

**Abstract**—Two sympatric populations of “transient” (mammal-eating) killer whales were photo-identified over 27 years (1984–2010) in Prince William Sound and Kenai Fjords, coastal waters of the northern Gulf of Alaska (GOA). A total of 88 individuals were identified during 203 encounters with “AT1” transients (22 individuals) and 91 encounters with “GOA” transients (66 individuals). The median number of individuals identified annually was similar for both populations (AT1=7; GOA=8), but mark-recapture estimates showed the AT1 whales to have much higher fidelity to the study area, whereas the GOA whales had a higher exchange of individuals. Apparent survival estimates were generally high for both populations, but there was a significant reduction in the survival of AT1 transients after the *Exxon Valdez* oil spill in 1989, with an abrupt decline in estimated abundance from a high of 22 in 1989 to a low of seven whales at the end of 2010. There was no detectable decline in GOA population abundance or survival over the same period, but abundance ranged from just 6 to 18 whales annually. Resighting data from adjacent coastal waters and movement tracks from satellite tags further indicated that the GOA whales are part of a larger population with a more extensive range, whereas AT1 whales are resident to the study area.

Manuscript submitted 1 June 2011.  
Manuscript accepted 18 October 2011.  
Fish. Bull. 110:143–155 (2012).

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

## Contrasting abundance and residency patterns of two sympatric populations of transient killer whales (*Orcinus orca*) in the northern Gulf of Alaska

**Craig O. Matkin (contact author)**<sup>1</sup>

**John W. Durban**<sup>2,3</sup>

**Eva L. Saulitis**<sup>1</sup>

**Russel D. Andrews**<sup>4</sup>

**Janice M. Straley**<sup>5</sup>

**Dena R. Matkin**<sup>1</sup>

**Graeme M. Ellis**<sup>6</sup>

Email address for contact author: [cmatkin@acsalaska.net](mailto:cmatkin@acsalaska.net)

<sup>1</sup> North Gulf Oceanic Society  
3430 Main St., Suite B1  
Homer, AK 99603

<sup>2</sup> National Marine Mammal Laboratory  
Alaska Fisheries Science Center  
National Marine Fisheries Service, NOAA  
7600 Sand Point Way NE  
Seattle, WA 98115

<sup>3</sup> Protected Resources Division  
Southwest Fisheries Science Center  
National Marine Fisheries Service, NOAA  
3333 N. Torrey Pines Ct.  
La Jolla, CA 92037

<sup>4</sup> School of Fisheries and Ocean Sciences  
University of Alaska Fairbanks  
and Alaska SeaLife Center  
301 Railway Ave.  
Seward, AK 99664

<sup>5</sup> University of Alaska Southeast  
Sitka Campus  
1332 Seward Ave.  
Sitka, AK 99835

<sup>6</sup> Department of Fisheries and Oceans  
Pacific Biological Station  
3190 Hammond Bay Rd.  
Nanaimo, British Columbia, V9R 5K6 Canada

Killer whales (*Orcinus orca*) in the eastern North Pacific can be genetically and acoustically separated into three nonassociating lineages: “resident,” “transient,” and “offshore” (Ford and Ellis, 1999; Matkin et al., 1999; Barrett-Lennard, 2000; Yurk et al., 2002). Of these lineages, Morin et al. (2010) found the transients to be the most genetically divergent and indicated that they should be considered a separate species. Only the transient form has been observed consuming marine mammals in this region and observations indicate that they feed on marine mammals exclusively (Ford et al., 1998; Saulitis et al., 2000; Herman et al., 2005; Matkin et al., 2007a, 2007b; Barrett-Lennard et al., 2011). The potential for these whales to affect trajectories of prey populations has led to considerable debate over the role of predation by transient killer whales in the decline of coastal pinnipeds and sea otters in western Alaska (e.g., Estes et al., 1998, 2009; Springer et al., 2003, 2008; DeMaster et al., 2006; Wade et al., 2007, 2009). In

addition to data on feeding habits, evaluation of their top-down impact requires data on abundance and residency patterns of these transient killer whales within specific marine systems, particularly with respect to the abundance and trends of their primary prey.

The coastal waters of Prince William Sound and the Kenai Fjords in the northern Gulf of Alaska are unique in being regularly used by two sympatric populations of transient killer whales (Matkin et al., 1999). Members of both the Gulf of Alaska-Aleutian Islands-Bering Sea transient stock and the AT1 transient stock (Allen and Angliss, 2010) have been photographically identified over the past 27 summer seasons (Matkin et al., 1999, 2008). Individuals from both populations regularly use the same region but have never been recorded swimming together and do not associate (Matkin et al., 1999), and they can be separated by behavior (Matkin et al., 1999; Saulitis et al., 2000), by acoustics (Yurk et al., 2002, 2010; Saulitis

et al., 2005), and by genetics (Barrett-Lennard et al., 2000).

Because of the lack of conclusive studies of genetic divergence across their range, the Gulf of Alaska–Aleutian Islands–Bering Sea transient stock includes all transient killer whales found in Alaskan waters west of southeastern Alaska other than the AT1 stock (Allen and Angliss, 2010). However, photographic mark-recapture analyses indicate little apparent overlap between the Gulf of Alaska whales and the western segment of the stock (Matkin et al., 2007a; Durban et al., 2010). In this article we will refer to the non-AT1 transients in the study area only as the Gulf of Alaska (GOA) transient population and consider their range to be the Gulf of Alaska and north gulf coast, which stretches from southeastern Alaska west through the Kodiak Island region. Although the full range and offshore distribution of the GOA transients is poorly defined, they have been photographed irregularly to the southwest of Prince William Sound–Kenai Fjords study area in Kachemak Bay, lower Cook Inlet, and Kodiak Island waters (Maniscalco et al., 2007; Matkin et al., 1999; C. Matkin, unpubl. data).

The AT1 transients are considered a separate stock, are classified as depleted under the Marine Mammal Protection Act, and currently number only seven individuals (Allen and Angliss, 2010). The home range of the AT1 transient population appears much more restricted than that of the sympatric GOA transients (Matkin et al., 1999; Scheel et al., 2001) or the parapatric west coast transients of southeastern Alaska, British Columbia, and Washington State coastal waters (Ford and Ellis, 1999). AT1 individuals have not been identified outside of the coastal waters of Prince William Sound and the Kenai Fjords (Matkin et al., 1999; Saulitis et al., 2005). Because of its limited range, small population size, and the consistent resightings of subgroups and individuals, the population dynamics of the AT1 population have been monitored directly from annual photographic data (Matkin et al., 2008). However, for the GOA transients, the infrequent resightings of individuals, fluidity in group structure, and larger population size have made it impossible to directly track births and deaths and require a mark-recapture sampling approach to estimate abundance and assess population changes.

In this article we fit mark-recapture models to long-term photographic identification data (1984 to 2010) to examine abundance trends, site fidelity, and demography for the AT1 and GOA transients in the coastal waters of Prince William Sound and the Kenai Fjords. We compare our results with previously described changes in the AT1 population (Matkin et al., 2008) and contrast these results with our parallel analysis of the GOA transient population. We use photographic resighting data and satellite telemetry data to further differentiate the range of the two populations and provide a context for their differing abundance trends.

