15

Energetic linkages between short-term and long-term effects of whale-watching disturbance on cetaceans

An example drawn from northeast Pacific resident killer whales

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Introduction

Many studies have demonstrated short-term behavioural responses by whales and dolphins in the presence of vessels, but the population-level implications of such changes are poorly understood (Lusseau, 2003, 2004; Bejder *et al.*, 2006a; Lusseau & Bejder, 2007). One means for developing such an understanding is to use a modelling framework such as the Population Consequences of Acoustic Disturbance (PCAD) model. PCAD identifies four levels at which data can be collected, and allows for estimates of modelling parameters at one level to be based on measured data at another level (National Research Council, 2005).

The first level contains short-term behavioural responses, such as those that have been the typical focus of studies on effects of whale-watching. Effects vary within and between species, and include changes in respiration patterns, surface active behaviours, swimming velocity, vocal behaviour, activity state, inter-individual spacing, wake riding, approach and avoidance, and displacement from habitat. Collisions may result in injury or death (Wells & Scott, 1997; Laist *et al.*, 2001). More detailed reviews of vessel effects can be found in Lien (2001) and Ritter (2003).

Fewer studies have addressed the second functional level effects of vessels on whales – quantifying how behavioural responses can affect critical life functions, such as feeding and breeding (Williams *et al.*, 2006; Lusseau *et al.*, 2009; Aguilar Soto *et al.*, 2006). A number of studies have shown vessels to displace whales from habitat, but it is not clear whether it negatively affects feeding behaviour (e.g. Morton & Symonds, 2002; Olesiuk *et al.*, 2002; Richardson *et al.*, 1995a). Even fewer studies have considered the third and fourth functional level effects – namely, the outcome of these disruptions of normal behaviour in the form of altered birth and death rates, and the translation of such changes in the vital rates of individuals to population-level effects (Bejder *et al.*, 2006a,b).

In this chapter, we use data from fish-eating or 'resident' form of killer whales (*Orcinus orca*; Ford *et al.*, 2000) to illustrate how the PCAD framework can be employed to describe the relationship between short-term behavioural responses and population-level consequences. Numerous mechanisms may contribute to population-level consequences. These include stress (Wasser *et al.*, 2010; Ayres *et al.*, 2012), toxin exposure (Ross *et al.*, 2000; Lachmuth *et al.*, 2011), vessel collision (Carretta *et al.*, 2010; Ford *et al.*, 2000), energy expenditure (Williams & Noren, 2009), energy acquisition (Williams *et al.*, 2006; Lusseau *et al.*, 2009), separation of mothers from calves, and disruption of mating (National Research Council, 2003). For the purpose of illustrating PCAD, we chose to limit our quantitative consideration to the energetic

Whale-watching: Sustainable Tourism and Ecological Management, eds J. Higham, L. Bejder and R. Williams.
Published by Cambridge University Press.

consequences of short-term disturbances on population numbers. Specifically, we were interested in cases in which human-caused disturbance could alter the balance between energy intake and expenditure. Whale-watching disturbance has been shown to increase energy expenditure for a number of cetacean species (from increased travelling time or speed, breaching, etc.) or decrease energy intake (e.g. by reducing time spent foraging; Williams *et al.*, 2006; Lusseau *et al.*, 2009).

We chose to treat energetic consequences as mathematically equivalent to changing intraspecific competition. That is, we combined levels 3 and 4 of the PCAD model into a single level after recognizing that intraspecific competition may result in the individual suffering a change in vital rates being different than the individual exposed directly to the disturbance.

We focused on resident killer whales for several reasons. First, they are extensively watched in the wild (see Figure 15.1 for a map of locations where the bulk of this work has been done). Prior to 1980, recreational whale-watching with northern residents was incidental to recreational boating or an opportunistic portion of commercial cruises. Then, Stubbs Island Charters began offering cruises in British Columbia where the primary focus was whale-watching. Initially, this was a small portion of their business. However, as interest grew, and road access to the north end of Vancouver Island improved, it became a more regular part of their business, eventually becoming a primary focus and growing to include a second vessel. By the mid-1980s, other companies in the region were also regularly offering whale-watching cruises. Subsequently, the geographic scope increased, with additional ports at Kelsey Bay and Campbell River serving passengers seeking to spend part of a day with northern resident killer whales (Jim Borrowman, pers. comm.). Scientific interest in the effects of whale-watching began in the early 1980s with work by Kruse (Kruse, 1991; Williams *et al.*, 2002a,b, 2009a,b; Lusseau *et al.*, 2009).

Commercial whale-watching began a few years earlier in the Southern Community of killer whales. The commercial whale-watch fleet grew slowly until the late 1980s, grew rapidly through the mid-1990s, and then levelled off (Koski, 2011). Ports regularly allowing passengers to see southern resident killer whales now extend from Seattle, WA to Vancouver, BC, through the San Juan Islands to Vancouver Island, and to the Olympic Peninsula.

Research and commercial whale-watching developed cooperatively, with researchers making it easier for commercial whale-watchers to find whales, and commercial whale-watchers providing logistical support and data to researchers (e.g. Hauser *et al.*, 2007). This cooperative relationship facilitated incorporation of scientific results into the whale-watch industry's own guidelines for self-regulation. Points in these guidelines included not approaching within 100 m (200 m for transients), a no-go zone in the Robson Bight (Michael Bigg) Ecological Reserve, the elimination of leap-frogging behaviour, and reduced operating speeds within 400 and 800 m of killer whales (Bain, 2001). Some of these guidelines were later adopted by one or more governments; in some cases government regulations remain less strict, while in other cases governments imposed stricter regulations (e.g. prohibition of parking in the path of killer whales, and setting a minimum approach distance of 200 m for residents).

In addition to studying the effects of vessels on killer whales in the wild, killer whales held in captivity have been available for detailed studies of their energetics (Kriete, 1995; Kastelein *et al.*, 2000, 2003; Kasting *et al.*, 1989), hearing (Bain & Dahlheim, 1994; Hall & Johnson, 1972; Szymanski *et al.*, 1999), and click production (Schevill & Watkins, 1966; Bain, 1986). Killer whales have also been the subject of a long-term study on their population dynamics (Olesiuk *et al.*, 1990, 2005). In addition, the primary prey of resident killer whales are commercially important, and hence have been extensively studied as well (Hilborn *et al.*, 2012; Ford *et al.*, 2005; Heise *et al.*, 2003; Hanson *et al.*, 2010; Baird & Hanson, 2004). Thus, there are extensive data to parameterize the first, second and fourth levels of the PCAD model, as well as data on mechanisms for how changes at one level may impact another.

