4 CETACEAN COMMUNITY STRUCTURE AROUND THE GALÁPAGOS IN RELATION TO ENVIRONMENTAL HETEROGENEITY AND SEASONAL CHANGE

4.1 ABSTRACT

A cetacean community consisting of seven small and medium-sized delphinids (*Stenella attenuata*, *S. longirostris*, *S. coeruleoalba*, *Delphinus delphis*, *Tursiops truncatus*, *Grampus griseus*, and *Globicephala macrorhynchus*), the sperm whale (*Physeter macrocephalus*), and the Bryde's whale (*Balaenoptera edeni*) was studied in relation to environmental conditions around the Galápagos Archipelago, using a compilation of sighting for the period 1973–2000. Sightings were gridded at a resolution of 0.25 degrees and seasonal composites were formed for analysis. Three major groups of sample units were obtained with cluster and indicator species analyses. The spatial distribution of two of the groups and their species composition showed a good correspondence with the main habitats found around the archipelago in all seasons. Areas of strong water-column stratification were characterized by presence of *S. attenuata* and *S. longirostris*, while upwelling and nearshore areas were characterized by presence *D. delphis*, *T. truncatus*, *B. edeni*, *G. griseus*, and *G. macrorhynchus*. The third group, characterized by presence of *S. coeruleoalba* and *P. macrocephalus*, was spatially incoherent. Ordination of the sample units *via* nonmetric multidimensional scaling yielded two axes, which represented 86% and 4.2%, respectively, of the information in the data set. The dominant environmental gradient in the study area (from cold, upwelling, and phytoplankton-rich conditions close to the islands to warm, stratified, and phytoplankton-poor conditions away from the islands) explained 27–35% of the variance in community structure along the first axis. Structure along the second axis was independent of the environmental variables considered.

4.2 INTRODUCTION

Located in the eastern equatorial Pacific, the Galápagos Archipelago lies in an area of rapid change in oceanographic conditions owing to its proximity to the Equatorial Front (EF). The EF is a regional feature that runs zonally between the South American coast and the international dateline, separating warm waters to the north from cool waters to the south. Biological production across this gradient is strongly influenced by the availability of macronutrients (i.e., nitrate) and micronutrients (i.e., iron). Conditions are generally oligotrophic north of the EF due to a meager nitrate supply across the strong pycnocline. South of the EF, wind-induced equatorial upwelling provides nitrate in adequate concentrations but iron is in limited supply, leading to "high-nutrient, low-chlorophyll" (HNLC) conditions through most of this region. Only at the Galápagos is this condition relieved owing to a localized phenomenon, the topographically forced upwelling of the Equatorial Undercurrent (EUC) on the western side of the archipelago. In this area, phytoplankton populations are able to use the upwelled nitrate in the presence of a local source of iron derived from the island platform. The productive habitat that develops in this area can be seen in ocean color satellite imagery as a plume of elevated phytoplankton pigment concentration extending westward for 100 km or more (Feldman et al., 1984; Feldman, 1986; Palacios, 2002). Thus, within oceanic Galápagos waters it is possible to find warm/oligotrophic, cool/HNLC, and cool/eutrophic conditions in close proximity to each other. In addition, a nearshore environment is found around the perimeter of the islands, and includes the shallow coastal waters and the underwater slopes of the volcanoes.

How does this environmental heterogeneity affect the occurrence patterns of top predators such as cetaceans? At the regional level, the distribution, abundance, and environmental associations of eastern tropical Pacific cetaceans have been the subject of a number of studies (Au and Perryman, 1985; Polacheck, 1987; Reilly, 1990; Reilly and Thayer, 1990; Wade and Gerrodette, 1993; Fiedler and Reilly,

1994; Reilly and Fiedler, 1994). In offshore waters, thermocline topography and watermass type appear to be the primary environmental factors that correlate with species distribution. Among the dolphins, the main patterns can be summarized as follows. Two geographically distinct stocks of spotted dolphins (*Stenella attenuata*) and spinner dolphins (*S. longirostris*) occupy the warmest waters of the region. Northeastern spotted dolphins and eastern spinner dolphins are found in Tropical Surface Water east of 120°W along the countercurrent thermocline ridge at 10°N. Western/southern spotted dolphins and whitebelly spinner dolphins are found in Subtropical Surface Water in the northwest and southwest corners of the region, where the thermocline is deep (Fiedler and Reilly, 1994; Reilly and Fiedler, 1994). Short-beaked common dolphins (*Delphinus delphis*), on the other hand, are found along the equatorial thermocline ridge east of 100°W in Equatorial Surface Water, and in the vicinity of the Costa Rica Dome, both areas of upwelling (Reilly, 1990; Reilly and Fiedler, 1994). Finally, striped dolphins (*S. coeruleoalba*) are widely distributed in the region and have no clear association with particular environmental conditions (Reilly, 1990; Reilly and Fiedler, 1994). In nearshore waters (i.e., off the coasts of Central America and northern South America), bottlenose dolphins (*Tursiops truncatus*), Risso's dolphins (*Grampus griseus*), short-finned pilot whales (*Globicephala macrorhynchus*), and, to a lesser extent, common dolphins are the dominant species, particularly in the Gulf of Panamá (Polacheck, 1987).

Among the large whales, the Bryde's whale (*Balaenoptera edeni*) is widely distributed in the region, but apparent areas of concentration are centered at the thermocline ridges along the equator and along 10°N, as well as in the Gulf of Panamá (Volkov and Moroz, 1977; Berzin, 1978; Wade and Gerrodette, 1993). Blue whales (*B. musculus*), on the other hand, have a clear preference for the upwelling-modified waters of the Costa Rica Dome and the Galápagos (Reilly and Thayer, 1990; Palacios, 1999a). Sperm whales (*Physeter macrocephalus*) are

widespread, although the Gulf of Panamá appears to be a particular area of concentration (Polacheck, 1987; Wade and Gerrodette, 1993).

All of the above species are known to occur in Galápagos waters, at least for part of the year (Palacios and Salazar, 2002), providing a unique opportunity to study the influence of strong environmental gradients on cetacean community structure at a local scale. It should be kept in mind that ocean conditions are not static, as processes acting at various temporal and spatial scales constantly modify them. These processes range from tidal mixing, equatorial waves and mesoscale eddies at one end of the spectrum, to El Niño and decadal oscillations at the other end. However, recognizing the importance of the seasonal cycle in the redistribution of forage at the regional scale (Blackburn et al., 1970; Dessier and Donguy, 1985; Fiedler, 2002), this study focuses on the effects of seasonal variability. The general patterns of species distribution, the relationships between species, and the associations between species and environmental variables around the Galápagos are described in this paper through community classification and ordination techniques.

4.3 METHODS

4.3.1 Cetacean data

The area for this study was defined as a 7 × 7-degree latitude-longitude box extending from 3°N–4°S and from 87°–94°W, with the geographic center of the Galápagos (0.5°S, 90.5°W) (Snell et al., 1995) at its center. The spatial extent of this area is about 605×10^3 km^2 or 597×10^3 km^2 once the area of the islands is subtracted. A database of marine mammal sightings collected by research expeditions and by scientific observers aboard fishing vessels operating in this area over the 28-yr period 1973–2000 was compiled for this study. Of the 4817 sightings in this database, 2879 belonged to 21 identified cetacean species, 165

belonged to two otariid pinnipeds, and 1773 corresponded to eight unidentiied categories. The database is described in detail in Appendix A (section 4.10.1).

For analysis, the target community was defined using the number of sightings for each species relative to the total number of identified cetacean sightings (see Table A4.1), as a criterion to identify dominant and rare species. Species with less than 4% of the total were considered rare and eliminated from the analysis. The remaining 2739 sightings involved nine species: *S. attenuata* (n = 519, 18%), *D. delphis* (n = 456, 15.8%), *T. truncatus* (n = 366, 12.7%), *B. edeni* (n = 316, 11%), *S. longirostris* (n = 303, 10.5%), *P. macrocephalus* (n = 284, 9.9%), *S. coeruleoalba* (n = 247, 8.6%), *G. macrorhynchus* (n = 131, 4.6%), and *G. griseus* (n = 117, 4.1%). In order to use the sighting data it was necessary to project them onto a uniform grid. The resolution for this grid was determined by the need to preserve the details of the distribution of each species of interest, but also to avoid a division so fine that the grid would be made up of mostly empty cells. A resolution of 0.25 degrees (27.7 km) was found to be a good compromise. The resulting 28 × 28 grid was projected onto the study area and sighting locations were assigned to the center of the grid cell in which they fell. Of the 784 cells making up the grid, 15 occurred on land and were eliminated, while the remaining 769 were allowed to take values.

This gridding scheme was applied on a seasonal basis by combining sightings made in each season without regard to the year, as a compromise between resolving relevant scales of temporal variability (i.e., seasonal to interannual) and obtaining sufficient spatial coverage of the study area. The four seasons were defined as: January–March (JFM), April–June (AMJ), July–September (JAS), and October–December (OND). The resulting seasonal grids contained 392 (JFM), 297 (AMJ), 196 (JAS), and 330 (OND) cells with marine mammal sightings (including rare and unidentified species). However, a grid cell was considered *valid* only if it had sightings of one or more of the nine species of interest. Accordingly, the final

grids contained 309 (JFM), 232 (AMJ), 140 (JAS), and 223 (OND) valid cells. Hereafter, the valid cells in these seasonal grids are referred to as *sample units*.

Associated with each sample unit was the number of sightings per species and per season, accumulated over the 28-yr period of the compilation. Use of these data as an indication of species "abundance" for community analysis would clearly be inappropriate due to the lack of an adequate measure of effort needed to standardize abundance in each sample unit (see Appendix A). However, for the purposes of this study, abundance was not needed because the important information is contained in the pattern of presences and absences of the different species (Fager, 1957; McCune and Grace, 2002). Therefore, the species data were transformed to presence-absence. This binary transformation is particularly useful in studies in which the heterogeneity of the sample units is large (in terms of the *number of species* present), by enhancing the performance of sociological distance measures (McCune and Grace, 2002), like the Sørensen-based coefficient used in section 4.3.3. In this case, the transformation had the added benefit of greatly reducing the problems associated with spatial differences in effort for a given season. After these manipulations, the sighting data set was more analogous to the climatological data sets described in the next section in that it emphasized the long-term seasonal patterns.

4.3.2 Environmental data

Environmental variables were chosen for the roles they play in structuring pelagic communities and for their potential relevance to cetacean ecology (e.g., Sournia, 1994; van der Spoel, 1994), as follows. Sea-surface temperature (SST) is a useful descriptor of horizontal gradients associated with subsurface processes and air-sea interaction. Thermal fronts, in particular, are effective boundaries for most oceanic biota (e.g., Olson, 2002), including cetaceans (e.g., Gaskin, 1968; Selzer and Payne, 1988; Goold, 1998). The tropical thermocline and pycnocline serve as

physical and ecological barriers in the water column (Longhurst, 1998). The oxygen minimum layer (OML), where oxygen concentrations fall below 1 ml l^{-1} due to bacterial decomposition, can be an effective barrier to many organisms, but it also offers refuge and increased food supply to species adapted to thrive in these conditions (Wishner et al., 1995). Considerable amounts of biota aggregate in these oxygen-deficient zones (Longhurst, 1967; Mullins et al., 1985), with the potential to attract large predators like cetaceans (e.g., Perrin et al., 1976). Finally, phytoplankton chlorophyll-*a* concentrations (chl) provide an indication of the standing stock of primary producers available as food to higher trophic levels, eventually reaching cetaceans *via* links in the food web (e.g., Smith et al., 1986).

Contemporaneous measurements of these environmental conditions at the sighting locations were not available for the vast majority of the observations. Environmental data had to be obtained from standard climatological compilations, and therefore they are neither real-time nor sighting-associated measurements. They should be viewed as indicators of the average ocean conditions for the study area. A description of the climatological products used and the procedures followed to extract the variables of interest are given in Appendix B (section 4.10.2). Eight environmental variables were extracted for each season: (1) depth of the thermocline (Z20), (2) thermocline strength (ZTD), (3) pycnocline strength (MBVF), (4) depth of the pycnocline (ZMBVF), (5) depth of the OML (ZOML), (6) thickness of the OML (ZOD), (7) SST, and (8) log-transformed chl (LCHL). These variables were re-gridded from their original resolution to a common resolution of 0.25 degrees for compatibility with the sighting grid (see Appendix B).

A ninth variable, distance from each cell center to the geographic center of the archipelago in the sigthing grid (or RAD), was derived as an attempt to account explicitly for the spatial dependence of cetacean distribution patterns on physiographic features associated with the presence of the archipelago. Because of

the local nature of these features, this was found to be superior to including latitude and longitude as geographic variables. The latter are more useful in large-scale studies where a regional gradient in species morphology may be present or when several stocks of a particular species are being considered (e.g., Reilly and Fiedler, 1994).

4.3.3 Analytical methods

The goals of the analyses were two: (1) to identify the major groups of sample units in terms of species composition, and (2) to characterize the main patterns of variation in the cetacean data sets and to determine the relationship of these patterns to environmental variability. For these purposes, classification and ordination techniques were applied using the implementations in the software package PC-ORD version 4.25 (McCune and Mefford, 1999). The gridded cetacean data sets were arranged into matrices with sample units in the rows and species in the columns for each season (309×9 for JFM, 232×9 for AMJ, 140×9 for JAS, and 223×9 for OND). Consistent with the goals, analyses were conducted in "Q mode" (Legendre and Legendre, 1998), which aims at uncovering relationships among sample units based on the observed species. A distance matrix was computed for each seasonal species matrix using the Sørensen distance (see Appendix C, section 4.10.3.2).

4.3.3.1 Classification: Recognizing the major groups of sample units

The purpose of classification was to delineate the major groups[1] of sample units based on differences in species composition. These differences are presumed to arise primarily in response to environmental variability (Fager, 1957; Legendre and Legendre, 1998; McCune and Grace, 2002). As described in the Introduction,

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[1] Throughout this paper, the word *group* is reserved to denote the major groups of sample units identified through cluster analysis and associated techniques.

most of the species in this study are known to have distinct habitat preferences, at least at the regional scale. For example, *S. attenuata* and *S. longirostris* are found in warm, offshore waters; *D. delphis* in upwelling-modified waters (e.g., Reilly, 1990; Reilly and Fiedler, 1994); and *T. truncatus* in nearshore environments (e.g., Polacheck, 1987). Because the study area can be readily divided into stratified *vs*. upwelling zones with regard to water-column structure, and into nearshore (i.e., within the 2000-m depth contour) *vs*. offshore zones with regard to distance from shore, it seemed reasonable to assume that at least three distinct cetacean habitats, stratified, upwelling, and nearshore, are present locally.

Cluster analysis was performed on the distance matrices, using flexible beta as the group linkage method, with ß = -0.25 (McCune and Grace, 2002). The program was instructed to partition the distance matrices into three groups of sample units, which were presumed to represent the three types of habitat described above. The statistical validity of the three groups was assessed with a multi-response permutation procedure (MRPP) (Mielke, 1984; Mielke and Berry, 2001) on the rank-transformed distance matrices. MRPP tested the null hypothesis of no difference in average within-group ranked distance. It also provided an agreement statistic (A) describing average within-group homogeneity compared to random expectation (A increases as distances become more similar, with maximum $A = 1$ when all distances within each group are identical) (McCune and Grace, 2002).

The differences in species composition between the groups was described with indicator species analysis (Dufrêne and Legendre, 1997). Indicator values for a species are formed by combining information about specificity (i.e., the abundance of a species in a group in relation to the mean abundances of that species across groups) and fidelity (i.e, the number of sample units in a group where a species was present in relation to the total number of sample units in that group). Indicator values are expressed as a precentage of perfect indication. A species is an indicator of the group for which it has the largest indicator value. The

collection of indicator species characteristic of a group is referred to here as an
assemblage. The indicator species provide a useful criterion in the ecological
interpretation of groups of sample units that are presumed to describe particular
environmental conditions. The significance of the indicator values was assessed
with a Monte Carlo procedure by randomly reassigning sample units to groups
1000 times (Legendre and Legendre, 1998; McCune and Grace, 2002).

