Effects of Nonrandomness on Line Transect Estimates of Dolphin School Abundance

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ABSTRACT: Line transect analysis is a census method that has been used to derive estimates of dolphin school abundance from sightings data collected by observers on tuna purse seine vessels. The method is based on the assumption that movements of the sighting platform (tuna vessel) and sighted objects (dolphin schools) are random with respect to each other. In practice, neither schools nor vessels move randomly. Stratification of sightings data has been used to alleviate partially the effects of this nonrandomness, but the effectiveness of this stratification cannot be tested with data from commercial vessels because the movements of the vessels cannot be controlled.

As an alternative, we have used a relatively simple mathematical simulation model to investigate the severity of bias introduced into school abundance estimates by nonrandom movements of schools and vessels, and by the data stratification procedure. Simulations show that nonrandom movements on a scale of a few hundred miles, coupled with the data stratification procedure, can lead to overestimates of dolphin school abundance by as much as a factor of two. These results focus attention on the need to understand patterns of dolphin school distribution in smaller scales of space and time than have been studied previously, and to develop data stratification methods more robust against the effects of small-scale nonrandomness.

The National Marine Fisheries Service (NMFS) monitors mortality of dolphins involved in fishing operations by the United States purse seine fleet for yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific Ocean (ETP), to determine whether mortality has exceeded an annual quota implemented by an act of the U.S. Congress. The quota levels depend upon whether dolphin populations are thought to be increasing or decreasing in number, relative to population levels during previous years.

The most effective method currently available for detecting trends in relative abundance is analysis of population abundance estimates collect-

ed over a period of 5-15 years. The most effective method currently available for making these abundance estimates is line transect analysis of dolphin school sightings data (Holt 1987; Buckland and Anganuzzi 1988). Two data sources are available for these line transect estimates of abundance: 1) data collected by observers during research surveys (RSOD-Research Survey Observer Data) and 2) data collected by observers during commercial fishing operations (TVOD-Tuna Vessel Observer Data). NMFS has used RSOD because research surveys can be designed specifically to satisfy the assumptions required by line transect analysis (Smith¹). However, research surveys are very expensive and are becoming more so. This expense causes RSOD to be sparse relative to TVOD and possibly unavailable in the future.

TVOD are a potential solution to these problems, having three significant advantages over RSOD: TVOD are much more abundant, are relatively inexpensive, and are likely to continue being collected as long as fishermen set on and kill dolphins. Observer-days from tuna vessels account for roughly 95% of the annual observer effort in the ETP, while observer-days from research vessels account for only 5%. TVOD are inexpensive relative to RSOD because TVOD are collected by the observers in addition to monitoring dolphin mortality, the latter being the main reason the observer program was initiated. This monitoring program has been in operation for the past 14 years, will continue into the foreseeable future, and monitors about 30% of trips by purse seiners (both U.S. and non-U.S. vessels) each year in the ETP². Ideally, TVOD could be used in place of RSOD to monitor changes in abundance of dolphins.

²Inter-American Tropical Tuna Commission, Annual Reports 1980–1988. Scripps Institution of Oceanography, La Jolla, CA 92038.



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¹Smith, T. D. 1975. Estimates of sizes of two populations of porpoise (*Stenella*) in the eastern tropical Pacific Ocean. Admin. Rep. No. L1-75-67. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

Reluctance to use TVOD to monitor the relative abundance of dolphins stem from concerns that TVOD 1) seriously violate some of the fundamental assumptions of line transect analysis (Polachek 1983), 2) are subject to serious but unquantified and possibly inconsistent biases, and 3) may be plagued with artifacts arising from the data collection process. Artifacts include, for example, differences between RSOD and TVOD in the sighting frequencies of various dolphin species reported by observers on research vessels compared to tuna vessels (Barlow and Holt³), environmental factors affecting sighting ability (e.g., sun glare, sea state, and cloud cover; Holt and Cologne 1987), and shifting areas of concentrated search effort (Buckland and Anganuzzi 1988). However, problems of this type are common to most commercial fisheries data and analyses derived from them. It is important to determine whether, despite these difficulties, useful estimates can be derived from such data sets.

