

NOAA Technical Memorandum NMFS



MAY 2010

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NOAA-TM-NMFS-SWFSC-457

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
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Variation and Predictors of Vessel-Response Behavior in a Tropical Dolphin Community

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ABSTRACT

Dolphins exhibit a range of vessel-response behaviors, from readily approaching and bow-riding, to other behaviors that are indifferent, or actively evasive. However, the factors responsible for this variation have not been examined. We used a tree-based modeling method to investigate the influence of geography, time of day, species composition, and fishery exposure on the responses of five species (10 management stocks) of dolphins in the eastern tropical Pacific, comprising ten management stocks. Data were collected for 2,667 sightings during four research cruises between 1998 and 2003. The relative frequency of five responses (approaching the vessel, bowriding, running, school splitting, and low-swimming) showed significant ($p < 0.0005$) variability among species, as well as among stocks within the same species. Striped (*Stenella coeruleoalba*), whitebelly spinner (*S. longirostris*), and western-southern spotted dolphins (*S. attenuata attenuata*) tended to be evasive, while coastal spotted (*S. attenuata graffmani*) and common bottlenose dolphins (*Tursiops truncatus*) tended to be attracted to the vessel. There was a strong tendency of dolphins sighted farther offshore to be significantly more evasive than those less than about 100nm from the coast. The degree of evasiveness in stocks that are frequently targeted by the tuna purse-seine fishery

(northeastern spotted – *S. a. attenuata*, eastern spinner – *S. longirostris orientalis*, and short-beaked common – *Delphinus delphis*) was greater with more purse-seine activity in the vicinity, while no significant relationship was found for those stocks that are rarely set on. For each stock, vessel-response had a relatively unique suite of predictors, indicating an interplay of intrinsic, natural extrinsic and anthropogenic factors.

INTRODUCTION

Small cetaceans respond to vessels at sea in a variety of ways, ranging from attraction, usually by approaching the boat to ride pressure waves, to apparent indifference, to clear avoidance (Leatherwood & Reeves 1983, Würsig et al. 1998, Ritter 2002). This range of reactions likely results from a combination of factors including ecological adaptation, historical experience, natural predisposition, habituation or learning, demographic effects of school size or composition, time of day, season, and weather (Würsig et al. 1998).

Some species are relatively consistent in their behavior. For example, Dall's porpoises (*Phocoenoides dalli*) and bottlenose dolphins (*Tursiops* spp.) are well-known as bow-riders of transiting vessels throughout their range, whereas harbour porpoises (*Phocoena phocoena*) and humpback dolphins (*Sousa* spp.) almost never ride the bow despite being nearshore species with ample opportunities (Barlow 1988, Würsig 2002, Jefferson 2000, Jefferson 2002). In other species, however, vessel-response behavior varies geographically. For example, striped dolphins (*Stenella coeruleoalba*) readily bow-ride in the Mediterranean Sea (Gaspari et al. 2007), do so less often in the Gulf of Mexico (Würsig et al. 1998), and rarely bow-ride in the eastern tropical Pacific (this study).

In addition to the factors mentioned above, there are also some anthropogenic activities that are known to modify vessel-response behavior. For example, several species of small cetaceans, such as common bottlenose dolphins, rough-toothed dolphins and false killer whales (*Pseudorca crassidens*) are attracted to and follow a wide variety of fishing vessels to feed on bait, catch, or discarded bycatch (Nitta & Henderson 1993,

Chilvers & Corkeron 2001, Gilman et al. 2006), while tour boats may variously attract or repel animals (Lusseau 2003, Goodwin & Cotton 2004, Neumann and Orams 2006).

In the eastern tropical Pacific (ETP), an oceanic region including the coastal waters of southern California to northern Peru and oceanic habitat out to Hawaii, a speciose dolphin community exists that displays a wide range of behavior in response to vessels and experiences a range of anthropogenic activities. Thirteen species of delphinids are regularly recorded here (Wade & Gerrodette 1993); some of which have been divided into stocks for management purposes. Each stock occupies overlapping but different habitats within the region, has differing patterns of association with other species, and has differing degrees of interaction with human activity (Reilly 1990, Perrin et al. 1991, Wade & Gerrodette 1993).

For many of these stocks, the primary anthropogenic factor in their environment is a large purse-seine fishery for yellowfin tuna (*Thunnus albacares*). Since the late 1950s, this fishery has utilized a unique ecological association between dolphins and large tuna by chasing and encircling the more visible dolphins at the surface to capture the tuna swimming below (National Research Council 1992). This association is specific to certain dolphin stocks and does not occur with equal frequency throughout the ETP. In the 1960s and early 1970s, the incidental dolphin mortality in the fishery was on the order of hundreds of thousands of dolphins per year, but through management action and modified fishing practices, recorded mortality has declined by over 99% (Wade 1993, Gosliner 1999, IATTC 2006). While mortality in the nets has dropped to approximately 1000 dolphins per year, the purse-seine fishery continues to conduct about 8,000 - 14,000 sets on dolphins per year, chasing, capturing and releasing millions of dolphins annually

(Perkins & Edwards 1999, Archer et al. 2002, IATTC 2006). The two main targeted stocks, the northeastern offshore spotted dolphin, *Stenella attenuata attenuata*, and the eastern spinner dolphin, *S. longirostris orientalis*, are currently listed as “depleted” under the U.S. Marine Mammal Protection Act, and show little, if any, sign of recovery (Gerrodette & Forcada 2005, Wade et al. 2007).

Since the early days of the fishery, tuna fishermen and scientists have observed that in regions of heavy fishing, dolphins of targeted stocks tend to be wary of purse seiners, require longer chases, and are more difficult to encircle (Orbach 1977, Norris et al. 1978, Holts et al. 1979, Stuntz & Perrin 1979, Allen et al. 1980, Pryor & Kang 1980, Schramm Urrutia 1997, Heckel et al. 2000, Lennert-Cody & Scott 2005). For example, as the seiner and its speedboats approach, offshore spotted dolphin schools in more fished areas are reported to "explode", breaking the school into smaller subgroups and sometimes forcing the set to be aborted (Orbach 1977, Stuntz & Perrin 1979, Allen et al. 1980). The dolphins are also known to swim low in the water with nearly imperceptible movement, only to "blow through," or rapidly swim out of the containment circle formed by the seiner and the speedboats, thus escaping capture (Holts et al. 1979, Allen et al. 1980).

In this paper, we describe patterns of vessel-response for the five most commonly encountered dolphin species in the ETP based on four dolphin survey cruises conducted by the Southwest Fisheries Science Center (SWFSC) during 1998, 1999, 2000 and 2003. Using a tree-based modeling method, we then examine the relative influence of a set of spatial, temporal, phylogeographic, social, and anthropogenic factors on dolphin vessel-response in this tropical ocean community.

METHODS

The Study Area and Species/Stocks

Our study area encompasses some 21 million km² of ocean in the ETP, a heterogeneous oceanic region centered on the eastern Pacific warm pool (Ballance et al. 2006, Fiedler & Lavín 2006). The region is characterized by moderately high productivity and a strong and shallow thermocline (Wyrski 1966, Fiedler & Talley 2006, Pennington et al. 2006) and supports a diverse and abundant community of dolphins (Wade & Gerrodette 1993). For this analysis, we selected the five most frequently sighted species, comprising ten management stocks (Table 1, Figure 1). The stocks have different geographic distributions, live mainly in different habitats within the ETP, have different patterns of association with other delphinid species, and have differing degrees of interaction with the fishery.

Ten species and stocks were examined (Table 1:

1) the common bottlenose dolphin (*Tursiops truncatus*), which is widespread in the ETP but more common closer to shore (Wade and Gerrodette 1993),

2-4) the short-beaked common dolphin (*Delphinus delphis*), which is divided into three management stocks (northern, central and southern) based on disjunct geographic distributions and subtle morphological differences (Perrin et al. 1985),

5-7) the spotted dolphin, *Stenella attenuata*, which is divided into coastal (*S. a. graffmani*) and offshore (*S. a. attenuata*) subspecies (Perrin 1990), with two offshore stocks recognized: the northeastern spotted dolphin inhabits the core area of the ETP and the western-southern inhabits the outer region,

8-9) spinner dolphins, including the eastern form, *S. l. orientalis*, which occurs in the core area and is known for its marked sexual dimorphism and distinct male reproductive features (Perrin & Mesnick 2003), and the “white-belly” spinner, occurring in the outer region and thought to be a hybrid between the eastern spinner and the pantropical Gray’s spinner (*S. l. longirostris*) and found farther west and to the south (Perrin et al. 1985, Perrin et al. 1991, Dizon et al. 1994), and

10) the striped dolphin, *S. coeruleoalba*, a pelagic species with no named subspecies.

Common dolphin habitat is characterized by cool, upwelling-modified waters; spotted and spinner dolphins are primarily found in warm, tropical waters; striped dolphins occupy habitat that in many features is intermediate between the other two patterns; and common bottlenose dolphins occur throughout the region from coastal to offshore waters (Au & Perryman 1985, Reilly 1990, Reilly & Fiedler 1994, Ballance et al. 2006).

Data Collection

The primary objective of the SWFSC cruises was to conduct line-transect surveys to estimate cetacean abundance in the area affected by the tuna purse-seine fishery and adjacent parts of the ETP. In this study, we use data collected from 1998 - 2000 and 2003 onboard four different research vessels (NOAA ships *David Starr Jordan*, *McArthur*, *McArthur II*, and University of Rhode Island vessel *Endeavor*) between July and December of each year. The ships are similar in length (52 - 68m) and observer eye

height above the water (~10m). Over 100,000 km of trackline were covered on effort during this time, over the coastal, core and outer regions of the study area.

Methods of collecting dolphin abundance data followed standard protocols for line-transect surveys conducted by the SWFSC (Kinzey et al. 2000). During daylight hours and in good weather, a visual search for cetaceans was conducted on the flying bridge as the ship moved along the trackline at approximately 10 knots. While on duty, two observers, one on each side of the ship, scanned a 100° wedge that started abeam of the vessel on their side and ended 10° past the trackline on the opposite side of the bow with 25x pedestal-mounted "big-eye" binoculars. A third observer searched by eye and with hand-held 7x binoculars, covering the area close to the trackline.

When marine mammals were sighted, the ship diverted from the trackline and approached the school in order to identify species and stock composition, estimate group size, and observe the school's response to the research vessel. After counts were completed and all species were identified, typically requiring 5 – 45 minutes, observers recorded their observations on a standardized sighting form (NOAA Form 88-208) that asked for answers to a series of behavioral questions and a written narrative of the event. Prior to the cruises, all observers attended a training course detailing the observation and recording of behavioral observations using standardized terms. While observers had varying levels of experience, at least one-third had 20+ years of experience observing the behavior of pelagic dolphins. For this study, we used the observers' account of the presence or absence of each of five discretely coded objective vessel-responses to give a profile of a school's reaction to the vessel: approaching the boat (Approach), bow-riding (Bow-ride), running from the boat (Run), low swimming (Lowswim), and school-

splitting (Split). These behaviors were specifically chosen because they were unambiguous to define, clearly visible from the flying bridge, and indicative of whether the dolphins were attracted to or avoiding the research vessel. The behaviors Run, Lowswim and Split resulted in the dolphins leaving the area, ceasing surface activity and parts of the school moving off in opposite directions, respectively. Conversely, Approach and Bow-ride caused animals to close the distance between the school and the ship and in the case of Bow-ride to come so close as to swim in the wake of the vessel. Observers were also asked to categorize the general evasiveness of each group (Evasive) based on the presence or absence of the above responses, additionally observed behaviors, and their experience with pelagic dolphin behavior. One form was filled out for each sighting, representing a consensus opinion of all observers on duty at the time.

