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Estimates of Cetacean Abundance and Distribution in the Eastern Tropical Pacific

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ABSTRACT

Large-scale research vessel surveys were conducted annually from 1986 through 1990 by the US National Marine Fisheries Service to monitor the abundance of dolphin populations in the eastern tropical Pacific Ocean (ETP). Stratified line-transect surveys with two vessels sampled an area of 19 x 10^6 km^2. Sightings of all cetaceans were recorded, leading to the identification of 29 species. Distribution maps are presented for all species. Data from all five surveys were pooled to give single estimates of abundance in the ETP for 24 stocks of cetaceans representing 19 species or genera. Abundance estimates totaled 9.6 million animals for all dolphin species (subfamilies Delphininae and Steninae), 292,800 for all species in the subfamily Globicephalinae, 45,300 for all species in the family Ziphiidae (beaked whales), 33,881 for all species in the superfamily Physeteroidea, representing 22,666 sperm whales and 11,215 dwarf sperm whales, and 14,431 for two species in the family Balaenopteridae (rorquals), representing 13,023 Bryde's whales and 1,415 blue whales.

KEYWORDS: ETP; ASSESSMENT; SURVEY-SHIP; SMALL CETACEANS – GENERAL; SPOTTED DOLPHIN; STRIPED DOLPHIN; SPINNER DOLPHIN; COMMON DOLPHIN; FRASER'S DOLPHIN; BOTTLENOSE DOLPHIN; RISSO'S DOLPHIN; ROUGH-TOOTHED DOLPHIN; PILOT WHALE; MELON-HEADED WHALE; FALSE KILLER WHALE; PYGMY KILLER WHALE; BEAKED WHALES; CUVIER'S BEAKED WHALE; PYGMY BEAKED WHALE; BLAINVILLE'S BEAKED WHALE; SPERM WHALE; DWARF SPERM WHALE; BRYDE'S WHALE; BLUE WHALE.

INTRODUCTION

In 1986 the US National Marine Fisheries Service (NMFS) initiated a long-term, large-scale research program to monitor trends in the abundance of dolphin populations in the eastern tropical Pacific (ETP). The program utilized two research vessels annually for 120 days each, from 1986 to 1990, for a total of five surveys. Although the purpose of the surveys was to monitor dolphin abundance, sightings of all cetaceans were recorded. These surveys provided a unique opportunity to describe the abundance of the entire cetacean fauna in the ETP. Here we pool all five years of data to estimate abundance in the eastern tropical Pacific for 24 stocks of cetaceans representing 19 species or genera. A stratified analysis incorporating line-transect methods similar to Wade and Gerrodette (1992) was used.

There are few previous estimates of abundance for most of the species considered here. Polacheck (1987) compared the relative density of eight species of cetacean in the ETP, using encounter rates of cetacean schools with tuna purse-seiners, but did not make abundance estimates. Data from the tuna purse-seiners have also been used to estimate trends in relative abundance for three dolphin species that experience mortality in the fishery, a recent example being Buckland *et al.* (1992). Annual abundance estimates have been made for stocks of four species of dolphins that experience mortality in the fishery (Wade and Gerrodette, 1992), using the same data as in this paper. Abundance estimates for those four species are repeated here, but as single pooled estimates rather than as annual estimates. Estimates are presented for the first time for 15 other species or genera of cetaceans. Additionally, distribution maps for sightings of all 29 species are presented.

MATERIALS AND METHODS

Study area and survey methods

The five surveys occurred between late July and early December each year between 1986 and 1990. The surveys were designed to replicate each other as closely as possible, using the same methods, the same vessels and many of the same observers each year. The outside boundary of the study area was described by Au *et al.* (1979). The study area was partitioned into four areas or strata: inshore; middle; west; and south (Fig. 1). The size of each stratum was calculated by Holt and Sexton (1990). The number of ships, the total amount of survey effort needed to achieve a given precision and the allocation of survey effort by stratum were described in Holt *et al.* (1987).

The NOAA research vessels *David Starr Jordan* and *McArthur* traversed randomly placed predetermined tracklines in the ETP for approximately 120 days at sea in each year (Fig. 1). While on duty, two observers searched from directly ahead to abeam of the ship using 25x binoculars while a third searched directly ahead of the ship when not recording data. When a school was initially detected, the observers estimated the angle and radial distance to the school. Angles were read directly to the nearest degree from a scale on the binocular stand, while radial distances were measured by reading calibrated reticles in the binocular eyepiece. Perpendicular distances were calculated as the radial distance multiplied by the sine of the angle, in radians. When possible, cetacean schools were approached to confirm species identification and to make estimates of school size. Dolphin schools more than 5.6km (3 n.miles) from the trackline were not routinely approached. Whale sightings were only approached when

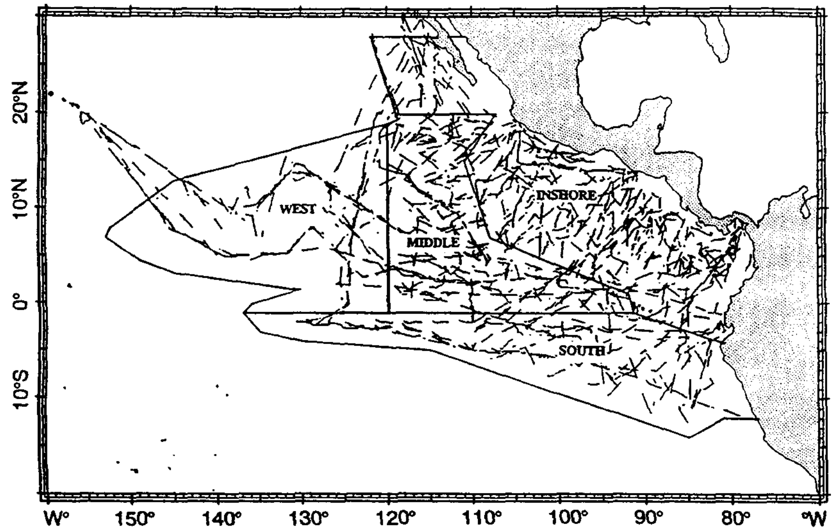

Fig. 1. Study area, strata, and survey tracklines 1986–90 in the eastern tropical Pacific. Solid, continuous lines define outer perimeter of study area and partitions between the 4 strata: inshore, middle, west, and south. Broken lines represent 'on-effort' tracklines of the marine mammal survey.

convenient; consequently, many of these sightings were not identified to species, but to some larger category such as 'rorqual'.

Data selection

Legs of effort from Beaufort states 0–5 were used, discarding a small amount of Beaufort 6 effort. Only schools detected within 5.5km (2.97 n.miles) perpendicular distance of the trackline were used (this is lower than the value of 7.4km used by Tobayama *et al.*, 1992). The perpendicular distances were grouped into eleven bins of 0.50km width for the analysis. For each sighting, from one to six observers estimated school size, with the most frequent number being three. Therefore, school size estimates were averaged across observers to obtain the mean of their estimates. Sightings with only a reported minimum estimate of school size were not used in the calculation of mean school size, but were used otherwise, contributing to n_{jk} and the estimation of $f_{jk}(0)$ (see Eq. 1 below).

Stocks estimated

The term 'stock' will be used to refer to the category for which an abundance estimate was made. Dolphins from some stocks are killed during tuna purse-seining operations in the ETP. The major populations affected by the fishery are the offshore stocks of spotted dolphins (*Stenella attenuata*) and the eastern and whitebelly stocks of spinner dolphins (*S. longirostris*) (Smith, 1983). A number of other species, including common dolphins (*Delphinus delphis*), striped dolphins (*S. coeruleoalba*), Fraser's dolphins (*Lagenodelphis hosei*), rough-toothed dolphins (*Steno bredanensis*), bottlenose dolphins (*Tursiops truncatus*) and short-finned pilot whales (*Globicephala macrorhynchus*), have also been killed (e.g., Hall and Boyer, 1989).

For the three species of *Stenella* and *Delphinus delphis*, abundance estimates were made for the nine stocks, described in Dizon *et al.* (1992). With the exception of the three stocks of *Stenella attenuata* and the one stock of *Stenella coeruleoalba*, these were the same stocks used in Wade and Gerrodette (1992). The rest of the stocks represent species level estimates, with the exception of two genus level categories. Abundance estimates were made for three additional species of dolphin (i.e. members of the subfamily Delphininae or Steninae), one genus and four species in the subfamily Globicephalinae, two species in the superfamily Physeteroidea, one species and one genus in the family Ziphiidae, and two species in the family Balaenoptera.

Subfamily **Delphininae**

Stenella attenuata

Abundance estimates were made for three spotted dolphin stocks: the coastal spotted stock (subspecies *S. attenuata grafmani*); and two offshore stocks, the northeastern spotted and western/southern spotted, using the stock boundaries of Dizon *et al.* (1992) shown in Fig. 2.* This was a substantial revision of the offshore stock boundaries described in Perrin *et al.* (1985), based on a re-examination of cranial morphology (Perrin *et al.*, 1991). The northeastern spotted dolphin (378 sightings) has a stock area that corresponds to the inshore and middle strata, with the exception that the southern boundary is at 5°N, rather than at 1°S (Fig. 2; dashed line is dividing line between the two stocks). The western/southern spotted dolphin (210 sightings) has a stock area that is both to the south and the west of the northeastern stock area, and corresponds to the south stratum (previously the southern spotted stock area) combined with the west stratum and the portions of the inshore and middle strata south of 5°N. The coastal spotted dolphin (16 sightings) has a stock area which is a narrow band 185km (100 n.miles) offshore along the Central American and Mexican coast (Fig. 2; solid line), and is entirely contained within the offshore stock areas.

* Figures 2 to 19 are at the end of the paper.

Stenella longirostris
Abundance estimates were made for two stocks of spinner dolphin: eastern spinner and whitebelly spinner (Dizon *et al.*, 1992; Fig. 3). The eastern stock of spinner dolphin (236 sightings) is considered a subspecies, *S. longirostris orientalis,* endemic to the ETP, while the whitebelly stock of spinner dolphin (154 sightings) is considered a hybrid between the eastern spinner and the pantropical spinner dolphin, *S. longirostris longirostris* (Perrin, 1990). The eastern and whitebelly stocks have a considerable region of overlap in their stock areas (Fig. 3; eastern stock, dotted line; whitebelly stock, dashed line). There were no sightings during the surveys of the Central American spinner dolphin, *S. longirostris centroamericanus,* as very little survey effort was spent in its distribution area, which is within 80km of the Central American coast (Fig. 3; solid line).

