Capture rate as a function of school size in pantropical spotted dolphins, *Stenella attenuata*, in the eastern tropical Pacific Ocean

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Abstract.–The frequency with which dolphins from the northeastern offshore stock of the pantropical spotted dolphin, *Stenella attenuata*, experience chase and capture by tuna purse-seiners in the eastern topical Pacific Ocean was estimated by comparing dolphin school-size frequencies in sighting data from research vessel observer records, with those recorded in set data by tuna vessel observers. The objective of the study was to provide a preliminary basis for estimating stock-wide effects of fishery-induced disturbance in these dolphins.

Our analyses indicate two major characteristics for this stock: first, capture frequency appears to increase rapidly with increasing school size, and second, approximately half of the stock at any given time occurs in schools smaller than those apparently preferred by purse-seiners. This implies that if individual dolphins have a preference for associating with schools of a particular size, then individuals associating primarily with large schools would be subjected to chase and capture much more frequently than those associating with small schools. However, because the largest schools are relatively rare and account for a small percentage of individuals, the majority of dolphins in the stock would experience relatively few captures per year, although some would experience a high rate. It is not known whether dolphins do indeed exhibit such a preference, or if instead individuals associate with schools from a wide range of sizes at different times.

Schools of 1000 or more dolphins are estimated to be set on approximately once a week each on average, but such schools are estimated to represent just under one tenth of the animals in the northeastern offshore stock. Schools set on most often by tuna purse-seiners, containing from about 250 to 500 dolphins, are estimated to be set on between two and eight times each per year and are estimated to include approximately one third of the stock. An estimated one half of the stock occurs in schools smaller than 250 animals; schools of this size are estimated to be set on less than twice per year each.

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Tuna fishermen in the eastern tropical Pacific Ocean (ETP) commonly catch large yellowfin tuna (*Thunnus albacares*) by locating a school of dolphins visually and then surrounding it with a large purse-seine net in order to capture the tuna that are often closely associated with ETP dolphin schools. The dolphins are released from the net and the tuna are then loaded aboard (NRC, 1992). This method, known as "fishing on dolphin," historically has been a significant cause of dolphin mortality (NRC, 1992) but has also recently been suggested as a significant cause of fishery-related physiological stress in the dolphins involved, perhaps to the point of causing unobserved mortality or changes in reproductive success (e.g. Myrick and Perkins, 1995).

Although it has not been possible to measure physiological stress directly in these dolphins, it is possible to use existing data to estimate how often an animal experiences chase and capture. Capture frequency provides at least a rough measure of the amount of fishery-induced disturbance that dolphins affected by the ETP tuna fishery experience. Here, we estimate capture frequency for the northeastern offshore stock of the pantropical spotted dolphin (*Stenella attenuata*) (Dizon et al., 1992). This is the species most commonly associated with tuna and historically most often used in fishing on dolphin (greater than 70% of dolphin sets annually for about the last 30 years (e.g. IATTC[1]).

A simple calculation (see "Discussion" section) leads to a rough estimate for the mean number of times an individual dolphin is set on per year of (number of dolphins set on) ÷ (number of dolphins) ≈ 8 times per year. However, simply knowing the overall average rate of capture is not sufficient to evaluate the potential adverse effects on individuals because the rate for different animals may vary widely, depending on a number of interrelated factors including school size, geographic location, time of year, and the amount of tuna associated with a school. In this paper, we investigate the effects of school size. Specifically, we show that large dolphin schools (more than several hundred animals) are much more likely to be captured than are small schools (less than one hundred animals) because of a tendency for fishermen to concentrate their effort on larger schools, which tend to carry more tuna, and to virtually ignore smaller ones. However, this result does not directly give the capture rate for an

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[1] IATTC. 1992. Annual report: 1990. Inter-American Tropical Tuna Commission, La Jolla, CA, 261 p.

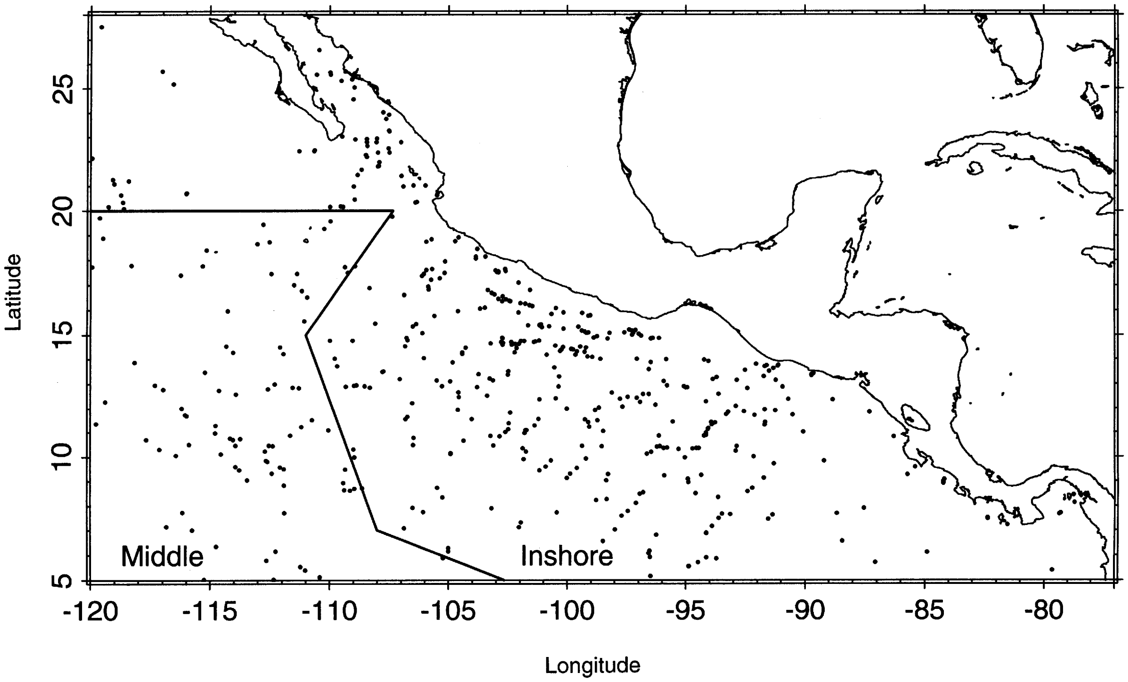

Figure 1

Geographic stock boundaries for the northeastern offshore stock of the pantropical spotted dolphin (*Stenella attenuata*). The stock is defined by the region in the ETP north and east of 5°N and 120°W, bounded at 28°N. The two strata pictured are based on those defined by Holt et al. (1987). The inshore and middle strata have total areas of 4,544,000 km^2 and 2,019,000 km^2, respectively. Points represent on-effort sightings from the research vessels, 1986–90 and 1992–93.

individual dolphin because animals may associate with schools of different sizes at different times. We consider implications for individual dolphins in the "Discussion" section.