Toward this end, we have developed a relatively simple model simulating the TVOD collection process. Our purpose in developing the model was twofold: 1) to test the effect of suspected biasing factors on line transect estimates of abundance and 2) to test new methods of abundance estimation prior to conducting expensive field tests. There are two unique advantages of simulation modeling in this context. First, we are simulating dolphin abundances and vessel movements within the model itself; therefore, we have available the "truth" against which to compare our modelgenerated estimates of abundance. Second, we have the capability of investigating effects on estimates that are due to combinations of biasing factors which may not have occurred during the years we happen to have been collecting data, but which can be expected to occur. Biasing factors include, for example, small-scale nonrandomness in school and vessel movements and spatial distributions, choice of data stratification method, changes in fishing objectives, practices, and areas of concentrated search, and changes in sighting protocol and recording procedures. We chose to focus first on the effects of nonrandomness and on the method of data stratification because recently developed methods of line transect analysis to estimate dolphin abundance from TVOD (Buckland and Anganuzzi 1988) raised serious but unanswered questions about the effects of these factors on the abundance estimates derived.

The philosophy behind building a relatively simple model was that biases shown to be troublesome and methods shown to be inadequate in a simple computer model are likely to be even more troublesome and inadequate in the real world. It is both more efficient and more economical to investigate these biases and methods first with a simple simulation model, prior to developing expensive field experiments. We have specifically applied the tenets of Occam's Razor in developing this model, making it as simple as possible while still incorporating the major processes and features contributing to the TVOD data collection process. In this study, we focused only on estimating abundance of dolphin schools, leaving questions about abundance of *individual* dolphins for a later day. We also assumed that data were collected without artifacts, leaving also that problem for a later set of simulations. Both of these omissions are examples of factors that probably have strong effects on analyses of TVOD, but which are at this stage unnecessary refinements to the simulation model. Such refinements could be added later if no problems were identified during simulations with the early, most simplified versions of the model.

This paper presents results of testing one hypothesis about one of the most fundamental factors suspected to affect seriously line transect estimates of dolphin abundance derived from TVOD. Specifically, we tested the effect of nonrandom clustering by dolphin schools on abundance estimates. As part of this analysis we tested also the effects of three types of data stratification prior to line transect estimation of school abundance: 1) no stratification, 2) stratification by raw encounter rate per 1° square, and 3) stratification by smoothed encounter rate per 1° square, using the smoothing and interpolation algorithm developed by the Inter-American Tropical Tuna Commission for deriving estimates of dolphin abundance from line transect analysis of TVOD (Buckland and Anganuzzi 1988). We were primarily interested in the third type of stratification, because the properties of the smoothing algorithm are poorly understood. The other two stratifications were conducted to provide a basis for comparison with the smoothing procedure.

³Barlow, J., and R. S. Holt. 1986. Geographic distributions of species proportions for dolphins in the eastern tropical Pacific. Admin. Rep. No. LJ-84-27. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA. La Jolla, CA.

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THE MODEL

Model Structure

This section presents a general description of model structure. A detailed technical explanation of the model can be found in Kleiber and Edwards⁴. The model (TOPS: Tuna-vessel Observer Program Simulator) simulates the movements of 75 tuna purse seiners and either 2,500 or 1,250 dolphin schools within a 1,200 \times 1,200 square nautical mile area. Figure 1 provides a graphical comparison of the "study area" simulated by the model, to the entire area within which the tuna-dolphin association is exploited by the purse seine fleet. Twenty-five hundred dolphin schools is the nominal number of schools expected within a 1,200 \times 1,200 nmi area of the ETP, based on Holt's (1985, ^{5,6} 1987) estimates of the total number of dolphins, average size of dolphin schools, and species proportions for the ETP, prorated from the entire ETP to an area $1,200 \times 1,200$ nmi. Simulations were also run with half this number of schools to investigate the ability of abundance estimates derived under different conditions to reflect changes in actual abundance in the model. Number of vessels is based on reported size of the ETP purse seine fleet, assuming about 50% of the fleet will be fishing a given area of this size at any one time (see IATTC Annual Reports 1983–87).

All dolphin schools are assumed to be identical (i.e., are replicates); all schools include only the

⁵Holt, R. S. 1985. Estimates of abundance of dolphin stocks taken incidentally in the eastern tropical Pacific yellowfin fishery. Admin. Rep. No. LJ-85-16. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA. ⁶Holt, R. S. 1985. Estimates of population size of dolphins in the eastern tropical Pacific using line transect methods. Admin. Rep. No. LJ-85-20. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.



FIGURE 1.—Approximate extent of the eastern tropical Pacific Ocean (ETP) tuna purse seine fishery. Boxes enclose two areas the size of the area simulated by TOPS (1.200×1.200 nmi), indicating relative sizes of the entire fishery area compared to the area encompassed by the simulation.

