

1 **Estimating relative energetic costs of human disturbance to**  
2 **killer whales (*Orcinus orca*)**

3

4 Running title: Williams, Lusseau & Hammond: Estimating energetic cost of  
5 disturbance

6

7 ROB WILLIAMS<sup>a,b\*</sup>, DAVID LUSSEAU<sup>c,1</sup> AND PHILIP S. HAMMOND<sup>a</sup>

8

9 a - Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, St  
10 Andrews, Fife KY16 8LB, Scotland, UK

11 b - Pearse Island, Box 193 Alert Bay BC, V0N 1A0, Canada

12 c - Lighthouse Field Station, University of Aberdeen, George Street, Cromarty, Ross-  
13 shire IV11 8YJ, Scotland, UK

14 1 – Present address: Dalhousie University, Department of Biology, 1355 Oxford Street,  
15 Halifax NS, B3H 4J1, Canada

16 \* - To whom correspondence should be addressed (E-mail: [mew@st-andrews.ac.uk](mailto:mew@st-andrews.ac.uk); Tel: +1  
17 250 974 7103; No fax number)

18 Abstract: 248 words

19 6 keywords/phrases

20 5263 words

21

22 **Estimating relative energetic costs of human disturbance to**  
23 **killer whales (*Orcinus orca*)**

24

25 **Abstract**

26 This study examined the activities of “northern resident” killer whales (*Orcinus*  
27 *orca*) in Johnstone Strait, British Columbia, Canada, in July and August, from 1995  
28 to 2002. Disturbance from vessels has been identified as a conservation concern  
29 for this population. The primary aims of the study were to test whether boat  
30 presence altered whales’ activities, and if so, to estimate whether behavioural  
31 responses were likely to have carried energetic costs. A land-based observation  
32 site near a vessel-exclusion marine protected area allowed us to conduct a natural  
33 experiment to monitor whale activities in the presence and absence of boats. Using  
34 Time-Discrete Markov Chain models, boat presence was linked to significant  
35 changes in the probability that focal whales would switch from one activity state to  
36 another, which led to significantly different activity budgets in the presence and  
37 absence of boats. We estimated that the energetic cost of meeting these budgets  
38 differed by only 3-4%. In the presence of boats however, whales reduced their  
39 time spent feeding and the time spent rubbing their bodies on smooth pebble  
40 beaches. These lost feeding opportunities could have resulted in a substantial  
41 (18%) estimated decrease in energy intake. Our sensitivity analysis provides  
42 preliminary evidence that disturbance could carry higher costs to killer whales in  
43 terms of reducing energy acquisition than increasing energetic demand, and future  
44 research should address this directly. Meanwhile, our observations suggest that  
45 protected areas would confer greatest conservation benefit to endangered killer  
46 whale populations if they were designed to protect important foraging areas.

47

48 **Keywords:** behavioural response, marine protected area, cetacean, whalewatching,  
49 bioenergetics, activity budget

50

## 51 **Introduction**

52 Some predators are valued by humans, either for their ecological or aesthetic attributes,  
53 whereas others are viewed as pests. Increasingly, applied ecologists are asked to  
54 consider effects of anthropogenic activities on valued predators (Gill et al., 2001 ;  
55 Ormerod, 2002). For reasons of tractability, animals' behavioural responses are often  
56 used to indicate their vulnerability to disturbance, although the relationship between the  
57 strength of these responses and the underlying sensitivity of wildlife is unlikely to be  
58 straightforward (Beale and Monaghan, 2004a, b). Certainly, equating lack of response  
59 with indifference is incorrect – those animals least likely to exhibit avoidance responses  
60 may simply be those that can least afford to demonstrate their sensitivity, namely those  
61 in poorest body condition (Beale and Monaghan, 2004b).

62

63 This complexity becomes especially apparent when dealing with conservation and  
64 management of cetaceans (whales, dolphins and porpoises), which are long-lived and  
65 elusive study animals. Cetaceans are also exposed to a variety of both targeted and  
66 incidental human activities in the marine environment. While the effects of direct  
67 mortality impacts, such as by-catch or whaling, can be unambiguously related to  
68 population-level consequences (Slooten et al., 2000), it is very challenging to assess the  
69 potential long-term effects of anthropogenic activities, such as whalewatching, which  
70 elicit subtle, short-term reactions (Bejder et al., 1999; Williams et al. 2002a, b;

71 Lusseau, 2003a). Clearly, linking short-term behavioural responses to long-term  
72 population-level impacts presents difficulties, a fact that can lead to the false, or at least  
73 premature conclusion that human activities have no biologically significant effects on  
74 the targeted animals. In 1993, the International Whaling Commission (IWC) adopted a  
75 resolution that declared its desire "to encourage the further development of whale  
76 watching as a sustainable use of cetacean resources" (IWC, 1994). Recent studies  
77 however have raise concerns about the consequences of anthropogenic activities in the  
78 marine environment on cetacean populations generally, and an unchecked development  
79 of the whalewatching industry more specifically. There are indications that repeated  
80 short-term avoidance tactics can lead to long-term impacts at the population level, either  
81 through habitat displacement (Morton and Symonds, 2002; Lusseau, 2005; Bejder et al.,  
82 In press), which can reduce the fitness of targeted populations, or via physiological  
83 constraints at the individual level (Lusseau, 2003b), which may lead to decreased  
84 reproductive output (Lusseau, 2003b). For a food-limited population, energetics can  
85 provide the missing causal link between demonstrable short-term behavioural responses  
86 and difficult-to-detect population-level impacts. This study presents the results of a  
87 sensitivity analysis to assess whether short-term behavioural responses were likely to  
88 carry energetic consequences for killer whales (*Orcinus orca*) in the northeast Pacific.

89

90 Three killer whale ecotypes are found in the coastal waters of British Columbia (BC),  
91 Canada (Ford et al., 2000): mammal-hunting *transients*; recently identified and poorly  
92 studied *offshores*; and northern and southern communities of fish-eating *resident* killer  
93 whales. A core area for "northern residents" is found in Johnstone and Queen Charlotte  
94 Straits (Fig. 1; JSKWC, 1991). The northern resident community comprises 34  
95 matriline, the basic killer whale social unit (Ford et al., 2000). Many matriline return

96 to the area each summer to mate, feed on salmon, and rub their bodies on smooth pebble  
97 beaches (Ford et al., 1998, 2000; Ford and Ellis, In press). One of the area's benefits to  
98 killer whales is the tendency for narrow Johnstone Strait to concentrate migratory  
99 salmon (Nichol and Shackleton, 1996). Commercial fishing vessels, freighters, cruise  
100 liners and commercial and recreational whalewatching boats also use the area heavily.  
101 Part of this area has been set aside in 1982 as a killer whale sanctuary (Robson Bight-  
102 Michael Bigg Ecological Reserve, RBMBER) to prevent boaters from approaching the  
103 gravel beaches on which the whales rub (Ford et al., 2000). The functional role of this  
104 activity is unknown, but beach-rubbing behaviour is rarely seen in other cetaceans.

