

Estimation of relative exposure of dolphins to fishery activity

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ABSTRACT: For the past half-century, the purse seine fishery for yellowfin tuna has been a significant factor in the lives of dolphins in the eastern tropical Pacific (ETP). However, little is known about how frequently an individual dolphin is exposed to the fishery, and there are no methods available for accurately assessing the prior exposure of dolphins encountered at sea. Here we present a method to estimate an index of exposure based on a model of dolphin movement derived from data collected from multiple tracking studies. Based on this movement model, the method weights purse seine sets given their distance from a particular school of dolphins sighted at sea and how long ago they occurred. The method also takes into account the species composition and school size in the set. As a demonstration, we use the method to examine the spatial and temporal distribution of this index over an 11 yr period for which we have detailed data on purse seine sets. While the method has been designed for examining exposure to the ETP purse seine fishery, it is also applicable to studies of other anthropogenic effects where there is concern about exposure rates, such as underwater sound, pollution, or ship strikes.

KEY WORDS: Fishery exposure · Dolphin · Eastern tropical Pacific

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INTRODUCTION

Since the late 1950s, a large commercial purse seine fishery in the eastern tropical Pacific (ETP) has exploited the association of large schools of dolphins with yellowfin tuna *Thunnus albacares* by chasing and encircling the dolphins to capture the tuna below (National Research Council 1992, Gerrodette 2002). Historically, many dolphins, predominantly pantropical spotted *Stenella attenuata* and spinner *S. longirostris* dolphins, were killed during fishery operations (Wade 1994); however, modifications to fishing gear and practices in the 1970s and 1980s led to a drastic reduction in the number of dolphins killed in each set (IATTC 2009). Dolphin populations are not recovering at expected rates (Gerrodette & Forcada 2005, Wade et al. 2002), and several recent studies have suggested that the experience dolphins in some populations have of being repeatedly chased, captured, and released may have negative effects on survival or

reproduction through a variety of possible factors, such as separation of mothers and calves (Archer et al. 2001, Edwards 2006), or a decrease in calf production or the length of time calves spend nursing (Cramer et al. 2008).

From 1998 to 2007, there were ~11 000 dolphin sets yr⁻¹ in the ETP purse seine fishery (IATTC 2009). Although this estimate provides an aggregate measure of the impact of the fishery on dolphins, it does not encapsulate spatial or temporal variation in intensity of fishery activity. Current population estimates of the management stocks most frequently involved in the fishery are ~860 000 (coefficient of variation [CV] = 23%) for northeastern spotted *Stenella attenuata*, and ~1 100 000 (CV = 26%) for eastern spinner *S. longirostris orientalis* dolphins (Gerrodette et al. 2008). On average, there are ~120 (CV = 17%) northeastern spotted dolphins and ~200 (CV = 15%) eastern spinners in a school (Gerrodette et al. 2008). Thus, if sets were randomly spread in space and time, then a

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given dolphin might be exposed to 1 to 2 sets yr^{-1} . On the one hand, the stress related to chase, capture, and release (Curry 1999) might be relatively low across the population for an event that occurs this infrequently. On the other hand, if sets were spatially and temporally more concentrated such that a subset of the population experienced them relatively more frequently, there is a strong potential for multiple acute stress episodes to occur and lead to a general state of prolonged chronic stress along with associated negative physiological effects. To evaluate the potential magnitude of any of these effects on the population level, the frequency at which dolphins are exposed to purse seine operations needs to be quantified.

Perkins & Edwards (1999) estimated annual set frequency by comparing the size distributions of schools that were set on to schools observed during research cruises. Because larger schools tend to carry more tuna, they are preferentially targeted by the fishery. For the school sizes most likely to be set on, it was estimated that sets occur between 2 and 8 times yr^{-1} . The problem with extrapolating these results to the population is that we have very little information about how dolphin schools are structured and how individuals move among schools of different sizes. If these large schools are the result of ecological heterogeneity, and individuals randomly move in and out of them as the 'fission-fusion' model suggests (Perrin et al. 1979, Scott & Cattanach 1998), the average annual capture rate of any given dolphin is likely to be on the low end of the estimates given by Perkins & Edwards (1999). Conversely, stability of school membership or demographic structuring would tend to increase the frequency of sets for some individuals to values closer to the high end of these estimates.

Mesnick et al. (2002) found that fishery exposure was significantly correlated to short-term evasive behavior for those stocks most frequently set on in the ETP. In their study, fishery exposure for individual dolphin sightings was estimated by counting the number of sets occurring within a specified time and distance window (an 'ambit'). While it serves as a convenient summary metric of likely set activity around a sighting, this simple count may not accurately summarize the recent exposure that individuals may have had to the fishery. Using this method, sets on either the temporal or spatial periphery of the ambit will contribute as much to the metric as sets close to the sighting, although they have a lower chance of having been encountered by dolphins in that sighting. Likewise school size and stock composition were not taken into account; consequently sets on small schools are weighted equally with sets on large schools, and sets that are not on the species of interest contribute to the metric.

Here we present a method that overcomes these shortcomings and measures relative fishery exposure for any given location and time (such as for a dolphin or dolphins encountered at sea, which we refer to as a 'sighting') by weighting sets based on a model of spotted dolphin movement derived from empirical tracking and mark/recapture data. As an example of the type of study that can be conducted with this algorithm, we also present an examination of the spatial and temporal patterns of exposure for 3 species of dolphins involved in the ETP tuna purse seine fishery. The applicability of this method is not limited to this problem or region. By replacing a field of purse seine sets with any other anthropogenic effect such as underwater sound sources, pollution outflows, or vessel traffic, the method can easily be extended to studies of other types of potentially harmful exposure.