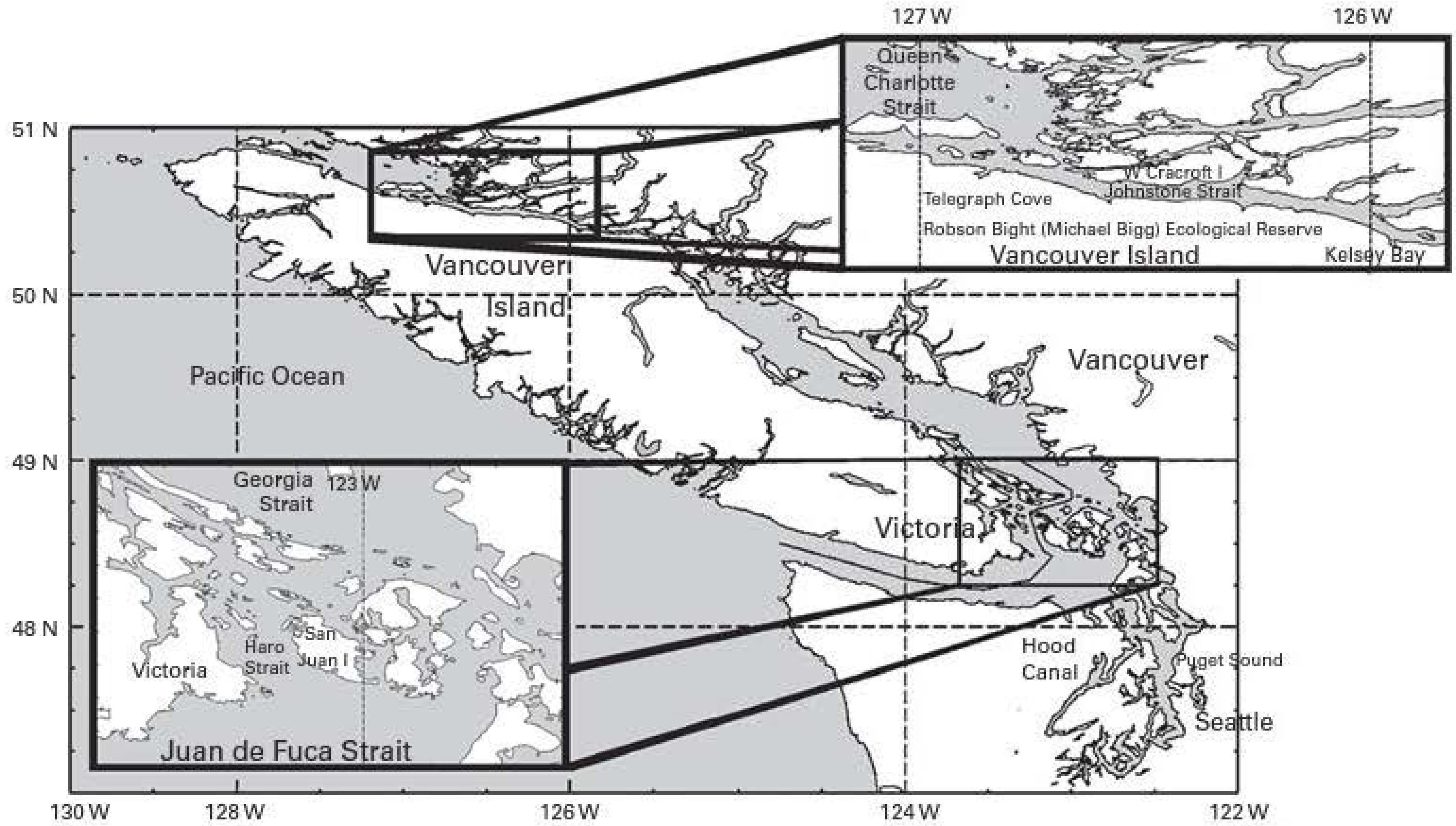

Figure 15.1 Map showing core areas for resident killer whale research. Northern resident killer whale research was centred in Johnstone Strait. Shore-based studies of the effects of whale-watching were conducted from West Cracroft Island, near the Robson Bight Michael Bigg Ecological Reserve. Southern resident killer whale research was centred in Haro Strait. Shore-based studies of the effects of whale-watching were conducted from San Juan Island.

The PCAD approach allows population growth to be projected for an undisturbed population, and to contrast that to the growth of populations experiencing varying degrees of disturbance. Any differences would represent the population-level consequences of disturbance. This modelling framework also allows interaction effects to be examined between disturbance and other factors that affect population growth, such as prey availability (Ward *et al.*, 2009; Ford *et al.*, 2010).

The resident killer whale case study

Under good conditions, resident killer whale populations have increased at a rate of 2.6% per year (Olesiuk *et al.*, 2005). However, the southern resident population of killer whales has failed to achieve this rate of growth since the early 1990s, and in fact declined from a high of 98 individuals in early 1995 to a low of 79 in 2001 (Fisheries and Oceans Canada, 2008; Krahn *et al.*, 2004). The Center for Whale Research reported the 1 July 2012 population was 82 (http://whaleresearch.com/research.html). The causes of the decline have not been confirmed, but may be related to a decline in food availability, and exposure to toxic chemicals, whale-watching and vessel traffic in general (Baird, 2001; Krahn *et al.*, 2004).

Williams *et al.* (2002a,b) and Williams and Ashe (2007) have demonstrated experimentally that whale-watching boats affected the swimming behaviour of ‘northern resident’ killer whales. Males travelled approximately 13% further when approached by a boat following whale-watching guidelines than when travelling unaccompanied, and females changed direction more from one pair of surfacings to another when accompanied by the experimental boat than when on their own

(Williams *et al.*, 2002a). When followed by a boat that 'leapfrogged', the male whales travelled approximately 17% further than in the absence of boats (Williams *et al.*, 2002b). As a result, it took more energy for whales to travel from one place to another when accompanied by boats than under control conditions, although the metabolic cost of swimming in killer whales is relatively low across a wide range of swimming speeds (Williams & Noren, 2009). Williams *et al.* (2006) estimated that the energetic cost of meeting an activity budget in the presence of boats was only 3–4% higher than that under control conditions. In the presence of boats, however, whales reduced their time spent feeding, which could have resulted in a substantial (18%) decrease in energy intake (Williams *et al.*, 2006). In similar work on 'southern resident' killer whales, Lusseau *et al.* (2009) showed a 25% reduction in the proportion of time spent feeding in the presence of boats.

Bain and Dahlheim (1994) demonstrated that killer whale hearing ability was impaired by masking noise such as vessel noise. A consequence of this is that active space (the range over which biologically important signals are functional) is reduced in the presence of noise (Miller, 2000; Erbe, 2002; Jensen *et al.*, 2009; Clark *et al.*, 2009). In general, the ability of a killer whale to generate echolocation clicks limits the source level, and should be independent of the level of ambient noise. Target strength is a property of the prey, and should also be independent of noise. Thus, a whale in an increasingly noisy environment must be closer to its prey to detect it. Holt (2008) estimated that a boat at cruising speed 400 m from a whale would reduce its echolocation range by 90%. Reducing active space, in turn, should reduce foraging efficiency (Clark *et al.*, 2009). Temporary and permanent threshold shifts are additional mechanisms that may reduce active space (Au *et al.*, 1999; Erbe, 2002).

Increasing the energetic requirements of individuals within the population and reducing effective prey availability are equivalent to reducing the carrying capacity in food-limited populations. Olesiuk *et al.* (2005) produced an equation relating population size and carrying capacity to population growth rate. This model was based on the concept that as populations increase, there is stronger competition for resources such as food, which in turn slows population growth (Gilpin *et al.*, 1976).

Whale-oriented vessel traffic has been monitored for many years (Koski, 2011; Osborne, 1999), as has the population of southern resident killer whales since the mid-1970s (e.g. Bigg *et al.*, 1990; Olesiuk *et al.*, 1990). In addition, the portion of the range of southern resident killer whales that is shared extensively with whale-watching boats has been documented (Osborne, 1999). These data form a basis for testing the strength of relationships between the magnitude of whale-watching and population trends and distribution.

Vessels have been seen accompanying whales passing through a study site off the west side of San Juan Island approximately 90% of the time during daylight hours (Lusseau *et al.*, 2009; Williams *et al.*, 2009a). Combining this estimate with the observation that whales have been regularly seen from April to October suggests that vessels accompanied whales approximately 25% of the time during the year (i.e. 50% of the time during the 6-month whale-watching season).

The following considers the possibility that whale-watching has negatively affected the population dynamics of southern resident killer whales. Specifically, we examined whether whale-watching could affect population dynamics by requiring greater energy expenditure and/or reducing foraging efficiency. To accomplish this, we estimated the increase in energy expenditure due to whale-watching, and estimated reductions in foraging efficiency due to vessel noise. We also developed a model to relate changes in energy balance to changes in population dynamics, and tested whether a significant correlation exists between exposure to whale-watching and population trends. We then assessed whether the model was consistent with (1) the increase in population size in the presence of vessel traffic prior to 1995, (2) the apparent absence of change in range, and (3) pod-specific population trends and patterns of exposure to whale-watching and other vessel traffic.

Methods

Changes in energy expenditure due to whale-watching

We assumed that killer whales that swam 13% or 17% further along a circuitous path would have less time to rest than killer whales that were not being followed by a vessel and swam along a relatively straight-line path. This increase in swimming distance would result in an approximate 13% or 17% increase in energy consumption (Waite, 1988; Kriete, 1995). We multiplied the increased energy expenditure by the proportion of time that whales were exposed to whale-watching to estimate the total increase in energy expenditure (approximately 50% of the time during 50% of the year, or 25% overall over the course of a year).

Changes in energy acquisition due to noise from whale-watching

We used the sonar equation to convert dB of masking or reduced sensitivity due to temporary or permanent threshold shifts to change in detection range. For echolocation at maximum range,

$$DT = SL - 2TL + TS - NR,$$

where DT is the detection threshold, SL is the source level, TL is one-way transmission loss, TS is target strength, and NR is received noise.

At short range in deep water, one-way transmission loss can be approximated by the formula $TL = 20 \log (R)$, where R is the transmission distance (Au, 1993). A correction to this equation for directivity is needed, but insufficient data are available to make this correction quantitatively (Bain & Dahlheim, 1994). Fortunately, the correction for directivity is likely to be the same for any given noise source, independent of absolute noise level. Thus, the equation for passive detection becomes

$$DT = SL - TL - NR.$$

As can be seen from the sonar equation, an increase in noise will result in a decrease in tolerable transmission loss, and hence detection range will decline. In the absence of wind and current, natural ambient noise can be as low as 20 dB re 1 $\mu Pa^2/Hz$ at 20 kHz (Richardson *et al.*, 1995b). Ambient noise from wind, currents and non-whale-oriented traffic in Haro Strait was typically 50 dB re 1 $\mu Pa^2/Hz$ at 20 kHz (Bain, 2002). This corresponds to an outboard engine operating at high speed at a distance of several kilometres. Thus, noise from whale-watching vessels above this level will increase masking and reduce echolocation range. Received level decreases approximately 6 dB with each doubling of distance. That is, the target will need to be twice as close to offset the masking noise of 12 dB (i.e. 6 dB less loss on the way to the target, and 6 dB less loss on the way back to the whale). For passive listening, two halvings of distance will be required (i.e. the source will need to be four times closer). As a result, for killer whales using passive listening to locate prey (e.g. 'transient' – mammal-hunting killer whales: Barrett-Lennard *et al.*, 1996), the change in distance producing the transmission loss required to offset noise would be approximately twice as large as for whales using echolocation (resident killer whales). Furthermore, whales that use social facilitation in foraging (e.g. resident killer whales (Ford & Ellis, 2005), humpback whales (D'Vincent *et al.*, 1985)) will face the restrictions in range due to masking noise experienced in passive listening.