105

106 The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) currently  
107 lists northern resident killer whales as *Threatened* (Baird, 2001). Their listing was  
108 made partly in response to lack of population growth; and more recently, a population  
109 decline observed in annual censuses (Ford et al., 2000). While the cause(s) of the  
110 decline remains unknown, it is generally agreed that both northern and southern resident  
111 communities face a variety of threats (Baird, 2001) in the form of reduced prey  
112 availability (Allendorf et al., 1997), high toxin loads (Ross et al., 2000), and  
113 anthropogenic disturbance (Williams et al., 2002a, b). The most contentious example of  
114 human disturbance may be commercial whalewatch operators, however these represent  
115 only a small fraction of the vessels that use the same waters as northern resident killer  
116 whales in Johnstone Strait, and their compliance with the Reserve boundaries was  
117 highest of the ten vessel types in the area (Wong and Williams, 1998; Ashe and  
118 Williams, 2003).

119

120 The decision to create a reserve proved prescient when, subsequently, studies began  
121 reporting correlations between vessel traffic and whale behaviour (Kruse, 1991). Even  
122 non-whale-oriented vessel traffic, such as fishing boats, altered the behaviour of killer  
123 whales (Williams et al., 2002a). It is unclear whether these subtle avoidance responses  
124 observed in experimental studies carried energetic costs to whales and it is unknown  
125 whether animals were equally vulnerable to disturbance in all activity states. Previous  
126 experimental studies targeted only whales engaged in typical “travel/forage” activity, in  
127 order to avoid confounding effects of activity state and vessel traffic on whale  
128 behaviour (Williams et al., 2002a, b). No quantitative attempt has been made to assess  
129 whether the sensitivity of these animals to disturbance varies with the whales’ activity  
130 state. Consequently, it is unclear whether the focal animals sampled in impact  
131 assessments conducted to date were representative of population-level responses. An  
132 impact assessment should include subjects from all age-sex classes and span the entire  
133 repertoire of activity states.

134

135 The primary goal of this study was to test whether whale activity budgets differed when  
136 boats were present from activity budgets when boats were absent. The fact that time-  
137 activity budgets can be linked to energetic demands in this species (Kriete, 1995) set a  
138 secondary goal: to estimate whether the energetic demand of killer whales in the  
139 presence of boats was greater than in their absence. This framework, using killer  
140 whales as an example, can serve as a model linking field observations of short-term  
141 responses to human activities to longer-term energetic effects at individual and  
142 population levels. This study illustrates the utility of integrating behavioural studies and  
143 physiology into conservation strategies for large mammals (Sutherland, 1998).

144

145 **Methods**

146

147 DATA COLLECTION

148 Data were collected from a cliff on West Cracroft Island (Fig. 1) approximately 50m  
149 above mean water level, which offered an expansive view across Johnstone Strait. Field  
150 seasons varied in length among years (1995-2002), but the longest period common to all  
151 years was 1 July - 31 August. A minimum of three observers recorded boat and whale  
152 activity from 08h00 to 20h00 daily. The study area was divided into eight zones, four  
153 inside the Reserve and four in the waters immediately adjacent to the Reserve. These  
154 zones were readily identifiable from the cliff based on sightlines drawn to prominent  
155 landmarks. Every 15 min, these observers scanned the area with 7X50 binoculars and a  
156 25X50 spotting scope to record the number of boats in each zone of the study area.

157

158 Whale activity was recorded on the same 15-min schedule by scanning the main activity  
159 of whales in focal groups (Altmann, 1974). Whales were recorded as being in a group if  
160 they were within approximately ten body lengths of one another, and displaying the  
161 same behaviour at the surface. Once whales entered the study area, observers used both  
162 visual and acoustic cues to identify individuals using photo-identification catalogues  
163 (Ford et al., 2000). The exact identification of individuals was not always necessary to  
164 follow groups because of the ease of tracking separate schools across sampling periods.  
165 Focal groups were defined post-hoc from the subset of the data in which group  
166 composition remained constant across a sequence of samples.

167

168 Whale activity recorded during each 15-min scan sample was assigned to one of five  
169 mutually exclusive and cumulatively inclusive activity states (Table 1). The definitions

170 of these states were adapted from those used in other killer whale behaviour and  
171 bioenergetics studies (Felleman et al., 1991; Hoelzel, 1993; Kriete, 1995; Barrett-  
172 Lennard et al., 1996; Ford et al., 2000; Lusseau et al., 2004; Ford and Ellis, In Press). At  
173 each scan, the whales were recorded as being either inside or outside the reserve, based  
174 on zone boundaries. This allowed subsequent accounting for known effect of location  
175 on whale behaviour (e.g., beach-rubbing). They are presented roughly in order of  
176 increasing energetic cost of the activity, as estimated from captive and field experiments  
177 on killer whales by Kriete (1995) (Table 1).

178

#### 179 DATA ANALYSES

180 Adjacent 15-minute observations were unlikely to be statistically independent, so the  
181 scan sample data were analysed as a series of time-discrete Markov chains (TDMC)  
182 (Lusseau, 2003a, 2004). This technique allowed us to model the probability of a focal  
183 group switching from one activity state to another as a function of a given factor (in this  
184 case, boat presence in the same zone as the whale), and therefore to quantify the effect  
185 of this factor.

186

187 Two binary grouping variables were created. First, each scan sample of whale activity  
188 was given a value for location, either inside or outside the Reserve. The dataset was  
189 further categorised depending on the presence of boats. If no boats were present in the  
190 same zone as a focal group of animals, then that scan was identified as a control (i.e.,  
191 no-boat) observation, regardless of whether boats were present in other parts of the  
192 study area. Similarly, observations were scored as treatment (i.e., boat-present)  
193 observations only when boats were present in the same zone as the focal animal. Focal

194 follows were separated into four data files: those in the presence versus absence of  
195 boats, and those inside versus outside the Reserve.

196

197 Program UNCERT (available from <http://uncert.mines.edu>) was used to tally the  
198 number of times one state was observed following another from these series of samples,  
199 conditional on location of the focal group and boat presence in the same zone as the  
200 whales. Four-way contingency tables were constructed with the following categories:  
201 preceding activity (5 possible states, factor labeled P in the model on Fig. 2), succeeding  
202 activity (5 possible states, labeled S in the model), boat traffic (present or absent,  
203 labeled B) and location (inside or outside the Reserve, labeled L).

