

Cetaceans of the Marquesas Islands (French Polynesia): distribution and relative abundance as obtained from a small boat dedicated survey

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Abstract

A dedicated survey of the cetacean population of the Marquesas Islands in French Polynesia, located at about 9°S and 140°W, took place from a 15-m ketch between 29 November 1998 and 27 January 1999 and included visual searching (with three observers on duty) and acoustic sampling with a towed hydrophone. A total effective effort of 2255 km was logged in the study area (63 250 km²), around all islands, as well as in the open sea between the islands. The boat moved on zig-zag tracks dictated by sea and wind conditions, cruising on engine most of the time, at a mean speed of 9 km/h. Sighting rates for individuals were obtained by processing visual data obtained at \leq Beaufort 3 sea conditions, using *Distance 2.2* software. A total of 101 on-effort sightings were made of 10 identified species including the pantropical spotted dolphin *Stenella attenuata* (37), spinner dolphin *Stenella longirostris* (24), bottlenose dolphin *Tursiops truncatus* (17), melon-headed whale *Peponocephala electra* (14), and rough-toothed dolphin *Steno bredanensis* (4). Five other delphinids, *Grampus griseus*, *Orcinus orca*, *Pseudorca crassidens*, *Globicephala macrorhynchus*, and *Feresa attenuata* were each sighted once. The population diversity was high, with a Shannon-Weaver index of 1.8, the melon-headed whale and the spotted dolphin representing 51% and 29% of the observed population, respectively. A sighting rate for individuals of 0.95 ind/km (CV=27%) was estimated for inshore waters (<10 km from coastline) and 0.26 ind/km (CV=23%) for offshore waters. The delphinid community displays higher diversity and relative abundance than that in the Society Islands and appears to be different than observed in the Eastern Tropical Pacific, Galapagos Islands, Solomon Islands, southern Sulu Sea and Savu Sea.

Key words: boat-survey, delphinid, distribution, relative abundance, Marquesas Islands, tropical Pacific.

Introduction

The Marquesas Archipelago lies in the middle of the tropical Pacific at a latitude of 9°S and a longitude of 140°W, between the Eastern Tropical Pacific (ETP) and the Society Islands (Fig. 1a). It includes ten elevated islands, extending over an area of 91,750 km² (Fig. 1b). The archipelago is located close to the mesotrophic equatorial band, in contrast to oligotrophic waters found further south (Longhurst & Pauly, 1987; Longhurst, 1999). More than 20 species of cetaceans frequent the waters of French Polynesia, at least seasonally (Reeves *et al.*, 1999). Sightings in the Society Archipelago, about 1300 km southwest of the Marquesas, indicated that the humpback whale (*Megaptera novaeangliae*), spinner dolphin (*Stenella longirostris*), rough-toothed dolphin (*Steno bredanensis*), and Blainville's beaked whale (*Mesoplodon densirostris*) are frequent species, while the melon-headed whale (*Peponocephala electra*), Fraser's dolphin (*Lagenodelphis hosei*), short-finned pilot whale (*Globicephala macrorhynchus*), and Cuvier's beaked whale (*Ziphius cavirostris*) are commonly seen. The bottlenose dolphin (*Tursiops truncatus*), pantropical spotted dolphin (*Stenella attenuata*), Risso's dolphin (*Grampus griseus*), pygmy killer whale (*Feresa attenuata*), dwarf sperm whale (*Kogia simus*), and sperm whale (*Physeter macrocephalus*) have also been sighted in the Societies (Gannier & Gannier, 1998; Gannier, 2000). In the ETP, 29 species have been identified (Wade & Gerrodette, 1993), including 14 in the southwestern part of the ETP, immediately northeast of the Marquesas, where baleen whales of the genus *Balaenoptera*, striped dolphins (*Stenella coeruleoalba*), and several beaked whales are present.

We carried on a 9-week boat survey to evaluate distribution, diversity and relative abundance in the Marquesas, from 29 November 1998 to 27 January 1999, and compared results to adjacent areas, such as the Society Islands and the ETP.

