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RELATIVE ABUNDANCE, DISTRIBUTION AND INTER-SPECIFIC RELATIONSHIP OF CETACEAN SCHOOLS IN THE EASTERN TROPICAL PACIFIC

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ABSTRACT

The relative abundance of the most common cetacean schools in the eastern tropical Pacific Ocean for 1977–1980 are estimated based on encounter rates with tuna purse-seiners. No temporal trends were apparent in the relative abundance estimates. The geographic distributions for eight different school types are described. Multivariate statistical techniques are used to investigate interrelations between species and relationships to parameters of the physical environment. The results suggest three major species groupings: (1) an inshore grouping of bottlenose dolphins (*Tursiops truncatus*), Risso's dolphin (*Grampus griseus*), pilot whales (*Globicephala macrorhynchus*) and, to a lesser extent, common dolphins (*Delphinus delphis*); (2) an offshore pelagic grouping of spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*); and (3) an association between pilot whales and common dolphins that overlaps the first grouping in inshore areas and also tends to be segregated from the second grouping. The results also suggest that relative densities of different school types are strongly related to physical environmental parameters, the most important being sea surface temperature, depth of the thermocline and thickness of the oxygen minimum layer.

Key words: abundance, distribution, *Delphinus delphis*, *Globicephala macrorhynchus*, *Grampus griseus*, *Stenella attenuata*, *Stenella longirostris*, *Tursiops truncatus*, multivariate, temperature, thermocline, oxygen minimum.

A large number of cetacean species is known to inhabit the eastern tropical Pacific Ocean (Leatherwood *et al.* 1972). Little is known about the structure of this group of marine mammals or the factors influencing the spatial distribution of its members. A knowledge of the distribution and association between species is central to an understanding of the ecology of any community. Without such knowledge, it is impossible to accurately define the structure of a com-

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munity, much less to address the question of what factors are actually structuring the community and controlling its dynamics. Interest and management concerns about the cetacean species inhabiting the eastern tropical Pacific have developed because of the involvement and incidental killing of some of these species in the purse-seine fishery for yellowfin tuna (*Thunnus albacares*) (Perrin 1968, 1969). A knowledge of the spatial distribution and associations of these cetacean species is important for a complete assessment and management of these species.

Until recently, no reliable information was available on the distributional ranges of many of the major species. As a result of extensive research by the National Marine Fisheries Service into the tuna purse-seine fishery and the incidental involvement of dolphins in the harvesting process, a large body of data has been collected on the more abundant marine mammal species. The distributional ranges of the more abundant species (including distinct morphological races) have been described from this information (Perrin 1975, Perrin *et al.* 1976, 1979, 1983, Holt and Powers 1982). However, uncertainty remains about the boundaries of these ranges, particularly in the far-western and southern portions of the eastern tropical Pacific.

Within these distributional ranges, only a few analyses exist of the distributional patterns of some of the more common species (Reilly 1977, Au *et al.* 1979, Leatherwood *et al.* 1980). Except for Reilly's (1977) study on the relative densities of pilot whales, none of these studies has been based on direct quantitative measures of density. Their primary focus has been to describe the major areas of distribution of one or more species. In addition, Au *et al.* (1979) examine the relationship between environmental variables and the spatial frequency of sightings without regard to searching effort for the four most common dolphin species. The authors note the existence of apparently strong relations between the number of sightings and sea surface temperature, thermocline depth, and areas of frontal convergences. Because of a statistical mistake, Reilly (1977) found no relationship between environmental variables and his measure of relative densities for pilot whales (Reilly, pers. comm.). Scattered within other studies are comments, but no quantitative analyses, on the apparent association of various cetacean species with environmental parameters. The possible inter-relations between species have been discussed only qualitatively (*e.g.*, Au *et al.* 1979, 1980, Au and Pitman 1981).

In this paper, the spatial distribution of the relative densities of schools is estimated and examined for the eight most commonly sighted cetacean species based on encounter rates with tuna purse-seiners. The inter-relations among these spatial distributions and their relations to the general physical environment are explored with multivariate statistical methods.

Materials and Methods

The Data

The data used for estimating relative densities in this paper were collected by trained scientific observers from the National Marine Fisheries Service aboard operating U.S. tuna purse-seiners. These observers collected information on all sightings of marine mammals and on the searching activities of the vessels. Details on the data gathered, the collection procedures and their preparation can be found in Polacheck (1983, 1984) and Perrin *et al.* (1983). The analyses presented below are based on data collected from 1977 to 1980. While data are available from other years, sample sizes are considerably smaller and collection procedures differed in earlier years.

Since the data were gathered aboard working purse-seiners, the sampling distribution of searching effort was not random. Purse-seiners concentrate their effort both seasonally and at relatively fine spatial scales (Polacheck 1983). Also, observers do not generally have access to the 25× binoculars used by the crew for searching. For schools sighted at a distance, but not approached by the vessel, positive identifications were usually not made. Thirty-eight percent of the dolphin schools reported were not positively identified by the observer. Schools not identified are probably not random with respect to species (*i.e.,* schools associated with tuna are more likely to be investigated). Both of these factors may induce unknown biases into the results. The problem of non-random search is compensated in part in the analyses below by the fact that all calculations have been performed based on a 5° square stratification of the data. The analyses presented below are dependent upon the relative spatial patterns of the sighting rates and not absolute rates. As such, the problem of unidentified schools should not induce serious bias unless species are selectively non-identified by area. However, the problem of non-identification means that the number of schools sighted is smaller than might be expected for species not involved in the tuna fishery. In these cases, caution should be used in interpreting lack of positive results and relationships. This is particularly true for the striped dolphin, which had the third lowest encounter rate by purse-seiners of the species considered below, but is the most frequently sighted dolphin species on research cruises (Holt and Powers 1982).

School Types

Relative densities for nine types of schools are examined. These represent the eight species most frequently encountered by purse seiners. They are:

1. Schools of spotted dolphins (*Stenella attenuata*)
2. Schools of spinner dolphins (*S. longirostris*)
3. Schools of common dolphins (*Delphinus delphis*)
4. Schools of striped dolphins (*S. coeruleoalba*)
5. Mixed schools of spotted and spinner dolphins (*S. attenuata* and *S. longirostris*)
6. Schools containing bottlenose dolphins (*Tursiops truncatus*)
7. Schools containing Risso's dolphins (*Grampus griseus*)
8. Schools containing pilot whales (*Globicephala macrorhynchus*)
9. Schools containing sperm whales (*Physeter catodon*)

A school was classified as one of the first four types if its estimated composition contained at least 90 percent of the species referred to. Mixed schools of spotted and spinner dolphins were defined as any school for which the estimated composition contained more than 10 percent for each species. For the last four school types, a school was included if it contained any identified individuals of that species. This was done because the actual number of individuals seen in any single sighting of these four species tends to be small. Thus, even when seen in a mixed school, these animals represent a significant collection of individuals for that species, whereas the frequency of mixed schools of these species was too infrequent to consider separate classifications. For these school types, a few mixed schools may be counted as more than a single type. Common and striped dolphins rarely represented less than 90 percent of a school. Spotted dolphins rarely constituted less than 10 percent of the school. The spinner dolphin was most frequently found as a minor constituent in schools dominated by other species (primarily spotted dolphins). Thus, ~20 percent of all schools containing any spinner dolphins were composed of less than 10 percent of spinner dolphins. However, even for this species, this represents only ~1 percent of all individuals encountered. Although information on species identification was collected from crew members as well as from the observers, only positive identifications made by the observer are used here because of the uncertainty involved in the crew identifications for many of the species.

