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Observations on the distribution and behaviour of Dall's porpoise (*Phocoenoides dalli*) in Monterey Bay, California

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Summary

A study of Dall's porpoise distribution and behaviour between September 1986 and February 1989 confirmed the year-round presence of these animals in Monterey Bay, California. Dall's porpoises in the Bay preferred deep (mean = 264 m) waters near the head of the Monterey Submarine Canyon. Mean group size was 5.7, but aggregations of up to 20 animals periodically developed. Most porpoises sighted in the Bay were subadults, and cow-calf pairs were uncommonly seen. Bow-riding was common, occurring in over half of the sightings, and rooster-tailing was the predominant surfacing mode. Monterey Bay Dall's porpoises spent most of the day feeding, resting, and playing in scattered subgroups of 2–6 individuals.

Introduction

Dall's porpoise (*Phocoenoides dalli*) is common to the cooler waters of the North Pacific Ocean, and is the most frequently-sighted small cetacean off central and northern California (Dohl *et al.*, 1983). Several thousand are taken incidentally each year in driftnets in the western Pacific (Jones, 1984) and recently a directed harpoon fishery off Japan has expanded and now threatens certain stocks there (International Whaling Commission, 1989). Little is known about this species in most sections of its range, and this makes difficult the tasks of assessing the effect of the take on the populations, and finding methods of preventing entanglement.

In the late 1960s and early 1970s, an extensive study was conducted on Monterey Bay Dall's porpoises, which provided much information on distribution, behaviour, feeding habits, and morphology (Loeb, 1972; Morejohn *et al.*, 1973; Morejohn, 1979). Despite this, the population status and movement patterns of porpoises in the Bay are not known with any certainty. Also, information on general behaviour and ecology of this commonly-sighted, but little-studied, species is generally lacking.

This study was undertaken to provide information relative to these needs. Strip or line transect analysis of sighting surveys was rejected as a focus of research due to indications that Dall's porpoises strongly react to the presence of survey vessels, thus biasing resulting population estimates (Bouchet *et al.*, 1983). Instead, an attempt was made to characterize the population through photographic identification of individuals (see review by Würsig & Jefferson, 1990). Photo-identification of Monterey Bay Dall's porpoises proved to be difficult, but much useful information was obtained in the process.

Methods and study area

Information on Dall's porpoise sightings was collected between September 1986 and February 1989. Sighting information was obtained by the author on 16 Dall's porpoise observation cruises, and opportunistically on 31 cruises dedicated to other activities. Cruises included all seasons, but there was relatively little effort in summer.

The research vessel used on most cruises was the 10.7 m R/V *Ed Ricketts*, operated by Moss Landing Marine Laboratories. Observations were generally conducted between 07.00 and 15.00. Usually, there was no set transect; the vessel travelled along the edge of the Monterey Submarine Canyon, a region of known high porpoise density (Loeb, 1972). In October and November 1988, a set of transects was run across the axis of the Monterey Submarine Canyon, to examine Dall's porpoise distribution relative to water depth (Fig. 1). Legs 1 and 2 were run three times each, and legs 3 and 4 only twice each.

Information collected during sightings included time, position, initial sighting angle and distance, sea surface temperature, water depth, sighting conditions, estimated aggregation size, response to boat, and various behavioural data. The primary objective of the cruises was to obtain photos for individual recognition. This was most often attempted by stopping the boat while the animals were bow-riding, and photographing them if they remained close. Most close-up observations of Dall's porpoises were during times when animals approached the vessel to ride the bow wave, and so it is not certain that natural

