Abundance and distributional ecology of cetaceans in the central Philippines

M. Louella L. Dolar*, William F. Perrin+, Barbara L. Taylor+, Gerald L. Kooyman# and Moonyeen N.R. Alava++

Contact e-mail: Ldolar@san.rr.com

ABSTRACT

In general, little is known about cetacean abundance and distribution in Southeast Asia. This paper investigates the species composition, interactions/associations, abundance and distribution of cetaceans in an archipelagic tropical habitat characterised by deep, oceanic waters approaching the shore, high water temperatures and deep, stable thermoclines. Abundance is estimated using line transect methods. In addition, the cetacean fauna of the Sulu Sea is compared with those of other tropical marine ecosystems: the eastern tropical Pacific, the western Indian Ocean and the Gulf of Mexico. The most abundant species in the two study sites (eastern Sulu Sea and the Tañon Strait) was the spinner dolphin, *Stenella longirostris*; with a population estimate of 31,512 (CV=26.63%) in the eastern Sulu Sea and 3,489 (CV=26.47%) in the Tañon Strait. Other abundant species were the pantropical spotted dolphin (*S. attenuata*), Fraser's dolphin (*Lagenodelphis hosei*) and the short-finned pilot whale (*Globicephala macrorhynchus*). Density and species-abundance rank varied between the two study sites, with generally higher densities in the Sulu Sea than in the Tañon Strait. An exception was the dwarf sperm whale, *Kogia sima*, whose density was 15 times higher in the Tañon Strait. Fraser's dolphin ranked third in abundance in the Sulu Sea but was absent from the Tañon Strait. Environmental factors such as depth, site and temperature were observed to have a significant influence on the distributions of various species.

KEYWORDS: SPINNER DOLPHIN; PANTROPICAL SPOTTED DOLPHIN; FRASER'S DOLPHIN; PILOT WHALE; DWARF SPERM WHALE; MELON-HEADED WHALE; RISSO'S DOLPHIN; BOTTLENOSE DOLPHIN; BRYDE'S WHALE; ROUGH-TOOTHED DOLPHIN; PYGMY KILLER WHALE; SPERM WHALE; ECOLOGY; HABITAT; SULU SEA; TAÑON STRAIT; ASIA; SURVEY-VESSEL; *g*(0); ABUNDANCE ESTIMATE; DISTRIBUTION; SCHOOL SIZE

INTRODUCTION

With few exceptions, there is a general lack of information on cetacean habitat, abundance and distribution in Southeast Asian waters. Habitat degradation and cetacean bycatch in numerous fishing operations are widespread and are possibly threatening many dolphin populations in the region (Perrin *et al.*, 2005). One of the reasons for this lack of information is the high cost of abundance surveys. Line transect surveys mounted by developed countries use large ships suitable for high-seas travel, with high sighting platforms and long cruising ranges (e.g. Wade and Gerrodette, 1993; Barlow, 1995; Forney *et al.*, 1991; Jefferson, 1995). These surveys are often prohibitively expensive for developing countries. The survey methods used here follow the same distance-based approach (e.g. Buckland *et al.*, 1993) as the studies mentioned above but modified to utilise a small boat with a relatively low sighting platform and shorter cruising range in order to reduce costs. Estimates of abundance are critical to assessing the impacts of fisheries known to incidentally kill cetaceans (Dolar, 1994).

Sites included in this study were habitats that are more or less representative of the Philippines (Fig. 1): deep, oceanic waters close to shore (as seen in the Sulu Sea); narrow, semi-enclosed areas with terraced slopes (the Tañon Strait); and shallow, flat areas contiguous to deep waters (northeastern part of the Sulu Sea). The Sulu Sea and the Tañon Strait are connected via the Mindanao Sea and are only approximately 85km apart. It is assumed that large, highly mobile animals such as cetaceans can move freely between them, but whether the species assemblages, relative densities and species associations of cetaceans in these two areas are similar has not been known. These questions are addressed by comparing and contrasting the cetacean fauna in the two marine habitats, including species composition, abundance or relative density and associations among species and relating these patterns to physical parameters such as water depth and water temperature. The cetacean fauna of the Sulu Sea was also compared to faunas in other tropical oceans/seas to broaden the understanding of tropical cetacean habitats.

The study sites

The study sites were the eastern part of the Sulu Sea with an area of 23,014km², or approximately 9% of the total Sulu Sea's area of approximately 250,000km², and all of the Tañon Strait with an area of 4,544km² (Fig. 1). The Sulu Sea is a semi-isolated deep marine basin completely surrounded by a shelf, most of which is shallower than 100m (Linsley *et al.*, 1985). Shallow straits connect it to the South China Sea, the Pacific Ocean and the Celebes Sea. In general, surface water of the basin exhibits high temperature (27-28°C), low salinity (34.2-34.4 ppt) and a deep, stable thermocline, located at about 250m (Linsley *et al.*, 1985), that gets uplifted during tropical cyclones (Frische and Quadfasel, 1990). Deep waters approach very close to shore.

The Tañon Strait in contrast is much smaller and shallower. It is only 15-27km wide and 220km long. The deepest portion (~555m) is central (Hayasaka *et al.*, 1987) and extends south. Although the near-surface circulation is also subjected to the seasonal reversal of the monsoon

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[*] *Tropical Marine Research for Conservation, 6363 Lakewood St., San Diego, CA 92122, USA.*
[+] *Southwest Fisheries Science Center, NMFS, NOAA, 8604 La Jolla Shores Drive, La Jolla, California, 92037, USA.*
[#] *Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California, CA 92037, USA.*
[++] *Conservation International-Philippines, 6 Maalalahanin St., Teachers Village, Quezon City, Philippines.*

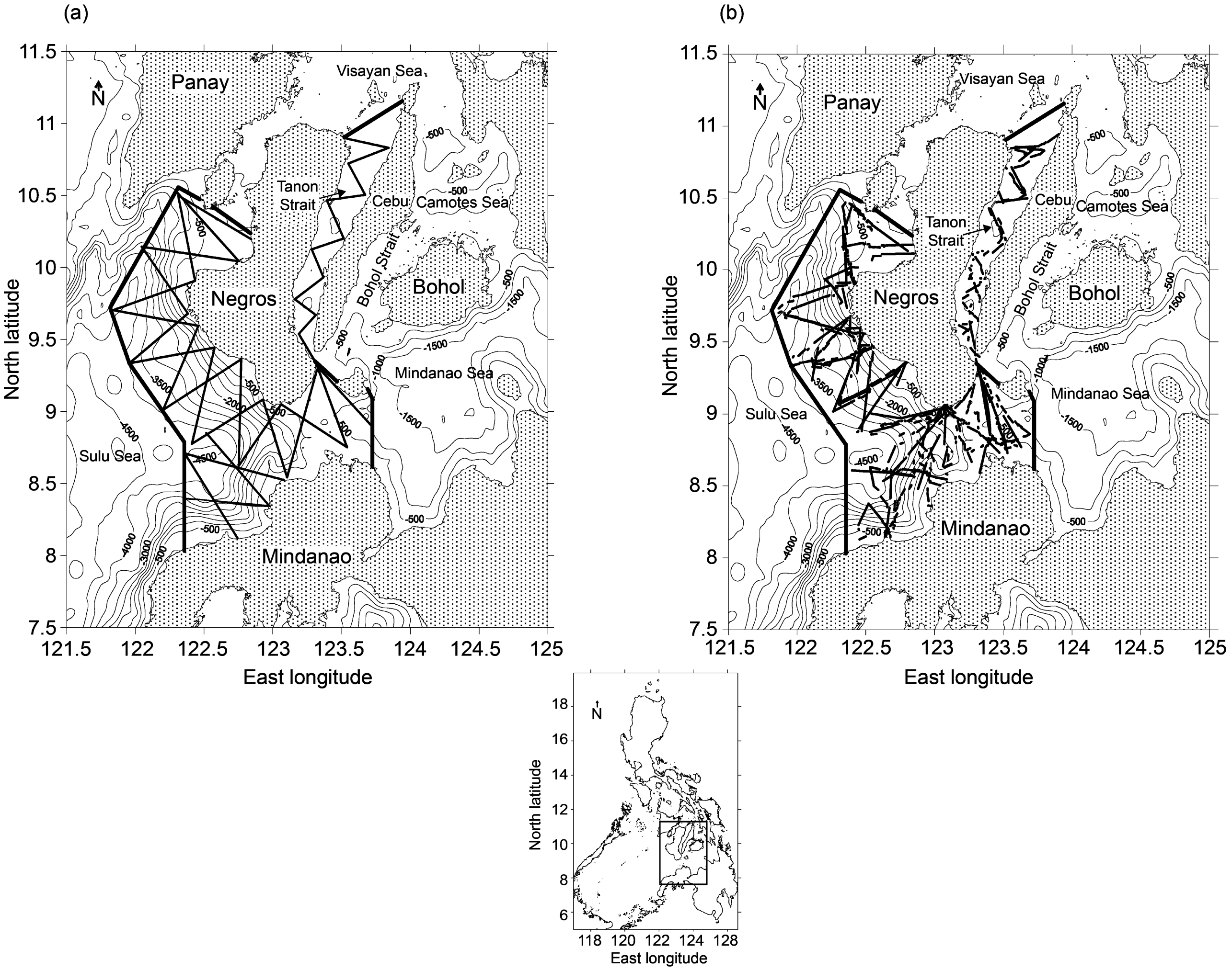


Fig. 1A. The study sites and planned tracklines, B. completed tracklines. Boundaries (thick lines) of study sites are shown. Mapping with SURFER 7.0.

winds, the strait is partially protected by the islands of Negros and Cebu. Sea surface temperature (SST) is about 30°C, gradually decreasing to about 25°C at 100m (Hayasaka *et al.*, 1983). The temperature from 200m to the bottom is relatively stable at about 17°C. The salinity is 32-34 ppt and the thermocline is 100-150m deep. Transverse and longitudinal profiles of the strait show very steep slopes with submarine terraces (Hayasaka *et al.*, 1983).

Both sites belong to the ecoregion with the highest marine biological diversity in the world. The interesting bottom topography in the Sulu Sea provides a rich and dynamic ecosystem of coral reefs, seamounts, seagrasses, lagoons, steep slopes and deep sea communities that supports a myriad of marine organisms. It shares with its contiguous Sulawesi Sea more than a thousand species of fish, 500 species of corals, about 400 species of algae, possibly up to 30 species of marine mammals and 5 species of marine turtles. It also has one of the two most important turtle breeding and nesting sites in Southeast Asia. The Tañon Strait, though much smaller, is home to more than 70 species of fish and over 20 species of crustaceans (Dolar, 1991; Fishbase website *http://www.fishbase.org/search.php*). Its narrow shelf is fringed with intermittent strands of coral reefs, mangroves and seagrasses. It has a thriving squid fishery and an abundant nautilus population.

MATERIALS AND METHODS

Survey

Cetacean distribution and abundance were determined using line transect methods developed to estimate abundance of small cetaceans in the eastern tropical Pacific (Holt, 1987; Wade and Gerrodette, 1993). These methods were modified to suit the local conditions and the resources available. Since the boat used was relatively small and the area surveyed was not safe from dangers of piracy and possibility of being run over by large ships, drifting at sea at night was not an option. To maximise the distance covered from shore seaward, yet still being able to dock on shore at night, our transect lines were systematically designed in a continuous zigzag or sawtooth design based on waypoints along the boundaries of the study sites. This type of design is recommended for efficiency when time and/or cost of a survey platform are an issue (Buckland *et al.*, 2001). The systematic spacing of the zigzag lines did not coincide with a regular topographic or spatial feature. Twenty four 60-70km long transect lines were traversed in the Sulu Sea extending from the coast seaward set at 20km apart at their base, with 22 lines approximately 20km long and 30km apart at their base in the Tañon Strait (Fig. 1A).