We assumed that normal foraging efficiency equated to that of a whale with normal hearing in quiet conditions, and expressed foraging efficiency impaired by noise as a percentage of normal foraging efficiency. We also assumed that foraging killer whales ensonified a 'tube' surrounding their travel path, with the radius of the tube reflecting the detection range of prey (active space).

Whether a-priori knowledge of prey distribution affected the ratio of prey detected in noisy conditions to quiet conditions was treated in four ways (see Figure 15.2).

First, the *fixed-location model* assumed that prey were in a fixed location known to the whales (e.g. a particular territory within a reef, as would be the case for many bottomfish species). Whales

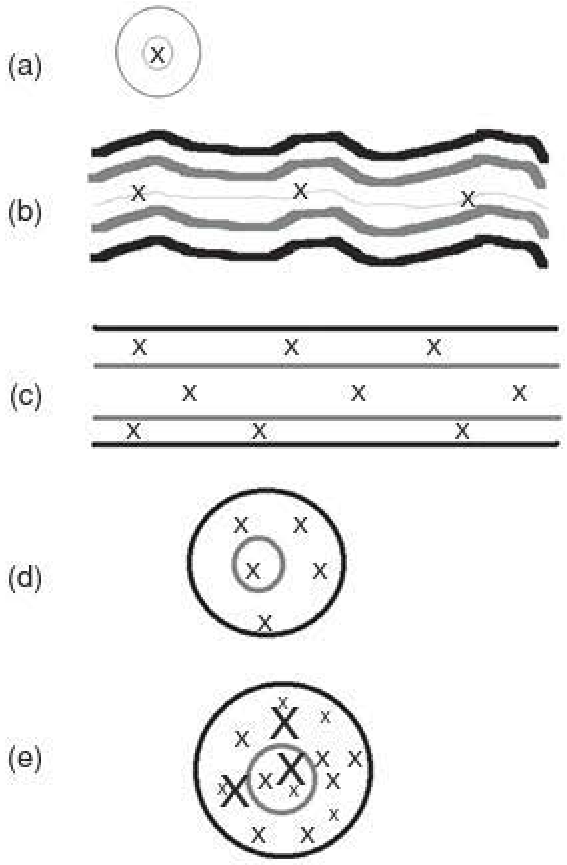

Figure 15.2 Search patterns by killer whales for prey (X) in the water column. (a) known prey location; (b) unknown prey location along a known line; (c) unknown prey location within a plane with search within the plane; (d) unknown location within a plane with search perpendicular to the plane; (e) no information on prey location. X's within the grey boundaries represent prey that would be detected even when hearing is impaired. X's between the grey and black boundaries represent prey that would be missed due to hearing impairment. In (e), large and small X's also represent prey that would be missed.

successfully located prey when they arrived within detection range of this location.

The second model, the *linear search model*, assumed that prey occurred along a line (e.g. a depth contour along the bottom), but at an unknown position. Whales successfully located prey when they arrived within the detection range of the prey.

Our third model, the *within-plane search model*, assumed that prey items lay in a plane (e.g. at a fixed depth or along the bottom), but at an unknown position. Whales were assumed to travel in the plane of the prey. In this model, prey within detection range of passing whales were detected, but prey sufficiently distant from the paths of whales were undetected. A variation of this is the *across-plane search model*, which assumes that prey are at an unknown position in the plane (e.g. along the mouth of a channel or a current shear). Whales are assumed to travel perpendicular to the prey plane, and successfully locate prey only when they penetrate the plane within detection range of the prey (see Jefferson, 1987).

Our fourth and final model, the *volumetric search model*, assumed that prey could be anywhere in the water column. Whales only located prey if they passed within the detection range of this location. A species such as Chinook salmon may be distributed in a way that requires volumetric searches (Candy & Quinn, 1999).

Population dynamics

Population growth of southern resident killer whales was modelled with the generalized logistic equation (Gilpin *et al.*, 1976) using parameters calculated by Olesiuk *et al.* (2005):

$$\frac{\Delta N}{\Delta t} = 0.026N\left(1-\left(\frac{N}{100}\right)^{40}\right),$$

where N is the population size, ΔN is the change in population per unit time (Δt), the intrinsic rate of increase of 2.6% per year, and the shape parameter z was 40. Population carrying capacity was estimated to be 100 individuals based on the size of the southern resident population when it peaked around 1960 and again in the mid-1990s (Bain & Balcomb, 1999).

Relationship between fleet size and whale population changes

We performed four statistical analyses to assess whether there was a significant relationship between fleet size and changes in southern resident killer whale population size. The first two analyses used data from 1977 to 2001 (Koski, 2011), while the latter two used only data from five years before the 1996 peak in 1 July population size to five years following the peak (1991–2001).

For each time-frame (i.e. 1977–2001 or 1991–2001), we evaluated two time lags. The first pair of analyses assumed that overall exposure to whale-watching was related to fleet size in that year. That is, we tested whether fleet size predicted population change over the year following exposure. The second pair of analyses assumed that overall exposure to whale-watching was related to consumer demand for whale-watching services. We assumed that operators based their fleet sizing decisions on the number of trips made in the previous year. Thus we tested whether fleet size predicted population change over the year preceding exposure to that particular fleet, as both may have been based on whale-watching activity in the previous season. In summary, we tested for correlation on the assumptions that

1. fleet size determined the amount of exposure to vessels that whales experienced in a given year, and
2. the amount of exposure to vessels that whales experienced in a given year was determined by the same factors as fleet size the following year.

We calculated correlation coefficients for each of the four conditions, as well as the probability that a correlation of that magnitude or higher could occur by chance.

To visualize the data, we plotted the actual values of the variables, as well as moving averages of both variables.

Olesiuk *et al.* (1990) reported 502 encounters with southern residents during the course of their research: 311 sightings of J Pod, 240 of K Pod, and 198 of L Pod (more than one pod was present on many occasions). We used these values as a rough estimate of the relative exposure of the three pods to whale-watching traffic.

Sensitivity

To determine the population-scale effect of whale-watching, we compared the projected population growth in the presence of whale-watching to what growth would have been in its absence. As some parameters were estimated somewhat arbitrarily, and others were best estimates with broad confidence intervals, we calculated relative population growth rates for a variety of values to determine the sensitivity of the analysis to the values employed.

Results

Changes in energy expenditure due to whale-watching

The extra energy expenditure due to a whale being followed by a single vessel operating in accordance with whale-watch guidelines would total 3.25% over the course of the whale-watching season. A whale being followed by a leapfrogging vessel would expend about 4.25% more energy over the course of a season. This is consistent with the findings of Williams *et al.* (2006) that the energetic cost of meeting an activity budget in the presence of boats was 3–4% higher than during no-boat conditions.

Changes in energy acquisition due to noise from whale-watching

The relative ranges at which whales can detect prey are shown in Figure 15.3 for a variety of detection thresholds related to noise or threshold shifts. Figure 15.3 also shows corresponding reductions in area and volume remaining in the active space.

Population dynamics and sensitivity

Annual changes in the number of killer whales that would be expected at different population sizes according to the generalized logistic model are shown in Figure 15.4 for a range of shape parameters ($z = 1$–40). In general, all of the models predicted a constant per-capita growth rate at low population sizes, and a rapid slowing of growth as the population exceeded 90% of carrying capacity. The models also predicted a loss of 1–4 individuals per year if the population exceeded carrying capacity

