Available online at www.sciencedirect.com
SCIENCE DIRECT®
Biological Conservation 117 (2004) 299–307
BIOLOGICAL CONSERVATION
www.elsevier.com/locate/biocon

Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour

Rochelle Constantine*, Dianne H. Brunton, Todd Dennis

School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

Received 12 July 2002; received in revised form 4 December 2003; accepted 8 December 2003

Abstract

Over the last decade there has been considerable growth in marine mammal-watching tourism throughout the world. Due to the species use of coastal habitats, bottlenose dolphins are most frequently exposed to dolphin-watching tourism. We conducted boat-based focal follows of schools of bottlenose dolphins to determine the effect of boats on dolphin behaviour. A CATMOD analysis showed that behaviour differed by boat number, in particular, resting behaviour decreased as boat number increased. Dolphins rested less and engaged in more milling behaviour in the presence of permitted dolphin-watching boats compared to non-permitted boats. An increase from 49 to 70 permitted trips per week and a change in their departure times resulted in a further decrease in resting behaviour. Currently the effects of boats, in particular permitted boats, on dolphin resting behaviour whilst they are in the Bay of Islands, are substantial. In the light of these findings we suggest that current legislation in New Zealand is not affording this isolated population protection from disturbance.

Keywords: Dolphin-watching; Tourism; Bottlenose dolphin; Human disturbance

1. Introduction

Marine tourism is a rapidly growing industry throughout the world (Miller, 1993). Potential benefits of nature-based tourism include the potential to change people's attitudes towards the environment (Orams, 1995) and generating considerable revenue for local communities (Duffus and Dearden, 1993; Hoyt, 2001). One of the greatest challenges of marine tourism is protecting and conserving the habitat and wildlife whilst managing the needs of tourists (Giannecchini, 1993). There have been concerns over the impact of tourism on cetaceans (Beach and Weinrich, 1989; Bejder et al., 1999; Corkeron, 1995; Constantine, 2001) but the burden of proof often is placed upon those trying to manage the whale-watching industry (which includes whales, dolphins and porpoises) rather than those profiting from it (Mangel et al., 1996; Yaffee, 1997).

Cetaceans are charismatic animals with a wide appeal for many people. Their popularity has resulted in the rapid growth of the whale-watching industry throughout the world. The most recent estimate (Hoyt, 2001) found that commercial whale-watching tours are available in at least 87 countries and territories, and the industry is worth at least US$1 billion. Despite this rapid growth, very little is known about the short- or long-term effects of tourism on cetacean behaviour.

Bottlenose dolphins, *Tursiops truncatus* and *Tursiops aduncus*, are the species of small cetacean most likely to be exposed to tourism (Samuels et al., 2003). Despite the global distribution of the species, they are frequently found in isolated populations that range along discrete areas of coastline (Shane et al., 1986; Wells et al., 1987; Wilson et al., 1999; Connor et al., 2000). Because they are long-lived mammals (40–50 years; Connor et al., 2000), populations that include individuals with limited home-ranges can regularly be exposed to tourism. Research on mammals exposed to tourism has shown that they usually become habituated to, or tolerant of benign human presence, e.g., chimpanzees, *Pan troglodytes*, (Johns, 1996) and grey whales, *Eschrichtius robustus*, (Jones and Swartz, 1984). If animals perceive a situation to be threatening, however, then they are more likely to become sensitised to human presence, e.g., bottlenose dolphins (Irvine et al., 1981; Constantine,

* Corresponding author. Fax +64-9-3737-417.
E-mail address: r.constantine@auckland.ac.nz (R. Constantine).

0006-3207/$ - see front matter
doi:10.1016/j.biocon.2003.12.009

2001) and gorillas, *Gorilla gorilla beringei* (Fossey, 1972). Killer whales exposed to experimental approaches by a research boat have been observed using avoidance tactics similar to those observed when prey are escaping a predator (Williams et al., 2002). Mother-calf pairs of bottlenose dolphins increase their dive duration in the presence of boats suggesting some form of avoidance behaviour (Nowacek, 1999).

An isolated population of 400–500 bottlenose dolphins, *Tursiops truncatus*, ranges along the northeastern coast of New Zealand (Constantine, 2002). The nearest coastal population of bottlenose dolphins is approximately 1000 km south (Bräger and Schneider, 1998) and there is no evidence of interchange between these populations (Constantine, 2002). This population of free-ranging, non-provisioned dolphins has been exposed to dolphin-swim/watch tours in the Bay of Islands since 1991 (Constantine, 2002). Unlike most operations elsewhere in the world, these tours operate under a permitting system that restricts the number and frequency of tour-boats operating and allows no more than three boats of any type within 300 m of a school of dolphins. Here we describe the effect of boats on bottlenose dolphin behaviour. We examined the effect of permitted dolphin-watching boats compared to non-permitted boats, and we quantify the change in dolphin behaviour when further permits were issued allowing an increase from 49 to 70 trips per week.