204

205 Dependence of transitions in activity states on location and boat traffic variables was  
206 tested for in SPSS 10.0 (SPSS, Inc.) using General Log-Linear Analysis. The candidate  
207 independent covariates in this case were boat traffic and location, and the response  
208 variable was the number of times one state was observed following another. The G-  
209 statistic for goodness-of-fit was computed for each model and the difference between  
210 the G-values was used to test the significance of the term being left out (Caswell, 2001).

211 To test for the effects of location and boat presence, these terms were added  
212 sequentially to the null model assuming that succeeding state was dependent on  
213 preceding state (included terms **PS** and **PBL**, Table 2) (Lusseau, 2003a). The effect of  
214 both boat and location were then tested by adding the dependence of **S** on each of these  
215 factors (by adding the terms **BS** and **BPS**) (Lusseau, 2004). The best fitting model was  
216 selected using Akaike's Information Criterion (Burnham and Anderson, 1998) (Fig. 2).  
217 This analysis therefore provided not only a way of identifying the best fitting model, but

218 also a way of quantifying the significance of the contribution of each factor to  
219 explaining the variance observed in the dataset.

220

221 The transition probability matrices obtained from the contingency tables were  
222 eigenanalysed using the PopTools add-in for Excel, to estimate the stationary  
223 distribution of each matrix, which corresponded to the left eigenvector of the dominant  
224 eigenvalue (Caswell 2001). This eigenvector corresponds to the time-activity budget of  
225 the population (Caswell 2001; Lusseau 2004). Activity budgets were calculated in the  
226 presence and absence of boats.

227

228

## 229 ESTIMATING ENERGETIC REQUIREMENTS FROM TIME-ACTIVITY

### 230 BUDGETS

231 The time-activity budgets observed with respect to boat presence were converted to  
232 rough estimates of the energetic demand of free-ranging killer whales (Kriete, 1995).  
233 Only Kriete's data from *Hyak* (a 4 733kg adult male) and *Yaka* (a 2 800kg adult female)  
234 were used, rather than values for both adult and sub-adult subjects, because data on the  
235 sub-adult female were thought to be unreliable (Kriete, 1995). For comparative  
236 purposes, we also calculated theoretical field metabolic rates for individuals of known  
237 weights to estimate energetic demand (Kleiber, 1975). The estimates presented thus  
238 illustrate the energetic demand for two hypothetical adults of the same mass as the  
239 captive adult subjects. Caloric demand was presented using the category-specific (Table  
240 2) estimates of the energetic cost of each activity state (Kriete 1995). Time-activity  
241 budgets were converted to rough estimates of the energetic requirements of a free-  
242 ranging 4 733kg adult male and a 2 800kg adult female. Male and female energy

243 budgets were estimated using the average activity budget described above, rather than  
244 using sex-specific activity budgets.

245

246

## 247 **Results**

248 This study synthesises observations from eight seasons, during 496 days (5 952 hours)  
249 of effort, including 2 000 hours observing killer whales. After censoring, 7 517  
250 transitions of focal groups from one activity state to another were observed.

251

### 252 LOG-LINEAR ANALYSES

253 Both variables affected the behaviour of the whales (Table 3: testing components BS,  
254 BPS for the effect of boat presence and components LS, LPS for the effect of location).

255 When starting with a null model in the log-linear analyses (i.e., that adjacent scans are  
256 dependent, and that location and boats have no effect on succeeding whale activity), the  
257 best model considered both location and boat factors (AIC = -32.8, Table 3). The effect  
258 of location was much stronger than the effect of boats, but adding the boat effect  
259 explained a significant portion of the variance (Table 3). There was no significant  
260 interaction between the boat and location terms (Table 3), which meant that whale  
261 response to boats was similar inside and outside the Reserve.

262

### 263 EFFECT OF BOAT PRESENCE ON TRANSITION PROBABILITIES

264 Boat presence showed strong effects on the probability of whales switching from one  
265 activity state to another for most initial activity states (Fig. 2). The strongest effect of  
266 boat presence on transition probabilities was observed in Activity State B. Animals  
267 were less likely to enter Activity State B from any other state when boats were present.

268

269 Whales were less likely to switch from Activity States C to D when boats were present  
270 than in their absence (Fig. 2). In addition, whales observed in Activity State D were  
271 less likely to remain in that state (and more likely to switch to lower-energy Activity  
272 States C or A) when boats were present than when boats were absent. Whales engaged  
273 in Activity State C were more likely to remain in that state when boats were present.

274

#### 275 EFFECT OF BOAT PRESENCE ON ACTIVITY BUDGET

276 Whales spent far less time in Activity States B and D when boats were present (Fig. 3).  
277 The proportion of time spent in Activity States A, C and E was significantly greater  
278 when boats were present.

279

#### 280 EFFECT OF BOAT PRESENCE ON ENERGETIC REQUIREMENTS

281 While activity budgets were significantly different in the presence and absence of boats,  
282 the effect of boat presence on energetic demand was relatively small after converting  
283 the time spent in each activity state (Table 2) to estimates of 12h energetic demand in  
284 the presence and absence of boats (Table 4). Our estimates fell well within the range of  
285 other estimates of killer whale's energetic demand calculated in various ways (Table 4).  
286 Williams (2004) obtained estimates using the scaling relationship between mass and  
287 both basal and field metabolic rate (Kleiber, 1975). The estimates of Barrett-Lennard et  
288 al. (1995) were also based on Kriete's measures (1995); while Baird (1994) derived  
289 estimates for mammal-eating killer whales from observed prey ingestion rate. Overall,  
290 estimated energetic demand over 12h for a free-ranging 4 733kg male and a 2 800kg  
291 female represented approximately 3% greater demand in the presence of boats than in  
292 the absence of boats. However, the lost opportunities to gain energy translating from

293 the decrease in time spent feeding (Activity State D) had the potential to carry a heavier  
294 burden. A decrease from 12.5% of time spent feeding to 10.2% when interacting with  
295 boats corresponds to an 18% decrease in the amount of time spent feeding when boats  
296 were present. No attempt was made to test for statistical significance of these  
297 differences, because variance estimates have not been presented for the estimates of  
298 energetic costs of the different activity states (Kriete, 1995).

299

300

### 301 **Discussion**

302 This study has provided evidence that the way in which whales used the study area  
303 changed when boats were present, and presented a point estimate of the extent to which  
304 these changes in activity may have carried energetic costs to whales. These objectives  
305 were met using a non-invasive, inexpensive behavioural study while addressing two  
306 shortcomings of previous studies: this study included observations of all age-sex  
307 classes of whales in the population, and sampled across the entire repertoire of killer  
308 whale activity in Johnstone Strait. Most importantly, the striking difference in potential  
309 relative costs between energetic expenditure and acquisition provides a clear mandate to  
310 prioritise future research.