MATERIALS AND METHODS

The exposure index that we have developed is based on a model of dolphin movement derived from empirical data. This model produces a probability distribution for a dolphin travelling a given distance in a specified amount of time, which we use to weight purse seine sets occurring in the vicinity of dolphins sighted at sea. In addition, the size and species composition of the dolphin schools involved in the set are used in the weighting scheme. The weights for each set are summed to produce the final index of exposure. In the following, we detail how each component of the index is calculated.

Dolphin movement model. The data used to model dolphin movement were collected during a tagging project conducted from 1969 to 1978 (Perrin et al. 1979, Hedgepeth 1985) and a radio-tracking study conducted from 1992 to 1993 and in 2001 (Scott & Chivers 2009). In the tagging study, technicians onboard purse seiners attached a variety of tags, most of which were 'spaghetti' tags, to dolphins as they were released from the net. Biological data on the dolphin and information about the tagging event, such as tag type, tag number, location, and date were recorded on release. If the tagged dolphins were subsequently resighted or recaptured, the date and location were recorded.

In the radio-tracking study, focal spotted dolphins were captured by a purse seiner and fitted with radio-transmitters. These dolphins were then followed for up to 3 d and recaptured by the purse seiner as part of a larger study designed to examine their blood chemistry for evidence of stress-related changes (Forney et al. 2002). Because the data from these dolphins indicated rapid straight-line swimming immediately after release that was likely due to escape from the area of

the tagging operation, we selected the position and time 1 h after release to be the initial point of normal movement (Scott & Chivers 2009). The end point for the track was the position and time immediately preceding the initiation of the chase for recapture. After their first recapture, 2 dolphins were released with the radio-transmitter still attached and captured again at a later point. These multiple capture/recaptures from the same dolphin were used in the analysis, with each pair used as an independent time/distance point. In total, 31 tracks were available from 29 dolphins tracked in this study.

For this analysis, the tagging and tracking datasets described above were combined. We used only 1 sample when multiple dolphins were released and resighted in the tagging dataset. To avoid potentially confounding variation due to annual movement patterns of both dolphins and the tuna purse seiners that collected resight and recapture data (Perrin et al. 1979), we restricted samples in the analysis to those animals recaptured within half a year (183 d). One outlying tag return of 1608 nautical miles (n miles) in 107 d was removed from the analysis. The final sample size from the combined datasets was 146 tracks, or pairs of release and resight/recapture points.

We modeled the relationship between dolphin travel distance and time using a standard random walk model (Pielou 1969, Okubo 1980, Gerrodette 1981). For diffusing particles with no directional movement, the distance traveled, x , from a point of origin is described by a power function of the form

$$x = a \times t^b \quad (1)$$

where a is a positive proportionality constant, and time t is raised to the power b which determines the diffusion rate, defined as a positive real value in a random walk model. In our data, the distance traveled (x) was calculated as the great circle distance between release and recapture locations in n miles, and time at liberty (t) was calculated to the nearest minute.

We estimated the parameters of the random walk model using a Bayesian analysis of the movement data. The likelihood function was based on a normal distribution using a log-transform of Eq. 1, which converts the power function to a linear function,

$$\log(x) \sim N(a' + b \times \log(t), \tau) \quad (2)$$

where a' is $\log(a)$, and τ is the precision, or the inverse of the variance (σ^2). Priors for a' , b were Uniform(0, 10), and τ was Gamma(shape = 10^{-3} , rate = 10^{-3}). Six independent Markov chain Monte Carlo (MCMC) chains were run, with each chain initialized from random draws from the prior distributions. A burn-in period of 10 000 updates was conducted for each chain, followed by another 100 000 updates. Every 100th update was

saved to produce a total of 1000 samples from each chain. The 6000 samples from all chains were then combined to create a single sample from the final posterior probability distribution for a' , b , and σ^2 . The analysis was conducted using the package BRugs v0.5-1 running OpenBUGS v3.0.3 on R v2.9.0 (R Development Core Team).

Using the joint posterior distribution on the parameters from the above Bayesian model, the probability distribution that a dolphin would have traveled x n miles in t d is given as

$$\Pr(x | t, a', b, \sigma^2) = \frac{1}{\sqrt{2\pi\sigma^2}} \cdot e^{-\left[\frac{(\log(x) - (a' + b \cdot \log(t)))^2}{2\sigma^2}\right]} \quad (3)$$

Exposure index. The exposure index for a given dolphin sighting is best visualized as a weighted sum of purse seine sets that have occurred prior to that sighting. The first component of the weighting scheme is the probability that a dolphin from the sighting was involved in each set. A set is assumed to have a region of influence, represented by a circle around its reported location. For this study, circles of 2 radii were examined: 6 n miles, representing the average distance to the horizon for a visual observer, and 12 n miles, representing the average detection distance of the onboard 'bird' radar (M. Scott pers. comm.). Thus, the probability that a dolphin was exposed to a set is

$$\Pr(\text{exposure}_i) = \int_j \text{median}(\Pr(x_j | t_i)) \quad (4)$$

where j represents all points within the set circle, x is the distance from any given point to the sighting, and t_i is the time elapsed between the set and the sighting in minutes. For this study, we used the time recorded as the beginning of the chase to represent the time the set occurred.

