A MODEL LINKING ENERGETIC EFFECTS OF WHALE WATCHING TO KILLER WHALE (*ORCINUS ORCA*) POPULATION DYNAMICS

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INTRODUCTION

The Southern Resident population of killer whales (*Orcinus orca*) has declined from a high of 98 in early 1995 to a low of 78 in 2001 (Bain and Balcomb 1999, Balcomb unpublished data). The causes of the decline are not well understood, but have been reported to be primarily due to a decline in food availability and exposure to toxic chemicals (Dahlheim et al. 2000). Whale watching has been raised as one of the other possible causes. However, critics of the importance of this last factor have argued that:

1) killer whale populations have grown in the presence of whale watching boats. If disturbance from whale watching were significant at the population growth level, the impact should have been observed long ago;
2) if whale watching disturbed whales, whales would move to another part of their range, and there is no evidence for this;
3) if whale watching were a significant factor in the decline of this population, the impact on J Pod would be greatest, and the impact on L Pod would be the least. In fact, J and K pods have declined to 1993 levels, while L Pod has declined to 30% below its 1993 level.

Three models were employed to address these points. The first model describes population growth of killer whale populations (Olesiuk et al. 2000). This model is 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). This was used to convert energetic costs experienced by whales due to whale watching (Williams et al. in press) to population growth effects.

The second model addresses potential effects of noise on hearing ability (Bain and Dahlheim 1994). This was used to model the decline in active space experienced by whales (Miller 2000, Erbe 2000 and 2001) due to noise.

The third model addresses the impact on foraging efficiency of reduced active space. In turn, the three models were combined to estimate the range of population scale effects possible from the reduction in foraging efficiency due to noise.

Following development of the models, the results of this study were used to discuss the validity of the arguments raised above to suggest that whale watching has no population scale effects. Finally, I assessed whether the population scale effect of whale watching could exceed the Potential Biological Removal (Wade and Angliss 1997) allowed for the Southern Resident killer whale population.

It is important to emphasize that this paper uses models and thus will not answer the question of whether whale watching **actually** has contributed in any way to the decline of this population. However, additional data required to answer this important question in the future are identified.

Exposure to Whale Watching

Whale watch activity gradually increased from 1976 to1991. There was a small jump in 1992 to a level that was sustained through 1993, followed by a rapid increase through 1997. There was a small decline from 1997 to 1998. From 1998-2001, overall whale watching activity was roughly constant, although the number of boats engaged in whale watching near Lime Kiln lighthouse declined during this period, and the number of boats in the whale watch fleet fluctuated (Otis and Osborne 2001).

In addition to the overall increase in number of boats engaged in whale watching from 1976 to 2001, there has been an increase in the number of hours per day whale watching boats are on the water, and the number of days per year whale watchers operate. In 2001, whale watch activity began picking up in April, and continued into October. A small number of operators went out before or after the core whale watching season. Recreational and scientific whale watchers were active by around 6 a.m., and some commercial whale watching continued until around sunset. There was also a small amount of effort after dark for commercial filming. Thus multiple vessels can be expected to be whale watching consistently for about 12 hours a day, six months out of the year. (While there will be some time during this core period when no whales can be located, these gaps are likely to be offset by "out of season" whale watching [pers. obs.].)

The composition of the whale watching fleet has also changed over the years. Prior to 1992, the fleet was dominated by boats operating from American ports. From 1992 through 1996, the fleet was split roughly equally between vessels from American and Canadian ports. Subsequent to 1996, the fleet consisted primarily of vessels from Canadian ports. (Otis and Osborne 2001, The Whale Museum SoundWatch Program [unpublished data]). While there are exceptions, in general, the American boats are large and operate their engines at relatively low RPM and Canadian boats are small and operate at high RPM. The shift from primarily large, low RPM vessels to small, high RPM vessels may have resulted in an increase in the average noise exposure experienced by whales.

In the early years, killer whale watching was conducted primarily by scientific researchers and professional photographers. While few in number, these individuals worked long hours in close proximity to whales to obtain photographs with sufficient detail to identify individuals or market. These early workers suspected their vessels impacted whale behavior, and began to develop guidelines they believed would minimize impact on whales. These guidelines address proximity between vessels and whales, vessel operating speeds, and orientation of the vessels relative to the whales. There are two sets of guidelines, one for Northern Residents developed by the Johnstone Strait Killer Whale Committee with the assistance of outside whale watch operators and researchers, and one for Southern Residents developed by the Whale Watch Operators Association Northwest. As commercial and recreational whale watching have surpassed photography-oriented whale watching in numerical importance, and compliance with such guidelines has increased, the nature of exposure to vessels may have changed as well.

Both sets of guidelines suggest a closest approach of about 100 meters. Both presume vessels at this range will be travelling at the same speed as the whales, which is typically around 2 m/s. That is, engines will be operating at relatively low RPM, and hence noise produced will be relatively low both in amplitude and frequency. The guidelines for Southern Residents envision faster vessel travel (3.5 m/s) at a distance of about 400 m from the whales. They also allow for travel at unlimited speeds at distances of greater than 800 m. As speed increases, the total amount of noise and the emphasis on high frequencies both increase (see Figure 1). Both sets of guidelines suggest that whales be approached from behind or to the side, not from in front.

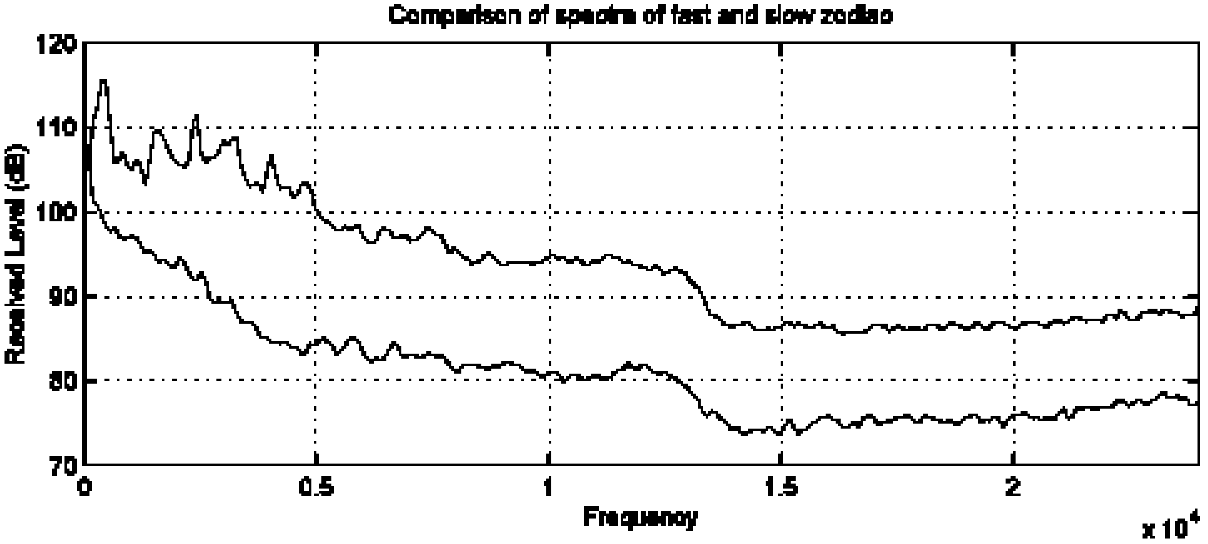

Figure 1. Noise received from an outboard powered boat at two different speeds. Note that at higher speed, the power spectral density is higher at all frequencies. Also note that for any given spectral density level, it occurs at higher frequency in the high-speed recording (Williams and Miller, pers. comm.).