⁴Kleiber, P. K., and E. F. Edwards. 1988. A model of tuna vessel and dolphin school movement in the eastern tropical Pacific Ocean: technical description of the model. Admin. Rep. No. LJ-88-28. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

northern offshore stock of spotted dolphins, Stenella attenuata, all have the same number of animals, all are equally visible, and all move independently of each other. All vessels are assumed to be identical also; they are the same size, are equally adept at sighting dolphin schools, and do not communicate with each other. Dolphin schools move at speeds varying between 0.5 and 2.4 knots, depending on conditions of the local environment (see below). All vessels move at 15 knots continuously. Speeds are based on reported averages for dolphin schools (Perrin 1979) and for vessels (vessel activity records, NMFS data bases). Vessels are assumed to chase and set upon all sighted schools. Vessels that have set on a school are "removed" from the simulation for 5 hours, simulating the average time to chase, set, collect tuna, release dolphins, and get back under way. Sighted schools are removed from the position of sighting and replaced randomly within 0 to 50 nmi of the sighting, simulating a variable "rest" period of 0 to 24 hours between one set and the next for sighted schools.

Dolphin schools move in response to the local height and gradient of an "environmental topography". The topography is a grid of equally spaced peaks of good habitat interrupted by valleys of low-quality habitat. Habitat quality varies between a value of 1 at the peaks for optimum habitats to 0 at the least favorable habitats midway between peaks. Topographies are generated as a function of sine waves in two-dimensional space and are either stationary or made to slide from right to left at 1 knot. Two combinations of peak spacing and peak shape were used for the simulations reported here: 1) a simple topography of 4 equally spaced peaks with relatively gentle slopes (Fig. 2a), and 2) a more complex topography of 16 equally spaced peaks with relatively steep slopes (Fig. 2b).

These choices for peak number generate spaces between peak tops of 300 and 600 miles. These spacings were chosen based on approximate distances between clusters of dolphin school sightings from research vessel data⁷. Peak steepness was chosen to simulate either slow spatial changes in environmental conditions (gentle slope) or rapidly changing conditions (steep slope) such as those which pertain at ocean fronts (Owen 1981).

Spacings of 600 miles between gently sloping peaks generates distances of 300 miles between maximum and minimum values of the environ-

⁷R. S. Holt, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla. CA 92038, pers. commun. July 1987.



FIGURE 2.—Geometric configuration of the simple environmental

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mental topography, representing a 300 mile gradual gradient from "best" to "worst" conditions (Fig. 2a). In the complex, steep environment the precipitous slopes generate a distance of only about 75 miles between maximum and minimum values for environmental quality, the slopes being separated by a "desert" of unfavorable habitat about 150 miles wide (Fig. 2b).

These two topographies were chosen to bracket a range of reasonable possibilities for patterns in environmental characteristics that may cause nonrandom clustering of dolphin schools. The factors of peak gradient and peak spacing (number of peaks) are confounded here because we tested only the two topographies, simple:gentle and complex:steep. Gentle gradients are confounded with few peaks; steep gradients are confounded with many peaks. We did not test the other two possibilities (simple:steep and complex:gentle) because these are both intermediate topographies that would have generated intermediate results. In the interest of simplicity, we restrict this simulation study to the two extreme cases.

The rate at which the topography moved (1 knot) was chosen to simulate movement of major habitat features affecting dolphin school movements. Because direct identification and measurements of such features have yet to be

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made, the choice of rate was based on reported speeds of major ocean currents in the eastern tropical Pacific and apparent seasonal movements of major concentrations of dolphin schools. Reported current speeds include 0.1 to 0.3 knots for the core of the Pacific North Equatorial Current bordering the fishery area on the north (Seckel 1975), 1.2 to 2.4 knots for the equatorial undercurrent underlying the fishery area (Wyrtki 1966), and 1.2 to 2.4 knots for maximum speed of the Equatorial Countercurrent surface waters encompassing a majority of the fishing area (Wyrtki 1966). School sightings data from research ships indicate that major concentrations of dolphin schools may move seasonally between distant areas at approximately 0.3 knots (200 nmi/mo)8.

Our choice of 1 knot was based on the assumption that the mechanism(s) responsible for aggregating dolphin schools are most probably related to distributions of prey and water mass signatures indicating presence or absence of the prey. Dolphins in the ETP consume small (10–50 cm) fish and squid (Perrin et al. 1973). This mobile prey base will in turn be responding to

COMPLEX TOPOGRAPHY



topography (a) and the complex topography (b).