Data and methods

To quantify the tendency for purse-seiners to set on large schools, we compared the relative frequency with which different sizes of schools are selected by fishermen for encirclement with the relative frequency with which schools of various sizes occur naturally. First, we estimated the probability distribution of sizes for spotted dolphin schools within the geographic boundaries of the northeast (NE) offshore stock[2] (Fig. 1), using observations from research vessels. This distribution models the relative number of schools of each size in the study area. Then we fitted a smooth probability distribution to dolphin school sizes from tuna vessel sets. This distribution models the relative number of times schools of each size were set on. Finally, we used the ratio of the two estimated density functions, suitably scaled, to estimate the average number of times per year a dolphin school of a given size was set on. This estimated effect includes not only the tendency of fishermen to preferentially set on larger schools, but also any tendency to search in areas where large schools may be more prevalent.

Research vessel sighting data

In 1986, the U.S. National Marine Fisheries Service (NMFS) initiated a multiyear research program to monitor trends in the abundance of dolphin populations in the ETP. The program used research vessels to conduct line transect surveys in the ETP and record sightings of all cetaceans encountered (Wade and Gerrodette, 1993). The surveys were designed to provide a spatially unbiased sample of the survey area and to be as similar as possible across years. Typically, three independent observers estimated school size and species composition for each sighting. For detailed descriptions of the survey design, materials, and methods, see Holt et al. (1987), Hill et al. (1991), and Mangels and Gerrodette (1994).

The research vessel data used in this study consisted of spotted dolphin school sightings from the

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[2] Coastal and NE Offshore stocks of the pantropical spotted dolphin exist sympatrically: however, schools are for the most part distinguishable.

Table 1

Summary of research vessel data by year and stratum. Search effort is defined as the distance travelled along the trackline as observers actively search during a sea state of Beaufort 5 or less. Sighting rate is defined as the number of northeastern offshore spotted dolphin schools sighted on-effort, within 5.5 km of the ship's trackline, per 1000 km of search effort. Middle and inshore strata are defined in Figure 1.

	Inshore stratum		Middle stratum		Pooled	
Year	Search effort (km)	Sighting rate	Search effort (km)	Sighting rate	Search effort (km)	Sighting rate
1986	9260	6.26	3457	4.92	12,716	5.90
1987	8523	7.27	4322	5.09	12,845	6.54
1988	6303	6.98	3371	3.26	9674	5.69
1989	8375	9.67	3996	4.00	12,371	7.84
1990	7036	8.10	4744	3.79	11,780	6.37
1992	10,189	5.99	0	—	10,189	5.99
1993	7953	6.29	584	3.42	8537	6.09

1986–90 and 1992–93 marine mammal surveys (Table 1). These seven surveys each occurred between 28 July and 10 December, referred to here as the "study period." We used sightings only from search effort within the NE offshore stock boundaries, for which observers were actively searching ("on-effort") and for which Beaufort sea state was 5 or below. We excluded sightings farther than 5.5 km from the trackline because school size estimates were generally unreliable for such distant schools. A total of 499 sightings were included in this study.

The median estimated school size was 106 dolphins; 48% of the estimates were less than 100, and only 1% greater than or equal to 1000 (Fig. 2A). These quantities are not corrected for size selection bias (see "Statistical model" section). The true distribution of school sizes was estimated to include a larger percentage of small schools.

Tuna vessel set data

Since the late 1970s, the Inter-American Tropical Tuna Commission (IATTC) and NMFS have placed trained observers aboard a significant percentage of ETP tuna purse-seiner vessels larger than 400 tons capacity. A single observer is placed aboard a vessel when a trip is selected for observation. These observers collect data on the dolphins with which commercial species of tuna in the ETP commonly associate, and monitor dolphin mortality due to purse-seine fishing operations. For a more detailed description of the observation programs, see IATTC (1989), IATTC,[1] or Jackson (1993).

Detailed observer data were available from tuna sets made by U.S. vessels. From these data, we used observer estimates of school size and species composition from spotted dolphin schools set on by tuna vessels within the NE offshore stock boundaries and during the study period for the years 1986–90. We used the observer's final "best" estimates, made after the set, which included counts of any animals that evaded or were cut out of net encirclement[3] (IATTC, 1991; NMFS, 1992). The tuna vessel data used here included only schools that were actually set on, and not observations of schools that were sighted but not set on. We assumed that there was no "observer effect" on a captain's choice of schools to be set on. A total of 3454 set observations were included in this study (Table 2).

The tuna vessel set data represent about 77% of the search effort during the study period for the U.S. purse-seine fleet (29 to 40 vessels during the years 1986–90). To increase search efficiency, tuna vessels often travel at 15 knots, and crews use helicopters and communicate in "code groups" (Orbach, 1977) in addition to searching with binoculars from the ship. Not all schools that are sighted are set upon, and thus the observed sets represent a much larger effective sample size in terms of sightings, and the "missing" schools tend to be small. The median estimated size of schools that were set upon was 560 dolphins. Only 4% of the estimates were less than 100, whereas 26% were greater than or equal to 1,000 (Fig. 2B).

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[3] Using the pre-encirclement school size means that although we are estimating the rate at which schools of a given size were set on, it is likely that some dolphins involved in a given set were chased by the tuna vessel and its speedboats but not actually encircled by the purse-seine net. For the purposes of estimating numbers of sets as a measure of adverse impact, we do not distinguish chase from capture.

Data from individual sets made by non-U.S. vessels were not available; however, count data summarizing observed numbers of sets and trips made by all vessels were available. From these data, we used the numbers of sets on the target stock observed each year, by both U.S. and non-U.S. vessels, during the study period and for the entire year (Table 2). Additionally, the total annual number of fishing trips that involved sets on dolphins has been estimated each year from tuna vessel logbook data (e.g. IATTC[1]). Dividing the annual number of observed trips by the annual total number of trips gives the annual trip sampling fraction ("coverage"), which we took as known exactly. We further assumed that observer coverage was constant throughout the year and took the sampling fractions as applicable for the study period as well as the entire year.