To assure good sighting conditions, surveys were carried out during the break between the two alternating monsoon seasons, i.e. 9-27 May 1994 (Sulu Sea) and 3 May-5 June 1995 (Sulu Sea and the Tañon Strait), using a 20m boat with a sighting platform 2.5m above the water at a cruising speed of 17-20km hr^{-1}. Some segments of the trackline were cancelled due to three days of bad weather. Five observers rotated through four primary positions (positions 1-4) on an hourly basis and took a break on the fifth hour, and two additional observers alternated on position 5 on an hourly basis (Fig. 2). The five positions and their coverage were as follows:

position 1: In front using 20x spotting binoculars mounted on the deck of the boat; covered 180°;

positions 2 and 3: Using 10x handheld binoculars; covered 90° from directly in front to the right and the left sides of the boat;

position 4: In the bow of the boat (without binoculars) guarding the trackline;

position 5: A professional dolphin spotter (ex dolphin hunter) who scanned the waters 180° forward to the horizon without using binoculars.

Searching covered the entire region from directly in front of the vessel to 90° left and right and out to the horizon. Two other members were assigned permanently to record data and navigate. Four of the seven observers were present in both years of survey.

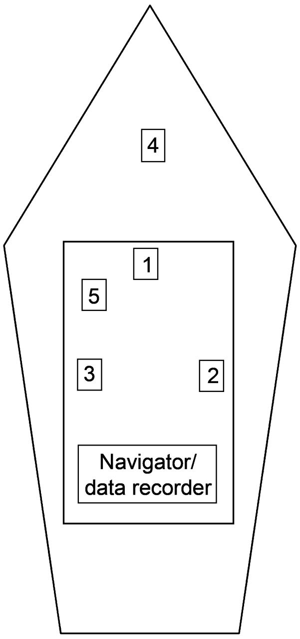


Fig. 2. Observer positions during the survey.

When an observer saw a positive cue (e.g. splash, blow or the animals), all observers were alerted to the animal's location and searching effort was suspended. Vessel position was noted using the global positioning system (GPS) and the angle of the sighting to the trackline was measured using binoculars with a compass (*Fujinon* 7 × 50 FMTRC). The best estimator as determined by previous training and exercises estimated the distance to the sighting. Distances were also measured using the GPS whenever animals were seen to be just logging on the surface. Deviations between estimated and measured distances were then determined. The binocular reticle scale was not used to estimate distance because the sighting platform was so low that pitching of the boat greatly affected the reading and islands also often obscured the horizon. Sightings were approached and the species (collectively decided by the team), group size and exact location of the animals were recorded. Photographs and behavioural notes were also taken. The trackline was then resumed by following a convergent course towards the end of the trackline leg, rather than returning to the exact point where the sighting was made. Sighting effort was maintained between 06:00 and 18:00 hours whenever weather conditions allowed (Beaufort sea state 0-4).

Auxiliary data were recorded: time, geographical location, boat speed and bearing, viewing conditions (sea state, wind direction, sun position, visibility and presence of rain or fog) and observer's identification and position. This information was updated hourly or whenever conditions changed. The tenth member of the team recorded SST and salinity hourly and at locations of sightings, using a bucket thermometer and a refractometer.

Analysis

The program *REPORT*, developed by the Protected Resources Division of the Southwest Fisheries Science Center, was used to summarise information on the total number of sightings, the species sighted, average school size for each species, species association, total distance of effort covered, sighting rates at different Beaufort sea states and perpendicular distances needed for density and abundance estimations. The total areas of the study sites were estimated using *ArcView GIS* (3.0).

Calibration of distance estimates

The regression between the distance estimated by eye and the GPS-measured distance was significant (R^2= 0.996 and P<0.001) with a slope of 0.851 that differed significantly from zero (one tailed t-test [α= 0.05] P<0.005; Fig. 3). The distances estimated by eye were corrected using the inverse prediction method (Zar, 1996) in order to be able to gauge the general magnitude of how systematically biased observer distance estimates may affect abundance estimates.

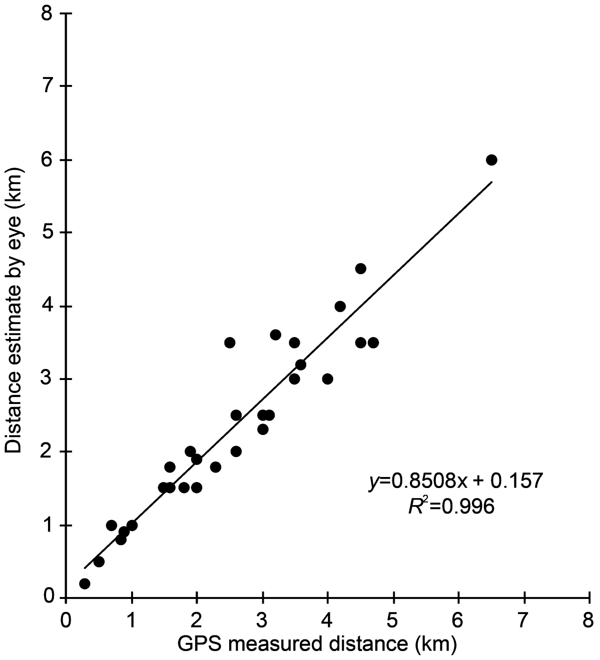


Fig. 3. Regression of the on distance estimated by eye on measured distance. N=32.

Density and abundance estimates

Density and abundance of species with sufficient sample sizes were estimated using the program *DISTANCE* 4.1, Release 2 (Buckland *et al.*, 2001; Laake *et al.*, 1993; Thomas *et al.*, 2003). Generally, a sample size of at least 60-80 sightings for the determination of the probability density function is desired, but occasionally 40 may be considered adequate (Buckland *et al.*, 1993; 2001). Sightings from the two study sites for two years of survey, and in some cases for two species, were pooled to obtain an adequate sample size. Encounter rate, school size, density and abundance were estimated by stratum, i.e. for each species, site and year of survey. Before pooling, the distribution of perpendicular distances was tested to determine if it differed between the two study sites, between years or between species (Kolmogorov-Smirnov test). The hypothesis that school size differed between species (Wilcoxon rank test) was also tested. For only four species (spinner dolphin, *Stenella longirostris*; pantropical spotted dolphin, *S. attenuata;* Fraser's dolphin, *Lagenodelphis hosei*; and short-finned pilot whale, *Globicephala macrorhynchus*) were there adequate numbers of sightings for the two study sites and two survey years (148, 61, 39 and 42 sightings, respectively) to allow reasonably precise estimation of abundance. Sightings data for Fraser's dolphin and the short-finned pilot whale were pooled because they were often found associated with each other, e.g. 62% of Fraser's dolphins sighted in 1994 and 49% in 1995 were with short-finned pilot whales. On these occasions, the very large dorsal fins of the pilot whales contributed to the sightability of the associated Fraser's dolphins (Kolmogorov-Smirnov test on the distributional pattern of perpendicular distances between the two species, P=0.183). Rather than providing no estimates for the more rare species (bottlenose dolphin, *Tursiops truncatus*; melon-headed whale, *Peponocephala electra;* dwarf sperm whale *Kogia sima* and Risso's dolphin, *Grampus griseus*), provisional estimates were calculated with caveats. Sightings of the bottlenose dolphin and melon-headed whale (total=31) were pooled because of the similarity in their general body size, behaviour, school size (Wilcoxon rank test, P=0.225) and distribution of perpendicular distances (Kolmogorov-Smirnov test, P=0.156).

For the estimation of abundance (using the multivariate mode of *DISTANCE* 4.1), the strata site and year were used as factor covariates and Beaufort sea state as a non-factor covariate. School size, however, was not used as a covariate because its use prevented analysis by stratum (a limitation of the program). Thus, in order to avoid an upward bias in abundance brought about by large schools having greater probabilities of detection at greater distance than small schools, a size-bias regression was performed on the logarithm of school size and the detection probability. Statistical power was estimated whenever the mean school size was used in the calculation of abundance (Zar, 1996). Knowledge of statistical power helps with interpretation of the results and evaluation of the strength of conclusions (Taylor and Gerrodette, 1993). Low power to reject the null hypothesis of no difference (and hence the use of the mean school size) could result in overestimation of abundance.

For cetaceans, the assumption that all groups on the trackline were detected (i.e. $g(0)=1$) may be violated because some cetaceans (e.g. dwarf sperm whales and beaked whales) may be beneath the surface during the entire passage of the boat and therefore missed. This negatively biases abundance estimates. Barlow (1999) developed a simulation model to estimate the probability of detecting species that dive for long periods, such as the dwarf sperm whale and beaked whales, during line-transect effort. He found that the detection probability, $g(0)$, was 0.35 for dwarf and pygmy sperm whales (*Kogia* spp.). This value was used to estimate dwarf sperm whale abundance in this study. For dolphins and whales occurring in medium-to-large schools, the assumption that $g(0)=1$ is probably true.

Models of the detection probability function, $f(0)$, were fitted to the data and the best fitting model chosen using the Akaike Information Criterion, AIC (Akaike, 1973; Buckland *et al.*, 2001). In addition, results of the Qq plot, Kolmorov-Smirnof Test and Cramer von-Misses Family Tests were also considered when choosing the best-fit model. The CV and the 95% confidence intervals (CI) were calculated for density and abundance estimates using bootstrap methods (Efron and Tibshirani, 1993; Buckland *et al.*, 1993) built into the program *DISTANCE*, with 200 resamples with replacement. Density and abundance of other species such as the rough-toothed dolphin (*Steno bredanensis*), pygmy killer whale (*Feresa attenuata),* Bryde's whale (*Balaenoptera edeni* or *B. omurai*), sperm whale (*Physeter macrocephalus)* and killer whale (*Orcinus orca*) were not estimated owing to insufficient sightings.

The abundance estimates and encounter rates obtained were compared with those from other tropical seas such as the eastern tropical Pacific (ETP), the western tropical Indian Ocean (WTIO) and the Gulf of Mexico (GM) by comparing the abundance ranks and standardising the encounter rates obtained in this study using the method described by Ballance and Pitman (1998). These standardised encounter rates are referred to as corrected encounter rates.

Distribution

The same data collected for the abundance estimations were used for the determination of the distributional patterns of selected species (only species with more than 20 sightings were included).

Bathymetric data were obtained from the General Bathymetric Chart of the Oceans (GEBCO) Digital Atlas[1] and depths were interpolated from the data points on a gridded field having a cell resolution of 0.01° latitude by 0.01° longitude using the software *ArcView GIS* (v.3.0). Similarly, SSTs and sea state contours were interpolated from the temperature and sea state data points collected during the survey, on a gridded field having a cell resolution similar to that of the water depth and using the same software. Survey effort and number of sightings under the same environmental parameters were summarised using *ArcView GIS*. A constant 0.001 was added to each value to avoid a value of zero in transects where there were no sightings.