As the distance between a sighting and a set increases, the probability that a dolphin in that sighting was exposed to that set decreases, not only according to Eq. 3. It also decreases because the dolphin could have travelled to the sighting location from an increasingly larger area. Specifically, the set makes up a smaller fraction of the area that the dolphin could have inhabited in the past. Consequently, we also weight a set by the fraction of the area around the sighting it occupies

$$W_i = \frac{A(\text{set}_i)}{A(\text{extent}_i)} \quad (5)$$

where extent_i is defined as a circle around the sighting of radius $d + r$, where d is the distance from the sighting to the set center, and r is the set radius (Fig. 1). If the set circle or set extent intersected the coastline, only the area over water was used in the above calculation.

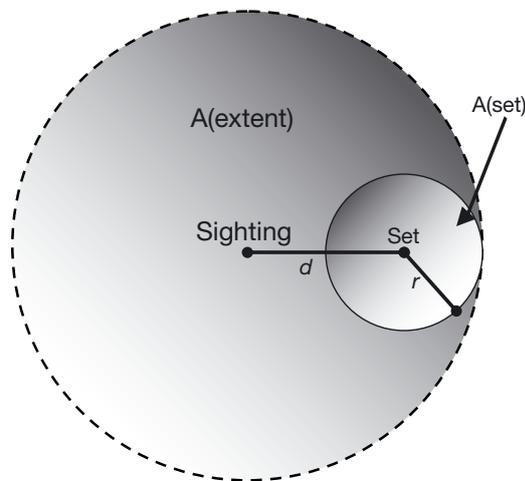


Fig. 1. Set area, $A(\text{set})$, and extent area, $A(\text{extent})$, for Eq. 5 in text (see 'Materials and methods'), where d is the distance from the dolphin sighting to the set and r is the search radius of the set

The final component of the exposure index weighting is the species-specific group size of dolphins in the set (N_{species_i}). For example, all other things being equal, an eastern spinner dolphin is 10 times more likely to have been involved in a set where 200 spinners were chased than in a set with 20 spinners. Conversely, the exposure index for a set with no spinners chased should be 0 regardless of its distance and temporal proximity to a spinner sighting.

To simplify calculations, we limited the number of sets considered around a sighting to those occurring within 60 d and the upper 95th percentile of the estimated distance a dolphin could travel within 60 d (≈ 481 n miles). Thus, for a sighting with k sets in this ambit, the exposure index for a sighting of a given species is

$$\text{Index}(\text{sight}_{\text{species}}) = \sum_{i=1}^k (\text{Pr}(\text{exposure}_i) \times W_i \times N_{\text{species}_i}) \quad (6)$$

Spatial and temporal exposure analyses. We examined the spatial and temporal distribution of the exposure index for the 3 dolphin species most commonly involved in the ETP tuna purse seine fishery: offshore spotted dolphins, eastern spinner dolphins, and pooled northern, central, and southern stocks of short-beaked common dolphins *Delphinus delphis*. Offshore spotted dolphins are composed of 2 management stocks (northeastern and western/southern; Perrin 1990, Dizon et al. 1994), and common dolphins are composed of 3 stocks (northern, central, and southern; Perrin et al. 1985). In all analyses, data for these stocks were combined. To estimate the exposure for each species,

we multiplied the exposure index for that species by an estimate of its density for each day of survey effort on research cruises conducted by the Southwest Fisheries Science Center from 1979 to 1990 (Table 1). These years were selected because we had access to detailed data on the position, time, and dolphin composition of tuna purse seine sets for a significant portion of the fleet, as described below.

For each survey day in which there were at least 10 n miles of survey effort (~ 1 h of effort), the density of a species was estimated as

$$\text{Density}(\text{species}) = \frac{\sum S_{\text{species}} \times f(0)_{\text{species}}}{2 \times e \times g(0)_{\text{species}}} \quad (7)$$

where S is the group size of each sighting of that species, estimated from the average of the 'best' estimates provided by observers. If no 'best' estimates were made, the observers' 'low' estimate was used. If a sighting was composed of multiple species, species-specific group sizes were calculated as the average of each observer's estimate multiplied by their estimate of the percentage of individuals of that stock. Only sightings made while on-effort (sensu Kinzey et al. 2000) were used in the calculation. Effort (e) is the linear distance covered while on-effort each day. The line-transect variables, $f(0)$ and $g(0)$, respectively correct for decreasing detection probabilities with distance from the transect and failure to detect all animals on the transect (Buckland et al. 2001). Species-specific $f(0)$ and $g(0)$ values were taken from Ferguson & Barlow (2001). We did not subsample data to account for sea state constraints in Ferguson & Barlow (2001), but applied the $f(0)$ and $g(0)$ values to all data, which may negatively bias densities estimated in sea states higher than Beaufort 5. For spotted and common dolphins, multiple values of $f(0)$ and $g(0)$ for different stocks in the ETP were averaged. Details of survey methodology

Table 1. Southwest Fisheries Science Center research cruises conducted in the eastern tropical Pacific used to estimate daily density. PPAS: Porpoise Population Assessment Survey; MOPS: Monitoring of Porpoise Stocks

Year	Cruise name	Ships (n)	On effort days (n)
1979	PPAS	2	120
1980	PPAS	2	108
1982	PPAS	1	66
1983	PPAS	1	78
1986	MOPS	2	198
1987	MOPS	2	198
1988	MOPS	2	185
1989	MOPS	2	202
1990	MOPS	2	210

