Abstract.—The results of a canonical correspondence analysis (CCA) of data from research vessel surveys of the eastern tropical Pacific were applied to time series of estimated dolphin abundances from tuna vessel sightings. The research vessel survey data consisted of daily dolphin school sightings and concurrent environmental variables for August–November of 1986 through 1990. Seasonal fields of habitat quality for 1975-90 were calculated from historical bathythermograph data by using the CCA ordination results. For spotted (*Stenella attenuata*) and eastern spinner (*S. longirostris orientalis*) dolphins, annual abundance estimates or interannual changes in those estimates are significantly correlated with habitat quality. This effect is at least partly due to expansion of high quality habitat beyond the geographic ranges assumed for the abundance estimate. We discuss ways that environmental data could be used to reduce error in dolphin abundance estimates.

Interannual variability of dolphin habitats in the eastern tropical Pacific. II: Effects on abundances estimated from tuna vessel sightings, 1975–1990

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The eastern tropical Pacific Ocean (ETP) supports a diverse and abundant cetacean fauna. By the late 1960s, it had become clear that large numbers of dolphins were being killed in tuna purse seine operations (Perrin, 1969). The dolphin species affected by the tuna fishery, known as "target species," are spotted dolphin (*Stenella attenuata*), the "whitebelly" form and "eastern" subspecies of spinner dolphin (*S. longirostris* and *S. l. orientalis*, Perrin, 1990), common dolphin (*Delphinus delphis*), and striped dolphin (*S. coeruleoalba*). In 1973, the U.S. government initiated a formal program to place observers on purse seiners to monitor dolphin mortality (Smith, 1983). In 1975, the Inter-American Tropical Tuna Commission began putting observers on the international fleet. The tuna vessel observer data from these programs includes sightings of cetaceans, as well as mortality data and biological samples from incidental catches.

Time series of target species abundance have been estimated from tuna vessel observer data (Buckland et al., 1992). These are yearly estimates of stocks of spotted, spinner, and common dolphins within nominal stock boundaries known as the Status of Porpoise Stocks or SOPS boundaries.[1]

Buckland et al. (1992) analyzed smoothed time series of these estimates and detected significant trends for some stocks.

Time series of dolphin abundance estimates are subject to considerable sampling error plus the effects of environmental variability on abundance and distribution. The effect of environmental factors on abundance estimates must be quantified before such a time series can be properly interpreted in terms of abundance changes or trends. This paper analyzes relationships between abundance estimates from tuna vessel observer data and environmental variability. Since little or no environmental data are collected on these ships, we base our analysis on species-environment relationships derived from research vessel data (Reilly and Fiedler, 1994).

National Marine Fisheries Service research vessels have surveyed the ETP several times since 1974 to collect data for abundance estimates and supplement the tuna vessel observer data (Holt et al., 1987). The most extensive research vessel observer data were collected

[1] Au, D. W. K., W. L. Perryman, and W. F. Perrin. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. NOAA/SWFC Admin. Rep. No. LJ-79-43, 59 p.

for the Monitoring of Porpoise Stocks (MOPS) program during August-November in 1986 through 1990 (Wade and Gerrodette, 1992). The MOPS surveys were designed to cover the SOPS spotted, spinner, and common dolphin stock boundaries. Reilly and Fiedler (1994) showed that sighting rates of dolphin species or school types on the MOPS surveys were related to concurrently measured environmental variables. We used a robust and efficient multivariate technique, canonical correspondence analysis, to examine relations between spatial distributions of dolphin species and environmental variables.

Canonical correspondence analysis (CCA) was developed to relate community composition to known variation in the environment. It is a form of direct gradient analysis that directly estimates ordination axes as linear combinations of observed environmental variables (Ter Braak, 1986). The advantages of CCA for multivariate species-environment analyses and details of the method are discussed by Reilly and Fiedler (1994). CCA estimates unimodal (Gaussian) responses of species along the ordination axes. In general, the response is observed abundance or probability of occurrence. We assume that a species response (abundance observed at a site in time and space) reflects the suitability of environmental conditions at that site relative to the species' optimal habitat or niche. This suitability, or habitat quality, is defined by the response distribution along the axes. An observed response will also include error caused by behavioral responses to the environment that affect the detectability of schools.

In this paper, we analyze relations between abundance estimates and habitat quality. It must be stated at the outset that in a 15-year record of populations with growth rates of only ~0.02 yr^{-1} (Reilly and Barlow, 1986), we are able to detect short-term environmental effects on sampling but not long-term effects on population size. Nevertheless, we demonstrate that some of the interannual variability in estimated abundances of ETP dolphins can be explained by environmental factors.

Methods

We used archived bathythermograph data to quantify variability of surface temperature, thermocline depth, and thermocline thickness in the MOPS study area since 1975. These variables were shown to be important in explaining variations in encounter rates in the MOPS surveys (Reilly and Fiedler, 1994). Other important variables (salinity and chlorophyll concentration) have not been routinely ob-

served with sufficient frequency to be used in this historical analysis. Seasonal fields (gridded values) of surface temperature, thermocline depth, and thermocline thickness for the period 1975–90 were derived from a bathythermograph data base originally described by Fiedler (1992) and augmented with data from other sources for this study (Table 1). Thermocline depth is defined as the depth of the 20°C isotherm. Thermocline thickness is defined as the difference in depth between the 20°C and 15°C isotherms.

Data were objectively gridded by seasons (December–February, March–May, June–August, September–November from 1975 through 1990) on a 2-degree latitude-longitude grid from lat. 20°S to 30°N latitude and from the coast out to long. 160°W. Decorrelation scales, the distances required for a substantial change in surface temperature or thermocline depth, have been estimated as 3 degrees latitude and 15 degrees longitude in this region (Sprintall and Meyers, 1991). At each grid point, means of at least 20 observations within up to 4 degrees latitude and 20 degrees longitude were calculated. The observations were weighted by the re-

Table 1

Numbers of bathythermograph profiles, after screening for errors and replicates, used to define habitat quality in yearly seasonal grids (1975–90) and in climatologies (1960–91). **NODC** = NOAA/NESDIS/National Oceanographic Data Center CD-ROM NODC-03: Global Ocean Temperature and Salinity Profiles, vol. 2, Pacific Ocean; **MOODS** = Navy Master Oceanographic Observations Data Set, including non-NODC observations through 1983 obtained from the Naval Oceanographic Office through NODC and 1985–90 observations obtained from Steve Pazan, Scripps Institution of Oceanography; **SOP** = French-American ship-of-opportunity observations obtained from NOAA/ERL/Pacific Marine Environmental Laboratory (Kessler, 1990); **FSFRL** = Japanese Far Seas Fisheries Research Laboratory MBT data obtained from PMEL and from NOS/Ocean Applications Branch (these data will be added to the NODC data set in the near future).

