Evasive behavior of spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*) during fishing for yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean

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Abstract—This study examines the question of whether the evasive behavior of northeastern offshore spotted dolphins (*Stenella attenuata*) during fishing for tuna (by the Mexican fleet) varies in geographic areas of the eastern Pacific Ocean (EPO). It also investigates whether evasion differs between northeastern offshore spotted and eastern spinner dolphins (*Stenella longirostris orientalis*). Observations recorded in the database of the Mexican Programa Nacional de Aprovechamiento del Atún y de Protección de Delfines (PNAAPD) from 1992 to 1995 were analyzed. The calculated evasion index was the estimated percentage of dolphins that evaded capture in relation to the herd's estimated initial size in each set.

Evasion index by set was averaged in 2 2 quadrants and then used to draw a contour map. Three areas were outlined with low (25%), medium (44.44%), and high (71.80%) median evasion indices. These areas were significantly different ($P<0.0001$) according to the Kruskal-Wallis nonparametric multisample test, thus indicating a spatial pattern in evasive behavior of northeastern offshore spotted dolphins during fishing operations of the Mexican fleet. Spatial patterns in evasive behavior might be related to the dolphins' learning capacity, hence experience of individual dolphins or herds with tuna purse-seining in the EPO should be estimated to demonstrate this. To be representative, future research should utilize available historical fishing effort data for the international fleet. Furthermore, a multivariate approach to this issue is necessary.

One of the investigated areas (mouth of the Gulf of California) was further analyzed regarding differences between two stocks of dolphins. Evasion indices for eastern spinners were significantly different from those for northeastern offshore spotted dolphins ($P<0.0001$, Kolmogorov-Smirnov two-sample test). This difference may correspond to different evasive strategies used by the two stocks to evade capture in the net, such as evasion under the net and dispersion (division of herd into subgroups during the set). Eastern spinners apparently evaded more frequently than northeastern offshore spotted dolphins by diving under the net. During the three set stages of tuna fishing (before chase, during chase, and during encirclement), eastern spinner dolphins dispersed less often than spotted dolphins, behavior that may permit them to coordinate their evasive movements more effectively than northeastern offshore spotted dolphins. Evasion over the net was rarely observed in either stock.

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The tuna fishery in the eastern Pacific Ocean (EPO) sets purse seines in three major modes: school, log, and dolphin fishing. Yellowfin tuna (*Thunnus albacares*) and certain species of dolphins are found to associate in the EPO. The spotted dolphin (*Stenella attenuata*) is by far the most important species from the point of view of its frequency of association with tuna and its use by fishermen for catching tuna (Perrin, 1969). The frequent appearance of spinner dolphins (*Stenella longirostris*) in sets also makes this species significant, although in almost all cases it appears in mixed herds with the spotted dolphin (National Research Council, 1992).

During "dolphin fishing" or "fishing on dolphins," the net is set around the tuna and the dolphins after a period of chase. Once a dolphin herd is sighted with high-power binoculars (25), four to six speedboats are lowered, and the chase begins. The speedboats herd the dolphins and the accompanying tuna into a tight group that can be encircled by the seiner. The dolphins may try to evade the boats to avoid capture. Those that do not succeed are released by the fishing crew during the "backdown" procedure (a procedure in which the vessel is run in reverse to pull the corkline underwater and thus release the dolphins) (Barham et al., 1977).

Impact of the fishery on cetacean populations has been assessed by estimating cetacean abundance and distribution involved in tuna purse-seining, as well as by estimating mortality rates. By 1988, the estimated abundance of the northeastern offshore spotted dolphin had been reduced to between 19% and 28% and that of the eastern spinner dolphin and to between 32% to 58%

in relation to estimated pre-exploitation levels (Wade, 1993; Wade[1]). Therefore, these stocks have been designated as depleted under the U.S. Marine Mammal Protection Act. However, when compared to abundance estimates from 1986–90 research surveys (Wade and Gerrodette, 1993), preliminary estimates from the most recent surveys (Gerrodette[2]) show a noticeable increase in the abundance of the northeastern offshore spotted and the eastern spinner dolphin compared to previous estimates (Wade and Gerrodette, 1993).

In addition to abundance estimation, the total incidental mortality (all species and stocks involved in the fishery and for the international fleet) was estimated at 3274 for 1995, which represents 0.03% of the total population (Hall and Lennert, 1997) of 9.6 million for all dolphin species involved in the tuna fishery (Wade and Gerodette, 1993). The Mexican Programa Nacional para el Aprovechamiento del Atún y de Protección de Delfines (PNAAPD) estimated the incidental mortality (of all species and stocks) of the Mexican fleet to be 1819 dolphins in 1994 (Compeán et al.[3]).

Important efforts have been aimed at reducing mortality rates, such as improving fishing gear (Barham et al., 1977; Coe et al., 1984), placing quotas on the number of dolphins killed for each stock (Wade[4]), placing a quota on the number of dolphins killed by fishing vessel and making the backdown procedure mandatory (Colson, 1992).

Other efforts in reducing mortality have been directed towards research on dolphin behavior during tuna purse-seining (Norris et al., 1978; Pryor and Kang[5]). Mortality rates may also be reduced by understanding more about the dolphins' behavior, so that they are less likely to injure themselves or die during fishing practices (Norris et al., 1978).

[1] Wade, P. R. 1993. Estimation of historical population size of the northeastern stock of offshore spotted dolphin (*Stenella attenuata*). Southwest Fisheries Science Center Administrative Report LJ-93-18, 18 p. Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038-0271.

[2] Gerrodette, T. 1999. Preliminary estimates of 1998 abundance of four dolphin stocks in the Eastern Tropical Pacific. http://swfsc.ucsd.edu/IDCPA/Abund98.html. Southwest Fisheries Science Center., Natl. Mar. Fish. Serv., NOAA, P.O. Box 271. La Jolla, CA 92038

[3] Compeán J., G. A., I. Méndez G.-H. and I. Méndez R. In preparation. Annual estimates of incidental mortality for dolphin species associated with the Mexican tuna fishery during 1992–1995. Programa Nacional para el Aprovechamiento del Atún y de Protección de Delfines (PNAAPD). Km 107 Carretera Tijuana-Ensenada, Campus CICESE, 22800 Ensenada, B.C., México.