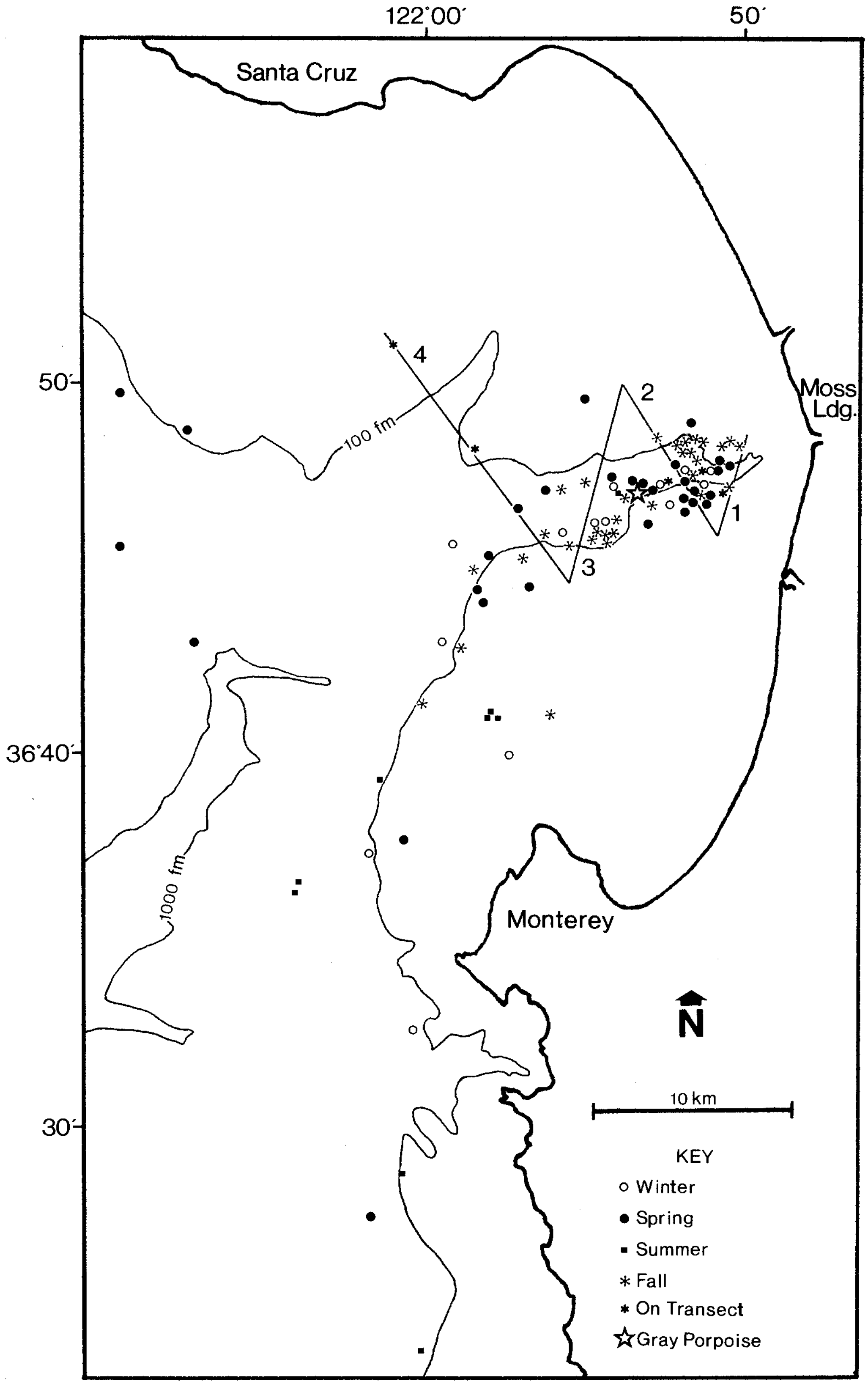

Figure 1. Map of the study area with the 100 and 1000 fathom (180 and 1830 m) curves, and transect lines shown. The 100 fathom curve denotes the boundaries of the Monterey Submarine Canyon. Plotted are locations for 90 Dall's porpoise sightings, including an anomalous all-grey individual. It must be cautioned that differences in the seasonal distribution of sightings are not necessarily real, and at least partially reflect seasonal differences in searching effort.

behaviour patterns were being observed at these times.

Notes on the age/sex composition of porpoise groups were recorded when the animals were seen well, following the classification scheme of Jefferson (1990). Calves and juveniles can be reliably distinguished, based on their smaller size and muted colour patterns. Immature porpoises (also called subadults) show a great deal of overlap in external appearance with adult females, but younger subadults tend to have still somewhat-muted patterns.

The study area consisted of Monterey Bay and the immediately adjacent waters off central California (Fig. 1). Monterey Bay is 37 km wide at its mouth. The major physical feature is the Monterey Submarine Canyon, which brings deep oceanic waters (> 180 m) to within 3 km of the shore at its head (or apex) directly west of Moss Landing. The Bay is highly productive, supporting extensive and varied fish and cephalopod populations, and several major fisheries (Cailliet *et al.*, 1979; Heimlich-Boran, 1988).

The oceanography of the area is characterized by three major periods: the upwelling period (February to September), the oceanic period (September to October), and the Davidson Current period (November to February) (Bolin & Abbott, 1963). These 'oceanographic seasons' are likely to be important for marine organisms, so data were analysed accordingly. The 'solar seasons' were defined as follows: spring (March to May), summer (June to August), fall (September to November), and winter (December to February).

Results

Distribution

There were sightings during all four solar seasons, and in every month in which at least one cruise was conducted. There were no cruises in June or July, but Dall's porpoises were sighted in the Bay in these months during the study period (Black, 1989).