	1975–90	1960–91
NODC	61,486	127,365
MOODS	10,741	15,077
SOP	2,859	11,305
FSFRL	2,350	4,744
Total	77,436	158,491

ciprocal of the distance from the grid point. The range of observations around a grid point was increased in increments of 0.4 degrees latitude and 2 degrees longitude to obtain a minimum sample size of 20 for each grid point. Thus, local grid resolution decreases in data-poor regions, generally south of the equator where the maximum distance required was up to 20 degrees longitude. Within the MOPS area, sufficient observations were available within 2 degrees latitude and 10 degrees longitude of 71% of the gridpoints, and within 4 degrees latitude and 20 degrees longitude of 95% of the gridpoints. We converted observations to anomalies (deviations from the seasonal mean) before gridding to reduce the spatial variability of the observations. This minimized bias caused by interpolation over or extrapolation into large data gaps.

Relationships among abundances of dolphin species and environmental variables were analyzed by using CCA as described in Reilly and Fiedler (1994). Encounter rate, equal to number of schools sighted per unit of sighting effort (trackline distance), was used as a measure of relative abundance. The final abundance estimate also depends on school size and effective track width. However, Reilly and Fiedler (1994) found that weighting encounter rates by estimated school size in the CCA produced essentially the same species-environment patterns. Therefore, schools of all sizes occupied approximately the same habitats and school size variability within these habitats was not related to the environmental variables included in the analysis.

CCA was performed on MOPS sightings and environmental data as in Reilly and Fiedler (1994), except that mixed schools of spotted and spinner dolphins were counted as schools of both species rather than as an additional "species." Also, we used Hill's symmetric scaling of species and site scores (S=–3 in our implementation of CANOCO[2]). This alternative scaling of the ordination had no qualitative effect on species-environment patterns but seemed to give more reasonable results at the edges of the study area when scores were combined to quantify species habitat distributions.

Habitat quality for species i (H_i) at a gridpoint was calculated from the Gaussian responses fit to the two dominant canonical axes by CCA. The response to each environmental axis was calculated as a normal probability density function:

$$H_{ij} = t_{ij}^{-1} \exp\left(-0.5 * \left((x_j - u_{ij})/t_{ij}\right)^2\right),$$

where,

x_j = the site (gridpoint) score on environmental axis j,

u_{ij} = the species i score (optimum) on axis j,

t_{ij} = the tolerance (standard deviation) of species i on axis j.

Species scores and tolerances (u_{ij} and t_{ij}) were output by CANOCO as part of the CCA. Site scores (x_j) were calculated as linear combinations, defined by the output canonical axis coefficients, of normalized and gridded environmental observations. Habitat quality, H_i, was then calculated as the geometric mean of H_{ij}'s; each H_{ij} was scaled so that the mean value is 1.0 during 1975–90. Thus, H_i is equal to the abundance expected at a site, based on local environmental conditions, divided by the mean abundance in the study area during 1975–90.

Point estimates of annual abundance were provided by Anganuzzi[3] for pooled stocks: spotted dolphins include northern and southern offshore spotted dolphins, whitebelly spinner dolphins include northern and southern whitebelly spinner dolphins, and common dolphins include northern, central, and southern common dolphins. No estimates were made for striped dolphins, which were rarely set on by tuna vessels.

Results

The species-environment biplot (Fig. 1) summarizes the results of the CCA of five species and three environmental variables observed during 1986–90 MOPS research surveys. The eigenvalues of the three canonical axes were 0.296, 0.074, and 0.001. The first two axes explained 99.7% of the species-environment variance accounted for by all three axes. Therefore, the third axis was not used. The first two axes explained 20.5% of the total variance of species encounter rates (Table 2).

Positive scores on canonical axis 1 indicate cool surface temperature and a shallow, weak thermocline (Table 3). These are characteristics of the productive "cool upwelling" habitat that we identified with the first axis in the complete CCA (seven species and six environmental variables, Reilly and Fiedler, 1994). This habitat is found in the equatorial and eastern boundary current (Peru and Cali-

[2] Ter Braak, C. J. F. (1988). CANOCO—a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (version 2.1). Tech. Rept. LWA-88-02, Groep Landbouwwiskunde, Postbus 100, 6700 AC Wageningen, The Netherlands.

[3] Anganuzzi, A. Inter-American Tropical Tuna Commission, 8604 La Jolla Shores Drive, La Jolla, CA 92038. Pers. commun. December 1991.
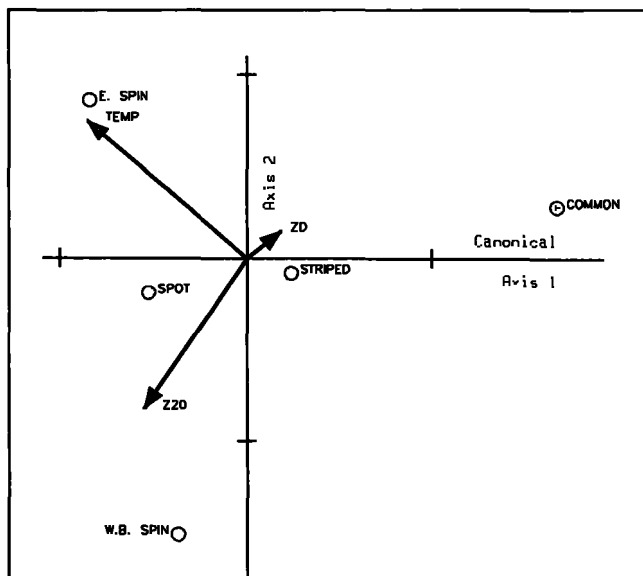
Figure 1

Ordination biplot of first two canonical axes from CCA of species-environment data from 1986–90 MOPS surveys of the ETP. Points represent species scores (optima) and vectors represent the regression relationships of environmental variables with the canonical axes. TEMP = surface temperature, Z20 = thermocline depth, ZD = thermocline thickness. SPOT = spotted dolphin (*Stenella attenuata*), COMMON = common dolphin (*Delphinus delphis*), E. SPIN = eastern spinner dolphin (*S. longirostris orientalis*), W. B. SPIN = whitebelly spinner dolphin (*S. longirostris*), STRIPED = striped dolphin (*S. coeruleoalba*).

