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REPORT

Parallel influence of climate on the behaviour of Pacific killer whales and Atlantic bottlenose dolphins

David Lusseau,[1]* Rob Williams,[2]
Ben Wilson,[1,3] Kate Grellier,[1,2]
Tim R. Barton,[1]
Philip S. Hammond[2] and
Paul M. Thompson[1]
[1]Lighthouse Field Station, School of Biological Sciences, University of Aberdeen, George St, Cromarty, Ross-shire IV11 8YJ, UK
[2]Natural Environment Research Council Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, St Andrews, Fife KY16 8LB, UK
[3]Marine Mammal Research Unit, University of British Columbia, 6248 Biological Sciences Road, Vancouver, V6T 1Z4 BC, Canada
**Correspondence: E-mail: d.lusseau@abdn.ac.uk*

Abstract

The grouping behaviour of animals is governed by intrinsic and extrinsic factors which play an important role in shaping their social organization. We investigated the influence of ocean climate variation on the grouping behaviour of two widely separated populations of cetaceans, inhabiting north Atlantic and north Pacific coastal waters. The group size of both bottlenose dolphins in the Moray Firth, UK, and killer whales in Johnstone Strait, Canada, varied from year to year in relation to large-scale ocean climate variation. Local indices of prey abundance were also related both to climate indices and predator group sizes. The cetaceans tended to live in smaller groups when there was less salmon available in both areas which seem to occur 2 years after a lower phase of the North Atlantic and Pacific Decadal Oscillations. These findings suggest that, even in highly social mammals, climate variation may influence social organization through changes in prey availability.

Keywords

Bottlenose dolphin, climate influence, grouping pattern, killer whale, mean-field model, North Atlantic Oscillation, Pacific Decadal Oscillation, salmon.

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INTRODUCTION

There is increasing evidence for impacts of large-scale climate variation on ecological processes in animal populations (Ottersen *et al.* 2001; Stenseth *et al.* 2002), but the underlying mechanisms often remain unclear (Stenseth *et al.* 2003). The effects of climate variations on higher trophic levels can be difficult to understand because they involve several relationships that may be non-trivial and nonlinear. There may also be lags in responses to local climate (Hallett *et al.* 2004) which, coupled with nonlinear population dynamics, make it hard to determine these complex associations. Studies of the influence of climate variation on behaviour can provide important insights into causal links between these large-scale processes and population dynamics (Sutherland & Norris 2002). However, it can be difficult to quantify meaningful behavioural indices. For example, comparisons of grouping patterns are complicated because group formation is, at least partially, to be expected by chance. Relying on indices that are based on simple assumptions may therefore help in minimizing the difficulties in relating observations to climate variations.

Nonlinear modelling is proving useful to highlight the effects of climate variations on prey availability and cascading population ecology impacts at higher trophic levels (Mysterud *et al.* 2001; Post & Forchhammer 2001; Belgrano *et al.* 2004; Ellis & Post 2004; Hjermann *et al.* 2004). Recently developed models also show that the aggregation behaviour of animals may be governed by simple rules (Krause & Ruxton 2002; Couzin & Krause 2003) and therefore modelled using techniques for describing the movement of physical particles (Okubo 1986). For species ranging from aphids (*Aphidiodea* spp.) to buffalos (*Syncerus caffer*), it appears that aggregation patterns can be explained by simple mean-field models (Bonabeau *et al.* 1999; Sjöberg *et al.* 2000), where the frequency of occurrence, $D(n)$, of group of size n, follows a power law, with exponent b, truncated at a given critical group size (n_c) by a faster decaying function such as an exponential, $D(n) \propto n^{-b} e^{(-n/n_c)}$. This truncation is related to density-dependent factors, such as predation and food availability, affecting the stability of groups larger than n_c and therefore the likelihood that an individual should join or leave a group. Groups larger than n_c are rarer, therefore, the probability of sighting these groups decays faster past n_c (Bonabeau *et al.* 1999). Bonabeau *et al.*'s model describes the movement of animal groups between 'sites' in a 'field' and relies on the simple assumption that groups of individuals tend to aggregate when they meet. At each time t, a group can move from one site to the next within the field and a fraction p of individuals can leave the group (p can be 0). The principal assumption of mean-field models is that the fluctuation of neighbours is not correlated (Mandl 1989). Bonabeau's model also assumes that the motion of groups between sites does not depend on time. The likelihood, $D(n,t+1)$, that at time $t+1$ a group will be of size n, is calculated by counting how many sites in the field are occupied by groups of size n at that time. It is related to the likelihood that groups present at site s at time t move and merge with others at new sites and that fraction of them leave as these departing individuals are re-injected in the field (see Bonabeau *et al.* 1999 for more details about the model). The long-term behaviour of $D(n,t)$ is expressed by $D(n)$ as explained above.

