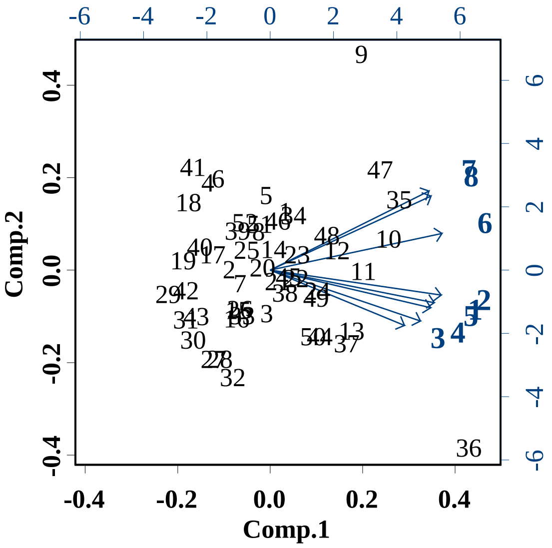


Figure 5.21: Biplot loadings of the monthly averaged chlorophyll-$a$ concentration. The zones are plotted in blue and the data are plotted in black.

The positive correlations of the chlorophyll-$a$ between all the zones (table 5.10) indicate that they vary together. However, it points to stronger correlations the zones 1 and 2; and between 6, 7, and 8 (table 5.10). The zone 3 followed by 4 represent the weakest correlations when comparing all the chlorophyll-$a$ combinations between the zones. The variations of chlorophyll-$a$ concentration over time are better investigated below in the section 5.2.4.

Overall, the monthly averaged chlorophyll-$a$ values vary through the study region, and in accordance with the previous results, may be divided into two distinct groups of (a) northern zones 1 and 2, and (b) southern zones 5 to 8; with the zones 3 and 4 as a transitional group.

| Zones | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| 1 | 1.000 | 0.942 | 0.678 | 0.731 | 0.795 | 0.786 | 0.731 | 0.708 |
| 2 | | 1.000 | 0.693 | 0.789 | 0.830 | 0.844 | 0.769 | 0.771 |
| 3 | | | 1.000 | 0.554 | 0.610 | 0.640 | 0.563 | 0.554 |
| 4 | | | | 1.000 | 0.807 | 0.733 | 0.591 | 0.648 |
| 5 | | | | | 1.000 | 0.842 | 0.653 | 0.697 |
| 6 | | | | | | 1.000 | 0.905 | 0.912 |
| 7 | | | | | | | 1.000 | 0.940 |
| 8 | | | | | | | | 1.000 |

Table 5.10: Correlation matrix of monthly chlorophyll-$a$ values for the latitudinal zones over 4 years data set.

### 5.2.4 Chlorophyll-$a$ Temporal Variability

The monthly-averaged images of chlorophyll-$a$ concentration from SeaWIFS off the southern Brazilian coast, from January 1998 to December 2000, are illustrated in the appendix B (figures B.4 to B.6). Pixels located in shallow coastal water are the main source of high chlorophyll-$a$ values (see figure 5.4 in the methodology section for the extracted pixels of the study area).

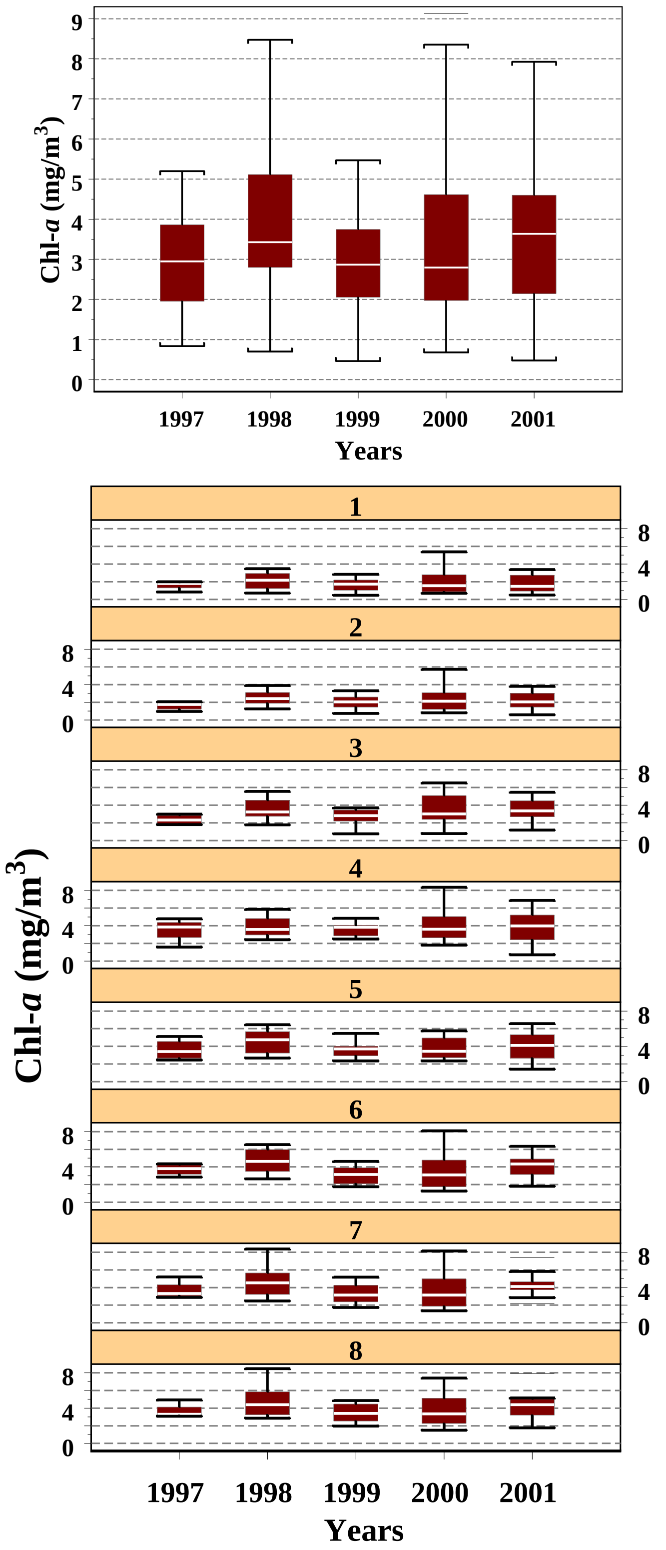


Figure 5.22: Monthly-averaged chlorophyll-$a$ (mg/m$^3$), between September 1997 and December 2001, for the whole study area (top) and discriminated by the latitudinal zones (bottom) over years (1997 is an incomplete year).

Maps of sea surface temperatures in the study area for comparable years (1998 to 2000), are illustrated in the same appendix B (figures B.1 to B.3).

Generally, chlorophyll-$a$ concentration values start increasing from June, and reaching high values during winter time (July to September). Reduced values (<3mg/m$^3$) occur through summer (January to March). High pigment concentration values appear in the southern portion of the study area normally in May, and appear migrating northwards near to the coast. Around July, except for 1999, it is possible to notice higher chlorophyll-$a$ values mainly in the southern section of the study area.

Notably, the greater concentrations occur south of 32$^o$S, reducing considerably close to 31$^o$S, and only occasionally (*e.g.* September 1998, July 2000) reaching north of this latitude.

Moreover, in the vicinities of 32$^o$S closer to the coast, some increases in chlorophyll-$a$ concentration are observed (*e.g.* January to March 98), perhaps not associated with these northward migrations. This region is close to the mouth of the Patos Lagoon, which is a very representative estuary on the southern Brazilian coast.

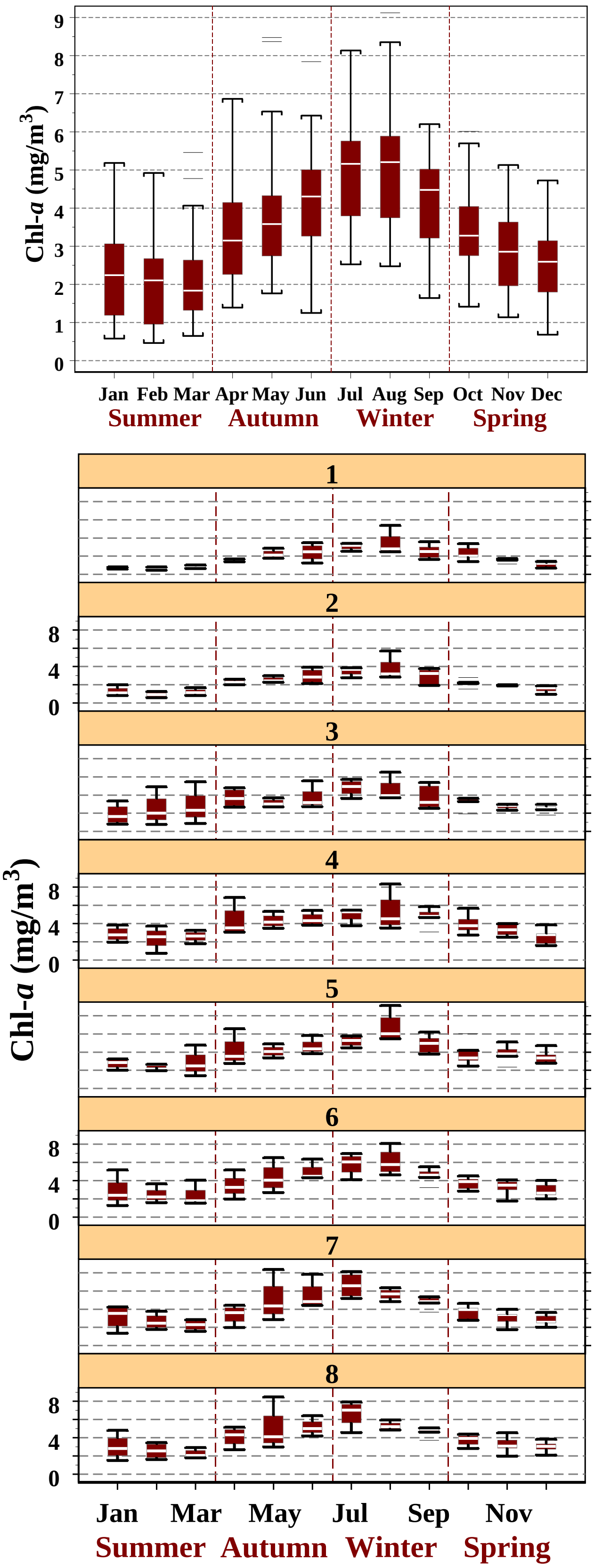


Figure 5.23: Monthly-averaged chlorophyll-$a$ (mg/m$^3$), between September 1997 and December 2001, for the whole study area (top) and discriminated by the latitudinal zones (bottom) over months.

On the whole, chlorophyll-$a$ seems to exhibit a temporal evolution pattern in the study area, which can be investigated in further analyses.

The following figures (5.22 and 5.23) summarise the temporal variation (years, months, and seasons). The analyses are expressed firstly for the whole study region, and also divided into latitudinal zones. Two-way ANOVA was also applied to look for seasonal variation from year to year, the interaction effect, of monthly-averaged chlorophyll-$a$ for the whole area and for each zone.

The results revealed significant inter-annual differences in the chlorophyll-$a$ concentration (df= 3, F= 5.52, $p$= 0.002, not considering the incomplete year 1997, see top graphic of figure 5.22). However, this is comparing only 4 years of data. When the chlorophyll-$a$ concentration were compared over years for each of the latitudinal zones individually, no significant differences were found (table 5.12, see bottom graphic of figure 5.22). The seasonal variation revealed significant differences throughout months (df= 11, F= 23.52, $p$<0.001, see top graphic of figure 5.23). The seasonal variation over years (interaction between month and year effects) showed significant differences for the whole area (df= 11, F= 1.69, $p$= 0.012), although no significant differences were found when dividing the area into the latitudinal zones (table 5.11, right side).

Additionally, the concentrations according to month are also significantly different when analysed separately for each latitudinal zone (table 5.11, see bottom graphic of figure 5.23).

| **Chl *a* Month analysis** | | | | | | | | | | | | | | | | **Interaction effect** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | **Estimated means (mg m$^{-3}$)** | | | | | | | | | | | | **Month : Year** | | | |
| **Zone** | **df** | **F** | ***p*** | **Jan** | **Feb** | **Mar** | **Apr** | **May** | **Jun** | **Jul** | **Aug** | **Sep** | **Oct** | **Nov** | **Dec** | **Zone** | **df** | **F** | ***p*** |
| **1** | 11 | 9.25 | <0.001 | 0.7 | 0.6 | 0.8 | 1.6 | 2.2 | 2.4 | 3.1 | 3.4 | 2.5 | 2.3 | 1.6 | 1.1 | **1** | 11 | 1.01 | 0.462 |
| **2** | 11 | 9.24 | <0.001 | 1.3 | 0.9 | 1.2 | 2.3 | 2.5 | 2.9 | 3.5 | 3.7 | 2.9 | 2.2 | 2.0 | 1.5 | **2** | 11 | 1.94 | 0.076 |
| **3** | 11 | 2.46 | 0.019 | 1.9 | 2.4 | 2.7 | 3.7 | 3.1 | 3.7 | 4.8 | 4.5 | 3.8 | 3.1 | 2.7 | 2.5 | **3** | 11 | 1.95 | 0.075 |
| **4** | 11 | 3.37 | 0.002 | 2.8 | 2.4 | 2.6 | 4.2 | 4.3 | 4.5 | 5.0 | 5.2 | 4.7 | 4.0 | 3.3 | 2.6 | **4** | 11 | 0.76 | 0.671 |
| **5** | 11 | 4.74 | <0.001 | 2.7 | 2.5 | 2.8 | 4.1 | 4.1 | 4.6 | 5.2 | 6.7 | 4.9 | 3.8 | 3.8 | 3.5 | **5** | 11 | 1.80 | 0.101 |
| **6** | 11 | 4.87 | <0.001 | 2.8 | 2.4 | 2.3 | 3.4 | 4.3 | 4.9 | 5.8 | 6.1 | 4.5 | 3.7 | 3.2 | 2.9 | **6** | 11 | 1.05 | 0.430 |
| **7** | 11 | 6.19 | <0.001 | 3.2 | 2.6 | 2.3 | 3.4 | 5.0 | 5.5 | 6.6 | 5.6 | 4.7 | 3.7 | 3.0 | 2.8 | **7** | 11 | 1.33 | 0.260 |
| **8** | 11 | 5.98 | <0.001 | 3.0 | 2.5 | 2.2 | 4.1 | 4.9 | 5.2 | 6.6 | 5.3 | 4.7 | 3.7 | 3.2 | 3.0 | **8** | 11 | 2.12 | 0.053 |

Table 5.11: The results of the ANOVA analysis of the chlorophyll-$a$ (mg/m$^3$) over months (left side), and the two-way ANOVA of the interaction between month and year (right side) to investigate the monthly cycle (seasonal) over years. The analyses are discriminated by the latitudinal zones.

Nevertheless, those cycles seem to differ within the area. The northern zones presented lower chlorophyll-$a$ concentration cycles, whereas towards the southern zones the cycles exhibit higher concentrations. This behaviour is opposite to the temperature seasonal cycle in the area, where lower temperature cycles occur at southern zones and increasing towards northern (see figure 5.12). The chlorophyll-$a$ concentrations start increasing about April-May with higher values on July for the southern zones 8 to 6 and from the zone 5 the higher concentrations are later on August. It is possible that there is a northward flowing of waters with higher chlorophyll-$a$ from southern to northern zones through Autumn-Winter, which may explain such temporal variation along the coast.

| **Chl *a* Year analysis** | | | | **Estimated means (mg m$^{-3}$)** | | | |
|---|---|---|---|---|---|---|---|
| **Zone** | **df** | **F** | ***p*** | **1998** | **1999** | **2000** | **2001** |
| **1** | 4 | 0.37 | 0.829 | 2.1 | 1.7 | 2.0 | 1.8 |
| **2** | 4 | 0.70 | 0.597 | 2.5 | 2.1 | 2.4 | 2.2 |
| **3** | 4 | 1.59 | 0.191 | 3.5 | 2.7 | 3.5 | 3.5 |
| **4** | 4 | 0.17 | 0.951 | 3.9 | 3.6 | 4.0 | 3.8 |
| **5** | 4 | 0.74 | 0.572 | 4.6 | 3.6 | 4.1 | 4.1 |
| **6** | 4 | 1.89 | 0.128 | 4.7 | 3.1 | 3.6 | 4.1 |
| **7** | 4 | 1.53 | 0.210 | 4.8 | 3.3 | 3.7 | 4.3 |
| **8** | 4 | 1.20 | 0.324 | 4.7 | 3.5 | 3.8 | 4.2 |

Table 5.12: The results of the ANOVA analysis of the chlorophyll-$a$ (mg/m$^3$) over years, discriminated by the latitudinal zones. The year 1997 was discarded as it is incomplete.

The monthly time series (from September 1997 to December 2001, N= 52) exhibits regular chlorophyll-$a$ cycles for all the latitudinal zones (figure 5.24). However, these cycles are much less reproducible when compared with the SST time series models (see figure 5.13).

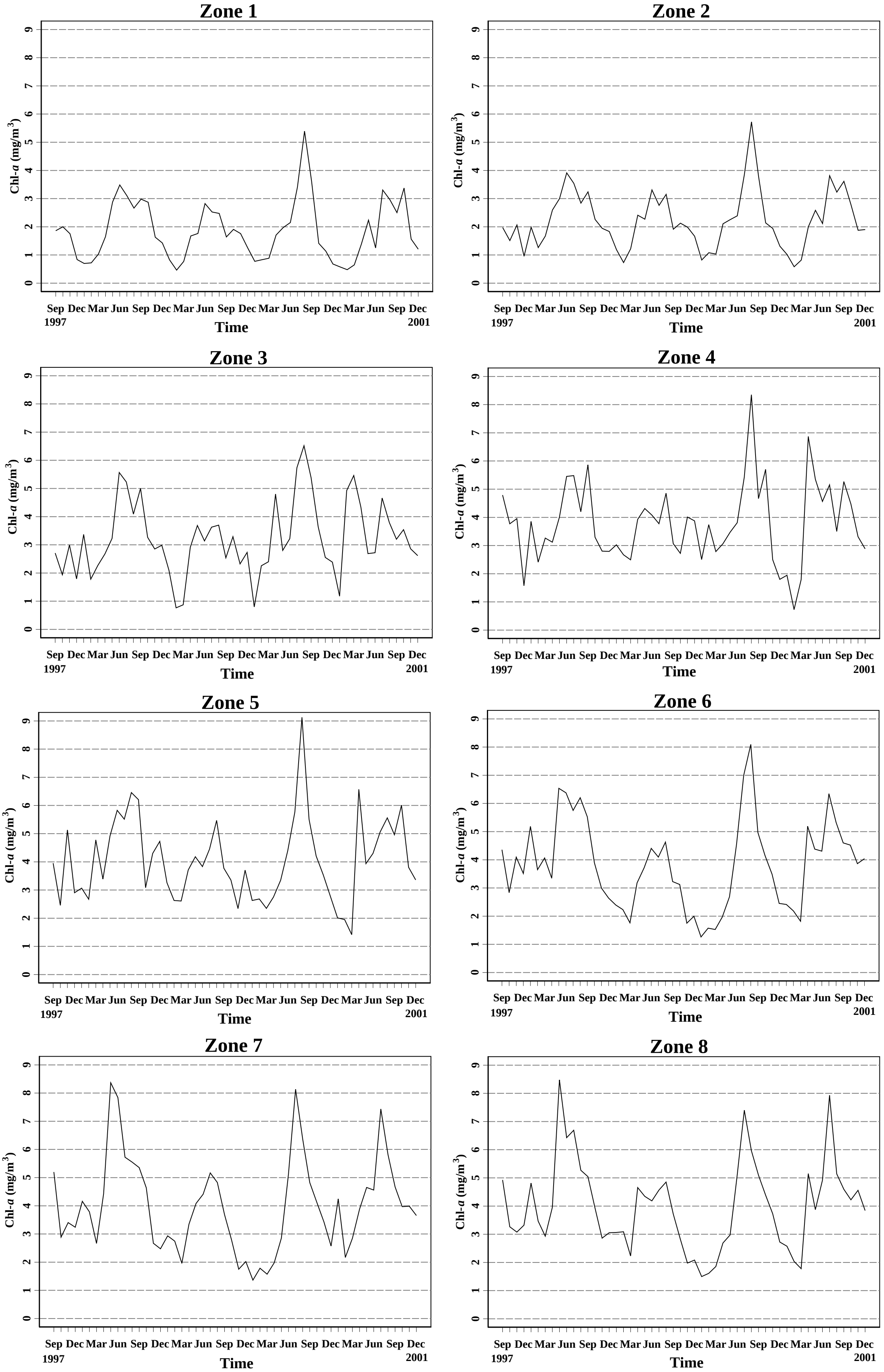


Figure 5.24: Monthly time series, of chlorophyll-*a* from November 1981 to April 2001 (N=52 months).

Moreover, the southern zones show higher amplitude of chlorophyll-$a$ concentrations cycles (figure 5.24). Furthermore, these figures also illustrate that the seasonal pattern is rather variable over time, though generally higher concentrations are in the winter seasons (July to September). Additionally, the seasonal pattern looks less clear in the transitional region along the area, the zones 3 to 5.

The data appear to be cyclical, and we test for the existence of significant cyclical behaviour by the autocorrelation plot (figure 5.25). The plot shows significant cycles of chlorophyll-$a$ concentrations (periods of approximately 12 months) for the zones 5 to 8, and 1 to 2. The $y$ axis shows the correlation between chlorophyll-$a$ taken different values of months apart (lag) (see PCA methodology on section 5.1.2 for further information). Therefore, there is a strong negative correlation between the chlorophyll-$a$ in month "12" and the chlorophyll-$a$ 6 months previous, and a reasonably strong and significant correlation between this chlorophyll-$a$ and 11-12 months previous. Remember that the horizontal dotted lines show significant correlations at the 5% level.

In fact, zone 3 series exhibits barely significant positive autocorrelation at lags 1 and 12, and

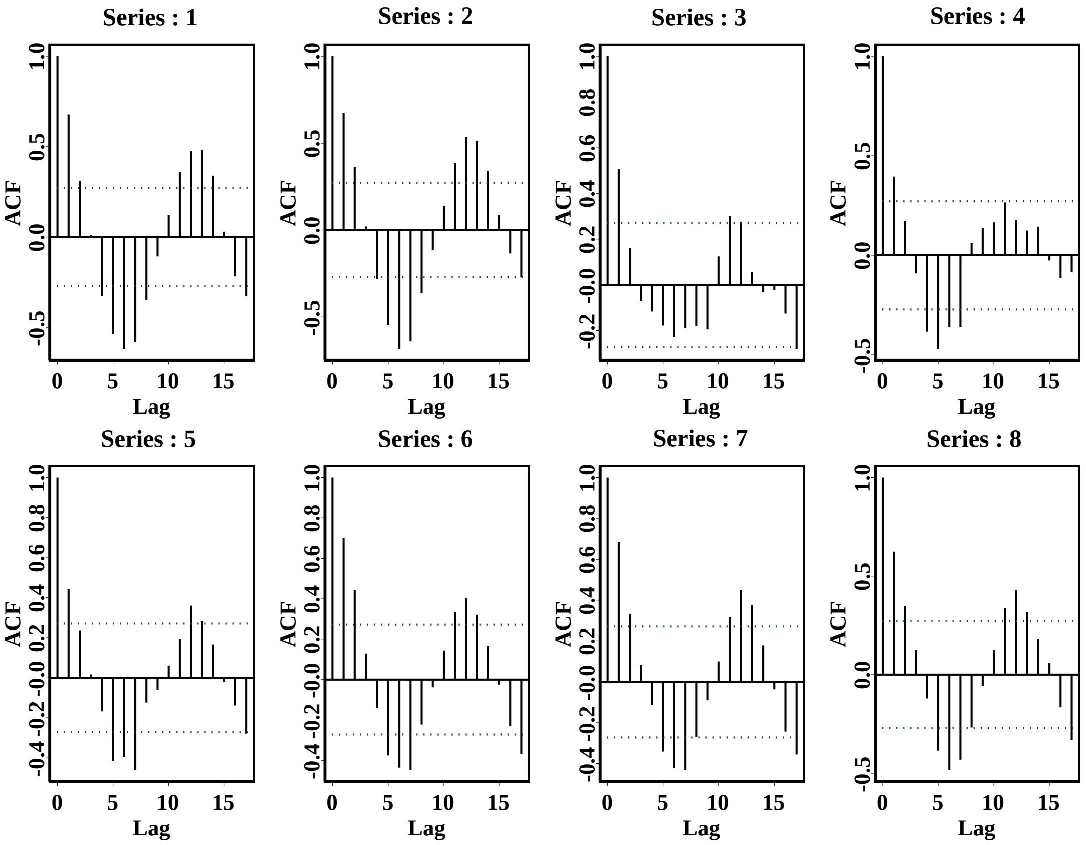


Figure 5.25: Autocorrelation plots of the multiple chlorophyll-$a$ time series to look for evidence of cyclical behaviour (seasonal pattern).

a significant negative correlation at lag 18. It can be noticed that these lags denote similar months (1 and 12) and the opposite month (18), which represent that the cycle just become significant at some extreme seasons (summer and winter). Equivalent results can be found for the zone 4 series (figure 5.25). It confirms the previous results with central zones may reflecting a transitional behaviour along the study area.

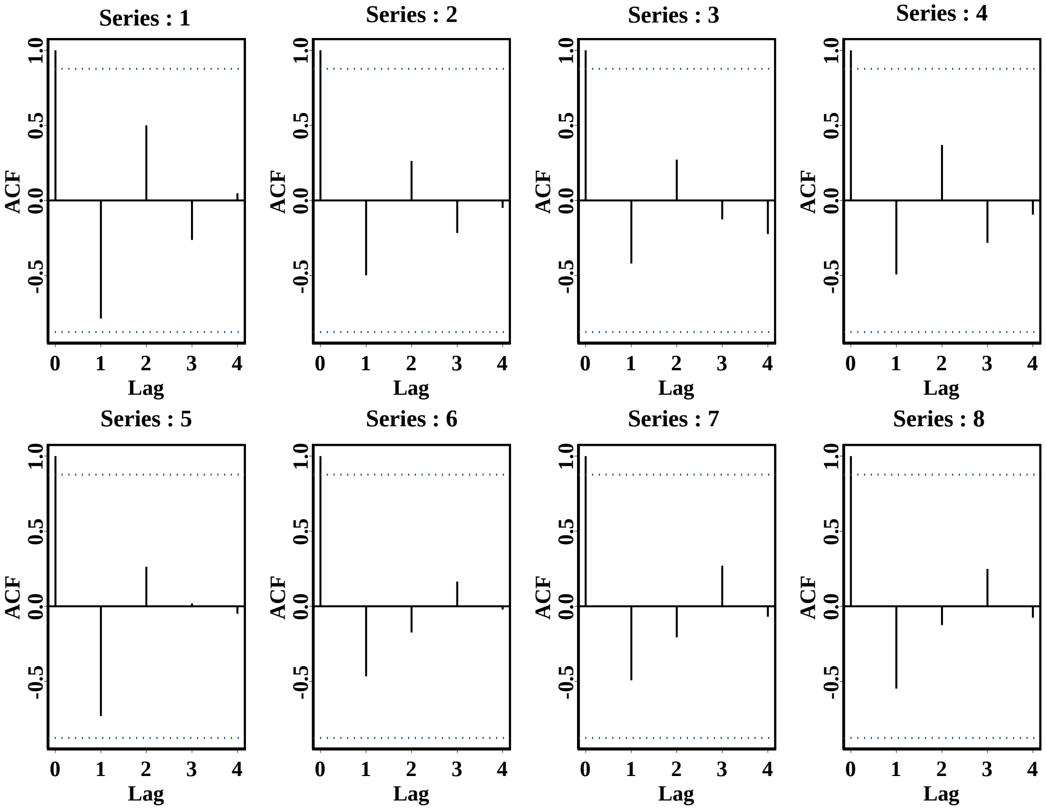


Figure 5.26: Autocorrelation plots of the multiple chlorophyll-$a$ time series to look for patterns across years.

So there are significant cycles of chlorophyll-$a$ concentration from the time series (figure 5.25) and their period is about 1 year, although it is not known yet about patterns across years. We use the same autocorrelation function considering the yearly means (figure 5.26) to test for such cycles.

There are no significant cycles across years (figure 5.26), as no ACF line reaches the dotted lines (correlations that would be significant at the 5% level). Nonetheless, there is some suggestion of an alternation between successive years, at least for zones 1 to 4, of positive and negative chlorophyll-$a$ correlations. That is to say that where a year presents lower concentrations of chlorophyll-$a$, the following year has somewhat higher concentrations, and so on, even though these cycles are not significant (see figure 5.26). Thus, there is no inter-annual cyclic pattern of chlorophyll-$a$ concentration in the study area through the 4 years period analysed.

### 5.2.5 Sea Surface Temperature *vs.* Chlorophyll-$a$

From the previous sections (5.2.3 and 5.2.4) we have found very similar behaviour of water temperature and chlorophyll-$a$ concentrations. It seems that SST may be a useful predictor of chlorophyll-$a$ in the study area (figure 5.27). This shows a clear negative correlation between both parameters.

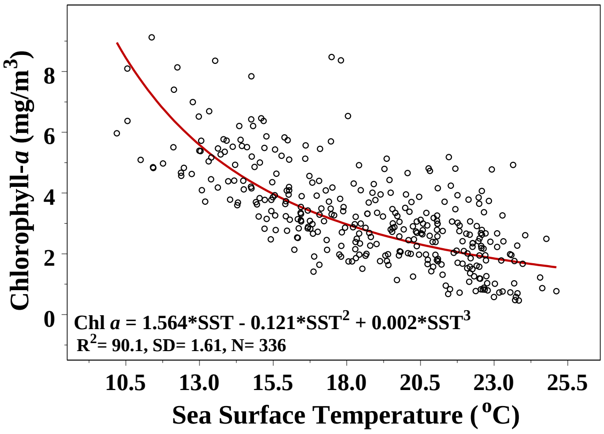


Figure 5.27: Chlorophyll-$a$ and SST monthly means relationship in the study area.

Fitting a linear model with the SST as the response variable and including not only the chlorophyll-$a$ variable as a predictor but also the year, month, and latitudinal zone as possible covariates, it is possible to visualise all the relationships at once (table 5.13).

| | Parameter | SST | SE | *t*-value | *p*- value |
|---|---|---|---|---|---|
| 1 | **Intercept** | 24.45 | 0.25 | 98.62 | <0.001 |
| 2 | **Chl *a*** | -0.39 | 0.05 | -7.91 | <0.001 |
| | **Month** | | | | |
| 3 | Jan | 0 | | | |
| 4 | Feb | 0.50 | 0.19 | 2.53 | 0.012 |
| 5 | Mar | 1.10 | 0.21 | 5.04 | <0.001 |
| 6 | Apr | -0.82 | 0.22 | -3.71 | <0.001 |
| 7 | May | -2.76 | 0.22 | -12.02 | <0.001 |
| 8 | Jun | -4.96 | 0.23 | -20.72 | <0.001 |
| 9 | Jul | -6.51 | 0.25 | -25.91 | <0.001 |
| 10 | Aug | -7.17 | 0.26 | -27.60 | <0.001 |
| 11 | Sep | -6.70 | 0.22 | -30.01 | <0.001 |
| 12 | Oct | -5.33 | 0.21 | -25.37 | <0.001 |
| 13 | Nov | -3.41 | 0.21 | -16.43 | <0.001 |
| 14 | Dec | -1.80 | 0.21 | -8.70 | <0.001 |
| | **Year** | | | | |
| 15 | 1997 | 0 | | | |
| 16 | 1998 | -0.63 | 0.17 | -3.63 | <0.001 |
| 17 | 1999 | -1.18 | 0.17 | -6.86 | <0.001 |
| 18 | 2000 | -1.36 | 0.17 | -7.92 | <0.001 |
| 19 | 2001 | -0.90 | 0.27 | -3.28 | 0.001 |
| | **Zones** | | | | |
| 20 | 1 | 0 | | | |
| 21 | 2 | 0.00 | 0.17 | 0.01 | 0.995 |
| 22 | 3 | 0.14 | 0.18 | 0.76 | 0.444 |
| 23 | 4 | 0.28 | 0.19 | 1.47 | 0.142 |
| 24 | 5 | -0.43 | 0.20 | -2.14 | 0.033 |
| 25 | 6 | -0.89 | 0.19 | -4.61 | <0.001 |
| 26 | 7 | -1.10 | 0.20 | -5.57 | <0.001 |
| 27 | 8 | -1.59 | 0.20 | -8.04 | <0.001 |
| | **R$^2$ = 0.95 and df = 312** | | | | |

Table 5.13: Linear model: parameters for the water temperature (SST) in the study area.