⁸S. B. Reilly, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1987.

movements of its own prev base of smaller animals. We reasoned that it is unlikely that this food chain is being swept along as rapidly as the maximum current speeds, but, especially on smaller scales, the distributions of prey and predator are probably moving faster than the speeds apparently characteristic of large-scale seasonal movements. We chose 1 knot as a conservative approximation. It is possible that dolphin aggregating mechanisms move, overall, more slowly than 1 knot, but probably not faster. Thus by comparing simulation results from nonmoving topographies versus topographies moving at 1 knot, we have tried to bracket the range of responses likely to occur in the real system.

In our model, dolphin schools were made to respond to these topographies by adjusting their speed according to the quality level and by adjusting their direction according to the gradient in quality experienced during the previous time step. The range of speeds chosen for dolphin schools (0.5 to 2.4 knots) was based on average observed cruising speeds of dolphin schools in the ETP⁹. In the model, dolphin speed is fastest at the lowest quality levels and slowest at the highest quality levels. Direction choice is stochastic with probabilities biased in the forward direction when the gradient is positive (conditions improving) and in the reverse direction when the gradient is negative (conditions deteriorating). Thus the rules for school speed and direction cause schools to circle slowly in "favorable" areas (i.e., on the peaks) and to move rapidly straight ahead in "unfavorable" areas (i.e., the valleys between peaks).

Vessel movements were controlled by each vessel's history of dolphin school sightings, through a "sightings memory" variable. The value of the variable increases by one unit each time a school is sighted and it decays constantly by a given proportion with each time step. Thus, the value of the variable will be high when a vessel is in a "good" area (i.e., has seen lots of schools) and will be low when the vessel is in a "bad" area (schools are few). Vessel direction is stochastic and affected by the value of this "sightings memory" variable. When the value is high, direction choice is biased in the reverse direction; i.e., the vessel is most likely to turn approximately 180 degrees. When the value is low, small angles are much more likely to be chosen; i.e., the vessel will tend to continue moving forward. Each vessel maintains its own sightings variable independent of the sightings variables of other vessels, so that each vessel moves independently of all other vessels.

Generation of Simulated TVOD

Each simulation began with totally random distributions of both vessels and dolphin schools. Nonrandom spatial distributions of vessels and schools then developed as a function of the environmental topography and of the movement rules for schools and vessels. Each simulation continued for 600 time steps of 1 h/step.

Estimates of school abundance were based only on TVOD collected during the last 200 steps. By this time, the model had in all cases settled into a quasi-steady state (Fig. 3). TVOD for each vessel, collected during each of these last 200 steps, included vessel number, total number of miles searched during that step, position of the vessel at the end of the step, and presence or absence of a school sighting. Only one school could be sighted per vessel per time step.

TVOD were "collected" for all dolphin schools moving within 2 nmi of any vessel. Two nautical miles is the effective strip width found commonly with line transect analyses of real TVOD.¹⁰ All vessels were assumed to carry observers. Observers were always on duty collecting data (i.e., were never "off effort"). Vessels searched continuously (i.e., did not stop at "night").

Data Analyses

TVOD were aggregated subsequently into 1° squares prior to abundance estimation. Onedegree squares are the smallest geographic subdivision that retains, with real TVOD, sufficient data for line transect analysis (Polachek 1983; Buckland and Anganuzzi 1988).

Four replicated simulations were conducted for each of eight different cases representing two

⁹Hedgepeth, J. 1985. Database for dolphin tagging operations in the eastern tropical Pacific. 1969-1978, with discussion of 1978 tagging results. Admin. Rep. No. LJ-85-03. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

¹⁰M. Hall, Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92093, pers. commun.

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FIGURE 3.—Time course of total school abundance estimates derived from unstratified TVOD. Estimates were derived during each of 600 time steps for 4 replicated runs of 8 different starting conditions. The cases differed in environmental topography (simple, gentle vs. complex, steep), in whether the topography was static or dynamic (sliding left at 1 knot), and in underlying abundance of dolphin schools (1,250 or 2,500). Numbers in parentheses (2, 1; 4, 5) are parameters used in the equations generating the topographies.

levels for each of three factors. The factors and levels included 1) complexity of the environmental topography (simple, with 4 gently sloping peaks vs. complex, with 16 steeply sloping peaks), 2) topography dynamics (static vs. moving at 1 knot) and 3) dolphin school abundance (2,500 vs. 1,250 schools). Topography movement was implemented by causing the grid

of peaks and valleys to slide uniformly sideways from "right" to "left".

Stratification Schemes

TVOD collected under each of the eight cases were subjected to three types of stratification: 1) none, 2) raw encounter rate, and 3) smoothed encounter rate.

In the case of no stratification, school abundance was estimated simply as

$$(TE/AS) * (TA) \tag{1}$$

where TE is total number encounters by all vessels during time steps 400 to 600, AS is total area searched during that time, and TA is total area simulated (1,200 × 1,200 nmi). In this case, all 1° squares were treated as a single group or stratum.