Several density-independent factors have been related to grouping patterns in Cetartiodactyla (even-hoofed ungulates, whales, dolphins and porpoises), particularly the openness and complexity of the habitat in which they live (Shane *et al.* 1986; Gerard & Loisel 1995; Gerard *et al.* 2002; Lusseau *et al.* 2003). The grouping pattern of sympatric populations of delphinids has been related to their feeding habits (Baird *et al.* 1992), yet the fluctuation around these general grouping principals have not been explored at ecological scales. In the absence of predation or changes in population density, density-dependent factors should lead to variations in these critical group sizes, n_c, under different resource levels. These models remain untested, but potentially provide a novel tool for exploring the responses of social species to climate variation and climate change. Here we test whether this mean-field model can explain the grouping behaviour of two populations of dolphins living in two different ocean basins, and whether critical group sizes can be related to food availability and climate variation.

MATERIALS AND METHODS

Cetacean groups

We tested the hypothesis that critical group sizes vary under different resource levels using data from two predator-free populations of highly social species of marine mammal, that each inhabits widely separated ocean systems. No sign of predation has ever been recorded in either population; living individuals do not bear scars from bites, or have dead stranded animals been observed with bite marks as in other locations where shark and killer whale predation occur (Heithaus 2001; Heithaus & Dill 2002; Naessig & Lanyon 2004). In addition, the distribution of potential predators does not include the Moray Firth (http://www.fishbase.org) and killer whale–large shark interactions tend to lead to the death of sharks (Fertl *et al.* 1996; Pyle *et al.* 1999).

In the north-east Atlantic, we used an 11-year data set from a coastal population of bottlenose dolphins (*Tursiops truncatus*) in the Moray Firth, UK (Wilson *et al.* 1999), and in the north-east Pacific, we used a 9-year data set on the northern resident community of killer whales (*Orcinus orca*), from Johnstone Strait, Canada (Ford *et al.* 1998; Fig. 1). The Moray Firth data were collected during summer months (May to September) from 1990 to 2000 using standardized boat-based surveys (Wilson *et al.* 1997). In Johnstone Strait, killer whale group sizes were estimated every 15 min from a cliff top on West Cracroft Island (Fig. 1) during the summer months (May to September) of 1995 to 2003. In both cases the same study area was consistently surveyed throughout the years. Sampling techniques did not violate the assumption of Bonabeau *et al.*'s model (see *Introduction*). Yearly surveys show that the population abundance of killer whales (Ford *et al.* 2000) and bottlenose dolphins (Wilson *et al.* 1999; Durban 2002) did not vary significantly throughout the study periods and the variations observed were not large enough to affect the interannual comparisons. Group size in both locations was estimated using a combination of direct counts and identification of individuals present (Wilson *et al.* 1999).