[4] Wade, P. R. 1993. Revised estimates of fisheries kill of dolphin stocks in the eastern tropical Pacific, 1959–1972. Southwest Fisheries Science Center Administrative Report LJ-93-17, 19 p. Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 8604 La Jolla Shores Dr., La Jolla, CA 92038-0271.

[5] Pryor, K., and I. Kang. 1980. Social behavior and school structure in pelagic porpoises (*Stenella attenuata* and *S. longirostris*) during purse seining for tuna. Southwest Fisheries Center. Admin. Rep. LJ-80-11C. Southwest Fisheries Science Center, 8604 La Jolla, Shores Drive, La Jolla, CA 92038-0271.

Some research indicates that some dolphin stocks may have reduced mortality through behavioral adaptations. The first ethological research on *Stenella attenuata* and *Stenella longirostris* during fishing operations was accomplished by Norris et al. (1978). They focused on overall herd movements and interanimal distances and developed the first ethogram for these animals during a net set for tuna. Pryor and Kang (1980) also made observations during seining operations but focused more on individual and subgroup behavior. Although Norris et al. (1978) described high stress levels in dolphins that were involved in sets, Pryor and Kang interpreted their own data as indicating much learned adaptive behavior and low stress levels. By analyzing records from observers on tuna boats, Stuntz and Perrin[6] noted and discussed the fact that dolphins (*Stenella* spp.) were more difficult to capture in areas where fishing effort had been higher and the authors concluded that dolphins had been able to learn to evade capture from tuna boats.

Data collected by observers on board tuna purse-seiners from 1992 to 1995 (PNAAPD database) were used to investigate whether the evasive behavior[7] of northeastern offshore spotted dolphins (*Stenella attenuata*) during fishing for yellowfin tuna varied geographically in the EPO. Differences in evasive behavior between the northeastern offshore spotted and the eastern spinner dolphin (*Stenella longirostris orientalis*) were also assessed. Furthermore, differences in evasive strategies[8] between these two stocks were described.

Methods

Data collection

Data from 1992 to 1995 from the PNAAPD database (Mexican fleet) were used to study evasive behavior of two stocks of different species in the EPO: the northeastern offshore spotted dolphin, a stock of the pantropical spotted dolphin (*Stenella attenuata*), and the eastern spinner dolphin (*Stenella longirostris orientalis*), a subspecies and stock of the spinner dolphin (*Stenella longirostris*) (Dizon et al., 1994; Perrin and Gilpatrick, 1994; Perrin et al., 1994).

Observers (also referred to as scientific technicians) from the Inter-American Tropical Tuna Commission (IATTC)

[6] Stuntz, W. E., and W. F. Perrin. 1979. Learned evasive behavior by dolphins involved in the eastern tropical Pacific tuna purse seine fishery. Unpubl. abstract. Third Biennial Conference on the Biology of Marine Mammals, October 7–11, 1979, Seattle, WA.

[7] Evasive behavior: In this study, calculated as a percentage of the estimated number of dolphins that avoided capture in the net relative to the best estimate of the initial herd size (before the set started) by the observer or scientific technician. See "Methods" section.

[8] Evasive strategies: movements of the herd or subgroups of dolphins in relation to seiner, speedboats, and net (when it has been set and before rings up) by which dolphins attempt to avoid capture in the net.

and corresponding national programs have worked on board tuna vessels. Since 1991, the PNAAPD has placed observers on board 50% of the trips by Mexican tuna boats (the remaining 50% is covered by IATTC observers). Observers record data during dolphin sets, using standardized data forms and instructions provided by the PNAAPD (which are very similar to those used by the IATTC). A detailed description of data collection and procedures can be found in Perrin et al. (1983) and Polachek.[9] In summary, in the "Daily Activity Record" (DAR), observers keep a daily log on events (date, time of day, departure, arrival, sightings, sets, geographic position, aerial assistance during a set, etc.), weather conditions (cloud cover, sea state, visibility, water temperature), and tuna catch. In other forms they also record the vessel's features and all data concerning marine mammal sightings and sets, school and log sets, sea turtle sightings, and more recently, bycatch.

When a marine mammal group is sighted (which might lead to a net set for tuna catch), observers fill out the "Record of Marine Mammal Observations and Set Data" (RMMOSD). Herd size and composition (percent and species or stock identification) is annotated as estimated by the observer (usually with 7 50 or 10 50 binoculars), a crew member on board (with 20 or 25 binoculars), and another crew member from the helicopter. At the end of a set, the observer has to decide on his "best estimate" of the herd size and composition before the actual set occurred. During a set, the observer estimates the number of dolphins (identified by species or stock) that actively evade the boats and net before the chase, during the chase, and during the encirclement, as well as the number of groups within the herd during each of the three set stages. The number of dolphins deliberately cut out by the skipper, those that evade by diving under the net or escape by leaping out of the net are also estimated and identified by the observer All these data were of interest for our study (except dolphins deliberately cut out because this action was not considered evasion actively achieved by dolphins). Other data recorded by the observer are chase and set times, number of speedboats used, whether or not explosives were used, the number and composition of captured marine mammals (those that were encircled), number of animals rescued and the manner of their rescue, start and end of backdown, number of dolphins hurt or killed, and further details about the fishing procedure.

