

## Possible indirect interactions between transient and resident killer whales: implications for the evolution of foraging specializations in the genus *Orcinus*

Robin W. Baird<sup>1</sup>, Peter A. Abrams<sup>2</sup>, and Lawrence M. Dill<sup>3</sup>

<sup>1</sup> Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6, and Marine Mammal Research Group, Box 6244, Victoria, B.C., Canada V8P 5L5

<sup>2</sup> Department of Ecology, Evolution and Behavior, University of Minnesota, 318 Church St. S.E., Minneapolis, MN, USA 55455

<sup>3</sup> Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6

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**Summary.** Two distinct forms of killer whale (*Orcinus orca*) occur off the coast of British Columbia, Alaska and Washington State. These have different diets, and may be reproductively isolated. Because the primary food of transient whales (pinnipeds) is a potential competitor for the primary food of resident whales (salmon), or for the smaller fishes on which salmon feed, there should be an indirect interaction between the two forms of killer whale. We use simple mathematical models to show that this interaction will be either of a “plus-minus” type, or a “plus-plus” type (indirect mutualism), depending on whether or not pinnipeds and residents are on the same trophic level. In the case of the “plus-minus” interaction, increasing the population density or improving the environmental conditions of transients will increase the population density of residents, while increasing resident populations will reduce the equilibrium population size of transients. In the case of the “plus-plus” interaction, increasing the population density or improving the environmental conditions of transients will increase the population density of residents, and vice versa. Such effects may not be currently manifest due to reduced populations at most levels in the food web. Regardless, considering such indirect interactions may be important for the management of many of the species involved, and can also provide a valuable framework for examining the evolution of the two forms of killer whales. Frequency-dependent indirect interactions, acting in concert with density-dependence within populations and disruptive selection on prey-type specific foraging characteristics, may have favoured reproductive isolation of the two forms of killer whales. We suggest that these two forms of whale are in the process of speciating, i.e., the two forms are incipient species.

**Key words:** Foraging – Sympatric speciation – Killer whales – Indirect interactions

It has recently been recognized that there are two forms of killer whale (*Orcinus orca*) found in the coastal waters of western North America from Washington State through Alaska, with the forms differing in foraging behaviour, habitat use and group dynamics. Differences in association patterns, shape of dorsal fin, pigmentation patterns, and mitochondrial DNA (Bigg et al. 1987; Baird and Stacey 1988a; Hoelzel 1989; Stevens et al. 1989) suggest limited gene flow between the two forms at best. The two were originally termed transient and resident based on their presumed associations with particular areas (Bigg et al. 1976). As noted by Guinet (1990), this distinction based on association with a certain area has since become less clear, but the two names have been retained, mainly because of their widespread use and the lack of appropriate alternative designations. Bigg et al. (1987) have suggested that these two forms could be considered separate “races”. For our purposes, it will be assumed that all residents (there are several “communities”) form a single population, that the same is true of transients, and that the two killer whale populations are totally distinct. While the possibility of occasional exchange of individuals between social groups of the two forms cannot be entirely ruled out, there have been no documented cases during the past 15 years, during which time all residents and most transients have been recognized individually.

The population of transient whales feeds primarily on pinnipeds (i.e. harbour seals, *Phoca vitulina*), while the resident whale population feeds primarily on fish (i.e. salmon, *Oncorhynchus* spp.) (Bigg et al. 1990). The fact that pinnipeds also feed primarily on fish (Spalding 1964; Perez and Bigg 1986; Olesiuk et al. 1990b) raises the possibility that the two whale groups may influence each other’s food supply indirectly. The present study uses simple mathematical models to explore these potential indirect effects. The potential exists for each population to have an impact on the average population size and evolutionary changes that occur in the other. The simple types of models presented are meant to suggest possibili-

ties rather than to make precise predictions about the dynamics of the species/forms under consideration. None of the indirect effects discussed below are likely to be important unless one or both whale populations experience significant density dependence in mortality and/or natality. Largely due to human exploitation, resident killer whales now appear to be significantly below their carrying capacity (Olesiuk et al. 1990a), while the status of transients relative to their carrying capacity is not known. Also due to human exploitation, the populations of many of the other species in the food web are well below aboriginal levels. However, it is important to be aware of the possibility of indirect effects, as such effects are relevant to the management of several of the species included in the models. As well, the theoretical framework presented to examine potential indirect effects is useful in considering the evolution of the two forms of killer whale. This is explored further in the discussion.