In this study we used the average of the on-duty observers' best estimates of school size. Calibration studies have shown that while these values may be a slight underestimate of the true school size, there is no significant difference in the relative values between observers or between sightings (Gerrodette and Perrin 1991).

Data Used in Analyses

We only used data from sightings for which all five objective vessel-responses were recorded as either present or absent and the general evaluation of evasiveness of the group was recorded as either Evasive or Non-Evasive. Thus, all responses were treated as binary variables. By taking the five objective responses together, a series of 32 behavioral profiles were formed (= all 2^5 possible combinations of objective vessel-responses).

Each group was classified as “pure” if dolphins of only one stock were present, or “mixed” if otherwise. We estimated the distance to shore for a group by calculating the distance to the nearest landmass (including islands) using ArcView v3.1. The school size and stock composition of each group was taken from data recorded by the observers on the flying bridge. The school size used was the mean of the three on-effort observers’ best estimates (Kinzey et al. 2000).

Two measures were used to evaluate the exposure that individual dolphins within a group may have had with purse-seining in the ETP. First, we counted the number of purse-seine sets that occurred prior to the sighting within a 300-nautical-mile (556 km) radius during the previous 70 days. The spatial and temporal extent of this ambit was chosen based on the results of studies of movements by spotted dolphins in the ETP (Perrin et al. 1979, Hedgepeth 1985) and of stress effects (Southern et al. 2002). The number of purse-seine sets within the specified area was only available from Inter-American Tropical Tuna Commission (IATTC) observer data, which represent approximately 50% of the total number of sets made, as they do not include sets made by vessels carrying observers from the various national programs (IATTC 2006).

Second, we calculated the average annual estimated fishery mortality for each stock from 1998-2000 (Archer et al. 2002). During the years of this study, purse-seine sets were predominantly made on northeastern offshore spotted dolphins and eastern spinner dolphins, while striped, bottlenose and coastal spotted dolphins were rarely set upon (IATTC 2006). To account for this differential exposure to the fishery, we ranked each stock based on the average mortality in the fishery as reported in the IATTC Annual

Reports (IATTC 2006). These mortality ranks were then used in the analysis described below.

Behavioral Differentiation of Stocks

Restricting the data to sightings of only pure schools, we used a χ^2 -test to examine differences in the frequency distribution of each behavior and the behavioral profiles among stocks. Significance was determined with a standard permutation test of 5000 replicates. Additionally, χ^2 -tests were performed between all pairs of stocks. The χ^2 -statistic from the pairwise test was used as a distance metric in a *k*-means cluster analysis to identify stocks that exhibited similar behavioral profiles. All statistical analyses were conducted using R v2.5.0 (R Development Core Team 2007).

Predictors of Vessel-Response Behavior: Random Forest Analysis

In order to evaluate the relative influence of geography, time of day, species composition, and fishing activity on the vessel-response behaviors we used the Random Forest analysis (Breiman 2001) as implemented in the *randomForest* package coded for R (Liaw & Weiner 2002). Random Forest is an extension of the standard Classification and Regression Tree algorithm (CART – Breiman et al. 1984) in which the goal is to identify variables which are “important” predictors for the response under consideration. Random Forest operates in the following manner: In each iteration, a CART tree is built on a bootstrap sample of the data. During the building process, at each node, a set of predictor variables are randomly selected and the best of these predictors are used to split the sightings. The sightings continue to be split in this manner until a full, un-pruned tree

is grown, where each terminal node predicts a single sighting. In our analyses, each forest was created from 1000 repetitions of the above procedure.

The suite of predictor variables used is given in Table 2. The response variables examined were the five objective vessel-responses described above (Approach, Bow-ride, Run, Lowswim, and Split) as well as the general evaluation of evasiveness (Evasive). One Random Forest was built for each of these six response variables using all sightings containing the ten stocks of interest. Additionally, we built six forests for each of the ten stocks by iteratively selecting only those sightings in which a given stock occurred. Thus, a total of 66 Random Forests were built. In this analysis, all sightings without missing data for the response and predictor variables were used. In order to account for heterogeneity in the frequencies of any given response and allow under-represented behavioral responses to have equal weight in the model, the size of the bootstrap sample of sightings for each category (response present or absent) was constrained to be equal. The sample size was selected as the minimum of the size of the smallest category, or half of the total number of sightings.

The error rate of a forest is estimated by examining the prediction error of sightings not in the bootstrap sample for each tree. The aggregate misclassification rate for these “out-of-bag” or “OOB” cases is called the “OOB error rate”. The “importance” of a predictor variable in a forest is assessed by examining how the prediction error increases when that predictor is permuted in the OOB cases. The measure of variable importance that we used was the “mean decrease in accuracy” as defined in Liaw & Wiener (2002). For each random forest run, null distributions of variable importance scores were generated by 1000 random permutations of the response variable. Variables

with importance scores greater than 95% of their null distribution were considered significant.

Finally, in order to visualize the relationship between the response variable and each predictor variable determined to be important in a given forest, we examined all plots of partial dependency for significant predictors. These plots depict the relationship between the predictor variable of interest on the x -axis and the log-odds of the presence of the response variable on the y -axis given the classification patterns of that predictor in the assembled forest. The full formula is provided in the documentation for *partialPlot* (Liaw & Wiener 2002) with a detailed description given by Friedman (2001).

In our presentation of these results and the discussion that follows, we will refer to responses to vessels as being more or less likely given a particular predictor. In these presentations, one should keep in mind that these determinations are relative to an overall probability of the given response and that the value of the predictor is modifying this probability. As an example, a response with a low probability ($\log\text{-odds} < 0$) in the absence of a predictor can have an even lower probability in its presence, indicated by a smaller (more negative) log-odds value. Thus, for some partial dependency plots we discuss with significant relationships, all of the log-odds may be positive (behavior tends to be present) or negative (behavior tends to be absent).

RESULTS

Frequency, Composition and Group Size of Sightings

In the four surveys conducted from 1998 to 2000, and 2003, complete vessel-response data (all five responses and general evasiveness) were collected for 1,443

sightings of the ten stocks of interest (Table 1). Of these, over 90% of common (northern, central, and southern stocks), coastal spotted, and striped dolphin sightings were of pure schools. Approximately 75% of the bottlenose dolphin sightings were pure, with most of the remaining mixed-species sightings containing Risso's dolphins (*Grampus griseus*), short-finned pilot whales (*Globicephala macrorhynchus*), rough-toothed dolphins (*Stenobredanensis*), or offshore spotted dolphins (*Stenella attenuata attenuata*). Both eastern and whitebelly spinner dolphins were sighted the majority of the time in mixed-species schools (74% and 67% respectively), and both were predominantly sighted with northeastern offshore spotted dolphins. Conversely, northeastern and western-southern offshore spotted dolphins were only slightly more likely than not to be sighted in a mixed-species school (55% and 58% respectively). When found in a mixed school, these two dolphins were predominantly schooling with eastern or whitebelly spinners.

Average estimated school size for all groups was 108 dolphins with a median of 56, ranging from 1 to 2,795. Short-beaked common dolphins, eastern and whitebelly spinners, and western-southern offshore spotted dolphins tended to occur in the largest schools, while common bottlenose, striped, and coastal spotted dolphins tended to be sighted in smaller schools. For all stocks but southern short-beaked common dolphins, the median school size of mixed-species schools was larger than that of pure schools.

Variation in Response among Stocks

There was significant variation in the distribution of behavioral responses among stocks (Figure 2). Both common bottlenose and coastal spotted dolphins frequently approached and rode the bow, rarely exhibited any of the three evasive responses (Run, Lowswim, Split) and were rarely characterized as Evasive. The reverse pattern was seen

in southern common, whitebelly spinner, western-southern spotted, and striped dolphins, which were much more likely to exhibit evasive responses. The remaining four stocks (northern and central short-beaked common, eastern spinner, and northeastern spotted dolphins) exhibited a range of responses, although northern short-beaked common dolphins tended to be less evasive than the other three.

As expected, there was significant correlation among responses such that the distribution of response profile frequencies (Figure 3) closely mirrored that of the individual responses. The χ^2 -test indicated a significant differentiation of the profile frequency distributions among stocks ($p < 0.001$). Only four of the 45 pairwise comparisons (Table 3) were non-significant ($p > 0.05$): eastern spinner v. central short-beaked common ($p = 0.18$), eastern spinner v. northeastern spotted ($p = 0.40$), central v. southern short-beaked common ($p = 0.58$), and western-southern spotted v. whitebelly spinner ($p = 0.29$), suggesting greater similarity between these stocks.

The similarities of the stocks' response profiles as revealed by the pairwise χ^2 -tests were summarized in the cluster analysis (Figure 4), which indicate three well-defined nodes. The most distinct represents the three highly evasive stocks: striped, whitebelly spinner, and western-southern spotted. Common bottlenose and coastal spotted dolphins, while having significant differences in their response profile frequencies, are grouped together in the center of the figure, indicating their similar tendencies to be attracted to the vessel. The final node contains the remaining five stocks, which exhibited both attractive and evasive responses to the vessel. Within this node, the two stocks frequently found together, eastern spinner and northeastern spotted dolphins,

share a node, as do central and southern short-beaked common dolphins, with northern short-beaked common dolphins external to these two groups.

Exposure to the Fishery

Two measures were used to evaluate the exposure that dolphins in a group may have had to the tuna purse-seine fishery: the number of dolphin sets occurring around the sighting within 300 nm and the previous 70 days (“dsets”), and the rank of the total mortality (“mort.rank”) of each stock from 1998-2000. Figure 5 summarizes these two measures for the ten stocks examined. While central short-beaked common dolphins had the largest median number of sets (211), they were only ranked fifth in terms of magnitude of kill in the fishery. Likewise, while eastern spinner dolphins had the highest reported kill, they only ranked fourth in terms of the median number of sets in the ambit ($n = 75$). The three stocks with the lowest number of individuals killed were striped, coastal spotted, and common bottlenose dolphins. Additionally, southern short-beaked common dolphins ranked low on both measures. No stock had both a large number of sets in the ambit and a high kill in the fishery.

Predictors of Vessel-Response Behavior

In the Random Forest analyses (see Appendix), the distance from the coast was found to be the most important variable in classifying whether or not a sighting would be Evasive, Approach, Bow-ride, or Run ($p < 10^{-4}$). It was also a significant predictor for analyses of Lowswim and Split, being second and fourth most important respectively. In all analyses, the response variables exhibited consistent relationships with distance from

coast, tending to reflect more evasion and less attraction to the vessel the farther offshore (Figure 1). From Figure 6 we estimate that sightings are equally as likely to be evasive as non-evasive approximately 100nm offshore.

Variables related to the stock composition of the sighting were also identified as being significantly important in these analyses. Patterns of the variable “stock” were similar to those seen in the cluster analysis. Groups which approached the vessel, rode the bow, or were judged to be non-evasive were most likely to contain bottlenose or coastal spotted dolphins. Those which ran were most likely to contain southern short-beaked common, whitebelly spinner, western-southern offshore spotted, or striped dolphins. Western-southern offshore spotted and striped dolphins were also the most likely to exhibit low-swimming behavior. Pure schools (those composed of a single stock) were three times less likely to split than mixed-stock schools. Schools composed of a relatively larger fraction (approximately > 60%) of common bottlenose or coastal spotted dolphins were significantly less likely to split.