2. Methods

2.1. Field methods

Non-systematic surveys were conducted in the Bay of Islands, New Zealand, from an independent research boat (a 4.7 m or 6.0 m boat powered by an outboard engine), between December 1996 and February 2000. There was an average of 1.2 schools (as defined by Connor et al., 1998) of dolphins (median school size = 12) (Constantine, 2002) in the Bay per day, resulting in most boats encountering the same school on any given day. The research boat was manoeuvred carefully in order to minimise its potential effects on the dolphins' behaviour. This involved driving the boat at a speed that matched that of the focal school. If the school was milling, stationary, or moving at slow speed for a period of time then the boat was either placed in neutral or the engine was turned off. If the dolphins were travelling, they would often approach the boat and bowride. On these occasions, both speed and course remained consistent allowing the dolphins to determine the length of time they would bowride, rather than the boat being driven to either initiate or maintain contact. Differences in the schools' behavioural state resulted in varying distances being maintained from the focal school, but where possible, a distance of 50 m was maintained. Even with these precautions, the presence of the research boat was also considered as a potential disturbance factor.

When a school of bottlenose dolphins was encountered, data on school size and age-class composition were collected. A focal-follow observation was then initiated and data on the number of boats within 300 m of the school, the identity of those boats (i.e., permitted dolphin-watching, non-permitted commercial or recreational boats), and the dolphins' behavioural state were collected. The dolphins' behavioural state was determined by using a 2-min focal-school scan sampling methodology and assigning a predominant school activity after an instantaneous scan of each individual in the school (Altmann, 1974; Mann, 1999). A school consisted of any number of dolphins moving in a similar direction, engaged in similar behaviours and within five body lengths of any other dolphin. The dolphins' behavioural states were assigned to one of eight categories modeled on Shane et al. (1986). These were:

(i) Social. Dolphins observed leaping, chasing, and engaged in body contact with each other. Involved aspects of play and mating with other dolphins. Might serve a social and/or sexual role.
(ii) Forage. Dolphins involved in any effort to capture and consume prey as evidenced by chasing fish on the surface, co-ordinated deep diving with loud exhalations (but not chuffing), and rapid circle swimming (but not chasing another dolphin). There was usually no contact between individuals (as often observed when socialising). Prey was sometimes observed in the dolphin's mouth and frequently observed during the foraging bout.
(iii) Rest. Dolphins engaged in slow movements as a tight group (i.e., less than one body length between individuals). Movements during rest were slower than those seen in slow travelling behaviour (approximately one knot) and the dolphins were occasionally stationary. Resting lacked the active components of the other behaviours described.
(iv) Slow travel. Dolphins involved in persistent directional movement at speeds less than three knots.
(v) Slow travel—other. Dolphins involved in persistent directional movement at speeds less than three knots but were also engaged in equal amounts of another behaviour (forage, social and/or mill).
(vi) Travel. Dolphins involved in persistent directional movement at speeds of greater than three knots but not involving porpoising, i.e., leaping clear of the water.

(vii) Fast travel. Dolphins porpoising in a persistent, directional movement.
(viii) Mill. Dolphins showed frequent changes in heading that sometimes appeared as a transition behaviour between other behavioural states. Milling was sometimes associated with foraging, socialising or play.

Ambiguous states were infrequently observed and were excluded from the data-set. A boat encounter was initiated whenever a boat of any type came within 300 m of the focal school with the intention of viewing the dolphins. This distance was consistent with the New Zealand Marine Mammals Protection Regulations (1992).

2.2. Analyses

2.2.1. Data-set

Behavioural sampling units consisted of focal-follows where school size and composition remained unchanged. Only follows where the duration of the encounter exceeded 60 min were included. The two-minute subsamples collected during focal-follows were pooled within each sampling unit to give a proportion of time spent in each of the behavioural states (see Section 2.1). During any given focal follow, the number of boats present changed frequently so therefore, continuous sequences of behaviour were necessarily fragmented for analysis when placed into the appropriate boat number category. This fragmentation reduced the degree of autocorrelation to $P = <0.05$ and minimised pseudoreplication. Additionally, schools could not be used as the sampling unit because the fission-fusion nature of dolphin schools meant the composition of individual dolphins within a school varied from day to day. The statistical model used was the CATMOD procedure (SAS, 1996) which compared the proportions of all behavioural states for a variety of factors (see below for details of specific models) using a maximum likelihood estimator and incorporating a test of autocorrelation [AR(1)]. All statistical tests used a significance level of $\leqslant 0.05$.

The number of boats encountering the dolphins was recorded as 1, 2, 3, and 4+, where '1' was the research boat. The category of 4+ boats was in consideration of the Marine Mammals Protection Regulations (1992), which allows no more than three vessels within 300 m of a school of dolphins. Dolphin school sizes were recorded using four categories; 2–10, 11–20, 21–30, and 31–50 dolphins. To avoid potential confounding factors (Hurlbert, 1984) due to temporal changes in the dolphins' habitat use (Constantine, 1995, 2002), each season was analysed separately.

2.2.2. Number and type of boats

Changes in the dolphins' behaviour due to the number of boats, type of boat (i.e., research, permitted, and non-permitted boats), season, and school size were tested using the CATMOD procedure (SAS, 1996). From this model a Chi-squared approximation was used to estimate the probability for each factor in the model. The model included an interaction term (school size×number of boats). *A priori* comparisons of the research boat vs. all others were performed for all seasons to determine whether observations when the research boat was the only boat present were significantly different to when other boats were present. *A priori* comparisons were also performed for permitted vs. non-permitted boats. Data collected when there was a combination of permitted and non-permitted boats were not included in the analysis.