## Materials and methods

### Photographic mark-recapture

Identification photographs of killer whales were obtained from the waters of Prince William Sound, Kenai Fjords National Park, and the adjacent coastal waters of the northern Gulf of Alaska (Fig. 1A). The entire region was not surveyed in any given year; however, survey effort was focused towards Prince William Sound in the earlier years of the study (1980s) and was more evenly balanced across the region in later years. Photographic surveys were conducted between April and September over the 27-year period between 1984 and 2010. In order to increase capture probabilities, survey effort was focused in areas known to be used by killer whales, or in response to sighting reports. Data were collected from a variety of platforms; all were small vessels less than 15 meters in length powered by either gasoline-outboard or diesel-inboard engines.

During an encounter, whales were approached at a distance of 15 to 45 m and photographs were taken of the left side of each whale present, showing details of the dorsal fin and saddle patch (Matkin et al., 1999). Photographs were obtained with either 1) a Nikon F-100 SLR camera<sup>1</sup> with fixed 300-mm lens and Fuji Neopan 1600 black and white film, or 2) Nikon D70 and D200 digital cameras with 80–200 mm zoom or 300-mm fixed lenses. Individual whales were distinguished by the shape and pattern of natural markings on their dorsal fins and adjacent saddle patch (Matkin et al., 1999) and were subsequently matched to catalogs of photographs from previous years. Individual matches were corroborated by using co-occurrence with consistent associates because transient killer whales have been shown to travel in stable (and often life-long) matrilineal groupings (Ford and Ellis 1999; Matkin et al., 1999). Photographs were evaluated for quality, and only photographs resulting in reliable identifications were used. Typically, the entire group was photographed. Membership in the AT1 or GOA transient population was determined either by genetic sampling, acoustic analysis, or observation of repeated association with other members of the population.

We treated these photographic identifications and re-identifications as “captures” and “recaptures” to which analytical mark-recapture techniques could be applied for estimation of abundance and demographic parameters (Hammond, 1986, 1987, 1990).

Individual whales were not seen in every year that they were known to be alive, likely in part because of the movement patterns of whales relative to the geographical boundaries of the study area. This factor highlighted the need to allow for temporary emigration in the capture-recapture modeling. The popular Cormack Jolly Seber (CJS) model for estimating survival

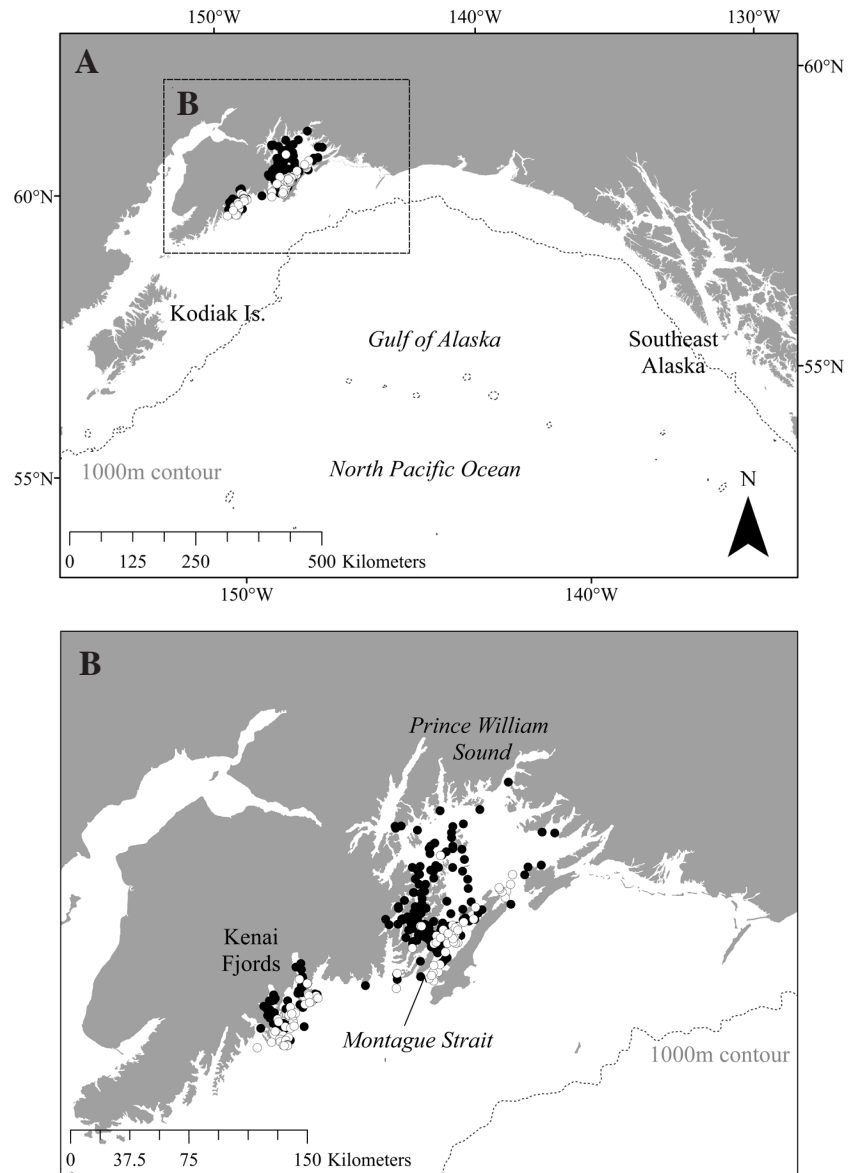
<sup>1</sup> Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

(Lebreton et al., 1992) does not account for animals that emigrate from the study area and return later. Instead, we followed Whitehead (1990) in developing a mark-recapture model that parameterized emigration and re-immigration probabilities in addition to survival. Our model was based on an individual-specific factorization (e.g., Schofield et al., 2009), allowing modularization into conditional distributions for capture probability, availability of whales for capture (temporary emigration), and death. This formulation allowed imputation of partially observed data on availability in the study area (available in the study area when actually identified) and survival status (alive when identified and between years of repeat identification), providing identifiability of parameters and enabling time-varying formulations. Specifically, the model had the parameters  $\phi_t$ ,  $\kappa_t$ ,  $\lambda_t$ , and  $\omega_t$ , where  $\phi_{t-1}$  is the probability of survival from time  $t-1$  to time  $t$ ;  $\lambda_{t-1}$  is the probability of temporary emigration from the study area at time  $t-1$ ;  $\kappa_t$  is the annual probability of re-immigration back into the study area; and  $\omega_t$  is the probability of capture at time  $t$  for whales alive and available to be captured in the study area. Note that owing to the geographic restrictions of the surveys and the likely wider ranging patterns of the whales, survival in this case represented apparent survival that could comprise either death or permanent emigration (at least for the duration of the study).

To fully quantify uncertainty about the unknown parameters, we adopted a Bayesian approach to model fitting and inference, where estimates were presented as full probability distributions (Gelman et al., 1995). The Bayesian approach requires prior distributions to be specified for all model parameters, and we adopted similar hierarchical priors for each set of probability terms  $\phi$ ,  $\lambda$ ,  $\kappa$ , and  $\omega$ . To allow temporal variation across each parameter vector, each annual probability was initially specified as a function of a mean for each parameter vector and annual random effects terms:

$$\begin{aligned} \text{logit}(\phi_t, \lambda_t, \kappa_t, \text{ and } \omega_t) &= \text{logit}(\mu^{\phi, \lambda, \kappa, \omega}) + g^{\phi, \lambda, \kappa, \omega} \varepsilon_t^{\phi, \lambda, \kappa, \omega} \\ \varepsilon_t^{\phi, \lambda, \kappa, \omega} &\sim N(0, \sigma^{\phi, \lambda, \kappa, \omega}) \\ g^{\phi, \lambda, \kappa, \omega} &\sim \text{Bernoulli}(0.5), \end{aligned} \quad (1)$$

where  $\text{logit}(a) = \log(a/(1-a))$ .