A Generalised Additive Model (GAM) was used to investigate possible patterns in the distribution of the selected species (Forney, 1999; Barlow *et al.*, 2006). Encounter rate and school sizes were used as response variables, and water depth, SST and site (Sulu Sea *versus* the Tañon Strait) were included as predictor variables. The predictor variables help define the habitat and can potentially affect the distributional patterns of cetaceans. Beaufort sea state was also included in the model to account for potential bias that it can cause in the sightability (and therefore of the encounter rate) of animals and the estimation of school sizes. Effort covered under Beaufort 0 and 1 were combined, owing to the low survey effort in

[1] *http://www.ngdc.noaa.gov/mgg/gebco/gebco.html*

Beaufort sea state 0, and effort under 3 and 4 were also pooled due to the low survey effort in Beaufort sea state 4. A step-wise model selection was used with each variable added sequentially, using the GAM function of the statistical package *S-PLUS* (v.3.3). The GAM extends the generalised linear model (GLM) by fitting non-parametric functions (which were estimated from the data using smoothing operations) of predictor variables to estimate the relationships between the response variable and the predictors. The general form of GAM is (Hastie and Tibshirani, 1990):

$$g(E(Y|x)) = g(\mu) = \alpha + \sum_{i=1}^{p} f_i(x_i) = \eta(x)$$

where g is the link function, α is a constant intercept term, f_i corresponds to the non-parametric function describing the relationship between the mean response and the i^{th} predictor and $\eta(x)$ is the additive predictor (analogous to the linear predictor for a GLM). The level of smoothing was explored from 1 to 4 degrees of freedom for water depth. The s function which fits cubic B-splines was used to estimate the smooth relationship between the response and the predictors. Exploratory plots indicated linear relationships between the response variables (encounter rate and school size) and Beaufort sea state as well as sea surface temperature, so they were added into the model as linear terms. An Analysis of Deviance was used to compare the various models (Forney, 1999). Deviance is defined as (McCullagh and Nelder, 1997):

$$D = \sum i \left(r_i^D\right)^2$$

with signed residual deviance, $r_i^D = sign(y_i - \hat{\mu})\sqrt{d_i}$, where y_i is each observation and d_i is the contribution of the ith observation to the deviance.

RESULTS

A total of 2,313km of on-effort trackline were covered over an area of 23,014km^2 during the two survey years in the Sulu Sea and 434km over an area of 4,544km^2 in one year of survey in the Tañon Strait (Fig. 1B). The ratios of the on-effort trackline to area were nearly equal: 10.0km/km^2 for Sulu Sea and 10.5km/km^2 for the Tañon Strait. These surveys yielded a total of 578 cetacean sightings, 510 of which were on-effort and 451 (or 78%) identified to the species level. Table 1 summarises the percentage of effort spent in each sea state.

Table 1

Percentage of effort spent at different Beaufort sea states.

	Percentage of effort		
	Sulu Sea Area = 23,014km^2		Tañon Strait Area = 4,544km^2
Beaufort Sea state	1994 (1,161km)	1995 (1,152km)	1995 (434 km)
0	2.6	6.0	8.2
1	19.4	30.4	25.8
2	51.6	29.4	24.4
3	22.4	25.3	29.1
4	4.0	8.9	12.5

Species composition and school sizes

Fourteen cetacean species were identified in the Sulu Sea; only six of these were seen in the Tañon Strait (Table 2). In addition, two unidentified beaked whales (*Mesoplodon* sp. and an unidentified large ziphiid whale with a pronounced bulbous head and long beak, possibly Longman's beaked whale (*Indopacetus pacificus*) were seen in the Sulu Sea during the 1994 survey. Only two large whale species were sighted, Bryde's and sperm whales, both in 1994. No large whales were sighted in the Tañon Strait. 'Unidentified cetaceans' were cetaceans seen from afar which disappeared when approached; most were singletons but a few were in groups of two to fifteen. There were four species with notably high encounter rates in the Sulu Sea (spinner dolphin, spotted dolphin, short-finned pilot whale and Fraser's dolphin) and two in the Tañon Strait (spinner dolphin and dwarf sperm whale) (Table 2). The spinner dolphin had the highest number of sightings and highest encounter rates in both areas. Although Fraser's dolphins ranked fourth in the Sulu Sea, they were absent in the Tañon Strait.

Mean school size varied greatly from one for dwarf sperm whales to 143 for melon-headed whales (Table 2). Large schools of up to more than a thousand animals were observed when several species occurred together. Mean school sizes for spinner and spotted dolphins were significantly smaller in the Tañon Strait than in the Sulu Sea (Wilcoxon-rank sum test, P=0.009 for spinner and P=0.018 for spotted dolphins).

Species associations

Sulu Sea

In the Sulu Sea (Table 3), spinner dolphins were found in pure schools 59% of the time, with the remainder of the time in mixed schools with eight other species: spotted dolphins, short-finned pilot whales, Fraser's dolphins, Risso's dolphins, bottlenose dolphins, rough-toothed dolphins, pygmy killer whales and Bryde's whales. Association was highest between Fraser's dolphins and short-finned pilot whales, which were found together more than half of the time. A similar close association was also observed between spinner and spotted dolphins. Excluding species with fewer than five sightings, Fraser's dolphins had the highest percentage of mixed-species sightings (84.2%) and Risso's dolphins the lowest (26.8%) (Table 4).

Tañon Strait

Spinner dolphins in the Tañon Strait (Table 3) were found more commonly in pure than mixed schools (86% compared to Sulu Sea's 58%). Although dwarf sperm whales were seen associated with other species, only approximately 15% of the total sightings were of mixed species associations (Table 3). Overall, there was a predominance of pure schools over mixed-species sightings in the Tañon Strait, and mixed species sightings did not involve more than three species at a time (Table 4).

Density and abundance estimates

Overall, sea state affected sighting rates in both the Sulu Sea and the Tañon Strait. As one would expect, encounter rates (per 1,000km) were highest at Beaufort zero (355 in Sulu Sea and 428 in the Tañon Strait) and lowest at Beaufort 4 (31 in Sulu Sea and 74 in the Tañon Strait).

The best-fit model for all but one species was the half-normal model (Table 5). The model that best fitted the data for the dwarf sperm whale was the hazard rate model, with the probability plot showing a rather peaked nature. The AIC increased by 31% when the half-normal model was tested for this species. In addition, the results of the Qq plot showed a poor fit for the half-normal model, as did the Kolmogorov Smirnoff and the Cramer von-Misses family

Table 2

Summary of cetacean sightings for the two years of survey in the Sulu Sea and one year of survey in Tañon Strait. N_t=total number of sightings, n_e=number of on-effort sightings, S=mean school size, E=encounter rate (number of schools 1,000km^{-1}).

	Sulu Sea				Tañon Strait			
Species	N_t (n_e)	S	S range	E	N_t (n_e)	S	S range	E
1. Spinner dolphin	111 (97)	90	1-644	42.0	52 (51)	39	1-900	117.5
2. Spotted dolphin	63 (57)	84	1-540	24.6	4 (4)	8	1-25	9.2
3. Short-finned pilot whale	48 (42)	52	1-350	18.2	1 (0)	50	50	2.3
4. Fraser's dolphin	44 (39)	92	3-475	16.9				
5. Risso's dolphin	26 (22)	8	1-40	9.5				
6. Bottlenose dolphin	24 (21)	26	1-93	9.1	3 (2)	6	1-12	4.6
7. Dwarf sperm whale	12 (9)	1.6	1-4	3.9	27 (21)	2.4	1-10	48.0
8. Melon-headed whale	7 (6)	34	7-52	2.6	2 (2)	143	40-210	4.6
9. Rough-toothed dolphin	3 (3)	2	1-4	1.3				
10. Bryde's whale	3 (3)	1.8	1-3	1.3				
11. Pygmy killer whale	1 (1)	3	3	0.4				
12. Sperm whale	1 (0)	4	4	-				
13. Killer whale	1 (1)	3	3	0.4				
14. Blainville's beaked whale	1 (1)	4	4	0.4				
15. Ziphiid whale	1 (1)	1.3	1-2	0.4				
16. *Mesoplodon* sp.	16 (8)	2	1-4	3.5				
Summary	**362 (311)**			**134**	**89 (80)**			**184**
Unidentified cetaceans	112 (104)	3.6	1-15	45.0	15 (15)	1	1-5	34.0

Table 3

Species associations. Numbers are percentages of on+off effort sightings (can total more than 100 since several species can co-occur). Numbers in bold diagonal represent the percentage of the time the species seen in pure schools. There is no symmetry in the matrix because the number of sightings varies by species.

	Spinner dolphin	Spotted dolphin	Short-finned pilot whale	Fraser's dolphin	Risso's dolphin	Bottlenose dolphin	Melon-headed whale	Rough-toothed dolphin	Pygmy killer whale	Bryde's whale	Dwarf sperm whale
A. Sulu Sea											
Spinner dolphin (111)	**59**	30	6	11	3	4		0.9	0.9	2	
Spotted dolphin (63)	52	**46**	6	10		5			2		
Short-finned pilot whale (48)	12	8	**38**	50	6	12		4	2		
Fraser's dolphin (44)	30	14	54	**16**	7	6	8		2		
Risso's dolphin (26)	12	8	12	12	**73**	4					
Bottlenose dolphin (24)	17	12	25	25	4	**50**	4		4		
Melon-headed whale (7)				43		14	**57**				
Rough-toothed dolphin (3)	3		66							33	
Pygmy killer whale (1)	100	100	100	100		100					
Bryde's whale (3)	66							33		**33**	
B. Tañon Strait											
Spinner dolphin (52)	**87**	6	6			2	2				6
Spotted dolphin (4)	75	**25**									
Dwarf Sperm whale (27)	11						4				**85**
Melon-headed whale (2)	50		50				50				
Bottlenose dolphin (3)	33					**67**	33				

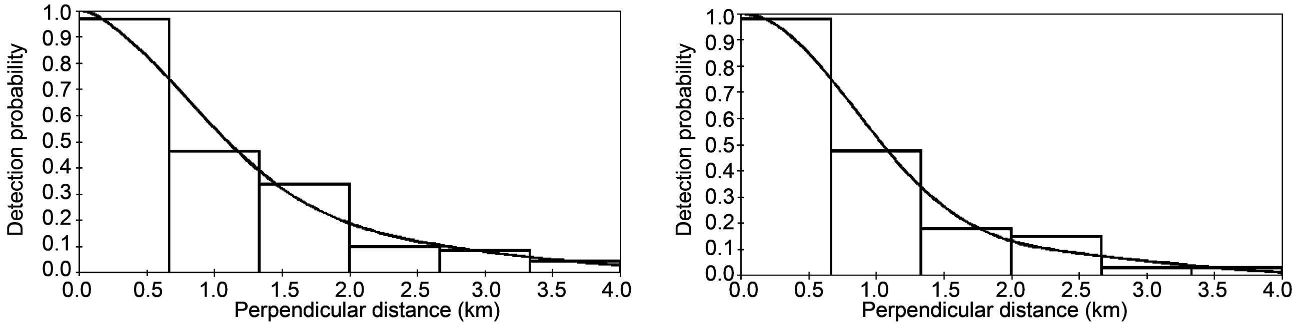
tests (uniform weighting and cosine weighting; p=0.03, 0.02, 0.01 respectively). Fig. 4 shows histograms of the perpendicular sighting distance data and the fitted models for the seven cetacean species. Abundance and density estimates with their corresponding confidence intervals for the seven cetacean species are given in Table 6. In all cases, the estimates using the corrected distance did not vary statistically from the uncorrected estimates. Based on data pooled over the two years of survey, the most abundant species in both sites was the spinner dolphin, although the density in the Tañon Strait was only about half that of the Sulu Sea. This lower density was owing to smaller school sizes rather than lower encounter rates; in fact encounter rate in the Tañon Strait was almost three times higher than in the Sulu Sea (Table 2). Other relatively abundant species in the Sulu Sea were the spotted dolphin, Fraser's dolphin and the short-finned pilot whale (Table 6). One significant observation was the much higher density (15×) of dwarf sperm whales in the Tañon Strait than in the Sulu Sea. The abundance estimate was double, despite the fact that the Tañon Strait is only approximately one-fifth of the size of the eastern Sulu Sea study site.