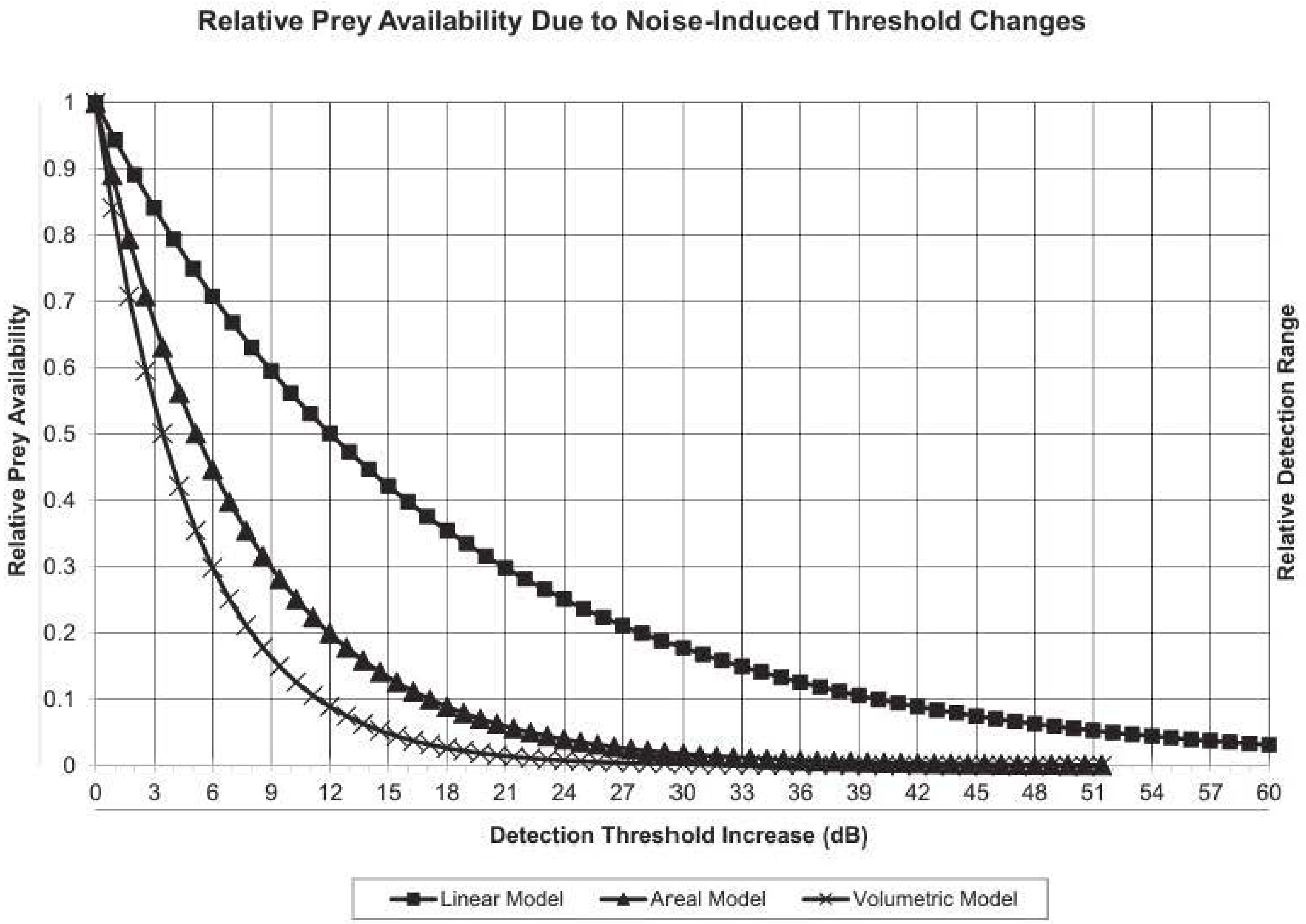

Figure 15.3 Detection range and detection efficiency for killer whales when hearing is impaired. The upper curve shows the relationship between relative detection range and magnitude of hearing impairment. This is also the curve for relative prey detection efficiency for the search within the plane model. The middle curve shows relative prey detection efficiency for the perpendicular-to-prey-plane search model. The lower curve shows the relative prey detection efficiency for the volumetric search model. It is important to note that small elevations in detection thresholds (e.g. 3 dB) can have large effects on the proportion of prey that remain detectable. Points of interest include 6 dB (proposed PTS), 12 dB (proposed TTS), and 30 dB (typical ambient above sea state 0).

by up to 10%. Thus, the most dynamic changes in effects on killer whale numbers appear to occur as they approach or exceed carrying capacity.

The projected energetic effect of whale-watching on killer whale numbers is shown in Figures 15.5 and 15.6. Assuming that population growth follows current patterns (i.e. $z = 40$) and whale-watching increases the energy needs of killer whales by 3% (to compensate for increased swimming and decreased foraging averaged over the course of a year), the model predicted a net loss of one individual per year as the population approached K (Figure 15.5). In other words, increasing the energy requirements of a population of killer whales due to whale-watching would mean that an environment that once supported 100 killer whales could now support only 97 whales, and equilibrium would be restored over about a three-year period. An increase of 5% would lower carrying capacity to 95 whales, and result in an initial compensation of about two individuals per year. Population-level impacts appeared to be negligible when the population was below 90% of K. Varying z (the shape parameter) or the assumed energetic cost for

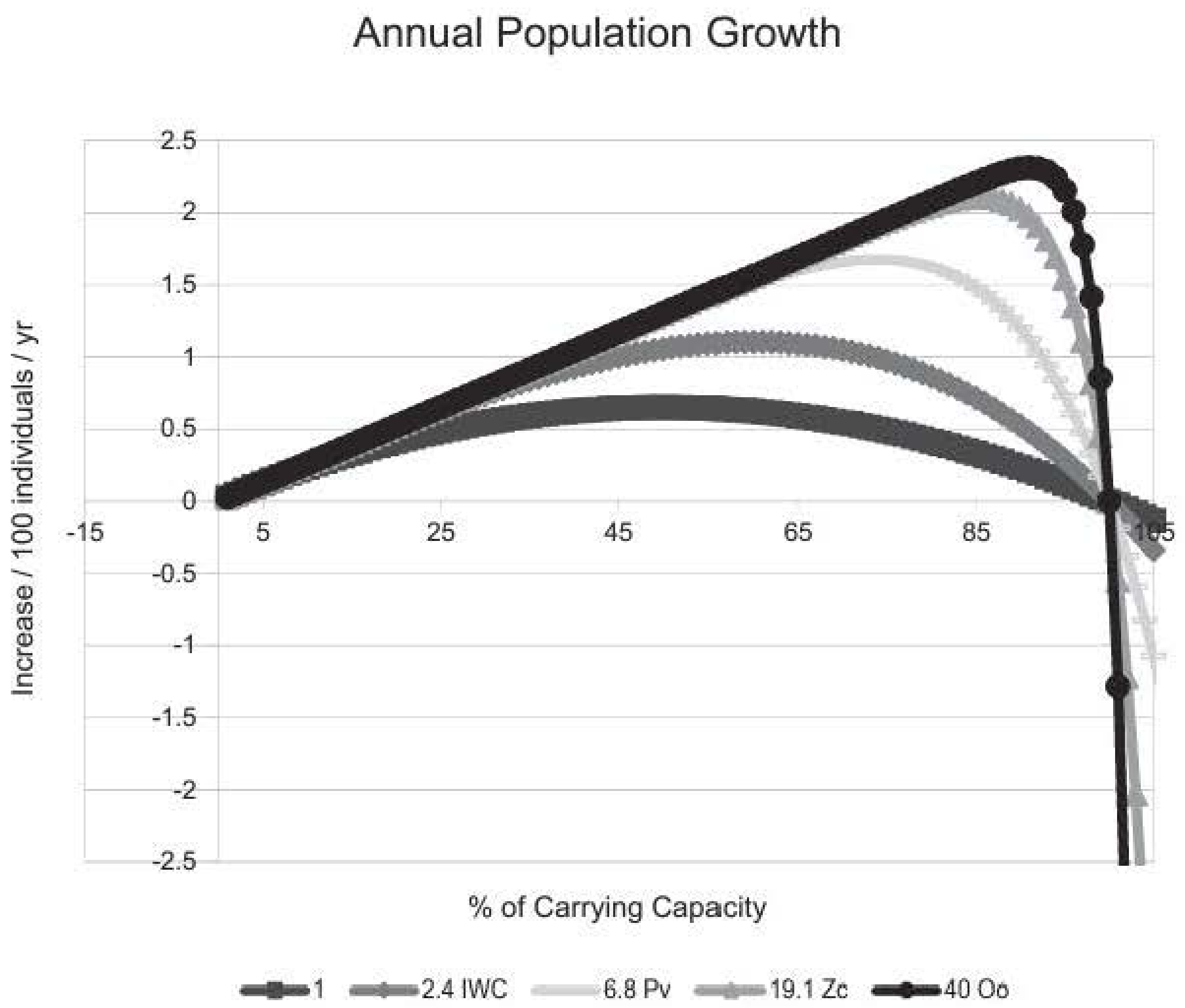

Figure 15.4 Population growth rates as a function of population size for a variety of shape parameters.

whales that were disturbed altered the population response by varying amounts (Figures 15.5 and 15.6). However, all realistic scenarios suggest that responses are negligible until the population is near its carrying capacity.

Relationship between fleet size and whale population changes

Numbers of commercial whale-watching vessels and annual changes in numbers of southern resident killer whales from 1977 to 2001 are shown in Figure 15.7. Regressing vessels on whales (with various time lags) yielded significant correlations. However, correlations over the long term (1977–2001) were weak ($r^2 = 0.18$, $p < 0.05$ for fleet size leading whale change; and $r^2 = 0.24$, $p < 0.01$ for fleet size following whale population change). In contrast, correlations over the more recent 1991–2001 period were stronger ($r^2 = 0.52$, $p < 0.01$, for fleet size leading whale population change; and $r^2 = 0.70$, $p < 0.001$, for fleet size following whale population change). This is consistent with the model result that population-level responses are only to be expected when the population is near carrying capacity.