The ship from which the observations were made was a significant predictor both of overall evasiveness and for each of the five specific behaviors. The probability of observing evasive behaviors was slightly less on the *David Starr Jordan* than on the other three ships. However, there was no consistent pattern among the *McArthur*, *McArthur II*, and *Endeavor*. Although tracklines were randomly assigned so as to ensure complete coverage throughout the survey area, operational constraints resulted in the *David Starr Jordan* tending to survey the coastal sections and offshore regions closer to the shore, while the *McArthur*, *McArthur II*, and *Endeavor* tended to work in the offshore

regions. Thus, this result possibly reflects more of the relationship between behavior and distance from shore than a ship-specific reaction.

Stock-Specific Predictors of Vessel-Response

Given that stock composition was a significant predictor of vessel-response behavior, we also conducted a Random Forest analyses for each response on sightings consisting of each of the ten stocks separately. Because some stocks did not exhibit a sufficient variety of some responses, we were only able to conduct 48 of the possible 60 Random Forest analyses. For each of the ten stocks grouped into their respective species below, we report the significant results of these analyses.

Common bottlenose dolphins. Approaching the vessel and bow-riding were significantly related to the size of schools, with larger schools being more likely to exhibit these two responses. Most of the significant predictors of evasiveness for these dolphins tended to relate to the species composition of the group. For example, an increase in the fraction of rough-toothed dolphins was significantly related to an increased likelihood that a bottlenose dolphin group would be evasive. The likelihood that a school would split increased with an increasing fraction of eastern spinner dolphins, offshore spotted dolphins, or rough-toothed dolphins. Conversely, the presence of a higher percentage of short-finned pilot whales, coastal spotted dolphins, or false killer whales in a group tended to decrease the likelihood of school splitting.

Short-beaked common dolphins. For all three stocks, overall evasiveness was significantly related to distance from coast (Figure 7), although the stocks tended to have varying degrees of evasiveness as previously noted. The number of dolphin sets in the ambit was a significant predictor for all responses in northern short-beaked common dolphins except school splitting. The pattern was consistent with an increase in the number of sets being related to an increase in the likelihood of evasive behaviors (Evasive, Lowswim, and Run – Figure 8), and a decrease in Approach and Bow-ride.

For central short-beaked common dolphins, the number of dolphin sets in the ambit was only significant ($\alpha = 0.05$) for Approach, with a pattern similar to that seen in the northern stock. However, the p -value for the relationship with Evasive in this stock was 0.07, and the pattern for this behavior was also similar to that seen in the northern stock. The most important predictor of school splitting in the central stock was school composition, with mixed schools ($n=3$) being three times as likely to split as pure schools.

Aside from the above-mentioned relationship of distance to coast to overall evasiveness, there were almost no significant predictors of behavior for southern common dolphins. An exception is school splitting, for which the only significant predictor was time of day. Groups of this stock sighted later in the day were less likely to exhibit splitting behavior.

Spinner dolphins. Evasiveness in eastern spinners was significantly related to the distance from the coast as described above. The number of dolphin sets in the area was a significant predictor for Evasive, Approach, Bow-ride, Run, and Lowswim, with evasive

behaviors being more prevalent for sightings with more than approximately 100 sets (Figure 8). The likelihood of school splitting was related to school composition, with mixed-species schools, or schools with a large fraction of northeastern spotted dolphins, tending to split more. Although there were no significant predictors for any response for whitebelly spinners, the number of dolphin sets was the most important predictor for Evasive ($p = 0.12$) and Run ($p = 0.18$), and distance to coast was the most important predictor for Lowswim ($p = 0.27$) and the second most important predictor for Split ($p = 0.16$).

Spotted dolphins. The three stocks of spotted dolphins exhibited considerably different vessel-response patterns. Because coastal spotters were relatively consistent in their attraction to the vessel, most responses only had a few predictors identified as being significant, but many of these did not seem to be biologically important. The analysis did suggest that this stock was about 1.5 times more likely to approach the vessel after approximately 9am.

Evasive behavior for northeastern spotted dolphins was primarily predicted by distance from the coast. At approximately 280nm offshore, sightings were equally likely to be evasive as non-evasive. Various predictors related to school composition played a secondary role. Schools of moderate size (10-200) tended to be more evasive than those smaller or larger. An increase in the proportion of spinner dolphins in a group tended to make that group more evasive. The third significant predictor of evasiveness was the number of purse-seine sets in the ambit. An increase in the number of recent sets from 0 to approximately 100 increased the probability of evasiveness approximately 35%

(Figure 8). This pattern was also seen in the analyses of Run, Split, and Lowswim, however the number of sets was only significant in the analysis of Lowswim. The reverse of the above patterns were more strongly seen in the analyses of Approach and Bow-ride.

For western-southern spotted dolphins, Evasive, Bow-ride, and Run were also significantly related to the distance from shore. Pure schools were more likely to run and less likely to split. However, there was no significant relationship with any behavior nor with the frequency of a particular secondary stock or species in the school. There were no significant predictors of Lowswim. Unlike with northeastern spotted dolphins, none of the behaviors were significantly related to the number of recent sets, which was fourth lowest overall in rank for this stock.

Striped dolphins. Unlike the other species, striped dolphins are found mainly in offshore areas and do not have a named neritic population. Although striped dolphins were relatively evasive throughout their range, schools in regions closer to the coast tended to be less evasive. School splitting was the only other behavior for which there were significant predictors. These predictors tended to be factors related to school composition; mixed-species groups were three times as likely to split as pure schools.

DISCUSSION

The results of our analysis show clear patterns of behavior in response to vessels among the species of dolphins most frequently encountered in the eastern tropical Pacific (ETP). Previous research on ETP dolphin behavior has largely been restricted to observations made of schools involved in purse-seine operations (Orbach 1977, Norris et

al. 1978, Stuntz & Perrin 1979, Pryor & Kang 1980, Hecke et al. 2000, Lennert-Cody & Scott 2005). This study expands the literature by describing the behavioral variability of these animals from the vantage point of a research vessel and by covering a larger geographic area. We also employ a comparative approach which explores some of the potential causal factors of this variation, the significant patterns of which are discussed below.

Distance from Shore

Our study area encompasses approximately 21 million km² of ocean in the ETP including coastal waters from southern California to northern Peru and oceanic habitat out to Hawaii. As is evident from Figure 1 and the results of the Random Forest analysis, there is a strong geographic trend in all species and stocks examined in which non-evasive behaviors are seen more frequently closer to shore, while evasive behaviors are more common offshore. One factor which may be related to this onshore-offshore pattern that we did not quantify in this study is the exposure of the various stocks to boat traffic in general. Dolphins in the wild often surf waves, whether they are waves breaking on the beach, swell or wind waves in the open ocean, pressure waves of large whales, or bow waves of boats (Würsig 2002). Dolphins that live nearer to the coast undoubtedly experience both more and a wider variety of vessels and have possibly become habituated to boats, thus making them more likely to bow-ride.

Many environmental variables, such as productivity and thermocline depth and strength, vary in a complex manner across the ETP, overlaid on a roughly onshore/offshore gradient and reflecting the heterogenous oceanographic nature of the

region (Wyrteki 1966, Fielder & Talley 2006, Pennington et al. 2006). These oceanographic characteristics have been found to be significant predictors of dolphin distribution and abundance (Au & Perryman 1985, Reilly 1990, Ballance et al. 2006), and the availability of resources is well known to alter behavior in other species (Würsig & Würsig 1980, Rubenstein & Wrangham 1986, Beale & Monaghan 2004). Thus it is possible that further analyses would identify a relationship between the response patterns described here and measures of productivity or forage.

Time of Day

In our study, time of day was not consistently an important predictor of response to vessels. The only two notable relationships were for southern short-beaked common dolphins, which were less likely to exhibit school splitting later in the day, and coastal spotted dolphins, which were slightly less likely to approach the vessel early in the morning. Other studies have shown that schooling behavior varies on a regular, daily cycle (Norris & Dohl 1980, Norris et al. 1994, Scott & Cattanach 1998). In offshore spotted dolphins, school size and mixing with other species increases in the morning and decreases in the afternoon (Scott & Cattanach 1998), which may be related to protection from predation (Norris & Dohl 1980).

Phylogeographic variation among species and stock

Our data show that vessel-response behavior varies significantly both among species and among stocks within species. Both striped and western-southern spotted dolphins tended to be evasive in almost all sightings, while common bottlenose and

coastal spotted dolphins were largely non-evasive. The behavioral profile of northeastern spotted dolphins was more similar to those of eastern spinner and all three stocks of short-beaked common dolphins than to the conspecific western-southern offshore or coastal spotted dolphins. These results demonstrate that response behavior can be highly variable within a species, likely driven by environmental factors. The behavioral variability observed in spotted, spinner and common dolphins is consistent with the pronounced morphological, life history and ecological differences among the geographically distinct stocks of these species in the ETP (Figure 1; Perrin 1975, Perrin et al. 1985, Perrin 1990, Perrin et al. 1991, Perrin et al. 1994, Dizon et al. 1994). In contrast, common bottlenose dolphins and striped dolphins were relatively consistent in their behavior across vast distributions in the ETP. Bottlenose dolphins were usually attracted to the research vessel and striped dolphins invariably evaded. These species showed similar differences in behavior in other regions as well, such as the Gulf of Mexico (Würsig et al. 1998).

School Composition and School Size

In addition to stock-specific behaviors, response to vessels was also significantly affected by school composition, with pure schools being significantly less likely to split. However, small schools were also very unlikely to split; therefore, it is possible that this relationship is largely due to pure schools tending to be smaller on average.

In some cases, it was also apparent that the presence of particular species in a school affected vessel-response behavior. As an example, eastern spinners and northeastern offshore spotters are most commonly found in schools together. While

tending to be evasive overall, schools with relatively more spotted dolphins had a higher likelihood of approaching the vessel and bow-riding, while presence of more spinner dolphins tended to increase general evasiveness and low-swimming and decrease the non-evasive responses. Heckel et al. (2000) also found differences in the evasive behavior of northeastern offshore spotted and eastern spinner dolphins during tuna purse-seine fishing operations. They observed that eastern spinner dolphins tended to be more cohesive during chase and evaded capture more frequently by diving under the net after it was set, whereas northeastern offshore spotted dolphins were more likely to be fragmented before the chase and to evade capture by dispersing or “exploding” as the net was set and pursued.

The presence of common bottlenose dolphins tended to increase the likelihood of a school approaching and bow-riding and decrease the evasive responses. Common bottlenose dolphins are well known as bow-riders the world over, “hitching” rides on transiting vessels (Würsig et al. 1998, Würsig 2002). As a consequence of their distribution in coastal waters, and their tendency to associate in schools with a variety of other species, common bottlenose dolphins may have more experience with bow-riding on vessels and this behavior may have spread to other populations and even other species – a form of cultural transmission (Rendell and Whitehead 2001) - facilitated by their fluid social structure and habit of mixing with other species (Wells et al. 1980, Scott & Chivers 1990, this study). Mixed-species groups that contained even a small percent of bottlenose dolphins tended to be non-evasive (e.g., the northeastern spotted dolphins noted above; western-southern offshore spotted), and species which rarely approached vessels in pure schools were observed to approach and sometimes bow-ride when they were in mixed-

species schools with common bottlenose dolphins (e.g., Risso's dolphins and rough-toothed dolphin; data not shown). The behavioral response of common bottlenose dolphins to vessels has been studied in a number of coastal locations around the world (Shane 1990, Janik & Thompson 1996, Chilvers & Cockeron 2001, Nowacek et al. 2001, Lusseau 2003, Goodwin & Cotton 2004, Lusseau 2004, Lusseau 2005, Bejder et al. 2006a, b). Results show a wide range of short- and long-term evasive and non-evasive responses based on factors such as vessel type, duration and degree of exposure, whether vessels provide foraging opportunities and whether vessels maintain a predictable course.

