

Distribution of the Rough-Toothed Dolphin (*Steno bredanensis*) around the Windward Islands (French Polynesia)¹

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Abstract: The rough-toothed dolphin (*Steno bredanensis*) has been described as a primarily pelagic cetacean species that is found in tropical and subtropical oceans throughout the world. Information on distributional patterns or habitat preference in most regions where *S. bredanensis* has been reported is limited. This study reports on the distribution of *S. bredanensis* around the Windward Islands of French Polynesia. Data were obtained from vessel surveys between 1996 and 2000, where rough-toothed dolphins were sighted 38 times. Group sizes of rough-toothed dolphins ranged between 1 and 35 individuals, with an average size of 10.8 individuals. When corrected for effort, results indicated that in French Polynesia *S. bredanensis* is found over a wide area but is more commonly distributed inshore than offshore. Rough-toothed dolphins were usually sighted 1.8 to 5.5 km from the barrier reef, in water depths between 1,000 and 2,000 m. Our results also demonstrate the year-round presence of this species around Tahiti and Moorea. *Steno bredanensis* has been reported in many oceanic archipelagos, and our findings may provide insight into preferred habitat and small-scale oceanographic conditions associated with regions where this cetacean species is relatively abundant.

INFORMATION ON rough-toothed dolphin (*Steno bredanensis*) distributions is limited, but published reports that include this species are quite widespread (Miyazaki and Perrin 1994). *Steno bredanensis* is rarely the focus of field studies but is often mentioned from a few

sightings. Although it is present in almost all tropical and subtropical regions, cetacean sighting data suggest that *S. bredanensis* is not a particularly common species in any area (Au and Perryman 1985, Hewitt 1985, Wade and Gerrodette 1993, Miyazaki and Perrin 1994, Mullin et al. 1994).

Previous reports on the distribution of rough-toothed dolphins are primarily from the eastern tropical Pacific, where very large regions of open ocean waters were surveyed. These studies have extended over 50 degrees of latitude, and for this open-ocean environment a large-scale distribution map for *S. bredanensis* has been generated from approximately 40 sightings (Wade and Gerrodette 1993). Other large-scale surveys in the eastern tropical Pacific indicate the presence of *S. bredanensis* in relatively low abundances compared with other delphinid species in that area (Au and Perryman 1985, Hewitt 1985). Cetacean surveys covering large areas of the western tropical Indian Ocean have also mapped *S. bredanensis* sightings; there the percentage of cetacean abundance represented by this species appears similar to that

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in the eastern tropical Pacific and the Gulf of Mexico, where this species is also present (Ballance and Pitman 1998). An aerial cetacean survey in the Gulf of Mexico documented only a single *S. bredanensis* sighting but in a water depth very similar to that of the inshore areas of French Polynesian islands (~1,000 m) (Mullin et al. 1994, Gannier 2000).

Although *S. bredanensis* distributions have been assessed over the wide eastern tropical Pacific and this may allow for insight into preferred habitat associated with large-scale oceanographic conditions, smaller-scale studies on the distribution of this species have yet to be undertaken. In French Polynesia, cetacean surveys have indicated that *S. bredanensis* is the second most commonly ob-

served species after *Stenella longirostris* (Gannier 2000). This provides an opportunity to investigate the habitat preference of this species around small oceanic islands. Based on multiple sightings of rough-toothed dolphins and on sampling effort spread over 4 years, this study reports on seasonal and temporal variation in distribution around the islands of Tahiti and Moorea.

MATERIALS AND METHODS

Area of Study

The study focused on Tahiti and Moorea in the Windward Islands (Society Archipelago), located at a latitude of 18° S and a longitude of 150° W (Figure 1). Both inshore and off-