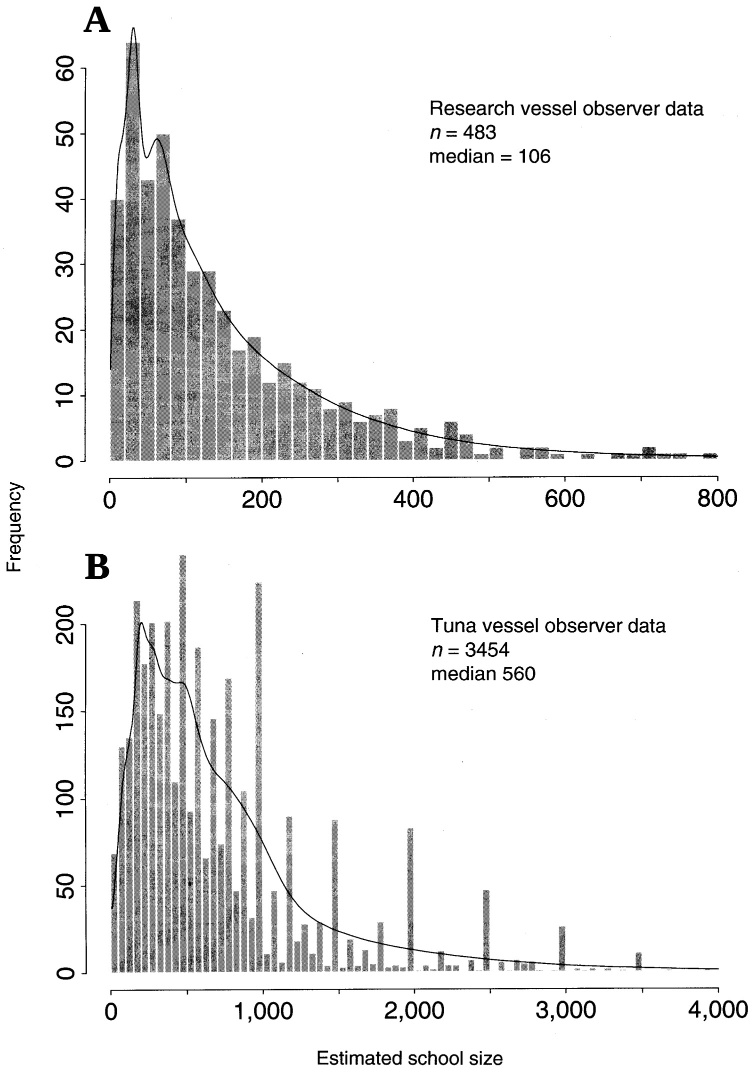

Figure 2

Estimated observed school sizes for northeastern offshore spotted dolphins. These data include observations from both geographic strata. The fitted lines are kernel density estimates (see text) for these observations. Note the different x- and y-axis scalings. (**A**) Research vessel sightings, 1986–90 and 1992–93. These data are the mean observer estimates and are not corrected for size selection bias (see text). They include on-effort sightings with perpendicular distance <5.5 km; 8 observations >800 are not shown. (**B**) Tuna vessel sets, 1986–90; 19 observations >4000 not shown.

Statistical model

We modeled the true population of NE offshore spotted dolphin schools within the stock boundaries as an independent identically distributed (i.i.d.) sample of unknown size from a hypothetical infinite superpopulation of schools having a smooth probability density for their school sizes. To characterize the true population of school sizes, both the total number of schools, $N_{schools}$, and the probability density from which their school sizes were drawn, $\pi(s)$, needed to be estimated. Although school size is really a discrete quantity, we approximated it using a continuous-valued random variate.

Dolphin school sightings are made from visual clues such as surface disturbances or associated bird flocks, and larger schools in general provide a more visible target. Thus, the sighting probability for schools at a given range depends on school size, leading to a selection bias (relative to $\pi(s)$) towards larger schools in the research vessel observations. We modeled these observations as a biased sample of size $n_{schools}$ from the true population. Because the ships' tracklines were random with respect to the dolphin population, we assumed that there were no other selection biases. We denoted the probability density of observed school sizes by $\pi^*(s)$ to distinguish it from $\pi(s)$, and note that

$$\pi(s) = \frac{w_{eff}}{w_{eff}(s)} \pi^*(s),$$

where $w_{eff}(s)$ = the line transect effective strip halfwidth for schools of size s ; and
w_{eff} = the size-averaged effective strip halfwidth (Appendix D in Burnham et al., 1980).

Table 2

Summary of tuna vessel data by fleet, year, and stratum. Coverage is defined as the percentage of fishing trips, involving sets on dolphins by vessels over 400 tons, that carried a scientific observer. Coverages and annual numbers of trips are taken from IATTC Annual Reports (e.g. IATTC, see Footnote 1 in main text). Observed sets per trip is defined as the mean number of observed sets on northeastern offshore spotted dolphin schools for trips that involved sets on dolphins. Middle and inshore strata are defined in Figure 1.

			Observed sets per trip 28 Jul–10 Dec ("study period")				Observed sets per trip annual			
Fleet	Year	Coverage	Trips	Inshore	Middle	Pooled	Trips	Inshore	Middle	Pooled
U.S.	1986	41.7	25	9.60	1.96	11.6	43	14.4	4.53	18.9
	1987	91.5	61	17.3	5.25	22.6	119	21.9	6.89	28.8
	1988	57.6	33	13.7	4.88	18.6	76	13.0	4.86	17.9
	1989	99.1	50	14.9	3.66	18.6	115	15.3	3.77	19.1
	1990	100.0	14	16.3	3.21	19.5	73	12.3	3.62	15.9
	Total	76.9	183	14.9	4.14	19.0	426	16.2	4.88	21.1
Intl.	1986	25.3	29	12.3	2.90	15.2	68	14.9	2.84	17.7
	1987	28.3	44	15.8	0.409	16.2	82	17.9	0.988	18.9
	1988	35.8	54	8.70	3.52	12.2	111	10.3	3.87	14.2
	1989	37.0	57	13.6	2.61	16.2	141	13.3	2.41	15.7
	1990	42.0	66	8.35	6.92	15.3	147	12.3	4.77	17.1
	Total	34.3	250	11.4	3.60	15.0	549	13.3	3.18	16.5

Both $w_{eff}(s)$ and w_{eff} depend upon the data truncation distance (Burnham et al., 1980), denoted by w and equal to 5.5 km in this analysis. $\pi^*(s)$ was estimated from the observed school sizes. However, to estimate $\pi(s)$, we also needed to estimate $w_{eff}(s)$, as described in "Estimation" section.

Anecdotal reports consistently imply that tuna vessel captains do not search for or set on dolphin schools at random when fishing on dolphin in the ETP. Because larger dolphin schools are observed to carry more tuna, they are presumably sought out and set upon preferentially, and the set data would have a selection bias towards large schools. We modeled the schools associated with purse-seine sets (both observed and unobserved) as a biased sample, with replacement, of unknown size from the true population of schools. To characterize these schools, both the total number of sets, N_{sets}, and the effective probability density from which their sizes were drawn, $p(s)$, needed to be estimated. $p(s)$ represents the superposition of the tuna fishermen's school-size selection preference upon $\pi(s)$. Sizes were recorded for all sets on trips carrying observers, and therefore there was no additional observer selection bias (in relation to $p(s)$). Assuming a random selection of trips, we treated the observed sets as an unbiased subsample of size n_{sets} and estimated $p(s)$ directly from the observed sizes. There was some concern with serial correlation between sets (see "Independence of observations" section).