The observers' estimates of herd size and number of dolphins evading capture may be biased owing to differing experience and estimation between observers. However, they attend a complete training course at the institution they work for (IATTC, PNAAPD, or other national programs), where they learn to identify fauna species they may encounter at sea (marine mammals, fish, birds, and sea turtles), how the fishing operation proceeds, and how to collect data. At the end of each trip, experienced editors at the institutions review the observers' collection of data. These procedures give credence to the data collected. Moreover, reactions of dolphins to approaching survey vessels have been studied previously by means of field experiments (Au and Perryman, 1982; Hewitt, 1985). Their results might be compared to the dolphins' behavior "before chase" because sighting distance in those studies (as during the fishing operation) was usually between 2 and 6 or 7 nmi (nautical miles), aided with 20 or 25 binoculars. Dolphins started to react (by changing their swimming speed and course) between 1.5 to 3 nmi distance to the ship (Hewitt, 1985) with one exception, where the herd reacted at 6 nmi (Au and Perryman, 1982). Almost half of the herds observed by Hewitt (1985) did not react at all. Therefore, the observer's estimate of initial herd size (which is also compared to the estimate by a crew member on board and by the crew member in the helicopter) was assumed to be reliable. We also relied on the observer's estimation of number of dolphins evading capture during all set stages (before chase, during chase, and during encirclement) because of their training and experience.

The logbooks with these observations are collected by the institution for which the observer works. To improve the accuracy and reliability of the observers' records, careful debriefing and editing is accomplished by skilled technicians (with considerable experience at sea) at the institutions (in our study, the PNAAPD). The observations are then entered into the corresponding computerized databases which are also checked for errors that might have occurred during "capture" (entry) of the data into the database (Perrin et al., 1983; Polacheck[9]).

Confidence in the databases of the IATTC and national programmes (PNAAPD and the U.S National Marine Fisheries Service) is acknowledged with the publication of studies that have analyzed some of these data. A few examples of such studies are the following: dolphin distribution (Perrin et al., 1983; Perrin et al., 1985), dolphin abundance estimation (Anganuzzi et al., 1992; Polachek[9]), incidental kill of dolphins in tuna fishing nets (Hall and Lennert, 1997; Wade[4]), dolphin life history (Chivers and De Master, 1994), tuna-dolphin association (Edwards, 1992; Scott and Cattanach, 1998), blue whale distribution in the eastern tropical Pacific (Reilly and Thayer, 1990), and aspects of the Mexican tuna fishery (Compeán and Dreyfus, 1996).

In our study, spatial patterns in evasive behavior of the northeastern offshore spotted dolphin were described, as well as differences in evasive behavior and strategies (herd dispersion,[10] evasion under and over the net) between

[9] Polachek, 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. Southwest Fisheries Science Center Admin. Report LJ-84-33, 26 p. National Marine Fisheries Service.

[10] Herd dispersion: to establish if a herd dispersed during a set, the grouping codes applied by the observers in paragraph 3 of the RMMOSD were used. The codes are the following: 1, herd is in one group; 2, herd has divided into two or three groups; 3, herd consists of more than three groups. These codes are recorded during three set stages: before chase, during chase, and during encirclement. For each species, the number of sets where the specified grouping code occurred was counted during each set stage. If codes were in ascending order, this was interpreted as herd dispersion during the fishing operation.

the northeastern offshore spotted and the eastern spinner dolphin (*Stenella longirostris orientalis*). A subset of the PNAAPD database (1992–95) was extracted from sections of the DAR (those referring to date and set position) and the RMMOSD (observer's best estimation of herd size and composition by species and stock, number and identification [also by species and stock] of evading and escaping dolphins, as described previously), and grouping codes. Data from sets that were interrupted (due to loss of tuna catch because all dolphins escaped from the chase or mechanical problems of the vessel or net performance, etc.) were excluded from the analyses.

Because data collected by the Mexican observer program (PNAAPD) represented 50% of the Mexican fleet's effort in the EPO, we assumed that the data set in our study was sufficiently large to represent the dolphins' evasive behavior in relation to Mexican tuna fishing boats during the sampled period.

Data analysis

Evasion index by set Evasion index by set was calculated in order to search for spatial patterns in evasive behavior of the northeastern offshore spotted dolphin and to analyze differences between northeastern offshore spotted and eastern spinner dolphins. This index is defined as the estimated percentage of dolphins that evaded capture during each set in relation to the herd's estimated initial size:

$$\hat{I}_{ij} = \left(\frac{\hat{E}}{\hat{H}}\right)100,$$

where $\hat{I}_{ij}$ = estimated evasion index during set i in quadrant j;
$\hat{E}$ = number of dolphins that evaded capture during set i in quadrant j, i.e. the sum of escaping dolphins estimated by the observer before the chase, during the chase, and during the encirclement as recorded in the RMMOSD;
$\hat{H}$ = herd size before chase started during set i in quadrant j, i.e. the observer's best estimate as recorded in the RMMOSD.

Evasion index by set was stratified by stock by selecting from the database only sets on pure herds (i.e. those herds composed 100% of a species) of northeastern offshore spotted dolphins and sets on pure herds of eastern spinner dolphins. Because only these two stocks were studied, results should not be considered representative of the corresponding species (pantropical spotted dolphin, *Stenella attenuata*, and spinner dolphin, *Stenella longirostris*).

Sets in which no dolphins escaped and therefore the calculated evasion index was zero were included in all analyses because they indicated that evasive behavior did not occur or failed. This action is contrary to common practice where "zeros" are often eliminated because they represent missing data that tend to bias calculations.

Spatial patterns in evasive behavior of northeastern offshore spotted dolphins To evaluate if there were spatial patterns in evasive behavior for the data in our study a computer program based on Matlab version 4.2c was used to plot the evasion index by set of the northeastern offshore spotted dolphin on a map of the EPO. The program calculated average evasion index by set in 2 2 quadrants to smooth the data which were then used to draw a contour map with the commercial surface mapping program Surfer version 6.01 (Smith et al., 1995). This software interpolated the average evasion index by set in 2 2 quadrants to form a regular rectangular array of grid values. This procedure was chosen because the smoothness of contours on a contour map is partially a function of the number of X and Y lines in the grid. When a grid is created, reducing the number of lines in the X and Y directions can result in more angular contours on the contour map. Most of the gridding methods in Surfer use a weighted average interpolation algorithm. The gridding method called "Kriging" with a linear variogram was chosen because it incorporates anisotropy and underlying trends in an efficient and natural manner and has been proven to be quite effective for many data sets in different fields (Smith et al., 1995).