**Figure 1**

(A) Location of the coastal study area of Prince William Sound and Kenai Fjords. (B) Locations of encounters with AT1 (203, closed circles) and Gulf of Alaska (GOA) (91, open circles) transient killer whales (*Orcinus orca*) between 1984 and 2010, during which photo-identification data were collected.

The prior distribution for each parameter was thus determined by two hyper-parameters:  $\mu$  represented the mean value across each set of parameters and the standard deviation term  $\sigma$  represented the year-to-year variability over the set, on the logit scale. Uniform(0,1) prior distributions were placed on each of the five mean probabilities  $\mu^{\phi, \lambda, \kappa, \omega}$  and a uniform(0,10) prior distribution was adopted for  $\sigma^{\phi, \lambda, \kappa, \omega}$  to allow annual differences from the logit-transformed means to emerge. The probability (evidence) of temporal variability in each parameter vector was assessed through indicator vari-

ables  $g^{\phi, \lambda, \kappa, \sigma}$  (e.g., Kuo and Mallick, 1998). Each of these indicators was assigned a Bernoulli prior distribution, such that the prior probability of including any annual effect was 0.5.

We used the freely available WinBUGS software (Lunn et al., 2000) to implement Markov Chain Monte Carlo (MCMC) sampling to make repeated draws from the “posterior distribution” of each parameter—the prior distribution was updated conditionally on the data and structural relationships of the model. We sampled 10,000 values from the posterior distribution of each parameter, after discarding an initial burn-in determined by the method of Brooks and Gelman (1998). The sampled values were then used to estimate summary statistics for the posterior distributions. MCMC approaches can similarly be used to sample from the posterior distribution of quantities that can be derived as functions of parameters. Notably, we used the same MCMC simulation approach to generate predictive observations from the model parameters and compared the fit of our re-immigration model to a standard Cormack Jolly Seber model based on the mean squared predicted error (MSPE; Gelfand and Ghosh, 1998; Durban et al., 2010). As with other model selection methods, this predictive approach achieves a compromise between the goodness-of-fit and a penalty for model complexity (Gelfand and Ghosh, 1998). As such, the model with the smallest MSPE was estimated to provide the best fit.

### Assessing trends

We used estimates of the capture probabilities ( $\omega_t$ ) to derive estimates of the abundance of animals ( $N_t$ ) using the study area in any given annual survey period ( $t$ ). These parameters were linked to the observed data by specifying the number of individuals actually observed in the study area ( $n_t$ ) as a binomial sample from the study area abundance ( $N_t$ ) with the binomial proportion given by the estimated  $\omega_t$ . To assess trends across years, we modeled each  $N_t$  as Poisson distributed and adopted a model for the unknown Poisson means ( $m_t$ ) that governed the form of the variation between years. Specifically, we therefore adopted a flexible change-point model to describe temporal transitions (e.g., Carlin et al., 1992):

$$\begin{aligned} \log(m_t) &= \beta_0 + g^\beta \beta_1 \delta(t - c) + \varepsilon_t^N \\ \varepsilon_t^N &\sim N(0, \sigma^N) \\ g^\beta &\sim \text{Bernoulli}(0.5). \end{aligned} \quad (2)$$

The parameter  $\beta_0$  described the general intercept of the model (or level of abundance on the log scale before the change-point), and the function  $\delta()$  represented a step function, defined as 1 if its argument was zero or positive and zero otherwise. The parameter  $\beta_1$  described the magnitude of a step change (on a log scale), at time  $c$  (known as a change-point). We assumed the timing of the change-point was unknown and used the data to assess the evidence for a change-point in each of the 27 years. This problem therefore involved estimating the

posterior distribution of the unknown temporal change-point ( $c$ ) to identify when a change-point may have occurred, and with what probability. The model offers a flexible approach for modelling changes in abundance, because uncertainty about the year of the change-point results in uncertainty over how the trend is apportioned over the time series of between-year transitions. Because the step function  $\delta()$  was specified on a discrete time period ( $t - c$ ), we placed a discrete uniform prior for  $c$  over  $T=27$  years) (e.g., Carlin et al., 1992):

$$c \sim U(1, T) \quad (3)$$

with discrete prior probability of  $1/T$  being placed on each of the 27 years. We assumed that the direction and magnitude of the change was unknown, and we therefore assigned diffuse prior distributions for the hyperparameters  $\beta_0$  and  $\beta_1$ , each with mean 0 and standard deviation of 10. We assessed the probability of a trend in abundance by estimating the indicator probability  $g^\beta$  of including the trend parameter  $\beta_1$  in the model for the abundance estimates.

Rather than perform this trend analysis independently of the mark-recapture model, we combined these two components into a single Bayesian hierarchical model to propagate uncertainty in estimation of capture probabilities ( $\omega_t$ ) into estimates of abundance ( $N_t$ ) and trend parameters. We did not assume that the  $N_t$  fell exactly on the trend line, or had a common variance, but instead we included annual random-effects terms ( $\varepsilon_t^N$ ) that allowed over-dispersion in contrast to a fixed-effects Poisson trend model. A normal random effects distribution was adopted for the  $\varepsilon_t^N \sim N(0, \sigma^N)$ , with overdispersion controlled by the standard deviation ( $\sigma^N$ ), which was assigned a uniform (0,10) prior distribution. As with the mark-recapture parameters, we used WinBUGS to sample 10,000 values from the marginal posterior distributions for the annual estimates of abundance,  $N_t$ . Additionally, interest was focused on making inference about the posterior distributions of the parameters of the trend model, specifically the change-point ( $c$ ), the rate of change ( $\beta_1$ ), and the probability of a trend ( $g^\beta$ ).

### Tracking whale movements

To examine movements of whales relative to our mark-recapture modeling estimates (extent of temporary emigration away from the study area), we compared photographs used in our analysis with those taken during parallel research efforts in southeastern Alaska, British Columbia, and Washington State (e.g., Ford and Ellis, 1999) to identify annual overlap of individuals. Previous analyses had shown no overlap of AT1 or GOA transients with those in the Aleutian Islands (Durban et al., 2010). In addition, we attached satellite transmitter tags to individual GOA and AT1 transient whales to provide fine-scale tracks of daily movements. The tag design was a low impact minimally percutaneous external-electronics transmitter (LIMPET) satellite tag (Andrews et al., 2008). In this tag, the main electronics package, an Argos-linked, location-only SPOT

