

**EASTERN TROPICAL PACIFIC DOLPHIN HABITATS -
INTERANNUAL VARIABILITY 1986-2000**

S.B. Reilly, P.C. Fiedler, T. Gerrodette, L.T. Ballance,
R.L. Pitman, J. M. Borberg, and R.C. Holland

Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
8604 La Jolla Shores Drive
La Jolla, California 92037

JULY 2002

ADMINISTRATIVE REPORT LJ-02-21

ABSTRACT

We examined patterns of habitat use among schools of dolphins in the eastern tropical Pacific during the three-year period 1998, 1999, 2000, and compared those patterns to previously reported results from approximately a decade earlier (1986-1990). We used canonical correspondence analysis (CCA) to help define relationships between dolphin distributions and oceanographic conditions, compared CCA models, and the geographic distributions of preferred habitats between the two periods. When using a common set of six basic oceanographic variables the habitat models were essentially the same for the MOPS and STAR periods, and geographic distributions of patterns during 1998-2000 were within the same range of interannual variability observed during 1986-1990. After removing variation associated with the six basic oceanographic variables, remaining variance associated with inter-decadal differences was trivial. Improvements to the ordination were realized by including information on geographic locations, separating common dolphins into three stocks, and by including additional explanatory variables representing seabirds, fishes and cephalopods. The best model explained approximately 30% of the total variance in dolphin abundance. Individual species values ranged from 62% for southern common dolphins, to just 8% for eastern spinner dolphins.

INTRODUCTION

Qualitative descriptions of cetacean habitats have been advanced since the 19th century, but quantitative study of their habitats is a relatively new endeavor. Initial descriptions were for large whales in the form of maps of commercial catch locations (e.g. Townsend 1935). This was followed by mid-20th century interpretations of catch patterns in relation to general patterns of oceanographic properties and processes (e.g. Nasu 1963). More recently, whale catch locations have been analyzed quantitatively in relation to oceanographic variables (e.g. Gregr and Trites, 2001).

Study of habitat ecology of dolphins in the eastern tropical Pacific (ETP) followed a later but similar pattern of development. Perrin (1975) described overall distribution ranges and large-scale patterns based on localities of catches and visual sightings from the ETP tuna purse seine fishery. Au and Perryman (1985) evaluated distribution and oceanographic patterns qualitatively, and provided the first focused hypotheses on the oceanographic patterns and processes underlying observed distributions. Reilly (1990) tested Au and Perryman's (1985) hypotheses using multivariate statistics, and contrasted seasonal patterns. Reilly and Fiedler (1994) fit multivariate, Gaussian models to dolphin abundances using canonical correspondence analysis (CCA: Ter Braak, 1986), and examined interannual patterns during the five-yr Monitoring of Porpoise Stocks (MOPS) expedition of 1986-1990. (Details of habitat patterns are presented below).

The primary objective of this study was to compare habitat patterns observed during the three years of the *Stenella* Abundance Research (STAR) expedition (1998-2000) with those observed approximately a decade earlier during the MOPS years (1986-1990). We followed the analytical approach taken by Reilly and Fiedler (1994) for dolphins in the eastern tropical Pacific, using CCA to quantify patterns of habitat use in relation to environmental characteristics. Two types of changes would be of

particular interest. 1) Changes in the underlying patterns of association of the dolphin species/stocks with the region's oceanography could indicate that the patterns observed during the 1970s and 1980s were not robust, ecological-scale patterns, or, that there had been some fundamental ecosystem shift or change in the intervening decade. 2) Substantial changes in the spatial patterns of preferred habitats might also be indicative that fundamental ecosystem changes had occurred since the late 1980s. Either of these types of changes would bear directly on our interpretations of recent population recovery, or lack thereof, as we attempt to answer the question posed by the US Congress as to whether or not the ETP tuna purse seine fishery is having a significant adverse impact on these dolphin populations.

An independent scientific peer review of this work was administered by the Center for Independent Experts located at the University of Miami. Responses to reviewer's comments can be found in the Appendix.

STUDY AREA

The basic physical features of the upper ocean in the eastern tropical Pacific have been described by Wyrki (1966), and Tsuchiya (1974). Fiedler (1992) updated this description and summarized seasonal and interannual variability. Major surface water masses and currents are depicted in Fig. 1. The center of the region is the east Pacific warm pool, occupied by warm, low-salinity Tropical Surface Water. The equatorial cold tongue of cooler, higher-salinity Equatorial Surface Water is found south of about 3°N. Peru Current and California Current Waters are found along the coasts of Peru-Ecuador and Baja California, respectively. These eastern boundary currents feed into the westward South and North Equatorial Currents (SEC, NEC). The North Equatorial Countercurrent (NECC) flows eastward between the NEC and SEC into the center of the east Pacific warm pool. The NECC is strong during September-December and weak or absent during February-April.

A permanent shallow thermocline underlies most of the region, shoaling towards the coast (Wyrki 1966). Zonal thermocline ridges are associated with the geostrophic balance of the zonal equatorial currents. Thus, surface divergences occur in the SEC above the equatorial thermocline ridge and between the NEC and NECC above the countercurrent thermocline ridge along 10°N (Fiedler 1992, 2002). Upwelling driven by equatorward longshore winds off Peru and Baja California and by trade winds along the equator brings cold, nutrient-rich water from below the shallow thermocline (nutricline) into the surface layer. This nutrient input maintains high concentrations of nutrients at the surface and results in high levels of new production in equatorial and eastern boundary current systems (Chavez and Barber 1987). Biological productivity is also enhanced by upwelling at the Costa Rica Dome (Wyrki 1964, Fiedler 2002), and by intermittent, topographically-induced offshore winds at several points along the coast of Central America (e.g., the Gulf of Tehuantepec, McCreary et al. 1989). Secondary and higher level productivity and standing stocks are generally high in areas of high primary productivity (Blackburn et al. 1970). Within this and other large oceanic regions, the abundance of animals from plankton to large nekton is patchy on a variety of spatial and temporal scales (Haury et al. 1978), with major consequences for the ecology of pelagic predators (e.g., Carr 1987).

ETP Dolphin Habitats

At least three complementary patterns have been described. Spotted and spinner dolphin habitat is primarily north of the equator extending offshore from the coast of Central America and Mexico, but also south of the Galapagos Islands. The dominant offshore pattern is centered approximately along the 10N thermocline ridge. That is, spotted and spinner habitat is characterized generally by stable, warm, low-salinity tropical waters where the thermocline shoals in relation to the rest of the open sea (Au and Perryman, 1985, Reilly, 1990). In contrast, common dolphin habitat is characterized by cooler, more saline upwelling-modified waters, with major concentrations occurring at the terminations of the California Current off Baja California, along the equator especially east of the Galapagos Is, and a third concentration off Central America, centered around the Costa Rica Dome. Striped dolphins occupy habitat that is in many respects intermediate between these two patterns (Reilly, 1990).

There are apparent shifts in the offshore direction by spotted, spinner and striped dolphins, coincident with seasonal shoaling of the 10 N thermocline ridge (Reilly, 1990). This seasonal shoaling is part of the dominant pattern of seasonal change in the ETP, associated with the north-south movement of the inter-tropical convergence zone between the trade winds (Fiedler 1992). Statistical tests supported the habitat hypotheses of Au and Perryman (1985) for spotted, spinner, and common dolphins, but not for striped dolphins. During the summer, striped dolphins occupied habitat that was geographically complementary with habitats of both common dolphins and spotted/spinner dolphins. Striped dolphin habitat was indistinguishable statistically from either the tropical or upwelling-modified habitats with the variables used, indicating that other factors or processes act to separate these dolphins from the others (Reilly 1990).

CCA models clearly reflected the descriptive habitat patterns (Reilly and Fiedler, 1994). Environmental variables included in Reilly and Fiedler's (1994) analyses were: surface temperature, salinity, sigma-t, and chlorophyll, and thermocline depth and thickness. The dominant pattern in the species-environment relationship (1st canonical axis) separated common dolphins from spotted and spinner dolphins, based on their associations with cool upwelling habitat and warm tropical habitat, respectively. The second axis separated whitebelly spinners from eastern spinners. Both occurred in tropical water, but were separated primarily by thermocline topography. The species - environment correlations were 0.67 on the first axis, 0.42 on the second. Overall, the environmental data explained 15% of the variance in the species data. For individual school types this ranged from 36% for common dolphins to 6% for striped dolphins. When latitude and longitude were added to the analyses the total variance explained was increased to 21%. Interannual variability in the species data was small, but judged significant by a Monte Carlo randomization test. Residual interannual variance was insignificant after removing variance associated with environmental variables.

METHODS

Data Collection

Dolphin Sightings. Sighting methods used are documented in detail in Barlow et al. (2001). In brief, line transect sighting surveys were conducted using teams of three observers who searched from a viewing height of 10 m above the sea surface. Two observers searched with 25x pedestal-mounted binoculars. The third observer searched with unaided eye and occasionally with 7x binoculars, and also served as data recorder. The ship turned toward sighted cetaceans for species identification, when necessary. Search effort was considered to be within a continuous leg until either sighting conditions changed, the ship was diverted to examine a sighting, or searching stopped for some other reason.

Oceanographic Data. Shipboard data collection and laboratory techniques are documented in Fiedler and Philbrick (2002). In brief, oceanographic data were collected in two general modes: continuous surface measurements as the ship was underway, and at discrete stations where vertical data were collected by deploying expendable bathythermographs (XBTs) or lowering a conductivity, temperature, depth (CTD) system equipped with a seawater collection rosette system. Continuous surface measurements included temperature and salinity. Instruments were calibrated regularly with discrete water samples. CTD casts were made at least once each day, before sunrise. Water samples were taken on each cast for phytoplankton pigment analysis and primary productivity estimation. Vertical profiles from XBTs were taken at least twice per day, usually at 1000 and 1400 local time.

Data Processing

Dolphin Sightings. For this study daily encounter rates were estimated for the seven types of dolphin schools most frequently set upon by the purse seine fishery, i.e. target schools, as in this study's predecessor (Reilly and Fiedler 1994):

Spotted Dolphins (*Stenella attenuata*)

Common Dolphins (*Delphinus delphis*)

Spotted with Eastern Spinner dolphins (*S. longirostris orientalis*)

Spotted with Whitebelly Spinner dolphins (*S. longirostris*)

Eastern Spinner dolphins

Whitebelly spinner dolphins

Striped dolphins (*S. coeruleoalba*)

Distinctions by stocks were not made here for spotted dolphins or common dolphins, rather, patterns were examined at the species level for these taxa. Eastern and whitebelly spinners are recognized as distinct subspecies, and past studies have indicated they have somewhat distinct habitat preferences (e.g. Reilly and Fiedler, 1994). Dolphin abundance was indexed as encounter rates with groups, i.e. number of groups sighted per distance searched. The sightings data, collected for line transect estimation of abundance within the entire study area, are separated into effort segments of uniform sighting conditions.

We pooled the segments of effort collected during fair or better visibility conditions (Beaufort scale 4 or lower) for each calendar day, and computed our relative abundance index for the day as the number of groups sighted divided by the total km searched that day. This resulted in sampling units of about 160 Km each, separated temporally and spatially by about 10-12 hrs and 130-160 Km, because the ships continued to run during the nights.

Environmental Data. As noted above, for the primary analyses conducted here oceanographic patterns and processes were represented by the same six variables as used by Reilly and Fiedler (1994):

Temp, Sea surface temperature, from along-track continuous measurements.

Sal, Sea surface salinity, from along-track continuous measurements.

SIGMAT, Surface water density index (a function of temperature and salinity).

LogCHL, Sea surface chlorophyll, log-transformed.

Z20, Depth of 20C isotherm, to index thermocline depth.

ZDIFF, Difference in meters between depths of the 20C and 15C isotherm depths to index thermocline strength.

We calculated daily averages for comparisons with the daily cetacean encounter rates. For the continuous surface variables (**Temp, Sal, and SIGMAT**), data were averaged from one hour before the start of effort to one hour after the end of effort. Daily average **LogCHLs** were calculated from hydrocast and underway surface samples during the same time interval. **Z20** and **ZDIFF** were estimated from XBT and CTD data. For days with missing data, daily average values were interpolated from gridded fields.

For some analyses, noon position (**Lat**, latitude, and **Lon**, longitude) were included to represent geographically fixed aspects of the dolphin habitats that are not represented by the six oceanographic variables. This was found to add to the overall explanatory power of the CCA by Reilly and Fiedler's (1994) analyses of the 1986-1990 data. Year and decade effects, represented by categorical variables, were included in some analyses to determine interannual and interdecadal variability respectively.

Multivariate Analyses of Species-Environment Relationships

Correspondence analysis is an eigenvector ordination technique, similar to principal components analysis, that can be used to investigate community structure. These methods extract dominant, orthogonal axes of variation in abundance indices for multiple species at multiple sites. Typically, the ordination axes are then interpreted indirectly with the help of external knowledge and data on environmental gradients, either qualitatively or with regression methods (Gauch 1982). As our primary focus is on habitats, we take advantage of an additional characteristic of CCA, the direct quantitative description of environmental gradients and patterns of habitat use, as described below.