Because the number of dolphin schools is not constant over time, we interpreted $N_{schools}$ as the time-averaged expected number of schools, and in particular did not use a finite population estimator. Similarly, we interpreted N_{sets} as the expected number of sets rather than making finite population estimates of the actual realized number of sets.[4]

Estimation

U.S. vessels—study period The observed school-size distributions from both the research vessel sighting data and from the tuna vessel set data were roughly lognormal in shape (Fig. 2). We estimated $\pi^*(s)$ and $p(s)$ using an adaptive kernel density estimator on the logs of the observed school sizes and then transformed the estimated density back to the original scale (Silverman, 1986). This variable bandwidth algorithm was chosen in order to make reasonable density estimates in the right tails where there were few data, while not oversmoothing near the modes. We chose the bandwidth scaling parameters as a trade-off between smoothness and fit to the data. We treated the observer estimates (mean estimates in the case of research vessel data) as exact measure-

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[4] Technical details and a discussion of our estimators for $N_{schools}$ and N_{sets} can be found in Perkins, P. C., and E. F. Edwards, 1997, SWFSC Admin. Rep. LJ-97-03, Southwest Fisheries Science Center, La Jolla CA, 36 p.

ments and did not attempt to correct for the possibility of size estimation biases in either data set (see "Discussion" section) or use a deconvolution kernel to account for estimation variance.

Our estimates of $w_{eff}(s)$ were based on modelling the inherent selection bias in the research vessel sighting data. We used a bivariate hazard-rate detection function in a size-dependent line transect analysis of the perpendicular sighting distances and sizes of the observed schools (Drummer and McDonald, 1987; Palka, 1993). Perpendicular distances were binned to reduce the effect of rounding in the data. School sizes were not binned because we did not use a parametric model for their distribution.

We define the average capture frequency for a school of size s as

$$N_{capture}(s) = \frac{N_{sets}(s)}{N_{schools}(s)} = \frac{N_{sets}\,p(s)}{N_{schools}\,\pi(s)}.$$

Setting the observed counts $n_{schools}$ and n_{sets} equal to their expectation gives

$$n_{schools} \approx E\left[n_{schools}\right] = \left(\frac{2Lw_{eff}}{A}\right) N_{schools} \text{ and}$$
$$n_{sets} \approx E\left[n_{sets}\right] = f_{trips} N_{sets},$$

where L = the total distance searched by the research vessels;

A = the total area within the stock boundaries; and

f_{trips} = the fraction of tuna vessel trips that carried an observer.

Using the relationship between $\pi(s)$ and $\pi^*(s)$, and these moment equations for $n_{schools}$ and n_{sets}, we estimated the capture frequency for a school of size s as

$$\hat{N}_{capture}(s) = \frac{n_{sets}}{f_{trips}} \frac{2L\hat{w}_{eff}}{An_{schools}} \frac{\hat{p}(s)}{\hat{\pi}^*(s)}.$$

Note that the factor w_{eff} cancels out and only $w_{eff}(s)$ remains.

Because there were so few schools smaller than 100 animals set on by tuna vessels, and so few schools larger than 1000 animals sighted from research vessels, we restricted our analysis to schools from 100 to 1000 animals, and computed estimates of capture frequency at intervals of 100 animals.

Stratification and pooling There were many school size data from tuna vessel sets (n_{sets}=3454), however, there were far fewer research vessel sighting data ($n_{schools}$ = 499) and these had an uneven spatial distribution. We decided that research vessel sightings were too sparse to stratify our estimates of $\pi^*(s)$ and $w_{eff}(s)$ geographically. We did make stratified estimates of $p(s)$, but this had very little effect in absolute terms on the estimates of capture frequency, and so we present only pooled estimates for simplicity.

Similarly, we did not stratify by year in any of our estimates. Set data, trip sampling fractions, sighting data, and search effort were combined to make a single estimate of the average N_{sets} and $N_{schools}$ over all years.

Extrapolation to the international fleet and to annual estimates Data from individual sets came only from U.S. tuna vessels, so that estimating capture frequency due to the entire fleet required extrapolation. We made the assumption that a captain's preference for dolphin school sizes upon which to make sets did not vary with the vessel's country of origin and thus extrapolated our estimate of $p(s)$ to the entire fleet. Our estimates of total numbers of target sets were based on separate observed counts and sampling fractions for the U.S. and the international fleets,

$$\hat{N}_{sets} = \hat{N}_{sets}^{(US)} + \hat{N}_{sets}^{(Intl)} = \frac{n_{sets}^{(US)}}{f_{trips}^{(US)}} + \frac{n_{sets}^{(Intl)}}{f_{trips}^{(Intl)}}.$$

This expression was substituted in for (n_{sets} / f_{trips}) in our estimates of capture frequency for the combined fleet. For non-U.S. vessels, we had only the total number of target sets observed, and we were unable to estimate the variance in $\hat{N}_{sets}^{(Intl)}$. Thus, our estimates for the combined fleet do not include estimates of precision.

Our estimates of capture frequency are strictly valid only for the study period. However, if we assume that the same patterns in school sizes and captain's preference for school sizes hold for the entire year, then the annual capture frequency can be estimated by using the corresponding annual set counts for U.S. and non-U.S. vessels. Because we had only the total number of target sets observed during times other than the study period, our estimates of annual capture frequency do not include estimates of standard error.

Independence of observations

Because of the geographically correlated nature of consecutive research vessel sightings or tuna vessel sets, successive school size observations from a single vessel may not have been independent. This is particularly a concern for the set data, because of the possibility of repeated sets on the same school (see

"Discussion" section). Although dependence does not add a bias to our estimates, it does decrease the effective sample size, which affects our estimates of precision. We accounted for this problem by using bootstrap standard error estimates, and by defining our bootstrap resampling units so as to make them as independent as possible while keeping a reasonably large sample size. For research vessel data, we took days as the resampling unit; for tuna vessels, we resampled by trips. For each bootstrap iteration, we resampled from the research vessel data to achieve approximately the same amount of search effort in each stratum as was actually achieved. We resampled from the tuna vessel data to achieve exactly the actual observed number of trips.

Results

Estimated distribution of school sizes

Figure 2 shows the kernel estimates of the densities $\pi^*(s)$ and $p(s)$. Both estimated densities were much smoother at large school sizes than at small school sizes. This is partially due to the variable bandwidth in the kernel estimator, but primarily due to the data themselves.