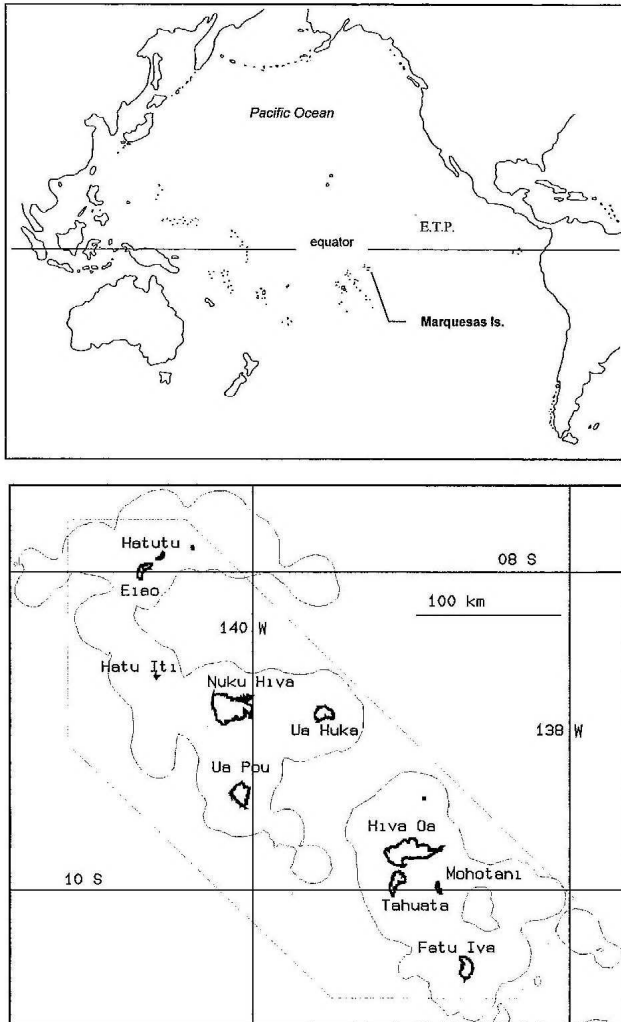


Figure 1. (a) Location of the Marquesas Islands in the Pacific Ocean (b) area of study (the 3000 m isobath is drawn).

Materials and Methods

Study area

The study area extends from Hatutu (7°55'S, 141°25'W) to Fatu Iva (10°35'S, 139°20'W), over a distance of 400 km (Fig. 1b), with an area 63,250 km².

The Marquesas are volcanic islands, but unlike most islands of French Polynesia, they are each surrounded by a 3–5 km wide shelf, where depth is less than 100 m. The whole archipelago emerges from a 3500 m deep abyssal plain, where at least six large seamounts can be found, rising to depths of less than 500 m. Depth of over 2000 m are generally found within 7–12 km from shore, the slope of submarine volcanic cones being about 10–14°. Most of the islands feature cliff-like coastline, although sometimes indented by bays. The bottom topography is not completely known; in some sectors bottom depth can only be estimated from satellite remote sensing data, with a precision of about 500 m.

The hydrobiology of the area is poorly known, although some large-scale results have been presented by Rougerie & Rancher (1994): vertical density and nutrients profiles show an upward sloping of the pycnocline from 25°S to 5°S (for example the nitracline depth rises from about 400 m to 160 m). Enhanced primary production is caused by the equatorial divergence lying between about 5°N and 5°S (Longhurst, 1999), affecting at least the northern part of the Marquesas Islands. Farther south, the South Pacific Subtropical Gyre Province is characterized by a deep pycnocline (100–175 m) and accentuated oligotrophy (Longhurst, 1999). In the Marquesas, sea-surface temperature features some seasonal change, with an average lower value of 26°C in September and a higher value of 29°C in March, during a normal year (non-ENSO situation). Recently, Signorini *et al.* (1999) clearly identified production processes in the Marquesas, from *Seavifs* colour imaging system. An 'island effect' could be caused by an interaction between oceanic islands and currents (Heywood *et al.*, 1990), or by nutrient inputs from rivers, or by some endo-upwelling phenomenon (Rougerie & Wauthy, 1986).

In summary, due to its geographical position (close to the Pacific Equatorial Divergence area) and its particular topography (featuring a narrow continental shelf), the Marquesas Archipelago offers a truly unique ecosystem to marine community organisms, and particularly to cetaceans.

Survey platform and material

A 15-m ketch was used in the survey. A 120-hp diesel engine made possible an average cruising speed of 9 km/h during sampling. When motor-sailing, the particular shape of the front sail left the

front sector unobscured. A Garmin GPS unit was used for navigation and positioning (50–100 m accuracy). Passive acoustic equipment was used, consisting of a 200 Hz to 20 kHz single towed hydrophone with 60 m of cable (Magrec Ltd, U.K.), an adjustable high-pass filter, and a recording device. A standard crew of six allowed four people to be on scientific duty. Three observers searched with the naked eye: one stood in front of the mast, and two sat on the cabin top. Both observer had their eyes located about 3.5 m above sea level. One additional crew member performed the acoustic monitoring.

Sampling

A combined visual and acoustic sampling protocol was adopted during the survey: sampling was done either on diesel propulsion (81% of the time) or motorsailing (19% of the time). In the first case, a nominal speed of 9 km/h was maintained, while in the second speeds were in the 7.5 to 11 km/h range. Two distinct strata were defined: the inshore area (within 10 km from shore) and the offshore area (often deeper than 2000 m). Sampling was carried out with sea state \leq Beaufort 4 and consisted of random zig-zag patterns within inshore areas, weather permitting. Offshore sampling was obtained during good weather journeys among the islands. Whenever cetaceans were sighted, they were approached for species determination and school size estimation.

Acoustic monitoring was carried out every 30 min (4.5 km of sampling in average) by reducing boat speed to 3–5 km/h, for 1 min. The result of each monitoring session was logged, using a five-level scale for both signal and noise. Whenever good quality cetacean emissions were heard during sightings, a 5–10 min recording was made.