In contrast to principal components analysis and other linear methods, correspondence analysis (CA, also called reciprocal averaging) fits non-linear Gaussian (unimodal) models to species abundance data. Canonical correspondence analysis is an extension of CA in which the species ordination is done directly and iteratively in relation to environmental variables. CCA is an efficient ordination technique when species have bell-shaped response curves or surfaces with respect to environmental gradients (Ter Braak 1986), which is consistent with general ecological knowledge (e.g. Whittaker et al. 1973). We used the implementation of CCA in the computer program CANOCO (Ter Braak 1988). The models and algorithm used in CANOCO are documented in Ter Braak (1986).

As part of the species-environment ordination, CCA estimates a series of site scores (here, site = day) that are linear combinations of the environmental variables that maximize the species-environment correlation. One set of site scores is estimated for each canonical ordination axis. In terms of the models specified above for oceanographic and geographic patterns, one set of coefficients would be estimated for each ordination axis, so that in a typical analysis there are four statistically independent environmental gradients estimated in association with the four dominant, independent patterns of species variation. The interpretation of environmental gradients represented by the axes is made from the correlation coefficients and the multiple regression or canonical coefficients of the original environmental variables with the canonical axes (Ter Braak 1986).

The results of canonical correspondence can be best interpreted from an ordination biplot, on which species and/or sites can be represented by points and environmental variables by arrows. The biplot displays the mean species scores or optima on two canonical axes, usually the first two, which explain the majority of the variance. The directions and relative lengths of the arrows for environmental variables represent their contributions to the ordination. More important environmental variables are therefore represented by longer arrows. In making biplots we used Hill's scaling (Ter Braak 1986) in which site scores are computed as weighted averages of species scores. Following Reilly and Fiedler (1994) we found it instructive also to map contours of environmental axes associated with dominant species axes, and plot sighting localities of relevant species over the contours.

RESULTS

STAR Years: 1988, 1989, 2000

A total of 102,811 Km of search effort from the STAR expedition met our quality criterion (Beaufort 4 or better). Figure 2 displays completed sighting effort, by year. The MOPS years are shown as well to allow comparisons of effort distribution across years. The combined STAR yrs effort resulted in 1,570 sightings of the seven species/stock categories of immediate interest here (Table 1). Continuous oceanographic measurements were recorded during periods additional to those meeting the sighting effort quality criterion, so that a total of 105,060 Km of continuous data on surface temperature and salinity were available (Table 2). Additionally there were 2,830 discrete chlorophyll measurements, 2209 XBT deployments and 1352 CTD stations. Considerable additional detail can be found in Philbrick et al.

(2001).

Table 3 gives the weighted correlation matrix for the STAR years, using the same six oceanographic variables as reported for the MOPS years by Reilly & Fiedler (1994). The species-environment correlations are the values for equivalent species and environment axes. For example, the correlation between the first or dominant species axis and the dominant environment axis is 0.7216, the correlation between the second set of axes is 0.4577, and so on. The first environmental axis includes negative correlations with surface temperature (TEMP, -0.6285) and thermocline depth (Z20, -0.5329), and significant positive correlations with surface water density (SIGMAT, 0.4704), surface chlorophyll (LogCHL, 0.4325) and thermocline strength (ZDIFF, 0.3336). As discussed further below, this axis essentially contrasts cool, dense upwelling modified waters with more tropical, less-productive warm waters over deeper thermoclines.

Table 4 reports results of a CCA ordination of the STAR yrs, structured to replicate the 'basic' six-variable ordination of the MOPS yrs reported by Reilly and Fiedler (1994, Table 4). The eigenvalues are similar in magnitude and pattern to the MOPS results, with about 90% of the species-environment patterns explained by the first two axes. As with the MOPS data, the total amount of sighting variance explained by the ordination in relation to these oceanographic variables is modest (14.7% for MOPS, 16.3% for STAR). The patterns among individual species/stocks are also similar overall, but show a few notable differences. During the MOPS years, the ordination explained 8.1% of spotted dolphin variance, 35.5% for common dolphins, while the STAR ordination explained 20.5% for spotted and 49.7% for common. Decreases were realized for spinner dolphins, both in mixed and unmixed schools. An increase was realized for striped dolphins, from 5.9% in MOPS to 15.9% in STAR. This increase related primarily to axis 2, which overall was not a strong axis.

CCA methods assume unimodal distributions of species data in relation to canonical axes (multivariate combinations) of environmental variables. With the original species definitions this assumption was met adequately for the MOPS years (Reilly and Fiedler 1994) for spotted dolphins and eastern spinner dolphins, but common dolphins showed evidence of bimodality on axis 1. Initial runs for the STAR years produced the same pattern, so we separated the common dolphin observations by stock, for the northern stock off Baja California, the central stock off Central America and the southern stock off South America and along the Equator (Dizon et al. 1994). As shown in Figure 3, the separated common dolphin stocks all have unimodal distributions on both axes 1 and 2. However, the distribution for the northern stock on axis 1 was very flat in comparison to the other stocks.

Monte Carlo randomization tests resulted in rejection of the hypothesis of no relation between the species and environmental data sets. One thousand permutations randomly pairing species and environmental data produced no ordinations with eigenvalues larger than the observed trace value of **0.501** (table 4), giving a P-value <0.001.

The species-environment biplot from the base ordination (Figure 4a) is very much like that for the MOPS ordination (redrafted here as Fig. 4b). The primary axis separates common dolphins from the spotted and spinner dolphins, while the second axis separates eastern spinner from whitebelly spinner dolphins, both in pure schools and in combinations with spotted dolphins. Positive values on axis 1 represent areas with cooler, more dense surface waters, a shallower thermocline and relatively more chlorophyll, which are characteristic of cool upwelling habitat, the preferred habitat of common dolphins. Negative scores on axis 1 represent warmer, less dense surface water, over slightly deeper thermoclines (in relation to upwelling areas where the 20C isotherm reaches near or to the surface). These conditions are characteristic of Tropical Surface water (Fig 1) and represent preferred habitat of offshore spotted dolphins and eastern and whitebelly spinner dolphins.

Axis two is, by definition, uncorrelated with axis one. Axis two patterns are significant, but explain only a small part of the species variance (about 3.5%). Environmental patterns represented by this axis include, in general, nearshore vs offshore properties. Axes three and four explain very small amounts of species variance and so are not considered further.

Spatial patterns of axis 1 scores are mapped by year in Figure 5. MOPS years also are represented here for ease of comparison. Contours are shaded for positive values to aid visual interpretation. Noon positions for days when spotted and common dolphins were sighted are represented by open triangles and closed circles, respectively. There is a general pattern for spotted dolphins to occur in areas of negative scores, and common dolphins to occur in areas of positive scores.

For consistency with the presentation of Reilly and Fiedler (1994) maps of axis 2 scores are also shown by year in Figure 6, with noon positions displayed for days when eastern spinners (open triangles) and whitebelly spinners (closed circles) were seen.

Additional Explanatory Variables: latitude, longitude and year

Extension of the primary, six variable ordination to include fixed geographic effects (latitude and longitude) notably improved the explanatory power of the ordination, increasing the percentage of species variance explained from 16.3% to 21.4% (Table 5). Greatest improvements from adding latitude and longitude were realized for mixed schools of spotted and whitebelly spinner dolphins, from 8.9% to 27.9%. Adding year (1998, 1999, 2000) as a covariate improved the overall fit just slightly, from 21.4% to 21.7%. No significant among-year differences remained after removing variance associated with the oceanographic variables.

Analyses with full data set, MOPS plus STAR years

A set of ordinations with the full 8-yr data set, combining the MOPS and STAR sets, is reported in Table 6. As expected, results are quite similar to ordinations of the two sets alone. The combined ordinations were run primarily to examine patterns of difference between the two decade-apart subsets,

after removing variance associated with oceanography. This result appears as column six in Table 6. The amount of species variance explained is trivial, 0.9% with an eigenvalue sum of 0.021. This was judged to be significantly different from zero by the permutation tests, but we view it as ecologically of little to no importance, given the very small eigenvalue.

There is a pattern of separation among the eight years worth noting, however, and the pattern appears different within the core and outside parts of the study area. Figure 7a is a biplot from the ordination of combined MOPS and STAR data (with just the six base environmental variables, for ease of presentation), including also the mean conditions observed throughout the study area in each year. The first thing to observe is that as expected the combined patterns are not notably different from the individual MOPS or STAR biplots. A second observation is that the STAR and MOPS years are separated by a small amount on the biplot, with STAR years clustering in the upper right quadrant (positive scores on both axes). To address the possibility that these small but apparent differences between the decades were a result of the differences in allocation of search effort between the decades (Figure 2) we defined a new variate, with two values each year, one for the core area, another for the outside area. Figure 7b displays the year/area variates on the biplot. It is clear that there is a much larger distinction between core and outside areas than between MOPS and STAR periods. All core observations cluster closely together, while outside observations are more spread and do show a consistent separation between the decades. That is, inter-decadal variability is small, but different patterns were apparent in the outside part of the study area, but not within the core habitat of both NEO spotted and E spinner dolphins.

Additional Analyses: Separation of Common Dolphins

As reported above for the STAR years and by Reilly and Fiedler (1994) for the MOPS years, the distribution of common dolphin observations on canonical axis 1 was bimodal. To address this problem we separated the common dolphin observations by stock, for the northern stock off Baja California, the central stock off Central America and the southern stock off South America and along the Equator (Dizon et al. 1994). This not only resulted in unimodal distributions as reported above, but also improved model fit by a modest amount, from explaining just 13.8% with the basic 6 environmental variables (Table 6, col. 1) to 16.1% (Table 6b, Col. 7).

Additional Analyses: Inclusion of variables on seabirds and surface fauna

In an attempt to increase explanatory power we added a set of recently-developed indices of abundance for other animals: seabirds from strip-transect sighting surveys (Ballance et al. 2002) and surface fishes and squids (Pitman et al. 2002) that are potential prey of dolphins. The full list of variables entered is given in Table 7. This extensive list of potential variables was screened by stepwise selection in CANOCO, with variables contributing less than 1% additional explanatory power excluded. The reduced set thus selected (Table 7) included all six original oceanographic variables, latitude and longitude, MOPS and STAR categorical variables, but just two of nine seabird indices, and two of seven fish/squid indices. This reduced set explained a total of 30% of the dolphin variance, down just 1% from the full set of all potential explanatory variables (Table 6b, cols. 9 and 10). This is a net increase of 10% from the previous best set which was comprised of the 6 base oceanographic variables, plus lat/long and years.

DISCUSSION

In terms of the basic questions addressed in this study, whether there had been substantial changes in patterns of habitat use between the decades sampled by the MOPS and STAR expeditions, the answer appears to be no. The basic patterns are very similar, both in terms of the multivariate habitat models as depicted in the biplots, and in terms of the geographic distributions of 'preferred' habitats, as depicted in the maps of Figures 5 and 6. One conclusion arising from this set of results is that the basic habitat descriptions arising from CCA of MOPS (Reilly and Fiedler 1994) appear robust. These depictions were in fact quantifications of the qualitative descriptions advanced by Au and Perryman (1984), based on observations made during the 1970s, so in total we have three decades of data giving very consistent pictures of habitat use by ETP dolphins. These patterns as a whole fit clearly within McGowan's (1974) ETP Biotic Province, which he defined based on a climatological analysis of multiple taxa from multiple trophic levels.

Some minor differences were observed between the decades of the 1980s and 1990s. STAR yrs are in general cooler, more productive and with shallower thermoclines, very similar in nature to the prominent La Nina of 1988. This pattern of variability is within the range expected for ENSO patterns. When stratum (core vs. outside) was considered in addition to the year sampled, the dominant pattern of separation was according to stratum, with only minor differences among years and decades. Interestingly, the small but consistent separation between the MOPS and STAR years was largely confined to the more offshore outside stratum. Within the core area occupied by both NEO spotted and E spinner dolphins there was almost no apparent difference between the MOPS and STAR periods.

Modest but notable improvements in model resulted from separating the common dolphins into separate stocks. Given the bimodality on the dominant axis for combined common dolphins, this is not too surprising. The amount of dolphin variance explained was increased by just over 2%. A more substantial improvement resulted from including information on seabirds and surface fauna. This increased explanatory power by an additional 10%, up to a total of about 30% for the dolphin species. Apparently much of the correlation structure among the birds and fishes/squids was redundant, as stepwise selection removed all but two each of the bird and fish/squid variables. The four added variables indexed the abundance of Tahiti petrel, white winged petrel, lanternfishes (myctophids) and large squids.