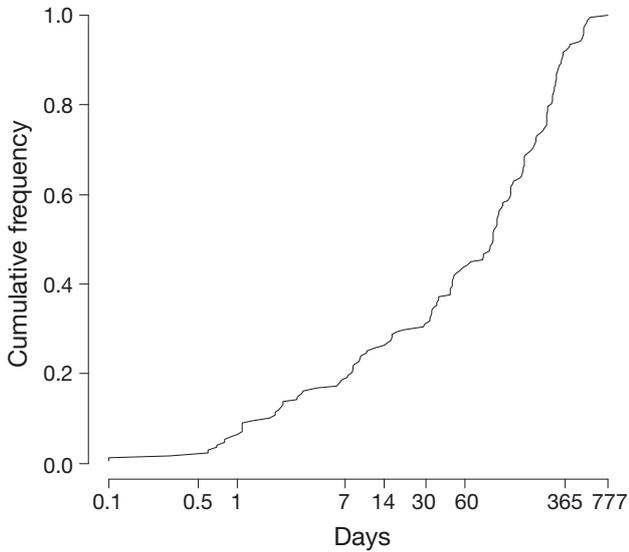


Fig. 2. Cumulative frequency distribution of number of days between release and recapture for 214 dolphins tagged between 1969 and 1978. x-axis is log-scaled

can be found in Kinzey et al. (2000) and Gerrodette & Forcada (2002) and references therein. For the exposure index calculation, the location chosen for each day with a density estimate was the position of the ship at noon, and the time used was 23:59:59 local time, to ensure all sets occurring on that day were included in the calculations.

Set data were extracted from the US National Marine Fisheries Service (NMFS) tuna purse seine observer database (described by Edwards 1989) covering US fleet activity from 1971 to 1990. Set times were recorded to the nearest minute and locations to the nearest degree. Dolphin school size was taken as the observer’s best estimate prorated by the percent composition of spinner, spotted, or common dolphins in the school.

Spatial and temporal patterns were interpolated with inverse distance weighting (IDW) as implemented in the *gstat* package in R. The IDW power factor was 0.8 for all analyses. Spatial grid sizes were 0.5 degrees of latitude and longitude. Monthly grids were used for temporal scales.

RESULTS

Dolphin movement

Over the 11 yr of the mark-recapture project, 4267 tags were deployed and 214 were opportunistically recovered from dolphins killed during sets or resighted on dolphins released from the net (Hedgpeth 1985).

An examination of the distribution of the time to recapture for these tags (Fig. 2) shows that ~93% occurred within 1 yr, 35% within 1 mo, 22% within 1 wk, and 8% within 1 d. The median time to recapture was 95 d. Converted to an annual rate, the median of this distribution is 3.7 captures yr⁻¹ with a central inter-quartile range of 1.4 to 33 captures yr⁻¹.

The joint posterior distribution of the parameters a' and b from the Bayesian movement model (Eq. 2) shows that the 2 are negatively correlated as expected for the intercept and slope parameters of a linear model (Fig. 3). Both parameters were uncorrelated with σ . Diagnostics of the MCMC chains indicate that there was good mixing after the burn-in period and there was no significant autocorrelation after a lag of 2 (data not shown). The probability distribution of movement (Fig. 4, from Eq. 3) broadens rapidly within the first week, such that after 7 d, a dolphin is most likely to be ~60 n miles from its point of origin, with a 95% highest posterior density (HPD) interval of 16 to 223 n miles. After 30 d, the most likely distance is 117 n miles with a 95% HPD of 31 to 433 n miles.

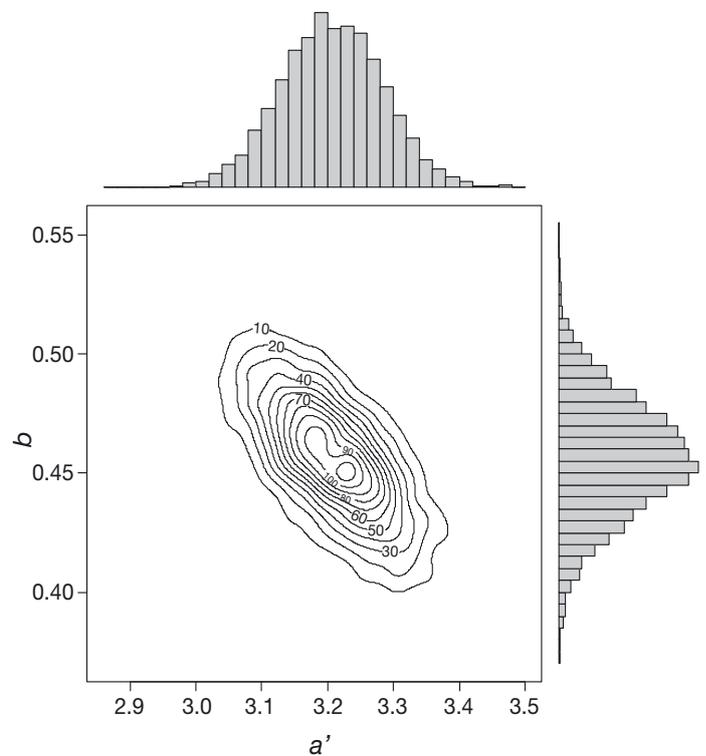


Fig. 3. Contour of joint posterior distribution of a' and b parameters from the dolphin movement model with marginal histograms along respective axes. Area under histograms sums to total number of samples from the posterior chain distribution ($n = 6000$). Values in contour are frequency of samples from Markov chain Monte Carlo (MCMC) chains

