
Decline in Relative Abundance of Bottlenose Dolphins Exposed to Long-Term Disturbance

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Abstract: *Studies evaluating effects of human activity on wildlife typically emphasize short-term behavioral responses from which it is difficult to infer biological significance or formulate plans to mitigate harmful impacts. Based on decades of detailed behavioral records, we evaluated long-term impacts of vessel activity on bottlenose dolphins (*Tursiops sp.*) in Shark Bay, Australia. We compared dolphin abundance within adjacent 36-km² tourism and control sites, over three consecutive 4.5-year periods wherein research activity was relatively constant but tourism levels increased from zero, to one, to two dolphin-watching operators. A nonlinear logistic model demonstrated that there was no difference in dolphin abundance between periods with no tourism and periods in which one operator offered tours. As the number of tour operators increased to two, there was a significant average decline in dolphin abundance (14.9%; 95% CI = -20.8 to -8.23), approximating a decline of one per seven individuals. Concurrently, within the control site, the average increase in dolphin abundance was not significant (8.5%; 95% CI = -4.0 to +16.7). Given the substantially greater presence and proximity of tour vessels to dolphins relative to research vessels, tour-vessel activity contributed more to declining dolphin numbers within the tourism site than research vessels. Although this trend may not jeopardize the large, genetically diverse dolphin population of Shark Bay, the decline is unlikely to be sustainable for local dolphin tourism. A similar decline would be devastating for small, closed, resident, or endangered cetacean populations. The substantial effect of tour vessels on dolphin abundance in a region of low-level tourism calls into question the presumption that dolphin-watching tourism is benign.*

Keywords: cetacean, human disturbance, *Tursiops sp.*, whale, wildlife management, wildlife tourism

Declinación de la Abundancia Relativa de Delfines Expuestos a Perturbaciones de Largo Plazo

Resumen: *Los estudios que evalúan los efectos de la actividad humana sobre la vida silvestre generalmente enfatizan respuestas conductuales de corto plazo a partir de las cuales es difícil inferir un significado biológico o formular planes para mitigar los efectos perjudiciales. Con base en décadas de registros, evaluamos los impactos de largo plazo de la actividad de embarcaciones sobre delfines (*Tursiops sp.*) en la Bahía Shark, Australia. Comparamos la abundancia de delfines en dos sitios (de turismo y control) adyacentes de 32 km².*

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a lo largo de tres períodos consecutivos de 4.5 años en los que la actividad de investigación fue relativamente constante pero los niveles de turismo incrementaron de cero, a uno y a dos operadores de observación de ballenas. Un modelo logístico no lineal demostró que no había diferencia en la abundancia de delfines entre períodos sin turismo y en períodos en los que un operador ofrecía excursiones. Cuando el número de operadores incrementó a dos, hubo una declinación significativa en la abundancia promedio de delfines (14.9%; 95% IC = -20.8 a -8.23), cercana a la declinación de unos de cada siete individuos. Al mismo tiempo, dentro del sitio control, el incremento en la abundancia promedio no fue significativa (8.5%; 95% IC = -4.0 a $+16.7$). Debido a la substancialmente mayor presencia y proximidad de embarcaciones turísticas en relación con embarcaciones de investigación, la actividad de embarcaciones turísticas contribuyó más que las de la investigación a la declinación en el número de delfines en el sitio de turismo. Aunque puede que esta tendencia no ponga en peligro a la población de delfines, grande y genéticamente diversa, de la Bahía de Shark, la declinación probablemente no es sustentable para el turismo de delfines local. Una declinación similar sería devastadora para poblaciones de cetáceos pequeñas, cerradas, residentes o en peligro. El considerable efecto de las embarcaciones turísticas sobre la abundancia de delfines en una región de turismo de bajo nivel cuestiona la suposición de que el turismo de observación de delfines es benéfico.

Palabras Clave: ballena, cetáceo, gestión de vida silvestre, perturbación humana, turismo de vida silvestre, *Tursiops* sp.