Stenella coeruleoalba
Abundance estimates were made for one stock of striped dolphin, from a total of 799 sightings (Fig. 4). Earlier work suggested that there were geographical stocks of striped dolphin in the eastern tropical Pacific (Perrin *et al.*, 1985). However, recent investigations indicate they should be considered as one stock (Dizon *et al.*, 1992).

Delphinus delphis
Abundance estimates were made for three stocks of common dolphin: northern common; central common; and southern common (Dizon *et al.*, 1992). These also correspond to the recommended management units of Perrin *et al.* (1985). The dividing lines relative to the study area between the northern (47 sightings) and central (70 sightings) stocks, and between the central and southern (92 sightings) stocks, are shown in Fig. 5 (dashed lines).

A fourth stock, the Baja neritic common dolphin (Perrin *et al.*, 1985), occurs within the northern stock area within 100 n.miles of the coast of Baja California, Mexico. Recent morphological and genetic evidence suggests that the two sympatric forms, referred to as the shortbeak (or offshore) form and the longbeak (or Baja neritic) form, are sufficiently different to deserve separate species status (Heyning and Perrin, 1991; Dizon *et al.*, 1992; Rosel *et al.*, In press). The shortbeak appears synonymous with *Delphinus delphis* while the longbeak form appears to be equivalent to the nominal species *Delphinus bairdii.* Criteria sufficient to distinguish the two forms in the field were not established until the last year of the surveys; consequently, only one identified sighting of the longbeak form was made in the study area (Fig. 5). Since insufficient information existed to distinguish sightings of the two forms for most of the surveys, all sightings within the northern stock area were pooled.

Lagenodelphis hosei
An abundance estimate was made for one stock of the Fraser's dolphin, from a total of 25 sightings (Fig. 6).

Tursiops truncatus
An abundance estimate was made for one stock of the bottlenose dolphin, from a total of 298 sightings (Fig. 7). Although it has been suggested that there are coastal and offshore forms of *Tursiops* in the eastern Pacific (Walker, 1981), there has been no conclusive study to establish stock areas or criteria for identifying the stocks in the field.

Grampus griseus
An abundance estimate was made for one stock of the Risso's dolphin, from a total of 194 sightings (Fig. 8).

Other delphinids
Due to the small number of sightings and the fact that most of its range was to the north of the study area, no abundance estimate was made for the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, for which there were 13 sightings at the northern extreme and north of the study area (Fig. 6). Similarly, no abundance estimate was made for the dusky dolphin, *Lagenorhynchus obscurus*, for which there was one sighting just south of the southern extreme of the study area (Fig. 6).

Subfamily **Steninae**
Steno bredanensis
An abundance estimate was made for one stock of the rough-toothed dolphin, from a total of 135 sightings (Fig. 9).

Subfamily **Globicephalinae**
Globicephala sp.
An abundance estimate was made for one stock of the pilot whales, from a total of 222 sightings (Fig. 10). This stock was referred to as *Globicephala* sp., although the majority of the sightings were probably *G. macrorhynchus.* An unknown quantity of sightings of *G. melas* were probably encountered at the southern extreme of the study area in the Peru current, but identification in the field is not possible, hence the designation of *Globicephala* sp.

Peponocephala electra
An abundance estimate was made for one stock of the melon-headed whale, from a total of 14 sightings (Fig. 6).

Pseudorca crassidens
An abundance estimate was made for one stock of the false killer whale, from a total of 34 sightings (Fig. 11).

Feresa attenuata
An abundance estimate was made for one stock of the pygmy killer whale, from a total of 29 sightings (Fig. 11).

Orcinus orca
An abundance estimate was made for one stock of the killer whale, from a total of 57 sightings (Fig. 11).

Family **Ziphiidae**
Ziphius cavirostris
An abundance estimate was made for one stock of Cuvier's beaked whale, from a total of 91 sightings (Fig. 12).

Mesoplodon sp.
An abundance estimate was made for one stock of *Mesoplodon* sp. There were 125 total *Mesoplodon* sightings including 88 sightings unidentified to species (Fig. 13). The remaining 37 sightings were distributed among three species: 19 sightings of a possibly un-named *Mesoplodon* sp. (Pitman *et al.*, 1987; sp. 'A' in Fig. 13); 12 sightings of Blainville's beaked whale, *Mesoplodon densirostris*; and three sightings of the recently named pygmy beaked whale, *Mesoplodon peruvianus* (Reyes *et al.*, 1991). It is not clear whether the relative abundance of species of *Mesoplodon* was reflected in the frequency of species identification. *Mesoplodon* sp. 'A' was possibly identified the highest percentage of the time, as the

substantial white chevron that is seen on larger animals is visible at a great distance (Pitman *et al.*, 1987). Information on how to identify the new species *M. peruvianus* was not available to the observers until during the 1988 survey, so it is likely that several sightings of this species were called unidentified *Mesoplodon* prior to that time. Its small size and short beak (Reyes *et al.*, 1991) may have made it relatively easy to identify since then. *M. densirostris* was only definitively identified when an excellent view of the head was obtained, allowing a view of the teeth or the high arching mouth-line. It is likely that it was identified the lowest percentage of the time, and the majority of unidentified *Mesoplodon* may therefore have been *M. densirostris*. Since the different species are likely to have had different probabilities of being identified, only a pooled abundance estimate for *Mesoplodon* sp. was made.

Other ziphiids

Due to the small number of sightings, no abundance estimates were made for the Southern bottlenose whale, *Hyperoodon* sp. cf *H. planifrons*, for which there were four sightings, or for Baird's beaked whale, *Berardius bairdii*, for which there were two sightings (Fig. 14).

Superfamily **Physeteroidea**

Physeter macrocephalus

An abundance estimate was made for one stock of the sperm whale, from a total of 148 sightings (Fig. 15).

Kogia simus

An abundance estimate was made for one stock of the dwarf sperm whale, of which there were 84 sightings (Fig. 16). There were an additional 11 sightings which were identified as being either *K. breviceps* (pygmy sperm whale) or *K. simus*. *K. breviceps* is thought to have a more northerly distribution than *K. simus* (Leatherwood *et al.*, 1988), and during the survey, *K. breviceps* was only sighted four times in the study area. These four sightings were all north of 24°N, close to the boundary of the study area, while all *K. simus* sightings were south of 24°N, indicating agreement with the suggested distribution (Fig. 16). All unidentified *Kogia* sightings south of 24°N (a total of 10) were therefore considered *Kogia simus* for the abundance estimate, for a total of 95 sightings. There was one unidentified *Kogia* sighting north of 24°N that was not used in the abundance estimate. No abundance estimate was made for *Kogia breviceps*.

Family **Balaenopteridae**

Balaenoptera musculus

An abundance estimate was made for one stock of the blue whale, from a total of 31 sightings (Fig. 17).

Balaenoptera edeni

An abundance estimate was made for one stock of the Bryde's whale. There were 42 confirmed sightings of *B. edeni* where the auxiliary ridges on the head were seen, a character which distinguishes this species from *B. borealis*, the sei whale (Leatherwood *et al.*, 1988) (Fig. 18). There were also 67 sightings identified as being either *B. edeni* or *B. borealis*, where the head was not seen well enough to determine if the auxiliary ridges were present or not. B. borealis is known to have a more northerly, temperate distribution in the eastern Pacific (Leatherwood *et al.*, 1988). Therefore, the 67 *B. edeni/B.* borealis sightings were considered *B. edeni* for this abundance estimate, for a total of 109 sightings.

Other rorquals

Due to the small number of sightings, no abundance estimates were made for the three other species of rorqual seen during the surveys. There were 14 sightings of the humpback whale, *Megaptera novaeangliae*, six sightings of the minke whale, *B. acutorostrata* and one sighting outside of the study area of the fin whale, *B. physalus* (Fig. 17).

Abundance estimation

The same methodology as in Wade and Gerrodette (1992) was used, with minor exceptions, but was applied to the pooled data set of all five years, rather than to each year separately. Estimates of population abundance (N_j) of stock j were computed by line-transect methods (Burnham *et al.*, 1980; Hiby and Hammond, 1989) as:

$$N_j = \sum_{k=1}^{4} N_{jk} \qquad (1)$$

where

$$N_{jk} = \frac{n_{jk} f_j(0)}{2L_k} \qquad (2)$$

and

N_{jk} = abundance estimate of stock j in stratum k,
n_{jk} = number of schools of stock j in stratum k,
$f_{jk}(0)$ = detection function of stock j in stratum k, evaluated at zero distance,
S_{jk} = mean school size of stock j in stratum k,
L_k = total effort in stratum k in kilometers,
A_k = total area in stratum k in square kilometers.

This represents a stratified analysis, where only cetacean sightings from stock j were used to calculate the density and therefore abundance of stock j within stratum k, with the abundance summed across the four strata for a total estimate for the stock.

In Wade and Gerrodette (1992), data were pooled across strata for the estimation of $f(0)$. The increased quantity of data obtained by pooling across years allowed, in some cases, a fully stratified analysis, where $f(0)$ was calculated separately for each stratum. However, not all stocks had enough sightings in every stratum. Therefore, where less than 50 sightings existed in a stratum, data were pooled across strata for the calculation of $f(0)$ until more than 50 sightings were available. The inshore and middle strata had similar levels of effort per unit area (9.3 and 10.1km/1000km^2, respectively), as did the west and south strata (3.7 and 5.6km/1000km^2, respectively). Therefore, where possible, these strata were pooled first. Details for each stock are explained below. A hazard rate model (Hayes and Buckland, 1983; Buckland, 1985) was fitted to the data to estimate $f_{jk}(0)$.

The standard error of N_j was estimated using bootstrap methods (Efron, 1982). Within each stratum and year, the total distance of searching effort was tabulated, and then legs of effort were randomly selected with replacement until that amount of effort was equaled. This effort and the associated sightings were then pooled across years and used to calculate $f_{jk}(0)$, S_{jk}, n_{jk} and finally N_j. This process was repeated 1,000 times. The standard error and coefficient of variation of N_j were calculated using these 1,000 estimates. A 95% confidence interval on N_j was estimated by the central 95% of the bootstrap estimates.