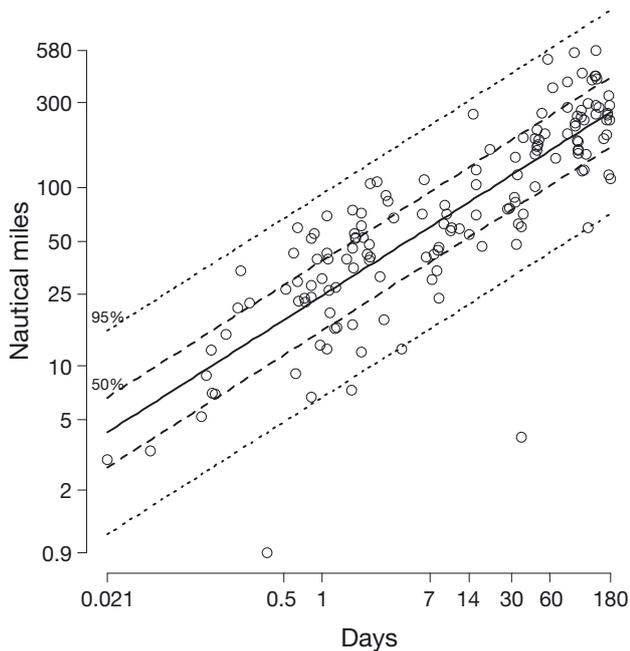


Fig. 4. Fit of Bayesian model to movement data from tagged dolphins. Both axes log-scaled. Lines: solid = median, dashed = central 50%, dotted = central 95% of posterior fit

Exposure index

Daily density was estimated for 1365 d of effort during 10 cruises from 1979 to 1990 (Fig. 5). Most survey effort occurred close to the coast of Central America and offshore to about 120° W, between 20° N and the equator. The ambit around each day was defined as a circle of 481 n miles and the previous 60 d, the same spatial and temporal limits placed on sets used in calculating the exposure index. For these days, the median number of sets within this ambit was 12. Approximately 30% of the days ($n = 404$) had no sets in the ambit. The maximum number of sets in an ambit was 295.

For all species, the distribution of the daily exposure index was heavily skewed towards 0. Specifically, exposure indices were 0 for 70, 87, and 96% of the days for offshore spotted, eastern spinner, and common dolphins, respectively. These indices represent both cases with 0 sets on the species in the ambit and days when the species was not sighted (density estimate = 0). The maximum

exposure index for the 3 species was 64.6 for spotted dolphins, 15.6 for spinner dolphins, and 1.65 for common dolphins.

Spatial and temporal exposure analyses

The spatial and temporal distribution of the exposure index weighted by density is given in Fig. 6. Exposure of common dolphins to the US tuna purse seine fishery was highest along the coast of Central America, remaining high but decreasing in intensity southward along the coasts of Colombia, Ecuador, and northern Peru (Fig. 6a). Exposure in this area for common dolphins was relatively low in the late 1970s as indicated by the blue region in Fig. 6b from ~0° to ~20° N, increasing to its peak in the late 1980s along this band. There is a stronger east-west gradient of exposure for this species (Fig. 6c), with very low values west of ~100° W. Exposure east of this line also increases over time, peaking around 90° W in 1990.

For both eastern spinner and offshore spotted dolphins, exposure was greatest in the core of the ETP (Fig. 6d,g), between ~10° and ~20° N, around 100° W. There is evidence of a latitudinal shift in exposure for these 2 species in which the center of fishery exposure in the late 1970s, which was at ~15° N, shifted ~5° far-

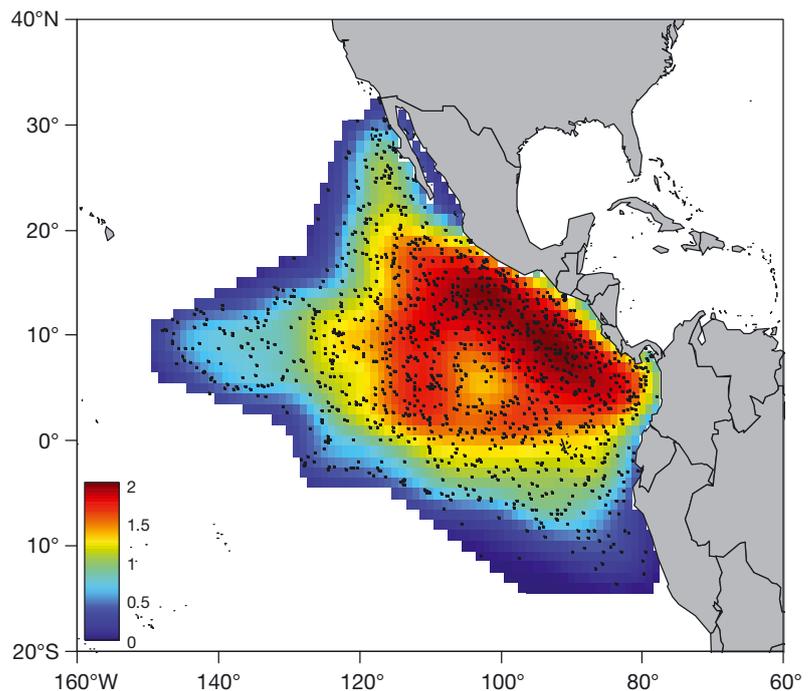


Fig. 5. Locations of days of survey effort in the eastern tropical Pacific (ETP) from 1979 to 1990. Color scale is a 2D kernel density smoother estimate of the number of points representing 1 d of survey effort within a 1° square area. Some overlap of points occurs in areas of high effort (red)