Discussion of the killer whale case study

Changes in energy expenditure due to whale-watching

The increases in energy expenditure and reduction in prey capture due to whale-watching are probably small – of the order of 10–20%. The cumulative effect will be smaller still (our best estimate is that it is on the order of 3–4%), as not all whales are watched all

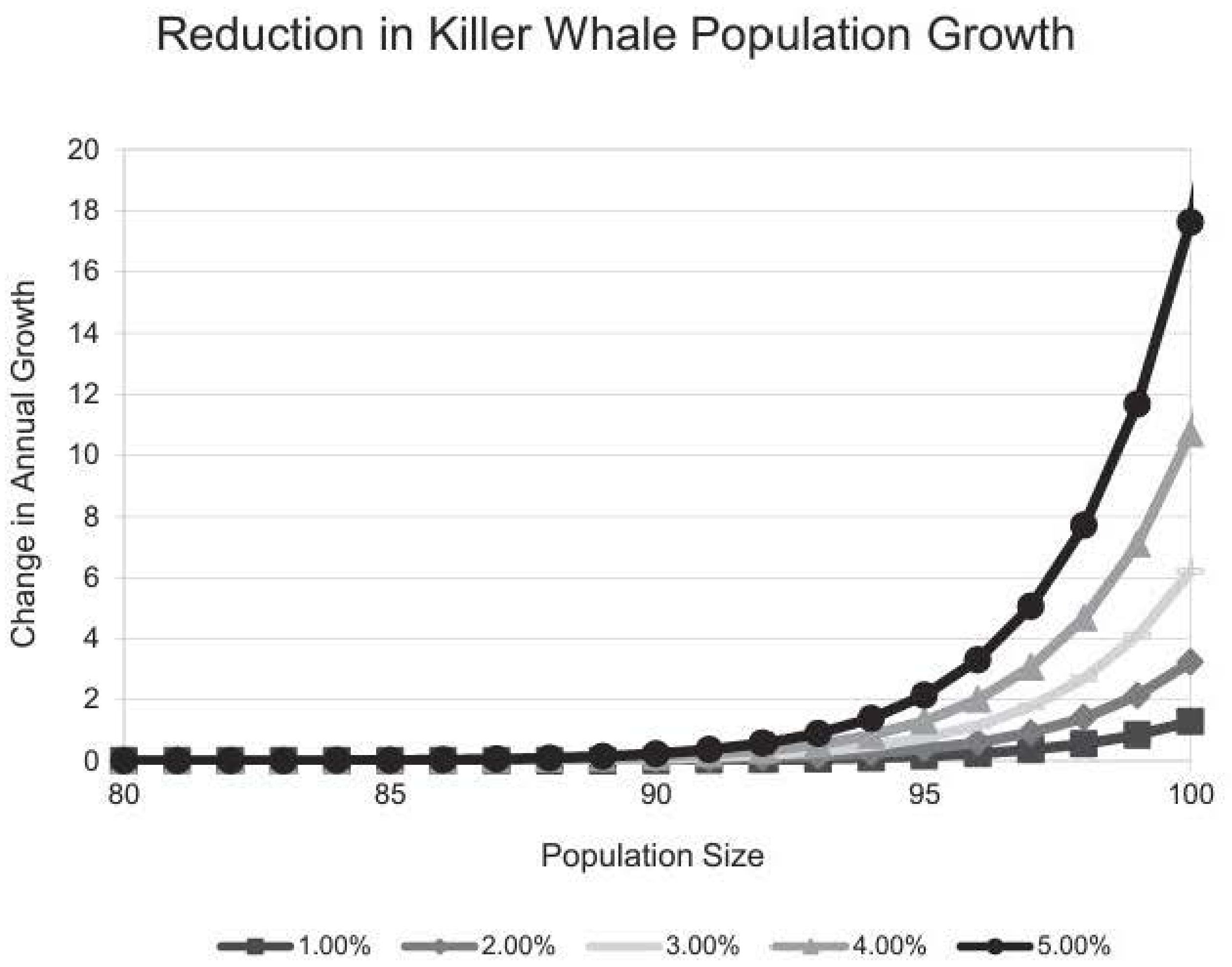

Figure 15.5 Population-scale effects for a variety of total energetic impacts (1–5%) when the shape parameter $z = 40$. Note that the curve at 3% is the best estimate for a whale-watching fleet that follows guidelines, while the curve at 4% is the best estimate for a fleet that continually speeds up to 'leapfrog' whales' predicted paths.

of the time. However, commercial whale-watching is now becoming a year-round industry, and public sighting networks have also allowed recreational whale-watchers to take advantage of viewing opportunities year round.

The commercial fleet has reached a size where all members of the southern resident community can be approached closely at the same time. In the absence of management intervention (e.g. regulation and/or boater education programmes), there is the potential for the frequency of interactions between boats and whales to increase. Although habituation might be expected to reduce or eliminate responses of whales to boats, Williams and Ashe (2007) were able to demonstrate behavioural changes of the magnitude assumed here in northern residents that had over 30 seasons of experience with researchers, commercial photographers, and other whale-oriented vessels, including > 20 seasons of commercial whale-watching. Similarly, Williams *et al.* (2009a) and Lusseau *et al.* (2009) found changes of this magnitude in southern residents after over 30 seasons of exposure to research vessels and 25 seasons of exposure to commercial whale-watching.

Changes in energy acquisition due to noise from whale-watching

Small increases in detection threshold resulted in a dramatic reduction in the ability of killer whales to detect prey. Au (1993) suggested that echolocation clicks could be detected reliably at about 10 dB above ambient noise, which for a killer whale corresponds to the signal-to-noise ratio at auditory threshold at Sea State 0 (Szymanski *et al.*,

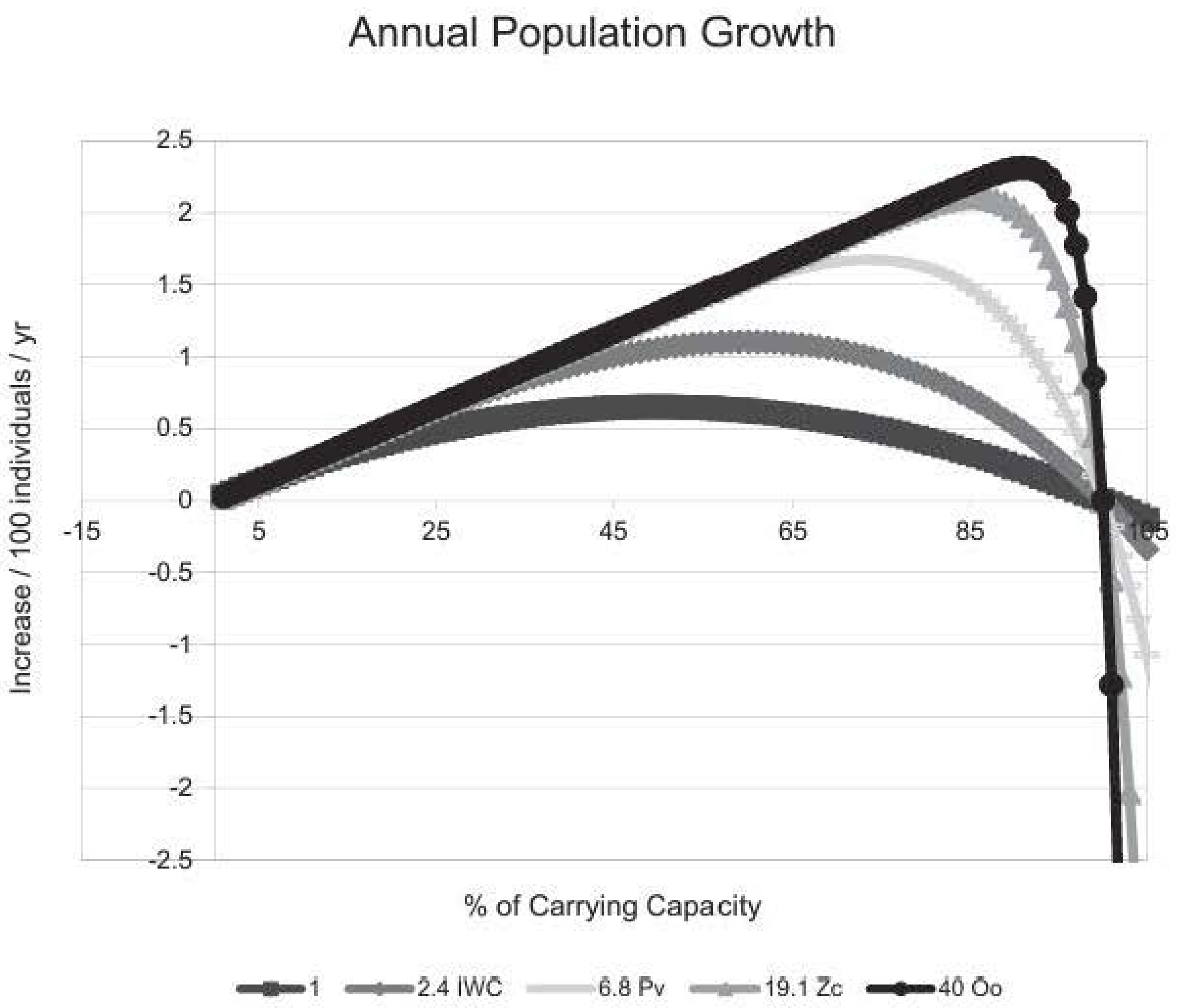

Figure 15.6 Population growth when total energetic impact on carrying capacity is 3% and the shape parameter *z* ranges from 1 to 40.

1999). Additional noise, whether from natural or man-made sources, would reduce the range of echolocation detection.