Data processing

Data were logged on two forms, one for sampling and acoustic parameters and the other for sighting information, and then entered into a computer database. The geographical software package *Oedipe* (Massé & Cadiou, 1994) was used for mapping and effort calculations, as well as for determining distance to shore for every sighting. Digitized isobaths were available for 500, 1000, 2000, 3000, and 4000 m depths. Sightings were plotted both on nautical chart and computer-based depth data. Delphinid diversity was evaluated with the Shannon-Weaver index (Frontier & Pichod-Viale, 1995), by using all on-effort sightings:

$$H = - \sum (N_k/N_t) \log_2 (N_k/N_t)$$

where, N_k is the number of observed individuals belonging to species k and N_t is the total number of observed delphinids.

Sighting rates for individuals (SRI) were defined from the formulation of the density estimator in the line transect method (Buckland *et al.*, 1993), by assuming $2 \cdot \text{esw}$ as constant across different strata, and calculated for both inshore and offshore areas:

$$D = (n \times S) / (L \times 2 \cdot \text{esw})$$

$$\text{SRI} = n \times S / L$$

where, n is the number of on-effort sightings, S is the mean school size, L is the sampling effort and esw the effective search half-width.

SRI may provide unbiased indications of the relative abundance in the inshore and offshore stratum if the effective search width is assumed to be constant in both strata. For a given survey protocol (i.e., same platform and number of observers), and a given species or group of species, the assumption of constant esw holds if sighting conditions are assumed to be constant on average in both strata. Sighting conditions vary with wind speed, swell height, sun angle, and cloud cover. Since wind in excess of Beaufort 4 have adverse effects on the detection of small cetaceans (Hiby & Hammond, 1989; Buckland *et al.*, 1993; Hammond *et al.*, 1995), we only used data obtained with sea state \leq Beaufort 3 to estimate sighting rates and SRI. Mixed-species schools were entered as single detections.

Because of the scarcity of sightings for most single species, we estimated the sighting rate and SRI for all delphinid species pooled. Sighting rates and SRI were estimated with *Distance 2.2* software (Laake *et al.*, 1994). Variance, SE, and CV were obtained from empirical estimates of components with the delta-method (Buckland *et al.*, 1993). Confidence intervals were estimated at 95% CL on the basis of a log-normal distribution of SRI and T-tests were used to compare logarithms of different SRI.

Distribution patterns for each species, j , were calculated as the sighting rate for individuals in each of three strata, k (coastal, inshore, offshore), a coastal domaine (distance from shore < 5 km) being delimited within the inshore stratum. To provide easy comparison among species, the effort-corrected distribution was then expressed as a relative parameter, F_{jk} :

$$F_{jk} \% = (\text{SRI}_j)_k / (\text{SRI}_j)_k$$

In this paper, acoustic data were only used for assessment of sperm whale presence.

Results

Effort

Sampling effort totaled 2255 km, of which 729 km were obtained with Beaufort 4 sea state, 1125 km

with Beaufort 3, 322 km with Beaufort 2, and 80 km with Beaufort 0-1. Effective effort with sea state of \leq Beaufort 3 was 1526 km in total: 1003 km for the inshore stratum (70.9% of sampling effort), and 523 km for the offshore stratum (62.1% of sampling effort). The inshore waters around the islands of Nuku Hiva, Hiva Oa, Ua Pou, Ua Huka and Tahuata were sampled on two occasions, while Eiao, Hatutu, Fatu Iva, Mohotani and Hatu Iti Islands were covered once (Fig. 2). The leeward side of islands was often sampled under better conditions than the windward side.

Sightings

A total of 101 on-effort sightings were made on ten delphinid species (*S. attenuata*, *S. longirostris*, *T. truncatus*, *P. electra*, *S. bredanensis*, *G. macro-rhynchus*, *P. crassidens*, *F. attenuata*, *G. griseus*, *O. orca*), and one unidentified beaked whale (Table 1). Five species were sighted more than once in the Marquesas: the pantropical spotted, spinner, bottlenose, rough-toothed dolphins, and the melon-headed whale.

The pantropical spotted dolphin was the most common species, with 37 schools observed on-effort (30 inshore and seven offshore) and a mean group size of 17.6 individuals. This dolphin was sighted in the three strata, including deep open sea waters (Fig. 3): its affinity was higher for the coastal domaine ($F=59.8\%$) than for the inshore and offshore strata ($F=18.9\%$ and 21.3% , respectively) (Table 1). Spotted dolphins sometimes formed mixed groups with spinner dolphins, always outnumbering that species. The spinner dolphin ranked second in sighting frequency, with a total of 23 schools observed on-effort and a mean school size of 7.6 individuals (Table 1). Spinner dolphins were often seen in coastal or inshore waters ($F=59.9\%$ and $F=29.1\%$, respectively), often in sheltered locations such as bays inlets and sometimes less than 50 m from shore (Fig. 4). They were observed once offshore in a mixed group with spotted dolphins ($F=11\%$). Bottlenose dolphins were sighted on 17 occasions, off almost every island (Fig. 5) with an average group size of 8.2 individuals (Table 1). During bow-riding sessions, several individuals were estimated to be about 4 m long. This species was mostly sighted in coastal waters ($F=89.3\%$), and sometimes in the inshore area, close to the shelf break ($F=10.7\%$). Melon-headed whales were sighted 14 times, usually in large groups with a mean school size of 85.1 individuals (Table 1). The schools sighted from late December to January included a small proportion of small calves. They were always observed in coastal waters (Fig. 6), one sighting being located over 300 m of depth, close to the shelf break. Rough-toothed dolphins were sighted four times (Fig. 5), in groups of

