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Distribution of cetaceans off the Society Islands (French Polynesia) as obtained from dedicated surveys

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Abstract

Small boat surveys were organised off the Society Islands (French Polynesia), with 2–3 active observers on board. Sampling was done with Beaufort 4 sea state or less, cruising at 10 km/h mostly on engine power, from March 1996 to May 1999. The area of study extends over 400 km from Tahiti at the southeast, to Maupiti at the northwest, and was divided into 4 sectors: the lagoon area, the inshore stratum (<10 km from the barrier reef) of the Windward and Leeward Islands, and the offshore stratum. For a seasonal analysis the survey data were divided into a September–November period and a March–May period. A sighting rate and a relative abundance index (individual/km of effort) was estimated for delphinids, for each stratum and each period. Mean and variance estimates were computed with Distance 2.2 software. Some 134 sightings were obtained during a total effective effort of 6482 km, including 5222 km with sea state less than Beaufort 3. The humpback whale (*Megaptera novaeangliae*) was observed 35 times, the sperm whale (*Physeter macrocephalus*) and the dwarf sperm whale (*Kogia simus*) once, two species of beaked whale (*Mesoplodon densirostris* and *Ziphius cavirostris*) were observed 8 times, and seven species of delphinid were sighted 91 times, in order of decreasing frequency: *Stenella longirostris, Steno bredanensis, Globicephala macrorhynchus, Peponocephala electra, Lagenodelphis hosei, Tursiops truncatus* and *Grampus griseus*.

The inshore strata had relative abundance indices of 0.258 delphinid/km (Windward Islands) and 0.219 delphinid/km (Leeward Islands), while only 0.021 delphinid/km were found in the offshore stratum. Cetaceans in general favour the inshore waters. An index of 0.123 delphinid/km was found during the March–May period, compared to 0.345 during the September–November period. Factors influencing the distribution of cetaceans are discussed and comparisons given with results obtained in other archipelagos and the eastern tropical Pacific.

Key words: survey; distribution; relative abundance; Society Islands; delphinids; beaked whales.

Introduction

The Society Archipelago lies in the middle of the tropical Pacific at a latitude of 17°S and a longitude of 150°W and includes nine elevated islands and four atolls. The local hydrobiology is dominated by oligotrophy, with superficial primary biomass of less than 0.1 g Chla/m^3, because the Society Islands are located far to the south of the narrow equatorial band, where moderate primary production occurs (Longhurst & Pauly, 1987). More than 20 species of cetaceans frequent the waters of the Society Islands, at least seasonally (Leatherwood & Reeves, 1983). From reports issued by various sources, Poole (1993) listed 13 confirmed species, including 12 odontocetes and one mysticete. Eleven species were identified from preliminary surveys in a sailboat and a research vessel, including the southern humpback whale (*Megaptera novaeangliae*), two beaked whales (*Ziphius cavirostris* and *Mesoplodon densirostris*) and eight delphinid species (Gannier & Gannier, 1998). From these previous sightings, the spinner dolphin (*Stenella longirostris*) and the rough-toothed dolphin (*Steno bredanensis*) were common species, while the melon-headed whale (*Peponocephala electra*) and Fraser's dolphin (*Lagenodelphis hosei*) appeared to be more frequent than the short-finned pilot whale (*Globicephala macrorhynchus*), the bottlenose dolphin (*Tursiops truncatus*), the spotted dolphin (*Stenella attenuata*) and the pygmy killer whale (*Feresa attenuata*). An accentuated preference for the inshore waters was also suggested by the preliminary results, more than 80% of the sightings being obtained less than 10 km offshore. Among the twelve species reported by Reeves *et al.* (1999) as confirmed sightings or strandings in the Society Islands, the Risso's dolphin (*Grampus griseus*) is not listed above.

We describe here in the distribution of cetaceans off the Society Islands, from a series of dedicated small boat surveys undertaken from 1996 to 1999.

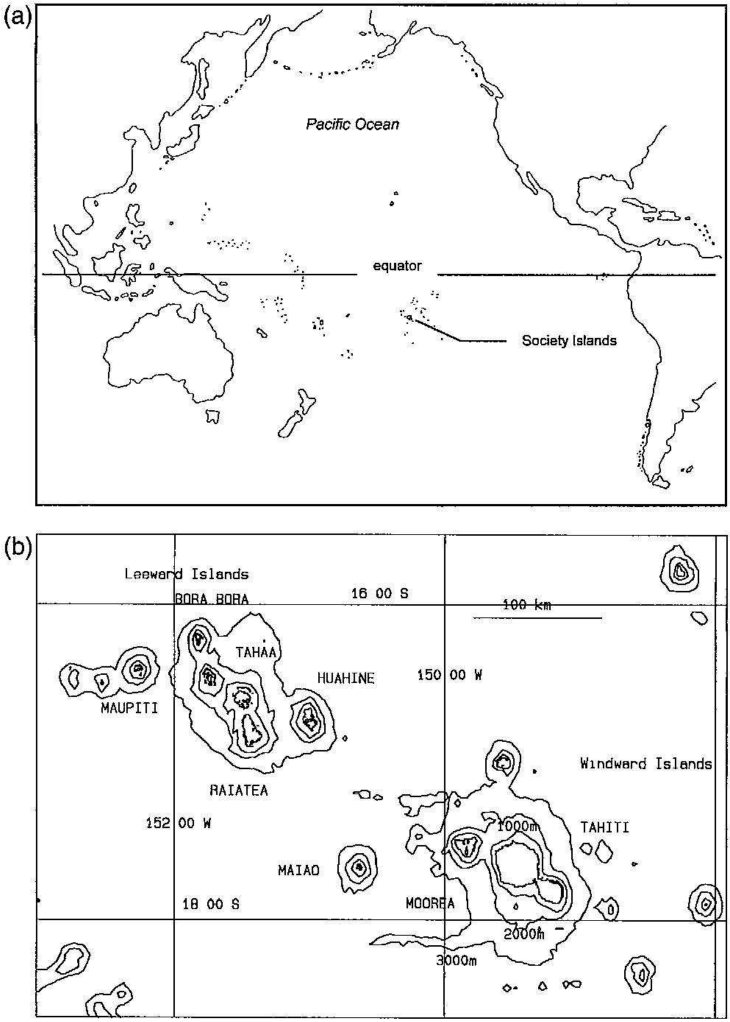

Figure 1. (a) Location of the Society Islands in the Pacific Ocean; (b) Area of study.

Material and Methods

Area of study

The area of study extends from Tahiti (Windward Islands) to Maupiti (Leeward Islands), over a distance of 400 km (Fig. 1). Eight surveys were organised from March 1996 to May 1999 on a 12 m auxiliary sailboat (Table 1). This survey programme totalled 143 days, during which the 0–100 km area around the islands was covered. Due to the 13°–18°

Table 1. Details of surveys (March 96–May 99).