A 20 dB increase in noise corresponds to approximately a 3-fold decrease in detection range for echolocation (Figure 15.3). A 60 dB increase in noise corresponds to approximately a 30-fold decrease in detection range. Received noise levels from benign whale-watching (a single outboard-powered vessel that is 100 m to the side, travelling at approximately the same speed as the whale) is on the order of 105–110 dB re 1 μPa, with power spectral densities of approximately 70–80 dB re 1 $\mu Pa^2/Hz$ at 20 kHz (Richardson *et al.*, 1995b). Thus, benign whale-watching likely results in masking on the order of 20–30 dB in excess of normal levels of ambient noise.

Temporary threshold shifts due to whale-watching are unlikely to be large enough to exceed the effects of masking. Similarly, permanent threshold shifts are likely to be small relative to temporary threshold shifts and masking. However, temporary threshold shifts may be important in quiet water, where a 12 dB threshold shift would result in a 2-fold decrease in detection range. Similarly, a permanent threshold shift of 6 dB would reduce detection range in quiet water to 70% of the optimum.

Masking will only reduce detection range while whales are in the presence of boats, and is likely to occur for approximately 25% of the year (or 50% of the time during the core whale-watching season). Where temporary threshold shifts occur, the effect might persist for up to 24 hours after

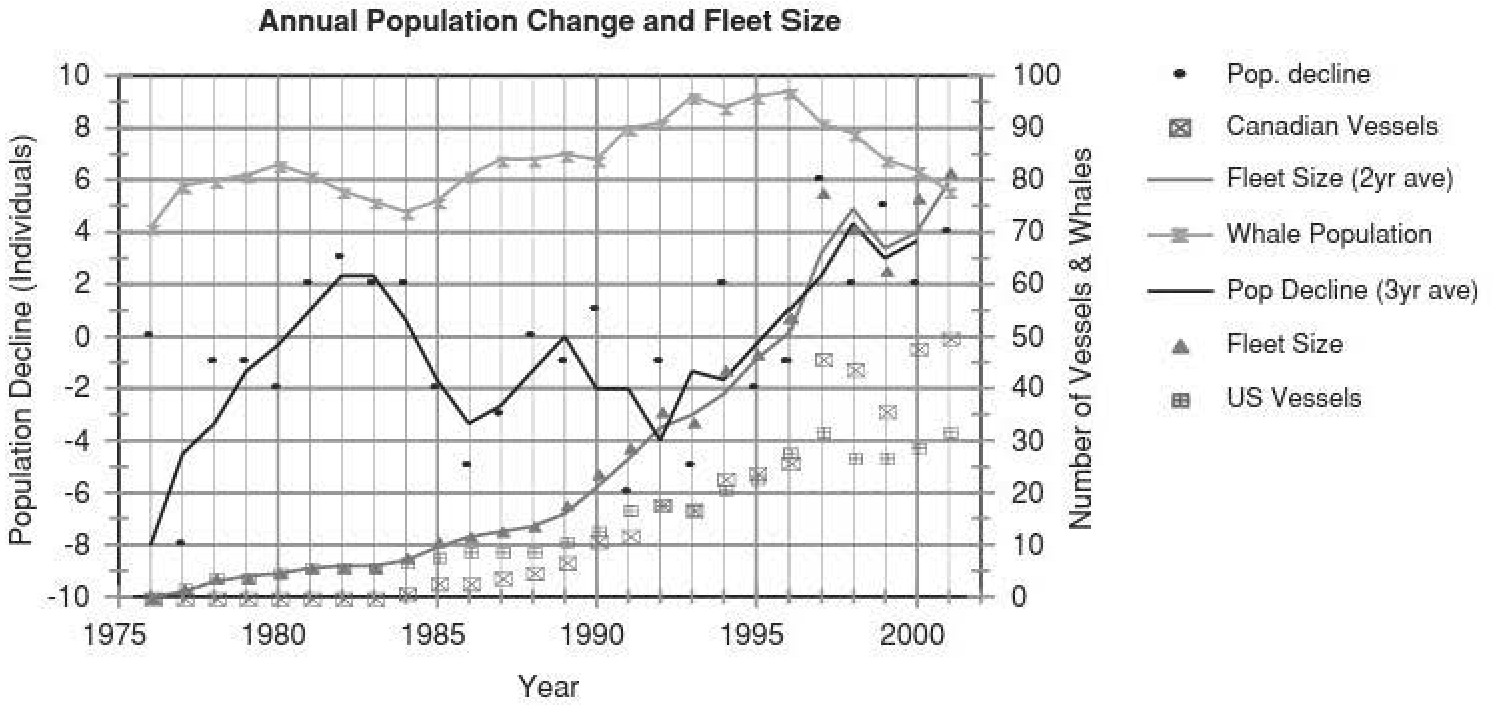

Figure 15.7 Relationship between fleet size and killer whale population changes. 1 July counts of southern resident population size are shown (Krahn *et al.*, 2004). The total number of commercial vessels actively engaged in whale-watching, along with the number based in American and Canadian ports, are shown (after Koski, 2011). Annual changes in whale population size are plotted in the year of the latter count. A three-year moving average of annual whale population change is plotted along with a two-year moving average of total fleet size. Fleet size is used as an index of exposure to whale-watching, although other factors not represented in this graph that affect overall exposure may include: efficiency of whale-watch operators in locating whales; hours per day spent with whales; number and type of engines employed, operating speed, distance, orientation and relative position. Note the tight fit of smoothed whale population change with smoothed fleet size beginning in the early 1990s. Also note that the number of vessels in the commercial whale-watching whale fleet exceeded the number of whales in the population in 2001 (although typically, not all vessels operated simultaneously).

exposure to noise if the duration of the effect in killer whales is the same as that in humans (Erbe, 2002). Because whales may only have 9–12 hours between bouts of whale-watching, this effect might be nearly continuous for half the year. Alternatively, the effect may disappear almost completely within an hour, as is the case with bottlenose dolphins (*Tursiops truncatus*; Nachtigall *et al.*, 2003). Temporary threshold shifts of such a short duration would only slightly increase the effect of noise relative to masking alone. In contrast, permanent threshold shifts would reduce detection range and would be a problem year-round.

The implications for foraging efficiency of reducing active space depend on the foraging tactics that killer whales use to locate prey (Figure 15.1). Assuming that prey are in a fixed location known to the whales (fixed-location model), killer whales will find prey with the same efficiency regardless of whether their echolocation ability is impaired. Similarly, whales should also find prey with the same efficiency regardless of whether their echolocation ability is impaired if they are on the same path (linear search model) and the whale travels faster than the fish and retains minimal navigation and sensory capability. However, detection efficiency will be impaired if the probability of detecting prey is proportionately related to detection range or the square of the detection range (within- and across-plane search models, respectively). Detection efficiency will be further impaired by noise if prey are randomly located in the water column (volumetric search model), in which case detection efficiency is proportional to the cube of the reduced detection range.

Holt (2008) cited noise levels recorded from a fixed location along San Juan Island. Average midday levels were about 12 dB above midnight levels at 15 kHz, suggesting echolocation range would likely be reduced by a factor of at least 3–5 off San Juan Island (average noise received by whales was likely higher than the average received at the fixed site). In the absence of knowledge about prey distribution, this would result in a reduction of available prey by over 95%. Under the planar model (across-plane approach), available prey could be reduced by ~90–95%. Even with approximate knowledge of prey location (planar model, within-plane approach), most prey that would be detected in quiet water could be missed. With outboard-powered whale-watching vessels, even under present guidelines, there would be losses of similar magnitude relative to the already reduced level from other sources of ambient noise (i.e. total reductions in excess of 99%).

It should be pointed out that directional hearing capabilities might reduce the magnitude of the effect of noise on prey detection range relative to that calculated above. Vessels operating to the side or behind whales may have a masking effect that is 10–20 dB lower than the same noise source in front of whales (Bain & Dahlheim, 1994). There is also potential for temporal pattern processing to improve extraction of signal from noise (Szymanski *et al.*, 1998). Even with these corrections, there is still the potential for decreasing foraging efficiency due to noise from increasing whale-watch activity to be more important than changes in foraging efficiency due to changing prey abundance. An 80% reduction in effective prey availability due to noise from whale-watching would be the right order of magnitude to account for the decline in southern residents during the 1990s. This corresponds to an increase in noise received by killer whales of only 9 dB if they have no a-priori knowledge of prey locations.

Population dynamics and sensitivity

The impact of whale-watching on the modelled population dynamics was very sensitive to the shape parameter. When the shape parameter used was 1 (i.e. Maximum Net Productivity Level (MNPL) at 50% of K), the population-scale effects of changes in effective carrying capacity were limited. That is, it would take the population a long time to reach equilibrium with the new carrying capacity. As a result, the change in population growth in any given year would be small.

There were two obvious changes in population-scale effects as the shape parameter increased. The rate of population growth remains near the intrinsic rate of increase even when the population was well above 50% of K. Furthermore, the per capita growth rate remains near the intrinsic rate of increase at higher population sizes as the shape parameter increases (i.e. the production curve became more asymmetrical, with MNPL occurring at higher percentages of K as the shape parameter increases – the reason for the name 'shape parameter'). With a shape parameter of 40 as estimated by Olesiuk *et al.* (2005), for example, changes in effective carrying capacity had essentially no effect on population growth rate as long as the population remained below 90% of both the old and new values of K. In contrast, the rate of population growth changed very rapidly when the population was near K. That is, small changes in K produce large changes in population growth rate when the population is near K. Populations that are over K rapidly fall below equilibrium.