### Biological background

Table 1 lists some of the behavioural and ecological differences between transient and resident killer whales. For present purposes, the most important differences relate to diet and habitat use. Transient killer whales in British Columbia have been recorded eating four of the five species of pinnipeds found there (summary in Jefferson et al. 1991): harbour seal; elephant seal, *Mirounga angustirostris*; Steller sea lion, *Eumetopias jubatus*; and California sea lion, *Zalophus californianus*. The fifth species of pinniped found in B.C., the northern fur seal (*Callorhinus ursinus*), has not been recorded as prey there, but has been recovered from stomach contents of killer whales off Alaska (Zenkovich 1938). Recent evidence collected around southern Vancouver Island suggests that harbour seals may be the most common prey of transients (Baird et al. 1989, 1990). For the purposes of simplifying the models, however, all species of pinnipeds are lumped together, and equations dealing with

**Table 1.** A summary of differences between resident and transient killer whales (from Bigg et al. 1987; Baird and Stacey 1988b; Bain 1989; Morton 1990)

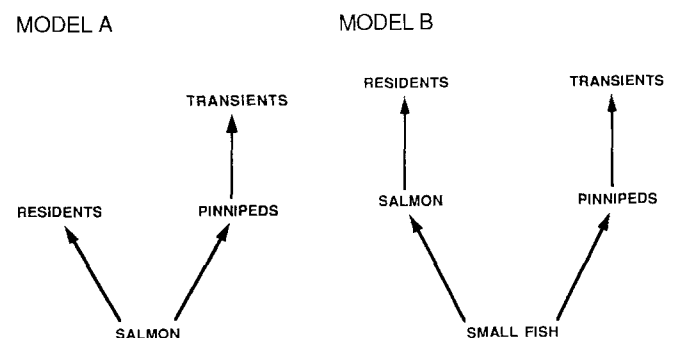
	Resident	Transient
Group size	large (3–80)	small (1–15)
Dispersal from maternal group	no	yes
Seasonal occurrence	w/salmon runs	unpredictable
General foraging area	deep water	shallow water
Dive duration	short, consistent	long, variable
Echolocation during foraging	yes	no
Prey type	fish	marine mammals
Prey size	small	large
Sharing of prey	generally no	generally yes

pinnipeds consider a hypothetical “average” species. The diet of residents is much easier to characterize; in British Columbia and Washington State, the vast majority (approx. 90%) of prey observed to be eaten have been salmon (Bigg et al. 1990). However, the possibility remains that other fish species may be taken but consumed underwater or at times of the year when observer effort is minimal.

Resident and transient killer whales generally use the various portions of the habitat to different degrees (Heimlich-Boran 1988; Morton 1990). This can be related to their prey choice, since there is some habitat separation between the major prey of residents (salmon), and the major prey of transients (pinnipeds). Since pinnipeds eat fish (including salmon) they obviously do not occupy completely different habitats from salmon, but they spend a significant proportion of their time associated with haul-out sites, and other nearshore areas. Salmon are generally found in major waterways, especially during migration. Since pinnipeds are air-breathing mammals and must return to the surface to breath, it is also likely that the distribution in the water column of the two prey types is different, with pinnipeds spending more time nearer the surface, and salmon spending more time in deeper water. Of course, this may vary among pinniped and salmon species, with the age and sex of the individual, and with the time of year.

There is some dietary overlap of pinnipeds and resident killer whales (see Fisher 1952; Spalding 1964; Olesiuk and Bigg 1988; Olesiuk et al. 1990b; Bigg et al. 1990). In addition, pinniped diets overlap with those of salmon (Hart 1973). Present information is inadequate to assess the type and degree of overlap accurately (see Discussion). However, the possibility of the indirect effects illustrated in the two food webs shown in Fig. 1 exists.