fornia Currents) waters of the ETP and is also present seasonally in the region of the Costa Rica Dome at 10°N, 90°W (Fiedler, 1992). Positive scores on canonical axis 2 indicate warm surface temperature and a shallow thermocline (Table 3). These are characteristics of the "coastal tropical" habitat of Reilly and Fiedler (1994). This habitat is centered in the warmest tropical surface water of the ETP, along the coast of Mexico south of Baja California.
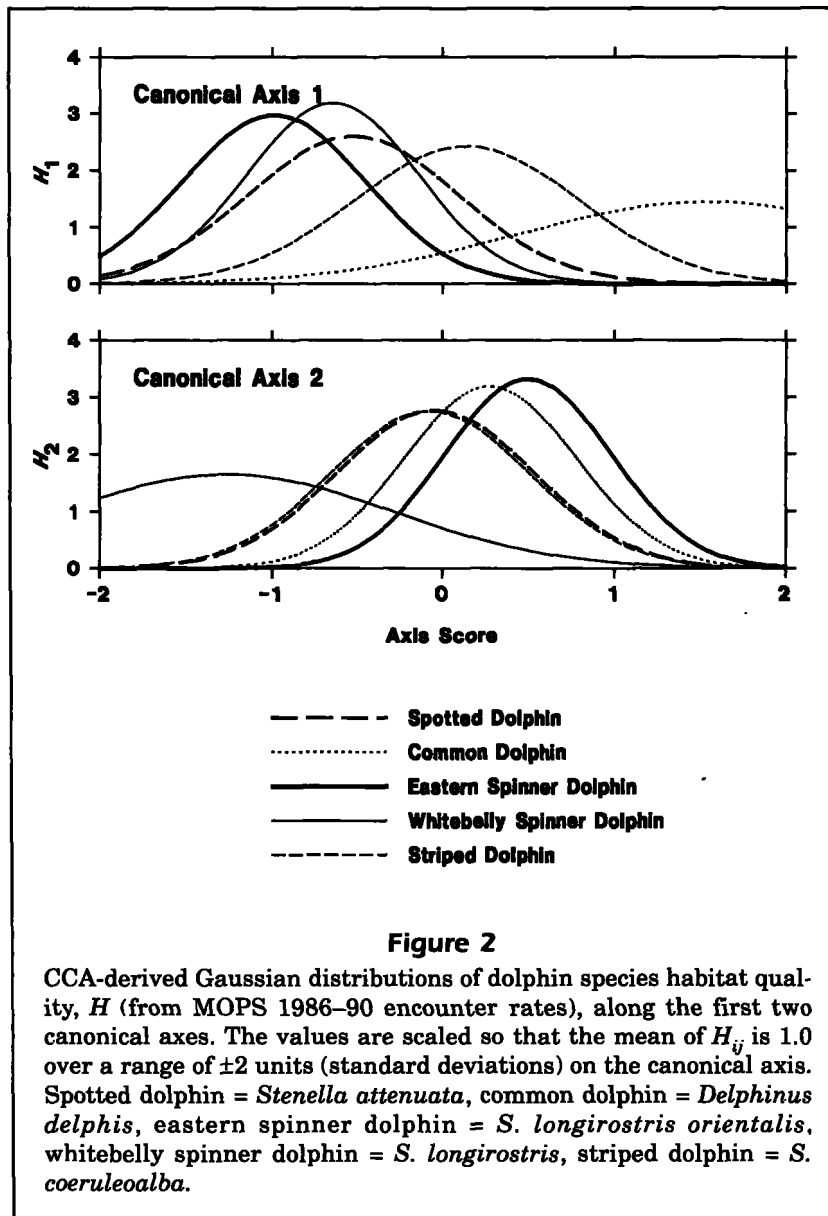
Species responses along the canonical axes (Fig. 2) showed some separation of species habitats, as in the complete CCA (Reilly and Fiedler, 1994). Axis 1 separated common dolphins from spotted and spinner dolphins, while axis 2 separated eastern and whitebelly spinner dolphins. The means (optima, Table 4) of a species distribution on the two canonical axes in Figure 2 are equal to the species scores plotted in the ordination biplot (Fig. 1).

The validity of the species/environment relationships calculated by CCA was confirmed in three ways. First, distributions of climatological H, derived from the CCA results and climatological values of environmental variables at each gridpoint in the MOPS area (Fiedler, 1992), were consistent with stock ranges indicated by the SOPS population boundaries, with the exception of whitebelly spinner dolphins (Fig. 3). Second, the distributions were similar to patterns in maps of tuna and research vessel sighting records (Perrin et al., 1985), although such maps can give only a rough indication of habitat distribution because the sighting or collection frequencies are not standardized by effort. Third, the distributions of H calculated for climatological September–November environmental conditions were significantly correlated with gridded fields of mean (August–November, 1986–90) MOPS encounter rates as follows: spotted dolphin $r = 0.52$, common dolphin $r = 0.45$, eastern spinner dolphin $r = 0.65$, whitebelly spinner dolphin $r = 0.36$, striped dolphin $r = 0.41$ ($P<0.01$ for all relationships).

Table 2

Fractions of individual and total species variances explained by canonical correspondence analysis (CCA). AX1 = canonical axis 1, AX2 = canonical axis 2. Dolphin species: spotted = *Stenella attenuata*, common = *Delphinus delphis*, eastern spinner = *S. longirostris orientalis*, whitebelly spinner = *S. longirostris*, striped = *S. coeruleoalba*.

	AX1	AX2	AX1+AX2
Spotted	0.191	0.000	0.191
Common	0.321	0.004	0.325
Eastern spinner	0.169	0.089	0.258
Whitebelly spinner	0.014	0.118	0.132
Striped	0.037	0.002	0.039
Total	0.164	0.041	0.205

Table 3

Regression/canonical coefficients for standardized environmental variables on two environmental axes (AX1 and AX2). TEMP = surface temperature, Z20 = thermocline (20°C isotherm) depth, ZD = thermocline thickness (difference between 20°C and 15°C isotherm depths).

	TEMP	Z20	ZD
AX1	−0.501	−0.326	+0.111
AX2	+0.439	−0.486	+0.088

Figure 2

CCA-derived Gaussian distributions of dolphin species habitat quality, H (from MOPS 1986–90 encounter rates), along the first two canonical axes. The values are scaled so that the mean of H_{ij} is 1.0 over a range of ±2 units (standard deviations) on the canonical axis. Spotted dolphin = *Stenella attenuata*, common dolphin = *Delphinus delphis*, eastern spinner dolphin = *S. longirostris orientalis*, whitebelly spinner dolphin = *S. longirostris*, striped dolphin = *S. coeruleoalba*.

Spotted dolphin habitat was centered south and southwest of the southern coast of Mexico to about 3°N (Fig. 3). This corresponds to the warm, tropical surface water mass of Wyrtki (1966, see Fig. 1 in Reilly and Fiedler, 1994). The Costa Rica Dome (10°N, 90°W) was a notable gap in favorable spotted dolphin habitat.

Eastern spinner dolphins were even more closely associated with warm tropical surface water. Highest values of H for this stock were found off southern Mexico, in the center of the "coastal tropical" habitat defined by canonical axis 1 (Reilly and Fiedler, 1994). Whitebelly spinner dolphins were associated with subtropical surface water (Wyrtki, 1966) to the northwest and southwest of the tropical surface water in the core of the MOPS area.

Table 4

Dolphin species scores (standardized) ±tolerances on the first two canonical axes from canonical correspondence analysis (CCA). Dolphin species: spotted = *Stenella attenuata*, common = *Delphinus delphis*, eastern spinner = *S. longirostris orientalis*, whitebelly spinner = *S. longirostris*, striped = *S. coeruleoalba*.