Calculations and Statistical Methods

The relative densities within a geographic stratum were calculated as the total number of encounters by all vessels divided by the sum of distance searched by all vessels. This is equivalent to the weighted average of the encounter rate for each vessel when the weights are equal to the distance searched by a vessel within a stratum. In Polacheck (1983), the question of appropriate weights is discussed. Estimates of the variance of these relative density estimates within a stratum can be calculated using standard formulae for the variance of a weighted mean (Seber 1973).

In this paper, all calculations are based on 5° square stratifications of the data. This scale was selected because encounter rates tend to be too variable at any finer scale, given the total number of sightings. Similarly, encounter rates were only considered if a minimum of 500 mi of searching was conducted within any stratum in order to remove the variability associated with very small numbers of encounters.

Average annual estimates of the overall encounter rates from 1977 to 1980 for each species were calculated as the simple average of the encounter rates in each 5° square. The method used for estimating the variance of these average annual rates is detailed in Polacheck (1983).

For the common and spinner dolphins, the annual rates were calculated based on their known historical ranges from Holt and Powers (1982). For the other species, these rates were calculated for the area of the known historical range of the spotted dolphin, also from Holt and Powers (1982). This area was chosen because the distributional ranges for most of these other species within the eastern tropical Pacific are not well known. This area provides a common basis for comparison. Given the lack of searching effort in the western and southern areas of the eastern tropical Pacific (Polacheck 1983), the exact choice of the offshore boundaries tends to be immaterial to the final results. Revised and expanded estimates of these historical ranges have been produced by Perrin *et al.* (1983). In comparison with the ranges provided in Holt and Powers (1982), these revised ranges contain no new areas in which substantial searching by purse-seiners has occurred. These revised ranges were not available at the time when the calculations in this paper were performed. These annual rates were calculated primarily to see if there were any pronounced time trends for any of the species.

Inter-relations among the species were examined initially by calculating the correlation matrix between the encounter rates within a year for all 5° squares south of 25°N and with a minimum of 500 mi searching. An overall correlation matrix was also calculated utilizing the four annual estimates for a 5° square as independent replicates. This overall correlation matrix thus takes into account variation between years.

Factor analyses based on principal components (Kendall 1980) were conducted based on these correlation matrices. The resulting factor loading provides a measure of the association between the relative density estimates. The spatial patterns for the factor scores for each 5° square were examined to see if the implied associations from the factor analyses corresponded to any spatial relationships. Separate factor analyses were done for each year's data as well as an analysis based on the combined correlation matrix. Comparison of the results among these analyses provides an indication of the robustness and consistency of the results. Both weighted and unweighted factor analyses were run. In the weighted analyses, the weights were made equal to the total distance searched within a 5° square to reflect the differences in variances of the estimates owing to differences in search effort. The results were similar for both the weighted and unweighted analyses. Only the results of the unweighted analysis are presented. Rotation of the factor loadings was by the varimax method.

The relationship between the encounter rates and the spatial variation in the oceanic environment was examined for 13 variables. Only scattered information, derived from various sources over various time periods, is available on environmental or climatological conditions in the eastern tropical Pacific. The data that are used here are from the compilation put together by Schnell *et al.* (1982) (modified slightly in Polacheck [1983]). They are neither real-time nor sighting associated measurements. They are meant as a rough measure of the average conditions prevailing in the eastern tropical Pacific. Table 1 lists the variables used and their abbreviations.

To test for any relationship among these environmental variables and the observed encounter rates, a principal component analysis was performed on the 13 environmental variables, followed by a multiple regression analysis of the estimated encounter rate for each school type against these principal components.

Reilly (1977) performed a similar analysis on his estimates of the relative

Table 1. Descriptions and abbreviations of the 13 environmental measurements.

Abbreviation	Description
1. N. Current	Average northerly component of the sea surface current in winter
2. W. Current	Average westerly component of the sea surface current in winter
3. Depth	Average sea depth
4. Jan. Solar Insol.	Average incoming solar radiation for January (g cal/cm)
5. Ann. Solar Insol.	Average annual incoming solar radiation (g cal/cm)
6. Jan. Temp.	Average sea surface temperature in January
7. July Temp.	Average sea surface temperature in July
8. Temp. Var.	Average annual sea surface temperature variation
9. Depth O_2 Min.	Average depth at which oxygen content of sea water falls below 1.0 ml/l
10. Thick. O_2 Min.	Thickness of the subsurface layer with an oxygen content of less than 1.0 ml/l
11. Salinity	Average salinity of surface sea water
12. W. Thermocline	Average depth of the mixed layer for January, February and March
13. Thermocline Var.	Average annual variation in the depth of the center of the permanent thermocline

densities of pilot whales. Regression analysis was done on the principal components because large correlations exist between the environmental variables that would make a meaningful interpretation of simple multiple regression analyses on the original data difficult. The principal components are a mutually orthogonal and independent linear combination of the environmental data (Kendall 1980) and the resulting regression parameters are mutually independent. With this method, the independent contribution of each principal component to the variance in the encounter rate is easily assessed while the contribution of each of the environmental variables to any principal component can also be examined for an indication of the most important environmental variables. The order in which components were entered into the analyses was by rank of their correlation with the dependent variable.

The principal components are numbered in order of the amount of the total variance that they explain in the environmental data. As such, by noting which components are important predictors in the regression analyses, one has an indication of whether the major variation in the environment as measured by the independent variables correlates with variation in relative densities as measured by the encounter rates.

The combined set of encounter rates for all four years was used for these regression analyses since the environmental data have no annual component but are only estimates of the average conditions prevailing in the eastern tropical Pacific. This combined data set contains up to four independent estimates of the encounter rate within a 5° square. Thus, these analyses include within them a measure of the variation in the encounter rates between years. The same set of geographic squares that was used in the factor analyses was used in these regression analyses. The environmental variables were transformed to standardize normal scores before the principal components were calculated in order to reflect relative and not absolute variations.

In addition to the regressions on principal components, a canonical correlation analysis is presented for the relationship between the set of encounter rates for all species and the set of environmental variables. Canonical correlations reduce the dependency between the sets of data to their simplest possible form and provide an indication of the degree of inter-relatedness between them (Pielou 1977, Kendall 1980). Canonical correlation analyses have not been widely used by ecologists although Pielou (1977) suggests that they may be a powerful tool for providing insights into the inter-relation between two sets of ecological variables. The same data sets that were used in the factor analyses and the regression on principal components are used for this canonical correlation analysis. Both sets of variables were transformed to their standardized, normal scores.

Results

Annual Rates

The average annual encounter rates suggest no consistent trend in abundances over the four years of data (Table 2). The amount of variation associated with individual estimates tends to be high (*e.g.*, coefficients of variations between 7 and 20 percent) because of the relative rarity of encounters for many of these school types. The rate for mixed spotted and spinner schools show the most consistent trend (downward), but, given the associated variability and fluctuations in the estimates, no conclusion about temporal changes is warranted. The encounter rates for 1977 are always the highest except for schools containing Risso's dolphins.

Spatial Distributions

For all of the species considered, the spatial density of schools based on these encounter rate estimates is non-uniform throughout the eastern tropical Pacific (Fig. 1). The values in this figure are the weighted averages of the estimated yearly encounter rate within a 5° square where the weights equal the annual distance searched. For the sperm and pilot whales and for the common, bottlenose and Risso's dolphins, high encounter rates tend to be mainly in nearshore areas. For common dolphins and perhaps pilot whales, there appears to be an additional offshore concentration but of considerably lower densities, centered at about 10°N and 135–140°W. Reilly (1977) noted an offshore concentration of pilot whales, describing it as a distinct population center. The inshore distribution for common dolphins are concentrated in two areas at 25°N and 5°N with a hiatus between them. The distribution of almost pure schools of spotted dolphins roughly parallels the distribution pattern for all spotted dolphin schools examined in detail in Polacheck (1983). The distribution of schools of spinner and striped dolphins is more diffuse. Highest encounter rates for schools of

Table 2. Estimates of the average annual encounter rate for nine types of cetacean schools in the eastern tropical Pacific. Encounter rates are number of schools per 1,000 mi of searching. Numbers in parentheses are estimates of the standard deviations (based on equation 2 of Chapter VIII in Polacheck 1983).