In Fig. 1A, resident whales and pinnipeds are shown as direct competitors for a common food resource; each would have a negative effect on the other's population size. In Fig. 1B, resident whales and pinnipeds have a more indirect interaction, with pinnipeds primarily consuming the smaller fish species that are the food of salmon (Hart 1973), which, in turn, are the primary food of resident whales. The interaction illustrated in Fig. 1B



**Fig. 1A, B.** Potential food web types. **A.** In Model A, pinnipeds and residents compete for salmon and other fish. **B.** In Model B, pinnipeds compete with salmon for smaller fishes (e.g. herring)

implies that larger pinniped populations indirectly reduce salmon populations (by reducing their food supply), and therefore reduce the food available to resident whales. Higher resident whale population density decreases salmon density, which increases the supply of smaller fish consumed by pinnipeds. Available data are not sufficient to determine positively which of these two food webs is a better representation of the whale-pinniped-fish system; therefore models of both types of system will be explored below. They have very different consequences for the interactions between the two types of whales.

## Lotka-Volterra type models

### A. Resident whales and pinnipeds are competitors

The simplest representation of the system described in Fig. 1A includes three populations. The transient whales may be modeled as predators that consume only one of two competing species. If the population densities of pinnipeds, residents, and transients are denoted P, R, and T, respectively, then the basic interactions are represented by:

$$\begin{aligned} dR/dt &= r_R R(K_R - R - \alpha P)/K_R && \text{(resident whales)} \\ dT/dt &= T(BCP - D_T) && \text{(transient whales)} \\ dP/dt &= r_P P[(K_P - P - \beta R)/K_P] - CPT && \text{(pinnipeds)} \end{aligned} \quad (1)$$

where  $r_R$  and  $K_R$  are the intrinsic rate of increase and carrying capacity, respectively, for resident whales;  $r_P$  and  $K_P$  are the equivalent values for pinnipeds;  $\alpha$  and  $\beta$  are competition coefficients between pinnipeds and resident whales, and vice versa; C is the number of pinnipeds captured per unit time per unit pinniped density by an average transient whale; B is the efficiency with which transient whales consume and assimilate pinnipeds; and  $D_T$  is the density-independent death rate of transient whales.

This is a special case of the Lotka-Volterra type of one predator-two competing prey model that has been explored by Vance (1978) and Gilpin (1979). Hutson and Vickers (1983) present a more general analysis which does not assume that per capita growth rates are linear functions of population densities. The pinniped-whale system is a special case of these models because the predator (transient whales) eats only one of the two competitor types (pinnipeds). Present knowledge of the natural history of these species suggests limitations on some of the parameter values. Because there appear to be differences in the relative species composition of the diets of pinnipeds and resident whales (Fisher 1952; Spalding 1964; Perez and Bigg 1986; Olesiuk and Bigg 1988; Olesiuk et al. 1990b; Bigg et al. 1990), the product of the competition coefficients should be less than one (Abrams 1983). Because whales are much larger and consume a much greater amount of prey than do pinnipeds,  $K_R$  should be significantly smaller than  $K_P$ , and  $\beta$  should be much greater than  $\alpha$ .

The model assumes that the instantaneous per capita population growth rate of transient whales is indepen-

dent of their own population density. Because of the complex social behaviour of this species and the presence of group hunting, this assumption is probably invalid at sufficiently low whale population densities. However, we are more interested in what occurs at higher whale densities, when per capita growth rates are probably less influenced by whale density and more influenced by food supply.

Equations (1) have a single equilibrium point with positive population densities of all three types. This is specified by:

$$\begin{aligned} P &= D_T/BC \\ R &= K_R - (\alpha D_T/BC) \\ T &= (r_P/CK_P)[K_P - (D_T/BC) - \beta K_R + (\alpha \beta D_T/BC)] \end{aligned} \quad (2)$$

Standard methods (see e.g. Sanchez 1968) show that this equilibrium point is always locally stable (assuming positive equilibrium populations of all species).

The expressions for equilibrium densities can be compared with the equilibrium density that each type of whale would attain in the absence of the other. These are:

$$\begin{aligned} R &= (K_R - \alpha K_P)/(1 - \alpha \beta), \\ T &= (r_P/CK_P)[K_P - (D_T/BC)] \end{aligned} \quad (3)$$

Comparison of the formulas for resident density in (2) and (3) shows that when both types are present at equilibrium the density of resident whales (R) must be larger than when transients are absent. Conversely, it seems probable that the transient whale population will be smaller when both whales are present; the condition for the presence of residents to decrease the transient population equilibrium is:

$$BCK_R > \alpha D_T \quad (4)$$

It is necessary that  $BCK_P$  be greater than  $D_T$  in order for transients to exist in the absence of residents. Although  $K_R$  is much smaller than  $K_P$ ,  $\alpha$  is very much less than one because pinnipeds have a much lower fish consumption rate than whales, and because of likely differences between pinnipeds and whales in the species of fish that they exploit. This makes it very likely that condition (4) is satisfied, and that the presence of residents decreases the equilibrium population size of transients.