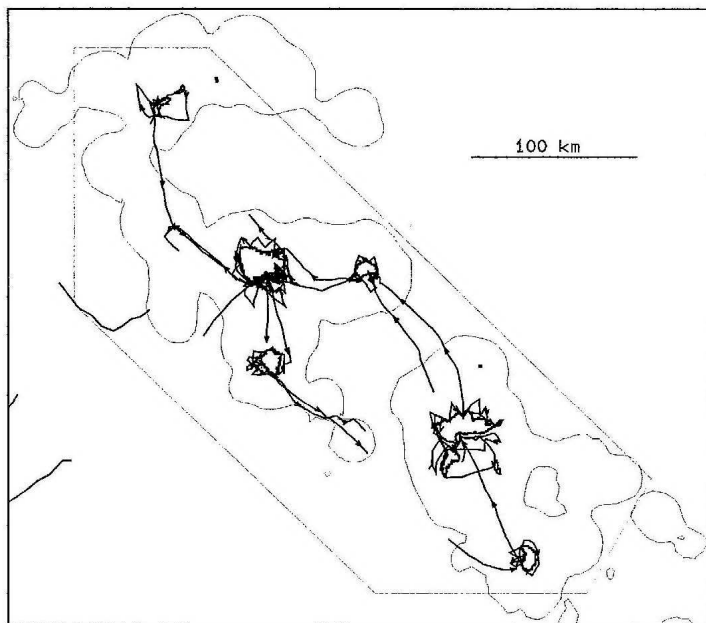


Figure 2. Sampling effort in the Marquesas 1998-99 (the 3000 m isobath is drawn).

Table 1. Sighting frequency and effort-corrected distribution pattern in (F %), calculated for each delphinid species in each stratum (100 sightings).

Species	Number of sight.	Sighting frequency	F % coastal	F % inshore	F % offshore
<i>Stenella attenuata</i>	37	0.370	59.8	18.9	21.3
<i>Stenella longirostris</i>	23	0.230	59.9	29.1	11.0
<i>Tursiops truncatus</i>	17	0.170	89.3	10.7	0
<i>Peponocephala electra</i>	14	0.140	100.0	0	0
<i>Steno bredanensis</i>	4	0.040	29.8	62.8	7.4
<i>Grampus griseus</i>	1	0.010	0	100.0	0
<i>Globicephala macrorhynchus</i>	1	0.010	0	100.0	0
<i>Pseudorca crassidens</i>	1	0.010	0	0	100.0
<i>Feresa attenuata</i>	1	0.010	0	100.0	0
<i>Orcinus orca</i>	1	0.010	0	100.0	0

17.7 individuals in average (Table 1). This species was sighted once in coastal waters (F=29.8%), twice in the inshore stratum (F=62.8%), over the

continental slope (Fig. 5), and once in offshore waters (F=7.4%). Mixed groups involved two or three species. Groups combining *P. electra*,

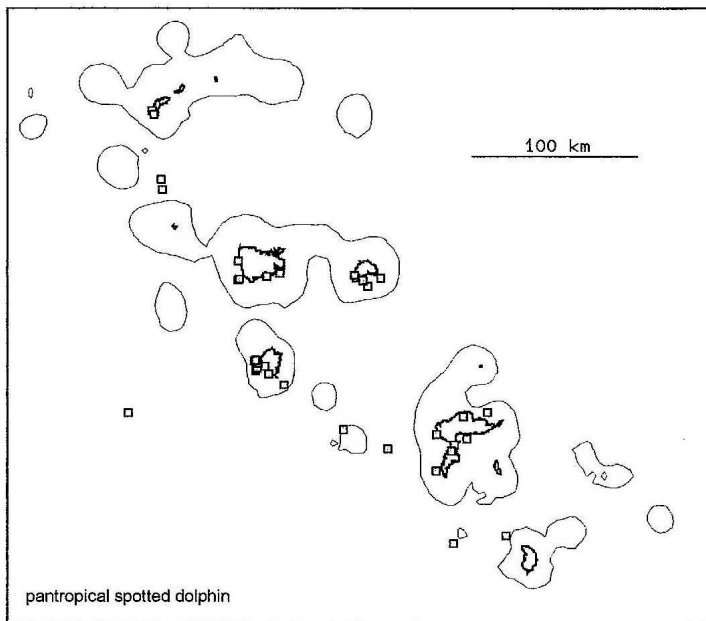


Figure 3. Sightings of pantropical spotted dolphins in the Marquesas 1998–99 (the 2000 m isobath is drawn).

T. truncatus, and *S. longirostris* were seen twice, while the most common association was *S. attenuata*–*S. longirostris* (8 times). An association of *T. truncatus* with *S. attenuata* was observed once.