Species	1977	1978	1979	1980
Spotted dolphin	5.555	3.631	5.455	3.853
	(0.200)	(0.204)	(0.250)	(0.199)
Spinner dolphin	0.899	0.571	0.408	0.609
	(0.066)	(0.104)	(0.048)	(0.097)
Mixed spotted/spinner	1.631	1.368	1.369	1.032
	(0.090)	(0.104)	(0.103)	(0.098)
Common dolphin	1.177	0.510	1.102	0.673
	(0.127)	(0.043)	(0.099)	(0.116)
Striped dolphin	0.378	0.351	0.314	0.408
	(0.050)	(0.042)	(0.033)	(0.061)
Bottlenose dolphin	0.876	0.539	0.740	0.581
	(0.101)	(0.043)	(0.064)	(0.052)
Risso's dolphin	0.098	0.129	0.112	0.098
	(0.036)	(0.027)	(0.023)	(0.023)
Pilot whale	0.878	0.334	0.554	0.507
	(0.148)	(0.030)	(0.061)	(0.066)
Sperm whale	0.324	0.258	0.362	0.276
	(0.032)	(0.024)	(0.050)	(0.030)
No. of 5° squares[a]	44	45	42	41
Total distance searched (mi)	435,808	487,956	354,555	224,148

[a] Number of squares and total distance searched vary slightly for common and spinner dolphins because of the different areas used to define the boundaries for these two species.

striped dolphins are found southwest of the Galapagos and for pure schools of spinner dolphins, off western Mexico. The lack of a stronger pattern may be due partially to the poor resolution in the data because of the overall low encounter rates for these two species. The distribution of mixed schools of spotted and spinner dolphins is also diffuse, but their encounter rates tend to be highest in the offshore area around 10°N.

Spatial Relations between Species

The estimates of the correlation coefficient for the encounter rates within a 5° square between species suggest that relatively strong associations in densities between species may exist (Table 3). These correlation coefficients can be considered minimal estimates, given the large sampling error associated with the individual encounter rate estimates.

When factor analyses are used to classify these associations between species, the results suggest two or three main species groupings. Factor analysis on the correlation matrix for the encounter rates for all four years' combined data

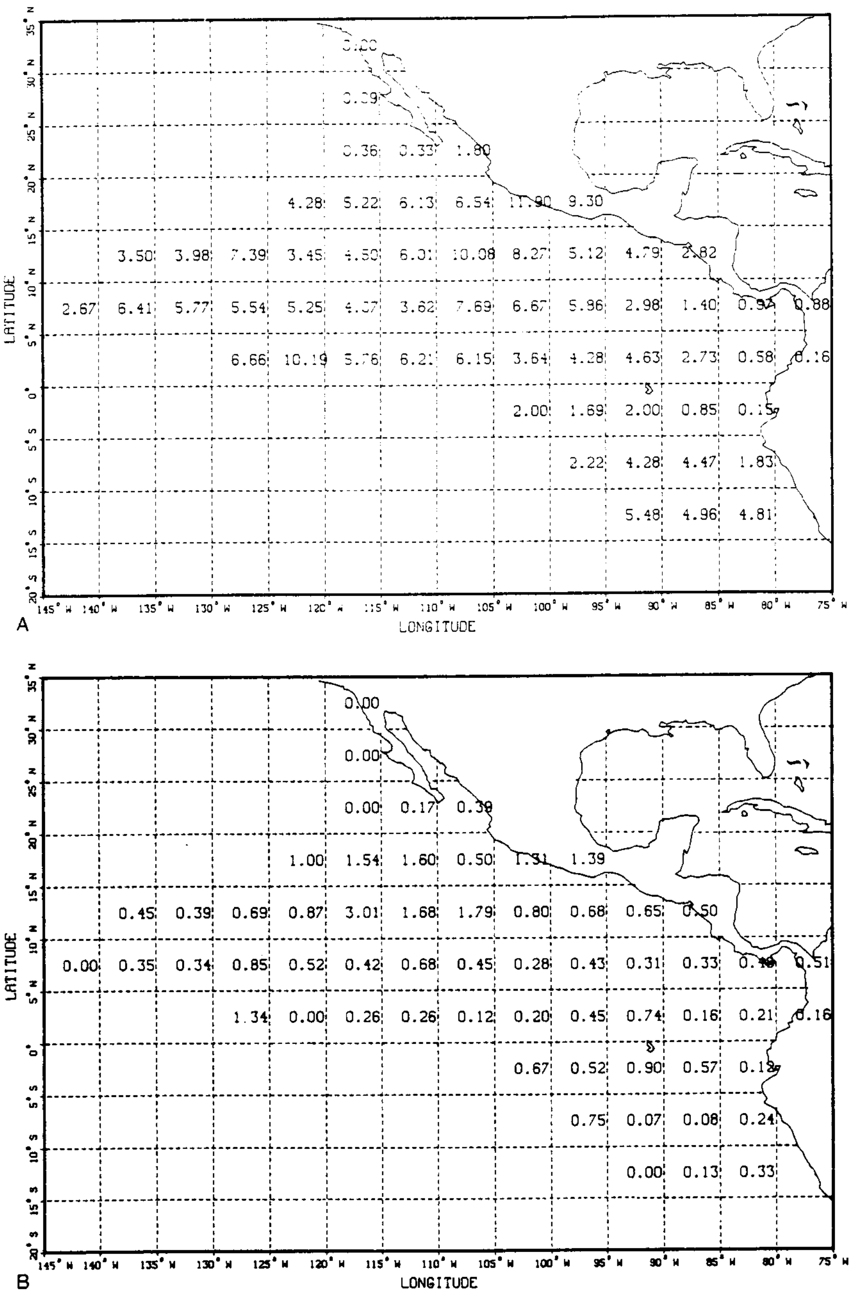
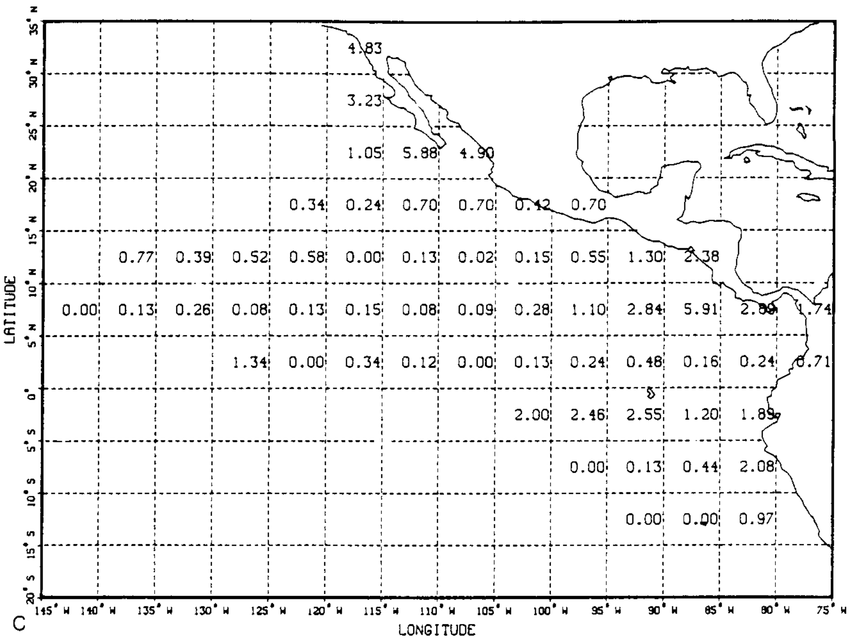


Figure 1. Weighted average estimates of the annual encounter rates (number of schools/1,000 mi searched) from 1977–1980 by 5° squares for marine mammal schools in the eastern tropical Pacific. (A) Pure spotted dolphin schools. (B) Pure spinner dolphin schools.