A geographic difference in evasive behavior was observed in the contour map (see "Results" section, Fig. 1), and the 60%, 50%, and 40% contours were considered the limits between three areas with different evasive behavior (as defined by the evasion index) during the study period and for the Mexican fleet. In addition, the following statistical procedures were applied to test for significant differences in mean evasion indices of the three areas.

Analysis of variance (ANOVA) can be used to compare the mean of three groups of proportions (i.e. for each area) (Zar, 1999). Because proportions (like the evasion index) have a binomial distribution, the individual data should be transformed as follows in order to meet normality and homoscedasticity assumptions (Zar, 1999):

$$\hat{I}'_{ij} = 0.5\left(\arcsin\sqrt{\frac{\hat{E}}{\hat{H}+1}} + \arcsin\sqrt{\frac{\hat{E}+1}{\hat{H}+1}}\right),$$

where $\hat{I}'_{ij}$ = estimated transformed evasion index during set i in quadrant j;
$\hat{E}$ = estimated number of dolphins that evaded capture during set i in quadrant j; and
$\hat{H}$ = estimated herd size before chase during set i in quadrant j.

After transformation, the data still did not have a normal distribution (Kolmogorov-Smirnov goodness-of-fit test, D=0.0704, P<0.01, n=808; Zar, 1999). Therefore, distribution-free tests were used to search for significant differences between the three evasion areas (Conover, 1980; Neave and Worthington, 1988).

To search for significant differences between the medians (usual group average measure in nonparametric statistics) of three groups (evasion areas), the nonparametric Kruskal-Wallis multisample test seemed to be the most appropriate for the data in our study. The reasons for this

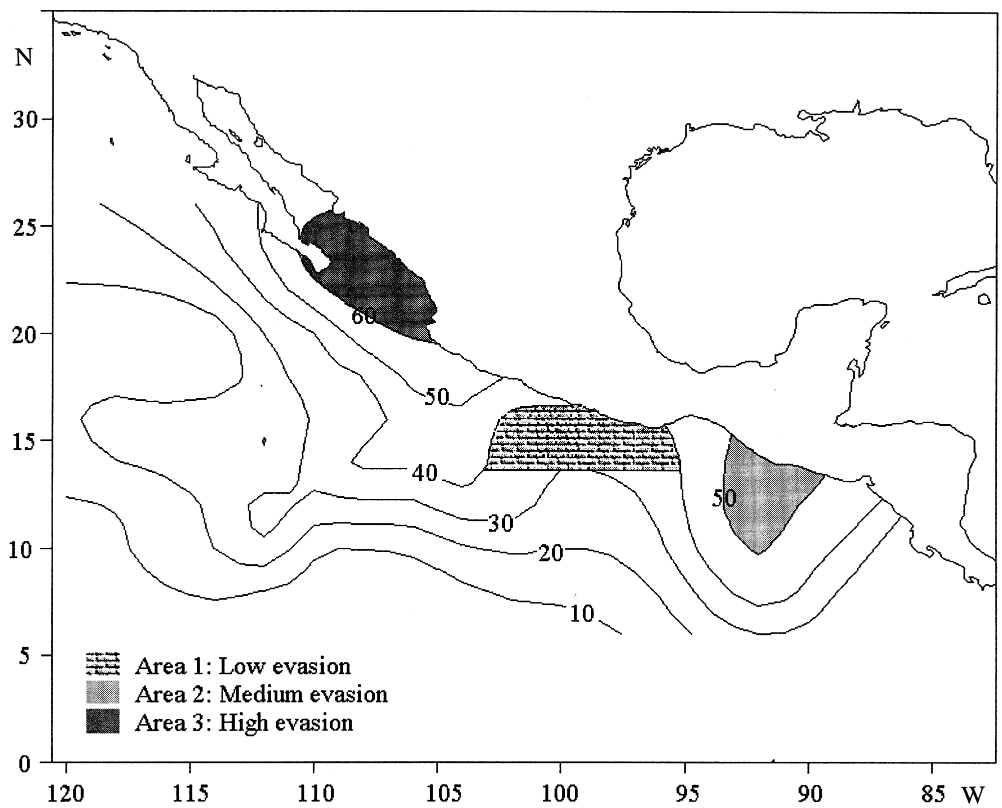

Figure 1

Estimated evasion index by set (estimated percentage of dolphins that evaded capture during each set in relation to estimated initial herd size) for northeastern offshore spotted dolphins (1992–95, Mexican fleet, PNAAPD data). Three areas were delimited according to 60%, 50%, and 40% evasion index contours.

are that data were measured in an interval scale (the test requires at least an ordinal scale), and samples are considered to be independent when it is assumed that dolphins remain approximately in the same area. Even though the swimming capacity of dolphins is well known, it is difficult to establish how fast or far they are able to travel. The Kruskal-Wallis test was preferred over the median test (with simpler calculations) because the latter uses the data more crudely than the former, and so the median test will generally be somewhat less powerful (Conover, 1980).

The Kruskal-Wallis test ranks all observations from 1 to n, and its statistic (H) is based on comparing each group's mean rank with the mean of all the ranks, weighted by the appropriate sample size to compensate for the effect of unequal sample sizes (Neave and Worthington, 1988). If the differences among the three evasion areas proved to be significant, nonparametric multiple comparisons could be executed to find which areas could be most confidently claimed to have different medians from each other (Conover, 1980; Neave and Worthington, 1988). The statistic for multisample comparisons (T) is obtained by calculating the absolute differences between the means of ranks assigned to the samples and then dividing these difference by their standard deviations. The T statistic has approximately the standard normal distribution; therefore H_0 will be rejected if $T>z$ (Conover, 1980; Neave and Worthington, 1988). Statistical procedures were performed with computing packages Statistica version 4.2 (StatSoft, 1993) and BMDP (Dixon, 1990).