Survey period	Number of days	Effective effort Beaufort <4 (km)	Number of sightings	Remarks
March–April 1996	9	368	4	—
October–November 1996	18	881	18	—
April–May 1997	13	590	13	—
September–November 1997	17	1168	44	w/hydrophone, humpback
April–May 1998	10	421	6	Windward
September–October 1998	18	893	30	w/hydrophone, humpback
March 1999	6	255	5	Leeward
May 1999	12	647	14	focused on rough-toothed dolphin

slope of the volcanic islands, water reaches depths of over 2000 m within 6–8 km from the barrier reef. The area of study comprised three distinct sectors: the lagoon area, the inshore area and the offshore area. Most islands are surrounded by a barrier reef, extending sometimes more than 2 km off the true coast line; a lagoon area is found within the barrier reef, where water may be deep enough to shelter dolphin schools (especially in the bays, passes and channels). The inshore area is located within 10 km of the reef barrier. The southern central tropical Pacific does not feature large-scale primary production, as found in the eastern tropical Pacific (Longhurst, 1999). Passes and edge effects may bring nutrient into the photic zone, in particular due to the outflow of lagoon and river waters and to some eddy-induced vertical mixing. The offshore stratum lies off the 10 km limit: it is an oceanic area with waters generally deeper than 3000 m. Its hydrobiology is dominated by oligotrophy and a deep (200–300 m) and stable thermocline. However, the sea-surface temperature features a significant seasonal change, with an amplitude of about 4°C. During a normal year (non-ENSO situation), lower temperatures of 25–26°C are found in August–September and higher temperatures of 28–29°C in February–April.

Sampling
The same visual protocol was adopted during all surveys: sampling was usually (81% of the time) done on diesel propulsion (speed 10 km/h), with sea state less than or equal to Beaufort 4. Sampling within the lagoon was constrained by topography and limited to deep waters. Sampling inshore consisted of random zig-zag patterns around the islands. Sampling offshore was obtained during fine-weather journeys between the islands, whenever possible. Positioning and navigation were accomplished with a GPS and an auto-steering device. Sampling was interrupted whenever sea state exceeded Beaufort 4 and resumed the following day, or later if necessary.

During visual sampling, two or three observers stood on the roof and shared the frontal sector, searching with naked eye. When cetaceans were sighted, radial distance and bearing estimates were recorded immediately. Schools were then carefully approached for species determination and school size estimation. Sampling effort and sighting data were recorded on two separate forms. A passive acoustic device was used during two surveys, whose main focus was the distribution of humpback whales (Table 1). In these instances, regular acoustic monitoring was carried on during inshore zig-zag sampling by decreasing boat speed to 3–5 km/h, every 3 km of sampling. The result of each monitoring session was logged on the form, using a five-level scale for both signal and noise. When a high quality humpback whale song was heard, a longer stop (10–25 min) was decided in order to properly record the session; however such interruptions of sampling were not common.

Data processing
Species identification was in some cases confirmed from examination of colour transparencies, especially for several sightings of beaked whales. In particular, positive identification of *M. densirostris* was only recorded when the distinctive head of a male could be recognized, either on a picture or during binocular aided observation.

Data were first entered into a computer database (dBase IV), and processed with a geographical software package (*Oedipe*) used for mapping and effort calculations (Massé & Cadiou, 1994).

Indices of relative abundance were estimated for the inshore stratum of both the Windward and Leeward Islands (separately), and for the offshore stratum (as a whole). Two variables were calculated

Table 2. Details of survey effort (in kilometres).

Sighting conditions	Beaufort 0–2 2204	Beaufort 3 3018	Beaufort 1262
Area	Offshore 551	Inshore Windward 3423	Inshore Leeward 1216
Period	Cold water 2632	Warm water 2007	Total inshore 4639

for each stratum: sighting frequency (number of observations per km), and relative abundance index (RAI) (number of animals seen per km):

$$RAI = n \times S/L$$

where, n is the number of on-effort sightings, S is the mean school size and L is the effective sampling effort. From the formulation of the density estimator in the Line Transect Method (Buckland *et al.*, 1993), RAI provides unbiased indications of the relative abundance if the effective search half-width *esw* is assumed to be constant in different strata:

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

Numerous parameters can cause the effective search width to vary. However, 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 supposed to be constant on average. Sighting conditions may vary with wind speed, swell height and luminosity. Wind in excess of Beaufort 3 can have adverse effects on the detection of small cetaceans (Hiby & Hammond, 1989; Buckland *et al.*, 1993; Hammond *et al.*, 1995). Hence, for the processing of sighting rates and RAI, we retained only sampling effort obtained with sea state of Beaufort 3 or less.

Because of the general scarcity of sightings for most single species, we estimated the sighting rate and the RAI for all delphinid species pooled. Sighting rates and RAI were estimated with Distance 2.2 software (Laake *et al.*, 1994), only primary sightings were considered; the mixed species schools were entered as single detections, and global school size was used. The *esw* was arbitrarily taken as 1 km for delphinids, a value larger than any perpendicular distance estimated during the survey. Confidence intervals were estimated on the basis of a log-normal distribution of the relative abundance index. T-tests were used to compare the RAI estimates, after having tested the equivalence of variances with an F-test. The Shannon–Weaver index was used to evaluate the diversity of odontocetes (Frontier & Pichod-Viale, 1995):

$$H = -(\Sigma N_i/N_t) \, Log_2 \, (N_i/N_t)$$

where, N_i is the number of observed individuals belonging to the species i and N_t is the total number of observed odontocetes.

Seasonal sighting rates and RAI were investigated by splitting inshore data into two temporal strata, a ‘cold water’ season for data collected from September to November and a ‘warm water’ season for data from March to May. No survey data were obtained either in July–August or in December–January.

Results

Effort

Survey effort totalled 6452 km, of which 5190 km were obtained with Beaufort 3 sea state or less. Effective effort was 4639 km for the inshore stratum, leaving 551 km in the offshore stratum (Table 2). Sampling effort was unequally divided between the Windward Islands inshore stratum (3423 km) and the Leeward inshore stratum (1216 km). The islands of Tahiti, Moorea, Huahine, and Raiatea-Tahaa were more favoured by the sampling effort than the distant islands of Maiao, Bora Bora and Maupiti (Fig. 2). Sampling effort was evenly distributed between the two temporal strata, with 2632 km obtained during the ‘cold water’ period and 2007 km during the ‘warm water’ period (Table 2).

Sightings

A total of 134 groups of cetaceans were observed on-effort (Table 3), including humpback whales (*M. novaeangliae*), sperm whales (*Physeter macrocephalus*), dwarf sperm whales (*Kogia simus*), two species of beaked whales (*M. densirostris* and *Z. cavirostris*) and seven delphinids (*S. longirostris*, *S. bredanensis*, *P. electra*, *L. hosei*, *T. truncatus*, *G. macrorhynchus*, *G. griseus*). From this total, 4 sightings were obtained with sea state higher than Beaufort 3 and therefore not used for estimates of sighting rate and relative abundance. The spinner dolphin was the only species observed in the lagoon area.

The humpback whale was observed 35 times, in groups of 1–4 animals during surveys in the period September–November. Sightings occurred only in the inshore stratum and generally at less than 2 km

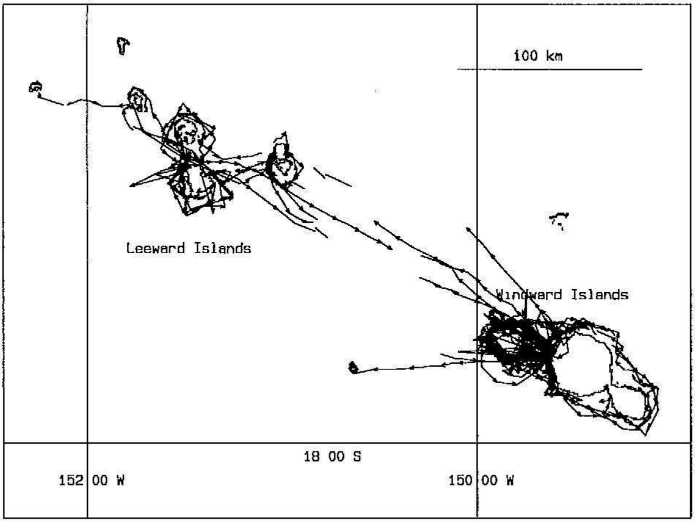

Figure 2. Sampling effort.