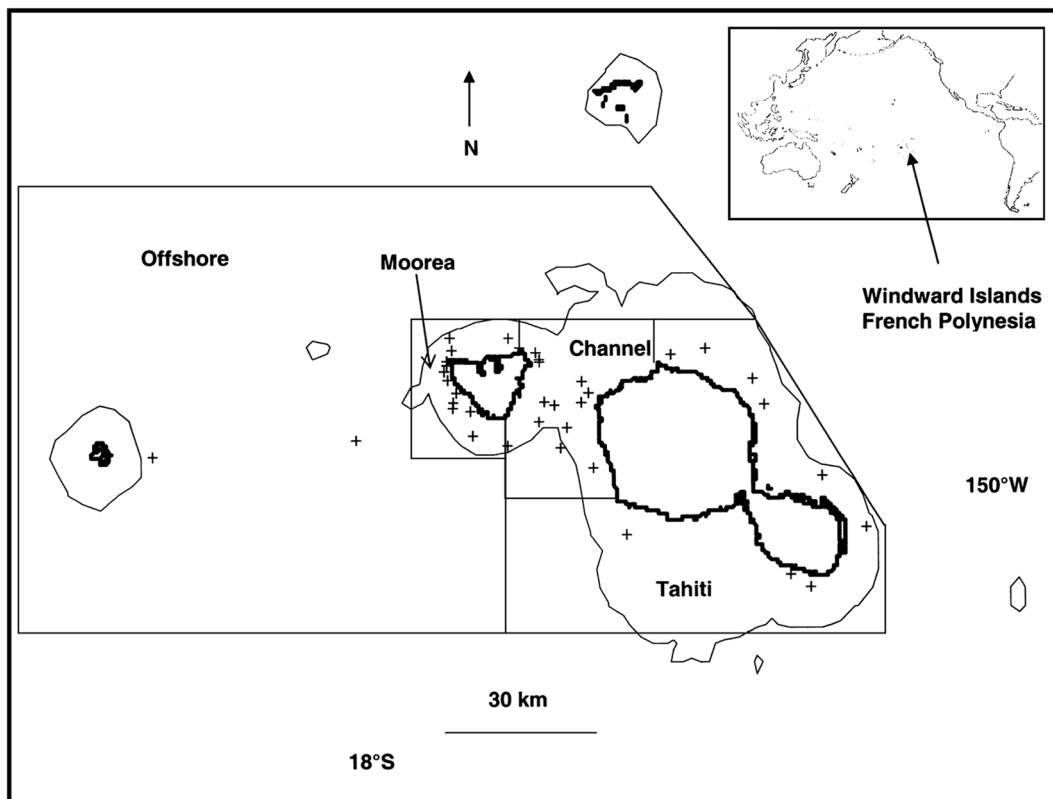


FIGURE 1. Windward islands of Moorea and Tahiti located within the French Polynesian archipelago. Survey regions were categorized as channel, Moorea, Tahiti, and offshore areas. + indicates sighting location of *Steno bredanensis*.

shore areas were surveyed. Due to the 12–18° slope of these volcanic islands, the water rapidly reaches depths in excess of 2,000 m within the inshore area. Oceanic waters are oligotrophic (Longhurst 1999) but passes may provide nutrients into the photic zone and edge effects may cause local eddy-induced vertical mixing as shown around several tropical oceanic islands (Aristegui et al. 1997). The offshore area lies beyond 10 km of the barrier reef, with waters generally deeper than 3,000 m. Water masses are characterized by a very deep (200–300 m) and stable thermocline, but the sea surface temperature features a substantial seasonal change, with lower values of 25–26°C in August–September and higher temperatures of 29–30°C in February–April (non-ENSO situation).

The study area was divided into four regions to investigate distribution of rough-toothed dolphins (Figure 1). The first region was described as the channel located between the islands of Tahiti and Moorea; the second covered the rest of Moorea, which is essentially a leeward area, and extended up to 10 km from shore. The third region comprised all areas off Tahiti, except for the channel, which was primarily a windward exposure and also extended to 10 km from shore. The last region was defined as offshore waters, including areas surveyed that were more than 10 km from shore (Figure 1).

A series of 11 surveys were conducted between March 1996 and May 2000 using a 12 m sailboat. Sampling took place when wind speed was less than or equal to Beaufort 4, primarily using diesel propulsion at an average speed of 9.5 km · hr⁻¹. Both inshore and offshore strata were sampled, and zigzag tracks were conducted around the islands whenever possible. A GPS (global positioning system) was used for positioning and navigation. During the surveys, two or three observers stood on the deck, about 2 m above sea level, and searched the side and frontal sectors. Position was recorded approximately every 3 km, as well as wind, sea state, and relative cloud cover. When cetaceans were sighted, a GPS position was recorded immediately and radial distance and bearing were

estimated. Schools of rough-toothed dolphins were approached systematically to estimate school size, composition, and pod activities.

Data Processing

Data obtained from sampling were entered into a database (*Dbase IV*) and made compatible with *Oedipe* Ifremer Mapping System (Massé and Cadiou 1994), also used for data poststratification and effort calculations. Bottom depth and distance to the barrier reef for each sighting were obtained from nautical charts issued by SHOM, the French Navy Hydrographic Service.