Differences between stocks To evaluate differences in evasive behavior between eastern spinner and northeastern offshore spotted dolphins, estimated evasion indices by set for both stocks in evasion area 3 (as outlined in Fig. 1) were compared. Areas 1 and 2 were excluded from the analysis because eastern spinner sample sizes were smaller than 30 and these sizes were considered insufficient for statistical analysis when compared to sample sizes in area 3. Northeastern offshore spotted data were not normally distributed, and nonparametric tests were again used to compare the two independent samples (two stocks).

To decide which test was the most appropriate, "box-and-whisker" plots (Du Toit et al., 1986) were drawn to look for general distribution similarities or differences between both data sets (Fig. 2). The apparent difference in the medians would be worthwhile testing with the Mann-Whitney two-sample test (Conover, 1980; Neave and Worthington, 1988). However, data sets seemed to be different in spread (Mann-Whitney assumes equal spread); therefore a more

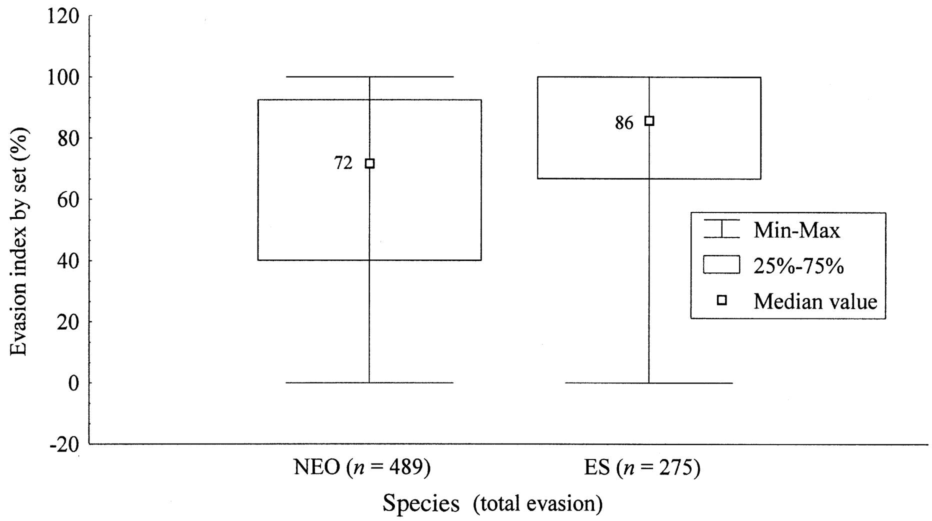

Figure 2

"Box and whiskers" plot for estimated total evasion index by set (estimated percentage of evaded dolphins that evaded capture during each set related to estimated initial herd size) for northeastern offshore spotted (NEO) and eastern spinner (ES) dolphins (Mexican fleet, PNAAPD data

cautious approach would be to apply the nonparametric Kolmogorov-Smirnov two-sample test because differences in location (average) and spread are tested simultaneously (Conover, 1980; Neave and Worthington, 1988). The Kolmogorov-Smirnov test compares the cumulative distribution function of two samples and uses the maximum vertical difference between them as the test statistic D (Neave and Worthington, 1988).

Eastern spinner and northeastern offshore spotted dolphins were also compared with respect to the dolphins' evasive strategies, such as evasion under and evasion over the net. The Kolmogorov-Smirnov test for two independent samples was used to evaluate estimated evasion indices by set between the stocks when they evaded capture by swimming under the net. The one-sided test was used to confirm if the evasion indices by set in one stock were larger than in the other. Differences in estimated evasion indices by set, when dophins evaded capture by swimming over the net, were not tested owing to very low sample sizes (n=3 in the northeastern offshore spotted, n=5 in the eastern spinner dolphin).

Furthermore, differences between the two stocks were described with respect to the dolphins' dispersion, i.e. the ability of the herds to "explode" (separate suddenly) (Allen et al., 1980) into subgroups in relation to the herds' configuration before the chase. For this description, the grouping codes applied by the observers in paragraph 3 of the RMMOSD were used. The codes used were the following: 1, herd is in one group; 2, herd has divided into two or three groups; 3, herd consists of more than three groups. These codes were recorded during three set stages: before chase, during chase, and during encirclement. For each stock, the number of sets where the specified grouping code occurred was counted during each set stage. If codes were found in ascending order, this was interpreted as herd dispersion during the fishing operation.

To test for significant differences in dispersion behavior between northeastern offshore spotted and eastern spinner dolphins, only data for evasion area 3 (Fig. 1) were used because sample sizes for both stocks were largest there. A multiway frequency table seemed to be the appropriate statistical tool, since counts of grouping codes was the response variable during each set stage and for each stock. However, one of the most important assumptions of multiway frequency analysis, independence, was not met. Only designs for comparisons between subjects may be analyzed with this analysis, so that the frequency in each cell is independent of the frequencies in all other cells. If the same case contributes values to more than one cell, those cells are not independent (Tabachnik and Fidell, 1996). In our study, each case (i.e. each set) contributed to three different cells (the three set stages).

Consequently, to test for differences in dispersion behavior between the stocks, data were rearranged by using the grouping code as the response variable and set stages as the repeated measures in each set (Table 1). Therefore, this design resembled a repeated-measures analysis with one among-subjects factor (stocks) and one within-subjects factor (set stage). If the response variable were in interval scale, a repeated-measures analysis of variance (ANOVA) would have been appropriate to test for differences between stocks (Zar, 1999). However, the response variable in our study was the grouping code, a categorical variable in ordinal scale.