Introduction

Studies to detect and mitigate threats of human activity on wildlife usually need to produce time-sensitive information in crisis situations. With insufficient resources, time, and background information, these investigations typically emphasize readily obtainable, short-term behavioral measures that can be directly related to disturbance factors (e.g., de la Torre et al. 2000; Duchesne et al. 2000; Lacy & Martins 2003). Unfortunately, it is seldom possible to infer biological significance based on short-term behavioral change. It is rarely known whether, and in what ways, short-term responses translate to longer-term change in reproduction, survival, or population size (e.g., Gill et al. 2001; Beale & Monaghan 2004a). Moreover, traditional interpretations of behavioral change in response to disturbance have been questioned recently (e.g., Nisbet 2000; Gill et al. 2001; Beale & Monaghan 2004b; Bejder et al. in press). For example, animals demonstrating the strongest responses are not necessarily those most vulnerable to disturbance (e.g., Creel et al. 2002; Stillman & Goss-Custard 2002; Beale & Monaghan 2004b). These uncertainties challenge the utility of conventional impact assessment research to identify valid indicators of disturbance and accurately inform wildlife management.

The same problems complicate efforts to interpret impacts of wildlife tourism. Cetacean (whale, dolphin, and porpoise) watching is a growing form of wildlife tourism, targeting at least 56 (including endangered and threatened) species in all oceans and involving more than US\$1 billion and 9 million people/year (Hoyt 2001; Samuels et al. 2003). Cetacean-watching tourism is commonly presented as a benign alternative to whaling (e.g., Hoyt 1993) that enhances public attitudes toward the marine environment (e.g., Orams 1997) and bolsters local economies (e.g., Hoyt 2001). Nevertheless, given the na-

ture of this tourism—such that specific cetacean communities in small, coastal ranges are repeatedly sought for prolonged, close-up encounters—there exists a considerable potential for harmful consequences for targeted animals. Impact assessment for cetaceans typically emphasizes immediate behavioral responses to human activity (e.g., Bejder et al. 1999; Constantine et al. 2004; Samuels & Bejder 2004), the biological relevance of which is rarely known (Corkeron 2004).

Based on one of the best-studied cetacean populations—the Indo-Pacific bottlenose dolphins (*Tursiops* sp.) of Shark Bay, Australia—we documented a long-term response to dolphin-watching tourism. The unique, longitudinal behavioral database enabled us to use a treatment-control experimental design. Given the scarcity of studies with adequate controls or longevity to fully evaluate tourism impacts, we suggest that management deliberations draw strong inference from the few well-documented sites, such as Shark Bay, where pre- and post-tourism data on individually known animals can be considered.

Methods

Field Site, Study Population, and Long-Term Database

Shark Bay, Western Australia (26°S, 114°E; Fig. 1), is inhabited by approximately 2700 bottlenose dolphins (Preen et al. 1997). The marine habitat consists of shallow sea grass beds (<4 m), embayment plains, and deeper channels (≤15 m). Dolphin tourism and dolphin research occur in the eastern gulf, based from the resort settlement of Monkey Mia.

Two forms of dolphin tourism occur in Shark Bay. Since the 1960s, several dolphins have received fish handouts from humans at Monkey Mia (Connor & Smolker 1985).

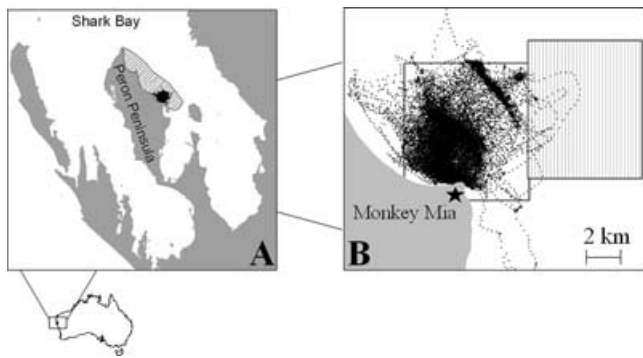


Figure 1. Study site in Western Australia: (a) Shark Bay and Peron Peninsula (hatched area, approximately 300-km² site of long-term dolphin research) and (b) 36-km² tourism site (black dots, tour-vessel movements) and an adjacent control site of equal size (shaded square).