In stratifying by raw encounter rate, encounter rates (schools encountered per nautical miles searched during the last 200 time steps) were calculated for each 1° square. The squares were subsequently ranked in ascending order of encounter rate, and grouped into (n) strata. Strata were demarcated on the basis of including at least (m) schools (encounters) per stratum. Both (n) and (m) were calculated using an algorithm developed by the Inter-American Tropical Tuna Commission for their line transect analyses of dolphin abundance in the ETP (Buckland and Anganuzzi 1988). School abundance was then estimated for each stratum separately. Total school abundance in the entire 1,200 \times 1,200 nmi area was then estimated simply as the sum of these estimates per stratum.

In stratifying by smoothed encounter rate, encounter rates in each 1° square were smoothed according to the algorithms developed by Buckland and Anganuzzi (1988). Squares were then ranked and assigned to strata based on these smoothed encounter rates. This smoothing algorithm generally creates strata composed of contiguous areas of squares, arrayed in decreasing order from area of apparent high density to areas of lower density. It is not uncommon, however, for some squares in a given strata to be scattered in areas isolated from the majority for that stratum.

The smoothed encounter rates generated by the algorithm were used only during this stratification step; school abundances were estimated for each stratum using the raw (actual) encounter rate. Total abundance of dolphin schools was then estimated as the sum of the estimates for each stratum.

Estimates Derived

Two types of estimates were derived from these simulated TVOD: total abundance of dolphin schools in the entire simulated area, and change in school abundance from one sampling period to another, where this change was estimated simply as the ratio of school abundance estimates derived under two different sets of initial conditions in the model. Thus, school abundances were estimated first, and change estimates derived subsequently from these abundances. These estimates of change were calculated as a very simple analogy to a trend estimate, extending in this case over two sampling periods instead of over series of estimates. This two-sample change estimate is only a rough approximation to a trend estimate derived from a series of measurements (Gerodette 1987). However, conclusions about the effects of inconsistent biases on this *change* estimate will be valid for trend estimates also, except for the unlikely case in which effects of various inconsistent biases cancel each other out, so that the trend estimate reflects the actual trend, but only fortuitously.

Change estimates were derived under two conditions. Under the first condition the estimate was simply the ratio of the abundance estimate when true density was 1,250 schools (low density) to the estimate when the true density was 2,500 schools (high density). All other conditions in the model remained the same. This simulates the situation of consistent biases.

Under the second condition, the trend estimate was the ratio of one low-density estimate to one high-density estimate, but the ratio was constructed by selecting abundance estimates from cases which differed in other factors in addition to differing in dolphin abundance. This simulates the situation of biases being inconsistent from one sampling period to the next. Three ratios were selected from the many possibilities, to simulate three reasonable scenarios in the real ETP and to bracket a range from mild to severe inconsistencies.

The first of the three ratios was an estimate of abundance change in the simple environment, where in one case the environment was static during the sampling period and in the other the environment was moving at 1 knot. The second

ratio was an estimate of abundance change coupled with a change in the environment from simple to complex (environments remaining static in both cases). The third ratio was an estimate of abundance change coupled with a change from a simple and static environment to a complex and moving environment. These three cases simulated ratio estimates of abundance changes from, for example, one year to the next, where conditions in the environment have also changed between years.

RESULTS

Development of Nonrandom Distributions

Relatively similar dynamics occurred within the four replicated runs of each of the eight cases (Fig. 3). In all cases, nonstratified estimates of total school abundance, calculated for each of the 600 time steps, developed progressively positive biases. Early during each simulation, estimates were relatively accurate. But as schools and vessels became progressively nonrandomly distributed (Fig. 3a-h), estimates deteriorated owing to the concentration of search effort by tuna vessels in the areas where dolphin school were prevalent and to the concomitant avoidance by vessels of areas with few schools.

Although positive bias developed in all cases, the degree and progression of bias was strongly influenced by environmental topography, both configuration and dynamics. Relatively little bias developed in cases where the topography was relatively noncomplex (Fig. 3a, c) or was moving at 1 knot (Fig. 3b, d, f, h). Very large biases developed in cases where the topography was complex and static (Fig. 3e, g).