For the ETP, we know relatively little about the nature or duration of association in the mixed species schools, as our observations lasted only as long as required to accurately count and identify the stocks present. However, the frequency and specificity of school mixing differed significantly among stocks (Table 1). Encounters with mixed schools of spotted and spinner dolphins are not only more common than encounters with pure schools, but these species are more often encountered with each other than with any other species. For spotted and spinner dolphins, occurring in mixed schools with the other species is a fundamental aspect of their biology in the ETP (Perrin 1975, Perrin et al. 1979), as is their association with tuna and seabirds (Perrin 1969, Orbach 1977, Au & Pitman 1986, Au 1991, Edwards 1992). School mixing rarely involves common or striped dolphins, and while bottlenose dolphins occur in mixed species groups frequently, they mix with a variety of species. As stocks show differing tendencies to mix, it is reasonable to predict that behaviors which disrupt mixed schools, such as school splitting, will have differing affects on the individuals, depending on the nature of the association

and whether it is causal or longer term, opportunistic or obligatory, and the duration of the disassociation.

Fishery Interactions

Our results indicate that changes in behavior are not only apparent in the long-term as demonstrated by Heckel et al. (2000) and Lennert-Cody & Scott (2005) but are also evident in the short-term. Those dolphins which have historically been targeted by the fishery (northeastern spotted, eastern spinner, and northern short-beaked common) changed their response behavior in correlation with the number of recent purse-seine sets in the vicinity of the group within a relatively small window of time and space (70 days and 300 nm). Conversely, no significant correlation was found for stocks which are less involved with the fishery.

Our measure of exposure to the fishery was a simple count of the number of IATTC-observed dolphin sets made within the above-defined window. Because approximately half of the purse seine trips carry IATTC observers and the remaining half carry national-program observers, we did not measure the total number of sets occurring around the sighting, albeit fishing effort can be expected to be correlated in time and space to some extent between sampled and un-sampled vessels. If we assume that the national program-observed sets are similar to the IATTC-observed sets, then our measure of fishery exposure should be approximately half that, of the true exposure. Because these extra sets would be evenly distributed with respect to our sightings we would not expect their omission in this study to affect our conclusions. However, if national program-observed sets tend to fish more heavily in one area, then their exclusion could

affect the patterns we have reported.

Dolphins are long-lived, large-brained animals, and long-term exposure to the fishery represents considerable opportunity for learning. Since the late 1960s and early 1970s, the purse-seine fishery has conducted about 8,000 - 14,000 sets on dolphins per year (IATTC 2006), extending over generations of dolphins and across the ranges of several stocks. The overall capture frequency per individual dolphin is estimated to be about eight times per year (Perkins & Edwards 1998). Although greater than 99% of the dolphins are released alive, it is clear that dolphins have learned from their exposure and interactions with the industry. As dolphins show an increase in evasive behaviors due to their recent interaction with the fishery, it will be important to assess whether these behaviors, while presumably effective in preventing temporary capture in a purse-seine net, may over the long-term be detrimental to the integrity and the social functioning of the school itself (Norris 1974, Curry 1999, Archer et al. 2001, Edwards 2005).

It should be emphasized that some of the dolphin stocks targeted by the tuna purse seine fishery are not recovering as expected, and management efforts are focused on better understanding both direct and indirect fishery effects on the populations (Gerrodette & Forcada 2005). While the effects of direct mortality can be related to population-level impacts (Gerrodette & Forcada 2005, Wade et al. 2007), it is much more difficult to assess the potential impacts of indirect effects. Presumably, evasive behaviors decrease the chances of dolphins being encircled. However, if avoidance carries costs, then dolphins must balance these costs against the benefit of reduced encirclement. These costs may include physical exertion, physiological stress, separation of mothers and calves, shark fatalities, and other as yet unknown aspects of social and ecological

disruption (Norris 1974, Orbach 1977, Curry 1999, Archer 2001, 2004, Edwards 2005). In addition, avoidance behaviors create a trade-off between avoiding risk and other fitness-enhancing activities, such as feeding, predator avoidance, parental care, and mating (Frid & Dill 2002). Even in better studied coastal populations (e.g., Lusseau 2003, Williams et al. 2006), linking short-term behavioral changes to long-term population-level impacts is challenging and the relationship is not expected to be straightforward (Gill et al. 2001, Beale & Monaghan 2004). However, in both marine and terrestrial species, there are indications that repeated short-term avoidance behaviors can lead to long-term impacts at the population level, through behavioral changes in habitat use and foraging (Yarmoloy et al 1988, Gerrodette & Gilmartin 1990, Nellemann et al. 2000, Phillips & Alldredge 2000, Lusseau 2005), communication (Slabbekoorn & Ripmeester 2008, stress physiology (Foley et al 2001 Müllner et al., 2004) and social functioning (Poole & Thomsen 1989, Bejder et al. 2006a). Further investigation of these factors is important, because while being chased has been implicated in the lack of recovery, the mechanism is not yet understood.

It is important to emphasize that the behaviors we have examined reflect the reaction of dolphins to our research vessel. While several other studies have examined the reaction of dolphins to purse-seiners during chase, encirclement and release, it is unknown to what extent these behaviors are similar to those exhibited around other kinds of vessels the dolphins may encounter. Additionally, our observations began when the school was detected and usually lasted only as long as was necessary to make reliable abundance estimates and stock identifications. In order to get accurate group size estimates and make species identifications, our research vessels actively pursued groups.

Therefore, in many of the sightings the interactions were initiated by us and may not reflect the response of the dolphins to a vessel that maintains its course and does not close on them.

While we have examined several vessel-responses and a variety of potentially mediating factors, dolphin vessel-response behavior is even more variable than discussed here. Differences among groups may also be influenced by factors such as recent social interactions, other human activities such as the overall concentration of vessel traffic, season, weather, and ecological and oceanographic conditions. Our analyses could be enhanced by employing better estimates of recent fishing activity and the frequency of interaction and exposure that an individual dolphin experiences, either via modeling efforts, or by collecting empirical data from electronic tagging experiments.

ACKNOWLEDGEMENTS

We are indebted to the field biologists, officers, and crews of the *David Starr Jordan*, *McArthur*, *McArthur II*, and *Endeavor* who are responsible for collecting the observations for this study. We would like to thank Tim Gerrodette and Andrew Dizon who helped guide the early phases of this study. We especially want to acknowledge the contributions of Bob Pitman, Paula Olson, Doug Kinzey, Richard Rowlett, Laura Morse, and Jim Cotton. We relied heavily upon their experience in the ETP to ensure that our data collection methodology accurately reflected the vessel-responses of pelagic dolphins. We thank Melissa Paine, who entered the 1999 behavioral data. This manuscript was improved by thoughtful reviews from Tim Gerrodette, Thomas Jefferson,

Bill Perrin, Bob Pitman, and Lisa Ballance. The Office of Protected Resources of the NOAA Fisheries funded the project.

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Table 1. Stock designations, number of sightings, school size distribution, and frequency of species in mixed sightings. “Pure” sightings are those in which only one stock is present, “mixed” sightings contain one or more stocks. Data from 1,443 sightings used in analyses in this study. Stock definitions taken from Dizon *et al.*, 1994.

Stock Code	Latin Name Common Name	Pure Sightings # sightings mean size (sd) median size (range)	Mixed Sightings # sightings mean size (sd) median size (range)	Sighting mixing frequency
BOTTLE	<i>Tursiops truncatus</i> Bottlenose	206 43 (198) 16 (1 – 2795)	70 68 (63) 46 (6 – 313)	16 <i>Grampus griseus</i> 16 <i>Globicephala macrorhynchus</i> 11 <i>Steno bredanensis</i> 10 <i>Stenella attenuata attenuata</i> 5 <i>Stenella longirostris orientalis</i> 4 <i>Stenella attenuata graffmani</i> 3 <i>Pseudorca crassidens</i> 1 <i>Lagenorhynchus obscurus</i> 1 <i>Lissodelphis borealis</i> 1 <i>Stenella longirostris</i> spp 6 Unidentified
COMM.N	<i>Delphinus delphis</i> Short-beaked common (northern stock)	68 210 (286) 134 (7 – 1700)	2 187 (91) 187 (123 – 251)	1 <i>Stenella coeruleoalba</i> 1 <i>Tursiops truncatus</i>
COMM.C	<i>Delphinus delphis</i> Short-beaked common (central stock)	79 127 (98) 95 (14 – 426)	3 208 (291) 62 (18 – 543)	2 <i>Stenella attenuata attenuata</i> 1 Unidentified
COMM.S	<i>Delphinus delphis</i> Short-beaked common (southern stock)	37 284 (237) 232 (9 – 1025)	4 211 (132) 166 (111 – 400)	2 <i>Stenella coeruleoalba</i> 2 <i>Delphinus delphis</i>
SPIN.ES	<i>Stenella longirostris orientalis</i> Eastern spinner	33 165 (197) 82 (7 – 807)	93 172 (117) 144 (40 – 783)	88 <i>Stenella attenuata attenuata</i> 5 <i>Tursiops truncatus</i> 1 <i>Stenella attenuata graffmani</i> 4 Unidentified
SPIN.WB	<i>Stenella longirostris longirostris</i> Whitebelly spinner	19 92 (94) 65 (10 – 398)	39 270 (239) 227 (56 – 1348)	38 <i>Stenella attenuata attenuata</i> 1 <i>Stenella coeruleoalba</i> 1 <i>Stenella longirostris longirostris</i> 4 Unidentified
SPOT.NE	<i>Stenella attenuata attenuata</i> Offshore spotted (northeastern stock)	104 74 (65) 56 (6 – 375)	128 168 (114) 147 (26 – 783)	95 <i>Stenella longirostris orientalis</i> 12 <i>Stenella longirostris longirostris</i> 8 <i>Tursiops truncatus</i> 7 <i>Stenella longirostris</i> spp 1 <i>Stenella longirostris</i> (southwestern form) 1 <i>Stenella coeruleoalba</i> 1 <i>Steno bredanensis</i> 7 Unidentified
SPOT.WS	<i>Stenella attenuata attenuata</i> Offshore spotted (western-southern stock)	31 79 (58) 57 (12 – 208)	43 292 (239) 242 (28 – 1348)	26 <i>Stenella longirostris longirostris</i> 8 <i>Stenella longirostris</i> (southwestern form) 4 <i>Stenella longirostris</i> spp. 3 <i>Stenella coeruleoalba</i> 1 <i>Delphinus delphis</i> 1 <i>Tursiops truncatus</i> 1 Unidentified
SPOT.CO	<i>Stenella attenuata graffmani</i> Coastal spotted	119 68 (97) 33 (3 – 620)	10 100 (66) 70 (44 – 255)	7 <i>Tursiops truncatus</i> 1 <i>Stenella longirostris orientalis</i> 1 <i>Delphinus delphis</i> 1 Unidentified
STRIPED	<i>Stenella coeruleoalba</i> Striped	338 46 (41) 33 (2 – 258)	17 163 (142) 116 (28 – 580)	6 <i>Delphinus delphis</i> 4 <i>Stenella attenuata attenuata</i> 1 <i>Stenella longirostris</i> (southwestern form) 1 <i>Stenella longirostris longirostris</i> (whitebelly) 1 <i>Grampus griseus</i> 1 <i>Orca orcinus</i> 3 Unidentified

Table 2. Predictor variables examined in Random Forest analyses.