The model summarise all the relationships found previously, as a negative relationship of temperature with chlorophyll-$a$ (row 2), a higher decrease in temperature with the winter months (rows 9 to 11) and towards southern zones (rows 24 to 27).

On the whole, the model demonstrated that all the parameters are good indicators of SST, which implies in a predictable pattern of water temperature temporally and spatially in the study area.

Similar relationships were found fitting the model with chlorophyll-$a$ as the response variable (not shown), although the power of the model decreased (R$^2$= 0.76). The SST parameter is more predictable than the chlorophyll-$a$ variable in the study area.

Overall, all the analysis for the oceanographic parameters SST and chlorophyll-$a$ demonstrated fairly stable spatial and temporal variations. Furthermore, the northern and southern zones reveal significative differences according to the oceanographic parameters analysed, with the zones 3 and 4 revealing some divergences between the other latitudinal zones.

## 5.3 Discussion

The study area (SBCS, see Chapter 3 for details) is a very complex region affected by important water masses, variability in freshwater discharges from Patos Lagoon, and upwelling phenomenon. Moreover, Lima et al. (1996) also suggested wind forcing in the southern Brazilian shelf affects the water circulation. Additionally, the SBCS can generate particular oceanographic features due to rapid changes of topography along the coast. These suggest that geographical areas from a complex and dynamic environment may be influenced differently by different parameters, and should be divided into smaller regions than a unique great area (Gonzales-Silvera et al., 2004).

Therefore, the analysis from this Chapter has taken into account the analysis of the biophysical parameters chlorophyll-$a$ and SST according to the latitudinal zones along the study area in order to investigate how they vary.

### 5.3.1 Sea Surface Temperature

The study area is characterized by high variability in SST (see table 5.1), which is probably associated with the Brazil-Malvinas Confluence (BMC), the frontal zone formed by the meeting of the southward flowing, warm and salty Brazil Current (BC) and cold, relatively fresh Malvinas Current (MC) flowing north (Gordon, 1989).

The results of this study reveal great temperature ranges, over $10^oC$ for all the latitudinal zones (table 5.1 and figure 5.6), which is consistent with other studies. Zavialov et al. (1999) found that the south Brazil and Uruguay coastal waters exhibit an extremely large cycle of SST (annual ranges 7 to over $10^oC$), and Legeckis (1978) in his pioneering work showed that the SST gradients in the BC/MC front could exceed values of $10^oC$ in a distance of several kilometres.

According to our results, temperatures around $20^oC$ are representative for all latitudinal zones over many months, demonstrating the higher temporal influence of warm waters in the study area (see SST colour maps, figures B.1 to B.3). Souza (2000) describes the BC distribution in the SBCS for practically all seasons, which explain the higher temperatures for all the zones. Additionally, computations of the southward transport of the BC at 32-33$^o$C suggest that during most of the year tropical water is transported over the shelf (Garfield, 1990).

However, higher temperatures heavily influence the zones 1 to 4 (mean values higher than 20$^o$C) decreasing towards the south, with significant differences starting between the zones 4 to 5 (table 5.2 and figure 5.7). Additionally, the analysis of variance, MCA and PCA all confirmed similar temperature differences between northern and southern zones (figure 5.10), starting from the central zone 4 (figure 5.8).

Loder et al. (1998) reported that the majority of boundary currents flowing along the outer shelf are influenced by boundary currents in the adjacent continental shelves and coastal waters, and their influence increases with decreasing shelf width. In the study area, for instance, the BC influence in the shelf can expected to be greater because of a narrow shelf width of less than 50km (northern zones region) in comparison to a typical width of 150 km in the southern zones region (Loder et al., 1998). Figure 5.1 illustrates how the width of the shelf in the SBCS increases around the latitudinal zone 4. Thus, the narrow shelf width in the northern zones may facilitate the higher influence of the BC (warm waters), which therefore gives rise to significant higher temperatures.

Furthermore, Piola et al. (2000) states that warmer waters from the BC are oriented in the north-south direction, located on average near the 50m isobath at 32$^o$S, and extend southward toward the shelf break near 36$^o$S. Between 32$^o$S and 34$^o$S the current follows the 100 to 200m isobath. Thus the influence of the BC is greater in the coastal waters above the latitude of 32$^o$S, i.e. the northern latitudinal zones region.

Finally, Belem (1993) analysing SST in the Southern Brazilian waters over 30 years (1946-1979) from ships of opportunity, and for 8 years (1981-1989) by MCSST/AVHRR, also distinguished different regions. The author described 3 regions: region 1 from 29 to 31$^o$S, region 2 from 31 to 33$^o$S, and the third region from 33 to 35$^o$S. The same author suggests that region 2, of which the coastal region is similar to the zones 4 to 7 in this study, as an intermediate area between the maximum and minimum limits of the warm BC in coastal waters.

Overall, even though those studies have taken into account larger study areas, a greater range of latitudes and distant regions from the coast, in this study it has also been possible to reveal differences in the influence of warm waters along shallower coastal areas.

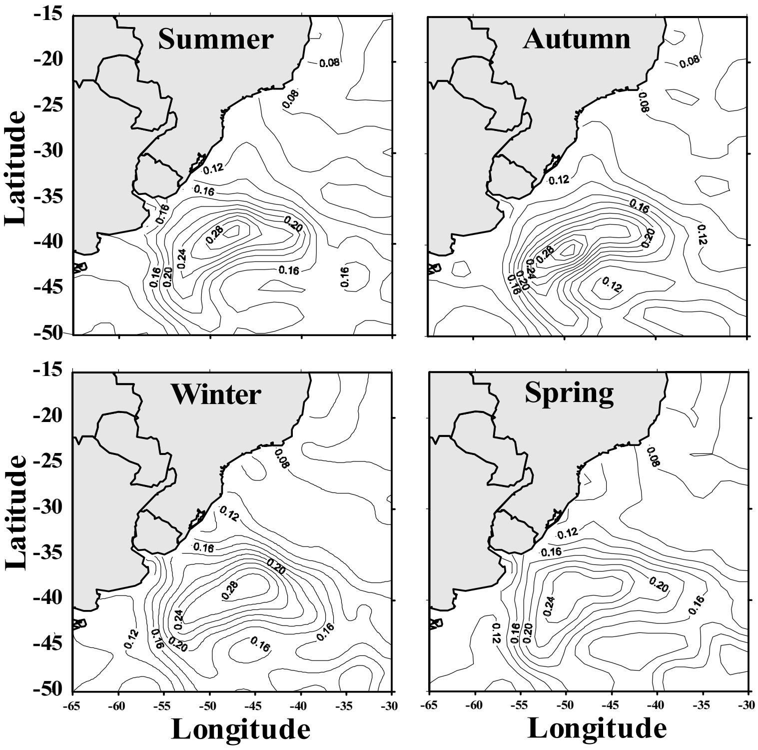


Figure 5.28: Seasonal surface oceanic topography variability from altimetry data (1993/1994) obtained by TOPEX/POSEIDON (values in metres). Source: Mata and Garcia (1996).

However, the significant results in the study area are not only influenced by the presence of warm currents but also by colder water masses, which explain the significant lower temperatures for the southern zones 5 to 8 (figure 5.6). The Brazilian Coastal Current (BCC) is actually an extension of the MC carrying cool coastal waters principally in latitudes lower than 32$^o$S over the study area (Souza, 2000). Considering that the BCC is an extension of the MC towards the coast in the region of the SBCS, we will simply refer to the BCC (cold current).

Overall, both the behaviour of the BC and BCC explain much of the significant differences of SST found between the northern (1 to 4) and southern (5 to 8) zones.

Water temperatures could also be influenced by surface oceanic topography. Satellite altimeters determine elevations and depressions present in the oceans. These variations in sea surface height characterise the dynamic topography of the ocean, which is intimately linked to the oceanic surface circulation (Mata and Garcia, 1996).

Mata and Garcia (1996) analysed surface oceanic topography variability in the southwestern Atlantic using altimetry data, obtained by TOPEX/POSEIDON satellite. They found that the BMC region showed the strongest variability on the study area. Lower values of variability have been found north of 30$^o$S, dominated by the BC and the south Atlantic subtropical gyre, and south of 45$^o$S, where the MC is present. The lower values reflect a less dynamic system compared to the high variability area (between 30 and 45$^o$S). The vicinity of 31-32$^o$S, central latitudinal zones, shows an increase of variability of surface oceanic topography towards the south, with some seasonal variability (see figure 5.28 on the top).

Nonetheless, despite several results pointing to a significant distinction of SST between the northern and southern zones, it seems that such differences may not be smooth along the study area. From the simple analysis of means and ANOVA, the significant differences started between the neighbouring zones 4 and 5, and continued for the distant zones (*e.g.* 4 and 6, 4 and 7). Additionally, despite the strong temperature correlations between all sites (>90.1%), the weakest correlations were noticed for zone 4 (see table 5.4). From the PCA, greater PC differences were found for the zone 4 (see figure 5.9), which explained a great variance of the data (98%, table 5.3). Thus the vicinity of the latitudinal zone 4 could suggest a dynamic-edge region in terms of temperature behaviour along the study area. Those results and previous literature may suggest that in the SBCS this zone could be affected distinctly by both the BC and BCC, as their behaviours are linked to the shelf width and latitude, respectively (Loder et al., 1998; Souza, 2000).

The SST spatial variability in the study region is also influenced by temporal migrations of the BMC, strongly related to the seasonal fluctuation of the the BC and the BCC. Thus the following paragraphs principally address seasonal variability of SST along the zones.

A clear annual variation in the analysis of SST was found (figure 5.12), with higher temperatures for summer (mainly February-March), and lower values for winter (mainly August).

The BMC shows large meridional migrations, moving from 40-46$^o$C in austral summer (Legeckis and Gordon, 1982) to as far north as 35-30$^o$C in austral winter (Zavialov et al., 1999). Campos et al. (1996) suggests northern limits of the BMC extending itself to the north of Santa Marta Cape ($\sim$28$^o$S) or perhaps 27$^o$S (Piccolo, 1998). Zavialov et al. (1999) proposes that in some years (although exceptional) the front can be traced up to as far north as 27$^o$S, whereas Souza (2000) found the mean latitude of the BMC penetration to be $\sim$25$^o$S.

The BC/BCC front retracts to its southernmost position in February (austral summer), when the position of the 20$^o$C isotherm is about 36$^o$S (Souza, 2000). It means that by this time the whole study region is influenced by the BC, in agreement with results for mean SST values in all zones higher than 20$^o$C. Especially for the northern latitudinal zones relatively higher SST mean values are found in the summer, possibly caused by the greater temporal influence of the BC in the northern zones of the study area.

The lower temperatures are strongly related to the intrusion of the BCC during winter and spring time in the study area. The BCC extreme position is continuous along the SBCS and restricted to isobaths shallower than 200m in the inner shelf (Souza, 2000). The 17$^o$C isotherm is adopted as an indicator of the extreme position of the BCC (Zavialov et al., 1999; Souza, 2000). Souza (2000) cited that the vicinity of 32$^o$ ($\sim$ zone 5) marks the extremity of occurrence of the BCC during summer and autumn months. Moreover, to the north of 32°S the BCC only penetrates the SBCS during the winter and spring months.

This is consistent with the mean SST values in wintertime lower than 17°C for all latitudinal zones, and also for autumn season (April to June) in the southern zones. From the SST images (figures B.1 to B.3), there are clearly lower temperatures in the southern coastal region in comparison to the northern during colder months (figure 5.12).

Lima et al. (1996) analysed sea surface temperature for bi-monthly periods, incorporating historical data from 1854 to 1979, for the area between 28°S-35°S and 46°W-54°3OW (figure 5.29). Their results are consistent with those of this study in terms of the influence of the BCC in the study area not only in winter but also in spring.

From figure 5.29, the curvature of the isotherms suggests northward flow near the coast in wintertime. Beyond that, Zavialov et al. (1999) found that along the southern Brazil and Uruguay coasts the expected tongue-like spatial pattern can be observed, also illustrated in the figure 3.2 (Souza, 2000) in Chapter 3, and in this study (figures B.1 to B.3).

The tongue-like shape is probably associated with alongshore intrusions of the BCC and, possibly, with variability of freshwater discharges from the Rio de la Plata and Patos-Mirim estuaries, which flow northwards (Zavialov et al., 1999). Winter and early spring constitute the rainy season in southern Brazil, which is therefore the period when freshwater discharge of the Patos Lagoon reaches its maximum in the year (Castello and Moller, 1978).

Lower temperature values (outliers) were also found, mainly in the spring, but also in the summer and autumn (figure 5.12), which may indicate colder water invasions in the area. These water mass intrusions could have their origins in eddies or upwelling processes.

According to Garcia (1997), upwelling is common in the SBCS region. The upwelling occurring at the coast, our study area, is more likely to happen in the spring and summertime, and occur between 28°S and 32°S, according to Miranda (1972) and Hubold (1980). Lima et al. (1996) also investigated the interaction between eddy-induced upwelling and wind-generated transport which results in enhanced upwelling and a strong bottom intrusion of sub-Antarctic waters on the shelf in summer.

Not only are there temporal variations of SST along the zones illustrated by the clear annual SST cycle (figure 5.14), but the seasonal pattern is fairly stable over time (see figure 5.13 and the two-way ANOVA in table 5.5), at least for the 20 years covered by this study.

From the time series graphs (figure 5.13) it can be seen that there are some higher values of

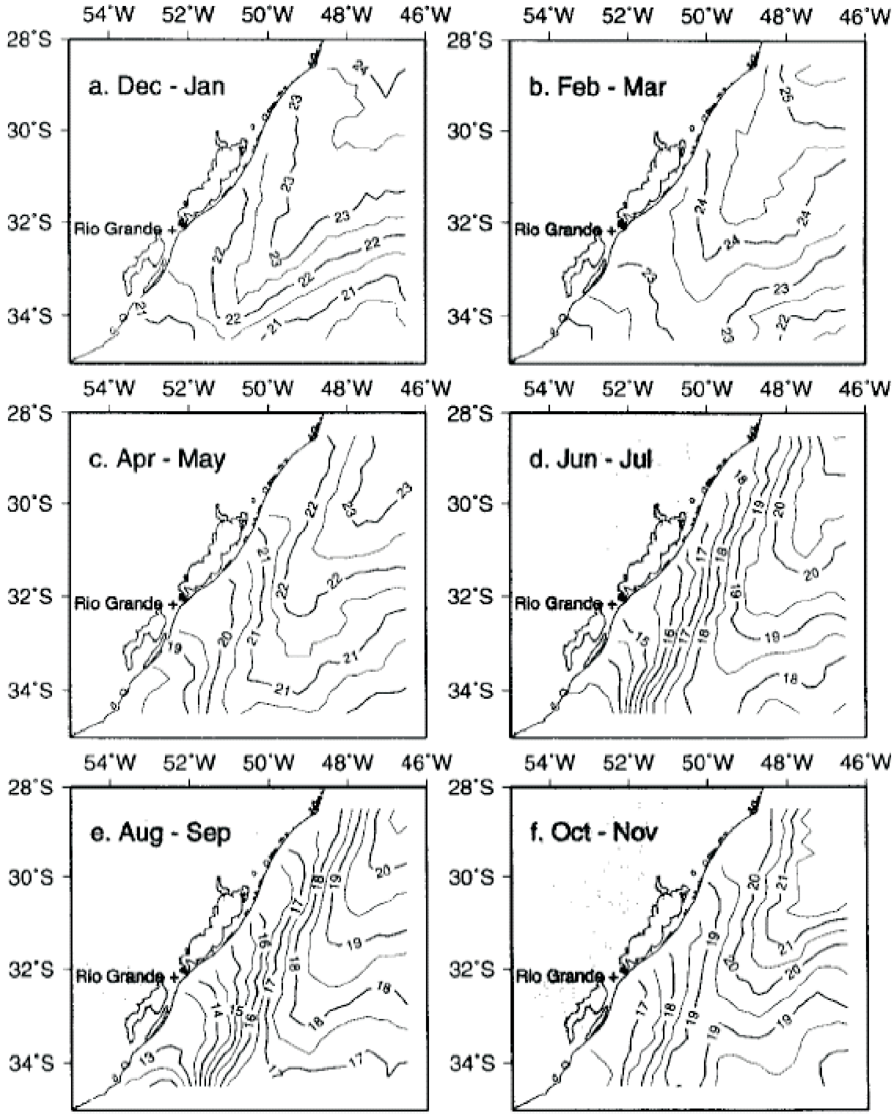


Figure 5.29: Sea surface temperature distribution for 2 month segments of the seasonal cycle, from 1854 to 1979 period. Units are in degrees Celsius. (a) December-January; (b) February-March; (c) April-May; (d) June-July; (e) August-September; (f) October-November. Source: Lima et al. (1996).

temperature in the northern zones, which has already been discussed in the previous paragraphs. However, the series of southern latitudinal zones reveal larger ranges of temperature. The greater seasonal range in these areas may be attributed to the dynamic influence of the BCC intrusion from the south, whereas it decreases in temperature towards the north as mixing occurs with warmer waters. The northern zones perhaps do not experience such impact from the BCC, also suggested by weakest cyclic behaviours from the residuals (figure 5.15), and stronger cycles toward south zones.

Belem (1993) mentioned that in the northern area of the south Brazilian coast, despite the influence of the BCC, the BC presence is still important. Souza (2000) also described how thermal gradients in the BC/BCC front were smaller towards the north, owing to the distance of the MC influence. In addition, similar results were found by Zavialov et al. (1999), which demonstrated that in the shelf off the southern Brazil and Uruguay the annual range generally increases southwards.

Additionally, the presence of tropical waters (BC) over the shelf during the summer causes high monthly mean surface temperatures with a low standard deviation, whilst high monthly surface temperatures deviations are typical for the heterogeneity of water masses in the winter (Belem, 1993; Lima et al., 1996) (see figure 5.12).

Overall, all the latitudinal zones seem strongly exposed to annual cycles of the BCC and BC, even though the northern zones reflect less evident cyclical behaviour.

From the results of ANOVA (table 5.6), and the autocorrelation function of time series (figure 5.16, no consistent overall trend or differences in the systematic cycles was found in the temperatures through the years for the temporal data set analysed in this study (20 years, figure 5.11). The inspection of inter-annual variation, the seasonal variation from year to year (not systematic cycles or trends), also did not reveal significant differences (see interaction analysis of table 5.5).

The results of this work did not find any inter-annual differences of temperature through the 20 years analysed, and since the temporal duration of the biological data set is only 7 years, further analyses in Chapter 6 will just take into account a seasonal explanatory variable.

### 5.3.2 Chlorophyll-*a*

The results revealed systematically lower concentrations of chlorophyll-*a* for the northern zones (1 and 2), with an increase through zones 3 and 4, and higher values in the southern zones 5 to 7 (table 5.7 and figure 5.17).

For the values in the southern zones, the results are similar to those found by previous authors. Gonzales-Silvera et al. (2004) analysed monthly composites of chlorophyll-*a* from SeaWIFS between $5^o$N and $45^o$S, and discovered highest pigment values appearing approximately below $30^o$S. They discuss whether their results may be linked with the geographical limit between tropical and temperate zones described by Lentini (1997). Furthermore, surface chlorophyll-*a* concentration over the shelf between the latitudes of 31 and $34^o$S has been reported to be high in coastal waters (Ciotti et al., 1995).

For the lower values in the northern zones, Brandini et al. (2000) found similar results and suggest low chlorophyll-$a$ concentrations due to nutrient limitation of subtropical oligotrophic waters of the BC. As discussed earlier, the BC has a strong influence on the northern latitudinal zones.

However, the analyses of significance in the chlorophyll-$a$ concentrations between the zones, using t-tests (table 5.8 and figure 5.18) and ANOVA (pairwise differences; figure 5.19), illustrate significantly different chlorophyll-$a$ values for zone 3 compared to all the other zones. Beyond that, the weakest correlations between the zones are related to the zone 3, followed by 4 (table 5.10). Finally for PCA, zones 3 and 4 demonstrated divergent PCs, which explains 77.6% of the total variance (table 5.9). PCA results of the chlorophyll-$a$ variance also suggest a very distinct group 6 to 8; follow by 1, 2 and possibly 5; and finally latitudinal zones 3 and 4 (figure 5.21).

In particular, zone 6 appears somewhat distinct from 7 and 8, with different PCs values and sign (figure 5.20). This difference in variance could be associated with the discharge from Patos Lagoon (~32$^o$S). The area 6 is located at the mouth of the estuary, and it receives a large amount of water, rich in chlorophyll-$a$, to the adjacent coastal region through the year, mainly in autumn and winter (Abreu, 1987).

From the SeaWIFS images (figures B.4 to B.6) it is possible to see relatively high concentrations of chlorophyll-$a$ in adjacent coastal areas around 32$^o$S (*e.g.* November 97, March 98, September 2001), which is likely to be caused by the Patos Lagoon outflow at this latitude.

Those results do not suggest a homogeneous increase, or decrease, in the chlorophyll-$a$ values along the study area, but an anomalous change in the vicinities of zones 3-4. In fact, if we look at the ACF plots (figure 5.25), the areas 3 and 4 demonstrate a weak indication of cyclic patterns, whereas all the other latitudinal zones show up clear, and significant, cyclic behaviours.

Garcia et al. (2004) studying the eddy-like structures in the BMC from SeaWiFS and AVHRR images together with altimetry data obtained by the TOPEX/POSEIDON, have shown that chlorophyll-$a$ concentration from cold waters reduces rather rapidly upon mixing with warmer northern waters. Frontal regions resulting from the horizontal interaction of the water masses were also coupled with high chlorophyll-$a$ concentrations (Ciotti et al., 1995).

In the previous discussion, SST results pointed to clear differences of temperatures between the northern and southern zones an either side of zone 4, suggesting that the mixing influence of the BC and BCC is significant at this location. Thus the rapid decrease in the chlorophyll-$a$

from the south towards north may be explained by the mixing of BC and BCC in the vicinity of 31$^o$S.

Preceding studies in the area have shown the temporal presence of subantarctic water increases pigment concentration values over the continental shelf (Ciotti et al., 1995). Similar results were found, here, with chlorophyll-$a$ concentrations starting to increase in autumn months from southern zones, and moving northwards with higher values during winter months (figure 5.23), showing the same pattern as the BCC in the study area.

Looking at the maps of SST and chlorophyll-$a$ (figures B.1 to B.3, and B.4 to B.6), colder waters (from 17$^o$C) show up in about May for the southern coastal region and move towards the north, which is also observed in the chlorophyll-$a$. On the other hand, during summer and spring where the inner shelf is heavily influenced by the BC, the chlorophyll-$a$ concentration on the coast show lower values.

Garcia et al. (2004) also concluded that on the Brazilian shelf there are peaks of chlorophyll-$a$ and primary production rates at the end of winter (August−September) (figure 5.30). In our data, peaks of high chlorophyll are also observed during late winter and spring (figure 5.24), possibly associated with stabilisation of the water column with concomitant nutrient enrichment from cold currents, freshwater outflow, and previous near shore bottom turbulence (Odebrecht and Garcia, 1997).

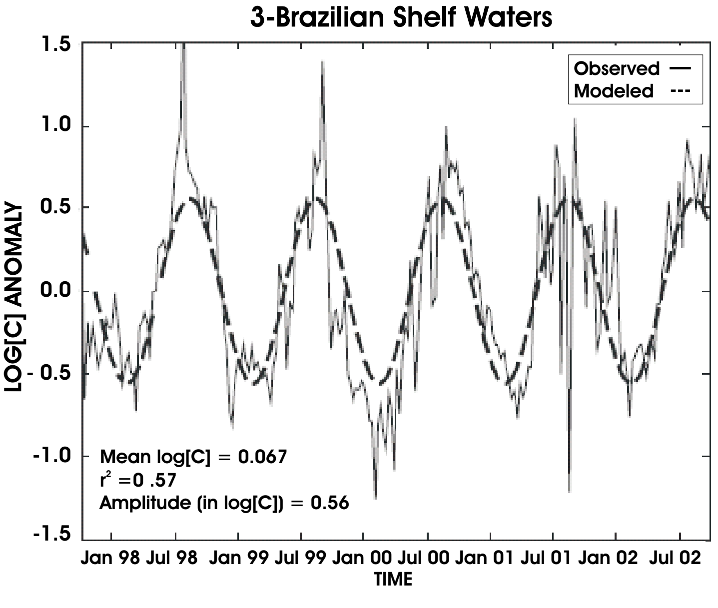


Figure 5.30: Modeled and observed log*[C]* (log chlorophyll-$a$ values) anomalies, in conjunction with a model based on variance preserving spectra, for the October 1997 to September 2002 period. Source: (Garcia et al., 2004).

Furthermore, in the inner shelf of ~32-35$^o$S, the annual amplitude of chlorophyll-$a$ is strongly influenced by the La Plata and Patos Lagoon. This is probably also partially due to persistent presence of suspended sediments from the estuaries, which result in high average values (>4mg/m$^3$) (Garcia et al., 2004).

Notably, there are high peaks of chlorophyll-$a$ during 1998, mostly in southern zones (figure 5.24). Garcia et al. (2004)

explained that the unusually high-chlorophyll signal over the southern Brazilian shelf at this occasion (figure 5.30) is probably caused by the strong reflectance signal of suspended matter from the anomalously high La Plata River and Patos Lagoon discharges following the 1997/1998 El Niño event.

Indeed, the year 2000 showed even greater peaks, which could be associated with an anomalous discharge of the estuaries, but not related to the ENSO event, or a higher influence of the BCC. The SST images (figures B.1 to B.3) illustrated lower temperature values in the end of winter and early spring in 2000, when compared with the previous years 1998/99. However the real cause for such an increase of chlorophyll-*a* concentration in 2000 it still unclear.

The results of ANOVA (table 5.12) revealed no trend in the chlorophyll-*a* over years for each zone, though the temporal data set analysed in this research is very limited. The inspection of chlorophyll-*a* seasonal variation through years also revealed no significant results (table 5.11).

Beyond that, for the northern zones 1 to 4 there is the same suggestion of alternating years of higher and lower concentrations (figure 5.26), but these are not statistically significant. However looking at the chlorophyll-*a* images (figures B.4 to B.6), it is possible to see higher concentrations north of zone 4 in the winter of 1998, lowest in 1999, and higher again in 2000. It may be that these alternate years explain the significant inter-annual differences of chlorophyll-*a* values and its seasonal variation (interaction analysis) when summing up all zones (whole area).

Overall, not all chlorophyll-*a* is carried by currents or influenced by freshwater discharges, as there is also a local cycle of production, consumption, etc., which makes its behaviour considerably more variable.

### 5.3.3 Sea Surface Temperature *vs.* Chlorophyll-*a*

Overall, both the SST and chlorophyll-*a* behaviour in the study area show a clear seasonal cyclical pattern. However, the SST cycle behaviour is considerably more regular than that of chlorophyll-*a*, as illustrated in the time series analysis.

The SST in the study area is basically influenced by the two water masses, BC and BCC, whose presence is strongly seasonal, leading to an evident cycle over time. The chlorophyll-*a* concentration with a strong signal in the winter time is possibly also largely controlled by the cold waters of BCC, exhibiting a negative correlation with temperature (figure 5.27).

However, because chlorophyll-$a$ is also controlled by other factors (*e.g.* reflectance signals of suspended matter, the mixing edge of the BC and BCC, La Plata River and Patos Lagoon discharges), the cyclic pattern is less regular as might be expeccted. Because other parameters may play an important influence on chlorophyll-$a$, it is poorly predictable in comparison with SST in the study area. This is evident when fitting LM considering SST and chlorophyll-$a$ as response variables, and the temporal and spatial parameters as possible explanatory variables. The LM for the SST shows a strong power (95%, table 5.13), in comparison to the chlorophyll-$a$ model (76%, see section 5.2.5). However, both models' power show that the spatial and temporal variables are good indicators of SST and chlorophyll-$a$ variability.

The convergence between the different cold and warm water masses, as well as the freshwater input from the La Plata River and Patos Lagoon, all with distinct phytoplankton communities, results in high phytoplankton diversity over shelf and slope in the study area (Odebrecht and Garcia, 1997). Descriptions of these phytoplankton species off southern Brazilian shelf showed a large number of diatom and dinoflagellate species (Ciotti, 1990).

According to Ciotti (1990) the principal factors controlling primary production in the southern Brazilian shelf were the nutrients and chlorophyll-$a$ concentration of microplankton, which were dominated by diatoms. Because of the large sizes of these species they allow the establishment of short pelagic food webs with high ecological effectiveness.

Abreu (1987) stated that the phytoplankton biomass in the mouth of Patos Lagoon is very important for the larger zooplankton, ichthyoplankton, and juvenile fish densities occurred in association with higher concentration of phytoplankton. Additionally, from the pelagic fish species of the SBCS, Engraulidae species are the most abundant, mainly the *Engraulis anchoita*, which feed on zooplankton and occasionally in phytoplankton (Castello and Habiaga, 1982).

Thus the franciscana prey, mainly juvenile fishes and the Engraulidae species (*Engraulis anchoita*, *Anchoa marinii*) (see Chapter 4), are likely to related with phytoplankton (expressed as chlorophyll-$a$) distribution in the region. This relationship will be explored in the following chapter.

### 5.3.4 The study area and the environmental parameters

The results of the present study show a clear seasonal and spatial variability of the environmental parameters within the study area.

In general, according to its oceanographic characteristics, the study area could again be divided into two main regions, the northern region from the latitudinal zone 1 to 4 ($\sim$29 to 31.5$^o$C), and a southern region from zones 5 to 8 ($\sim$31.5 to 33.5$^o$C).

However, the latitudinal zones 3 and 4 have showed some particular and significant divergences from the other zones. Thus it may be more realistic to conclude that these latitudinal zones are probably an intermediate zone along the coast, which has not been previously described in detail.

Therefore, the study area could be partitioned into three different sectors: a northern sector that correspond to the latitudinal zones 1 and 2; a middle sector of zones 3 and 4; and a southern sector from zones 5 to 8.

As previously discussed, other research studies had also discussed the variability of SST and chlorophyll-$a$ behaviours in southern Brazil (Belem, 1993; Ciotti et al., 1995; Mata and Garcia, 1996; Lima et al., 1996; Campos et al., 1996; Loder et al., 1998; Zavialov et al., 1999; Souza, 2000; Garcia et al., 2004). However, they generally considered a great range environment, extending to distant areas from the coast and greater latitude ranges. Here we have addressed a relatively small area with an average of 50 m isobath and a limit of 100 m isobath, and extending only 240 nm ($\sim$6$^o$ in latitude, see figure 5.1).

Although the area is relatively small, we could identify significant differences along the study area which lead to a more detailed description of different environments, particularly for this shallow coastal region.

On the whole, all the sectors are influenced by the Brazil Current (BC) in austral summer, and by the Brazilian Coastal Current (BCC), as an extension of the Malvinas/Falkland Current (MC), in austral winter. However, the arrival and permanency of such currents in different latitudes certainly control the SST and chlorophyll-$a$ variations through the zones.