Dall's porpoises were observed in water depths ranging from 46–915+ m (mean = 264.4 ± 180.62 m, n = 71). This is a biased sample, however, because most observation cruises preferentially searched for porpoises near the 100 fm (180 m) contours of the Monterey Submarine Canyon.

Despite this bias, it can be said with some certainty that Dall's porpoises in Monterey Bay avoid shallow waters. Only 4% of sightings occurred in waters shallower than 90 m, and the shallowest sighting was at 46 m. This is despite a fair amount of sighting effort in shallower waters (usually on opportunistic cruises). For instance, several cruises followed parallel to shore north or south of Moss Landing in waters 9–27 m deep, and Dall's were never sighted there. Instead, harbour porpoises (*Phocoena phocoena*) were generally sighted in these shallow coastal areas. Also, Dall's porpoises were never sighted between Moss Landing Harbour and the head of the Canyon (water depths of 8–180 m), even though this area was generally traversed twice on nearly every cruise.

The four transect legs (see Fig. 1) were designed to examine distribution relative to water depth, by traversing the Canyon from shallow (27–90 m) through deep (> 180 m) waters. Small sample sizes precluded statistical analysis, but 4 of the 5 sightings that occurred during transects fell near the 180 m contours of the Canyon.

Dall's porpoises were sighted on 85% of the 39 cruises that covered the waters of the head of the Monterey Submarine Canyon, as opposed to only 15% of the 20 cruises that departed from Monterey Harbour and searched only the waters within several kilometers of the Monterey Peninsula. Thus, despite the presence of suitably deep waters off Monterey, Dall's porpoise density appears to be greater over the head of the Canyon, especially near the steep edges, as suggested by Loeb (1972).

Surface water temperature was available for a subset of 26 sightings. For these, temperatures ranged from 12.4–14.7°C, near the centre of the species' known range (Kasuya, 1978).

Sighting conditions

Mean initial sighting distance was 170.5 ± 142.90 m (range = 3–800 m, n = 76). Initial sighting distance decreased steadily with increasing sea states (higher Beaufort numbers) (Fig. 2). This is likely because in higher sea states porpoises become more difficult to see, and only those groups close to the boat are likely to be observed. Slow rolling porpoises are difficult to spot among whitecaps (Beaufort 3 or greater). The dynamic sighting cue provided by rooster-tailing animals makes them easier to spot, but at long distances the splash can be difficult to distinguish from large whitecaps.

Aggregation size

Collected data on group size may not always have reflected natural situations, since often what appeared to be animals from several different groups converged on the vessel to ride the bow wave. At other times, groups of porpoises split-up, and only some animals approached the boat. Attempts were made to note the sizes of the original groups, but this was often difficult or impossible. Thus, the term 'aggregation size' is used here (following Miller, 1990). Aggregation size represents the total number of porpoises in the immediate vicinity of a sighting.

Estimated aggregation sizes ranged from 1–20, with a mean of 5.7 ± 4.23 (n = 96). Most groups consisted of 2–6 individuals (Fig. 3). This is in close agreement with data collected by Barham (1982) in