Currently, four adult females are provisioned daily under strict ranger supervision. This phenomenon is the area's main tourist draw, with 100,000 annual visitors, of which 69% come primarily to see dolphins (Reark Research 1995; Western Australian Department of Conservation and Land Management, unpublished data).

Commercial, vessel-based dolphin watching began with one operator in May 1993. A second operation began in August 1998. The two tour vessels are 17 m and 19 m sailing catamarans, with turbo 140 hp and 50 hp twin engines, respectively. Since the arrival of the second operator, eight trips are offered on a near-daily basis.

Dolphin behavioral research began in 1984. Within a 300-km² study area (Fig. 1a), approximately 800 dolphins have been studied through survey and focal-follow techniques conducted from small vessels (4–6 m length; ≤50 hp 2- and 4-stroke outboard engines). In group “survey records” (Mann 1999), individual dolphins were identified by comparing dorsal fin photographs taken at sea with a catalog (Würsig & Jefferson 1990), with group membership defined based on a 10-m “chain rule” (Smolker et al. 1992). A long-term database of survey records yielded individually specific information about dolphins, including age, sex (Smolker et al. 1992; Mann et al. 2000; Krützen et al. 2004a), and distribution. We analyzed data from March 1988 to January 2003.

In surveys dolphin locations were based on the global positioning system (GPS) since June 1994 and previously on compass bearings taken from dolphins to prominent landmarks. When landmarks were later located with GPS, dolphin locations derived from ≥3 bearings could be converted to latitude and longitude with Locate II software (<http://www.npac.nsw.gov.au/envsci/staff/vnams/Locate.htm>). We conducted an independent error assessment to evaluate conversion precision. Distances between locations derived from each method had an average discrepancy

of 260 m ($n = 32$ locations, $SD = 239$ m, $95\% CI = \pm 82.7$). Because dolphin-group locations recorded via GPS had a random error of ≤200 m (due to selective availability applied by the U.S. government through May 2000), conversion accuracy from bearings to latitude and longitude was reasonably close to the usual margin of error for GPS.

Experimental Design

We selected experimental sites based on movements of the tour vessels (Fig. 1b). We defined our tourism site as the 36-km² area wherein the tour vessels operated primarily. We tracked tour-vessel movements at 75-second intervals via automatic GPS downloading during 188, 84, and 100 tour-vessel trips monitored in 2000, 2002, and 2003, respectively (177 and 195 trips per tour vessel). Our control site was an adjacent area of equal size with little activity by research vessels and no activity by tour vessels. The close proximity of tourism and control sites equalized potential influence of environmental factors. No aquaculture sites were included in our study area (e.g., Watson-Capps & Mann 2005).

We selected three consecutive approximately 4.5-year periods based on the temporal pattern with which dolphin-watching licenses were issued. Thus, T0, represented a time period prior to the onset of tourism (March 1988–April 1993); T1 began with issuance of the first dolphin-watching license and encompassed the period in which only one tour vessel was operating (May 1993–July 1998); and T2 began with issuance of the second dolphin-watching license and represented a period in which two tour vessels were operating (August 1998–January 2003). Research activity remained relatively constant throughout the study period.

Dolphin exposure to tour and research vessels was estimated per site and time period, with encounters defined as ≥1 minute spent within 50 m of dolphins. The distance criterion was based on operator license conditions (Western Australian Wildlife Conservation (WAWC) Notice 1998 [Close Season for Marine Mammals]; WAWC Regulations 1970, Regulation 15 Marine Mammal Interaction License).