For a given survey protocol (i.e., same platform and same number of observers) and a given species, the assumption of constant dolphin detectability holds if sighting conditions are constant. Because wind in excess of Beaufort 3 may have adverse effects on the detection of small cetaceans (Hiby and Hammond 1989, Buckland et al. 1993), only survey efforts in conditions from Beaufort 0 to 3 were used to estimate sighting rates. Because our survey efforts were not homogeneous across the different strata (regions, periods, areas), distribution was effort-corrected: a mean sighting rate (y_p) was computed, relating to the number of rough-toothed dolphins seen per kilometer. For estimating y_p , we retained the same sampling unit as that used for data recording and computed a sighting rate y_i for each sample,

$$y_i = n_i \cdot S_i / l_i$$

where n_i is the number of rough-toothed dolphin schools detected during the sample (in fact, $n = 0$ or $n = 1$), S_i is the school size, and l_i is the sample length.

The short sample length (2–5 km) was used to enable distribution to be estimated in small areas. Our data set included many 0 values, and the arithmetic mean was not adequate for estimating sighting rates. A Pennington estimator (Pennington and Berrien 1984) was used instead to compute average sighting rates. This estimator is based on the log-normal distribution of the nonzero values of a series of data (Aitchison and Brown 1957) and produces unbiased estimates of mean and

variance in such cases. For a distribution of n samples with m nonzero values ($m > 1$), with y_m the sample mean of the nonzero \log_e values and s^2 a sample variance of the \log_e values, Aitchison and Brown (1957) gave the estimate of the mean, y_p , as:

$$y_p = m/n \cdot \exp(y_m) \cdot G_m(s^2/2)$$

Pennington (1983) gave the estimator of the variance, $\text{var}(y_p)$ as:

$$\begin{aligned} \text{var}(y_p) = m/n \cdot \exp(2 \cdot y_m) \\ \cdot [m/n \cdot G_m(s^2/2) - (m - 1/n - 1) \\ \cdot G_m([m - 2/n - 1] \cdot s^2)] \end{aligned}$$

where $G_m(x)$ is defined by:

$$\begin{aligned} G_m(x) = 1 + (m - 1/n) \cdot x \\ + \sum_{2, \infty} [(m - 1)^{2j-1} \cdot x^j] / \\ [m^j(m + 1)(m + 3) \dots \\ (m + 2j - 3) \cdot j] \end{aligned}$$

T -tests were then used to compare the mean y_p estimates.

The seasonal variation of the rough-toothed dolphins sighting rate was investigated by processing data collected in the channel and Moorea areas, where the sampling effort was highest. The data were split into three temporal periods: a cold-water season (September to November), an intermediate season (December to February), and a warm-water season (March to May). Seasonal sighting rates were estimated as described previously.

RESULTS

Effort

Our total survey effort over the entire study area was 6,458 km, and effective effort was calculated for each region and expressed according to Beaufort conditions experienced during the survey (Table 1). Average sighting conditions were similar (Table 1), except for the offshore area, where Beaufort 3 conditions were more prominent and composed a high percentage of the effective effort. Three different time periods during the year were investigated for seasonal effects in regions 1 and 2: an effective effort of 2,157 km of effort between September and November, 559 km between December and February, and 2,475 km during March to May.

Sightings and Group Size

Rough-toothed dolphins were observed 38 times during the study period. Smaller schools of *S. bredanensis* were more common than larger groups. Average school size was 10.8 ± 9.5 SE individuals with a range between 1 and 35 individuals. Out of our 38 total sightings, 29% of rough-toothed dolphin groups had at least one calf present. Rough-toothed dolphin group size was found to be homogeneous across all four regions (F -test = 0.345, $df = 33$; F 5% = 2.89 [Table 2]). In the Windward Islands, the rough-toothed dolphin was sometimes found in mixed schools, once associated with bot-

TABLE 1
Survey Effort and Sighting Conditions with Percentage of Total in Each Column in Parentheses

Parameter	Entire Study Area (%)	Region 1 (Channel) (%)	Region 2 (Moorea) (%)	Region 3 (Tahiti) (%)	Region 4 (Offshore) (%)
Total effective effort (km)	6,458	3,441	1,706	758	553
Effort in Beaufort 0–1 conditions (km)	864 (13.4%)	482 (14.1%)	213 (12.5%)	117 (15.0%)	52 (9.4%)
Effort in Beaufort 2 conditions (km)	2,442 (37.8%)	1,383 (40.2%)	678 (39.7%)	242 (31.9%)	139 (35.1%)
Effort in Beaufort 3 conditions (km)	3,152 (48.8%)	1,576 (45.7%)	815 (45.7%)	399 (52.6%)	362 (65.4%)

TABLE 2
Number of Sightings and Average Group Size by
Region Surveyed

Region	No. of Sightings	Average Group Size (SE)
1: Channel	13	10.4 (10.0)
2: Moorea	14	12.5 (11.2)
3: Tahiti	8	8.1 (3.1)
4: Offshore	3	13.0 (13.1)

tlenose dolphins and twice with melon-headed whales and Fraser's dolphins. *Steno bredanensis* was also observed interacting with humpback whales on two occasions. Although both spinner dolphins and pilot whales are commonly found in French Polynesia (Gannier 2000), rough-toothed dolphins were never seen associated with either of these species during our surveys.