Table 4

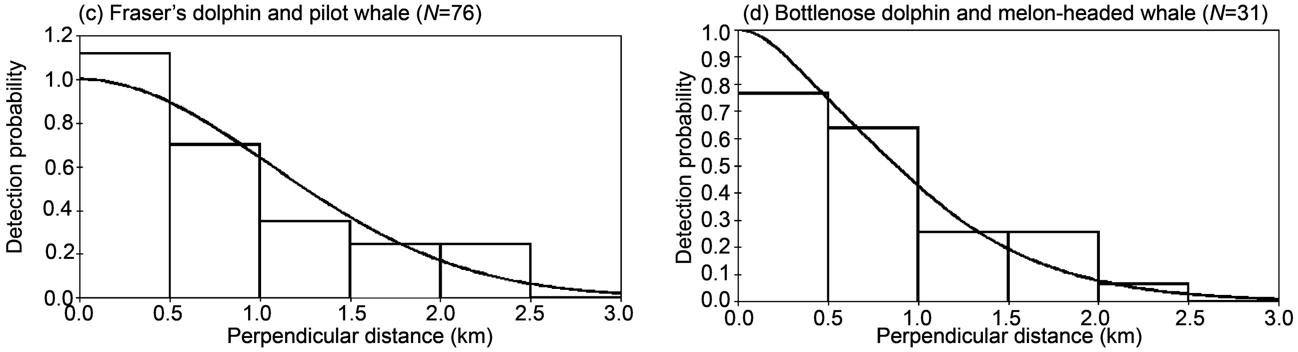
Percentage of on+off effort sightings associated with 1, 2, 3, 4 and 5 other species at one time. Percentage of mixed and pure schools also shown.

Species (no. of on-effort sightings) plus	Percentage of sightings associated with other species at one time 1*sp*	2*spp*	3*spp*	4*spp*	5*spp*	% mixed school	% pure school
A. Sulu Sea							
Spinner dolphin (111)	32.1	4.6	2.8	0.9	0.9	41.3	58.7
Spotted dolphin (63)	44.4	3.2	3.2	1.6	1.6	54.0	46.0
Short-finned pilot whale (48)	43.8	8.3	6.2	2.1	2.1	62.5	37.5
Fraser's dolphin (44)	61.4	11.4	6.8	2.3	2.3	84.2	15.8
Risso's dolphin (26)	19.2	3.8		3.8		26.8	73.2
Bottlenose dolphin (24)	29.1	12.5	4.2		4.2	50.0	50.0
Melon-headed whale (7)	28.6	14.3				42.9	57.1
Rough-toothed dolphin (3)	66.7	33.3				100	
Bryde's whale (3)	33.3	33.3				66.6	33.4
Pygmy killer whale (1)					100	100	
B. Tañon Strait							
Spinner dolphin (52)	11.5	1.9				13.4	86.6
Dwarf sperm whale (27)	14.8					14.8	85.2
Spotted dolphin (4)	75.0					75.0	25.0
Bottlenose dolphin (3)		33.3				33.3	66.7
Melon-headed whale (2)	50.0	50.0				100	0.0

(a) Spinner dolphin (*N*=142) (b) Spotted dolphin (*N*=62)



(c) Fraser's dolphin and pilot whale (*N*=76) (d) Bottlenose dolphin and melon-headed whale (*N*=31)



(e) Dwarf sperm whale (*N*=30) (f) Risso's dolphin (*N*=21)

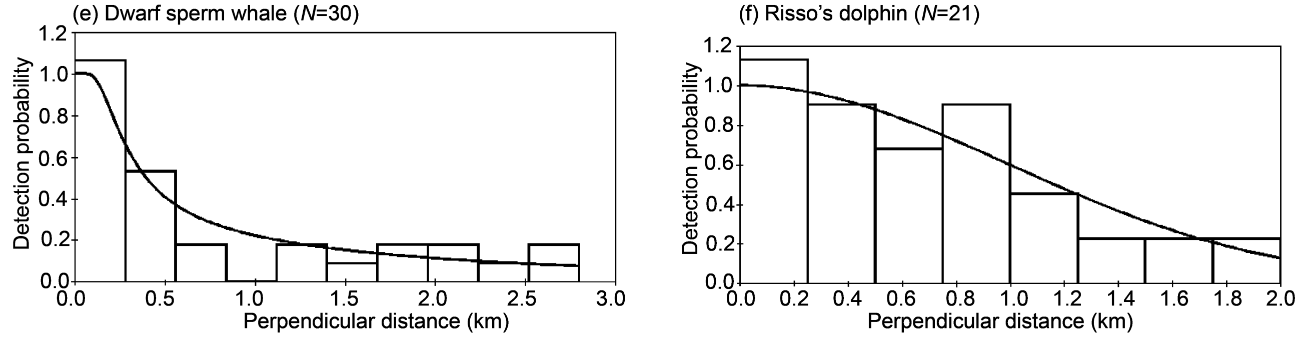


Fig. 4. Probability detection plot and model fit for A=spinner dolphin, B=Pantropical spotted dolphin, C=Fraser's dolphin and short-finned pilot whale, D=bottlenose dolphin, E=dwarf sperm whale and F=Risso's dolphin.

Table 5

Truncation distance (w), number of sightings used after truncation (n), estimated value of probability density function [$f(0)$], effective strip width (ESW), Akaike Information Criterion value (AIC) and the model used for different species and species groups.

Species/species group	w (km)	n	$f(0)$ (km^{-1})	*ESW* (km)	AIC	Model
Spinner dolphin	4.0	142	0.75	1.3	265.0	Half-normal
Spotted dolphin	4.0	62	0.81	1.2	112.4	Half-normal
Fraser's dolphin and short-finned pilot whale	3.0	76	0.75	1.3	119.6	Half-normal
Bottlenose dolphin and melon-headed whale	3.0	31	1.01	1.0	37.5	Half-normal
Risso's dolphin	2.0	21	0.85	1.2	29.3	Half-normal
Dwarf sperm whale	2.8	30	1.34	0.7	41.1	Hazard-rate

Table 6

Parameters for density estimation, estimates of density (D)(km^{-2}), species abundance (N), the 95% upper and lower estimations of abundance and the coefficient of variation (*CV*) for seven species of cetaceans. The *CV*s were computed by the program *DISTANCE* using the bootstrap method, with samples=200 with replacement. n=number of sightings after truncation; E(s)=school size (either mean or regressed school size). The last column shows the abundance estimates using uncorrected observer distance estimation.

Species	n	$E(s)$	P	D	N	L95%	U95%	%*CV*	Uncorrected N (%*CV*)
Spinner dolphin									
Sulu Sea 1994	46	88.4	0.99	1.24	28,586	16,121	52,601	35.37	24,886 (37.90)
Sulu Sea 1995	45	97.9	---	1.33	30,707	14,901	63,278	37.32	33,845 (33.50)
Sulu Sea 1994 and 1995	91	92.4	0.79	1.37	31,512	18,760	52,931	26.63	33,272 (23.60)
Tañon Strait	51	17.4	---	0.77	3,489	2,074	5,876	26.47	3,433 (21.00)
Spotted dolphin									
Sulu Sea 1994	23	92.5	0.69	0.75	17,325	7,466	40,203	43.04	17,041 (47.75)
Sulu Sea 1995	35	82.4	0.68	0.94	21,715	9,755	48,336	41.61	18,402 (55.56)
Sulu Sea 1994 and 1995	58	66.4	---	0.65	14,930	6,841	32,583	40.88	16,413 (44.08)
Tañon Strait	4	7.9	0.73	0.14	640	284	1,443	26.64	624 (42.72)
Fraser's dolphin									
Sulu Sea 1994	21	107.6	0.84	0.73	16,931	9,032	31,738	31.16	13,199 (28.61)
Sulu Sea 1995	16	83.5	0.79	0.43	10,080	4,315	22,547	43.06	7,178 (61.12)
Sulu Sea 1994 and 1995	37	97.2	0.64	0.58	13,518	7,958	22,962	26.93	10,914 (28.00)
Tañon Strait	---	---	---	---	---	---	---	---	---
Short-finned pilot whale									
Sulu Sea 1994	19	41.0	0.95	0.25	5,827	2,348	14,460	45.86	5,138 (42.90)
Sulu Sea 1995	19	63.0	0.95	0.40	9,170	4,044	20,793	41.71	9,462 (37.00)
Sulu Sea 1994 and 1995	38	52.4	0.92	0.32	7,492	4,189	13,400	29.67	7,292 (27.15)
Tañon Strait	1	50.0	---	0.04	179	23	1,407	95.64	159 (88.76)
Bottlenose dolphin									
Sulu Sea 1994 and 95	22	23.7	0.96	0.11	2,628	1,211	5,703	40.23	2,469 (43.03)
Tañon Strait	1	5.7	---	0.01	30	3	269	104.87	88 (64.86)
Melon-headed whale									
Sulu Sea 1994 and 1995	6	30.5	0.97	0.04	921	211	4,019	82.62	875 (80.16)
Tañon Strait	2	143.5	---	0.30	1,383	167	4,268	81.57	1,299 (128.25)
Risso's dolphin									
Sulu Sea 1994 and 1995	21	8.4	0.90	0.03	1,514	611	3,754	47.16	1,682 (54.60)
Tañon Strait	---	---	---	---	---	---	---	---	---
Dwarf sperm whale									
Sulu Sea 1994 and 1995	10	1.7	0.96	0.01	326	129	827	58.41*	381 (36.11)
Tañon Strait	20	1.7	---	0.15	670	179	2,512	62.33*	866 (64.01)

Comparison of the Sulu Sea with other tropical seas

Abundance rank, school size and corrected encounter rate were compared with those for cetaceans found in the WTIO, ETP and the GM, as reported in Ballance and Pitman (1998) using the same standardising procedure used by them (Table 7). All the species found in the Sulu Sea were also seen in all three of the other tropical regions. The most abundant species in the Sulu Sea, the spinner dolphin, was also the most abundant in the WTIO, second in rank in the GM, but only fourth in the ETP. The second most abundant, the pantropical spotted dolphin, ranked first in the GM and second in the ETP but only sixth in the WTIO. The additional differences observed were: (a) the two other more abundant species in the Sulu Sea, Fraser's dolphin and the short-finned pilot whale, ranked lower in the other three tropical regions; (b) the striped dolphin, *Stenella coeruleoalba* and a species of common dolphin, *Delphinus* sp., were absent from the Sulu Sea but highly abundant in the WTIO and the ETP; (c) the clymene dolphin, *S. clymene,* which ranked fourth in the GM, was not found in the Sulu Sea (it is endemic to the Atlantic); (d) school sizes of spinner, spotted and Fraser's dolphins and melon-headed whales in the Sulu Sea were smaller than those of the WTIO and the ETP; and (e) corrected encounter rates of spinner, spotted and Fraser's dolphins and pilot whales were notably higher in the Sulu Sea than in the WTIO, ETP and the GM.