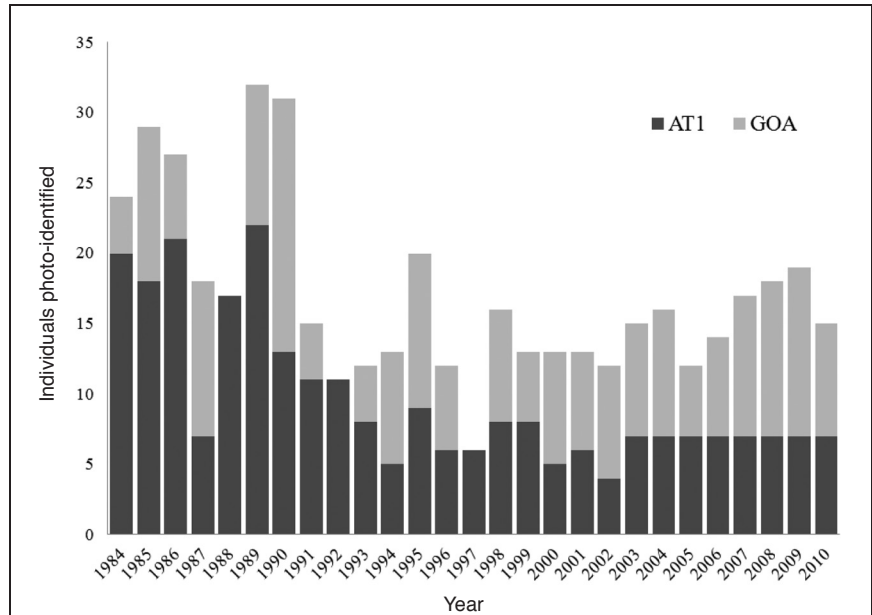


5 transmitter (Wildlife Computers, Redmond, WA), is housed in an epoxy casing with dimensions of 65×30×22 mm. The tag is held externally on the dorsal fin of the whale by two 4-mm-diameter medical-grade titanium darts that were affixed to the bottom of the tag, for a total mass of 49 g. The darts were designed to penetrate 6.5 cm into the connective tissue in the dorsal fin and remain embedded with a series of backward-facing barbs which acted as anchors for the darts. The LIMPET tags were projected onto the whales by using a crossbow with 150-lb draw weight, and the tag was held on the end of an arrow in a special rubber boot.

This type of satellite tag transmits ultra-high frequency (UHF) radio signals to Argos receivers onboard weather satellites in sun-synchronous polar orbits. To conserve power, transmissions are limited by a submersion sensor to times when the whale is at the surface. Locations were calculated by the Argos system by the method of least squares (<http://www.argos-system.org>, accessed October 2007), and we determined the plausibility of each location using the Douglas Argos filter, vers. 7.03 (Douglas<sup>2</sup>). We retained locations with high location accuracies (LC2 and LC3), as well as consecutive points separated by less than 3 km. All other locations were removed if the rate of movement between consecutive locations exceeded 25 km/h or the angle formed by the previous and subsequent locations indicated extreme return-movements. The angle of each triad of points and the distance between the shortest leg of the triad was assessed by the filter and compared with the dimensionless rate coefficient (Ratecoef) that was set to 25. Location data were imported into Google Earth (Google, Mountain View, CA) for basic visual inspection and into ArcMap 9.3.1 (ESRI, Redlands, CA) for further analysis. Distance traveled was calculated for each tagged animal, as well as a calculation of oceanic home range developed by subtracting the land area from the total area in the Minimum Convex Polygon, which was the polygon that described the perimeter of all filtered satellite locations received during the period of attachment.

## Results

During the 27 years of this study we averaged 106 (range=29–249) vessel days per year with at least 59



**Figure 2**

The number of individuals photographically identified from the AT1 and Gulf of Alaska (GOA) transient killer whale (*Orcinus orca*) populations in each annual April–September period, 1984–2010.

days logged in all years except for 1987 (29 days). During these surveys we recorded a total of 203 encounters with members of the AT1 transient population and 91 encounters with members of the GOA transient population (Fig. 1). Over 27 annual (May–September) periods, a total of 88 individual whales were documented. There were three times as many GOA individuals (66) as AT1 individuals (22), but the average number of individuals identified in each summer interval was similar for both populations (GOA: median=8, range 0–18; AT1: median=7, range 4–22; Fig. 2). This finding reflected a higher resighting rate for individual AT1 whales; individuals were seen in a median of nine different annual intervals (range 3–25) compared with a median of just two intervals (range 1–16) for GOA whales (Fig. 3). It is notable that 7 of 22 total AT1 whales were identified in more than 20 annual intervals, whereas only 1 of 66 GOA whales was identified in more than 10 intervals (Fig. 3). The number of AT1 individuals seen each year clearly declined across the study period from around 20 individuals in the 1980s to fewer than 10 individuals in the 2000s, whereas the number of GOA individuals remained at a more consistent but low number with a median 8 individuals identified per year (Fig. 2). However, to formally assess changes in abundance, we adjusted our sighting data for capture probabilities using mark-recapture models.

The mark-recapture model with emigration and re-immigration provided a better fit to the photo-identification data than the standard CJS model, for both AT1 and GOA individuals. For GOA whales, there were 49 discrepancies between 1079 observed and predicted data

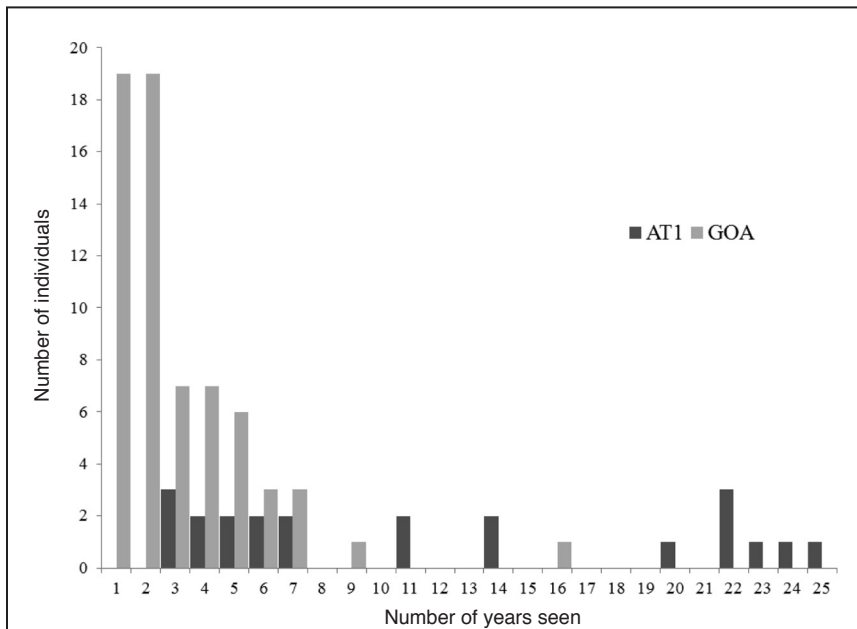
<sup>2</sup> Douglas, D. 2007. The Douglas Argos-Filter. [Available at <http://alaska.usgs.gov/science/biology/spatial/manual.html>, accessed 1 October 2007.]

points under the re-immigration model, compared with 190 of 1079 data points for the CJS model, translating to a mean squared predicted error of 0.04 and 0.18 respectively. For AT1 whales, there were 25 discrepancies from 569 data points under the re-immigration model, compared with 91 in 569 for the CJS model, corresponding to MSPEs of 0.04 and 0.16, respectively. Inference was therefore based on parameter estimates from the flexible emigration-re-immigration model, which in-

dicated notable differences in the fidelity of the two populations to the study area (Table 1).