School Abundance Estimates

Nonstratified estimates of total school abundance, calculated from TVOD collected during the last 200 time steps, show the positive bias indicated in the time courses shown in Figure 3. The degree of positive bias in unstratified estimates was not constant, but varied with model conditions (Fig. 4). Bias was least for the case of a simple, moving environment, slightly higher for the complex, moving environment, slightly higher again for the simple, static environment, and dramatically higher for the complex, static environment. Estimates of school abundance based on stratification by raw encounter rate were in all cases relatively accurate, although estimates tended to be negatively biased for the cases of a simple environment (Fig. 4).

Estimates based on stratification by smoothed encounter rate also tended to be negatively biased for the cases of a simple environment (Fig. 4). The case of a complex, moving environment led to a slight positive bias in abundance estimates. But the complex, static environment led to pronounced overestimates of abundance that rivaled results from the unstratified analyses.

Reducing the underlying density of schools by half, from 2,500 to 1,250 schools, was mirrored by decreases of approximately one half in school abundance estimates (Fig. 4). Patterns of overor underestimation under various model conditions remained consistent over both densitites. For example, the most severe bias occurred in both cases under conditions of a complex, static environmental topography.

Change Estimates

When change estimates were derived by comparing cases in which only the underlying density of schools was changed (i.e., when biases remained consistent between sampling periods) the estimates based on raw or smoothed encounter rate stratification were very accurate (Fig. 5). Estimates based on unstratified data were strongly biased but analyses of real TVOD are never conducted on unstratified data, so this case is useful only as an indication of improvement in estimation achieved by stratifying.

Inconsistent biases produced a dramatically different result. Even relatively small changes in underlying model conditions produced moderate to large biases in the change estimates. Also, these biases were neither consistently positive nor consistently negative, even within a single set of comparisons (Fig. 5).

DISCUSSION

School Abundance Estimates

Stratification

Overestimates were derived from nonstratified data in all cases because vessels (and therefore observers) spent more time (expended more effort) in areas where dolphin schools were abun-



FIGURE 4.-Estimated vs. actual school density (total number of schools in simulated area) under 8 different cases for model conditions and under 3 types of data simulation for each condition. Each set of 4 columns is a set of 4 replicated runs for a given case. The cases differed in 1) environmental topography (simple, gentle vs. complex, steep), 2) whether the topography was static or dynamic (sliding left at 1 knot), and 3) actual abundance of dolphin schools (1.250 or 2,500). Numbers in parentheses (2, 1; 4, 5) are parameters used in equations generating the topographies. Two and 4 refer to the number of peaks arrayed along each axis of the spatial plane, generating a regular square grid of peaks. One and 5 are values of the parameter controlling peak slope; 1 generates a gradual slope, 5 generates a precipitous slope. Heavy lines across the figures indicate the true density (abundance) of schools in each set of simulations. Data treatments include A) no stratification before estimating school abundance, B) stratification of 1° squares based on observed (raw) encounter rates per square, and C) stratification of 1° squares based on smoothed encounter rates per square.

dant, and avoided areas where schools were few (Fig. 6). Overestimates of average school abundance per 1° square resulted from this pattern of effort because few samples from low density squares contributed to the average. Overestimates of total school abundance then followed directly by extrapolating this overestimate to the entire area.

Overestimation of school abundance was especially pronounced for the case of a complex,





FIGURE 5.-Comparisons of estimated versus actual change ("trend") in school abundance from one sampling period to another. Changes in abundance were estimated as the ratio of school abundance (estimated or actual) under one set of model conditions (SD1) to school abundance (estimated or actual) under some other set of conditions (SD2). Lo and Hi refer to actual abundance of schools (Lo = 1,250 schools, Hi = 2,500 schools). S and NS refer to topography dynamics (S = topography sliding sideways at 1 knot (dynamic), NS = static topography). Number in parentheses refer to parameters generating topographies. Two and 4 refer to number of peaks along each axis. One and 5 refer to peak gradient (1 = gradual slope, 5 = precipitous slope). Three change estimates, resulting from three different types of data stratification, were generated for each comparison: A) no stratification before estimating school abundance, B) stratification of 1° squares based on observed (raw) encounter rates per square, and C) stratification of 1° squares based on smoothed encounter rates per square. Comparisons are expressed as (1 - (Estimated change/actual change))*100, so that differences appear as percentages. Differences are 0 when estimated changes equal actual changes.

static environment because this condition led to very concentrated clumping of schools within a few 1° squares. Vessels concentrated most of their effort in these few squares with very high density. Overestimates were less pronounced in the cases of a simple environment because here the areas of higher density were much more diffused and not so different from areas of low density. The gradient of increasing density toward the topographic peaks built up much more slowly, so that vessels sampled many more squares with relatively low density than had been the case for the complex, static environment. The overestimate of abundance was relatively lower for the case of the complex, dynamic environment for essentially the same reason; the