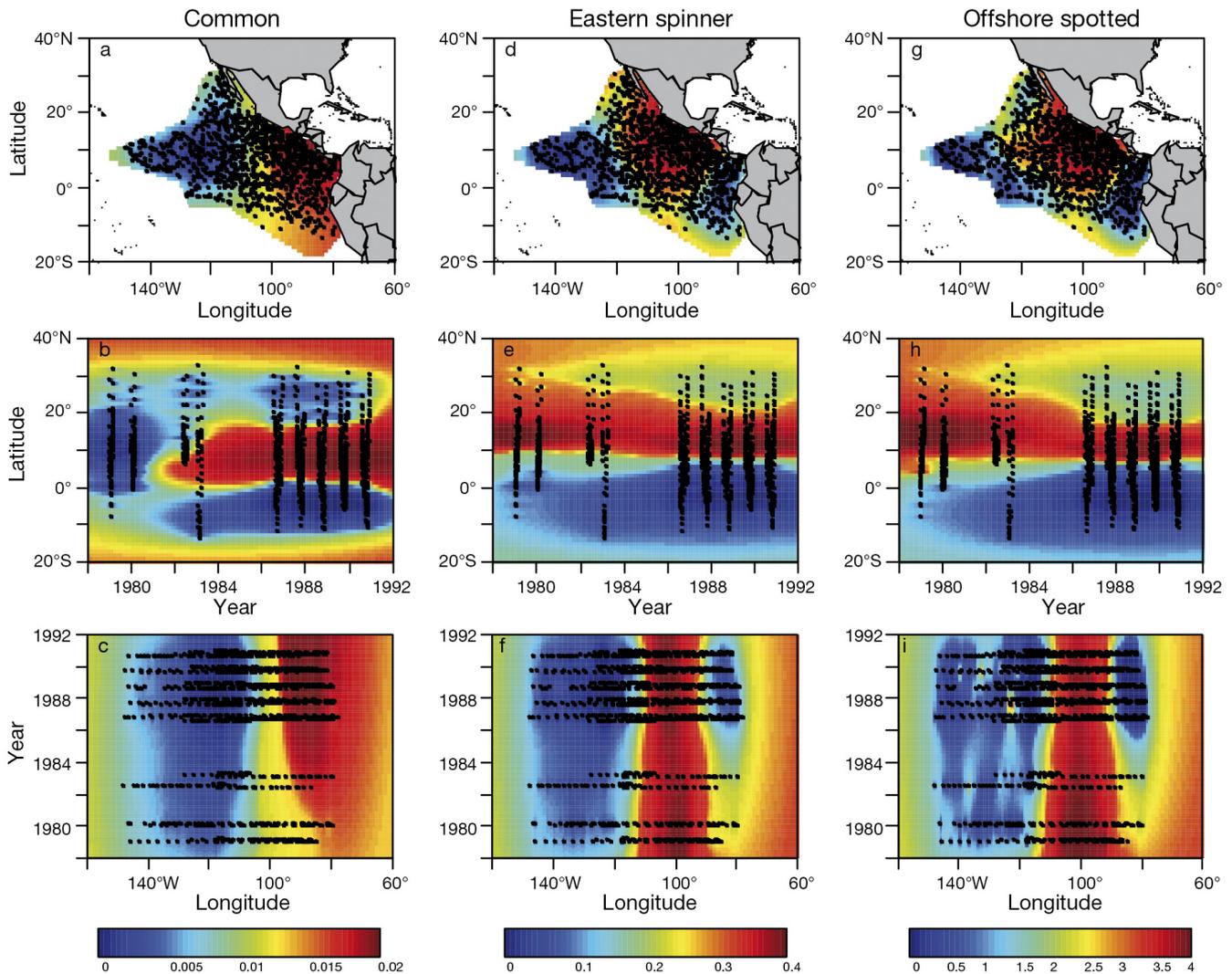


Fig. 6. *Delphinus delphis*, *Stenella longirostris* and *S. attenuata*. Inverse distance weighted smoothed distributions of exposure indices weighted by daily density for (a–c) common, (d–f) eastern spinner, and (g–i) offshore spotted dolphins. First row: spatial distribution. Second row: distribution of latitude by year. Third row: distribution of longitude by year. Values range from minimum (blue) to maximum (red) within a species (color scale for each column is given on bottom row)

ther south by the late 1980s (Fig. 6e,h). During this time frame, there is also westward shift of exposure for eastern spinners from $\sim 100^{\circ}$ to $\sim 105^{\circ}$ W (Fig. 6f), which is not as evident in the plot for offshore spotted dolphins (Fig. 6g). Additionally, exposure was relatively low for both spotted and spinner dolphins along the coasts of Colombia and Ecuador (Fig. 6d,g).

DISCUSSION

We present a new method of quantifying the exposure of dolphins to the tuna purse seine fishery using an algorithm that weights purse seine sets based on the time and distance at which they occurred, their

species composition, and a model of dolphin movement. The result is an index in which sets with more dolphins or those that occurred closer in time or space have more influence, thus measuring relatively 'recent' exposure to the fishery. The necessity for this algorithm stems from a need to estimate exposure on a finer temporal and spatial scale than has been done previously to better examine the effects of repeated chase, capture, and release.