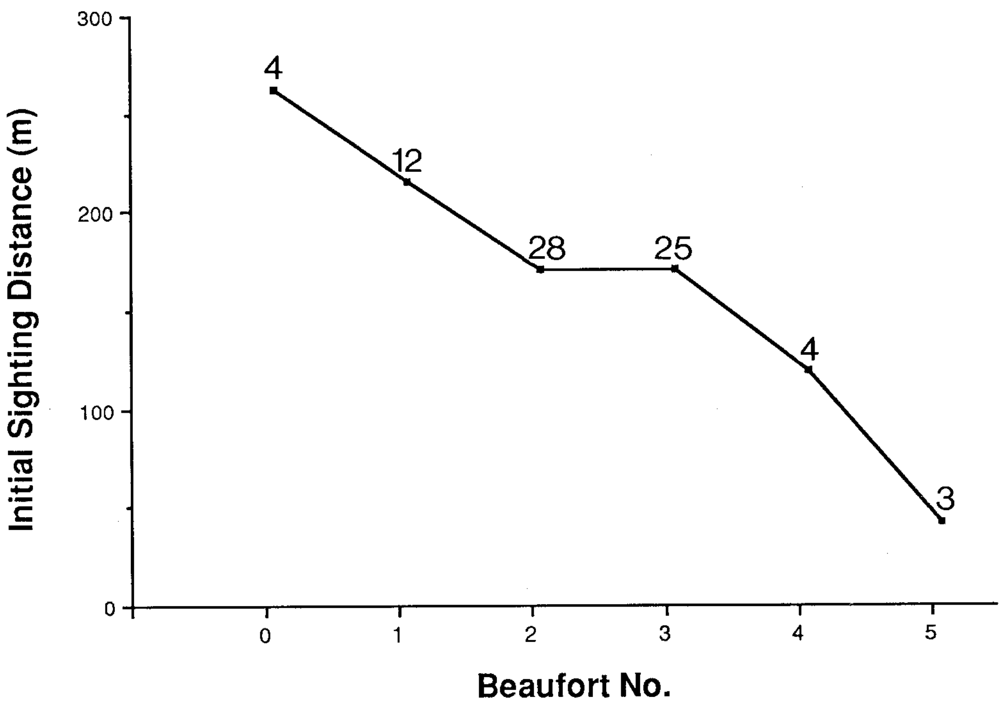

Figure 2. Relationship of mean initial sighting distance and Beaufort sea state. Numbers above points are sample size.

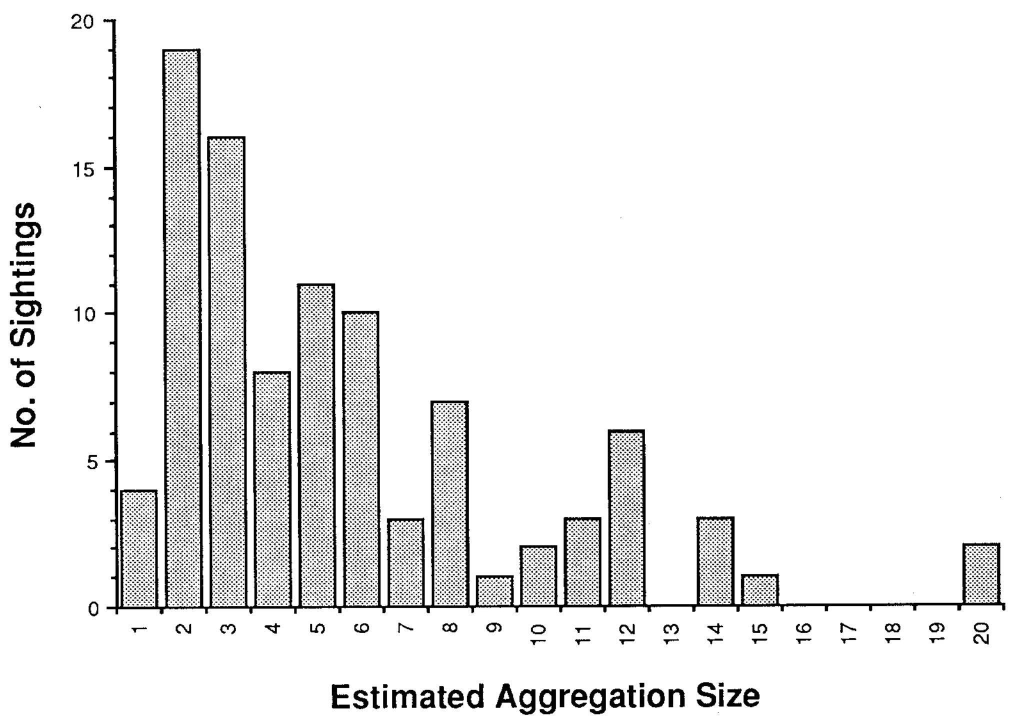

Figure 3. Frequency graph of estimated aggregation sizes for Dall's porpoise sightings.

the 1950s and Morejohn (1979) in the 1960s and 1970s.

There was no significant difference in aggregation size between morning (mean $= 5.7 \pm 4.68$, $n = 34$) and afternoon sightings (mean $= 5.7 \pm 4.00$, $n = 62$) ($t = 0.004$, $df = 94$, $p > 0.05$). Nor was there any significant variation in aggregation size either with solar season (ANOVA $= 2.174$, $df = 95$, $p > 0.05$) or with