4.3.3.2 Ordination: Representing sample units and environment in reduced space

The purpose of ordination was to characterize the main patterns of variation
among sample units in the species matrices and to establish the influence of
environmental variability on those patterns. As a preliminary step, the species data
were transformed with the Beals smoothing function (McCune, 1994). This
transformation replaces the presence-absence data for a given species in a sample
unit with a probability of occurrence (hereafter referred to as *synthetic abundance*)
estimated on the basis of observed species co-occurrences in that sample unit,
according to the formula given in Appendix C (section 4.10.3.3). Transformation
was necessary in order to improve the stability of the solution in the ordination
procedure (see below) because the Sørensen distances among sample units obtained
from the presence-absence data produced two "populations" with little or no
overlap (see Appendix C), leading to unstable solutions. Although the Beals
transformation enhances the detection of the main compositional gradient (i.e., the
pattern of joint occurrences) in heterogeneous and sparse community matrices, it
does so at the expense of weaker patterns (McCune, 1994; Ewald, 2002). By
filtering out the noise from the signal, the procedure sacrifices the use of inferential
statistics, and therefore, the results of the ordination can only be used for
descriptive purposes.

The Beals-transformed seasonal matrices were combined into a single 904 ×
9 matrix, and a distance matrix was computed from this array of synthetic

abundances using the Sørensen distance. Community ordination of the distance matrix was sought through nonmetric multidimensional scaling (NMS) (Legendre and Legendre, 1998; McCune and Grace, 2002). Details of the setup and the intermediate steps of the analysis are provided in Appendix C (section 4.10.3.4).

For assessment of the relationship between the ordination axes and the environmental variables, values were extracted from the 0.25-degree gridded environmental data sets for grid cells with valid data in the corresponding species matrices (see section 4.3.2). The extracted environmental/spatial data were re-arranged into a matrix with sample units in the rows and variables (Z20, ZTD, MBVF, ZMBVF, ZOML, ZOD, SST, LCHL, and RAD) in the columns for each season. A principal component analysis was performed on the variables describing direct effects of physical forcing on the system (i.e., Z20, ZTD, MBVF, ZMBVF, ZOML, ZOD, SST) as a data reduction strategy, but also to eliminate the multicollinearity and improve the normality of these variables (see Appendix B for a description of the principal components). The resulting matrix containing the scores of the first three principal components (PC1, PC2, and PC3), was combined with LCHL and RAD. This 904×5 matrix contained the "external" variables of interest (environmental and spatial descriptors). Relationships between the external variables and the solution of the NMS ordination were established through rotation, overlays, correlations, and biplots (McCune and Grace, 2002).

4.4 RESULTS

4.4.1 Distribution

The predominant cetacean community was composed of seven small and medium-sized delphinids (*S. attenuata*, *S. longirostris*, *S. coeruleoalba*, *D. delphis*, *T. truncatus*, *G. griseus*, and *G. macrorhynchus*), the sperm whale (*P. macrocephalus*), and the Bryde's whale (*B. edeni*). The quarterly number of sightings for these nine species combined is shown in Figure 4.1. Maps with

sighting locations for each species are shown in Figure 4.2. These maps indicate clear differences in distribution within the study area. Two species were found along the northern and southern margins (*S. attenuata* and *S. longirostris*), three species had scattered distributions (although with some clustering near the islands) (*S. coeruleoalba*, *G. macrorhynchus*, and *P. macrocephalus*), and the remaining four species were primarily concentrated near the islands (*D. delphis*, *T. truncatus*, *G. griseus*, and *B. edeni*), especially around the western islands of Isabela and Fernandina.

4.4.2 Classification

MRPP supported the statistical significance of the three-group partition obtained with cluster analysis for all seasons (*p*-value < 0.0001) (Table 4.1). The hierarchical structure of the groups is shown in the dendrograms in Figure 4.3. The number in bold type inside each box indicates the number of sample units for that group. Also listed is the species assemblage characteristic of each group from the indicator species analysis, along with the indicator value (i.e., the percentage of perfect indication) for each species, in parenthesis. The spatial distribution of the groups is shown in Figure 4.4.

At this level of partition, within-group homogeneity (quantified by the agreement statistic *A* in Table 4.1), was fairly high for all seasons (*A* range: 0.38–0.46). Average within-group Sørensen distances were generally low for groups 1 and 2, and higher for group 3 (Table 4.1). These differences were directly related to the number of species characteristic of that group, as described below. Group sizes were varied, with groups 1 and 3 having the largest number of sample units in all seasons except JAS (Fig. 4.3). The branching in the dendrograms indicated that group 2 was more similar to group 3 in JFM and JAS, and more similar to group 1 in AMJ and OND.
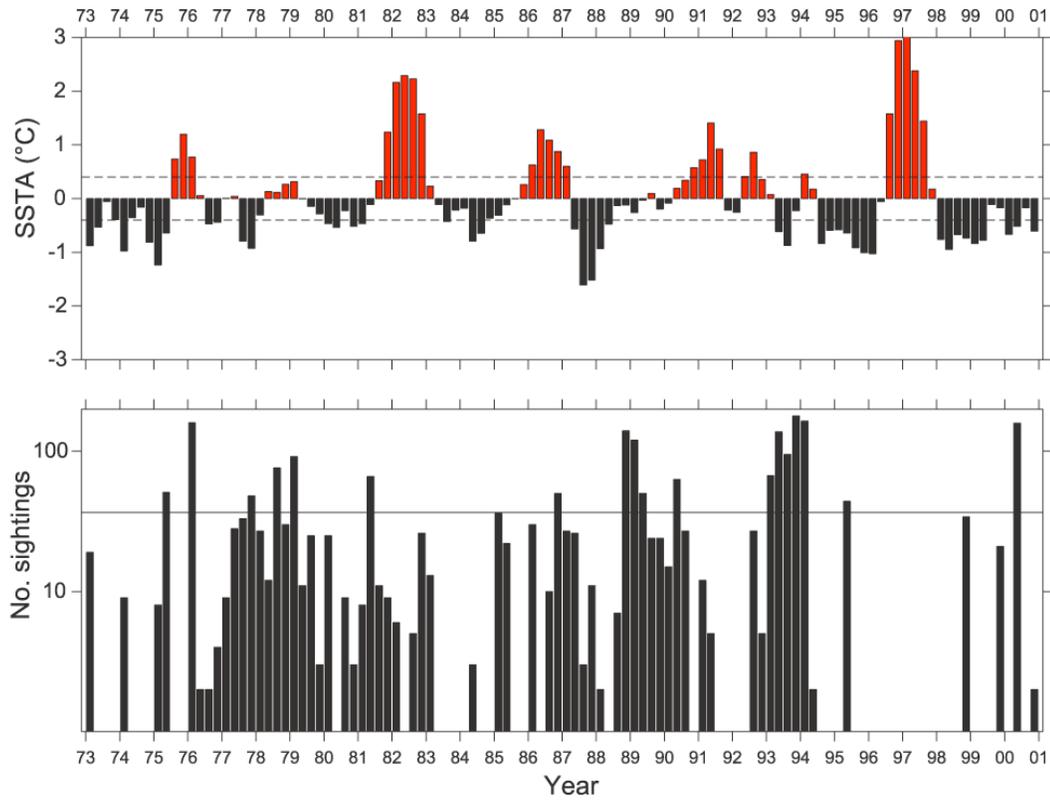
Figure 4.1: Time series for the period 1973–2000. Top: quarterly-averaged SST anomaly (SSTA) from the 5-month running mean of the CDRS monthly record (see p. 123). Bottom: quarterly number of sightings (in log scale) for the nine species of interest. The horizontal line indicates the average (36.5). Blank spaces are times during which no sightings were made.
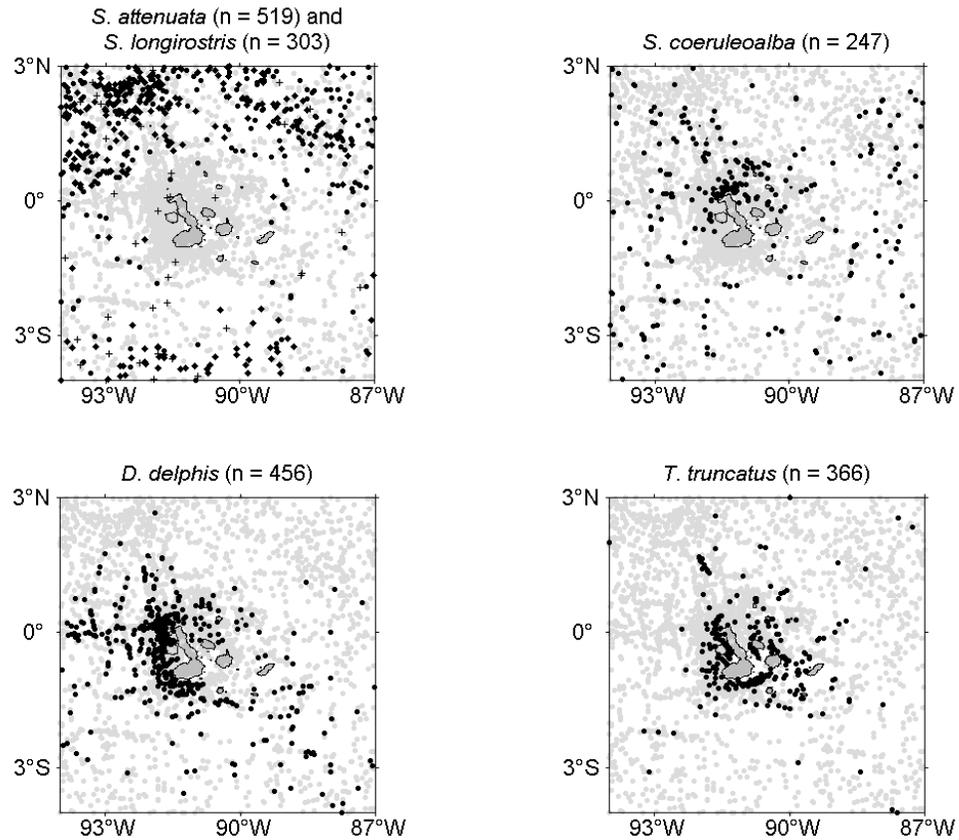
Figure 4.2: Cumulative sighting locations for *S. attenuata*, *S. longirostris* (plus symbols), *S. coeruleoalba*, *D. delphis*, and *T. truncatus*, for the period 1973–2000. Gray dots are the locations of all marine mammal sightings (identified and unidentified) in the study area (n = 4817).
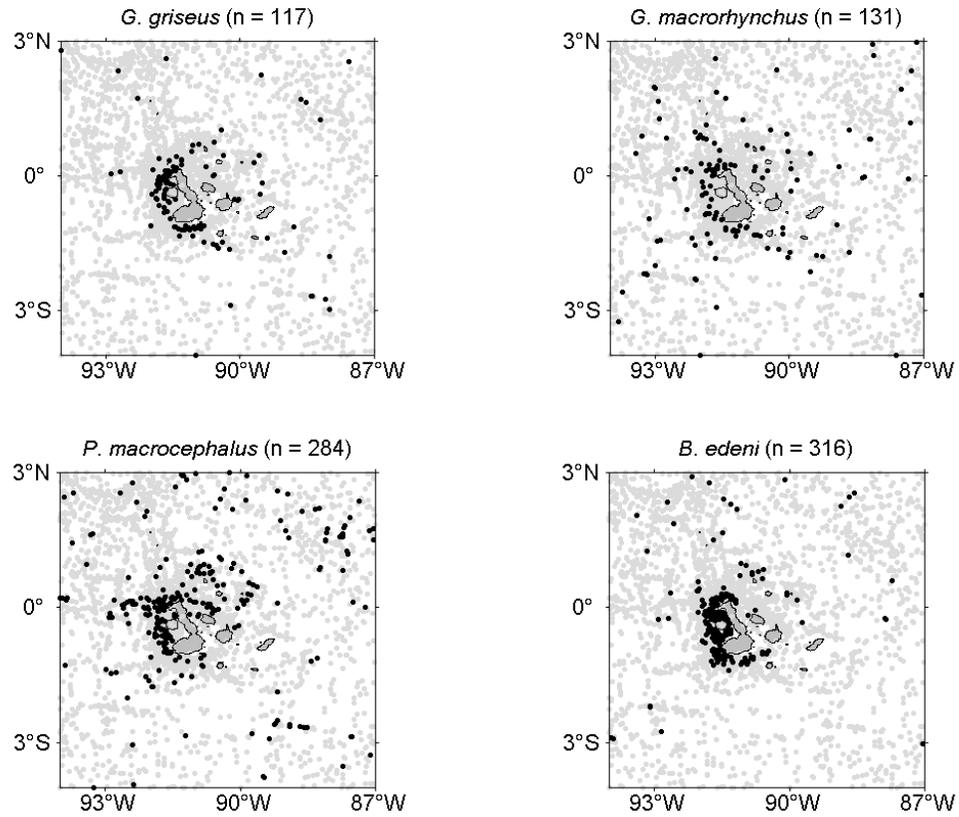
Figure 4.2: Continued. Cumulative sighting locations for *G. griseus*, *G. macrorhynchus*, *P. macrocephalus*, and *B. edeni*, for the period 1973–2000. Gray dots are the locations of all marine mammal sightings (identified and unidentified) in the study area (n = 4817).
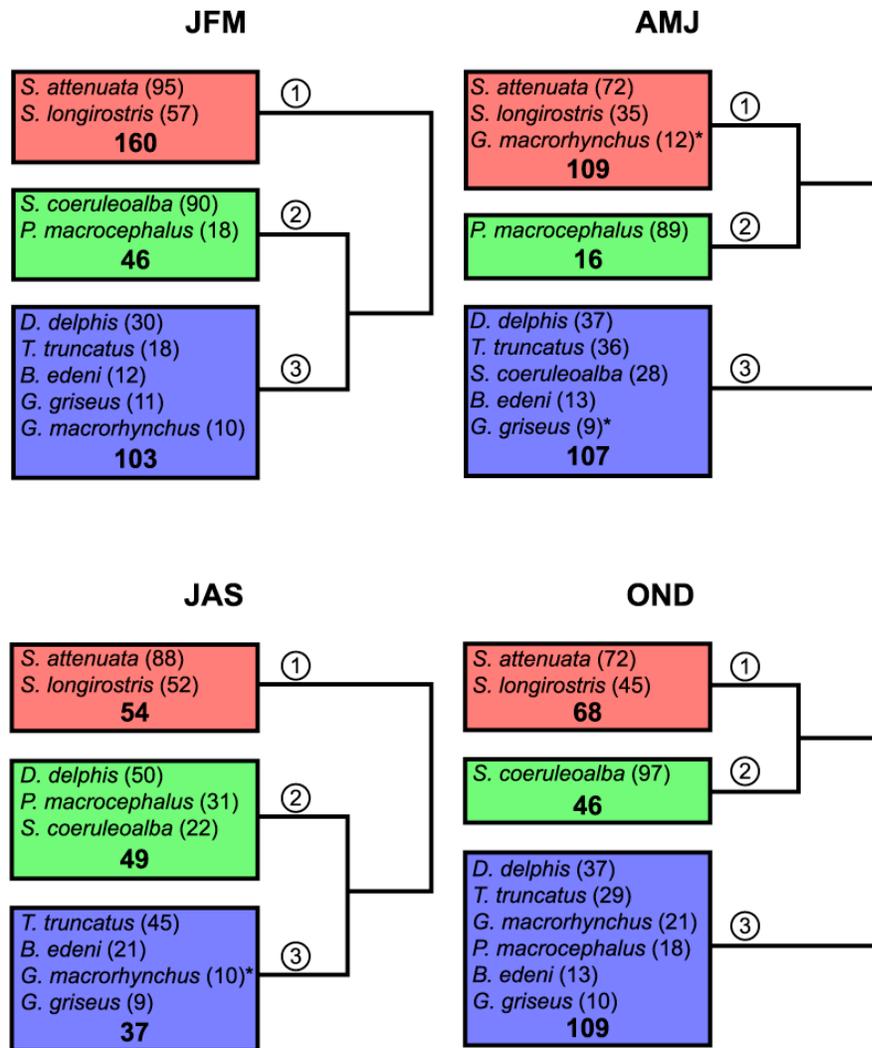
Figure 4.3: Schematic dendrograms of the three major groups of sample units extracted with cluster analysis for each season. The number of sample units within each group is shown in bold type. The species assemblage characteristic of each group from the indicator species analysis is listed, along with the indicator value for each species (in parenthesis). An asterisk next to a species name indicates that the indicator value for that species was statistically non-significant according to the Monte Carlo test.
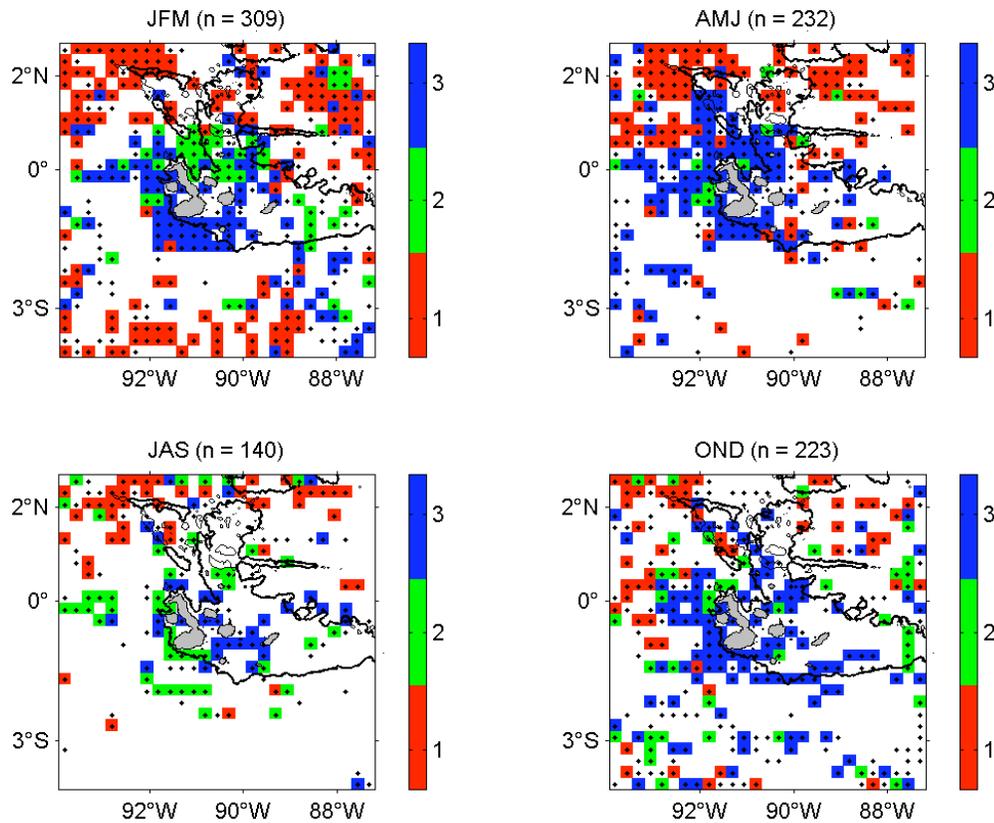
Figure 4.4: Spatial distribution of the three groups of sample units identified through cluster analysis for each season. The 2000-m depth contour is indicated. Black dots represent grid cells with with marine mammal sightings (including rare and unidentified species). The number of sample units (i.e., valid grid cells) is shown in parenthesis.