Table 3. On-effort sightings.

Species	Inshore stratum	Offshore stratum	Lagoon area	School size min; max	School size mean; S.E.
Megaptera novaeangliae	35	0	0	1; 4	1.83; 0.89
Physeter macrocephalus	0	1	0	1	—
Kogia simus	1	0	0	2	—
Mesoplodon densirostris	4	0	0	2; 4	
Ziphius cavirostris	1	1	0	2; 2	—
Unidentified beaked whale	2	0	0	1; 2	—
Stenella longirostris	19	0	24	3; 100	33.53; 23.17
Steno bredanensis	30	2	0	1; 35	10.47; 10.36
Peponocephala electra	4	0	0	50; 120	—
Lagenodelphis hosei	4	0	0	25; 30	—
Tursiops truncatus	2	0	0	3; 5	—
Grampus griseus	1	0	0	4	—
Globicelphala macrorhynchus	5	0	0	10; 35	26.0; 12.4

from the reef barrier, around both the Windward and the Leeward Islands (Fig. 3). Also, if no humpback was seen around the islands of Raiatea-Tahaa, singers were heard and recorded there. Twelve sightings were of single individuals and pairs of animals. Groups of two animals included 6 mother-calf pairs. Groups of 3–4 individuals were detected on 7 occasions, and often included whales of adult or subadult size. Although humpback whales were never detected inside the lagoon, on two occasions groups detected at the outside were observed to enter the lagoon soon afterwards (and while the observer boat was at a great distance). Both cases relate to groups of three animals: one in Tahiti (3 adults-sized animals) and one in Moorea. In this latter case, a female with a 5 m long calf was apparently escorted by a male, a loud song being heard simultaneously.

Beaked whales were sighted mostly in the inshore stratum, both in the Leeward and Windward

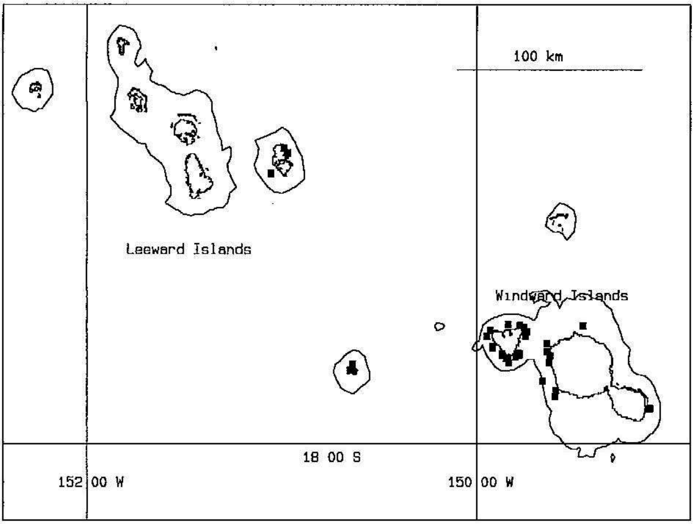

Figure 3. Sightings of humpback whale (the 2000 m isobath is drawn).

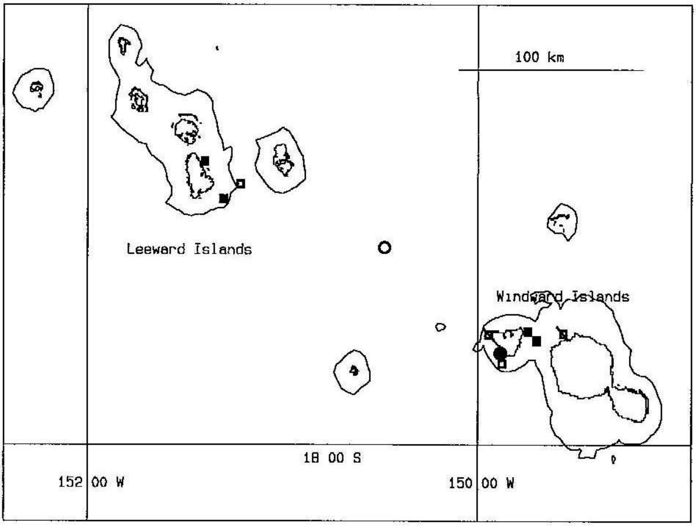

Figure 4. Sightings of Cuvier's (open square), Blainville's (dark square) and unidentified beaked whale (slashed square), of sperm whale (open circle) and pygmy sperm whale (dark circle).

Figure 5. Photograph of two Blainville's beaked whales (from a pod of four) seen between Tahiti and Moorea (Windward Islands) on 20 September 1998.

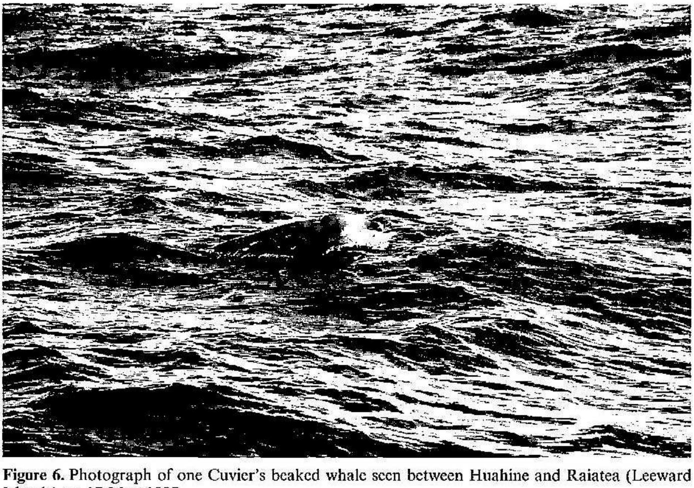

Figure 6. Photograph of one Cuvier's beaked whale seen between Huahine and Raiatea (Leeward Islands) on 17 May 1997.