Estimated effective strip halfwidth

Figure 3 shows the estimated values for the effective strip halfwidth as a function of school size. Because $\pi^*(s) \propto w_{eff}(s)\pi(s)$, $w_{eff}(s)$ represents the relative amount of "thinning" for schools of different sizes, i.e. $w_{eff}(s)/w$ is the probability of a school of size s being detected from the research vessel, given that it is within the truncation distance w. The estimated values indicate that approximately one third of schools of size 100 within the truncation distance (5.5 km) were missed by the research vessel observers, and essentially all schools of size 1000 were detected. The result shown in Figure 3 is, qualitatively at least, partially constrained by the bivariate line transect model, i.e. if the data indicate dependence of detectability upon school size, then the parametric form for $w_{eff}(s)$ dictates that the estimated curve must vary smoothly and monotonically with size and must approach w asymptotically. However, the model fit need not have any dependence on school size, and the specific direction and rate of increase shown in Figure 3 are due to the data, and agree with observer experience in terms of reaching the limiting value within the range of sizes shown.

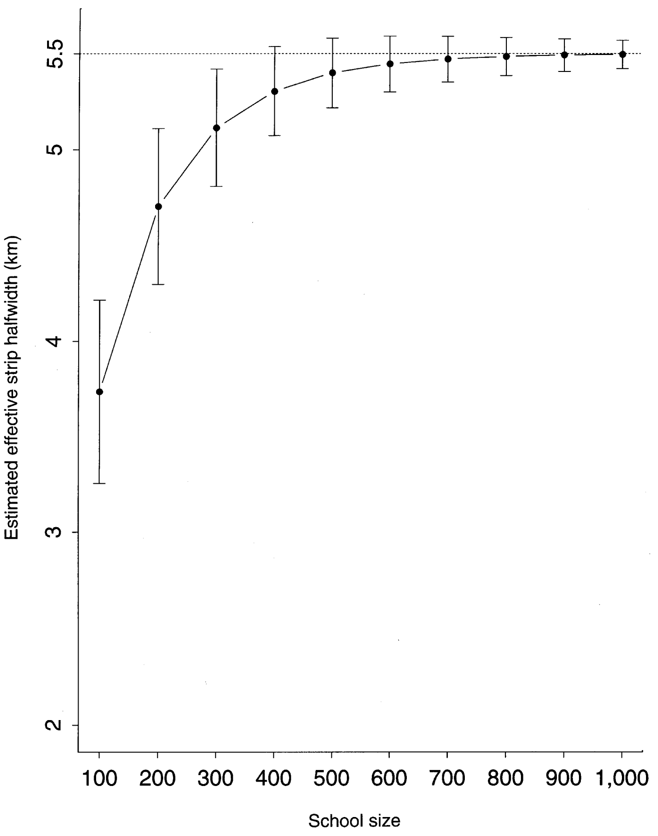

Figure 3

Estimated effective strip halfwidth as a function of dolphin school size. These maximum likelihood estimates are from the bivariate hazard rate line transect model as discussed in the text, and are based on northeastern offshore spotted dolphin school sightings from observers aboard NMFS research vessels during the months July to December, 1986–90 and 1992–92. Error bars indicate plus or minus one standard error and should not be interpreted as confidence intervals. The horizontal line at 5.5 km indicates the perpendicular truncation distance in the line transect model.

The standard error bars in Figure 3 exceed w in some cases, although it is not possible for $w_{eff}(s)$ to exceed the truncation distance w. These error bars are presented simply to represent the estimated precision for each estimate, and should not be interpreted as confidence intervals. Confidence intervals for the estimated halfwidths would tend to be asymmetric and would not exceed the truncation distance.

Estimated capture frequency

Figure 4 shows the estimated capture frequency due to U.S. tuna vessels. These estimates represent the average number of times a school of a given size was set on each year during the study period. The estimates are an integration of the information presented in Figure 2 and Figure 3, i.e.

$$\hat{N}_{capture}(s) \propto \hat{w}_{eff}(s)\hat{p}(s)/\hat{\pi}^*(s),$$

scaled by a suitable estimate of the overall average capture frequency. The magnitude and direction of the trend in $\hat{N}_{capture}$ was almost entirely due to the estimates of $p(s)$ and $\pi^*(s)$. Estimates of the factor $w_{eff}(s)$ varied only by about 50% over the range of sizes considered, whereas the estimated ratio of $p(s)$ to $\pi^*(s)$ varied by two orders of magnitude.

The precisions of our estimates of capture frequency depended on the precisions of the individual estimated factors involved in $\hat{N}_{capture}(s)$. We were able to estimate those different precisions using the output of the bootstrap procedure and found that they varied widely. Much of the variability was in our estimates of $\pi^*(s)$, with bootstrap estimates of CV ranging from 9% at a school size of 100 up to 24% at 1000. Bootstrap CVs for $\hat{w}_{eff}(s)$ were low, ranging from 13% down to 1%, but, as mentioned above, $w_{eff}(s)$ was the factor most constrained by the model. Bootstrap CV's for $\hat{p}(s)$ were lower than those for $\hat{\pi}^*(s)$, ranging from 14% at a school size 100 down to 6% at 1000. Set counts and sighting counts both had bootstrap CV's of approximately 6.5%.

Figure 5 shows the estimated annual capture frequencies due to the U.S. fleet and due to the combined U.S. and international fleet. The estimate of the combined capture frequency for schools of size 1000 is 36.1 sets per year, or one set every 10 days, compared with well under once a year for schools of 100 animals. The estimate for the median school size set on (560 animals) was 10.1 sets per year, or just under once per month. The U.S. fleet accounted for an estimated 31% of sets during the years 1986–90. Although we were not able to estimate standard errors in these annual estimates, the error bars in Figure 4 should give at least a rough idea of the potential precision.

Because of the extrapolation of school-size distributions necessary to make annual and combined fleet estimates, the two curves in Figure 5 are identical in shape to that in Figure 4, but have different scale factors. The scale factor for the lower curve was an estimate of the overall (size-averaged) annual capture frequency, $N_{sets}/N_{schools}$, due to the U.S. fleet, whereas the scale factor for the upper curve was the corresponding estimate for the combined fleets. These two overall capture frequency estimates were not extrapolated from data collected during the study period, but were based on annual set counts for the two fleets.