Summing up, the different sectors can be described as followed:

- Northern Sector = Zones 1 to 2 (29$^o$ 11' to 30$^o$ 41' S): highly influenced temporally by the BC; exhibits a seasonal cycle of SST although lower temperature amplitudes than southern section; lowest values of chlorophyll-$a$ concentration; seasonal cycle of chlorophyll-$a$ with peaks in winter time.
- Central Sector = Zones 3 to 4 (30$^o$ 11' to 31$^o$ 40' S): a dynamic-edge region in terms of temperature behaviour probably caused by the mixing of BC and BCC, as these zones

explain most of the variance in the data; less clear seasonal variation of chlorophyll-$a$ concentration, with intermediate values and peaks in winter months; narrowest continental shelf, mainly around 100m isobath, implying in a particular hydrographic system.

- Southern Sector = Zones 5 to 8 ($31^o$ 40' to $33^o$ 26' S): highly influenced temporally by the BCC; also exhibiting a seasonal cycle of SST but with larger temperature ranges than the northern section; highest values of chlorophyll-$a$ concentration; seasonal cycle of chlorophyll-$a$ with higher peaks in winter time as well as high values in autumn and spring seasons; influenced by Patos Lagoon freshwater discharge, mainly during winter and early spring.

### 5.3.5 The study area and the franciscana diet

From Chapter 4, the comparisons of past analysis of franciscana diet (Ott, 1994) with the franciscana diet from this study revealed an increase of species associated with warm currents, the fishes *Stellifer rastrifer* and *Trichiurus lepturus* (see section 4.4.4). This raised the question whether this increase could be associated with changes of warm currents over the years in the study area (*e.g.* a trend towards warming). However, according to our results, this does not seem to be the case.

Moreover, the diet analyses has shown that the southern zones exhibit more temporal variation in terms of fish species (see section 4.3.4 and 4.6.1, Chapter 4). From the significant prey species of franciscana diet from northern zones, only the fish *Anchoa marinii* and the family Engraulidae are related to cold waters, whereas in the southern zone diets there are many significant species characteristic of cold waters (*e.g. Anchoa marinii*, *Cynoscion guatucupa*) as well as many from warm currents (*e.g. Umbrina canosai*, *Argonauta nodosa*, *Trichiurus lepturus*, *Peprilus paru*).

The water temperature variability along the coast confirmed those occurrence of cold and warm water related species of franciscana prey. The southern zones exhibit a seasonal cycle with larger temperature ranges, highly influenced by warm and cold currents, whereas the northern zones are less influenced by colder water masses, exhibiting lower temperature ranges (see the previous section 5.3.4).

Furthermore, the principal component analysis of franciscana diet along the coast identified similar spatial differences of the prey species occurrence (discriminated as northern, southern, and central zones groups, see figure 4.37 in Chapter 4) with the environmental characteristics of the habitat analysed in this chapter (see the habitat description in the previous section 5.3.4).

Most likely there is an influence of such oceanographic parameters in the franciscana diet variability throughout the coast. Therefore the main goal of the following Chapter 6 is to analyse how these environmental parameters of the habitat may influence the franciscana dolphin diet.

# Chapter 6

# The environmental-biological coupling

The dynamic hydrography of the study area, analysed in the previous Chapter, has an important influence on the distribution and abundance of many species (Seeliger et al., 1997), including the prey species of franciscana dolphin. However, there are currently no studies on how this would affect the franciscana feeding habits.

Therefore, understanding some of the environmental determinants in the franciscana prey species is the principal objective of this Chapter, and it is one of the main aims of this research study.

The present Chapter will study the relationship between the frequency and size of the franciscana prey, previously described in the Chapter 4, and a suite of variables describing the environment (*SST* and *chlorophyll-a*), which were assessed in the Chapter 5.

A usual approach is to treat the franciscana prey as a function of the oceanographic variables, as well as the spatial variables (*latitude* and *water depth*), and temporal (*season*) parameters.

Statistical methods such as LM, GLM, and GAM, have been used in recent years as more useful means to integrate biological and physical data. However, only recently has grown interest in the use of such techniques, and there is as yet no standard methodology in common use.

LM are popular because they describe the relationship between the expectation of a response (dependent) variable and a set of explanatory (independent) variables very clearly. However, LM are based on the assumption that response variables have normal distributions with constant variance, and that a linear relationship between the response variable and the explanatory variables.

GLM accommodate response variables with nonnormal (conditional) distributions through a transformation called the link function. These models can be easily formulated by selecting an appropriate response distribution (*e.g.* Poisson, binomial) and link function (*e.g.* log link). In this respect, GLM provide a simplified and flexible approach to statistical modeling (Venables and Ripley, 1997).

GAM is a nonparametric regression technique offering advantages over conventional regression techniques because it is not tied to a particular functional relationship (*e.g.* linearity). In GAM the covariates are assumed to affect the dependent variable through additive, unspecified (not linear, not parametric) smooth functions (Venables and Ripley, 1997).

We have used LM and GLM as the modelling approaches, and GAM to verify the shape of the relationships (i.e. linearity), to test the hypotheses that the explanatory parameters might be important predictors in the diet composition of the franciscana dolphin.

## 6.1 Methods

### 6.1.1 The physical parameters

To characterise the thermal environment and the phytoplankton production where the franciscana were caught, a number of variables were derived from weekly AVHRR SST and SeaWIFS chlorophyll-$a$ images. Detailed information about the source and process of those parameters can be accessed in the "Methods" section 5.1 (Chapter 5).

The SST nighttime and chlorophyll-$a$ images were plotted for the time of each franciscana dolphin capture (N= 270). Figure 6.1 shown an example of the catch of a franciscana dolphin, sample number N514, plotted for both images. From those plots the SST and chlorophyll-$a$ values at the time and location of each capture event were obtained. Therefore all the physical parameters were linked with the corresponding geographic position and time of the capture event of each animal.

We recognise that the prey structures may remain in fact for one day or more (especially cephalopod beaks) in the stomach contents, and the animals could travel some distance before being captured. Therefore the analyses will take into account the SST average values close to the capture event (local environment), as well as values for a wider environment.

The purpose is to analyse the influence of the environmental variables on the franciscana prey considering those two spatial scales. The same procedure is applied for the chlorophyll-*a* parameter.

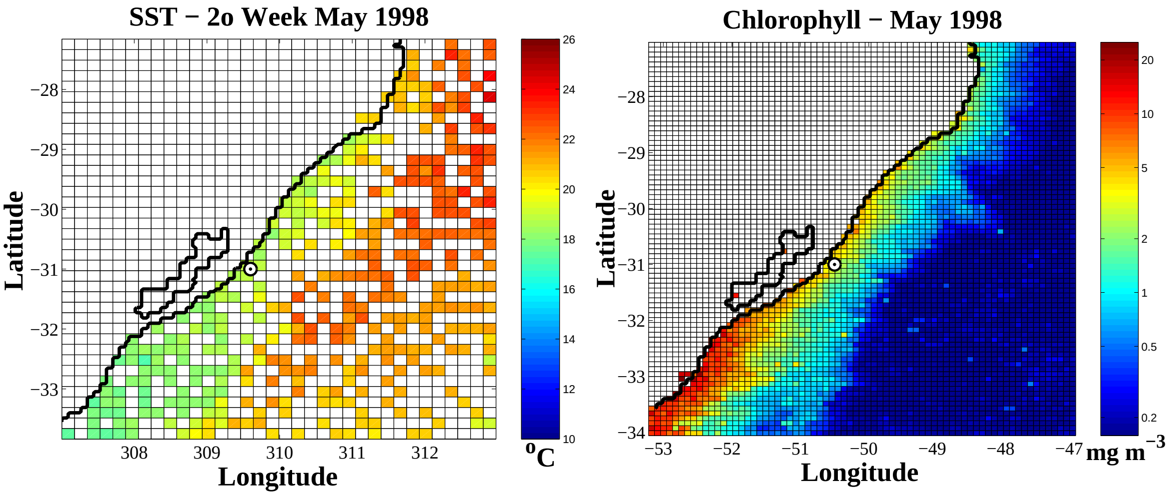


Figure 6.1: Weekly-averaged SST from AVHRR image for May 1998 (left), and monthly-averaged chlorophyll-*a* concentration from SeaWIFS image for May 1998 (right). The circles indicate the capture event of one franciscana dolphin (sample N514) on 12 May 1998.

The SST ($^o$C) values chosen for the analyses were (1) the weekly-averaged SST of the pixel region (9km resolution, see figure 6.1) including the franciscana capture event (N= 249), representing the local environment; and (2) the weekly-average SST of the latitudinal zone of the catch (N= 252), representing a wider environment. The latitudinal zone dimension is illustrated in the figure 5.2 (section 5.1.2, Chapter 5).

For the SST data it was possible to use more accurate values for the time of the dolphin capture, in this case the weekly-averaged values ($^o$C). However, for the chlorophyll-*a* data was only possible to get monthly values of concentration. Unfortunately it was also only possible to obtain values of chlorophyll-*a* concentration commencing in September 1997, thus not all franciscana captures could be analysed with respect to this parameter. The monthly average values of chlorophyll-*a* concentration of both the pixel region (18km resolution, see figure 6.1) and the latitudinal zone of the dolphin catch were recorded (N= 98). The latitudinal zone dimension is illustrated in the figure 5.4 (section 5.1.3, Chapter 5).

### 6.1.2 The biological parameters

Data from the stomachs of 270 franciscanas captured between 1994 and 2001 were used in the analysis. Detailed information about the source and process of the biological parameters concerning franciscana prey can be accessed in the "Methods" section (4.2, Chapter 4).

| Group/Species | Common name | Habitat and region | Depth ranges* | Code** |
|---|---|---|---|---|
| **Fish** | | | 0-600m | fish |
| *Cynoscion guatucupa* | striped weakfish | shelf-demersal/pelagic as juveniles | 0-180m (0-60m) | Cg |
| *Cynoscion jamaicensis* | Jamaica weakfish | shelf-demersal | 0-180m (40-80m) | Cj |
| *Paralonchurus brasiliensis* | banded croacker | shelf-demersal | 0-80m (0-60m) | Pbr |
| *Umbrina canosai* | Argentine croacker | shelf-demersal | 0-180m (>40m) | Uc |
| *Stellifer rastrifer* | rake stardrum | shelf-demersal | 0-40m | Sr |
| *Urophycis brasiliensis* | squirrel codling | shelf-demersal | 0-250m (0-180m) | Ubr |
| *Trichiurus lepturus* | cutlassfish | shelf-demersal/pelagic as juveniles | 0-350m (0-250m) | Tl |
| *Porichthys porosissimus* | lantern midshipman | shelf-demersal | 0-250m (20-120m) | Pp |
| *Peprilus paru* | American harvestfish | shelf-pelagic | 0-200m (25-70m) | Ppa |
| *Merluccius hubbsi* | Argentine hake | shelf-demersal/pelagic as juveniles | 20-600m (40-180m) | Mh |
| *Anchoa marinii* | anchoita | shelf-pelagic | 0-200m (0-40m) | Am |
| **Cephalopod** | | | 0-500m | *see* Ls |
| *Loligo sanpaulensis* | common long-finned squid | shelf-demersal/pelagic | 0-250m (0-60m) | Ls |
| *Loligo plei* | slender inshore squid | shelf-demersal/pelagic | 15-280m | Lp |
| *Argonauta nodosa* | Knobby argonaut | shelf-epipelagic | 20m-500m | An |
| **Crustacean** | | | | |
| | marine shrimp | estuary/shelf-benthic | 0-70m | shrimp |

* The range in which the animals are most abundant is given in parenthesis. ** See figure 6.2 for illustration.

Source: a) Seeliger, U., Odebrecht, C. and Castello, J. P. (Eds.) 1997. Subtropical Convergence Environmemts. Springer Editora, Berlin, Germany. 308pp.
b) Santos, R. A. 1999. Cephalopods and them food web importance in South Brasil. PhD Thesis. University of Rio Grande. Rio Grande, Brasil. 150pp.
c) Haimovici, M. 1998. Present state and perspectives for the southern Brasil shelf demersal fisheries. Fisheries Management and Ecology. 5, 277-289p.
d) http://www.fishbase.org

Table 6.1: General information of the prey species of the franciscana dolphin from the southern Brazilian coast, which were chosen as the biological parameters for the models. The last column is the code reference for each species used in the figures through this Chapter.

The franciscana prey species and groups selected for the models are the fishes *Cynoscion guatucupa*, *Stellifer rastrifer*, *Trichiurus lepturus*, *Anchoa marinii*, *Paralonchurus brasiliensis*, *Porichthys porosissimus*, *Umbrina canosai*, *Urophycis brasiliensis*, *Cynoscion jamaicensis*, *Peprilus paru*, *Merluccius hubbsi*, and the prey group of ”total fish specimens”; the cephalopods *Loligo sanpaulensis*, *Loligo plei* (squids), and *Argonauta nodosa* (argonaut); the crustacean representative is the ”shrimp specimens group” (figure 6.2). The squid *Loligo sanpaulensis* represents 99% of all cephalopods analysed, thus the total cephalopod specimens ingested is practically represented by this single species. Table 6.1 shows those species common names and some ecological information.

These prey species and groups were chosen for the interaction models in this Chapter because of their significant contribution (frequency, spatial, and/or temporal) in the franciscana feeding ecology (see section 4.6 in Chapter 4).

### 6.1.3 The temporal and the spatial parameters

Season is the temporal parameter taken into account for the models. The year variable was discarded since the temporal range of the biological data set is only 7 years, and the data

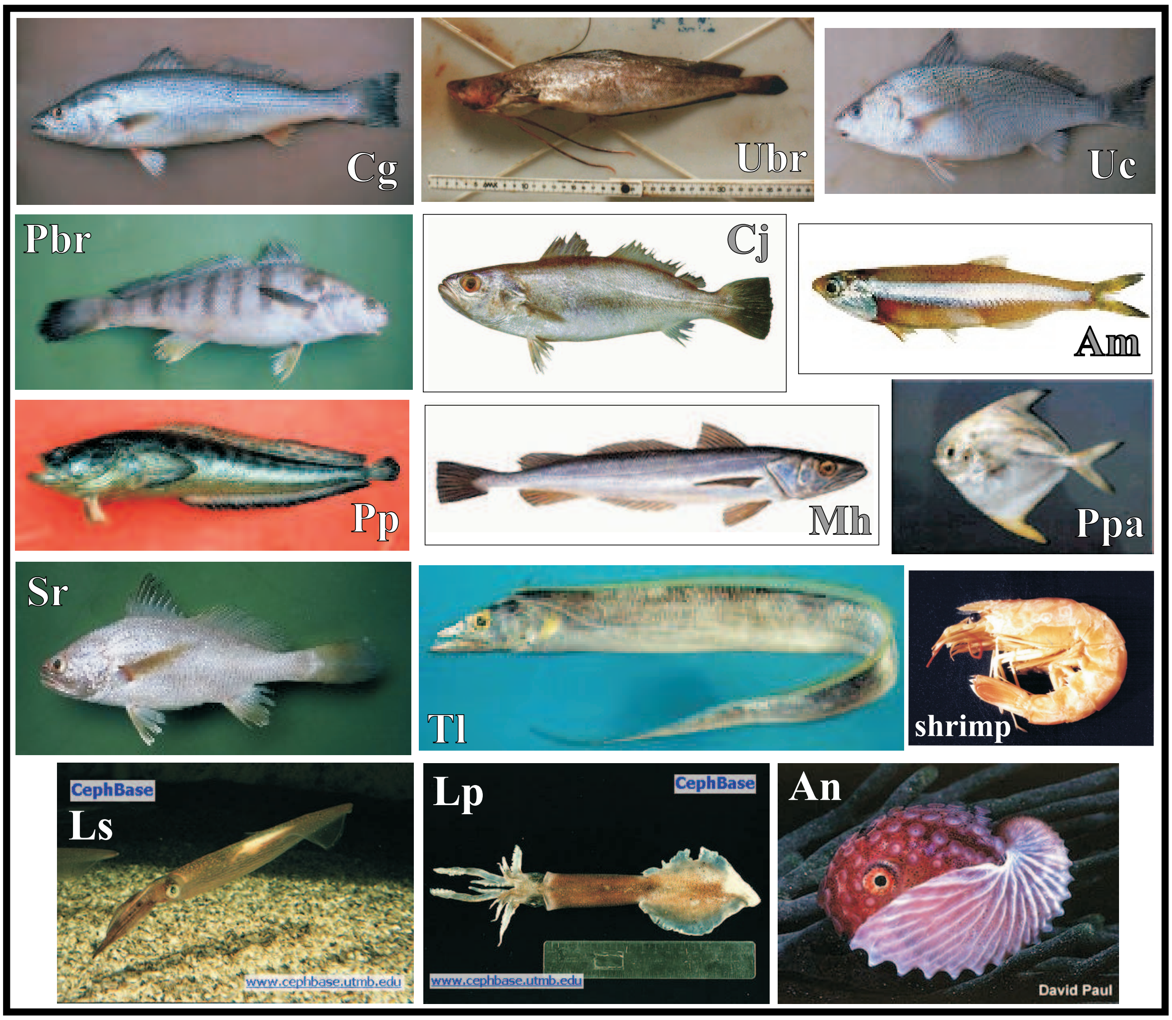


Figure 6.2: Franciscana dolphin principal prey species (fish, cephalopod, and crustacean): the biological parameters. See the species code reference and its ecological information in the table 6.1. Sources: www.fishbase.org, www.cephbase.utmb.edu, www.tolweb.org, and www.ecomarina.com.ar.

is biased with many animals sampled during 1994 and 1997 (57% of the data). In addition the results from the environmental predictors in the previous Chapter (section 5.2) did not find significant inter-annual temperature variation through 20 years, or of chlorophyll-$a$ trend throughout 4 years, for which data are available.

The spatial variables are the latitude and the water depth at the time of the dolphin capture.

The latitude is expressed in $^o$S. Because the latitude is a continuous variable this was preferred to the latitudinal zone since this generates fewer parameters to be estimated in the models. The latitudinal zone is a categorical variable with 7 levels, and together with season (4 levels) this produces too many parameters compared to the number of observations since 5 more environmental variables also are taken into account in the models (see table 6.2).

Spatial bathymetric data, provide information about the water depth of the capture, another important physical habitat characteristic which was recorded. Most of these data were obtained directly from the fisherman at the time of the capture, and some also from a global data set (GEBCO) when plotting the capture coordinates. The known water depths of particular franciscana captures were very similar to those from the global data set. We did not use the *distance from the coast* or *longitude* descriptors because this information is already effectively represented by the depth, as the water depth and longitude increase with the distance from the coast.

For the stranded dolphins only the oceanographic values of the latitudinal zones (SST zone and Chl *a* zone) in which the dolphins were found were considered. Obviously the water depth parameter was not recorded for those individuals.

### 6.1.4 Statistical analysis

The suite of predictor variables (table 6.2) included those related to the environmental parameters SST (nighttime) and chlorophyll-*a*; and those related to the time (season) and location (latitude and water depth). All these are linked to the capture event of each franciscana dolphin. The response variables are the franciscana dolphin prey - the prey species frequency and the fish and cephalopod prey specimens length (mm) (table 6.3).

Response variables that meet the assumption of a normal distribution, *i.e.* the log-transformed fish prey length and the log-transformed cephalopod prey length, were analysed with LM. Response variables measuring non-normal counts, *i.e.* the preys species number, were analysed with GLM based on a Poisson (log link) model structure. However, some GLM results showed overdispersion, and the errors are expected to be highly skew because of the low mean numbers and many zeros in the data. In such cases a negative binomial family (with a log link) provided a parametric alternative way of modelling allowing for overdispersion (Venables and Ripley, 1997). Hence we modeled overdispersion assuming a different error distribution from the negative binomial family.

It was chosen GLM because they are statistically more robust procedure than GAM (non-parametric technique), and also produces less complex mathematical expressions, but it requires preliminary exploration of the functional relationships. However, this requirement was checked through the use of GAM (see Chapter 1 for more detail), and the relationships proved to be linear.

Therefore for individual prey species we used GLM (poisson or negative binomial family), as employed for other faunal groups (Scott et al., 2000), and for specimens size we applied LM.

| Type | Parameter | Explanation | Units | Mean | Range |
|---|---|---|---|---|---|
| Predictors | SST pixel | Mean of weekly SST nighttime from the pixel of the franciscana dolphin capture | $^o$C | 18.1 | 12.3; 24.9 |
| | SST zone | Mean of weekly SST nighttime from the latitudinal zone of the capture (or stranding) | $^o$C | 18.4 | 12.5; 24.9 |
| | Chl *a* pixel | Mean of monthly chlorophyll-*a* concentration from the pixel of the capture | mg $m^{-3}$ | 3.9 | 0.4; 10.4 |
| | Chl *a* zone | Mean of monthly chlorophyll-*a* concentration from the latitudinal zone of the capture (or stranding) | mg $m^{-3}$ | 3.8 | 0.5; 8.4 |
| | Water depth | Water depth of the catch | m | 24.1 | 10; 57 |
| | Latitude | Latitude | $^o$S | 31.5 | 29.4; 33.4 |
| | Season | Season | n/a | n/a | Sum; Aut; Win; Spr |

Table 6.2: A summary of the predictors parameters used in the LM and GLM analyses.

| Type | Parameter | Explanation | Units | Mean | Range |
|---|---|---|---|---|---|
| Response | *Cynoscion guatucupa* | Fish prey species | number | 17.2 | 0; 269 |
| | *Stellifer rastrifer* | Fish prey species | number | 14.1 | 0; 219 |
| | *Trichiurus lepturus* | Fish prey species | number | 3.6 | 0; 19 |
| | *Anchoa marinii* | Fish prey species | number | 8.2 | 0;65 |
| | *Paralonchurus brasiliensis* | Fish prey species | number | 5.5 | 0; 28 |
| | *Urophycis brasiliensis* | Fish prey species | number | 5.2 | 0; 64 |
| | *Porichthys porosissimus* | Fish prey species | number | 4.2 | 0; 51 |
| | *Umbrina canosai* | Fish prey species | number | 7.9 | 0; 56 |
| | *Cynoscion jamaicensis* | Fish prey species | number | 7.4 | 0; 41 |
| | *Peprilus paru* | Fish prey species | number | 4.2 | 0; 28 |
| | *Merluccius hubbsi* | Fish prey species | number | 3.3 | 0; 12 |
| | *Loligo sanpaulensis* | Cephalopod prey species | number | 23.1 | 0; 332 |
| | *Loligo plei* | Cephalopod prey species | number | 2.3 | 0; 8 |
| | *Argonauta nodosa* | Cephalopod prey species | number | 3.4 | 0; 20 |
| | shrimp | Total shrimp specimens prey | number | 0.36 | 0; 17 |
| | Fish group | Total fish specimens prey | number | 26.6 | 0; 364 |
| | Cephalopod group | Total cephalopod specimens prey | number | 23.7 | 0; 332 |
| | Fish prey length | All fish specimens length | mm | 96.4 | 2.9; 889.0 |
| | Cephalopod prey length | All cephalopod specimens mantle length | mm | 105.5 | 4.3; 256.6 |

Table 6.3: A summary of the response parameters used in the LM and GLM analyses.

GLM and LM were fitted using the S statistical language in the S-PLUS software (6.1 for Windows, Math-Soft Inc., Seattle, Washington). Inference for a GLM is based on the theory of maximum likelihood estimation, and likelihood ratio tests and analysis of deviance replace the classical F-tests and analyses of variance of the standard LM (Crawley, 2002). For more information about GLM and LM see "Methods" section (4.2.4), in Chapter 4.

In building the LM and GLM continuous predictors were used where possible, rather than categorical predictors which require more parameters to describe relationships, as this would also have made the equations cumbersome and not very portable. Obviously, *Season* effect had to be included, however, as a categorical variable in all models.

Exploratory GLM analyses were run to assess the importance of the various predictors for each individual prey species. Model selection is based on stepwise procedure using the Akaike information criterion (AIC), -2 *log* Likelihood + 2*effective degrees of freedom*, with smaller values of the AIC being preferred. Final models included only those predictors and interactions whose deviance reduction was significant against $\chi^2$ at the 0.05 confidence level. The percent change in deviance between the final model and the null model was calculated as a measure of the amount of variation explained by the model ($D^2$). The contribution of each predictor in the final model was obtained from the GLM deviance tables.

LM was chosen to assess the influence of the predictors for the prey specimens length, and model selection also followed the AIC procedure. Predictors and interactions whose the variance reduction was significant at the 0.05 confidence level were included in the final models. $R^2$ and the variance explained for each predictor or interaction was obtained from the variance tables of the models.

Model parameters and their associated values, as well as model $R^2$ and $D^2$ and adjusted $R^2$ and $D^2$, are showed. The adjusted fraction of variance/deviance explained by the models considers the effects of the explanatory variables after other variables have been fitted. The adjusted measure therefore combines information of the effect of each variable considering all other variables, and the degrees of freedom used (Graphen and Hails, 2002).

To test the predictive power of the resultant models, the selected models (LM and GLM) were subsequently constructed from the first randomly 50% of the data, and the remaining data were used to validate the model predictions. The predicted values were compared to observed (real) prey species numbers in the case of GLM, and prey specimens length in the case of LM. Simple Pearson correlation coefficients were used to evaluate the observed and the predicted values (Jaberg and Guisan, 2001).

## 6.2 Results

The average number of the franciscana prey species did not meet the assumptions of normality and were examined with respect to the predictor variables using a GLM appropriate for count data. The prey specimens size, log-transformed fish and cephalopod lengths, did meet the assumptions of normality and were examined with respect to the predictor variables in a LM.

Because most effects vary with prey species and the specimens size, we choose to present the results by species and specimens length rather than by predictor parameter or group of parameters. At the end a summary of predictor effects is presented to place the results into a different framework.

### 6.2.1 GLM selection: factors affecting franciscana prey species

The purpose is to find the minimum adequate model for each one of the dolphin prey species and its possible predictors and interactions, and the influence of those in the response variable.

Both the AIC and an examination of residuals from the fitted models showed that a poisson and negative binomial GLM with a log-link function were the most appropriate models for prey species frequency as a function of the environmental, spatial and temporal parameters.

- **Fish species**

The results for the fishes that showed the simplest minimum adequate models (with non interactions), area listed in table 6.4. Latitude and season were the most frequent parameters appearing to affect these fish prey species numbers in the franciscana diet.

**(Ubr)** ***Urophycis brasiliensis***. The model for this fish ended (after the stepwise AIC procedure) with the single term latitude, even though it is not significant. Hence none of the predictors seem to influence this fish species in the franciscana diet.

**(Pp, Ppa, Sr)** ***Porichthys porosissimus*, *Peprilus paru*, *and Stellifer rastrifer***. The latitude and season predictors together explain 15%, 16% and 77% of the total deviance of *Porichthys porosissimus*, *Peprilus paru*, and *Stellifer rastrifer*, respectively. The fish *Porichthys porosissimus* was most influenced by latitude, with a negative trend, whereas the *Peprilus paru* has a significant positive relationship with latitude (figure 6.3).

However, season contributed most to the deviance of *Peprilus paru* (table 6.4). Both have greater positive coefficients for summer and autumn. Latitude influence seemed strong for the *Stellifer rastrifer*, as it explains a great portion of its model deviance, followed by a contribution of only 2.7% from season. There is a significant negative relationship between latitude and *Stellifer rastrifer* frequency, with higher numbers during winter (figure 6.3).

| **Model** | **Predictors** | **% explained deviance** | ***P*-level** |
|---|---|---|---|
| *Urophycis brasiliensis* | Latitude | 1.9 | 0.076 |
| | $D^2 = 0.02$ /adj.$D^2 = 0.015$ | | |
| *Porichthys porosissimus* | Latitude | 10.6 | <0.001 |
| | Season | 5.7 | 0.041 |
| | $D^2 = 0.16$ /adj.$D^2 = 0.15$ | | |
| *Peprilus paru* | Latitude | 5.1 | <0.001 |
| | Season | 12.5 | <0.001 |
| | $D^2 = 0.18$ /adj.$D^2 = 0.16$ | | |
| *Stellifer rastrifer* | Latitude | 75.5 | <0.001 |
| | Season | 2.7 | 0.009 |
| | $D^2 = 0.78$ /adj.$D^2 = 0.77$ | | |
| *Paralonchurus brasiliensis* | Depth | 13.6 | <0.001 |
| | Season | 15.1 | <0.001 |
| | $D^2 = 0.29$ /adj.$D^2 = 0.27$ | | |
| *Anchoa marinii* | Chl *a* zone | 16.3 | <0.001 |
| | Latitude | 7.6 | <0.001 |
| | Season | 27.8 | <0.001 |
| | SST pixel | 15.2 | <0.001 |
| | $D^2 = 0.67$ /adj.$D^2 = 0.64$ | | |

Table 6.4: Fish prey frequency models (GLM) of six chosen species. % explained deviance= percentages of deviance explained successively by each predictor; *P*-level= significance level associated with the chi-test for each predictor; $D^2$= total proportion of deviance explained by the model; adj.$D^2$= same as $D^2$ but corrected for the number of degrees of freedom used to build the model.

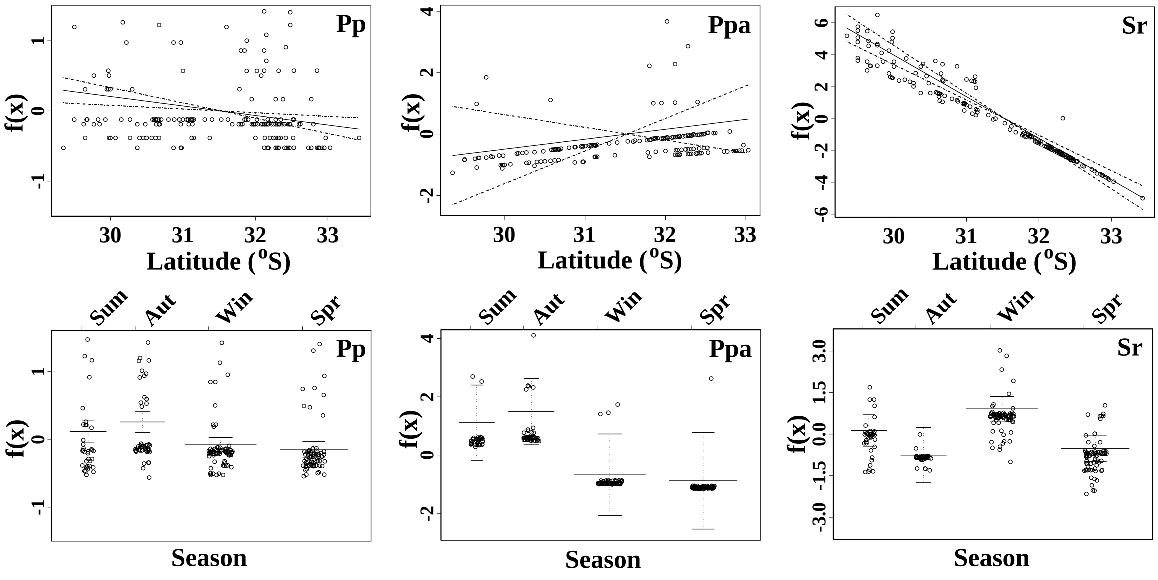


Figure 6.3: GLM functions generated from the most-parsimonious models relating fish number of *Porichthys porosissimus* (Pp, left graphs), *Peprilus paru* (Ppa, middle graphs), and *Stellifer rastrifer* (Sr, right graphs), and their predictors. Solid lines are the fitted GLM. Dashed lines are approximate 95% point-wise confidence intervals.

**(Pbr) *Paralonchurus brasiliensis*.** Water depth appeared to affect this prey species (14% of deviance, table 6.4), while at lower depths the number of this prey seems higher (negative relationship, figure 6.4).