The bird species remaining (white winged petrel and Tahiti petrel) were not the first we would have predicted, as neither is a key member of the multispecies flocks that typically associate with dolphins in the ETP (Ballance et al. 1997) but they do provide representative contrast in both their geographical distributions and in their predator-prey relationships. Tahiti petrels are found along the 10N convergence, with both nearshore and far offshore areas of higher density; they scavenge for squids and are regarded as not dependent on tunas for foraging success (Ballance et al. 2002). In contrast, white winged petrels occur primarily at the southern edge of the study area, i.e. within the south equatorial counter current (Figure 1); they are also generally independent of tunas for foraging success, and prey on micronekton, primarily myctophids (Ballance et al. 2002). Both large squids and myctophids are preyed

upon by dolphins of the region, with spotted dolphins emphasizing squids and rarely consuming myctophids, while spinner dolphins are presumed to feed at different depths and/or times of day, and they do consume mid-water animals such as myctophids. We intend to pursue this aspect of the habitat modeling in greater depth in the near future.

In table 6b, it appears that the added seabird and fish/squid data gave the greatest increased explanation for the 3 common dolphin categories (particularly N and S) and striped dolphins.

Some caveats are worth noting. The small amounts of variance explained overall (30%) indicate that much of the place-to-place variance in dolphin abundance, as indexed by encounter rates, is not related to the oceanographic and geographic variables available for this analysis. Group size effects were not included in this analysis, and for completeness probably should be added in future studies. However, Reilly and Fiedler (1994) found no significant habitat associations with group sizes for the MOPS years, so it is not likely this will have changed substantially in more recent years.

LITERATURE CITED

- Au, D.W.K. and W.L. Perryman (1985). Dolphin habitats in the eastern tropical Pacific. *Fish. Bull. US* 83(4): 623-643.
- Ballance, L. T., R. L. Pitman, and S. B. Reilly (1997). Seabird community structure along a productivity gradient: importance of competition and energetic constraint. *Ecology* 78:1502-1518.**
- Ballance, L. T., R. L. Pitman, L. B. Spear, P. C. Fiedler (2002).** Investigations into temporal patterns in distribution, abundance and habitat relationships within seabird communities of the eastern tropical Pacific. Administrative Report No. LJ-02-17, NMFS, Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037.
- Barlow, J., T. Gerrodette and J. Forcada (2001). Factors affecting perpendicular sighting distances on shipboard line-transect surveys for cetaceans. *Journal of Cetacean Research and Management* 3(2):201-212.
- Blackburn, M., R.M. Laurs, R.S. Owen & B. Zeitschel (1970). Seasonal and areal changes in standing stocks of phytoplankton, zooplankton and micronekton in the eastern tropical Pacific. *Mar. Biol.* 7: 14-31.
- Carr, A. (1987). New perspectives on the pelagic stage of sea turtle development. *Conserv. Biol.* 1(2): 103-121.
- Chavez, F. P. & R. T. Barber (1987) An estimate of new production in the equatorial Pacific. *Deep-Sea Res.* 24: 1229-1243.
- Dizon, A.E., W.F. Perrin, and P.A. Aiken (1994). Stocks of dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific: a phylogeographic classification. NOAA Technical Report NMFS 119: 1-20.
- Fiedler, P.C. (1992). Seasonal climatologies and variability of eastern tropical Pacific surface waters. NOAA Tech. Rep. NMFS 109, 65 p.
- Fiedler, P. C. (2002) The annual cycle and biological effects of the Costa Rica Dome. *Deep-Sea Res. I* 49: 321-338.
- Gregr, E.J. and A.W. Trites (2001). Predictions of critical habitat for five whale species in the waters of coastal British Columbia. *Can. J. Fish. Aquat. Sci.* 58: 1265-1285.
- King, F.D. (1986). The dependence of primary production in the mixed layer of the eastern tropical Pacific on the vertical transport of nitrate. *Deep-Sea Res.* 33(6): 733-754.
- McCreary, J. P., H. S. Lee & B. B. Enfield (1989) The response of the coastal ocean to strong offshore winds: with application to circulations in the Gulfs of Tehuantepec and Papagayo. *J. Mar. Res.* 47: 81-109.
- McGowan, J.A. (1974). The nature of oceanic ecosystems. In: Miller, C.B. (ed.) *The Biology of the Oceanic Pacific*. Oregon State Univ. Press, Corvallis, p. 9-28.
- Nasu, K. (1963). Oceanography and whaling ground in the subarctic region of the Pacific Ocean. *Sci. Rep. Whales Res. Inst.* 17: 105-135.
- Perrin, W.F. (1975). Distribution and differentiation of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific. *J. Fish. Res. Bd Can.* 32: 1059 - 1067.

- Philbrick, V.A., P.C. Fiedler, J.T. Fluty and S.B. Reilly (2001). Report of oceanographic studies conducted during the 2000 eastern tropical Pacific Ocean survey on the research vessels David Star Jordan and McArthur. NOAA Technical Memorandum NMFS-SWFSC-309. 20 p.
- Reilly, S.B. (1990). Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. *Mar. Ecol. Prog. Ser.* 66: 1-11.
- Reilly, S.B and P.C. Fiedler (1994). Interannual variability of dolphin habitats in the eastern tropical Pacific. I: Research vessel surveys, 1986-1990. *Fish. Bull US* 92: 434-450.
- Ter Braak, C.J.F. (1986). Canonical correspondence analysis: a new eigenvector ordination technique for multivariate direct gradient analysis. *Ecology* 67(5): 1167-1179.
- Townsend, C.H. (1935). The distribution of certain whales as shown by logbook records of American whaleships. *Zoologica* 19: 1-50.
- Tsuchiya, M. (1974) Variation of surface geostrophic flow in the eastern intertropical Pacific Ocean. *Fish. Bull. U.S.* 72(4): 1075-1086..
- Wyrski, K. (1964). Upwelling in the Costa Rica Dome. *Fish. Bull., U.S.* 63: 355-372
- Wyrski, K. (1966). Oceanography of the eastern equatorial Pacific Ocean. *Oceanogr. Mar. Biol. Ann. Rev.* 4: 33-68

LIST OF TABLES AND FIGURES

Tables

1. Search effort and number of cetacean schools recorded by yr, 1998-2000, from the STAR expedition in the ETP.
2. Environmental data from the STAR expedition by yr, 1998-2000, used in the CCAs.
3. Correlation coefficients among environmental variables, canonical species axes and environmental axes estimated by a canonical correspondence analysis of cetacean abundances in the eastern tropical Pacific during the STAR expedition of 1998, 1999 and 2000.
4. Ordination results from the base-case CCA of the STAR data set.
5. Comparative CCA ordinations for the STAR data set.
6. Comparative CCA ordinations for the combined STAR and MOPS data set.
7. Full and reduced variable sets for ordination of combined MOPS and STAR data.

Figures

1. Schematic representation of the surface circulation and water masses of the ETP.
2. Study area with STAR and MOPS cruise tracks for each year.
3. Frequency histograms, transformed to percentages, of first two environmental axis scores in locations where dolphin schools were sighted, for seven species/stocks.
4. Biplots: STAR (4a) vs MOPS (4b).
5. Maps of axis 1 for all 8 yrs.
6. Maps of axis 2 for all 8 yrs.
7. Biplot: combined data with years' means.

Table 1. Search effort and number of cetacean schools recorded by year, 1998-2000, from the *Stenella* Abundance Research expedition in the eastern tropical Pacific.

	Year			Total
	1998	1999	2000	
Km Searched	42,724	29,817	30,270	102,811
Number of Sightings of				
Spotted dolphins ¹	93	158	100	351
Common dolphins ²	69	226	97	392
Spotted with Eastern Spinner ³	37	89	52	178
Spotted with Whitebelly Spinner ³	12	16	17	45
Eastern Spinner	18	22	15	55
Whitebelly Spinner	4	13	6	23
Striped dolphins ⁴	135	240	151	526
Total sightings used in this analysis	368	764	438	1570
Other cetacean sightings	1603	401	698	2702
Totals	1971	1165	1136	4272

¹ *Stenella attenuata*.

² *Delphinus delphis*.

³ *S. longirostris*.

⁴ *S. coeruleoalba*.

Table 2. Oceanographic data from the *Stenella* Abundance Research expedition, 1998-2000, used in the canonical correspondence analyses. Table entries list numbers of observations for discrete measurements, or number of km covered during continuous measurements. XBT = expendable bathythermograph; CTD = conductivity-temperature-depth.

Data type	Year			Total
	1998	1999	2000	
Surface temperature, salinity (km)	43,952	30,241	30,867	105,060
Surface chlorophyll measurements	1215	809	806	2830
XBT measurements (drops)	895	655	659	2209
CTD measurements (stations)	547	393	412	1352

Table 3. Correlation coefficients among environmental variables, canonical species axes and environmental axes estimated by a canonical correspondence analysis of cetacean abundances in the eastern tropical Pacific during the *STAR expedition* of 1998, 1999 and 2000.

SPEC AX1	1.0000							
SPEC AX2	.0242	1.0000						
SPEC AX3	-.0239	-.1543	1.0000					
SPEC AX4	-.0580	-.0507	.1130	1.0000				
ENVI AX1	.7216	.0000	.0000	.0001	1.0000			
ENVI AX2	.0000	.4577	.0000	.0000	.0000	1.0000		
ENVI AX3	.0000	.0000	.2570	.0000	.0000	.0000	1.0000	
ENVI AX4	.0000	.0000	.0000	.1519	.0000	.0000	.0000	1.0000
Temp	-.6285	.1704	-.0745	-.0158	-.8710	.3723	-.2899	-.1039
Sal	.0663	-.1003	.0585	.0130	.0919	-.2193	.2275	.0855
Simgat	.4704	-.1858	.0783	.0150	.6519	-.4060	.3044	.0987
LogCHL	.4325	.1831	.0231	.0035	.5993	.4001	.0897	.0231
Z20	-.5329	-.0226	.1635	-.0272	-.7385	-.0493	.6360	-.1789
ZDIFF	.3336	.2002	.0493	-.0853	.4623	.4375	.1916	-.5618
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ENVI AX4
Temp	1.0000							
Sal	-.3192	1.0000						
Simgat	-.8662	.7484	1.0000					
LogCHL	-.3957	.0243	.2802	1.0000				
Z20	.4553	.1282	-.2522	-.3317	1.0000			
ZDIFF	-.2526	.0423	.1844	.1304	-.1872	1.0000		
	Temp	Sal	Simgat	LogCHL	Z20	ZDIFF		

Table 4. Ordination results from a CCA of the 1998-2000 STAR expedition, for the simple six variable model reported in Table 3, including only oceanographic variables. This simple model ordination is presented as a base-case comparison with Table 4 of Reilly and Fiedler (1994), for the 1986-1990 MOPS expedition.

	Canonical Axes				<u>Eigenvalues</u>
	1	2	3	4	
Eigenvalues :	.339	.113	.037	.011	
Species-environment correlations :	.722	.458	.257	.152	
Cumulative percentage variance					
of species data :	11.0	14.7	15.9	16.3	
of species-environment relation:	67.5	90.1	97.5	99.7	
Sum of all unconstrained eigenvalues					3.073
Sum of all canonical eigenvalues					0.501
			<u>Species Total</u>		
Cumulative percentage variance					
spotted dolphin ¹	12.2	18.5	20.2	20.5	
common dolphin ²	49.0	49.4	49.6	49.7	
spotted and eastern spinner ³ dolphins	5.5	7.5	9.7	10.5	
spotted and whitebelly spinner ³ dolphins	3.9	6.9	8.1	8.9	
eastern spinner dolphin	3.1	7.3	7.4	7.4	
whitebelly spinner dolphin	1.4	2.8	4.0	4.0	
stiped dolphin ⁴	1.0	13.7	15.4	15.9	

¹ *Stenella attenuata*.

² *Delphinus delphis*.

³ *Stenella longirostris*.

⁴ *S. coeruleoalba*.

Table 5. STAR comparative ordinations.

Comparative ordination from canonical correspondence analyses of seven types of dolphin schools in the eastern tropical Pacific with six different sets of environmental variables for STAR data (1998-2000). Set 1 = surface temperature (SST), thermocline depth (Z20), thermocline strength (ZD), surface salinity (SAL), surface chlorophyll (LOGC) and surface density (SIGMA-T). Set 2 = Set 1 plus years (1-3) as categorical variables. Set 3 = Set 1 plus latitude and longitude. Set 4 = Set 1 plus both latitude and longitude and years. Set 5 = years (1-3) as categorical variables, after removing variance associated with all other environmental variables (Set 3).

	Environmental variable set				
	1	2	3	4	5
Eigenvalue sum	0.501	0.513	0.659	0.672	0.013
P-value	0.001	0.001	0.001	0.001	0.154
Percent variance accounted for					
total species data	16.3	16.5	21.4	21.7	0.5
Spotted dolphins ¹	20.6	20.7	21.0	21.1	0.2
Common dolphins ²	49.7	50.5	51.0	51.9	0.8
Spotted with Eastern Spinner ³	10.5	10.8	11.3	11.6	0.2
Spotted with Whitebelly Spinner ³	8.9	9.0	27.9	28.1	0.2
Eastern Spinner	7.7	7.7	8.1	8.1	0.0
Whitebelly Spinner	4.0	4.9	8.9	9.7	0.8
Striped dolphins ⁴	15.9	16.2	18.7	19.2	0.6

¹ *Stenella attenuata*.