Table 4.1: Average within-group distance, chance-corrected within-group agreement (*A*), and *p*-value from MRPP analyses on the seasonal rank-transformed distance matrices. The number of sample units in each group is given in parenthesis.

Group	Average within-group distance			
	JFM	AMJ	JAS	OND
1	0.14 (160)	0.24 (109)	0.12 (54)	0.11 (68)
2	0.18 (46)	0.10 (16)	0.38 (49)	0.10 (46)
3	0.44 (103)	0.36 (107)	0.36 (37)	0.41 (109)
A	0.46	0.38	0.41	0.45
p	< 0.0001	< 0.0001	< 0.0001	< 0.0001

In terms of species composition (Fig. 4.3), group 1 was characterized by the presence of *S. attenuata* and *S. longirostris* in all seasons. *Stenella attenuata* had the highest indicator value (72–95%) for this group. *Globicephala macrorhynchus* was also included with group 1 in AMJ, but its indicator value was not significant (*p*-value = 0.173). The relatively small group 2 was characterized by one to three species, depending on season. *Stenella coeruleoalba* was the predominant indicator species for this group in JFM (90%) and OND (97%), although it was also present in JAS. *Physeter macrocephalus* was present in JFM, AMJ, and JAS, and it was the only species in the group in AMJ. *Delphinus delphis* was the most characteristic species of group 2 in JAS (50%). The assemblage typical of Group 3 included four

to six species. *Delphinus delphis* had the highest indicator value (30–37%) for this group in all seasons except for JAS, when it associated with group 2, as mentioned above. *Tursiops truncatus* had the second highest indicator values in JFM, AMJ, and OND (18–36%), and it was the characteristic species of group 3 in JAS (45%). Other species characteristic of this group in most seasons included *B. edeni*, *G. griseus*, and *G. macrorhynchus*.

The sample units in each group tended to occupy distinct zones. Group 1 occupied the offshore waters along the northern and to some extent southern sectors of the study area, especially in JFM (Fig. 4.4). Group 3 was associated with the periphery of the archipelago in JFM, AMJ, and OND, particularly with its western sector. During JAS, group 3 occupied the shallow central waters. The comparatively few sample units that made up group 2 were concentrated between northern Isabela, Santiago, Marchena, Pinta and Genovesa islands in JFM. During JAS, group 2 occupied the western and southern periphery of the archipelago. No clear pattern was evident in AMJ and OND, as sample units for this group were scattered throughout the study area.

4.4.3 Ordination

The two-dimensional solution obtained with the NMS procedure was rotated by 231° to maximize the loading of RAD onto the main axis of the ordination. The intent was to account for the spatial component in cetacean distributions associated with the presence of the archipelago, while removing the variation associated with this variable in the second axis. After rotation, the first axis captured 86% of the variance in the species data, while the second axis represented 4.2%, for a total of 90.2%. The arrangement of sample units, environmental variables, and average species locations in the ordination space is shown in Figure 4.5. Maps depicting the spatial distribution of sample unit scores

on axis 1 and axis 2 for each season are shown in Figure 4.6 and Figure 4.7, respectively.

The results of the principal component analysis on the environmental variables describing direct effects of physical forcing on the system are given in Table 4.2. The dominant component, PC1, was characterized by a deep (shallow) thermocline (Z20) and pycnocline (ZMBVF), a strong (weak) thermocline (ZTD), a high (low) pycnocline stability (MBVF), a shallow (deep) and thick (thin) OML (ZOML and ZOD, respectively), and warm (cold) SST. These conditions describe the main environmental gradient in the study area, from warm, stratified conditions offshore, to cold, upwelling conditions close to the islands. Since the second and third components had negligible correlations with the ordination axes (see below), they are not described here. The interested reader is referred to Appendix B.

After rotation, the point cloud was primarily aligned with axis 1 (Fig. 4.5). Scatter about axis 2 was greater on the negative side of axis 1, while there was very little scatter on the positive side. Average species scores were located on the negative side of axis 1 for seven species (*S. coeruleoalba*, *P. macrocephalus*, *G. macrorhynchus*, *B. edeni*, *D. delphis*, *G. griseus*, and *T. truncatus*), and on the positive side for two (*S. attenuata* and *S. longirostris*) (Fig. 4.5). On axis 2, the average scores were near zero for all species.

The spatial distribution of the ordination scores on axis 1 (Fig. 4.6) shows that the negative scores were found around the periphery of the archipelago in all seasons, whereas the positive scores were primarily associated with the northern sector of the study area (and also with the southern sector in JFM). Relatively few sample units had intermediate values. Scores were most negative in JAS and most positive in OND. Scores on axis 2 followed a cycle with negative values becoming more negative and positive values becoming more positive as the year progressed
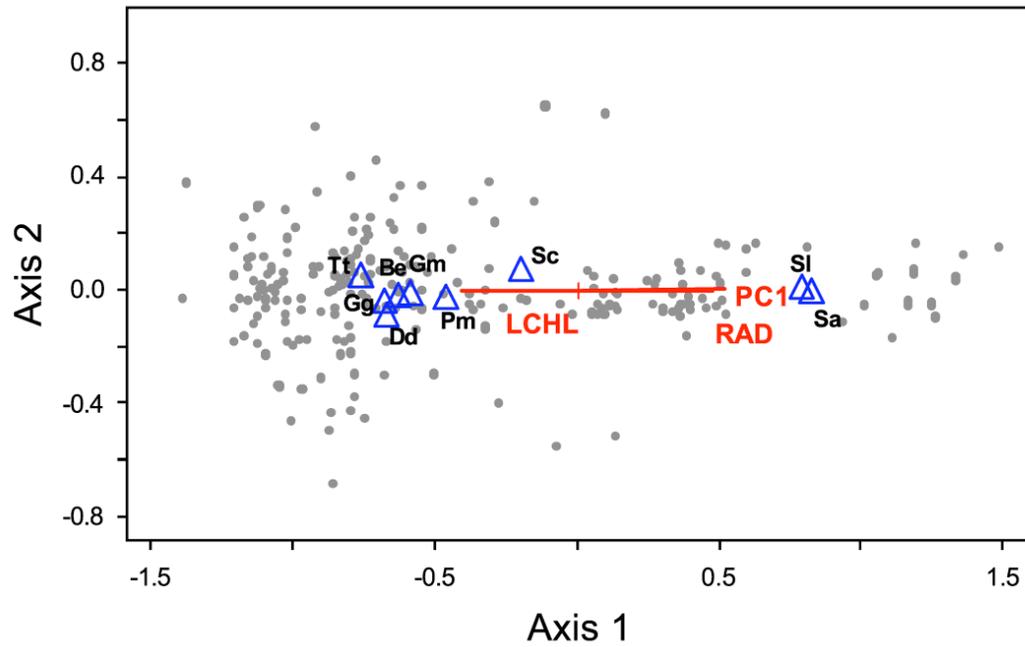
Figure 4.5: Biplot of NMS ordination (after 231° rotation). Gray dots represent sample units and open triangles are the average positions of the nine species of interest, calculated by weighted averaging. Vectors for environmental variables with $r^2 < 0.2$ in respect to both axes are not shown.
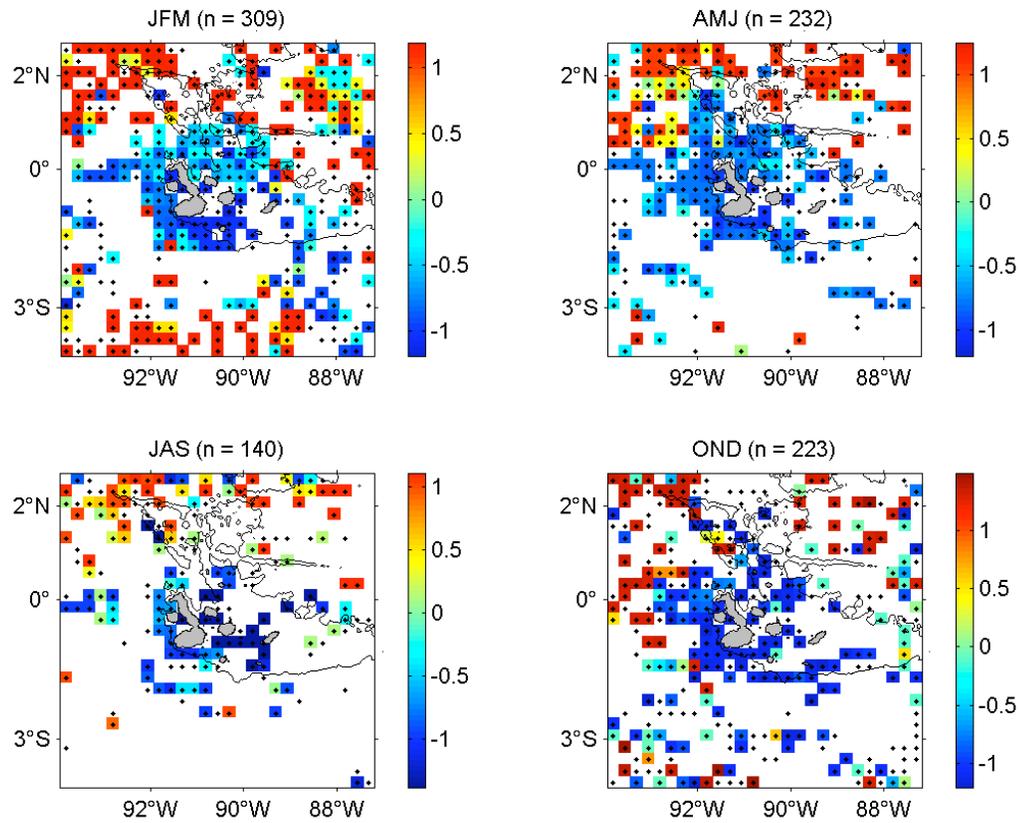
Figure 4.6: Spatial distribution of NMS scores on axis 1 (after 231° rotation) for each season. The 2000-m depth contour is indicated. Black dots represent grid cells with marine mammal sightings (including rare and unidentified species). The total number of sample units (i.e., valid grid cells) is shown in parenthesis.
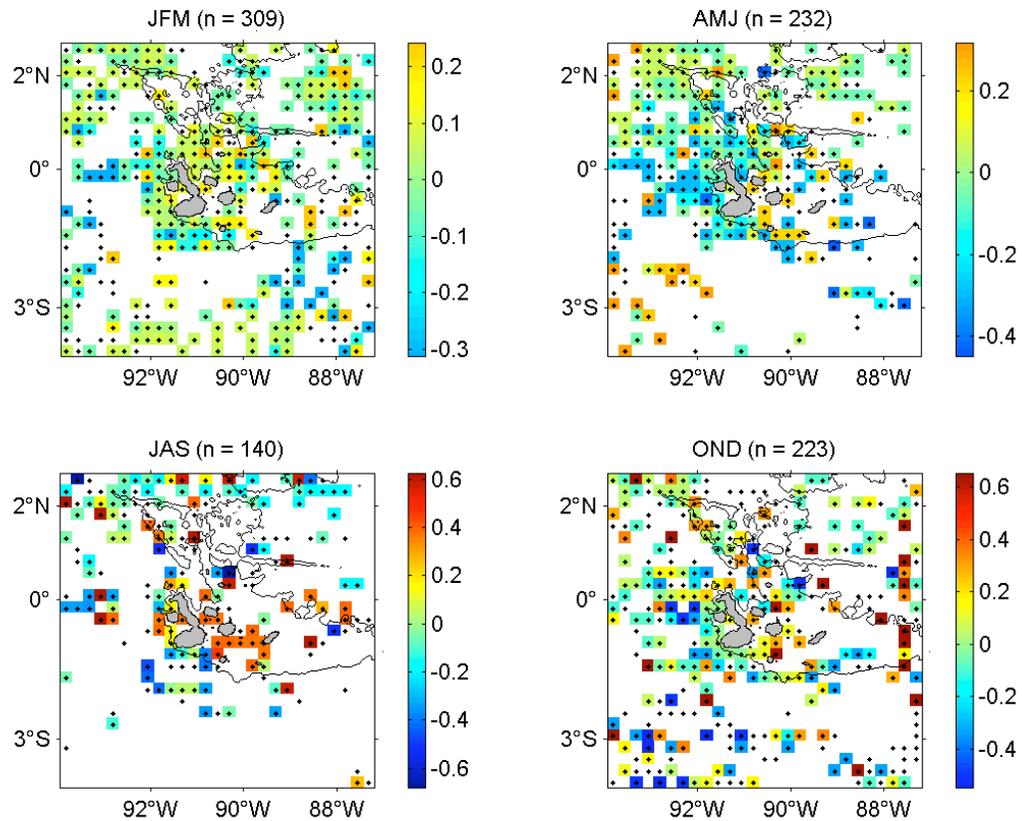
Figure 4.7: Spatial distribution of NMS scores on axis 2 (after 231° rotation) for each season. The 2000-m depth contour is indicated. Black dots represent grid cells with marine mammal sightings (including rare and unidentified species). The total number of sample units (i.e., valid grid cells) is shown in parenthesis.