Islands (Fig. 4): Blainville's beaked whales were always (4 times) sighted at less than 8 km from the reef barrier (Fig. 5), while one sighting of Cuvier's beaked whale was in the offshore stratum, 12 km from the barrier reef, and the other 4 km off the barrier reef (Fig. 6). *M. densirostris* were consistently seen in groups of 2–4 individuals, school size of *Z. cavirostris* being lower (2 individuals). The Blainville's beaked whales were observed in water 300 m to 1400 m deep and the Cuvier's beaked

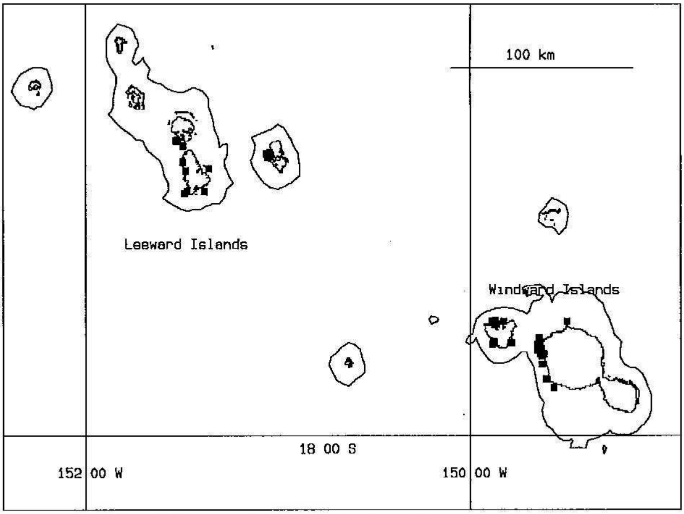

Figure 7. Sightings of spinner dolphin (the 2000 m isobath is drawn).

whales in slightly deeper waters (1100 m and 2100 m). Two sightings of beaked whales were not identified to species, due to the short duration of the visual contact; however, their description corresponded either to a species of *Mesoplodon* or to a medium sized *Z. cavirostris*. They were obtained 1 km and 2.5 km off the barrier reef.

One sighting of a solitary sperm whale was obtained in deep water (3500 m) offshore in October 1997, after a series of positive hydrophone sessions. From its estimated size the animal was assumed to be a large male. The dwarf sperm whale sighting occurred in May 1999, 0.6 km to the reef barrier of Moorea island (Fig. 4) in shallow waters (120 m). Two individuals resting at the surface were approached at 40 m during the 25 mn contact and were photographed.

Of 91 delphinid schools sighted on-effort, the majority were inshore, usually less than 5 km from the reef. It is worth noting that almost all species recorded more than once were observed both off the Leeward and Windward Islands.

The spinner dolphin was the most common species, with a total of 43 schools observed on-effort and a mean school size of 33.5 individuals (Table 3). Nineteen sightings were obtained inshore and 24 within the lagoon area (Fig. 7), where spinner dolphins were usually seen at particular locations, often close to a pass. They were observed to stay at these favoured locations until the afternoon. Sightings made later in the evening were often obtained less than 5–10 km from a known favoured site. *S. longirostris* occurred over quite shallow waters, ranging from 20 m while resting in lagoons, to 500–1000 m. Spinner dolphins were seen year-round in the Society Islands.

The rough-toothed dolphin was observed 32 times, in the Leeward and Windward Islands, and around every island but Maupiti and Maiao. It was represented both in the inshore and offshore strata (two sightings in the latter), occurring from 0.1 km off the reef to 24 km offshore (Fig. 8). However, 68% of the sightings were obtained within 4 km of the barrier reef. *S. bredanensis* occurred in variable water depths, ranging from less than 100 m to over 3000 m, although apparently favouring the 500–1500 m range. Group size ranged from one to 40 individuals, with an average of 10.5 individuals (Table 3). Rough-toothed dolphins were observed year-round. Small schools (5–8 animals) were sighted twice with mixed schools of melon-headed whales and Fraser's dolphins.

The short-finned pilot whale was sighted 5 times, around the islands of Huahine, Tahiti and Moorea (Fig. 9). Sightings occurred in various periods of the year, with group sizes ranging from 10 to 35 animals (mean 26.0 individuals). This species showed a predilection for inshore waters, being occasionally

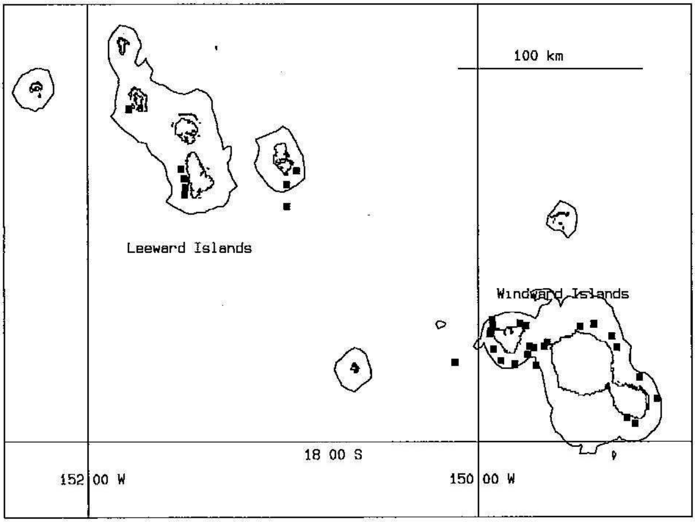

Figure 8. Sightings of rough-toothed dolphin (the 2000 m isobath is drawn).

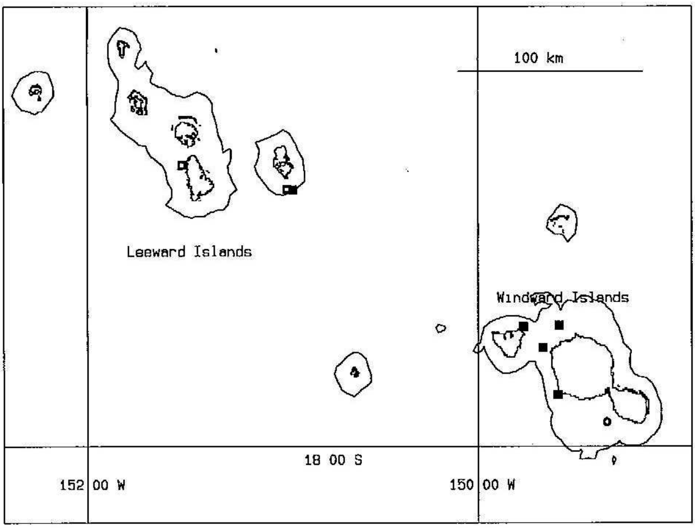

Figure 9. Sightings of large and medium-sized delphinids: bottlenose dolphin (open square), short-finned pilot whale (dark square) and Risso's dolphin (open circle).

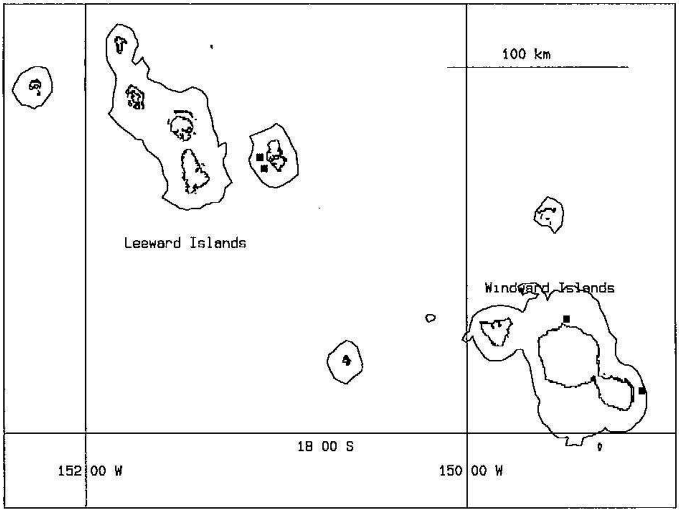

Figure 10. Sightings of Fraser's dolphin and melon-headed whale.

seen at less than 0.5 km from the barrier reef and up to 7 km offshore. It occurred over moderate water depths, ranging from 300 m to 1400 m. On one occasion, a school of pilot whales included three bottlenose dolphins.

