Dusky dolphins (*Lagenorhynchus obscurus*) in New Zealand waters

Present knowledge and research goals

Bernd Würsig, Nicholas Duprey and Jody Weir

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ABSTRACT

Dusky dolphins (*Lagenorhynchus obscurus*) occur near shore and in waters up to c. 2000 m in depth in much of the cooler-temperate southern hemisphere. In New Zealand, they are found off most of the South Island and the southern part of the North Island, but have been studied intensively in only two areas, Kaikoura and Admiralty Bay, South Island. Dusky dolphins off Kaikoura have been investigated since 1984 by radio tracking, shore-based theodolite (surveyor's) tracking, and boat-based behavioural descriptions and photographic identification of natural markings; in Admiralty Bay, theodolite tracking and boat-based studies have been conducted since 1998. Off Kaikoura, dusky dolphins feed at night on myctophids and squid; in Admiralty Bay, they feed during the daytime on schooling fishes in shallow waters. Group sizes, behaviours, social affiliations and general habitat-use patterns differ between Kaikoura and Admiralty Bay, even though some of the same animals utilise both habitats in different seasons. Off Kaikoura, there are daily and seasonal differences in behaviours and movement patterns, with daytime rests around midday, social activities in the mornings and afternoons, and feeding in deeper oceanic waters at night. The discovery of midday resting has led to a voluntary 'down-time' of no tourism boats by a local dolphin tourism enterprise, Dolphin Encounter. Dolphins tend to move in deeper waters in winter than in summer, but there is great variation in the areas traversed. Research is making inroads into understanding dusky dolphin social dynamics, foraging strategies and predator avoidance tactics. Basic research is being augmented by targeted investigations into tourism effects, to allow recommendations to be made on permitted areas, times and numbers.

Keywords: cetacean, dusky dolphin, *Lagenorhynchus obscurus*, marine mammal, delphinid, habitat use, dolphin tourism, dolphin behaviour, marine mammal tourism, swim-with-dolphin tourism

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1. Introduction

The dusky dolphin (*Lagenorhynchus obscurus*) is a small, robust delphinid with a short rostrum and slightly falcate pointed dorsal fin (Fig. 1) (Jefferson et al. 1993). It is countershaded in mute fashion, without the strong white/black shading of many other species. Its paintbrush-like lateral stripes might assist in conspecific visual communication, as dolphins travel in staggered fashion, side-by-side. Its white ventrum is often used to 'flash' at schooling prey, causing them to herd more tightly due to a fright reaction. Dusky dolphins, or 'duskies', have 27–36 pairs of small, pointed teeth in both the upper and lower jaw (Jefferson et al. 1993). Specimens of dusky dolphins found in New Zealand range up to 186 cm long, with most mature males and females reaching between 170 cm and 180 cm. While specimens from southwestern Africa are similar in size to those in New Zealand, those off Peru grow considerably larger (Cipriano 1992; Van Waerebeek 1992, 1993). Tooth growth ring analysis recorded the oldest dusky dolphin off Kaikoura as being approximately 35–36 years old (Cipriano 1992), although average age is probably only 20–25 years.

Dusky dolphins are gregarious wherever they occur, varying from social groups of as few as three or four animals (rarely), to more common groupings of a dozen or more, and large 'open-ocean' schools of hundreds to several thousand (Würsig et al. 1997). Studies to date have shown that dusky dolphins tend to change affiliation frequently, with fission-fusion societies resulting in many animals changing school memberships (and thus partially changing travelling partners) over a timeframe of hours to days. We suspect that temporary aggregations allow for efficient restructuring according to different food-finding and predator-avoidance requirements in different habitats and at different times. For example, off Kaikoura, New Zealand, dusky dolphins are mostly found in the open-ocean school configuration (with satellite all-male, mixed and nursery groups travelling up to several kilometres from the main school), presumably to provide safety in numbers whilst in open and deep waters where sharks and killer whales (*Orcinus orca*) are common (Würsig et al. 1997; Markowitz 2004). In contrast, in the relatively protected and largely shark-free, semi-enclosed Marlborough Sounds, dusky dolphins occur in much smaller bands as they feed on schooling fishes (Markowitz et al. 2003; McFadden 2003). Dusky dolphins that occur off coastal Argentina oscillate between small schools of a dozen or so animals while resting and foraging, to aggregated schools of hundreds for efficient feeding on schools of fish (Würsig & Würsig 1980; Würsig et al. 1989).

Figure 1. Dusky dolphin, *Lagenorynchus obscurus*, photographed off Kaikoura.

Perhaps because of their pronounced social nature, dusky dolphins produce varied sets of sounds (Yin 1999; Au & Würsig 2004), and perform leap and other surface splash-causing behaviours (Würsig & Würsig 1980). They perform varied leaps associated with stages of herding, fusion of groups, feeding and after-feeding socialising in Argentina (Würsig & Würsig 1979, 1980), and crescendos of acrobatic leaps during periods of socialising off Kaikoura (Markowitz 2004). Leaps are likely to be a reflection of levels of alertness, possibly synchronising excitement among many members of an extended school (as suggested by Norris & Dohl 1980; Norris et al. 1994). Certain leaps that end in loud splashes also appear to serve as contact calls, being louder and more omni-directional than internally created ('vocal') sounds. The dolphin shown in Fig. 1 is leaping low and about to re-enter the water in 'noisy' fashion, or with a considerable sideways twist and concommitant splash. It has been shown that such demonstrative leaps can be a part of stages of feeding, but in this case it is likely to be an expression of a high level of social activity, or individual exuberance.

This paper is designed to summarise what is currently known about the distribution and movement patterns of dusky dolphins, both globally and around New Zealand; describe potential population relationships as found by recent genetic work; discuss the impacts of tourism on dusky dolphin populations off Kaikoura, New Zealand; and outline current research and recommend directions for future studies, with particular reference to the management of this species.

2. Distribution and movement patterns

2.1 GLOBAL

Dusky dolphins may be considered 'semi-pelagic', as they associate with coastal zones as well as shallow shelves and slopes of the continental shelf. Dusky dolphins occur off South America (Peru, Chile and Argentina), southwestern Africa (Namibia and South Africa), New Zealand, the Falkland and Tristan da Cunha Islands in the South Atlantic, and the Prince Edward, Amsterdam and St. Paul Islands in the eastern Indian Ocean (Van Waerebeek et al. 1995). Dusky dolphins are not common in water deeper than 2000 m, and any deeper water sightings are generally related to abrupt continental shelf or island drop-offs (Jefferson et al. 1993).