2.2.3. Discrete vs staggered tours

During the research period there was an increase in the number of permitted dolphin-watching tours and a corresponding change in their departure times from discrete departures (i.e., three boats leaving at 0800 and 1230 and one boat leaving at 1000) to staggered departures (i.e., two boats leaving at 0800, two at 0900, two at 1000, two at 1230, one at 1300, and one at 1330). The effect of the discrete vs. staggered departures on dolphin behaviour for summer and autumn was tested using CATMOD (SAS, 1996). Summer and autumn were the only seasons with sample sizes that allowed statistical analyses. The full model used in the analysis included 'school size' and 'number of boats' and the interaction term.

3. Results

3.1. Sample size

Between December 1996 and February 2000, 261 hours were spent observing dolphins during 55 focal-school follows. Only one school was followed per day. The average focal-follow lasted 4 h 43 min (SE = 13.79 min, range = 1–7 h 45 min) and a total of 7595 2-min scan samples were collected. Sample sizes for the four school-size categories were: 2–10 ($n = 17$), 11–20 ($n = 20$), 21–30 ($n = 8$), and 31–50 ($n = 10$). Dolphins were accompanied by boats in addition to the research boat in 58% of scans ($n = 4403$).

3.2. Number of boats

Comparisons of dolphin behaviour in the presence of the research boat vs. all other boats showed a significant difference for all seasons (Table 1). This suggests the research boat could be considered as a suitable observation platform to contrast behaviour in the presence of boats other than a carefully driven research boat. This does not suggest that the research boat itself had no impact (Nowacek et al., 2001) but that measured changes occurred over and above the effect of the research boat.

Dolphin behaviour varied significantly with school size and the number of boats present for all seasons (Table 2). Examination of the predicted values for the categorical responses showed the behavioural state most affected by boat number was resting (Fig. 1). The trend was for resting behaviour to decrease with increasing numbers of boats, especially for the commonly observed schools of 2–10 and 11–20 dolphins. Resting behaviour was most often observed in the presence of the research boat (67.8% out of 837) and rarely observed when there were more than three boats present (0.5% out of 837). Milling behaviour generally increased in frequency with increasing numbers of boats across all seasons. Milling was most frequently observed whenever three or more boats were present (46.4% out of 1088) and declined when the research boat was the only boat present (28.4% out of 1088).

Table 1
Analysis of contrasts of dolphin behaviour in the presence of the research boat vs all other boats by season

Season	χ^2	d.f.	P	2-min samples
Summer	28.96	7	0.0001	3086
Autumn	16.00	7	0.0251	2530
Winter	18.08	7	0.0116	1393
Spring	38.43	7	<0.0000	586

3.3. Type of boat

There were significant changes in dolphin behaviour due to the presence of permitted dolphin-watching boats vs. non-permitted boats in summer ($\chi^2_7 = 64.24$, $P < 0.000$), autumn (for school size 2–10 dolphins

Table 2
Analysis of behaviour by season for boat number. The interaction terms were not significant for winter and spring, hence a main effects model was used

	Summer			Autumn			Winter			Spring		
2-min samples	3086			2530			1393			586		
Number of schools	22			19			9			5		
Effect	χ^2	d.f.	P	χ^2	d.f.	P	χ^2	d.f.	P	χ^2	d.f.	P
School size	217.98	7	<0.0001	78.48	21	<0.0001	38.04	7	<0.0001	33.70	7	<0.0001
Boat number	94.24	21	<0.0001	77.84	21	<0.0001	87.19	21	<0.0001	62.76	21	<0.0001
Interaction	119.20	63	<0.0001	149.44	63	<0.0001						

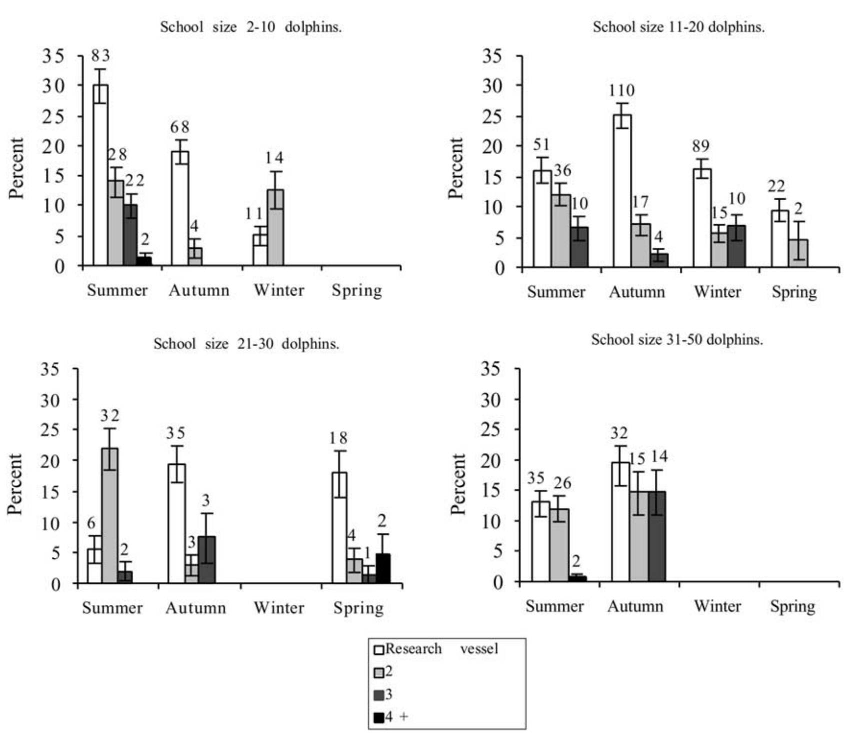

Fig. 1. Resting behaviour by number of boats and season for different school sizes. *N* values above error bars.