We calculated dolphin exposure to research vessels directly from the long-term database, based on actual locations and durations of all surveys and follows conducted during the study period. We extrapolated dolphin exposure to tour vessels from the 188 tour-vessel trips monitored in 2000, during which the number, duration, and location of dolphin encounters were recorded. We considered monitored trips representative of each operator's activity throughout all years of operation (D. Charles & H. Raven, personal communication).

We based dolphin abundance measures on individual identification of dolphins from photographic analyses. A total of 21,240 individual dolphin identities (including

Table 1. Number of identified dolphins, including recounts, per site and time period.

Time period*	No. of dolphins (identified as individuals)	
	tourism	control
T0	2714 (90.4%)	42 (71.4%)
T1	6261 (90.7%)	1548 (73.2%)
T2	8863 (94.6%)	1812 (76.3%)

*Abbreviations: T0, before tourism; T1, one tour vessel operating; T2, two tour vessels operating (dates provided in text).

recounts) were obtained from 6008 survey records from both sites (control: $n = 978$; tourism: $n = 5030$) over all time periods (Table 1). There was no statistical difference in proportions of dolphins identified as individuals within sites among periods (chi-squared $p = 0.14$, control; $p = 0.11$, tourism [Table 1]); thus, any observed difference in site abundance among periods cannot be attributed to a difference in our ability to recognize individuals.

Statistical Analyses

For dolphin abundance calculations, we subdivided tourism and control sites into grid squares. Grid-square size was calculated as the smallest scale with an acceptable error margin. Based on 0.2-km random error for GPS dolphin locations (see above), the probability of assigning an animal to an incorrect square was simulated as 19%, 10%, and 5% for 0.5-, 1- and 4-km² squares, respectively. Grid square sizes of 1 and 4 km² yielded acceptable assignment errors (10; 5%) and sample sizes ($n = 36$, 1 × 1 km squares; $n = 9$, 2 × 2 km squares). Both scales were selected for analyses to evaluate potential effect of square size on abundance calculations.

Dolphin abundance was calculated per square per time period. A nonlinear logistic model (Eqs. 1 & 2) related total number of identified individuals to total number of survey records per square per period. The model included a term for changes in abundance (p) per square between time periods. The model was fitted with least-squares estimates, with parameter confidence intervals estimated by bootstrapping on squares (1000 times):

$$y(j, 1) = s(j) \times q \times x(j, 1) / (1 + q \times x(j, 1)) \quad \text{and} \quad (1)$$

$$y(j, 2) = s(j) \times q \times x(j, 2) \times (1 + p) / [1 + q \times x(j, 2)], \quad (2)$$

where the dependent variable $y(j, t)$ is the number of dolphins (y) observed in square j per period t ; $x(j, t)$ is the number of survey records (x) within square j per period t .

The model estimated the following parameters: $s(j)$, number of dolphins using square j in the first of con-

secutive periods; p , proportional change in number of dolphins within a square between consecutive periods (assumed equal for all squares within a given site); q , rate of increase in number of dolphins detected in a square relative to effort (number of survey records) (assumed equal for all squares and periods). We used least squares and maximum likelihood to estimate $s(j)$, q , and p .

Results

Dolphin Exposure to Tour and Research Vessels

Tour vessels were within 50 m of dolphins during an average of 1.86 encounters per trip (SD = 1.07), with mean encounter duration of 10.63 minutes (SD = 7.33 minutes, $n = 188$ monitored trips, 349 encounters). An average of 2.5 and 5.5 (of 4 and 8 possible) trips were conducted daily during T1 and T2, respectively (D. Charles, personal communication).

Based on these measures, we calculated time spent with dolphins by tour vessels as 0, 0.82, and 1.81 hours/day during T0, T1, and T2, respectively, with corresponding values for research vessels within the tourism site as 0.54, 0.41, and 0.77 hours/day (Fig. 2) respectively. Thus, within the tourism site, dolphin exposure to tour vessels increased substantially over the study period, whereas exposure to research vessels remained relatively constant. Time spent with dolphins by all vessels increased by 78.4% from T1 to T2, of which 74.9% was attributed to tour vessels. During T2, tour vessels were with dolphins for 140% more time than research vessels.