311

312

### 313 EFFECTS OF BOATS ON KILLER WHALE ACTIVITY BUDGETS

314 Commercial salmon catches and whale activity in the Reserve indicated that Robson  
315 Bight offers good fishing opportunities. The ability of the Reserve to provide good  
316 feeding habitat to resident killer whales, however, may be compromised when boats  
317 enter it. Overall, whales reduced their time spent feeding from 13% to 10% when boats

318 were present. Focal whales not only showed a lower probability of continuing feeding,  
319 but also a lower probability of initiating a feeding bout (i.e., switching from  
320 travel/forage to feeding activity) when boats entered the Reserve (Fig. 2). Recall that  
321 the vast majority of boats in the study area were not engaged in whalewatching, but  
322 rather were commercial fishing vessels (Wong and Williams, 1998). While the  
323 exponential increase in commercial whalewatching activity has caused some to question  
324 the benign nature of that industry (Corkeron, 2004), it is important to note that the  
325 disturbance (primarily commercial fishing traffic) driving the trend we report was  
326 largely tangential to the whales. In addition, whales spent nearly 17% of their time in  
327 the study area rubbing when boats were absent, compared with 3% when boats were  
328 present in the same zone as the whales (Fig. 3). The whales increased their travel  
329 budget by 12.5% (Fig. 3). This echoes a previous finding that whales' avoidance  
330 reactions to an experimental boat would result in their having to travel 13% farther  
331 along a circuitous route to cover the same effective distance that they were covering  
332 prior to the arrival of the boat (Williams et al., 2002a).

333

334 Noise, rather than simple presence of the boats, seems the likeliest mechanism for boats  
335 to disturb whale behaviour. Evidence exists for killer whales evading annoying noise  
336 on fine temporal and spatial scales (Williams et al., 2002b) and harmful noise on annual  
337 and regional spatial scales (Morton and Symonds, 2002). Empirical evidence exists that  
338 boat noise can impair killer whales' ability to detect pure tones (Bain and Dahlheim,  
339 1994) and low-frequency lateral components of calls (Miller, 2002) thereby reducing  
340 the whale's 'active space', the volume of water that is within acoustic range of a whale.  
341 Whalewatching vessels can increase anthropogenic noise in substantial fractions of  
342 killer whale foraging habitat (Erbe, 2002). However, these analyses are the first to

343 suggest that vessel traffic *did* impact feeding activity of free-ranging northern resident  
344 killer whales.

345

346

347 POTENTIAL EFFECTS OF BOAT TRAFFIC ON KILLER WHALE ENERGETIC  
348 DEMAND AND ACQUISITION

349 Overall, killer whale activity budgets varied markedly between absence and presence of  
350 boats, but the net energetic effect was relatively small (Table 4). This reflects the  
351 tendency for whales to replace one low-energy activity (e.g., beach-rubbing) with  
352 another (e.g., resting) in the presence of boats. As a result, the point estimates of the  
353 total energetic demand spent in the two different activity budgets are quite similar,  
354 suggesting that at low traffic levels, northern resident killer whales may be able to  
355 balance the energetic cost of avoiding boats.

356

357 This exercise was presented to illustrate the point that short-term behavioural responses  
358 can carry energetic costs that could have long-term population effects if the population  
359 were food-limited. The point estimates of the energetic cost of each activity state  
360 (Kriete, 1995) reflect categorization of a continuum of energetic costs, and carry  
361 uncertainty that has not been quantified, and therefore could not be included in this  
362 exercise.

363

364 However, this is the third study to suggest that, while responding to boats may carry  
365 some energetic cost to northern resident killer whales, the upper limit of that cost is  
366 currently likely to be low (Williams et al., 2002a, b). The question therefore becomes  
367 whether whales are able to satisfy their energetic demands either under disturbed or

368 undisturbed conditions. In the context of a conservation strategy for northern resident  
369 killer whales where prey availability is already a concern (Baird, 2001), the real issue  
370 may not be increased energy expenditure in the presence of boats so much as the  
371 potential for boats to cause a reduction in overall energy acquisition, via masking effects  
372 of boat noise, interruption of feeding bouts or replacement of feeding activity with boat-  
373 avoidance activities.

374

375 This study provides indirect evidence that feeding activity is disrupted by the presence  
376 of boats, which could lead to a substantial decrease in energy gain opportunities in the  
377 presence of boats. Several studies have associated the fast, non-directional swimming  
378 typical of activity state D (Feeding, Table 1) with successful fish captures as evidenced  
379 by finding scales or bits of fish floating near the surface (Felleman et al., 1991; Hoelzel,  
380 1993; Ford et al., 1998; Ford and Ellis, In press), thus its functional role appears to be  
381 related to feeding – prey detection, if not prey capture. Killer whale populations will  
382 respond numerically in the same way to reduced prey abundance as they will to an  
383 equivalent reduction in prey detection due to masking effects of boat noise. In a food-  
384 limited population, this is one mechanism that could link short-term consequences of  
385 vessel traffic to long-term, population-level consequences. Prey availability has been  
386 cited as a concern for both the Threatened northern resident and Endangered southern  
387 resident killer whales (Baird, 2001). The difficulties inherent in assessing prey  
388 preference, prey availability and quantity of prey acquisition in free-ranging killer  
389 whales are obvious. Indirect impact assessments such as this one may represent a  
390 practical first step while methods are developed to assess impact of boat traffic on  
391 feeding activity directly in free-ranging cetaceans. The need to rely on indirect methods

392 of assessing environmental impact of human activity is a recurring problem in marine  
393 research (Inglis and Gust, 2003).