Individuals are known to move within locations; for example, within the waters around Argentina (Würsig et al. 1997), New Zealand (Würsig et al. 1997), Peru (Van Waerebeek 1992) and South Africa (Smithers 1983; Cassens et al. 2005). However, it is unlikely that individuals have moved between continents in recent times. Genetic evidence suggests that dusky dolphins may have evolved from an ancestral population that resided in the South Atlantic (Cassens et al. 2005); however, this assertion is not at all clear. The Peruvian population may be the oldest, having separated from the ancestral stock roughly 200 thousand years ago (kya). The New Zealand population is thought to have been the next to break off from the ancestral population, c. 50–100 kya, and the South African and Argentine populations are the most recently isolated at c. 12 kya (Harlin 2004).

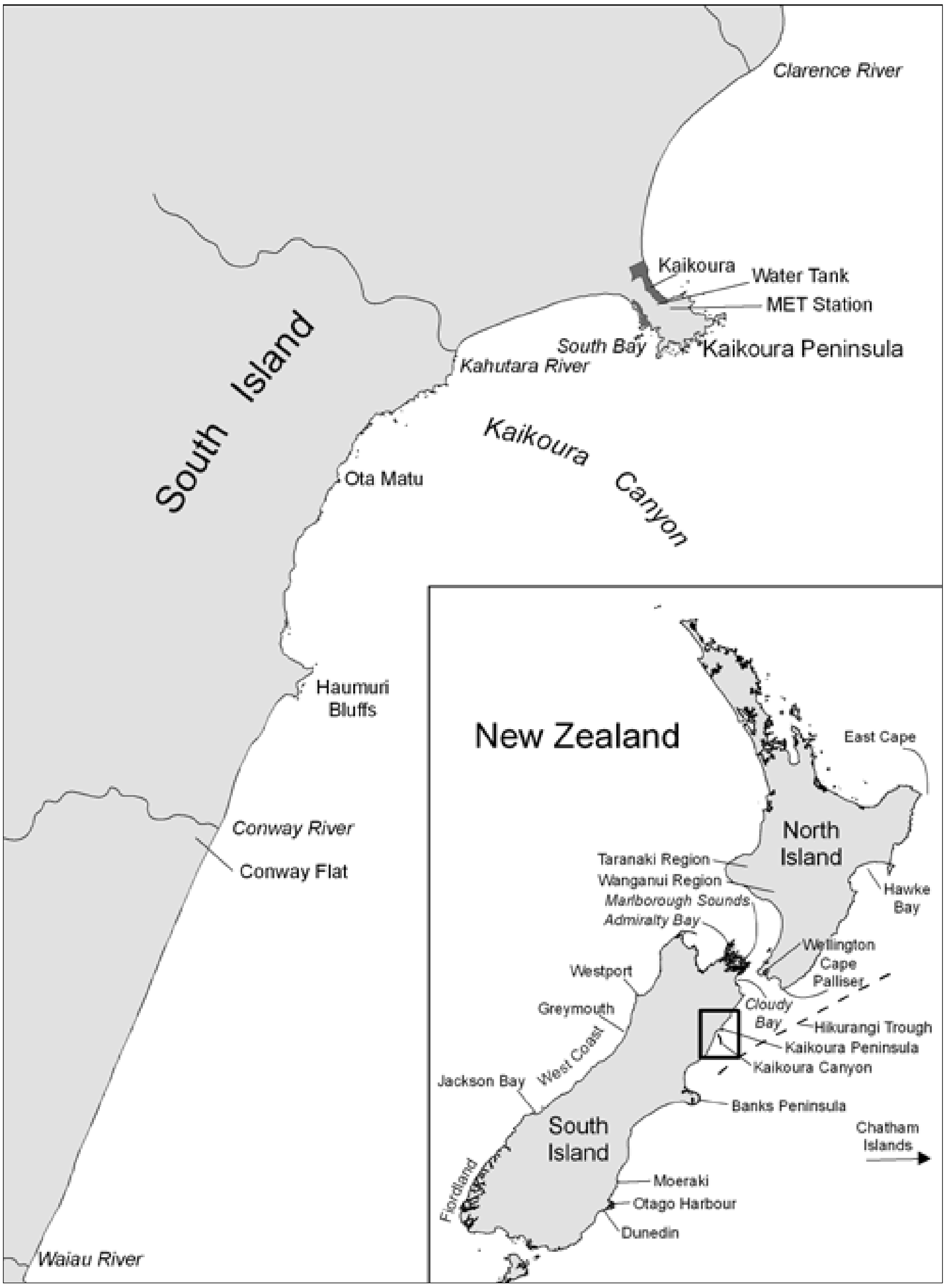
2.2 NEW ZEALAND

In New Zealand, most research on dusky dolphins has been concentrated in two regions: an area off the northeast of the South Island that lies between the Kaikoura Peninsula and the Haumuri Bluffs, which are 20.5 km southwest of the peninsula; and (more recently) in Admiralty Bay, Marlborough Sounds (Fig. 2). Therefore, although the animals occur in many areas around New Zealand, relatively little is known about their behavioural ecology except in these two better-studied areas.

2.2.1 Distribution

Dusky dolphins occur off most of the South Island, the lower part of the North Island, the subantarctic Campbell and Auckland Island groups, and along the Chatham Rise to the east of the South Island (Würsig et al. 1997). Baker (1990) reported that large groups of up to 100 individuals are commonly sighted south of East Cape in the North Island but rarely north of this (Fig. 2). Constantine (1996) summarised opportunistic sightings around both the North and South Islands, and found that during winter, both small and

Figure 2. Map showing main study area for dusky dolphin (*Lagenorynchus obscurus*) research and other localities at which dusky dolphins have been sighted (inset).



large groups of dusky dolphins were reported in the Hawke Bay area. North of this area, sightings were very rare. Historical sightings reported dusky dolphins in the Taranaki/Wanganui region, and it is possible that they still frequent this area. Reports from Wellington describe sightings during summer. Moving further south, there are regular reports for the Marlborough Sounds during April–July, sightings of groups of 3–100 individuals off Westport and Jackson Bay in February, reports of groups of up to 5000 for southeastern Fiordland during February, and sightings 22–60 km offshore from Greymouth during March. There were occasional sightings of groups of < 20 dolphins near Moeraki during January and February, and in Otago Harbour, small groups of < 10 individuals per group were sighted in November–December, with larger groups of up to several hundred individuals during February and March (Constantine 1996). Dusky dolphins also appear to occur infrequently in the inshore waters of Banks Peninsula, between the Conway and Waiau Rivers, and to the north of Otago Harbour (Würsig et al. 1997). They occur around Kaikoura in all seasons, and in Cloudy Bay during March–May and October–September (Würsig et al. 1997). There have also been reports of dusky dolphins around the Chatham Islands (c. 800 km to the east of the South Island) in October (Würsig et al. 1997). However, they may also occur there in seasons other than spring, possibly even year-round. Gaskin (1968) suggested that seasonal shifts in near-surface water temperatures influence the distribution of dusky dolphins on the eastern side of New Zealand, with the dolphins being associated with waters of 9.8–16.0°C; however, it is likely that this pattern is driven more by prey than by temperature.