Distribution

Steno bredanensis was sometimes observed less than 100 m from the reef barrier and occasionally more than 30 km offshore, indicating a wide distribution range. When considering

the entire study area, the total distributions corrected for effort indicate that *S. bredanensis* was found at a rate of 0.124 individual per kilometer. Inshore regions (regions 1 to 3) had a higher number of *S. bredanensis* than the offshore area (region 4), with 0.239 (Table 3) and 0.079 ± 0.130 SE individual per kilometer, respectively. Although sample size in the offshore region was small, this difference was significant (*t*-test, $t = 2.82$, $df = 35$, $P = 0.08$).

Effort-corrected distribution of rough-toothed dolphins was considered according to distance from the barrier reef, bottom depth, and different regions sampled (Table 3). Overall, *S. bredanensis* was more frequently sighted 1.8–5.5 km from shore, with 0.422 individual per kilometer ($n = 19 \pm 0.166$ SE), than in the 0–1.8 km area, with 0.063 individual per kilometer ($n = 8 \pm 0.031$ SE). This difference was significant (*t*-test, $t = 5.44$, $df = 29$, $P = 1.18 \cdot 10^{-5}$). Likewise, rough-toothed dolphins were more frequently sighted in depths between 1,000 and 2,000 m, with 0.190 individual per kilometer ($n = 13 \pm 0.079$ SE), than in the 0–1,000 m category, with 0.173 individual per kilometer ($n = 18 \pm 0.061$ SE), although this difference was not significant (*t*-test, $t = 0.067$, $df = 29$, $P = 0.548$).

Effort-corrected distributions were similar off Tahiti and Moorea (regions 3 and 2), with

TABLE 3
Mean Sighting Rates for Different Categories (in Dolphins per 100 km of Effort)

Mean Sighting Rates (n ; SE)	Channel	Moorea	Tahiti	Inshore (Both Islands)
Whole region	18.62 (15; 8.51)	27.56 (11; 13.47)	32.59 (9; 13.16)	23.89 (35; 6.93)
Distance to shore 0 to 1.8 km	—	12.49 (7; 6.73)	1.05 (1; 0.59)	6.29 (8; 3.12)
Distance to shore 1.8 to 5.5 km	—	29.20 (8; 17.70)	47.80 (11; 20.17)	42.24 (19; 16.64)
Depth 0 to 1,000 m	—	19.87 (10; 10.07)	13.60 (8; 5.27)	17.34 (18; 6.12)
Depth 1,000 to 2,000 m	—	23.95 (6; 13.37)	14.46 (7; 7.66)	18.98 (13; 7.90)

respective values of 0.326 ($n = 9 \pm 0.132$ SE) and 0.276 ($n = 11 \pm 0.135$ SE) individual per kilometer, and somewhat lower in the channel region (region 1), with a value of 0.186 ($n = 15 \pm 0.085$ SE) individual per kilometer (Table 3). Pairwise statistical comparison indicated that only Tahiti and the channel region were significantly different (t -test, $t = 2.734$, $df = 20$, $P = 0.0127$).

Seasonal Variation

Differences in distribution were found between the colder-water season (September to November), intermediate water temperature range (December to February), and the warmer-water season (March to May). During the cold-water season (September to November), a sighting rate of only 0.10 individual per kilometer ($n = 8 \pm 0.05$ SE) was obtained, which was much lower than for the two other periods. In December to February the sighting rate was 0.21 individual per kilometer ($n = 5 \pm 0.14$ SE), which is close to the warm-season (March until May) sighting rate of 0.15 ($n = 11 \pm 0.08$ SE). However, the cold-water season estimate was probably influenced by an uneven effort distribution during that period (September–November) because sampling favored inshore waters where surveys were focused on humpback whales during the winter months.