394

395 Assuming that the fast, non-directional swimming behaviour observed in Activity State  
396 D was associated with prey capture attempts (as reported by Felleman et al. (1991),  
397 Hoelzel (1993), Ford et al. (1998), and Ford and Ellis (In press)), it is perhaps  
398 unsurprising that killer whales near boats shortened their feeding bouts and initiated  
399 fewer of them than in the absence of boats. It has been demonstrated that many bird  
400 species respond to tourism presence by shortening feeding bouts (Burger et al., 1997;  
401 Galicia and Baldassarre, 1997; Ronconi and St Clair, 2002). This has been found also  
402 in numerous studies of terrestrial mammals, where feeding activity is easier to observe  
403 than in free-ranging cetaceans. Bighorn sheep (*Ovis canadensis nelsoni*) reduced food  
404 intake dramatically when approached by helicopters near the Grand Canyon (Stockwell,  
405 1991), and woodland caribou (*Rangifer tarandus*) exposed to tourists reduced their time  
406 spent feeding in the Charlevoix Biosphere Reserve (Duchesne et al., 2000). Terrestrial  
407 carnivores, as well as herbivores, have been shown to reduce food intake as a  
408 consequence of increased vigilance in the presence of humans. Grizzly bears (*Ursus*  
409 *arctos*) spent 53% less time feeding on army cutworm moths (*Euxoa auxiliaris*) in  
410 Glacier National Park, Montana, USA after detecting the presence of climbers in the  
411 area (White et al., 1999). This represented a substantial reduction in the caloric value of  
412 estimated food intake. Similarly, Amur tigers (*Panthera tigris altaica*) in Krai, Russia  
413 showed strong vulnerability to human disturbance in the form of roads (Kerley et al.,  
414 2002). Tigers at undisturbed sites spent more time at kills and consumed more of the  
415 kill than tigers disturbed by humans. Ultimately, disturbance to tigers was linked to  
416 lower reproductive success and higher adult mortality than tigers that occupied sites far

417 from roads (Kerley et al., 2002). Thus, a range of disparate studies has found that  
418 feeding activity of large mammals was disrupted by human activity.

419

420 Although this study has provided evidence that boat traffic disrupted feeding activity,  
421 the case for boat traffic reducing energy acquisition in resident killer whales is  
422 equivocal. Fast, non-directional swimming does not always indicate prey location and  
423 capture (Wilson *et al.*, 2002). Neither is the relationship between time spent searching  
424 for food and energy acquisition a straightforward one. Increasing the cost of transport  
425 to foraging fur seals caused adult females to stay away from their pups longer than the  
426 control group, but animals appeared to be able to alter their diving behaviour to  
427 compensate for this cost (Boyd et al., 1997). Mothers must have been able to  
428 compensate for the cost of longer foraging trips and higher swimming costs, since pup  
429 growth in treatment and control groups was similar (Boyd et al., 1997). In our study,  
430 longer traveling/foraging bouts and shorter feeding bouts for killer whales when boats  
431 were present could mean that whales near boats had to search for food longer, but not  
432 find it. Alternatively, it could mean that boats improved the whales' foraging  
433 efficiency. Perhaps the location of fishing boats and their nets helped whales to find  
434 fish quickly, enabling whales to return to other activities. However, the masking effects  
435 of boat noise on killer whale echolocation ability (Bain and Dahlheim, 1994) are well  
436 established. The energetic cost of avoiding boats is likely to be small. The energetic  
437 consequences of reducing energy acquisition are unknown, but we demonstrate that they  
438 have the potential to be much larger than the cost of avoidance behaviour. Thus,  
439 research that investigates the feeding ecology of resident killer whales is a higher  
440 priority than that which investigates energetic cost of avoiding boats.

441

442

## 443 IMPLICATIONS FOR ENDANGERED SOUTHERN RESIDENT KILLER WHALES

444 It is useful to examine these findings in the context of the Endangered southern resident  
445 killer whale community, which is not only in a more vulnerable conservation status than  
446 the Threatened northern resident community, but also experiences far greater levels of  
447 boat traffic (Baird, 2001). One major implication for ongoing studies of the impact of  
448 vessels on southern resident killer whales is apparent immediately from the results of  
449 this study. These studies should target the most vulnerable activities and individuals to  
450 be most informative and precautionary. Therefore, southern resident vessel-impact  
451 studies should incorporate scan-sampling to record activity of all individuals in a study  
452 area to avoid unintentionally excluding the most challenging (but perhaps the most  
453 informative) scenarios from behavioural studies. Similarly, experiments that  
454 unintentionally exclude females and calves (e.g., Williams et al., 2002b), due to the  
455 difficulty in discriminating them reliably from conspecifics on each surfacing, may  
456 inaccurately reflect the average response of whales to disturbance.

457

458 If southern residents were influenced by boat traffic in a similar way to their northern  
459 counterpart, then our study has implications for the use of small, but well-chosen marine  
460 protected areas to mitigate impact of anthropogenic activities on whales. The southern  
461 residents' Depleted status under the U.S. Marine Mammal Protection Act requires a  
462 management plan that reduces 'take', including harassment, of whales. Marine  
463 protected areas could play a role in reducing 'take' of southern resident killer whales, as  
464 long as no-entry zones are placed in areas where whales feed, rather than along travel  
465 corridors, or in areas used primarily by whales for resting or socialising. Killer whales  
466 do indeed have preferred habitats, some of which are strikingly obvious in nature.

467 Some populations of killer whales intentionally strand themselves to capture prey off  
468 beaches with unique topographic features that lend themselves to allowing this to take  
469 place (Lopez and Lopez, 1985; Guinet et al., 2000). The data presented here were  
470 collected in a similarly blatant example of preferred habitat – the ecological reserve was  
471 set aside to protect the unusual smooth gravel beaches on which these killer whales rub  
472 their bodies – although the reserve parenthetically has turned out to be protecting  
473 important feeding habitat as well. It would be useful to identify whether preferred  
474 feeding habitat exists for southern resident killer whales, and if so, to protect it. The  
475 results of the present study suggest that recovery of at-risk populations of killer whales  
476 would benefit from concerted efforts to identify and protect other areas of important  
477 foraging habitat. Protecting seemingly trivial fractions of the range of cetaceans may at  
478 first appear futile, but ultimately, small marine protected areas may offer utility both for  
479 measuring and mitigating impact of human activity on cetaceans.

480

#### 481 WIDER IMPLICATIONS

482 Studies of animal behaviour have an important role to play in conservation biology, but  
483 linking the two fields has been slow (Sutherland, 1998; Blumstein and Fernández-  
484 Juricic, 2004). Partly, conservation biologists may be skeptical of equating animal  
485 disturbance (a function of human activity that is confounded by the animal's sensitivity,  
486 tolerance, habituation and tradeoffs) with conservation risk (Gill et al., 2001). One way  
487 that behavioural studies can be integrated into biological conservation is to help  
488 quantify the extent to which human disturbance might reduce quality of habitat or  
489 resources. Increasing whales' energetic costs or reducing their ability to acquire prey, if  
490 the effect is sufficiently strong, can change the demographic parameters that influence  
491 effective population size (Anthony and Blumstein, 2000).