The above discussion suggests that there should be a "plus-minus" interaction between the densities of the two types of whale, i.e., the presence of transients increases the equilibrium density of residents, while the presence of residents decreases the equilibrium density of transients. However, such a simple characterization can obscure the variety of effects that may occur as the result of indirect interactions between two types (Abrams 1987). If the two whale populations are in fact genetically isolated, evolutionary changes may occur independently in the two, and environmental changes may affect the parameters of population growth of one but not the other. The indirect interaction may be better understood by considering the effects of evolutionarily favoured changes in the parameters of the growth equation of one

type on the two equilibrium densities. Increases in the carrying capacity of residents ( $K_R$ ) will increase their equilibrium population size, while decreasing the equilibrium population size of transients. If the food intake rate required for zero population growth in the transients ( $D_T/B$ ) is decreased, the equilibrium density of both types of whales will increase. If the consumption rate constant ( $C$ ) of transient whales increases, the population density of residents will increase, while that of transients will increase if  $C < 2D_T(1 - \alpha\beta)/B(K_p - \beta K_R)$ .

All of these results are consistent with the generalization that favourable environmental changes (or evolutionarily favoured changes) in the resident whales will decrease the population density of the transients, while environmentally favourable or evolutionarily favoured changes in the transients will increase the population density of residents. Further, it can easily be shown that if the population density of transients is maintained above its normal equilibrium level (e.g. by immigration), this will increase the equilibrium density of residents; if the density of residents is maintained above its normal equilibrium level, this will decrease the equilibrium density of transients.

There are many reasons why a Lotka-Volterra type model is too simple a description of whale and pinniped population dynamics. However, the simple model analyzed above makes several points that are likely to be true for a wide range of models that have the same trophic structure. If there is competition between resident whales and pinnipeds, there is likely to be a positive effect of the transient whales on the population density attained by the residents, and a negative effect of resident density on transient density. Of course, these conclusions depend upon our assumptions about the biology of the system: (i) the existence of competition, and (ii) the absence of other direct or indirect interactions between residents and transients.

#### *B. Resident whales and pinnipeds have an indirect interaction*

If pinniped diets overlap with salmon diets (as shown in Fig. 1B), then a Lotka-Volterra type model of the system must contain at least four different populations. The basic interactions may be represented as follows:

$$\begin{aligned} dR/dt &= R(B_R C_R S - D_R) \text{ (resident whales)} \\ dT/dt &= T(B_T C_T P - D_T) \text{ (transient whales)} \\ dP/dt &= r_p P [1 - (P/K_p) - (\alpha S/K_p)] - C_T P T \text{ (pinnipeds)} \\ dS/dt &= r_s S [1 - (S/K_s) - (\beta P/K_s)] - C_R S R \text{ (salmon)} \end{aligned} \quad (5)$$

The parameters have meanings analogous to the parameters in equations (1), except that  $\alpha$  and  $\beta$  are now competition coefficients between pinnipeds and salmon. The assumption of a linear relationship between food consumption and per capita population growth is common in food web models (Pimm 1982). It is again probable that the product  $\alpha\beta$  is less than one because of dietary differences between salmon and pinnipeds. The equilibrium population sizes in this system are:

$$\begin{aligned} S &= D_R/B_R C_R \\ P &= D_T/B_T C_T \\ R &= (r_s/C_R)[1 - (D_R/K_s B_R C_R) - (\beta D_T/K_s B_T C_T)] \\ T &= (r_p/C_T)[1 - (D_T/K_p B_T C_T) - (\alpha D_R/K_p B_R C_R)] \end{aligned} \quad (6)$$

This sort of system has been studied by ecologists interested in indirect effects (Vandermeer 1980), and it is known that increases in either of the two top predators (the two whale populations) will cause increases in the equilibrium density of the other; such a "plus-plus" interaction is referred to as indirect mutualism. It also follows directly from equations (6) that evolutionarily favoured changes in any of the parameters of either whale population growth equation (larger  $B$ , larger  $C$ , lower  $D$ ) will increase the equilibrium population size of the other. The system described by equations (5) again always has a stable equilibrium when  $\alpha\beta < 1$ . The models considered here are more likely to have a stable equilibrium than are models that incorporate convex functional responses (Murdoch and Oaten 1975). Results on other simple three and four-species models suggest that adding or deleting a species is likely to have an effect on the stability of the remainder of the food web (e.g. Abrams 1987).