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 $F_{IGURE 6}$.—Tracks of simulated purse seine vessels after 400 time steps during a simulation with a complex, static environmental topography. Vessel movements are concentrated near peaks in the topography, in response to the high density of dolphin schools in these areas.

characteristics of the environment produced many more squares with relatively low densitites. But here the process generating these relatively low-density squares was very different from the simple environment case. In the complex, moving environment the peaks were moving at 1 knot. Aggregating the data from the last 200 time steps generated a smeared version of the underlying 16-peak array. Integrated over the entire period of data collection, the areas of dolphin concentration appear as bands across the simulated area, rather than as individual peaks (Fig. 7). The dolphin schools spread themselves out over a larger number of squares than in the static case, producing lower estimates of average density per square.

Stratification By Raw Encounter Rate

Estimates derived from stratification by raw encounter rate were relatively unbiased in all cases because in these simulations we "collected"

an unrealistically large number of TVOD with unrealistically complete coverage of the simulated area. Of the four hundred 1° squares in our 1,200 × 1,200 nmi area, no more than six went unsampled during any simulation. As a result, encounter rates in each square reflected very accurately the true school density in each square. Stratifying by these encounter rates, deriving a different estimate of average school density for each stratum, taking the weighted average of these estimates, and then extrapolating this weighted average to the entire area produced quite accurate estimates of total school abundance.

The slight negative bias in the cases of a simple environment may be due to a curious effect that was not obvious until we made a movie of vessel and school movements generated by TOPS for a simulation of the simple moving topography. It appears in this movie that vessels tend to undersample the areas of highest density in the center of the gradual peaks, because the vessels encounter enough schools along the periphery to keep them from turning into these high density, central areas. Undersampling the highest densities of course will lead to an underestimate of the average density per square and thus to an underestimate of total abundance.

This avoidance of peak centers did not occur with the complex, static environment used in our simulations, apparently because most of the peak area in this topography occurred within only a few squares (Fig. 2b). Vessel speed was apparently sufficient to carry most vessels into the highest density areas before the effects of sightings caused the vessels to slow down.

Stratification by Smoothed and Interpolated Encounter Rate

Given the apparent accuracy of estimates derived under the stratification by raw encounter rate, it would seem irrelevant to proceed to the more complicated and sometimes ineffective stratification by smoothed encounter rates. However, real world tuna vessels never sample the ETP as completely as the simulated vessels sampled the TOPS environments. In most years, fewer than half the vessels carry observers, the fleet as a whole samples less than half the entire ETP, and the sampling that is done tends to be concentrated seasonally in variable geographic areas (Buckland and Anganuzzi 1988). This leaves many 1° squares unsampled.

For management purposes, we cannot assume

that squares with no effort contained no dolphins; therefore, we are left with the necessity of estimating densities in those unsampled areas. We have to fill in the holes somehow, so an interpolation method, either a more robust method than used to date, or some new method, is required.

In most of the TOPS simulations, Buckland and Anganuzzi's (1988) smoothing and interpolation routines worked quite well, with accuracy rivaling that of the raw encounter rate stratification. The very poor performance of the smoothing algorithm in the case of a complex, static environment, however, is troubling because we have no data from the field to determine whether or not such topographies exist in the ETP. We suspect that such topographies do exist because the parameters used in the TOPS model were chosen specifically to be reasonable. In particular, the distances between peaks were chosen to bracket the apparent distances between clusters of dolphin schools as indicated by sightings from research vessels.¹¹ Also, the movement rates by vessels, schools, and topography were specifically selected to approximate observed rates.

The severe bias in the complex static case arises owing to an interaction between the effective sampling frequency (in this case, 1° squares), the peak topography, and the mechanics of the smoothing algorithm. The algorithm works by calculating, for each square, a smoothed encounter rate that is a weighted average of encounter rates for all squares within a radius of at least four squares. Thus the smoothed rate in each square is affected by rates across a diameter of at least eight 1° squares, or a distance of at least 480 nmi (8 \times 60 nmi). In the case of the complex, static topography, this minimum distance is greater than the distance between peaks (300 nmi). Also, the relatively precipitous peaks encompass only 3 or 4 squares and are separated by low-density areas several squares across. The smoothing algorithm tends to "fill in" these low-density areas, elevating apparent encounter rates in the intervening squares and causing squares to be assigned to strata out of proportion to the true densities of dolphin schools in the squares.

It is possible that the relatively precipitous slopes of the peaks in the complex environment

¹¹R. S. Holt, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1987.