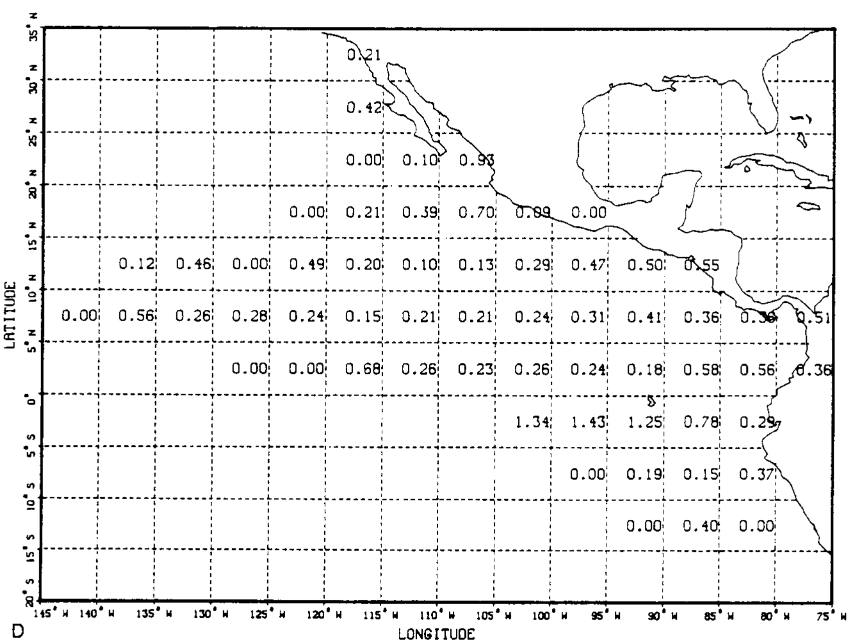
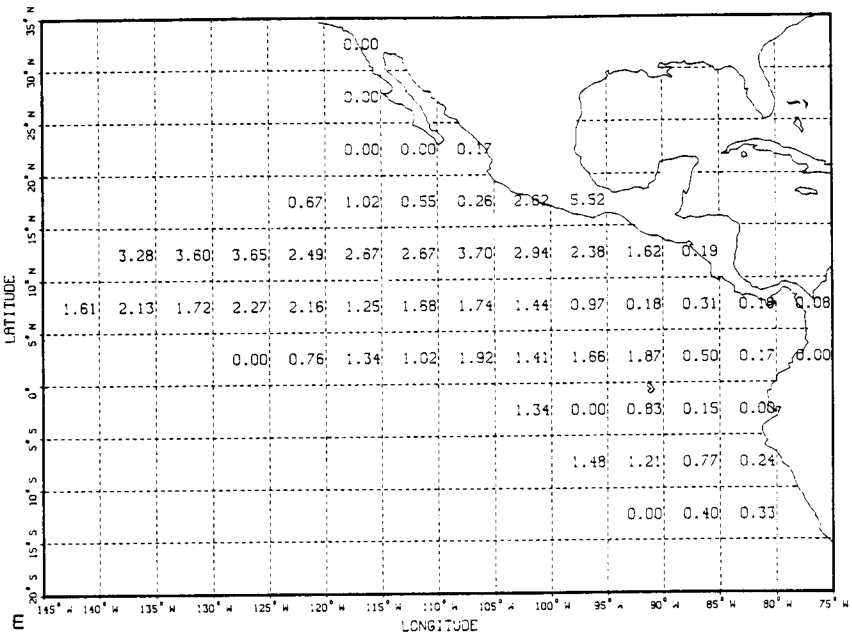


Figure 1. Continued. Weighted average estimates of the annual encounter rates (number of schools/1,000 mi searched) from 1977–1980 by 5° squares for marine mammal schools in the eastern tropical Pacific. (C) Pure common dolphin schools. (D) Pure striped dolphin schools.



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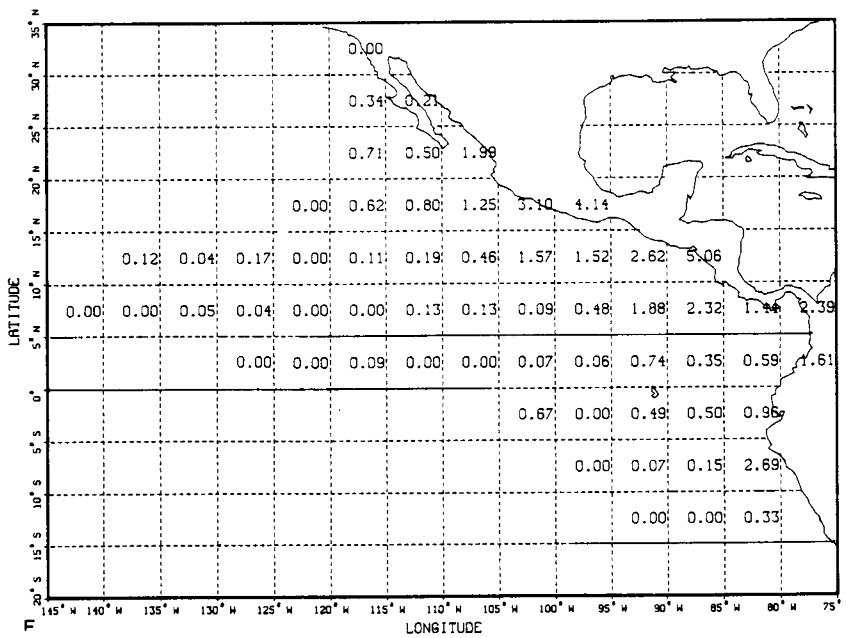

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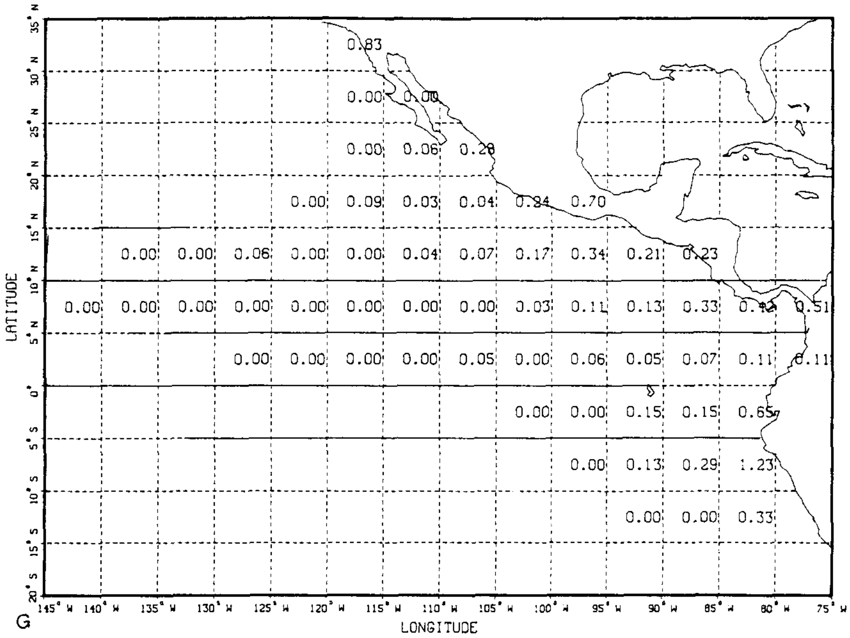
Figure 1. Continued. Weighted average estimates of the annual encounter rates (number of schools/1,000 mi searched) from 1977–1980 by 5° squares for marine mammal schools in the eastern tropical Pacific. (E) Mixed spotted and spinner schools. (F) Bottlenose dolphin schools.