Variable Name	Type	Description
<i>ship</i>	factor	Identifier of vessel from which observations were made (MAC = McArthur, DSJ = David Starr Jordan, END = Endeavour, MACII = McArthur II)
<i>hour</i>	continuous	Hour of day of sighting in local time (minutes and seconds converted to decimal)
<i>stock</i>	factor	One of ten stocks listed in Table 1
<i>pure</i>	factor	Sighting was of a single stock (TRUE) or mixed stocks (FALSE)
<i>best</i>	continuous	Best estimate of total school size in sighting
<i>pct.XXX</i>	continuous	Percent of sighting composed of stock XXX (n = 23 stock codes in all sightings)
<i>dist.coast</i>	continuous	Distance to nearest coast in nautical miles (including Hawaiian and Galapagos Islands)
<i>dsets</i>	continuous	Number of dolphin sets made within 300 nautical miles and previous 70 days
<i>mort.rank</i>	discrete	Rank of average mortality for stock from IATTC Annual Reports

Table 3. Results of pairwise χ^2 -test of behavioral profiles. χ^2 -statistic is given below the diagonal, p -value from 5000 replicates above the diagonal. Shaded values indicate nonsignificant results ($p > 0.05$). Results using all sightings are in table A, results from sightings of “pure” schools are in table B.

A) All Sightings

	BOTTLE	COMM.C	COMM.N	COMM.S	SPIN.ES	SPIN.WB	SPOT.CO	SPOT.NE	SPOT.WS	STRIPED
BOTTLE		0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002
COMM.C	161		0.0088	0.5777	0.1818	0.0002	0.0002	0.0018	0.0002	0.0002
COMM.N	69	30		0.0002	0.0004	0.0002	0.0002	0.0002	0.0002	0.0002
COMM.S	187	15	43		0.0444	0.0088	0.0002	0.0202	0.0020	0.0374
SPIN.ES	172	20	40	23		0.0006	0.0002	0.4001	0.0002	0.0002
SPIN.WB	234	39	74	18	34		0.0002	0.0032	0.2905	0.0354
SPOT.CO	52	145	77	142	142	180		0.0002	0.0002	0.0002
SPOT.NE	210	40	56	34	21	38	166		0.0002	0.0002
SPOT.WS	257	49	80	20	46	7	189	45		0.0026
STRIPED	477	106	233	36	137	32	451	148	38	

B) Pure Sightings

	BOTTLE	COMM.C	COMM.N	COMM.S	SPIN.ES	SPIN.WB	SPOT.CO	SPOT.NE	SPOT.WS	STRIPED
BOTTLE		0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002
COMM.C	152		0.0128	0.7688	0.8520	0.5013	0.0002	0.0514	0.0656	0.0002
COMM.N	70	29		0.0002	0.0936	0.0006	0.0002	0.0004	0.0002	0.0002
COMM.S	160	13	38		0.1914	0.6113	0.0002	0.0754	0.4121	0.0290
SPIN.ES	104	10	21	11		0.0256	0.0002	0.1562	0.0006	0.0002
SPIN.WB	148	15	38	6	15		0.0002	0.6047	0.4959	0.6145
SPOT.CO	40	134	69	128	93	128		0.0002	0.0002	0.0002
SPOT.NE	145	26	43	23	20	12	123		0.2855	0.0002
SPOT.WS	177	23	45	8	24	6	140	16		0.5971
STRIPED	422	104	223	36	80	10	424	104	12	

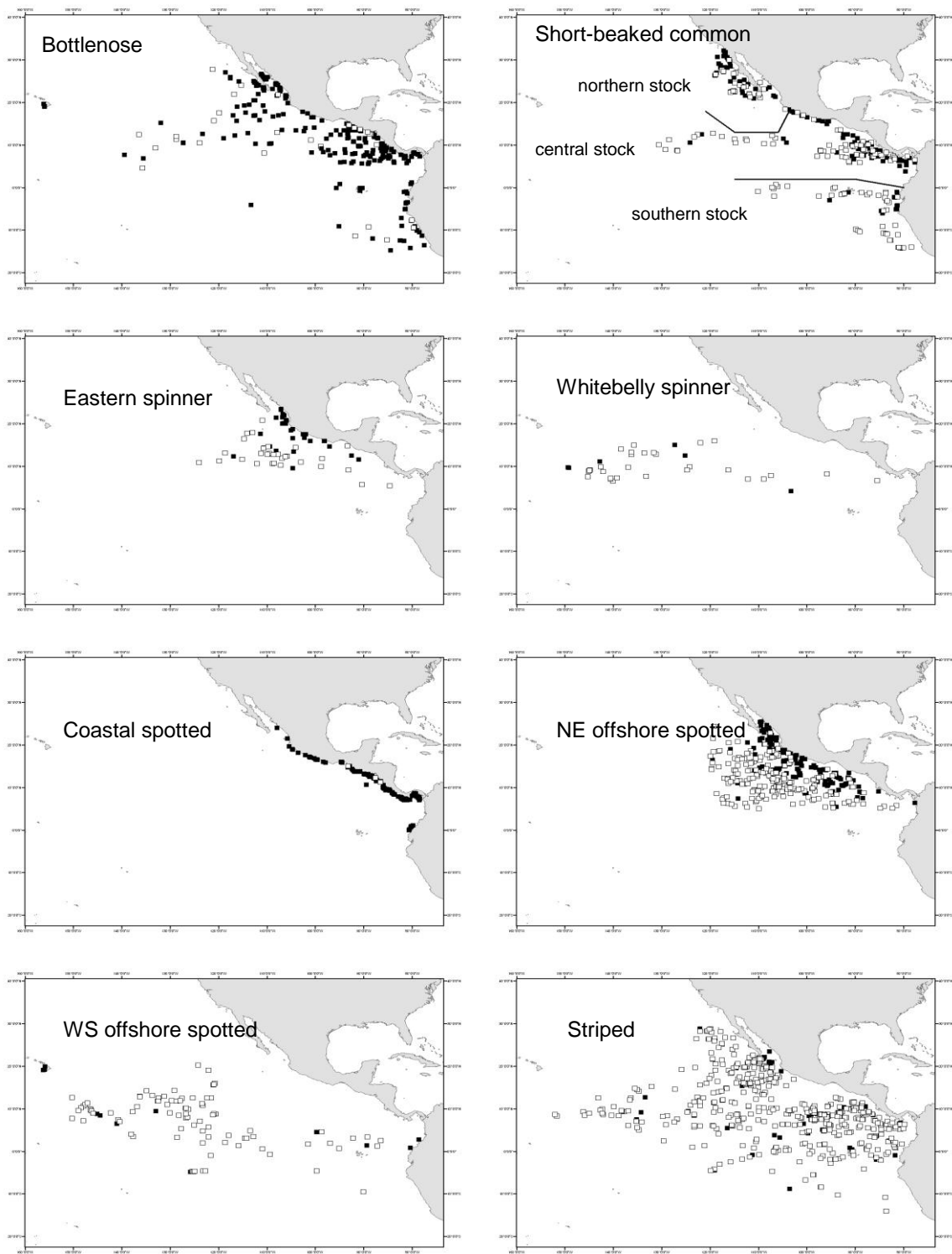


Figure 1. Research vessel sightings by stock. Open squares indicate sightings in which the school was evasive relative to the research vessel and closed squares indicate sightings in which the response to the research vessel was non-evasive.

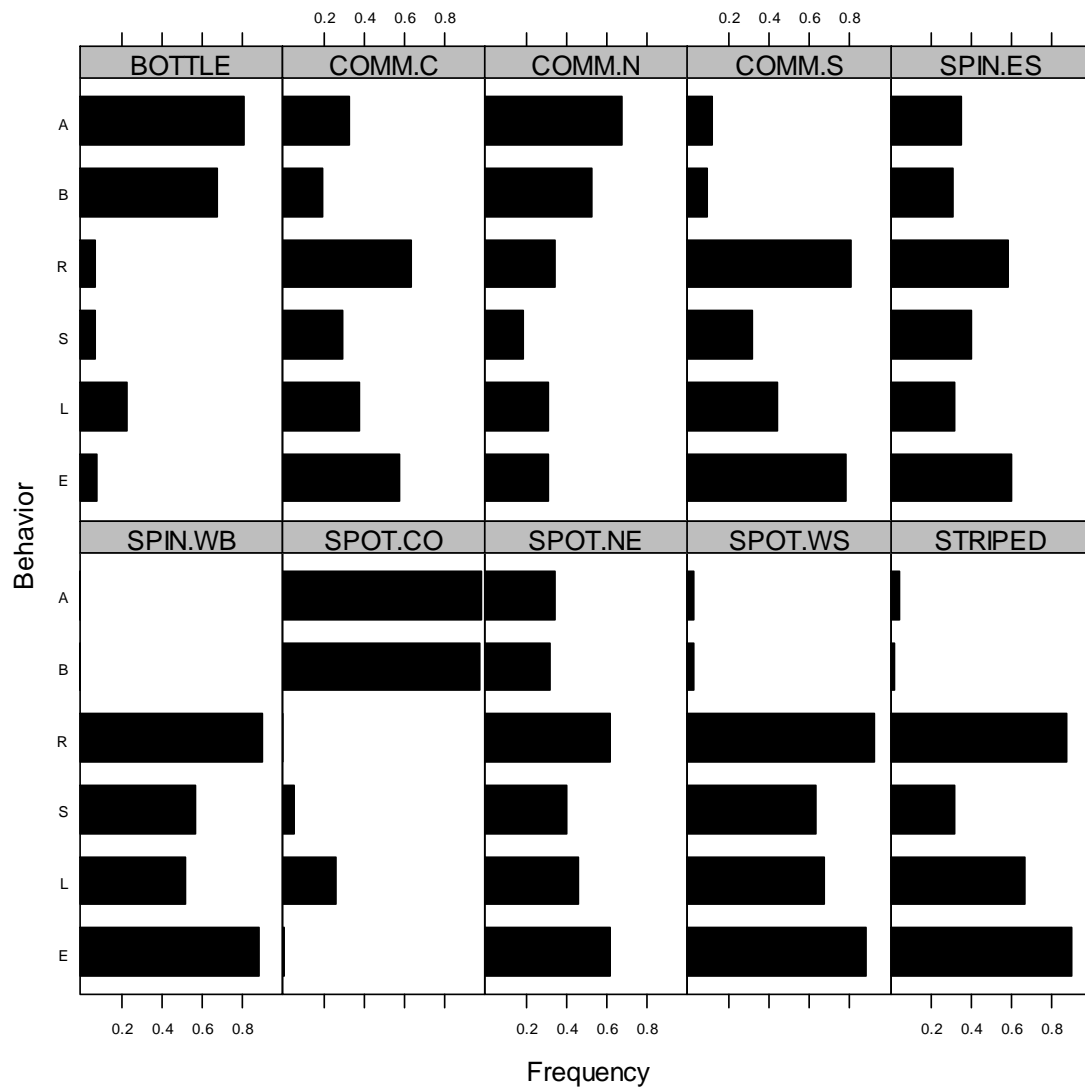


Figure 2. Frequency of six vessel-response behaviors for each stock. Behavior abbreviations on y-axis are A)pproach, B)owride, R)un, S)plit, L)owswim, and E)vasive.