Proration of unidentified sightings

There were a number of sightings that were not identified to a stock but were identified to a broader category. Abundance estimates for these unidentified categories were prorated to every stock that was included in the broader category. A full description of the stocks in each category will follow. The general method used to calculate a revised abundance estimate N_j^* for stock j by prorating the sightings from these unidentified categories was:

$$N_j^* = \sum_{k=1}^{4} N_{jk}^* \qquad (3)$$

where

$$N_{jk}^* = N_{jk} + N_{uk}\left(\frac{N_{jk}}{N_{jk} + \sum_{i=1}^{m} N_{ik}}\right) \qquad (4)$$

and

N_{jk}^* = revised abundance estimate for stock j in stratum k,
N_{jk} = abundance estimate for stock j in stratum k using only identified sightings of stock j (from Eq. 1),
N_{uk} = abundance estimate for the unidentified category containing stock j in stratum k,
N_{ik} = abundance estimate(s) for other stock(s) also contained in the unidentified category in stratum k,
m = number of additional stocks also contained in the unidentified category.

Within each stratum, this represents a proration of the unidentified abundance estimate to each stock based on the ratio of the abundance estimate of that stock divided by the sum of the abundance estimates of all the stocks in that unidentified category. This proration method assumes that all stocks within a category had an equal probability of being unidentified when seen. There were six different unidentified categories, described below.

(1) Unidentified spotted dolphins

The northeastern stock of offshore spotted dolphin partially overlaps the range of coastal spotted dolphins, which extends out 185km (100 n.miles) from the west coast of Central America (Fig. 2; Perrin *et al.*, 1985). There were seven unidentified spotted dolphin sightings that occurred within the overlap region. An abundance estimate based on those seven sightings was prorated between these two stocks, using an $f(0)$ calculated from all spotted dolphin sightings within this overlap region. Eq. 4 was modified slightly to use an abundance estimate for northeastern spotted dolphins just within the overlap region with the coastal stock area. The range of the coastal spotted dolphin also partially overlaps the range of the western/southern stock of offshore spotted dolphin. No coastal spotted dolphins were seen in this overlap region during the surveys; therefore the one unidentified spotted sighting within this region was allocated to the western/southern stock of offshore spotted dolphin.

(2) Unidentified spinner dolphins

There were 16 unidentified spinner dolphin sightings within the region of overlap between the eastern and whitebelly stock areas (Fig. 3). An abundance estimate based on these 16 sightings was prorated between the two stocks, using an $f(0)$ calculated from all spinner dolphin sightings with the region of overlap. As in the case for unidentified spotted dolphins, Eq. 4 was modified slightly by using abundance estimates for the eastern and whitebelly stocks calculated just within the area of overlap, rather than abundance estimates from the entire stratum.

(3) Unidentified dolphin sightings

Sightings not identified to species or stock but known to be a dolphin due to body size or the presence of a distinct beak were categorized as unidentified dolphins. These were sightings that were lost before an adequate identification was made. Generally these represented sightings that were small in school size or were sighted at a large distance from the ship, or both. There were 701 of these sightings, from which an unidentified dolphin abundance estimate was made. This abundance estimate was prorated among the fourteen stocks in the Delphininae and Steninae: *Stenella* sp. (six stocks); *Delphinus delphis* (three stocks); *Lagenodelphis hosei, Tursiops truncatus; Steno bredanensis;* and *Grampus griseus*. The only other dolphin seen in the study area was the Pacific white-sided dolphin, *Lagenorynchus obliquidens*, of which there were only three sightings available for an abundance estimate, all at the northern extreme of the study area close to the coast of Baja, Mexico (Fig. 6). These sightings were ignored for this proration of unidentified dolphin sightings.

(4) Unidentified Ziphiids (beaked whales)

Over 97% of the 225 beaked whale sightings identified to genus or species were *Mesoplodon* (128) or *Ziphius cavirostris* (91) sightings. The other species identified were a bottlenose whale, *Hyperoodon* sp. cf H. *planifrons* (4) and Baird's beaked whale, *Berardius bairdii* (2). There were a total of 104 unidentified Ziphiid sightings, which could be prorated among all four stocks. However, the six sightings of *Hyperoodon* sp. and *Berardius bairdii* represent less than 3% of the total number of beaked whales identified to genus, and were ignored for this calculation. The abundance estimate for unidentified Ziphiids was therefore prorated between the two stocks of *Ziphius cavirostris* and *Mesoplodon* sp.

(5) Unidentified Balaenopteridae (rorquals)

Some whale sightings could be identified as rorquals, but were not identified to species. There were 97 of these sightings, categorized as unidentified Balaenopteridae (Fig. 19). Although all six rorqual species were seen during the surveys, only two, *B. edeni* (109 sightings) and *B. musculus* (31 sightings), were seen with enough frequency to estimate their abundance. The numbers of sightings of other rorquals were six humpback whales, *Megaptera novaeangliae*, six minke whales, *B. acutorostrata*, and one sighting of the fin whale, *B. physalus* north of the study area, which were insufficient numbers from which to estimate abundance, as required in Eq. 4. Therefore, Eq. 4 was modified slightly to prorate unidentified Balaenopteridae to *B. edeni* and *B. musculus*. The summation in the denominator on the right side of Eq. 4 was replaced by a pooled abundance estimate based on all rorqual sightings identified to species, excluding sightings of stock j. For example, for *B. edeni*, the summation was replaced by a pooled estimate from the sightings of *B. musculus*, *B. acutorostrata*, and *M. novaeangliae*, for a total of 44 sightings. Similarly, for *B. musculus*, the summation was replaced by a pooled estimate from the sightings of *B. edeni*, *B. acutorostrata*, and *M. novaeangliae*, for a total of 121 sightings.

(6) Unidentified large whales

There were also 82 whale sightings which were determined to be either sperm whales or rorquals but were not identified to species. These were termed unidentified large whales, and an abundance estimate from these sightings was prorated between sperm whales and rorquals. Again, abundance estimates were not available for the infrequently seen rorqual species, so a pooled estimate for all rorqual sightings was used to prorate this abundance estimate between *P. macrocephalus* and all rorquals, using Eq. 4. The amount prorated to all rorquals was further prorated to *B. edeni* and *B. musculus*, using the same term in parentheses on the right hand side of Eq. 4 as was used in prorating the unidentified Balaenopteridae sightings described in the previous section.

RESULTS AND DISCUSSION

A total of 135,324km of on-effort trackline was surveyed during the five years (Table 1) and approximately 4,600 cetacean sightings contributed to the abundance estimates. This resulted in an encounter rate of 32.2 cetacean schools per 1,000km. Total density of cetaceans in the ETP was estimated as 0.52 animal per km^2.

Table 1

Eastern tropical Pacific study area and survey effort. Area A_k (in thousands of square kilometers, from Holt and Sexton 1990a), % of total study area, achieved survey effort L_k (in thousands of kilometers) in each stratum, summed over the 5 surveys from 1986-90, % effort achieved in each stratum, and the target % effort as calculated in Holt *et al.* 1987.

	Inshore	Middle	West	South	Total
Area (1000km^2)	5693.0	3798.0	5298.0	4359.0	19148.0
Percent of Total	29.7	19.8	27.7	22.8	100.0
Effort (1000km)	52.8	38.0	19.8	24.4	135.3
Percent	39.0	28.3	14.6	18.0	100.0
Target percent	35.8	28.7	14.0	21.5	100.0

Abundance estimates for all 24 stocks, both before and after proration, are summarized in Table 2. Abundance estimates totaled 9.6 million animals for all species in the subfamilies Delphininae and Steninae (dolphins), 292,800 for all species in the subfamily Globicephalinae, 45,300 for all species in the family Ziphiidae (beaked whales), 33,881 for all species in the superfamily Physeteroidea (sperm and pygmy sperm whales) and 14,431 for both species in the family Balaenopteridae (rorquals).

The most numerous species was estimated to be *Delphinus delphis*, as the three stocks summed to 3,100,000, with the majority in the southern stock. When the three *Stenella* species were summed across stocks, each was estimated at 1,600,000–2,100,000 animals. In total, these four species were estimated to number 8,700,000. Estimated dolphin density (in animals per km^2) was 0.50 for the entire study area, and was highest in the south stratum (0.70), followed by the inshore (0.55), the west (0.38) and finally the middle stratum (0.35). The total estimated number of dolphin schools in the study area was 103,828, which represents a school density of 0.0054/km^2, or one school/185km^2.

The highest estimate for an individual stock was for the southern common dolphin, estimated at 2,100,000 with relatively large confidence limits. The second highest estimate was for the striped dolphin at 1,900,000, followed by the western/southern offshore spotted dolphin (1,300,000) and the whitebelly spinner dolphin (1,000,000).

Excluding the four most abundant species, the next highest dolphin estimates were for *Lagenodelphis hosei* (281,000) and *Tursiops truncatus* (226,200). The highest estimate for a small whale was for the pilot whale, *Globicephala* sp. (160,200); only 8,500 killer whales, Orcinus orca, were estimated to be in the ETP. Coefficients of variation (CV) ranged from 0.112 (*Stenella coeruleoalba*) to 0.636 (*Pseudorca crassidens*), with most being less than 0.40.

The most frequently encountered cetacean species was *Stenella coeruleoalba*, which was seen at the rate of 5.4 schools per 1,000km, followed by *S.attenuata* (4.1/1,000km) and *S.longirostris* (2.8/1,000km). The most frequently encountered small whale was *Globicephala* sp. (1.7/1,000km), while the most frequently encountered large whale was *Physeter macrocephalus* (1.0/1,000km).

Comparisons with previous estimates

The eastern tropical Pacific Ocean is a distinct oceanographic region characterized by a shallow thermocline and relatively high production (Fiedler *et al.*, 1991). The extensive line-transect efforts summarized here have produced the most comprehensive mammal and bird surveys ever undertaken in this part of the ocean. The estimates combine sightings between 1986 and 1990, and thus represent cetacean abundance averaged over five years. Annual estimates of dolphin abundance vary considerably from year to year (Buckland *et al.*, 1992; Wade and Gerrodette, 1992). Such interannual variability in the estimates is due to both sampling variability and to oceanographic variability associated with the El Niño-Southern Oscillation (Fiedler *et al.*, 1992).

For most of the species in this report (with the exception of the dolphins caught in the tuna fishery), previous estimates of abundance in tropical waters have been crude, or not possible at all from occasional sightings. The estimates of abundance in Table 2 are based on surveys specifically designed for marine mammals. Because the estimates are based on a statistical model, a coefficient of variation (CV; the ratio of the standard error to the point estimate) and a confidence interval are calculated for each estimate. The precision of the estimates of abundance varies considerably, with CVs ranging from 0.112 to 0.636. Estimates for the more frequently seen species tend to have lower CVs and shorter confidence intervals.