Melon-headed whales and Fraser's dolphins were observed 4 times in mixed schools totalling 75–160 animals (Fig. 10), always with higher numbers of melon-headed whales (school size ranging from 50 to 120 individuals) than Fraser's dolphins (school size 25–30 individuals). These aggregations also included several rough-toothed dolphins on two occasions. Mixed groups were observed twice each around Huahine and Tahiti, 2 to 5 km off the barrier reef, over depths of 500 m to 1500 m. In the former case, one of the two sightings was probably a duplicated detection occurring after a 3-h survey interruption and was discarded for the relative abundance estimate.

With only two sightings in the Leeward Islands (including the mixed school with pilot whales), the bottlenose dolphin was not frequent. Group sizes were of 3 and 5 individuals. Risso's dolphin presence was also limited, with one sighting in inshore waters 6 km close to Tahiti (Fig. 9). The group apparently consisted of only 4 animals. Both species were observed in inshore waters.

In summary, our present results show a local cetacean community limited to 11 species, giving a high Shannon–Weaver diversity index of 1.57 for the odontocetes. One striking feature is perhaps the relatively high frequency of beaked whales in relation to other taxa (8 sightings of 134). Delphinids are the most frequent cetaceans, with dominance of the spinner and the rough-toothed dolphins, and the common occurrence of melon-headed whale, Fraser's dolphin and short-finned pilot whale. Humpbacks are frequently sighted during their wintering season. While it can be inferred from the simple observation of distribution maps that cetaceans are much more frequent in inshore waters, this will be better shown in the following section.

Inshore and offshore relative abundances

There was about a five-fold difference in sighting rates between the offshore ($0.362\ 10^{-2}$ group/km) and the inshore strata for both groups of islands. The values obtained in the Leeward and Windward inshore strata were close to each other, with 0.112 group/km and 0.091 group/km respectively (Table 4). Mean school size estimates in both inshore areas were also similar: 22.7 animals (SE=4.7) in the Windward Islands and 24.2 (SE=6.2) in the Leeward Islands (Table 4). Consequently, two RAI estimates are similar, with 0.258 delphinid/km in the Windward Islands and 0.219 in the Leeward Islands (Table 4). However, they are statistically different

Table 4. Sighting rates and relative abundance indices for delphinids.

Estimate	Inshore stratum (Windward)	Inshore stratum (Leeward)	Offshore stratum
Sighting rate (group/km) and SE	$1.15\ 10^{-2}$ ($0.168\ 10^{-2}$)	$0.91\ 10^{-2}$ ($0.244\ 10^{-2}$)	$0.362\ 10^{-2}$ ($0.295\ 10^{-2}$)
Mean school size and SE	22.7 (4.74)	24.2 (6.23)	6.0 (1.0)
Relative abundance index (ind/km) and SE	0.258 (0.066)	0.219 (0.081)	$0.217\ 10^{-1}$ (—)

Table 5. Seasonal variation of the delphinids relative abundance.

Estimate	March to May (warm water)	September to November (cold water)
Sighting rate (group/km) and SE	$0.946\ 10^{-2}$ ($0.229\ 10^{-2}$)	$1.215\ 10^{-2}$ ($0.176\ 10^{-2}$)
Mean school size and SE	13.05 (2.51)	28.47 (5.77)
Relative abundance index (ind/km) and SE	0.123 (0.038)	0.345 (0.086)

(T-test, $P=0.012$). The RAI estimate in offshore area is about one order of magnitude lower, i.e. 0.0217 delphinid/km. It is clear that delphinids favour the inshore areas, around islands, rather than open sea waters.

These results show an homogeneity in the delphinid population between the Windward and the Leeward Islands (in sighting rate, mean school size and RAI). Furthermore, except for the Risso's dolphin, the dwarf sperm whale (only seen in the Windward Islands), and the bottlenose dolphin (only observed in the Leeward Islands), all species were sighted in both groups of islands. Although no RAI estimates could be produced for the beaked whales, they occurred similarly in both groups of islands, suggesting that the Society Islands can be considered as a whole as far as the odontocete fauna is concerned.

Seasonal variation

Four dolphin species were observed during both periods: the spinner dolphin, the rough-toothed dolphin, the short-finned pilot whale and the bottlenose dolphin. The melon-headed whale and the Fraser's dolphin were only observed during the 'cold water' season. For all delphinid species pooled, there was similarity between the sighting rates obtained during the two seasons, with an estimate of $0.946\ 10^{-2}$ group/km for the March–May period against about $1.21\ 10^{-2}$ group/km for the September–November period (Table 5). These values were not significantly different. But the mean school size estimates are significantly different, with 13.0 individuals during the 'warm water' season and 28.5 animals during the 'cold water' season. Consequently, the two RAI estimates differ significantly, with 0.123 delphinid/km for the March–May period and 0.345 during the September–November period (Table 4), as confirmed by a T-test ($P<0.0001$). Our results indicate that delphinids were relatively more abundant during the 'cold water' season.

Seasonal variation could not be assessed for beaked whales, but both Blainville's and Cuvier's beaked whales were observed during the 'cold water' and 'warm water' seasons. Humpback whales were only sighted during surveys in the 'cold water' season, up to the beginning of November when mother-calf pairs were still observed around Tahiti and Moorea.

Discussion

Occurrence

To date, little survey work has been dedicated to waters surrounding the Polynesian and Micronesian Archipelagos (Hawaii excepted). With 10 species sighted, the local odontocete population displays a high diversity, while mysticetes are represented only by the humpback whale. All species observed during our surveys were within previously reported ranges (Ridgway & Harrison, 1989; 1994; 1999; Leatherwood & Reeves, 1983; Reeves *et al.*, 1999).

The humpback was the most frequently sighted species during the September–November period. Although full comparative analysis has still to be done, the structure of songs recorded in French Polynesia during the 1997 season (Gannier, unpublished report) shows some similarities with songs recorded in the eastern Australia–New Caledonia–Tonga wintering area (Helweg *et al.*, 1998).

The rarity of sperm whale in our records was surprising if one considers the ancient whaling history of Polynesia (Dodge, 1971). During a recent survey (Gannier, 2000), we observed a school of about 16–20 sperm whales in offshore waters of the Windward Islands. Maps published by Townsend (1935) did show several sperm whale catches around the Society Islands, although more Yankee Whalers catches were recorded in the Tuamotu Archipelago. In the tropical Pacific Ocean, a major concentration of catches lies "On The Line", i.e. close to the equator (Townsend, 1935). Although sperm whale distribution in the South Pacific is not well known presently, the species is supposed to inhabit subtropical and tropical waters during the austral winter (Rice, 1989).

Both Cuvier's and Blainville's beaked whales are cosmopolitan and inhabit both tropical and temperate waters. Both species have been observed in the tropical Pacific, although their distributions are better known from stranding records (Heyning, 1989; Mead, 1989). The dwarf sperm whale is also cosmopolitan and could prefer coastal waters in its tropical-to-temperate range; the species has already been observed in the tropical Pacific (Caldwell & Caldwell, 1989).

The short-finned pilot whale inhabits tropical waters of all oceans and temperate waters in the north Pacific; the species has been observed in the eastern and western tropical Pacific (Bernard & Reilly, 1999). The bottlenose dolphin is known to inhabit tropical and temperate waters in all world oceans (Wells & Scott, 1999) and Risso's dolphin distribution is almost as extended, although the species is not frequently recorded in the central tropical Pacific (Kruse *et al.*, 1999).