Estimating prey abundance

Uncertainty over the diet composition of both dolphin populations and the abundance of all potential prey prevent direct estimates of resource availability. Instead, we identified both large scale and local proxies of resource availability that could be compared with critical group sizes in different years. First, the winter North Atlantic Oscillation (NAO) (Hurrell 1995) and the Pacific Decadal Oscillation (PDO) (Mantua *et al.* 1997) provided large-scale proxies for bottlenose dolphins and killer whales respectively. The NAO index reflects the atmospheric pressure difference between the Azores high pressure zone and the low pressure located over Iceland (Hurrell 1995). Values for the winter NAO index were obtained from the Climatic Research Unit, University of East Anglia, Norwich, UK (http://www.cru.uea.ac.uk/cru/data/nao.htm). The PDO is a reflection of the North Pacific sea surface temperature (Mantua *et al.* 1997). Values for the PDO index were obtained from the Joint Institute for the Study of the Atmosphere and Ocean, University of Washington and National Oceanic and Atmospheric Administration, Seattle, USA (http://tao.atmos.washington.edu/pdo/). Both these indices of climate variation influence many aspects of marine productivity in their respective ocean basins,

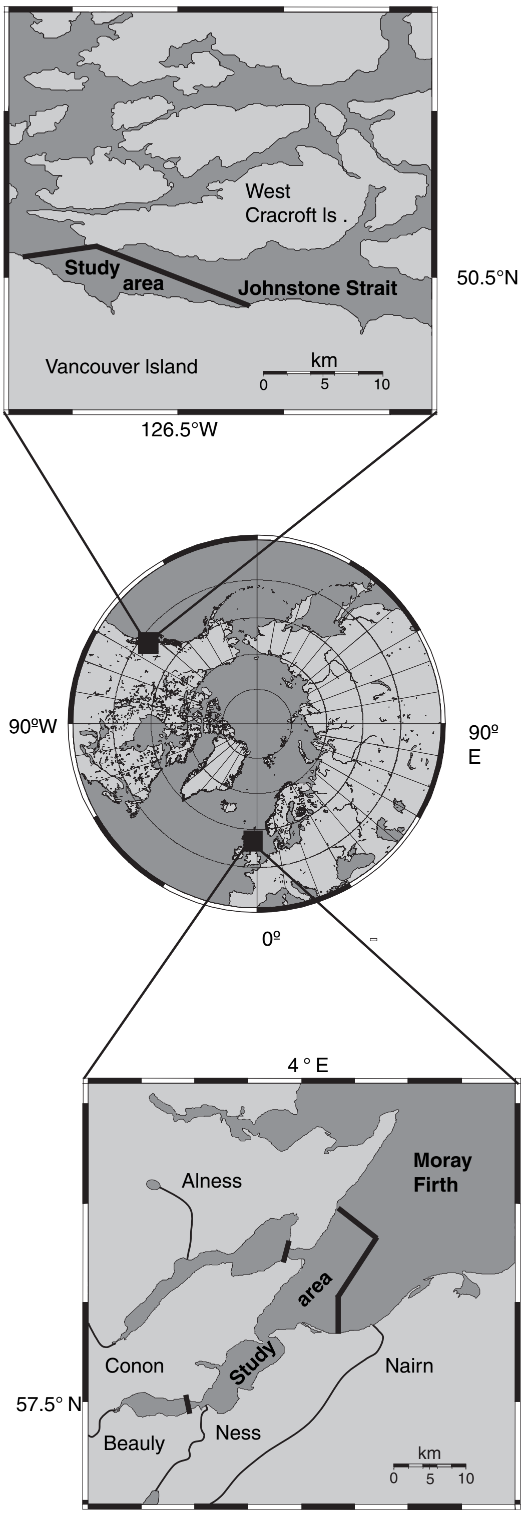

Figure 1 Location of the two study areas, including a map of the inner Moray Firth, UK and a map of northern Johnstone Strait, Canada. Study areas are delineated in black. In Scotland, salmon catches were available for Conon, Alness, Beauly, Ness and Nairn rivers.

including the availability of several known prey (Alheit & Hagen 1997; Ottersen *et al.* 2001; Arnott & Ruxton 2002; Friedland *et al.* 2003).