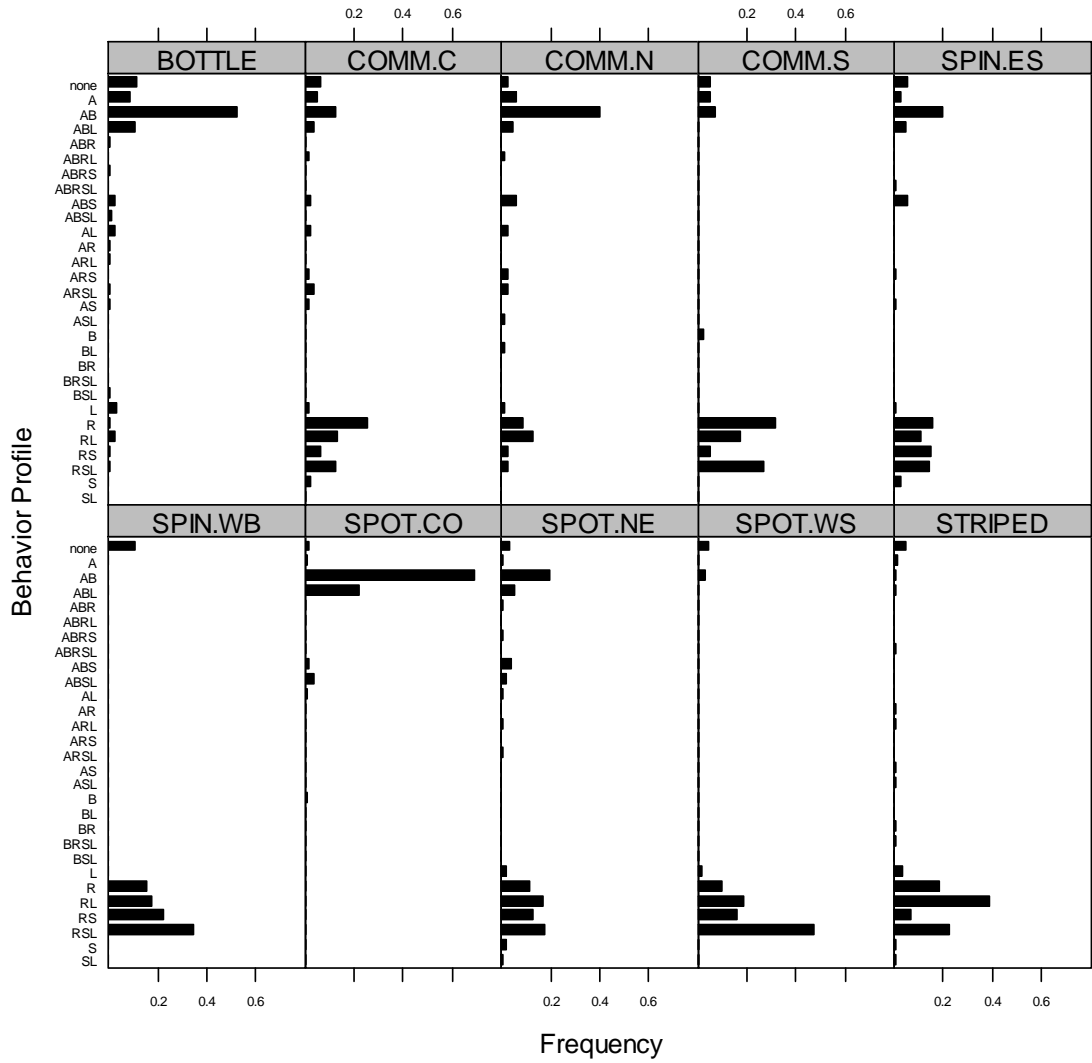


Figure 3. Frequency of behavioral profiles for each stock. Profile designations on y-axis indicate presence of listed vessel-responses where A)pproach, B)owride, R)un, S)plit, and L)owswim (e.g. RSL = running, splitting, and lowswimming were observed, while approaching and bowriding were not). “none” indicates that none of the responses were observed.

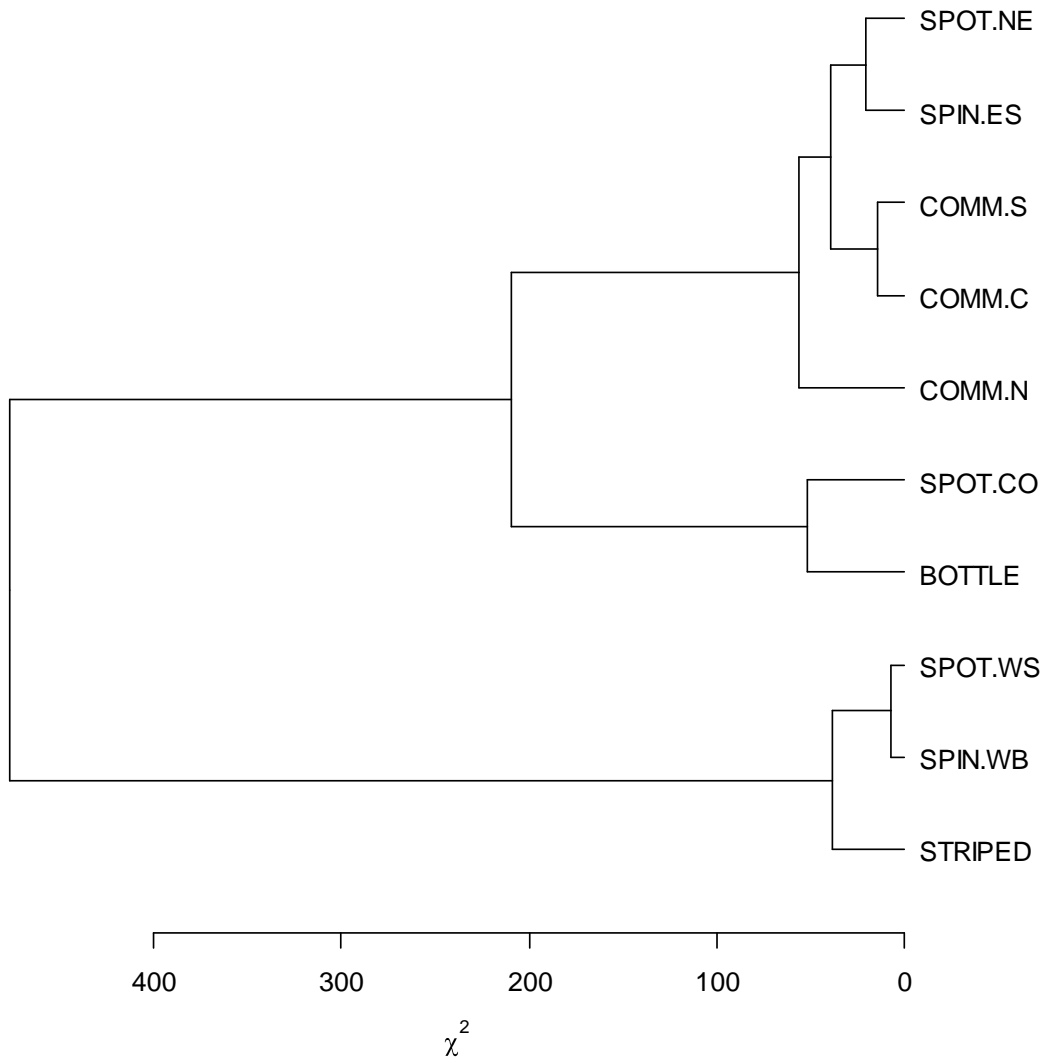


Figure 4. Cluster dendrogram from χ^2 values of behavioral profiles presented in Figure 3.

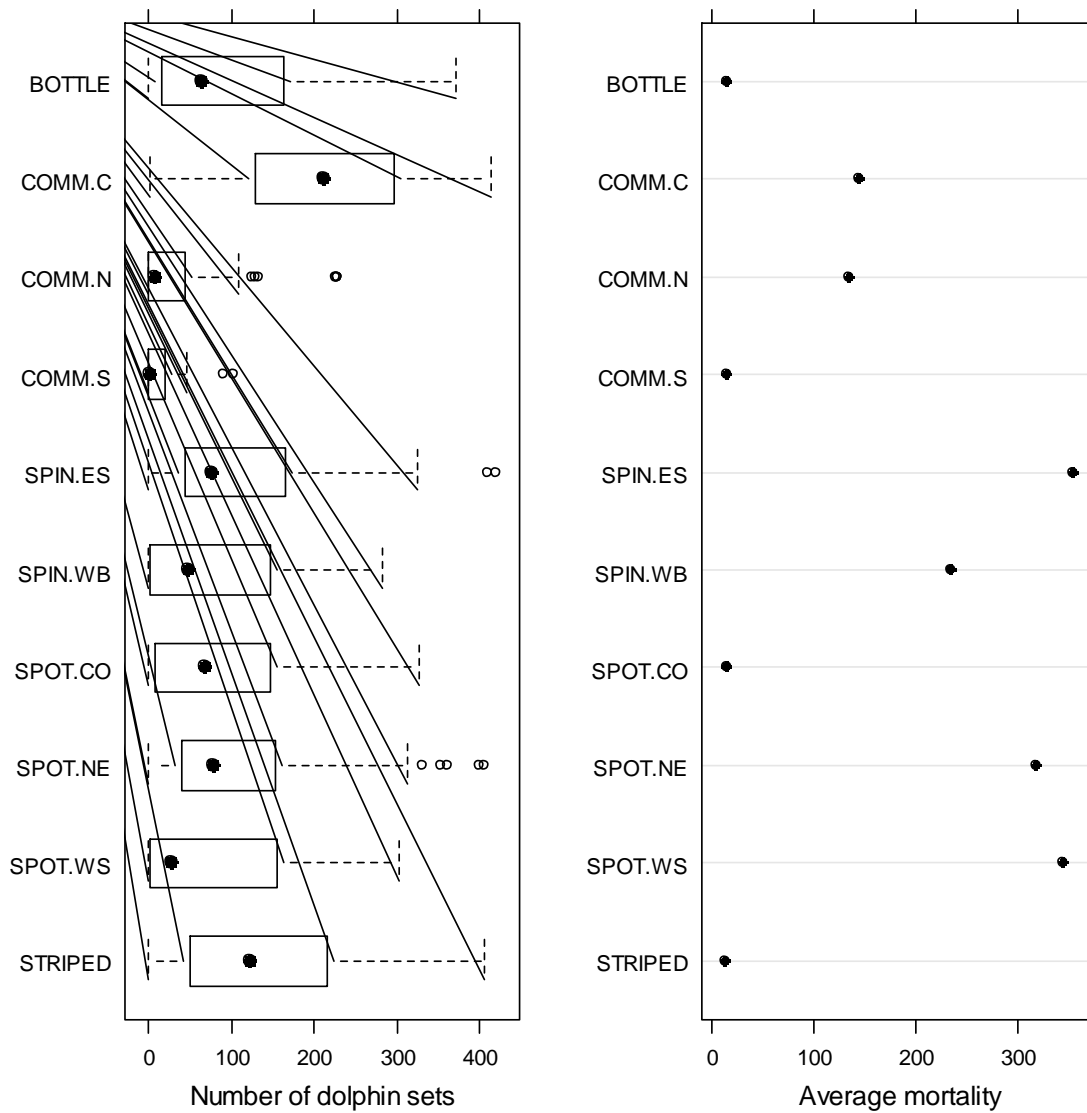


Figure 5. Fishery exposure of each stock. Left panel depicts distribution of number of dolphin sets made around sightings of each stock. Right panel indicates average mortality for each stock from IATTC Annual Reports from 1998-2000.