Researchers spent little time in the area when not observing dolphins, so the above measures are good approximations of total research-vessel activity within the tourism site. In contrast, tour vessels, which did not travel elsewhere to look for dolphins, were estimated to spend a total of 4.4 and 9.6 hours/day within the tourism site during T1 and T2, respectively. Thus, during T2, overall

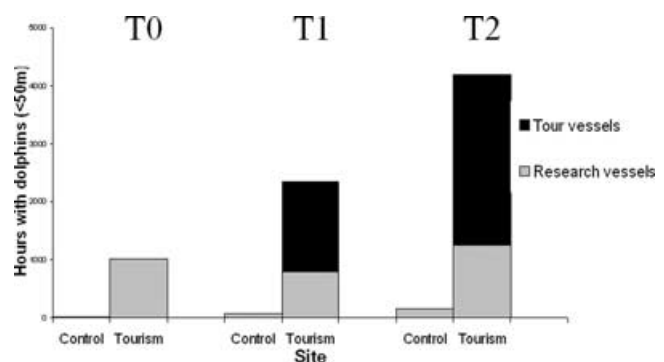


Figure 2. Total time spent within 50 m of dolphins by tour and research vessels in tourism and control sites during the time periods, T0 (pre-tourism), T1 (one tour vessel operating), and T2 (two tour vessels operating).

presence of tour vessels within the tourism site was an order of magnitude greater than that of research vessels.

Within the adjacent control site, tour vessels were never observed within 50 m of dolphins, whereas, research vessels were near dolphins for 0.006, 0.039, and 0.099 hours/day during T0, T1, and T2, respectively (Fig. 2). To put this into perspective, during the period of greatest research activity (T2) research vessels were with dolphins for <6 minutes/day.

Changes in Dolphin Abundance

Comparing periods of no tourism (T0) with periods when there was one tour-vessel operator (T1) within the tourism site, there was no significant difference in dolphin abundance per grid square, regardless of scale used (1 km², 4 km²), although power to detect change was low. As the number of tour operators increased to two (T1 to T2), the average dolphin abundance declined significantly (14.9%/km²; 95% CI = -20.8 to -8.23; Fig. 3). At the larger scale average abundance also declined significantly (18.2%/4 km²; 95% CI = -0.77 to -25.02). Concurrently, within the adjacent control site, increased dolphin abundance was not significant (8.5%/km²; 95% CI = -4.0 to +16.7; Fig. 3). At the larger scale increased abundance was also not significant (2.4%/4 km²; 95% CI = -14.16 to +20.57).

Thus, from T1 to T2, change in dolphin abundance was similar regardless of scale: abundance declined substantially within the tourism site and increased slightly within the adjacent control site. The 4-km² scale yielded a more dramatic decline; however, the corresponding con-

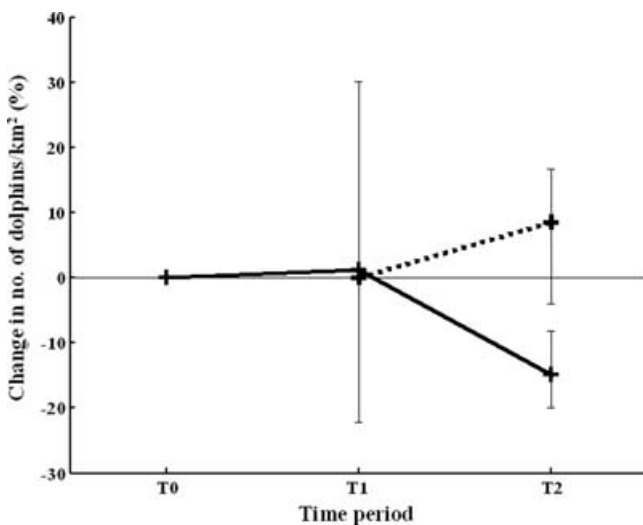


Figure 3. Average percent change in dolphin abundance within tourism (solid) and control (dotted) sites among the time periods, T0 (before tourism), T1 (one tour vessel operating), and T2 (two tour vessels operating). Vertical lines depict 95% confidence intervals.

fidence interval was broader due to the smaller sample of squares. Therefore, subsequent discussion of impacts is based on findings calculated from the more conservative 1-km² scale. Overall, as the number of tour operators increased, there was a concurrent decrease in dolphin abundance within the tourism site, equating to a decline of approximately one in every seven individuals.