² *Delphinus delphis*.

³ *S. longirostris*.

⁴ *S. coeruleoalba*.

Table 6. Combined MOPS and STAR ordinations.

Comparative ordination from canonical correspondence analyses of seven types of dolphin schools in the eastern tropical Pacific, with six different sets of environmental variables for the combined MOPS and STAR data. Set 1 = surface temperature (SST), thermocline depth (Z20), thermocline strength (ZD), surface salinity (SAL), surface chlorophyll (LOGC) and surface density (SIGMA-T). Set 2 = Set 1 plus years (1-8) as categorical variables. Set 3 = Set 1 plus latitude and longitude. Set 4 = Set 1 plus both latitude and longitude and years. Set 5 = years (1-8) as categorical variables, after removing variance associated with all other environmental variables (Set 3). Set 6 = expedition (MOPS and STAR) as categorical variables, after removing variance associated with Set 3.

	Environmental variable set					
	1	2	3	4	5	6
Eigenvalue sum	0.422	0.469	0.588	0.633	0.044	0.021
P-value	0.001	0.001	0.001	0.001	0.001	0.001
Percent variance accounted for						
total species data	13.8	15.1	19.2	20.4	1.8	0.9
Spotted dolphins ¹	12.9	14.3	13.5	15.0	1.4	0.7
Common dolphins ²	38.2	41.5	42.9	45.9	3.0	1.9
Spotted with Eastern Spinner ³	15.4	15.7	17.5	17.8	0.3	0.0
Spotted with Whitebelly Spinner ³	8.6	9.5	18.5	20.0	1.5	0.4
Eastern Spinner	7.3	7.9	8.5	9.0	0.6	0.1
Whitebelly Spinner	4.9	6.0	14.3	14.8	0.5	0.1
Striped dolphins ⁴	3.8	7.2	11.4	14.5	3.1	1.8

¹ *Stenella attenuata*.

² *Delphinus delphis*.

³ *S. longirostris*.

⁴ *S. coerulesoalba*.

Table 6b. Combined MOPS and STAR ordinations, continued.

Comparative ordination from canonical correspondence analyses of nine types of dolphin schools in the eastern tropical Pacific (the same as those in table 6 but with Common dolphins divided into 3 new categories: Northern Common, Central Common and Southern Common dolphins). Four different sets of environmental variables for the combined MOPS and STAR data were run with the inclusion of these new dolphin categories. Set 7 = Set 1 (see Table 6). Set 8 = Set 7 plus years (1-8) within the core study area and years in the outer study area as categorical variables. Set 9 = Set 7 plus latitude and longitude, expedition (MOPS and STAR), and 16 additional variables representing seabirds and surface fauna (detailed in Table 7). Set 10 = Set 9 after stepwise selection of variables, reducing the predictor set (detailed in Table 7).

	Environmental variable set			
	7	8	9	10
Eigenvalue sum	0.742	0.968	1.504	1.441
P-value	0.001	0.001	0.001	0.001
Percent variance accounted for				
total species data	16.1	20.0	31.0	30.0
Spotted dolphins ¹	12.9	15.6	20.1	18.4
Northern Common dolphins ²	17.5	22.2	48.9	48.1
Central Common dolphins ²	17.0	19.5	27.6	26.8
Southern Common dolphins ²	42.6	46.2	65.0	62.8
Spotted with Eastern Spinner ³	15.4	17.5	24.8	22.5
Spotted with Whitebelly Spinner ³	8.6	20.9	30.8	30.2
Eastern Spinner	7.3	10.2	10.8	8.1
Whitebelly Spinner	4.9	11.7	20.3	20.0
Striped dolphins ⁴	3.8	9.6	26.1	23.2

¹ *Stenella attenuata*.

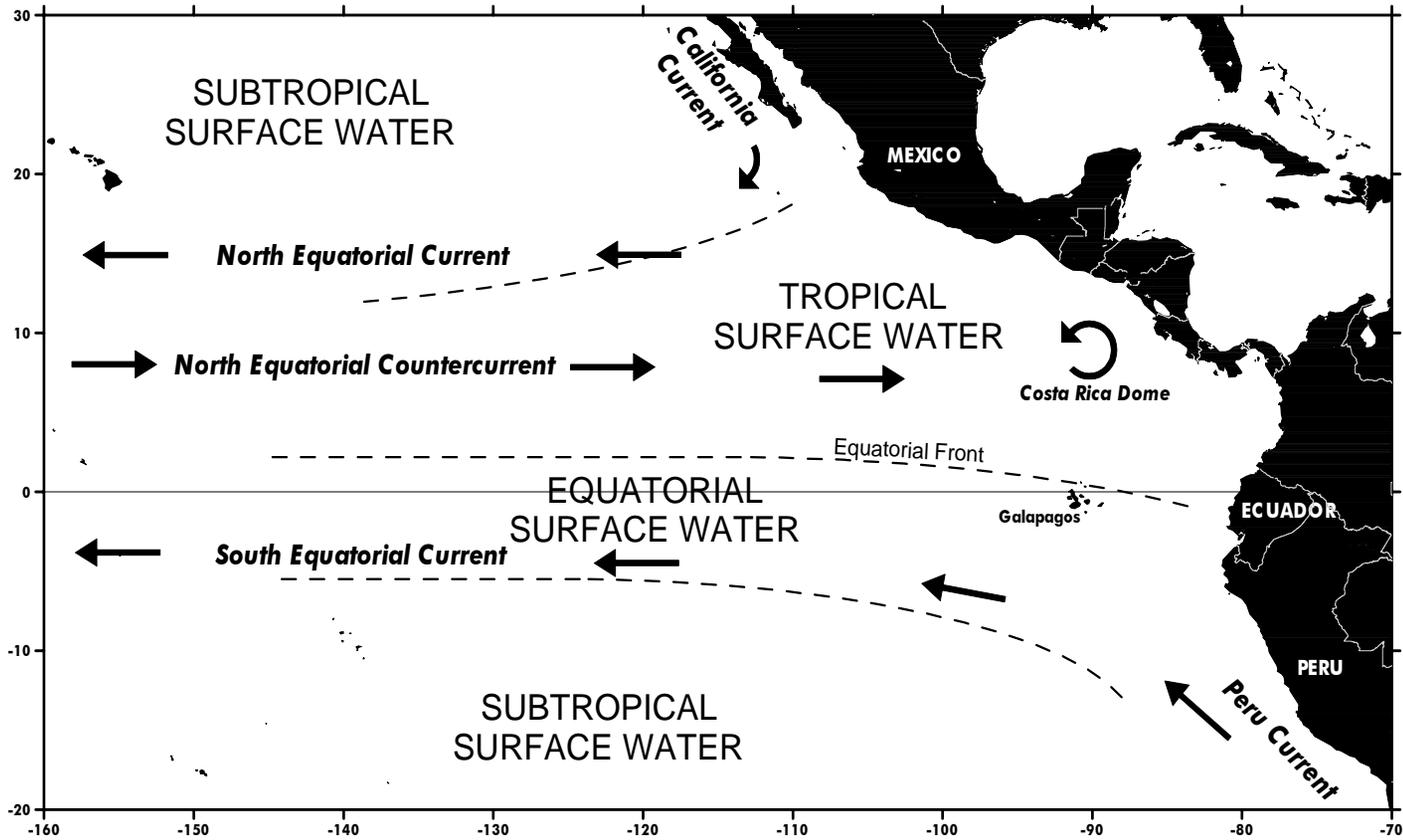
² *Delphinus delphis*.

³ *S. longirostris*.

⁴ *S. coerulesoalba*.

Table 7. Full and reduced variable sets for ordination of combined MOPS and STAR data.

Variables Entered	Variables Selected
Temperature	Temperature
Salinity	Salinity
Simgat	Simgat
LogCHL	LogCHL
Z20	Z20
ZDIFF	ZDIFF
Latitude	Latitude
Longitude	Longitude
MOPS	MOPS
STAR	STAR
White-winged Petrel	White-winged Petrel
Tahiti Petrel	Tahiti Petrel
Myctophids	Myctophids
Large Squid	Large Squid
Red-footed Booby	
Sooty Tern	
Wedge-rumped Storm Petrel	
Phalarope spp.	
Wedge-tailed Shearwater	
Juan Fernandez Petrel	
Leach's Storm Petrel	
Oxyporhamphus	
Exocoetus	
Four-winged Flyingfish	
Medium Squid	
Small Squid	



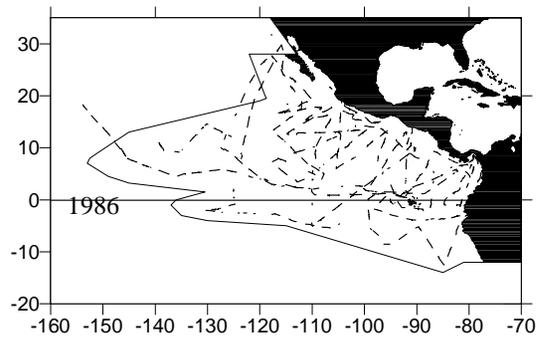


Figure 1. Schematic representation of the surface circulation and water masses of the eastern tropical Pacific Ocean.