Table 7

Comparison of abundance ranks, mean school sizes and corrected encounter rates of cetaceans found in the Sulu Sea (SS), western tropical Indian Ocean (WTIO), the eastern tropical Pacific (ETP) and the Gulf of Mexico (GM). Table obtained from Ballance and Pitman (1998) with the results of the present study added (ne=no estimate; nd=no data).

	Abundance rank				Mean school size (*CV*)				Corrected encounter rate (schools 1,000km^{-1})			
Species	SS	WTIOO	ETP	GM	SS	WTIO	ETP	GM	SS	WTIO	ETP	GM
Stenella longirostris	1	1	4	2	91.8 (0.14)	169.8 (1.37)	120.5	70.8 (24.62)	39.14	7.39	5.19	14.28
Stenella attenuata	2	6	2	1	83.5 (0.27)	147.2 (1.52)	127.9	57.7 (7.67)	21.35	1.13	5.97	9.68
Lagenodelphis hosei	3	10	5	16	87.6 (0.18)	183.3 (0.57)	394.9 (0.20)	34.0 (---)	16.86	0.25	0.25	8.48
Globicephala sp.	4	8	8	13	56.7 (0.26)	30.7 (0.66)	18.3 (0.08)	16.6 (21.16)	18.16	2.17	3.66	3.87
Tursiops sp. (*truncatus*)	5	4	6	3	23.9 (0.21)	53.1 (2.39)	22.7 (0.22)	14.0 (11.81)	7.87	4.92	4.72	10.16
Peponocephala electra	6	7	10	6	56.8 (0.38)	283. (0.97)	199.1 (0.20)	119.6 (22.50)	2.24	0.38	0.10	8.36
Grampus griseus	7	5	7	8	8.4 (0.18)	48.3 (2.29)	11.8 (0.08)	10.7 (9.44)	6.34	4.85	6.27	3.49
Kogia sima	8	15	17	14	1.3 (0.14)	1.6 (0.55)	1.7 (0.07)	2.2 (13.77)	1.29	3.19	3.20	1.93
Mesoplodon sp.	ne	14	13	17	2 (---)	2.0 (0.53)	3.0 (0.11)	1.9 (13.56)	ne	3.03	3.10	4.82
Ziphiid whale (*Z. cavirostris*)	ne	19	15	20	1.3 (---)	3.0 (---)	2.2 (0.06)	1.2 (16.67)	ne	0.16	3.25	4.73
Steno bredanensis	ne	9	9	9	2.0 (---)	21.4 (0.70)	14.7 (0.18)	14.4 (12.18)	ne	2.58	4.63	19.09
Balaenoptera edeni	ne	18	16	19	1.8 (---)	1.2 (0.37)	1.7 (0.07)	2.7 (45.07)	ne	0.91	2.46	4.69
Feresa attenuata	ne	13	12	11	3.0	15.8 (0.44)	27.9 (0.12)	29.2 (62.44)	ne	1.17	0.63	5.73
Orcinus orca	ne	17	18	15	3.0	8.0 (---)	5.4 (0.09)	10.0 (15.28)	ne	0.33	0.66	4.09
Physeter macrocephalus	ne	12	14	10	1	2.8 (0.96)	7.9 (0.17)	2.6 (7.87)	ne	9.78	1.24	3.67
Stenella coeruleoalba	---	2	3	5	---	42.6 (0.99)	60.9 (0.05)	36.1 (11.63)	0	8.44	14.34	1.79
Delphinus spp.	---	3	1	---	---	221.2 (1.32)	380.1	---	0	1.63	3.02	---
Pseudorca crassidens	---	11	11	12	---	41.3 (0.88)	11.4 (0.12)	20.4 (42.07)	0	0.84	1.21	4.98
Balaenoptera musculus	---	16	19	---	---	1.6 (0.39)	1.5 (0.13)	---	---	1.93	0.36	---
Kogia breviceps	---	20	nd	18	---	1.0 (---)	nd	2.2 (11.75)	---	0.32	nd	3.32
Stenella clymene	---	---	---	4	---	---	---	63.7 (26.67)	---	---	---	14.13
Stenella frontalis	---	---	---	7	---	---	---	21.2 (15.89)	---	---	---	5.46

	SS	WTIO	ETP	GM
Total number of species:	15	20	19	20
Area (km^2):	23,014	----	19,148,000	----
On-effort transect line (km):	2,313	9,784	135,300	----
Encounter rate for all cetaceans (animals 1,000km^{-1})	134	60.2	32.2	----

Distribution

Fig. 5 is the plot of sighting locations in relation to water depth and Fig. 6 shows the results of the smoothed functions of the predictor variables incorporated into the encounter rate GAM for the various species. Table 8 summarises the results of the GAM analysis. The results of the GAM analysis for school size and encounter rate as response variables are similar for all species except the spinner and bottlenose dolphins. For the spinner dolphin, the encounter rate does not appear to be affected by Beaufort sea state (cues were leaping and splashing), whereas estimation of school size was affected. For the bottlenose dolphin, water depth appears to be an important factor in its distribution (as shown by a much higher encounter rate in shallow waters), whereas school size was more or less the same at various depths (Table 8, Fig. 6). Beaufort sea state affected encounter rates for the spotted, Fraser's and Risso's dolphins and dwarf sperm whale (Fig. 6). After adjusting for sea state, water depth appeared to be an important determinant in the distribution of Fraser's, bottlenose and Risso's dolphins and the short-finned pilot whale. SST also appeared to be important in the distribution of all species except Fraser's and Risso's dolphins. Site was an important factor for spotted, Fraser's and Risso's dolphins and dwarf sperm whale.

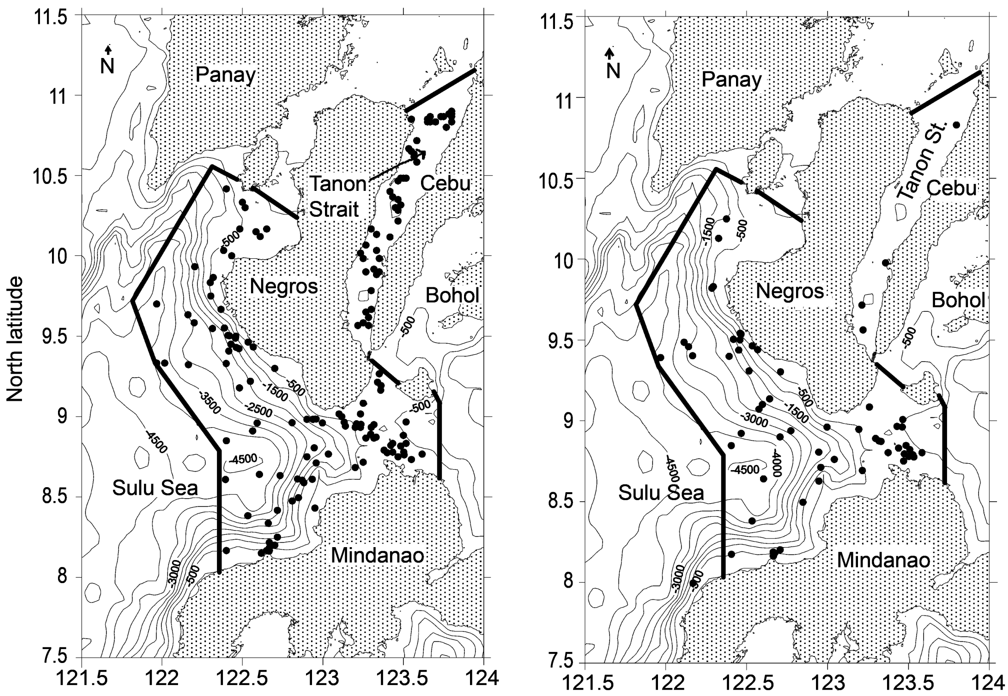
DISCUSSION

The 14 species observed in the Sulu Sea and the Tañon Strait in this survey constitute 54% of the total number of cetaceans known from Philippine waters and 47% of the total number of cetacean species recorded in Southeast Asia. Species not seen in this survey but which are found in Philippine waters include the striped dolphin, Irrawaddy dolphin (*Orcaella brevirostris*), Indopacific humpback dolphin (*Sousa chinensis*), Indopacific bottlenose dolphin (*T. aduncus*), pygmy sperm whale *(K. breviceps*), false killer whale (*Pseudorca crassidens*), Blainville's beaked whale (*M. densirostris*), Cuvier's beaked whale (*Ziphius cavirostris*), fin whale (*B. physalus*), humpback whale *(Megaptera novaeangliae*), blue whale (*B. musculus*) and Longman's beaked whale (Leatherwood *et al.*, 1992; Perrin *et al.*, 1995; Dolar, 1999b; Yaptinchay, 1999; Bautista, 2002; Dolar *et al.*, 2002; Perrin *et al.*, 2005; Acebes *et al.*, 2005; Trono and Wang, pers. comm.; Yaptinchay and Alava, pers. comm.; Digdigan, pers. comm.).

Interspecific interactions

Almost half of the sightings of spinner dolphins in the Sulu Sea were with eight other species, and the relative frequency that they were seen with them appeared to be positively correlated with the abundance of the species. For example, 30% of the sightings were with spotted dolphins (abundance rank=2), 11% with Fraser's dolphins (rank=3), 6% with short-finned pilot whales (rank=4), etc. In the Tañon Strait, the great majority (87%) of sightings were of pure schools and the most frequent associations were with dwarf sperm whales and spotted dolphins. This association with dwarf sperm whales was not observed in the Sulu Sea, where density of dwarf sperm whales was 15 times less than in the Tañon Strait. A close association between spinner and spotted dolphins was also observed in the ETP, where 73% of spinner dolphin sightings were with spotted dolphins (Reilly, 1990) and in the WTIO (Ballance and Pitman, 1998). In the GM, however, these two species did not form mixed schools (Jefferson and Schiro, 1997).