Discussion

Relative Contribution of Tour Versus Research Vessels

Dolphin abundance declined within the tourism site during a period of increased exposure to tour vessels but a relatively constant, and substantially lower, exposure to research vessels. During the period of decline, time spent by tour vessels within the tourism site and near dolphins was 10 and 2.4 times greater, respectively, than that of research vessels. Given their substantial presence and proximity to dolphins, tour vessels were considered the primary contributor to declining dolphin abundance.

Vessel size may be a source of disturbance, and larger tour vessels are likely to be more intrusive than research vessels. Engine size and consequent underwater noise may also be a source of disturbance, given cetacean reliance on acoustics for communication, orientation, and predator/prey detection (e.g., Richardson et al. 1995; Tyack 1998). Acoustically, research vessels with their smaller, quieter engines were probably less intrusive than tour vessels, which, although sailing catamarans, were frequently motored and operators shifted gears on average once every 21 seconds when they were near dolphins (Bejder 2000).

Although tour vessels were the principal contributor to declining dolphin abundance, our results draw attention to a dilemma; that is, research that documented the decline necessarily increased the animals' overall exposure to vessels. Disturbance by research vessels is often balanced by enhancements to welfare, management, and conservation of study subjects. Moreover, research vessels may be less invasive than other vessel types (Nowacek et al. 2001; Lusseau 2003; Constantine et al. 2004). Nevertheless, our results highlight a need to carefully weigh costs and benefits of research activity for targeted subjects.

Potential Explanations for Declining Abundance in Response to Disturbance

Within the tourism site, the decline in dolphin abundance was equivalent to a loss of approximately one in every seven individuals. This local decline cannot be attributed to an overall population decline because an opposite trend occurred within the adjacent control site. Neither can the decline be explained by ecological factors, effects of which would be similar in contiguous sites.

At this time we cannot discount possible differences in immigration or mortality between the two sites. There is, however, another potential mechanism: differential recruitment via reproduction (Bejder 2005).

Our findings indicate that the decline is due, at least in part, to the displacement of more sensitive animals away from the area of disturbance. During the period of greatest tour-vessel activity, dolphin abundance declined within the tourism site, whereas dolphin numbers slightly increased in an adjacent region. This suggests a long-term shift in habitat use from an area of high to low vessel traffic.

Habitat shift is a form of avoidance, which occurs on a continuum of temporal and spatial scales. Dolphins may remain in an area of vessel disturbance while responding behaviorally to minimize impacts (e.g., Bejder et al. 1999; Williams et al. 2002; Lusseau 2003). Marine mammals may temporarily move away during periods of heavy vessel activity but reinhabit the same area when traffic is reduced (e.g., Allen & Read 2000; Lusseau 2004), or they may abandon a once-preferred region for as long as disturbance persists (Gerrodette & Gilmartin 1990).

Animals faced with disturbance must evaluate the costs and benefits of relocating to less-disturbed locations, an assessment analogous to decision making under predation risk, wherein the decision is influenced by availability, distance, and quality of suitable habitat elsewhere and the animal's condition and ability to cope or flee (Lima & Dill 1990; Gill et al. 2001; Frid & Dill 2002; Beale & Monaghan 2004a, 2004b). When animals switch from short-term evasive tactics to long-term site avoidance in response to escalating disturbance, costs of tolerance have likely exceeded benefits of remaining in previously preferred habitat. Thus, for Shark Bay dolphins, cumulative vessel activity, with addition of a second tour vessel, may have exceeded tolerance levels of some dolphins, and may have resulted in their long-term displacement away from the disturbance.