The most common cetaceans on these surveys were the spotted, spinner, common and striped dolphins. The large number of sightings made it possible to estimate population sizes separately for several stocks of these species. No estimate of the Central American subspecies of spinner dolphins (Perrin, 1990) was possible because our surveys had little effort in the limited area where that subspecies occurs (Fig. 3). We do compute an estimate for another geographically restricted subspecies, the coastal spotted dolphin, but we consider this estimate somewhat questionable because the distribution of search effort in its range near the coastline (Fig. 2) was not completely random, but tended to be concentrated near ports.

Total dolphin density was highest in the south stratum during these surveys. Previous estimates of abundance have generally shown highest dolphin school density near the Mexican and Central American coastline (Holt *et al.*, 1987; Polacheck, 1987), the inshore stratum in these surveys. Purse-seining has operated most intensively in this area, and historically the highest dolphin kills have been on the stocks that occur here, the northeastern spotted and eastern spinner dolphins (Smith, 1983). However, whether

Table 2

Abundance estimates for eastern tropical Pacific cetaceans in thousands of animals. N_j is the estimate based only on identified sightings of the stock. $N_j^*(int)$ represents intermediate pro-rated abundance estimates from three unidentified categories involving 6 stocks. N_j^* represents final abundance estimates, some of which were pro-rated from three unidentified categories. Note that the abundance estimates for species in the *Globicephalinae* and *Kogia simus* did not involve any pro-rating. *CV* represents the coefficient of variation for N_j^*. N_j^*U and N_j^*L represent, respectively, the upper and lower 95% bootstrap confidence limits, calculated using the percentile method (Efron 1982).

	N_j	N_j^*(int)	N_j^*	CV	$N_j^*{}_L$	$N_j^*{}_U$
Delphininae						
Stenella attenuata						
Northeastern spotted	663.3	668.8	730.9	0.142	588.7	970.4
Western/southern spotted	1258.9		1298.4	0.150	918.7	1654.1
Coastal spotted	25.6	27.2	29.8	0.346	15.1	50.8
Stenella longirostris						
Eastern spinner	568.1	583.5	631.8	0.238	389.5	938.3
Whitebelly spinner	988.6	992.2	1019.3	0.187	694.4	1456.2
Stenella coeruleoalba	1824.5		1918.0	0.112	1531.8	2249.3
Delphinus delphis						
Northern common	433.7		476.3	0.367	200.6	807.3
Central common	371.2		406.1	0.383	200.3	766.0
Southern common	2127.7		2210.9	0.217	1536.6	3488.2
Lagenodelphis hosei	281.5		289.3	0.335	138.0	508.1
Tursiops truncatus	226.2		243.5	0.286	190.9	409.9
Grampus griseus	164.1		175.8	0.381	90.0	375.4
Steninae						
Steno bredanensis	136.7		145.9	0.320	89.4	256.8
Globicephalinae						
Globicephala sp.			160.2	0.138	112.3	198.4
Peponocephala electra			45.4	0.467	34.2	110.3
Feresa attenuata			38.9	0.305	18.5	63.1
Pseudorca crassidens			39.8	0.636	11.5	109.5
Orcinus orca			8.5	0.368	4.7	15.9
Ziphiidae						
Ziphius cavirostris	16.1		20.0	0.265	13.8	34.5
Mesoplodon sp.	20.2		25.3	0.195	17.4	34.4
Physeteroidea						
Physeter macrocephalus	21.2		22.7	0.224	14.8	34.6
Kogia simus			11.2	0.294	7.7	16.2
Balaenopteridae						
Balaenoptera musculus	1.1	1.3	1.4	0.243	1.1	2.5
Baleanoptera edeni	9.9	12.0	13.0	0.202	8.9	19.9

there have been shifts in dolphin species composition and abundance and, if so, whether such changes are due to the incidental kill in the tuna fishery is uncertain.

The five-year combined estimates for spotted, spinner, striped, and common dolphins are close to, but not the same as, the average of the annual estimates of abundance for these species based on the same surveys (Wade and Gerrodette, 1992). The differences are due to (a) pooling data over all five years, (b) including unidentified sightings by proration, (c) changing stock definitions for the spotted and striped dolphins, and (d) slight changes in the data selection criteria. Populations of several stocks, notably the northeastern spotted and eastern spinner dolphins, have been considerably reduced as a result of mortality in tuna purse-seine nets (Smith, 1983; Wade, 1993), but indications are that populations have not, in general, been decreasing over the last ten years (Buckland *et al.*, 1992; Wade and Gerrodette, 1992).

Omura and Ohsumi (1974) estimated 1,340 blue whales in the North Pacific in 1970, and Wada (1975) estimated 1,600 whales for the 1973 season. These numbers were subsequently summarized by Gambell (1976) and most recently by Braham (1991). We estimate 1,415 blue whales in the eastern tropical Pacific area, with a 95% confidence interval from 1,078 to 2,501. The non-overlap in study area makes comparison with previous estimates difficult. The tropical blue whales may represent a second population center in the north Pacific Ocean, or they may be the same whales migrating seasonally between high and low latitudes. Because the surveys reported here took place from late July to November, one might expect that Northern Hemisphere blue whales would be at their high latitude feeding grounds during our surveys. The blue whales seen in our study area might thus represent a year-round population in high productivity areas (Reilly and Thayer, 1990) or, possibly, migrants from the Southern Hemisphere winter.

A ship survey in 1991 off the coast of California using the same procedures as described here has produced an estimate of 2,332 blue whales (J. Barlow, pers. comm., Southwest Fisheries Science Center, National Marine Fisheries Service, La Jolla, CA, 92308, USA). Because this survey took place at the same time of year as the ETP surveys, a minimum estimate of blue whale abundance in the eastern Pacific is the sum of these two point estimates, or 3,779 blue whales. An August ship survey and aerial surveys throughout the year did not find any blue whales off the coast of Oregon and Washington (Green *et al.*, 1992).

Many of the same comments apply when trying to interpret our estimate of sperm whale abundance. Recent estimates of the number of mature sperm whales in the eastern North Pacific are about 275,000 (Gosho *et al.*, 1984). Our total population estimate of approximately

23,000 with a 95% confidence interval of 14,791 to 34,639 is an order of magnitude lower, but applies to a different area. Sperm whales also undergo seasonal migrations, so the presence of these sperm whales in tropical water from August to November may, as with blue whales, either indicate a small resident tropical population or migrants from the Southern Hemisphere.

Based on sightings from commercial tuna vessels, Polacheck (1987) computed cetacean school encounter rates (schools encountered per 1,000 n.miles searched) in the eastern tropical Pacific. To produce an estimate of abundance from a school encounter rate one must also have estimates of school size and effective strip width (Eq. 1). Because both school size and effective strip width may differ by species, time and area, using school encounter rate as an index of relative abundance can be misleading. In Table 3 we have computed weighted mean school size, effective strip width (related to the ease of sighting each species) and the school encounter rate.

Although Polacheck's (1987) data were collected 10 years earlier, some comparisons of school encounter rates are interesting. For comparative purposes, we averaged the encounter rates over the four years of Polacheck's table 2 and converted from nautical miles to kilometers. For the three main dolphin species that associate with tuna and are therefore of primary interest to the tuna fishermen (spotted, spinner, and common dolphins), school encounter rates given by Polacheck are higher than our rates. For other cetacean species not used by the fishery, encounter rates given by Polacheck are all lower than our rates. These differences are probably related to the efficiency with which fishermen can find and report cetaceans of interest to them.

School sizes and effective strip widths

Although the stratified Equation 1 was used to calculate these abundance estimates, for ease of inspection and comparison between stocks, summary estimates of the parameters of Equation 1 are presented in Table 3. School size, f(0), and encounter rate are presented as mean values for the entire study area, calculated as appropriate weighted means of the four stratum values. Note that the parameter $f(0)$ is expressed as the 'effective strip width' (ESW) in km, which is equal to twice the inverse of $f(0)$. The hazard rate model provided an adequate fit to the data for estimating $f(0)$ in all cases except two: for *Pseudorca crassidens* (pooled estimate across all strata using 34 sightings, $p<0.05$, 1-tailed test, $chi^2 = 15.91$, df=8) and for one of two estimates of $f(0)$ for *Tursiops truncatus* (pooled estimate for the inshore and middle strata using 227 sightings, $p<0.01$, 1-tailed test, $chi^2 = 20.88$, df = 8).

The range in mean school sizes observed during these surveys is striking, ranging from just over two for *Ziphius cavirostris*, to nearly 500 for the southern stock of common dolphins (Table 3). The mean school size estimates may be positively biased because small schools are more likely to be missed than large ones. At least for the schooling dolphins, school size is a dynamic feature of behavior, changing with time of day (Scott and Cattanach,

Table 3

Mean school size, effective strip width in km (ESW, equal to 1/f(0) times 2), number of sightings going into the estimate of school density (n), and the school encounter rate per 1000km (ER). School size, effective strip width, and encounter rate are weighted mean values for the entire study area. Coefficients of variation for the estimates of school size and effective strip width are in parentheses.

	School size	ESW	n	ER
Delphininae				
Stenella attenuata				
Northeastern spotted	115.9 (0.09)	6.97 (0.11)	378	2.09
Western/southern spotted	149.4 (0.08)	4.27 (0.13)	210	1.88
Coastal spotted	75.0 (0.15)	5.04 (0.24)	16	0.09
Stenella longirostris				
Eastern spinner	111.7 (0.09)	5.17 (0.17)	236	1.34
Whitebelly spinner	134.1 (0.16)	3.70 (0.13)	154	1.47
Stenella coeruleoalba	60.9 (0.05)	3.40 (0.09)	799	5.39
Delphinus delphis				
Northern common	385.9 (0.23)	4.47 (0.37)	47	0.26
Central common	254.4 (0.13)	5.70 (0.36)	70	0.43
Southern common	472.8 (0.11)	2.99 (0.21)	92	0.70
Lagenodelphis hosei	394.9 (0.20)	6.06 (0.32)	25	0.23
Tursiops truncatus	22.7 (0.22)	3.85 (0.22)	298	1.98
Grampus griseus	11.8 (0.08)	1.89 (0.38)	194	1.45
Steninae				
Steno bredanensis	14.7 (0.18)	1.78 (0.19)	135	0.86
Globicephalinae				
Globicephala sp.	18.3 (0.08)	3.70 (0.13)	222	1.70
Peponocephala electra	199.1 (0.20)	8.26 (0.36)	14	0.10
Feresa attenuata	27.9 (0.12)	2.83 (0.20)	29	0.21
Pseudorca crassidens	11.4 (0.12)	1.72 (0.75)	34	0.31
Orcinus orca	5.4 (0.09)	5.28 (0.31)	57	0.43
Ziphiidae				
Ziphius cavirostris	2.2 (0.06)	1.71 (0.27)	91	0.67
Mesoplodon sp.	3.0 (0.11)	2.52 (0.14)	128	0.88
Physeteroidea				
Physeter macrocephalus	7.9 (0.17)	7.30 (0.16)	148	1.02
Kogia simus	1.7(0.07)	1.81 (0.15)	95	0.61
Balaenopteridae				
Balaenoptera musculus	1.5 (0.13)	5.19 (0.19)	31	0.20
Baleanoptera edeni	1.7 (0.07)	2.70 (0.27)	109	0.84

Submitted) and sometimes dramatically between years (Wade and Gerrodette, 1992).