2.2.2 Movement patterns

Dusky dolphins travel and disperse over distances greater than 100 km (Würsig & Bastida 1986; Würsig et al. 1997; Harlin et al. 2003). A radio-tagged individual from Kaikoura moved c. 150 km to a location south of Cape Palliser off the North Island in less than 2 days (Cipriano 1992). Photo-identification studies of dolphins' natural marks (Würsig & Jefferson 1990) were begun off Kaikoura in 1984 (Cipriano 1992), and continue to this day. Markowitz (2004) compared records from Kaikoura with those gathered more opportunistically in other regions around New Zealand and found that three individuals that had been photographed in Kaikoura in March and April were recorded on the West Coast in February. One of these individuals was also photographed in Admiralty Bay, Marlborough Sounds, in the winter of the same year. Though limited, these data indicate that at least some dusky dolphins travel c. 1000 km between locations around the South Island.

Markowitz (2004) identified 39 dolphins in Admiralty Bay during winter, all of which had originally been photographed in Kaikoura during summer/autumn. At least some of these dolphins have been recorded in both locations in successive years. Markowitz (2004) estimated a mean population size of 220 dusky dolphins in Admiralty Bay during any given week in winter. It is possible that these seasonal migrations are a cultural phenomenon for only a part of the population, which has been learned from parents, other elders or other conspecifics (Whitehead et al. 2004). Work is currently underway to describe the association and habitat-use patterns of dusky dolphins off Kaikoura and in Admiralty Bay.

Genetic analyses of dusky dolphins from four areas around the South Island were conducted by Harlin et al. (2003). Their results showed no evidence of population differentiation between the four sites, indicating at least sporadic travel and mating between areas. Genetic analyses also suggested a potential seasonal bias in sex ratio in the different areas. In Kaikoura, the sex ratio was 1:1; from limited studies off the Otago Peninsula, the ratio of females to males was 13:1; and in Admiralty Bay, the ratio appeared to be c. 1:2 females to males. These data are preliminary and ratios may not be as skewed as they suggest. Recent photographic analysis has revealed that some new mothers that were first photographed with calves in Kaikoura in summer/autumn have been recorded in Admiralty Bay during the following spring/summer months. Nevertheless, the genetic data suggest that the Marlborough Sounds may be used predominantly by males for overwintering, whereas females may be more common off Otago and the West Coast during the breeding season (Harlin et al. 2003). We suggest caution in interpreting these early data, however, as the genetic samples could be biased by, for example, males preferentially allowing themselves to be sampled in Admiralty Bay, while they are bow-wave riding near the boat; and more females being sampled off Otago and the West Coast due to the sampling vessel having been quite close to shore (within 3 km), and the generally known bias towards more females and young near shore in other areas (Argentina: Würsig & Würsig 1980; off Kaikoura: Würsig et al. 1997).

2.3 KAIKOURA

2.3.1 The marine environment

Both bathymetric and oceanographic systems contribute to a unique marine ecosystem off Kaikoura. The subtropical convergence, a mixing of Antarctic and tropical waters that exhibits relatively higher primary productivity than areas further north and south (Boyd et al. 1999), is found at roughly the same latitude as Kaikoura. In addition, very deep, productive waters are brought to within 500 m of the Kaikoura coastline via the Hikurangi Trough and the Kaikoura Canyon (Fig. 2). The resulting nutrient availability leads to a high concentration of plankton, fish, squid and marine mammals in the area.

Hydroacoustic studies showed a deep scattering layer (DSL) of plankton, invertebrates and fishes migrating vertically to within 50–100 m of the surface at night along the east coast of the South Island (Kerstan & Sahrhage 1980). The DSL is probably most pronounced in oceanic waters, and comes close to shore as a result of the Kaikoura Canyon and its associated trenches. This canyon system makes the open-ocean bay between the Kaikoura Peninsula and the Haumuri Bluffs (Fig. 2) especially attractive to dusky dolphins, which feed on fishes and squid within the DSL offshore when it rises during the night (Benoit-Bird et al. 2004), and rest, socialise and seek protection from predators in the shallower waters near shore during the day. This system also extends south of the Haumuri Bluffs, and dolphins follow the canyon edge to the south.

2.3.2 Distribution

Stonehouse (1965) found dolphins (most likely dusky dolphins) in large concentrations near the Kaikoura Peninsula, with sightings being more frequent south of the peninsula (to as far south as the Conway River and Conway Flat) than north of it. These findings are echoed by Cipriano (1992), who recorded more regular sightings of dusky dolphins between the Kaikoura Peninsula and Haumuri Bluffs than in the waters north of the peninsula. This general trend, with sporadic intra- and inter-seasonal exceptions, still occurs (pers. obs). Nevertheless, dusky dolphins also occur with some frequency north of Kaikoura Peninsula, regularly as far north as at least the Clarence River (Dolphin Encounter, Kaikoura, unpubl. data). Aside from radio-tracking of dolphins in that area in the 1980s (Cipriano 1992), no detailed investigations of dusky dolphins have been conducted to the north of Kaikoura and south of the Marlborough Sounds.