For animals such as bottlenose dolphins that exhibit enduring, individually specific social relationships (e.g., Wells et al. 1987; Smolker et al. 1992), disruption of bonds through displacement, based on a continuum of individual tolerance levels, may have far-reaching repercussions. Tracking long-term movements of individuals and identifying the more sensitive age, sex, or reproductive classes and/or social networks within the Shark Bay dolphin community will be crucial to understanding how disturbance affects social structure (e.g., Lusseau & Newman 2004).

Managing Dolphin-Watching Tourism

Protecting Dolphins and Tourism, Locally

That dolphin-watching tourism in Shark Bay should have minimal impact on targeted animals is vital, not only for dolphin welfare and conservation, but also given the im-

portance of this tourism to the regional economy (CALM 1993). Although declining dolphin numbers within the tourism region may not jeopardize the entire population, which is large and genetically diverse (Preen et al. 1997; Krützen et al. 2004b), the current rate of decline may not sustain dolphin-watching tourism over the long term. Moreover, the decline is incompatible with stated management objectives, which specify that wildlife tourism be managed in ways that preserve ecological values (CALM 1996).

The Western Australian Department of Conservation and Land Management (CALM) is empowered to intervene when human activities are incompatible with conservation goals. Our results offer some guidance as to appropriate mitigation action. A reduction in dolphin exposure to research vessels is not warranted, given the lesser effect of research activity, and contributions of vessel-based research to dolphin welfare and management. Nevertheless, it seems prudent that vessel-based research be monitored over the long term and curtailed with detection of significant effects (e.g., Clutton-Brock 2003).

Modifying tourist operations to reduce dolphin exposure to tour vessels does seem warranted, given the greater impact of tour-vessel activity. The CALM has accepted this finding and is revising conditions of commercial operator licenses.

Shifting the Burden of Proof Globally

In Shark Bay the dolphin-watching tourism industry is licensed and controlled, yet we found a measurable impact over a relatively brief period. Extrapolating from this site of low-level, regulated tourism, it must be assumed that cetacean-watching tourism is less benign than commonly believed. Worldwide, there are many sites where tourism pressure on cetaceans is substantially greater than in Shark Bay (e.g., British Columbia, Canada [e.g., Williams et al. 2002]; Bay of Islands and Fjordland, New Zealand [e.g., Constantine et al. 2004; Lusseau 2004]; Port Stephens, Australia [e.g., Allen 2005]; Hawaii, U.S.A. [e.g., Forest 2001]). Given the scarcity of studies with adequate controls or longevity to fully evaluate tourism impacts, a cumulative impact, like that detected in Shark Bay, could go unnoticed for decades. Thus, management deliberations must draw strong inference from the best-documented sites, such as Shark Bay, where long-term, individually specific information can be taken into account.

An adaptive, precautionary approach is essential to managing tourism that targets small, closed, resident communities of cetaceans, wherein effects of anthropogenic activity will be amplified. Special care is needed to manage tourism targeting endangered cetacean species (e.g., Northern right whale [*Eubalaena glacialis*], Cape Cod Bay, U.S.A., and Bay of Fundy, Canada; vaquita [*Phocoena sinus*], Baja California, Mexico), where management errors could contribute to extinctions.

In many cases, cetacean-watching tourism is seen as a way to “save” a species or population from direct exploitation; however, our findings suggest that dolphin-watching tourism can have harmful impacts. Given the substantial effect of tour-vessel activity on dolphins in a region of low-level tourism, it is time to shift the burden of proof. It should be incumbent upon tour operators to demonstrate that their activities are sustainable and not harmful to targeted animals (e.g., by supporting bona fide monitoring programs). It may also be time to raise the question as to when, where, and under what circumstances, cetacean-watching tourism should not occur at all (Corkeron 2004).

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