	AX1	AX2
Spotted	−0.53 ± 0.57	0.19 ± 0.54
Common	1.68 ± 1.16	0.28 ± 0.48
Eastern spinner	−0.84 ± 0.49	0.86 ± 0.71
Whitebelly spinner	−0.37 ± 0.55	−1.51 ± 1.19
Striped	0.24 ± 0.69	−0.08 ± 0.55

Common dolphin habitat was centered in cool, upwelling-modified water in three regions: off Baja California, along 10°N with a maximum at the Costa Rica Dome, and in the equatorial surface water

mass of Wyrtki (1966). These three habitat centers are occupied by the northern, central, and southern stocks of common dolphins (Perrin et al., 1985). The offshore H maximum along 10°N at 120–130°W does not correspond to high encounter rates in the MOPS data, but reflects a shoaling of the countercurrent thermocline ridge at that location (Fiedler, 1992).

Striped dolphins are the most widespread and abundant of the target species. The highest H values tended to be in regions between or offshore of the centers of spotted/eastern spinner dolphin habitat in tropical surface water near the coast of southern Mexico and northern, central, and southern common dolphin habitats off Baja California, near the Costa Rica Dome, and in equatorial water (see also Reilly, 1990).

Both seasonal and interannual variability were evident in time series of mean seasonal habitat quality, H (Fig. 4). The strongest interannual signal for all species can be attributed to the El Niño events of 1982–83 and 1986–87. During both events, H increased for spotted and spinner dolphins and decreased for common and striped dolphins. Seasonal variability, indicated by the deviations of the seasonal from the smoothed H values, was low for species with large geographic ranges (e.g. striped dolphin) and high for species with more restricted ranges (e.g. eastern spinner dolphin). Seasonal variability of H was as great as interannual variability for eastern spinner dolphins.

Annual dolphin abundance estimates, N_t, or interannnual change in abundance estimates, N_t-N_{t-1}, were related to changes in the environment, H, for spotted and eastern spinner dolphins. Annual spotted dolphin abundance was not significantly correlated with H, but interannual change in abundance was negatively correlated with H (Fig. 5, $r=-0.65$, $P=0.01$). Calculating year-to-year changes in abundance eliminates multi-year trends in the time series. Buckland et al. (1992) found significant trends in estimated spotted dolphin abundance which might complicate the relation between annual N and H values. An increase in H for spotted dolphins indicates an expansion of favorable habitat to the south of the SOPS population boundary west of 100°W (Fig. 6A).

Annual eastern spinner dolphin abundance was negatively correlated with H ($r=-0.49$, $P=0.05$). An increase in H for eastern spinner dolphins indicates an expansion of favorable habitat to the west and south of the SOPS population boundary (Fig. 6B).
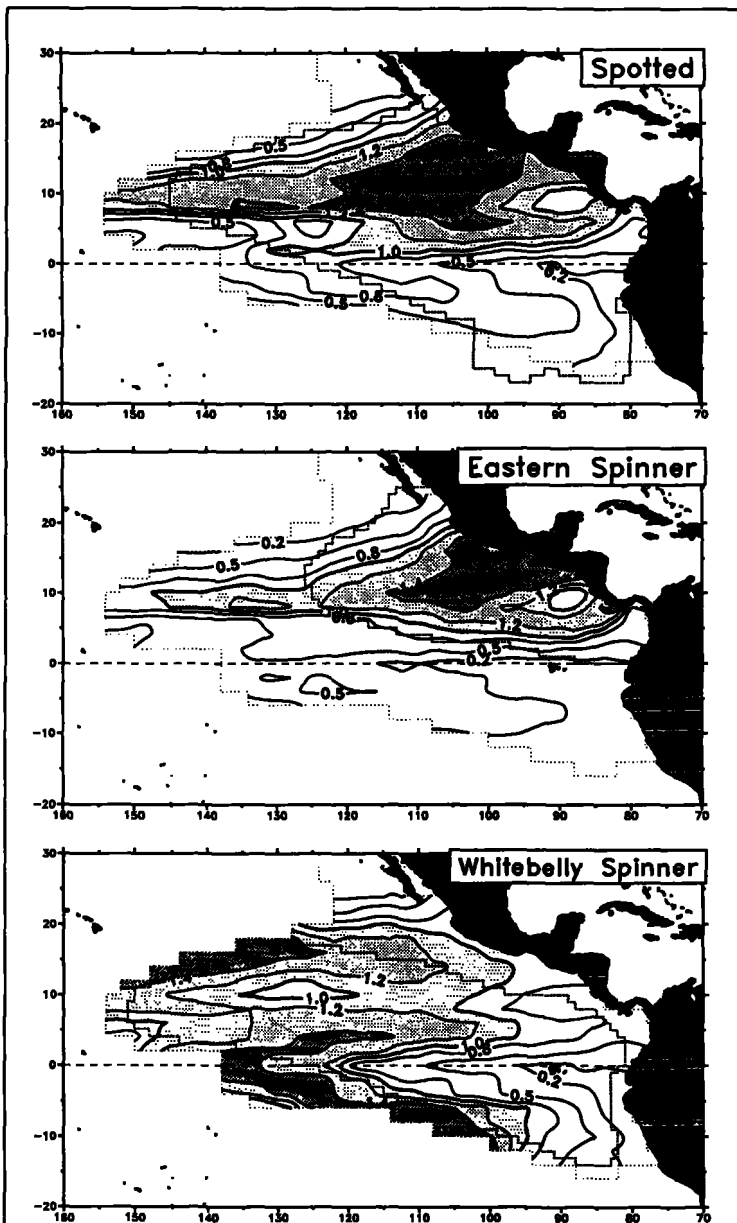

Figure 3

Mean habitat quality (H) for spotted (*Stenella attenuata*), eastern spinner (*S. longirostris orientalis*), whitebelly spinner (*S. longirostris*), common (*Delphinus delphis*), and striped (*S. coeruleoalba*) dolphins. H was calculated from climatological fields of surface temperature, thermocline depth, and thermocline thickness in the MOPS area. Heavy dashed lines delimit SOPS population areas used by Anganuzzi and Buckland (1989) and Anganuzzi et al. (1991) or, for striped dolphins, as defined by Au et al. (Footnote 1.)
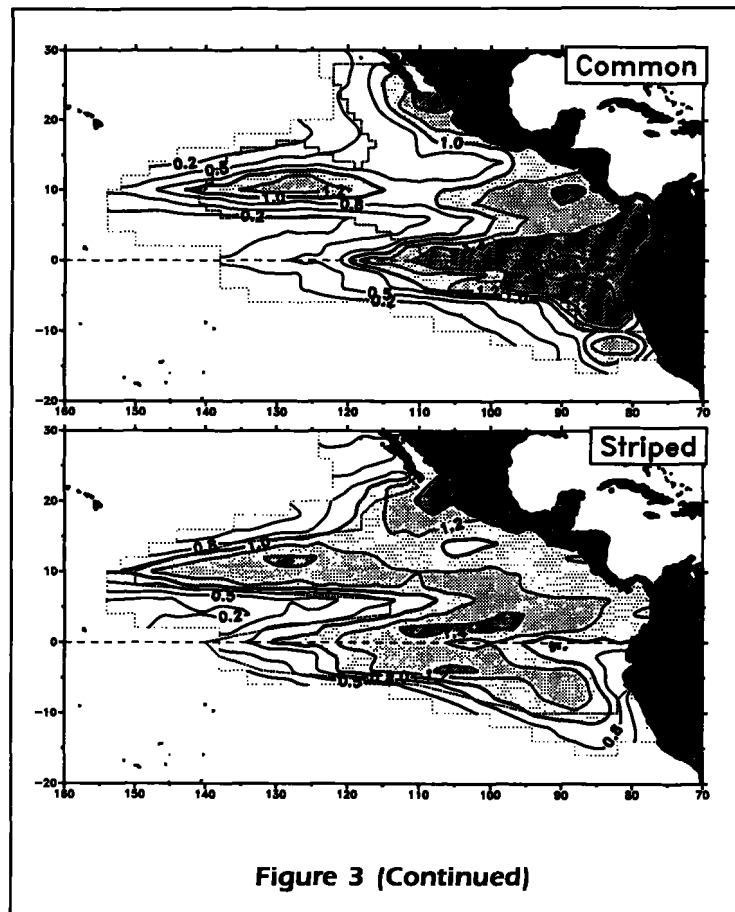
Figure 3 (Continued)