492

493 The approach that we outline could serve as a model for integration of physiological  
494 information into behavioural studies toward a conservation goal, by modeling data from  
495 captive and free-ranging animals. The key requirement is that the energetic cost of a  
496 variety of activity states must be known. This integration has been done for wintering  
497 great cormorants (Gremillet et al., 2003) and similar behaviour-based modeling has  
498 allowed managers to predict how oystercatcher (*Haematopus ostralegus*) populations  
499 would respond to a changing environment (Stillman et al., 2000). The difficulty of  
500 acquiring physiological data for cetaceans makes this approach extremely challenging.  
501 These data are available readily for many pinniped species that come ashore for  
502 moulting or breeding. One application might be the northern elephant seal, where  
503 metabolic rates have been measured when the animals are resting on land, in warm  
504 water and in cold water (Noren, 2002). We see this approach as particularly useful for  
505 conducting pilot studies to assess quickly and non-invasively whether the magnitude of  
506 a stressor is likely to be large enough to justify investing resources into more  
507 sophisticated studies. If a stressor is found to be large enough to be of concern, refuge  
508 areas can play a role in conservation and recovery strategies.

509

### 510 **Acknowledgements**

511 We thank BC Parks (Ian MacLellan, Linda Phillip and Rik Simmons) for permission to  
512 use these data, and the people who have been involved with us in data collection over  
513 the past eight years (Bion Research, Beaveridge Consulting and Johnstone Strait Killer  
514 Whale Interpretive Centre Society, especially Cheryl Ciccone and David Briggs). RW  
515 thanks The Russell Family and Jane Marcher Foundations for support. DL thanks the  
516 University of Otago - Bridging grant scheme for financial support during the analysis.

517 Doug Sandilands produced the map in Fig. 1. We thank David Bain, Robin Baird,  
518 Graeme Ellis, John Ford, Dawn Noren, David Rosen, Andrew Trites, Terrie Williams  
519 and Arliss Winship for constructive comments.

520

521 **References**

522 Allendorf, F.W., Bayles, D., Bottom, D.L., Currens, K.P., Frissell, C.A., Hankin, D.,  
523 Lichatowich, J.A., Nehlsen, W., Trotter, P.C., Williams, T.H., 1997. Prioritizing Pacific  
524 salmon stocks for conservation. *Conservation Biology* 11, 140-152.

525

526 Altmann, J., 1974. Observational study of behaviour: sampling methods. *Behaviour* 49,  
527 227-267.

528

- 529 Anthony, L.L., Blumstein, D.T., 2000. Integrating behaviour into wildlife conservation:  
530 the multiple ways that behaviour can reduce N-e. *Biological Conservation* 95, 303-315.  
531
- 532 Ashe, E. & Williams, R., 2003. Voluntary Compliance with the boundaries of a killer  
533 whale sanctuary. In *Abstracts of the 14<sup>th</sup> Biennial Conference on the Biology of Marine*  
534 *Mammals*, Greensboro, NC.  
535
- 536 Bain, D.E., Dahlheim, M.E., 1994. Effects of masking noise on detection thresholds of  
537 killer whales, In *Marine Mammals and the Exxon Valdez*. ed. R.R. Loughlin, pp. 243-  
538 256. Academic Press, San Diego.  
539
- 540 Baird, R.W., 1994. Foraging behavior and ecology of transient killer whales (*Orcinus*  
541 *orca*), Unpublished PhD thesis in Zoology. Simon Fraser University, Vancouver, British  
542 Columbia, Canada.  
543
- 544 Baird, R.W., 2001. Status of Killer Whales, *Orcinus orca*, in Canada. *Canadian Field-*  
545 *Naturalist* 115, 676-701.  
546
- 547 Barrett-Lennard, L., Heise, K., Saulitis, E., Ellis, G., Matkin, C., 1995. The impact of  
548 killer whale predation on Steller sea lion populations in British Columbia and Alaska.  
549 North Pacific Universities Marine Mammal Research Consortium, Vancouver, British  
550 Columbia, Canada.  
551
- 552 Barrett-Lennard, L.G., Ford, J.K.B., Heise, K.A., 1996. The mixed blessing of  
553 echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales.  
554 *Animal Behaviour* 51, 553-565.  
555
- 556 Beale, C. M., and P. Monaghan. 2004a. Human disturbance: people as predation-free  
557 predators? *Journal of Applied Ecology* 41:335-343.  
558
- 559 Beale, C. M., and P. Monaghan. 2004b. Behavioural responses to human disturbance: a  
560 matter of choice? *Animal Behaviour* 68:1065-1069.  
561
- 562 Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., Heithaus, M.,  
563 Watson-Capps, J. and Flahert, C., In Press. Decline in relative abundance of bottlenose  
564 dolphins exposed to long-term disturbance. *Conservation Biology* 00: 0000-0000.  
565
- 566 Bejder, L., Dawson, S.M., Harraway, J.A., 1999. Responses by Hector's dolphins to  
567 boats and swimmers in Porpoise Bay, New Zealand. *Marine Mammal Science* 15, 738-  
568 750.  
569

- 570 Blumstein, D.T., Fernández-Juricic, E., 2004. The emergence of conservation behavior.  
571 Conservation Biology 18, 1175-1177.  
572
- 573 Boyd, I.L., McCafferty, D.J., Walker, T.R., 1997. Variation in foraging effort by  
574 lactating Antarctic fur seals: Response to simulated increased foraging costs. Behavioral  
575 Ecology and Sociobiology 40, 135-144.  
576
- 577 Burger, J., Niles, L., Clark, K.E., 1997. Importance of beach, mudflat and marsh  
578 habitats to migrant shorebirds on Delaware Bay. Biological Conservation 79, 283-292.  
579
- 580 Burnham, K.P., Anderson, D.R., 1998. Model selection and inference: a practical  
581 information-theoretic approach. Springer-Verlag, New York.  
582
- 583 Caswell, H., 2001. Matrix population models: construction, analysis, and interpretation,  
584 2nd edn. Sinauer Associates, Inc., Sunderland.  
585
- 586 Corkeron, P.J., 2004. Whale watching, iconography, and marine conservation,  
587 Conservation Biology 18, 847-849.  
588
- 589 Duchesne, M., Cote, S.D., Barrette, C., 2000. Responses of woodland caribou to winter  
590 ecotourism in the Charlevoix Biosphere Reserve, Canada. Biological Conservation 96,  
591 311-317.  
592
- 593 Erbe, C., 2002. Underwater noise of whale-watching boats and potential effects on killer  
594 whales (*Orcinus orca*), based on an acoustic impact model. Marine Mammal Science  
595 18, 394-418.  
596
- 597 Felleman, F.L., Heimlich-Boran, J.R., Osborne, R.W., 1991. The feeding ecology of  
598 killer whales (*Orcinus orca*) in the Pacific Northwest, In Dolphin Societies: Discoveries  
599 and Puzzles. eds K. Pryor, K.S. Norris, pp. 113-147. University of California Press,  
600 Berkeley.  
601
- 602 Ford, J.K.B. and Ellis, G.M., In Press. Selective foraging by fish-eating killer whales  
603 (*Orcinus orca*) in British Columbia. Marine Ecology Progress Series 00:0000-0000.  
604