Schools of whales consist of subgroups. Some of these subgroups consist of maternally related family members, while others are composed of distantly related individuals. Subgroups typically consist of a few individuals, although some individuals occasionally travel on their own. The result is that although the Southern Resident population consisted of 71-98 individuals, in general it takes fewer than 20 boats to have boats in close proximity to all whales in the population. This implies there may be a saturation level above which increased numbers of vessels will not increase impact on the population substantially. In fact, Southern Resident guidelines provide for how to take turns when the number of whale watching vessels exceeds the number of subgroups of whales.

Population Dynamics

The generalized logistic equation (Gilpin et al. 1976) models change in population growth rate as population size approaches carrying capacity. The equation takes as parameters actual population size, carrying capacity, the intrinsic rate of increase, and a shape parameter.

Olesiuk and colleagues (1990, 2000) have calculated population parameters. They found an intrinsic rate of increase of 2.92%, and a shape parameter $z=11.3$. Brault and Caswell (1993), using data from Olesiuk et al. (1990), estimated a slightly lower value of $r=0.0254$, but this does not differ significantly from Olesiuk et al.'s value. Bain and Balcomb (1999) estimated the population peaked at near 100 individuals around 1960 and again in the mid-1990's, so this was taken as an approximation of K.

Thus, the equation for annual population growth becomes:

$$\frac{\Delta N}{\Delta t} = 0.0292N\left(1-\left(\frac{N}{100}\right)^{11.3}\right)$$

Effects of Whale Watching on Whale Behavior

A variety of studies have demonstrated short-term effects of whale watching on killer whales (e.g., Kruse 1990, Williams et al. in press). Trites and Bain (2000) pointed out that energetic mechanisms could be used to estimate the magnitude of population scale effects from short-term behavioral changes.

Williams et al. (in press) found that whale watching affected swimming behavior of Northern Residents. Males traveled approximately 13% farther when being followed by boats than when traveling unaccompanied. Females changed direction more from one pair of surfacings to another when accompanied by boats than when on their own. As a result, it takes more energy for whales to travel from one place to another when accompanied by boats than under natural conditions. Nowacek et al. (2001) observed similar responses to boats by bottlenose dolphins (*Tursiops truncatus*).

Effects of Noise on Whales

Given the history of whale watching experienced by southern residents, it seems appropriate to divide exposure into five epochs. The first epoch would be the time before the introduction of motorized vessels. The second would have been the period during which motorized vessels shared coastal waters with orcas, but did not follow them. At times during this epoch, orcas may have been exposed to very loud noise from military activities and collections for public display (Hoyt 1981). The next lasted from the beginning of whale watching in the mid-1970's through 1991. During this time, the number of vessels engaged in whale watching was small relative to the number of whales. Many of the vessels in the whale watch fleet were likely to be relatively low noise vessels. From 1992-1996, the number of vessels in the fleet was often sufficient to expose all whales to noise simultaneously. The fleet probably had a roughly even mix of low and high-noise vessels. From 1997-2001, there were more than enough vessels in the fleet to expose all whales to noise a large proportion of the day. The fleet was probably composed primarily of high noise vessels.

Bain and Dahlheim (1994) found that noise could mask echolocation and impair communication required for cooperative foraging. Erbe (2000, 2001) noted that exposure to noise could result in threshold shifts, resulting in impairment of echolocation and communication even after noise exposure is terminated.

Bain and colleagues have studied hearing abilities of killer whales in the presence and absence of noise (Bain and Dahlheim 1994, Szymanski et al. 1998, Szymanski et al. 1999). These studies have shown that killer whales experience a masking effect from noise as other mammals do. The masking effect was strongest when both the test signal and the noise source were located directly in front of the whale. The relative masking effect varied on the order of 20 dB depending on orientation at 20 kHz, and to a smaller degree at lower frequencies. Whales were much more sensitive to frequencies above 4 kHz than they were to lower frequencies, and showed best sensitivity at about 20 kHz at 30 dB re 1 :Pa.

Noise can exclude killer whales from small bodies of water. In Barnes Lake, Alaska, where killer whales had become entrapped, noise generated by banging on metal pipes was used to drive the whales out of the lake. The distance maintained by the whales between themselves and the drivers suggested they were maintaining noise levels at or below the 135 db re 1 :Pa level that induced strong behavioral responses in a captive whale (Bain 1995). Morton and Symonds (in press) found that noise from acoustic harassment devices used to protect fish farms from seal predation excluded killer whales from the waters exposed to high levels of noise.

Similar effects have been found with other species of marine mammal, although different species appear to have different thresholds for leaving the immediate vicinity of the source. The noise level at which individuals transitioned from a random direction of travel to travel oriented away from airguns was relatively tight for each species, however (Calambokidis et al. 1998).

Noise produced by vessels tends to increase both in frequency and intensity as vessel speed increases. Because sound dissipates with distance, received levels fall as the distance between the vessel and the whales increases.

Outboard powered vessels operating at full speed are estimated to produce a total noise level of approximately 165-175 dB. The frequency spectrum will contain significant amounts of energy to frequencies above 10 kHz. At a distance of 800 m, the noise will have dissipated to a received level of approximately 107-117 dB. This would correspond to source levels of 147-157 dB at 100 m and 159-169 dB at 400 m. These both appear to be reasonable estimates of source levels for vessels travelling at the moderate speeds cited in the Southern Resident guidelines. That is, the Southern Resident guidelines could be interpreted as designed to limit noise exposure to the ambient level generated by non-whale related traffic in areas open to sport and commercial fishing (Bain 2001).

The admonition in both guidelines against approaching from in front parallels the finding that masking noise had its strongest effect when directly in front of whales.

Active Space. Active space is a way of describing the range over which biological signals remain biologically meaningful. This is a function of signal intensity, hearing ability, and ambient noise. As ambient noise increases (e.g., due to vessel traffic), active space decreases. The consequence of this decrease is that prey items outside the active space are undetectable by echolocation, and coordinated movements (e.g., for cooperative foraging) are impossible with individuals outside the active space.

For echolocation at maximum range,

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

where

DT = Detection Threshold,
SL = source level
TL = one way transmission loss,
TS = target strength, and
NR = 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 and Dahlheim 1994). For a given noise source, the correction for directivity is likely to be the same independent of absolute noise level.

As can be seen from the sonar equation, an increase in noise will be offset by a decrease in 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 : Pa^2 / Hz at 20 kHz (Richardson et al. 1995, see Figure 2). Ambient noise from wind, currents, and non-whale oriented traffic in Haro Strait was typically at 50 dB re 1 : Pa^2 / Hz at 20 kHz (Bain in prep.). This corresponds to an outboard operating at high speed at several kilometers distance. Thus noise from whale watching vessels above this level will increase masking and reduce echolocation range.