Table 4.2: Loadings (eigenvectors) for the first three principal components (PC) of the seven variables describing direct effects of physical forcing in the water column and at the surface. Values greater than 0.3 are shown in bold to highlight the variables with the greatest contribution to each PC. The eigenvalues and the fraction of the variance represented by each PC are also indicated.

Variable	PC1	PC2	PC3
Z20	**-0.47**	0.07	**-0.31**
ZTD	**0.30**	**0.52**	0.20
MBVF	**-0.34**	**0.49**	0.15
ZMBVF	**-0.35**	**-0.51**	-0.24
ZOML	0.27	0.08	**-0.81**
ZOD	**-0.45**	-0.07	**0.35**
SST	**-0.42**	**0.45**	0.10
Eigenvalue	3.4	1.4	1.0
Variance fraction (%)	48.4	19.7	14.7

from JFM to JAS, and then returning in OND (Fig. 4.7). In JAS, spatially cohesive positive-negative contrasts were apparent between sample units in the central shallow waters and those to the north, south, and west. Contrasts between sample units were also evident in OND, but they were scattered and did not have a clear pattern.

Correlation coefficients (r) between scores on the ordination axes and synthetic abundances for each species are given in Table 4.3. Most species showed intermediate to high correlations with the first axis ($0.773 \le |r| \le 0.978$), with only two species (*S. coeruleoalba* and *P. macrocephalus*) showing a low degree of linear correlation ($|r| < 0.5$). Correlations with the second axis were moderate for

three species, *D. delphis* ($r = $ -0.4), *S. coeruleoalba* ($r = $ 0.35), and *T. truncatus* ($r = $ 0.2), and they were low or neglible for the other six (Table 4.3).

Table 4.3: Pearson (*r*) and Kendall (tau) correlations of synthetic abundances with ordination axes (after 231° rotation) for the nine species of interest.

Axis	1			2		
	r	r^2	tau	*r*	r^2	tau
Stenella attenuata	0.978	0.957	0.778	-0.009	0.000	-0.011
Stenella longirostris	0.937	0.878	0.777	0.060	0.004	0.154
Stenella coeruleoalba	-0.221	0.049	-0.207	0.349	0.121	0.047
Delphinus delphis	-0.773	0.597	-0.644	-0.401	0.161	-0.206
Tursiops truncatus	-0.743	0.551	-0.686	0.210	0.044	0.070
Grampus griseus	-0.614	0.377	-0.570	-0.137	0.019	-0.036
Globicephala macrorhynchus	-0.536	0.287	-0.647	-0.028	0.001	-0.075
Physeter macrocephalus	-0.483	0.233	-0.452	-0.083	0.007	-0.052
Balaenoptera edeni	-0.588	0.346	-0.649	-0.041	0.002	-0.060

The synthetic abundances corresponding to each sample unit for each species are shown in the ordination space in Figure 4.8 as dots of different sizes. A few sample units with *scores* higher (lower) than ± 0.5 on axis 2 (which are beyond ± 2 standard deviations and are probably outliers to the ordination) stand out as having large abundances for only two species: *S. coeruleoalba* and *P. macrocephalus* (Fig. 4.8). The scatterplots on the sides of the main ordination space show the abundance along axis 1 and axis 2 separately. The fitted curves highlight the species responses to the compositional gradients (and, for most species, demonstrate the limitations of using the correlation coefficient for this purpose). The responses on axis 1 were linear with maximum abundance at the negative end of the gradient for *T. truncatus* and *G. griseus*. For *S. attenuata* and *S. longirostris* the response had a linear trend with abundance increasing toward the positive end, but with distinct humps along the gradient. *Globicephala macrorhynchus* and *B. edeni* showed a similar response, but with abundance increasing toward the negative side. Species that showed unimodal or more complex responses with maxima at intermediate locations along the gradient were *S. coeruleoalba*, *D. delphis*, and *P. macrocephalus*. On axis 2, both *S. attenuata* and *S. longirostris* had a unimodal response with maximum abundance at the middle of the gradient. *Delphinus delphis* and *T. truncatus* also showed distinct unimodal responses, but their maxima were on opposite sides of the axis. The response curve of *G. griseus* was rather flat and broad, while *G. macrorhynchus* and *B. edeni* had bimodal responses with minima near the middle of the gradient. Finally, the response curves for *S. coeruleoalba* and *P. macrocephalus* appeared to be driven by the outliers (to the ordination) at both ends of the gradient, and otherwise would have been unimodal with peaks near the middle (Fig. 4.8).
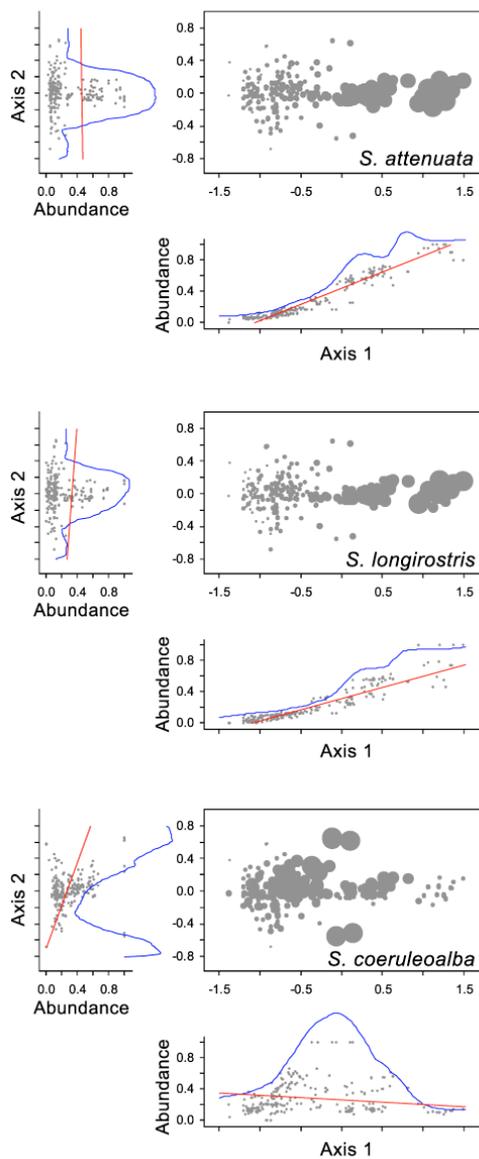
Figure 4.8: Synthetic abundance for *S.attenuata*, *S. longirostris*, and *S. coeruleoalba* overlaid on ordination. Size of dots is proportional to the abundance of the species. Side scatterplots show abundance *vs*. scores for axis 1 (below) and axis 2 (left). Blue curve is an envelope that includes points falling within two standard deviations of a running mean along the axis. Red line is the least-squares fit.
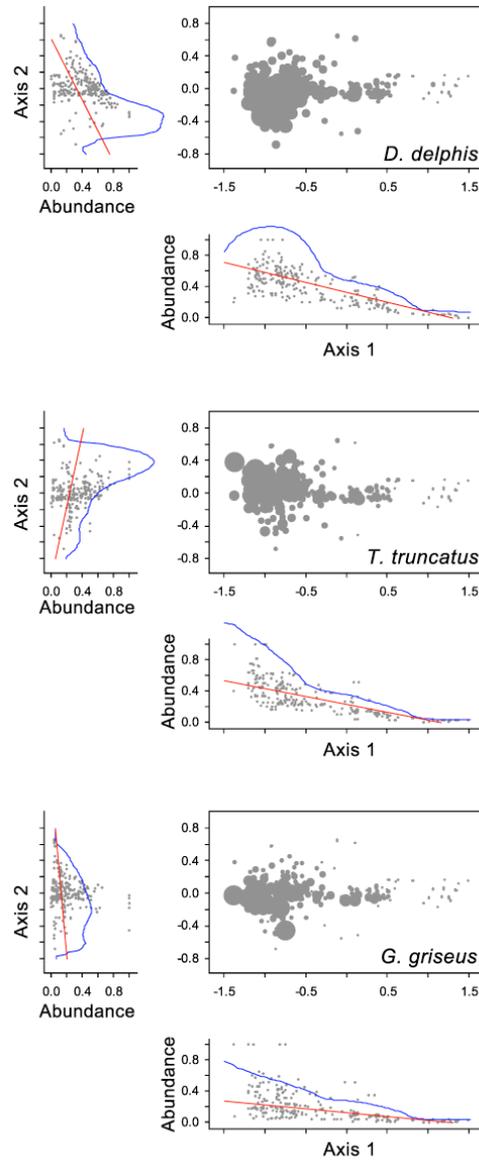
Figure 4.8: Continued. Synthetic abundance for *D. delphis*, *T. truncatus*, and *G. griseus* overlaid on ordination. Size of dots is proportional to the abundance of the species. Side scatterplots show abundance *vs*. scores for axis 1 (below) and axis 2 (left). Blue curve is an envelope that includes points falling within two standard deviations of a running mean along the axis. Red line is the least-squares fit.
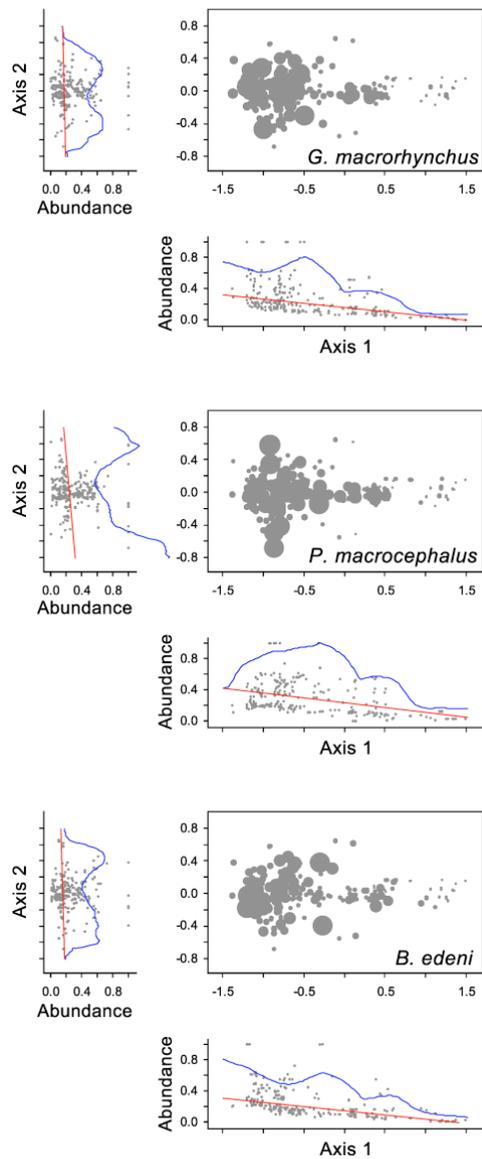
Figure 4.8: Continued. Synthetic abundance for *G. macrorhynchus*, *P. macrocephalus*, and *B. edeni* overlaid on ordination. Size of dots is proportional to the abundance of the species. Side scatterplots show abundance *vs*. scores for axis 1 (below) and axis 2 (left). Blue curve is an envelope that includes points falling within two standard deviations of a running mean along the axis. Red line is the least-squares fit.

Correlations among environmental variables and with each axis are listed in Table 4.4. Three of the five variables, LCHL, RAD, and PC1, had intermediate correlations with the scores on axis 1 (r = -0.52, 0.56, and 0.59, respectively). The percentage of the variance in axis 1 explained by these variables (i.e., the square of the correlation coefficient) ranged between 27.4 and 34.2%. PC2 and PC3 had negligible correlations with this axis 1, and all five variables had negligible correlations with axis 2. These correlations are evident in the biplot in Figure 4.5, which shows that the three environmental vectors (not just RAD) were almost completely aligned with axis 1 after the rotation. A fairly high degree of collinearity was evident among the dominant environmental variables (r = -0.78 for LCHL vs. PC1; r = -0.69 for LCHL vs. RAD; and r = 0.73 for PC1 vs. RAD) (Table 4.4).

Table 4.4: Pearson correlations among environmental variables and ordination axes (after 231° rotation).

	PC1	PC2	PC3	LCHL	RAD	Axis 1	Axis 2
PC1	1.00						
PC2	0.00	1.00					
PC3	0.00	0.00	1.00				
LCHL	-0.78	0.11	0.01	1.00			
RAD	0.73	-0.09	0.23	-0.69	1.00		
Axis 1	0.59	0.04	0.08	-0.52	0.56	1.00	
Axis 2	0.06	0.01	0.07	-0.03	-0.02	0.04	1.00

4.5 DISCUSSION

4.5.1 Sample unit groups and species assembalges as indicators of community
        types and habitat preferences

Although the groups extracted with cluster analysis had a number of
similarities across seasons, direct comparisons are limited because the sample units
that entered the analysis were different for each season (only 54 sample units were
common to all four seasons). In particular, it is not possible to determine whether
the observed seasonal differences in group size or in species composition are
related to shifts in habitat use or community structure, or if they are due to
differences in sampling effort. Nevertheless, it is possible to draw several
generalizations about these groups and the species assemblages that were
associated with them.

Groups 1 and 3 were fairly persistent in terms of size, distribution, and
species composition. Group 1 occupied the warm, stratified habitat found north of
the EF and was characterized by *S. attenutata* and *S. longirostris* (this group also
occupied the seasonally warm waters along the southern sector of the study area in
JFM). Group 3 occupied the periphery of the archipelago, particularly the western
sector where the EUC upwells. The species assemblage associated with this group
was characterized by *D. delphis*, which typifies upwelling-modified habitats (see
Introduction), but it also included species that associate with nearshore habitats (*T.
truncatus*, *B. edeni*, *G. griseus*, and *G. macrorhynchus*).

The comparatively fewer sample units that made up group 2 make it
difficult draw ecological interpretations. Sample units were scattered throughout
the study area in all seasons except JFM, when a discrete cluster occupied an area
between northern Isabela, Santiago, Marchena, Pinta and Genovesa islands. This
group was consistently characterized by *S. coeruleoalba* and/or *P. macrocephalus*.
Even though the group did not occur in a habitat of known characteristics, the
persistence of the indicator species suggests that the sample units meet specific

requirements or that the species composition is the result of interactions with the species in the other groups.

Other studies in the eastern tropical Pacific have remarked on the apparent lack of a preference for particular oceanographic conditions by *S. coeruleoalba*. The species tends to occur wherever *S. attenuata*, *S. longirostris*, and *D. delphis* are least abundant (Au and Perryman, 1985; Reilly, 1990; Reilly and Fiedler, 1994), implying some sort of segregation. There is further evidence that niche partitioning takes place between *S. coeruleoalba* and *D. delphis* in the Mediterranean and the northeast Atlantic, where *S. coeruleoalba* is a highly opportunistic feeder, taking cephalopods, crustaceans, and mesopelagic fishes, whereas *D. delphis* appears to be somewhat more piscivorous (Hassani et al., 1997; Sagarminaga and Cañadas, 1998; Das et al., 2000). It is also interesting to observe that *P. macrocephalus* tended to occur with *S. coeruleoalba* (or in its own group in AMJ). The scattered distribution of *S. coeruleoalba* and *P. macrocephalus* appears to occur throughout the eastern tropical Pacific (Polacheck, 1987), but has not been adequately explained because of the lack of consistent association with other species or with particular environmental conditions.