2.3.3 Seasonal and intra-seasonal trends

Cipriano (1992) and Markowitz (2004) found that dusky dolphins in the Kaikoura area were closest to shore during summer, farthest from shore in winter, and at an intermediate distance in autumn and spring. Theodolite tracking gave evidence of resting and socialising in waters between 50 m and 500 m depth during the middle of the day in early May, whereas tracks from winter showed that groups were generally further offshore (Würsig et al. 1991). Using radio transmitters mounted on the dorsal fins of ten individuals, Würsig et al. (1991) and Cipriano (1992) tracked individuals in winter 1984 and spring-summer 1987–88. For three individuals tracked in winter, tagged dolphins and their groups frequently travelled > 5 km from the tip of the Kaikoura Peninsula and up to 9 km offshore of the Haumuri Bluffs. They consistently moved far from shore throughout the day, and each remained within the radio reception range of c. 50 km for only a few days. An adult male moved a considerable distance to the north in 1.5 days, reappeared a few days later, and then moved out of range to the south 2 days after this. Overall, there were greater than expected periodic movements away from the Kaikoura area, and it is likely that this pattern is more common than the 'daily' occurrence of groups near shore would suggest.

Markowitz (2004) also noticed a significant seasonal difference in the longitude and latitude of groups encountered during non-systematic boat-based surveys in the Kaikoura region between 1997 and 2003. Dolphins were found further north in autumn/winter than in summer, and furthest from shore (i.e. furthest east) in winter. From December to February, Markowitz (2004) found that most groups were south of the Kahutara River, whereas from March to May, groups were more evenly spread between the Kaikoura Peninsula and just south of Haumuri Bluffs. These patterns were also observed in the 2004–2006 field seasons (unpubl. data).

2.3.4 Diurnal and nocturnal trends

Shore-based studies by Cipriano (1992) found that dusky dolphins were further from shore in late afternoon during autumn and summer. Markowitz (2004) found that dolphin groups headed in a more westerly direction during the early morning and in a more easterly direction from midday to late afternoon. Overall, it is apparent that there is a strong bias towards shore during the day and offshore or at least into deeper canyon waters during the night. This is commensurate with the idea that dolphins rest and socialise near shore during the day when the DSL is too deep for them to obtain meso-pelagic prey, and feed during the night, when the DSL organisms travel closer to the surface (Würsig et al. 1997).

3. Population biology and behaviour

3.1 POPULATION SIZE AND INDIVIDUAL RESIDENCY

From mark-recapture analyses of naturally marked and photo-identified dolphins, Markowitz (2004) estimated a mean of just under 2000 dusky dolphins in the Kaikoura area at any one time, from a population of over 12 000 individuals. His study showed that some individual dolphins were seasonal residents of the Kaikoura area, with dolphins remaining in the area for an average of 3.4 (± 1.27) months and returning to the area at roughly the same time in subsequent years.

3.2 GENETICS

In most years, there is a marked difference in group sizes, aspects of behaviour, inshore/offshore distribution, and even some aspects of colouration patterns of dusky dolphins that frequent Kaikoura during summer v. winter. However, Harlin et al. (1999) concluded that 'winter' and 'summer' groups are not different with respect to maternal lineages. The current unsubstantiated working hypothesis is that the dolphins seen in Kaikoura in winter may spend the summer in the Chatham Islands and/or off Dunedin or other areas further south. However, this hypothesis still needs to be tested through dedicated photographic and genetic surveys in other areas.

3.3 DIET

Cipriano (1992) analysed the stomach contents of 26 dusky dolphins that were found dead in the Kaikoura area, and identified a total of 17 735 prey pieces. Of these, fish and squid were the predominant prey. Lanternfish (Myctophidae), including *Symbolophorus* sp., *Diaphus* sp., *Myctophum* sp., *Hintonia* sp. and 'unknown' species represented 14%–100% of stomach contents by number in samples where they were present. Hoki (*Macruronus novaezelandiae*) was found in the analysis of some dolphins in each season, whereas red cod (*Physiculus bacchus*), hake (*Merluccius australis*), hatchetfish (Gonostomatidae/Sternoptychidae), carapids (Carapidae), *Bathylagus* sp. and some unidentified fishes appeared to be taken only occasionally. The most common type of squid species were *Nototodarus/Todaroides* spp. These were found in the stomach contents in all seasons, whereas other squid types were only taken occasionally. Although myctophids are smaller than the other main food types, they are the most energy-rich. Dusky dolphins that feed in Admiralty Bay in winter eat pilchard (*Sardinops sagax*), yellow-eyed mullet (*Aldrichetta forsteri*) and sprat (*Sprattus antipodum*). Photographic records indicate that some of these dolphins also frequent Kaikoura at other times of the year, showing that individual dolphins alter their foraging strategies and prey types on a seasonal/regional basis (Markowitz et al. 2003).

3.4 NOCTURNAL FORAGING STRATEGIES

Benoit-Bird et al. (2004) used a specially adapted, 200 kHz echosounder to determine the distribution of dusky dolphins relative to their prey during night surveys off Kaikoura. A total of 250 transect kilometres were surveyed continuously from 1800 h to 0530 h between 27 July and 2 August 2002. Results indicated that while surface foraging behaviour began at around 1800 h in winter, dolphins were not found in the DSL until it rose to within c. 130 m of the surface at 2000 h. Dolphins dove most shallowly near midnight, when the shallowest part of the DSL rose to 30 m. Dolphins were detected in subgroups of 1–5 individuals. From 1600 h to midnight, average subgroup size increased by small increments each hour; after midnight, subgroup size gradually decreased again. Thus, dolphins foraged (and presumably fed) in small subgroups at the shallowest dive depths, but individually dove down to as far as 130 m. We suspect that the animals may be herding prey as a social unit while diving shallowly, but do not have the time to do so during deeper dives of over c. 100 m depth. Dolphins were not detected swimming deeper than 130 m. Results suggest a possible foraging window of 9 h in winter; we assume that this is briefer during the summer. It is presently unclear whether or to what degree dolphins socially coordinate night-time feeding at any depth. Studies by the authors and colleagues that used a more sophisticated sonar array of 38, 120 and 200 kHz transducers operating simultaneously were conducted in late summer to early autumn 2006. It is hoped that these will shed light on seasonal differences in prey and foraging behaviour, differences by moon phase, and details of social strategies at depth.

3.5 BEHAVIOURS AND ACTIVITIES

Markowitz (2004) found that group size off Kaikoura was largest in winter, with 30% of groups recorded during this time containing over 1000 individuals. Dolphins travelled more and rested less in winter than in summer. In spring and summer, the spacing between individuals was tighter than in winter. Noisy leaps (defined as ‘breaches’ and ‘slaps’ that make a splash) were the most commonly recorded leap type during all seasons, but occurred most often during winter.

During the morning, dolphin groups were spread out, leaping often and closest to shore. Around midday, dolphins tended to rest in tight groups. They then spread out again and moved offshore in late afternoon/early evening. Large groups of hundreds of individuals exhibited coordinated travel and noisy leaps; Markowitz (2004) hypothesised that the latter serve as directional signals for others.