- 605 Ford, J.K.B., Ellis, G.M., Balcomb, K.C., 2000. Killer whales: the natural history and  
606 genealogy of *Orcinus orca* in British Columbia and Washington State, 2nd edn.  
607 University of British Columbia Press, Vancouver.  
608
- 609 Ford, J.K.B., Ellis, G.M., Barrett-Lennard, L.G., Morton, A.B., Palm, R.S., Balcomb,  
610 K.C., 1998. Dietary specialization in two sympatric populations of killer whales  
611 (*Orcinus orca*) in coastal British Columbia and adjacent waters. Canadian Journal of  
612 Zoology 76, 1456-1471.  
613
- 614 Galicia, E., Baldassarre, G.A., 1997. Effects of motorized tourboats on the behavior of  
615 nonbreeding American flamingos in Yucatan, Mexico. Conservation Biology 11, 1159-  
616 1165.  
617
- 618 Gill, J.A., Norris, K., Sutherland, W.J., 2001. Why behavioural responses may not  
619 reflect the population consequences of human disturbance. Biological Conservation 97,  
620 265-268.  
621
- 622 Guinet, C. Barrett-Lennard, L.G. and Loyer, B., 2000. Coordinated attack behaviour and  
623 prey sharing by killer whales at Crozet Archipelago: strategies for feeding on  
624 negatively-buoyant prey. Marine Mammal Science 16, 829-834.
- 625
- 626 Hoelzel, A.R., 1993. Foraging Behavior and Social Group-Dynamics in Puget-Sound  
627 Killer Whales. Animal Behaviour 45, 581-591.  
628
- 629 International Whaling Commission, 1994. Forty-fourth report of the International  
630 Whaling Commission. Cambridge.  
631
- 632 International Whaling Commission, 2001. Report of the workshop on assessing the  
633 long-term effects of whalewatching on cetaceans. Annex N. Journal of Cetacean  
634 Research and Management 3 (supplement): 308-315.  
635
- 636 Johnstone Strait Killer Whale Committee (cited as JSKWC), 1991. Background report.  
637 BC Min. of Environment, Land and Parks and Dept. of Fisheries and Oceans.  
638
- 639 Kerley, L.L., Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Quigley, H.B.,  
640 Hornocker, N.G., 2002. Effects of roads and human disturbance on Amur tigers.  
641 Conservation Biology 16, 97-108.  
642
- 643 Kleiber, M., 1975. The fire of life: an introduction to animal energetics. R.E. Kreiger  
644 Publishing, Huntington, New York, USA.  
645
- 646 Kriete, B., 1995. Bioenergetics in the killer whale, *Orcinus orca*., Unpublished PhD  
647 thesis in Zoology. University of British Columbia, Vancouver.  
648
- 649 Kruse, S., 1991. The interactions between killer whales and boats in Johnstone Strait,  
650 B.C., In Dolphin Societies: Discoveries and Puzzles. eds K.S. Norris, K. Pryor.  
651 University of California Press, California.  
652

- 653 Lopez, J.C. and Lopez, D., 1985. Killer whales (*Orcinus orca*) of Patagonia and their  
654 behavior of intentional stranding while hunting nearshore. *Journal of Mammalogy* 66,  
655 181-183.
- 656
- 657 Lusseau, D., 2003a. Effects of tour boats on the behavior of bottlenose dolphins: Using  
658 Markov chains to model anthropogenic impacts. *Conservation Biology* 17, 1785-1793.  
659
- 660 Lusseau, D., 2003b. Male and female bottlenose dolphins *Tursiops* spp. have different  
661 strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. *Marine*  
662 *Ecology Progress Series* 257, 267-274.  
663
- 664 Lusseau, D., 2004. The hidden cost of tourism: detecting long-term effects of tourism  
665 using behavioral information. *Ecology and Society* 9, 2.  
666
- 667 Lusseau, D., 2005. The residency pattern of bottlenose dolphins (*Tursiops* spp.) in  
668 Milford Sound, New Zealand, is related to boat traffic. *Marine Ecology Progress Series*  
669 295, 265-272.  
670
- 671 Lusseau, D., Williams, R., Wilson, B., Grellier, K., Barton, T., Hammond, P.S. and  
672 Thompson, P.M., 2004. Parallel influence of climate on the behaviour of Pacific killer  
673 whales and Atlantic dolphins. *Ecology Letters* 7, 1068-1076.  
674

- 675 Miller, P.J.O., 2002. Mixed-directionality of killer whale stereotyped calls: a direction  
676 of movement cue? Behavioral Ecology and Sociobiology 52, 262-270.  
677
- 678 Morton, A.B., Symonds, H.K., 2002. Displacement of *Orcinus orca* (L.) by high  
679 amplitude sound in British Columbia, Canada. ICES Journal of Marine Science 59, 71-  
680 80.  
681
- 682 Nichol, L.M., Shackleton, D.M., 1996. Seasonal movements and foraging behaviour of  
683 northern resident killer whales (*Orcinus orca*) in relation to the inshore distribution of  
684 salmon (*Oncorhynchus* spp.) in British Columbia. Canadian Journal of Zoology 74,  
685 983-991.  
686
- 687 Ronconi, R.A., St Clair, C.C., 2002. Management options to reduce boat disturbance on  
688 foraging black guillemots (*Cepphus grylle*) in the Bay of Fundy. Biological  
689 Conservation 108, 265-271.  
690
- 691 Ross, P.S., Ellis, G.M., Ikononou, M.G., Barrett-Lennard, L.G., Addison, R.F., 2000.  
692 High PCB concentrations in free-ranging Pacific killer whales, *Orcinus orca*: Effects of  
693 age, sex and dietary preference. Marine Pollution Bulletin 40, 504-515.  
694
- 695 Slooten, E., Fletcher, D., Taylor, B.L., 2000. Accounting for uncertainty in risk  
696 assessment: Case study of Hector's dolphin mortality due to gillnet entanglement.  
697 Conservation Biology 14, 1264-1270.  
698
- 699 Stockwell, C.A., 1991. Behavioral Reactions of Desert Bighorn Sheep to Avian  
700 Scavengers. Journal of Zoology 225, 563-566.  
701
- 702 Sutherland, W.J., 1998. The importance of behavioural studies in conservation biology.  
703 Animal Behaviour 56, 801-809.  
704
- 705 White, D., Kendall, K.C., Picton, H.D., 1999. Potential energetic effects of mountain  
706 climbers on foraging grizzly bears. Wildlife Society Bulletin 27, 146-151.  
707
- 708 Williams, R., Trites, A.W., Bain, D.E., 2002a. Behavioural responses of killer whales  
709 (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental  
710 approaches. Journal of Zoology 256, 255-270.  
711
- 712 Williams, R., Bain, D.E, Ford, J.K.B & Trites, A.W., 2002b. Behavioural responses of  
713 male killer whales (*Orcinus orca*) to a 'leapfrogging' vessel. Journal of Cetacean  
714 Research and Management, 4(3), 305-310.  
715
- 716 Williams, T.M., Estes, J.A., Doak, D.F., Springer, A.M., 2004. Killer appetites:  
717 assessing the role of predators in ecological communities. Ecology 85, 3373-3384.  
718