Comparing the distribution of the number of sets in the ambit and the exposure index for each species shows that the exposure index is not a simple monotonic function of the number of sets (Fig. 7). With few sets in an ambit, exposure is limited to relatively small values. As the number of sets increases, the potential for

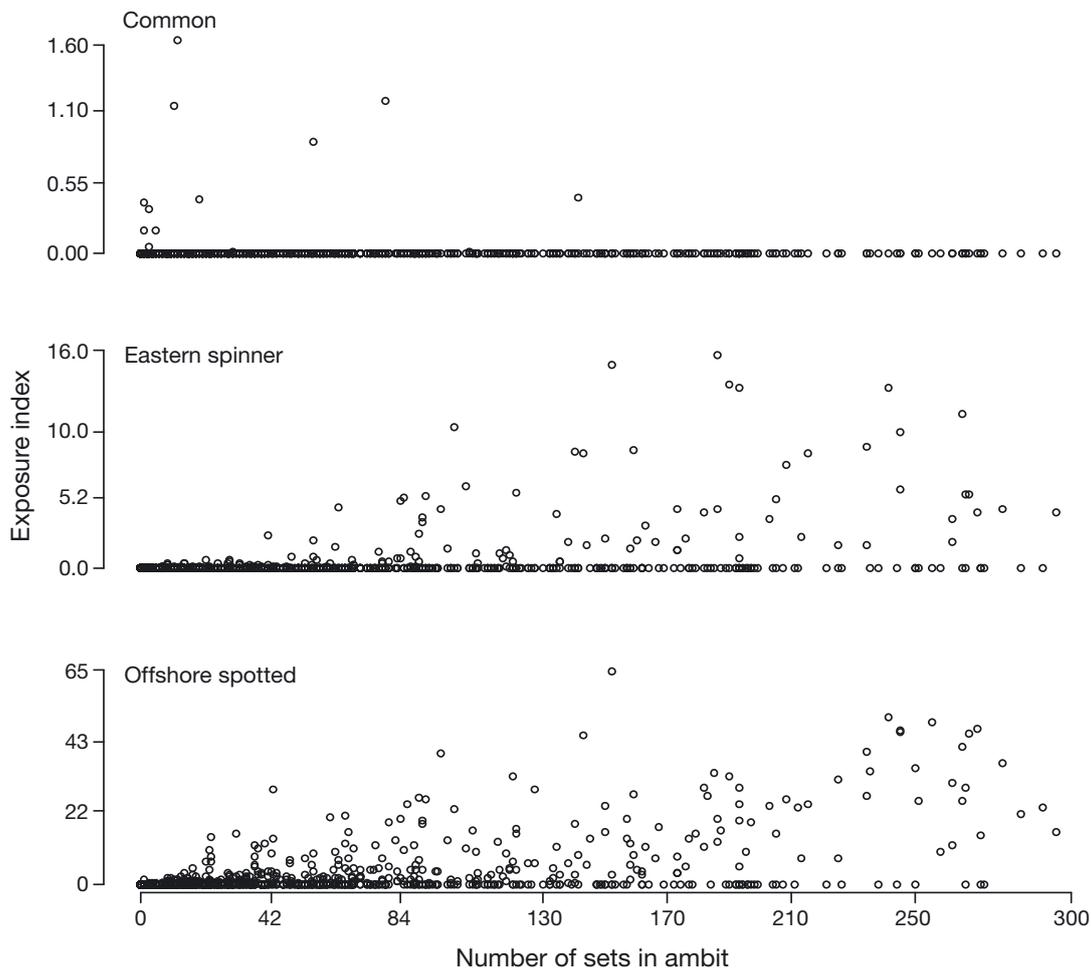


Fig. 7. *Delphinus delphis*, *Stenella longirostris* and *S. attenuata*. Relationship of exposure index to number of sets in ambit for days of survey effort

exposure also increases, but can also remain at low levels. Even with several hundred sets in the ambit, exposure can be equal or close to 0, indicating that either most of these sets occurred at a great temporal or spatial distance, or did not involve many dolphins of that particular species. The pattern seen for common dolphins reflects the fact that exposure was 0 for a large proportion of days for these species. However, although the maximum exposure for common dolphins is low relative to spotted and spinner dolphins, it is notable that days with non-0 exposure were based on relatively few sets in the ambit. This suggests that when common dolphins are set on, sets are relatively more concentrated in space and time. This result makes sense given the concentration of this species around the Costa Rica Dome, a highly productive upwelling region centered around 90° W, 10° N (Danil & Chivers 2006).

It is clear that the ETP purse seine fishery has been a significant factor in the lives of dolphins since its inception (Gosliner 1999, Reilly et al. 2005, Edwards 2007).

One of the best indicators of its impact has been the relationship between dolphin evasiveness and fishery exposure (Schramm Urrutia 1997, Heckel et al. 2000, Mesnick et al. 2002, Lennert-Cody & Scott 2005). In a review of historical observer data, Lennert-Cody & Scott (2005) showed that the ~40 yr westward and southward movement of the fishery is correlated with an increase in evasiveness of spotted and spinner dolphins. The authors hypothesized that the cumulative exposure of dolphins triggers and maintains heightened evasive behaviors. Consequently, schools of highly evasive dolphins, including those labeled 'the untouchables' by fishermen (Pryor & Norris 1978), become prevalent in regions that have been fished the longest.