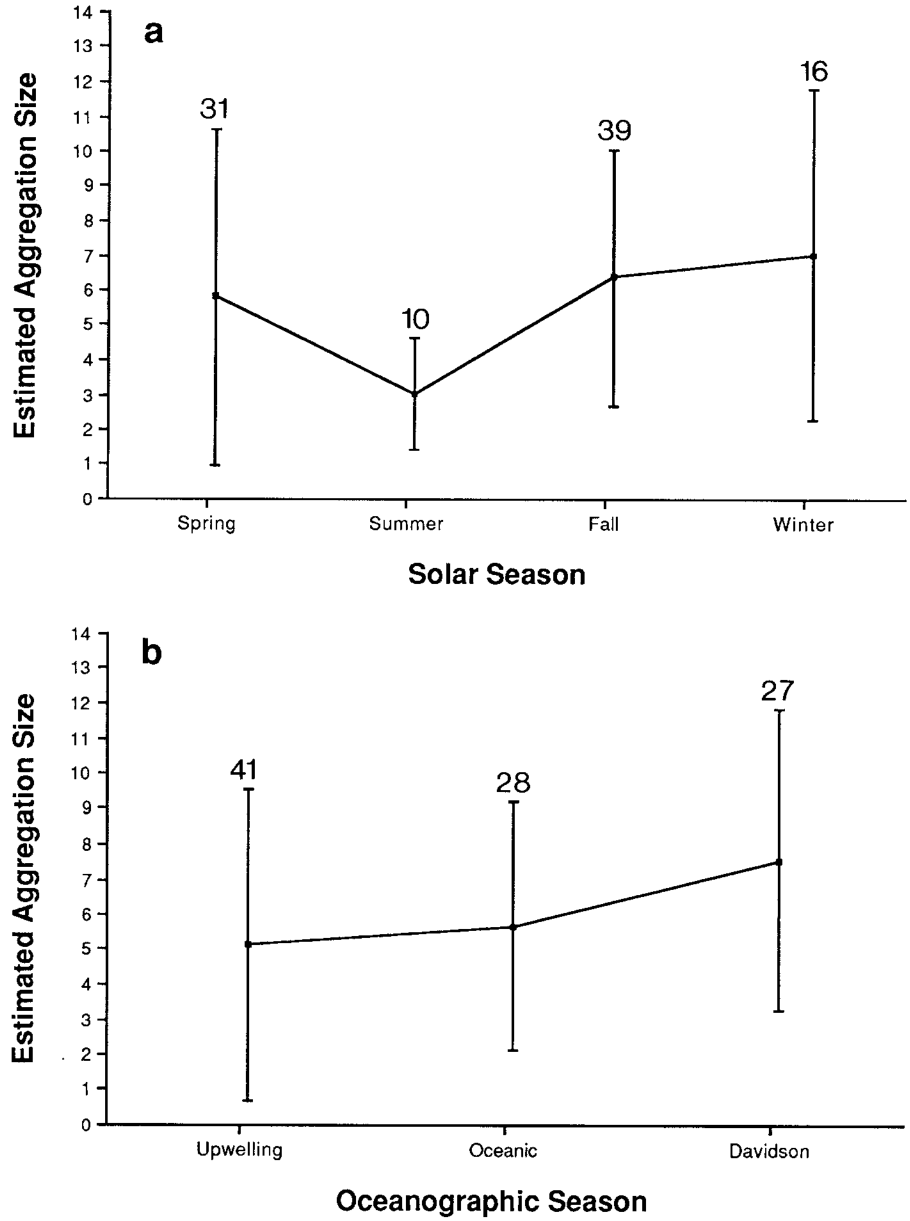

Figure 4. Variation in estimated aggregation size with: (a) solar season, and (b) oceanographic season of Bolin and Abbot (1963). Points are mean, bars are ± 1 standard deviation, and numbers are sample size.

oceanographic season (ANOVA $= 2.815$, df $= 95$, $p > 0.05$) (Fig. 4).

Population composition

Calves were rarely seen in Monterey Bay (representing 0.5% of all individuals sighted). Small calves were seen on 24 and 27 October 1986, and a larger calf (still accompanied by its presumed mother, but with frosting developing on the dorsal fin) was seen on 12 December 1988. Based on its size (about 65–75% of adult size) and colour pattern development, this latter calf was estimated to be 3–6 months old. These observations are consistent with the late spring to early fall calving season suggested for eastern Pacific Dall's porpoises (Jefferson, 1989).

Juveniles were seen throughout the year in Monterey Bay, but most individuals observed appeared to be larger subadults (or immatures), based on the incomplete development of their colour patterns. Very few large adult-type animals with the full colour pattern development were seen in the Bay.

Behaviour

Three surfacing modes were recognized: slow rolling, rooster-tailing, and fast surfacing (defined in Jefferson, 1987). Rooster-tailing was the most