719 **Table 1.** List of activity state codes (A-E) used in this study with their equivalent  
 720 energetic cost categories defined by Kriete (1995). Activity State B, beach rubbing, is  
 721 considered equal to rest in terms of energetic cost, but probably plays a social role (Ford  
 722 *et al.* 2000). Probable functional roles for the other activity states are inferred from  
 723 earlier studies of behavior and feeding ecology in northern and southern resident killer  
 724 whales (Felleman *et al.* 1991; Hoelzel, 1993; Ford *et al.* 1998).  
 725

Activity state (this study)	Energetic cost (Kriete, 1995)	Definition	Probable function
A	1	Whales were swimming at slow speed with highly predictable sequences of several short (30s) dives followed by a long dive of 3-5 minutes. This activity state was characterized by the absence of surface-active behavior (e.g., breaching or tail-slapping).	Resting
B	1	Whale presence within 50m of a gravel beach; independent surfacing and diving of individuals; long periods spent stationary at the surface, followed by slow swim speeds toward a beach; at which point, bubbles or splashing could be observed in the vicinity of the beach.	Beach-rubbing
C	mean(2+3)	Whales surfaced and dove independently but all whales in the group were heading in the same general (east-west) direction. The dive sequences of individuals showed regular patterns of several	Traveling /Foraging

---

		short dives followed by a long one, and whales swam at moderate speeds.	
D	mean(2+3)	Individuals were spread out across the Strait; individuals were surfacing and diving independently in irregular sequences of long and short dives; and individuals displayed fast, non-directional surfacings in the form of frequent directional changes.	Feeding
E	3	Animals surfaced in tight groups with individuals engaged in tactile behavior; whales showed irregular surfacing and diving sequences and swim speeds; irregular direction of movement; and high rates of surface-active behavior.	Socialising

---

726

727

728 **Table 2.** Approximate energetic cost of five activity states on equivalent categories  
 729 used by Kriete (1995), and proportion of time spent in each state in the presence and  
 730 absence of boats.

731

Activity	Cost of activity (kcal/kg/h) <sup>1</sup>		Proportion of time in activity	
	Male	Female	No-boat	Boat
A	1.17	0.91	0.152	0.230
B	1.17	0.91	0.168	0.029
C	1.935	1.79	0.533	0.598
D	1.935	1.79	0.125	0.102
E	2.19	2.28	0.023	0.040
Transitions observed			3500	4017

732 <sup>1</sup> After Kriete (1995)

733

734

735

736

737

738

739

740

741

742

743

744

745

746 **Table 3.** Results of the log-linear analyses. P: preceding behavior, S: succeeding  
 747 behavior, B: boat presence, L: location. The null model assumed that succeeding  
 748 behavior was independent of boat and location effects, given preceding behavior, as  
 749 defined by a first-order Markov chain. However, there was strong support from the data  
 750 for a model that included effects of vessel traffic and location on succeeding behavior.

751

<b>Model</b>	<b>Component added</b>	<b><math>\Delta G^2</math>, df, p-value</b>	<b>AIC</b>	<b><math>\Delta AIC</math></b>
Null (PS, PBL)			348.3	381.1
	BS,BPS	164, 20, <0.0001		
Boat effect (BPS, PBL)			224.3	257.1
	LS,LPS	297.1, 20, <0.0001		
Boat + Location (BPS, LPS, PBL)			-32.8	0
	BLS,BLPS	7.2, 20, 0.996		
Boat * Location (PSBL)			0	32.8

752 **Table 4.** Estimated 12h energetic demand of a free-ranging male and female killer  
 753 whale in activity budgets observed in the absence and presence of boats. Energetic  
 754 requirement is presented in terms of both caloric demand and lost energetic gain  
 755 opportunities. Both these requirements are presented in kcal/12H. Energetic gain  
 756 represents the amount of energy whales need to acquire while feeding to meet their total  
 757 energetic demand. When boats are present, the energetic gain is the amount of energy  
 758 they can acquire (related to the amount of time they can spend feeding) assuming the  
 759 same acquisition rate as during control (no-boat) situations. Other published values of  
 760 killer whale's energetic demand are provided for comparison.  
 761

	Male (4733 kg)		Female (2800 kg)	
	No-boat	Boat	No-boat	Boat
<b>Energetic demand</b> (kcal/12H) (this study)	96356	99216	51080	53138
<b>Theoretical field metabolic rate</b> <sup>1</sup>	121750		81750	
<b>Reported range</b> (kcal/12H) <sup>2</sup>	71000 - 146723		42000 - 86800	
Increase in energetic demand	2.9%		3.2%	
<b>Energetic gain</b> (kcal/H spent feeding)	64237	46507	34054	24655
Decrease in energetic gain	27.6%		27.6%	

762 <sup>1</sup>(Williams et al., 2004)

763 <sup>2</sup>(Baird, 1994; Barrett-Lennard et al., 1995; Williams et al., 2004)

764 **List of Figures**

765 **Fig. 1.** The study area bounded by lines drawn from the cliff-top observation site (\*).  
766 Shaded area of zones 3-6 marks the boundaries of RBMBER, and zones X and 2a-c  
767 indicate the boundaries of the study area outside the Reserve.

768

769 **Fig. 2.** Difference between the transition probability of the no-boat chains and the boat  
770 chains. A negative value on the y-axis means that the transition probability of the  
771 impact chain was lower than the control one. The significance of the difference between  
772 two transition probabilities was assessed using a Z-proportion test. Stars mark  
773 significant differences ( $P < 0.05$ ). For the P-value of any given comparison, please refer  
774 to the text.

775

776 **Fig. 3.** Effect of boat presence on activity budget. Bars represent 95% confidence  
777 intervals, and all differences are significant at the conventional level ( $P < 0.05$ ).

778



Zone	Area (ha)
2a	493
2b	1089
2c	552
x	357
3	307
4	420
5	342
6	176