Cipriano (1992) recorded mean swimming speeds ranging from 1.26 m/s to 3.38 m/s (1.00 m/s = 3.60 km/h). During 'directional travel', maximum burst speeds ranged from 3.08 m/s to 10.04 m/s, but these were sustained for only a few minutes at most.

3.6 REPRODUCTION

Cipriano (1992) estimated that both males and females become reproductively mature at c. 7–8 years and 160–165 cm total length. Markowitz (2004) observed the highest frequencies of mating behaviours in summer. Chasing was the most common behaviour recorded in mating groups, which on average were composed of six males chasing one female. Calves were most often documented in spring and summer (November–January), and no newborn calves were recorded by Markowitz (2004) during autumn/winter. Cipriano (1992) calculated a gestation period of c. 11.4 months and lactation is estimated to last c. 18 months (Leatherwood et al. 1983). A seasonal difference in testis size of adult males suggests that the breeding season is restricted mainly to spring–summer (Würsig et al. 1997).

Five very young calves, measuring between 97 cm and 120 cm in length, had only milk in their stomachs; another dolphin that measured 118 cm had eaten myctophids and other types of fish (Cipriano 1992). From this, we surmise that solid prey is taken at c. 118 cm length at the earliest.

4. Tourism impacts

In 1989, shortly after sperm whale (*Physeter macrocephalus*) watching started in Kaikoura, swim-with-dolphin tourism began. Dolphin Encounter (formerly Dolphin Mary Charters) began to conduct tours on small vessels, and participants were given the opportunity to swim with groups of dusky dolphins (that at times also included short-beaked common dolphins, *Delphinus delphis*). As tourism grew, Dolphin Encounter expanded; it is now the only swim-with-dolphin operation in the area. Two marine mammal watching permits, issued under the Marine Mammal Protection Regulations of 1992, allow three swim trips a day, with 13 swimmers per trip. Another permit allows eight trips per week, also with a maximum of 13 swimmers per trip. All three permits allow additional passengers on-board to view dolphins. Therefore, up to 50 trips per week are taking a maximum of 650 participants to swim with dolphins.

Whale Watch Kaikoura, the only boat-based whale-watching company operating in the Kaikoura area, holds four marine mammal watching permits to operate whale-watching tours, each permit allowing four trips per day. While their focus is on sperm whales, they are also permitted to view dolphins during these tours and often stop to view dusky dolphins, New Zealand fur seals (*Arctocephalus forsteri*) and sea birds. Whale Watch Kaikoura's permits also allow their tourists to swim with dolphins; currently, they do not take advantage of this.

Kaikoura has benefited from whale and dolphin tourism activities. The number one stated reason that tourists travel to Kaikoura is for the proximity to marine mammals (Simmons & Fairweather 1998). An estimated 356 000 overnight visitors came to Kaikoura in 1998, a large number for a town of only c. 2000 permanent residents; in that same year, approximately 30% of all jobs in Kaikoura either directly or indirectly relied on tourism (Simmons & Fairweather 1998; Hoyt 2001).

4.1 RESEARCH INTO EFFECTS OF DOLPHIN-BASED TOURISM

Several studies have been conducted in New Zealand investigating interactions between boats and cetaceans in an attempt to better understand how animals might be impacted and ways of mediating potential effects. Examples of species studied include sperm whales (*Physeter macrocephalus*) in Kaikoura (Gordon et al. 1992; Richter et al. 2003), Hector's dolphins (*Cephalorhynchus hectori*) in Akaroa Harbour (Nichols et al. 2001), bottlenose dolphins (*Tursiops truncatus*) in Fiordland National Park (Lusseau 2003), and bottlenose dolphins in the Bay of Islands (Constantine et al. 2004).

In Kaikoura, research into interactions between commercial tourist operations and dusky dolphin groups began in 1993. Over the past 13 years, small (Yin 1999) and large (Barr 1997) groups of dusky dolphins have been studied, in an attempt to investigate potential impacts of recreational and commercial tourist boats. In 1998, the long-term effects of tourism were investigated using pre-tourism data collected in the mid-1980s (Brown 2000, who used pre-tourism data from Cipriano 1992). Recently, two projects were completed in the Kaikoura area: a detailed study on nursery groups (Weir 2007), and an investigation into movement patterns of the larger dusky dolphin groups and associated levels of vessel traffic (Duprey 2007).

4.1.1 Methodology used

Theodolites, or surveyor's transits, have been used to study cetacean species around the world. A theodolite provides vertical and horizontal measurements (each measurement being a 'fix') that can be used to accurately calculate the latitude and longitude of objects at the surface of the water (Würsig et al. 1991; Gailey & Ortega-Ortiz 2002). Since the station is shore-based, researchers can remove any potential effects of a research vessel affecting the behaviour of the animals under study. The topography of the Kaikoura area is ideal for theodolite work, with high cliffs and hilltops providing vantage points directly beside the sea. Several studies conducted in the Kaikoura area on the interactions between tourism and dusky dolphins have used shore-based theodolite platforms.

4.1.2 Directed studies

As tourism activities increased in Kaikoura, two studies began to investigate the dusky dolphin population and how it was being affected by boats and swimmers. Barr (1997) examined responses of large groups of dusky dolphins to boats and swimmers during two field seasons, December 1993 to April 1994, and October 1994 to April 1995, over 118 days. Theodolite surveys were conducted from Ota-Matu lookout (42°29′S, 173°31′E), the same station as had been used in an earlier study (Cipriano 1992). Groups were followed for 10-min sessions, no more than four times per hour. For each 10-min session, group size, dispersion and swimmer activity were recorded. Dispersion was recorded by fixing the front and back of the group as it moved. Data were later sectioned into 2-h time blocks, beginning at sunrise; this allowed the potential effects of time of day to be analysed. For calculation of leg speed (the speed of travel between two fixed points), a maximum of 240 s was allowed between fixes. Any boats approaching within 500 m of the focal group were recorded. A total of 776 10-min observations were used to analyse boat interactions; 710 of these observations were used in statistical tests on dolphin behaviour.

Barr (1997) found that dolphin groups were more dispersed during the morning than the afternoon, and that the mean speed of groups was lowest during late morning and at midday. She postulated that low speed indicated resting, and that dolphins were therefore most likely using midday to rest. Although not statistically significant, there was a trend for mean dolphin density to increase later in the day. A higher number of tight groups was found later in the day; the number of dispersed groups decreased as the number of tight groups increased. More groups travelled close to shore in summer (December–February) than in autumn (March–April). Dolphins typically swam in water shallower than 800 m.