Salmonids are regularly eaten by both bottlenose dolphins (Janik 2000) and killer whales (Ford *et al.* 1998). Diet analysis of killer whales show that 96% of fish taken were salmonids (Ford *et al.* 1998). Relationship between the behavioural ecology of the two delphinid species in the study areas and salmonids lead to the assumption that salmon play an important role in the diet of the dolphins (Nichol & Shackleton 1996; Mendes *et al.* 2002; Hastie *et al.* 2004). However, it remains uncertain whether salmonids predominate in the diet of the Moray Firth bottlenose dolphins or whether they play a qualitative function (Santos *et al.* 2001). We therefore also used routinely collected salmon fishery statistics as local proxies of resource variability in both study areas. In Scotland, these are predominantly Atlantic salmon (*Salmo salar*), for which we used data on total catches from each of the five rivers running into our study area (Fig. 1) as a local index of abundance. Annual rod and line catch data provide the best available indicator of year to year variations in salmon abundance (Youngson *et al.* 2002). These data are not available at the scale of individual rivers, but analysis of 1990–2000 data from the whole of the Moray Firth showed that total catches were significantly related to rod and line catches ($F_{1,10} = 28.9$, $P < 0.001$, $R^2 = 0.763$). Catch data were obtained from Scottish Executive Statistical Reports (available from The Stationary Office Bookshop, Edinburgh EH3 9AZ). Five salmon species migrate through the Canadian study area; Chinook (*Oncorhynchus tshawytscha*), Sockeye (*O. nerka*), Coho (*O. kisutch*), Pink (*O. gorbuscha*), and Chum (*O. keta*)(Nichol & Shackleton 1996). The Canadian Department of Fisheries and Oceans conduct standardized annual test-fisheries in Johnstone Strait. Data on effort and catch of all five species are available at http://www.pac.dfo-mpo.gc.ca

Data analyses

An exponentially truncated power law (Tables 1 and 2) was fitted to the group size data sets for each year in order to determine the fit of the model and its parameters, including the critical group size, using the SPSS nonlinear regression (NLR) algorithm in SPSS 11.5 (SPSS, Inc., Chicago, IL, USA). Asymptotic standard errors are derived for each parameter by the NLR algorithm.

The relationship between cetacean group size statistics (mean, median and critical group size), independently obtained for each year, and indices of prey abundance was tested using stepwise (forward and backward) regression analyses available from MINITAB Release 14 (Minitab, Inc., State College, PA, USA). In the Moray Firth each river was used as an independent variable, while in Johnstone Strait

Table 1 Yearly variation in group-size distribution of bottlenose dolphins in the inner Moray Firth, UK

Year	Goodness-of-fit (R^2)	Critical group size (n_c±SE)	Scaling exponent (b ± SE)	Fitting constant (a ± SE)	Mean	Median
1990	0.995	4.2 ± 0.22	−0.18 ± 0.041	1.29 ± 0.02	6.2	5
1991	0.998	3.9 ± 0.15	−0.19 ± 0.032	1.31 ± 0.02	5.7	5
1992	0.995	7.1 ± 0.33	−0.019 ± 0.029	1.19 ± 0.02	8.1	6
1993	0.990	6.5 ± 0.38	−0.21 ± 0.042	1.14 ± 0.03	9.3	9
1994	0.994	4.9 ± 0.24	−0.26 ± 0.040	1.22 ± 0.03	7.7	7
1995	0.992	6.1 ± 0.29	−0.27 ± 0.037	1.14 ± 0.03	9.9	9
1996	0.995	4.3 ± 0.20	−0.31 ± 0.041	1.24 ± 0.03	7.1	7
1997	0.991	3.6 ± 0.29	−0.17 ± 0.066	1.34 ± 0.04	5.4	4
1998	0.975	9.3 ± 0.93	−0.03 ± 0.056	1.10 ± 0.04	9.4	9
1999	0.991	9.6 ± 1.02	0.25 ± 0.045	1.13 ± 0.03	6.1	4
2000	0.987	5.8 ± 0.46	−0.14 ± 0.056	1.14 ± 0.03	7.3	7

For each year, a truncated power law, $p(n) = an^{-b}e^{-n/n_c}$, was fitted to the cumulative frequency distribution, $p(n)$, of group sizes, n, observed in that year. The fit of the model (R^2) was significant for all years ($P < 0.0001$). R^2, the critical group size (n_c) and the scaling exponent (b), and the fitting constant (a) were determined using the nonlinear regression procedure from SPSS 10.1 (SPSS Inc.). The mean and median group size for each year is given for comparison.