## Discussion

The interactions between resident and transient whales may be either "plus-plus" or "plus-minus", depending on the particular food web used in the model. Given what is currently known about the diets of pinnipeds, Model B (and thus a "plus-plus" interaction) seems more likely. Regardless of which food web is assumed the model predicts a stable equilibrium ratio of resident and transient densities. Model B further suggests that each population's equilibrium density will be higher in the presence of the other than it would be if there were only one form of killer whale. It is also worth noting, based on trophic level efficiency arguments and equations (4) and (5), that resident population size should be greater than that of transients. This is supported by the current population estimates for the two forms (Bigg et al. 1987).

#### *A. The model vs. the real world*

As noted above, the simple types of models explored here are meant to suggest possibilities rather than to make predictions about the precise dynamics of the species/forms under consideration. If an attempt were made to use these or similar models to derive quantitative testable predictions about population dynamics, many additional factors would have to be taken into consideration. First is the question of how to delineate the populations to be considered. At the present time, information on the total geographic range of populations of killer whales is unknown, particularly with regard to offshore movements. In fact, there is evidence of an offshore "community" of killer whales off British Columbia, of which little, beyond their existence, is known (Bigg pers. comm.). Since the range of individual transient whales may span the range

of two or more “communities” of resident whales (Bigg 1982), it would be difficult to draw the lines for which populations to include. Similarly, the entire pinniped population fed upon by transients does not compete with residents (since their ranges only overlap partially). Seasonal movements of some of the pinniped species also make it difficult to estimate the overall extent of such competition, and it is likely that this would have to be done separately for each pinniped species in any event.

We have had to make assumptions about the diets of each species/form as well, based on the best current information. However, methods of evaluating food habits vary between species and studies, and have numerous biases which make accurate comparisons difficult (e.g. Bigg and Fawcett 1985; Antonelis et al. 1987; Harvey 1989). Current population sizes are not well established for any of the species for the area under consideration, but all are probably lower than historical levels due to culling, hunting, and live-capture. Thus, population sizes may have been reduced by human activities to such an extent that no indirect effects are currently manifested. If an attempt were made to assess whether indirect effects were occurring in the real world, details on the life histories, food habits, seasonal movements and population sizes of five species of pinnipeds (harbour seal, elephant seal, Steller sea lion, California sea lion and northern fur seal), both forms of killer whales, and an untold number of species of fish would need to be available. Depending on the food web model used, it might even be necessary to include Dall's porpoise (*Phocoenoides dalli*) and harbour porpoise (*Phocoena phocoena*), both of which are found in B.C., eat fish, and are consumed by transient killer whales (Jefferson et al. 1991).

The models assume that all species/types experience indirect density dependence via depletion of their food supply. There has been no evidence of density-dependence in population growth parameters for resident killer whales during the period 1973–1989 (Olesiuk et al. 1990a). Surveys of density-dependence in many species (Fowler 1988) suggest that large, slowly growing species generally do not experience density-dependence until their population sizes are significantly above one-half of their carrying capacity. If this is true of both whales and pinnipeds, then the predicted indirect effects may not be evident until whales are closer to their carrying capacity.

The true situation may be even more complicated than indicated in Fig. 1. Firstly, the residents may compete with only some pinniped species; other pinniped species may compete more directly with salmon. Thus, a more realistic scenario may contain elements of both food webs illustrated in Fig. 1. Secondly, some pinnipeds may feed on fish which feed on salmon (i.e., lamprey and dogfish) (see Beverton 1985). If so, transient predation on pinnipeds would decrease pinnipeds but increase the abundance of other salmon predators, which would tend to dampen any indirect effect of transients on residents.