Common and whitebelly spinner dolphins did not show significant linear relationships between N and H (Fig. 7). For all four species, log-transformation of the abundance estimates or lagging N_t by up to four seasons did not change the significance levels of the linear relationships. However, common dolphin abundance appeared to be maximum at H near 1.0 and to decrease at lower or higher H values, except in 1983. Scatterplots of N_t vs. H_t for spotted and whitebelly spinner dolphins suggest similar nonlinear relationships. For common dolphins at low values of H, as in early 1983, very little high-quality or favorable habitat was available in the ETP (Fig. 6C). The only favorable habitat with $H>1$ was in equatorial water west of the Galapagos. Half of this favorable habitat was outside the SOPS boundary. At high values of H, as in early 1985, favorable habitat for the central and southern stocks (along 10°N and the equator, respectively) expanded. Favorable habitat along the equator extended beyond the SOPS boundary. At the same time, favorable habitat for the more abundant northern stock, off Baja California, was reduced.

Discussion

Estimated abundances of spotted and eastern spinner dolphins in the eastern tropical Pacific were correlated with changes in the environment, as described by the CCA-derived habitat quality index H. The time scale of the changes and the patterns of favorable habitat relative to nominal population boundaries (Fig. 6) suggest that the correlations resulted from a sampling effect, rather than a population effect. Thus, we have explained biases in annual population estimates that result in apparent population changes. For example, Anganuzzi and Buckland (1989) suggested that their low 1983 abundance estimate for spotted dolphins might be explained by dispersal of local concentrations of schools during the strong El Niño. Our results showed that spotted dolphin schools may have moved outside the nominal species range when the "coastal tropical" habitat expanded into equatorial water west of 100°W during this unusual event. Similarly, estimated eastern spinner dolphin abundance decreased slightly with increasing H because

of the dispersal of schools outside the nominal range used in calculating the abundance estimate. The center of distribution of spotted and eastern spinner dolphins is the warm tropical surface water in the core of the ETP. Therefore, the apparent responses of the two populations to environmental variability are similar.

The different effects of environmental variability on the habitats of the three stocks of common dol-

phins appear to complicate the response of the population as a whole. Data collected during surveys of the central and northern stocks of common dolphins in fall 1992 and 1993, respectively, will allow us to quantify stock-specific habitats and, perhaps, responses to environmental variability. We detected no effect of environmental variability on the abundance estimates of whitebelly spinner dolphins, but the CCA results inadequately define the geographical
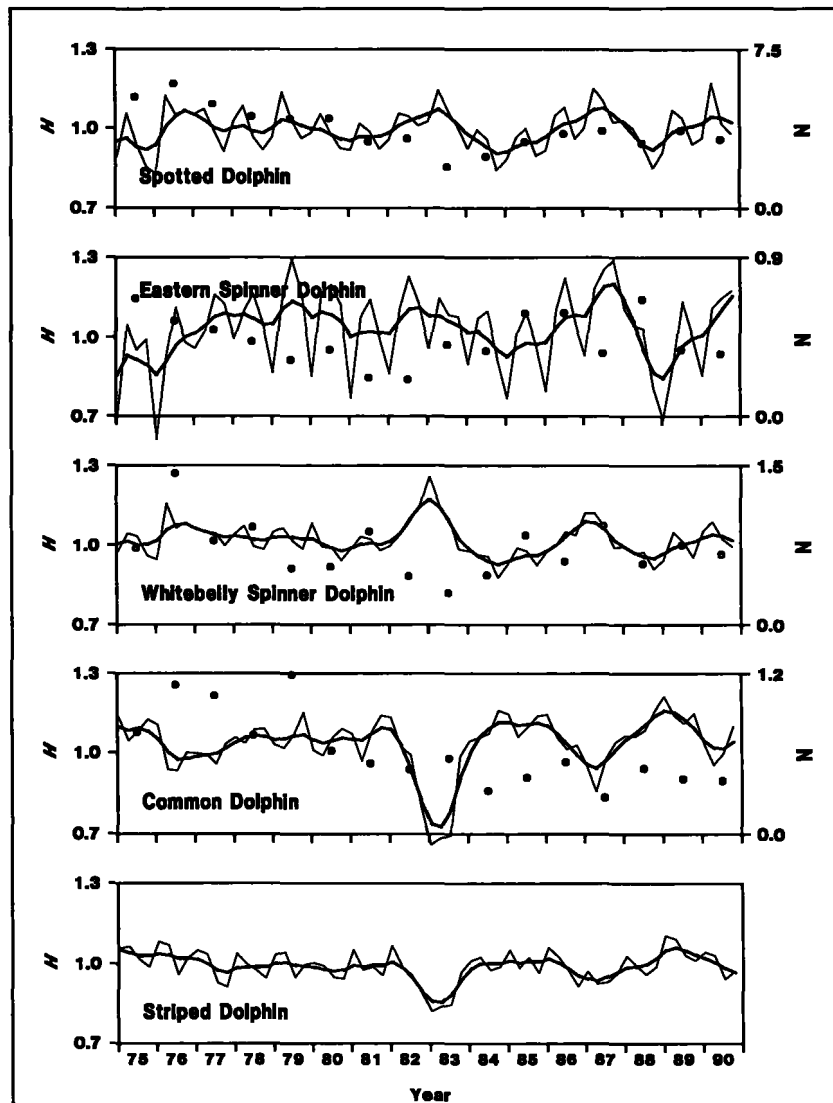
Figure 4

Mean SOPS area habitat quality (H) for five dolphin species: seasonal values (thin line) and smoothed values (five-season running mean, thick line). Dots are point estimates of species abundance ($N \times 10^{-6}$). Spotted dolphin = *Stenella attenuata*, common dolphin = *Delphinus delphis*, eastern spinner dolphin = *S. longirostris orientalis*, whitebelly spinner dolphin = *S. longirostris*, striped dolphin = *S. coeruleoalba*.

extent of the habitat of this stock (see Fig. 3). The apparent westward extension of the habitat outside the MOPS area is consistent with the recognition of the "whitebelly" form as a hybrid/intergrade between eastern and pantropical subspecies of spinner dolphins (Perrin, 1990). The partial separation of eastern and whitebelly spinner dolphin habitats defined by H is consistent with the management boundary between the two forms proposed by Perrin

et al. (1991): eastern spinners north of 10°N and east of 125°W, and whitebelly spinners south of 10°N or west of 125°W.