The species with the largest average school sizes were *Delphinus delphis* and *Lagenodelphis hosei*, with mean school sizes all above 250 animals, and as high as 473 for the southern stock of *D. delphis*. Both offshore *Stenella attenuata* stocks, as well as both *Stenella longirostris* stocks, had mean school sizes above 110 animals. Since many of the spotted and spinner schools were actually part of the same school (70% of spinner schools were with spotted dolphins, while 50% of offshore spotted schools were with spinner dolphins), many of these schools numbered more than 300 animals. All four of these dolphin species were seen in schools greater than 1,000 animals, with the largest schools seen estimated to be about 4,000 for *D. delphis*, 2,400 for *S. attenuata*, 1,700 for *S. longirostris*, and 1,500 for *L. hosei*. The striped dolphin occurs in much smaller schools than its congeners, but was the most frequently encountered dolphin on our surveys, particularly in the south. The only other species with an average school size of more than 100 was *Peponocephala electra*, with a mean school size of nearly 200. Many of these schools of melon-headed whales were found in association with large schools of *L. hosei*, the Fraser's dolphin, forming some of the largest mixed-species cetacean schools observed during the surveys. For the larger whale species, mean group sizes were much smaller (approximately 8 for *Physeter macrocephalus*, 5 for *Orcinus orca*, 3 for *Mesoplodon* beaked whales, 2 for *Ziphius cavirostris, Balaenoptera edeni* and *Kogia simus,* and 1.5 for *Balaenoptera musculus*).

In line-transect theory, $f(0)$ is the value of the probability-density function evaluated at zero distance from the trackline. Twice the inverse of this number has an intuitive interpretation as the ESW covered along the trackline, and we have computed this width for each stock in Table 3. The width of this effective strip depends on a number of factors, such as sea state and size and behavior of the animals. A larger ESW means, roughly speaking, that the animals are easier to see, other things being equal. Viewed in this way, the ESW values in Table 3 are generally consistent with what we know of the behavior of the different species. Species that occur in large schools tend to have large ESWs – for example, Fraser's dolphins. The widest effective strip widths, all at more than 6km, were for *Stenella attenuata* (northeastern stock), *Lagenodelphis hosei, Peponocephala electra* and *Physeter macrocephalus. Delphinus delphis* stocks had relatively narrow ESWs considering the large schools in which they usually occur; this may be because common dolphins are not found in association with seabird flocks as often as spotted and spinner dolphins (seabird flocks act as a cue and make the school more likely to be seen).

Not surprisingly, the smallest ESWs in Table 3 belong to the beaked whales and the cryptic *Kogia simus*. Among the delphinids, *Steno bredanensis* and *Grampus griseus* have the narrowest strip widths; these species occur in small schools and are the least 'showy' of the delphinids in their behavior. The small whales are intermediate between these, with ESWs ranging from 1.4 to 3.3km. *Peponocephala electra* has the largest ESW among the small whales, probably due to the large schools in which it is found. *Orcinus orca* occur in small schools, but have prominent dorsal fins and behavior. *Globicephala* sp. also have relatively prominent dorsal fins. The narrowest ESWs among the small whales belong to *Pseudorca crassidens* and *Feresa attenuata*, which have neither prominent fins nor behavior.

The wide ESW for *Physeter macrocephalus* is probably due to its prominent and distinctive blow, and to the fact that it tends to occur in larger groups than the two rorquals. The difference in ESW between *Balaenoptera musculus* and *B. edeni* is probably due to the larger blow of the former.

Possible bias

Violations of the assumptions of the line-transect model may lead to biases in the estimates of abundance. Of primary concern is the assumption that all animals on the trackline are seen. This is usually expressed in terms of the detection probability $g(x)$ of an animal at distance x, with $g(0)=1.0$ meaning that it is certain that an animal on the trackline will be seen (Burnham *et al.*, 1980). If $g(0)$ is less than 1.0, the abundance will be underestimated unless $g(0)$ is explicitly estimated, which was not done here. Our estimates are unadjusted for animals missed on the trackline and are therefore likely to be underestimates of the true population sizes for some species. Although estimates of $g(0)$ are generally species and area specific, estimates for similar species from other studies may give some indication of the magnitude of the potential bias. The assumption that $g(0)=1.0$ is unlikely to be true for sperm and beaked whales because they have long dive times and may not be at the surface during the time the ship passes by. Kasamatsu and Joyce (1991) estimated that $g(0)$ for beaked whales in the Antarctic was 0.25–0.50. Therefore, our estimates of abundance for the beaked whales *Ziphius cavirostris* and *Mesoplodon* sp. and for the sperm whales *Physeter macrocephalus* and *Kogia simus* are likely underestimates, perhaps by as much as one half.

The rorquals (blue and Bryde's whales) may also be missed on the trackline due to submergence when the ship passes close to their position, although their dive times are much less than sperm and beaked whales. An independent-observer experiment estimated $g(0)$ for minke whales off Spitsbergen to be significantly less than 1.0 (Oien, 1990). However, the platform had an obstructed view, which was not the case on our research vessels, so it is uncertain how appropriate these g(0) estimates would be to our abundance estimates for blue and Bryde's whales. Schweder *et al.* (1991) estimated $g(0)$ as 0.43 for northeastern Atlantic minke whales using a parallel ship experiment, and Schweder *et al.* (1992) updated that analysis with additional data to estimate g (0) as 0.506 for the same population. These estimates for minke whales may have some relevance to our estimate of abundance of the slightly larger Bryde's whale. However, the tall visible blow of the blue whale makes it unlikely that they were frequently missed, as they were often seen at a great distance from the ship and probably did not stay submerged the entire time that they were in the field of view of the ship.

None of the other species were likely to stay submerged as a group for significant periods of time. The globicephalids were unlikely to be missed because of their prominent profile at the surface. It is possible that *Steno bredanensis* and *Grampus griseus*, because of their small school size and/or low profile in the water, may be occasionally missed close to the trackline. The smaller delphinids, spotted, spinner, common, striped, Fraser's and bottlenose dolphins, all tend to occur in large schools and have short dive times. It is unlikely that any such schools were missed on the trackline, although it may be possible for some of the smaller schools of striped dolphin. A limited independent-observer experiment during the 1990 cruise indicated that no large schools were missed on the trackline; if small schools are occasionally missed, it will have little effect on the estimates for these species.

For the small delphinids that have a large range in school size, another possible bias arises from the overestimation of mean school size due to the decreased probability of detection of smaller schools at greater perpendicular distance. A preliminary investigation indicated that some of the stocks have a significant relationship between school size and perpendicular distance, while some do not. A linear regression of the logarithm of school size against $g(x)$, the estimated probability of detection (Laake *et al.*, 1993), was performed for one stock from each of the four most abundant dolphin species. The eastern spinner stock did not have a significant regression, and therefore its school size estimate was not apparently biased in this way. However, the other three stocks did have significant regressions, indicating that their school size estimates, and hence abundance estimates, were biased. Estimates of the corrected school sizes were lower by 14% for the northeastern offshore spotted dolphin, 12% for the striped dolphin, and 33% for the central common dolphin. This indicates that there is a small bias for most of the small delphinid stocks, with the possibility of more substantial biases in the estimates of the species that can occur in very large schools, such as the common and the Fraser's dolphin. Future estimates of abundance for these species should fully utilize a school size correction method such as the regression technique used preliminarily here.

The estimate of mean school size may also be biased due to errors by the observers in estimating school size. However, aerial photography during the surveys has shown that, on average, observers estimated school size accurately, although for the largest schools there was a tendency to underestimate school size (Gerrodette and Perrin, 1991). Another source of bias could result from reaction of the dolphins to the ship before detection, leading to a negative bias if they avoided the ship or a positive bias if they were attracted to the ship. To be a significant bias, dolphin schools would have to perceive and react to the ship at a large distance, because the average detection distance from the ship was approximately 5km. Aerial observations on a limited number of ETP dolphin schools have shown that some dolphin schools turn away from the ship at more than this distance, but that most schools are detected by observers before they react to the ship (Au and Perryman, 1982; Hewitt, 1985). Therefore, ship avoidance behavior by the dolphins may result in a small negative bias in the estimates presented here.

In general, the proration of unidentified sightings to the groups in Table 2 had little effect on the estimates. This is because, for most species, unidentified sightings form a small part of the total sightings. The differences between estimates before (N_j) and after (N_j^*) assignment of the unidentified sightings are most noticeable with the beaked and rorqual whales. The number of unidentified sightings was higher for these species groups because: (1) beaked whales were hard to identify to species in the field, although relatively easy to determine that they belonged to the 'beaked whale' group; and (2) rorquals could be identified as such at a great distance, but the ship did not always 'close' on these sightings. The proration of unidentified rorquals to blue whales, which added about 200 to the abundance estimate (Table 2), may be an overestimate, because the observers were more likely to investigate and identify rorqual sightings with the potential to be a blue whale, such as those exhibiting a large blow.

The surveys were designed to estimate the abundance of pelagic dolphin populations. Consequently, the coast and continental shelf were not systematically surveyed, and may have been proportionally under-represented (Fig. 1). As previously mentioned, the study did not reliably survey the areas inhabited by the coastal spotted and the Central American spinner dolphins. This may also have lead to an underestimate of abundance of the bottlenose dolphin, as it was encountered more frequently very close to shore (Fig. 7). Also affected were probably the sighting rates of some of the rorqual species other than the pelagically distributed Bryde's whale. For example, many of the few humpback whale sightings were very close to the coast (Fig. 17), and humpbacks are known to winter and breed in Mexican waters (Urban and Aguayo-L, 1987) and off Costa Rica (Steiger *et al.*, 1991). Therefore, the distribution maps may not fully describe the occurrence of coastal species throughout the study area, as many coastal areas were not surveyed.