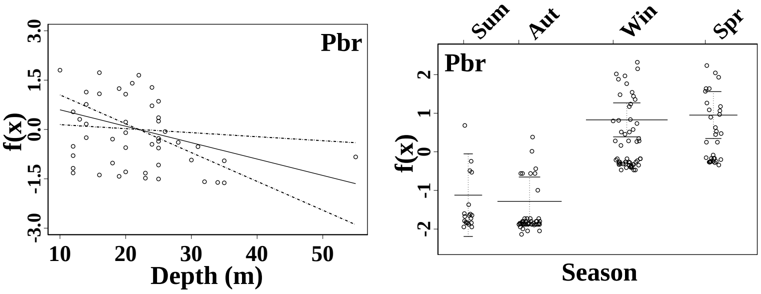


Figure 6.4: GLM functions generated from the most-parsimonious model relating fish number of *Paralonchurus brasiliensis*(Pbr) and its predictors.

If only depths shallower than 36m are considered, the effect still significant (12.5% of the total deviance, $P$-level$<$ 0.001). Together with season these predictors are responsible for 27% of the total deviance of this prey number in the dolphin diet. Winter and spring are the time of the year with higher numbers of *Paralonchurus brasiliensis*.

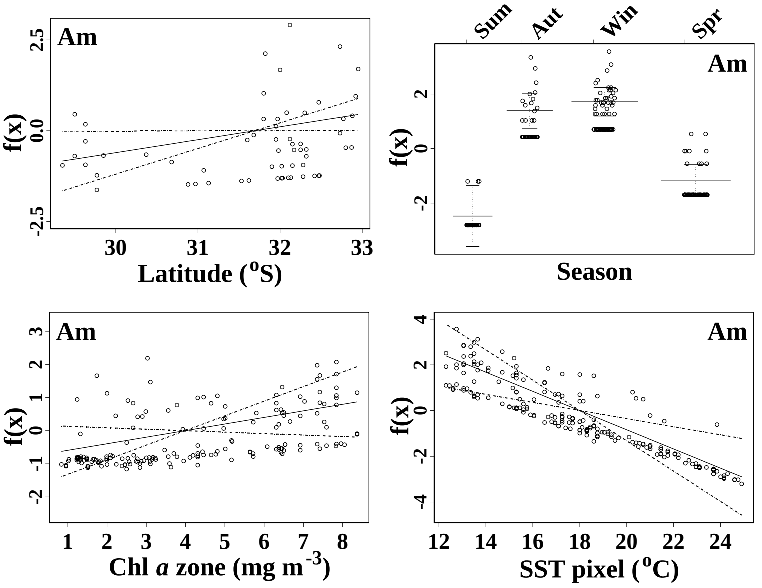


Figure 6.5: GLM functions generated from the most-parsimonious model relating fish number of *Anchoa marinii* (Am) and its predictors.

**(Am) *Anchoa marinii*.** The fish showed four significant predictors affecting its frequency in the franciscana feeding regime, which represent 64% of the total deviance (table 6.4). Season was the parameter with the greatest influence (27.8% of deviance), with a very low incidence of *Anchoa marinii* during summer, and higher number during autumn and winter (figure 6.5). There is a positive relationship between the *Anchoa marinii* and the latitude, although a lower contribution to the model (7.6%). The influence of environmental parameters chlorophyll-$a$ and water temperature seemed relatively strong (figure 6.5), as they together explained up to 31% of the total deviance. Lower temperatures appear to be highly significant for the presence of *Anchoa marinii* in the franciscana diet, followed by higher chlorophyll-$a$ concentrations.

The next set of results are for the fishes that showed more complex models (table 6.5), where interaction terms were not discarded by the AIC procedure. The environmental predictors are influential for the number of these fish prey in the franciscana food habits.

| Model | Predictors | % explained deviance | *P*-level |
|---|---|---|---|
| *Cynoscion jamaicensis* | Latitude | 0.8 | 0.010 |
| | Season | 2.7 | <0.001 |
| | SST zone | 25.0 | <0.001 |
| | Season : SST zone | 5.5 | <0.001 |
| | $D^2 = 0.34$ /adj.$D^2 = 0.32$ | | |
| *Merluccius hubbsi* | Depth | 31.7 | <0.001 |
| | Latitude | 12.1 | <0.001 |
| | SST zone | 3.0 | 0.022 |
| | SST pixel | 12.3 | <0.001 |
| | Latitude : SST zone | 0.1 | 0.663 |
| | Latitude : SST pixel | 0.6 | 0.310 |
| | SST zone : Depth | 0.8 | 0.229 |
| | SST pixel : Depth | 6.2 | <0.001 |
| | SST pixel : SST zone | 1.3 | 0.126 |
| | Latitude : SST pixel : SST zone | 5.6 | 0.002 |
| | $D^2 = 0.74$ /adj.$D^2 = 0.72$ | | |
| *Umbrina canosai* | Season | 6.8 | 0.001 |
| | SST zone | 5.6 | 0.002 |
| | SST pixel | 0.6 | 0.453 |
| | SST zone : SST pixel | 5.0 | 0.030 |
| | Season : SST zone | 3.9 | 0.010 |
| | $D^2 = 0.22$ /adj.$D^2 = 0.20$ | | |

Table 6.5: Fish prey frequency models (GLM) of three chosen species. More information about the parameters is described in the table 6.4.

Because the parameters of sea surface temperature (pixel and zone) are strongly correlated (share the same information), the presence of one SST parameter displaced or make less informative the other SST variable. The same for chlorophyll-*a* variables. Thus we illustrate just the most significant of them when both appear in the models.

**(Cj) *Cynoscion jamaicensis*.** This species seems strongly influenced by sea temperature, being more frequent in warmer waters (figure 6.6), and summer is the season with higher numbers. Although the latitude is significant for *Cynoscion jamaicensis* number in the franciscana diet, its influence for the total deviance of the model is low (0.8%).

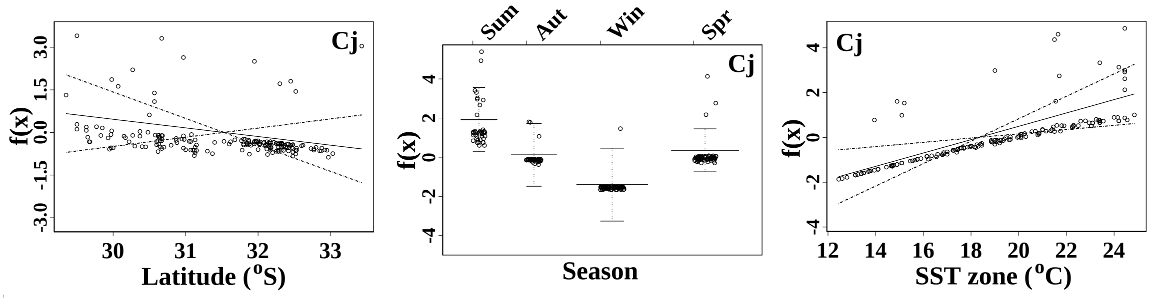


Figure 6.6: GLM functions generated from the most-parsimonious model relating fish number of *Cynoscion jamaicensis* (Cj) and its predictors.

**(Mh)** ***Merluccius hubbsi***. In contrast to *Cynoscion jamaicensis*, *Merluccius hubbsi* has a negative correlation with temperature, and a positive correlation with latitude (figure 6.7). Both of these and their interactions explain more than 32% of the model deviance (table 6.5). However, the depth parameter alone also explains this amount of deviance, and is therefore the most influential predictor for *Merluccius hubbsi* number in the franciscana diet.

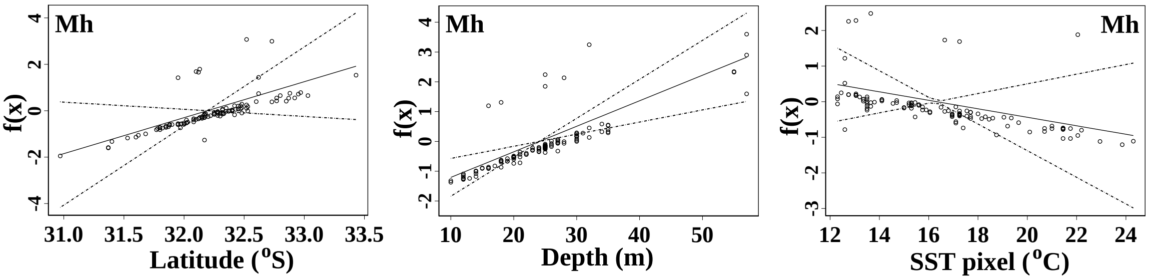


Figure 6.7: GLM functions generated from the most-parsimonious model relating fish number of *Merluccius hubbsi* (Mh) and its predictors.

**(Uc)** ***Umbrina canosai***. This species seems to be positively influenced by temperature (figure 6.8), and similarly by warm seasons. It appears that there is not a strong influence of a single predictor in the *Umbrina canosai* number in the franciscana diet, as season, temperature and their interaction all have a similar influence in the model (table 6.5).

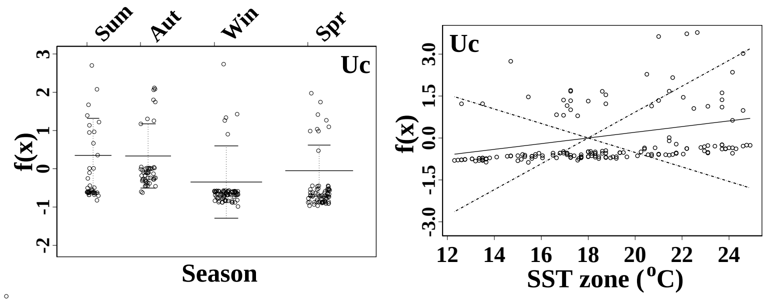


Figure 6.8: GLM functions generated from the most-parsimonious model relating fish number of *Umbrina canosai* (Uc) and its predictors.

**(Cg, Tl)** ***Cynoscion guatucupa and Trichiurus lepturus*** (table 6.6). These fish are very important prey of franciscana (see Chapter 4). They exhibit opposite relationships with respect to the sea temperature and season parameters (figures 6.9 and 6.10). *Trichiurus lepturus* seems higher in number during warmer seasons and has a high positive correlation with temperature, whereas *Cynoscion guatucupa* appears during colder seasons and has a negative relationship with temperature. Both predictors and interactions together explain about 48% of the total deviance for *Trichiurus lepturus*, and 33% for *Cynoscion guatucupa* (table 6.6). Furthermore, latitude is a relatively important predictor of *Cynoscion guatucupa*, responsible alone for more 13% of the deviance in the model. The depth appears to influence significantly only *Trichiurus lepturus*, despite a modest contribution to the total deviance of the model (4.1%).

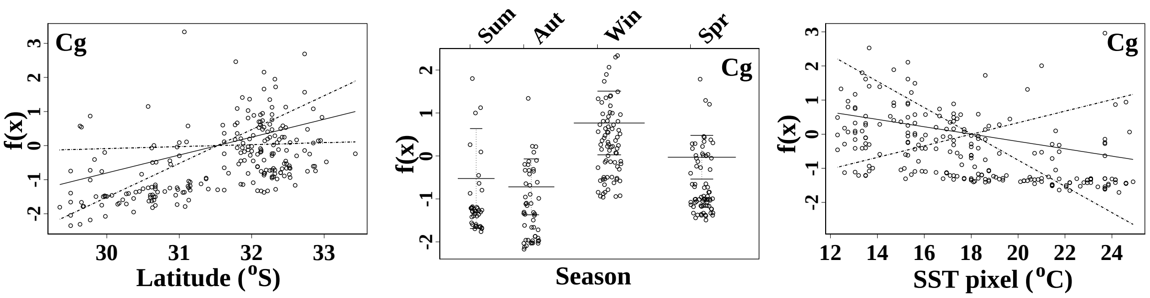


Figure 6.9: GLM functions generated from the most-parsimonious model relating fish number of *Cynoscion guatucupa* (Cg) and its predictors.

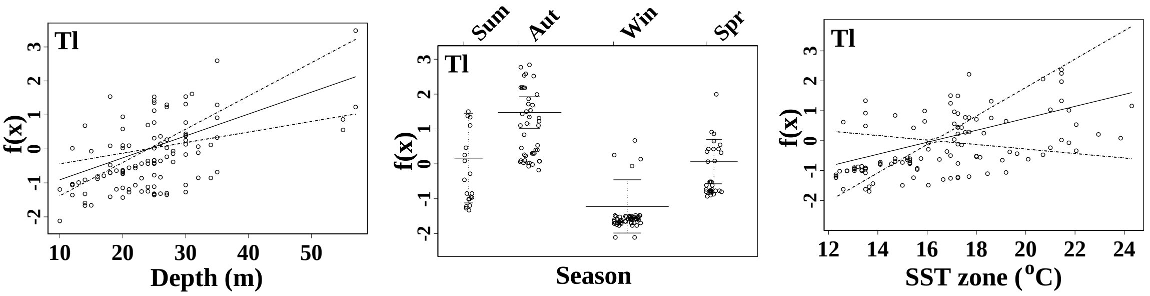


Figure 6.10: GLM functions generated from the most-parsimonious model relating fish number of *Trichiurus lepturus* (Tl) and its predictors.

| **Model** | **Predictors** | **% explained deviance** | ***P*-level** |
|---|---|---|---|
| *Trichiurus lepturus* | Depth | 4.1 | <0.001 |
| | Season | 26.0 | <0.001 |
| | SST zone | 1.3 | 0.075 |
| | SST pixel | 10.3 | <0.001 |
| | Depth : SST pixel | 2.8 | 0.010 |
| | Season : SST pixel | 4.7 | 0.011 |
| | SST zone : SST pixel | 2.0 | 0.031 |
| | Season : SST zone : SST pixel | 7.4 | <0.001 |
| | $D^2$ = 0.59 /adj.$D^2$ = 0.56 | | |
| *Cynoscion guatucupa* | Latitude | 12.9 | <0.001 |
| | Season | 4.3 | <0.001 |
| | SST zone | 0.9 | 0.035 |
| | SST pixel | 15.8 | <0.001 |
| | Latitude : Season | 1.5 | 0.067 |
| | Latitude : SST zone | 2.4 | <0.001 |
| | Latitude : SST pixel | 1.7 | 0.003 |
| | Season : SST zone | 3.6 | <0.001 |
| | Season : SST pixel | 3.9 | <0.001 |
| | SST zone : SST pixel | 0.6 | 0.076 |
| | Latitude : Season : SST zone | 0.7 | 0.361 |
| | Latitude : Season : SST pixel | 1.3 | 0.105 |
| | Latitude : SST zone : SST pixel | 0.6 | 0.080 |
| | Season : SST zone : SST pixel | 4.3 | <0.001 |
| | $D^2$ = 0.55 /adj.$D^2$ = 0.49 | | |

Table 6.6: Fish prey frequency models (GLM) of two chosen species. More information about the parameters is described in the table 6.4.

***Total fish specimens.*** There are three factors influencing the total number of fish specimens number in the franciscana diet, the sea temperature, the depth, and the season (table 6.7). It seems that at lower temperatures there are higher number of fish in the franciscana diet. Although the season parameter is significant, the differences between the seasons do not seem large (figure 6.11). Depth is the second influential predictor, with 6% of the total deviance, and together with its interactions its influence on the deviance is twice more (table 6.7).

| Model | Predictors | % explained deviance | *P*-level |
|---|---|---|---|
| Total fish specimens | Depth | 5.9 | <0.001 |
| | Season | 4.0 | 0.012 |
| | SST pixel | 16.5 | <0.001 |
| | Depth : Season | 1.6 | 0.217 |
| | Depth : SST pixel | 1.2 | 0.066 |
| | Season : SST pixel | 2.5 | 0.080 |
| | SST zone : SST pixel | 2.9 | 0.005 |
| | Depth : Season : SST pixel | 3.0 | 0.040 |
| | $D^2 = 0.38$ /adj.$D^2 = 0.30$ | | |

Table 6.7: Total fish prey specimens frequency model (GLM). More information about the parameters is described in the table 6.4.

Shallower depth is associated with high number of fish specimens. However, the influence of fewer samples from deeper waters could affect its significance. Hence a model including only depth values under 36m was fitted. The effect of depth was lower but still significant (4.2% of the total deviance, *P*-level= 0.003, figure 6.11).

Even though the best-fit models explained a significant amount of variation (deviance) in many fish prey species number, model validations revealed little predictive power of all the defined models. Pearson correlation values were generally not significant (values between 0.20 and 0.45).

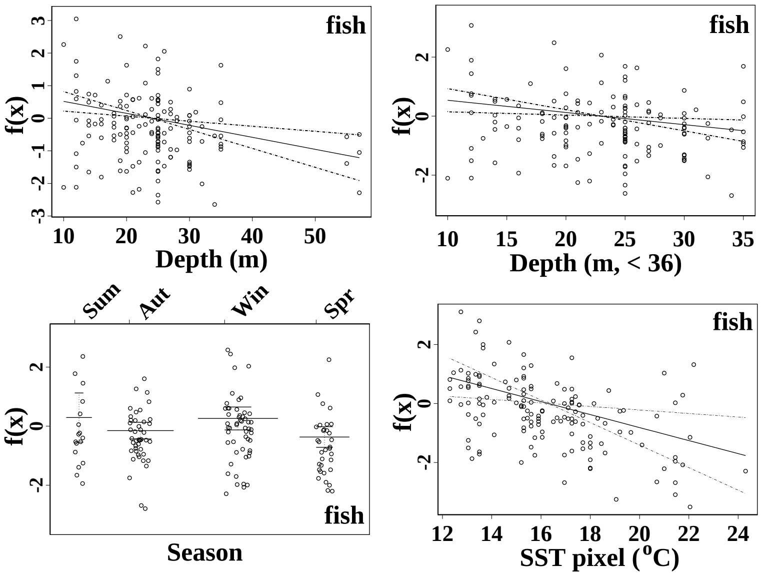


Figure 6.11: GLM functions generated from the most-parsimonious model relating total fish specimens and its predictors.

- **Cephalopod and crustacean species**

Analysis of deviance indicated strong support for the effects of the oceanographic parameter SST and the temporal parameter season for all the cephalopod prey species number, and the crustacean group "shrimp", in the franciscana feeding (table 6.8). Nevertheless, the models of the squid *Loligo sanpaulensis* and the shrimp specimens individually did not explain a great amount of variation for their frequency in the franciscana diet (19% and 12%, respectively).

| Model | Predictors | % explained deviance | ***P*-level** |
|---|---|---|---|
| *Loligo sanpaulensis* | poly (Latitude$^2$) | 6.7 | <0.001 |
| | Season | 7.4 | <0.001 |
| | SST pixel | 4.1 | <0.001 |
| | poly (Latitude$^2$) : SST pixel | 3.2 | 0.003 |
| | $D^2 = 0.22$ /adj.$D^2 = 0.19$ | | |
| *Loligo plei* | Latitude | 3.1 | 0.004 |
| | Season | 12.3 | <0.001 |
| | SST zone | 14.7 | <0.001 |
| | Latitude : Season | 2.7 | 0.060 |
| | Latitude : SST zone | 1.4 | 0.052 |
| | Season : SST zone | 3.1 | 0.034 |
| | Latitude : Season : SST zone | 10.5 | <0.001 |
| | $D^2 = 0.48$ /adj.$D^2 = 0.44$ | | |
| *Argonauta nodosa* | Depth | 17.4 | <0.001 |
| | Season | 8.3 | <0.001 |
| | SST pixel | 32.4 | <0.001 |
| | Depth : Season | 3.3 | 0.010 |
| | Depth : SST pixel | 1.9 | 0.011 |
| | Season : SST pixel | 1.4 | 0.192 |
| | $D^2 = 0.65$ /adj.$D^2 = 0.62$ | | |
| Total shrimp specimens | Season | 4.6 | 0.012 |
| | SST zone | 2.4 | 0.016 |
| | Season : SST zone | 7.8 | 0.003 |
| | $D^2 = 0.15$ /adj.$D^2 = 0.12$ | | |

Table 6.8: Cephalopod prey and shrimp specimens frequency models (GLM). More information about the parameters is described in the table 6.4.

**(Ls, Lp)** ***Loligo sanpaulensis and Loligo plei*****.** Both squids showed similar predictors despite the differences in their influences (table 6.8). The temperature affected negatively *Loligo sanpaulensis*, and positively *Loligo plei* (figures 6.12 and 6.13). Similarly there are high numbers during colder seasons for *Loligo sanpaulensis*, and during warmer seasons for *Loligo plei*. Season is the predictor that best explains the deviance in the *Loligo sanpaulensis* model, whereas it is temperature for *Loligo plei*. For the spatial predictor latitude, the squid *Loligo sanpaulensis* was the only prey with a polynomial shape (quadratic) for its number in the study area (figure 6.12), whilst *Loligo plei* showed a negative linear trend through latitude (figure 6.13).

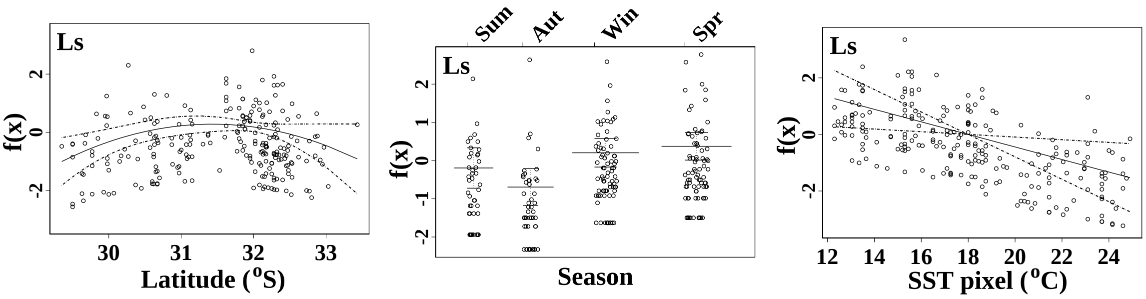


Figure 6.12: GLM functions generated from the most-parsimonious model relating cephalopod number of *Loligo sanpaulensis* (Ls) and its predictors.

**(An)** ***Argonauta nodosa*****.** This species had two main contributors to its model, the temperature and the depth (table 6.8). The temperature influences the numbers positively (figure 6.14), as do the warmer seasons. Depth appeared to affect the *Argonauta nodosa* number in the franciscana diet strongly, although between 10 and 35m its influence is small and not significant (0.2% of the total deviance, $P$-level= 0.591, see figure 6.14).

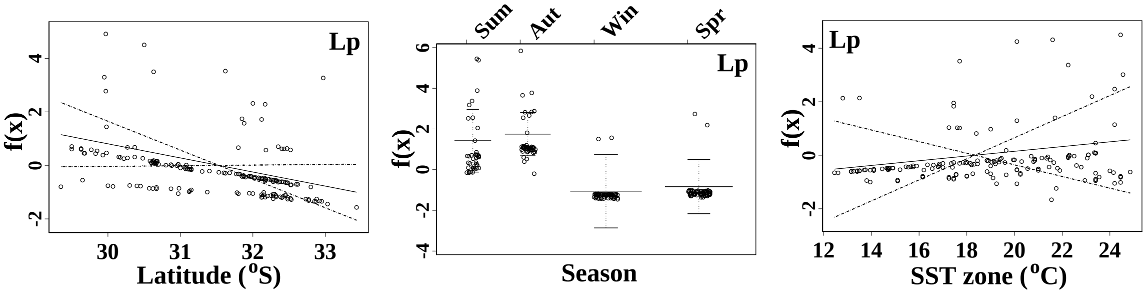


Figure 6.13: GLM functions generated from the most-parsimonious model relating cephalopod number of *Loligo plei* (Lp) and its predictors.

***Total shrimp specimens***. The shrimps show a significant positive influence with the spring season (figure 6.14), which is the parameter that most explained its variation (table 6.8). The temperature seems not to affect the shrimp numbers much in the dolphin diet, even though it has a significant negative correlation (figure 6.14).

Similarly to fish prey species, model validations revealed little predictive power for all the defined models. Pearson correlation values were again low (between 0.20 and 0.35).

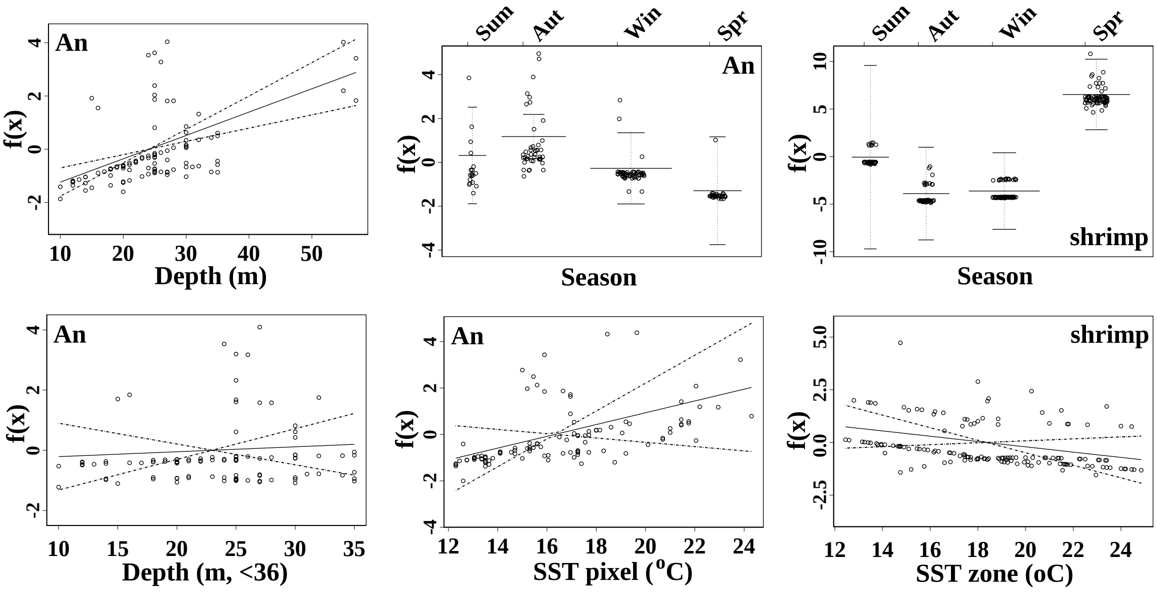


Figure 6.14: GLM functions generated from the most-parsimonious models relating the octopus *Argonauta nodosa* (An, left and middle graphs) and the shrimp specimens (shrimp, right graphs), and their predictors.

### 6.2.2 LM selection: factors affecting franciscana prey specimens size

The purpose is to find the minimum adequate model for the prey specimens length (mm) and the influence of possible predictors and their interactions. LM of log-transformed fish and cephalopod lengths were appropriate models for prey specimens size as a function of the explanatory parameters.

- **Fish specimens length**

The LM constructed for the fish specimens size revealed that sea temperature is the predictor that best explained its variance in the diet of franciscana (table 6.9). Although season and depth do not explain a large amount of variance, they are significant predictors. However, all the parameters and their interactions explain only 25% of the fish prey length variance in the franciscana feeding regime.

| Model | Predictors | % explained variance | *P*-level |
|---|---|---|---|
| *log* (Fish length) | Depth | 1.8 | <0.001 |
| | Season | 2.5 | <0.001 |
| | SST zone | 1.2 | 0.058 |
| | SST pixel | 7.8 | <0.001 |
| | SST zone : SST pixel | 3.7 | <0.001 |
| | Depth : SST pixel | 2.6 | <0.001 |
| | Depth : SST zone | 0.7 | <0.001 |
| | Season : SST pixel | 2.2 | <0.001 |
| | Season : SST zone | 1.8 | <0.001 |
| | Depth : Season | 0.4 | 0.007 |
| | Depth : SST zone : SST pixel | 0.1 | 0.038 |
| | Season : SST zone : SST pixel | 0.3 | 0.001 |
| | Depth : Season : SST pixel | 0.3 | 0.032 |
| | Depth : Season : SST zone | 0.1 | 0.045 |
| | Depth : Season : SST zone : SST pixel | 1.0 | <0.001 |
| | $R^2 = 0.26$ /adj.$R^2 = 0.25$ | | |

Table 6.9: Fish prey specimens length (LM). % explained variance= percentages of variance explained successively by each predictor; *P*-level= significance level associated with the F-test of variance for each predictor; $R^2$= total proportion of variance explained by the model; adj.$R^2$= same as $R^2$ but corrected for the number of degrees of freedom used to build the model.

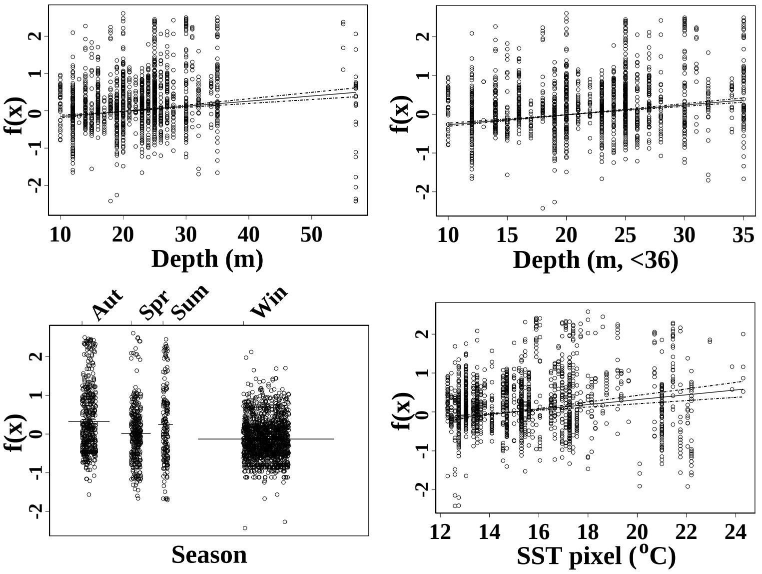


Figure 6.15: LM functions generated from the most-parsimonious model relating fish specimens length and its predictors. Solid lines are the fitted LM. Dashed lines are approximate 95% point-wise confidence intervals.

There is a positive relationship between the fish size and depth (figure 6.15), similarly considering water depth under 36m in the LM (increase to 4.7% of the explained variance, $p < 0.001$, figure 6.15). The model shows a positive trend of the fish prey length with temperature, with larger fish during warmer seasons.

Little predictive power of the model was again found with a

Pearson correlation coefficient between the predicted and observed values from the validation sets of 0.21.

- **Cephalopod specimens length**

Even though all the parameters and their interactions are significant in the best fit LM, it only explains 18% of the cephalopod specimens length variance in the franciscana diet (mainly from *Loligo sanpaulensis* measurements, table 6.10).

| Model | Predictors | % explained variance | *P*-level |
|---|---|---|---|
| *log* (Cephalopod length) | Depth | 3.1 | <0.001 |
| | polynomial (Latitude$^2$) | 3.7 | <0.001 |
| | Season | 1.8 | <0.001 |
| | SST pixel | 4.1 | <0.001 |
| | poly (Latitude$^2$) : SST pixel | 0.7 | <0.001 |
| | poly (Latitude$^2$) : Season | 1.0 | <0.001 |
| | Season : SST pixel | 1.5 | <0.001 |
| | Depth : poly (Latitude$^2$) | 0.3 | <0.001 |
| | Depth : SST pixel | 0.1 | 0.009 |
| | Depth : Season | 0.3 | <0.001 |
| | Depth : poly (Latitude$^2$) : Season | 0.6 | <0.001 |
| | Depth : Season : SST pixel | 1.0 | <0.001 |
| | Depth : poly (Latitude$^2$) : Season : SST pixel | 0.4 | <0.001 |
| | $R^2 = 0.19$ /adj.$R^2 = 0.18$ | | |

Table 6.10: Cephalopod prey specimens mantle length (LM). More information about the parameters is described in the table 6.9.