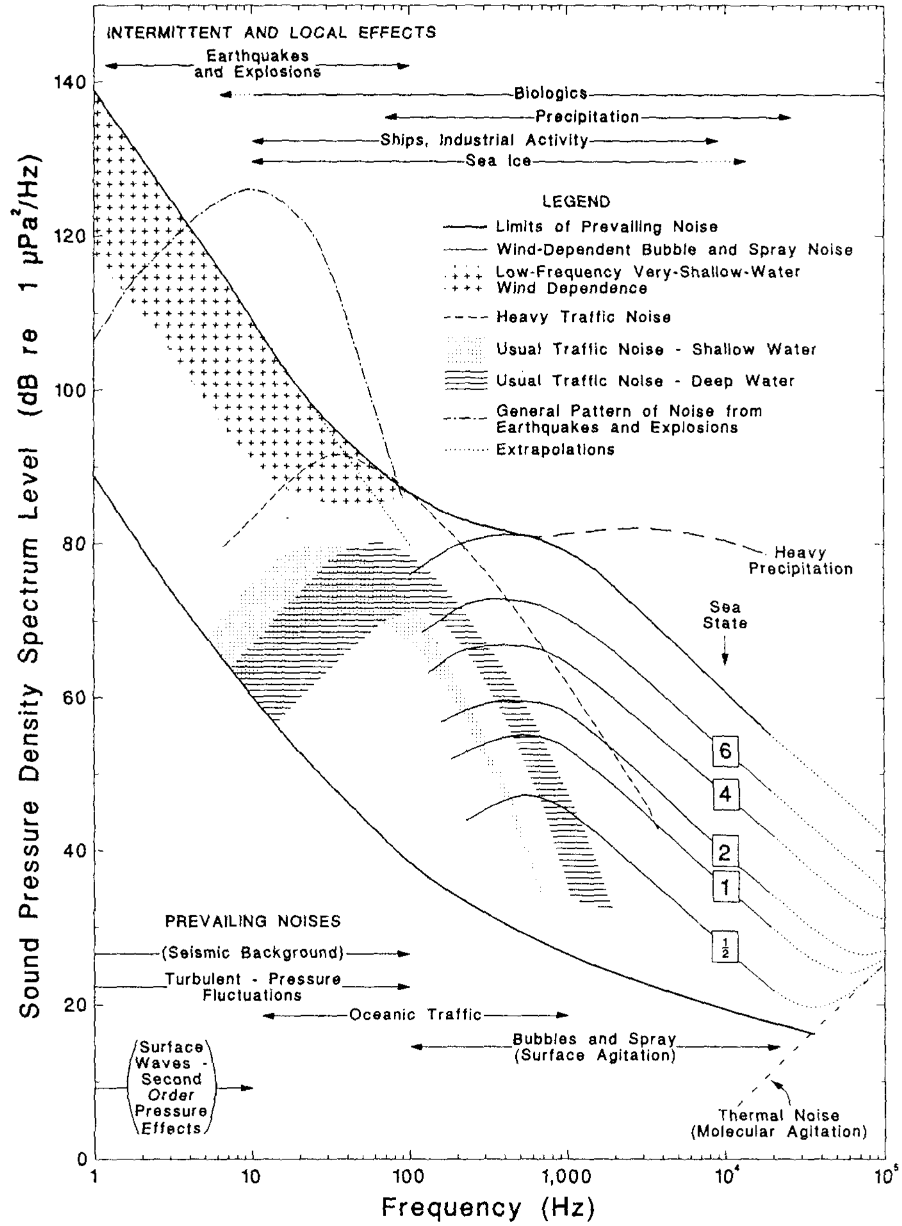

FIGURE 5.3. Generalized ambient noise spectra attributable to various sources, compiled by Wenz (1962) from many references and replotted in presently used units.

Figure 2. Ambient Noise. The figure is from Richardson et al. (1995, p. 92).

METHODS

Population Dynamics

The population growth parameters found by Olesiuk et al. (2000) were taken as best estimates for Southern Resident killer whales. These were allowed to vary to encompass the sometimes broad confidence limits in parameters they reported. Excess energy expenditure was treated as a proportional reduction in carrying capacity. Changes in population growth due to whale watching were calculated by subtracting expected growth in the absence of whale watching from that calculated with a reduced carrying capacity due to whale watching as described below.

Relationship Between Fleet Size and Whale Population Changes

Four statistical analyses were performed to assess whether there is a significant relationship between fleet size and changes in southern resident killer whale population size. The first two analyses used data from 1977 through 2001 (i.e., the whole record provided by Otis and Osborne [2001]), while the latter two used only data from five years before the 1996 peak in July 1 population size through five years following the peak (1991-2001).

For each time frame, two different time lags were evaluated. The first pair of analyses assumes overall exposure to whale watching is related to fleet size in that year. That is, the relationship tested was whether fleet size predicted population change over the year following exposure. The second pair of analyses assumed that overall exposure was related to consumer demand for whale watching services. Operators were assumed to base their fleet sizing decisions on economic conditions in the previous year. That is, the relationship tested was whether fleet size predicted population change over the year preceding exposure to that particular fleet, since both may have been based on whale watching activity in the previous season.

Correlation coefficients were calculated for each of the four conditions, and the probability of a correlation of that magnitude or higher occurring by chance was calculated. These numbers represent the strength of the relationship between fleet size and population size. They do not address whether the relationship is causal or both parameters are correlated with causal factors not considered in this analysis.

To visualize the data, raw plots were presented, which represent the “true” magnitude of the relationship. In addition, moving averages of both variables were plotted. This representation is biased toward exaggerating the relationship between the parameters, in that it discards information generated by factors that operate on different time frames than those that survive the smoothing process. With this caution in mind, this approach can be useful in structuring hypotheses for future testing.

For example, fleet size was averaged over a two year period. A strong impression resulting from this curve would suggest testing whether fleet sizing decisions were based on whale watching the previous two seasons rather than only the previous season as assumed above. That is, one would acquire data beyond the scope of this study to test whether the relationship was due to a biased effort to identify the strongest relationship out of many possibilities, or captured a heretofore unknown component of the relationship. Whale population changes were averaged over a three year period, the typical calving interval for killer whales.

Changes in Energy Expenditure due to Whale Watching

The reported 13% increase in swimming distance was assumed to replace resting behavior. This corresponds to an approximately 13% increase in energy consumption (Waite 1988, Kriete 1995). This amount was multiplied by a variety of factors to simulate different levels of whale watching. It was assumed that due to energy storage in the blubber, the temporal distribution of excess energy expenditure within the ranges considered here was not important to the calculation of population scale effects, although it may become important through other mechanisms (e.g., toxin concentration) or when effects are more extreme.

Changes in Energy Acquisition due to Noise from Whale Watching

Killer whale call and echolocation signal intensity is taken from Miller (2000). Hearing ability is taken from Bain and Dahlheim (1994) and Szymanski et al. (1999). A variety of noise levels were examined to allow interpretation of different source levels and operating distances.

Frequency structure and overall source noise level generated by vessels were estimated from the literature (e.g., Richardson et al. 1995, Erbe 2001). Noise was estimated to dissipate according to a standard spherical spreading model, to allow estimation of the noise level received by whales. Noise was considered to come from different distances to simulate different levels of whale watching intensity.

Masking effects of vessel noise were taken from Bain and Dahlheim (1994). The sonar equation was used to convert dB of masking to change in detection range.

Temporary threshold shifts were estimated from Au et al. (1999) and Erbe (2000). The reduced sensitivity to echolocation clicks was converted from dB to detection range using the sonar equation.

The potential for permanent threshold shifts in killer whales is unknown, but shifts were estimated by Erbe (2000) based on data from humans. Although the length of exposure she assumed exceeds the life span of most orcas, her proposed value was converted from dB to detection range using the sonar equation.

Normal foraging efficiency was taken as that for a whale with normal hearing in quiet conditions. Foraging efficiency impaired by noise was then expressed as a percentage of normal foraging efficiency. The following prey search tactics were considered.

Killer whales were assumed to ensonify a "tube" surrounding their travel path. The radius of the tube reflected the detection range of prey (active space). The relative probability of prey falling within the active space was taken as the ratio of detection range in the presence and absence of the effects of noise. Whether *a priori* knowledge of prey distribution affected this ratio was considered as described below (see Figure 3).

Fixed location model. In this model, prey items are assumed to be in a fixed location known to the whales (e.g., a particular territory within a reef). Whales successfully locate prey when they arrive within detection range of this location.

Linear Search Model. In this model, prey items are assumed to be along a line (e.g., a depth contour), but at an unknown position. Whales successfully locate prey when they arrive within detection range of the prey.