Distribution

The distributions of the three *Stenella* sp. and *Delphinus delphis* are well known from previous analyses, with *S. attenuata* (Fig. 2) and *S. longirostris* (Fig. 3) most abundant in warm, tropical waters, *D. delphis* (Fig. 5) most abundant in cold, upwelling-modified waters and *S. coeruleoalba* (Fig. 4) most abundant where the other three species are not, but without a strong correlation to one particular water mass (Reilly, 1990). One open question involves the stock identity of *D. delphis* seen farther west than 110°W in the central stock area, which are much closer to other sightings of *D. delphis* in the north stock area than they are to other sightings in the central stock area (Fig. 5). However, the central stock includes that offshore region because *D. delphis* in that region were bigger animals than those in the northern stock area, as were other *D. delphis* in the central stock area (Perrin *et al.*, 1985).

Lagenodelphis hosei has only recently been observed and recognized at sea, and earlier work speculated that its distribution in the eastern tropical Pacific would be similar to that of *Stenella longirostris* (Leatherwood *et al.*, 1988). All 33 sightings of *L. hosei* (25 used in the abundance estimate and eight 'off-effort') were south of 7°N (Fig. 6), and most were west of 100°W, far offshore, although there are other records of its occurrence in other parts of the ETP (Perrin *et al.*, In press). Therefore, the distribution of *L. hosei*, which is thought to be pantropical (Perrin *et al.*, In press), appears substantially different from the distribution of *S. longirostris* in the ETP (Fig. 3). Additionally, *L. hosei* appears to have an association with *Peponcephala electra*, as six of 18 sightings of *P. electra* were schools in which *L. hosei* and *P. electra* were found together. However, *P. electra* was also seen alone several times within the Gulf of Panama (Fig. 6) where *L. hosei* was absent, indicating *P. electra* are not restricted to equatorial waters, as previously thought (Au and Perryman, 1985). The association between *L. hosei* and *P. electra* has also been noted in other parts of the world (Perryman *et al.*, In press). *Lagenorhynchus obliquidens*, which occurs throughout much of the North Pacific (Leatherwood *et al.*, 1988), was seen only at the northern extreme of the study area (Fig. 6).

The three other small delphinids were found throughout most of the ETP. *Tursiops truncatus* was seen more frequently close to shore but was widespread in the ETP except offshore along 5°N latitude (Fig. 7), which suggests the offshore population may be divided into two populations, one north and one south of that parallel. *Grampus griseus* was seen most frequently in the shelf waters off Mexico and Guatemala, in the Gulf of Panama, and in the Peru current (Fig. 8). *Steno bredanensis* was seen at low densities everywhere except in the coldest parts of the Peru and California currents, where it was absent, with the most sightings in the warmest water close to the Mexican coast (Fig. 9), confirming its affinity for warm, tropical waters (Leatherwood *et al.*, 1988).

Globicephala sp. (probably all *G. macrorhynchus*, or nearly so, as discussed above) were most abundant in cold, upwelling-modified waters, and were absent from the warmest tropical waters off the Mexican coast (Fig. 10). There was a clear separation between short-finned pilot whales seen south of 15°N and those seen off the coast of Baja, Mexico (Fig. 10). These are likely to be separate stocks, and it is possible that the two populations represent two different forms in an analogous way to the cold-water and warm-water forms of short-finned pilot whales found in the western Pacific near Japan (Kasuya *et al.*, 1988). *Orcinus orca* was seen at low densities throughout the ETP, as were *Pseudorca crassidens* and *Feresa attenuata* (Fig. 11). However, more *P. crassidens* sightings were far offshore, while more *F. attenuata* sightings were close to the coast in the warmest water (Fig. 11). These patterns fit with what was known of their distributions (Leatherwood *et al.*, 1988).

Ziphius cavirostris was relatively abundant and found throughout the ETP (Fig. 12). Three sightings of *Mesoplodon peruvianus*, described from stranded animals in Peru (Reyes *et al.*, 1991) were seen, two off Peru and one off Mexico (Fig. 13). This agrees with the recent account of the first record of this species in the North Pacific, on the coast of Mexico (Urbán-Ramírez and Aurioles-Gamboa, 1992). *M. densirostris* was confirmed to have a fairly pelagic distribution (Leatherwood *et al.*, 1988), and appears to be distributed mostly in the southern portion of the ETP, as all 16 sightings of *M. densirostris* were south of 10°N (Fig. 13). Most of the 25 sightings of *Mesoplodon* sp. 'A' were off Mexico, although it was also seen off Central and South America, but not far offshore (Fig. 13). *Hyperoodon* sp. cf *H. planifrons*, previously described as having a population along the equator in the central Pacific (Leatherwood *et al.*, 1988), was seen only at 2°, 4°, 5° and 15°N, extending the known northern limit for this whale in the Pacific (Fig. 14). *Berardius bairdii*, which has a more northerly distribution (Leatherwood *et al.*, 1988), was only seen along the coast of Baja California, Mexico (Fig. 14).

Physeter macrocephalus was found throughout the ETP, but appeared to be most abundant in the Gulf of Panama (Fig. 15), formerly one of the primary sperm whaling grounds in the eastern Pacific (Leatherwood *et al.*, 1988). *Kogia simus* was also found throughout the ETP, but was seen most frequently near the coast (Fig. 16). *Balaenoptera musculus*, as has been previously described, was found in colder, nutrient-rich water of the California and Peru currents and the Costa Rican Dome (Reilly and Thayer, 1990; Fig. 17). *Megaptera novaeangliae* was similarly seen in the California and Peru currents, but was not seen in the Costa Rican Dome area, although it was seen once in the Gulf of Panama and once along the coast of Guatemala (Fig. 17). *Balaenoptera edeni* was widespread in its distribution, but appeared to have a hiatus in distribution from north to south, as no sightings were made between 7° and 9°N (Fig. 18). This suggests the possibility that there may be two stocks of *B. edeni* in the ETP. *B. acutorostrata* was only seen in the California and Peru currents, while *B. physalus* was only seen once, north of the study area along the coast of Baja, Mexico (Fig. 17). The majority of the unidentified *Balaenoptera* sp. sightings were probably *B. edeni*, or possibly *B. musculus* in the regions where it was found (Fig. 19).

ACKNOWLEDGEMENTS

Surveys on this scale require an enormous amount of work by many people over a long period of time, and it is impossible for us to thank individually all of the people responsible for the surveys' success. However, we wish to single out Douglas DeMaster, Rennie Holt, Stephanie Sexton, Scott Hill, and Alan Jackson for their contributions to the planning, execution, and analysis of the surveys. We particularly want to acknowledge the marine-mammal observers aboard both vessels; they collected the primary data on which these analyses are based, and the high quality of the data is largely due to their dedication and hard work. We would also like to thank Jay Barlow for providing the algorithm for fitting the hazard rate model, Howard Braham for references to recent whale literature, and James T. Enright and William F. Perrin for helpful comments and suggestions about the manuscript. Collectively we thank all of the other people at the Southwest Fisheries Science Center, as well as the officers and crews of the NOAA ships *David Starr Jordan* and *McArthur*, for their support.

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Legends for Figs. 2–5

Fig. 2. Sightings of the three spotted dolphin (*Stenella attenuata*) stocks, showing offshore spotted dolphins (squares); coastal spotted dolphins (pluses); and unidentified spotted dolphins in the coastal stock area (triangles). The dashed line represents the dividing line within the study area for assigning sightings to the offshore stocks, with all offshore spotted sightings to the north and east of the line assigned to the northeastern stock (northeast), and offshore sightings to the south and west of the line assigned to the western/southern stock (west/south). The coastal stock boundary is the solid line paralleling the coast 185km (100 n.miles) offshore.

Fig. 3. Sightings of the two spinner dolphin (*Stenella longirostris*) stocks, showing eastern spinner dolphins (open squares); whitebelly spinner dolphins (pluses); and unidentified spinner dolphins in the overlap area (filled triangles). Eastern refers to the area occupied by the eastern spinner dolphin, represented as a dotted line. Whitebelly refers to the area occupied by the whitebelly stock, represented as a dashed line. Overlap refers to the area of overlap between the eastern and whitebelly stock areas. Central Amer. refers to the stock area of the Central American spinner, in which there was little effort during the survey, and consequently no spinner dolphin sightings.

Fig. 4. Sightings of the striped dolphin, *Stenella coeruleoalba* (squares).

Fig. 5. Sightings of the three common dolphin (*Delphinus delphis*) stocks, showing shortbeak (or 'offshore') common dolphins (open squares); longbeak (or 'Baja neritic') common dolphins (open circles); and unidentified common dolphins (pluses). The two dashed lines represent the dividing lines within the study area for assigning common dolphin sightings to stocks. All sightings in the north area were assigned to the northern stock, in the central area to the central stock, and in the south area to the southern stock. Note that two morphological types, shortbeak and longbeak, are both in the northern stock (see text for explanation).

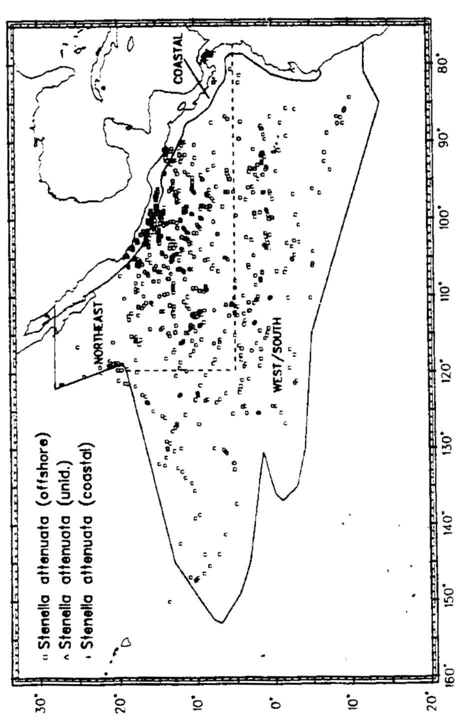
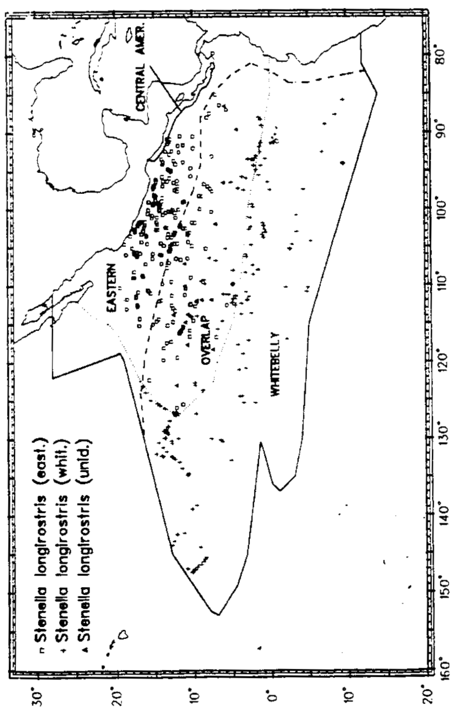


Fig. 2.