The model, like that for the fish group, revealed a greater effect on the variance from the environmental predictor sea temperature, with a positive correlation with the cephalopod length (figure 6.16). The spring and summer seasons seem to be the time with bigger cephalopods.

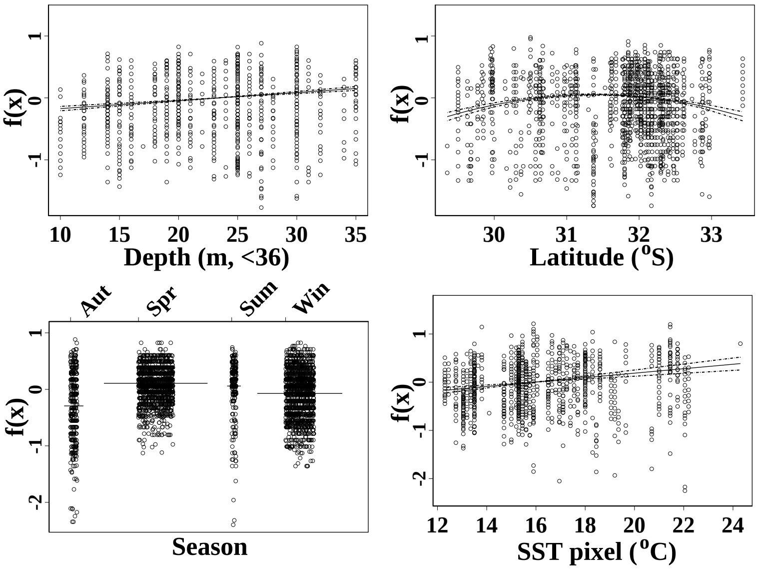


Figure 6.16: LM functions generated from the most-parsimonious model relating cephalopod specimens length (mainly *Loligo sanpaulensis*) and its predictors.

Relationship between cephalopod length and latitude was better reproduced as a polynomial (quadratic) regression (figure 6.16, top right graphic). The depth predictor has a positive correlation with cephalopod length for values lower than 36m (top left graphic).

There is little predictive power from the model with a small Pearson correlation coefficient (cor= 0.25).

### 6.2.3 Summary of predictor effects

In this section we summarise the effects associated with each predictor variable.

- **Sea Surface Temperature (SST)**

The relationship between the SST averaged values of the pixel region (SST pixel) and the latitudinal zone (SST zone) show a strong correlation ($R^2 = 0.88$) as expected, with the best fit model equation being $SST\ pixel = -0.367 + 1.003 \times SST\ zone$.

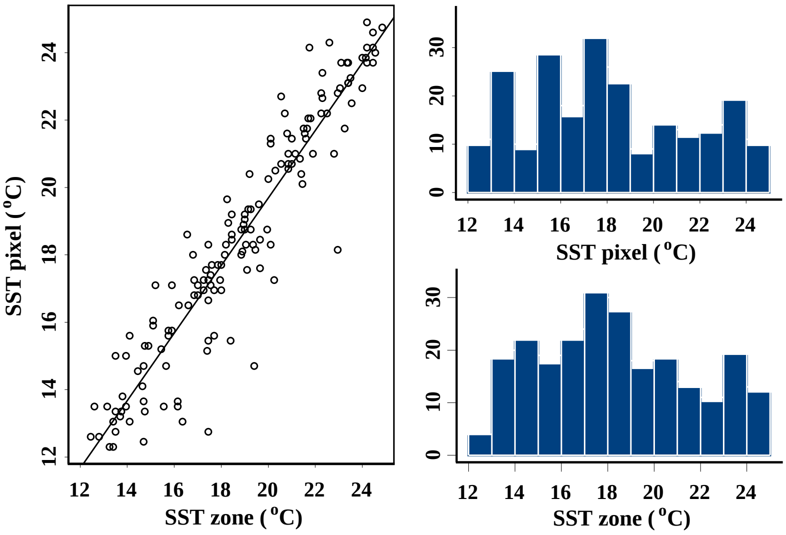


Figure 6.17: The relationship of the SST values parameters chosen for the LM and GLM analyses, and their histograms of distribution.

Therefore those variables share information, and the presence of one of them makes the other less informative. This can be seen in the GLM and LM tables (6.4 to 6.10). Thus the model choice for the SST zone or SST pixel normally takes into account only that one which better explains the variance/deviance, as well their interaction terms with other variables.

In the GLM, SST parameters (SST zone or/and SST pixel) generally explain a significant part of the deviance of many prey species. From the fourteen prey species analysed, nine were significantly influenced by temperature, as were the fish and shrimp prey groups too.

The most frequent prey from a warm environment, according to the models, were the fishes *Cynoscion jamaicensis*, *Umbrina canosai*, and *Trichiurus lepturus*, the squid *Loligo plei*, and the argonaut *Argonauta nodosa*. From colder waters the fishes *Anchoa marinii*, *Merluccius hubbsi*, and *Cynoscion guatucupa*, and the squid *Loligo sanpaulensis* were more abundant. Furthermore, some prey species were much less common in lower temperatures, as is the case of the fish *Trichiurus lepturus*, and in higher temperatures for example the fish *Anchoa marinii*. Total fish specimens eaten by franciscana were higher in number at lower temperatures, as were the shrimp specimens (although the effect is not large).

Judging by the effect on prey specimens size, bigger cephalopods and fishes were mostly associated with warmer temperatures.

- **Chlorophyll-a (Chl a)**

The relationship between the chlorophyll-$a$ monthly averaged values of the latitudinal zone (Chl $a$ zone) and pixel region (Chl $a$ pixel) of each capture event is demonstrated in the figure 6.18.

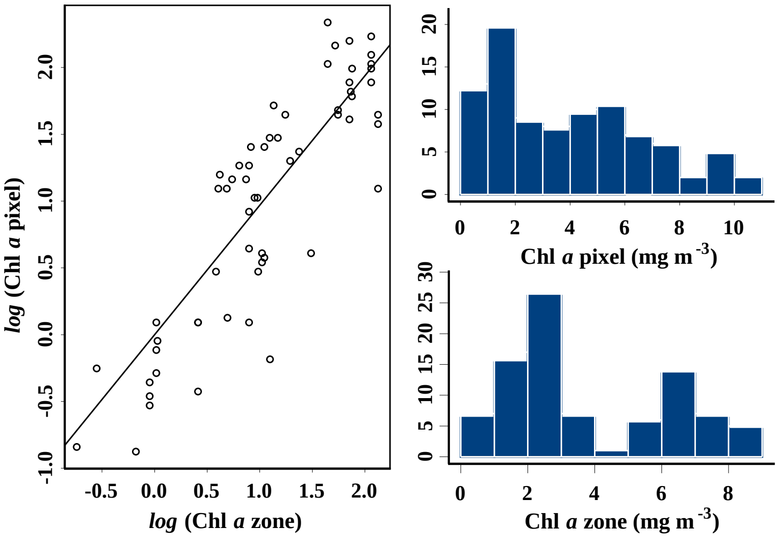


Figure 6.18: The relationship of the chlorophyll-$a$ values parameters chosen for the LM and GLM analyses, and their histograms of distribution.

Similarly to SST, and as expected the Chl $a$ parameters also show a strong correlation ($R^2 = 0.89$), with the best fit model (lower *AIC* criterion) equation being $log(Chl\ a\ pixel) = -0.802 + 0.969 \times log(Chl\ a\ zone)$.

The GLM modelling only considered the chlorophyll-$a$ predictor for the fish prey *Anchoa marinii*, showing a strong positive relationship. Considering the prey specimens size, no relationship was found with any Chl $a$ parameter.

- **Depth**

The majority (> 50%) of the franciscanas caught depths are between 15 and 30m (figure 6.19), and the greater samples are between 20 and 25m (mean= 24.1m). Because there is a gap in the samples between 35 and 50m (figure 6.19), in the case of significant results re-analysis of samples only considering water depth lower than 36m was conducted.

The water depth had a great influence for some fish prey species. As the water column deepens, there is an increase in the prey number of *Merluccius hubbsi*, *Trichiurus lepturus*, and the argonaut *Argonauta nodosa*; and a decrease in the frequency of *Paralonchurus brasiliensis*.

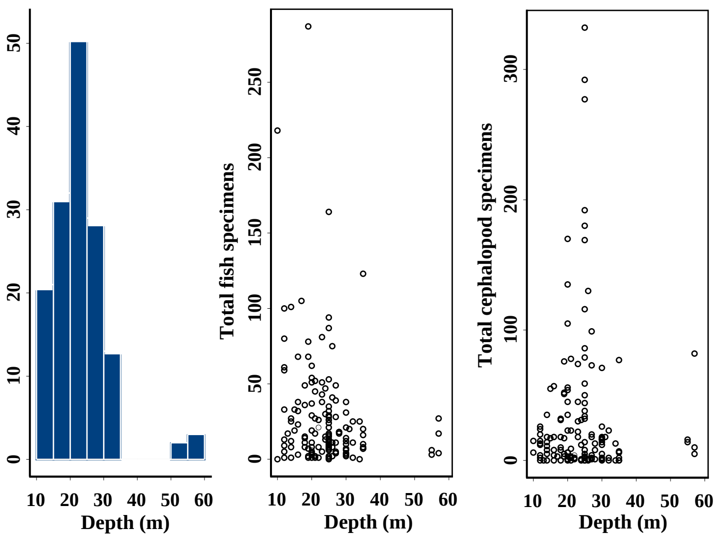


Figure 6.19: Histogram of the depth parameter, and the number of fish and cephalopod specimens plotted through depth.

The total number of fish specimens also decreases when water depth increases, probably because it is influenced by the body length of the fish specimens. This is because a great percentage of the franciscana prey ingested are smaller fishes and this parameter was significant affected by depth, because smaller fishes were more frequent in shallow waters. Smaller cephalopods also occurs in higher numbers in shallower water. Overall it is clear that water depth has a significant influence on the size of the franciscana prey.

- **Latitude**

This spatial parameter has a linear effect on many fish species number. Different prey species in the franciscana diet had a positive or negative linear relationship with the latitude predictor. The only species with a polynomial regression shape was the squid *Loligo sanpaulensis*. For the prey body length (LM), only cephalopod specimens varied significantly according to the latitude.

- **Season**

The temporal variable had the greatest effect of all the potential explanatory variables for almost all prey species. Practically all the prey vary seasonally in number, as well in body length. Only the fishes *Merluccius hubbsi* and *Urophycis brasiliensis* showed no significant variation through seasons, even though water temperature was significant for *Merluccius hubbsi*. Some features are not just related to the time in the year that some species appear in greater numbers, but also those in which some species are very infrequent. For example the fish *Trichiurus lepturus* and the squid *Loligo plei* occur with the lowest frequency during the winter, while the fishes *Anchoa marinii* and *Cynoscion guatucupa* are uncommon during the summer.

## 6.3 Discussion

Some comments and observations about the strengths and weaknesses of the modelled relationships are relevant, and are firstly considered.

Afterwards, the discussion of the present Chapter, the main goal of this study, is organised as follows:

We start discussing the results from factors affecting the franciscana diet according to the (i) prey species, and (ii) the prey specimens body length.

The discussion concerning prey species is organized by the influence of the sea temperature and season, where prey related to warm environment are firstly considered, followed by those related to a cold environment. Each prey species is discussed separately, together with the observations from other significant predictors.

Following this, the effects of chlorophyll-$a$ are included, and finally the spatial parameters latitude and depth are incorporated to summarize all the prey influenced by these predictors.

For the length of prey specimens, only two models (fish and cephalopod), are discussed.

This section continues with the approaches used in relation to the environmental-biological coupling analyses, which elucidate some findings from the Chapter 4, and reflect the dynamics of physical processes of the study area analysed in Chapter 5.

Finally we conclude with the implications of this research study.

### 6.3.1 The modelling approach: strengths and weaknesses

In this study we have developed and described a model-building approach to investigating the availability of franciscana prey as a function of a suite of easily measured environmental, spatial, and temporal variables. This versatile approach can be used to estimate linear relationships using GLM and LM. In addition, the models allow one to derive equations that help to understand the importance of different predictors for a particular prey species and also for the prey specimens body length.

However it must be recognized that the results from stomach contents are only an approximation of franciscana prey availability in the environment. Therefore some factors such as the prey behaviour (i.e. high mobility) may also influence their occurrence in the diet, and these are not included in the models.

Although simple covariates describing ocean properties have been found to be useful in explaining some of the variation in the foraging behaviour of apex predators, the predictive capacity of those models is rather variable (Bradshaw et al., 2004). That is also the case of our results. Even though some of the best-fit models explained a significant amount of variation in the franciscana prey, model validation tests revealed that these have rather little predictive power.

An important potential limitation for the models' predictive capacity may reside in the choice of some parameters from the spatial location of the capture event. Not all the animals had necessarily eaten in the immediate area surrounding its capture, consequently the predictor values of latitude and bathymetry might not correlate very well with the findings in the dolphin stomachs. However, when pixel and zone values for SST and Chl *a* were used, their influence on the response variables were generally very similar. This is because even at some distance from the dolphin capture, the water temperature and chlorophyll-*a* concentration are rather uniform, which makes them equally good as predictors.

Furthermore, the collective information from the modelling approaches indicates that prediction may still be difficult because the mechanisms influencing the prey in the franciscana diet may not be fully identified; rather, our modelling only indicates which of the factors considered impact on the franciscana feeding habits. Thus the ability to predict franciscana prey may be restricted by other factors such as the fish and cephalopod prey (i) biotic interactions - intra and interspecific competition and predation; (ii) physiological performance; (iii) segregation behaviour; (iv) recruitment time and location; and others as (v) fisheries exploration; (vi) ecosystem restraints, etc. Indeed, it is far from simple to isolate all the variables affecting prey aggregation or predator fidelity because marine trophic interactions are complex and interwoven (Laidre et al., 2004).

Nonetheless, the results indicated that the chosen predictors are often significant factors which explain, reasonably well, a significant proportion of the variation of many prey species in the franciscana food habits. However, latitude and season may explain dietary variability but they do not reveal the mechanism underlying the relationship. Unexplained variation from missing predictors may influence the power of our models, and non-random systematic sampling (unbalanced samples) may increase the "noise" in the data. Consequently it is not surprising that the models predictive power is rather low.

Research studies concerning different response variables related to several ecosystems predictors, using GLM and GAM, have more often than not found poor predictive models (Watts et al., 1999; Richardson et al., 2003; Bradshaw et al., 2004; Hastie et al., 2005), despite a wide range of potential and significant predictors analysed.

Overall, it is understandable that when dealing with observational data in many complex and dynamic ecosystems, not obtained with a designed and controlled experiment, it is difficult to find a powerful predicted model for any response variable. However, modelling potential predictors provides important information about their influence, significance and relationship with the response parameter, and it indubitably provide important information, even it is not complete.

Despite the poor predictive capacity of the models examined in this study, some of the mechanisms influencing the franciscana prey are congruent with expectations of distribution of marine food resources at the study region due to its oceanographic features (see Chapter 5). Thus we suggest that low predictive power is mainly due to environmental variability, not discarding also other factors cited previously, rather that to model inadequacy.

### 6.3.2 Factors affecting the franciscana prey

The major features of the franciscana feeding habits have been discussed in Chapter 4. Nevertheless, the findings from this Chapter further elucidate some of the results and observations from Chapter 4, and add new information.

In particular, the versatile modelling approach used permits one to (i) visualize the relationships between the prey abundance and its significant predictors; and (ii) understand the real influence of the significant predictors when considering them all together with their interactions in the same framework. Finally, this represents the first attempt to include environmental parameters in the analyses of franciscana feeding ecology.

- **Prey species**

The foraging behaviour and distribution of marine predators will be largely influenced by the distribution of their prey, the latter being influenced to various degrees by the physical and biological properties of the ocean (Richardson et al., 2003; Laidre et al., 2004; Bradshaw et al., 2004).

In our case, many of the franciscanas' prey were significantly influenced by an important ocean property, the sea surface temperature, represented by the SST zone and/or SST pixel parameters. As already reported in Chapter 5, the study region is affected by the encounter between the southward flowing and warm Brazil Current (BC), and the coastal cold current (BCC) flowing north (Gordon, 1989). Those currents fluctuate seasonally, and this explain why season emerges as a consistent predictor describing the variation on abundance of franciscana prey species. Season and the SST parameters represent the greater amount of variation from interaction terms in the models (see tables 6.5 to 6.8).

From the fish species related to a warm environment, the Argentine croacker *Umbrina canosai* seemed most influenced by SST (figure 6.8), followed by the Jamaica weakfish *Cynoscion jamaicensis* (figure 6.6). The frequency of the cutlassfish *Trichiurus lepturus* in the franciscana diet is also strongly influenced by higher temperatures (see figure 6.10).

According to Haimovici et al. (1996), the juveniles of *Umbrina canosai* (mostly those ingested by franciscana) occur in the coastal zone off southern Brazil from spring and mainly during summer, while the adults migrate to Uruguay and northern Argentina. The same authors stated that *Cynoscion jamaicensis* was highly associated to temperatures higher than $16^o$C, being higher abundant during spring and summer research cruises, and practically absent during the winter. Looking at the figure 6.6, there is a similar pattern of water temperature and seasonal influence on frequency of *Cynoscion jamaicensis* in the franciscana diet. Beyond that, GLM for *Cynoscion jamaicensis* showed significantly greater numbers for lower latitudes, and this region is more influenced by warmer temperatures in the study area (see Chapter 5 for more information).

*Trichiurus lepturus* is also known to be strongly affected by temperature. A research study about this fish showed similar findings (Martins and Haimovici, 1997). During research cruises in the study region, these authors found an increase of the mean CPUE of the *Trichiurus lepturus* from less than 10kg $h^-1$ at $11^o$C to around 100kg $h^-1$ at temperatures up to $16^o$C, remaining high in warmer waters. In the present research, *Trichiurus lepturus* is also found to be sensitive to lower temperatures, with very low frequency during winter time (see figure 6.10).

Water depth was also a significant predictor of the numbers of *Trichiurus lepturus* ingested, where this fish prey was more frequent in the franciscana diet in the deepest waters. However, there is a difference between the juvenile and sub-adult groups distributions according to water depth (Martins and Haimovici, 1997). From March to May there is a higher frequency of *Trichiurus lepturus* sub-adult group in the inner shelf (20-80m), whereas juveniles were more frequent in less than 20m of depth (Martins and Haimovici, 1997). The sub-adult group of *Trichiurus lepturus* (mean= 402.05mm, see table 4.5) was the most ingested by franciscana, and coincides with the high abundance. Additionally, its most important presence in the diet was during autumn (see figure 6.10), which also conforms temporally with its frequency in the study region according to Martins and Haimovici (1997).

The cephalopods related to warmer temperatures, the squid *Loligo plei* and the argonaut *Argonauta nodosa* (Costa and Haimovici, 1990; Santos, 1999), also had SST parameters as the main predictor in the present study, especially for *Argonauta nodosa*.

Along the coast of southern Brazil the *Loligo plei* is occasionally caught in the inner shelf (Costa and Haimovici, 1990), which explain the considerably lower frequency when compared with *Loligo sanpaulensis*, but it is frequent in the warm season (Haimovici and Andrigueto Jr., 1986). Besides season and temperature parameters, the latitude was also a significant predictor with greater *Loligo plei* numbers at lower latitudes. Costa and Haimovici (1990) stated that for the southern Brazilian coast, the squid is more abundant in the northern sector, and Haimovici and Perez (1991b) found that during summer and autumn the squid penetrates southward following the superficial BC.

The occurrence of *Argonauta nodosa* along the southern Brazilian coast is also highly related to the superficial warm waters of the BC (Haimovici and Perez, 1991b), which is why this argonaut was strongly affected by the SST (this variate alone explains 32% of the deviance in the model, see table 6.8). The second predictor in importance was water depth. This epipelagic species was most frequent in the diet of franciscana from deeper waters, and related studies from many predator stomachs (fishes, seabirds, and other marine mammals) found higher numbers of *Argonauta nodosa* from the stomachs of outer shelf and shelf break predators (Santos, 1999).

All these above prey species were positively influenced by sea temperature, which also influenced some other prey species negatively as in the case of *Merluccius hubbsi* (see figure 6.7), *Cynoscion guatucupa* (see figure 6.9) , *Anchoa marinii* (figure 6.5), and the squid *Loligo sanpaulensis* (see figure 6.12).

A research study in the study area (Haimovici et al., 1993) cited the Argentine hake *Merluccius hubbsi* as a fish related to a colder environment. Haimovici et al. (1993), during 329 bottom hauls between 10 to 587m in the southern Brazilian coast, found higher captures of *Merluccius hubbsi* during winter cruises, mainly from depths over 50m. Those authors also found that juveniles were more frequent between depth of 40 and 120m, and occasionally in coastal waters. Similarly, water depth was positive correlated with *Merluccius hubbsi* in the diet of franciscana (see figure 6.7), and mainly juveniles were preyed upon (mean= 25.5mm, see table 4.5). Finally, the highest catches of *Merluccius hubbsi* occurred south of 32$^o$S of latitude (Haimovici et al., 1993), and we also found that a higher number of *Merluccius hubbsi* in the franciscana diet occurred at similar latitudes (see figure 6.7).

Another important franciscana fish prey species, the striped weakfish *Cynoscion guatucupa*, was frequent at lower temperatures. Although the *Cynoscion guatucupa* is regarded as a cold water species, juveniles and sub-adults, which are mostly ingested by franciscana (mean= 55.2mm, table 4.5), occurred all year round, mainly in the coastal zone (spawning area) (Haimovici et al., 1996). It therefore seems that even though this prey is available all year, it is more ingested by franciscana during winter. An hypothesis could be the absence of other important prey species during this time, such as the warm water fish *Trichiurus lepturus*, which is mostly ingested during the other seasons, and practically absent in the winter (see figure 6.10). The *Trichiurus lepturus* is an important prey in terms of biomass ingested by franciscana (see tables A.1 and A.2 in appendix A), hence the franciscana could prefer it when this fish is abundant, rather than smaller fish species such as the *Cynoscion guatucupa*.

Not only season and temperature were significant predictors for *Cynoscion guatucupa*, but also the latitude, with higher numbers occurring at southern latitudes. Similar abundance pattern was found by Haimovici (1997a), where demersal fisheries cruises found *Cynoscion guatucupa* increasing in abundance south of 32$^o$S in the Brazilian coast, Uruguay and northern Argentina.

The anchoita *Anchoa marinii* was more frequent in colder temperatures and seasons. Those two predictors represent a large amount of variation in the GLM (43%, see table 6.4). Castello (1997) describe *Anchoa marinii* as a typical inhabitant of shallow waters in southern Brazilian coast, and the fish is associated with the low temperature waters of the BCC. Additionally, there is also a spatial variation of *Anchoa marinii* number in the franciscana diet through the study area (see figure 6.5). The negative relationship between anchoita and latitude is possibly because of the greater temporal influence of cold waters in the southern zones (see section 5.3.1, Chapter 5).

The main cephalopod ingested, the common long-finned squid *Loligo sanpaulensis*, was affected negatively by temperature. The species is the most abundant coastal squid in southern Brazil, and it is associated with colder and more productive areas of fronts between water masses, such as the northern influence of the MC/BCC (Andriguetto Jr. and Haimovici, 1991). Similarly, colder seasons are associated with higher numbers of the squid in this study, and it was a significant predictor (see table 6.8). These results are consistent with higher temporal abundance of *Loligo sanpaulensis*, where highest catches (over 15kg/h) were obtained in winter and spring research cruises off southern Brazilian coast (figure 6.20) (Andriguetto Jr. and Haimovici, 1991).

Figure 6.20 provides further information on the spatial distribution of *Loligo sanpaulensis*. The red line approximates the southern limit of the *Loligo sanpaulensis* distribution in the franciscana diet of this study (see figure 6.12). It seems that the squid abundance starts increasing again northwards with higher catches around 31$^o$S (figure 6.20), and a similar relationship of *Loligo sanpaulensis* and latitude in the franciscana diet was found (see figure 6.12). Unfortunately, north of 31$^o$S there is no information of catches from the work of Andriguetto Jr. and Haimovici (1991), when the number of *Loligo sanpaulensis* starts decreasing again in the franciscana feeding data. However, the number of *Loligo sanpaulensis* found in the stomachs of several marine predators (fish, birds and mammals) decrease northwards off the Brazilian coast (Santos, 1999).

Temperature was not a significant predictor for the banded croacker *Paralonchurus brasiliensis*, even though it was more frequent during winter and spring (see figure 6.4). However, this fish species occurs throughout the year off the southern Brazilian coast, and seems equally abundant during colder or warmer seasons (Haimovici et al., 1996; Haimovici, 1997a). The

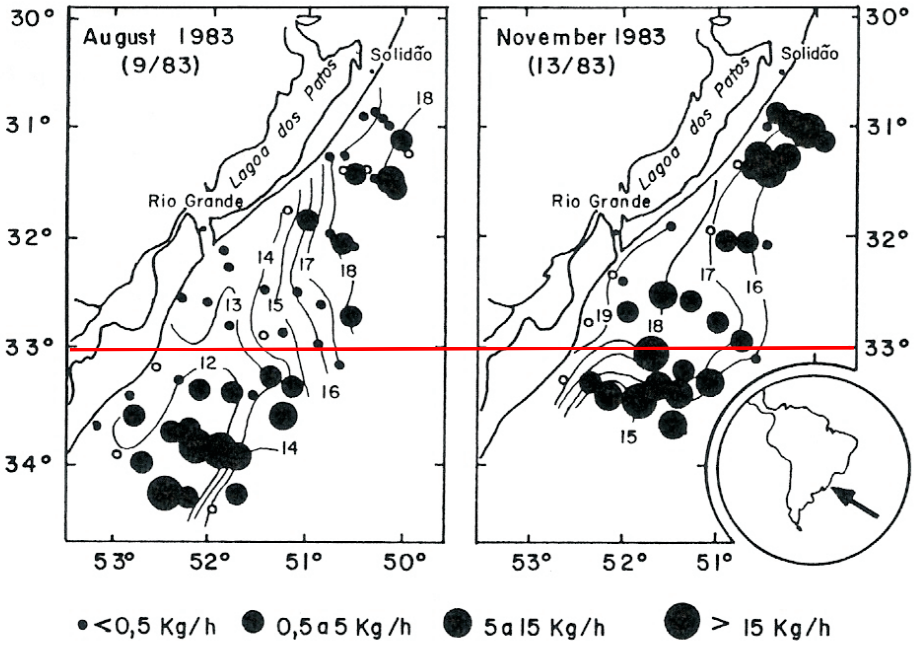


Figure 6.20: Catches in kilograms per hour (kg/h) of *Loligo sanpaulensis* and bottom isotherms in two seasonal surveys, winter (at left) and spring (at right), off southern Brazil. Source: Andriguetto Jr. and Haimovici (1991). Those two seasons represented the majority of the *Loligo sanpaulensis* found in the franciscana diet, and the red line shows around the southern limit of *Loligo sanpaulensis* distribution in this study (see figure 6.12).

fish has a negative relationship with water depth in the diet of franciscana. A similar trend was found by Haimovici et al. (1996) in research cruises, where the highest occurrence of this fish was between 0 and 20m of depth.

GLM results for the total fish specimens group were possibly influenced by higher number of some species such as the *Cynoscion guatucupa*, *Paralonchurus brasiliensis*, and *Anchoa marinii*. Mainly because those species, the fish group had the highest numbers in winter, and a negative correlation with temperature. The relationship with water depth is possibly influenced by a number of fish species (*e.g. Cynoscion guatucupa*, *Umbrina canosai*,*Cynoscion jamaicensis*, *Paralonchurus brasiliensis*) which were highly represented by juveniles (see table 4.5), and the shallower coastal waters of southern Brazil is an important spawning area for many demersal species through all year (Haimovici and Vieira, 1986; Haimovici, 1988; Reis, 1992; Haimovici et al., 1996; Castello et al., 1997; Haimovici, 1997a).

The GLM for the shrimp group was the weakest model, despite season and temperature being significant predictors. These results reflect its distribution in the study area (Boshi, 1969; Haimovici, 1997b). The marine shrimps are commercially important in the southern Brazil coast, and have been fished mainly from spring to summer (Boshi, 1969; Haimovici, 1997b). The slightly higher frequency of shrimps at lower temperatures could be because the spring season is still influenced by colder waters, especially in southern latitudes of the study area (see Chapter 5).

Many prey species were found to be affected by sea temperature, but only one fish species by chlorophyll-*a*, even though this covaries strongly with water temperature (see figure 5.27 in Chapter 5).

The anchoita *Anchoa marinii* had a significant positive relationship with chlorophyll-*a*. This relationship may be possibly linked with its food habits, because Engraulidae species are the most abundant of the pelagic fish species of the SBCS, these feed on zooplankton and occasionally in phytoplankton (Castello and Habiaga, 1982). However, as the water temperature decrease, the chlorophyll-*a* increases (see figure 5.27), suggesting that the chlorophyll-*a* may only be a significant predictor because it is correlated with temperature, and is not directly affecting the fish prey. Nonetheless, other species related to colder temperatures (*e.g. Cynoscion guatucupa*, *Merluccius hubbsi*) were not influenced by any Chl *a* parameter.

Among the spatial predictors, the latitude essentially indicates that some relevant prey species were fairly uniform, as the case of *Trichiurus lepturus*, *Umbrina canosai*, *Paralonchurus brasiliensis*, *Urophycis brasiliensis*, *Argonauta nodosa*, and shrimp specimens. Some prey species numbers decreased or increased linearly with latitude, as cited in several cases above.

All the prey species showing a negative relationship with latitude had a positive correlation with temperature, and the inverse was also true. This shows that the temporal influence of temperature is different throughout the latitude, which is confirmed according to the analyses of the sea surface temperature on Chapter 5. Hence warm water species are more likely to occur for longer periods at lower latitudes, and cold water species at higher latitudes.

Furthermore, some other species which were not affected by any SST parameter vary significantly in latitude, such as the lantern midshipman *Porichthys porosissimus*, the American harvestfish *Peprilus paru*, and principally the rake stardrum *Stellifer rastrifer*. Although temperature does not influence those species significantly, season was found to be a significant predictor.

Overall, it is clear that a lot of the spatial and temporal variations of the dolphin diet are closely linked with the environmental factors which are influenced by the water masses BC and BCC along the study region.

Most of the prey that varied in latitude in the franciscana diet showed variations which are consistent with their known distributions as found in many fish and cephalopod research studies along the southern Brazilian coast (Andriguetto Jr. and Haimovici, 1991; Haimovici and Perez, 1991b; Castello, 1997; Castello et al., 1997; Haimovici, 1997b; Santos, 1999). Additionally, the predictor water depth, which is a more specific spatial parameter, was also significantly correlated with some prey species that showed similar distribution results in the study region from research cruises (Haimovici et al., 1993, 1996; Haimovici, 1997a; Martins and Haimovici, 1997; Santos, 1999).

The results of the spatial predictors suggest firstly that the diet does closely reflect feeding near to the location of capture, and secondly that the dolphins seem to feed fairly opportunistically, since their diet is consistent with the prey distributions.

Finalizing this section we discuss a question raised in the franciscana diet analyses of Chapter 4. In the discussion of that Chapter we stated that the tropical species *Stellifer rastrifer* could be sensitive to lower temperatures, as this species was not found in the franciscana stomachs from southern zones. However, from the modelling analysis it seems that *Stellifer rastrifer* is not affected at all by water temperature, and actually it is found to be more frequent during winter time (SST average of $12^{o}$C). Additionally, from Chapter 5 we could see that southern zones are also influenced by warm currents. Therefore, the southern range limit of *Stellifer* *rastrifer* around $29^o$ (Tropical Data Base Program) corroborates the diet analysis, although our results do not support the view that the species is influenced by a warm environment as previously suggested by Menezes and Figueiredo (1980), at least for the specimens of southern limit distribution.