GOA transients showed a much higher rate of exchange of individuals in the study area, with a relatively high probability of emigration (posterior median  $\mu^\lambda=0.55$ ) and low rate of re-immigration ( $\mu^\kappa=0.17$ ), compared to a low rate of emigration and high rate of re-immigration for the AT1 population ( $\mu^\lambda=0.08$ ,  $\mu^\kappa=0.77$ ), implying high study area fidelity for the AT1 whales. Similarly, the average probability of capture was higher for AT1 ( $\mu^\sigma=0.98$ ) compared with GOA ( $\mu^\sigma=0.83$ ) individuals, implying that almost all of the AT1 individuals in the study area were photographed in each year, likely because of a higher fidelity to the study area and smaller range. Although the average apparent survival was high for both populations (GOA  $\mu^\phi=0.98$ ; AT1  $\mu^\phi=0.99$ ), there were noticeable annual deviations from the average (Fig. 4). Although there was a substantial dip in the GOA transients' apparent survival in one year, 1986, there was a consistent trend in the AT1 population, with survival from 1989 to 1990 showing a marked decrease (posterior median=0.68, 95% probability interval=0.48 to 0.86) compared with the overall average, with no overlap in 95% probability intervals between this estimate and those for most other years.

The trends in abundance of the two populations, based on estimates of abundance and parameters of the



**Figure 3**

Frequency plot of the number of individual whales photographed in different numbers of annual sampling periods, for both the AT1 and Gulf of Alaska (GOA) transient killer whale (*Orcinus orca*) populations.

**Table 1**

Fit of photographic identification data to the mark-recapture model with emigration and re-immigration, for both AT1 and Gulf of Alaska (GOA) transient killer whale (*Orcinus orca*) populations.  $l$ =the probability that an individual in the study area migrates out of it each year;  $\kappa$ =the probability that an individual not in the study area population migrates back into it each year;  $\phi$ =the annual probability of survival,  $\sigma$ =the annual probability of capture (identification) in the study area. Estimates are presented as the 0.025, 0.50, and 0.975 probability intervals of the posterior probability distribution (i.e., median surrounded by 95% probability intervals) for the average ( $\mu$ ) value across May–September periods, plus the probability of between-year differences in parameters over the 27 time periods, given by the posterior probability  $p(g=1)$  of each respective time-varying indicator variable  $g$ . Additionally, the parameter  $\beta_1$  is included to indicate the magnitude and direction of abundance trend (on the log scale).

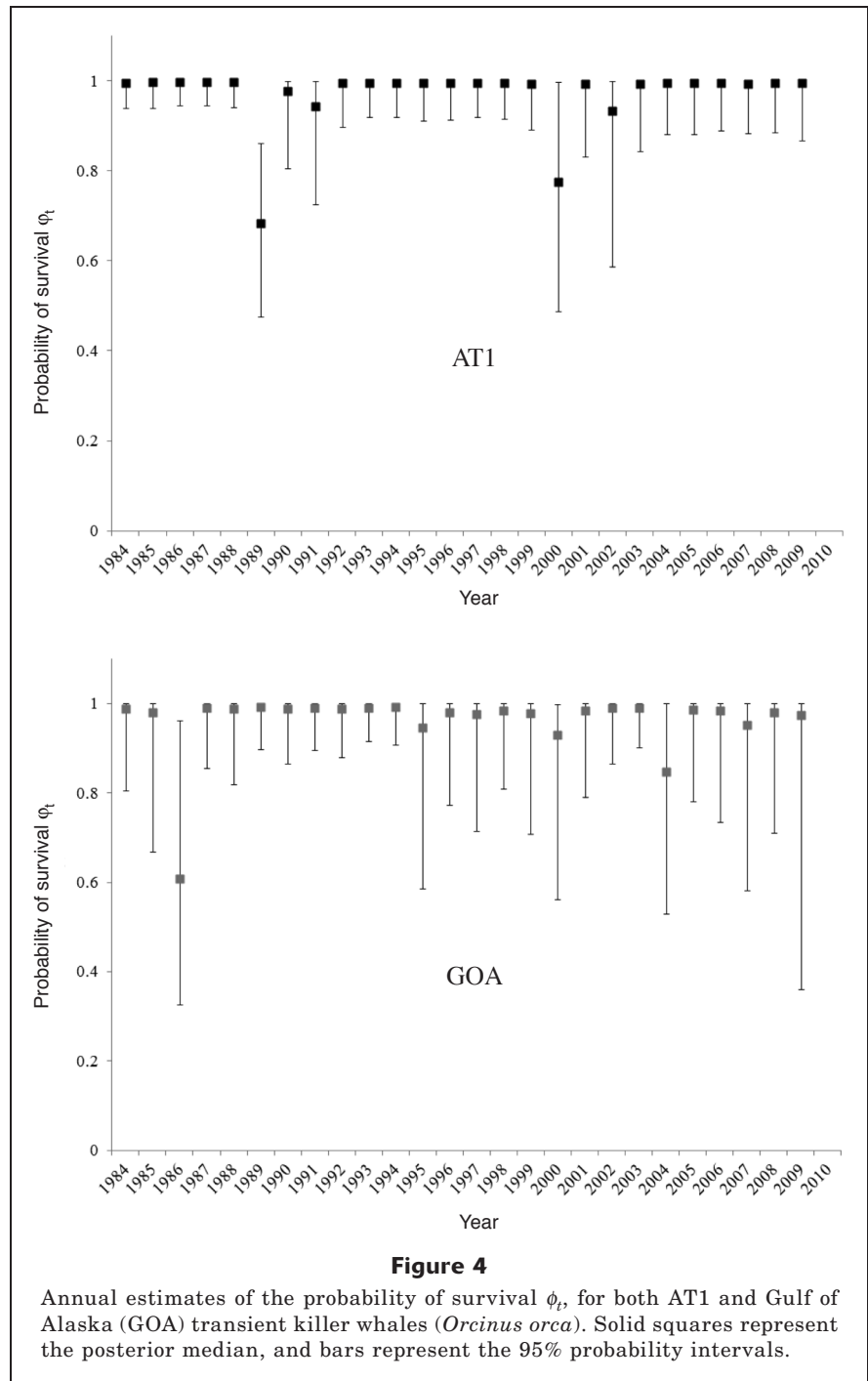
Population	Posterior estimates				
	Emigration $\mu^\lambda [p(g^\lambda=1)]$	Re-immigration $\mu^\kappa [p(g^\kappa=1)]$	Survival $\mu^\phi [p(g^\phi=1)]$	Capture $\mu^\sigma [p(g^\sigma=1)]$	Trend $\beta_1 [p(\beta_1=1)]$
GOA	0.21,0.55,0.80 [1.00]	0.02,0.17,0.67 [1.00]	0.94,0.98,0.99 [1.00]	0.55,0.83,0.99 [1.00]	-1.2,0.1,1.3 [0.02]
AT1	0.02,0.08,0.23 [1.00]	0.18,0.77,0.97 [0.71]	0.96,0.99,1.00 [1.00]	0.92,0.98,1.00 [0.64]	-1.1,-0.8,-0.5 [1.00]