The rough-toothed dolphin inhabits sub-tropical and tropical waters of all oceans and its presence is well documented in the tropical Pacific (Miyazaki & Perrin, 1994). The spinner dolphin is represented by different forms in the Pacific and well distributed in tropical waters around the world (Perrin & Gilpatrick, 1994). Fraser's dolphin is a cosmopolitan delphinid with a preference for tropical waters; its presence is well documented in the tropical Pacific (Perrin *et al.*, 1994). Melon-headed whales are also found in the tropical and sub-tropical waters of all oceans and widely distributed in the tropical Pacific (Perryman *et al.*, 1994).

Most of the literature published so far deals with the eastern tropical Pacific (ETP), which is essentially located to the north-east of French Polynesia, east of 140°W, on both sides of the equator. In particular, dolphin habitats have been studied there by Reilly (1990), Fiedler & Reilly (1994), and Reilly & Fiedler (1994). In the ETP, estimates of cetacean abundance have been provided by several authors, including Wade & Gerrodette (1993).

A comparison of the present results with the western area of the ETP (i.e., the sector closest to French Polynesia) can be obtained from the distribution maps and an extensive data set published by Wade & Gerrodette (1993): nine small delphinids, six larger odontocetes and one baleen whale are mentioned in this sector by these authors. From this list of 16 species, the Bryde's whale (*Balaenoptera edenii*), the killer whale (*Orcinus orca*), the false killer whale (*Pseudorca crassidens*), the pygmy killer whale (*Feresa attenuata*), the pantropical spotted dolphin (*Stenella attenuata*) and the striped dolphin (*Stenella coeruleoalba*) were not observed during our surveys off the Society Islands. But, we did observe both the pygmy killer whale and the pantropical spotted dolphin during an offshore research survey 200–400 km south of the Society Islands, in December 1996 (Gannier & Gannier, 1998). Reilly (1990) showed that striped dolphins in the ETP inhabit waters with a shallower thermocline than the spotted and spinner dolphins; it is not surprising, therefore, that striped dolphins were not seen in the deep-thermocline waters around the Society Islands. On the other hand, Wade & Gerrodette (1993) did not mention the dwarf sperm whale or the humpback whale in the western sector of the ETP, and we observed both species off the Society Islands.

From 390 reports obtained from various sources, Poole (1993) listed 13 confirmed species in French Polynesia, including the killer whale and the pantropical spotted dolphin, but the exact locations of those records were not indicated. It could be argued that reports from amateurs should be sometimes regarded with prudence, since correct identification of cetaceans in tropical waters can be difficult, especially when considering pairs of species like *P. electra–F. attenuata*, *S. longirostris–S. attenuata*, *M. densirostris–Z. cavirostris* or even *G. macrorhynchus–P. crassidens*.

During a recent survey in the Marquesas Archipelago (roughly located halfway between the Society Islands and the ETP), the killer whale, the false killer whale and the pygmy killer whale were each sighted once, while pantropical spotted dolphins were frequently observed (Gannier, 1999). The composition of dolphin species was different, with an accentuated presence of bottlenose dolphins, pantropical spotted dolphins and melon-headed whales; spotted and rough-toothed dolphins were well represented in offshore waters (Gannier, 1999).

Ballance & Pitman (1998) compared delphinid populations in three tropical ecosystems, the western tropical Indian Ocean (WTIO), the Gulf of Mexico (GM) and the eastern tropical Pacific. Among ten species of delphinids, *S. attenuata* ranked first in relative abundance in GM and ETP, while it was fifth in WTIO. *S. longirostris* displayed a less variable relative abundance, ranking first in WTIO, second in GM and third in ETP.

Furthermore, both species associate frequently in WTIO and ETP, when they do not in GM. The authors concluded that habitat requirements of both species may differ significantly. Present results and those obtained in the Marquesas (Gannier, 1999) provide further evidence of these subtle differences.

The present results also show some similarities with those obtained in the Solomon Islands, located at about 8°S, 160°E in the western tropical Pacific, by Shimada & Pastene (1995). Among delphinids, the spinner and spotted dolphin were common species, while the melon-headed whale, the killer whale, the false killer whale, the short-finned pilot whale, Risso's dolphin and Fraser's dolphin were also sighted. But the sperm whale and Bryde's whale were commonly sighted off the Solomons, when they are not frequent around the Societies.

Data obtained in the Philippines Archipelago (northwestern tropical Pacific) show a more diverse mysticete community, with the regular presence of Minke whale (*B. acutorostrata*) and Bryde's whale, probably related to food resources (Tan, 1997). The odontocete community is not dissimilar to that of the Society Islands, but pygmy sperm whales, false killer whale and finless porpoise (*Neophocaena phocaenoides*) have been observed in the Philippines (Tan, 1997) when they were not in the Societies. The two former species are probably present in the Society Islands, but they are still to be observed by the author. In the Sulu Sea and surroundings, spinner and Fraser's dolphins display markedly different distribution patterns, the former preferring shallower waters, when the latter is more frequent in deep waters, and Dolar (1999) has shown this is probably related to their respective feeding ecology.

Our results for the Society Archipelago offer a good example of a cetacean fauna around volcanic islands surrounded by tropical oceanic and oligotrophic waters. Comparisons with other areas in the tropical Pacific suggest some degree of commonality, while the differences can be related to topography of islands and their zonal and latitudinal position.

Distribution

Excluding one sighting of Cuvier's beaked whale, one of sperm whale and two of rough-toothed dolphins, all detections were obtained in the inshore stratum, mostly within 5 km of the barrier reef. Consequently, there is a ten-fold ratio between the Relative Abundance Index obtained in inshore waters (about 0.2 delphinid/km) and the lower value estimated for offshore waters. The latter estimate was obtained from a relatively low sampling effort (551 km). However, during a previous survey on board a large research vessel (Gannier & Gannier, 1998), 2166 km of effective sampling were achieved offshore south of the Society Islands and only three sightings were recorded farther than 27 km offshore, including one group of *F. attenuata* and one group of *S. attenuata*. The offshore area can be regarded as a desert in comparison to the inshore area while in the eastern tropical Pacific, offshore sectors are well inhabited by several species of dolphins as well as larger odontocetes (Reilly, 1990; Fiedler & Reilly, 1994; Reilly & Fiedler, 1994).

There is little doubt that such a balance between the inshore and offshore waters cetacean population can be attributed to hydrobiological factors. The extreme oligotrophy of water around the Societies was measured *in situ* (Rancher & Rougerie, 1993) and is also visible from CZCS satellite imagery (Longhurst, 1999). Longhurst includes the Society Islands within the oligotrophic 'South Pacific Subtropical Gyre Province', when the eastern tropical Pacific lies within the 'Pacific Equatorial Divergence Province', where mesotrophic conditions predominate. In the Society Archipelago, the vertical stratification of waters remains unchanged even close to the reef barrier (Rougerie & Rancher, 1994).

The distribution of odontocetes in the inshore stratum may be explained by an increase of prey availability. In the open ocean, the deep chlorophyll maximum lies at 100–150 m over a transition layer of 200–400 m thickness; this is not favourable to the feeding cetaceans unless they are deep divers. But small-scale productivity increase could evolve from eddies linked to the current flow around the islands, or from local nutrient inputs due to rivers and rainfall, or even from an endo-upwelling phenomenon occurring through the coral platform (Rougerie & Wauthy, 1986). Increased food availability might in turn be exploited by the pelagic or the deep demersal community (squid, fish), preyed upon by odontocetes, noticeably night-feeders like spinner dolphins or short-finned pilot whales. Unfortunately, *in situ* study of small scale hydrobiological features has still to be undertaken in French Polynesia, and satellite imagery is not yet accurate enough to yield suitable data.