$\chi^2_7 = 22.35$, $P < 0.002$) and spring ($\chi^2_7 = 15.93$, $P = 0.026$). There was no significant difference in winter ($\chi^2_7 = 11.89$, $P = 0.104$). In summer, the busiest season for all types of boats, there was significantly less resting behaviour, and significantly more milling behaviour when the permitted dolphin-watching boats were present (Fig. 2).

3.4. Discrete vs staggered departures

The change in departure times, and increased number of permitted dolphin-watching boats, resulted in a 54 min increase in the amount of time the dolphins were accompanied by one or more permitted dolphin-watching boats per survey (discrete— =98 min ± SE 10.4 min, staggered— =152 min ± SE 11.3 min, two-tailed $t_{49} = 3.529$, $P = 0.0009$). As expected, the number of scans where there was one or more permitted operators present also increased from 36.8% ($n = 1417$) of scans for discrete departures to 45.0% ($n = 1743$) for staggered departures.

There was a highly significant difference in dolphin behaviour between discrete vs. staggered departures in summer ($\chi^2_7 = 70.80$, $P < 0.000$) but not in autumn ($\chi^2_7 = 11.51$, $P = 0.118$). Examination of the predicted values showed the behavioural states most affected by boat number in summer were resting, milling, travelling, and foraging.

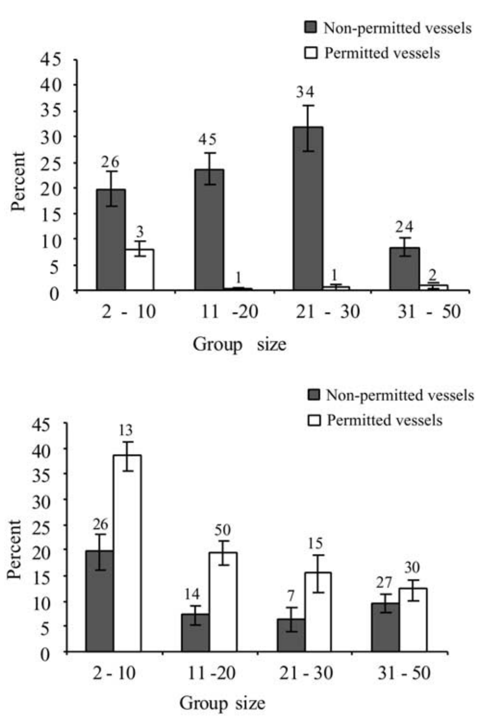

Fig. 2. Resting (top) and milling (bottom) behaviour with non-permitted vs. permitted boats by school size in summer. N values above error bars.

4. Discussion

Few countries have legislation to protect cetaceans from human disturbance. Whether the law in New Zealand is effective at protecting bottlenose dolphins from disturbance by differing numbers and types of boats has not been described elsewhere. The present study indicates that the behaviour of this isolated population of 400–500 bottlenose dolphins was affected by boat interactions. This varied with season and school size, but in all cases where there were significant differences, the frequencies or duration of resting and milling behaviours, in particular, were different. Dolphin behaviour was affected by the number of boats present and the type of boat. Their behaviour was also affected by an increase in the number of permitted operators and a change in departure times, but because these changes occurred simultaneously it is not known whether one of these factors affected the dolphins' behaviour more than the other or if there was a cumulative effect. Bottlenose dolphins were accompanied by between one and 20 boats, other than the research boat, during the 260 h of focal-school observations (Constantine, 2002). In particular, the data indicated the permitted boats had an impact above other boat types.

Eleven percent of all behaviour observed during the study was resting behaviour. This is similar to the 8–10% reported for the bottlenose dolphins in the Gulf of California, Mexico (Ballance, 1992) and 11–12% reported for the Doubtful Sound, New Zealand population (Schneider, 1999; Lusseau, 2003), but considerably lower than the 2% reported for the population in the Shannon Estuary, Ireland (Ingram, 2000) and 0.2% reported for the population in the Sado Estuary, Portugal (Harzen, 1998). The research sites in Ireland and Portugal have strong tidal currents and appear to be important areas for foraging and therefore probably do not provide an ideal habitat for resting. This may explain the lower rate of resting behaviour reported in these areas. In the present study, resting was observed during 69% of the scans when the research boat was the only boat present. The amount of resting decreased significantly with an increase in the number of boats. Resting was observed during only 0.5% of the observations when there were more than three boats associated with a school. It appears that resting behaviour was more likely to decrease for smaller schools of dolphins (i.e., 2–20 dolphins) in the presence of boats than for larger schools. With the majority (79.6% out of 201) of schools encountered during the study containing between 2 and 20 individuals, and the fact that there was usually only a single school of bottlenose dolphins in the Bay of Islands on any day (Constantine, 2002), disturbance to resting behaviour is likely to have affected the majority of schools.