Short-finned pilot whales were sighted south of Nuku Hiva, in a group numbering about 32 animals (Fig. 4), in water 700 m deep. Risso's dolphins were sighted north of Nuku Hiva (Fig. 4), in water about 800 m deep. False killer whales were sighted close to a sea-mount, in water about 2000 m deep (Fig. 6). The school comprised at least three adults and one calf. Good underwater recording of calls was obtained during the sighting and yellowfin tuna (*Thunnus albacares*) were simultaneously observed. Pygmy killer whales were sighted north of Hiva Oa (Fig. 6), in water 100 m deep, close to the shelf break. The school comprised at least three animals, two lifted their head above the surface, enabling identification. Two killer whales were sighted over the southern shelf-break of Nuku Hiva (Fig. 6). They were observed to travel faster than 12 km/h, parallel to the shore.

The sperm whale presence was not detected out of 501 listening stations in the Marquesas, while dolphinid signals were heard on 88 occasions.

In summary, coastal waters attracted the five common delphinids species, while the rough-toothed, spinner and pantropical spotted dolphins were also distributed in offshore waters, the latter being also sighted well off the 2000 m isobath. A Shannon-Weaver diversity index of 1.86 was calculated.

Inshore and offshore relative abundances

With 50 sightings obtained at \leq Beaufort 3 sea conditions, a SRI of 0.955 individual/km (CV=26.8%) was found for the inshore stratum against 0.263 ind./km (CV=32.7%) for the offshore stratum (11 sightings). This difference reflects the inshore distribution of most species, including bottlenose and spinner dolphins, and melon-headed whales. The nearly four-fold difference is due equally to a higher sighting rate (0.0355 group/km inshore against 0.0169 group/km offshore), and to a

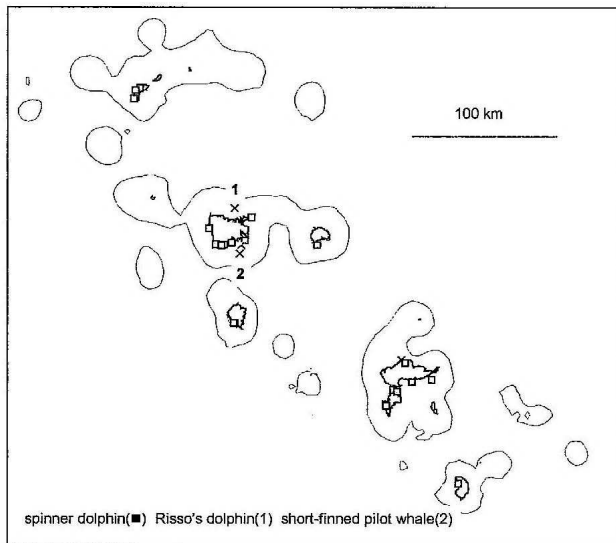


Figure 4. Sightings of spinner dolphin, short-finned pilot whale and Risso's dolphin in the Marquesas 1998–99 (the 2000 m isobath is drawn).

higher mean school size (26.9 inshore against 15.5 offshore). The high mean school size of the melon-headed whale — 85.1 — strongly influences the inshore estimate. When a Student's *t*-test was performed, the values of SRI in both strata were found to be significantly different ($P < 0.001$).

Discussion

A considerable amount of work has been published for the Eastern Tropical Pacific area: dolphin habitats have been studied by Au & Perryman (1985), Reilly (1990), Fiedler & Reilly (1994), Reilly & Fiedler (1994), and estimates of abundance have been provided by several authors, including Buckland *et al.* (1992), Wade & Gerrodette (1993), Anganuzzi & Buckland (1994). Distribution or relative abundance results exist for the Galapagos Islands, located about 90°W–0°S (Smith & Whitehead, 1999), the Society Islands, 150°W–17°S (Gannier, 2000), the Solomon Islands, 160°E–9°S (Shimada & Pastene, 1995) and the southern Sulu Sea, 120°E–7°N (Dolar *et al.*, 1997). We also consider survey work in the Savu Sea off Lombok

Island in the Indonesian Archipelago, 120°E–10°S (Rudolph, 1997).

Species occurrence

All species observed during our survey were within previously reported ranges (Leatherwood & Reeves, 1983). Delphinid sightings in the Marquesas are reported by Reeves *et al.* (1999), including spinner, Risso's, bottlenose, and pantropical spotted dolphins, melon-headed, and pilot whales. The pantropical spotted dolphin is a common species in the tropical Pacific, being found offshore, as well as close to islands (Perrin & Hohn, 1994). The spinner dolphin is represented by different forms in the Pacific and well distributed in tropical waters around the world, where it is often associated with inshore waters; in the ETP large schools are seen well offshore (Perrin & Gilpatrick, 1994). The bottlenose dolphin inhabits tropical and temperate waters in all world oceans; although primarily coastal it can be found in pelagic waters (Wells & Scott, 1999). Melon-headed whales are found in the tropical and sub-tropical waters of all oceans and are common in the eastern tropical Pacific