The plausible alternative to apply was logistic regression, often referred to as linear probability models (Tabachnik and Fidell, 1996). This technique is similar to multiple regression analysis in that one or more independent variables (the three set stages in our study) are used to predict a single dependent, categorical variable (the stocks). Linear probability models accommodate all types of independent variables (numerical and categorical) and they do not have to be normally distributed, linearly related, or of equal variance within each group. The assumptions of multivariate normality and equal variance-covariance matrices across groups do not have to be met, either. Furthermore, logistic regression might be preferable to multiple discriminant analysis because it is similar to regression with its straightforward statistical tests, ability to incorporate nonlinear effects, and wide range of diagnostics (Tabachnik and Fidell, 1996).

The model produced by logistic regression is nonlinear, and the outcome variable is the probability of having one outcome or another (in our study: one stock or the other) based on a nonlinear function of the best linear combination of predictors, with two outcomes (Tabachnik and Fidell, 1996):

$$\hat{Y}_i = \frac{e^u}{1+e^u},$$

where $\hat{Y}_i$ = the estimated probability that the ith case is in one of the categories and u is the usual linear regression equation:

$$u = A + B_1X_1 + B_2X_2 + \ldots + B_kX_k,$$

with constant A, coefficients B_j, and predictors, X_j (independent variables, the set stages in this study) for k predictors (j=1, 2, …, k).

This linear regression equation creates the log of the odds, that is, the linear regression equation is the (natural log of the) probability of being in one group divided by the probability of being in the other group. The procedure for estimating coefficients is maximum likelihood, and the goal is to find the best linear combination of predictors to maximize the likelihood of obtaining the observed outcome frequencies. Logistic regression can be used to fit and compare models. The researcher uses goodness-of-fit tests to choose the model that does the best job of predictions with the fewest predictors. (Tabachnik and Fidell, 1996).

Therefore, logistic regression analysis was applied to test the predictability of stock membership (the dependent or grouping variable) by grouping codes (response variables) during three set stages (independent variables). The simplest model (constant-only model) was compared with the full model (with the three independent variables) by computing their log-likelihoods and by using χ^2. Degrees of freedom were the difference between degrees of freedom for the full and the constant-only models. The constant-only model has 1 df (for the constant) and the full model for our study had 3 df (1 df for each individual effect and one for the constant); therefore χ^2 was evaluated with 3 df. If χ^2 was significant, the full model would be reliable (Tabachnik and Fidell, 1996).

Results

Spatial patterns in evasive behavior of northeastern offshore spotted dolphins

The evasion index by set of northeastern offshore spotted dolphins was averaged in 2 2 quadrants and the resulting contour map is shown in Figure 1. The highest evasion index by set contour was 60% and extended approximately from south of the Baja California peninsula, across the Gulf of California mouth, and to the Mexican mainland (approx. 20 northern latitude). The 55% and 50% evasion

Table 1

Repeated-measures design to test for differences in dispersion behavior[1] between northeastern offshore spotted and eastern spinner dolphins. The data (response variable) are grouping codes for case i, during set stage j, for species k (=X_{ijk}). (Mexican fleet, 1992–95, PNAAPD data.)

			Set stages		
Case (herd in each set)		Species	1 (before chase)	2 (during chase)	3 (during encirclement)
1 to 308	1	northeastern offshore spotted dolphin	$X_{1\,1\,1}$ $X_{308\,1\,1}$	$X_{1\,2\,1}$ $X_{308\,2\,1}$	$X_{1\,3\,1}$ $X_{308\,3\,1}$
309 to 544	2	eastern spinner dolphin	$X_{309\,1\,2}$ $X_{544\,1\,2}$	$X_{309\,2\,2}$ $X_{544\,2\,2}$	$X_{309\,3\,2}$ $X_{544\,3\,2}$

[1] Herd dispersion: to establish if a herd dispersed during a set, the grouping codes applied by the observers in paragraph 3 of the RMMOSD were used. The codes are the following: 1, herd is in one group; 2, herd has divided into two or three groups; 3, herd consists of more than three groups. These codes were recorded during the three set stages: before chase, during chase, and during encirclement. If observers documented an ascending order in the codes (1, 2, 3), this feature was interpreted as herd dispersion during the fishing operation.

index contours were approximately parallel to the 60% contour and in addition formed a triangle-shaped area off the coast of Guatemala. Evasion indices 40% and lower extended south and offshore west of Mexico (Fig. 1). Therefore, the 60%, 50%, and 40% contours were considered the limits between three areas with different evasive behavior of the northeastern offshore spotted dolphin for our study. Three areas were identified (shaded areas in Fig. 1):

1) Low evasion: south of Mexico (30% to 40% estimated evasion index by set)
2) Medium evasion: coastal area south of Guatemala (50% to 55% estimated evasion index by set)
3) High evasion: mouth of the Gulf of California (60% and higher estimated evasion index by set)

Not all data between these contours were used because of difficulty in extracting data throughout the geographic range and because sample sizes for each area (n>100) seemed to be adequate for the analysis. Average mean evasion indices differed significantly between the three areas (Kruskal-Wallis, n_1=206, n_2=111, n_3=491; total n=808, H=93.13, 2 df, P<0.0001). Hence, nonparametric multiple comparisons between all pairs of areas were executed, and all pairs were found to be significantly different (Table 2).

According to these results, there seemed to be a spatial pattern in evasive behavior (measured in our study as the estimated median evasion index by set in each evasion area) of northeastern offshore spotted dolphins during fishing operations of the Mexican fleet from 1992 to 1995.

Differences between stocks

The eastern spinner dolphin seemed to evade capture more effectively than the northeastern offshore spotted dolphin in evasion area 3 when estimated evasion indices by set for both stocks were compared (Fig. 2). The differences were significant according to the Kolmogorov-Smirnov one-sided test for two independent samples (spinner: n=275, spotted: n=489; D=0.2031, P<0.001).