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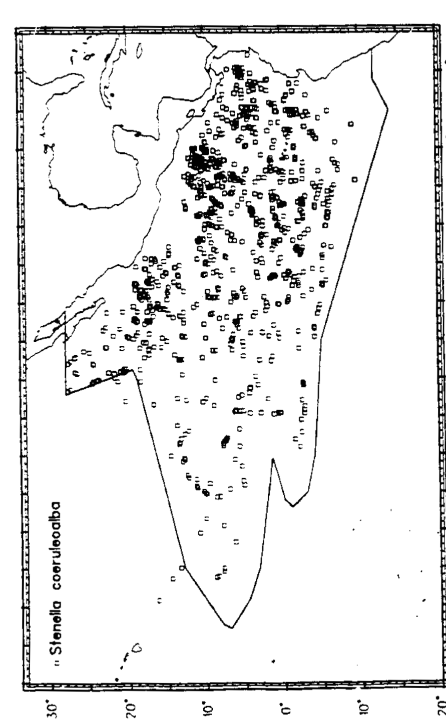

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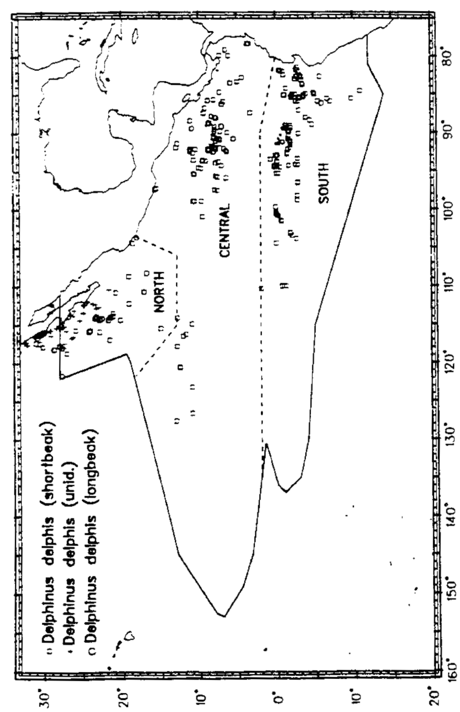

Fig. 5.

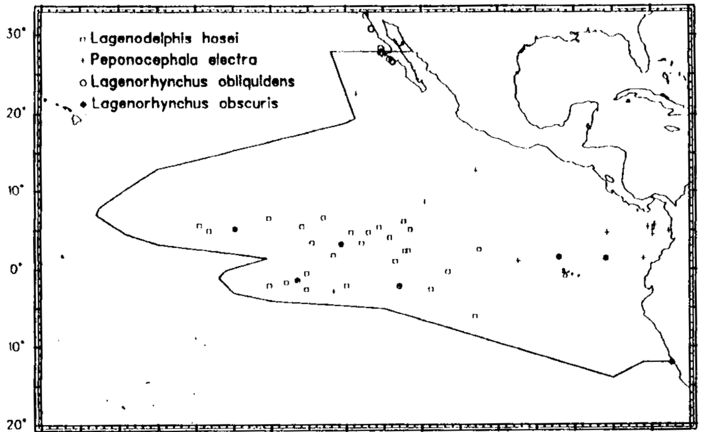

Fig. 6. Sightings of Fraser's dolphin, *Lagenodelphis hosei* (open squares); the melon-headed whale, *Peponocephala electra* (pluses); the Pacific white-sided dolphin, *Lagenorynchus obliquidens* (open circles); and the dusky dolphin, *Lagenorynchus obscurus* (filled diamond).

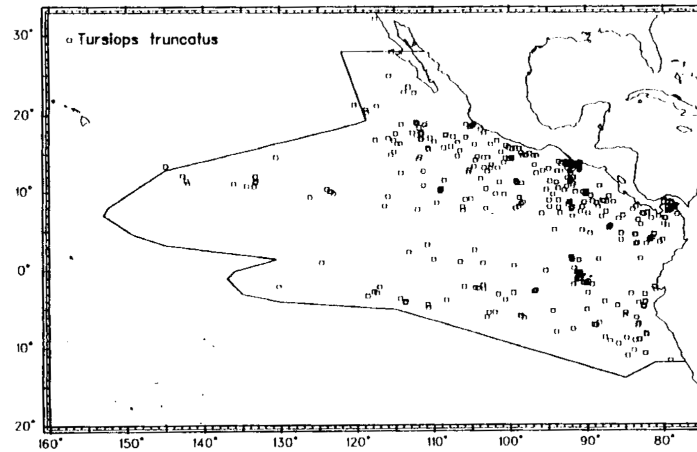

Fig. 7. Sightings of the bottlenose dolphin, *Tursiops truncatus* (squares).

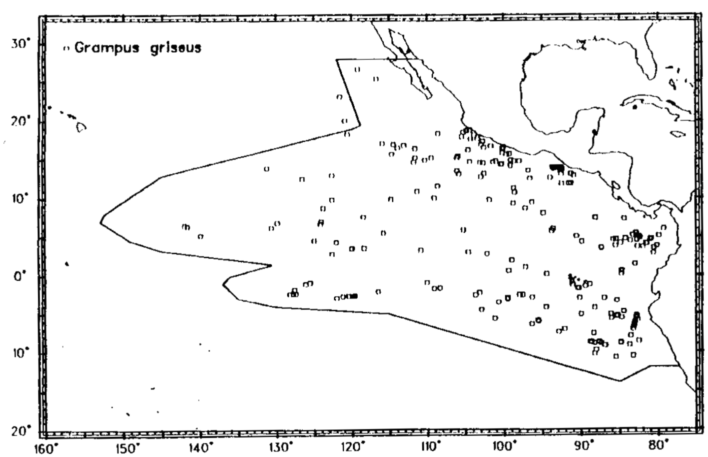

Fig. 8. Sightings of Risso's dolphin, *Grampus griseus* (squares).

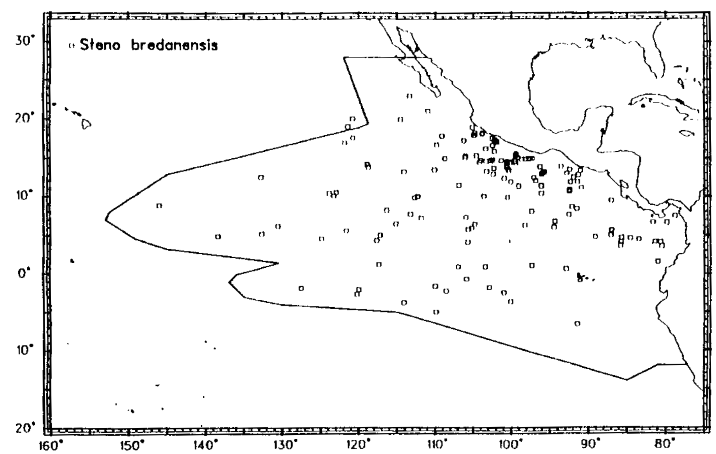

Fig. 9. Sightings of the rough-toothed dolphin, *Steno bredanensis* (squares).

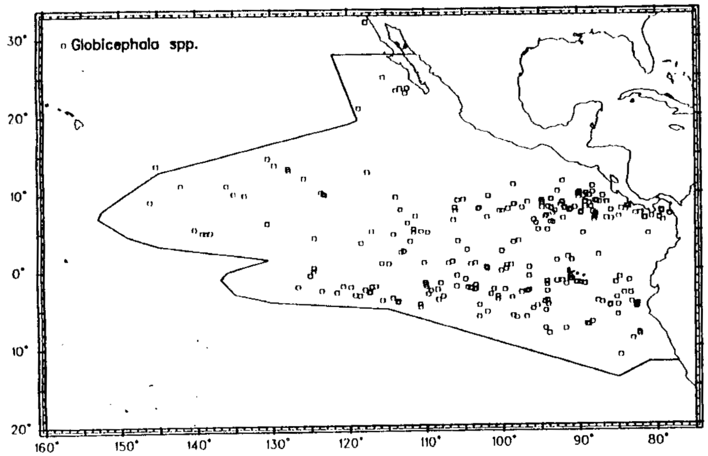

Fig. 10. Sightings of pilot whales, *Globicephala* sp. (squares).

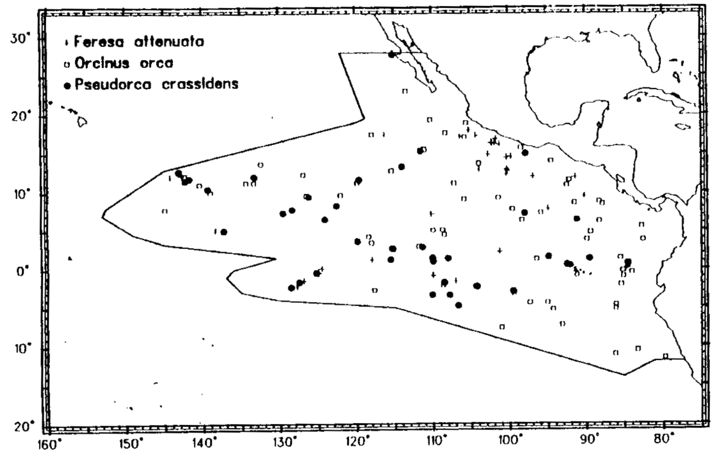

Fig. 11. Sightings of the pygmy killer whale, *Feresa attenuata* (pluses); the killer whale, *Orcinus orca* (squares); and the false killer whale, *Pseudorca crassidens* (filled circles).

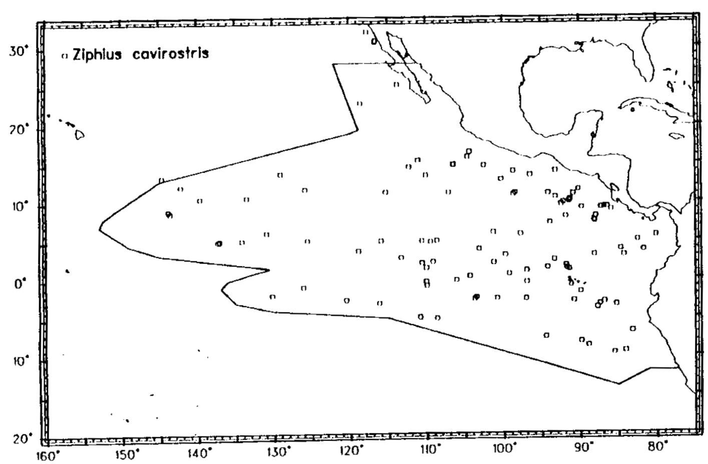

Fig. 12. Sightings of Cuvier's beaked whale, *Ziphius cavirostris* (squares).