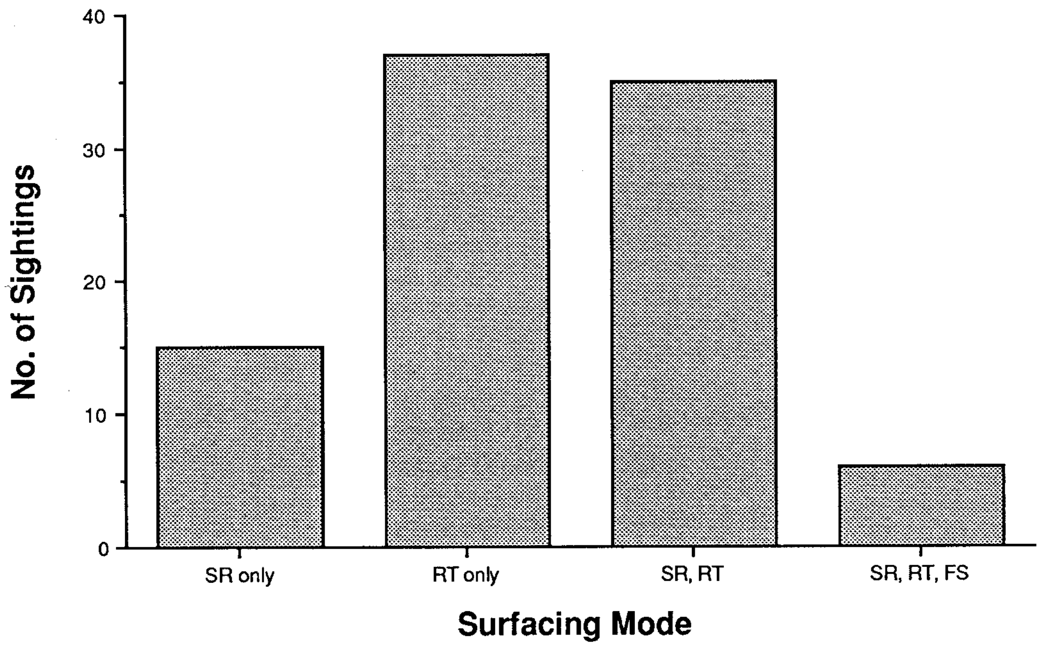

Figure 5. Frequencies of various combinations of surfacing modes seen in Monterey Bay. SR is slow roll, RT is rooster-tail, and FS is fast surface.

commonly observed surfacing mode, being seen at some point in 84% of all sightings (Fig. 5). This sample is biased, however, due to the fact that rooster-tailing porpoises are easier to spot than slow rolling ones, and porpoises always rooster-tail when they bow-ride.

Bow-riding on the research vessel occurred in 53% of all sightings, with no significant difference in tendency to ride in morning vs. afternoon (Chi-square = 0.360, df = 1, $p > 0.05$). The *Ricketts* apparently does not produce a good pressure wave, and porpoises generally crossed quickly back and forth in front of the bow, rather than stationing themselves there, as they do on some vessels. Bow-riding episodes were generally of short duration, often with the animals dropping off and moving back towards the area where they had begun bow-riding. This suggests that play, rather than assisted travel, was the primary motivation for bow-riding (Loeb, 1972).

Porpoises, while bow-riding, often periodically dropped back from the bow and surfaced in the stern wake of the vessel. On four instances during the study, porpoises were also observed riding breaking swells, or the presssure waves caused by the blunt heads of blue whales (*Balaenoptera musculus*). This 'snout-riding', as the latter was called, generally resulted in aggressive charging of the surface and 'snorting' blows by the whales, much like that described by Würsig & Würsig (1979) for southern right whales (*Eubalaena australis*) being ridden by bottlenose dolphins (*Tursiops truncatus*). The blue whales appeared to be disturbed by the much smaller porpoises 'buzzing' around their heads.

Fifty-four percent of the groups were attracted to the vessel, generally (but not always) to ride the bow wave. Fourty-four percent of the groups showed no apparent response, and only 2% appeared to avoid the vessel (by obviously changing direction and activity). Both of the groups that avoided the boat included cow-calf pairs. Mothers with calves were never seen to bow-ride.

The durations of most encounters were short, and it was not always possible to determine with any certainty what activity the animals were engaged in. However, there was almost no indication of directional travelling, such as that usually seen in herds of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), northern right whale dolphins (*Lissodelphis borealis*), Risso's dolphins (*Grampus griseus*), and common dolphins (*Delphinus delphis*) in the Bay. On a few occasions (generally near mid-day), the porpoises appeared to be resting, generally slow rolling with particularly low activity levels, and could not be induced to ride the bow wave of the research vessel.

Dall's porpoises most often appeared to be feeding, either slow rolling in small groups in a restricted area, or surface-splashing in larger groups, but also in a relatively small area. Surface-splash behaviour (defined in Bouchet *et al.*, 1983) was observed in 27% of the sightings, with no difference in its occurrence between morning and afternoon sightings (Chi-square = 0, df = 1, $p > 0.05$). Mean size of surface-splashing groups (mean = 9.6 ± 5.29, n = 26) was greater than for groups that did not surface-splash (mean = 4.6 ± 3.32, n = 70), a highly significant difference ($t = 9.298$, $df = 94$, $p < 0.001$). The proportion of surface-splashing groups observed may be biased upwards by the fact that surface-splashing porpoises rooster-tail in larger groups, making them more visible to observers.