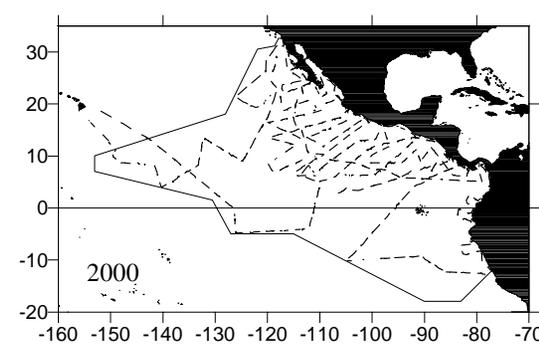
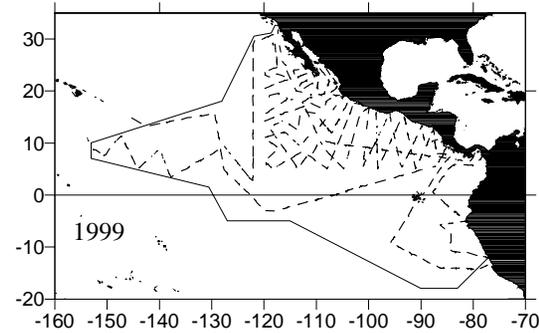
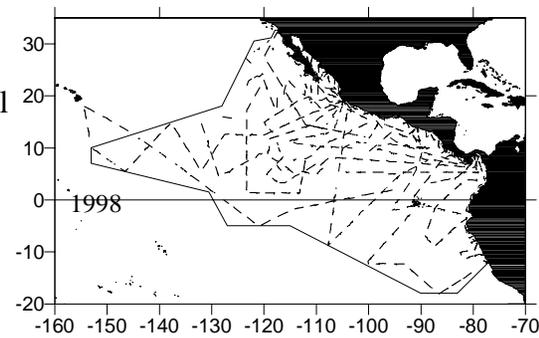
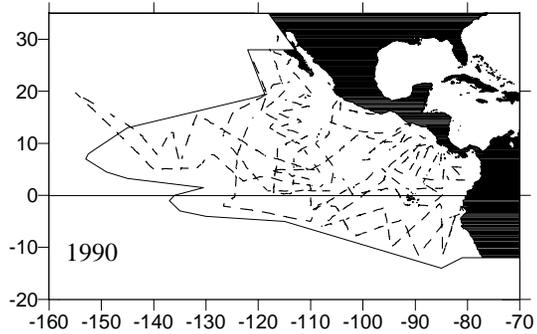
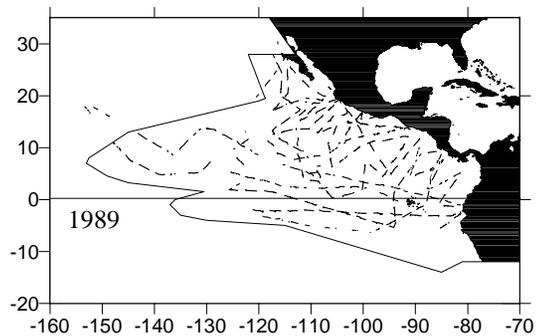
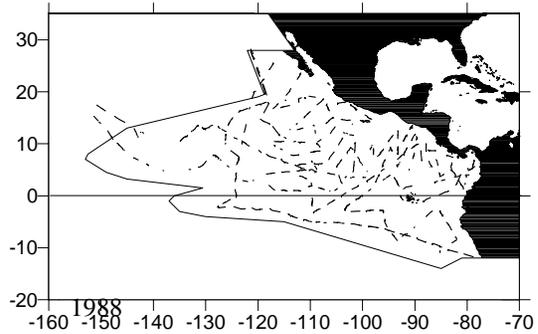
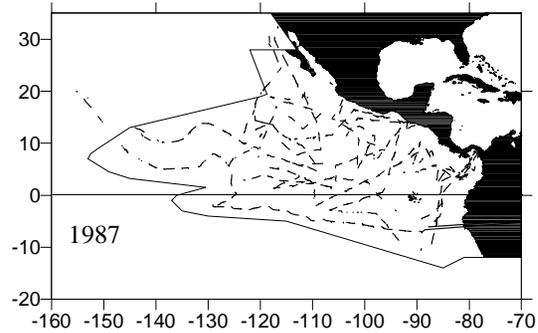
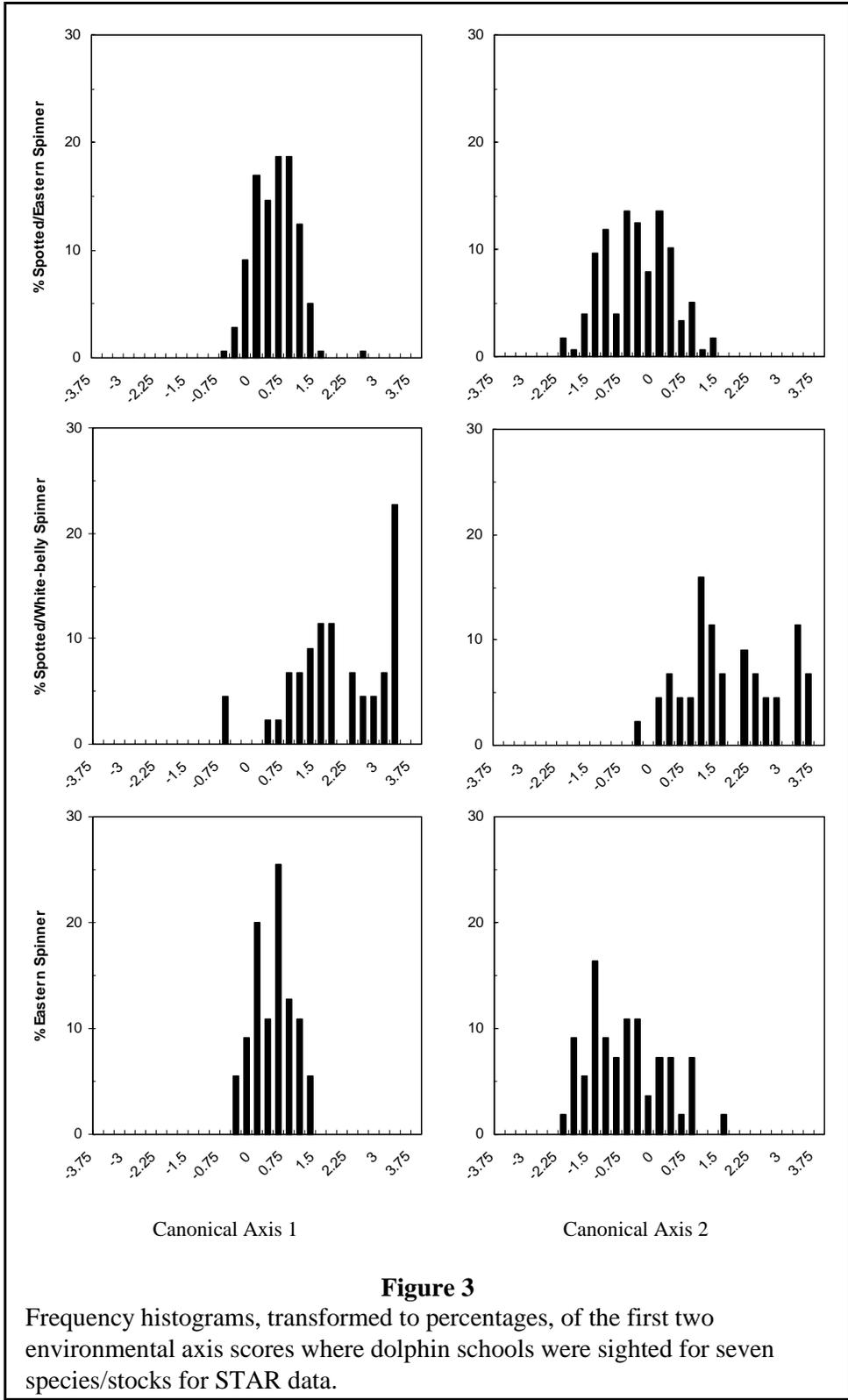


Figure Study with on-cruise for each the (1986- and (1998- expediti



2. areas effort tracks year of MOPS 1990) STAR 2000) ons.

Figure 3

Frequency histograms, transformed to percentages, of the first two environmental axis scores where dolphin schools were sighted for seven species/stocks for STAR data.

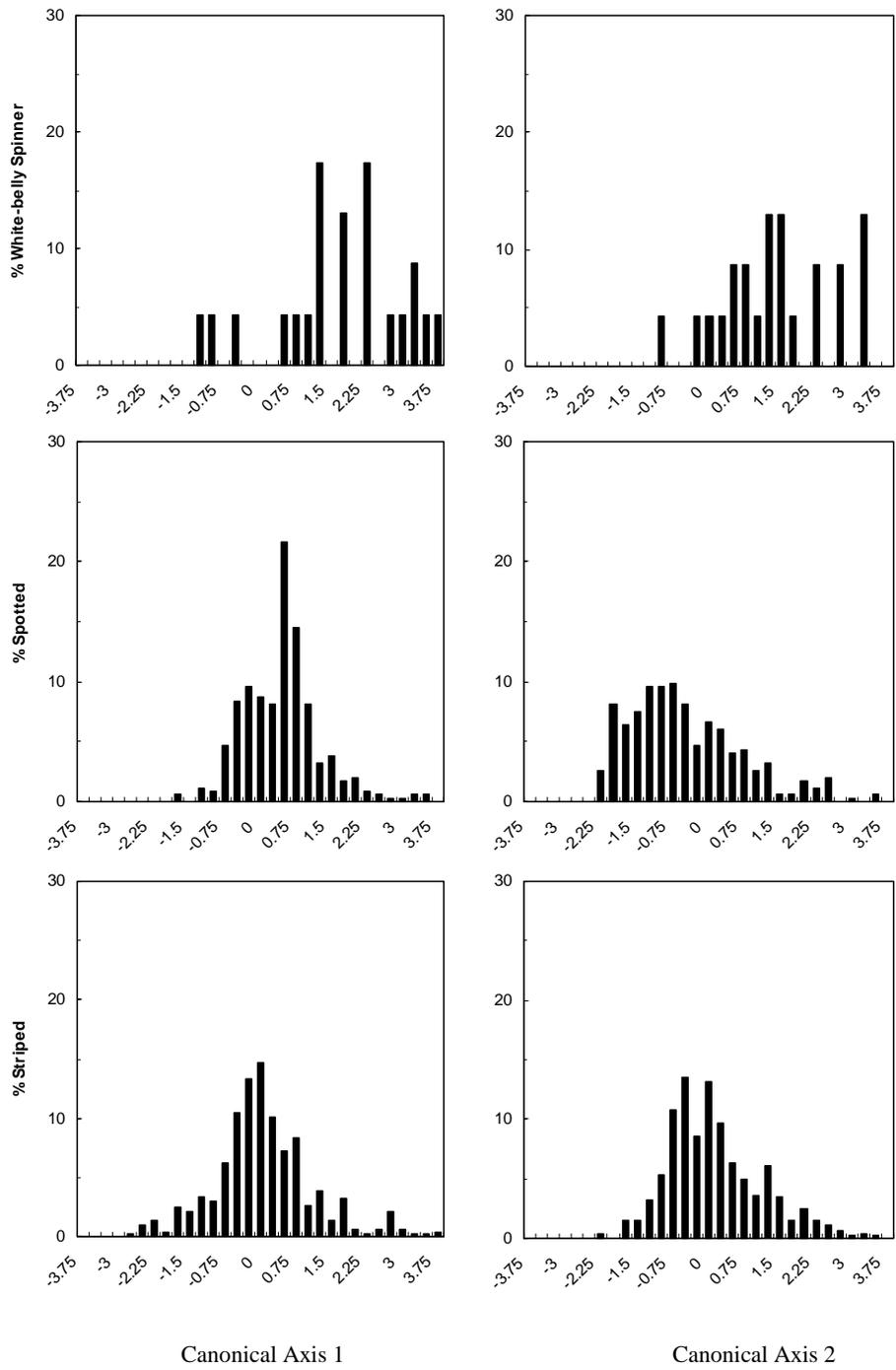
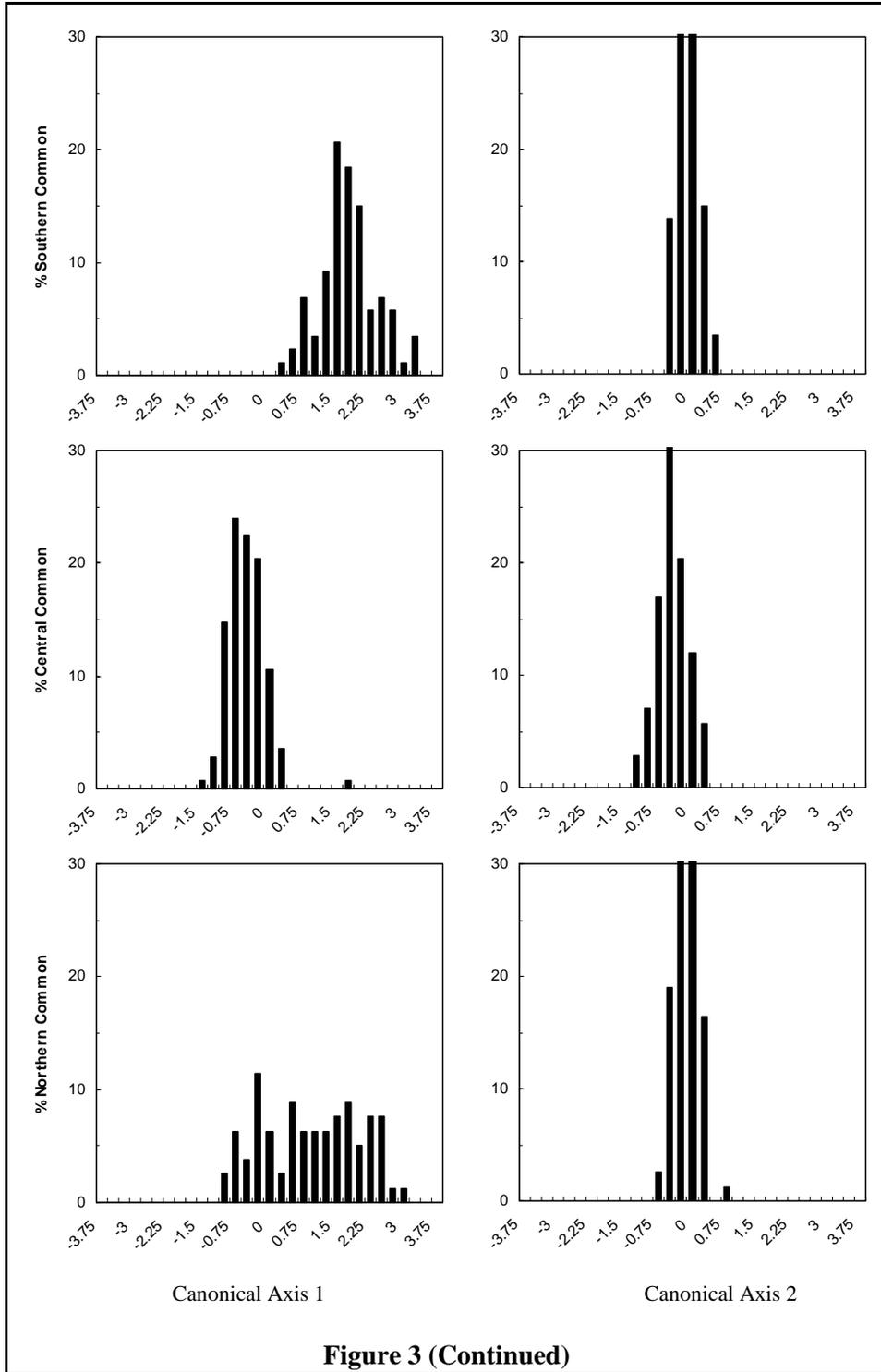


Figure 3 (Continued)