In summary, it is likely that franciscana dolphin is a good indicator of the abundance and distribution of many prey species along its habitat range. This provides strong support for past studies of franciscana diet, which had also detected trends in prey composition matching with known trends in fish stock abundance (Bassoi and Secchi, 1999). Therefore franciscana stomach contents also represent a useful and cost-effective way of studying prey distributions.

- **Prey body length**

The positive correlation of temperature with fish body length occurs because the bigger specimens are mainly warm water species (*e.g. Umbrina canosai*, *Trichiurus lepturus*). The relationship of fish body length with water depth is similar to the results of GLM for the total fish specimens, because the predominance of important fish species (*e.g. Cynoscion guatucupa*, *Stellifer rastrifer*, *Paralonchurus brasiliensis*) are composed mainly of juvenile and sub-adult groups (see table 4.5), which were abundant in shallower waters.

Cephalopod lengths are dominated by the squid *Loligo sanpaulensis* (99%), and will be discussed in relation to this species. Past research surveys for the area revealed smaller specimens of *Loligo sanpaulensis* during summer (mean mantle lengths: Summer= 58.4mm, Autumn= 52.5, Winter= 76.2, and Spring= 80.5) (Andriguetto Jr. and Haimovici, 1991). Nonetheless, in this work we have found bigger cephalopods for all seasons (mean mantle lengths: Summer= 111.1mm, Autumn= 94.4, Winter= 99.5, and Spring= 113.4). From both studies, the greater means are from spring, similarly mantle length trends in winter and autumn seasons, and the summer length average for the franciscana diet squid specimens is twice the size of the research survey. According to Clarke (1996) some cetaceans feed selectively on the larger individuals on the spawning grounds, and these data support that observation.

In short, franciscana does appear to select larger *Loligo sanpaulensis*, because the average size of squid preyed on by this dolphin was higher than those found during research surveys through all year (Andriguetto Jr. and Haimovici, 1991). However, the ingestion of the cephalopods is likely to follow similar trends of the average sizes and abundance as found in research cruises, with the exception of summer.

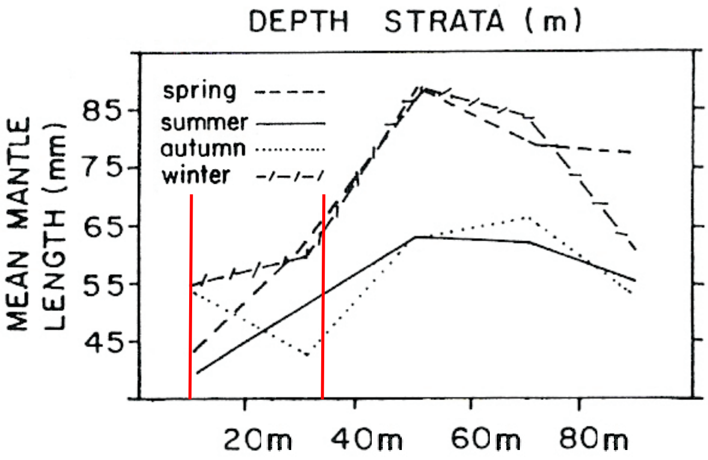


Figure 6.21: Mean mantle length (mm) of *Loligo sanpaulensis* per depth strata intervals in four seasons surveys off southern Brazil. Source: Andriguetto Jr. and Haimovici (1991). The red line shows the depth interval between 10 and 35m from the cephalopod mantle length model of this study (see figure 6.16, top left graphic).

The positive relationship between depth and the *Loligo sanpaulensis* mantle length (see figure 6.16) is similar to that found in catches of research cruises in the study region (figure 6.21). The figure 6.21 is divided into seasons, and 3 of them show a positive relationship with depth, whilst autumn had a negative correlation. Looking at the seasonal variation from figure 6.16, summer and spring showed higher means for the specimens length, and from the research cruise (figure 6.21) these seasons demonstrate strongly positive correlations with depth (to about 50m depth).

Furthermore, latitudinal differences in *Loligo sanpaulensis* eaten by franciscana show a polynomial shape, with bigger sizes near $31.5^o$ (see figure 6.16). This region in the study area has a peculiar feature of rapid change in bathymetry with a significant decrease in depth at about $31.5$-$31.0^o$ (see the 50m isobath, figure 5.1), and research cruises in the area had shown a peak of bigger squids at about 50m (figure 6.21). Thus the abundance of bigger specimens of *Loligo sanpaulensis* are higher in coastal regions at about $31.0^o$ of latitude, and bigger squids were also more abundant in the franciscana diet at this latitude.

The results of *Loligo sanpaulensis* size in the franciscana diet and the research catches (Andriguetto Jr. and Haimovici, 1991) are clearly similar, even for a more specific spatial resolution such as the water depth. However, cephalopod beaks may accumulate for several days or months in the stomachs of marine predators (Clarke, 1986b), and if this structure remains longer in the stomachs, the chance that the animal could have eaten the prey at different locations before being captured should be higher. Thus it might be expected that there would be no pattern in the diet at all. However, our results show patterns in the ingestion of *Loligo sanpaulensis* by franciscana which are very similar to those found in the habitat. Therefore it seems probable that the animals may be feeding for longer periods of time in the same areas.

Overall, the results of many prey in the diet of franciscana not only reveal a generally opportunistic feeding behaviour of franciscana in terms of prey abundance, but are also suggesting that the animals may be expending fairly long periods of time in the same areas, and/or not often moving to distant areas along the coast.

### 6.3.3 The approach from the environmental-biological interactions

In this first attempt to relate the environmental parameters of the franciscana habitat with its feeding, the results revealed important insights about the use of habitat by franciscana. Such findings are very important because the franciscana dolphin is hardly ever seen at sea, and research studies about its distribution and behaviour are still not possible for the study area. Therefore the biological data from accidental catches or stranded events are an important source of information about franciscana ecology.

The selection of prey types and the exact composition of the diet is affected by several factors including prey availability, time of year, prey quality, and prey behaviour. Among these, the effect of prey availability is most easily demonstrated and occurs, for example, because of marked differences in the habitat.

From the results of the present Chapter we can recognize many prey species that were significantly associated with spatial and temporal parameters, consistent with their known spatial and temporal abundance through the study area (Andriguetto Jr. and Haimovici, 1991; Haimovici and Perez, 1991b; Castello, 1997; Castello et al., 1997; Haimovici, 1997b; Santos, 1999). The results generally support the hypothesis of fairly opportunistic franciscana' feeding behaviour.

However, Pinedo (1982) analysed franciscana stomachs from southern Brazilian coast and concluded that the dolphin is selective according to the prey size, preferring fish prey under 50mm in total length. In Chapter 4 (see section 4.4) we already mentioned this and we suggested that the animals could be non-selective, eating the most available prey in the habitat. The modelling analysis in the present Chapter conforms to this hypothesis and matches that of the opportunistic behaviour of franciscana, where the prey found in the diet were similar to what found in the habitat (research cruises).

Marine mammals are generally considered to be opportunistic foragers which select from a number of alternative prey according to availability (Trites, 2002). However, little is known about the choices that marine mammals make when foraging. Presumably what they eat is a function of prey size and ease of capture, which are however linked to the aggregation and abundance of the prey.

From the present results it also seems that some selection in terms of prey size may nevertheless occur. The franciscana may still ingest greater numbers of "bigger specimens" when they are more available in the habitat. This was the case of larger *Loligo sanpaulensis* specimens, and the swordfish *Trichiurus lepturus* (see previous section). *Trichiurus lepturus* specimens ingested by franciscana had an average size of about 400mm, whereas the main prey *Cynoscion guatucupa* and *Stellifer rastrifer* were ∼50mm (see table 4.5). Changes in the relative costs and benefits of capturing particular prey items may lead to prey switching, which has been observed in other marine mammals (Williams et al., 1996).

Each potential prey item differs in the energy required to capture it and the amount of energy the predator will gain from eating it. Prey selection may also take the form of capturing a particular size of prey. For example, harbor seals in Scotland feed primarily on the most abundant fish species, but prefer fish 10-16cm in length (Pierce et al., 1991b).

Moreover, we recognize that from present results it could be suggested that (i) the animals could be expending longer periods of time in adjacent areas; or (ii) making mostly minor movements along the coast and not great excursions; or (iii) demonstrating a considerable degree of preference for some areas.

This possible use of habitat by franciscana might be explained in terms of minimizing energetic costs. The franciscana habitat, our study region, exhibits a wide range of temperature, from $\sim 10^{o}$ to $26^{o}$C (see Chapter 5), and sudden changes in water temperature alter the total energetic costs in dolphins (Williams et al., 1996). Several behaviours will enable a foraging dolphin to maintain low maintenance and thermoregulatory costs, and these include limiting foraging excursions to distant areas (Williams et al., 1996). Additionally, franciscana inhabit shallower waters (see Chapter 2) which minimizes the depths of foraging to which they must dive, and thus the costs. Swimming and diving represent major energetic expenditures in aquatic mammals (Heithaus and Dill, 2002), thus such strategies might help franciscana reducing foraging/energetic costs.

It is likely that relationships between locomotor (swimming and diving), thermoregulatory demands, and prey availability will be important factors in determining the range of foraging in dolphins (Wells et al., 1990). Therefore is it quite likely that franciscana dolphin may occupy, and possibly for long periods, a small spatial ranges.

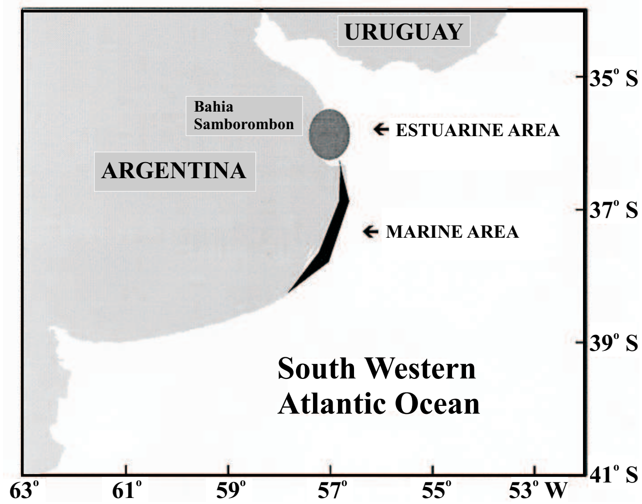


Figure 6.22: Map with indication of estuarine and marine areas from the franciscana diet study off northern Argentina. Source: Rodriguez et al. (2002).

Furthermore, diet study of franciscana from the northern coast of Argentina recorded different feeding regimes between animals inhabiting estuarine and marine areas (Rodriguez et al., 2002). The dolphins were incidentally caught in gillnets or found stranded in the external area of the Rio de la Plata estuary and the southern marine area (figure 6.22). The authors found a very different diet between the sites, and the most important feature of the estuarine area was the absence of cephalopods (stenohaline habits), whereas in the marine areas the squid *Loligo sanpaulensis* occurred in 67% of the stomachs. Therefore as suggested in the present work, this might indicate that franciscana demonstrate a fairy high preference for some areas, otherwise some cephalopod beaks would be expected to found in the stomachs of dolphins from the estuarine area, as these structures remain longer in the stomachs of predators (see section 4.1, Chapter 4). This can be also exemplified by a case of a stranded franciscana held in captivity for 7 days that was fed with several fish and only six squids, while after the animal died 123 squid beaks were found in its stomach (Bassoi et al., in review). Similar cases of other cetacean species held in captivity, some individuals for several months, recorded many beaks from the stomach contents, while they had never been fed with cephalopods (Clarke, 1986b).

Furthermore, the swordfish *Trichiurus lepturus* was absent in the diet of franciscana in Argentina but frequently reported as prey in waters off Uruguay (Fitch and Brownell, 1971; Praderi, 1986), only $1^o$ in latitude northwards (figure 6.22). The examples above also confirm that distinct franciscana diet can be observed from areas which are highly localised.

From the results of Chapter 4 we can also detect differences within the population (*e.g.* male and female, adult and juvenile), which could reflect a different use of habitat perhaps to minimize competition (Bordino et al., 1999, 2002). Naturally, the hypothesis proposed in this study about some preference for determined areas may also involve a degree of adaptation to reduce prey competition, besides the strategy is also probably to reduce energetic costs as suggested before.

Additionally, Bordino et al. (2002) proposed a seasonal differential use of habitat by adult and juvenile franciscana in two distinct areas of the Argentina coast. Overall, differential use of habitat was proposed by sex and age class of two franciscana populations (southern Brazilian coast and central Argentinean coast), and also seasonal movements were reported for Argentinean waters. Moreover, recent studies of franciscanas from the southern Brazilian coast suggest probable habitat preference by latitude (Danilewicz et al., 2004), although the authors advised that more research effort is needed.

Nonetheless, the present research is the first to indicate clearly a differential use of habitat by franciscana, with minor and small-scale movements patterns along the southern Brazilian coast, or with the animals spending long periods of time in the same areas. Possibly both suggestions may lead to a habitat preference, which can be latitudinal, by franciscana along the study area supporting the recommendations of Danilewicz et al. (2004).

### 6.3.4 Implications of the research

The results and hypothesis from the present study provide relevant information for effective conservation procedures in the study area, especially in view of the urgent need to reduce the incidental mortality of the species (Secchi et al., 2003).

The annual mortality of franciscana off the southern Brazilian coast has been estimated to range from several hundreds up to around a thousand individuals (Secchi et al., 1997; Ott, 1998; Ott et al., 2002), and it has been estimated that there is a 99% probability that the population is decreasing (Kinas, 2002). Franciscana from the southern Brazilian coast/Uruguay population have been recently classified as ”Vulnerable” by the IUCN Red List of Threatened Species (Secchi and Wang, 2003) (see more information on Chapter 1).

Therefore, if it is assumed that the use of habitat by franciscana is localised, as found in this study, distinct management procedures in the fisheries should be taken in order to minimize accidental entanglement of the species. For example, defining specific areas for the use of gillnets, rather than allowing their use throughout the whole of the coast as nowadays. Such procedures may not be the best option to protect individual groups of franciscana, if they do prefer some areas, but it is an effective alternative to conserve this population as a whole.

However, developing action plans and/or experiments to reduce the harmful effects of incidental catches and to increase the chances of long-term survival of the stocks or local populations must be the major task for governments, institutions, and fishing industry managers; and not only individuals, researchers and conservationists, interested in the franciscana's conservation. It is hoped that researchers, fishers, and decision-makers from Brazil, Uruguay, and Argentina, can cooperatively commit to the pursuit of this important endeavour.

# Chapter 7

# Summary and conclusions

The present study aimed to examine the bio-physical interactions between the franciscana prey composition and its marine environment. The main focus was placed on the franciscana diet variability (spatial and temporal) and the interplay with environmental parameters (*e.g.* sea temperature, chlorophyll-*a*, water depth). Hence the specific steps were twofold: Chapter 4 analysed the franciscana food habits from stomach contents data through the southern Brazilian coast; and in Chapter 5 the franciscana habitat has been analysed according to the environmental conditions of sea temperature and chlorophyll-*a*. Chapter 6 interacted the franciscana diet (Chapter 4) with the oceanographic parameters of its environment (Chapter 5) to assess the degree to which each habitat characteristic was responsible for the observed franciscana diet composition. Chapter 6 was our main interest in this research study. The following paragraphs will provide a summary of the key findings.

Firstly the franciscana diet was analysed from the two sources of the data, the northern and the southern areas (first part of Chapter 4), mainly based on Linear and Generalised Linear Models (LM and GLM). The franciscana diet and its biological aspects within the population were discussed, and some differences within the franciscana regardless to sex and sexual maturity were found. The smallest teleost fish, typical of dense schools of recruits through shallower waters, and shrimps are more often consumed by juveniles than adults. Adults seem to be more selective, consuming larger fish prey and more cephalopods. Females throughout the study area also eat more shrimps and crabs, specimens abundant in shallow waters, and consumed more fish than males, mostly of small sizes (recruit fish). In short, adult females may be distributed closer to the coast than adult males, at least in some periods, possibly related to the parental guidance of juveniles.

Differences in the franciscana diet among sex and sexual maturity categories from the northern area seemed more apparent than for the animals from the southern area. In general, variations on feeding regimes among sex and sexual maturity could indicate some degree of adaptation to minimise prey competition within the population.

Comparisons of franciscana feeding regimes from northern and southern areas of the study region revealed significant differences, as well as distinct temporal variability. The most important teleost species for the southern area were: *Cynoscion guatucupa*, *Trichiurus lepturus*, *Paralonchurus brasiliensis*, and *Anchoa marinii*, whilst for the northern they were: *Stellifer rastrifer*, *Trichiurus lepturus*, *Urophycis brasiliensis*, and *Paralonchurus brasiliensis*. Notably, only one occurrence of *Stellifer rastrifer* was found in the diet of southern franciscana (N= 172), while this teleost was the main prey of the northern area (N= 98). The squid *Loligo sanpaulensis* was consumed more by franciscana from the southern area, and animals from northern area ingested bigger fish on average, and the major contributor here was *Trichiurus lepturus*. There was a clear seasonal variation of prey species in the diet, and the importance of some prey in specific seasons is apparent, as is the case of *Anchoa marinii* which is more common during wintertime and *Trichiurus lepturus* during summer. The southern area exhibited more temporal variation in terms of fish species. From the prey species of the northern area, only the fish *Anchoa marinii* and the family Engraulidae are related to cold waters, whereas in the southern there are many prey species characteristic of cold waters (*e.g. Anchoa marinii*, *Cynoscion guatucupa*) as well many from warm currents (*e.g. Umbrina canosai*, *Argonauta nodosa*, *Trichiurus lepturus*, *Peprilus paru*).

Those results motivated more detailed analysis (second part of Chapter 4) with the study region divided into 7 smaller areas called latitudinal zones (1 to 7, from N to S). This analysis supports and validates the spatial and temporal differences of the franciscana diet through the study area. Additionally, it was verified that the differences of prey frequency and size do not change gradually along the zones. For example the important species *Cynoscion guatucupa* and *Stellifer rastrifer* showed abrupt changes in the central zones 3 and 4, and other fish species also decreased significantly in occurrence between these central zones (*e.g. Peprilus paru*, *Anchoa marinii*, and *Merluccius hubbsi*). The squid *Loligo sanpaulensis* showed a rapid increase of frequency in the franciscana diet in zone 4. Moreover, the mean sizes of both fishes and cephalopods are significantly higher for zones 3 and 4, respectively. This indicates that northern and southern zones of the study area could represent different environments in terms of available prey for franciscana, and the findings of central latitudinal zones (3 and 4) may represent another more diverse environment from the southern and northern zones regarding to prey species.

To conclude, many differences of this prey abundance, occurrence, and sizes were found by the spatial and temporal analysis. This raises the question whether variations in the environmental conditions along the coast may affect the distribution of franciscana prey, and consequently its feeding regime. Moreover, northern and southern zones may be differently affected by environmental parameters, and the middle geographic zones may represent another distinct area.

Indeed, there is a great temporal influence of warm temperatures from the Brazil Current (BC) in the northern zones, and cold temperatures related to the coastal branch of Malvinas/Falkland Current (BCC) in the southern zones (Chapter 5; using MANOVA, PCA, and time series analyses). Besides, the whole area is very influenced by BC for several months, which explain the occurrence of many warm prey species through all zones.

On the whole, all the zones are influenced by the BC in austral summer, and by the BCC in austral winter. The arrival and permanency of such currents in different latitudes clearly control the SST and chlorophyll-$a$ variations through the zones, describing it into 3 sectors: (1) Northern zones 1 and 2 ($29^o$ 11' to $30^o$ 41' S) are highly influenced temporally by the BC, exhibits a seasonal cycle of SST with lower amplitudes of temperature than southern zones, low chlorophyll-$a$ concentration, and seasonal cycle of chlorophyll-$a$ with peaks in winter time; (2) Central zones 3 and 4 ($30^o$ 11' to $31^o$ 40' S) showed a dynamic-edge region in terms of temperature behaviour probably caused by the mixing of BC and BCC, less clear seasonal variation of chlorophyll-$a$ with intermediate values and peaks in winter months, narrowest continental shelf, mainly around 100m isobath, possibly a particular hydrographic system; and (3) Southern zones 5 to 8 ($31^o$ 40' to $33^o$ 26' S) are highly influenced temporally by the BCC, also exhibiting a seasonal cycle of SST but with larger ranges of temperature than the northern zones, high chlorophyll-$a$ concentration, seasonal cycle of chlorophyll-$a$ with higher peaks in winter time as well as high values in autumn and spring, and influenced by Patos Lagoon freshwater discharge, mainly during winter and early spring.

Overall, the environmental characteristics along the study area are potential factors in the distribution and abundance of the prey species of franciscana. The next step was to understand these environmental determinants in the franciscana prey composition.

The franciscana prey (species and size) was treated as a function of the oceanographic variables (SST and chlorophyll-$a$), and the spatial (latitude and water depth), and temporal (season) parameters, through GLM and LM (Chapter 6). According to SST, the most frequent prey from warm temperatures were the fishes *Cynoscion jamaicensis*, *Umbrina canosai*, and *Trichiurus lepturus*, the squid *Loligo plei*, and the argonaut *Argonauta nodosa*. From colder waters the fishes *Anchoa marinii*, *Merluccius hubbsi*, and *Cynoscion guatucupa*, and the squid *Loligo sanpaulensis* were most significant. Furthermore, some prey species were much less common in lower temperatures, as the case of *Trichiurus lepturus*, and in higher temperatures such as *Anchoa marinii*. All the prey showing a negative relationship with latitude had a positive correlation with temperature, and the inverse was also true, showing the different influence of temperature throughout the latitude, which is confirmed from the SST analysis of its habitat (Chapter 5). As expected, warm water species are more likely to occur for longer periods at lower latitudes, and cold water species at higher latitudes. Judging by the effect on prey specimens size, bigger cephalopods and fish were most frequent in warmer temperatures, indicating that warm months are an important time for bigger prey specimens.

The chlorophyll-*a* predictor only influenced the fish prey *Anchoa marinii* (strong positive relationship), and is therefore not useful as an explanatory variable.

Among the spatial parameters, the latitude was a important predictor for many species. The only species with a significant non-linear (polynomial) regression shape was the squid *Loligo sanpaulensis*, with higher numbers at central latitudes. Latitude also influenced the cephalopod specimens size in the diet, with greater sizes at central latitudes. The water depth had a great influence in some fish prey species. As the water column deepens, the prey number of *Merluccius hubbsi*, *Trichiurus lepturus*, and the argonaut *Argonauta nodosa* increase; while the frequency of *Paralonchurus brasiliensis* decreases. Smaller fish and cephalopods occur in higher numbers in shallower water. Practically all the prey vary seasonally in number.

The influence of different environmental parameters on the franciscana prey species (number and size) is very similar to that found in the habitat by research cruises (Chapter 6). Because some structures analysed may remain longer in the stomachs, it seems likely that (i) the animals could be remaining for long periods of time in adjacent areas; or (ii) making relatively small movements along the coast but not great excursions; or (iii) demonstrating a certain degree of preference for some areas. This behaviour might be an strategy of minimizing energetic costs, ensuring low maintenance and thermoregulatory costs, by limiting foraging excursions to distant areas. Therefore it is likely that franciscana dolphin may occupy, possibly for long periods, small spatial ranges (Chapter 6).

In summary, this study demonstrated how the environmental conditions of the franciscana habitat influence its feeding regime revealing a strong opportunistic behaviour of franciscana, and also suggesting small ranges of habitat, which imply be an important factor for conservation issues along the southern Brazilian coast.

From this investigation the following conclusions can be drawn:

- Variations on franciscana feeding regimes between sex and sexual maturity categories indicate a degree of adaptation to minimise prey competition within the population, and a differential use of habitat between them.
- The franciscana dolphin has a fairly opportunistic behaviour in terms of prey abundance and occurrence, and has some preference for bigger prey specimens, mainly from adult individuals.
- The shallow coastal region off southern Brazil exhibits a clear seasonal and spatial variability of water temperature and chlorophyll-$a$, influenced by the Brazil Current (BC) in austral summer and by the Brazilian Coastal Current (BCC) in austral winter, which suggest three different environments along the coast: northern ($29^o$ 11' to $30^o$ 41' S); central ($30^o$ 11' to $31^o$ 40' S); and southern ($31^o$ 40' to $33^o$ 26' S).
- The environmental characteristics of water temperature and water depth strongly influence the prey species (number and size) ingested by franciscana. The temporal and spatial parameters, season and latitude, are also very important predictors of the franciscana diet composition, and chlorophyll-$a$ is not useful as a predictor.
- The new contribution of this study suggests that franciscana of southern Brazilian coast may occupy, and possibly for long periods, small range areas.

In terms of future work, the following points seem worthwhile as part of further investigations:

- A more detailed investigation of prey structures digestion, mainly fish otoliths and cephalopod beaks, could help to better understand and elucidate the real time at which the prey were ingested.
- The inclusion of further parameters in the LM and GLM (*e.g.* bottom temperature, zooplankton concentration) could increase their predictive power and the influence in the franciscana diet composition.
- Long-term monitoring of the franciscana feeding, not only in the southern Brazilian coast but also along its range distribution, and its interaction with habitat features

might yield new insights about the dolphin ecology. This is important because satellite tagging studies for franciscana dolphin still a remote future for almost all its distribution range.

- The use of stomach contents data from such monitoring studies could assist as indicators of variations of abundance of commercially important fish species, and it represents a low cost information.
- It is important to apply similar methods (i.e. GLM, or GAM) to other species of marine mammals off coast of Brazil in order to compare their feeding habits with several environmental parameters. This can help to elucidate how the diet of different marine mammals might be linked with their habitat, and consequently their behaviour.

# Appendix A

# Index of Relative Importance (IRI) Tables

| **Southern area** | | **Number of** | **Ocurrence in** | **Reconstituted** | **Importance Relative Index** |
|---|---|---|---|---|---|
| **Prey** | **Common name** | **prey %** | **stomachs %** | **mass (g) %** | **IRI (Pinkas *et al.*, 1971)** |
| **Fish** | | **46.95** | **95.93** | **12.29** | |
| *Cynoscion guatucupa* | striped weakfish | 23.05 | 65.12 | 2.18 | 1643.07 |
| *Trichiurus lepturus* | cutlassfish | 2.38 | 36.63 | 3.78 | 225.64 |
| *Anchoa marinii* | anchoita | 4.84 | 28.49 | 0.17 | 142.76 |
| *Paralonchurus brasiliensis* | banded croacker | 3.23 | 34.30 | 1.26 | 154.25 |
| *Urophycis brasiliensis* | squirrel codling | 2.04 | 28.49 | 1.58 | 103.17 |
| *Porichthys porosissimus* | lantern midshipman | 1.62 | 21.51 | 0.61 | 48.10 |
| *Umbrina canosai* | Argentine croaker | 2.25 | 12.79 | 0.75 | 38.29 |
| *Peprilus paru* | American harvestfish | 0.66 | 7.56 | 0.02 | 5.14 |
| *Engraulis anchoita* | anchoita | 0.54 | 7.56 | 0.09 | 4.76 |
| *Micropogonias furnieri* | white croaker | 0.51 | 5.23 | 0.33 | 4.42 |
| *Merluccius hubbsi* | Argentine hake | 0.27 | 4.65 | 0.01 | 1.29 |
| *Macrodon ancylodon* | king weakfish | 0.29 | 4.65 | 0.63 | 4.25 |
| *Cynoscion jamaicensis* | Jamaica weakfish | 0.22 | 3.49 | 0.27 | 1.70 |
| *Pomatomus saltator* | bluefish | 0.24 | 3.49 | 0.05 | 1.01 |
| *Prionotus* sp. | searobins | 0.26 | 2.91 | 0.07 | 0.95 |
| *Syacium papillosum* | dusky flounder | 0.21 | 1.74 | 0.12 | 0.57 |
| *Menticirrhus* sp. | southern kingcroacker | 0.07 | 2.91 | 0.06 | 0.38 |
| *Raneya fluminensis* | cuskeels | 0.05 | 1.74 | 0.21 | 0.46 |
| *Mugil* sp. | mullet | 0.02 | 1.16 | 0.08 | 0.12 |
| *Trachurus lathami* | rough scad | 0.03 | 1.74 | 0.002 | 0.06 |
| *Stromateus brasiliensis* | butterfish | 0.08 | 0.58 | 0.01 | 0.05 |
| *Paralichtys isoceles* | flounder | 0.01 | 0.58 | 0.002 | 0.01 |
| *Stellifer rastrifer* | rake stardrum | 0.01 | 0.58 | 0.003 | 0.01 |
| Scianidae | | 0.08 | 3.49 | | 0.29 |
| Engraulidae | | 0.69 | 12.21 | | 8.40 |
| unidentified | | 3.29 | 64.53 | | 212.62 |
| **Cephalopod** | | **51.65** | **81.98** | **87.71** | |
| *Loligo sanpaulensis* | common long-finned squid | 50.65 | 81.98 | 87.14 | 11295.73 |
| *Loligo plei* | slender inshore squid | 0.25 | 8.72 | 0.47 | 6.28 |
| *Argonauta nodosa* | Knobby argonaut | 0.68 | 11.63 | 0.09 | 8.93 |
| *Octopus tehuelchus* | tehuelche octopus | 0.04 | 1.74 | 0.01 | 0.08 |
| *Semirossia tenera* | lesser bobtail squid | 0.02 | 1.16 | 0.002 | 0.03 |
| *Eledone* sp. | octopus | 0.01 | 0.58 | | 0.01 |
| **Crustacean** | | **1.41** | **40.12** | | |
| *Pleoticus muelleri* | marine shrimp | 0.23 | 7.56 | | 1.71 |
| *Artemesia longinaris* | marine shrimp | 0.28 | 4.65 | | 1.29 |
| *Loxopagurus loxocheles* | marine crab | 0.06 | 3.49 | | 0.21 |
| *Dardanus insignis* | marine crab | 0.01 | 0.58 | | 0.01 |
| Penaeidae | "shrimps" | 0.20 | 8.14 | | 1.59 |
| Penaeoidea | "shrimps" | 0.12 | 6.98 | | 0.86 |
| Brachiura | "crabs" | 0.02 | 1.16 | | 0.02 |
| Pleocyemata | "crabs" | 0.08 | 4.07 | | 0.33 |
| Dendrobranchiata | "shrimps" | 0.01 | 0.58 | | 0.01 |
| Isopoda | "bugs" | 0.33 | 5.81 | | 1.91 |
| unidentified | | 0.07 | 3.49 | | 0.25 |
| **Total** | | **n = 9643** | **n = 172** | **281662.37** | |

Table A.1: Numerical abundance (n%), frequency of occurrence (O%), estimated mass (W%), and the Index of Relative Importance (IRI) of prey of franciscanas for southern area (N= 172), southern Brazilian coast.