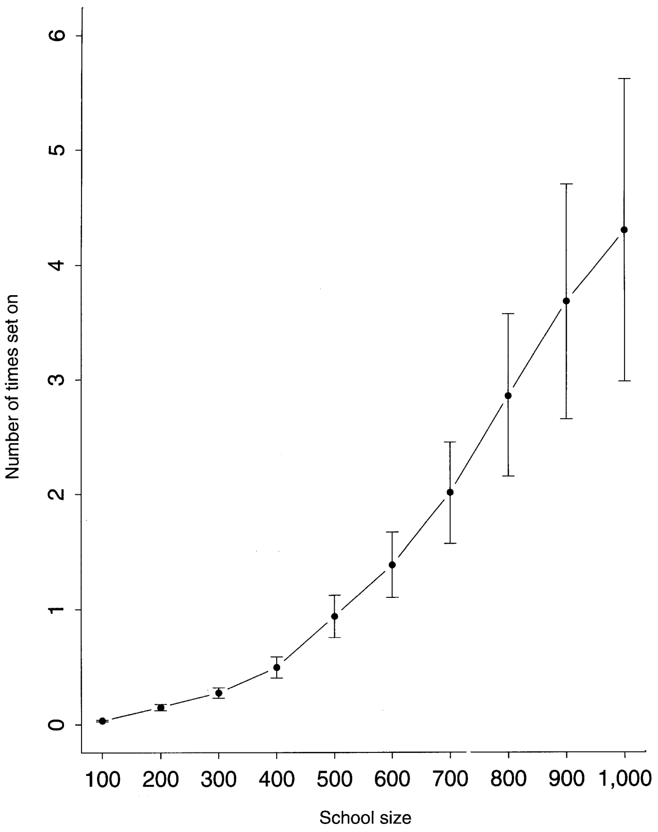

Figure 4

Estimated capture frequency as a function of dolphin school size, for schools of northeastern offshore spotted dolphins. The estimates are of the average number of times a school was set on each year by U.S. tuna purse-seiners, between 28 July and 10 December (19.4 weeks), for the years 1986–90. Error bars indicate plus or minus one standard error and should not be interpreted as confidence intervals.

Using the estimated school sizes from the sighting data, and weighting by the estimated effective strip width, $w_{eff}(s)$, we estimated the cumulative percentage of individual dolphins in schools greater than or equal to a given size, i.e.

$$H(s) \equiv \Pr\{\text{a dolphin is in a school of size} \geq s\}$$

$$= \int_s^\infty t\pi(t)dt \Big/ \int_0^\infty t\pi(t)dt$$

$$\hat{H}(s) = \frac{\sum_i s_i \hat{w}_{eff}(s_i) I\{s_i \geq s\}}{\sum_i s_i \hat{w}_{eff}(s_i)},$$

$$\text{where } I\{s_i \geq s\} = \begin{cases} 1, & \text{if } s_i \geq s \\ 0, & \text{otherwise} \end{cases}$$

and the sums are over research vessel sightings.

Combining $\hat{H}(s)$ with the combined-fleet capture frequency estimates (Fig. 5, upper curve), schools of 1000 animals or greater were estimated to be set on at least once every ten days and contained an estimated 9% of dolphins (Fig. 6). Schools set on most often by tuna purse-seiners, containing from about 250 to 500 dolphins, were estimated to be set on between 2 and 8 times each per year on average; these schools represented just under an estimated one third of the stock. An estimated one half of NE offshore spotted dolphins occurred in schools smaller than 250 animals; schools of this size were estimated to be set on less than twice per year each.

We note that $H(s)$ should not be used to quantify the school size preferences of individual dolphins. For example, although we estimated that schools larger than 1000 animals contained an estimated 9% of dolphins at any given time, this does not imply that the same 9% of dolphins always made up such schools.

Capture frequency for very large schools

Although no kernel estimate of $\pi(s)$ was possible for s greater than 1000 animals, the estimated detection probability for those schools was essentially one out to the truncation distance w, making a rough calculation for capture frequency possible. Because of the rounding tendency of tuna vessel observers, we made an estimate for schools greater than or equal to 1000. With the assumption that the effective strip halfwidth is equal to the truncation distance, an estimate of the average capture frequency due to the entire fleet is

$$\hat{N}_{capture}(s \ge 1000) = \frac{\hat{N}^{(large)}_{sets}}{\hat{N}^{(large)}_{schools}} = \frac{n^{(US,large)}_{sets}}{n^{(US)}_{sets}} \left(\frac{n^{(US)}_{sets}}{f^{(US)}_{trips}} + \frac{n^{(Intl)}_{sets}}{f^{(Intl)}_{trips}} \right) \frac{2Lw}{An^{(large)}_{schools}} .$$

The estimated average capture frequency for these very large schools was 51.3 sets per year, or just under once a week.

Discussion

Capture rates for individual dolphins

To interpret these capture frequency results in terms of individual dolphins, we must consider the size range of the schools with which a given individual tends to associate. If one assumes that dolphins have a strong fidelity for a characteristic school size, then the above results indicate that a fixed but relatively small percentage of the dolphin population was consistently subjected to a high rate of capture in purse-seine nets, whereas the majority of dolphins were subject to relatively little disturbance from the fishery. However, little is known about the spatial and temporal dynamics of dolphin schools and their sizes, and a range of other assumptions are possible.

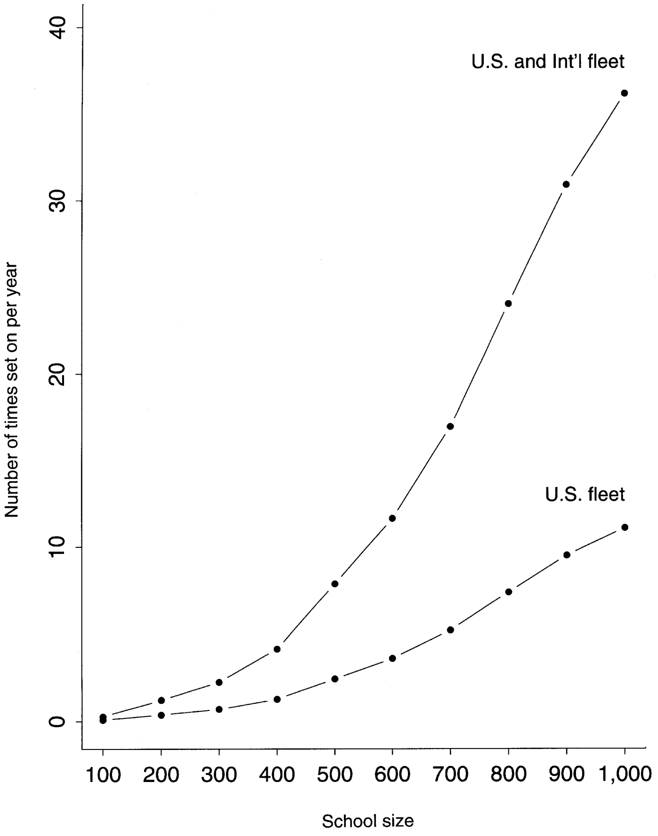

Figure 5

Estimated annual capture frequency as a function of dolphin school size for schools of northeastern offshore spotted dolphins. The estimates are of the average number of times a school was set on each year by tuna vessels in the ETP purse-seine fleet for the years 1986–90. The lower curve shows the number of sets due to U.S. vessels only; the upper curve shows the number of sets due to U.S. and non-U.S. vessels combined. Estimates of standard error were not possible for these estimates.