With respect to the evasive strategies of these two stocks, evasion index when the dolphins escaped under the net was compared by set. Eastern spinner dolphins apparently escaped more effectively under the net than northeastern offshore spotted dolphins (spinner n=177, spotted n=125, D=0.4097, P<0.001, Kolmogorov-Smirnov two-sample test; Fig. 3).

Dispersion behavior of northeastern offshore spotted and eastern spinner dolphins is presented for evasion area 3 (mouth of the Gulf of California, Fig. 4). Herds of both stocks tended to disperse from one set stage to the next; during encirclement, grouping code 3 (herd divided into more than 3 subgroups) had increased and was the most frequently recorded grouping code for northeastern offshore spotted dolphins in area 3 during our study. Northeastern offshore spotted herds tended to be more fragmented than eastern spinner herds before chase and to disperse in greater numbers during subsequent set stages (Fig. 4). Logistic regression analysis revealed a reliable full model (χ^2=60.209, P<0.001, df 3, n=544), i.e. the outcome of stock was predicted by the three independent variables (set stages). The prediction of stock outcome might further be interpreted as a difference between northeastern offshore spotted and eastern spinner dolphins with respect to dispersion behavior in our study.

In contrast, both stocks presumably escaped only on rare occasions by leaping out of the net because eastern spinners did so in only 5 of 275 sets (1.82%) and northeastern offshore spotted dolphins in 3 of 489 sets (0.61%) during the study period. Estimated evasion indices by set could not be compared because the samples were too small for any statistical test.

Discussion

Spatial patterns in evasive behavior

An apparent significant geographic difference in evasive behavior of northeastern offshore spotted dolphins was found between three areas in the EPO (Mexican fleet data, 1992–95, Fig. 1, Table 2). The lowest evasion area was located south of Mexico (area 1), the medium evasion area was in a relatively small coastal area south of Guatemala (area 2), and the highest evasion area was in the Gulf of California mouth (area 3, Fig. 1). About twenty years ago, fishermen noticed that dolphins were more difficult to capture in some areas than in others. Certain coastal dolphin

Table 2

Nonparametric multiple comparisons (according to Conover, 1980; Neave and Worthington, 1988) of estimated average (median) evasion index by geographic area (see Fig. 2) for the northeastern offshore spotted dolphin (1992–95, Mexican fleet, PNAAPD data). The null hypothesis (i.e. the median of two groups is equal) is rejected if the T statistic is larger than the critical Z value. All pairwise comparisons were significant (*indicates significant at P<0.05, where the critical Z-value for 3 groups (k–1)=2.39).

Area	n	Estimated median evasion index (%)	25–75% quartiles	Pairwise comparisons	T
1 (low)	206	25.00	0–66.67	1 and 2	3.17*
2 (medium)	111	44.44	20–83.33	1 and 3	9.49*
3 (high)	491	71.80	40–92.50	2 and 3	3.86*

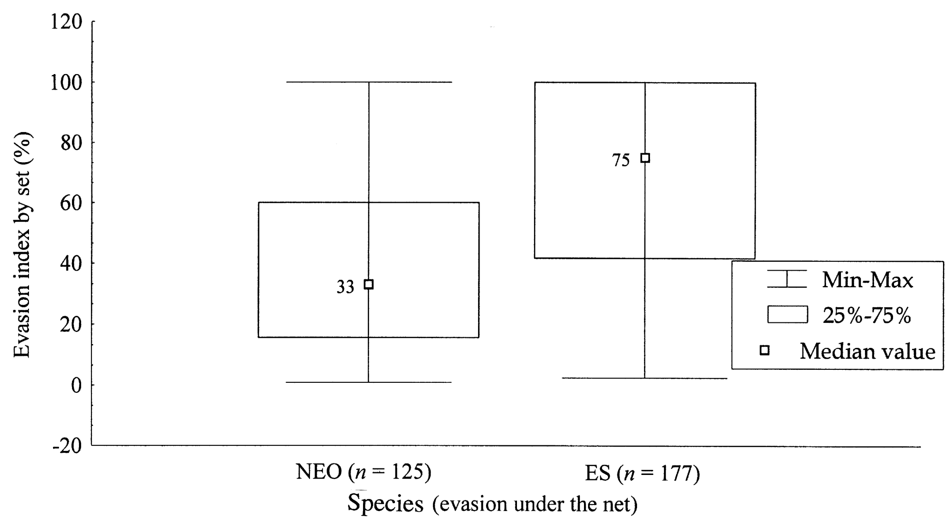

Figure 3

"Box and whiskers" plot for estimated evasion index by set for northeastern offshore spotted (NEO) and eastern spinner (ES) dolphins when dolphins evaded under the net (Mexican fleet, PNAAPD data 1992–95).

herds were called "the untouchables" by fishermen (Pryor and Norris, 1978) because the animals were capable (and still are) of completely evading the fishing operation even before the net has been set (National Research Council, 1992).

Several authors have suggested that the reasons for the detectable spatial patterns in evasive behavior seem to be related to the learning capacity of these mammals. Stuntz and Perrin[5] stated that dolphins (*Stenella* spp.) were more difficult to capture in areas where fishing effort had been greatest, therefore concluding that dolphins have learned to evade capture more effectively. Hewitt (1985) pointed out that the dolphins' reaction distance to survey vessels "may vary between geographic areas with the degree of animal naivete." This possibility was also considered by Hall and Boyer (1986) as an explanation for the spatial heterogeneity of mortality rates.

Although dolphin learning seems to be a logical explanation for geographic differences in evasive behavior, adequate measures for the dolphins' experience (i.e. their exposure to the tuna fishery) have to be designed. A measure may be the historical fishing effort (no. of chases per one-, two- or five-degree quadrant by the international fleet on the northeastern offshore spotted dolphin accumulated from 1959, when the tuna purse-seining fishery started, until today) standardized with respect to herd density (as described by Polachek, 1987; Reilly, 1990; or Reilly and Fiedler, 1994). Standardization is necessary because dolphins in areas with fewer herds will presumably have more opportunities to practice evading capture in comparison with areas where there are more herds (higher density) and effort has apparently been the same (number of chases per quadrant).