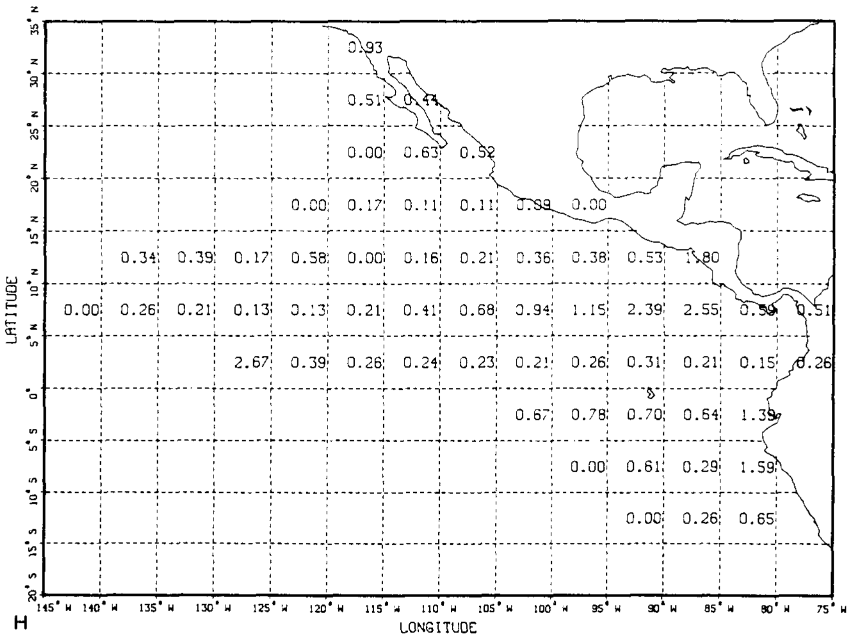


Figure 1. Continued. Weighted average estimates of the annual encounter rates (number of schools/1,000 mi searched) from 1977–1980 by 5° squares for marine mammal schools in the eastern tropical Pacific. (G) Risso's dolphin schools. (H) Pilot whale schools.

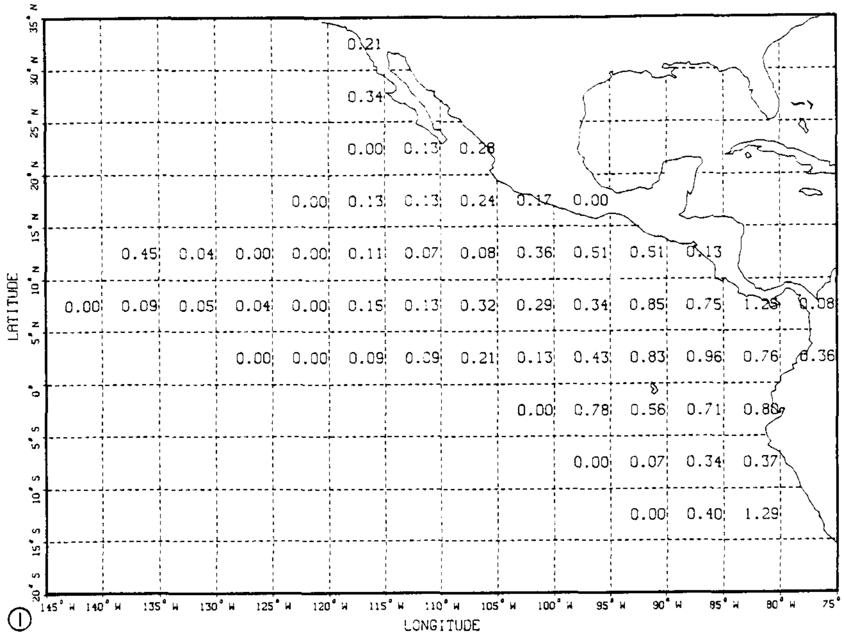


Figure 1. Continued. Weighted average estimates of the annual encounter rates (number of schools/1,000 mi searched) from 1977–1980 by 5° squares for marine mammal schools in the eastern tropical Pacific. (I) Sperm whale schools.

resulted in three factors with eigenvalues greater than 1.00. These three factors explain 63 percent of the variance in the original data.

Considering the factor loadings (Table 4), bottlenose dolphins, Risso's dolphins and pilot whales load strongly and are positively associated in the first factor. The common dolphin is also moderately associated with this first factor. The second factor is dominated by a positive association between spotted, spinner and mixed spotted and spinner schools. The common dolphin and to a lesser extent, the pilot whale are negatively associated with this factor. The third factor is dominated by the striped dolphin and sperm whales.

When separate factor analyses are performed on the data from each year, (1) the spotted, spinner and mixed spotted and spinner schools and (2) the bottlenose, common, Risso's and pilot whale schools tend to load together in the first few factors although there is some variability in this pattern, particularly in this latter grouping in 1980 (Table 5). Common dolphins also tend to be negatively associated with the factors associated with spinner and spotted dolphins. It is also interesting that, in 1978, schools of pure spinner dolphins appeared to be relatively independent of the distribution of either schools of mixed spotted and spinner or pure spotted dolphins.

The apparent association between sperm whales and striped dolphins suggested by the loading pattern for the third factor in the combined analysis may be spurious, given the factor loading patterns in the annual analyses, particularly

Table 3. Estimates of the correlation coefficients between nine types of cetacean schools based on the encounter rates in 5° squares from the combined data set for 1977–1980.

	Spotted dolphin	Spinner dolphin	Common dolphin	Striped dolphin	Mixed spotted/spinner	Bottle-nose dolphin	Risso's dolphin	Pilot whale	Sperm whale
Spotted dolphin	1.000								
Spinner dolphin	0.326	1.000							
Common dolphin	−0.325	−0.065	1.000						
Striped dolphin	−0.164	0.009	0.116	1.000					
Mixed spotted/spinner	0.478	0.370	−0.300	−0.173	1.000				
Bottlenose dolphin	0.054	0.240	0.307	0.029	0.061	1.000			
Risso's dolphin	−0.059	0.210	0.192	0.010	0.039	0.676	1.000		
Pilot whale	−0.188	−0.088	0.447	0.039	−0.221	0.551	0.389	1.000	
Sperm whale	−0.188	−0.152	0.273	0.197	−0.227	0.031	0.133	0.159	1.000

Table 4. The factor loading for the nine types of cetacean schools from the factor analysis on the combined set of encounter rate estimates by 5° square for 1977–1980. V.P. is the variance explained by a factor.

	Factor 1	Factor 2	Factor 3
Spotted dolphin	−0.092	0.712	−0.206
Spinner dolphin	0.209	0.743	0.140
Common dolphin	0.522	−0.430	0.237
Striped dolphin	−0.045	0.017	0.873
Mixed spotted/spinner	−0.046	0.755	−0.212
Bottlenose dolphin	0.885	0.188	0.008
Risso's dolphin	0.795	0.167	0.069
Pilot whale	0.760	−0.313	−0.017
Sperm whale	0.139	−0.271	0.580
V.P.	2.341	2.049	1.267

in light of the strong negative association between these two species in the third factor for 1977. However, these two species are known to be common in equatorial waters. Thus, the factor analysis may be picking out a true relationship and the reason the relationship does not appear stronger may be due to the fact that purse-seiners spend little time within the equatorial waters of the eastern tropical Pacific.