(a) Spinner dolphin (b) Pantropical spotted dolphin



(c) Fraser's dolphin (d) Short-finned pilot whale

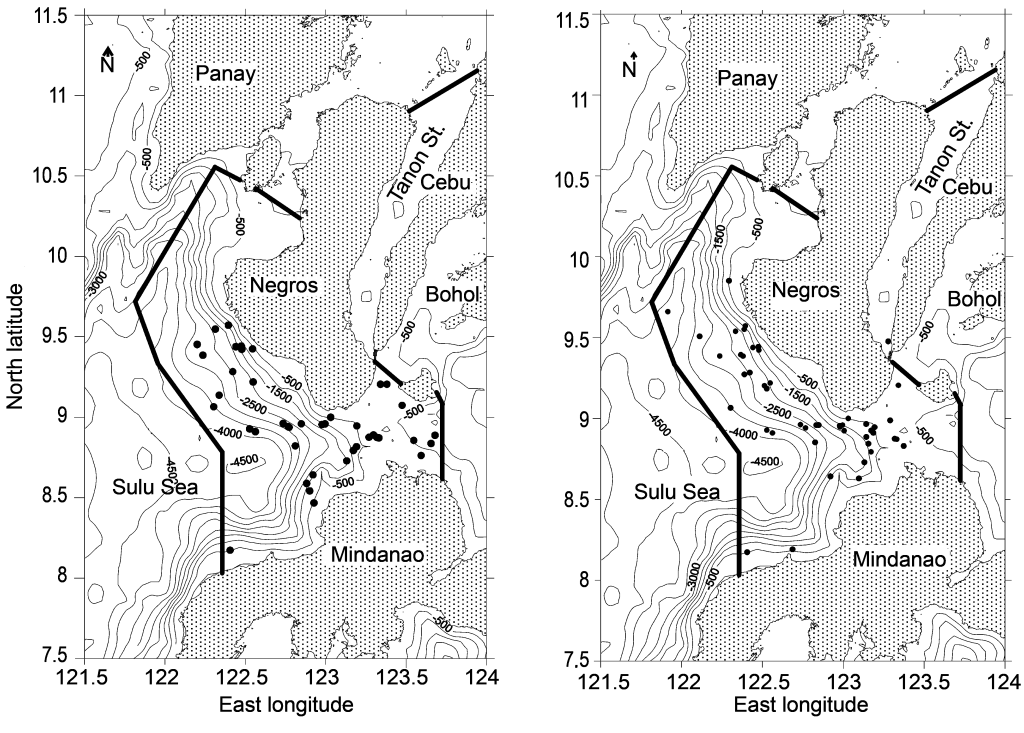
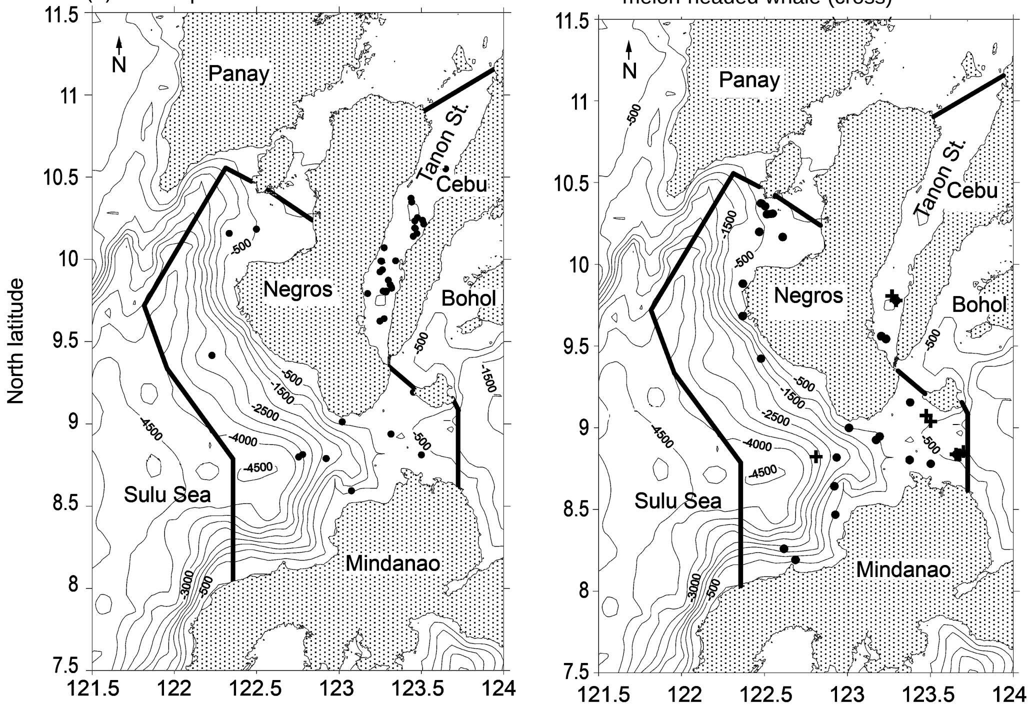


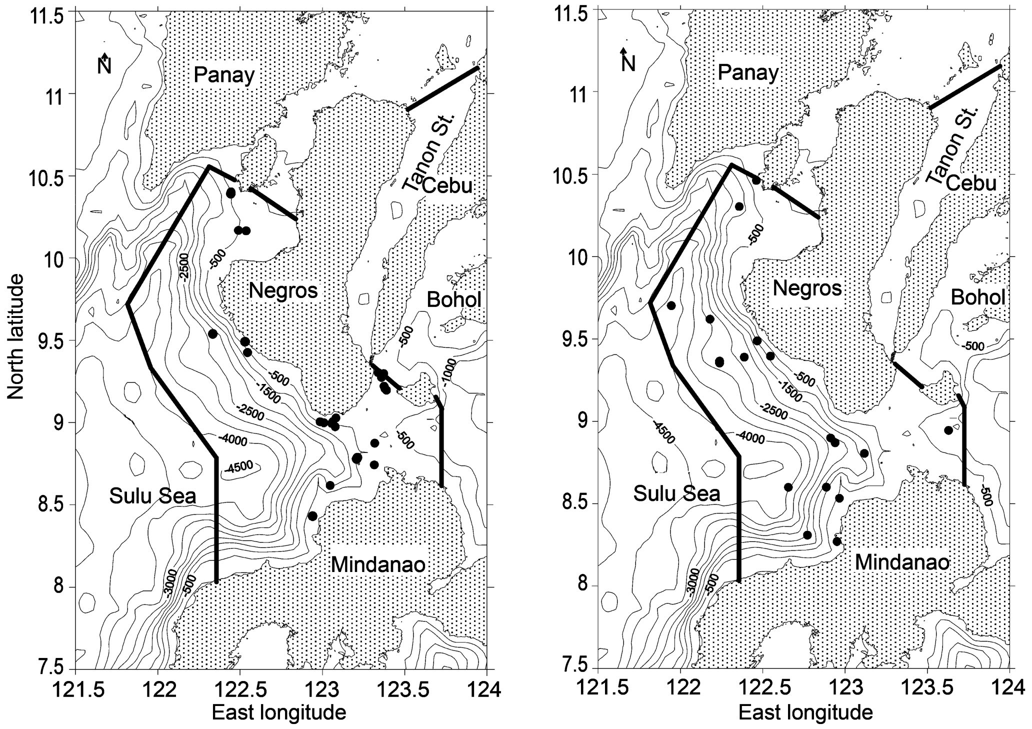
Fig. 5. Sightings of cetaceans in the Sulu Sea and the Tañon Strait (●) Other species: (□) Bryde's whale; (★) Rough-toothed dolphin; (+) Sperm whale; (▲) Pygmy killer whale; (✖) Killer whale.

[*Figure 5 continued*]



(e) Dwarf sperm whale

(f) Bottlenose dolphin (circle) and melon-headed whale (cross)



(g) Risso's dolphin

(h) Beaked whales

[*Figure 5 continued overleaf*]

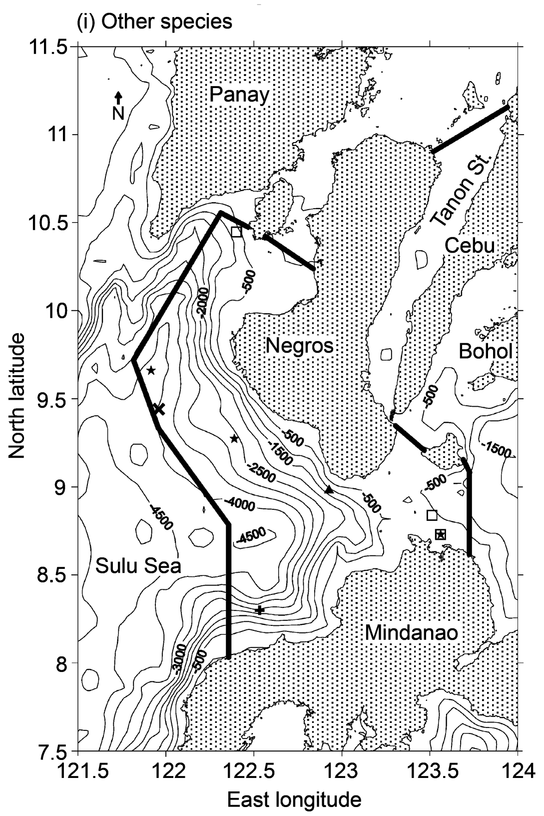


Fig. 5 (continued). Sightings of cetaceans in the Sulu Sea and the Tañon Strait (●) Other species: (□) Bryde's whale; (★) Rough-toothed dolphin; (+) Sperm whale; (▲) Pygmy killer whale; (✖) Killer whale.

Fraser's dolphins interacted with other species more than any of the other species seen in this study; 84.2% of all the sightings were of mixed schools. They were observed associated mostly with short-finned pilot whales and spinner dolphins when in deep waters and with melon-headed whales and bottlenose dolphins when in relatively shallow waters or when close to shore. The close association between Fraser's dolphins and short-finned pilot whales has not been observed elsewhere, even in the ETP where the species overlap in their habitats (Au and Perryman, 1985; Wade and Gerrodette, 1993)[2]. There and in the GM, Fraser's dolphins have been found to be associated with melon-headed whales (Au and Perryman, 1985; Perryman *et al.*, 1994). In the WTIO however, Fraser's dolphins have not been seen associated with other species (Ballance and Pitman, 1998).

The degree of association of pilot whales with other species in our study (63%) is among the highest observed for this species. In the ETP, only 15% of pilot whale sightings involved other cetaceans (Bernard and Reilly, 1999). When in the deep waters of the Sulu Sea it associated mostly with Fraser's dolphins and when in shallow waters mostly with bottlenose dolphins. Association with bottlenose dolphins in coastal waters has been reported to be common in the ETP (Bernard and Reilly, 1999), the Canary Islands (Heimlich-Boran and Heimlich-Boran, 1990) and in the WTIO (Ballance and Pitman, 1998).

There are no previous reports of dwarf sperm whales being associated with other species. In the Tañon Strait however, about 11% of the sightings of dwarf sperm whales were with spinner dolphins and 4% were with melon-headed whales.

Distribution and abundance

Although tropical waters seem more homogenous in terms of the habitat they provide than temperate or Arctic waters and thus may be expected to harbour similar patterns of cetacean habitat use, we found surprising differences between the two nearly contiguous bodies of tropical waters that we studied. The Sulu Sea has a more diverse cetacean fauna than the Tañon Strait, with more than twice as many species. It can be characterised as an area dominated by spinner, spotted and Fraser's dolphins and the pilot whale, whereas the Tañon Strait can be characterised mainly as a spinner dolphin and dwarf sperm whale area. The high cetacean diversity in the Sulu Sea can be explained in part by its much larger size, a greater variety of habitat types and a wider range of prey species. In contrast, the smaller Tañon Strait, with its narrower range of habitats, greatly favours certain species but cannot support many others. As in most ecosystems, the assemblage of species in each site is a result of the diversity of habitats as well as of competition among the various cetacean species. Below, the fairly abundant species have been grouped into two categories; those with (a) restricted and (b) general or flexible habitat preferences.