Planar Search Model.

> A) In this model, prey items are assumed to lie in a plane (e.g., at a fixed depth or along the bottom), but at an unknown position. Whales are assumed to travel in the plane of the prey. Prey within detection range of passing whales are detected, but prey sufficiently distant from the paths of whales are undetected.
>
> B) In this model, prey items are assumed to be at an unknown position in a plane (e.g., along the mouth of a channel or a current shear). Whales are assumed to travel perpendicular to the prey plane. Whales successfully locate prey only when they penetrate the plane within detection range of the prey.

Volumetric Search Model. In this model, prey items are assumed to be anywhere in the water mass. Whales will only locate prey if they pass within detection range of this location. A species such as chinook salmon may be distributed in a way that requires volumetric searches.

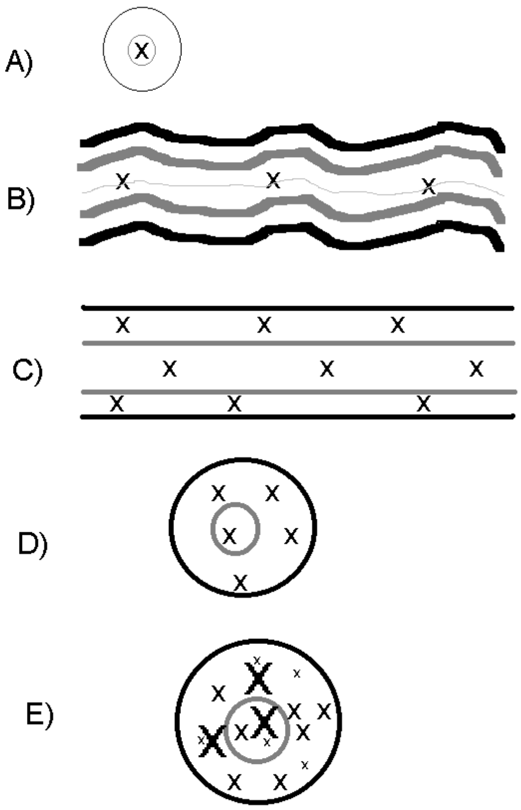

Figure 3. Search Patterns. A) known location; B) unknown location along a known line; C) unknown location within a plane with search within the plane; D) unknown location within a plane with search perpendicular to the plane; E) no information on prey location. X's within the grey boundaries represent 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.

RESULTS

Relationship Between Fleet Size and Changes in Population. The annual change in whale population size is plotted along with fleet size data in Figure 4. All four regressions yielded significant correlations. The correlations over the long term were weak (r^2=.18, p<.05 for fleet size leading whale change; r^2=.24, p <.01 for fleet size following whale population change). The correlations over the 1991-2001 period were stronger (r^2=.52, p<0.1 for fleet size leading whale population change; r^2=.70, p <.001, for fleet size following whale population change).

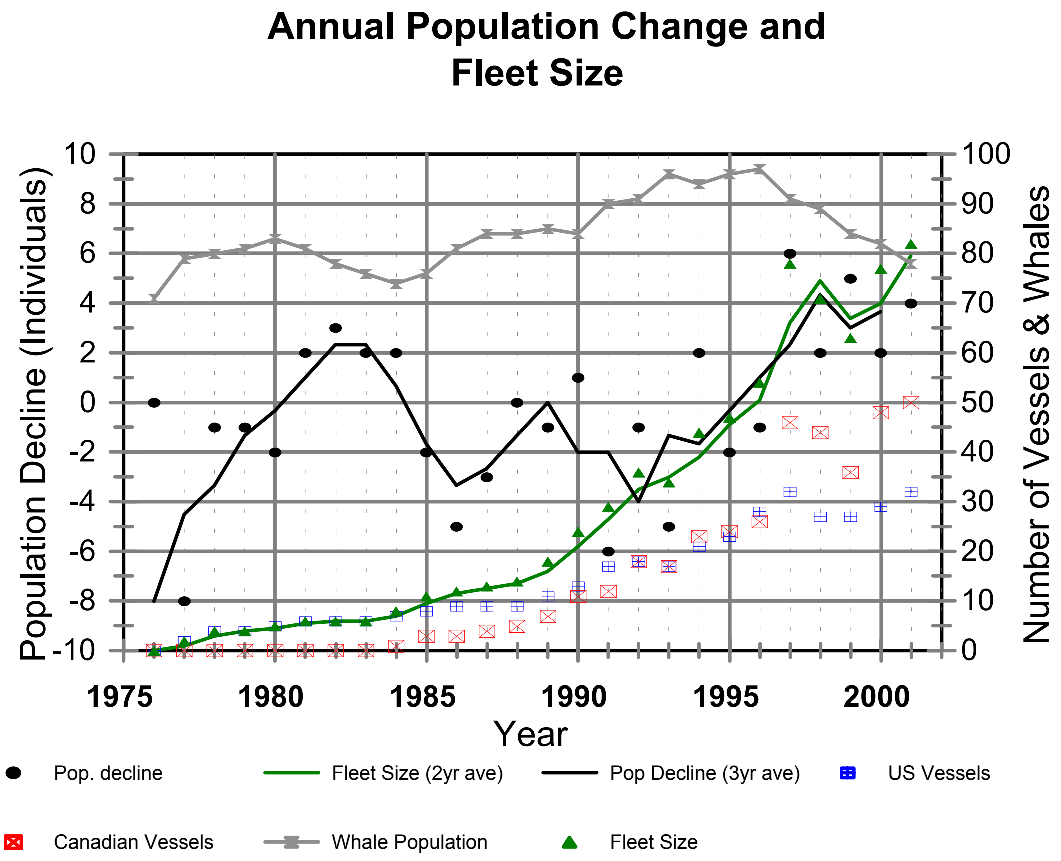

Figure 4. Relationship between fleet size and whale population changes. July 1 counts of Southern Resident population size are shown (after Wade et al. 2000 with unpublished data from Balcomb). The total number of commercial vessels actively engaged in whale watching, along with the number based in American and Canadian ports, are shown (after Otis and Osborne 2001). 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 actors 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 1990's. 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).

Changes in Energy Expenditure due to Whale Watching. Whales were observed regularly from April through October. Research and professional photography boats may approach whales beginning near dawn. In addition, sport fishing boats may opportunistically whale watch early in the morning. Commercial whale watching boats may remain with whales until shortly before sunset. Smith (unpublished data) found whales were accompanied by vessels when passing through her study site off the west side of San Juan Island approximately 90% of the time. Thus a realistic estimate is that whales are accompanied by vessels approximately 25% of the time during the year (50% of the time during the 6 mo. whale watching season). The best estimate for change in carrying capacity due to increased energy expenditure is roughly 3% (25% of 13%).

Changes in Energy Acquisition due to Noise from Whale Watching. The ability of the whale to generate echolocation clicks limits the source level, and this should be independent of noise level. Target strength is a property of the prey, and therefore is independent of noise. Thus it becomes clear that the consequence of an increase in received noise is a reduction in the one-way transmission loss that can be tolerated. That is, prey must be closer to the whale for it to be detected. Figure 5 shows the relative detection range for a variety of magnitudes of detection thresholds due to noise or threshold shifts. It also shows the corresponding reduction in area and volume remaining in the active space.