More direct evidence of feeding was obtained on three occasions when several small bait fish were seen jumping out of the water in front of surfacing Dall's porpoises. Also, in six sightings, small flocks of seabirds (most commonly gulls, *Larus* spp.) appeared to be associated with Dall's porpoise aggregations, suggestive of feeding.

On 18 November 1988, a group of six animals was observed engaged in possible cooperative feeding. Throughout the 45 min. observation period there was repeated synchronous fluke-up diving and surfacing within a small area. Between dives, the porpoises engaged in much socializing and body contact. Feeding was indicated by a scattering layer picked up on the depth sounder, the presence of associated birds, and fish seen jumping out the water in front of surfacing porpoises; as well as the behaviour of the porpoises themselves.

Interactions between individual porpoises were difficult to document, because the animals could only be seen through the water's surface when they were bow-riding. On two occasions in November 1986, however, a larger porpoise veered at a smaller individual that was bow-riding, thereby displacing the latter from its position at the bow. Similar behaviour was reported by Morejohn (1979).

Discussion

Photo-identification attempts

Attempts at photo-identification of individual Dall's porpoises in Monterey Bay provided little reward for the time invested. A total of only six distinctive individuals were observed during the study, and good photos were obtained of only three of these. There were no resightings of these animals. Loeb (1972) was able to identify several individuals in Monterey Bay by natural markings in the early 1970s, but since she did not take photos, some of her reported resightings must be considered unreliable.

No porpoises with anomalous colour patterns were observed by the author, but on 27 August 1988, an all-grey Dall's porpoise was seen bow-riding by other researchers in Monterey Bay (Black, 1989). Its location is plotted in Fig. 1. Morejohn *et al.* (1973) sighted several grey individuals in Monterey Bay in the early 1970s, but it is unlikely that any of these were the present individual, since most Dall's porpoises appear to live less than 10 years, and very few appear to live as long as 20 years (Kasuya, 1978).

Photographic identification of Dall's porpoises in this study proved to be difficult for the following reasons: (1) most animals that rode the bow wave were subadults, with few colour markings on their dorsal fins; (2) most had 'clean' fins with no obvious scratches or nicks; (3) porpoises can generally only be photographed usefully when slow rolling at close range, which they did not commonly do; (4) the location where a porpoise will surface cannot be predicted unless the sea is flat, and it can be followed visually underwater between surfacings (Monterey Bay characteristically has much rough weather); (5) Dall's porpoises spend short periods of time at the surface, allowing the photographer little time to focus and shoot; and (6) the research vessel was relatively large and unmanoeuverable, thus making it difficult to get into position to take good photos.

Future attempts to photo-identify Dall's porpoises will be hampered by the fact that their teeth are too small and blunt to cause the kinds of rake marks and nicks seen on most delphinids, and the fast-swimming and unpredictable surfacing patterns of the animals make it difficult to get good photos. Nonetheless, Dall's porpoises can be photo-identified. Miller (1989, 1990) has had success in applying this technique to Dall's porpoises in Puget Sound, Washington. Her study area is rather ideal because it is an inshore area, with much calmer waters; porpoises in her area spend much more time slow rolling; and the animals seem to be more recognizable, due to the presence of many adults and several individuals with grossly mangled dorsal fins (likely caused by boat collisions).

Dall's porpoise use of Monterey Bay

There appears to be some age segregation of the Monterey Bay Dall's porpoise population. The majority of individuals over the head of the Monterey Submarine Canyon appear to be subadults and they are present in approximately equal numbers year-round. Generally, animals appear to spend most of the day feeding, resting, and occasionally 'playing', in scattered subgroups of about two to six individuals. As suggested by Miller (1990) for Puget Sound animals, these subgroups appear to be labile, aggregating periodically to feed and play (for example, converging on a boat to bow-ride), and then splitting up again. However, without proper data on individual associations, it is impossible to determine if long-term associations exist within these aggregations in Monterey Bay.

Adults and calves appear to be largely distributed elsewhere, probably further offshore, where they may be part of a larger migratory population (as suggested by Loeb, 1972). When adults are seen in the Bay, they appear to preferentially use relatively shallow waters, perhaps reducing competition with subadults over the Canyon head. Four of five sightings of adult groups occurred in waters shallower than 100 m (range = 46–

95 m), much shallower than the overall mean sighting depth of 264 m.

Age/sex segregation has been documented in this species, especially for cow/calf pairs (Jefferson, 1987; Miller, 1989; Kasuya & Ogi, 1987). But, despite the discovery of several calving areas in the eastern North Pacific (Johnstone Strait, British Columbia, Jefferson, 1987; Puget Sound, Washington, Miller, 1989), the population status of eastern Pacific Dall's is not known.