Reilly and Fiedler (1994) suggested that species habitats defined by axis scores from CCA could be used to improve the precision and accuracy of abundance estimates from research vessel surveys. Precision could be increased by post-stratifying the sighting data based on the spatial distribution of axis scores. Bias could be reduced by using axis scores to quantify the amount of habitat available within a survey area. The present results suggest that this approach could be extended by using species habitat distributions incorporating environmental variability along more than one canonical axis. For example, a large area of suitable spotted dolphin habitat existed in equatorial water beyond the SOPS population boundary during 1983, apparently causing a serious underestimate of abundance. Gerrodette et al.[4] suggested similar approaches for using fields of H to adjust abundance estimates from MOPS research vessel surveys.
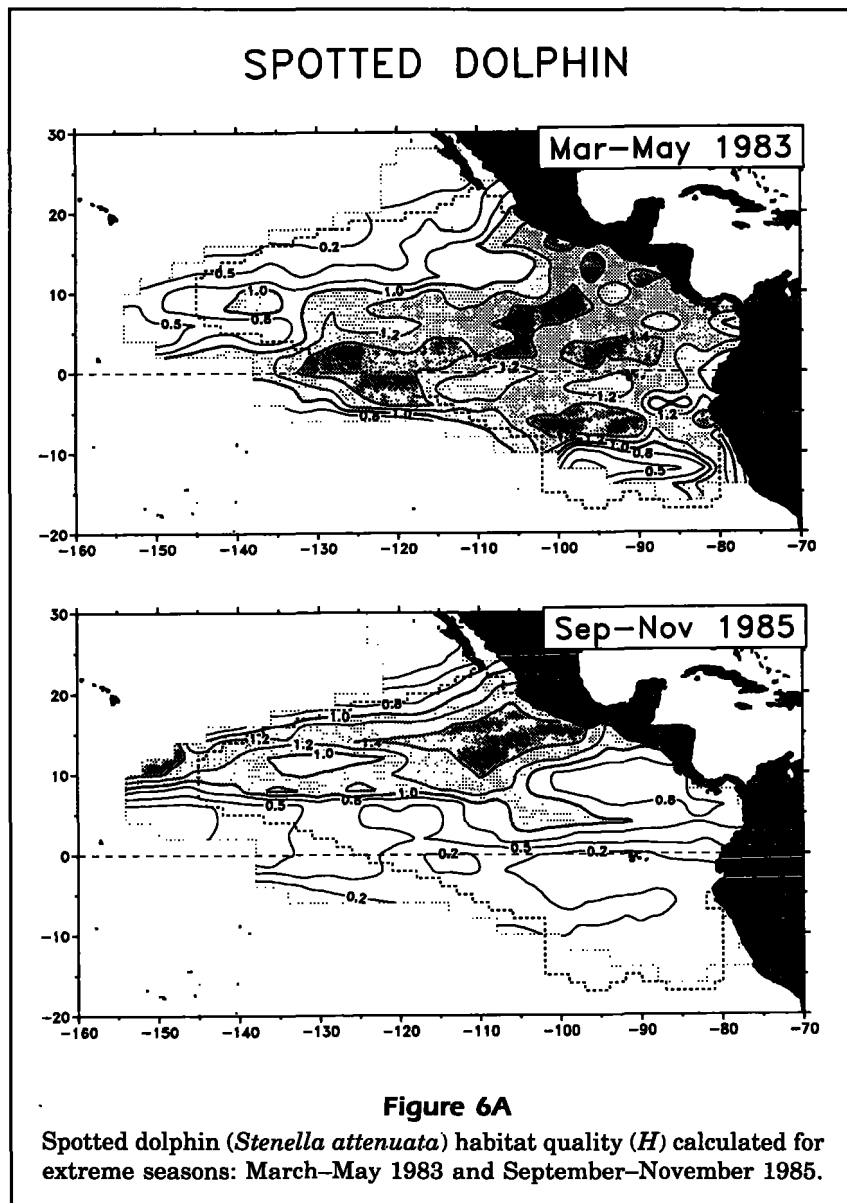
We utilized the results of a multi-species CCA for this study. While this approach yields useful information about community structure, as in the separation of eastern and whitebelly spinner habitat, it does not retain the maximum amount of information about any single species for management applications. A similar type of analysis for each individual species or stock might explain more of the variability in abundance and improve the quantification of habitat quality defined by Gaussian responses along dominant environmental gradients. In addition, CCA could potentially be used to account for environmental effects on school size and effective trackline width that cause error in dolphin abundance estimates. However, preliminary results of a CCA incorporating school size (Reilly and Fiedler, 1994) showed no meaningful relation between school size and environmental variability. We have only begun to exploit CCA in our work and believe it is a powerful new technique with great potential for quantitative ecological studies of populations of marine mammals and other organisms. For example, environmental variability dominates variations in recruitment of many fish stocks (Longhurst, 1984; Hollowed et al., 1987). Although our time series was not long enough to address population change, this study demonstrates the potential of CCA to detect environmental effects in multi-stock fisheries studies.
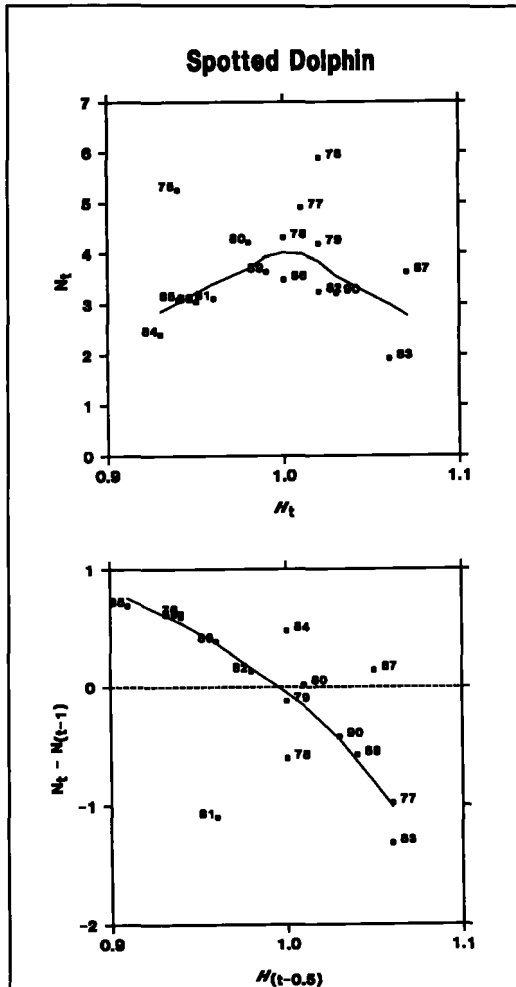
Figure 5

Abundance-environment relationships for spotted dolphins (*Stenella attenuata*) in the MOPS area: (**Top**) Annual abundance estimates ($N_t \times 10^{-6}$) vs. annual mean habitat quality (H_t). (**Bottom**) Interannual change in abundance estimates ($N_t - N_{t-1}, \times 10^{-6}$) vs. mean habitat quality from June of year t-1 through May of year t ($H_{t-0.5}$). Solid line connects lowess-smoothed values (Wilkinson, 1990).