In theory (and if data were available) it would be possible to construct a model incorporating the above complexities of food web organization and spatial scale. However, the very complexity of such a model would obscure its most important lesson – that transients and

residents may have effects on one another's population sizes, regardless of the precise mechanism by which these come about. One value of the models, even in their present simplified state, is that they stress the need to find out more about the indirect interactions between resident whales and pinnipeds, since these may have important implications for the population biology of transient whales. Additionally, over and above implications for potential present-day or future indirect interactions between the populations, the models can provide new insight into the evolution of the two forms. For this we assume that the above described indirect effects may have occurred in the evolutionary history of the local killer whales.

### *B. The evolution of foraging specializations in the genus Orcinus*

Consideration of the potential for indirect effects of various sorts to influence the equilibrium densities of residents and transients provides a new theoretical paradigm to understand the evolution of these very different forms of killer whale. Below, we will develop a scenario in an attempt to deduce how these two forms may have come to exist. For this purpose, we will assume the application of Model B.

We assume that at some point in the evolutionary past there was a single form of killer whale in the eastern North Pacific. If this early form specialized on a single type of prey (i.e., fish or marine mammal), as do the current forms, the first step in diversification would be for some individuals to begin to specialize on the alternative food-type. Since such a food-type would be abundant, its utilization would be profitable even if individuals were not initially well adapted to exploit it (Wilson and Turelli 1986). Foragers of the two types would likely differ behaviourally from one another in a number of ways. Differences in habitat and depth of the water column between pinnipeds and fish (Table 1) would require some habitat segregation, and different foraging tactics would be needed to encounter and subdue different sizes of prey. These differences are evident between residents and transients today.

Group sizes differ significantly between residents and transients, which can be related to the degree and type of cooperative hunting possible for their major prey types. Factors important in the evolution of cooperative hunting include prey size, and whether single or multiple prey are captured (Packer and Ruttan 1988). Fish can be considered multiple small prey, whereas pinnipeds can be considered single large prey. Whales feeding on fish could not share individual prey, and the capture of each fish would not significantly affect the capture by other individuals of other fish, or the subsequent capture of other fish by the same individual. This is because fish do not have the same options available for them to escape as seals or sea lions might. Fish may be able to evade killer whales to some degree, but would not be as effective at doing so as pinnipeds, since pinnipeds may escape onto land once they become aware of the presence of hunting

whales. Pinnipeds may also require extended handling to be subdued. Thus capture of one prey likely decreases the probability of the whales capturing subsequent prey. Also, due to their large size and agility, some pinnipeds (such as adult sea lions) may frequently be able to defend themselves successfully from attacking killer whales. Thus, the efficiency of a foraging group of pinniped eaters (transients) may be limited by the size of the prey, the number of individuals needed to subdue it, the division of the prey among members of the hunting group, and perhaps earlier detection (and thus avoidance) by the prey as group size increases. Such effects may lead to a maximum foraging group size for transients, and evidence is available that transients have a higher individual food intake rate when foraging in smaller groups (Baird et al. 1989, 1990). Fish eater (resident) group size is less likely to be constrained, given the large size of the fish schools on which they feed.

Resident killer whales use echolocation to detect fish, and the limited current evidence suggests that fish do not recognize the sound of echolocation as a threat (Schwarz and Greer 1984; Felleman 1986). Transients appear to be largely silent when foraging, presumably to limit detection by their mammalian prey (Ford 1984; Morton 1990; Hubbard-Morton 1990). Transients also appear to modify their respiratory rate (Morton 1990), and the amplitude of individual exhalations (Baird pers. obs.), in such a way as to decrease detection by marine mammal prey. To summarize, in order to maximize successful encounters with marine mammals, and thus presumably energy intake rate, transients hunt through stealth, and have habitat use patterns, respiration rates and group sizes which differ from those of residents.

In accordance with the indirect interactions outlined in Model B, both forms of killer whale would increase in density owing to a "plus-plus" interaction (indirect mutualism), and the relative frequency of individuals adopting the novel, alternative foraging strategy would increase in the population until density-dependent effects became important, i.e., close to overall carrying capacity. The two forms would eventually reach an equilibrium ratio by a combination of density- and frequency-dependence. Density-dependence (operating within the population as a whole) and frequency-dependence (in terms of indirect interactions operating between sub-populations) ensure that the fitness of each type of whale is equal at this equilibrium density ratio. (One of the early ideas about these two forms was that because of their smaller group sizes, and population size, transients were "relegated" to the less "desirable" niche [see e.g. Bigg 1979]. Our models suggest that this is not the case.)