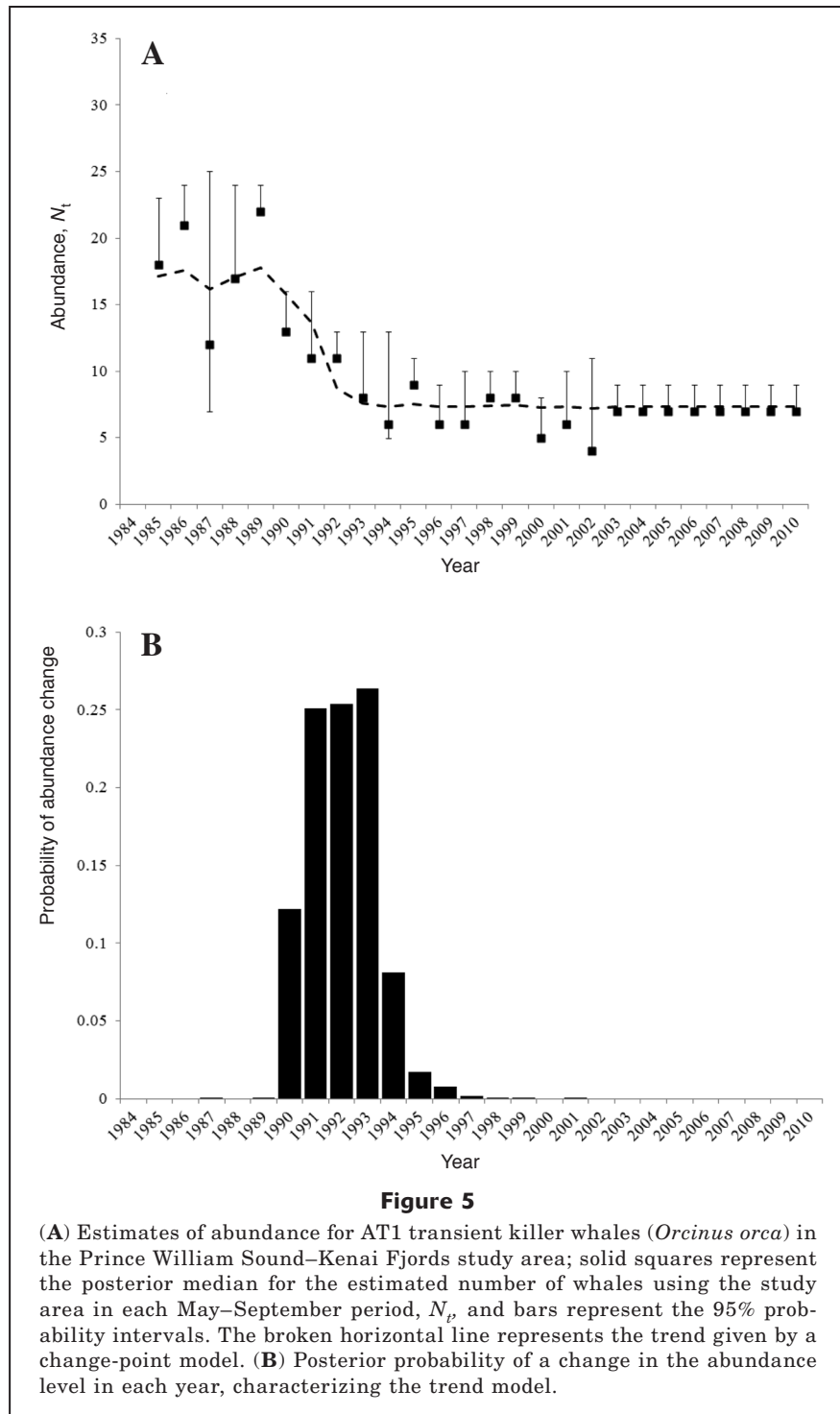
trend model, revealed contrasting patterns (Figs. 5 and 6). The estimated number of GOA whales using the study area in each annual period,  $N_t$ , showed relatively little variation from a low posterior median of six whales in 1996 and 2005 to a high of 18 in 1990. The AT1 whales showed evidence of greater abundance changes, from an estimated high of around 22 in 1989 to a low of seven at the end of the series. As a result, there was strong evidence that the abundance of AT1 whales declined over the study period and unequivocal support for inclusion of the trend model for abundance with  $p(g^\beta=1)=1$ . The entire posterior distribution for the trend parameter,  $\beta_1$ , fell below zero, indicating a probability of 1.00 of a downward trend. In contrast, the posterior distribution for the trend parameter was evenly spread above and below zero for GOA whales, with 51% of the posterior density in favor of a negative trend. As a result, there was little support for including a model for trends in abundance with  $p(g^\beta=1)=0.02$ . Correspondingly, the posterior density for the change-point was distributed evenly across all years for GOA whales and reflected no obvious changes in abundance. For AT1 transients, in contrast, there was a distinct peak in the posterior probability distribution for a change-point, and 97% of the posterior density for an abundance change occurred in the five years after 1989.

Emigration of GOA transients away from the study area was also supported by photographic resighting data from southeastern Alaska and British Columbia (Table 2). For 1995–2007 there were 16 encounters with GOA transient whales in these adjacent regions, including one (5 June 2001) with GOA transients in association with known members of the west coast transient population (Matkin et al., 2007b). There were no resighting data outside of Prince William Sound–Kenai Fjords for AT1 transients despite substantial survey effort in southeastern Alaska (Dahlheim and White, 2010) and in adjacent regions to the west of the study area (Matkin et al., 1999, 2007a; Durban et al., 2010; senior author, un-

publ. data). Additionally, the one tagged AT1 transient did not travel out of the area. All these observations support the inference from the mark-recapture model of high fidelity to the study area.

Satellite-monitored LIMPET tags were attached to GOA transients in Prince William Sound on four occasions for a total of 73 days of transmissions (Table 3). One individual (AT73) was tagged on two occasions in different years. Tagged whales traveled a total distance of 7107 km during 73 days for an average move-