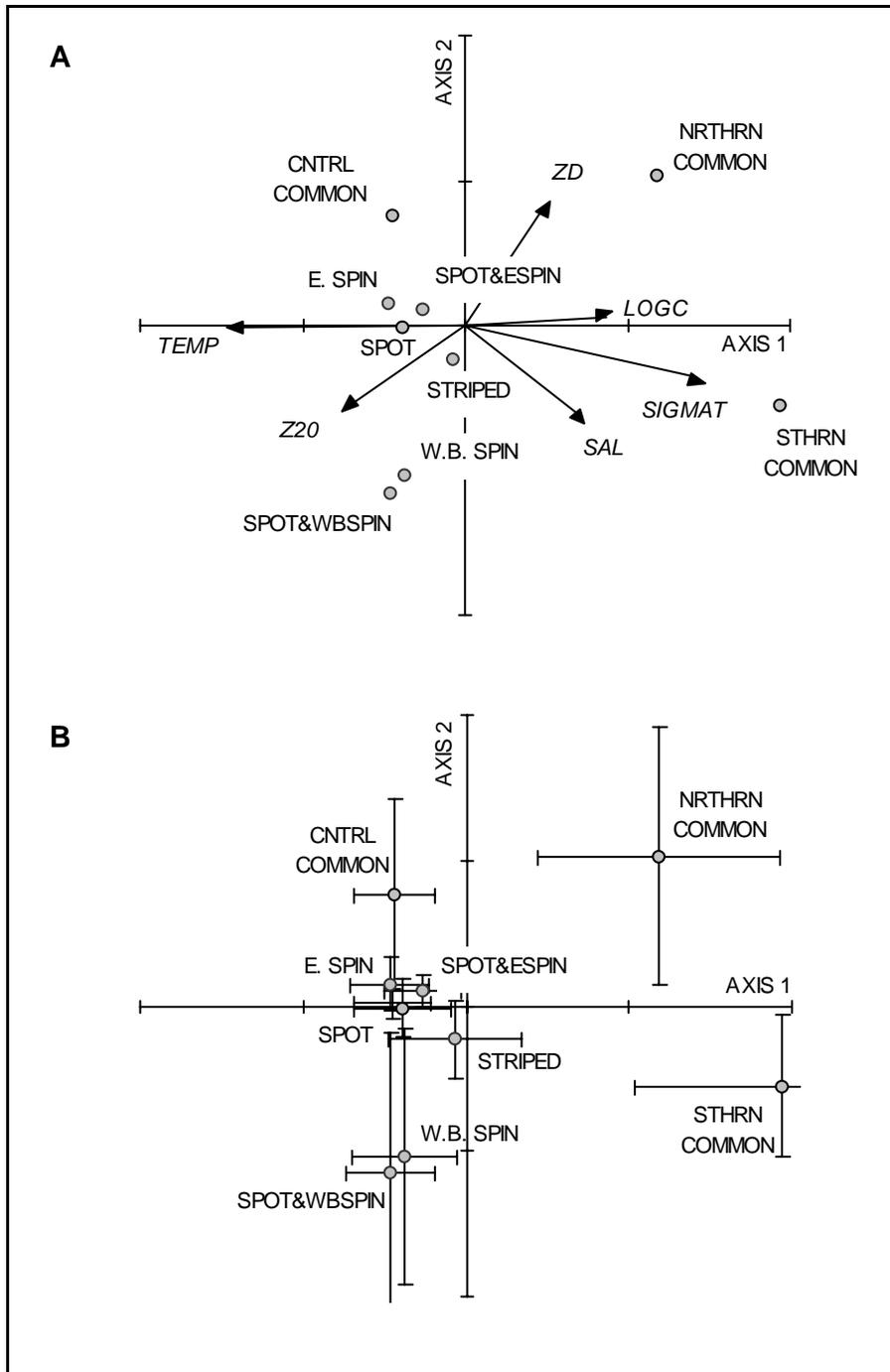


Figure 4a. Ordination results from CCA of cetacean species/stocks and environmental conditions in the ETP for **STAR** data (1998-2000). (A) Biplot of first two canonical axes and environmental variables. (B) Ordination showing 95% confidence limits for the species. In 5A, species are represented by circles and environmental variables by arrows.

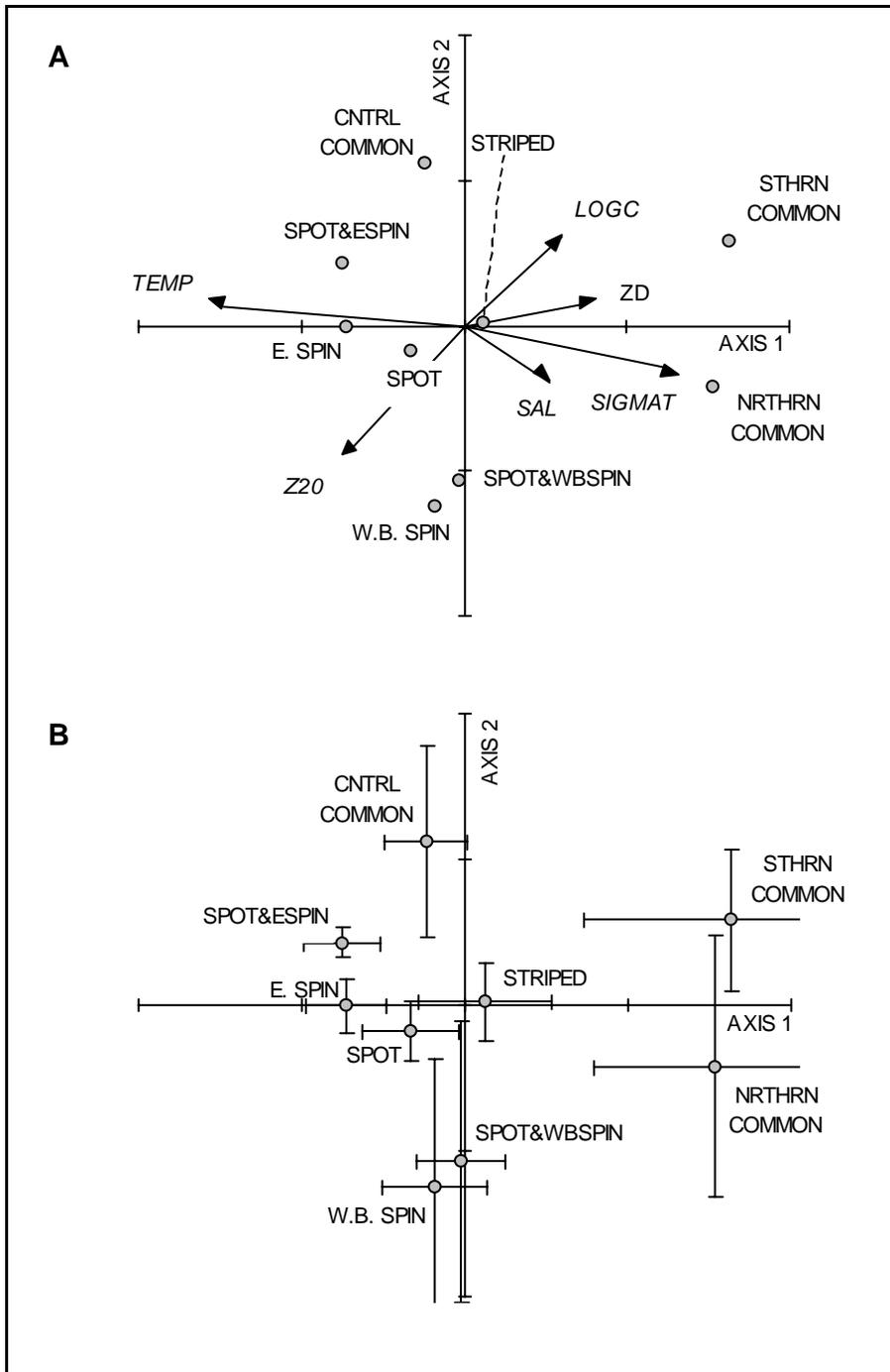


Figure 4b. Ordination results from CCA for **MOPS** years, 1986-1990.

Canonical Axis 1

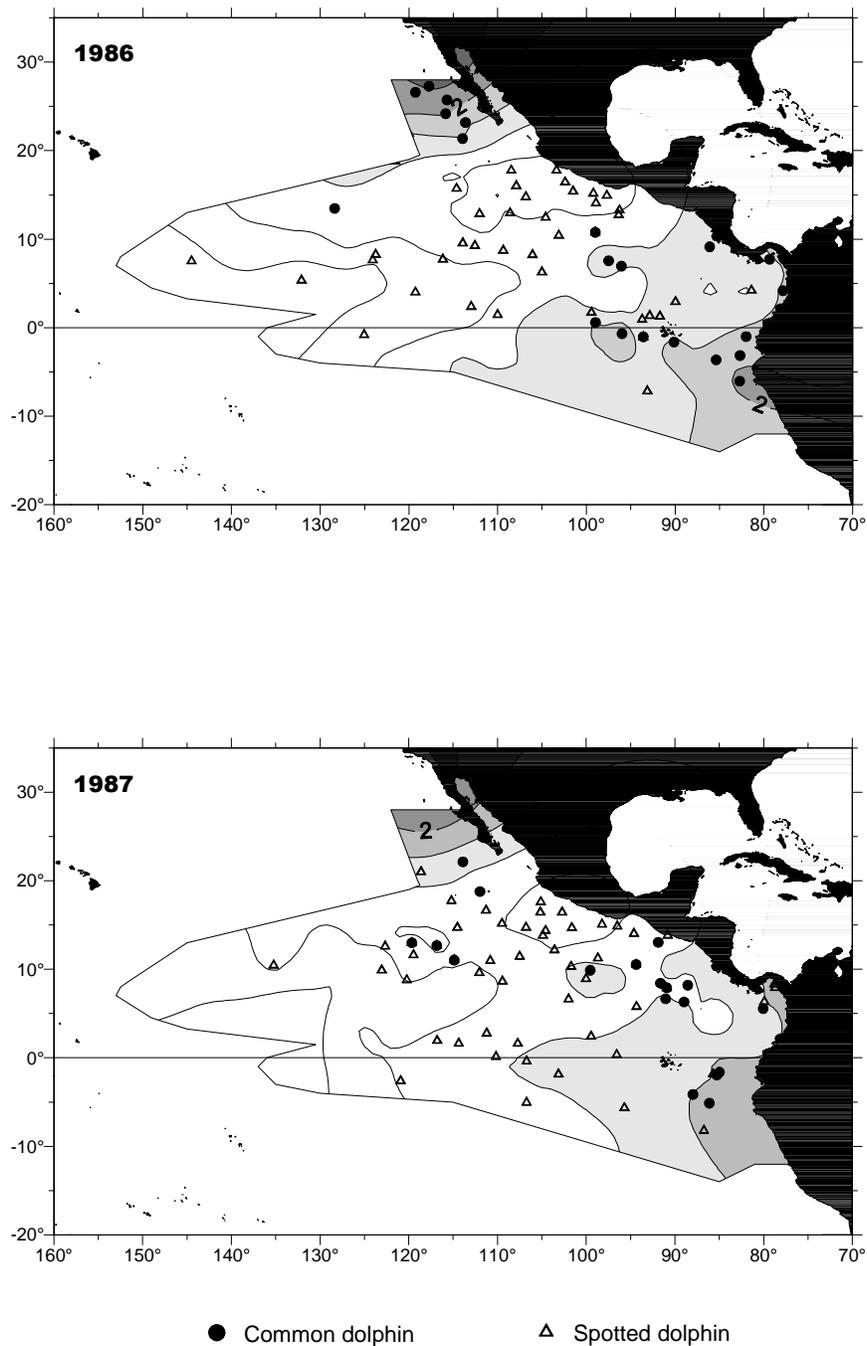


Figure 5. Maps of distribution of canonical axis 1 for 1986-2000. Positive areas are shaded. Spotted dolphin, *Stenella coeruleoalba*, sightings are represented by open triangles and common dolphin, *Delphinus delphis*, by closed circles.