Furthermore, the number of dolphins that evaded capture during a set might also be affected (reduced) by the number of speedboats, the fishing vessel's power, and the presence of a helicopter; explosives were also used to herd dolphins several years ago. In addition, the dolphins' distribution (and hence possibly the fleet's effort) is influenced by changes in oceanographic features between seasons (Au and Perryman, 1985; Reilly, 1990) and years (Fiedler and Reilly, 1994; Reilly and Fiedler, 1994). Therefore, all variables recorded by the observers regarding the fishing operation (vessel power, number of speedboats, aerial assistance, use of explosives), time, and environmental features should be considered. However, this thorough analysis, including the important (according to the literature) variable "fishing effort" was not performed with the available data because the effort of the Mexican fleet should not be considered representative of the international fleet (Mexican vessels tend to fish closer to Mexico than do other fleets). Our future research aims to consider these variables and the effort of the complete international fleet, which is possible only with data from the IATTC.

Differences between stocks

In the mouth of the Gulf of California (area 3, Fig. 1), eastern spinner dolphins (*Stenella longirostris orientalis*) showed significantly higher estimated evasion indices than those for northeastern offshore spotted dolphins (*Stenella attenuata*) in our study (Fig. 2). A stronger evasion behavior by the eastern spinner dolphin has been described by other authors (Norris et al., 1978; Pryor and Kang, 1980) and may relate to different evasive strategies used by the two stocks to evade capture in the net, some of which were analyzed in our study.

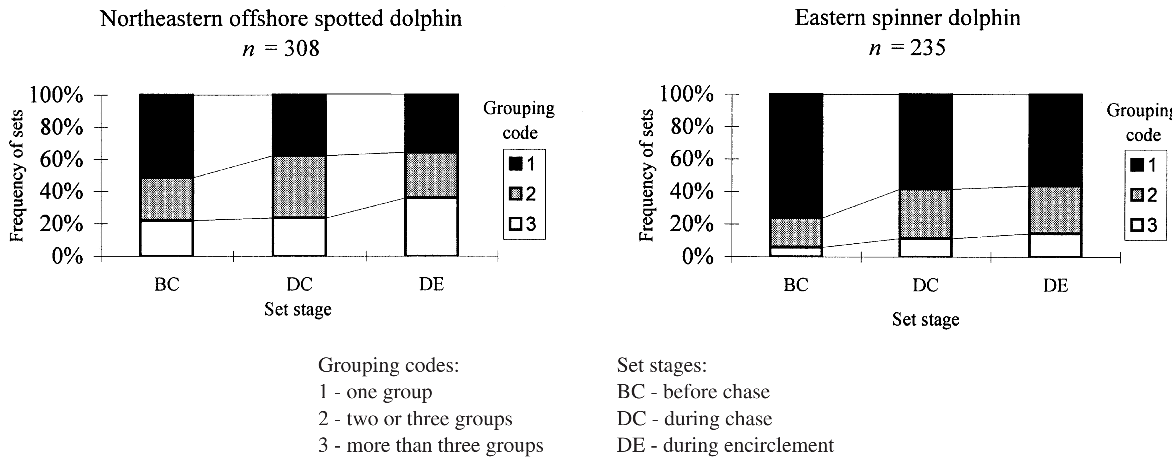

Figure 4

Dispersion (the ability of herds to "explode" (separate suddenly) into subgroups in relation to their configuration before chase) of northeastern offshore spotted and eastern spinner herds in evasion area 3 (Gulf of California mouth, Mexican fleet, PNAAPD data 1992–95).

Analysis of evasive strategies indicated that eastern spinner dolphins seemed to evade capture more effectively under the net than northeastern offshore spotted dolphins (Fig. 3). According to stomach-content analyses of spinner and spotted dolphins, the spinner dolphin is thought to forage deeper (approx. 250 m) than the spotted dolphin (approx. 30 m) (Fitch and Brownell, 1968). Therefore, the spinner dolphin may be more habituated to dive deeply enough to escape under the bottom of the net approximately 200 m from the surface, before the net is pursed.

In addition, even though herds of both stocks tended to disperse from one set stage to the next, there seemed to be a significant difference in dispersion between the stocks (according to logistic regression analysis results), i.e. eastern spinner dolphins apparently dispersed less often than the northeastern offshore spotted (Fig. 4). This evasive strategy (previously described as "school exploding" by Allen et al., 1980) also might have contributed to the eastern spinner dolphin's higher estimated evasion index in our study (Fig. 2). Because they disperse less and also tend to form larger subgroups than spotted dolphins during the fishing operation (Pryor and Kang, 1980), eastern spinner dolphin herds could be more cohesive and this behavior may coordinate their evasive movements more effectively than northeastern offshore spotted dolphins.

Moreover, the apparent higher evasive ability of eastern spinner dolphins might also be associated with different activity levels in these dolphins. Spinner dolphin activity level during the set tends to be higher than that of the spotted dolphin (Schramm, 1997) and could probably enhance evasion by spinners.

The frequency of evasion over the net was negligible in both stocks (spotted dolphins leaped over the net in only 0.61% of the sets analyzed; spinners, in 1.8%). Fishermen and scientists (Pryor and Kang, 1980) have also observed that dolphins encountered in fishing for tuna seldom attempt to leap out of the net to escape, even though individuals of both dolphin species are capable of doing so. The reasons why this event seems to be so rare are still unknown. Norris et al. (1978) mentioned that oceanic dolphins (like spinners and spotted) in captivity may take more time than coastal dolphins (like bottlenose dolphins, *Tursiops truncatus*) to cross a white line or a sunken rope on the tank bottom; this behavior might be explained by the fact that the animals may come from open waters where no barriers are present at all and there is no confinement. Thus, confinement in a tuna set may be foreign to these animals, as are the corkline and other features of a set (Norris et al., 1978).

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