Table 2 Yearly variation in group-size distribution of killer whales in Johnstone Strait, Canada

Year	Goodness-of-fit (R^2)	Critical group size (n_c±SE)	Scaling exponent (b ± SE)	Fitting constant (a ± SE)	Mean	Median
1995	0.997	3.3 ± 0.16	−0.09 ± 0.040	1.35 ± 0.02	4.2	3
1996	0.997	2.9 ± 0.21	−0.09 ± 0.059	1.41 ± 0.03	3.2	2
1997	0.996	3.6 ± 0.23	−0.02 ± 0.050	1.31 ± 0.03	4.3	3
1998	0.992	5.4 ± 0.37	−0.01 ± 0.046	1.19 ± 0.03	5.8	4
1999	0.996	3.4 ± 0.13	−0.36 ± 0.038	1.33 ± 0.02	6.0	5
2000	0.995	6.5 ± 0.27	−0.01 ± 0.026	1.17 ± 0.02	7.0	5
2001	0.998	9.3 ± 0.22	−0.03 ± 0.013	1.13 ± 0.01	9.3	6
2002	0.988	9.6 ± 0.43	0.13 ± 0.032	1.06 ± 0.03	7.5	6
2003	0.993	7.5 ± 0.30	−0.05 ± 0.025	1.15 ± 0.02	9.0	7

For each year, a truncated power law, $p(n) = an^{-b}e^{-n/n_c}$, was fitted to the cumulative frequency distribution, $p(n)$, of group sizes, n, observed in that year. The fit of the model (R^2) was significant for all years ($P < 0.0001$). R^2, the critical group size (n_c) and the scaling exponent (b), and the fitting constant (a) were determined using the non-linear regression procedure from SPSS 10.1 (SPSS Inc.). The mean and median group size for each year is given for comparison.

each species was treated as an independent variable. Therefore three multiple regression tests were carried out in for each location, testing the relationship between the mean, median, or critical group size and the prey abundance data. In the Moray Firth, there were four independent variables (The Conon and Alness rivers are represented as one catchment statistic) and there were five in Johnstone Strait.

The relationship between grouping behaviour and climate indices was then separately tested with a lag varying from 0 to 3 years. We therefore tested, separately, whether the mean, median or critical group size were related to NAO and PDO indices. We tested for lags because the influences of climate on higher trophic levels is often delayed as they are indirect (Stenseth *et al.* 2002). The range of lags was selected because of both the number of trophic levels we felt where involved in the climate–salmon–dolphin relationship and the lifespan of salmon (Post & Forchhammer 2001). Ocean climate variation influences returning numbers of both Atlantic and Pacific salmonids (Francis & Mantua 1996; Hare *et al.* 1999; Beaugrand & Reid 2003), with lagged effects of the NAO and PDO influencing either the freshwater environment of early life stages (Friedland *et al.* 2003) or the marine zooplankton prey of maturing adults (Beaugrand & Reid 2003). We therefore also determined whether salmon abundance indices were related to winter

NAO and PDO indices using similar stepwise regression analyses.

RESULTS

The truncated power law model provided a highly significant fit to the cumulative frequency distribution of 622 bottlenose dolphin groups encountered over 355 surveys (Fig. 2a) and 14 362 killer whale groups observed over 449 days (Fig. 2b) during the study. Thus, even in these highly social mammals, grouping behaviour over a large range of observed group sizes can be described by simple physical scaling rules. This model also fitted group-size distributions for individual years, and estimates of critical group size (n_c) for both species varied between years (Tables 1 and 2). Critical group sizes for both species were significantly and positively related to annual salmon catches in their respective study areas (bottlenose dolphins: $F_{4,10} = 5.05$, $P = 0.04$, $R^2 = 0.618$; Fig. 3a; killer whales: $F_{1,8} = 34.87$, $P = 0.001$, $R^2 = 0.833$; Fig. 3b). In Johnstone Strait, this relationship was only significant for Chinook, which, from stomach content analyses, are considered to be the preferred prey of the northern residents (Ford *et al.* 1998).