4.5.2 Community gradients in relation to environmental conditions

The maps of the ordination scores on axis 1 contrasted sample units clustered around the periphery of the archipelago with those found offshore, with little or no transition in between them. This suggests strong ecological differences among the two areas. Species abundances along axis 1 showed a clear compositional gradient, with *S. attenuata* and *S. longirostris* reaching their maximum abundance at the positive end; *S. coeruleoalba*, *P. macrocephalus* and *D. delphis* at intermediate locations; and *G. macrorhynchus*, *G. griseus*, and *B. edeni* at the negative end of the gradient (Fig. 4.8). This pattern represented 86% of the variance in the species data.

Rotation of the axes maximized the correlation of axis 1 with all three of the environmental variables which had any relationship with the ordination (PC1, LCHL, and RAD). These variables, which together describe a gradient from warm/ stratified/phytoplankton-poor conditions offshore to cold/upwelling/phytoplankton-rich conditions close to the islands, explained 27–35% of the variance contained in the compositional gradient on axis 1. Thus, the variety of environmental conditions found inside the study area appear to be responsible for the presence of communities of stratified, upwelling, and coastal habitats in close proximity to each other. In fact, the patterns of species abundance around the Galápagos mirror the response of eastern tropical Pacific cetaceans to large-scale thermocline topography and distance from land (e.g., Polacheck, 1987; Reilly, 1990; Fiedler and Reilly, 1994).

Although direct comparisons across seasons are limited because the sample units were not necessarily in the same locations, seasonal information was taken into account in the calculation of the ordination scores, as all 904 sample units were ranked and arranged together by the NMS procedure. The main observation is the shift toward more negative scores during JAS on axis 1 (Fig. 4.6), which implies that sample units become more favorable for those species whose abundance peaks in the negative region of the gradient (see Fig. 4.8). Thus, the shift is consistent with a community response to the expansion of the upwelling-modified habitat resulting from the intensification of wind-induced equatorial upwelling at this time of the year (see Chapter 3 and Appendix B).

Variability on axis 2 was most pronounced during JAS (Fig. 4.7). Comparison with the map showing the distribution of groups from cluster analysis for the same period (Fig. 4.4) indicates that most of the sample units with positive scores in the central shallow waters correspond with those in group 3, while several sample units with negative scores to the south, north, and west appear to correspond with those in group 2. These two groups were characterized by species

assemblages of nearshore and upwelling environments, respectively (see section 4.4.2). The response curves along axis 2 for the species with highest indicator value in these groups, *D. delphis* and *T. truncatus*, respectively (Fig. 4.8), show that their abundances peak at opposite sides of the gradient. Thus, axis 2 may suggest a separation between nearshore and upwelling-associated species, at least during JAS. Variability was also pronounced during OND, but the sample units were not organized in a recognizable pattern (Fig. 4.7). It should be stressed, however, that any interpretation of this axis is speculative, as it only described 4.2% of the variance in the species data (any pattern may have been weakened by the Beals transformation). Axis 2 was unrelated to environmental variability.

Because the compositional gradient along axis 1 appeared to be primarily driven by environmental conditions, it is possible to speculate on what would be the community response to strong El Niño-Southern Oscillation (ENSO) conditions. During El Niño events, conditions would be most similar (but more extreme) to those taking place at the peak of the warm season (March), when upwelling conditions are spatially restricted to the core of the topographic upwelling of the EUC, while stratified conditions are widespread. Thus, the environmental gradient would contract on the negative side and expand on the positive side. With the shrinking of favorable conditions for upwelling-adapted species, competition for space (i.e., food resources) in the vicinity of the islands would increase. Conversely, during La Niña, upwelling conditions are widespread while the stratified habitat shrinks. As discussed above for the changes observed during JAS, the upwelling-adapted species would expand their range with the expansion of the upwelling environment, while *S. attenuata* and *S. longirostris* would probably retreat to the north with the receding stratified waters. This picture is consistent with the regional responses described by Fiedler and Reilly (1994) to observed El Niño and La Niña events.

4.5.3 Implications for feeding ecology

Cluster and indicator species analysis demonstrated that most of the species in the study occupy distinct habitats that are persistent year-round (albeit with some degree of seasonal adjustment). Ordination further suggested strong ecological differences between waters around the periphery of the archipelago and those offshore. What is the basis for these differences? Addressing this question involves considering the way in which the species of interest use their habitats, particularly in regard to foraging strategies. Although the food and feeding habits of Galápagos cetaceans are largely unknown (with the exception of the sperm whale), insight can be gained from information available at the regional and global scale.

Stenella attenuata and *S. longirostris*, the two species that characterized the stratified environment, are known to feed mainly on mesopelagic organisms of the deep scattering layer at dawn and dusk, when they concentrate closer to the surface during their diel vertical migration (Perrin and Gilpatrick, 1994; Robertson and Chivers, 1997). The diet of *S. attenuata* is mainly composed of lanternfishes (family Myctophidae), enope squid (family Enoploteuthidae), and flying squid (family Ommastrephidae) (Roberston and Chivers, 1997). *Stenella longirostris* has a similar diet, but the size of the prey items and their depth distribution may be different (Perrin and Gilpatrick, 1994). These two dolphins are regularly found in polyspecific assemblages that include yellowfin tuna (*Thunnus albacares*), seabirds, and sharks (Au and Perryman, 1985; Au, 1991). As mentioned earlier, *S. coeruleoalba* is a highly opportunistic feeder, taking cephalopods (families Ommastrephidae and Histioteuthidae), crustaceans, and myctophids. It has been suggested that striped dolphins feed at great depths (200–700 m), on the basis of the luminescent organs often found on their prey (Perrin et al., 1994). The diet of *D. delphis*, the characteristic species of the upwelling environment, is primarily composed of epipelagic shoaling fishes (families Clupeidae and Engraulidae),

although it may also take cephalopods, myctophids, and bathylagids of the deep scattering layer (Evans, 1994; Young and Cockroft, 1994).

Grampus griseus, *G. macrorhynchus*, and *P. macrocephalus* feed primarily on cephalopods. However, *G. macrorhynchus* is also known to take fish (Bernard and Reilly, 1999), while *G. griseus* occasionally feeds on crustaceans (Kruse, 1999). Both species are presumed to be nocturnal feeders, and in the Galápagos they are regularly found in areas of steep slopes (although *G. macrorhynchus* appears to prefer deeper water). The diet of *P. macrocephalus* in Galápagos waters is primarily composed of histioteuthid squid (Smith and Whitehead, 2000). Animals typically forage at depths of 320–420 m (Papastavrou et al., 1989), both during daytime and nighttime (Smith and Whitehead, 1993). *Balaenoptera edeni* feeds on shoaling prey such as clupeids, engraulids, and euphausiids (Cummings, 1985), while *T. truncatus*, the most coastal species in this study, feeds on a wide variety of fishes and invertebrates, including demersal forms (Wells and Scott, 1999).

This information, together with knowledge of the local environmental conditions and other biological observations, can be of use in forming a general picture of trophic ecology in the different habitats indentified in this study. The warm, stratified habitat found along the northern sector of the study area (and seasonally along the south sector) overlays a thick and shallow OML. A distinct euphausiid assemblage (*Euphausia distinguenda*, *E. diomedeae*, *E. lamelligera*, *E. tenera*, and *Nematoscelis gracilis*) adapted to the oxygen-deficient conditions thrives in this habitat (Brinton, 1979). This assemblage is the dominant crustacean component of the deep scattering layer, while mesopelagic fishes (primarily myctophids) and cephalopods are the dominant nekton (e.g., Blackburn, 1968; Blackburn et al., 1970). Through trophic links among these groups, the deep scattering layer is believed to support the large populations of top predators like

yellowfin tuna (McGowan, 1971) and dolphins (Au and Perryman, 1985; Fiedler et al., 1998) found in this environment.

The upwelling habitat on the western side of the archipelago is created by the surfacing of the EUC. The waters of the EUC are well oxygenated (Anderson, 1977; Lukas, 1986), and are characterized by a different euphausiid assemblage (*E. eximia*, *E. paragibba*, and *Nyctiphanes simplex*) (Cornejo de González, 1977; Brinton, 1979). Observations of potential prey for cetaceans in this area include myctophids (*Myctophum nitidulum*), nail squid (*Onychoteuthis banksii*) (Palacios, 1999b), and Panamá lightfish (*Vinciguerria lucetia*) (García et al., 1993) among the mesopelagic organisms, and South American pilchard (*Sardinops sagax*), Pacific anchoveta (*Cetengraulis mysticetus*), and round herring (*Etrumeus teres*) (García et al., 1993; Grove and Lavenberg, 1997), among the epipelagic schooling fishes. The stomach contents of a Cuvier's beaked whale (*Ziphius cavirostris*), a deep-diving species collected in the upwelling habitat, contained beaks of several mesopelagic squid species (*Mastigoteuthys dentata*, *Histioteuthis heteropsis*, *Megalocranchia* sp., *Cranchia scabra*, *Ommastrephes bartrami*, *Liocranchia reinhardti*, and *Philidoteuthis* sp.), and the mesopelagic crustaceans *Gnathophausia ingens* and *Acanthephyra* sp. (Palacios, 1999b). Whitehead et al. (1989) have suggested that the strong flow of the EUC may transport and concentrate the slow-swimming histioteuthid squid that are the main prey of sperm whales in this area. The large ommastrephid *Dosidicus gigas* has also been collected in these waters (Palacios, 2000). Thus, its possible that other teuthivorous cetaceans like *G. macrorhynchus* and *G. griseus* also feed on several of the species just mentioned. Another marine mammal that feeds in the upwelling environment is the Galápagos fur seal (*Arctocephalus galapagoensis*). Its diet is composed of vertically migrating myctophids and bathylagids among the fishes (Dellinger and Trillmich, 1999), and *O. banksii* and ommastrephids among the squids (Clarke and Trillmich, 1980). *Delphinus delphis* is occasionally seen in daytime foraging aggregations with

Nazca boobies (*Sula granti*) and hammerhead sharks (*Sphyrna* sp.) (D.M. Palacios, personal observations), and given its food habits elsewhere, it probably preys upon *S. sagax* and the other shoaling fishes mentioned above. Au and Perryman (1985) have suggested that a shorter food chain in upwelling environments may be the basis for cetacean community differences with respect to stratified environments.

The EUC also plays a role in the productivity of the nearshore environment through branching and recirculation in the central part of the archipelago (Houvenaghel, 1978; also see Chapter 1). Two of the species in this study, *T. truncatus* and *B. edeni*, as well as the Galápagos sea lion (*Zalophus wollebaeki*) commonly occur there. Feeding frenzies involving some or all of these species, coastal seabirds (*Sula nebouxii*, *Pelecanus occidentalis*), and sharks are a common sight in these waters (D.M. Palacios, personal observations). Given that *S. sagax* is known to be the primary prey of *Z. wollebaeki* (Dellinger and Trillmich, 1999) and of the blue-footed booby (*S. nebouxii*) (Anderson, 1989), it is possible that the predators are converging on dense schools of this fish. Other schooling fishes that occur in high abundance in coastal waters are the black-striped and the white salema (*Xenocis jessiae* and *Xenichthys agassizi*, respectively; family Haemulidae), and the yellow-tailed and the Galápagos mullet (*Mugil rammelsbergii* and *M. galapagensis*, respectively) (Grove and Lavenberg, 1997). Large surface swarms of the euphausiid *N. simplex* have also been observed at a variety of nearshore locations, where they could be prey for *B. edeni* and other baleen whales (cf. Palacios, 1999a).

4.6 CAVEATS

Each of the different sources of sightings used in this study (see Appendix A) has its own set of biases due to the different protocols and platforms used to collect them. Combining these disparate data sets has the potential of compounding

the biases in an unknown way. However, this was necessary in order to obtain adequate coverage of the different environments occurring around the Galápagos (see the maps of distribution of sightings by sources in Fig. A4.1). The combined data set provided an opportunity to look at general patterns of species-species and species-environment relationships at a resolution rarely achieved in studies of cetacean ecology.

Although this study focused on the seasonal timescale, it is necessary to mention the possible effects of interannual (i.e., ENSO) variability in the sighting data, considering that, in the study area, seasonal and interannual variability are of the same order of magnitude (Fiedler, 1992; Delcroix, 1993). A time series of quarterly-averaged SST anomaly (SSTA) is shown for the same period of the marine mammal compilation in Figure 4.1. [SSTAs were computed from a monthly SST record collected by the Charles Darwin Research Station (CDRS) in Galápagos for the period 1965–2001. Monthly SSTAs were normalized by the standard deviation of SST, and a 5-month running mean was applied, from which the quarterly average was derived.] The dashed lines in the plot indicate the $\pm$ 0.4°C threshold that has been used to define El Niño and La Niña events in the study area (Trenberth, 1997). Trenberth (1997) found that under this definition, ENSO events occur about 55% of the time, while average conditions are less common. The continuous recurrence of warm and cold events suggests that long-lived animals like cetaceans should be adapted to them. With regard to unusually strong events, two El Niños (1982–1983 and 1997–1998) and one La Niña (1988–1989) took place during the period under consideration. However, only the 1982–1983 El Niño and the 1988–1989 La Niña are present in the sighting data set, because no survey effort took place between the third quarter of 1996 and the last quarter of 1998 (Fig. 4.1). Therefore, the effect of strong events on the data set are probably small.

Another important caveat is that the community analyses assume the contemporaneous presence of the different species in a sample unit (the Sørensen distance and the Beals smoothing computations are based on the patterns of co-occurrence). However, because the seasonal species matrices were constructed using cummulative sightings over a 28-yr period, species could have occurred in a sample unit at different times without ever being present together. For this reason, interpretation of the results is limited to the dominant patterns.

It should also be emphasized that the results presented here are primarily intended to give the broad outlines of community structure and its relationship to environmental variability. The relatively low percentage (27–35%) of the variance in community structure on axis 1 explained by the environmental variables may be due in part to the use of the coarse climatological data.

Finally, one particular set of variables not considered in this study which are known to influence cetacean distribution are those describing the physiography of the sea floor (i.e., depth and slope) (e.g., Hui, 1979; 1985; Baumgartner, 1997; Waring et al., 2001; Cañadas et al., 2002). These variables were not included in this study because it was felt that the spatial resolution imposed by the gridding scheme (~ 28 km) would smooth out the rapid changes in depth and other fine details of the steep topography around the archipelago. However, a preliminary examination of the distribution of the nine species with respect to these variables using a 3.7 km-resolution bathymetry data set indicated that *G. griseus* was strongly associated with the steepest underwater slopes around the volcanoes. This species is also known to have a close association with the steepest slopes of the northern Gulf of Mexico (Baumgartner, 1997).

4.7 CONCLUSION

Despite the caveats associated with the data sets, the community analyses provided a systematic characterization of the distribution patterns and

environmental associations of the nine cetaceans that commonly occur around the Galápagos (these were informally described in section 4.4.1 and Fig. 4.2). Seasonal change in community structure was only modest, in spite of the strong environmental variability in the region. This was attributed to the persistence of the upwelling of the EUC on the western side of the archipelago, which sustains a productive environment year-round.

Finally, available information on feeding habits and prey occurrence suggested that stratified, upwelling, and coastal environments are characterized by different types of trophic interactions which, in turn, are probably responsible for the type of cetacean assemblages found in them. Given the diversity of species in the upwelling habitat, further studies of cetacean distribution and abundance at finer scales have the potential of yielding useful information on interspecific interactions, niche specialization, and habitat partitioning in this complex environment.

4.9 REFERENCES

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4.10 APPENDICES

4.10.1 Appendix A: Compilation of the marine mammal database

Sighting records of marine mammals for the area defined in the Methods (section 4.3.1) were compiled from four principal sources. These were: (1) a historical database of cetacean sightings collected by scientific observers aboard

US tuna vessels during fishing trips to the eastern tropical Pacific for the period 1973–1990, available from the Southwest Fisheries Science Center (SWFSC) of the National Marine Fisheries Service (NMFS) (La Jolla, CA, USA); (2) a historical database of sightings collected during regional marine mammal surveys by the SWFSC throughout the eastern tropical Pacific between 1974 and 2000 (Lee, 1993; 1994; Wade and Gerrodette, 1993; Kinzey et al., 2001); (3) cetacean sightings collected opportunistically by scientists from Dalhousie University (Dalhousie, NS, Canada), during sperm whale research trips in Galápagos waters in 1985, 1987, 1989, 1991, 1992 and 1995 (Smith and Whitehead, 1999); and (4) sightings collected during three marine mammal studies in the Galápagos by the Ocean Alliance (OA) (Lincoln, MA, USA) in 1988–1989, 1993–1994 and 2000 (Lyrholm et al., 1992; Palacios, 1999b; 2000). The author participated in the 1993–1994 and 2000 studies, as part of a collaboration between OA and the Marine Mammal Program at Oregon State University (OSU) (Newport, OR, USA).