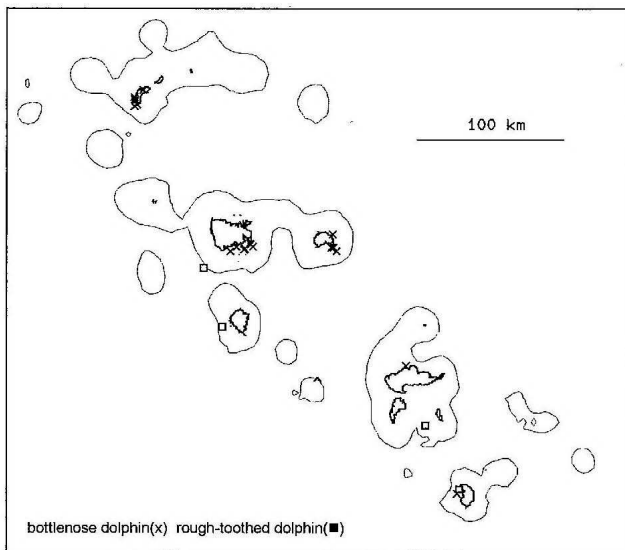


Figure 5. Sightings of bottlenose and rough-toothed dolphins in the Marquesas 1998–99 (the 2000 m isobath is drawn).

(Perryman *et al.*, 1994). Schools of up to 800 individuals are occasionally observed in the Marquesas (*unpublished data*, Nuku Hiva 27 December 1997). The rough-toothed dolphin inhabits sub-tropical and tropical waters of all oceans, in particular the tropical Pacific; it is primarily regarded as an oceanic species (Miyazaki & Perrin, 1994). Risso's dolphins are distributed extensively in tropical and temperate seas, although the species is not frequently recorded in the central tropical Pacific; it is most commonly encountered seaward of continental slopes (Kruse *et al.*, 1999). The short-finned pilot whale has been observed in the eastern and western tropical Pacific (Bernard & Reilly, 1999). The false killer whale inhabits tropical and temperate oceans, it is mostly seen in deep waters offshore, as well as close to oceanic islands (Odell & McClune, 1999). The pygmy killer whale is observed mainly in tropical areas or warm western boundary currents (Ross & Leatherwood, 1994). Killer whales are widely distributed from high latitudes to tropical waters; they are more abundant in coastal habitats (Dalheim & Heyning, 1999).

They were observed in the Marquesas by a SCUBA diving club, while engaged in feeding on manta rays (pers. comm. X. Curvat, Taihoae, Nuku Hiva, Marquesas; February 1999).

The absence of sperm whale in our records was surprising, owing to both bottom topography and geographical location. Based on historical whaling data (Townsend, 1935), a major concentration occurred close to the equator and whales were caught around the Marquesas. The sperm whale is thought to inhabit subtropical and tropical waters during the austral winter (Rice, 1989). The absence of baleen whales is also noteworthy, since the Marquesas are included in the Bryde's whale (*B. edeni*) distribution range (Leatherwood & Reeves, 1983). According to local people, humpback whales are rarely sighted in the Marquesas during their wintering period, but a mother-calf pair was seen on 24 August 1998 near Hiva Oa (pers. comm. M. Oberlin, Hanaïapa, Hiva Oa, Marqueses; January 1999). Humpback whales are common sightings in other archipelagos of French Polynesia during the July–November period (Gannier *et al.*, 2000).

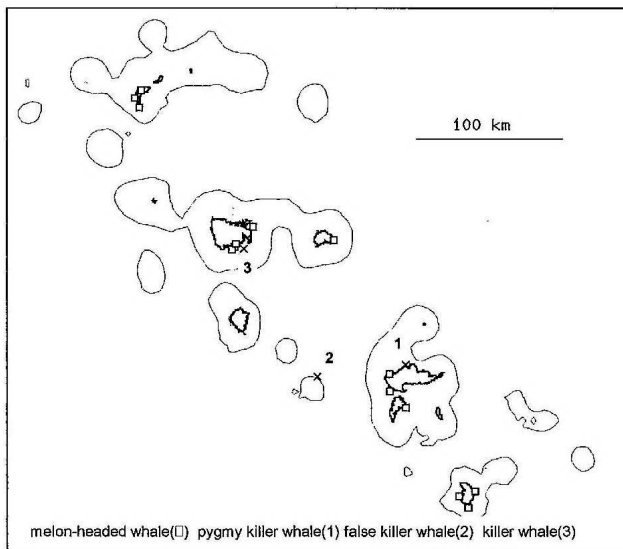


Figure 6. Sightings of melon-headed whale, false killer, killer and pygmy killer whale in the Marquesas 1998–99 (the 2000 m isobath is drawn).

Comparison with similar results in the Society Islands

Results in the Society Islands were obtained by the author with a 11.5-m sloop during surveys spanning over three years: a total of 134 on-effort sightings of seven species was gained during 6482 km of survey effort (Gannier, 2000). Spinner and rough-toothed dolphins and melon-headed whales were the most frequent delphinids, while, short-finned pilot whale and Fraser's dolphin were common, and bottlenose and Risso's dolphins were rare (Table 2). Two additional species, the pantropical spotted dolphin and the pygmy killer whale were identified during one research trip in offshore waters south of the Societies (Gannier & Gannier, 1998).