Species with restricted distributions

Fraser's dolphin

Fraser's dolphin distribution, as noted during this study, is influenced by water depth, with highest sighting rates and largest school sizes found in waters beginning at about 700-800m deep and extending to waters deeper than 3.5km. This species has been characterised as a tropical and oceanic species (Wade and Gerrodette, 1993; Perrin *et al.*, 1994). In the ETP, it was observed to occur at least 15km from the coast and mostly on the high seas approximately 45-110km offshore in waters 1.5-2km deep (Wade and Gerrodette, 1993; Perrin *et al.*, 1994). It has not been observed in shallow waters close to shore except when deep water approached the coast, as the case may be in the Lesser Antilles and Indonesia (Jefferson *et al.*, 1992). The occurrence of Fraser's dolphins in the shallow waters south of Negros Island, but not in the Tañon Strait gives support to this suggestion. A compilation of cetacean sightings over seven years also showed that although the Tañon Strait was the most surveyed area for cetacean occurrence, Fraser's dolphins were never seen within it (Dolar and Perrin, 1996). Hammond and Leatherwood (1984) observed high numbers only in the lower third of the Bohol Strait and at the centre of the Camotes Sea, where waters are deeper than 500m. Thus, as in the ETP, Fraser's dolphins in the Sulu Sea appear to prefer very deep waters. However, if deep waters approach the coast, as is the case in the Sulu Sea, then they can become coastal animals as well. The apparent dependence of Fraser's dolphins on deep waters could be associated with their preference for mesopelagic prey. In the Sulu Sea, they may dive to as deep as 600m to capture non-migrating deep-water fish, squids and shrimps (Dolar *et al.*, 1999; Dolar *et al.*, 2003).

Risso's dolphin

As noted previously, the Sulu Sea appear to be a better habitat for Risso's dolphin than the Tañon Strait (Dolar and Perrin, 1996). Its distribution clearly shows a preference for

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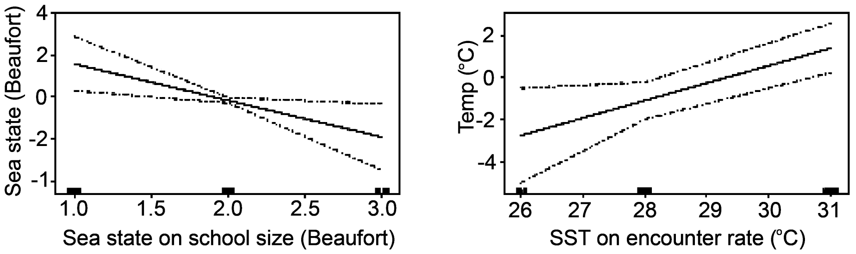
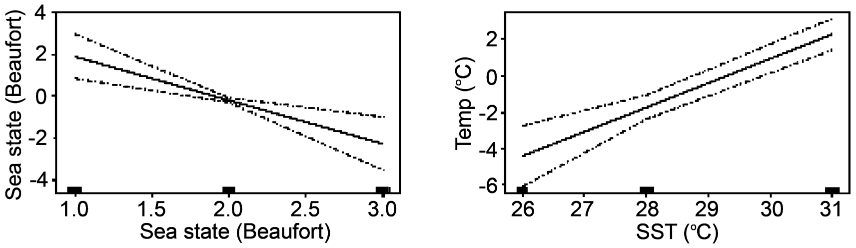
[2] The information in Dolar (2002) and Olson and Reilly (2002) regarding association between pilot whales and Fraser's dolphins was obtained from this study.

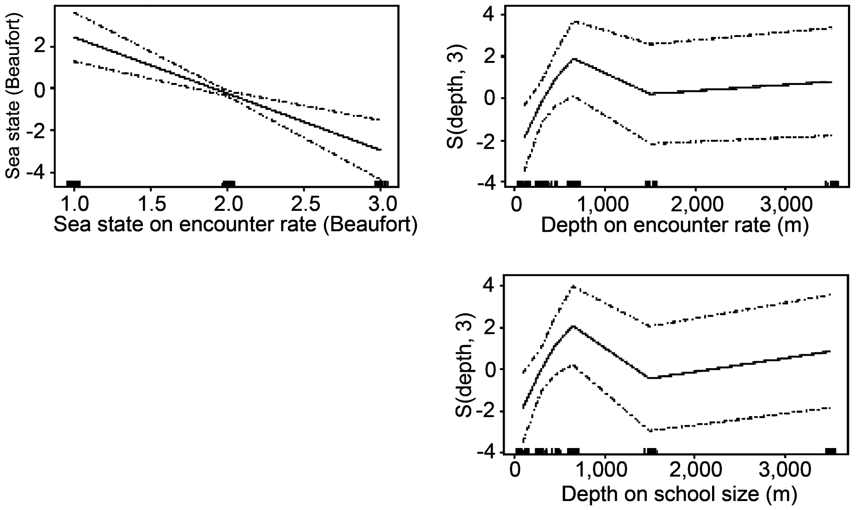
(a) Spinner dolphin



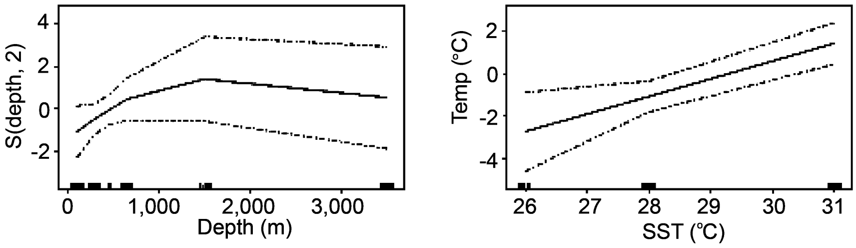
(b) Spotted dolphin (encounter rate)



(c) Fraser's dolphin

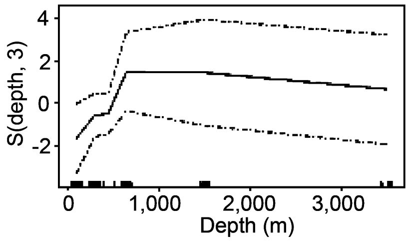


(d) Short-finned pilot whale



Depth on encounter rate

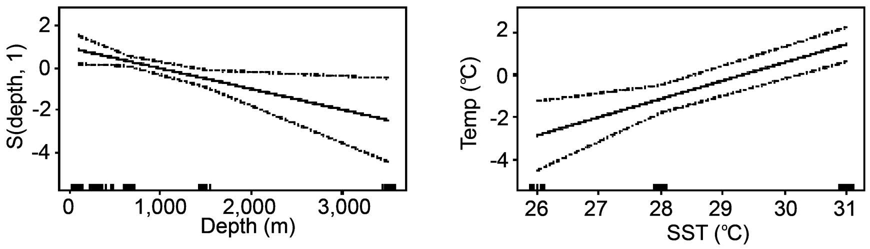
SST on encounter rate



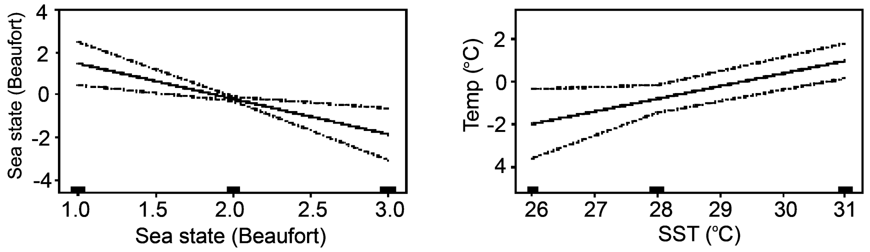
Depth on school size

[*Figure 6 continued overleaf*]

(e) Bottlenose dolphin (encounter rate)



(f) Dwarf sperm whale (encounter rate)



(g) Risso's dolphin (encounter rate)

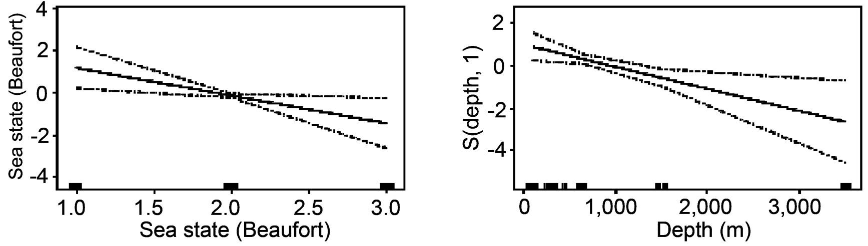


Fig. 6. Smoothed functions of the predictor variables included in the encounter rate and school size GAMs for selected cetacean species. When the trend of the smoothed functions of predictor variables is similar in both encounter rate and school size GAM, only the former is shown.

Table 8

Summary of the GAMs for seven cetacean species for encounter rate and school size. Change in deviance was calculated as: [(null deviance - residual deviance)/null deviance] x 100 (Barlow *et al.*, 2006).

Response variables	No. of sightings used	Change in deviance (%)	Predictor variables (associated degrees of freedom)
Spinner dolphin			
Encounter rate	146	7.172	SST(1)
School size		15.062	Beauf(1) + SST(1)
Spotted dolphin			
Encounter rate	62	37.433	Beauf(1) + SST(1) + Site(1)
School size		36.369	Beauf(1) + SST(1) + Site(1)
Fraser's dolphin			
Encounter rate	39	36.920	Beauf(1) + Depth(3) + Site(1)
School size		34.912	Beauf(1) + Depth(3) + Site(1)
Short-finned pilot whale			
Encounter rate	42	15.428	Depth(2) + SST(1)
School size		17.014	Depth(3) + SST(1)
Bottlenose dolphin			
Encounter rate	23	15.888	Depth(1) + SST(1)
School size		9.690	SST(1)
Dwarf sperm whale			
Encounter rate	30	28.622	Beauf(1) + SST(1) + Site(1)
School size		29.088	Beauf(1) + SST(1) + Site(1)
Risso's dolphin			
Encounter rate	22	8.854	Beauf(1) + Depth(1) + Site(1)
School size		19.199	Beauf(1) + Depth(1) + Site(1)

a depth range of 200 to 400m overlying a steep slope in the Sulu Sea (Figs 5 and 6). This depth is less than the 400 to 1,000m preferred depth observed in other tropical and subtropical areas (Leatherwood *et al.*, 1980; Kruse, 1989; Davis *et al.*, 1998; Baird, 2002). In the GM, it was found to have a very narrow core habitat, bounded by the 350 and 900m isobaths and depth gradients greater than 23 or 24m per 1.1km (Baumgartner, 1997). Steep slopes at the shelf break can enhance physical processes such as tidal stirring, dissipation of internal waves and or eddy-slope interaction that can cause increased vertical mixing. This in turn, can increase productivity of phytoplankton, fish and cetaceans (Huthnance, 1981; Baumgartner, 1997; Kruse *et al.*, 1999). As with other physical parameters, bottom topography can therefore influence cetacean distribution indirectly by concentrating prey species (Hui, 1979; Hui, 1985; Selzer and Payne, 1988).

Dwarf sperm whale

Although the raw data showed distinctly high encounter rates at depths of 200-400m, the GAM analysis and the Analysis of Deviance showed that the best-fit model did not include depth as an important predictor variable. It appears that site is the most important predictor (*p*=0.002). The unusually high abundance of dwarf sperm whales in the Tañon Strait suggests that it is a preferred habitat. The mean depth of all sightings here (255m) is much lower compared with those in the Sulu Sea (1,824m) (Table 9) and the GM (928m; Davis *et al.*, 1998). In general, dwarf sperm whales inhabit waters over the edge of continental shelves close to shore and feed mainly on cephalopods and occasionally on benthic fishes and crustaceans (Gaskin, 1982; Ross, 1979; McAlpine, 2002). The Tañon Strait, especially the southern half, has a complex bottom topography of very narrow shelves on either side and submarine terraces that go down to 555m. This and the warm bottom temperatures of about 17°C make the conditions there suitable for benthic cephalopods such as squids and nautilus and for benthic fish and crustaceans (Hayasaka *et al.*, 1987; Tucker and Mapes, 1978). In addition, there are fewer deep-diving competitors in the Strait such as the short-finned pilot whales and Risso's dolphins. Fraser's dolphins are absent from the strait.