These effects can also be seen over relatively short time frames. In a study of vessel response behavior of ETP dolphins during research cruises, Mesnick et al. (2002) found that the number of purse seine sets in the past 70 d and within 300 n miles of each dolphin sight-

ing is a significant predictor of whether that sighting will be evasive. However, this relationship only exists for those species frequently involved in purse seine fishing (spotted, spinner, and common dolphins). Species of other dolphins not involved in the fishery, and with varying degrees of 'natural' evasiveness, did not vary their evasive responses relative to prior fishery activity.

There is also evidence that the fishery is influencing reproduction in dolphin populations. Cramer et al. (2008) showed a significant negative relationship between the age at weaning of northeastern offshore spotted dolphins and the total number of dolphin sets made within 1 yr. The authors also suggested that previously observed differences in life history parameters between exploited and non-exploited management stocks (Perrin & Henderson 1984, Barlow 1985, Chivers & Myrick 1993) are consistent with negative impacts of the fishery on reproduction.

Each year, there are ~11 000 purse seine sets made on dolphins in the ETP (IATTC 2009). However, little is known about how frequently an individual dolphin is likely to experience a set within a year. The only empirical data available come from the 1969 to 1980 study on seasonality of dolphin movement in the ETP from which we acquired the mark-recapture data used in constructing the movement model in this paper (Perrin et al. 1979, Hedgpeth 1985). From the distribution of these recaptures, the median time to recapture was 98 d, which translates to ~3.7 captures yr⁻¹.

However, several aspects of these data prevent us from treating these values as true estimates of set frequency for spotted dolphins. Tag designs used during the majority of this experiment limited recovery to only those dolphins that were killed during sets. Thus, there is no way to account for dolphins which were tagged, set on, and released, perhaps multiple times prior to their death, introducing a positive bias in our data. Specifically, for any of the tagged dolphins that were recovered, the true time to recapture has the potential of being less, but not greater, which would increase estimates of annual capture rate.

An additional bias may occur in these data because the tags were placed on dolphins captured as a result of routine fishing activities. Consequently, these results may not be applicable to the 'average' dolphin because they do not take into account the probability of being captured in the first place, which likely varies both temporally and spatially. To accurately model movement for the entire population, data would have to be randomly collected across the range of the stocks in question, both from dolphins set on as well as those not involved in sets.

It should be noted that the exposure index that we have presented also does not allow one to estimate

actual set frequency. To convert it to set frequency, one would need some ground-truth data that would permit the correlation of the index with a known capture history. The advance that our method makes over other studies in the past is that it permits the calculation of a relative measure of set exposure for individual sightings of dolphins rather than aggregate measures over long time frames. As we have demonstrated here, this permits the examination of exposure on finer spatial and temporal scales than before.

While the spatial and temporal patterns of exposure agree with other analyses of these species during the same time frame (Lennert-Cody & Scott 2005), the analysis presented here using the NMFS observers set database is only intended as an example of how the exposure index can be employed. Because the data in the NMFS database represent from 1 to 48% of all purse seine sets made on dolphins between 1971 and 1990 (Edwards 1989, IATTC 2009), it is not considered complete and may not fully reflect the true patterns and intensity of the ETP tuna fishery. During these years, especially after the mid-1980s, fishing by vessels from other nations, primarily Mexico, was increasing. Over the past couple of decades, this international fleet has progressively moved from nearshore central Mexico to offshore regions to the south and west (Lennert-Cody & Scott 2005). A comprehensive spatial and temporal analysis following the template we have outlined would require data on the location and time of non-US observed sets from the IATTC observer and logbook databases, which were unavailable to us at the time of this writing.

Several components of our model of dolphin movement could be improved if more data become available. Our model is essentially 1-dimensional because it assumes that directionality of travel is random (with the exception of coastal waters). Perrin et al. (1979) found that movement <300 n miles was essentially random, while movements >300 n miles tended to be along an east-west axis, although sample sizes at these distances were low. Thus, it is unlikely that there is significant directional movement on the time scale that we are interested in. However, it may be possible to address potential spatial heterogeneity by integrating this model with models designed to predict dolphin density based on habitat variables (Barlow et al. 2009).

Finally, it should be noted that the movement data available to us were primarily collected from northeastern and southern/western offshore spotted dolphins. Movement patterns of individuals in stocks of other species are likely to differ. For example, from their series of tagging and radio-tracking studies, Perrin (1975) and Perrin et al. (1979) suggested that eastern spinner dolphins exhibit less net movement than offshore spotted dolphins. Thus, a stock-specific model

would require collecting sufficient movement data from each stock separately or exploring using habitat-density models as mentioned above.

Although this index has been explicitly developed for estimating the exposure of dolphins to the ETP tuna purse seine fishery, the basic algorithm can easily be modified to examine the exposure of cetaceans to a variety of other events. For example, the effects of anthropogenic noise on cetaceans have been receiving an increased amount of interest in recent years (Romano et al. 2004, Cox et al. 2006, Nowacek et al. 2007). By collecting the location and times of the sound sources of interest and constructing a movement model for the species in question, one could assess the cumulative impact of repeated sounds on populations over a period of time and examine physiological or behavioral correlates in sampled individuals. Similarly, one could extend this kind of analysis to estimate exposure to other anthropogenic sources which may be stationary in space, but vary in time, such as pollution outflows, spills, or interactions with static fishing gear.

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