There have apparently been only three detailed quantitative studies of Dall's porpoise behaviour (Jefferson, 1989; Miller, 1989, 1990; this study). Most other behavioural information comes from opportunistic sightings or data collected on cruises dedicated to other types of research. Until more long-term behavioural and ecological studies are undertaken in other areas throughout the species range, Dall's porpoise will remain one of the lesser known small cetaceans, and attempts at reducing and assessing the impacts of human-caused mortality will be hampered. Through photo-identification (and in areas like Monterey Bay, some tagging or radio-tracking) and systematic data collection on a particular population of porpoises over a period of several years, we stand to learn a great deal about this species.

Acknowledgements

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References

Barham, E. G. (1982) Marine mammals in Monterey Bay, California, during the years 1950–1955. *California Fish and Game* **68,** 213–223.

Black, N. (1989) Personal communication, Moss Landing Marine Laboratories.

Bolin, R. F. & Abbott, D. P. (1963) Studies on the marine climate and phytoplankton of the central coastal area of California, 1954–1960. *CalCOFI Rep.* **9,** 23–45.

Bouchet, G. C., Braham, H. W. & Tsunoda, L. M. (1983) Investigation of Dall's porpoise (*Phocoenoides dalli*) response to a survey vessel: Preliminary assessment. *Int. Whal. Commn. Sci. Comm. Rep.* SC/35/SM13, 15 pp.

Cailliet, G. M., Karpov, K. A. & Ambrose, D. A. (1979) Pelagic assemblages as determined from purse seine and large midwater trawl catches in Monterey bay and their affinities with the market squid, *Loligo opalescens*. *CalCOFI Rep.* **20,** 21–30.

Dohl, T. P., Guess, R. C., Duman, M. L. & Helm, R. C. (1983) Cetaceans of central and northern California, 1980–1983: Status, abundance, and distribution. Report prepared for Pacific OCS Regions, Minerals Management Service, 284 pp.

Heimlich-Boran, J. R. (1988) Marine resources and human activities in the Monterey Bay area. Unpublished report to Center for Marine Conservation, 123 pp.

International Whaling Commission (1989) Japan. Progress report on cetacean research, May 1988 to April 1989. *Int. Whal. Commn. Sci. Comm. Rep.* SC/41/ProgRep Japan, 9 pp.

Jefferson, T. A. (1987) A study of the behavior of Dall's porpoise (*Phocoenoides dalli*) in the Johnstone Strait, British Columbia. *Can. J. Zool.* **65,** 736–744.

Jefferson, T. A. (1989) Calving seasonality of Dall's porpoise in the eastern North Pacific. *Mar. Mammal. Sci.* **5,** 196–200.

Jefferson, T. A. (1990) Sexual dimorphism and development of external features in Dall's porpoise *Phocoenoides dalli*. *Fishery Bulletin, U.S.* **88,** 119–132.

Jones, L. L. (1984) Incidental take of the Dall's porpoise and the harbour porpoise by Japanese salmon driftnet fisheries in the western North Pacific. *Rep. Int. Whal. Commn.* **34,** 531–538.

Kasuya, T. (1978) The life history of Dall's porpoise with special reference to the stock off the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst.* **30,** 1–63.

Kasuya, T. & Ogi, H. (1987) Distribution of mother-calf Dall's porpoise pairs as an indication of calving grounds and stock identity. *Sci. Rep. Whales Res. Inst.* **38,** 125–140.

Loeb, V. J. (1972) A study of the distribution and feeding habits of the Dall porpoise in Monterey Bay, California. M.A. thesis, San Jose State University, 62 pp.

Miller, E. J. (1989) Distribution and behavior of Dall's porpoise (*Phocoenoides dalli*) in Puget Sound, Washington. M.Sc. thesis, University of Washington, 97 pp.

Miller, E. (1990) Photo-identification techniques applied to Dall's porpoise (*Phocoenoides dalli*) in Puget Sound, Washington. *Rep. Int. Whal. Commn.* (Spec. Iss. **12),** 429–437.

Morejohn, G. V. (1979) The natural history of Dall's porpoise in the North Pacific Ocean. In: *Behaviour of marine animals, Vol. 3: Cetaceans* (Eds H. E. Winn and B. L. Olla) Plenum Press, New York-London, 45–83.

Morejohn, G. V., Loeb, V. & Baltz, D. M. (1973) Coloration and sexual dimorphism in the Dall porpoise. *J. Mammal.* **54,** 977–982.

Würsig, B. & Jefferson, T. A. (1990) Methods of photo-identification for small cetaceans. *Rep. Int. Whal. Commn.* (Spec. Iss. **12**), 43–52.

Würsig, B. & Würsig, M. (1979) Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the South Atlantic. *Fishery Bulletin, U.S.* **77,** 399–412.