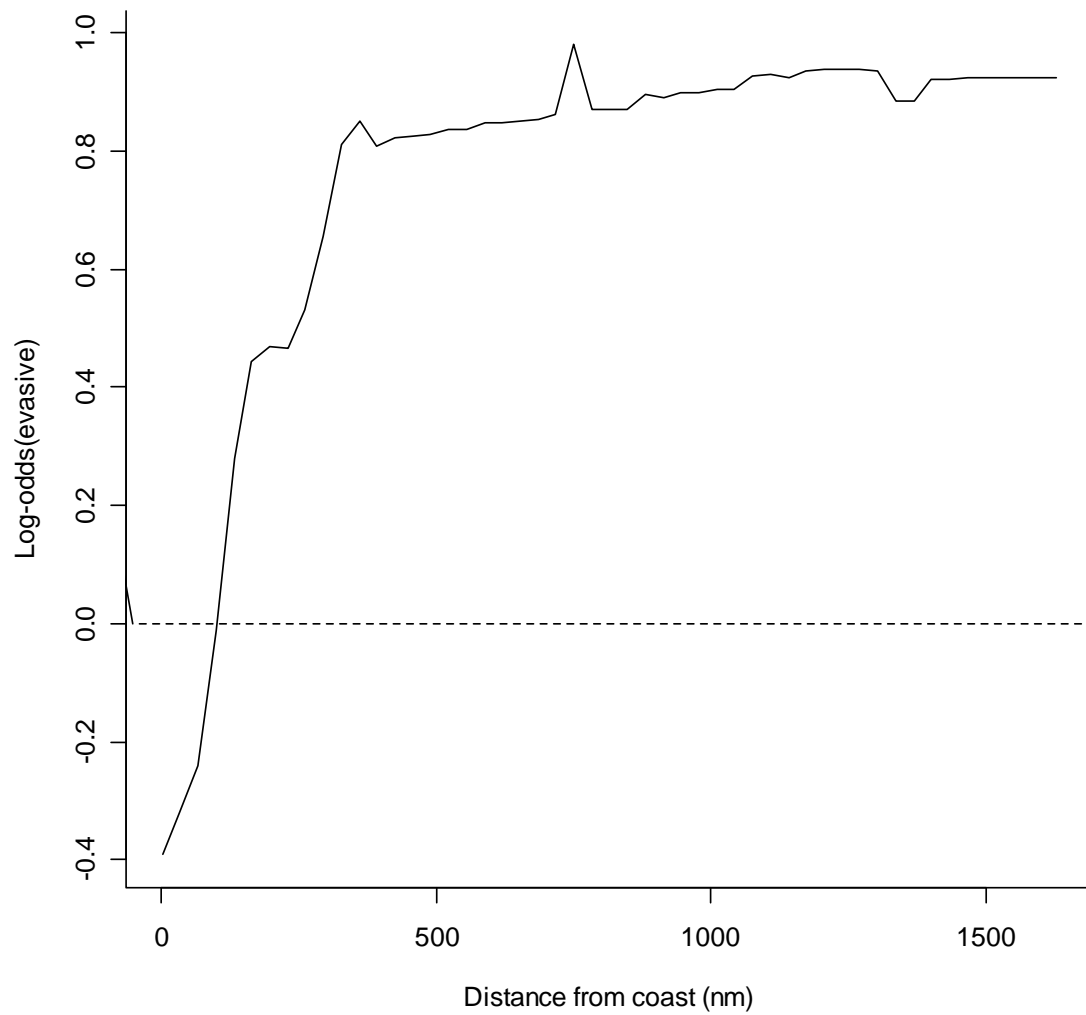


Figure 6. Partial plot of the log-odds of evasiveness relative to the distance from the coast using all sightings. Dashed line represents equal probability of being evasive or non-evasive.

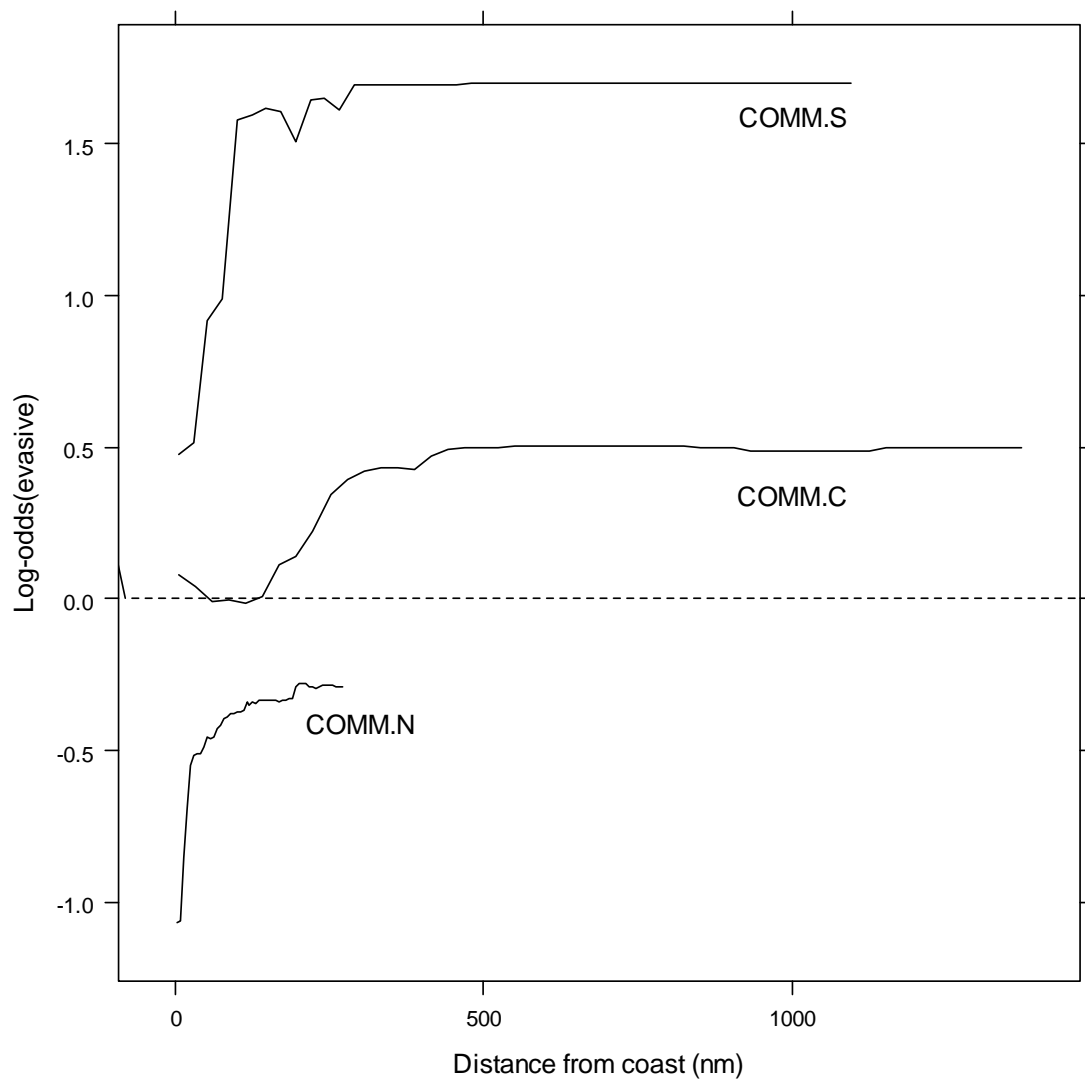


Figure 7. Partial plots of the log-odds of evasiveness relative to the distance from the coast for northern (COMM.N), central (COMM.C), and southern (COMM.S) common dolphins. Dashed line represents equal probability of being evasive or non-evasive.

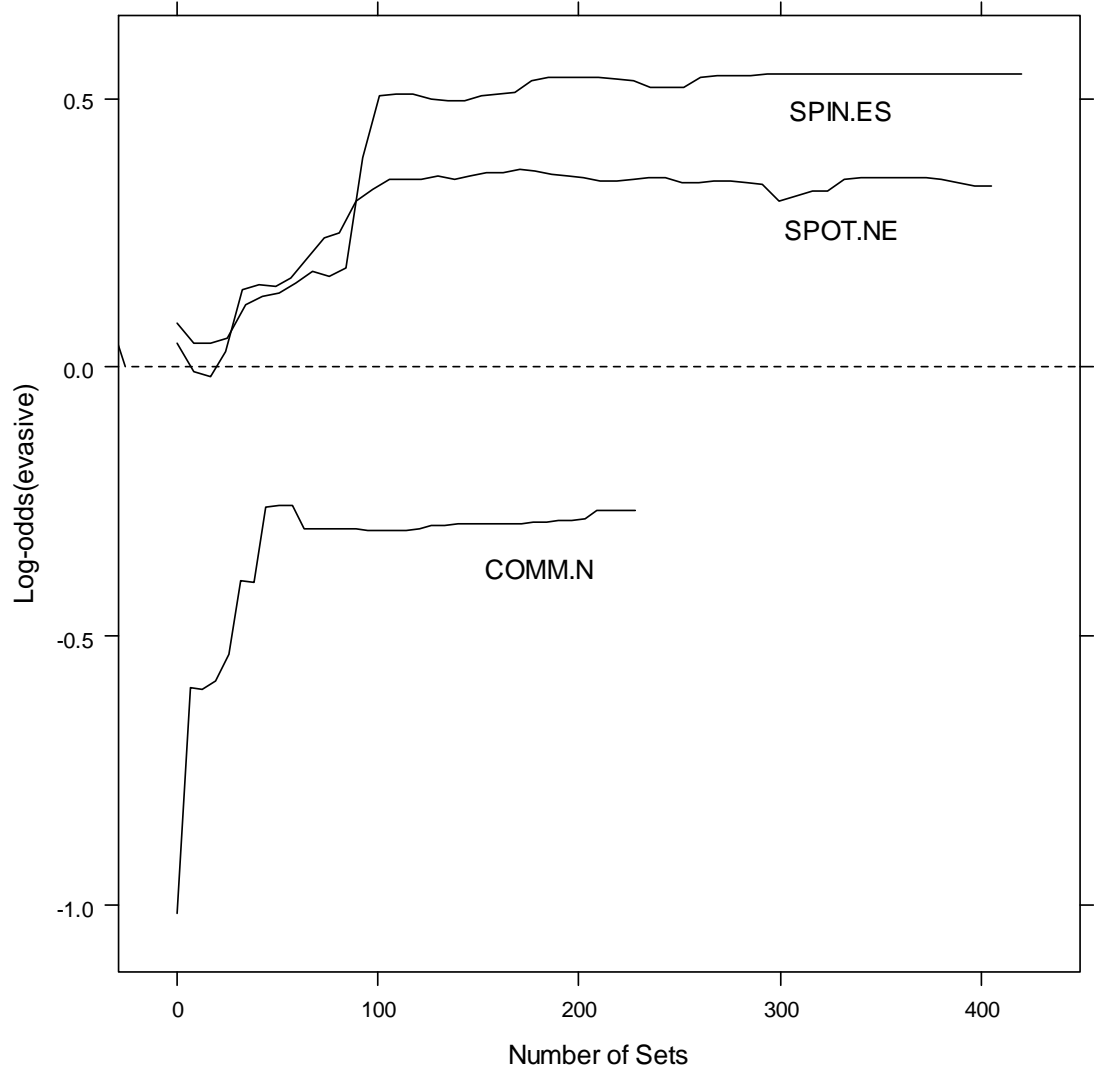
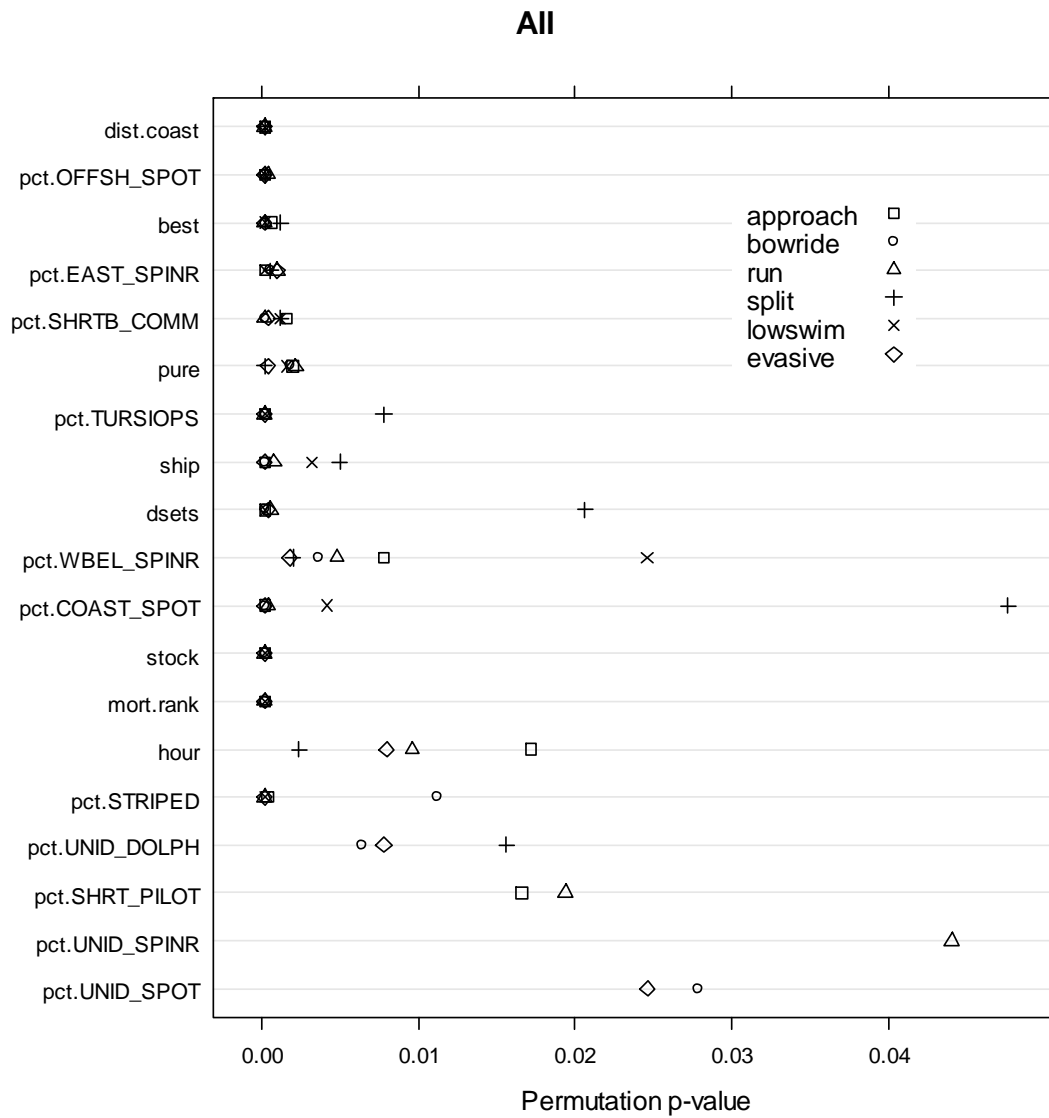
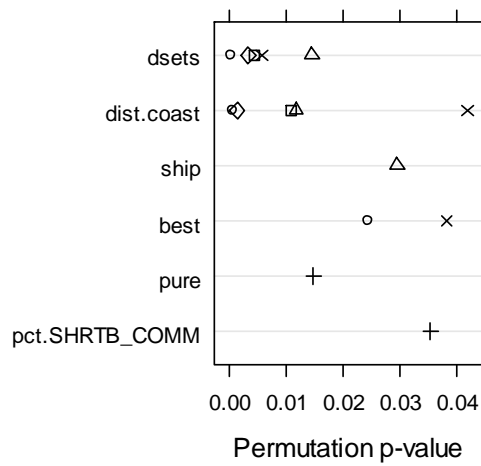