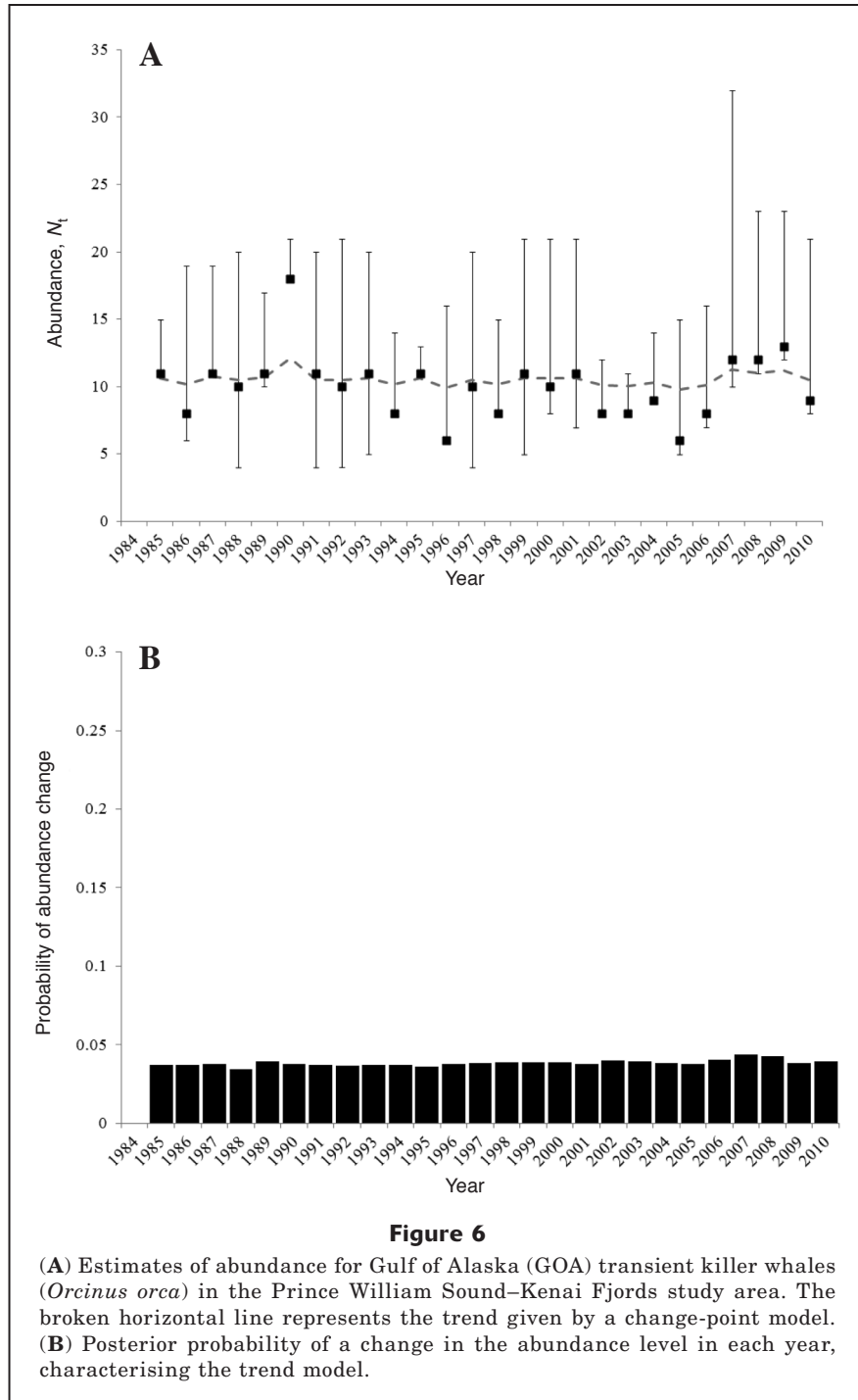




ment of 97km/day. Tagged GOA transients traveled as far offshore as 100 km and ranged from northern Kodiak Island to outside waters of southern southeastern Alaska (Fig. 7). The only areas used by the tagged whales in Prince William Sound were ocean entrances and Montague Strait. A single AT1 killer whale was tracked for five days in 2010, and it traveled an average distance of 95km/day. It moved offshore as far as

45 km but did not leave the Kenai Fjords–Prince William Sound area. It was the only tagged whale that traveled up into Prince William Sound, away from the ocean. The pattern of AT1 transients using more inside waters in Prince William Sound and Kenai Fjords, and of GOA transients using ocean entrances, Montague Strait, and the outer coastlines of Kenai Fjords was also reflected in our encounter locations (Fig. 1B).





## Discussion

Although approximately the same number of individuals was identified annually in the two transient killer whale populations we monitored in the coastal waters of Prince William Sound and the Kenai Fjords, the population parameters estimated by our mark-recapture model were notably different. The AT1 transients exhibited high site fidelity and high capture probability,

indicating that essentially every member of this small population was photographed annually in our coastal study area. In contrast, we estimated higher rates of turnover and lower capture probabilities in the study area for GOA transients. The most likely explanation for the latter pattern is that these whales were part of a significantly larger population with a more extensive range. The distribution of sightings was heavily weighted toward the ocean entrances and outer coast

**Table 2**

Photographic resighting date and location data of Gulf of Alaska (GOA) transient killer whales (*Orcinus orca*) in coastal south-eastern Alaska (SEA) and British Columbia (BC).

Year	Month	Day	Region	Location	Latitude N	Longitude W	GOA whales identified
1995	3	24	SEA	Sitka Sound	56°58'	135°33'	AT74
1997	11	5	SEA	Sitka Sound	57°0'	135°20'	AT70 AT71 AT72 AT73 AT73A AT75
1997	2	4	SEA	Sitka Sound	56°58'	135°33'	AT74
1997	1	9	SEA	Sitka Sound	56°58'	135°33'	AT74
1998	7	19	SEA	Glacier Bay	58°28'	136°1'	AT30 AT32
2000	3	10	SEA	Sitka Sound	57°6'	135°28'	AT70 AT71 AT72 AT73 AT75 AT80
2000	4	4	SEA	Sitka Sound	57°1'	135°21'	AT72 AT70 AT71 AT75 AT73 AT80
2001	6	5	SEA	Glacier Bay	58°28'	136°1'	AT30 AT32 AT74 AT74A
2001	7	23	BC	Skaat Harbor	52°24'	131°26'	AT30 AT32
2002	2	24	SEA	Sitka Sound	57°7'	135°31'	AT70 AT71 AT72 AT73 AT75 AT80
2003	2	28	SEA	Sitka Sound	56°55'	135°39'	AT74 AT74A
2003	3	2	SEA	Sitka Sound	56°55'	135°39'	AT74 AT74A
2004	5	16	BC	Hecate Strait	53°54'	131°0'	AT74 AT74A
2007	2	7	SEA	Sea Lion Rock	57°17'	135°57'	AT70 AT71 AT75
2007	2	19	SEA	Yasha Island	56°57'	135°35'	AT74 AT74A
2007	7	19	SEA	Glacier Bay	58°34'	136°6'	AT141, AT142, AT143

**Table 3**

Summary of attachment and movement data for satellite tags placed on Gulf of Alaska (GOA) and AT1 transient killer whales (*Orcinus orca*).

Population	Whale	First transmission date	Last transmission date	Duration (days)	Distance (km)	Range (km <sup>2</sup> )
GOA	AT109	7/4/2007	7/20/2007	17	1528	18415
GOA	AT73	9/20/2008	10/19/2008	30	3839	270503
GOA	AT122	6/12/2010	7/1/2010	19	1115	36222
GOA	AT73	9/21/2010	9/27/2010	7	625	2615
AT1	AT9	8/17/2010	8/22/2010	5	473	3982

for the GOA transients, whereas the AT1 transients were regularly encountered well inside Prince William Sound and Kenai Fjords, including glacial fjords headed by active glaciers (Fig. 1B).

Our trend analysis revealed an abrupt decline in the abundance of the AT1 transient population after the *Exxon Valdez* oil spill in 1989, corroborating earlier interpretations of photo-identification data (Matkin et al., 2008). This decline in abundance correlates with a spike of lower apparent survival from 1989 through 1990 and is almost certainly due to mortality, as supported by the low estimated rates of temporary emigration, high capture probabilities, and the lack of evidence of movement into other areas (Matkin et al., 1999, 2008). The AT1 population is currently exceptionally small at seven individuals, and the lack of recruitment since 1984 indicates their eventual extinction. Although the AT1 population appears to be a remnant group of

predators of near-coastal harbor seal (*Phoca vitulina*) and Dall's porpoise (*Phocoenoides dalli*) (Saulitis et al., 2000, 2005), their descent toward extinction was compounded by mortality after the oil spill. Additionally, harbor seals, a primary prey for AT1 killer whales, have declined substantially in our study area during the study period (Frost et al., 1999; Allen and Angliss, 2010).