Sighting rates for individuals of 0.258 and 0.219 delphinid/km were obtained for inshore waters in the Societies, respectively in the Winward and Leeward Islands, while SRI was only 0.022 delphinid/km in the offshore area of this archipelago (Gannier, 2000). In comparison with the present results of 0.955 (inshore area) and 0.263 delphinid/km (offshore area), the Society Islands

display a significantly lower relative abundance in both strata. Although survey platforms were of different sizes (15 m in the Marquesas and 11.5 m in the Societies), the vessels were of the same class (sailboats) and cruised at the same average speed. Hence, different sighting platforms are not likely to influence relative abundance comparisons among archipelagos. The four-fold (inshore stratum) and fifteen-fold difference (offshore stratum) can be related to respective oceanographic and topographic features in the two Polynesian archipelagos, discussed below. Moreover, a Shannon-Weaver index of 1.57 was reported for the Society Archipelago, lower than the index of 1.81 found in the Marquesas (Gannier, 2000).

Comparison with other areas of the tropical Indo-Pacific region

Eleven delphinids, one ziphiid, one physeterid, and two balenopterids were recorded by Wade & Gerrodette (1993) in the southwestern area of the ETP (i.e., a sector southwest of 5°N and 120°W, adjacent to the Marquesas) as seen on published distribution maps. Out of 99 delphinid sightings,

Table 2. Survey results in the tropical Indo-Pacific region, as reported in the literature.

Species Delphinidae	Galapagos (n=159) ^a	SW ETP (n=99) ^b	Marquesas (n=100) ^c	Societies (n=97) ^d	Solomons (n=19) ^e	Sulu Sea (n=51) ^f	Savu Sea (n=68) ^g
<i>S. longirostris</i>	0.012	0.094*	0.077	0.542	0.608	0.464	0.799*
<i>S. attenuata</i>	0.008	0.252*	0.287	0.020	0.178	0.381	0.150*
<i>P. electra</i>	0	0.079*	0.525	0.156	0.096	0	0.009
<i>G. griseus</i>	0.041	0.034*	0.001	0.001	0.003	0.009*	0.013
<i>Globicephala</i>	0.041	0.043*	0.014	0.057	0.068	0.014*	0.006
<i>L. hovei</i>	0.036	0.323*	0	0.092	0.027	0.023*	0.013
<i>S. bredanensis</i>	0	0.005*	0.031	0.128	0	0	0.003
<i>P. crassidens</i>	0	0.013*	0.002	0	0.016	0	0.004*
<i>F. attenuata</i>	0	0.013*	0.002	0.002	0	0	0.003
<i>Delphinus</i> sp	0.648	0	0	0	0	0	0
<i>S. coeruleoalba</i>	0.036	0.121*	0	0	0	0	0
<i>O. orca</i>	0.005	0	0.001	0	0.005	0	0.001
<i>T. truncatus</i>	0.173	0.010*	0.061	0.002	0	0.108	0
other delphinids	0	0	0	0	0	0.039	0
Ziphiidae	—	15	1	8	0	1	0
Kogiidae	—	0	0	1	0	3	1
Physteriidae	—	1	0	1	7	0	1
Balaenopteridae	—	11	0	35	14	0	3

Sighting frequencies for individuals were calculated in each area for delphinids. For other taxa, a simple number of sightings is given.

Bold figures apply to the first dominant pelagic species (excluding bottlenose dolphins), bold italics to the second, and italics for the third.

*Indicates that approximate school sizes were taken in the text of the corresponding paper.

References: ^aSmith & Whitehead (1999), ^bWade & Gerrodette (1993), ^cpresent study, ^dGannier (2000), ^eShimada & Pastene (1995), ^fDolaret *et al.* (1997), ^gRudolph (1997).

Fraser's, pantropical spotted, and striped dolphins ranked high in frequency (32.3%, 25.2% and 12.1% respectively); beaked whales accounted for 15 records, balaenopterids for eleven, and only one sperm whale sighting (Table 2). Among the 11 delphinids recorded by Wade & Gerrodette (1993), nine were sighted during our survey in the Marquesas: striped and Fraser's dolphins were not. Killer whales were not observed in the southwestern ETP. Much of the contrast between southwestern ETP and Marquesas delphinid communities involves 4 species: the Fraser's dolphin (32.3% of delphinids in SW-ETP against 0% in the Marquesas), the striped dolphin (12.1% against 0%), the melon-headed whale (7.9% against 52.3%), and the bottlenose dolphin (two sightings in ETP against 17 in the Marquesas). But, the two latter species have been mostly observed in coastal waters in the Marquesas, an habitat absent from the southwestern ETP. Striped dolphins tend to inhabit offshore temperate waters with a shallow thermocline in the ETP (Reilly, 1990) and were shown to be poorly related to six oceanographic variables (Reilly & Fiedler, 1994). Fraser's dolphins are typically seen in open sea habitat (Perrin *et al.*, 1994), and are frequently associated to melon-headed

whales in the ETP (Wade & Gerrodette, 1993), as well as in the Societies (Gannier, 2000).

In the Galapagos, eight delphinids were identified out of 159 sightings recorded during small-vessel surveys mainly focused on sperm whale ecology (Smith & Whitehead, 1999). The common dolphin (identified to genus level, 64.8% of individuals), Risso's dolphin, short-finned pilot whale, and bottlenose dolphin were the most common taxa, while the killer whale and spinner, spotted and Fraser's dolphins were less common or rare (Table 2). The local abundance of common dolphin is convergent with previous findings on its distribution in the ETP, closely related to cool upwelling water (Reilly & Fiedler, 1994). Hence, the absence of common dolphin in the Marquesas was not surprising.