FIGURE 7.—Average number of sightings of dolphin schools per 1° square during the last 200 a) simple, static, b) simple, sliding,





time steps of one simulation for each of the four types of environmental topography c) complex, static, and d) complex, sliding.

are unrealistic, but in fact these slopes extend over at least two 1° squares (Fig. 2b). This is a distance of at least 120 nmi. Conditions change across ocean fronts in distances much shorter than this, and ocean fronts are aggregating mechanisms for many marine biota (Owen 1981). Of course, such fronts are never static and the smoothing algorithm worked quite well in the complex, dynamic environment, apparently owing to the smearing effect discussed previously. However, as in the previous case, we have as yet insufficient data to identify the conditions actually pertaining in the real ETP.

The major point is that the simulations have shown that clustering characteristics on relatively small scales (10s to 100s of miles) can seriously bias estimates of abundance derived via the smoothing algorithm, which is a problem because as yet we know almost nothing about clustering on this scale in the real ETP. The model results indicate strongly that future research should be focused either on resolving this lack of information or on developing alternative analyses that are not as sensitive as this smoothing algorithm to these small-scale spatial effects.

Change Estimates

These demonstrated problems with estimating school abundance are serious but in real-world analyses could perhaps be ignored; the next set of dolphin quotas will be determined not on the basis of estimated absolute abundance at some point in time but rather on the basis of *estimated changes* in abundance (Holt et al. 1987). This is an advantage in the estimation process because as long as nothing other than dolphin abundance changes from one sampling period to the next (i.e., as long as biases remain consistent), then accurate estimates of those changes in abundance can be derived from TVOD.

However, we know almost as little about whether biases truly remain constant (consistent) in the ETP, as we know about small-scale spatial distributions of dolphin schools. It is obvious from Figure 5 that even relatively small changes in bias can lead to considerably inaccurate estimates of change and, by implication, estimates of trend. A change as simple as moving from a static to a slowly moving environment produced an overestimate in the ratio estimate of almost 20% (Fig. 5, Lo(2, 1)S/Hi(2, 1)NS). Not even the direction of bias remained consistent, changing from positive in some cases to negative in others.

The ratio estimate based on a simple static environment during one sampling and a complex static environment during the other period (Fig. 5) is of particular interest, because an effect of this type may be the basis for the anomalous and biologically unlikely dip in Buckland and Anganuzzi's (1988) estimates of abundance for northern offshore spotted dolphin, Stenella attenuata during 1983 (Fig. 8), the year of an exceptionally strong El Niño. Our simulation results in this case lead to a potentially testable hypothesis about a factor that may have significantly affected analyses of real TVOD. Preliminary analyses of apparent differences in distributions of dolphins during El Niño versus non-El Niño years support the hypothesis that changes in spatial distributions led to inconsistent biases and thus to inaccurate trend estimates during these years.12

SUMMARY

The results from these simulations are useful in a general sense; they show that significant biases can develop within the simple model structure used here. The quantitative results are specific to the parameter values and movement rules chosen for these particular simulations and are neither intended nor assumed to mirror specific distributions of either vessels or dolphin schools in the real environment of the ETP. Although parameter values controlling rates and abundances are "correct" to the best of our knowledge, choosing different parameters for the functions controlling dolphin responses to the environment, or vessel responses to dolphins, would probably change both the rates and spatial characteristics of pattern development and thus estimates of abundance derived.

Other clustering patterns could have been used, and other results generated. However, our purpose at this stage was not to generate a catalogue of patterns and responses. Our purpose was to test the effects of varying a simple but reasonably realistic (in terms of rates and spacings) aggregating pattern for dolphin schools, using the results to determine whether any insight could be gained into the problem of estimating abundance of dolphin schools in the real world, using real TVOD.

Indeed, we found that our simplified simula-

¹²S. B. Reilly, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun.



FIGURE 8.—Estimated abundance of northern offshore spotted dolphin, *Stenella at*tenuata, showing biologically unlikely recovery in 1984 following apparent decrease in abundance during 1983 (from Buckland and Anganuzzi 1988).

tion approach identified two critical problems that must be addressed if TVOD are to an effective source for estimates of dolphin abundance or changes in abundance in the eastern tropical Pacific Ocean. These critical problems are 1) the effect of small-scale nonrandomness of dolphin schools, and 2) the interactions between these small-scale patterns (sampling frequency and smoothing algorithms) on estimates of school abundance or change in abundance derived from line transect analysis of sightings data. Research effort should now be directed toward identifying and characterizing school distributions within these smaller spatial (and temporal) scales, and toward improving the efficacy of existing methods or developing new methods for analyzing TVOD.

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