A reduction in resting behaviour due to human disturbance has been observed in other studies. Lusseau (2003) found that the bottlenose dolphins in Fiordland, New Zealand substantially decreased their resting and socialising bouts in the presence of boats. He observed only 1% resting behaviour in the presence of boats other than the research boat, in contrast to 11% resting behaviour when the research boat was the only boat present. Duschene et al. (2000) found caribou (*Rangifer tarandus caribou*) were more vigilant in the presence of tourists and this resulted in a reduction of time spent resting and foraging. In a study on Amur tigers (*Panthera tigris altaica*), Kerley et al. (2002) found a decrease in foraging efficiency by tigers when disturbed by humans at kill sites. They suggested that tigers that were able to remain at kill sites expended less energy than those disturbed, and that this possibly resulted in an increase in energetic demands because tigers forced to eat less from each kill would spend more time hunting and less time resting. Harp seal pups (*Phoca groenlandica*) spent less time resting when disturbed by tourists and their mothers spent more time vigilant and less time suckling their pups in the presence of tourists (Kovacs and Innes, 1990). Harbor seals (*Phoca vitulina*) disturbed by boats when hauled out rested less than undisturbed seals, and there was an increase in seals entering the water when disturbed and then being reluctant to haul out again (Henry and Hammill, 2001). Disturbance of howler monkeys (*Alouatta pigra*) by tourists often elicited a vocal response involving bouts of roaring that was often followed by resting behaviour when the disturbance ceased. Roaring also frequently lead to inter-group conflict that increased the potential for aggression and injury (Grossberg et al., 2003). Whether the reduction in, or disturbance of, resting behaviour discussed in these studies had an energetic, reproductive or survival cost is unknown.

Resting is a fundamentally important behavioural state to the health of many species of animal. Bishop (1999) found that the heartbeat frequency that affects metabolic rate is considerably lower when birds and mammals are resting than when they are active. The effects of a reduction in resting behaviour shown in the present study are unknown but studies on birds and other mammal species have demonstrated physiological stress. Studies on free-ranging bighorn sheep (Macarthur et al., 1979) found that energy expenditure increased when they were exposed to human activity. Tietje and Ruff (1980) found that black bears (*Ursus americanus*) sometimes abandoned their dens in response to human approach and that this disturbance resulted in greater overwinter weight loss than non-disturbed bears. Fowler (1999) found Magellanic penguins (*Spheniscus magellanicus*) that were unfamiliar or infrequently exposed to humans had higher stress levels than penguins habituated to human presence. Adelie penguins (*Pygoscelis adeliae*) increased their heart rate when disturbed by humans and helicopters and it was found that disturbed birds had a lower breeding success than undisturbed birds (Culik et al., 1990). A reduction in rest is likely to result in a reduction of energy reserves, which could affect foraging efficiency, vigilance levels, and the level of parental care.

The synchronization of behaviours such as resting and foraging are thought to be important for group cohesion and that groups benefit through optimising care of offspring, anti-predator defence and increasing efficiency in exploiting food resources (Clark and Mangel, 1986; Emlen, 1991). It also can incur a cost to the individual in a social group but is necessary for maintaining social group cohesion (Conradt and Roper, 2000).

Synchronous behaviour is poorly understood in bottlenose dolphins but a recent study in the Moray Firth, Scotland showed that changes in synchronous surfacing in the presence of boat traffic may be detrimental to the population as it precludes them from engaging in other behaviours, e.g., foraging (Hastie et al., 2003).

The permitted operators spent an average of 57.5 minutes interacting with dolphins (Constantine, 2002). This was considerably more than the time spent with dolphins by other types of boats (i.e., 6.8–9.3 min for non-permitted boats, unpublished data). Because dolphin-watching boats usually operate in a manner different to other boats in order to maintain contact with the dolphins, similar prolonged encounters have been reported elsewhere. Janik and Thompson (1996) found the dolphin-watching boat in the Moray Firth, Scotland accounted for 64% of all interactions observed, despite a number of other boats using the area. Like the Bay of Islands, the dolphin population of the Moray Firth have been exposed to frequent boat traffic for many years, but boats historically did not follow the dolphins (Janik and Thompson, 1996). With permitted operators contributing the major boat presence for the population of dolphins in the present study (up to 70 trips per week), the difference in boat manoeuvring and duration of contact are likely to explain the dolphins' behavioural differences around the permitted boats. This finding needs to be considered independently of the effect of other types of boat.

The issuing of further permits allowed an extra 21 dolphin-watching tours to be conducted per week by the end of 1998. This change in permits provided an opportunity to collect data on the implications of increased dolphin-watching tours. The increased number of tours resulted in an increase in the amount of time the focal school was accompanied by permitted operators. It also caused an overlap between the tour-boats. Subsequently, there was a further decrease in resting behaviour when the operators changed from discrete to staggered departures. The consistent response of dolphins to the presence of permitted boats in the

Bay of Islands over the research period suggests that this population, despite frequent contact, have not habituated to these tours.