Figure 8. Partial plots of the log-odds of evasiveness relative to the number of purse-seine sets around the sighting for the three stocks of dolphins most frequently involved in purse-seine operations: northeastern-spotted (SPOT.NE), eastern spinner (SPIN.ES), and northern common (COMM.N) dolphins. Dashed line represents equal probability of being evasive or non-evasive.

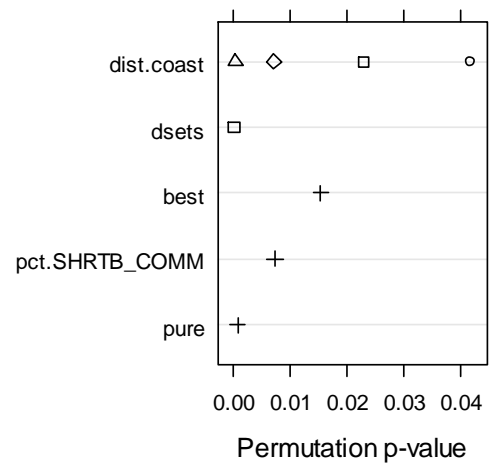
Appendix. Permutation p -values for significant predictors ($p \leq 0.05$) of vessel-response ($n = 1000$ permutations). Results for all sightings are listed first followed by sightings of each stock. Symbols represent results for each of the six responses as indicated in legend. Partial plots for all random forest runs are available from the author on request.



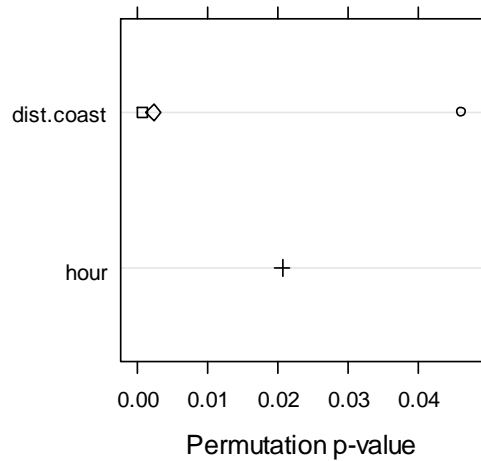
COMM.N



COMM.C

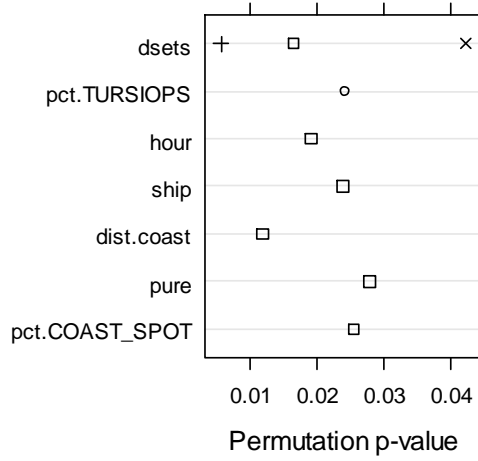


COMM.S

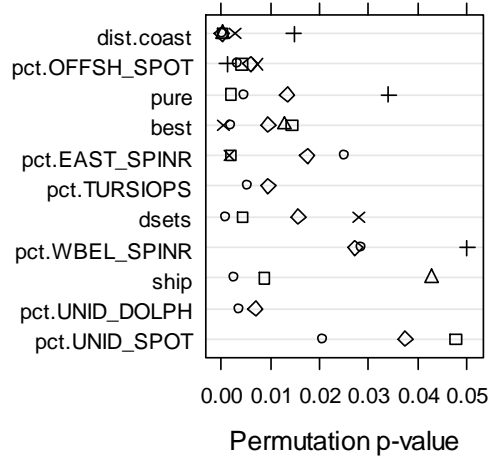


- approach □
- bowride ○
- run △
- split +
- lowswim ×
- evasive ◇

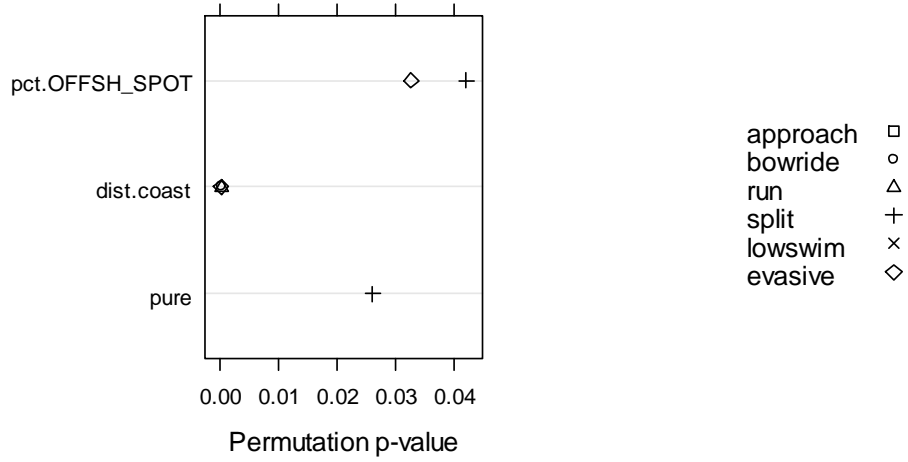
SPOT.CO



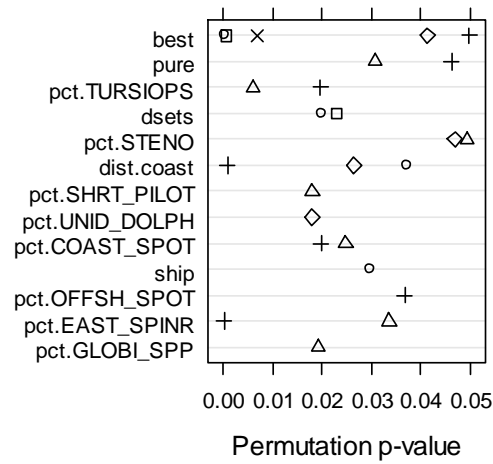
SPOT.NE



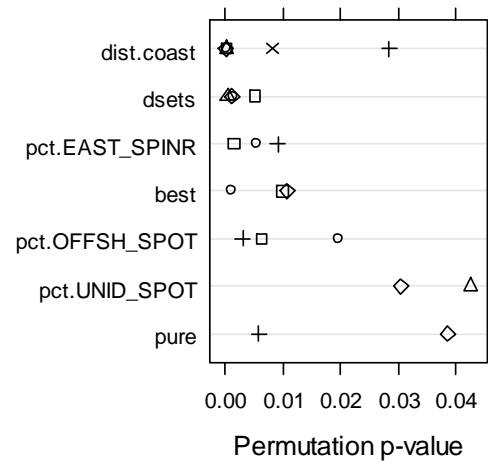
SPOT.WS



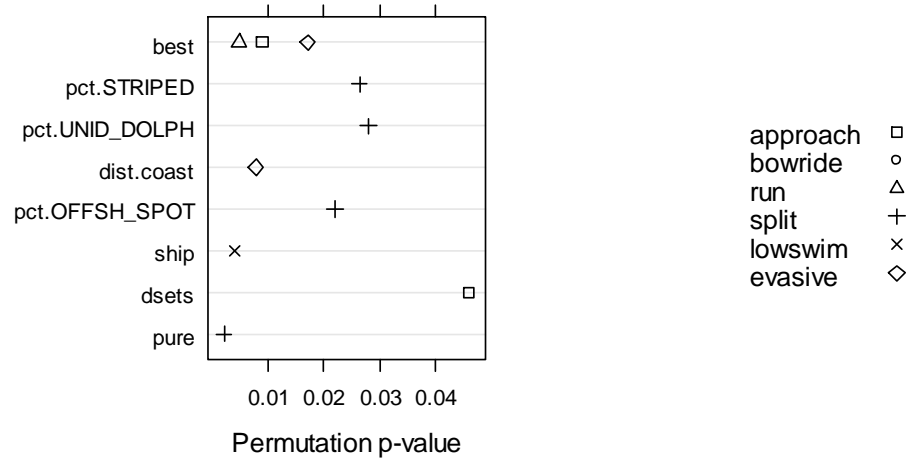
BOTTLE



SPIN.ES



STRIPED



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