Although inshore waters are locally favoured by dolphins, the sighting rates and the RAI estimates do not indicate that abundance is high; the overall sighting rate was less than one per day. Part of the spinner dolphin community is not included in the inshore relative abundance indices, since 24 sightings made in particular resting sites were relevant to the lagoon stratum (Table 3). Comparison of relative abundance estimates between different surveys can be delicate and sometimes unmeaningful, we may however refer here to some results in the literature. Anganuzzi & Buckland (1994) combined estimates for the offshore pantropical spotted dolphin in the ETP, as obtained from tuna vessel observer programmes; a sighting rate of 4.08 10^{-3} schools/km and an average school size of 597.2 dolphins lead to an estimate of 2.43 dolphin/km. It is likely that the tall platform and large effective search width (13.6 km) largely influence such a high relative abundance index. During a survey conducted with a 12 m sailboat (similar to the platform used here), we obtained an index of 0.67 striped dolphin/km in the Ligurian Sea (Gannier, 1998); this is still much higher than the 0.2 dolphin/km found in the inshore stratum of the Society Islands. Hence, the local delphinid population can not be described as 'very abundant'.

Seasonality

The sighting of humpback whales during the September–November period is obviously linked to the wintering and breeding of the humpback whale population. In 1998, humpback whales were sighted in the Societies from 10 July (Pierre-Philippe Tricottet, pers. com.) to 12 November (Kristi West, pers. com.) This extended time period corresponds broadly to data obtained in Tonga (Dawbin, 1997).

Our results show a three-fold ratio between the 'cold water' and the 'warm water' RAI estimates (0.345 and 1.232 delphinid/km, respectively). A seasonal thermal contrast in superficial waters (from about 25°C in August to 29°C in March) could be the cause of the seasonal change, triggering either a zonal or a latitudinal migration shift of several delphinid species. But the variation of the Relative Abundance Index owes much to the seasonal absence of the melon-headed whale and Fraser's dolphin from our records. The low 'warm water' RAI estimate is largely caused by the absence of large mixed schools of *L. hosei* and *P. electra* from the March–May data set. This is particularly reflected by the much lower mean school size estimate obtained during that season (13.05 against 28.45 in September–November). Due to the general scarcity of sightings, this seasonal absence could be incidental, since large mixed schools of melon-headed whales and Fraser's dolphins were observed off Moorea in January, February and March by other cetologists (Jay Sweeney & Kristi West, pers. com.)

According to Longhurst & Pauly (1987), the seasonal variability of standing biomass is low in tropical oceans, except in some wind-induced upwelling areas. During the austral winter, a weak deepening of the mixed layer could cause a short increase in primary and secondary biomass in the tropical waters (Longhurst, 1999). This process could arise in the September–October period around the Society Islands and would account for an increase of the cetaceans in the area. However, the present seasonal results are preliminary and deserve to be strengthened by additional data before the seasonal status of delphinid can be further described.

Conclusions

Cetaceans in the Society Islands are divided into two distinct components: the mysticete community, represented by the migratory southern humpback whale, and the odontocete community, which includes more than 12 species belonging to the Delphinidae, Ziphiidae and Physeteridae. The high diversity of the odontocetes is probably related to stability of the local hydrobiological conditions. The distribution of cetaceans largely favours inshore waters, and this reflects the accentuated oligotrophy of the open ocean in this part of the tropical Pacific. Even if numerous ecological factors are locally unknown, the paradigm of 'desert or oasis' can hardly be avoided by the marine ecologist involved in cetacean studies. In spite of obvious limitations, like the limited coverage of offshore waters and the use of a small survey platform, the present study offers an important set of results for a poorly known area of the tropical Pacific.

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Literature Cited

Anganuzzi, A. A. & Buckland, S. T. (1994) Relative abundance of dolphins associated with tuna in the Eastern Pacific Ocean: Analysis of 1992 data. *Rep. Int. Whal. Commn.* **44**, 361–366.

Balance, L. T. & Pitman, R. L. (1998) Cetaceans of the Western Tropical Indian Ocean: distribution, relative abundance, and comparisons with cetacean communities of two other tropical ecosystems. *Marine Mammal Science.* **14** (3), 429–459.

Buckland, S. T., Anderson, D. R., Burnham, K. P. & Laake, J. L. (1993) *Distance Sampling Estimating Abundance of Biological Populations.* Chapman and Hall Ed., London, 446 pp.

Bernard, H. J. & Reilly, S. B. (1999) Pilot whales-*Globicephala* Lesson, 1828. In: S. H. Ridgway & R. J. Harrison (eds.) *Handbook of Marine Mammals. Volume 6: The Second Book of Dolphins and Porpoises*, pp. 245–279. Academic Press, London, 486 pp.

Caldwell D. K. & Caldwell, M. C. (1989) Pygmy sperm whale-*Kogia breviceps* (de Blainville, 1838); Dwarf sperm whale-*Kogia simus* (Owen, 1866). In: Ridgway, S. H. & Harrison, S. H. (eds.) *Handbook of Marine Mammals. Volume 4: River Dolphins and the Larger Toothed Whales*, pp. 235–260. Academic Press, 442 pp.

Dawbin, W. H. (1997) Temporal segregation of humpback whales during migration in southern hemisphere waters. *Memoirs of the Queensland Museum* **42** (1), 105–138.

Dodge, E. S. (1971) Baleiniers à Tahiti. *Bulletin de la Société des Océanistes*, **11**, 32 pp. Musée de l'Homme, Paris.

Dolar, M. D. (1999) Comparative distribution, abundance and feeding ecology of two dolphin species in the Philippines. *Abstract from the Thirteenth Bienn Conf. Biol. Marine Mammals, Maui (Hawaii)*, 48.

Fiedler, P. C. & Reilly, S. B. (1994) Interannual variability of dolphin habitats in the eastern tropical Pacific. 2: Effects on abundances estimated from tuna vessel sightings, 1975–1990. *Fishery Bulletin* **92**, 451–463.

Frontier, S. & Pichod-Viale, D. (1995) *Ecosystèmes: Structure, Fonctionnement, Evolution*, 447 pp. Masson, Paris.

Gannier, A. (1998) Une estimation de l'abondance estivale du Dauphin bleu et blanc *Stenella coeruleoalba* (Meyen, 1833) dans le futur Sanctuaire Marin International de Méditerranée nord-occidentale. *Terre et Vie.* **53**, 255–272.

Gannier, O. & Gannier, A. (1998) First results on the distribution of cetaceans in the Society Islands (French Polynesia). *Abstract of the World Marine Mammals Science Conference, Monaco*, 49.

Gannier, A. (1999) Distribution of cetaceans in the Marquesas Islands (French Polynesia) as obtained from a dedicated survey. *Abstract of the Thirteenth Bienn. Conf. Biol. Marine Mammals, Maui (Hawaii)*, 64.

Gannier, A. (2000) Rapport sur la distribution des Mégaptères et autres cétacés aux Iles du Vent et aux Iles Australes (juillet–octobre 1999). Report to the Research Office of the Government of French Polynesia, 66 pp.