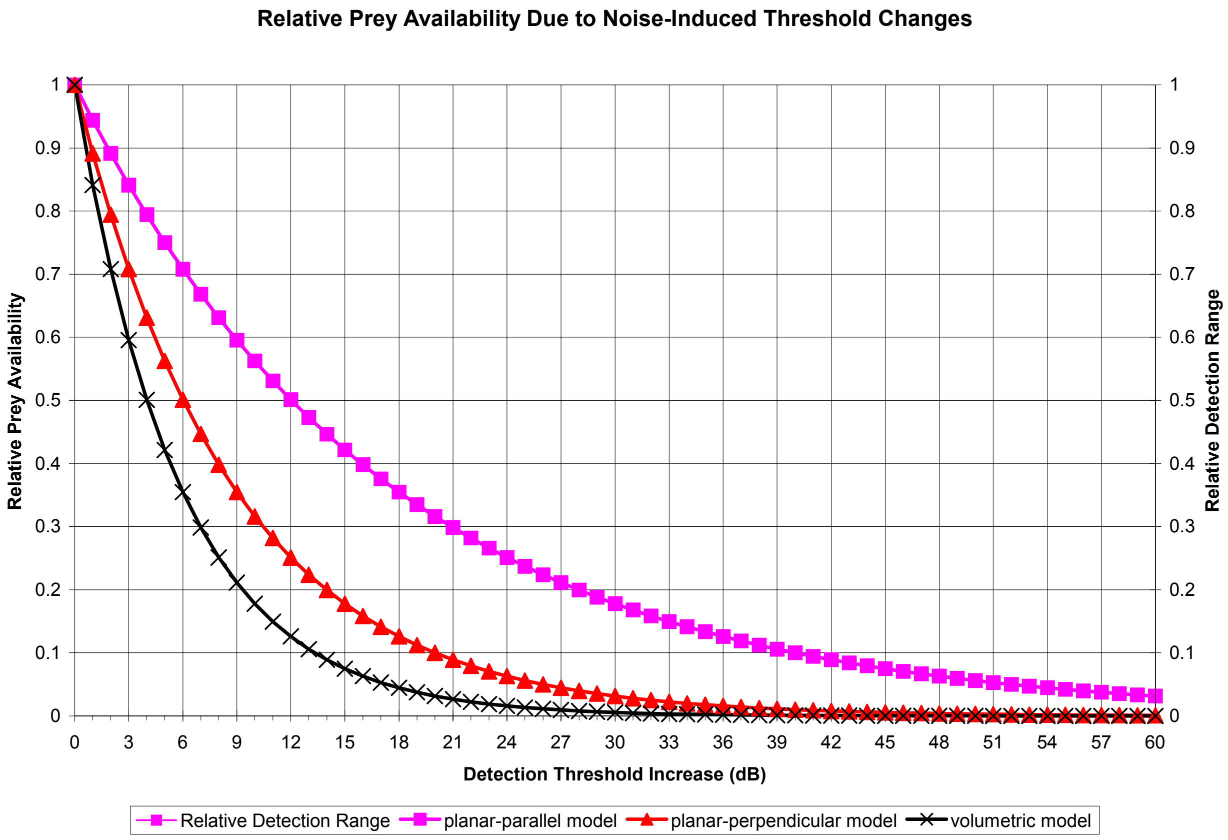

Figure 5. Detection Range and Detection Efficiency when hearing is impaired. The upper curve shows the relationship between relative detection range and magnitude of hearing impairment. This is also the curve for relative prey detection efficiency for the search within the plane model. The middle curve 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).

Masking. Received noise levels from benign whale watching (a single vessel 100 m to the side, traveling at approximately the same speed as the whale) would be on the order of 105-110 dB re 1 :Pa, with power spectral densities of approximately 70-80 dB re 1 :Pa^2 / Hz at 20 kHz (the equivalent of noise from heavy precipitation). Thus masking on the order of 20-30 dB in excess of high levels of ambient noise could be expected. As can be seen in Figure 5, a 20 dB increase in noise corresponds to approximately a 3-fold decrease in detection range. A 60 dB increase (relative to low levels of ambient noise) in noise corresponds to approximately a 30-fold decrease in detection range.

Temporary Threshold Shift. Temporary threshold shifts due to whale watching are unlikely to be large enough to exceed the effects of masking. However, in quiet water, threshold shifts may be important. E.g., a 12 dB threshold shift would correspond to a 2 fold decrease in detection range.

Permanent Threshold Shift. Permanent threshold shifts are likely to be small relative to temporary threshold shifts and masking. However, in quiet water, a permanent threshold shift of 6 dB would reduce detection range to 70% of the ideal.

Active Space. The implications of reduction in active space for foraging efficiency depend on the foraging tactics used to locate prey as described below.

Fixed location model. Since the location is known, as long as the whales retain the ability to navigate, they will find prey with the same efficiency regardless of whether their echolocation ability is impaired.

Linear Search Model. Since the whale and the fish are on the same path, as long as the whale travels faster than the fish and retains minimal navigation and sensory capability, they will find the prey with the same efficiency regardless of whether their echolocation ability is impaired.

Planar Search Model.

> A) In contrast to the previous cases, detection efficiency will be impaired if detection range is impaired. The whale detects prey within its active space on either side of its path. That is, prey detection probability is linearly related to detection range (Figure 5, upper curve).
>
> B) The decline in detection efficiency will be proportional to the square of the decline in detection range. Figure 5 (middle curve) shows detection efficiency as a function of impairment.

Volumetric Search Model. Detection efficiency will be impaired if detection range is impaired. The decline in detection efficiency will be proportional to the cube of the decline in detection range. Figure 5 (lowest curve) shows detection efficiency as a function of impairment.

Population Growth Rates. Figure 6 shows population growth under a variety of values of the shape parameter.

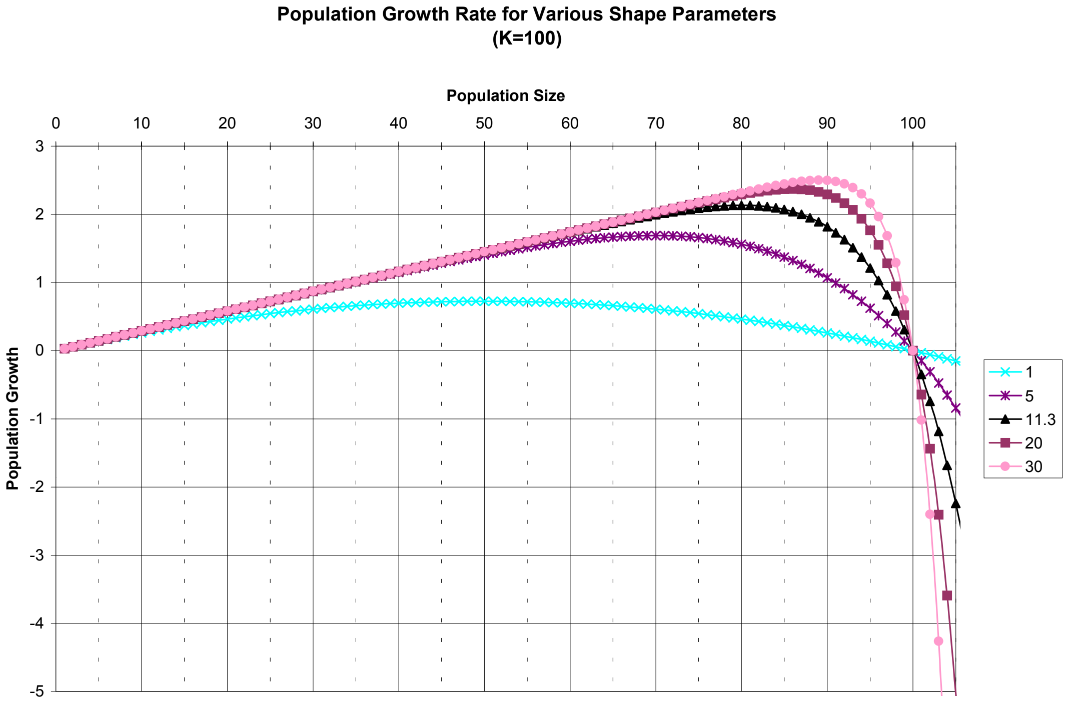

Figure 6. Population growth rates as a function of population size for a variety of Shape Parameters. The middle curve (z=11.3) is the best estimate.