DISCUSSION

Our distribution results from the Windward Islands suggest that rough-toothed dolphins prefer a specific habitat in French Polynesian waters. *Steno bredanensis* is most frequently found in water depths between 1,000 and 2,000 m, ca. 1.8 to 5.5 km from shore. These results do not demonstrate a purely pelagic habitat usage in this region, which is in contrast to many general reports describing *S. bredanensis* as only a deep-water species (Leatherwood et al. 1982, Leatherwood and Reeves 1983, Miyazaki and Perrin 1994). In Hawai'i *S. bredanensis* is apparently found farther offshore (Mobley et al. 2000, Baird et al. 2003) but where depths are similar to those found closer inshore in French Poly-

nesia (Schlais 1984). However, water depth alone was not found to be an important factor affecting sighting rates in our study (Table 3), despite a probable influence on prey availability. It is not known which specific species of cephalopods and fish *S. bredanensis* in French Polynesia feeds upon. During our study rough-toothed dolphins only were visually observed feeding on epipelagic fishes (including flying fishes) during the day. Mahimahi (*Coryphaena hippurus*) has been suggested as a prey item of *S. bredanensis* (Pitman and Stinchcomb 2002), which would be consistent with an abundance of mahimahi in the areas of French Polynesia where rough-toothed dolphins are most commonly sighted. Inshore prey species have been suggested from stomach contents of stranded individuals in Hawai'i, but those animals may not have represented healthy animals, which are normally found offshore in that region (Miyazaki and Perrin 1994, Mobley et al. 2000). Rough-toothed dolphins are known to enter inshore waters in some areas (for example, this species is sometimes caught as bycatch in coastal gill-net fisheries off northeastern Brazil [Monteiro-Neto et al. 2000]).

In the Windward Islands of French Polynesia, our overall average sighting rate of *S. bredanensis* was 0.124 individual per kilometer. Although comparisons are difficult because survey platforms and observation protocols are specific to each study, sighting rates in other oceans do indicate lower frequencies of *S. bredanensis*, with estimates of 0.0047 and 0.00258 individual per kilometer in the eastern tropical Pacific and western tropical Indian Ocean, respectively (Wade and Gerrodette 1993, Ballance and Pitman 1998). Rough-toothed dolphin importance in delphinid populations may better be compared in terms of sighting frequency. *Steno bredanensis* ranks second in the Society Islands, with 34% of on-effort delphinid sightings (Gannier 2000). In the Marquesas, the northernmost archipelago of French Polynesia, the species ranked sixth, with a sighting frequency of 4.0% (Gannier 2002). In the Solomons, rough-toothed dolphins ranked fifth among delphinids, with a sighting frequency of 5.0% (Shimada and Pastene 1995).

In the Sulu Sea in the Philippines, the species also ranked fifth, with a sighting frequency of 2.9% (Dolar et al. 1997). *Steno bredanensis* was ranked as the ninth most common cetacean species sighted in both the eastern tropical Pacific and the western tropical Indian Ocean (Wade and Gerodette 1993, Ballance and Pitman 1998). Hence from results available in the literature, French Polynesia, and in particular the Windward Islands, appears to be a favored area for *S. bredanensis*. Another region where *S. bredanensis* sighting frequency rates are greater than 20% has been identified in similar water depths off the Hawaiian islands of Kaua'i and Ni'ihau (Baird et al. 2003). Certainly, this species is present around many small oceanic islands in warm temperate to tropical regions and perhaps is found in habitat similar to that of Tahiti/Moorea and Kaua'i/Ni'ihau more abundantly than previously thought.

Our seasonal distribution results indicate surprising differences in that the lowest seasonal sighting rate was obtained during the cold-water season and the highest sighting rate during intermediate water temperature values (December to February). This does not agree with relative abundance estimates of Gannier (2000), which indicated that delphinids are generally three times more likely to be sighted during cold-water periods as in the warm season in the Society Islands. However, the melon-headed whale and Fraser's dolphin account for two of these four delphinid species, and those species were sighted in very large groups during the cold-water season, influencing the results presented for all delphinid species in Gannier (2000). It is also possible that our results for *S. bredanensis* seasonal distributions are at least partially affected by an unequal sampling effort regarding depth and distance from shore between the seasons. During the cold-water period our efforts were more concentrated on shallower areas, because surveys were sometimes focused on humpback whales during that portion of the year. Regardless of season, our results indicate that in French Polynesia *S. bredanensis* is most commonly found at a distance of 1.8 to 5.5 km from the barrier reef in water depths of ca. 1,000–2,000 m.

The Windward Islands are located in an oceanic region where oligotrophy is the rule, with a very deep thermocline (Longhurst 1999). However, small-scale biomass production may be generated by interaction between currents and oceanic islands (Heywood et al. 1990). This may account for higher relative abundance close to the Windward Islands, although *S. bredanensis* is also likely to favor areas where food availability is higher because of ocean floor proximity.

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