If school membership is completely fluid and dolphins mix perfectly among schools, then over the long term, all dolphins would experience the same capture rate. We made a rough estimate of this rate by estimating the total annual number of dolphins set on and the total number of dolphins. Using data from Table 2, we made a rough estimate of 7610 for the mean annual number of sets on NE offshore spotted dolphins during the period of this study. From tuna vessel observer data, an estimate for the mean school size for those sets is 773 animals. When combined with an estimate for the total number of NE offshore spotted dolphins (Wade and Gerrodette, 1993), this gives (7610 × 773 dolphins set on) ÷ (731,000 dolphins) = 8.04 sets per dolphin per year.

The true picture certainly lies between these two extremes. On the other hand, if the composition and spatial location of some large schools are static over periods of weeks or longer, then animals in those schools could be subject to short-term capture rates even higher than those of our estimates because of the clustered distribution of fishing effort.

Geographic stratification

Holt et al. (1987) partitioned the ETP into several geographic strata primarily on the basis of spotted dolphin density as observed from tuna vessels during years prior to the study period. In an alternate analysis for capture frequency, we used Holt et al.'s partition to fit separate densities for $p(s)$ in each of two strata (Fig. 1), and used separate counts n_{sets} and $n_{schools}$. The estimates of $p(s)$ from the two strata were significantly different (Kolmogorov-Smirnov goodness-of-fit test, P=0.002), but primarily at smaller school sizes, less than 200 animals, and this stratification made little difference in absolute terms from the unstratified estimates of capture frequency. The similarity in capture frequency estimates between strata indicates that fishing pressure was approximately proportional to dolphin school density.

We did not stratify geographically to estimate $\pi^*(s)$ or $w_{eff}(s)$ because we found that the number of observations in the middle stratum ($n_{schools}$=81) was too small to allow stratification and still have reasonable precision. A Kolmogorov-Smirnov test and Q-Q plots indicated that there was no substantial difference (P=0.62) in $\pi^*(s)$ between strata for the research vessel observers. On the other hand, we fitted the bivariate line transect model to data from the two strata separately and found that the estimate of $w_{eff}(s)$ for the middle stratum was 10–20% smaller than that for the inshore stratum, depending on school size. However, there were few data on which to base either result. One reason why $w_{eff}(s)$ might actually have differed between the two strata was a difference in observed sea state conditions; a higher average Beaufort sea state was reported in the middle stratum. The practical impact is that our estimates of capture frequency may have been overinfluenced by data from the inshore stratum.

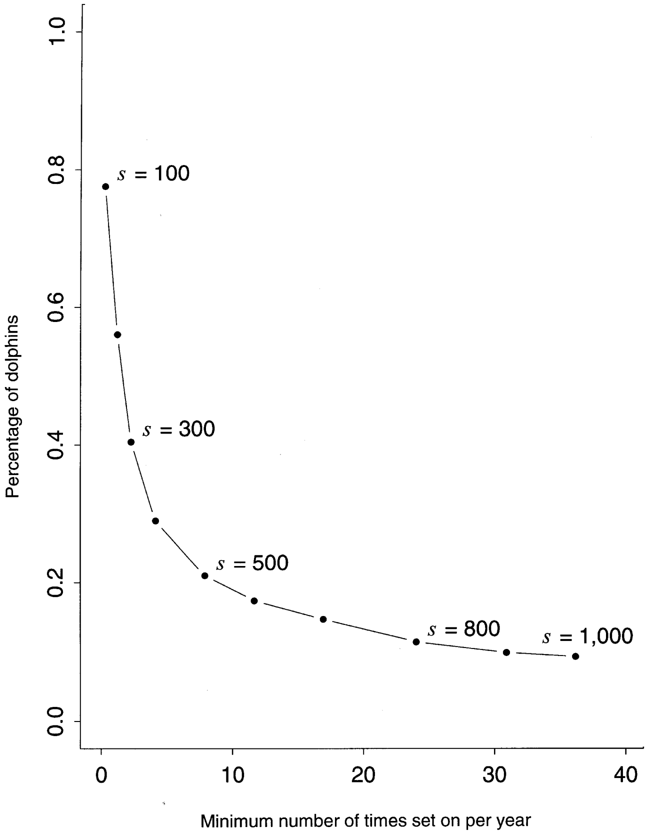

Figure 6

Estimated percentage of northeastern offshore spotted dolphins subject to different levels of capture frequency. The horizontal axis represents the minimum number of times a dolphin school is set upon per year by U.S. and non-U.S. tuna vessels in the ETP purse-seine fleet, for the years 1986-90. The vertical axis represents the estimated fraction of the stock (not the fraction of schools) subject to at least that rate of being set upon. s is the minimum school size accounting for that percentage.

Observer size-estimation errors

Our statistical model for the school size data included terms for selection biases, that is, which schools were included in the sighting or set data. However, there was also a potential for observer size-estimation biases. That is, given a sighting of, or a set on, a specific school, an observer had to estimate size of the school. The results presented here treated the observer estimates as exact counts. We did not include an error term for size estimates in either the kernel density estimates of $\pi^*(s)$ and $p(s)$ or the bivariate line transect estimates of $w_{eff}(s)$.

An observer size estimation bias would scale or otherwise deform those estimates of $\pi^*(s)$ or $p(s)$ (or both), depending on whether the bias was proportional to size or was more complex. Even if the observers were unbiased in their individual estimates, estimation variance would still increase both tails in the density estimates. Thus, if research vessel observers and tuna vessel observers consistently made different errors in estimating school sizes, then the trend in our estimates of capture frequency, e.g. Figure 4, could have been in part or entirely due to those errors.

Gerrodette and Perrin[5] studied dolphin school size-estimation errors for research vessel observers by ground-truthing observer estimates against aerial photo counts of the same school. They found that the counts from a single observer could be modeled as lognormally distributed given the true school size. They also found that a given observer in the study might have a substantial positive or negative bias.

Using their photo and observer dataset, we fitted a lognormal model for the geometric means of the observer estimates from each sighting.[6] The fit indicated that the observers had essentially no bias at a true school size near 100, but that there was a negative bias of 21% at a school size of 1000. Because the lognormal is a skewed distribution, this mean bias corresponds to essentially no median bias. The estimated CV for the estimates, given the true size, was 48%.

Given this information, it would have been possible in theory to correct the research vessel observer estimates for bias. However, we did not make that correction because the corresponding correction for the tuna vessel set data was not possible in the absence of a suitable ground-truth study. Significant differences between observers and observing conditions on research vessels and tuna vessels precluded the assumption that any size-estimation biases are similar in the two types of data.