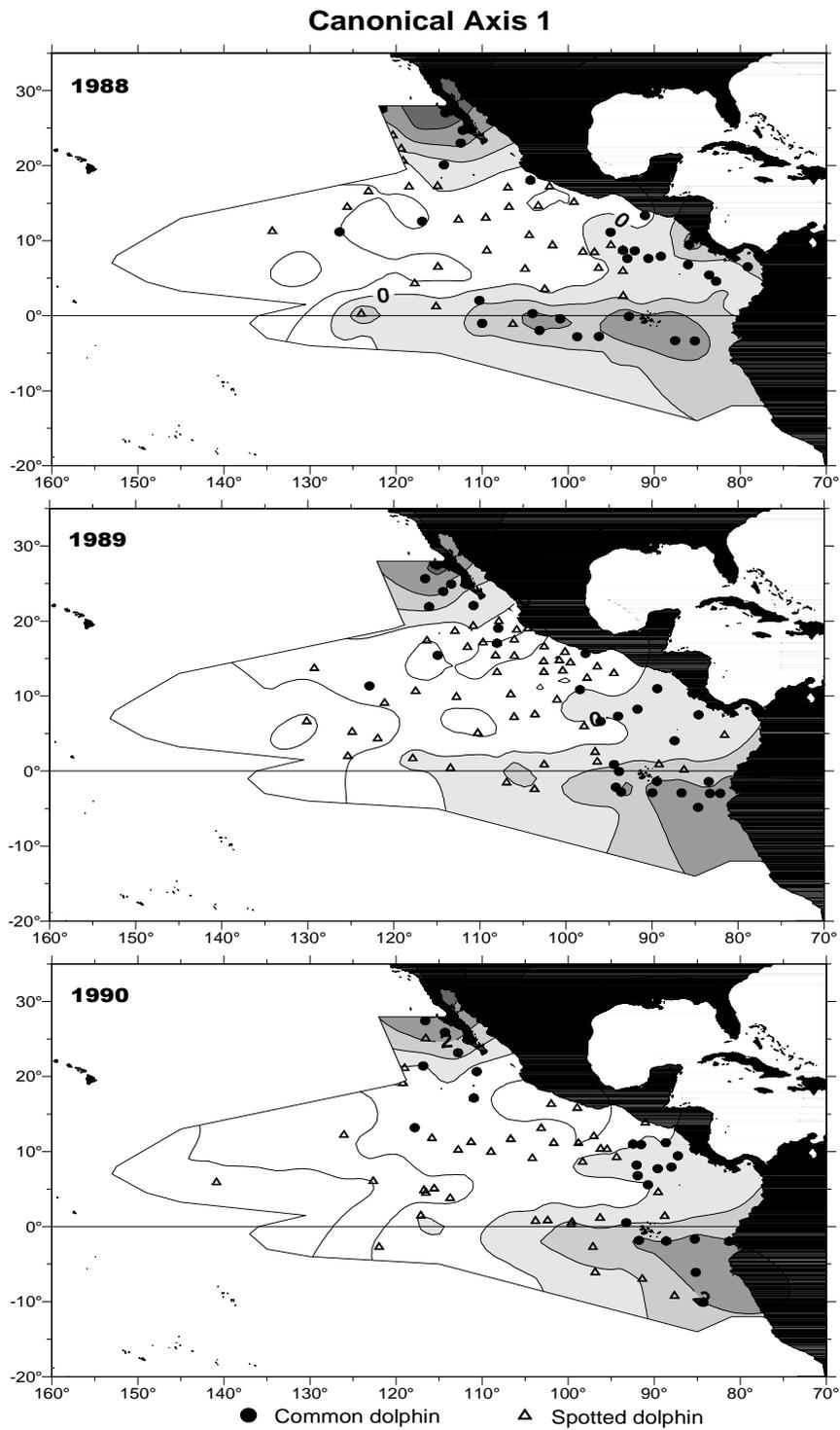


Figure 5 (Continued).

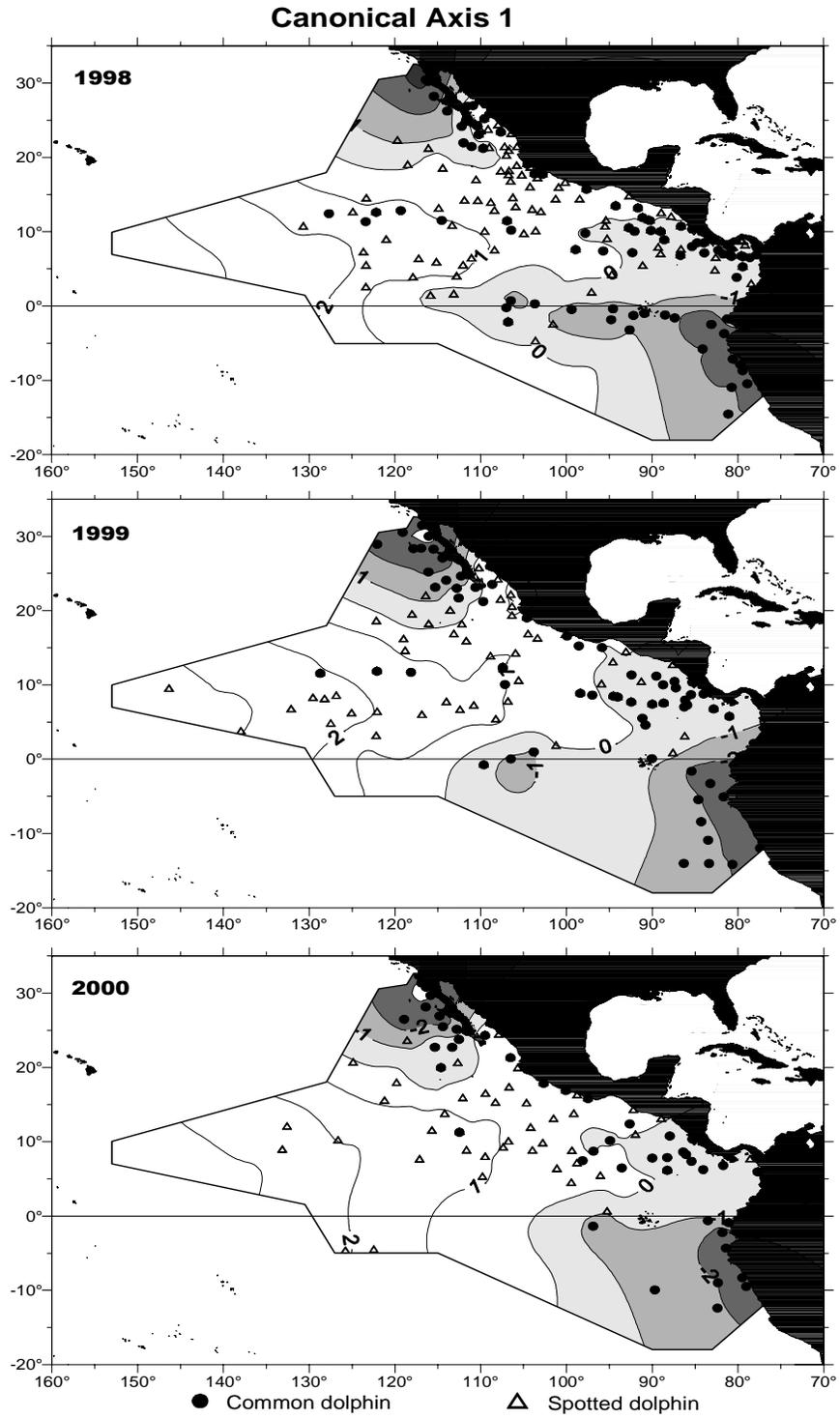


Figure 5 (Continued).

Canonical Axis 2

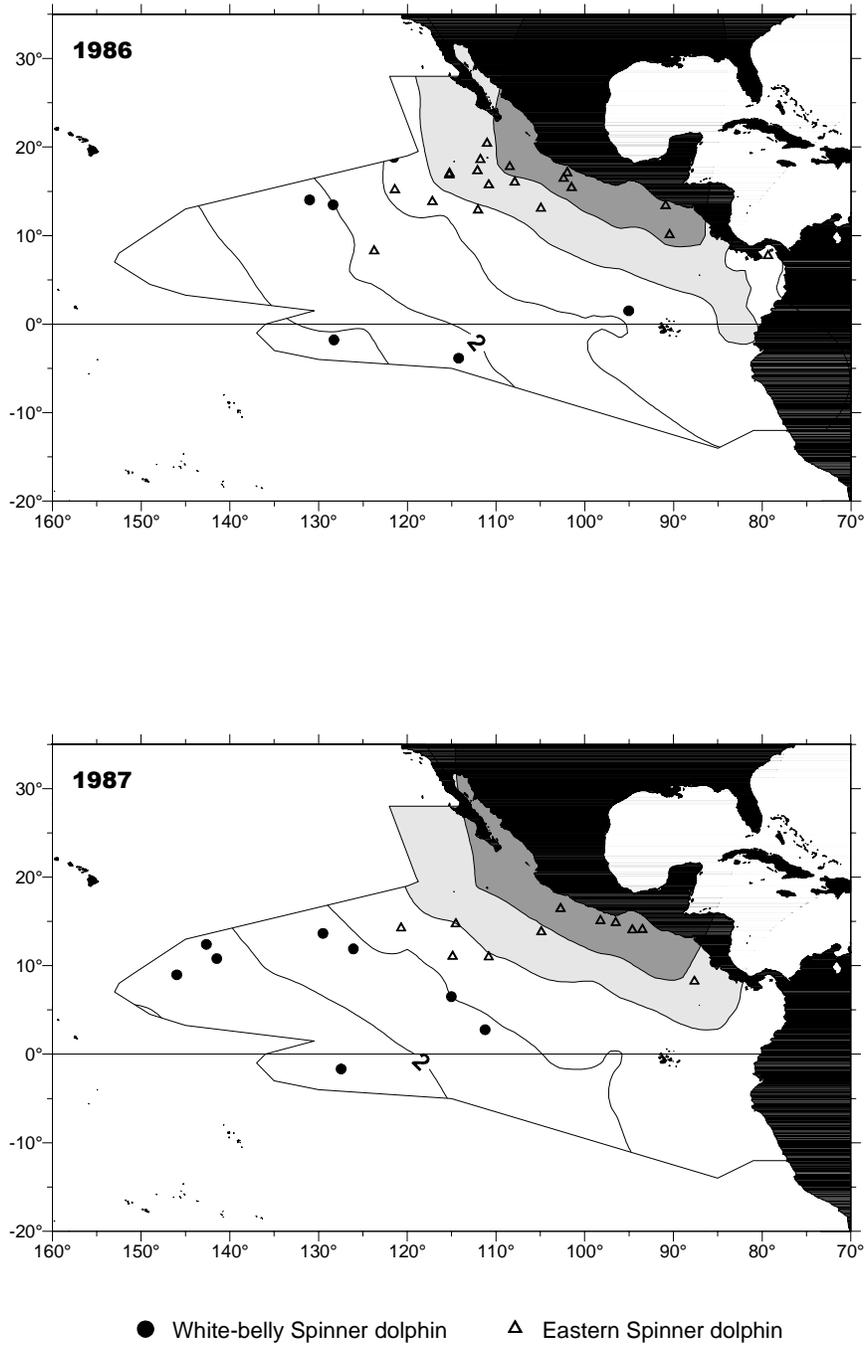


Figure 6. Maps of distribution of canonical axis 2 for 1998-2000. Negative areas are shaded. Eastern spinner dolphin, *Stenella longirostris*, sighting localities are represented by closed circles and whitebelly spinner dolphin, *S. longirostris*, by open triangles.

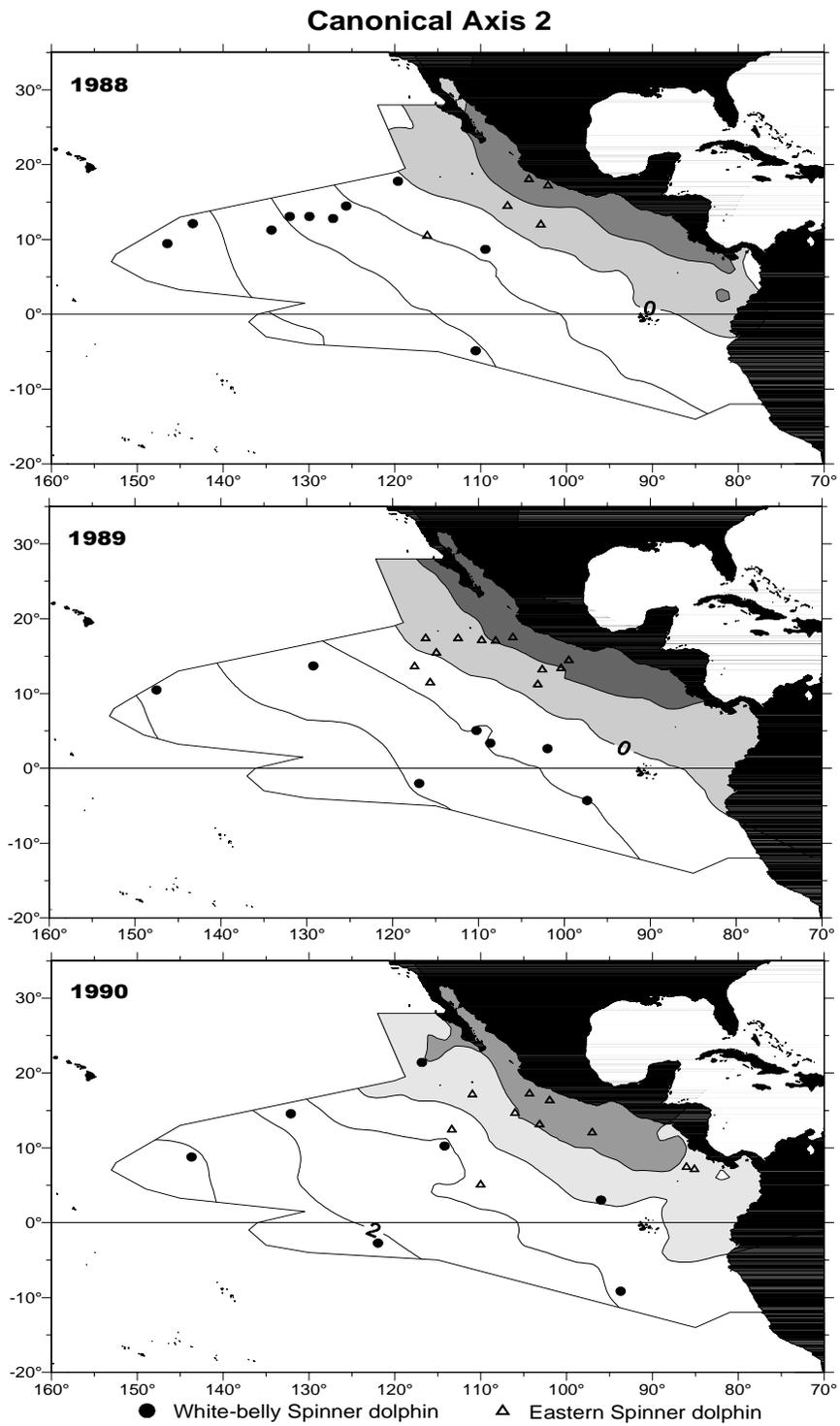


Figure 6 (Continued).