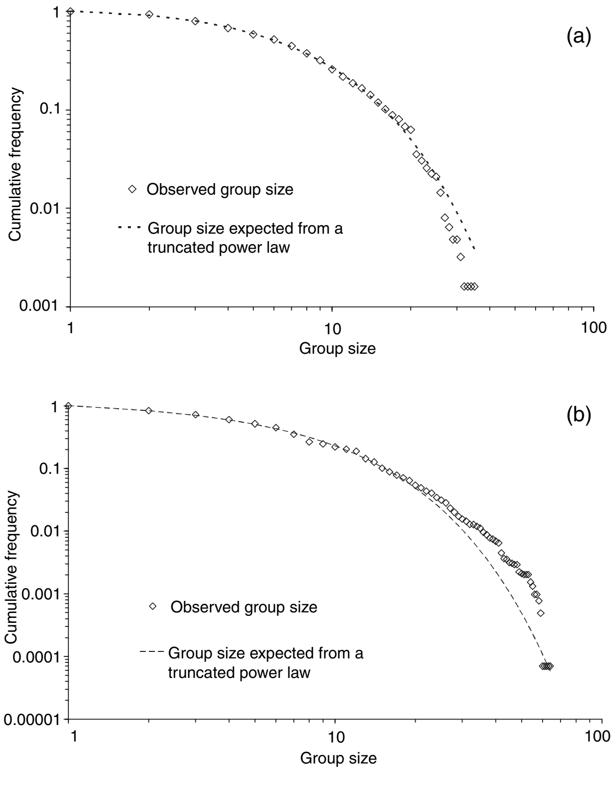

Figure 2. Group-size cumulative frequency distribution of all groups of (a) bottlenose dolphins and (b) killer whales. The truncated power law model, $p(n) = an^{-b}e^{-n/n_c}$, provided a significant fit to both distributions (bottlenose dolphins: $R^2 = 0.999$, $P < 0.0001$, $a = 1.20 \pm 0.008$, $b = -0.11 \pm 0.012$, $n_c = 5.7 \pm 0.10$. Killer whales: $R^2 = 0.998$, $P < 0.0001$, $a = 1.17 \pm 0.01$, $b = 0.05 \pm 0.016$, $n_c = 6.6 \pm 0.17$). The same model was fitted for each year separately and regression analyses results are presented in Table 1 (bottlenose dolphins) and Table 2 (killer whales).

Bottlenose dolphin critical group sizes were significantly related to the winter NAO index with a 2-year lag ($F_{1,10} = 7.38$, $P = 0.024$, $R^2 = 0.451$; Fig. 3c). Salmon catches in the Scottish study area were also related to the winter NAO index with a 2-year lag, both for the 12-year study period ($F_{1,11} = 24.03$, $P < 0.001$, $R^2 = 0.727$; Fig. 3e) and for the entire period for which catch data are available (1952–2001: $F_{1,50} = 8.3$, $P = 0.006$, $R^2 = 0.147$). The same pattern emerged for the killer whale critical group sizes, which were significantly related to the 2-year lagged PDO index ($F_{1,8} = 11.62$, $P = 0.011$, $R^2 = 0.624$; Fig. 3d). As seen in the Scottish study area, the 2-year lagged PDO index was also related to Chinook abundance estimates both at larger scales (Francis & Mantua 1996; Mote *et al.* 2003) and in Johnstone Strait ($F_{1,8} = 7.18$, $P = 0.032$, $R^2 = 0.506$; Fig. 3f).

The relationship between both mean and median group sizes and climate was inconclusive for both species, revealing the value of the new group size statistic (n_c). There were less pronounced relationships between salmon abundance and both mean and median killer whale group sizes (respectively $F_{1,8} = 7.74$, $P = 0.027$, $R^2 = 0.457$ and $F_{1,8} = 8.32$, $P = 0.023$, $R^2 = 0.478$). The same picture emerged with mean bottlenose dolphin group sizes but not medians (respectively $F_{4,10} = 6.15$, $P = 0.026$ and $F_{4,10} = 3.82$, $P = 0.070$). However, there was no significant relationship between climatic indices and either mean or median group sizes for killer whales and bottlenose dolphins.