The number of records in the study area available from each source was as follows: tuna vessel trips, 1323; SWFSC research vessel surveys, 610; SWFSC aerial surveys, 36; Dalhousie University trips, 479; and OA/OSU studies, 1969. The total of number of sighting records was 4417, belonging to 23 identified marine mammal species (21 cetaceans and two otariid pinnipeds endemic to the Galápagos) (Table A4.1) and to eight unidentified categories (i.e., sightings that could only be identified to the family level or higher) (Table A4.2). The compiled database spanned the 28-yr period 1973–2000, although no sightings were available for the years 1996 and 1997. Each record in the database contained fields for source, date, time, latitude, longitude, species identification (or unidentified sighting category), and group size.

The final numbers for certain species in Table A4.1 are the result of combining taxonomically related sighting categories. This pooling was based on regional knowledge of the distribution of the species involved, following the

practice in Wade and Gerrodette (1993). For example, sightings of short-beaked common dolphins represent sightings positively identified as such plus sightings of *Delphinus* sp. (unidentified common dolphin species). The only other species of common dolphin in the eastern Pacific, the long-beaked common dolphin (*D. capensis*), is associated with neritic habitats in the California and Perú Currents, and thus could not be reasonably expected to occur in the study area. Similarly, sightings of short-finned pilot whales (*Globicephala macrorhynchus*) were grouped together with sightings of *Globicephala* sp.; sightings of dwarf sperm whales (*Kogia sima*) were grouped with sightings of *Kogia* sp.; and sightings of Bryde's whales were combined with sightings only identified as "Bryde's or sei whale". Sei whales (*Balaenoptera borealis*) are very similar in appearance to Bryde's whales, but they have a more subtropical distribution and therefore it is unlikely that they occur in the study area.

Although the number of records in the database was 4417, mixed schools of two or more species occurred in 400 of these sightings. Because this study uses the sighting location of each species whether seen in monospecific or mixed-species schools, the numbers listed in Tables A4.1 and A4.2 add up to 4817 sightings.

In terms of temporal and geographic coverage of each source, the two SWFSC databases provided long-term coverage, but because of the regional scale of their operations, only a few days were spent inside the study area in a typical year. Also, these operations covered mostly the offshore waters of the study area. The local studies, on the other hand, consisted of multiple trips around the archipelago, providing coverage for a few months in the case of the Dalhousie data and up to one continuous year for the OA/OSU 1993–1994 data. These trips were typically closer to the islands than the tuna and SWFSC research vessel operations. Sighting locations by source are presented in Figure A4.1.

The protocols under which the sightings were collected differed in other fundamental ways. Some were collected under methods specifically designed to

survey marine mammal populations (Lee, 1993; 1994; Wade and Gerrodette, 1993; Palacios, 2000; Kinzey et al., 2001), while others were collected incidentally to fishing (tuna vessel trips) or other research operations (Lyrholm et al., 1992; Palacios, 1999b; Smith and Whitehead, 1999). The platforms from which the sightings were made also differed widely, ranging from large research and tuna vessels to sailing vessels to survey aircraft. For these reasons, it is not possible to provide a unified measure of search effort, which could be used to compute an index of marine mammal abundance. However, this study is not concerned with determining population size or population changes through time. Rather, its primary objectives are to investigate community structure and environmental associations, provided that coverage of the study area by the operations described above was adequate. Therefore, and given that under fair sighting conditions at least some marine mammals will normally be seen on any given day at sea, one can use the cumulative locations for all sightings (including the ones that went unidentified) as a general indication of coverage. Weather and other visibility-related conditions in the Galápagos region are excellent during the first part of the year (sea states 0–3 in the Beaufort scale) and fair during the second part, when SE trade winds tend to create whitecaps (Beaufort 2–4). The cumulative locations for all sightings by season are shown in Figure A4.2.

Table A4.1: Marine mammal species identified in the study area from sightings collected during 1973–2000. Mixed-species sightings are counted once for each species involved.

Scientific name	Common name	No. sightings
Stenella attenuata	Pantropical spotted dolphin	519
Stenella longirostris	Spinner dolphin	303
Stenella coeruleoalba	Striped dolphin	247
Steno bredanensis	Rough-toothed dolphin	5
Delphinus delphis	Short-beaked common dolphin	456
Tursiops truncatus	Bottlenose dolphin	366
Grampus griseus	Risso's dolphin	117
Lagenodelphis hosei	Fraser's dolphin	10
Peponocephala electra	Melon-headed whale	4
Feresa attenuata	Pygmy killer whale	2
Pseudorca crassidens	False killer whale	12
Globicephala macrorhynchus	Short-finned pilot whale	131
Orcinus orca	Killer whale	38
Physeter macrocephalus	Sperm whale	284
Kogia sima	Dwarf sperm whale	10
Mesoplodon spp.	*Mesoplodon* species	11
Ziphius cavirostris	Cuvier's beaked whale	22
Balaenoptera acutorostrata	Minke whale	4
Balaenoptera edeni	Bryde's whale	316
Balaenoptera musculus	Blue whale	18
Megaptera novaeangliae	Humpback whale	4
Arctocephalus galapagoensis	Galápagos fur seal	104
Zalophus wollebaeki	Galápagos sea lion	61

Table A4.2: Unidentified sighting categories (family level or higher).

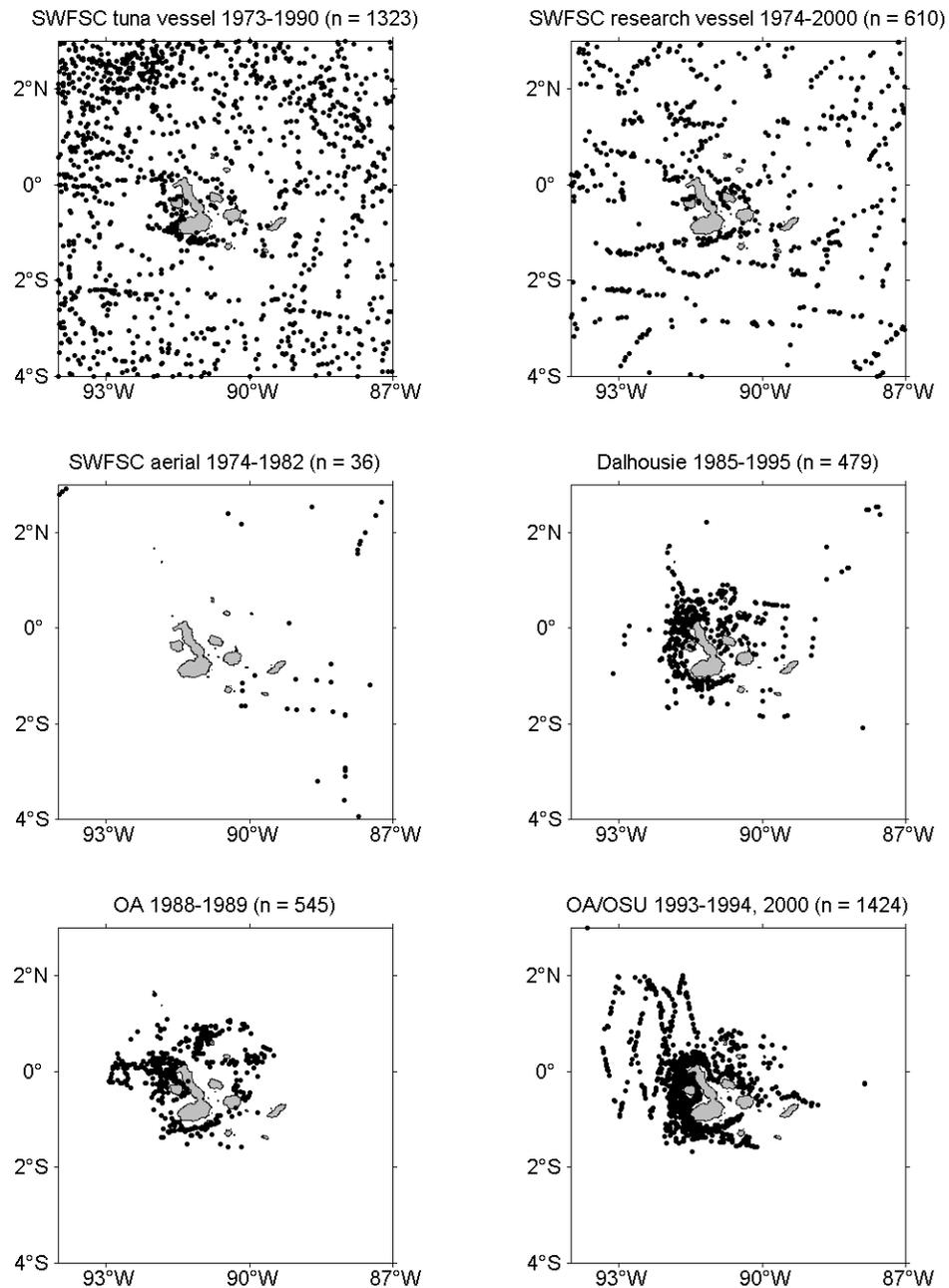| Category	No. sightings
Ziphiid whale	40
Unidentified rorqual	199
Unidentified dolphin	1148
Unidentified small whale	75
Unidentified large whale	101
Unidentified whale	144
Unidentified cetacean	33
Unidentified otariid	33

Figure A4.1: Marine mammal sighting locations (identified and unidentified) in the study area, by source, for the period 1973–2000.
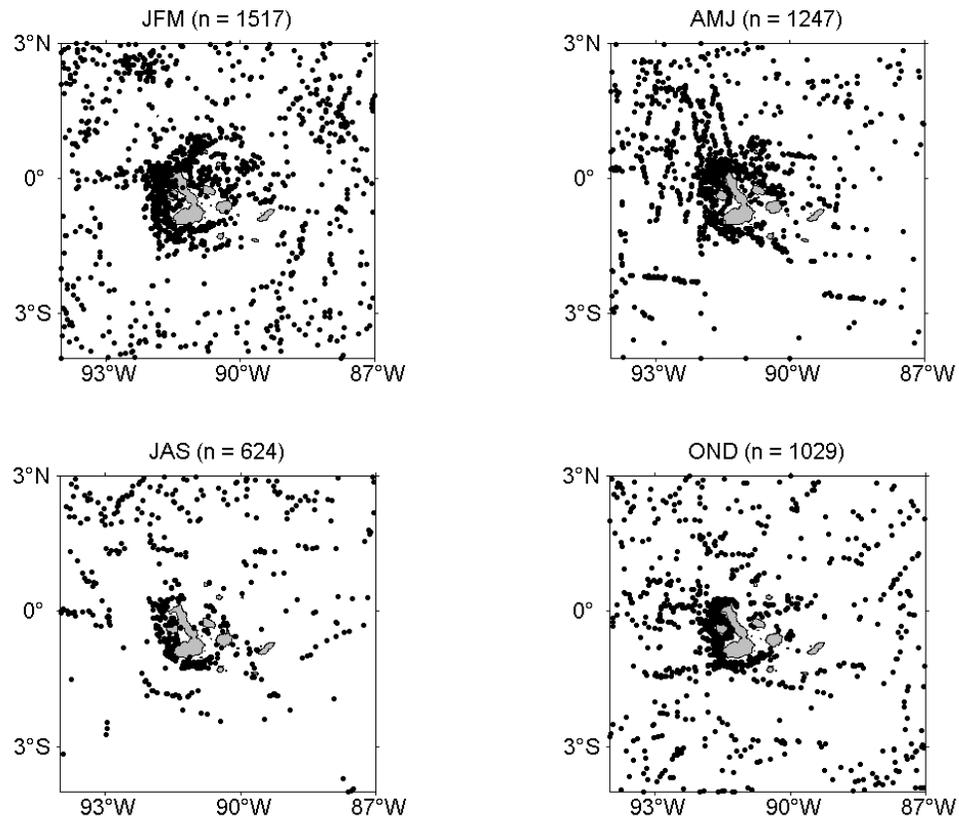
Figure A4.2: Cumulative locations of all marine mammal sightings (identified and unidentified) in the study area, by season, for the period 1973–2000.

4.10.2 Appendix B: Description of the seasonal climatologies

4.10.2.1 Data products and variable extraction

Global, gridded data sets were obtained, subset to the study area, and, where necessary, processed to derive the eight environmental variables of interest at seasonal timescales. Climatological monthly fields of satellite-derived SST were extracted from the "Pathfinder + Erosion" product, which was computed from the 13-yr base period 1985–1997 of Advanced Very High Radiometer (AVHRR) measurements (Casey and Cornillon 1999). Similarly, monthly climatologies of near-surface chl were obtained from satellite-derived ocean color measurements for the 5-yr base period 1996–2001 of combined data from the Ocean Color and Temperature Scanner (OCTS) and the Sea-viewing Wide-Field-of-view Sensor (SeaWiFS), as described in Chapter 3. Seasonal fields were produced from the monthly climatologies. Chl was log-transformed (LCHL) to account for the log-normal distribution of this variable. The original resolution of the SST and LCHL data sets was 9.28 km.

Seasonal climatologies of 1-degree resolution water-column properties were obtained from the World Ocean Atlas 1998 (WOA98) (Conkright et al., 1998). At each grid cell, 1-m vertical resolution profiles of temperature, salinity, and dissolved oxygen were extracted from the standard depth levels by cubic-spline interpolation. The following six variables were derived from these data: (1) depth of the thermocline (i.e., the depth of the 20°C isotherm, or Z20); (2) thermocline strength (i.e., the vertical distance between the 20°C and 15°C isotherms, or ZTD); (3) maximum Brunt-Väisälä frequency (i.e., the maximum resistance to turbulent mixing in the pycnocline, in cycles h^{-1}, or MBVF, also known as the maximum buoyancy frequency); (4) depth of the MBVF (or ZMBVF, also called the depth of the pycnocline); (5) depth of the OML (i.e., the depth at which dissolved oxygen concentrations were < 1 ml l^{-1}, or ZOML); and (6) thickness of the OML (i.e., the vertical distance between the upper and lower boundaries of the OML, or ZOD).

The eight variables were re-gridded from their original resolution to a common resolution of 0.25 degrees for compatibility with the sighting grid. For variables with a coarser resolution than the sighting grid, the value of a coarse cell was assigned to all of the 0.25-degree cells whose center fell inside the coarse cell. For variables with a finer resolution, the average of all cells inside a 0.25-degree cell was assigned to it.

4.10.2.2 Sea-surface and water-column variables: Seasonal patterns

Seasonal fields of SST and LCHL are presented in Figure B4.1. The dominant seasonal cycle is evident in these fields (see also Chapter 3), with high SST and low chl in JFM, and low SST and high chl in JAS. Also evident is the persistence of the area with lowest SST and highest chl on the western side of the archipelago in all seasons, which marks the location where the EUC upwells.

As mentioned in section 4.3.3.3, a principal component analysis was performed on the seven variables thought to describe the direct effects of physical forcing on the system (i.e., Z20, ZTD, MBVF, ZMBVF, ZOML, ZOD, and SST). The results were reported in section 4.4.3 for grid cells with valid data in the corresponding species matrices, with emphasis on the first component, since that component was the only one relevant to the ordination results. A description of the first three components is provided here based on analysis of the full data sets.