Canonical Axis 2

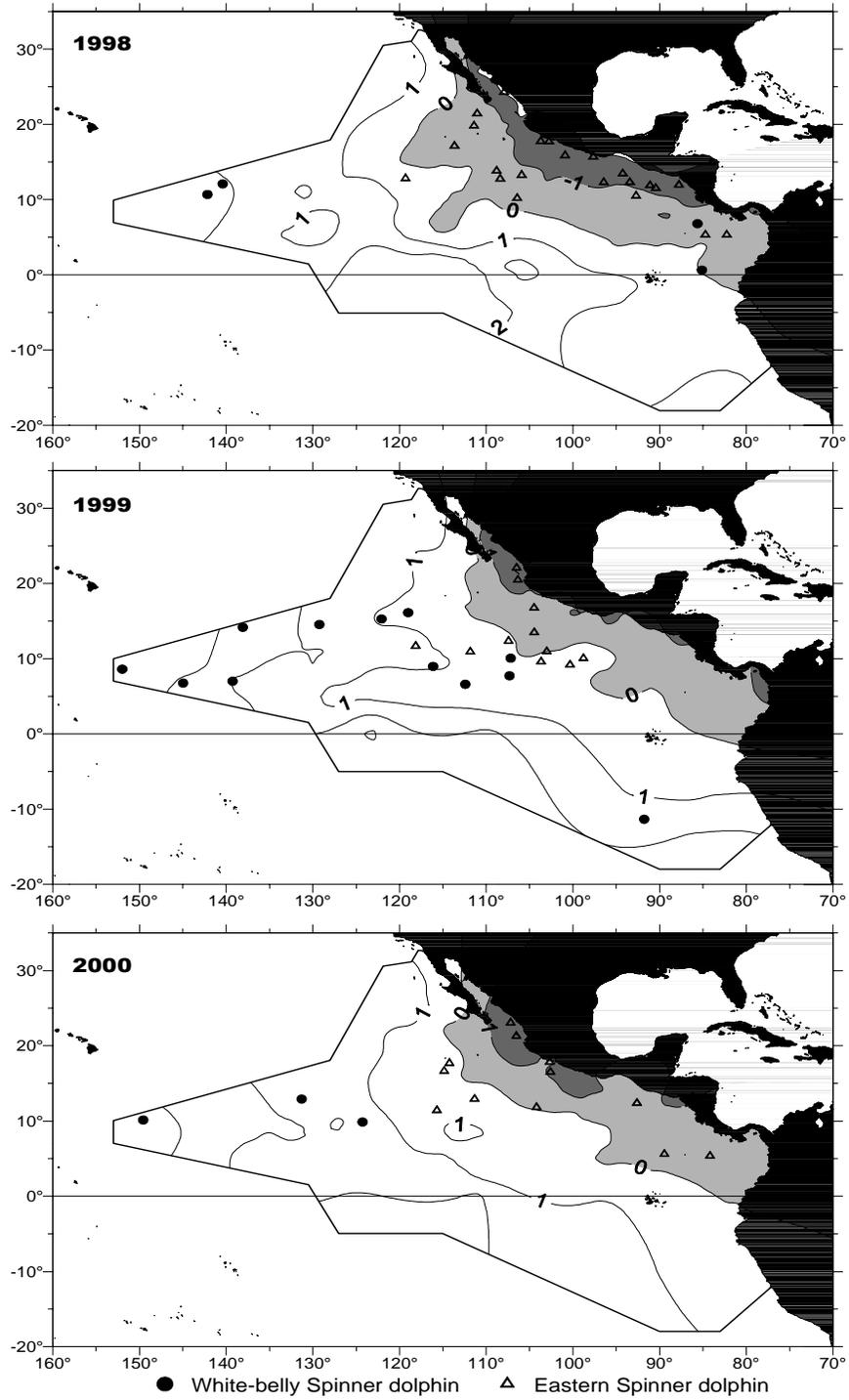


Figure 6 (Continued).

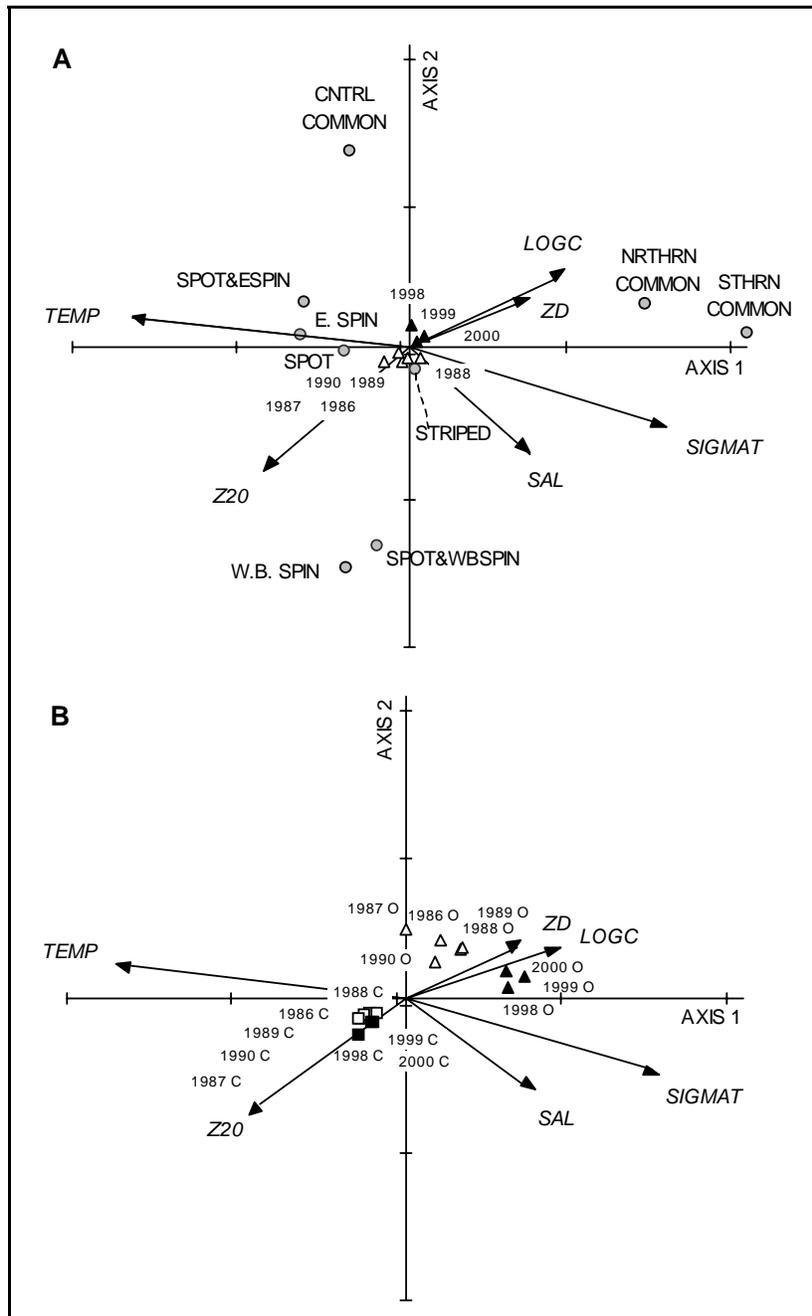


Figure 7. Combined STAR and MOPS ordination biplots. (A) Biplot of first two canonical axes with seven dolphin school types (circles), six oceanographic variables (arrows), and the eight years as categories (triangles). (B) Biplot with six oceanographic variables (arrows) and the eight years as categorical values for both the core area (C) and the outer area (O). Core area yearly means are

represented by solid and open squares and outer area values by solid and open triangles for STAR and MOPS years respectively.

APPENDIX

Responses to CIE Reviewer Comments

Hunt

Determine whether the degree of clumping, size, or frequency of observed foraging of cetacean groups has varied over time.

Response: This would be very interesting, but it is out of the scope of analyses possible in this CCA application. Further, it would be limited by the manner in which the sightings data are collected, with approximately 100km lengths of effort separated by roughly equivalent distances from the ships transiting at night. Clumping could be examined only on a relatively large scale, given the 100km average length of a unit of effort. This is a subject that we could pursue later, given time to dig into the data archives for other cruises (not standard line transect, dolphin abundance cruises) that could provide long sections of uninterrupted effort.

Where possible, it would be useful to examine whether data gathered prior to 1986 could be used in these analyses.

Response: We have looked into this, and it appears it could be done for some earlier cruises, but only with a subset of the basic six-variable set used here. This would require a procedure similar to that we used in an earlier paper (Fiedler and Reilly, 1994), estimating a reduced model for a subset of variables. In initial attempts recently we found this produced a model with substantially worse predictive ability (down to less than 10% variance explained) and so we judged it to be of limited help in addressing the larger questions related to possible decadal-level changes in habitat use patterns.

41

Oxenford

Incorporate some index of prey abundance (e.g. myctophidae, hemiramphidae and exocoetidae) for which good data exist (see Pitman et al. 2000, working paper 7) and bird associations into the CCA.

Response: Done. Good suggestion - it increased the model performance substantially.

Distinguish between common dolphin stocks, particularly as the models appear to be particularly strong for this species.

Response: Done. This eliminated the nagging bimodality for the combined common dolphins on the

dominant axis.

Post-stratify the data in all of the studies into core and outer areas, and further emphasis on looking for signals in the core area since this represents the key habitat of the target dolphin species.

Response: Done. This clarified that there was a small difference between the decades, but only in the outside stratum, which is of small importance to the stocks of primary interest, the NEO spotted and E spinners.

Dower

Include data on the presence of tuna or flyingfish.

Response: We did include data on flyingfish, other surface fishes and squids represented in the dip net data, and seabirds. Tuna data were not available contemporaneous with our daily sampling.

Drinkwater

Perform stepwise elimination as part of the CCA in order to highlight those independent variables contributing most of the explained variance of the dependent variables.

Response: Done, after also including the additional biological variables. This worked very effectively.

Include more independent variables in the CCA such as the SOI, an Equatorial Front index, nutrients, prey fishes and squids.

Response: Done for the prey fishes, squids and seabirds. Not feasible for the physical indices suggested, as they are not estimated on the spatial and temporal scales of our sampling (in the case of SOI and related climate/ocean summary statistics). It would be possible to estimate linear distance for each point in the ETP from the Equatorial Front (seasonally depicted, from satellite images?), but this would involve more new work than time allow for the present. We will look into this and similar distance measurements for follow up analyses we hope to conduct in the Fall.

Examine changes in the amplitude and frequency variability, not just mean values.

Response: This potentially could be done outside the context of the current paper, which somewhat specifically addressed habitat patterns using CCA via the software package CANOCO. This tool does consider variances explicitly, but not perhaps in the sense intended here. An entirely separate analysis, perhaps using GAMs could examine changes in amplitude and frequency variability. This is something we could pursue later, but not within the time constraints we now face.

Provide information on seasonal variability.

Response: Done. A brief section has been added to the text to summarize the seasonal patterns reported in my 1990 paper in Marine Ecology Progress Series.

Provide physical interpretation of each axis.

Response: Done, at least for the first two, dominant axes.

Clearly lay out hypotheses in the paper

Response: Casting the analyses within the context of hypothesis testing is not straightforward, nor does it seem to us to provide clear improvement to the presentation. [needs more text]

Thompson

Consider using a smaller suite of environmental variables, and using only those variables that are also available from other sources so that the temporal changes in the availability of preferred habitats across the whole ETP can be assessed.

Response: This of course can be done, and in fact we did so in an earlier publication (Fiedler and Reilly, 1994). However, our study area covers the entire range of eastern spinners and the vast majority of the range of NE spotted dolphins, so it isn't clear how much additional insight would be gained. This reduction to fewer variables also results in a reduction of explanatory power, to less than 10% of the dolphin abundance variances, so for this reason as well it might not help too much.

Additional analysis of cetacean distribution patterns should consider incorporating both oceanographic variables and information on potential prey and tuna catches to improve their predictive power.

Response: Done. Good suggestion. It increased the predictive power by adding an additional 10% to the approximately 20% explained, which is a notable improvement.

Alternatives to the software package surfer should be investigated for providing a more representative picture of inter-annual patterns in the distribution of key faunal groups.

Response: We have used other graphing packages in the past including coding our own, but have found SURFER to perform best, at least of those we've tried.