Hammond, P. S., Benke, H., Bergreen, P., Borchers, D. L., Buckland, S. T., Collet, A., Heide-Jorgensen, M. P., Heimlich-Boran, S., Hiby, A. R., Leopold, M. F. & Oien, N. (1995) *Distribution and Abundance of the Harbour Porpoise and Other Small Cetaceans in the North Sea and Adjacent Waters.* Life 92-2 /UK/027, Final report, 239 pp.

Helweg, D. A., Cato, D. H., Jenkins, P. F., Garrigue, C. & McCauley, R. D. (1998) Geographical variation in south Pacific humpback whale songs. *Behaviour.* **135**, 1–27.

Heyning, J. E. (1989) Cuvier's beaked whales-*Ziphius cavirostris* (Cuvier, 1823). In: S. H. Ridgway & R. J. Harrison (eds) *Handbook of Marine Mammals. Volume 4: River Dolphins and the Larger Toothed Whales*, pp. 289–308. Academic Press, 442 pp.

Hiby. A. & Hammond, P. S. (1989) Survey techniques for estimating abundance of cetaceans. *Rep. Int. Whal. Commn.* Special issue **11**, 47–80.

Kruse, S., Caldwell, D. K. & Caldwell, M. C. (1999) Risso's dolphin-*Grampus griseus* (Cuvier, 1812). In: In: S. H. Ridgway & R. J. Harrison (eds.) *Handbook of Marine Mammals. Volume 6: The Second Book of Dolphins and Porpoises*, pp. 183–212. Academic Press, London, 486 pp.

Laake, J. L., Buckland, S. T., Anderson, D. R. & Burnham, K. P. (1994) *DISTANCE User's Guide V2.2.* Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, 72 pp.

Leatherwood, S. & Reeves, R. (1983) *The Sierra Club Handbook on Cetaceans*, 302 pp. Sierra Club, San Francisco.

Longhurst, A. R. (1999) *Ecological Geography of the Sea*, 302 pp. Academic Press, San Diego.

Longhurst, A. R. & Pauly, D. (1987) *Ecology of Tropical Oceans*, 407 pp. Academic Press, San Diego.

Massé, J. & Cadiou, Y. (1994) *Oedipe—Manuel Utilisateur*, 38 pp. Ifremer, Nantes.

Mead, J. G. (1989) Beaked Whales of the Genus-*Mesoplodon.* In: S. H. Ridgway & R. J. Harrison (eds.) *Handbook of Marine Mammals. Volume 4: River Dolphins and the Larger Toothed Whales*, pp. 349–430. Academic Press, 442 pp.

Miyazaki, N. & Perrin, W. F. (1994) Rough-toothed dolphin-*Steno bredanensis* (Lesson, 1828). In: S. H. Ridgway & R. J. Harrison (eds.) *Handbook of Marine Mammals: The First Book of Dolphins*, pp. 1–21. Academic Press, 416 pp.

Perrin, W. F., Leatherwood, S. & Collet, A. (1994) Fraser's dolphin-*Lagenodelphis hosei* (Fraser, 1956). In: S. H. Ridgway & R. J. Harrison (eds.) *Handbook of Marine Mammals: The First Book of Dolphins*, pp. 225–240. Academic Press, 416 pp.

Perrin, W. F. & Gilpatrick, J. W. Jr (1994) Spinner dolphin-*Stenella longirostris* (Gray, 1828). In: S. H. Ridgway & R. J. Harrison (eds.) *Handbook of Marine Mammals: The First Book of Dolphins*, pp. 99–128. Academic Press, 416 pp.

Perryman, W. L., Au, D. W. K., Leatherwood, S. & Van Waerebeek, K. (1994) Melon-headed whale-*Peponocephala electra* (Gray, 1846). In: S. H. Ridgway & R. J. Harrison (eds) *Handbook of Marine Mammals: The First Book of Dolphins*, pp. 363–386. Academic Press, 416 pp.

Poole, M. (1993) A sighting/stranding network in French Polynesia, 1988–1993. *Abstract from the Tenth Bienn. Conf. Biol. Marine Mammals, Galveston*, 87.

Rancher, R. & Rougerie, F. (1993) *Hydropol. Situations Océaniques du Pacifique Central Sud*, 91 pp. Editions S.M.S.R., Montlhéry.

Reeves, R. R., Leatherwood, S., Stone, G. S. & Eldredge, L. G. (1999) *Marine Mammals in the Area Served by the South Pacific Regional Environment Program.* 48 pp. Report of the South Pacific Regional Environment Program (PO Box 240), Apia, Samoa.

Reilly, S. B. (1990) Seasonal change in distribution and habitat differences among dolphins in the eastern tropical Pacific. *Mar. Ecol. Prog. Ser.* **66**, 1–11.

Reilly, S. B. & Fiedler, P. C. (1994) Interannual variability of dolphin habitats in the eastern tropical Pacific. 1: Research vessel surveys, 1986–1990. *Fishery Bulletin*. **92**, 434–450.

Rice, D. W. (1989) Sperm whales-*Physeter macrocephalus* Linnaeus 1758. In: S. H. Ridgway & R. J. Harrison (eds.) *Handbook of Marine Mammals. Volume 4: River Dolphins and the Larger Toothed Whales*, pp. 177–23. Academic Press, 442 pp.

Ridgway, S. H. & Harrison, R. J. (1989) *Handbook of Marine Mammals. Volume 4: River Dolphins and the Larger Toothed Whales*, 442 pp. Academic Press, London.

Ridgway, S. H. & Harrison, R. J. (1994) *Handbook of Marine Mammals. Volume 5: The First Book of Dolphins*, 416 pp. Academic Press, London.

Ridgway, S. H. & Harrison, R. J. (1999) *Handbook of Marine Mammals. Volume 6: The Second Book of Dolphins and Porpoises*, 486 pp. Academic Press, London.

Rougerie, F. & Wauthy, B. (1986) Le concept d'endo-upwelling dans le fonctionnement des atolls-oasis. *Oceanologica Acta*. **9** (2), 133–148.

Rougerie, F. & Rancher, R. (1994) The Polynesian South Ocean: features and circulation. *Mar. Pollut. Bull.* **29**, 14–25.

Shimada, H. & Pastene, L. A. (1995) Report of a sighting survey off the Solomon Islands with comments on Bryde's Whale Distribution. *Rep. Int. Whal. Commn.* **45**, 413–417.

Townshend, C. H. (1935) The distribution of certain whales as shown by logbooks records of American whaleships. *Scientific contribution of the New York Zoological Society, Zoologica*. **19** (1), 1–50.

Tan, J. M. L. (1997) *A Field Guide to Whales and Dolphins in the Philippines*, 125 pp. Bookmark (264-A Pablo Ocampo Ave.), Makati City, Philippines.

Wade, P. R. & Gerrodette, T. (1993) Estimates of cetacean abundance and distribution in the Eastern Tropical Pacific. *Rep. Int. Whal. Commn.* **43**, 477–493.

Wells, R. S. & Scott, M. D. (1999) Bottlenose dolphin-*Tursiops truncatus* (Montagu, 1821). In: S. H. Ridgway & R. J. Harrison (eds.) *Handbook of Marine Mammals. Volume 6: The Second Book of Dolphins and Porpoises*, pp. 137–182. Academic Press, London, 486 pp.