DISCUSSION

It is well established that ocean climate variation influences animal phenology and demography, but few studies have yet recorded impacts on marine top predators (Stenseth *et al.* 2002). These similar effects of climate variation on grouping patterns of coastal cetaceans from both Atlantic and Pacific systems provide further evidence that the effects of climate variation can filter up to higher trophic levels. This is also the first study to identify a link between climate variation and social behaviour in a marine system, and illustrates the value of using generic physical models to explore the factors shaping animal societies (Bonabeau *et al.* 1999; Lusseau 2003a). Previous comparisons of fish-eating and mammal-eating killer whales led to suggestions that prey size influences grouping patterns (Baird & Dill 1996) and may be responsible for the differences in social organization of the two sympatric

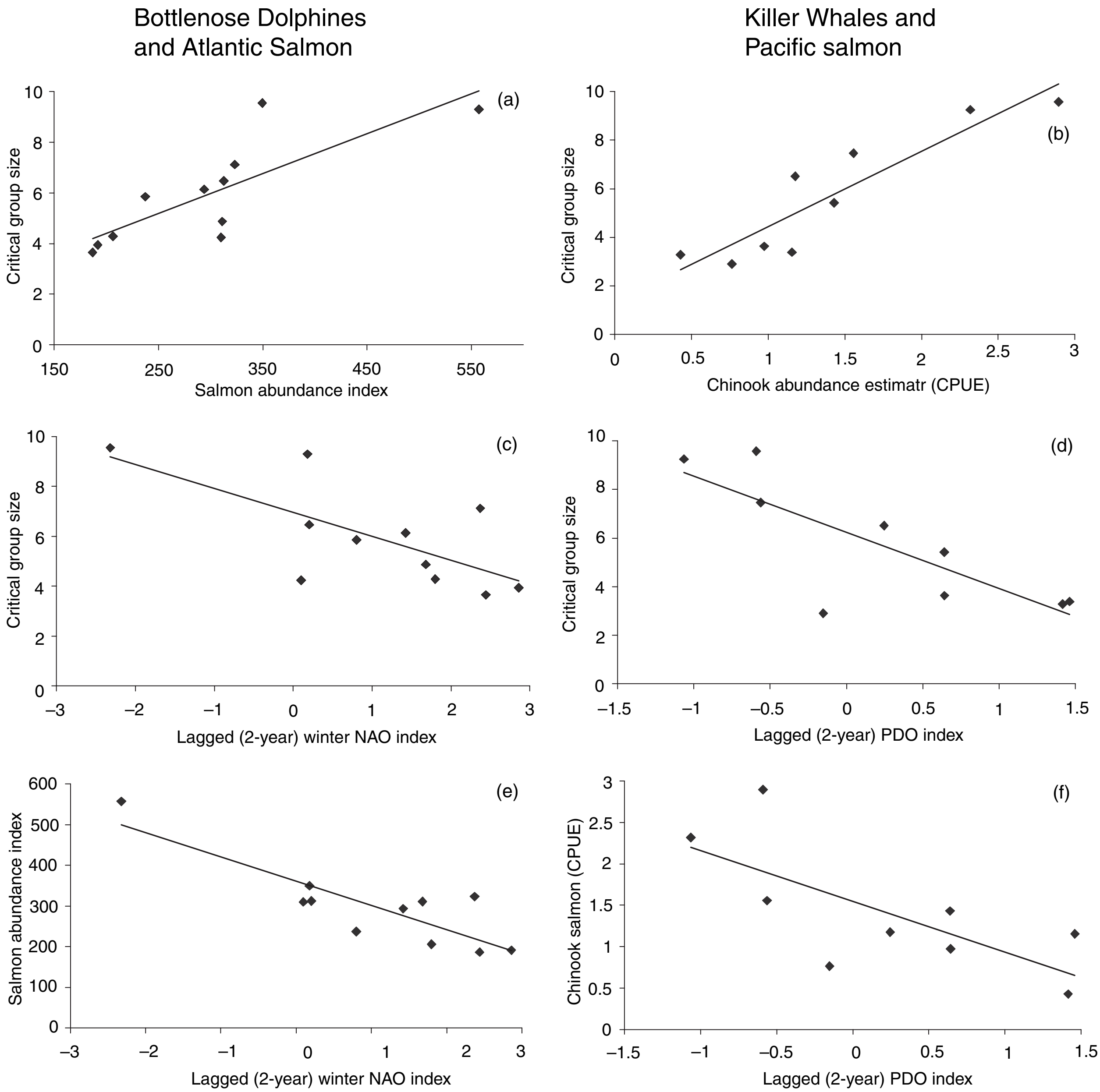

Figure 3 Relationships between grouping behaviour, climate variation and salmon abundance. (a) Bottlenose dolphin critical group size and annual catches of salmon in the Scottish study area. The salmon abundance index is calculated using partial regression coefficients for each river from the multiple regression analysis and the model includes all the rivers. (b) Killer whale critical group size and indices of Chinook salmon catch per unit effort (CPUE). (c) Bottlenose dolphin critical group size and the winter NAO index with a two-year lag. (d) Killer whale critical group size and the PDO index with a 2-year lag. (e) Salmon abundance index for the five Scottish rivers in relation to the winter NAO index with a 2-year lag. (f) Chinook abundance estimates (CPUE) and the PDO index with a 2-year lag.

populations of killer whales. Killer whales feeding on large prey caught one at a time (mammal eating) tend to live in smaller groups that maximize energy acquired to energy spent for each individual. The present findings now indicate that changes in the abundance of fish prey, or related changes in their distribution or grouping patterns, also result in interannual variation in grouping patterns in social odontocetes. This influence has consequences for the social organization of bottlenose dolphins and fish-eating killer whales. If density-dependent factors affect the size of groups, they affect the decision that individuals have to make to stay or leave groups. That is, they influence the choices made by individuals to interact with others and therefore can act as extrinsic factors guiding the structure of the social community and influencing parameters such as dispersal rate (Lusseau *et al.* 2003).