| **Northern area**<br>**Prey** | **Common name** | **Number of prey %** | **Ocurrence in stomachs %** | **Reconstituted mass (g) %** | **Importance Relative Index IRI (Pinkas *et al*., 1971)** |
|---|---|---|---|---|---|
| **Fish** | | **64.43** | **89.80** | **29.79** | |
| *Cynoscion guatucupa* | striped weakfish | 3.86 | 26.53 | 0.06 | 104.15 |
| *Trichiurus lepturus* | cutlassfish | 5.39 | 54.08 | 10.69 | 869.70 |
| *Paralonchurus brasiliensis* | banded croacker | 6.08 | 36.73 | 4.06 | 372.29 |
| *Urophycis brasiliensis* | squirrel codling | 7.37 | 36.73 | 4.51 | 436.22 |
| *Anchoa marinii* | anchoita | 1.56 | 14.29 | 0.12 | 23.96 |
| *Porichthys porosissimus* | lantern midshipman | 2.60 | 22.45 | 1.42 | 90.30 |
| *Umbrina canosai* | Argentine croaker | 2.84 | 18.37 | 0.82 | 67.28 |
| *Peprilus paru* | American harvestfish | 0.09 | 3.06 | 0.02 | 0.33 |
| *Engraulis anchoita* | anchoita | 0.69 | 7.14 | 0.22 | 6.49 |
| *Micropogonias furnieri* | white croaker | 0.72 | 5.10 | 0.51 | 6.27 |
| *Macrodon ancylodon* | king weakfish | 0.42 | 4.08 | 0.71 | 4.59 |
| *Cynoscion jamaicensis* | Jamaica weakfish | 2.93 | 10.20 | 0.80 | 38.08 |
| *Pomatomus saltator* | bluefish | 0.03 | 1.02 | 0.32 | 0.35 |
| *Menticirrhus* sp. | southern kingcroacker | 0.84 | 8.16 | 2.71 | 28.97 |
| *Trachurus lathami* | rough scad | 0.63 | 8.16 | 0.12 | 6.09 |
| *Stellifer rastrifer* | rake stardrum | 18.98 | 44.90 | 2.58 | 968.20 |
| *Stromateus brasiliensis* | butterfish | 0.03 | 1.02 | 0.04 | 0.07 |
| *Pagrus pagrus* | red porgy | 0.06 | 1.02 | 0.06 | 0.12 |
| *Ctenosciena gracilicirrhus* | barbel drum | 0.18 | 4.08 | 0.04 | 0.88 |
| *Licengraulis grossidens* | Atlantic sabretooth anchovy | 0.03 | 1.02 | | 0.03 |
| Scianidae | | 0.57 | 11.22 | | 6.39 |
| Engraulidae | | 0.78 | 12.24 | | 9.53 |
| undentified | | 7.78 | 58.16 | | 452.77 |
| **Cephalopod** | | **34.19** | **73.47** | **70.21** | |
| *Loligo sanpaulensis* | common long-finned squid | 32.37 | 73.47 | 67.27 | 7319.91 |
| *Loligo plei* | slender inshore squid | 0.90 | 8.16 | 2.81 | 30.26 |
| *Argonauta nodosa* | Knobby argonaut | 0.90 | 8.16 | 0.05 | 7.71 |
| *Octopus tehuelchus* | tehuelche octopus | 0.03 | 1.02 | 0.09 | 0.12 |
| **Crustacean** | | **1.35** | **39.80** | | |
| Penaeoidea | "shrimps" | 0.36 | 12.24 | | 4.40 |
| Isopoda | "bugs" | 0.96 | 32.65 | | 31.28 |
| undentified | | 0.03 | 1.02 | | 0.03 |
| **Total** | | **n = 3351** | **n = 98** | **71469.44** | |

Table A.2: Numerical abundance (n%), frequency of occurrence (O%), estimated mass (W%), and the Index of Relative Importance (IRI) of prey of franciscanas for northern area (N= 98), southern Brazilian coast.

| **Southern area** | **Male (N=100)** | | | | **Female (N=72)** | | | |
|---|---|---|---|---|---|---|---|---|
| **Prey** | % n | %O | %W | IRI | % n | %O | %W | IRI |
| **Fish** | | | | | | | | |
| *Cynoscion guatucupa* | 49.18 | 68.00 | 16.68 | 4478.64 | 59.46 | 61.11 | 18.72 | 4777.53 |
| *Trichiurus lepturus* | 5.69 | 38.00 | 37.18 | 1629.08 | 5.38 | 34.72 | 24.92 | 1051.84 |
| *Paralonchurus brasiliensis* | 7.38 | 35.00 | 12.85 | 708.05 | 7.74 | 33.33 | 7.95 | 522.95 |
| *Urophycis brasiliensis* | 5.00 | 31.00 | 8.07 | 405.31 | 4.46 | 25.00 | 17.20 | 541.63 |
| *Anchoa marinii* | 14.50 | 30.00 | 1.85 | 490.22 | 7.31 | 26.39 | 0.91 | 216.98 |
| *Porichthys porosissimus* | 4.87 | 19.00 | 1.19 | 115.15 | 2.42 | 25.00 | 8.47 | 272.23 |
| *Umbrina canosai* | 6.90 | 15.00 | 4.72 | 174.32 | 3.17 | 9.72 | 7.31 | 101.86 |
| *Peprilus paru* | 0.78 | 7.00 | 0.12 | 6.28 | 2.47 | 8.33 | 0.25 | 22.67 |
| *Engraulis anchoita* | 1.73 | 9.00 | 1.19 | 26.28 | 0.70 | 5.56 | 0.24 | 5.20 |
| *Micropogonias furnieri* | 0.73 | 5.00 | 1.88 | 13.06 | 1.77 | 5.56 | 3.45 | 29.04 |
| *Merluccius hubbsi* | 0.56 | 6.00 | 0.11 | 4.03 | 0.70 | 2.78 | 0.06 | 2.10 |
| *Macrodon ancylodon* | 0.39 | 4.00 | 6.02 | 25.64 | 1.02 | 5.56 | 4.25 | 29.29 |
| *Cynoscion jamaicensis* | 0.09 | 1.00 | 0.04 | 0.13 | 1.02 | 6.94 | 4.20 | 36.25 |
| *Pomatomus saltator* | 0.69 | 4.00 | 0.53 | 4.89 | 0.38 | 2.78 | 0.35 | 2.02 |
| *Prionotus* sp. | 0.13 | 1.00 | 1.11 | 1.24 | 1.18 | 5.56 | 0.09 | 7.08 |
| *Menticirrhus* sp. | 0.09 | 2.00 | 0.53 | 1.22 | 0.27 | 4.17 | 0.44 | 2.97 |
| *Raneya fluminensis* | 0.17 | 2.00 | 2.85 | 6.05 | 0.05 | 1.39 | 0.69 | 1.03 |
| *Trachurus lathami* | 0.13 | 3.00 | 0.03 | 0.49 | | | | |
| *Syacium papillosus* | 0.56 | 2.00 | 1.53 | 4.19 | 0.38 | 1.39 | 0.48 | 1.20 |
| *Mugil* sp. | 0.04 | 1.00 | 1.38 | 1.42 | 0.05 | 1.39 | 0.01 | 0.08 |
| *Paralichtys isoceles* | | | | | 0.05 | 1.39 | 0.03 | 0.11 |
| *Stellifer rastrifer* | 0.04 | 1.00 | 0.04 | 0.09 | | | | |
| *Stromateus brasiliensis* | 0.35 | 1.00 | 0.10 | 0.44 | | | | |
| *Pagrus pagrus* | | | | | | | | |
| *Ctenosciena gracilicirrhus* | | | | | | | | |
| *Licengraulis grossidens* | | | | | | | | |
| **Cephalopod** | | | | | | | | |
| *Loligo sanpaulensis* | 98.40 | 82.00 | 99.65 | 16376.01 | 97.38 | 81.94 | 98.56 | 16055.84 |
| *Loligo plei* | 0.26 | 7.00 | 0.25 | 3.60 | 0.94 | 11.11 | 1.30 | 24.90 |
| *Argonauta nodosa* | 1.34 | 11.00 | 0.10 | 16.14 | 1.25 | 12.50 | 0.10 | 16.87 |
| *Octopus tehuelchus* | | | | | 0.25 | 4.17 | 0.03 | 1.16 |
| *Semirossia tenera* | | | | | 0.13 | 2.78 | 0.01 | 0.37 |
| *Eledone* sp. | | | | | 0.06 | 1.39 | 0.001 | 0.09 |
| **Crustacean** | | | | | | | | |
| *Pleoticus muelleri* | 7.69 | 6.00 | | 46.15 | 27.12 | 9.72 | | 263.65 |
| *Artemesia longinaris* | 26.92 | 4.00 | | 107.69 | 10.17 | 5.56 | | 56.50 |
| *Loxopagurus loxocheles* | 2.56 | 2.00 | | 5.13 | 6.78 | 5.56 | | 37.66 |
| *Dardanus insignis* | | | | | 1.69 | 1.39 | | 2.35 |
| Penaeidae | 16.67 | 8.00 | | 133.33 | 10.17 | 8.33 | | 84.75 |
| Penaeoidea | 10.26 | 8.00 | | 82.05 | 6.78 | 5.56 | | 37.66 |
| Brachiura | 1.28 | 1.00 | | 1.28 | 1.69 | 1.39 | | 2.35 |
| Pleocyemata | | | | | 13.56 | 9.72 | | 131.83 |
| Dendrobranchiata | | | | | 1.69 | 1.39 | | 2.35 |
| Isopoda | 26.92 | 6.00 | | 161.54 | 18.64 | 5.56 | | 103.58 |

Table A.3: Numerical abundance (%n), frequency of occurrence (%O), estimated mass (%W), and the Index of Relative Importance (IRI) of prey of franciscanas for males and females (southern area).

| **Northern area** | **Male (N=100)** | | | | **Female (N=72)** | | | |
|---|---|---|---|---|---|---|---|---|
| **Prey** | % n | %O | %W | IRI | % n | %O | %W | IRI |
| **Fish** | | | | | | | | |
| *Cynoscion guatucupa* | 5.20 | 27.27 | 0.29 | 149.62 | 1.72 | 14.29 | 0.16 | 26.87 |
| *Trichiurus lepturus* | 6.53 | 59.09 | 37.65 | 2610.62 | 8.85 | 46.43 | 24.02 | 1525.91 |
| *Paralonchurus brasiliensis* | 6.09 | 34.09 | 13.25 | 659.34 | 20.88 | 46.43 | 19.93 | 1894.78 |
| *Urophycis brasiliensis* | 10.39 | 36.36 | 3.22 | 495.16 | 15.48 | 39.29 | 26.40 | 1645.41 |
| *Anchoa marinii* | 1.41 | 11.36 | 0.37 | 20.21 | 6.88 | 21.43 | 0.50 | 158.18 |
| *Porichthys porosissimus* | 2.30 | 25.00 | 4.35 | 166.26 | 6.88 | 28.57 | 4.67 | 330.07 |
| *Umbrina canosai* | 2.52 | 18.18 | 6.51 | 164.19 | 2.95 | 14.29 | 0.59 | 50.52 |
| *Peprilus paru* | 0.15 | 4.55 | | 0.67 | | | | |
| *Engraulis anchoita* | 0.97 | 6.82 | 1.32 | 15.55 | 2.21 | 10.71 | 0.53 | 29.38 |
| *Micropogonias furnieri* | 1.41 | 9.09 | 1.36 | 25.19 | 1.23 | 3.57 | 3.13 | 15.57 |
| *Merluccius hubbsi* | | | | | | | | |
| *Macrodon ancylodon* | 0.07 | 2.27 | 2.42 | 5.66 | 0.25 | 3.57 | 0.40 | 2.31 |
| *Cynoscion jamaicensis* | 6.61 | 15.91 | 6.91 | 215.06 | 1.47 | 3.57 | 0.02 | 5.34 |
| *Pomatomus saltator* | | | | | | | | |
| *Prionotus* sp. | | | | | | | | |
| *Menticirrhus* sp. | 1.56 | 6.82 | 5.33 | 46.97 | 0.74 | 10.71 | 15.02 | 168.78 |
| *Raneya fluminensis* | | | | | | | | |
| *Trachurus lathami* | 0.45 | 6.82 | 0.27 | 4.87 | 0.25 | 3.57 | 0.09 | 1.20 |
| *Syacium papillosus* | | | | | | | | |
| *Mugil* sp. | | | | | | | | |
| *Paralichtys isoceles* | | | | | | | | |
| *Stellifer rastrifer* | 40.91 | 47.73 | 16.36 | 2733.03 | 14.99 | 42.86 | 4.53 | 836.61 |
| *Stromateus brasiliensis* | 0.07 | 2.27 | 0.34 | 0.94 | | | | |
| *Pagrus pagrus* | 0.15 | 2.27 | 0.01 | 0.36 | | | | |
| *Ctenosciena gracilicirrhus* | 0.15 | 4.55 | 0.06 | 0.93 | | | | |
| *Licengraulis grossidens* | 0.07 | 2.27 | | | | | | |
| **Cephalopod** | | | | | | | | |
| *Loligo sanpaulensis* | 91.55 | 63.64 | 94.37 | 11831.29 | 97.14 | 78.57 | 97.70 | 15309.05 |
| *Loligo plei* | 3.30 | 11.36 | 5.51 | 100.11 | 1.98 | 7.14 | 2.30 | 30.54 |
| *Argonauta nodosa* | 5.15 | 13.64 | 0.12 | 71.87 | 0.88 | 3.57 | 0.00 | 3.15 |
| *Octopus tehuelchus* | | | | | | | | |
| *Semirossia tenera* | | | | | | | | |
| *Eledone* sp. | | | | | | | | |
| **Crustacean** | | | | | | | | |
| *Pleoticus muelleri* | | | | | | | | |
| *Artemesia longinaris* | | | | | | | | |
| *Loxopagurus loxocheles* | | | | | | | | |
| *Dardanus insignis* | | | | | | | | |
| Penaeidae | | | | | | | | |
| Penaeoidea | 33.33 | 13.64 | | 454.55 | 29.41 | 17.86 | | 525.21 |
| Brachiura | | | | | | | | |
| Pleocyemata | | | | | | | | |
| Dendrobranchiata | | | | | | | | |
| Isopoda | 61.11 | 25.00 | | 1527.78 | 70.59 | 42.86 | | 3025.21 |

Table A.4: Numerical abundance (%n), frequency of occurrence (%O), estimated mass (%W), and the Index of Relative Importance (IRI) of prey of franciscanas for males and females (northern area).

| **Southern area** | **Adult (N=72)** | | | | **Juvenile (N=99)** | | | |
|---|---|---|---|---|---|---|---|---|
| **Prey** | % n | %O | %W | IRI | % n | %O | %W | IRI |
| **Fish** | | | | | | | | |
| *Cynoscion guatucupa* | 45.41 | 65.28 | 13.97 | 3876.47 | 57.38 | 65.66 | 24.77 | 5393.67 |
| *Trichiurus lepturus* | 9.26 | 48.61 | 34.62 | 2132.77 | 3.95 | 28.28 | 23.57 | 778.38 |
| *Paralonchurus brasiliensis* | 11.71 | 40.28 | 7.69 | 781.15 | 5.73 | 30.30 | 15.12 | 631.98 |
| *Urophycis brasiliensis* | 6.88 | 34.72 | 18.45 | 879.60 | 3.84 | 24.24 | 2.43 | 152.03 |
| *Anchoa marinii* | 10.21 | 25.00 | 0.77 | 274.37 | 11.77 | 31.31 | 2.45 | 445.26 |
| *Porichthys porosissimus* | 4.11 | 20.83 | 5.87 | 207.98 | 3.64 | 22.22 | 3.38 | 155.90 |
| *Umbrina canosai* | 3.09 | 12.50 | 3.29 | 79.72 | 6.18 | 13.13 | 11.25 | 228.84 |
| *Peprilus paru* | 0.71 | 5.56 | 0.07 | 4.36 | 1.89 | 9.09 | 0.40 | 20.80 |
| *Engraulis anchoita* | 1.98 | 8.33 | 0.65 | 21.90 | 0.96 | 7.07 | 0.77 | 12.26 |
| *Micropogonias furnieri* | 0.79 | 4.17 | 2.73 | 14.67 | 1.37 | 6.06 | 2.65 | 24.39 |
| *Merluccius hubbsi* | 0.47 | 5.56 | 0.10 | 3.19 | 0.69 | 4.04 | 0.05 | 2.98 |
| *Macrodon ancylodon* | 0.47 | 5.56 | 3.78 | 23.66 | 0.75 | 4.04 | 7.53 | 33.49 |
| *Cynoscion jamaicensis* | 0.63 | 6.94 | 3.41 | 28.07 | 0.45 | 1.01 | 0.00 | 0.45 |
| *Pomatomus saltator* | 1.11 | 2.78 | 0.57 | 4.65 | 0.31 | 4.04 | 0.20 | 2.05 |
| *Prionotus* sp. | 0.16 | 2.78 | 0.04 | 0.56 | 0.79 | 3.03 | 1.57 | 7.13 |
| *Menticirrhus* sp. | 0.47 | 5.56 | 0.72 | 6.66 | 0.03 | 1.01 | 0.04 | 0.07 |
| *Raneya fluminensis* | 0.08 | 1.39 | 0.64 | 1.01 | 0.14 | 2.02 | 3.72 | 7.79 |
| *Trachurus lathami* | 0.08 | 1.39 | 0.01 | 0.13 | 0.07 | 2.02 | 0.02 | 0.19 |
| *Syacium papillosum* | 1.58 | 4.17 | 1.51 | 12.89 | | | | |
| *Mugil* sp. | 0.08 | 1.39 | 1.01 | 1.51 | 0.03 | 1.01 | 0.01 | 0.04 |
| *Paralichtys isosceles* | 0.08 | 1.39 | 0.02 | 0.14 | | | | |
| *Stellifer rastrifer* | | | | | 0.03 | 1.01 | 0.06 | 0.10 |
| *Stromateus brasiliensis* | 0.63 | 1.39 | 0.07 | 0.98 | | | | |
| *Pagrus pagrus* | | | | | | | | |
| *Ctenosciena gracilicirrhus* | | | | | | | | |
| *Licengraulis grossidens* | | | | | | | | |
| **Cephalopod** | | | | | | | | |
| *Loligo sanpaulensis* | 96.41 | 91.67 | 99.13 | 17924.15 | 99.15 | 66.67 | 99.51 | 13243.92 |
| *Loligo plei* | 0.66 | 12.50 | 0.65 | 16.38 | 0.36 | 9.09 | 0.46 | 7.43 |
| *Argonauta nodosa* | 2.78 | 20.83 | 0.22 | 62.46 | 0.36 | 15.15 | 0.02 | 5.73 |
| *Octopus tehuelchus* | 0.05 | 1.39 | 0.002 | 0.07 | 0.10 | 1.01 | 0.01 | 0.11 |
| *Semirossia tenera* | 0.05 | 1.39 | 0.001 | 0.07 | 0.03 | 1.01 | 0.002 | 0.04 |
| *Eledone* sp. | 0.05 | 1.39 | 0.001 | 0.07 | | | | |
| **Crustacean** | | | | | | | | |
| *Pleoticus muelleri* | 7.32 | 4.17 | | 30.49 | 20.43 | 10.10 | | 206.36 |
| *Artemesia longinaris* | 2.44 | 1.39 | | 3.39 | 24.73 | 6.06 | | 149.89 |
| *Loxopagurus loxocheles* | 9.76 | 5.56 | | 54.20 | 2.15 | 2.02 | | 4.34 |
| *Dardanus insignis* | 2.44 | 1.39 | | 3.39 | | | | |
| Penaeidae | 4.88 | 2.78 | | 13.55 | 18.28 | 12.12 | | 221.57 |
| Penaeoidea | 9.76 | 5.56 | | 54.20 | 8.60 | 8.08 | | 69.51 |
| Brachiura | 4.88 | 2.78 | | 13.55 | | | | |
| Pleocyemata | 14.63 | 6.94 | | 101.63 | 2.15 | 2.02 | | 4.34 |
| Dendrobranchiata | | | | | 1.08 | 1.01 | | 1.09 |
| Isopoda | 39.02 | 8.33 | | 325.20 | 17.20 | 4.04 | | 69.51 |

Table A.5: Numerical abundance (%n), frequency of occurrence (%O), estimated mass (%W), and the Index of Relative Importance (IRI) of prey of franciscanas for adults and juveniles (southern area).

| **Northern area** | **Adult (N=44)** | | | | **Juvenile (N=46)** | | | |
|---|---|---|---|---|---|---|---|---|
| **Prey** | % n | %O | %W | IRI | % n | %O | %W | IRI |
| **Fish** | | | | | | | | |
| *Cynoscion guatucupa* | 7.95 | 15.91 | 0.04 | 127.19 | 5.25 | 39.13 | 0.50 | 224.79 |
| *Trichiurus lepturus* | 12.31 | 56.82 | 34.24 | 2645.15 | 6.21 | 54.35 | 40.97 | 2563.97 |
| *Paralonchurus brasiliensis* | 21.97 | 38.64 | 15.19 | 1435.77 | 5.38 | 36.96 | 13.84 | 710.39 |
| *Urophycis brasiliensis* | 17.42 | 43.18 | 20.38 | 1632.26 | 9.60 | 32.61 | 3.37 | 422.89 |
| *Anchoa marinii* | 3.22 | 13.64 | 0.14 | 45.77 | 2.05 | 15.22 | 0.70 | 41.89 |
| *Porichthys porosissimus* | 5.49 | 15.91 | 5.85 | 180.40 | 3.65 | 30.43 | 3.36 | 213.43 |
| *Umbrina canosai* | 5.87 | 15.91 | 4.83 | 170.27 | 4.10 | 23.91 | 0.13 | 101.12 |
| *Peprilus paru* | | | | | 0.19 | 6.52 | | 1.25 |
| *Engraulis anchoita* | 2.65 | 6.82 | 0.91 | 24.27 | 0.51 | 6.52 | 0.55 | 6.90 |
| *Micropogonias furnieri* | | | | | 1.54 | 10.87 | 4.65 | 67.20 |
| *Merluccius hubbsi* | | | | | | | | |
| *Macrodon ancylodon* | 1.52 | 6.82 | 2.57 | 27.87 | | | | |
| *Cynoscion jamaicensis* | 1.33 | 4.55 | 2.73 | 18.42 | 5.76 | 15.22 | 3.13 | 135.24 |
| *Pomatomus saltator* | | | | | | | | |
| *Prionotus* sp. | | | | | | | | |
| *Menticirrhus* sp. | 1.33 | 11.36 | 12.61 | 158.35 | 1.34 | 6.52 | 5.58 | 45.16 |
| *Raneya fluminensis* | | | | | | | | |
| *Trachurus lathami* | 0.57 | 4.55 | 0.04 | 2.76 | 1.15 | 13.04 | 1.00 | 28.13 |
| *Syacium papillosum* | | | | | | | | |
| *Mugil* sp. | | | | | | | | |
| *Paralichtys isosceles* | | | | | | | | |
| *Stellifer rastrifer* | 3.22 | 31.82 | 0.11 | 106.03 | 39.12 | 60.87 | 21.62 | 3696.99 |
| *Stromateus brasiliensis* | 0.19 | 2.27 | 0.23 | 0.96 | | | | |
| *Pagrus pagrus* | | | | | 0.13 | 2.17 | 0.50 | 1.37 |
| *Ctenosciena gracilicirrhus* | 0.57 | 4.55 | 0.13 | 3.18 | 0.13 | 2.17 | 0.11 | 0.51 |
| *Licengraulis grossidens* | | | | | 0.06 | 2.17 | | 0.14 |
| **Cephalopod** | | | | | | | | |
| *Loligo sanpaulensis* | 95.56 | 81.82 | 96.57 | 15719.73 | 93.49 | 67.39 | 96.06 | 12774.15 |
| *Loligo plei* | 2.22 | 9.09 | 3.08 | 48.18 | 2.60 | 6.52 | 3.93 | 42.58 |
| *Argonauta nodosa* | 2.05 | 15.91 | 0.11 | 34.35 | 3.90 | 2.17 | 0.01 | 8.52 |
| *Octopus tehuelchus* | 0.17 | 2.27 | 0.24 | 0.94 | | | | |
| *Semirossia tenera* | | | | | | | | |
| *Eledone* sp. | | | | | | | | |
| **Crustacean** | | | | | | | | |
| *Pleoticus muelleri* | | | | | | | | |
| *Artemesia longinaris* | | | | | | | | |
| *Loxopagurus loxocheles* | | | | | | | | |
| *Dardanus insignis* | | | | | | | | |
| Penaeidae | | | | | | | | |
| Penaeoidea | | | | | 54.55 | 26.09 | | 1422.92 |
| Brachiura | | | | | | | | |
| Pleocyemata | | | | | | | | |
| Dendrobranchiata | | | | | | | | |
| Isopoda | 100.00 | 45.45 | | 4545.45 | 40.91 | 19.57 | | 800.40 |

Table A.6: Numerical abundance (%n), frequency of occurrence (%O), estimated mass (%W), and the Index of Relative Importance (IRI) of prey of franciscanas for adults and juveniles (northern area).

| **Southern area** | **Summer (N=24)** | | | | **Autumn (N=48)** | | | |
|---|---|---|---|---|---|---|---|---|
| **Prey** | % n | %O | %W | IRI | % n | %O | %W | IRI |
| **Fish** | | | | | | | | |
| *Cynoscion guatucupa* | 15.14 | 33.33 | 3.78 | 630.61 | 35.93 | 64.58 | 8.54 | 2872.25 |
| *Trichiurus lepturus* | 16.55 | 58.33 | 42.02 | 3416.72 | 14.39 | 52.08 | 47.06 | 3200.89 |
| *Paralonchurus brasiliensis* | 5.28 | 29.17 | 3.93 | 268.73 | 1.41 | 18.75 | 1.67 | 57.66 |
| *Urophycis brasiliensis* | 5.28 | 25.00 | 14.75 | 500.92 | 4.76 | 27.08 | 26.07 | 835.10 |
| *Anchoa marinii* | 0.70 | 8.33 | 0.05 | 6.29 | 17.75 | 27.08 | 0.93 | 505.95 |
| *Porichthys porosissimus* | 6.34 | 33.33 | 13.31 | 654.90 | 12.34 | 37.50 | 4.77 | 641.72 |
| *Umbrina canosai* | 23.59 | 20.83 | 12.33 | 748.28 | 1.62 | 16.67 | 0.09 | 28.64 |
| *Peprilus paru* | 14.08 | 12.50 | 0.36 | 180.55 | 2.16 | 14.58 | 0.31 | 36.08 |
| *Engraulis anchoita* | | | | | 2.38 | 8.33 | 0.54 | 24.32 |
| *Micropogonias furnieri* | 5.63 | 12.50 | 5.12 | 134.48 | | | | |
| *Merluccius hubbsi* | 1.06 | 4.17 | 0.26 | 5.47 | 0.54 | 6.25 | 0.01 | 3.43 |
| *Macrodon ancylodon* | | | | | 0.22 | 2.08 | 0.42 | 1.33 |
| *Cynoscion jamaicensis* | 5.28 | 8.33 | 0.12 | 45.02 | 0.22 | 4.17 | 3.16 | 14.08 |
| *Pomatomus saltator* | | | | | 2.27 | 8.33 | 1.26 | 29.40 |
| *Prionotus* sp. | | | | | 0.65 | 8.33 | 1.62 | 18.92 |
| *Menticirrhus* sp. | 0.35 | 4.17 | 1.44 | 7.47 | 0.54 | 6.25 | 0.29 | 5.21 |
| *Raneya fluminensis* | 0.35 | 4.17 | 2.52 | 11.98 | | | | |
| *Trachurus lathami* | | | | | 0.22 | 4.17 | 0.03 | 1.01 |
| *Syacium papillosus* | | | | | 0.65 | 2.08 | 1.19 | 3.83 |
| *Mugil* sp. | | | | | 0.11 | 2.08 | 1.89 | 4.17 |
| *Paralichtys isoceles* | | | | | | | | |
| *Stellifer rastrifer* | | | | | | | | |
| *Stromateus brasiliensis* | | | | | 0.87 | 2.08 | 0.13 | 2.08 |
| Scianidae (n.i.) | 0.35 | 4.17 | | | 0.11 | 2.08 | | |
| Engraulidae (n.i.) | | | | | 0.87 | 10.42 | | |
| **Cephalopod** | | | | | | | | |
| *Loligo sanpaulensis* | 86.36 | 100.00 | 96.76 | 13734.25 | 94.17 | 100.00 | 97.43 | 13571.65 |
| *Loligo plei* | 2.27 | 22.22 | 2.49 | 79.32 | 1.50 | 20.59 | 2.14 | 53.09 |
| *Argonauta nodosa* | 10.80 | 33.33 | 0.73 | 288.18 | 3.83 | 29.41 | 0.40 | 88.11 |
| *Octopus tehuelchus* | 0.28 | 5.56 | 0.01 | 1.24 | 0.17 | 2.94 | 0.02 | 0.38 |
| *Semirossia tenera* | 0.28 | 5.56 | 0.01 | 1.22 | 0.17 | 2.94 | 0.01 | 0.38 |
| *Eledone* sp. | | | | | 0.17 | 2.94 | 0.01 | 0.35 |
| **Crustacean** | | | | | | | | |
| *Pleoticus muelleri* | 10.00 | 10.00 | | 41.67 | 8.33 | 16.67 | | 69.44 |
| *Artemesia longinaris* | | | | | 16.67 | 16.67 | | 138.89 |
| *Loxopagurus loxocheles* | 10.00 | 10.00 | | 41.67 | 4.17 | 8.33 | | 17.36 |
| *Dardanus insignis* | | | | | 2.08 | 4.17 | | 4.34 |
| Penaeidae | 50.00 | 50.00 | | 1041.67 | 12.50 | 4.17 | | 26.04 |
| Penaeoidea | | | | | 10.42 | 20.83 | | 108.51 |
| Brachiura | | | | | 4.17 | 8.33 | | 17.36 |
| Pleocyemata | 20.00 | 20.00 | | 166.67 | 2.08 | 4.17 | | 4.34 |
| Dendrobranchiata | 10.00 | 10.00 | | 41.67 | | | | |
| Isopoda | | | | | 31.25 | 16.67 | | 260.42 |

Table A.7: Numerical abundance (%n), frequency of occurrence (%O), estimated mass (%W), and the Index of Relative Importance (IRI) of prey of franciscanas discriminated by summer and autumn (southern area) (n.i.= non identified).