During Barr's (1997) two seasons of field work, two companies held permits to take tourists to swim with dolphins: Dolphin Encounter and New Zealand Sea Adventures. Additionally, Whale Watch Kaikoura was permitted to visit dolphins, and three other companies (Wings over Whales (one permit), Kaikoura Aeroclub (one permit) and Kaikoura Helicopter (two permits)) were taking tourists to view dolphins or whales by plane or helicopter. Barr recorded 949 boats approaching dolphin groups and found no significant differences in the number of boats visiting dolphins between months. This intensity of tourism effort resulted in at least one boat being recorded within 300 m of a focal pod for 71.9% of the survey time, with the highest number of approaches occurring during mid-afternoon. Between Barr's first and second field season, there was a significant increase in the presence of boats, from 65.2% to 78.3% of survey time. Throughout her study, commercial cetacean tourism made up most of the traffic observed, at 84.4% of all boat traffic. Private boats represented a much smaller proportion (only 9.4%); the remainder were fishing vessels or unknown.

During Barr's (1997) boat-based research, an average of 3.17 swims were conducted per dolphin tour and swimmers were in the water for an average of 40 min per tour. The Marine Mammals Protection Regulations allow a maximum of three vessels to be within 300 m of a dolphin group. Barr (1997) found that this maximum was exceeded during 8.2% of all observations. Neither the number of boats nor types of boats was found to affect group dispersion, density or speed.

In a separate study, Yin (1999) followed groups of dusky dolphins from a shore-based theodolite station during the summers and springs of 1994–1997. Over 162 days (three field seasons), small groups of fewer than 25 dolphins were tracked with a digital Sokkia theodolite. Yin (1999) also used Ota-Matu lookout as her main tracking station; two other stations (the Kaikoura Peninsula Water Tower and the Meteorologic (MET) Station, both on Kaikoura Peninsula) were used as back-up stations when dolphin groups were in South Bay or offshore. Fixes that were greater than 120 s apart were not used to calculate leg speed, to avoid problems with non-linear travel. Both group size and calf presence were determined for each focal group. Sample sizes for Yin's (1999) study were generally low and while some trends were noticeable, most statistical analyses resulted in non-significance either due to low sample size or no apparent biological effect.

Mean leg speed ranged from a minimum of 3.2 km/h between 0800 h and 0900 h, to a maximum of 5.3 km/h between 1100 h and 1200 h. Mean leg speed did not vary significantly with season or time of day, which allowed data from all seasons to be pooled for analysis. However, sample sizes were still small, potentially meaning that real trends could not be detected. As group size increased from 5–10 to 10–15 and 15–20, mean leg speeds of the groups increased; however, this difference was not significant. Mean leg speeds of dolphin groups showed potential variance throughout the day, but, again, more data are needed for appropriate statistical testing. The mean leg speed of seven groups containing calves was not found to be different from non-calf groups; however, calf groups did show more linearity in their tracks than non-calf groups.

In 1994–1997 the mean leg speed of the small focal groups was not significantly affected by the distance (300 m v. 100 m) of boats from the group. However, mean leg speeds were higher when there were no boats within 100 m than when boats were present, and increased gradually over time after boats had left. Again, low sample sizes (30 samples with no boats present and only six samples with boats and to analyse post-boat interactions) could have impeded the detection of trends; therefore, a more thorough study is certainly warranted. If the present trends hold true, it would indicate that small dusky dolphin groups slow down in the presence of boats and gradually increase speed after boats have left them. Group track lines were more linear during and after boat encounters than when there were no boats present. Overall, boats did not interact very often with small groups; instead, the large main groups were the focus for most tourism. Most of the boats approaching close to small groups were simply travelling through the area and had fairly constant speeds and headings.

4.1.3 Effects of tourism on behaviour

Between December 1998 and April 1999, Brown (2000) studied dusky dolphin groups to compare pre- and post-tourism dolphin behaviour and movement patterns. Again using Ota-Matu as her primary field station, Brown tracked groups of all available sizes. By following the same methodology as Cipriano (1992) and using the same behavioural states as he did in his mid-1980s study, Brown (2000) was able to make comparisons between findings from the two studies. Over 262 h were spent theodolite tracking 274 groups (128 groups with > 50 dolphins; 146 groups with < 50 dolphins).

Brown (2000) found more groups of both sizes in the Kaikoura area than Cipriano (1992) had previously recorded. The movement patterns of these groups seemed to have changed since the mid- to late 1980s, with more groups travelling south. Brown speculated that this change may have been due to dolphins attempting to avoid the busy commercial ramp in the northern part of the survey area. Recent data indicate that inter-seasonal variation is of such a magnitude that the differences in group sizes and locations of dolphins may be related to variables other than boat/human contact, such as food distribution. Additional research is warranted in this area.

While studying the behaviours of large dolphin groups by boat, Markowitz (2004) found that boats other than his research boat were present during 55% of his observation periods: Dolphin Encounter—36%; Whale Watch—9%; New Zealand Sea Adventures—6%; and 'other' boats—4%. While no tour boats were recorded around nursery groups separate from large groups, calves were present during 71% of swims with large groups (Markowitz 2004).

Markowitz (2004) also collected information onboard dolphin tour vessels and found that the mean tour length was 2 h 7 min, with an average of 11.5 swimmers and 6.4 spectators per trip. Each swim lasted 8.3 min, on average, and involved approximately 10.8 swimmers. An average of 3.4 swims was made on each trip.

4.2 RECENT TOURISM-RELATED ACTIVITIES

4.2.1 Shore-based descriptions

In the late 1990s, Dolphin Encounter and Whale Watch Kaikoura began participating in a voluntary rest period, between 1130 h and 1330 h local time, from December to March. This was in response to research findings that dusky dolphin groups in the area were resting more during late morning and at midday than in the early morning and afternoon (Barr 1997; Yin 1999). Currently, only these two companies participate in the voluntary rest period; the other whale-watching companies, which use helicopter and plane platforms, visit dolphin groups throughout the day.