In the Solomons, eight species of delphinid were identified from a limited data set of 19 sightings recorded during large-vessel surveys (Shimada & Pastene, 1995): spinner and spotted dolphins were common (60.8% and 17.8% of individuals, respectively), the melon-headed whale, the killer and false killer whales, the short-finned pilot whale, and Risso's and Fraser's dolphins were also sighted (Table 2). The delphinid community of the

Solomons shows similarities with that of the Societies, as far as the spinner dolphins, melon-headed whales and pilot whales are concerned. Sperm whales and Bryde's whales were also sighted off the Solomons.

In the southern Sulu Sea, eight species were identified in 51 sightings of delphinid recorded during a survey (Dolar *et al.*, 1997): spinner (46.4% of dolphins), spotted (38.1%), and bottlenose dolphins were common, while the short-finned pilot whale, Risso's and Fraser's dolphins were rare (Table 2). *Orcaella brevirostris* and *Sousa chinensis*, two species inhabiting shallow Australasian waters were sighted.

In the Savu Sea, nine delphinids were identified in 68 sightings recorded mainly during small boat trips and some shore-based observations: spinner (79.9% of delphinids) and spotted dolphins (15%) were common (Rudolph, 1997). Risso's dolphins and killer whales were frequent too, while melon-headed, false killer, pygmy killer and short-finned pilot whales, and rough-toothed dolphins were rarely sighted (Table 2).

The whole set of results delivers an interesting picture for the tropical Pacific: (1) areas without a significant continental shelf domain do not shelter large densities of bottlenose dolphins, (2) a stable component of four pelagic or semi-pelagic species is present in all areas: spinner and pantropical spotted dolphins, Risso's dolphin and pilot whale, (3) the Marquesas features a very frequency for melon-headed whale (52.5% of individuals) compared to all other areas, and (4) spinner and pantropical spotted dolphins are among the two most frequent species in all areas, but the Galapagos, the spotted ranking second east of the Societies (over 25% in frequency) and the former being dominant west of this archipelago with frequencies of over 46% (Table 2). The two species' comparative distribution shown here is not unlike results shown by Ballance & Pitman (1998) for three tropical ecosystems: among ten species of delphinids, *S. attenuata* ranked first in relative abundance in the Gulf of Mexico and the ETP, but it was fifth in western tropical Indian Ocean whereas, *S. longirostris* displayed more consistent relative abundances, ranking first in western tropical Indian Ocean, second in Gulf of Mexico and third in ETP. Ballance & Pitman (1998) concluded that habitat requirements of both species differ significantly.

In summary, the Marquesas delphinid community appears singular, differing substantially from other areas to the west, and from the adjacent southwestern ETP. However, much of the difference with the latter area can be related to the presence of a continental shelf in the Marquesas and the open sea nature of SW-ETP: if frequencies for the spinner and spotted dolphins are

comparable in both areas (Table 2), much of the difference comes from the coastal bottlenose dolphins and melon-headed whales in the Marquesas, and the pelagic striped and Fraser's dolphins in the ETP. To a certain extent, the delphinid community of the Marquesas may be regarded as a coastal subset of the population found in south-western ETP.

Relationship with local oceanographic and topographic features

The Marquesas delphinid community is likely linked to both local oceanographic and topographic features. From averaged satellite imagery, as well as *in situ* measurements, Longhurst (1999) showed that the Pacific Equatorial Divergence Province is a distinct region from the South Pacific Subtropical Gyre Province located in higher latitudes. The Marquesas Archipelago lies at the frontier between those two regions. Furthermore, the circulation of the Southern Equatorial Current certainly produces eddies and local enrichment of the water upper column, as shown in the Canaries (Aristegui *et al.*, 1997) or around Aldabra-Cosmoledo, Indian Ocean (Heywood *et al.*, 1990). For example, a persistent phytoplankton bloom was observed in November 1998 (e.g., the beginning of our study) around the Marquesas by Signorini *et al.* (1999), using *SeaWiFS* satellite imaging system. The authors attributed this effect to a combination of turbulent mixing and advection, and possible inputs from land drainage. Small-scale edge effects could be visually detected during the survey, through sharp changes in surface colour. Hence, strong interactions between local oceanography and topography exist, certainly favouring abundance and diversity of delphinid populations, as may be seen when comparing delphinid communities in the Marquesas and the Societies.

Conclusions

The Marquesas offer a natural sanctuary to many marine species, the area being quite unpopulated and exempt of industrial or major agricultural activities. In the EEZ of French Polynesia, tuna fishing vessels are required to use long-line gear, assumed to cause relatively little damage to cetacean populations. The archipelago displays a diverse and abundant delphinid community, compared to other areas surveyed in French Polynesia. This is likely related to its geographical position, and to the presence of a continental shelf. On the other hand, large mysticetes and odontocetes (particularly sperm whales) were not encountered during our survey, although this might be due to the survey period (December-January).

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