Spatial distribution of schools and school sizes

Our analysis can be taken to imply full spatial mixing, that is, all schools of a given size within the stock boundaries (or within each stratum for the stratified case) have the same probability of being set upon. A more realistic model is that some schools have a higher or lower probability depending not only on their size but also on their geographic location in relation to areas of high school density or high fishing effort. Other factors, such as seasonal effects and the amount of associated tuna, are also interrelated with location in determining the rate of capture for a given school. Because we included only limited spatial information in our model, the appropriate interpretation of our results is that we estimated an average probability of being set upon, as a function of school size, for schools within the stock boundaries (or each stratum).

Observer experience suggests that pressure from fishing on dolphin can reduce average dolphin school size, i.e. areas of high fishing effort tend to have smaller schools.[7] This decrease in school size may be a result of chase and capture operations during sets intentionally or unintentionally splitting schools into smaller subgroups.[8] However, we did not find any indication of such a trend in our NE offshore spotted dolphin school-size data. We concluded that if fishing pressure did affect spotted dolphin school size, its effects may have been masked by size selection in the tuna vessel set data and by the relatively limited number of observations in the research vessel sighting data.

Dolphin schools

Variation in school size over time The simplest interpretation of this analysis would assume that a dolphin school is a fixed entity that does not change in size. If, on the other hand, a school is not a well-defined entity over any length of time, i.e. schools often fragment and reaggregate (e.g., Scott and Cattanach, 1998), then defining capture frequency for anything other than an individual dolphin becomes problematic. The superpopulation model that we used is one way to account for this fluid nature of dolphin schools. In particular, the research and tuna vessel school-size data represent time-averaged samples, i.e., averages over repeated realizations from the superpopulation. Estimated capture frequencies can be interpreted in terms of short-term rates.

Species composition Most schools in both the research vessel and tuna vessel data included not only NE offshore spotted dolphins, but other species as well, primarily spinner dolphins (*Stenella longirostris*). We did not differentiate between pure and

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[5] Gerrodette, T. and C. Perrin. 1991. SWFSC Admin. Rep. LJ-91-36, Southwest Fisheries Science Center, La Jolla CA, 74 p.

[6] Details of this exploratory analysis can be found in Perkins, P. C. and E. F. Edwards, 1997, SWFSC Admin. Rep. LJ-97-03, Southwest Fisheries Science Center, La Jolla CA, 36 p

[7] Rasmussen, R. 1997. Southwest Fisheries Science Center, La Jolla, CA. Personal commun.

[8] Hall, M. 1997. Inter-American Tropical Tuna Commission, La Jolla, CA. Some limited data have been collected to study school fragmentation and reaggregation (Perrin et al., 1979; Scott, M. 1997. Inter-American Tropical Tuna Commission, La Jolla, CA. Personal commun.

mixed schools in our analysis. Thus, we took as our population of schools not just those composed purely of NE offshore spotted dolphins, but all schools containing them. School sizes were taken as the total number of animals in each school. This approach would not have been appropriate if we had been estimating a stock-specific abundance (e.g. Wade and Gerrodette, 1993). However, as long as there is no bias in the species composition of schools that are set on, our approach is valid. An exploratory data analysis indicated that the distribution of species proportions was very similar for both research and tuna vessel data.

There was some indication that pure spotted schools tended to be smaller on average than mixed spotted-spinner schools. We did not pursue this because it did not affect our results.

Encounter rate for very large schools

Inspection of Figure 2 raises the question of why so few very large schools (1000 animals or greater) were sighted from the research vessels when so many were set upon by tuna vessels. Only five schools (1% of sightings) in that range were reported by research vessel observers, and the largest was estimated to be 2617 animals. In that range, 896 schools (26% of observed sets) were reported set upon by tuna vessel observers, and 97 were estimated to be larger than 2617 animals. These largest schools from the set data did tend to include slightly higher percentages of species other than spotted dolphins. However, they were still primarily made up of spotted dolphins (just over an estimated 70% on average), and it was not the case that they were due to an association with large groups of, for example, common dolphins (*Delphinus delphis*), which are known to form very large schools (e.g. Edwards and Perrin, 1993).

At least four explanations for this apparent discrepancy are possible. First, this may simply reflect the tuna vessel captains' preference for setting on large schools. Second, the difference may be due to relative bias in size estimation between the two types of observers, as discussed earlier. However, to explain all of the difference, the two sets of observers would have to differ on average by a factor of five in their estimates. Third, the research vessels may have missed a relatively rare segment of the population of schools, which the tuna vessels are able to seek out with a much greater search effort and a nonrandom search strategy. Fourth, some of these large observations in the set data may have been from intentionally repeated sets on the same schools. There is evidence in the tuna vessel observer data for both of these last two explanations, i.e., that localized areas of high density or school size (or both) may exist and that repeated sets on a single school may occur.

Conclusions

The results of this study indicate that tuna purse-seiners in the ETP fishing on NE offshore spotted dolphins have a strong preference for setting on larger than average dolphin schools, and that such schools were subject to being set on at a much higher rate than were smaller schools. Specifically, the largest schools considered, those of 1000 or more animals, were estimated to be set on approximately once every week, whereas the smallest schools considered, those of 100 animals, were estimated set on less than once a year. Our estimated capture rates should be taken as averages for a given school size and do not account for variation due to other factors, such as geographic location or the amount of associated tuna. Also, although we estimated rates in terms of sets per year, we do not assert that the short-term capture rate for a given school is constant, i.e. that sets occur at evenly spaced intervals throughout the year. For example, relatively few sets are made "on dolphin" in the NE offshore stock range during June and July (e.g. Edwards and Perkins, 1998).

These results do not account for any errors in estimation of dolphin school size. Although potential errors in school-size estimates made by research vessel observers were investigated, no corresponding study of potential errors for tuna vessel observer estimates was possible.

To draw conclusions about capture frequency for an individual dolphin, we must consider the size range of the schools with which a given individual tends to associate. Our results imply that dolphins associating primarily with large schools will be subjected to capture much more often than individuals associating primarily with small schools. However, we also estimated that the largest schools are relatively rare and account for a minority of the total number of individual dolphins at any given time. These results may imply that a fixed but relatively small percentage of the dolphin population was consistently subjected to a high rate of capture in purse-seine nets but that a majority of dolphins occur in schools smaller than those apparently preferred by purse-seiners, and experience relatively few captures per year.

However, little is known about the spatial and temporal dynamics of dolphin schools and their sizes, and other conclusions are possible. If dolphins associate with a wide range of school sizes, then the capture rates for individual dolphins would tend to "average out" and thus would vary less than the range of capture rates for schools. On the other hand, differences between schools in factors other than size could lead to short-term individual capture rates that are even higher than our estimates.

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