The second obvious effect of the shape parameter was that the maximum rate of increase in absolute population size increased with increasing shape parameter. For example, the maximum rate of increase for a species with a shape parameter of 1, intrinsic rate of increase of 2.6%, and a K of 100 would be less than one individual per year. When the population was at 105% of carrying capacity, the rate of decrease would be close to 0. In contrast, employing the observed shape parameter for resident killer whales of 40 put the maximum growth rate at over two individuals per year, and the decline of a population at 105% of K was over 16 individuals per year.

The implication of these two observations is that as the shape parameter increases, the potential magnitude of effects of changes in carrying capacity becomes smaller for populations well below carrying capacity, and becomes larger when the population is near K.

Relationship between fleet size and whale population changes

The sensitivity analysis performed above suggests that population growth rate will be independent of K when the population is depleted, as was the case for southern residents at the end of collections for public display (Bigg & Wolman, 1975; Bain & Balcomb, 1999). Once the population recovered, it would become very sensitive to changes in K. As a result, if carrying capacity is affected by whale-watching as suggested above, changes in population growth rate should not have correlated with changes in levels of whale-watching traffic when the population was small. Instead, it should have been tightly correlated with them when the population was large.

Similarly, when the size of the whale-watch fleet was small, the maximum possible cumulative effect would have been small. As fleet size increased, the potential cumulative effect increased, and hence one would expect stronger correlations when the fleet was large than when it was small.

This is the pattern that was observed. The correlation for all years was weak, and whale population size did not track fleet size when both were small. However, the correlation was strong when both were large.

Despite the consistency in the observed trends, we are unable to state whether the relationship between fleet size and population growth rate was causal or whether both parameters were correlated with causal factors that we have not considered. We have interpreted our data as implying that time spent whale-watching determines fleet size in subsequent years (i.e. consumer demand determines the number of trips and funds available to purchase and maintain vessels in future years), but this hypothesis needs testing.

Population growth in the presence of whale-watching

With relatively healthy fish stocks and depleted numbers of killer whales (due to past collections for public display), the southern resident population was probably well below carrying capacity in the 1970s. According to our model, whale-watching was unlikely to have had any population-scale effect during that period. In the 1980s to the early 1990s, the population may have tracked a fluctuating carrying capacity as fish abundance varied. While there was potential for impact, the small size of the fleet meant that total impact was probably small. As the amount of whale-watching increased through the 1990s, the magnitude of the change in energy balance due to whale-watching may have exceeded the magnitude of the change in energy balance due to changes in fish abundance. If so, this would account for the correlation between fleet size and changes in population size observed over that decade. Our model indicates that if the effect on the population is large, missed prey due to noise is probably a much more important mechanism than excess energy expenditure. The correlation between fleet size and whale population trends merits careful evaluation.

Smoothing fleet size and change in whale numbers by three-year intervals suggests a possible relationship between the two, beginning in the early 1990s (Figure 15.7). While this may be nothing more than coincidence, the smoothing eliminates noise associated with year-to-year variability in calving intervals (a three-year cycle) and possibly whale-watching business decisions.

The energetic consequences of whale-watching that we propose are only relevant when the population is food-limited (whether by reduction in food stocks (Washington Department of Fisheries *et al.*, 1993; Allendorf *et al.*, 1997) or the accessibility of these stocks is limited by disturbance). Other factors associated with whale-watching, such as stress or exposure to burned and unburned fuel, may also inflict population-scale effects in addition to the energetic consequences.

Displacement as a response to noise

Although Morton and Symonds (2002) found that noise excluded northern residents from peripheral habitat near a core area over a period of years, this does not imply that whales will always move in response to disturbance. Our models illustrate that relatively small impacts on effective fish availability can produce population-scale effects. However, population-scale effects of degraded habitat due to whale-watching in core areas (Hauser *et al.*, 2007) could be smaller than the effects of moving to habitat where prey density is lower and optimal foraging tactics may be unknown to the whales (e.g. Juan de Fuca Strait). This contrasts with the case described by Morton and Symonds (2002), in which nearby, familiar areas with similar prey densities (or perhaps higher prey densities, but with more intraspecific competition; Nichol & Shackleton, 1996) were available.

It is important to identify other sources of the decline that may act independently of or synergistically with whale-watching. For example, Ylitalo *et al.* (2001) found lipid concentrations in blubber samples collected from many individuals ranged by a factor of eight (from 7% to 59%). Some of this variation was likely due to methodological issues (e.g. the location on the body of the sample and handling and storage practices). However, some of the variation may have reflected real variation in fat reserves. Because a high proportion of lipids are in the blubber (Borrell *et al.*, 1995), total body concentrations of toxins may vary substantially with energy balance. Thus toxin concentrations could increase as a whale loses weight, even if total body burden remains constant.

Ross *et al.* (2000) found high PCB levels in southern residents, and Reddy *et al.* (2001) found PCB levels tended to be higher in mothers of captive *Tursiops* calves that died as neonates than in mothers of calves that survived the neonatal period. This indicates that reduction in lipid reserves due to impaired energy balance could negatively impact calf survival both through nutritional and toxicological mechanisms, and this may be related to the 50% reduction in calf recruitment rate in L Pod observed over the 1990s (Bain & Balcomb, 1999).

Future work on resident killer whales

Our study has several applications. First, focusing on a subset of the possible consequences of whale-watching provides a minimum estimate of the population-scale effects of whale-watching. Second, the quantitative model we constructed allows the impacts of a variety of scenarios to be evaluated (e.g. different levels of whale-watching – hours per day, days per year, noise exposure or impacts at different population levels, interaction effects of whale-watching and other factors such as prey availability). In addition, the consequences of mathematically equivalent factors can be considered (e.g. reduction in food availability due to fisheries- or climate-induced reductions in salmon stocks would be mathematically equivalent to a reduction in food availability due to noise).

Additional studies should be pursued to test our model predictions, such as that of Lusseau *et al.* (2009), who observed a reduction in foraging effort in the presence of whale-watching vessels. Additional work could address whether there is a detection probability threshold (prey items/unit volume within the masked detection range; Au *et al.*, 2004) for abandoning foraging on optimal foraging grounds that corresponds to this shift in behaviour. Our research could undertake a detailed analysis of whale-watch operators' logs to determine time spent with whales to rigorously assess whether the correlation between fleet size and whale population changes could reflect a causal relationship.

Another study should measure actual noise exposure to refine our estimates of acoustic impact on foraging efficiency (see Griffin & Bain, 2006, and Holt, 2008, as initial efforts toward this). Studies of foraging tactics used by killer whales would allow a better assessment of the importance of reduced prey detection ranges (see Baird & Hanson, 2004). Studies of the distances between whales cooperatively foraging (Ford & Ellis, 2005) successfully and ambient noise whales would also be of interest. Other studies of threshold shifts, directional hearing and masking using captive killer whales would also be valuable (in addition to Bain & Dahlheim, 1994).

Testing whether the correlation between prey availability and population growth (Ward *et al.*, 2009; Ford *et al.*, 2010) is stronger when corrected for whale-watching activity would be valuable. It may also be worthwhile to consider whether it is the timing or total amount of whale-watching that is important. For example, whale-watching could increase the duration of exposure to relatively high toxin concentrations if it slows the rate of weight gain as prey becomes seasonally more abundant. In addition, individuals expend far more energy when growing rapidly or lactating than at other stages of their life cycle (Kriete, 1995), so impairment of energy balance during these periods may have greater survival consequences than at other stages.

There is no doubt that more data are needed to determine whether the *actual* impact of whale-watching exceeds acceptable levels (0.2% of population size: Carretta *et al.*, 2010). The models developed here indicate there is potential for whale-watching to have important effects – mediated by energetic mechanisms – on population growth rates. The work of Ward *et al.* (2009) and Ford *et al.* (2010) suggest resident killer whale populations are near carrying capacity, so energetic effects are likely to be important to population growth rates.

Another area of work would be to develop a total ocean noise budget that includes noise from non-whale-oriented vessel traffic. It will be important to determine the conditions under which noise received from whale-watching vessels is exceeded by noise from other vessels. This will have important implications for regulating whale-watching (there may be minimal value to requiring whale-watching vessels to keep noise exposure below the actual ambient). It will also have implications for considering whether regulating non-whale-oriented traffic (e.g. commercial vessels operating within shipping lanes in critical habitat, commercial fishing, and other recreational traffic) is likely to promote recovery. If so, management actions specific to other vessels could complement whale-watching-directed actions (Clark *et al.*, 2009).