For the first factor from the combined analysis, there is a strong correlation between the factor scores for a 5° square in different years (Table 6). The annual factor score for a 5° square is a measure of the importance of the group of species that is strongly associated with a factor. The factor score is calculated as the sum of the products of the annual encounter rates for a 5° square for each species times its respective factor loading. A definite spatial pattern exists in these factor scores as can be seen in the tabulation of the annual score for each 5° square (Fig. 2A). Given the pattern in these factor scores, the positive factor loading for this first factor appears to represent a nearshore association of small cetaceans.

For the second factor from the combined analysis, the factor scores for a 5° square in different years also tend to be correlated (Table 6). A definite spatial pattern also exists for these factor scores (Fig. 2B). The positive values yield a pattern roughly similar to the pattern of relative density suggested by the detailed analysis of the encounter rate for spotted dolphins in Polacheck (1983). The areas with large negative values represent areas in which common dolphins and/or pilot whales are common and which lack schools of spotted and spinner dolphins.

Environmental Correlates

For almost all of the species, the maximum value of the estimated correlation coefficient between the encounter rates and any of the environmental variables has an absolute value between 0.30 and 0.45. The environmental variables

Table 5. The factor loading for the types of cetacean schools from the factor analyses on the annual encounter rate estimates by 5° squares. V.P. is the variance explained by a factor.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 1	Factor 2	Factor 3
	1977				1979		
Spotted dolphin	0.805	−0.096	0.122		0.562	−0.323	−0.254
Spinner dolphin	0.730	0.289	−0.108		0.739	−0.145	0.153
Common dolphin	−0.616	0.402	0.151		−0.278	0.703	0.195
Striped dolphin	−0.320	−0.160	−0.671		−0.530	−0.152	0.666
Mixed spotted/spinner	0.819	0.088	0.058		0.795	−0.256	−0.085
Bottlenose dolphin	0.093	0.952	0.007		−0.025	0.200	0.847
Risso's dolphin	0.226	0.887	0.009		0.137	0.385	0.680
Pilot whale	−0.426	0.747	0.030		−0.083	0.800	0.187
Sperm whale	−0.249	−0.101	0.776		−0.413	0.669	0.030
V.P.	2.635	2.548	1.106		2.050	1.984	1.792
	1978				1980		
Spotted dolphin	0.005	0.839	0.013	0.095	0.713	−0.341	−0.153
Spinner dolphin	−0.024	0.145	0.041	0.873	0.764	0.253	−0.152
Common dolphin	0.580	−0.480	0.154	0.191	0.030	0.914	0.042
Striped dolphin	0.011	−0.084	0.806	0.256	0.388	0.174	0.564
Mixed spotted/spinner	−0.052	0.809	−0.196	0.167	0.548	−0.454	−0.135
Bottlenose dolphin	0.886	0.161	0.069	−0.004	0.663	0.167	0.292
Risso's dolphin	0.516	−0.454	−0.115	0.255	−0.123	0.013	0.797
Pilot whale	0.691	−0.105	0.198	−0.192	0.066	0.735	0.232
Sperm whale	0.230	−0.058	0.715	−0.220	−0.134	0.220	0.837
V.P.	1.922	1.862	1.282	1.052	2.021	1.868	1.860

Table 6. Estimates of the correlation coefficient between years for the first and second factor scores for a 5° square from the combined factor analysis. The lower triangle is for the first factor and the upper for the second. (n = the number of 5° squares.)

	1977	1978	1979	1980
1977		0.65 n = 49	0.50 n = 48	0.52 n = 44
1978	0.68 n = 49		0.61 n = 49	0.36 n = 44
1979	0.37 n = 48	0.68 n = 49		0.74 n = 43
1980	0.48 n = 44	0.68 n = 44	0.80 n = 43	

that tend to show the highest correlations tend to be associated with sea surface temperature, depth of the thermocline, thickness of the oxygen minimum layer and depth. Where the correlation with depth is relatively high, it is primarily a reflection of the nearshore distribution for these species.

The results from the regression analyses of the encounter rates on the principal components of the environmental variables yielded a highly significant relationship (Table 7). For all species, the first three components entering the analysis are generally significant at least at the 0.01 level. However, the cumulative R^2 for the regression coefficients never exceeds 0.40 for the first four components. This indicates that a large component of the variance in these encounter rates is not explained by these environmental variables. The principal component that most frequently enters early into the regression equations is number 2 (7 of 9). This component is dominated by variables related to sea surface temperatures, the thermocline, solar radiation and the variance in the depth of the oxygen minimum layer. Species that tended to be associated in the factor analysis tend to have similar principal components playing dominant roles in their regression equations.

Although the first principal component for the environmental data explains approximately 36 percent of the variation in the environmental data, it enters as one of the first four variables in only one of the regression equations. Also, many of the higher principal components are important in the regression equations. This suggests that a major part of the variation in cetacean densities is unrelated to the variation in these physical environmental parameters.

Canonical Correlations

The first few canonical correlation coefficients between the set of encounter rates for all species and the set of environmental variables tend to be surprisingly high and highly significant (Table 8) according to Bartlett's test for the significance of the smallest set of eigenvalues (Dixon 1981). The first canonical variable for the species variables has relatively high loadings or correlations with the encounter rates for all species. Schools of spotted, spinner and mixed spotted

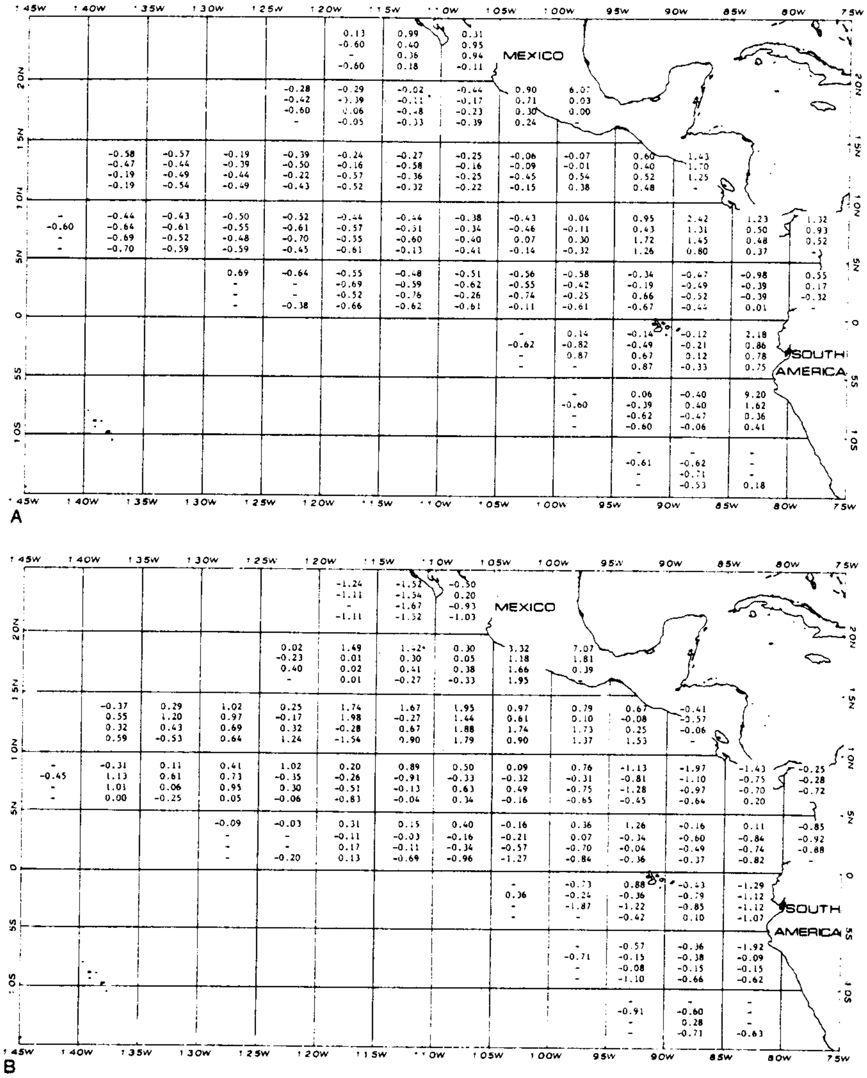


Figure 2. Estimates of the first (A) and second (B) factor scores for each year from 1977–1980 for a 5° square from the factor analysis on the combined data. The first value in a square represents the score for 1977, the second for 1978, *etc.* A dash indicates insufficient searching (*i.e.*, <500 mi) within a square during a given year.