Common bottlenose dolphin

Although found in both the Sulu Sea and the Tañon Strait it is clear that the bottlenose dolphin is restricted to shallow and intermediate depths on the inside of the shelf break. This coastal distribution is consistent with what is known about the distribution of the species in many areas (Würsig and Würsig, 1979; Shane, 1990; Jefferson and Lynn, 1994; Wells and Scott, 1999). The bottlenose dolphins observed in the Panay Gulf (or northeastern Sulu Sea) were seen on several occasions following shrimp trawlers. This ability to take advantage of human activities has also been observed in several other places (Leatherwood, 1975; Corkeron *et al.*, 1990).

Species with more general or flexible habitat preferences

Spinner dolphin

The spinner dolphin ranked first in abundance in both sites and was found inhabiting both coastal and oceanic and both shallow and deep waters. Neither depth nor site appears to be important in its distribution, though its density was slightly higher in the Tañon Strait than in the Sulu Sea. Its predominance in the two sites supports the hypotheses of Au and Perryman (1985), Reilly (1990) and Reilly and Fiedler (1994) regarding the characteristics of the habitat of this species, i.e. warm with low variation in surface conditions throughout the year. Surface temperatures recorded during the surveys were 25-32°C in both sites. The difference in the depth of the thermocline between the Sulu Sea and the Tañon Strait suggests that the thermocline may not be an important factor in the distribution of this species here. In the ETP, the depth of the thermocline was found to be an important oceanographic factor separating the distribution of the eastern from the whitebelly forms of spinner dolphins (Reilly and Fiedler, 1994). Overall, the thermocline in the ETP where spinner dolphins were found was shallower (mean = 67.72m; Reilly, 1990) compared to both the Tañon Strait and the Sulu Sea. Spinner dolphins in the Sulu Sea feed primarily on mesopelagic prey that migrate in the upper 200m at night and occasionally may dive to greater depths of perhaps to 400m (Dolar *et al.*, 2003). They appear to coexist with Fraser's dolphins, which are even deeper divers, by resource partitioning. The spinner dolphin has extended its foraging range horizontally to include shallow water; Fraser's dolphin on the other hand appears to have extended its foraging range vertically by diving deeper (Dolar *et al.*, 2003).

Spotted dolphin

The distribution of spotted dolphins is similar to that of spinner dolphins and is not affected by depth. A similarity in the distributions of these two species was also observed in the ETP (Au and Perryman, 1985; Reilly, 1990). Although it also occurs in the Tañon Strait, the Sulu Sea is its preferred habitat as shown by the best-fit model (GAM) and by the density, which is seven times higher in the Sulu Sea than in the Strait.

Short-finned pilot whale

To some extent, the distribution of the short-finned pilot whale in the Sulu Sea is similar to that of Fraser's dolphin (Figs 5 and 6). Globally, short-finned pilot whales are found in steep-slope waters, over continental breaks and in areas with high topographic relief (Olson and Reilly, 2002); these features are abundant in the Sulu Sea. Here, they were found in deep waters of 200-5,000m. Like Fraser's dolphins, they

Table 9

Depth and SST profiles for cetacean species that had 20 or more sightings.

		Depth (m)				SST (°C)			
Species and area	*N*	Range	Mean	SD	% *CV*	Range	Mean	SD	% *CV*
Spinner dolphin									
Sulu Sea	97	2-4,339	1,080	1,161	107.5	26.2-31.0	29.20	0.93	3.2
Tañon Strait	51	10-484	171	127	74.3	28.4-30.7	29.38	0.49	1.7
Spotted dolphin									
Sulu Sea	57	39-4,142	1,201	1,185	98.7	28.0-31.0	29.32	0.85	2.9
Tañon Strait	4	72-388	183	125	68.3	28.0-30.0	29.25	0.29	0.1
Fraser's dolphin									
Sulu Sea	39	158-3,793	1,341	1,141	85.0	27.0-31.0	29.33	1.08	3.7
Short-finned pilot whale									
Sulu Sea	42	222-3,406	1,334	923	69.2	26.0-31.0	29.64	0.83	2.8
Tañon Strait	1	160	160	0	0.0	29	29.00	0.00	0.0
Dwarf sperm whale									
Sulu Sea	9	117-3,744	1,824	797	43.7	29.0-31.0	30.40	0.66	2.2
Tañon Strait	21	94-443	255	96	37.6	28.0-30.0	29.30	0.37	1.3
Bottlenose dolphin									
Sulu Sea	21	19-2,381	498	560	112.4	27.0-31.0	29.56	0.85	2.9
Tañon Strait	2	24-328	141	133	94.3	29	29.00	0.00	0.0
Risso's dolphin									
Sulu Sea	22	150-1,872	420	377	89.8	28.2-30.4	29.16	0.63	2.2

are deep diving and feed mostly on squid (Bernard and Reilly, 1999), but unlike them they seem to move more freely in and out of the Tañon Strait. A separate study showed that short-finned pilot whales move between the southern part of the Tañon Strait and the Sulu Sea (unpublished data) and their occurrence in the Strait appears to be seasonal; timed with the influx of frigate mackerels (*Auxis thazard*), (pers. obs. by MLLD). Although short-finned pilot whales feed primarily on squid, they are also known to feed on fish such as cod, herring and mackerel and seasonally move onshore/offshore in pursuit of their prey (Bernard and Reilly, 1999; Olson and Reilly, 2002).

The relationship seen between water temperature and the distribution of the seven species tested is most likely an indirect one, a reflection of the distribution of the cetaceans' prey species. Following the migration of prey (e.g. mullet and snook), which in turn follow warmer waters, has been documented for bottlenose dolphins at Sanibel Island, Florida (Shane, 1990).

Other species

Except for the killer whale, all the species seen in this survey have been previously recorded in Philippine waters. The sighting of three killer whales (male, female and a calf) is the first record for the Philippines.

Bryde's whales have been hunted in the region for almost 100 years (Dolar *et al.*, 1994; Perrin and Dolar, 1998) and the very low sighting rate observed in this study is an indication that the population has decreased significantly in recent years. One of the two sightings off the northern coast of Mindanao was of a mother and a calf.

Survey method, assumptions, biases and limitations

The histograms of perpendicular distances (Fig. 4) are suitable for obtaining abundance estimates (Buckland *et al.*, 1993; 2001). The peaked nature of the histogram for dwarf sperm whale suggests that the ability to spot these whales drops drastically at about 0.5km from the trackline and could be attributed to the cryptic behaviour of this species. The modified technique used in this survey differed from those used in large-scale surveys using large ships in the following respects: (a) the range of the small boat was limited and it could not have been used to survey the high seas or areas farther than 70km offshore (therefore the species composition and abundances found within this distance from shore may be different from those at the centre of the Sulu Sea); (b) the survey could only be carried out in the period between the monsoon seasons when the seas were calm and therefore the results should only be interpreted to apply to this period in time; and (c) the low sighting platform, presence of islands which obscured the horizon and the pitching movement of the boat prevented the use of a reticle to measure distances accurately. Thus distance estimation could only be done by eye and therefore replicability may be compromised because of reliance on the skill of one observer to estimate distance.

Care was taken to ensure that the following three key assumptions necessary for a reliable estimation of density and abundance using the line transect method were met to a good approximation (Burnham *et al.*, 1980; Buckland *et al.*, 2001).

(a) Animals on the trackline are always detected. For delphinids, this may not be a serious problem (Marsh and Sinclair, 1989) but could present a problem for cetacean species which dive for long periods of time such as the dwarf sperm whale and beaked whales (Barlow, 1999). In order to limit this possible source of bias, three precautionary measures were taken. (1) Large (20×) binoculars were used at the trackline to enable the observer to examine the trackline for a relatively longer period of time. This however, may have also limited the observer's field of view and caused them to miss animals which surfaced near the boat. Therefore, (2) an observer without binoculars was assigned to the bow to ensure that the animals missed by the observer using the large binoculars were seen. (3) An experienced dolphin spotter without binoculars was assigned to scan the waters 180° forward to the horizon, including the trackline scanned by the observer assigned to the large binoculars. Even though these precautions were taken, it is possible that long-diving animals were missed. Therefore, for dwarf sperm whale 0.35 was used (Barlow, 1999) as an approximation to $g(0)$. Although vessel speed was similar to that of the vessel used in the simulation experiments, the platform height was much lower and only one 20× instead of two 25× mounted binoculars could be used. Therefore there is a chance that $g(0)$ could actually be lower than 0.35 for that species, which would cause underestimation of abundance. For other species, $g(0)$ was assumed to be equal to one.

(b) Animals are detected at their initial location (i.e. before they move in response to the observer). Although it was observed that some species like spinner and spotted dolphins were attracted to the boat and others such as Fraser's dolphins and dwarf sperm whales avoided it, the onset of these behaviours started after the animals had been detected, suggesting that most detections occurred beyond the likely range of the effect of the boat. The detection ranges of the binoculars used were from approximately 5km (for the 10×) to about 7km (for the 20×), and evasive or attractive behaviour was most often observed when the cetaceans were a kilometre or less away. Double counting was avoided by: (1) rejoining the trackline by following a convergent course towards the end of its leg being followed rather than returning to the exact point where the sighting was made; and (2) disregarding the animals sighted right after the vessel turned back to shore upon finishing the first of the day's two legs (see Fig. 1) unless they were of different species than seen just before the turn. Moreover, the probability that groups were counted again within the same line transect is small, since the cruising speed of the boat (17-20km hr^{-1}) was faster than the sustained swimming speed of most cetaceans.

(c) Distances and angles are measured correctly. The binoculars with the compass allowed measurement of angles to the nearest degree. Estimates of distance were made by the best estimator among the observers as determined by calibration exercises. The estimates were then further calibrated using the measurements made with the GPS, using animals that were not moving away or towards the boat. The use of a reticle would have introduced more errors, considering the low sighting platform, the small size of the boat and the presence of islands obscuring the horizon.

CONCLUSIONS AND RECOMMENDATIONS

The low-cost abundance surveys conducted resulted in population estimates that can serve as baseline information for the two study sites. This information is important in the assessment of fishery impacts in the area and in developing sound management advice for cetacean conservation. In the Sulu Sea dolphins are incidentally caught during various fishing operations and there are some indications that these takes may not be sustainable (Dolar, 1994; Dolar, 1999a).

This type of survey can be replicated in many areas in the Philippines and other developing countries where cetacean bycatch is prevalent but its impacts on cetacean populations are unknown. Equally important is the collection of good data on the anthropogenic induced cetacean mortality to determine sustainability of takes.

The archipelagic nature of the Philippines offers an interesting contrast with other tropical areas such as the ETP and the Indian Ocean where coastal and oceanic habitats are clearly defined. In the Philippines, islands are often surrounded by deep oceanic waters and some cetacean species, which are thought to be typically oceanic, can be found near shore. The relatively shallow Tañon Strait abutting the deeper oceanic basin of the Sulu Sea demonstrates the effect of depth on the distributions and interactions of certain species. It also shows that generalisations cannot be made regarding the habitat preferences of some species, as exemplified by the dwarf sperm whale whose preferred habitat in Tañon is 200-400m whereas in the Sulu Sea it is >1,000m. The relationships between the physical variables (such as water depth, slope and temperature) and cetacean distribution and abundance are often indirect, through links in the food web. Thus for species like the dwarf sperm whale, where there may be a shift in food preference depending on what is locally available, a global generalisation of habitat type may not apply.

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