Between late January and the end of March 2005, 31 days were spent conducting theodolite surveys from Ota-Matu, along the Kaikoura coast (Duprey et al. 2005; Duprey 2007). Scans for dolphin groups were conducted before surveys began and large groups (> 150 individuals) were followed until they were lost from sight, inclement weather forced a pause in research, or some other logistical constraint intervened. The position and behaviour of each focal group were recorded every 5 min, and any vessel (boat, plane, helicopter or kayak) that came within 400 m of a focal group had its arrival and departure times recorded along with its activity.

This study in 2005 was conducted to compare the number of boats and aircraft interacting with focal groups during rest and non-rest periods. We analysed all vessel traffic and divided data into rest (1130–1330 h) and non-rest (any other time of day) periods. Only data collected for at least 30 min were included in this analysis (for example, if a group was studied from 1110 h to 1155 h, it would not be included, as 20 min occurred during the non-rest period and 25 min during the rest period, so neither block amounted to 30 min). During the non-rest period, there was a mean of 3.28 visits/h (SD = 2.036, $n = 34$, total time = 89.63 h) and the rest period had a mean of 1.78 visits/h (SD = 1.584, $n = 17$, total time = 26.93 h). This decrease in the average number of visits made during the rest period was significant ($t = 18.826$, df = 49, $P < 0.005$); however, one tour operator was still making a mean of 0.62 visits/h (SD = 0.840) during this period. The other tour operator was never seen interacting with dolphin groups during the rest period. The number of private recreational vessels visiting groups was also high; a mean of 0.64 visits/h (SD = 0.847) and 0.91 visits/h (SD = 1.42) were made by private recreational boats during rest and non-rest periods, respectively (Duprey et al. 2005; Duprey 2007).

The length of swim-with-dolphin tours and total time spent swimming with dolphin groups were recorded during 2006 (Duprey 2007). On 34 tours between January and April 2006, on-board researchers collected data on the start and stop time of each tour and each swim attempt. The mean number of swims conducted per tour was 3.26 (SEM = 0.268), with swims lasting for a mean of 8.15 min (SEM = 0.581). Scans for calves were conducted on 17 tours, 15 (88.2%) of which had calves present for at least one swim. When scans for calves were conducted, calves were present during 42 (72.4%) of 58 swim attempts. Duprey (2007) found little change from Markowitz's (2004) 1997–2003 tour vessel research, the length and number of swim attempts with dolphin groups in the Kaikoura area changed very little. Markowitz (2004) found the mean tour length to be 2 h 7 min, mean swim attempt length to be 8.3 min, mean number of swims per tour to be 3.4 and observed calves during 71.4% of all swim attempts made.

We are currently analysing 35 group tracks to use positional data to determine whether dolphin groups in the area are experiencing different levels of traffic along the Kaikoura coast. Distance from shore and proximity to launch ramps will also be examined to determine whether there are significant differences in the number of boats interacting with groups found in different locations.

4.2.2 Boat-based studies: distribution and behaviour of nursery groups

In addition to the large groups of dusky dolphins that occur in the waters off Kaikoura, there are also smaller 'nursery groups' in the area. Beginning in January 2005, Weir et al. (2005) undertook systematic surveys to determine locations, behaviours and association patterns of these subgroups. Weir et al. (2005) and Weir (2007) defined a nursery group as a group composed of at least two calves for every six non-calves. Calves were defined as individuals estimated to be < 1 year old, based on small body size and poorly defined colouration pattern, 'cork-like' surfacing, and a consistent echelon position beside an adult.

The focus area for this study was between the Kaikoura Peninsula and Haumuri Bluffs. The survey track was 68.5 km long and covered an area of c. 97.5 km^2, with depths ranging from 2 m to over 1134 m. Beginning in January 2005, a 5.5-m semi-inflatable research boat powered by an 85 HP outboard motor was used to survey for nursery groups. To minimise sampling bias, surveys started at one of three pre-determined start locations on each survey day. When a nursery group was sighted, we marked our position on the survey route so that we could continue the route from the same location once finished with the group. We approached groups slowly to minimise disruption and recorded their location with the GPS unit. At this time, we would contact the shore-based theodolite station for a report of large dolphin groups and tour boat presence in the wider area. An attempt was made to photograph the dorsal fins and any other distinguishable body features of all members of the group, using a Nikon D1H digital camera. Behavioural data were collected by conducting 30–60-min focal follows of groups. Dolphins within 10 body lengths of another group member were counted as part of the nursery group. Environmental data were also collected in the vicinity of each group.

A total of 99 nursery groups were encountered on survey days between January and May 2005 and December 2005 to April 2006 (Weir 2007). While nursery groups were encountered significantly more often in shallow water (< 20 m) than in deeper water (> 20 m), this was not the case for other dolphin group types (Weir 2007). Boats, especially private recreational boats, were more frequently encountered in shallow waters than deeper waters (Weir 2007). The significant overlap between the areas used both by nursery groups and by boats indicates that nursery groups are at a greater risk from boat motors and recreational fishing gear in these areas (Weir 2007).

A total of 260 individuals were catalogued as members of nursery groups during the two field seasons (Weir 2007). Certain individuals photographed with young calves in nursery groups off Kaikoura were photographed later in the year in Admiralty Bay (Weir 2007).

5. Future research directions

We are at an exciting point in dusky dolphin research in Kaikoura. While in-depth studies require significant time, we are in the process of adding pieces to the puzzles of both social strategies and human-dolphin interactions. This is being accomplished largely by a suite of graduate students who are asking more directed questions while building on the low-level monitoring and several intensive studies of the past. We list their projects here, with the understanding that their goals and proposals may change pursuant to advice from their committee members, Department of Conservation personnel and others.

Nicholas Duprey and Jody Weir continued work in Kaikoura from December 2005 through to April 2006. Nursery groups continued to be the focus of boat-based work, with the emphasis being on focal follows of nursery groups. With these additional data, we will better understand how dolphin mothers are influenced by boat activity, aggressive male behaviour, and other potential impacts on energetic and life history requirements. Nicholas Duprey is currently collecting data on the movement patterns and duration of dolphin-swim tours in Kaikoura to better understand the number of swims per trip and movement patterns of boats during and after swimming. This information, combined with previously collected tracks of dolphin groups and vessel interactions, will help describe the quantity of interactions that dolphin groups are receiving in the area.