Table 1 lists the loadings for the first three principal components (PC). Together, they explained 83% of the variance in the original data sets. Figure B4.2 shows the site scores and their seasonal evolution for each PC. The first PC (41%) described the effects of the EUC around the archipelago (principally a shallow thermocline, weak pycnocline stratification, a thin OML, and low SST), which are most intense in JAS (see also Chapter 2). The OML is thin in this area because the EUC has a high-oxygen core (Anderson, 1977; Lukas, 1986), which effectively erodes the top of the OML directly beneath it. The second PC (26%) depicted a

NE-SW pattern principally driven by a strong, shallow pycnocline (resulting from
heavy precipitation in the Panamá Bight) and high SST. This pattern is strongest in
JFM. Finally, the third PC (16%) represented an W-E gradient, with a shallow,
thick OML, and a weak thermocline on the eastern sector. This pattern was also
strongest in JFM, and is probably associated with the W-E shoaling of the
thermocline in the eastern tropical Pacific (Fiedler, 1992), and the thickening of the
oxygen minimum layer off the coast of South America.

Table B4.1: Loadings (eigenvectors) for the first three principal components (PC)
of the seven variables describing direct effects of physical forcing in the water
column and at the surface. Values greater than 0.3 are shown in bold to highlight
the variables with the greatest contribution to each PC. The eigenvalues and the
fraction of the variance represented by each PC are also indicated.

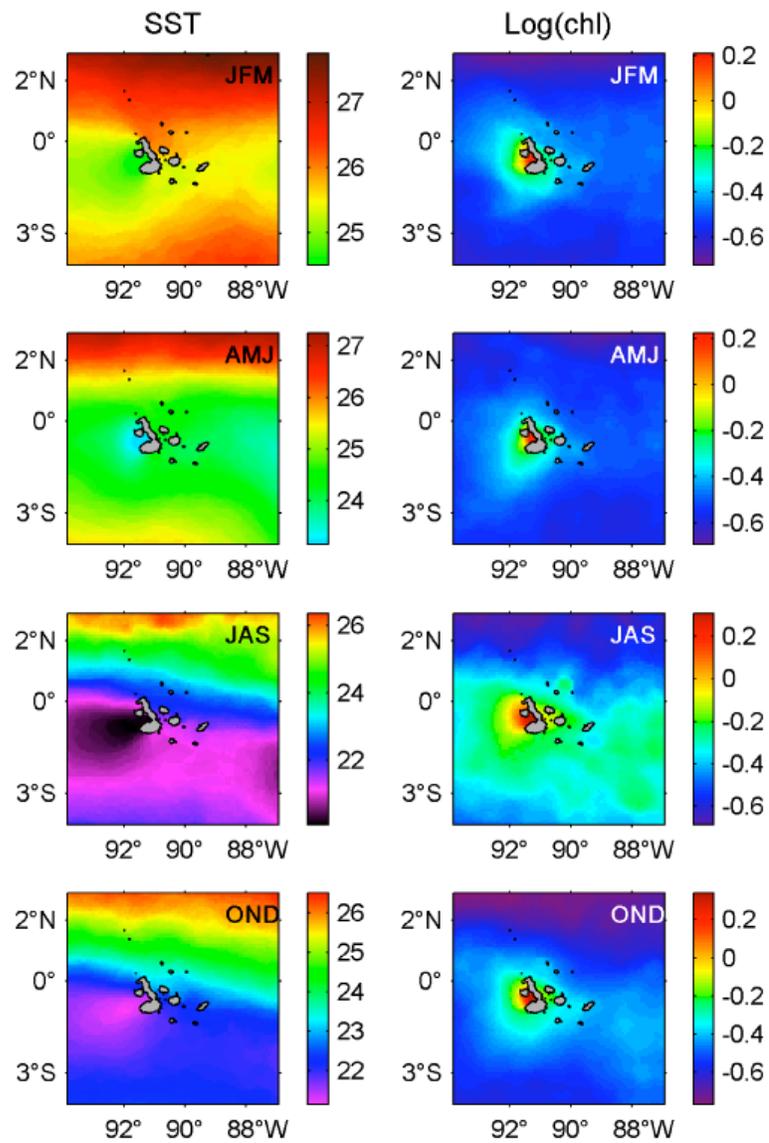| Variable	PC1	PC2	PC3
Z20	**-0.52**	0.13	-0.23
ZTD	0.27	**0.37**	**0.47**
MBVF	**-0.37**	**0.47**	0.02
ZMBVF	-0.27	**-0.50**	**-0.37**
ZOML	0.23	**0.39**	**-0.65**
ZOD	**-0.44**	-0.24	**0.40**
SST	**-0.45**	**0.41**	0.02
Eigenvalue	2.9	1.8	1.0
Variance fraction (%)	41.9	25.9	15.5

Figure B4.1: Seasonal climatologies of sea-surface temperature (SST) (°C) and log-transformed phytoplankton concentration (chl) (mg m^{-3}) for the study area.
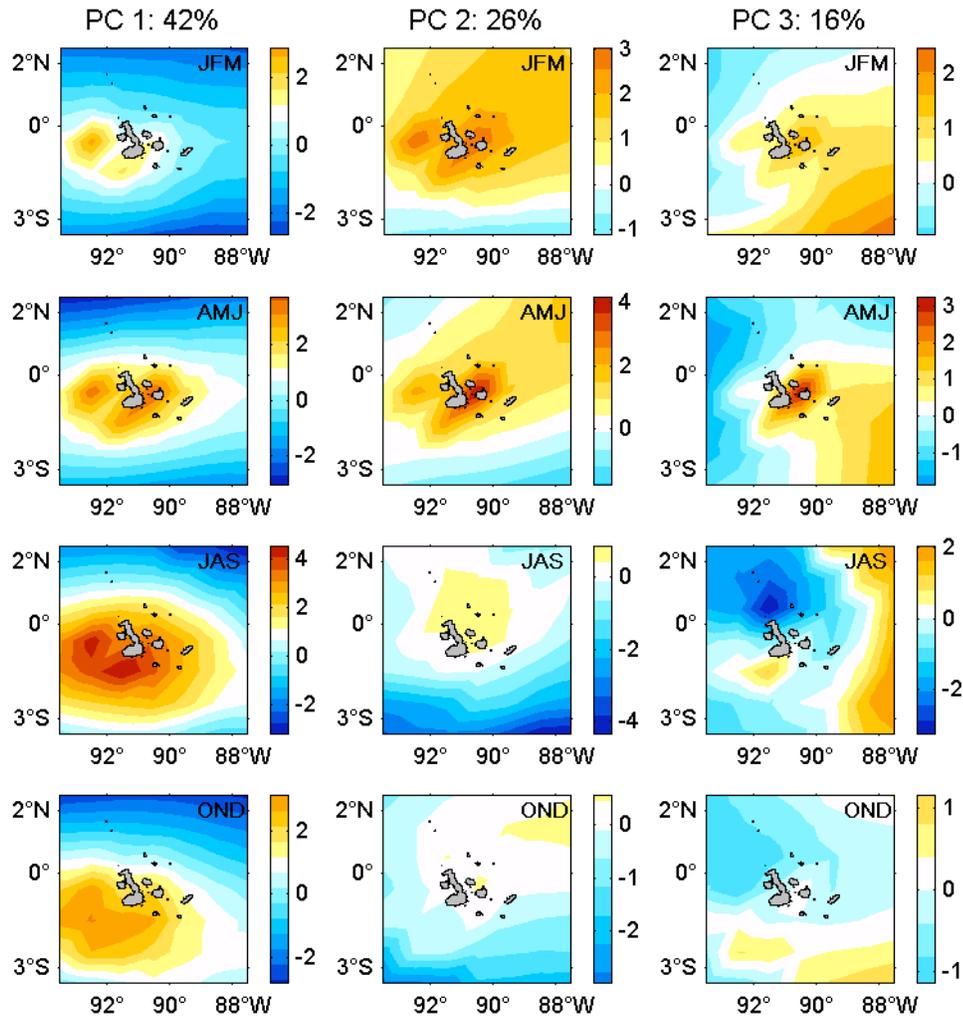
Figure B4.2: Seasonal evolution of the first three principal components (PC) of Z20, ZTD, MBVF, ZMBVF, ZOML, ZOD, and SST. The fraction of variance explained by each component is given.

4.10.3 Appendix C: Further details of the community analyses

4.10.3.1 Species diversity

Diversity measures provide concise summaries about the community and the properties of the data set. A measure of heterogeneity (see below), in particular, gives an indication of the degree of difficulty faced by ordination methods with a given data set (e.g., McCune and Grace, 2002). Common measures include Whittaker's (1972) three levels of diversity: alpha, beta, and gamma. Alpha diversity is the average number of species per sample unit (also known as species richness). Beta diversity is a measure of the amount of compositional heterogeneity in the data, which was estimated here as the ratio of the total number of species to the average number of species (gamma over alpha). Gamma diversity refers to the diversity of the study area, which is simply the total number of species across sample units (Whittaker, 1972). Three other widely used indices: Pielou's evenness, Shannon's entropy, and Simpson's diversity, are also included (Legendre and Legendre, 1998, McCune and Grace, 2002).

All these six diversity measures are reported for matrices containing the nine species of interest in Table C4.1 and for matrices containing all identified species in Table C4.2 for comparison. Also included in these tables are coefficients of variation for sample unit totals and for species totals, as well as average Sørensen distances among sample units in the distance matrices.

Table C4.1: Diversity measures and summary statistics for presence-absence matrices after removing rare species. SU is the number of sample units for each season. Pielou's evenness (E), Shannon's entropy (H), and Simpson's diversity (D) are also shown, along with the coefficient of variation (%) for row (CV_{su}) and column (CV_{sp}) totals. d is the average Sørensen distance among sample units in the distance matrices.

Season	SU	alpha	beta	gamma	E	H	D	CV_{su}	CV_{sp}	d
JFM	309	1.9	4.7	9	0.56	0.50	0.32	55.9	67.3	0.80
AMJ	232	1.8	5.0	9	0.50	0.44	0.28	57.4	55.4	0.83
JAS	140	1.6	5.6	9	0.39	0.35	0.23	58.9	52.2	0.86
OND	223	1.6	5.6	9	0.42	0.36	0.24	57.6	44.0	0.87

Table C4.2: Diversity measures and summary statistics for presence-absence matrices containing all identified species. SU is the number of sample units for each season. Pielou's evenness (E), Shannon's entropy (H), and Simpson's diversity (D) are also shown, along with the coefficient of variation (%) for row (CV_{su}) and column (CV_{sp}) totals. d is the average Sørensen distance among sample units in the distance matrices.

Season	SU	alpha	beta	gamma	E	H	D	CV_{su}	CV_{sp}	d
JFM	312	2.0	9.5	19	0.58	0.54	0.34	63.1	127.5	0.80
AMJ	237	1.9	10.0	19	0.55	0.51	0.32	64.4	111.5	0.84
JAS	151	1.7	12.4	21	0.38	0.37	0.23	71.1	115.9	0.89
OND	234	1.8	12.2	22	0.47	0.43	0.27	66.7	111.1	0.88

4.10.3.2 Distance among sample units in species space

The first step in the analyses was to obtain a matrix of distances among all sample units for each season (for the NMS ordination, a single distance matrix was obtained from the combined seasonal species matrices). Given a presence-absence species matrix **X** with *m* rows (i.e., sample units) and *n* columns (i.e., species)**,** the distance *D* between two sample units *i* and *h* was computed using the one-complement of Sørensen's coefficient of similarity (Legendre and Legendre, 1998; McCune and Grace, 2002) as:

$$D_{i,h} = \frac{\sum_{j=1}^{n} \left| x_{ij} - x_{hj} \right|}{\sum_{j=1}^{n} x_{ij} + \sum_{j=1}^{n} x_{hj}} \quad \text{for} \quad j = 1, \ldots, n \qquad (1)$$

The resulting distances were then arranged into a $m \times m$ matrix Δ, with elements δ_{ij}. *D* is referred to throughout this manuscript as the "Sørensen distance".

4.10.3.3 The Beals smoothing function

Prior to ordination, the data for each species in the presence-absence matrices were transformed with the Beals smoothing function, which yields quantitative values representing the "favorability" of each sample unit for each species (regardless of whether the species was present in the sample unit)**,** using the proportions of joint occurrences of the species of interest and the species that were actually in the sample unit (McCune, 1994). The main purpose of this transformation is to relieve the "zero truncation problem" (i.e., the lack of information about habitat quality outside of the observed range of a species because its abundance is zero), which is most severe in heterogeneous community data sets with a large number of zeros in the data matrix (McCune, 1994; Ewald, 2002). The

method also smoothes out differences due to varying sampling effort (McCune, 1994).

For a given presence-absence species matrix **X**, McCune (1994) defines the Beals smoothing function as:

$$b_{ij} \quad = \quad \frac{1}{S_i} \sum_k \left(\frac{M_{jk}}{N_k} \right) \quad \text{for all } k \text{ with } x_{ik} \neq 0 \qquad (2)$$

where b_{ij} is the adjusted value in the transformed data matrix **B** that replaces the original value in **X**, S_i is the number of species in sample unit i, M_{jk} is the number of sample units with both species j and k, and N_k is the number of sample units with species k.

The transformation was applied to improve the stability of the solution from the NMS ordination on the presence-absence data. Diagnostic analyses of the data indicated that although the matrix was about 81% sparse, all nine species were present in at least 8% of the sample units (i.e., there were no "rare species" remaining). Also, there were no outliers beyond ± 2 standard deviations in the distribution of Sørensen distances. However, a frequency histogram of the average Sørensen distance to each sample unit revealed that there were two "populations" with little or no overlap, as shown in Figure C4.1. A considerable number of sample units had low average Sørensen distances (< 0.71) and appeared grouped together at the low end of the histogram, while the remainder were spread more widely over the rest of the distance range. Examination of the spatial pattern of these distances (Fig. C4.2) indicated that the low-distance population corresponded with the group of sample units found in the northern sector of the study area (and also in the southern sector in JFM) that was characterized almost exclusively by the presence of *S. attenuata* and *S. longirostris* (see section 4.4.2). The NMS procedure interpreted the low-distance population as outliers competing with the main

population for a stable solution. In this case, the effect of the Beals transformation was to enhance the main compositional gradient. After smoothing, the Sørensen distances were more normally distributed (Figs. C4.1 and C4.3) and a low-stress, stable solution was reached. (see section 4.10.3.4)
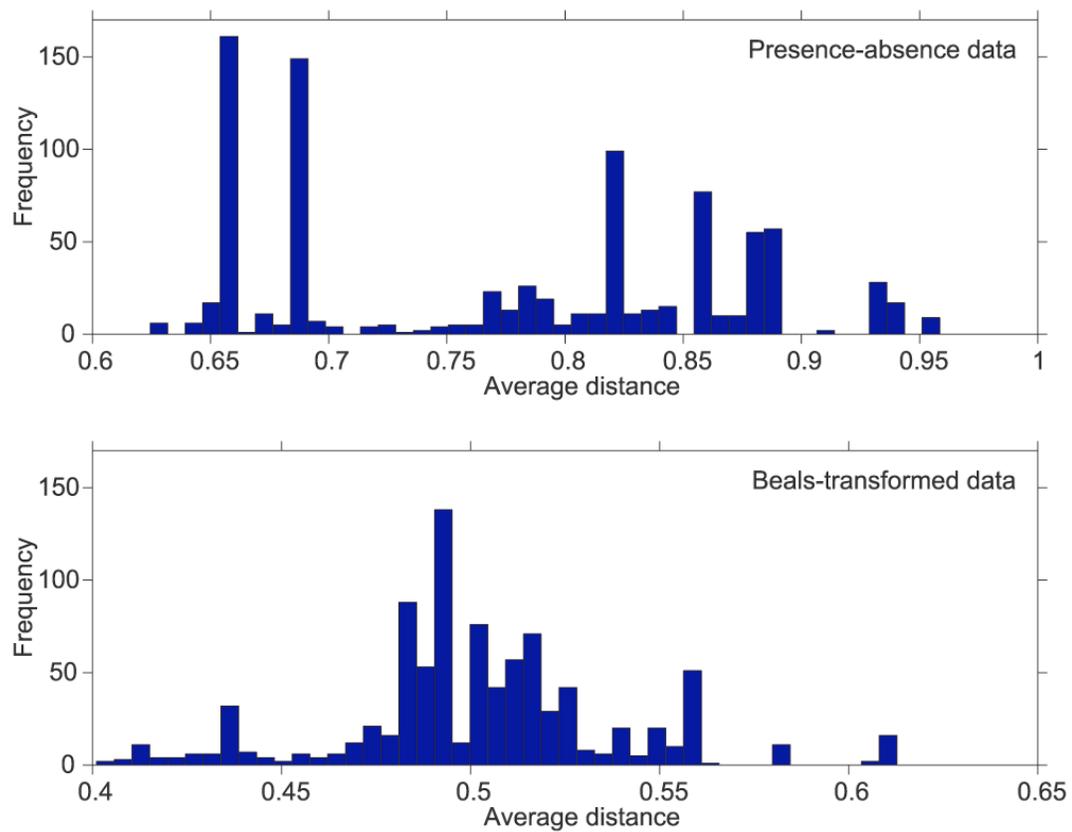