At this stage in their evolution individuals of the two forms might still have interbred freely, and the two strategies could be said to have co-existed in an evolutionary stable state (ESS) (Maynard Smith 1982; Gross 1984). An ESS involves two different pure strategies at the population level, with each strategy having equal fitness owing to negative frequency-dependence. The genetic structure is polymorphic, that is, individuals adopting each strategy are genetically distinct (this contrasts with a mixed ESS, which is monomorphic, with all individuals

capable of exhibiting both behaviours). The very behavioural adaptations which increase the ability of transients to feed on pinnipeds, are likely to decrease their ability to encounter scattered fish schools. Resident tactics to maximize encounters with fish would similarly decrease the likelihood of their encountering marine mammal prey. These mutually exclusive co-adapted suites of characteristic foraging tactics, corresponding to transient and resident strategies, suggest that the fitness of either prey specialist would be greater than that of a generalist who searched for both prey types simultaneously. This is another important feature of an ESS (Gross 1984).

There is another way to be a generalist, and that is to switch back and forth between tactics. But, if hunting tactics are learned, and require a long period of practice or guidance from other individuals, learning all tactics for both strategies might prohibit such switching. That learning is important for the development of killer whale hunting techniques was suggested by Lopez and Lopez (1985), and may be reflected in the long juvenile (2 to 6 years of age) and adolescent (6 to approx. 13 years of age) periods (Haenel 1986). The locations of pinniped or fish concentrations might also have to be learned.

Morphological adaptations specific to each foraging strategy could also have evolved. Morphological differences have been found between populations of killer whales in the Antarctic (Berzin and Vladimirov 1983), which might be due to differences in diet (Bain 1989). Bain (pers. comm.) has speculated that foraging related differences in the thickness of the proximal end of the mandible may exist, reflecting a trade-off of an increase in strength needed to withstand forceful movements of large prey, and a decrease in thickness for improved reception of sound. Improved sound reception through the mandible may be important for echolocating resident killer whales foraging for fish (see e.g. Brill et al. 1988). Unfortunately, testing for differences in morphology at this time is difficult, due to the paucity of available skeletal specimens.

It might seem beneficial for individuals specializing on different prey types to associate with one another, owing to what has been called the "skill pool effect" (Giraldeau 1984). According to this hypothesis, associations between individuals that have specialized on different prey types results in an overall increase in prey available to the group. However, if transients are constrained to a small group size by the size and availability of prey, and all individuals hunt cooperatively, then having an individual hunter who is unfamiliar with the foraging tactics needed, and thus unable to contribute to the hunt, would not be advantageous to the transient group, who presumably would therefore prohibit such joining. Resident groups might be more willing to include transients.

Extensive field observations (Bigg et al. 1987; Morton 1990; Baird unpub.) suggest that resident and transient groups remain spatially isolated, with no social interaction between the two forms; this sets the stage for reproductive isolation. Such isolation would be favoured by the sorts of disruptive selection on intermediates discussed above. Morphological and molecular divergence between the two forms, for which there is clear evidence

(see Introduction), would be the result. We therefore suggest that disruptive selection for prey type (= size) may have resulted in the two forms of killer whales found in the eastern North Pacific today.

Although we have not ruled out the possibility of allopatric speciation, our scenario is one of sympatric speciation, which is theoretically possible when frequency- and density-dependence are combined with disruptive selection (e.g. Wilson and Turelli 1986). Indeed, foraging specializations resulting in various degrees of sympatric isolation have been suggested for a variety of organisms, including Galapagos finches (Grant and Grant 1979, 1989), bluegill sunfish (Ehlinger and Wilson 1988), insects (Tauber and Tauber 1989), and possibly threespine sticklebacks (McPhail in press). We therefore suggest that killer whales in the eastern North Pacific are in the process of speciating, i.e., the two forms are actually incipient species. Only further work will show if this scenario seems plausible. This will require detailed examination of external and skeletal morphometrics (with emphasis on functional differences), genetic comparisons, and long-term behavioural, social and ecological research. Such ecological research should further explore the potential for competition and indirect effects with other organisms in the food web.

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