This study has some limitations. First, it uses regressive techniques and therefore does not demonstrate causal relationships between the variables described. However, the appearance of the same relationships in two widely separated systems strengthens the hypothesis that climate variation influences salmon abundance, which in turn influences dolphin grouping behaviour. The discrepancy in the percentage of critical group size variance explained by salmon abundance in both systems may be related to either data quality or diet. Bottlenose dolphins are known to be catholic feeders (Shane *et al.* 1986; Barros & Wells 1998) with some marked dietary preferences (Corkeron *et al.* 1990; Lusseau 2003b), compared with the more specialized diet of killer whales (Ford *et al.* 1998), and therefore other fish species may be affecting their grouping behaviour as well. However, the catch statistics of salmon for Scotland is only indicative of salmon abundance in the study area compared with the more robust dedicated surveys conducted in Canada (see *Materials and Methods*). This lack of accuracy may be reflected in the discrepancy in the percentage of variance explained by salmon abundance. Similarly, the large scale over which the climate is averaged by both climate indices explains the fit of the relationships with NAO and PDO in Fig. 3. Local climate indices are difficult to construct as many variables need to be taken into consideration and therefore despite their limitations large-scale climate indices remain more meaningful (Hallett *et al.* 2004).

Previous relationships between large-scale climate variation and ecological effects in top predators often lack clear causal links (Stenseth *et al.* 2003). Observed relationships between the climate variation indices, salmon abundance and critical group size provide strong support for the hypothesis that, in two different ocean basins, the link between climate variation and grouping behaviour results from the climate's influence on prey populations. In terrestrial systems, wolf (*Canis lupus*) group size is also affected by the NAO (Post *et al.* 1999; Post & Forchhammer 2001). There, greater snow cover in negative NAO years increased wolf group sizes, resulting in a top–down effect upon prey populations and primary producers (Post *et al.* 1999). In our study, however, climate variation influenced the behaviour of predators by indirectly influencing prey abundance, indicating that climate change may lead to bottom–up effects in marine ecosystems.

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