Research on other populations of dolphins exposed to increased levels of boat traffic has indicated corresponding behavioural changes. Land-based studies showed a decrease in aerial behaviours by spinner dolphins, *Stenella longirostris*, when boats were present (Forest, 2001; Ross, 2001). Forest (2001) also reported disruption to resting behaviours. Wells (1993) reported a significant increase in the number of bottlenose dolphins that used deep-water channels when there were high levels of boat traffic. These findings were supported by Allen and Read (2000), who found a shift in habitat preference in a population that had high levels of boat disturbance on weekends, compared to a population in a similar area but with no change in boat disturbance. Changes in behaviour with increased levels of human disturbance have been observed in other species of mammal, e.g., humpback whales, *Megaptera novaeangliae*, (Corkeron, 1995), chimpanzees (Johns, 1996), elephants, *Loxodonta africana*, (Andersen and Eltringham, 1997), and rhinoceros, *Rhinoceros unicornis* (Lott and McCoy, 1995). Just like dolphin-watching boats, these tours tried to approach the animals to observe them closely. Chronic disturbance to populations can cause behavioural changes, or even a population decline, that may persist several years after the disturbance has ceased [e.g., primates (Chapman et al., 2000) and dolphins (Heckel et al., 2000)]. In some cases human disturbance may cause animals to abandon or not use ideal habitat thereby potentially increasing the risk of mortality to their offspring, e.g., southern fur seals (*Arctocephalus australis*) (Stevens and Boness, 2003).

Currently the effects of boats (in particular permitted boats) on dolphin resting and milling behaviour in the Bay of Islands, are substantial. We therefore conclude that the implementation of the Marine Mammals Protection Act (1978) in the Bay of Islands is not affording the dolphins' sufficient protection from disturbance. A recent study found that over a period of five years, this population became sensitised to swim attempts from commercial swim-with-dolphin boats and increased their avoidance of swimmers (Constantine, 2001). It may be that research on this population in the future will show detrimental changes to this population's use of the Bay of Islands (as seen in Florida; Wells, 1993; Allen and Read, 2000), or to their behaviour around the permitted boats. The data reported here could be used to implement precautionary management schemes that take into account the potential long-term, cumulative effects of disturbance on this isolated population (Mangel et al., 1996; Yaffee, 1997). By restricting the number of trips, trip duration, and reducing the amount of time dolphins are exposed to tour-boats, these impacts would be minimised.

The challenges associated with understanding changes in the behaviour of complex social animals such as bottlenose dolphins are compounded by the need to produce effective management reform within a short time-frame. Ongoing evaluation of changes in population size, range, and habitat use is vital. Because bottlenose dolphins are frequently exposed to tourism, and the fact that this industry is growing rapidly, the need to understand detrimental changes in their behaviour and habitat use is important for understanding the effects of tourism on the long-term viability of the population. During the present study permits were issued in five other areas of this populations range. The effects of tourism on this population when outside the Bay of Islands are currently unknown but the potential for a cumulative effect from human disturbance is of concern.

The Bay of Islands forms an important part of the isolated study populations' range, with a high resight rate of individuals (Constantine, 2002). Consequently, the dolphins are unlikely to suddenly discontinue use of the area, even though they face increased human disturbance. Many factors affect animals' habitat use decisions, including proximity of equally high-quality sites, relative risk of predation, and density of competitors (Gill et al., 2001). In long-lived, slow-breeding species, such as bottlenose dolphins, the long-term effects of reduced resting behaviour on fitness, individual reproductive success and hence, population size, could take over 30 years to detect (Wilson et al., 1999, Thompson et al., 2000).

Acknowledgements

We thank Allen Rodrigo for statistical advice and C. Scott Baker and Simon Ingram for valuable comments on the manuscript. Many thanks to Nick Gales and Bernd Würsig for helpful discussions about this study. This research was generously funded through grants to R.C. by the Marine Mammal Trust Fund—Department of Conservation Northland, International Society for Marine Mammalogy—Emily B. Shane Award, Whale and Dolphin Conservation Society, Cetacean Society International, Whale and Dolphin Adoption Project, New Zealand Lotteries Grant Board, and the University of Auckland Post-Graduate Research Grant. Thanks to Jo Berghan, Noel Henry and Alan Fleming for assistance in the field. Many thanks to Dolphin Discoveries, Fullers Northland, Heritage Tours and Kings Tours, who were very supportive of this research. This manuscript was improved by the comments of two anonymous reviewers.

References

Allen, M.C., Read, A.J., 2000. Habitat selection of foraging bottlenose dolphins in relation to boat density near Clearwater, Florida. Marine Mammal Science 16, 81–824.

Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour 49, 227–267.

Andersen, K.F., Eltringham, S.K., 1997. Some preliminary observations on possible stress in the elephants of Mikumi National Park, Tanzania. African Journal of Ecology 35, 278–282.

Ballance, L.T., 1992. Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, Mexico. Marine Mammal Science 8, 262–274.

Beach, D.W., Weinrich, M.T., 1989. Watching the whales. Oceanus 32, 84–88.

Bejder, L., Dawson, S.M., Harraway, J.A., 1999. Responses by Hector's dolphins to boats and swimmers in Porpoise Bay, New Zealand. Marine Mammal Science 15, 738–750.

Bishop, C.M., 1999. The maximum oxygen consumption and aerobic scope of birds and mammals: getting to the heart of the matter. Proceedings of the Royal Society London B 266, 2275–2281.

Bräger, S., Schneider, K., 1998. Near-shore distribution and abundance of dolphins along the West Coast of the South Island, New Zealand. New Zealand Journal of Marine & Freshwater Research 32, 105–112.

Chapman, C.A., Balcomb, S.R., Gillespie, T.R., Skorupa, J.P., Struhsaker, T.T., 2000. Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. Conservation Biology 14, 207–217.