[4] Gerrodette, T., P. C. Fiedler, and S. B. Reilly. 1991. Including habitat variability in line transect estimation of abundance and trends. NMFS/SWFSC Admin. Rep. No. LJ-91-37.

Figure 6A

Spotted dolphin (*Stenella attenuata*) habitat quality (*H*) calculated for extreme seasons: March–May 1983 and September–November 1985.

Acknowledgments

Literature cited

Anganuzzi, A. A., and S. T. Buckland.
  1989. Reducing bias in trends in dolphin relative abundance, estimated from tuna vessel data. Rep. Int. Whal. Comm. 39:323–334.
Buckland, S. T., K. L. Cattanach, and A. A. Anganuzzi.
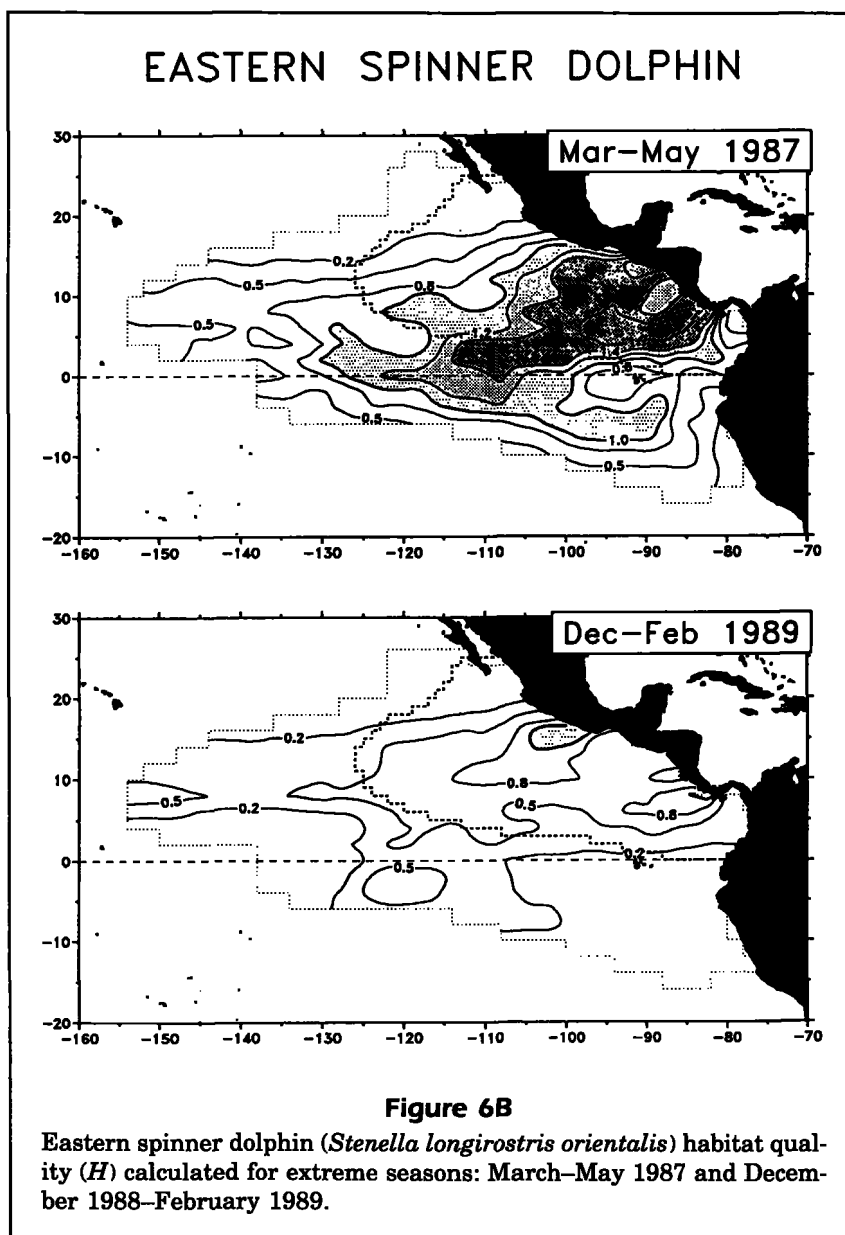 **1992.** Estimating trends in abundance of dolphins associated with tuna in the eastern tropical Pacific Ocean, using sightings data collected on commercial tuna vessels. Fish. Bull. 90:1–12.
Fiedler, P. C.
  1992. Seasonal climatologies and variability of eastern tropical Pacific surface waters. Dep. Commer., NOAA Tech. Rep. NMFS 109, 65 p.
Hollowed, A. B., K. M. Bailey, and W. S. Wooster.
  1987. Patterns in recruitment of marine fishes in

Figure 6B

Eastern spinner dolphin (*Stenella longirostris orientalis*) habitat quality (*H*) calculated for extreme seasons: March–May 1987 and December 1988–February 1989.

the northeast Pacific Ocean. Biol. Oceanogr. 5:99–131.

Holt, R. S., T. Gerrodette, and A. B. Cologne.
    1987. Research vessel survey design for monitoring dolphin abundance in the eastern tropical Pacific. Fish. Bull. 85:435–446.

Kessler, W. S.
    1990. Observations of long Rossby waves in the northern tropical Pacific. J. Geophys. Res. 95(C4):5183–5217.

Longhurst, A.
    1984. Heterogeneity in the ocean - implications for fisheries. Rapp. P.-v. Réun. int. Explor. Mer, 185:268–282.

Perrin, W. F.
    1969. Using porpoise to catch tuna. World Fish. 18(6):42–45.