Figure C4.1: Frequency distribution of average Sørensen distances to each sample unit ($m = 904$). Top: calculated from the presence-absence data. Bottom: calculated from the Beals-transformed data.
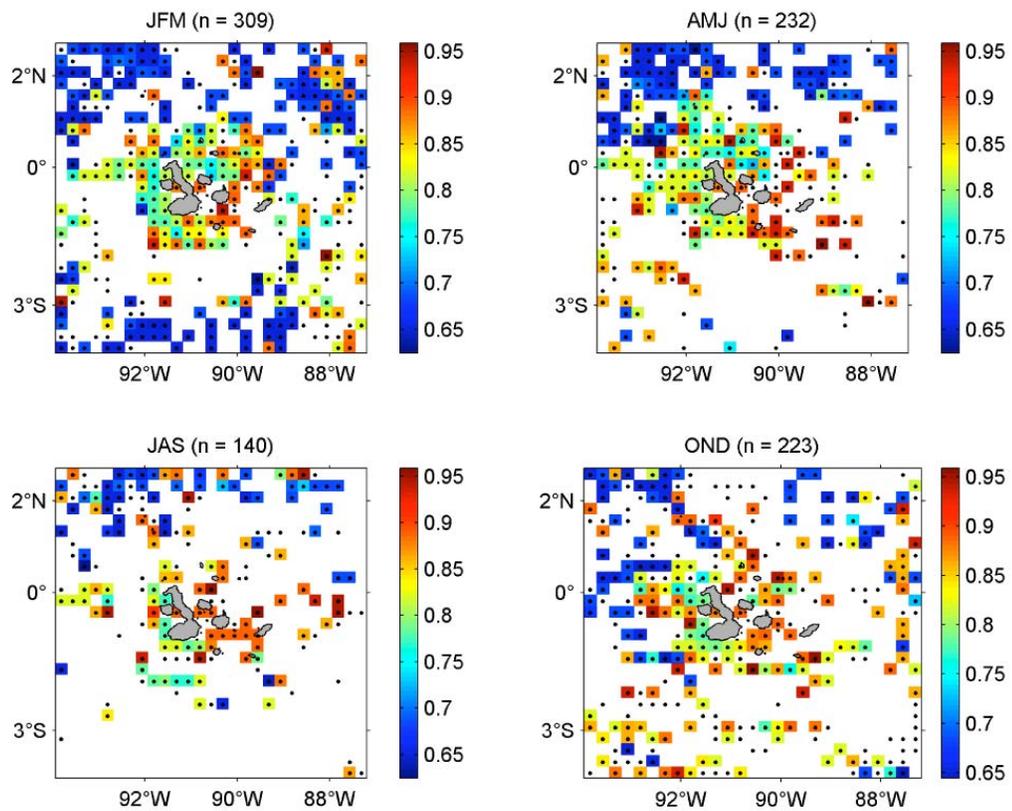
Figure C4.2: Spatial distribution of average Sørensen distance to each sample unit for each season in the presence-absence data set.
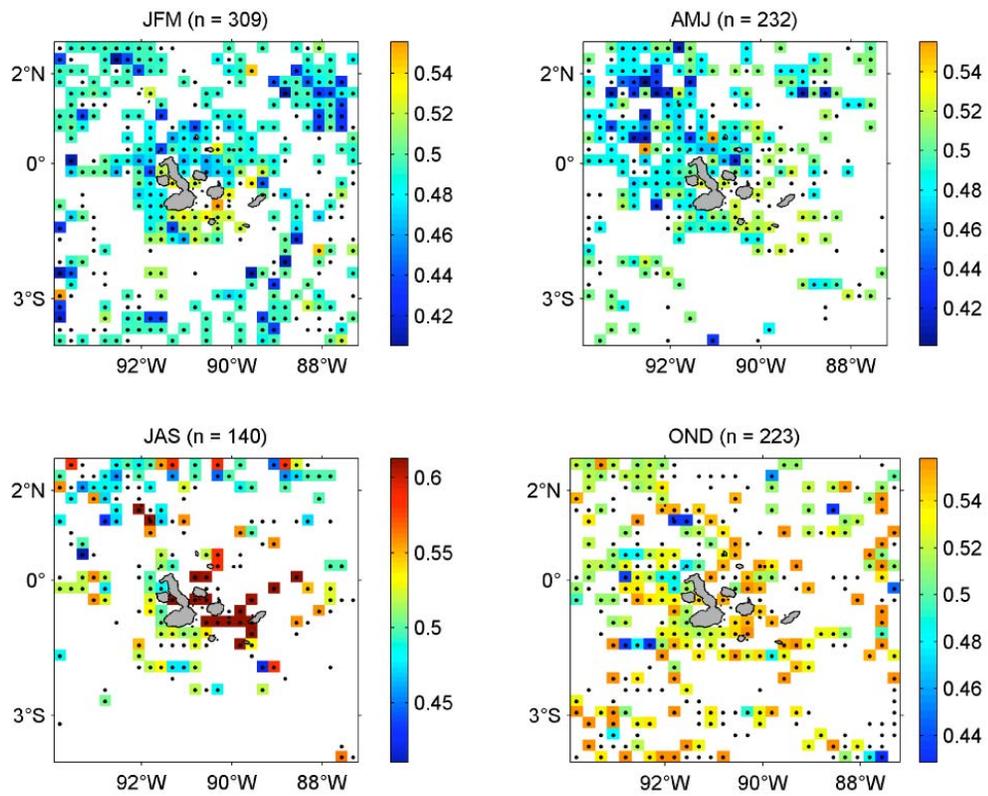
Figure C4.3: Spatial distribution of average Sørensen distance to each sample unit for each season after the Beals transformation.

4.10.3.4 Setup and intermediate steps of the NMS ordination

Unlike other ordination methods, NMS is not based on eigenanalysis, and it has no particular underlying model (either linear or unimodal). Its objective is to arrange dissimilar objects far apart and similar objects close to one another in a small and specified number of dimensions (i.e., number of axes). This preservation of ordering relationships among objects (sample units in this case) is accomplished by maximizing the rank-order correlation between distance in the full-dimensional space and distance in the ordination space. NMS operates as an iterative search for the best positions, which are assessed with "stress", an objective function that measures the lack-of-fit between the two kinds of distance. Improvements are accomplished by gradual changes to the configuration in a direction that progressively minimizes stress, using the method of steepest descent (an optimization algorithm) (Legendre and Legendre, 1998; McCune and Grace, 2002).

The search for the best solution was conducted in two stages, using the software package PC-ORD version 4.25 (McCune and Mefford, 1999). First, the sample units were configured at random and the program was allowed to run, starting with a six-dimensional solution and stepping down to a one-dimensional solution. The initial step length (i.e., the rate of movement toward minimum stress) was set at 0.2. At each step, 400 iterations of the calculations were performed. The stability criterion, defined as the standard deviation in stress over the preceding 15 iterations and used as a cut-off value to stop the iterative process if is a stable solution is reached before the predetermined number of iterations, was set at 0.00001. Forty runs with the real data and 50 runs with the randomized data were used as the basis for a Monte Carlo test of significance at each dimensionality, which tested the probability that a similar final stress could not have been obtained by chance. Selection of the final number of dimensions was done by examining a scree plot of stress values as a function of number of axes, choosing for the best solution the dimensionality where the change in stress became small. The final

solution was obtained in the second stage, by rerunning an NMS once, with the configuration of the chosen solution as the starting configuration. The number of iterations and the stability criterion were as with the preliminary runs.

The results from the initial unconstrained NMS run, which cascaded down from six to one dimensions, were assessed graphically with a scree plot of final stress *vs*. the number of dimensions (Fig. C4.4). The best ordination was obtained by selecting the number of dimensions after which additional dimensions provided only small reductions in stress; in this case at two dimensions. The Monte Carlo test of significance indicated a better than random solution for this dimensionality (*p*-value = 0.0196) (Table C4.1 and Fig. C4.4). The final two-dimensional solution was also assessed graphically using plots of stress, instability, step length, and magnitude of the gradient vector *vs*. iteration (see) (Fig. C4.5). From these plots it was evident that the stress curve stabilized at a low level after about 40 iterations and that the procedure ended with a periodic but low level of instability (Fig. C4.5). Since the final stress was low (12.4) and the final instability was about 10^{-3}, the ordination result was judged acceptable.

Table C4.3: Stress in relation to dimensionality (i.e., number of axes) from the initial unconstrained NMS runs for real and randomized data.

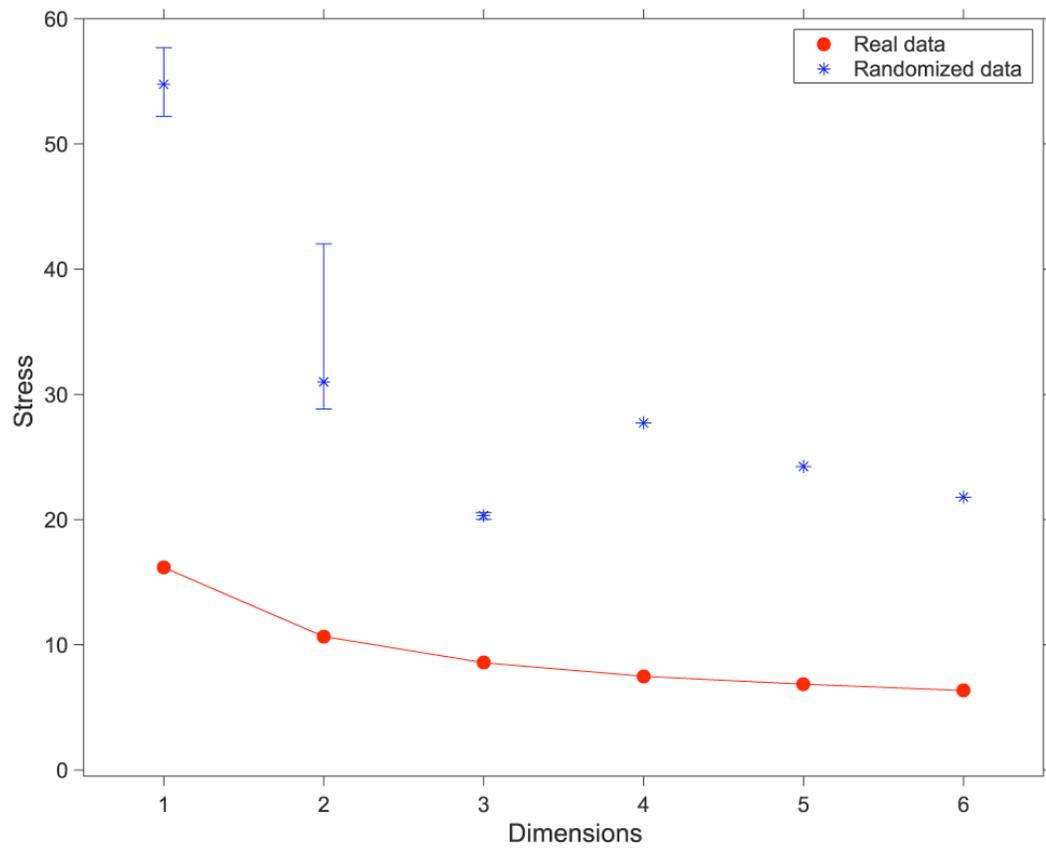| Axes	Stress in real data (40 runs)			Stress in randomized data (Monte Carlo test, 50 runs)			*p*
	Minimum	Mean	Maximum	Minimum	Mean	Maximum	
1	16.2	47.9	54.2	52.2	54.8	57.7	0.0196
2	10.7	12.4	17.6	28.8	31.0	42.0	0.0196
3	8.6	9.3	13.4	20.0	20.3	20.6	0.0196
4	7.5	8.1	9.9	27.7	27.7	27.7	0.0196
5	6.9	7.7	10.3	24.2	24.2	24.2	0.0196
6	6.3	9.2	23.3	21.8	21.8	21.8	0.0196

Figure C4.4: Scree plot of stress *vs*. dimensions from the initial unconstrained NMS runs for real and randomized data. Red dots are the minimum stress in the real data. Blue stars are the mean stress in the randomized data, while bars indicate the minimum and maximum (see Table C4.1).
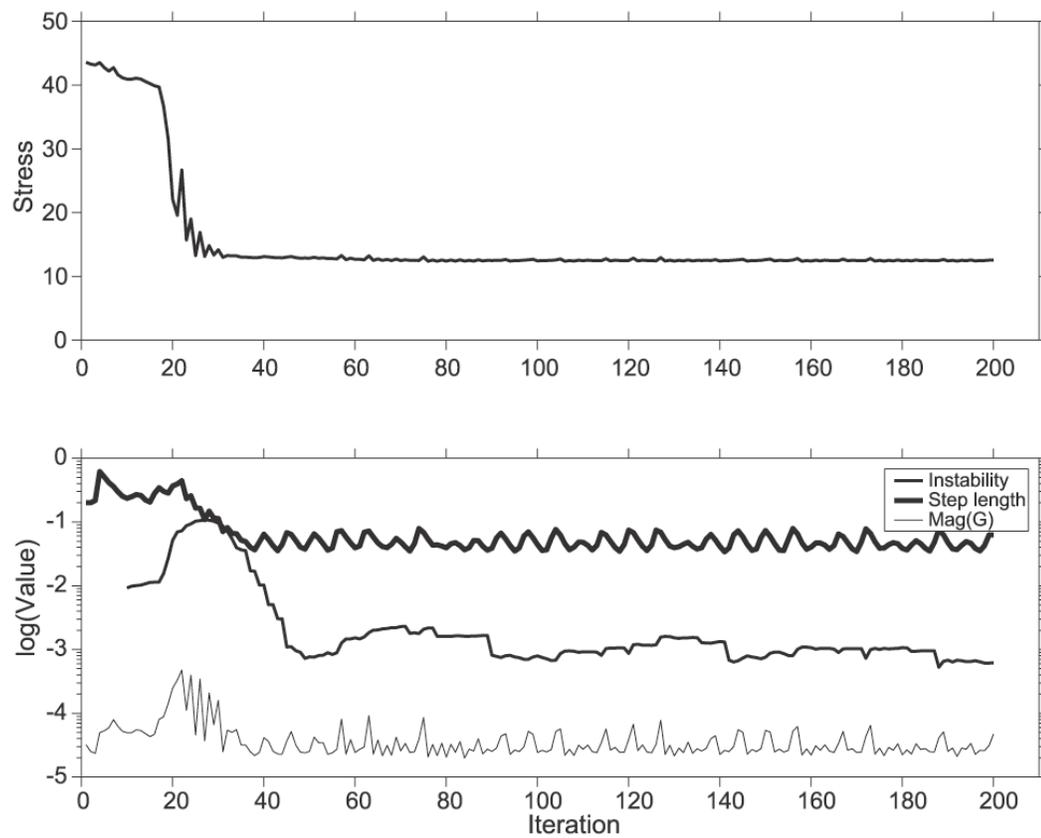
Figure C4.5: Stability of the final two-dimensional NMS solution. Top: stress *vs.* iteration. Bottom: instability, step length, and magnitude of the gradient vector *vs.* iteration. Only the first 200 iterations are shown.