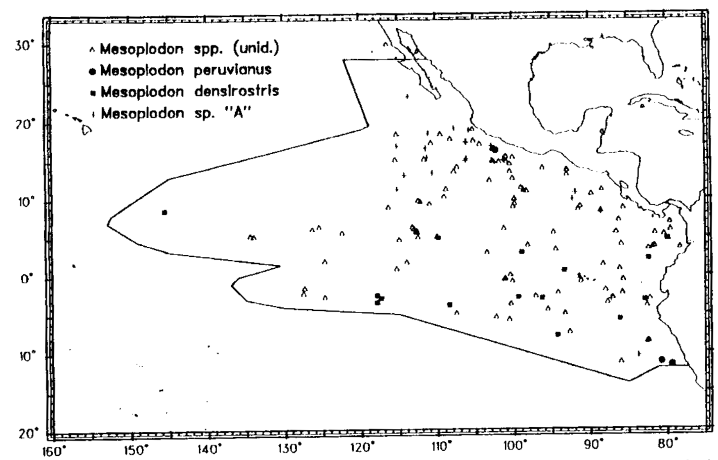

Fig. 13. Sightings of unidentified beaked whales, *Mesoplodon* sp. (open triangle); the pygmy beaked whale, *Mesoplodon peruvianus* (filled circles); Blainville's beaked whale, *Mesoplodon densirostris* (filled squares); and a possible new *Mesoplodon* sp. (Pitman *et al.*, 1987), called here sp. 'A' (pluses).

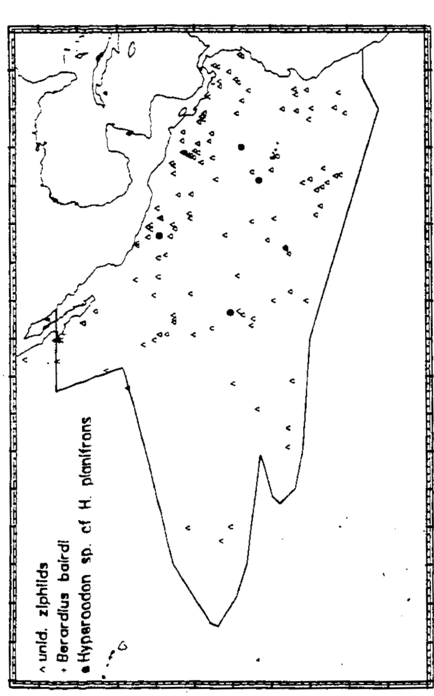

Fig. 14. Sightings of unidentified beaked whales, (ziphiids) (open triangles); Baird's beaked whale, *Berardius bairdi* (pluses), and a bottlenose whale, *Hyperoodon* sp. cf *H. planifrons* (filled circles).

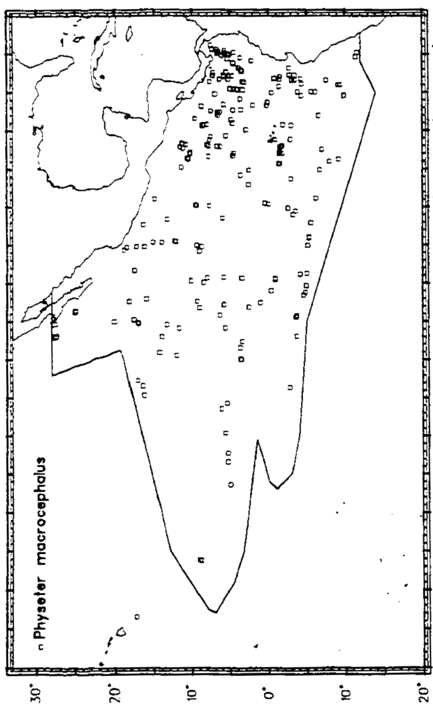

Fig. 15. Sightings of the sperm whale, *Physeter macrocephalus* (squares).

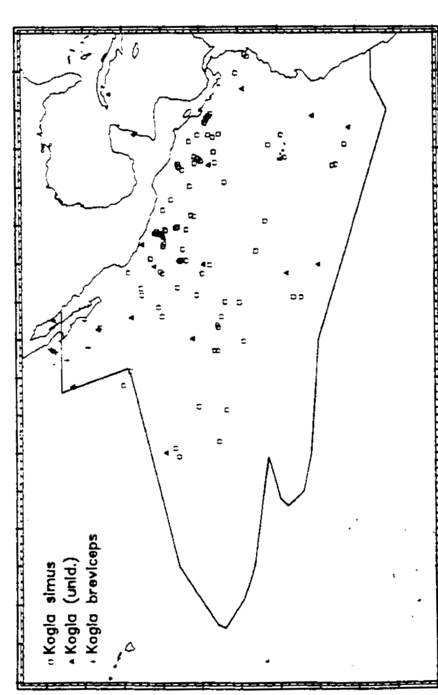

Fig. 16. Sightings of the dwarf sperm whale, *Kogia simus* (open squares); the pygmy sperm whale, *Kogia breviceps* (pluses); and unidentified *Kogia* (filled triangles).

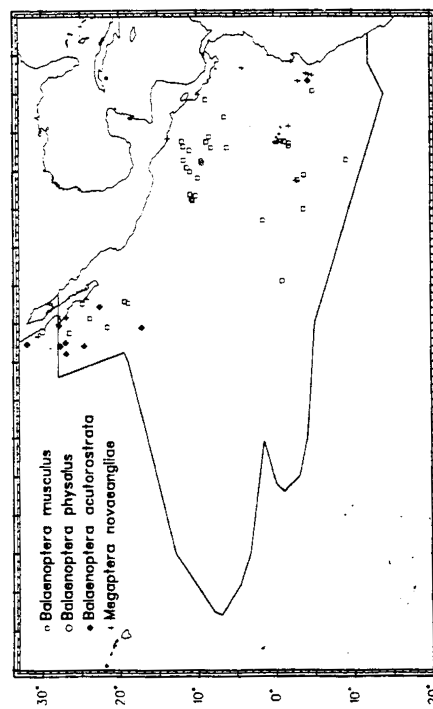

Fig. 17. Sightings of the blue whale, *Balaenoptera musculus* (open squares); the fin whale, *Balaenoptera physalus* (open circle); the minke whale, *Balaenoptera acutorostrata* (filled diamonds); and the humpback whale, *Megaptera novaeangliae* (pluses).

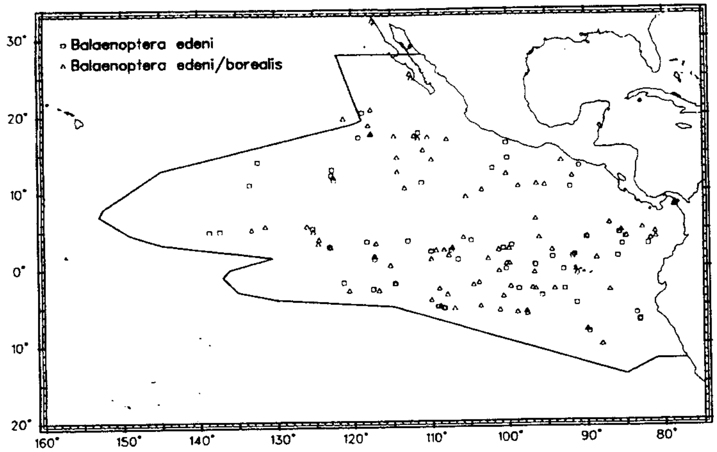

Fig. 18. Sightings of Bryde's whale, *Balaenoptera edeni* (open squares) and rorquals identified as either a Bryde's or a sei whale, *Balaenoptera edeni/borealis* (open triangles; see text for explanation).

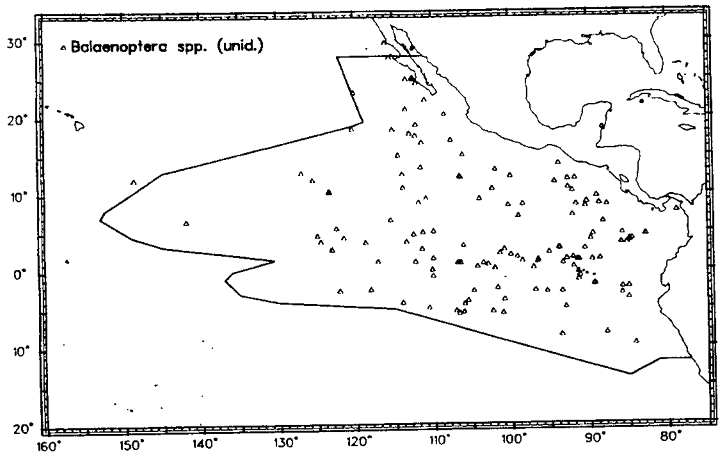

Fig. 19. Sightings of unidentified rorquals, *Balaenoptera* sp. (triangles).

ERRATA

For reasons outside our control, a number of errors found their way into paper SC/44/O 18.

p.478 **Data selection** Delete contents of bracket at end of 2nd sentence
p.478 **Stocks estimated** Last line, for 'Balaenoptera' read 'Balaenopteridae'
p.479 *Subfamily* **Globicephalinae**, for *Globicephala* sp. read *Globicephala* spp., throughout
p.479 *Family* **Ziphiidae**, for *Mesoplodon* sp. read *Mesoplodon* spp. throughout
p.480 Equation 2 should read

$$N_{jk} = \frac{n_{jk} f_{jk}(0)}{2L_k} \quad S_{jk} A_k$$

p.481 (2) *Unidentified spinner dolphins*, line 5, for 'with' read 'within'
p.481 (5) *Unidentified Balaenopteridae* (rorquals), line 4, for 'six' read 'five'; line 21, for '44' read '43'
p.482 2nd column, 2nd para. add reference to Table 3
p.483 Table 2 legend $N_j{}^*U$ and $N_j{}^*L$ should read N^*_{jU} and N^*_{jL}
p.487 line 19 for 'Baja, Mexico' read 'Baja, California, Mexico', throughout
p.487 Reference to Gerodette and Perrin, 1991, delete *Deep-Sea Res.* 39:199-219
p.488 Delete reference to Tobayama *et al.* 1992.