Clark, C.W., Mangel, M., 1986. The evolutionary advantages of group foraging. Theoretical Population Biology 30, 45–75.

Connor, R.C., Mann, J., Tyack, P.L., Whitehead, H., 1998. Social evolution in toothed whales. Trends in Ecology and Evolution 13, 228–232.

Connor, R.C., Wells, R.S., Mann, J., Read, A.J., 2000. The bottlenose dolphin: social relationships in a fission-fusion society. In: Mann, J., Connor, R.C., Tyack, P.L., Whitehead, H. (Eds.), Cetacean Societies: Field Studies of Dolphins and Whales. The University of Chicago Press, Chicago, pp. 91–126.

Conradt, L., Roper, T.J., 2000. Activity synchrony and social cohesion: a fission-fusion model. Proceedings of the Royal Society, London 267, 2213–2218.

Constantine, R., 1995. Monitoring the Commercial Swim-With-Dolphin Operations with the Bottlenose (*Tursiops truncatus*) and Common Dolphins (*Delphinus delphis*) in the Bay of Islands, New Zealand. MSc thesis. University of Auckland, Auckland, New Zealand.

Constantine, R., 2001. Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism. Marine Mammal Science 17, 689–702.

Constantine, R., 2002. The Behavioural Ecology of the Bottlenose Dolphins (*Tursiops truncatus*) of Northeastern New Zealand: A Population Exposed to Tourism. PhD thesis. University of Auckland, Auckland, New Zealand.

Corkeron, P.J., 1995. Humpback whales (*Megaptera novaeangliae*) in Hervey Bay, Queensland: behaviour and responses to whale-watching vessels. Canadian Journal of Zoology 73, 1290–1299.

Culik, B., Adelung, D., Woakes, A.J., 1990. The effect of disturbance on the heart rate and behaviour of Adelie penguins (*Pygoscelis adeliae*) during the breeding season. In: Kerry, K.R., Hempel, G. (Eds.), Antarctic Ecosystems: Ecological Change and Conservation. Springer-Verlag, Berlin, pp. 177–182.

Duchesne, M., Cote, S.D., Barrette, C., 2000. Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. Biological Conservation 96, 311–317.

Duffus, D.A., Dearden, P., 1993. Recreational use, valuation, and management, of killer whales (*Orcinus orca*) on Canada's Pacific coast. Environmental Conservation 20, 149–156.

Emlen, S.T., 1991. Evolution of cooperative breeding in birds and mammals. In: Krebs, J.R., Davies, N.B. (Eds.), Behavioural Ecology: An Evolutionary Approach. Blackwell Scientific Publications, UK, pp. 301–337.

Forest, A.M., 2001. The Hawai'ian Spinner Dolphin, *Stenella longirostris*: Effects of Tourism. MSc thesis. Texas A&M University, College Station, USA.

Fossey, D., 1972. Vocalizations of the mountain gorilla (*Gorilla gorilla beringei*). Animal Behaviour 20, 36–53.

Fowler, G.S., 1999. Behavioral and hormonal responses of Magellanic penguins (*Spheniscus magellanicus*) to tourism and nest site visitation. Biological Conservation 90, 143–149.

Giannecchini, J., 1993. Ecotourism: new partners, new relationships. Conservation Biology 7, 429–432.

Gill, J.A., Norris, K., Sutherland, W.J., 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation 97, 265–268.

Grossberg, R., Treves, A., Naughton-Treves, L., 2003. The incidental ecotourist: measuring visitor impacts on endangered howler monkeys at a Belizean archaeological site. Environmental Conservation 30, 40–51.

Harzen, S., 1998. Habitat use by the bottlenose dolphin (*Tursiops truncatus*) in the Sado Estuary, Portugal. Aquatic Mammals 24, 117–128.

Hastie, G.D., Wilson, B., Tufft, L.H., Thompson, P.M., 2003. Bottlenose dolphins increase breathing synchrony in response to boat traffic. Marine Mammal Science 19, 74–84.

Heckel, G., Murphy, K.E., Jimenez Compean, G.A., 2000. Evasive behavior of spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*) during fishing for yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. Fisheries Bulletin 98, 692–703.

Henry, E., Hammill, M.O., 2001. Impact of small boats on the haulout activity of harbour seals (*Phoca vitulina*) in Metis Bay, Saint Lawrence Estuary, Quebec, Canada. Aquatic Mammals 27, 140–148.

Hoyt, E., 2001. Whale Watching 2001: Worldwide Tourism Numbers, Expenditures, and Expanding Socioeconomic Benefits. International Fund for Animal Welfare, Yarmouth Port, MA, USA. ISBN: 1-901002-09-8.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54, 187–211.

Ingram, S.N., 2000. The Ecology and Conservation of Bottlenose Dolphins in the Shannon Estuary, Ireland. PhD thesis. University College Cork, Cork, Ireland.

Irvine, A.B., Scott, M.D., Wells, R.S., Kaufmann, J.H., 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. Fisheries Bulletin 79, 671–688.

Janik, V.M., Thompson, P.M., 1996. Changes in surfacing patterns of bottlenose dolphins in response to boat traffic. Marine Mammal Science 12, 597–602.

Johns, B.G., 1996. Responses of chimpanzees to habituation and tourism in the Kibale Forest, Uganda. Biological Conservation 78, 257–262.