Adrian Dahood (Texas A&M University), Kelly Benoit-Bird (Oregon State University) and Bernd Würsig continued and expanded their efforts to describe movements of dolphin groups relative to prey availability patterns, as gleaned from other studies and our own remote sensing of prey and predators in February–March 2006. This work, which was sponsored in part by the US-based National Geographic Society, is allowing a comparison of habitat-use patterns relative to both natural and potentially human-induced (tourism) factors. Although this work was completed in early 2006, Adrian Dahood continued to monitor movements of animals from shore through December 2006. She spent one-third of her time theodolite tracking dolphins from each of three sites: the Kaikoura Peninsula, the Ota-Matu site used since 1984, and a new site set up at Haumuri Bluffs, to yield new information on dolphin and boat movements in this less studied part of the study area.

Mridula Srinivasan (Texas A&M Univeristy) is investigating the potential effects of predator pressure on habitat use, grouping and sociality. This study will compare social aspects of dusky dolphins off the Kaikoura Peninsula and the closely related Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) of Monterey Canyon, Central California coast. Her study will also feed directly into questions of habitat use relative to human effects, as we believe that day-night and seasonal movement and social strategies are dictated largely by predators and prey. The study began in Kaikoura in January 2007, and will run for several years.

Sierra Deutsch (Texas A&M University) is interested in following up on social strategies and behaviours of mother-calf groups in the near-shore environment, with a special emphasis on the development of calf behaviours in their first year of life. She will be looking at whether calves imitate their mothers and others, as a partial attempt to describe social learning and potential cultural transmission of knowledge. This also has implications for human-dolphin interaction analyses, as it is possible that dolphin young, for example, are less disturbed by certain human activities if they are habituated to them by their elders. This study began in September 2006 and will run through to at least May 2007.

Three students are currently doing ancillary work to the directed Kaikoura-based studies, the results of which are anticipated to be comparable with the Kaikoura results to some degree. Heidi Pearson (Texas A&M University) is comparing social strategies of dusky dolphins in Admiralty Bay with dolphins and great apes from other studies. This work allows for a broader appreciation of the roles of sociality in large-brained mammals with very different evolutionary histories. Robin Vaughn (Texas A&M University) is studying foraging, feeding and cooperative communication of dusky dolphins in Admiralty Bay, with an eye towards an assessment of the flexibilities of behaviours as dolphins seasonally transition between the open deep waters of the Kaikoura coast and the semi-protected inshore, shallow waters of the Marlborough Sounds. Deborah Shelton (Texas A&M University) is analysing previously gathered genetic samples from both Kaikoura and Admiralty Bay to describe affiliation patterns and social group changes in these disparate habitats. All of these studies utilise basic life history and social strategy information not only to enhance our basic knowledge of the species, but also to directly assess human-dolphin interactions, enabling informed recommendations for conservation management to be made.

Finally, a new study focussed on dolphin responses to tourism was begun in January 2007, and is planned to finish in 2009 with a report to the Department of Conservation. The project, which involves both shore-based and boat-based studies, is funded by the Department of Conservation and Earthwatch, and is led by Tim Markowitz (now researcher at Massey University), Bernd Würsig, Sam DuFresne (of DuFresne Associates), and Mark Orams (The Peter Blake Society). It aims to assist the Department of Conservation in deciding whether the moratorium on tourism with dusky dolphins that was implemented in 1999 should be renewed or rescinded.

5.1 DATA FROM TOURISM

The directors of Dolphin Encounter, the major tourism organisation concerned with dusky dolphins in Kaikoura, have indicated that we could analyse their data showing where tourism vessels have gone in previous years. As we understand it, these data have been gathered sporadically, with special emphasis on good positional information over the past several years across all seasons. We believe that this dataset will be particularly valuable in ascertaining potential 'hot-spots' of habitat-use characteristics, and to show whether there is a correlation between the distribution of dolphins and their prey. Furthermore, we currently have no good information on the movements and distribution of dolphins south of the Haumuri Bluffs, and thus cannot shed an educated light on whether it is appropriate for the industry to be permitted to use the area south of the bluffs and, if so, how far south. The information recently gathered by the authors and colleagues, as well as the longer-term dataset from the tourism industry itself, should help to answer this.

6. General conclusions and recommendations

Dusky dolphins off Kaikoura have been studied for over 20 years, providing a long-term dataset of a long-lived, slowly reproducing, social mammal. Dusky dolphins utilise the Kaikoura near-shore and canyon environments throughout the year, resting near shore during the daytime and feeding in deeper waters, generally more offshore but also along-shore in the Kaikoura Canyon, at night.

While much has been learned about dusky dolphins off Kaikoura, and more recently about them in Admiralty Bay, Marlborough Sounds (for example, Markowitz et al. 2003), we have a dearth of information for other areas where they are known to occur, such as near Banks Peninsula and south of there, the west coast of the South Island, and the southern part of the North Island. At this time, we do not even know from where dolphins come as they aggregate off Kaikoura in April and May, and we suggest that dedicated census and photo-identification studies be planned for the above-mentioned areas, as well as for dusky dolphins of the Chatham Rise and Chatham Islands.

Swim-with-dolphin targeted tourism began c. 17 years ago, and has been quite intense for most of that time, especially outside winter. Nevertheless, dusky dolphins appear to be doing well, and areas used for rest, foraging and social activities have not noticeably changed due to human activities. However, the fact that an effect has not been detected is not proof that there is no effect; for example, the great variability of dolphin habitat use both intra- and inter-seasonally may be masking potential dolphin responses to humans. With increasing sophistication of remote-sensing of both prey and the dolphins at depth at night, we are now in a position to begin to understand overall dolphin movements in the area and to elucidate potential effects both by nature and humans. It helps that we have a strong dataset of background information, including over 2000 individually identified animals.

We recommend further natural history, life history strategy and ethological studies, similar to those outlined above. However, targeted studies with a hypothesis-driven framework are also required. Thus, for example, we could postulate the null hypothesis that dolphin 'nursery groups' that are composed largely of mothers and their newborn (less than 6-month-old) calves do not change movement patterns and behaviours relative to proximity of swim-with-dolphin tour vessels, other non-commercial vessels or fishing vessels. Any rejection of a part of the null hypothesis would allow us to further investigate that aspect and explore how and to what degree the potential disturbance (i.e. change) takes place. With our background information and present data-gathering capability, we could also investigate the null hypothesis that the large dolphin school envelope that tends to occur off Kaikoura does not change its daily back and forth movement regime relative to either prey density and occurrence patterns in and near the Kaikoura Canyon, or the amount and intensity of human interaction as it changes with season, day of the week, weather patterns and other factors (such as highly intense human activities during national school holidays, etc.).

Long-term projects such as the Kaikoura study are invaluable in informing management recommendations. Therefore, it is vital that this study be continued into the future.

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