Finally, additional research should address to what degree killer whales have mechanisms to partially overcome effects of noise. For example, Au *et al.* (2004) found that the high-frequency component of echolocation clicks likely returned the strongest echo from salmon, and Bain and Dahlheim (1994) found masking noise was less effective when it came from the side of or behind the whale than when it came from the same direction as a sound in front of the whale. However, because masking occurs up to at least two octaves above the maximum frequency in masking noise (Bain & Dahlheim, 1994), and vessels produce noise to over 20 kHz (Williams *et al.*, 2002b), masking will be an issue to over 80 kHz, a frequency at which hearing sensitivity is declining and that is above the most powerful part of the click. Further, high frequencies are directional, so even though the 40–60 kHz portion of clicks will be less masked than the 20 kHz portion, the high-intensity portion of the echolocation beam at these high frequencies are less likely to reach the fish than the 20 kHz portion. High frequencies also attenuate faster than lower frequencies. This suggests that killer whales may have the ability to overcome masking by increasing the high-frequency content of clicks, but is likely to be limited in its effectiveness.

Holt *et al.* (2008) found killer whales were able to increase the amplitude of calls in the presence of noise. However, the ability to increase intensity above average is presumably present even in the absence of noise when needed for long-range communication. That is, it remains to be determined whether the maximum ranges at which it is adaptive to communicate and echolocate are less than the maximum range at which successful communication and echolocation are possible in the presence of vessel noise.

Applications to other populations and species

Any attempt to model how cetacean populations respond to disturbance hinges on knowing how cetacean populations behave generally. Our PCAD model shows that the value of the population shape parameter z influences the likelihood that disturbance will lead to population-level consequences. Although the shape parameter is essential for computing population-level effects, we are not aware of it having been published for other cetacean species. The population shape parameter, z, has been reported for some harbour seal (*Phoca vitulina*) populations in the northeast Pacific: $z = 6.77$ for Strait of Georgia (Olesiuk, 2009); $z = 2.43$ and 1.75 for inland and coastal areas of Washington State, respectively (Jeffries *et al.*, 2003). Also, a value of $z = 19.01$ has been reported for pup production of California sea lions (*Zalophus californianus*; Carretta *et al.*, 2010).

There are a limited number of cetacean species (perhaps grey whales, bowhead whales, southern right whales and bottlenose dolphins) for which precise time series of abundance estimates are available that span moderate to high fractions of carrying capacity. Even in such cases, constructing a PCAD model may be more valuable in identifying data gaps than actually performing calculations, as interspecific variability in components of the PCAD model is unknown. However, the killer whale values we present could be used as defaults to make rough estimates while species-specific data are gathered. It should be noted that the default value of z used in baleen whale models in the International Whaling Commission is 2.39, but this does not appear to have been estimated empirically (May, 1980).

The sensitivity analysis shows that for species with a smaller shape parameter than that found for killer whales, the pattern of the onset of population-level changes would be different. Measurable changes would occur at lower population levels relative to carrying capacity in populations with small shape parameters, but the magnitude of changes in these populations near carrying capacity would be smaller than that in killer whales. Because the current carrying capacity must be used, historical estimates are of limited value in habitats that have changed significantly over time (e.g. changes to prey populations due to harvest or habitat degradation).

Only 0.5–2.5% of the daytime observations of ‘southern resident’ killer whales during the whale-watch season (from 2003 to 2005) occurred in the complete absence of vessels. The time without vessels within 1000 m ranged from 9.9% to 24.3%, 400 m ranged from 19.0% to 43.3%, and the time whales spent without any vessels violating the 100 m guideline then in effect was 71.2–76.7%. The nearly continuous presence of vessels was due to sport fishers present from first light, research vessels from early morning, and commercial whale-watchers from around 9 a.m. until sunset. At night, there is still significant freight traffic, although it is not whale-oriented. This is an issue for conducting control-exposure experiments, of course, but also raises concern about the broader tendency for commercial whale-watching activities to focus, for logistical reasons, on critical habitat areas (Williams *et al.*, 2009b).

Although researchers may be permitted to closely approach killer whales, they rarely do so (~10% of vessels observed within 100 m of whales were research vessels; Bain, 2007). Close approaches occur when researchers approach for photo-identification (Ford *et al.*, 2000), biopsy darting (Krahn *et al.*, 2007), breath sampling (Raverty *et al.*, 2007), or satellite (Andrews *et al.*, 2008) and other tagging (Baird *et al.*, 2005). Prey and faecal sampling may also require close approaches (Ayres *et al.*, 2012), although the use of dogs to locate scat, and the application of DNA techniques to identify prey in scat (Hanson *et al.*, 2010) have reduced the frequency of such approaches. Behavioural and acoustical studies are best conducted without close approaches to minimize the influence of the research vessel on measured behaviour.

As southern resident killer whales approached carrying capacity, population growth slowed due to an increase in non-calf mortality. Subsequently, calf recruitment to six months of age declined as well, resulting in a net decline during the last half of the 1990s (see data in Ford *et al.*, 2005). However, we would not be surprised if other mechanisms for population change are observed in other species.

Sensitivity analyses are useful to assist making management decisions. We have provided a mathematical framework for calculating likely outcomes of various management options. For example, managers could try to strike a balance between costs to the population of whale-watching, and the benefits resulting from changes in human behaviour once passengers return home. Managers could also calculate whether allowing whale-watching poses a risk to the survival of the population. However, it is important to emphasize that the models we outlined above have not been tested, so it is unknown whether they *actually* apply to killer whales, much less other species. However, we feel that our approach provides a quantitative framework to explore how changes in energy balance could lead to population-level consequences, and in the process could provide some critical insights into management issues and identifies additional data required to resolve important management questions.

Finally, we would like to emphasize that we have only addressed energetic mechanisms. As such, our findings provide a minimum estimate of impact. Other mechanisms, such as stress, exposure to toxins, and vessel collisions may be sufficiently important to further impair population growth. Stress may impair the immune system, making individuals more vulnerable to disease (Ayres *et al.*, 2012; Rosalind *et al.*, 2011). Exposure to toxins may also impair the immune system, increasing disease risk further (de Swart *et al.*, 1996). Toxins may also impair reproduction and calf survival (Reddy *et al.*, 2001). Toxins released from vessels include unburned fuel and exhaust (Lachmuth *et al.*, 2011). Although vessel collisions are rare, and many are survivable, mortalities associated with vessel collisions have been reported (Ford *et al.*, 2000). Synergistic effects of multiple mechanisms also need to be considered. For example, impaired energy balance leads to reduced lipid storage. Disease may lead to temporary cessation of food intake, resulting in further weight loss. Thus, body condition at the onset of disease and the time it takes to overcome pathogens together determine whether the disease is fatal. Similarly, when toxins impair reproduction, but are not fatal to the mother, she continues to compete with other whales in the population for food. Whether this influences population dynamics depends on the nutritional state of the rest of the population.

Concluding remarks

The core objective of efforts to understand and mitigate the effects of whale-watching has been to ensure the survival of populations. The first rigorous studies in the 1980s simply demonstrated that short-term behavioural responses existed. Managers, both in the private sector (whale-watch operators) and public sector responded with simple guidelines. Later studies showed some practices elicited stronger responses than others, and managers again responded with more effective guidelines to preclude activities that elicited strong evasive responses from killer whales. Recent work has shown that these guidelines are insufficient to prevent effects likely to be directly related to fitness (e.g. a reduction in foraging activity and increases in energy expenditure). As managers contemplate how to respond to such results, models such as ours can be constructed to address how short-term effects might relate to population dynamics, and whether data support a correlation between the quantity of exposure and shifts in population growth and decline. As better parameter estimates become available to inform these simple bioenergetics and population dynamics models, they should provide sufficient accuracy and precision to determine whether the effects of vessel traffic are sufficient to reduce the probability that the populations will survive in the long term (i.e. do they exceed potential biological removal (PBR); Wade & Angliss, 1997), or do the cumulative effects of whale-watching and other human activities put the population in jeopardy of imminent extinction?

The resident killer whales of the northeast Pacific represent an exceedingly data-rich case study of behaviour and population biology, but they also represent an interesting study in management. The degree to which management is or is not precautionary determines how much evidence of population-level effects is needed before management actions are imposed. And as some of the science that has been done on this population is applied to other cetaceans, it is important to spell out another lesson learned – namely, that it is essential to specify quantitative management objectives that identify how much of an effect managers are willing to tolerate (limits of acceptable change: Higham *et al.*, 2008; PBR: Wade & Angliss, 1997; and uncertainty: Taylor *et al.*, 2000). Otherwise, the science can and will continue without serving any practical purpose as long as the whales persist.

Acknowledgements

This chapter represents a synthesis of work conducted over the last 20 years, so we owe thanks to many individuals and organizations. Model development was supported primarily by the Orca Relief Citizens Alliance, with additional support from Six Flags Marine World Vallejo. Field studies that contributed to this work were supported by the National Science Foundation, National Marine Fisheries Service, Minerals Management Service, the US Geological Survey, BC Parks, Fisheries and Oceans Canada, and The Jane Marcher Foundation. We also thank whale-watch operators who made our experiments possible, particularly Jim Borrowman and Bill MacKay. Helpful comments on drafts of this manuscript were provided by Mark Anderson, Mike Bennett, Chris Clark, Brad Hanson, Rich Osborne and Bob Otis. We thank Ken Balcomb, Peter Olesiuk, Rich Osborne, Bob Otis and Jodi Smith for providing access to unpublished data. And finally, we would like to thank the many people who provided assistance in the field, not only for their hard work, but also for thoughtful discussions we have had with them over the years.

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