Population Scale Effects. Figures 7-9 show the impact of whale watching under a variety of scenarios. Impact is expressed in terms of energetic effects on carrying capacity. Figure captions outline scenarios of impact depicted in individual figures.

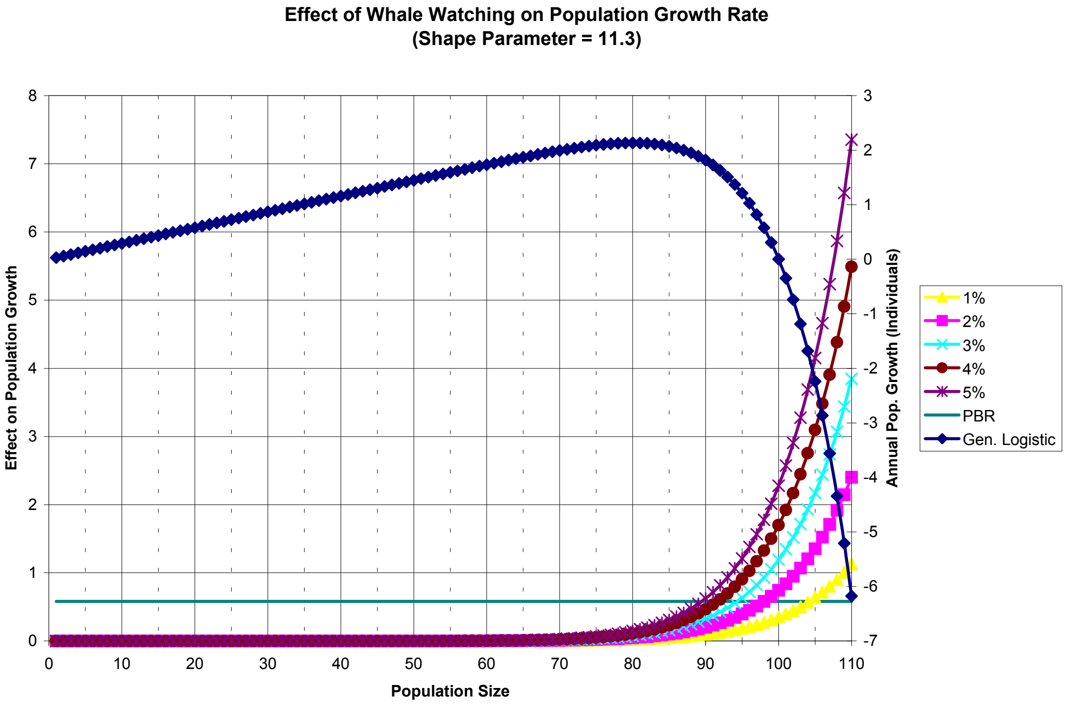

Figure 7. Population scale effects for a variety of total energetic impacts (1-5%) when the shape parameter z=11.3. Note that the curve at 3% is the best estimate. Note that only the 1% curve is below PBR at K. The 3-5% curves reach PBR at or below 95% of K. Finally, note that the impact is negligible when the population is at or below MNPL.

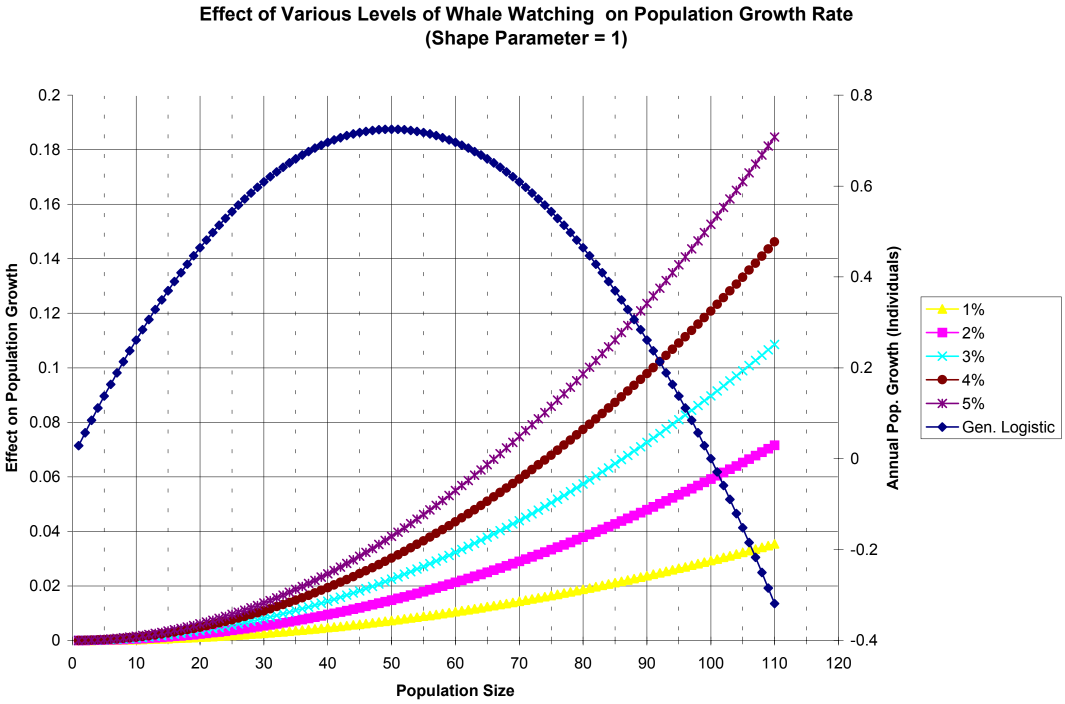

Figure 8. Population scale effects for a variety of total energetic impacts (1-5%) when the shape parameter z=1. Note that the curve at 3% is the best estimate. Also note, none of the effects on population growth exceeds PBR for this shape parameter.

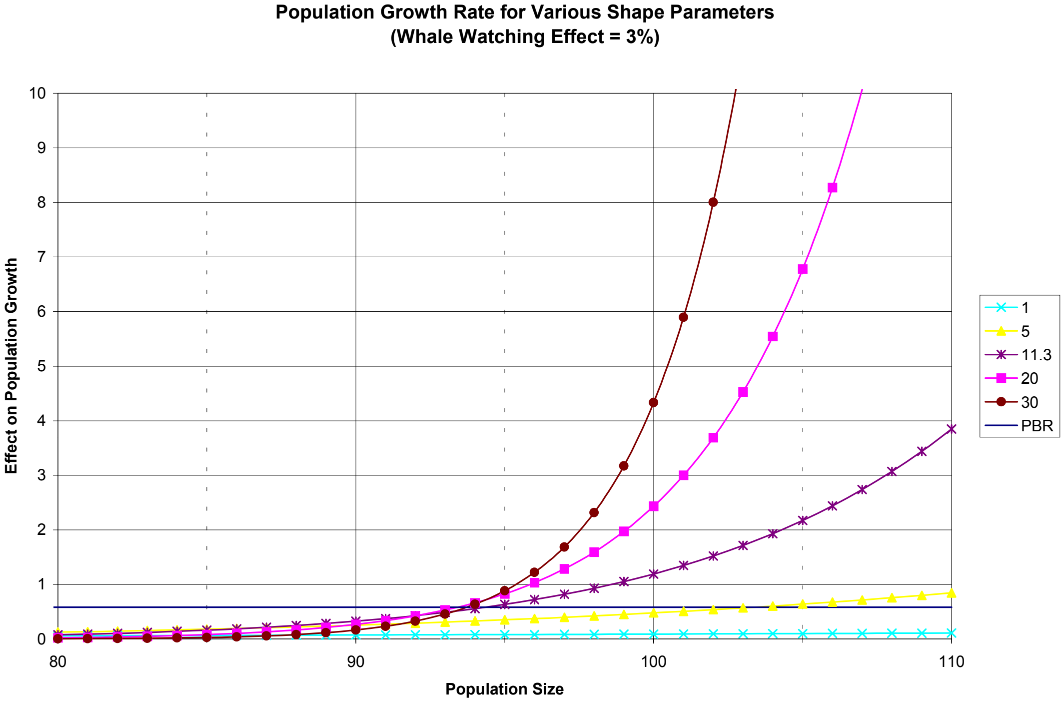

Figure 9. Population growth when total energetic impact on carrying capacity is =3% and the shape parameter z ranges from 1 to 30.