    1990. Subspecies of *Stenella longirostris* (Mammalia: Cetacea: Delphinidae). Proc. Biol. Soc. Wash. 103:453–463.

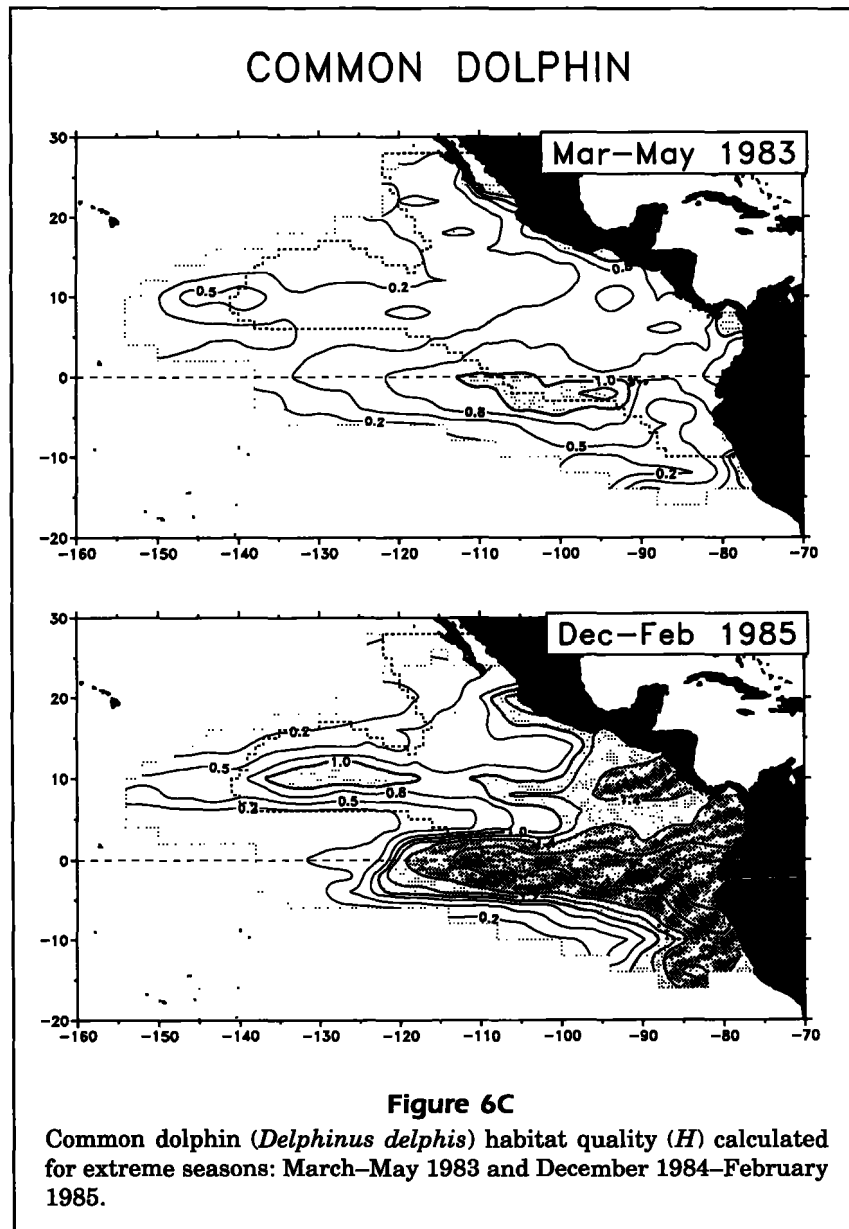**Perrin, W. F., M. D. Scott, G. J. Walker, and V. L. Cass.**
    1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. Dep. Commer., NOAA Tech. Rep. NMFS 28, 28 p.

Perrin, W. F., P. A. Akin, and J. V. Kashiwada.
    1991. Geographic variation in external morphology of the spinner dolphin *Stenella longirostris* in the eastern Pacific and implications for conservation. Fish. Bull. 89:411–428.

Reilly, S. B.
    1990. Seasonal changes in distribution and habitat

COMMON DOLPHIN

Mar–May 1983

Dec–Feb 1985

Figure 6C

Common dolphin (*Delphinus delphis*) habitat quality (*H*) calculated for extreme seasons: March–May 1983 and December 1984–February 1985.

differences among dolphins in the eastern tropical Pacific. Mar. Ecol. Prog. Ser. 66:1–11.

Reilly, S. B., and J. Barlow.
   1986. Rates of increase in dolphin population size. Fish. Bull. 84:527–533.

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. 92:434–450.

Smith, T. D.
   1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. Fish. Bull. 81:1–13.

Sprintall, J., and G. Meyers.
   1991. An optimal XBT sampling network for the

eastern Pacific Ocean. J. Geophys. Res. 96(C6): 10,539–10,552.

Ter Braak, C. J. F.
   1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179.

Wade, P. R., and T. Gerrodette.
   1992. Estimates of dolphin abundance in the eastern tropical Pacific: preliminary analysis of five years of data. Rep. Int. Whal. Comm. 42:533–539.

Wilkinson, L.
   1990. SYGRAPH: The system for graphics. SYSTAT, Inc., Evanston, IL.

Wyrtki, K.
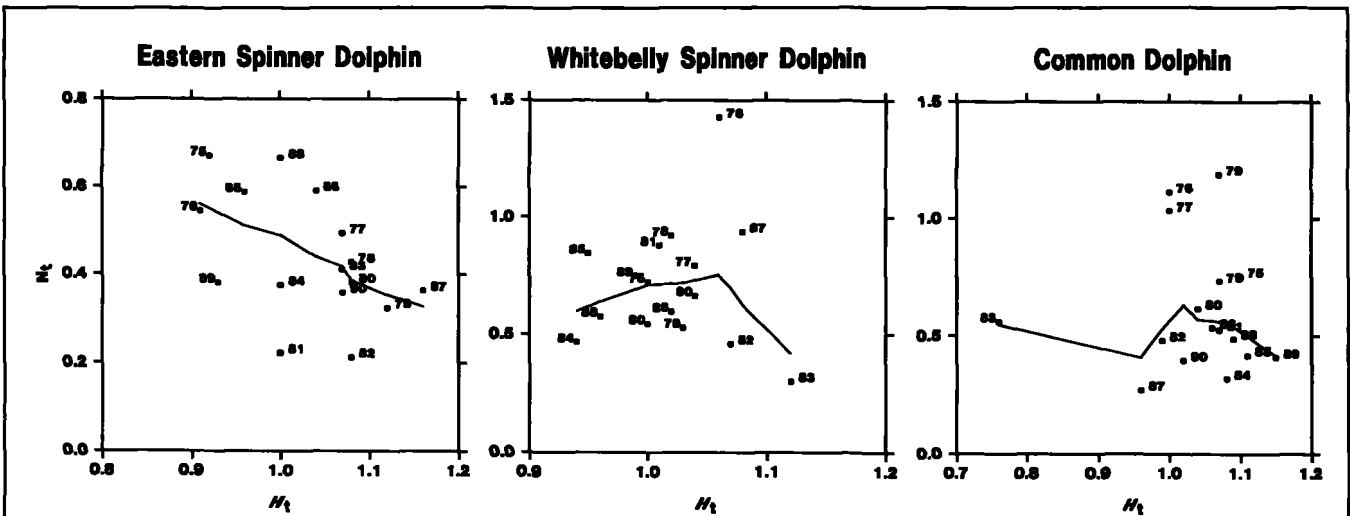   **1966.** Oceanography of the eastern equatorial Pacific Ocean. Oceanogr. Mar. Biol. Ann. Rev. 4:33–68.

Figure 7

Abundance-environment relations for eastern spinner (*Stenella longirostris orientalis*), whitebelly spinner (*S. longirostris*), and common (*Delphinus delphis*) dolphins in the MOPS area, annual abundance estimates ($N_t \times 10^{-6}$) vs. annual mean habitat quality (H_t). Solid line connects lowess-smoothed values (Wilkinson, 1990).