and spinner schools load positively and the other six species load negatively. Thermocline depth, sea surface temperature and depth load most heavily in the first canonical variable for the set of environmental parameters (*see* Polacheck 1983 for complete listing of the loading). In general, the results of this canonical correlation analysis suggest similar results to the factor analysis and regression

Table 7. Results of the regression analyses of the encounter rates for nine types of cetacean schools on the principal components of the 13 environmental variables. Results

	First component to enter				Second component to enter		
	Component number	Correlation with encounter rate	R^2	F-value to enter	Component number	Correlation with encounter rate	R^2
Spotted dolphin	11	0.41	0.17	40.39***	2	−0.34	0.28
Spinner dolphin	4	−0.37	0.14	31.55***	2	−0.27	0.21
Common dolphin	6	0.38	0.15	34.41***	5	0.21	0.19
Striped dolphin	10	0.19	0.04	7.47**	2	0.18	0.07
Mixed spotted/spinner	2	−0.38	0.14	33.25***	6	−0.29	0.23
Bottlenose dolphin	3	−0.42	0.18	43.64***	4	−0.34	0.29
Risso's dolphin	5	0.40	0.16	36.82***	2	0.21	0.20
Pilot whale	5	0.33	0.11	24.76***	8	−0.27	0.19
Sperm whale	2	0.34	0.12	26.05***	3	−0.29	0.20

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.005$.

on principal components, but emphasize the extent of the large amount of overall inter-relation between the set of environmental variables and the encounter rates.

Discussion

The above results indicate that the eastern tropical Pacific cannot be considered as a homogeneous community with respect to the common cetacean species found within it. The results of the factor analyses and estimates of the correlations between species suggest the existence of three major groupings in the spatial distributions of these species:

1. a nearshore grouping of bottlenose dolphins, Risso's dolphins, pilot whales and, to a lesser extent, common dolphins concentrated near the Gulf of Panama,
2. an offshore pelagic grouping of spotted and spinner dolphins, and
3. an association between pilot whales and common dolphins that overlaps the first grouping in nearshore areas and also tends to be segregated from the second grouping.

Striped dolphins and sperm whales have distributions overlapping all of these groupings and appear to have no strong association with any of the other species. The consistency of these major groupings both spatially and between years is surprising in view of the uncertainties and variability in estimates of relative are given for the first four components to enter the regression equations for each school type.

	Third component to enter				Fourth component to enter			
F-value to enter	Component number	Correlation with encounter rate	R^2	*F*-value to enter	Component number	Correlation with encounter rate	R^2	*F*-value to enter
31.42***	6	−0.25	0.34	18.28***	8	−0.19	0.38	12.00***
18.46***	6	−0.18	0.24	8.73***	11	0.16	0.27	7.06**
11.14***	7	0.21	0.23	11.03***	2	0.16	0.26	6.49*
6.71*	3	−0.17	0.10	6.50*	8	0.10	0.11	1.99
21.18***	1	0.18	0.26	9.00***	4	−0.18	0.29	8.88***
31.38***	5	0.24	0.35	17.59***	8	−0.19	0.39	11.04***
11.24***	3	−0.17	0.23	7.45**	4	−0.15	0.25	5.84*
18.17***	3	−0.19	0.22	8.94***	9	0.17	0.25	7.74**
20.73***	5	0.21	0.24	11.01***	9	0.11	0.26	3.42

densities. This consistency is what most strongly suggests that these statistical groupings may reflect actual associations. However, these groupings should be considered primarily as hypotheses for further exploration because of the coarseness of both the geographic and temporal straitifications. The variation between years indicates that there is flexibility in whatever associations do exist.

Of these three species groupings, the association between spotted and spinner dolphins has been noted previously (Au *et al.* 1979). The fact that the observed correlation coefficients between these two species (Table 4) are not even larger is somewhat surprising given the frequency with which these two species are found together in a single school. The absence of higher correlations could reflect either the limits of the precision in the estimates and/or limits of the degree of actual overlap. The estimated range map (Holt and Powers 1982, Perrin *et al.* 1983) indicate the species do not overlap completely. Also, the association between spotted and spinner dolphins is probably less for the southern stocks, which would weaken the overall correlation since the highest encounter rates for pure schools of spinner dolphins are in the south.

Au *et al.* (1979) also suggest that striped and common dolphins may be closely associated in their distributions. There is not strong support for this association in the quantitative measures examined here, although the second highest correlation for the encounter rate of striped dolphins is with common dolphins (Table 3). The lack of any association could reflect simply the imprecision in the estimates of relative densities, particularly considering that striped dolphins are rarely sighted. This rarity of sightings is most likely due to the problem of unidentified schools discussed under MATERIALS AND METHODS (above).

Au *et al.* (1980) and Au and Pitman (1981) suggest that there is a unique

Table 8. Estimates of the canonical correlation coefficients and the eigenvalues from the canonical correlation analyses between the set of environmental variables and the set of encounter rate estimates. Also given are the results from Bartlett's test for the significance of the smallest set of eigenvalues. The results in the first row are for the test that none of the eigenvalues are different from 0. The results in the second row are for the test that all but the first eigenvalue are equal to 0, *etc.* The number of canonical variables of practical value is less than or equal to the smallest number of eigenvalues for which Bartlett's test for the remaining eigenvalues is nonsignificant.

Canonical variable pair number	Canonical correlation	Eigenvalue	Bartlett's test for the remaining eigenvalues		
			d.f.	Chi-square	*P*
—	—	—	117	584.9	0.0001
1	0.802	0.643	96	391.7	0.0001
2	0.710	0.505	77	259.8	0.0001
3	0.599	0.359	60	176.5	0.0001
4	0.517	0.267	45	118.2	0.0001
5	0.435	0.189	32	78.8	0.0001
6	0.426	0.181	21	41.3	0.0051
7	0.362	0.131	12	14.9	0.2459
8	0.253	0.064	5	1.5	0.7828
9	0.114	0.013	—	—	—

association of cetaceans with the equatorial surface water mass within the eastern tropical Pacific. This water mass tends not be frequented by purse seiners. Therefore, the results of this paper have no bearing on any such association.

As with the results from the factor analyses, the relationships suggested by the regression analyses between the spatial distribution of encounter rates and environmental parameters are surprisingly strong, but require even more caution in attributing any form of casual association, particularly since both the seasonal and annual variability is ignored in the set of environmental variables. However, even in spite of the uncertainties in both sets of data, the high canonical correlations and the R^2s from the regression analyses suggest that a strong interdependence exists between the density of these cetacean schools and the environmental variation within the eastern tropical Pacific. These marine mammal species appear to have well-defined habits within the eastern tropical Pacific, determined in part by the physical environment. At the very least, the strong statistical relationships between these two sets of variables argue that the spatial patterns observed in the encounter rate estimates are unlikely to have arisen merely from sampling error, but reflect underlying patterns in the spatial densities of schools.