DISCUSSION

Population Growth in the Presence of Whale Watching

The strongest statistical relationship between changes in whale population and fleet size found was fleet size following population change over the 1991-2001 period. This could be interpreted in different ways. Since the change in whale population precedes deployment of the fleet, deployment could not be causally related to the change in whale population. The correlation between these parameters reflects that both are correlated with other variables that are causal and synchronized in time. If the causal variables are alternative measures of whale watching (e.g., high levels of whale watching in one season could both set limits on potential for whale population growth and lead to enlargement of the fleet the following season), then whale watching could cause the changes in whale population growth. Alternatively, interest in whale watching could drive fleet size, while something like salmon abundance could drive the changes in whale population. These two variables could be synchronized by a third variable, such as human population size, leading to correlation despite the lack of a causal relationship between whale watching and whale population growth.

There appears to be good agreement between the smoothed curves beginning in the early 1990's. This could reflect that whale watch operators typically base their business decisions on the previous two years, and that whales typically have a three year calving cycle. In this case smoothing would clarify the relationship by eliminating noise in the data. Alternatively, this could be the combination that produces the most "persuasive" results, but this would be misleading if the smoothing periods have no justification.

The energetic mechanisms discussed in this paper are only relevant when the population is food limited (whether by reduction in food stocks or accessibility of these stocks due to disturbance). Other mechanisms, such as stress or exposure to burned and unburned fuel, may lead to additional population scale effects of whale watching that are separate from energetic effects.

Relocation as a Response to Noise

It is apparent that a small increase in detection threshold will result in a dramatic reduction in prey detection capability. Au (1993) suggested that echolocation clicks could be detected reliably at about 10 dB above ambient noise. This signal-to-noise ratio would be achieved at auditory threshold for a killer whale in water at Sea State 0. That is, any additional noise, whether from natural or man-made sources, would reduce echolocation detection range. In an "urban" area like the inshore waters of Washington State, there will be nearly continuous vessel traffic affecting the acoustic environment. While whales are in these waters, the impacts of threshold shifts may be negligible, because other noise sources will have an impact of larger magnitude. However, when they are in other parts of their range, or on those rare occasions that they find quiet water, temporary or permanent threshold shifts may be important.

Where masking is the mechanism reducing detection range, this effect will only occur in the presence of boats. That is, approximately 25% of the year (or 50% of the time during the core whale watching season) would be the period of concern. Where temporary threshold shifts are the mechanism, the effect might persist for up to 24 hours after exposure to noise if the duration of the effect in killer whales is the same as that in humans. Since whales may only go 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 bottlenosed dolphins (*Tursiops truncatus*, Nachtigall et al. 2001). In that case temporary threshold shifts would only slightly increase the effect of noise relative to masking alone. Where permanent threshold shifts are the mechanism, reduced detection range would be a problem year round.

It is likely that noise from non-whale oriented recreational boating and commercial vessel traffic would reduce effective echolocation location range by a factor of about 3-5 off San Juan Island. In the absence of knowledge about prey distribution, this would result in a reduction of available prey by over 95%. Under the planar model (perpendicular approach), available prey could be reduced by around 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, 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. Even with this correction, 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 recent decline. This corresponds to an increase in noise received by killer whales on average of as little as 9 dB, depending on the foraging tactics used.

Although Morton and Symonds (in press) found noise excluded Northern Residents from peripheral habitat near a core area over a period of years, this does not imply whales will always move in response to disturbance. The model presented here illustrates that relatively small impacts on fish availability can produce population scale effects that exceed Potential Biological Removal. Thus population scale effects of whale watching could exceed PBR even when the effect on the population is too small for it to be adaptive for the population to relocate. Since whale watching takes place in what appears to be the best part of the Southern Resident range, relocation to much less desirable habitat may be maladaptive relative to remaining in degraded habitat. This contrasts with the case described by Morton and Symonds, in which nearby areas with similar prey densities (or perhaps higher prey densities, but with more intra-specific competition) were available.

Modifications of Whale Watching Practices to Reduce Impact

If the correlation between fleet size and population growth rate reflects a causal relationship between whale watching and killer whale population dynamics, this would have important implications. The 44% increase in the number of commercial whale watching boats between 1996 and 1997 is synchronous with the transition from the period of whale population growth to the period of rapid decline. Thus to stabilize the population it may be necessary to reduce whale watching to 1995 levels, when the fleet was about 60% of its 2001 size (~50 vessels). The population appears to have begun tracking fleet size in the early 1990's, when the fleet was about 40% of its 2001 size (~30 vessels). Reduction of both the number of vessels regularly engaged in whale watching, along with time-area closures to limit their effort to levels of the earlier years, may be necessary to restore healthy population growth.

Williams et al. (2001), in a study of northern residents, noted some behavioral responses to vessel traffic appeared to diminish between the mid-1980's and the mid-1990's, and one possible explanation was that operators had learned to maneuver their vessels in a way that had less impact on whales than practices in the early years. While measurements of noise under real-world conditions need to be made to be certain, it appears that guidelines for killer whale watching may reflect an understanding of the effects of noise at a "traditional knowledge" level, and responsible operators amended their practices accordingly. While it is also possible that some whales in the population habituated to the presence of vessels, this is at best a limited explanation since responses to vessels were still present after more than 20 years of whale watching (Williams et al. in press).

Southern Resident guidelines allow operators to periodically reposition their vessels in front of whales rather than travel to the side at a constant distance as recommended in the Northern Resident guidelines. When a vessel stops in front of whales, the whales have the option of changing their direction of travel to avoid the vessel or continue their previous course and closely approach it. Some operators use repositioning as way to get around distance guidelines because sometimes, "the whales come to them." However, it is important to note that travelling at a high rate of speed to get in front of whales increases the noise level received by the whales, and as the vessel approaches the path of the whales, its noise comes from the direction that maximizes masking. In light of the understanding that noise should be a consideration in establishing guidelines, it is not surprising that this practice is controversial.

Differential Effects on Different Pods

Olesiuk et al. (1990) reported that Southern Residents were identified a total of 502 times in their work: 311 sightings of J Pod, 240 of K Pod, and 198 of L Pod (more than one pod was present on many occasions). Since L pod was the least frequently sighted, it is probably less exposed to whale watching than the other pods. Therefore, it is unlikely that the excess decline in L pod was driven solely by whale watching.

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 ranged from 7.4 to 59%, a range of a factor of eight. Some of this variation is likely due to methodological issues (e.g., the location on the body of the sample). However, some of this variation probably reflects real variation in fat reserves. Since a high proportion of lipids are in the blubber (Borrell et al. 1995), total body concentrations of toxins may vary substantially with energy balance. That is, if whales lose weight, their toxin concentrations could increase even if total body burden remains constant.