Jones, M.L., Swartz, S.L., 1984. Demography and phenology of gray whales and evaluation of whale-watching activities in Laguna San Ignacio, Baja California Sur, Mexico. In: Swartz, S.L., Leatherwood, S. (Eds.), The Gray Whale. Academic Press, Orlando, Florida, pp. 309–374.

Kerley, L.L., Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Quigley, H.B., Hornocker, M.G., 2002. Effects of roads and human disturbance on Amur tigers. Conservation Biology 16, 97–108.

Kovacs, K.M., Innes, S., 1990. The impact of tourism on harp seals (*Phoca groenlandica*) in the Gulf of St. Lawrence, Canada. Applied Animal Behaviour Science 26, 15–26.

Lott, D.F., McCoy, M., 1995. Asian rhinos *Rhinoceros unicornis* on the run? Impact of tourist visits on one population. Biological Conservation 73, 23–26.

Lusseau, D., 2003. How do tour boats affect the behavioral state of bottlenose dolphins (*Tursiops* sp.)? Applying Markov chain modeling to the field study of behavior. Conservation Biology 17, 1785–1793.

MacArthur, R.A., Johnston, R.H., Geist, V., 1979. Factors influencing heart rate in free-ranging bighorn sheep: a physiological approach to the study of wildlife harassment. Canadian Journal of Zoology 57, 2010–2021.

Mangel, M., Talbot, L.M., Meffe, G.K., Agardy, M.T., Alverson, D.L., Barlow, J., Botkin, D.B., Budowski, G., Clark, T., Cooke, J., Crozier, R.H., Dayton, P.K., Elder, D.L., Fowler, C.W., Funtowicz, S., Giske, J., Hofman, R.J., Holt, S.J., Kellert, S.R., Kimball, L.A., Ludwig, D., Magnusson, K., Malayang, B.S., Mann, C., Norse, E.A., Northridge, S.P., Perrin, W.F., Perrings, C., Peterman, R.M., Rabb, G.B., Regier, H.A., Reynolds, J.E., Sherman, K., Sissenwine, M.P., Smith, T.D., Starfield, A., Taylor, R.J., Tillman, M.F., Toft, C., Twiss, J.R., Wilen, J., Young, T.P., 1996. Principles for the conservation of wild living resources. Ecological Applications 6, 338–362.

Mann, J., 1999. Behavioral sampling methods for cetaceans: a review and critique. Marine Mammal Science 15, 102–122.

Miller, M.L., 1993. The rise of coastal and marine tourism. Ocean and Coastal Management 20, 181–199.

Nowacek, S.M., 1999. The effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. MS thesis University of California Santa Cruz, California, USA.

Nowacek, S.M., Wells, R.S., Solow, A.R., 2001. Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. Marine Mammal Science 17, 673–688.

Orams, M.B., 1995. Using interpretation to manage nature-based tourism. Journal of Sustainable Tourism 4, 81–94.

Ross, G.L., 2001. Response of Hawaiian Spinner Dolphins to Boat Presence in Midway Atoll. MA thesis. San Francisco State University, San Francisco, USA.

Samuels, A., Bejder, L., Constantine, R., Heinrich, S., 2003. A review of swimming with wild cetaceans with a special focus on the Southern Hemisphere. In: Gales, N., Hindell, M., Kirkwood, R., (Eds.), Marine Mammals and Humans: Towards a Sustainable Balance. CSIRO Publishing, Collingwood, Australia.

SAS, 1996. The SAS System for Windows. SAS Institute Inc, Cary, North Carolina.

Schneider, K., 1999. Behaviour and Ecology of Bottlenose Dolphins in Doubtful Sound, Fiordland, New Zealand. PhD thesis. University of Otago, Dunedin, New Zealand.

Shane, S., Wells, R.S., Würsig, B., 1986. Ecology, behavior and social organization of the bottlenose dolphin: a review. Marine Mammal Science 2, 34–63.

Stevens, M.A., Boness, D.J., 2003. Influences of habitat features and human disturbance on use of breeding sites by a declining population of southern fur seals (*Arctocephalus australis*). Journal of Zoology, London 260, 145–152.

Thompson, P.M., Wilson, B., Grellier, K., Hammond, P., 2000. Combining power analysis and population viability analysis to compare traditional and precautionary approaches to conservation of coastal cetaceans. Conservation Biology 14, 1253–1263.

Tietje, W.D., Ruff, R.L., 1980. Denning behavior of black bears in boreal forest of Alberta. Journal of Wildlife Management 44, 858–870.

Wells, R. S., 1993. The marine mammals of Sarasota Bay. In: Sarasota Bay: 1992 Framework for Action. Sarasota Bay National Estuary Program, Sarasota, Florida, pp. 9.1–9.23.

Wells, R.S., Scott, M.D., Irvine, A.B., 1987. The social structure of free-ranging bottlenose dolphins. In: Genoways, H.H. (Ed.), Current Mammalogy, Vol. 1. Plenum Press, New York, pp. 247–305.

Williams, R., Trites, A.W., Bain, D.E., 2002. Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental approaches. Journal of Zoology, London 256, 255–270.

Wilson, B., Hammond, P.S., Thompson, P.M., 1999. Estimating size and assessing trends on a coastal bottlenose dolphin population. Ecological Applications 9, 288–300.

Yaffee, S.L., 1997. Why environmental policy nightmares recur. Conservation Biology 11, 328–337.