From the analyses of the relationship between these two sets of variables, parameters related to sea surface temperature, depth of the thermocline and thickness of the oxygen minimum layer tend to be the most important. These environmental parameters have been noted to correlate with the distributional ranges for the major dolphin species (Perrin *et al.* 1976, Au *et al.* 1979) and have also been noted to be related to tuna distributions (Blackburn 1965, Cole

1980, Forsbergh 1980, Sund *et al.* 1981). The significance, if any, of the thickness of the oxygen minimum layer is obscure.

The seven species other than the sperm whale considered in this paper are potentially major competitors. The available natural history information suggests that these seven species have overlapping diets, are opportunistic feeders on fish and squid in near-surface waters, have no significant predation pressure, are long-lived and have only limited capacities for rates of population growth (Leatherwood *et al.* 1972, Mitchell 1975; *see* also bibliographies of Johnson 1979, Rivers 1982). Traditional ecological theory on competition (*e.g.*, MacArthur 1968, May 1981) suggests that some form of resource partitioning must be occurring for these species to be co-occurring. The results from the factor and regression analyses are consistent with such partitioning. However, there is no direct evidence that any of these species are resource-limited. Even if this group has been structured by competition in the past, the large reduction in the abundances of spotted and spinner dolphins as the result of incidental kills during purse-seine operations (Smith 1979) suggests that the present should be a period of release from such competitive pressures. In this context, it would be interesting to examine changes in encounter rate estimates and in their spatial patterns if a longer time series of data becomes available.

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Literature Cited

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. National Marine Fisheries Service-Southwest Fisheries Center Admin. Report LJ-79-43. 59 pp.

Au, D. W. K., W. L. Perryman, R. L. Pitman and M. Sinclair. 1980. Cetacean populations and equatorial oceanography. Tropical Ocean-Atmosphere Newsletter 4:6, 10.

Au, D. W. K., and R. L. Pitman. 1981. The equatorial cetacean community of the eastern Pacific. (Abstract.) Page 95 *in* Proceedings of Fourth Biennial Conference on the Biology of Marine Mammals, December 14–18, 1981. San Francisco, CA.

Blackburn, M. 1965. Oceanography and the ecology of tunas. Oceanography and Marine Biology Annual Review 3:299–322.

Cole, J. S. 1980. Synopsis of biological data on the yellowfin tuna, *Thunnus albacares* (Bonnaterre 1788), in the Pacific Ocean. Pages 71–150 *in* W. H. Bayliff, ed.

Synopses of biological data on eight species of scombrids. Inter-American Tropical Tuna Commission Special Report No. 2.

DIXON, W. J. (Ed.) 1981. BMDP Statistical Software. 1981 edition. University of California Press, Berkeley, CA. 726 pp.

FORSBERGH, E. D. 1980. Synopsis of biological data on the skipjack tuna, *Katsuwonus pelamis* (Linnaeus 1758), in the Pacific Ocean. Pages 295–360 *in* W. H. Bayliff, ed. Synopses of biological data on eight species of scombrids. Inter-American Tropical Tuna Commission Special Report No. 2.

HOLT, R. S., AND J. E. POWERS. 1982. Abundance estimation of dolphin stocks involved in the eastern tropical Pacific yellowfin tuna fishery determined from aerial and ship surveys to 1979. U.S. Department of Commerce, NOAA Technical Memorandum SWFC-TM-NMFS-23. 95 pp.

JOHNSON, S. W. 1979. An annotated catalog of published and unpublished sources of data on populations, life history, and ecology of coastal marine mammals of California. National Marine Fisheries Service-Southwest Fisheries Center Admin. Report LJ-79-1. 193 pp.

KENDALL, M. 1980. Multivariate analysis. MacMillan, New York, NY. 210 pp.

LEATHERWOOD, S., W. E. EVANS AND D. W. RICE. 1972. The whales, dolphins and porpoises of the eastern North Pacific. A guide to their identification in the water. NUC-TP 282. 175 pp. Naval Undersea Research and Development Center, San Diego, CA 92132.

LEATHERWOOD, S., W. F. PERRIN, V. L. KIRBY, C. L. HUBBS AND M. DAHLHEIM. 1980. Distribution and movements of Risso's dolphin, *Grampus griseus,* in the eastern North Pacific. Fishery Bulletin 77:951–963.

MACARTHUR, R. H. 1968. The theory of the niche. Pages 157–176 *in* R. C. Lewontin, ed. Population biology and evolution. Syracuse University Press, Syracuse, NY.

MAY, R. M. 1981. Models for two interacting populations. Pages 78–104 *in* R. M. May, ed. Theoretical ecology (2nd edition). Sinauer Associates, Sunderland, MA.

MITCHELL, E. (Ed.) 1975. Review of biology and fisheries for smaller cetaceans: Report on the meeting of smaller cetaceans. Montreal, April 1–11, 1974. Journal of the Fisheries Research Board of Canada 32:889–983.

PERRIN, W. F. 1968. The porpoise and the tuna. Sea Frontiers 14:166–174.

PERRIN, W. F. 1969. Using porpoise to catch tuna. World Fishing 18:42–45.

PERRIN, W. F. 1975. Distribution and differentiation of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific. Journal of the Fisheries Research Board of Canada 32:1059–1067.

PERRIN, W. F., J. M. COE AND J. R. ZWEIFEL. 1976. Growth and reproduction of spotted porpoise, *Stenella attenuata,* in the off-shore eastern tropical Pacific. Fishery Bulletin 74:229–269.

PERRIN, W. F., G. J. SCOTT, J. WALKER, F. M. RALSTON AND D. W. K. AU. 1983. Distribution of four dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific with an annotated catalog of data sources. U.S. Department of Commerce, NOAA Technical Memorandum SWFC-TM-NMFS-38. 65 pp.

PERRIN, W. F., P. A. SLOAN AND J. R. HENDERSON. 1979. Taxonomic status of the "southwestern stock" of spinner dolphin *Stenella longirostris* and spotted dolphin *Stenella attenuata*. Report of the International Whaling Commission 29:175–184.

PIELOU, E. C. 1977. Mathematical ecology. John Wiley and Sons, New York, NY. 385 pp.

POLACHECK, T. 1983. The relative abundance of dolphins in the eastern tropical Pacific based on encounter rates with tune purse seiners. Ph.D. thesis, University of Oregon, Eugene, OR. 444 pp.

POLACHECK, T. 1984. Documentation of the time sequential file created from the tuna boat observer data bases for analyzing the relative abundance of dolphins in the eastern tropical Pacific. National Marine Fisheries Service-Southwest Fisheries Center Admin. Report LJ-84-33. 26 pp.

REILLY, S. B. 1977. The distribution of pilot whales, *Globicephala macrorynchus* Gray 1846, in the eastern tropical Pacific. Master's thesis, California Polytechnic State University, San Luis Obispo, CA. 80 pp.

RIVERS, V. 1982. Bibliography of marine mammal research programs at La Jolla Laboratory of Southwest Fisheries Center, 1963–1981. National Marine Fisheries Service-Southwest Fisheries Center Admin. Report LJ-82-25. 24 pp.

SCHNELL, G. D., M. E. DOUGLAS AND D. J. HOUGH. 1982. Geographic variation in morphology of spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*) from the eastern tropical Pacific. National Marine Fisheries Service-Southwest Fisheries Center Admin. Report LJ-82-15C. 213 pp.

SEBER, G. A. F. 1973. The estimation of animal abundance and related parameters. Griffin, London. 506 pp.

SMITH, T. D. (Ed.) 1979. Report of the status of the porpoise stock workshop (August 27–31, 1979, La Jolla, California). National Marine Fisheries Service-Southwest Fisheries Center Admin. Report LJ-79-41. 120 pp.

SUND, P. N., M. BLACKBURN AND F. WILLIAMS. 1981. Tunas and their environment in the Pacific Ocean: a review. Oceanography and Marine Biology Annual Review 19:443–512.

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