Evans et al. (2001) issued a report identifying mid-frequency sonar as a likely cause of the beaked whale stranding in the Bahamas in 2000. They indicated resonance was a potential mechanism for normally harmless sound levels to cause serious or lethal injuries. They indicated use in a restricted waterway may have prevented whales from moving to safe distances. The same type of sonar is used in the Southern Resident range, including in narrow waterways (pers. obs.). Since killer whales are similar in size to many of the whales impacted in the Bahamas (many were 17-18 feet, and larger minke whales [21-27'] were also affected), it is likely that killer whales would also be vulnerable to injury from this type of sonar. Impact from human activities such as this could differentially affect one pod.

Re-evaluation of PBR

The generalized logistic model with z=11.3 (Olesiuk et al. 2000) shows per capita growth is nearly independent of population size to at least 70% of K. Olesiuk et al. (1990) calculated the per capita growth rate while the Northern Resident population grew from less than 50% of K to less than 75% of K. In contrast to the situation where z=1, their estimate of R_{MAX} (0.0292) would be a valid estimate. Likewise, the calculation by Brault and Caswell (1993: 0.0254) would be valid. While it is not clear whether Olesiuk et al's (1990) or Brault and Caswell's estimate of R_{MAX} is more accurate, they are both less than the default value of 0.04. The Guidelines for Assessing Marine Mammal Stocks (Wade and Angliss 1997) suggest using stock specific values rather than the default value for R_{MAX} when available. Thus, R_{MAX} should be reduced in the calculation of PBR.

Currently, Potential Biological Removal due to human factors is

$$PBR = N_{MIN}\, ½\ R_{MAX}\, F_R = 0.8,$$

where N_{MIN}=84,
R_{MAX}= 0.04, and
F_R=0.5

for Southern Residents (Forney et al. 2000).

However, with the decline of the population since the count used in that estimate, and justification for accepting the lower R_{MAX} values rejected in that report, the PBR is reduced to about 0.5. Should the proposal to list the population as endangered be accepted, PBR would drop to 0.1. While mortality due to immediate injury appears to be 0, the model developed here suggests that in reality, there could be a non-zero take. A take of one whale every two years would justify classifying the stock as strategic, and a take of one whale every 15-20 years would not be considered insignificant for this stock. The model presented here indicates that under a range of reasonable assumptions, the impact of whale watching on this population could easily be of this magnitude or greater. Thus NMFS should consider actively managing this population, even if it does not list it under the Endangered Species Act.

Whale watching, by increasing energy expenditure and reducing foraging efficiency, may have an impact on population growth equivalent to lethal removal in excess of PBR. While the model suggests population growth would be indistinguishable between disturbed and undisturbed populations over a wide range of population sizes, it also suggests whale watching may have an important effect at high population density.

Future Work

This study will have several applications. By focusing on a subset of the consequences of whale watching, it will provide a minimum estimate of the population scale effects of whale watching. By generating a quantitative model, impacts can be estimated for a variety of scenarios (e.g., different levels of whale watching [hours / day, days / year, noise exposure], impacts at different population levels, interaction effects of whale watching and other factors such as prey availability). In addition, the consequences of other impacts that are mathematically equivalent could be evaluated (e.g., reduction in food availability due to reduction in salmon stocks would be mathematically equivalent to reduction in food availability due to noise).

To go from a model to something that is sufficiently likely to apply to the real world, several additional studies will be necessary.

This paper used the magnitude of behavioral responses observed in Northern Residents. It would be important to replace these data with data from Southern Residents.

A detailed analysis of whale watch operators' logs would allow determination of time spent with whales and a more rigorous assessment of whether the correlation between fleet size and whale population changes reflects a causal relationship.

It will be important to determine actual noise exposure to refine the estimate of acoustic impact on foraging efficiency. Further, it will be important to determine foraging tactics to assess the importance of reduced detection ranges. Studies of threshold shifts and more detailed studies of directional hearing and masking, conducted with captive killer whales, would also be valuable.

A quantitative determination of the relationship between prey availability and carrying capacity is also necessary. This is probably best addressed by a study of prey availability and its correlation with population growth that is more extensive than those conducted to date.

Further consideration of whether the timing of whale watching is important, or only the total amount, as modeled here, may be worthwhile. For example, if whale watching slows the rate of weight gain as prey seasonally becomes more abundant, it could increase the duration of exposure to relatively high toxin concentrations. In addition, individuals expend far more energy when growing rapidly or lactating than at other stages of the life cycle (Kriete 1995), so impairment of energy balance during these periods may have greater consequences than at other stages.

SUMMARY AND CONCLUSIONS

The analysis presented here discredits the first two arguments against whale watching having a population scale effect. While the third sets an upper bound indicating other factors in addition to whale watching are likely to be important, it still allows the effect of whale watching alone to be large enough that management intervention would be merited.

Although killer whale populations have grown in the presence of whale watching, the model indicates this was to be expected, as the population level effect would have been negligible until the population approached carrying capacity. In addition, the lack of population growth at current levels of whale watching undermines the premise of this argument.

While whale watching may well degrade habitat quality to the degree that it effects population growth, unless alternative habitat that is better than the degraded habitat is available, there will be no selection to move. For example, moving out to Juan de Fuca Strait may successfully evade most whale watching boats, but would place orcas in habitat where prey density may be far lower than in Haro Strait, and optimal foraging tactics are unknown to the whales.

Although whale watching is unlikely to be solely responsible for the excess decline in L Pod, the failure to grow of J and K pods indicates that there may be excess mortality that exceeds

Potential Biological Removal. If in fact, whale watching has increased mortality to this extent, Southern Residents should be declared a strategic stock and a take reduction team should be formed to reduce human induced mortality.

With the population depleted from collections for public display and fish stocks relatively healthy, the Southern Resident population was probably well below carrying capacity in the 1970's. According to this model, whale watching is unlikely to have any population scale effect under that condition. In the 1980's through the early 1990's, 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 1990's, 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 the last decade. The model indicates that if the effect on the population is large, missed prey due to noise is probably a more significant mechanism than excess energy expenditure. The correlation between fleet size and whale population trends merits careful evaluation.

Distance-based guidelines alone do not reflect all the expertise experienced whale watchers have gained about how to minimize their own impacts on whales. It may be that taking physical measurements of noise generated by whale watching vessels would allow more refined guidelines to be generated by combining traditional knowledge with scientific methods. It is important not only to consider distances between vessels and whales, but also how those vessels travel and where they are relative to the whales.

The high value of the shape parameter has many implications:

1) The maximum net productivity level for the population is over 80% of K, not the NMFS default of 50-60%.
2) The measured population growth rate is essentially equal to the intrinsic rate of increase at low to moderate values of N, rather than only at small values of N.
3) The population growing at the intrinsic rate of increase gives the population resilience to moderate catastrophes such as mass stranding, hence reducing its susceptibility to extinction due to random fluctuation.
4) PBR is lower than when calculated based on $z=1$.
5) The population level impact of disturbance is high when the population is near or above carrying capacity, as is likely to have been the case the last few years.
6) The population level impact of disturbance is low when the population is well below carrying capacity. Thus population growth in the presence of disturbance cannot be used to conclude that disturbance will not affect the population at high population densities.
7) The Southern Resident stock should be considered to be depleted, as it is currently below its maximum net productivity level.
8) Any human induced mortality or serious injury at levels exceeding one individual every two years to one individual every ten years needs to be reduced.

More data are needed to determine whether or not the **actual** impact of whale watching exceeds "insignificant levels approaching zero." However, following the precautionary principle would require regulation of the potential impacts of whale watching until data are available to indicate the regulations are unnecessary.

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