| **Southern area** | **Winter (N=56)** | | | | **Spring (N=44)** | | | |
|---|---|---|---|---|---|---|---|---|
| **Prey** | % n | %O | %W | IRI | % n | %O | %W | IRI |
| **Fish** | | | | | | | | |
| *Cynoscion guatucupa* | 69.03 | 87.50 | 43.08 | 9809.61 | 35.60 | 54.55 | 4.47 | 2185.80 |
| *Trichiurus lepturus* | 0.30 | 7.14 | 1.90 | 15.67 | 6.51 | 45.45 | 38.87 | 2062.64 |
| *Paralonchurus brasiliensis* | 7.48 | 41.07 | 15.85 | 958.02 | 16.06 | 45.45 | 23.36 | 1791.98 |
| *Urophycis brasiliensis* | 2.29 | 21.43 | 2.28 | 97.94 | 12.45 | 40.91 | 3.72 | 661.48 |
| *Anchoa marinii* | 12.45 | 48.21 | 3.17 | 752.84 | 1.88 | 15.91 | 0.24 | 33.68 |
| *Porichthys porosissimus* | 0.64 | 8.93 | 0.42 | 9.48 | 1.59 | 13.64 | 5.65 | 98.72 |
| *Umbrina canosai* | 0.30 | 5.36 | 0.32 | 3.28 | 18.81 | 13.64 | 21.99 | 556.41 |
| *Peprilus paru* | 0.08 | 3.57 | 0.02 | 0.37 | 0.29 | 2.27 | 0.08 | 0.84 |
| *Engraulis anchoita* | 1.02 | 12.50 | 1.49 | 31.32 | 1.01 | 4.55 | 0.26 | 5.77 |
| *Micropogonias furnieri* | 1.27 | 5.36 | 5.77 | 37.76 | 0.58 | 6.82 | 0.33 | 6.22 |
| *Merluccius hubbsi* | 0.76 | 7.14 | 0.12 | 6.32 | | | | |
| *Macrodon ancylodon* | 1.06 | 10.71 | 15.58 | 178.29 | 0.14 | 2.27 | 0.64 | 1.79 |
| *Cynoscion jamaicensis* | 0.08 | 1.79 | 3.43 | 6.27 | 0.29 | 2.27 | 0.22 | 1.16 |
| *Pomatomus saltator* | 0.04 | 1.79 | 0.01 | 0.09 | 0.14 | 2.27 | 0.001 | 0.33 |
| *Prionotus* sp. | | | | | 2.75 | 2.27 | 0.08 | 6.42 |
| *Menticirrhus* sp. | 0.04 | 1.79 | 0.46 | 0.89 | | | | |
| *Raneya fluminensis* | 0.17 | 3.57 | 4.19 | 15.57 | | | | |
| *Trachurus lathami* | 0.04 | 1.79 | 0.02 | 0.11 | | | | |
| *Syacium papillosus* | 0.59 | 3.57 | 1.85 | 8.71 | | | | |
| *Mugil* sp. | | | | | 0.14 | 2.27 | 0.02 | 0.37 |
| *Paralichtys isoceles* | | | | | 0.14 | 2.27 | 0.08 | 0.51 |
| *Stellifer rastrifer* | 0.04 | 1.79 | 0.07 | 0.20 | | | | |
| *Stromateus brasiliensis* | | | | | | | | |
| Scianidae (n.i.) | 0.08 | 3.57 | | | 0.58 | 4.55 | | |
| Engraulidae (n.i.) | 2.21 | 19.64 | | | 1.01 | 11.36 | | |
| **Cephalopod** | | | | | | | | |
| *Loligo sanpaulensis* | 99.57 | 100.00 | 99.86 | 17805.60 | 99.73 | 100.00 | 99.78 | 17683.64 |
| *Loligo plei* | 0.11 | 4.00 | 0.10 | 0.76 | 0.22 | 5.13 | 0.22 | 2.01 |
| *Argonauta nodosa* | 0.22 | 6.00 | 0.02 | 1.28 | 0.04 | 2.56 | 0.005 | 0.11 |
| *Octopus tehuelchus* | 0.11 | 2.00 | 0.02 | 0.22 | | | | |
| *Semirossia tenera* | | | | | | | | |
| *Eledone* sp. | | | | | | | | |
| **Crustacean** | | | | | | | | |
| *Pleoticus muelleri* | 5.56 | 7.14 | | 9.92 | 26.23 | 33.33 | | 417.29 |
| *Artemesia longinaris* | 5.56 | 7.14 | | 9.92 | 29.51 | 14.29 | | 201.19 |
| *Loxopagurus loxocheles* | 5.56 | 7.14 | | 9.92 | 3.28 | 9.52 | | 14.90 |
| *Dardanus insignis* | | | | | | | | |
| Penaeidae | 22.22 | 28.57 | | 158.73 | 6.56 | 19.05 | | 59.61 |
| Penaeoidea | 16.67 | 21.43 | | 89.29 | 6.56 | 19.05 | | 59.61 |
| Brachiura | | | | | | | | |
| Pleocyemata | 16.67 | 14.29 | | 59.52 | 3.28 | 9.52 | | 14.90 |
| Dendrobranchiata | | | | | | | | |
| Isopoda | 16.67 | 14.29 | | 59.52 | 22.95 | 19.05 | | 208.64 |

Table A.8: Numerical abundance (%n), frequency of occurrence (%O), estimated mass (%W), and the Index of Relative Importance (IRI) of prey of franciscanas discriminated by winter and spring (southern area) (n.i.= non identified).

| **Northern area** | **Summer (N=24)** | | | | **Autumn (N=6)** | | | |
|---|---|---|---|---|---|---|---|---|
| **Prey** | % n | %O | %W | IRI | % n | %O | %W | IRI |
| **Fish** | | | | | | | | |
| *Cynoscion guatucupa* | 1.31 | 12.50 | 0.10 | 17.55 | 2.86 | 16.67 | 1.59 | 73.55 |
| *Trichiurus lepturus* | 10.32 | 70.83 | 40.80 | 3621.11 | 12.86 | 33.33 | 26.83 | 1301.39 |
| *Paralonchurus brasiliensis* | 7.85 | 37.50 | 11.15 | 712.61 | 38.57 | 50.00 | 20.30 | 2919.23 |
| *Urophycis brasiliensis* | 4.36 | 20.83 | 13.46 | 371.31 | | | | |
| *Anchoa marinii* | 0.15 | 4.17 | 0.02 | 0.68 | 5.71 | 33.33 | 1.66 | 244.50 |
| *Porichthys porosissimus* | 5.23 | 33.33 | 6.16 | 379.91 | 2.86 | 16.67 | 2.40 | 47.62 |
| *Umbrina canosai* | 4.80 | 33.33 | 8.81 | 453.61 | | | | |
| *Peprilus paru* | 0.29 | 8.33 | 0.21 | 4.17 | | | | |
| *Engraulis anchoita* | | | | | | | | |
| *Micropogonias furnieri* | 2.62 | 12.50 | 0.36 | 37.17 | 7.14 | 16.67 | 31.07 | 624.50 |
| *Macrodon ancylodon* | | | | | | | | |
| *Cynoscion jamaicensis* | 9.01 | 29.17 | 6.79 | 460.78 | 1.43 | 16.67 | 0.05 | 24.55 |
| *Pomatomus saltator* | | | | | | | | |
| *Menticirrhus* sp. | 0.44 | 8.33 | 8.45 | 74.02 | | | | |
| *Trachurus lathami* | 1.02 | 4.17 | 0.06 | 4.48 | | | | |
| *Stellifer rastrifer* | 37.06 | 54.17 | 2.81 | 2159.78 | 14.29 | 50.00 | 18.49 | 1616.75 |
| *Stromateus brasiliensis* | | | | | | | | |
| *Pagrus pagrus* | 2.03 | 8.33 | 0.66 | 22.43 | | | | |
| *Ctenosciena gracilicirrhus* | 0.44 | 8.33 | 0.18 | 5.10 | | | | |
| *Licengraulis grossidens* | 0.15 | 4.17 | | 0.61 | | | | |
| Scianidae (n.i.) | 1.16 | 16.67 | | 19.38 | | | | |
| Engraulidae (n.i.) | 0.29 | 4.17 | | 1.21 | | | | |
| **Cephalopod** | | | | | | | | |
| *Loligo sanpaulensis* | 92.07 | 70.83 | 94.34 | 13203.96 | 66.67 | 66.67 | 0.08 | 4450.00 |
| *Loligo plei* | 3.42 | 20.83 | 5.41 | 183.94 | 8.33 | 16.67 | 0.08 | 140.21 |
| *Argonauta nodosa* | 4.32 | 16.67 | 0.01 | 72.31 | 25.00 | 16.67 | 0.02 | 417.02 |
| *Octopus tehuelchus* | 0.18 | 4.17 | 0.24 | 1.76 | | | | |
| **Crustacean** | | | | | | | | |
| Penaoidea | 20.00 | 20.00 | | 400.00 | | | | |
| Isopoda | 80.00 | 80.00 | | 6400.00 | 100.00 | 100.00 | | |

Table A.9: Numerical abundance (%n), frequency of occurrence (%O), estimated mass (%W), and the Index of Relative Importance (IRI) of prey of franciscanas discriminated by summer and autumn (northern area) (n.i.= non identified).

| **Northern area** | **Winter (N=22)** | | | | **Spring (N=43)** | | | |
|---|---|---|---|---|---|---|---|---|
| **Prey** | % n | %O | %W | IRI | % n | %O | %W | IRI |
| **Fish** | | | | | | | | |
| *Cynoscion guatucupa* | 8.70 | 45.45 | 0.29 | 408.57 | 7.97 | 27.91 | 0.09 | 224.79 |
| *Trichiurus lepturus* | 1.17 | 22.73 | 5.17 | 144.08 | 14.22 | 67.44 | 61.98 | 5139.29 |
| *Paralonchurus brasiliensis* | 9.61 | 59.09 | 21.43 | 1834.27 | 7.50 | 25.58 | 7.49 | 383.53 |
| *Urophycis brasiliensis* | 7.14 | 50.00 | 26.93 | 1703.48 | 25.16 | 46.51 | 7.00 | 1495.64 |
| *Anchoa marinii* | 5.58 | 40.91 | 0.93 | 266.48 | 1.09 | 6.98 | 0.08 | 8.21 |
| *Porichthys porosissimus* | 2.86 | 27.27 | 0.07 | 79.81 | 4.22 | 16.28 | 8.58 | 208.40 |
| *Umbrina canosai* | 0.39 | 9.09 | 0.01 | 3.61 | 9.22 | 18.60 | 0.75 | 185.48 |
| *Peprilus paru* | 0.13 | 4.55 | 0.01 | 0.59 | | | | |
| *Engraulis anchoita* | 1.30 | 22.73 | 0.83 | 48.40 | 2.03 | 4.65 | 1.33 | 15.64 |
| *Micropogonias furnieri* | 0.13 | 4.55 | 1.28 | 6.42 | | | | |
| *Macrodon ancylodon* | 0.78 | 4.55 | 2.81 | 16.33 | 1.25 | 6.98 | 4.11 | 37.41 |
| *Cynoscion jamaicensis* | | | | | 5.47 | 4.65 | 2.18 | 35.59 |
| *Pomatomus saltator* | 0.13 | 4.55 | 3.21 | 15.19 | | | | |
| *Menticirrhus* sp. | 2.47 | 13.64 | 14.94 | 237.44 | 0.94 | 6.98 | 5.10 | 42.11 |
| *Trachurus lathami* | 0.91 | 18.18 | 1.09 | 36.42 | 1.09 | 6.98 | 0.04 | 7.91 |
| *Stellifer rastrifer* | 42.21 | 63.64 | 21.00 | 4022.29 | 6.88 | 32.56 | 0.67 | 245.67 |
| *Stromateus brasiliensis* | | | | | 0.16 | 2.33 | 0.37 | 1.23 |
| *Pagrus pagrus* | | | | | | | | |
| *Ctenosciena gracilicirrhus* | | | | | 0.47 | 4.65 | 0.21 | 3.16 |
| *Licengraulis grossidens* | | | | | | | | |
| Scianidae (n.i.) | 0.26 | 9.09 | | | 1.41 | 11.63 | | |
| Engraulidae (n.i.) | 2.34 | 36.36 | | | 0.94 | 6.98 | | |
| **Cephalopod** | | | | | | | | |
| *Loligo sanpaulensis* | 100.00 | 81.82 | 100.00 | 16363.64 | 98.51 | 74.42 | 99.00 | 14698.40 |
| *Loligo plei* | | | | | 0.60 | 2.33 | 0.88 | 3.42 |
| *Argonauta nodosa* | | | | | 0.89 | 6.98 | 0.13 | 7.10 |
| *Octopus tehuelchus* | | | | | | | | |
| **Crustacean** | | | | | | | | |
| Penaoidea | 50.00 | 66.67 | | 3333.33 | 11.76 | 13.33 | | 156.86 |
| Isopoda | 50.00 | 66.67 | | 3333.33 | 82.35 | 93.33 | | 7686.27 |

Table A.10: Numerical abundance (%n), frequency of occurrence (%O), estimated mass (%W), and the Index of Relative Importance (IRI) of prey of franciscanas discriminated by winter and spring (northern area) (n.i.= non identified).

# Appendix B

# Colour Maps

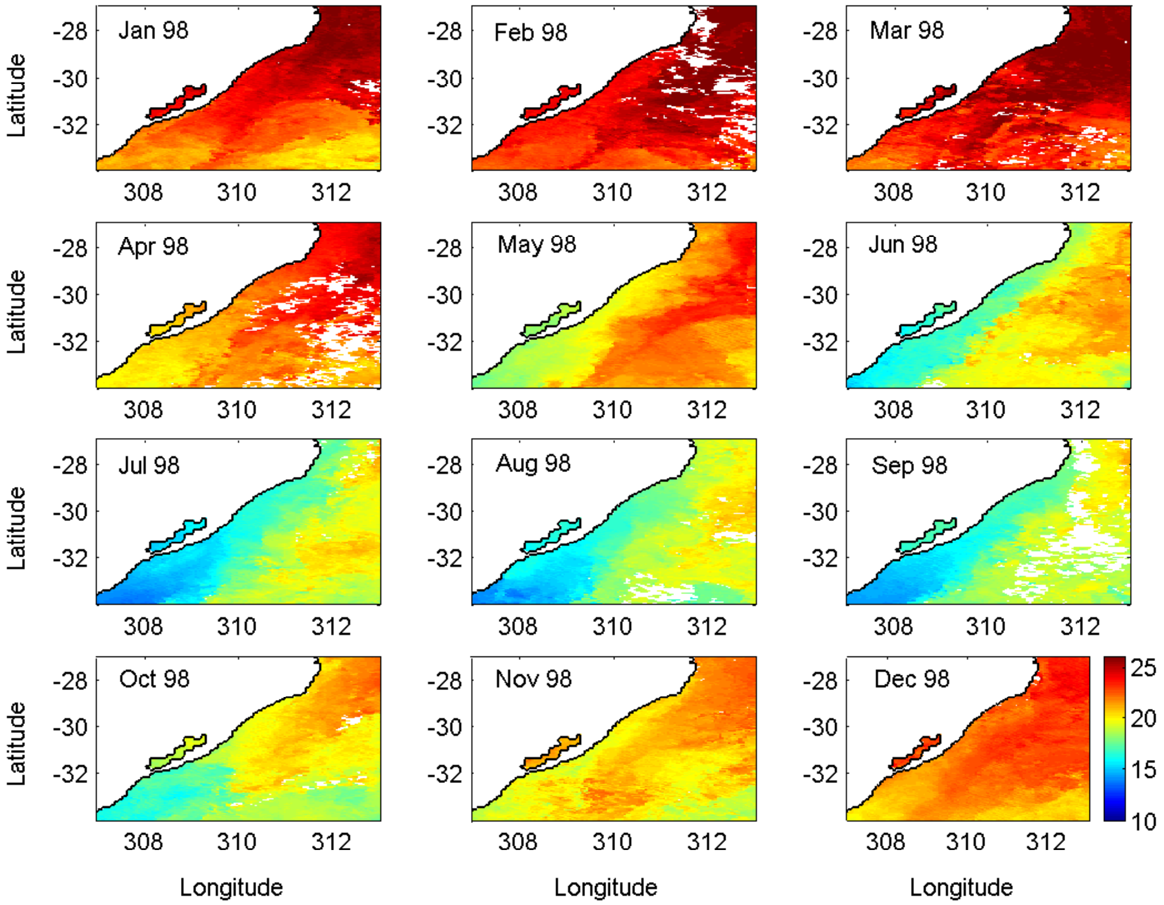


Figure B.1: Monthly averaged Sea Surface Temperature (SST) AVHRR images for the year of 1998. The legend bar at bottom right shows the values of temperatures in °C.

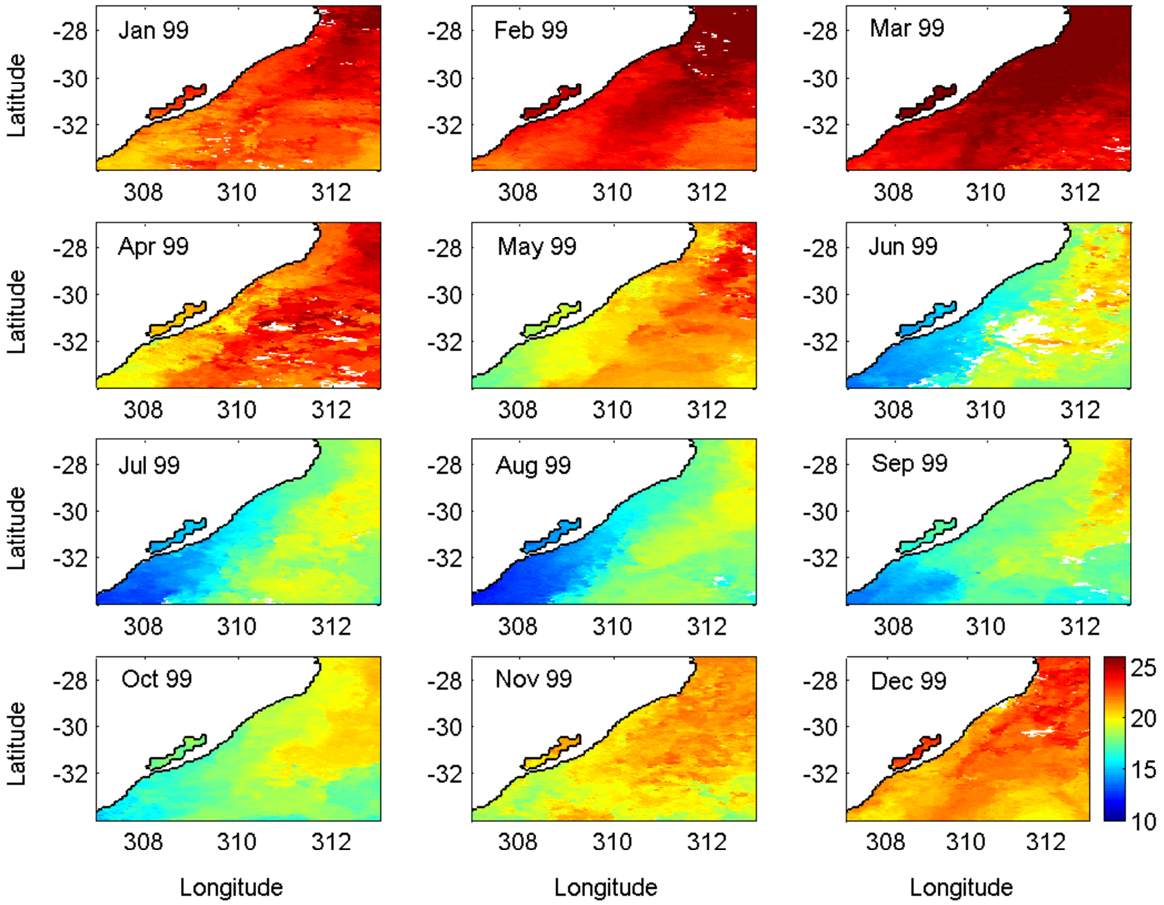


Figure B.2: Monthly averaged Sea Surface Temperature (SST) AVHRR images for the year of 1999. The legend bar at bottom right shows the values of temperatures in °C.

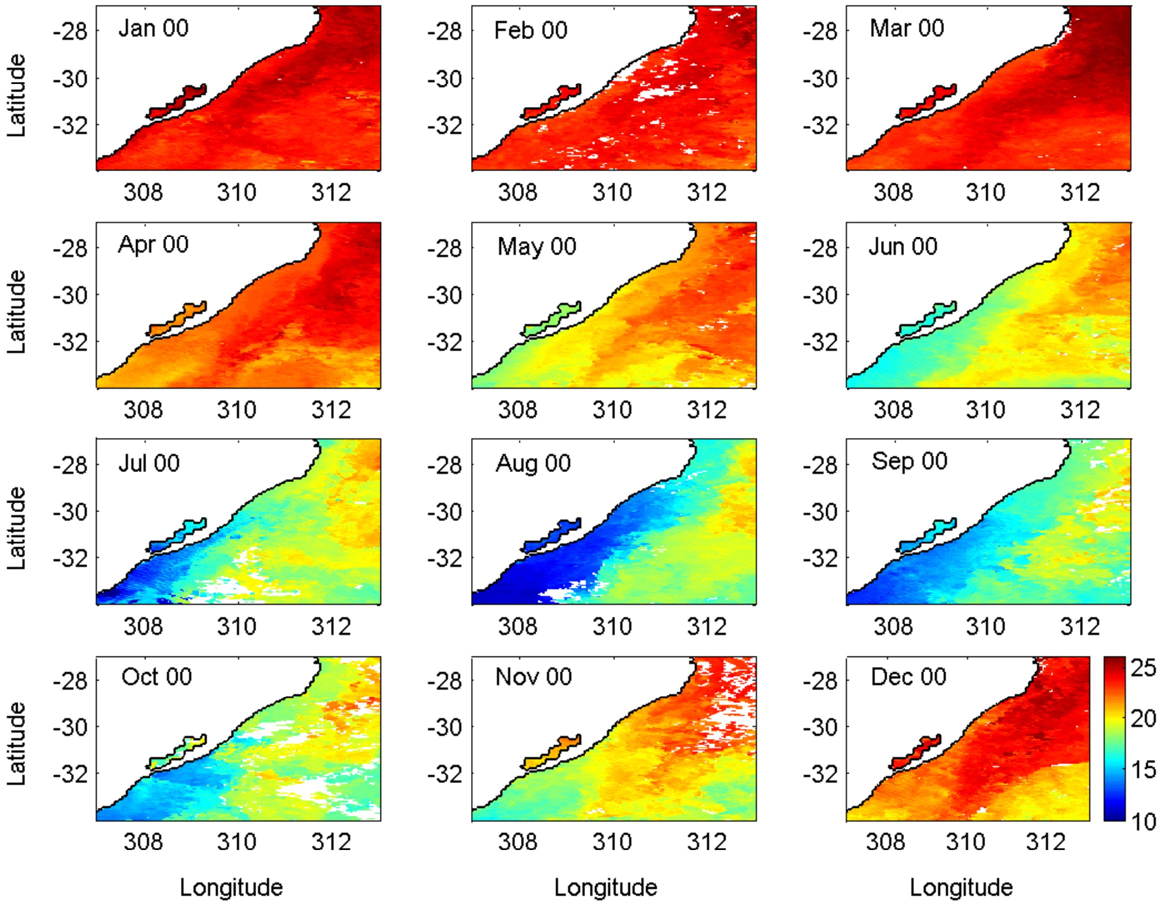


Figure B.3: Monthly averaged Sea Surface Temperature (SST) AVHRR images for the year of 2000. The legend bar at bottom right shows the values of temperatures in °C.

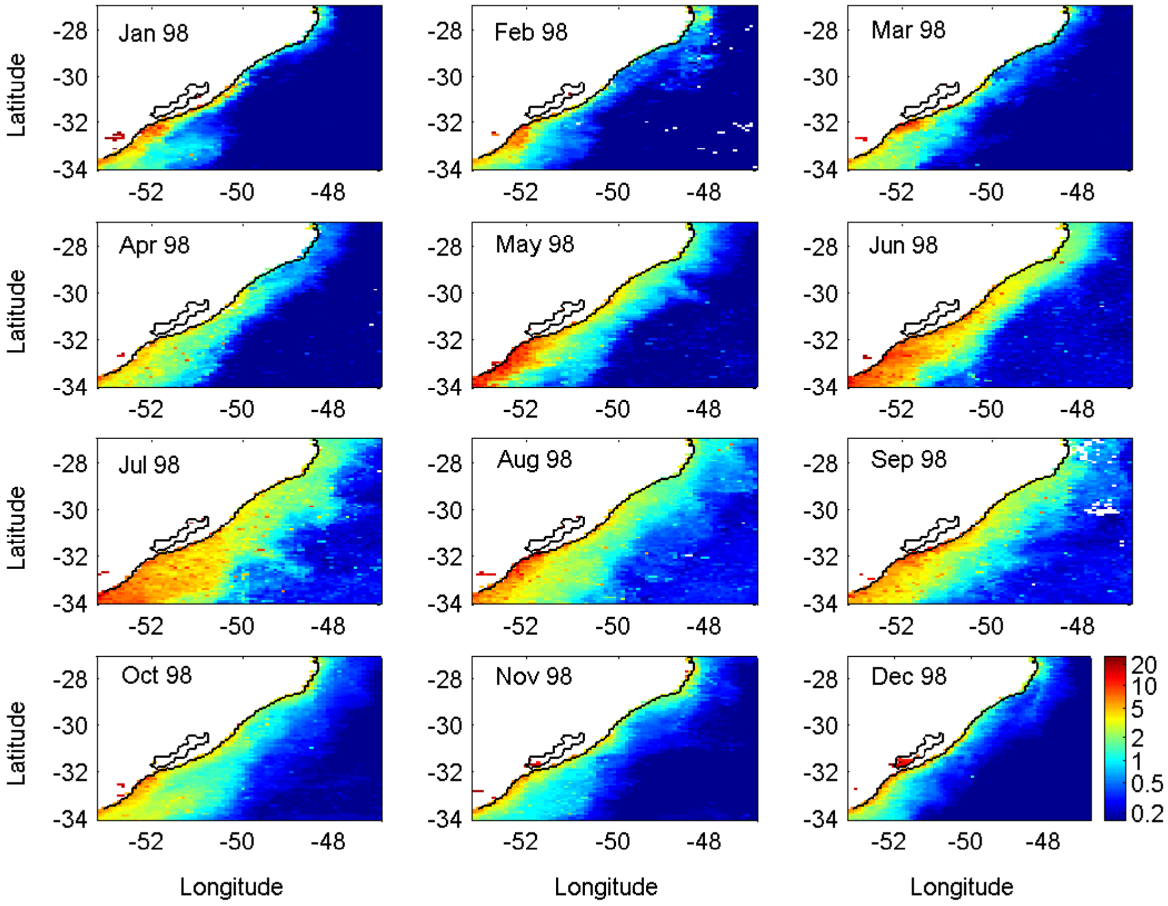


Figure B.4: Monthly averaged chlorophyll-$a$ concentration from SeaWIFS images for the year of 1998. The legend bar at bottom right shows the values of chlorophyll-$a$ concentration in mg/m$^3$.

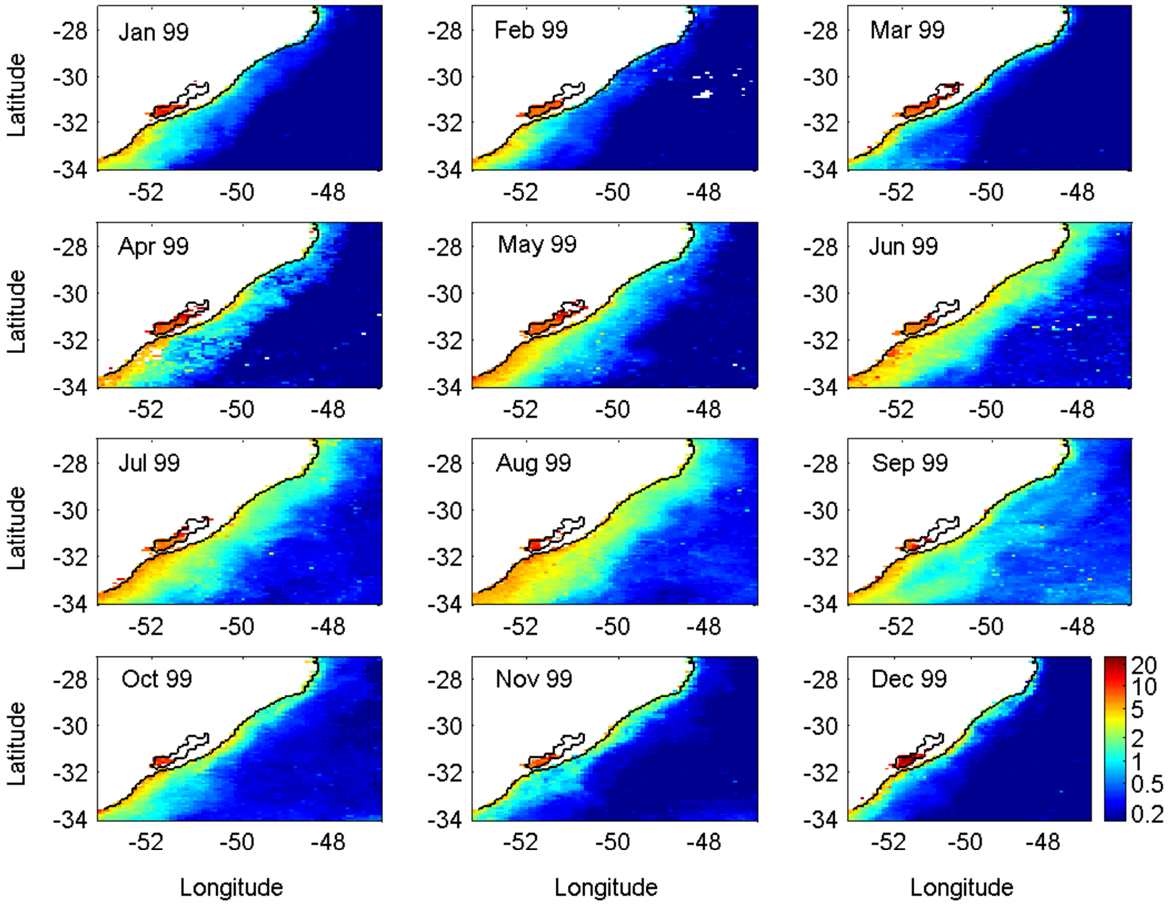


Figure B.5: Monthly averaged chlorophyll-$a$ concentration from SeaWIFS images for the year of 1999. The legend bar at bottom right shows the values of chlorophyll-$a$ concentration in mg/m$^3$.

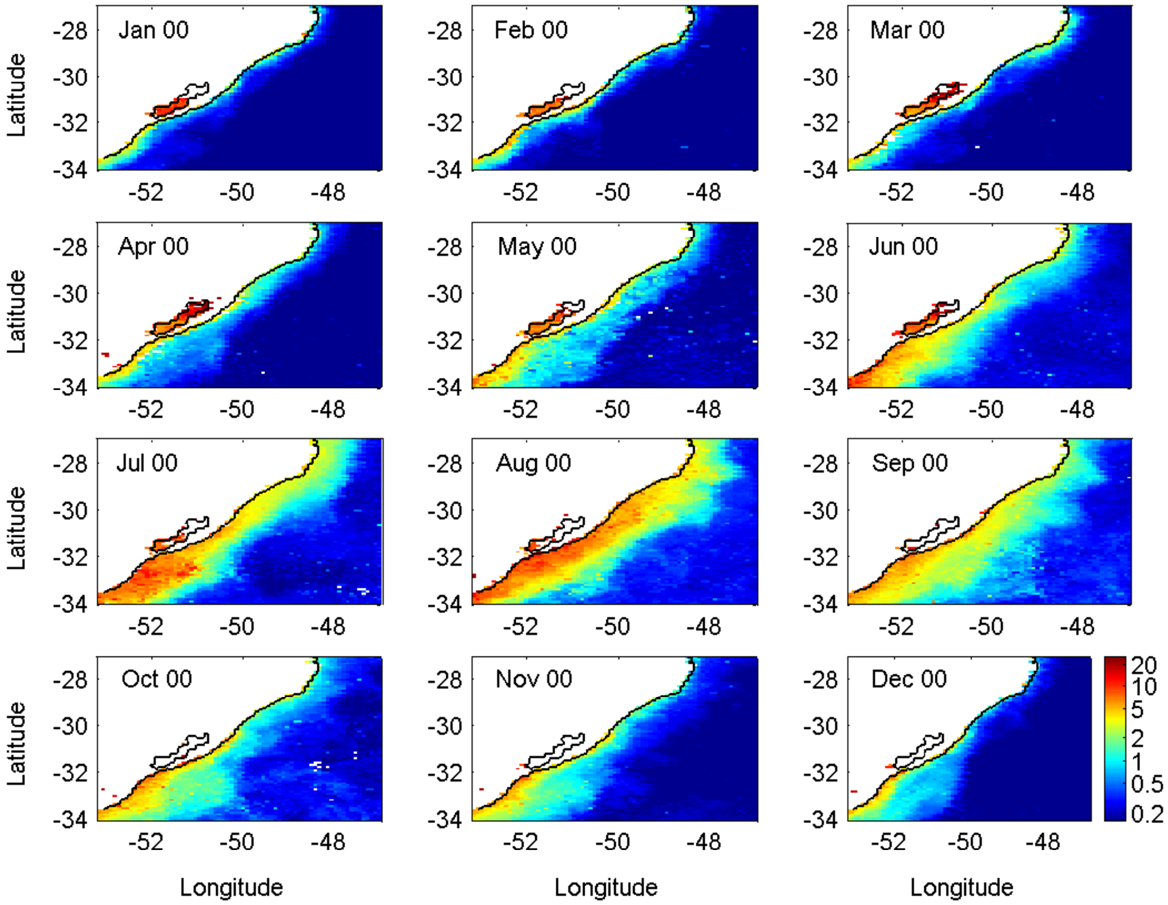


Figure B.6: Monthly averaged chlorophyll-$a$ concentration from SeaWIFS images for the year of 2000. The legend bar at bottom right shows the values of chlorophyll-$a$ concentration in mg/m$^3$.

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