There was no detectable decline in the GOA transient abundance over the period of study. As occasional visitors to the Prince William Sound–Kenai Fjords region, and because of their more extensive range (as supported by tagging data, Fig. 7A), they have likely been less affected by local changes to habitat and prey. Moreover, the documented prey items of GOA transients are notably different from those of the AT1 transients and include Steller sea lion (*Eumetopias jubatus*) (Saulitis et al., 2000; Heise et al., 2003; Maniscalco et al.,

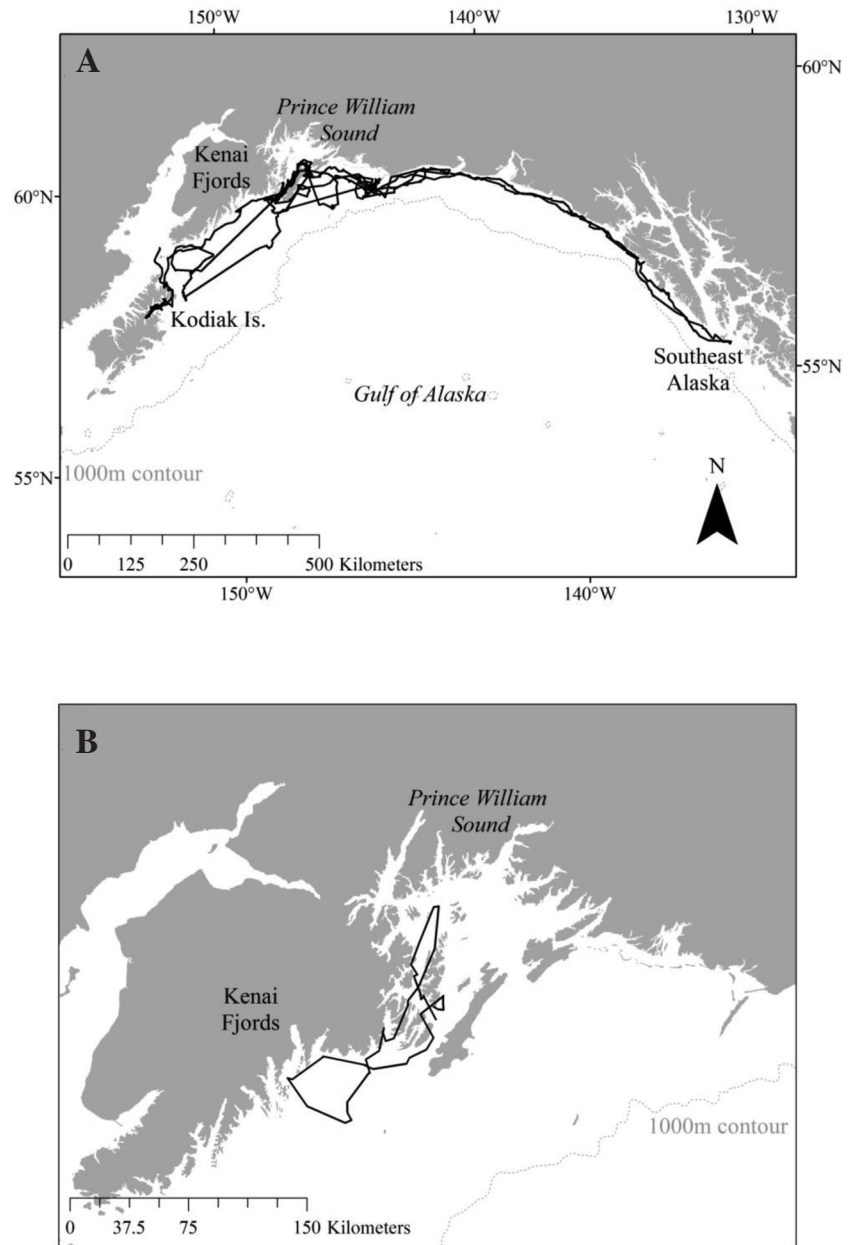
2007). Maniscalco et al. (2007) found Steller sea lions to be the dominant prey, at least during the non-winter periods in the Kenai Fjords region. Recent observations of GOA transients in southeastern Alaska, described in this article, indicate increased use of that region where, perhaps not coincidentally, Steller sea lion and harbor seal numbers have increased substantially in recent decades (Allen and Angliss, 2010).

The combined numbers of both GOA and AT1 transients that used Prince William Sound and Kenai Fjords over the course of a season was very low (currently estimated at ~16 whales in 2010) when compared with adjacent areas. In contrast, the parapatric west coast transient population in the coastal waters of southeastern Alaska, British Columbia, and Washington State numbers more than 200 individuals (Ford et al., 1999). Also, an annual aggregation of 80–100 transient whales has been reported in the Unimak Island region of the eastern Aleutian Islands in May and June (Matkin et al., 2007; Barrett-Lennard et al., 2011), and more than 300 transients use the coastal waters of a broader region of the Gulf of Alaska and Aleutian Islands (Durban et al., 2010). These differences likely reflect lower prey availability for mammal-eating killer whales in the northern Gulf of Alaska compared with adjacent regions.

Nuclear genetic diversity (Barrett-Lennard, 2000) indicates that the AT1 transients were once a much larger population. This, coupled with their more recent sharp decline, makes it unlikely that predation by these whales was a significant factor in dramatic decline of harbor seals in Prince William Sound in recent decades. Although it is conceivable that AT1 predation may have slowed harbor seal recovery, it is possible that the recent rebound in harbor seal numbers in Prince William Sound benefited from the AT1 decline. In the ten-year period 1997–2006, harbor seal numbers increased an average of 1.66% per year (95% confidence interval=0.34% , 2.98% per year) (Small<sup>3</sup>).

Maniscalco et al. (2007) suggested that Steller sea lions were a primary prey for GOA transients in Kenai Fjords, at least seasonally, and that the small number

<sup>3</sup> Small, R. 2010. Personal commun. Alaska Department of Fish and Game, Juneau, Alaska 99802.



**Figure 7**

Map of filtered movement tracks of (A) Gulf of Alaska (GOA) (4) and (B) AT1 (1) transient killer whales (*Orcinus orca*) tagged with a low impact minimally percutaneous external-electronics transmitter (LIMPET) and subsequently tracked in 2007–10 as summarized in Table 3.

of transients that used the area was not likely to have caused a decline in Steller sea lions. The consistent low numbers and lack of apparent increase in use of the area by GOA transients found in our study argue for a relatively even predation pressure on Steller sea lions in recent decades and support the conclusions of Maniscalco et al. (2007). In our population analysis we find little support for the hypothesis that declines in harbor seals or Steller sea lions in Prince William Sound and Kenai Fjords were a direct result of pre-

dition pressure by an increased number of transient killer whales.

It might be expected that the combination of reduced numbers of AT1 transient whales, the apparent rebound of harbor seals in the region, and a recent increase in Steller sea lion numbers, particularly in the eastern Gulf of Alaska (Allen and Angliss, 2010), would lead to increased use of these coastal waters by GOA transients. Because the local extinction of a killer whale population, as is likely for the AT1 population, is an unprecedented event, it is unknown whether members of the GOA population eventually will expand their use of the region. Our analysis indicates that, despite greatly reduced AT1 transient numbers and a slowly increasing prey population, this has not yet occurred.

## Conclusion

This study illustrates the importance of examining differing population trends and movements of individual killer whale ecotypes to reveal subtleties of population ecology and potential prey impacts. The Kenai Fjords–Prince William Sound region at the northern Gulf of Alaska supports two distinct non-associating transient populations that both occur at low numbers relative to other well-studied North Pacific regions. Despite their common position at the apex of marine food chains, each population exerts unique ecological impacts based on food preferences, prey abundance, and habitat use. These diverse impacts are reflected in the different range and trajectories of our study populations. The AT1 transients are a localized, inshore population apparently headed for extinction, whereas the GOA transients are a wider ranging, more oceanic population with relatively stable numbers.

Our study reveals that for small, infrequently observed populations such as the GOA transients, mark-recapture methods can be coupled with a Bayesian statistical approach to quantify important population parameters and examine population trends. With a combination of extensive geographically based photographic data and satellite tracking results, we can begin to define important aspects of population ecology.

## Acknowledgments

The majority of the long-term funds for the project were provided by the *Exxon Valdez* Oil Spill Trustee Council and the Alaska SeaLife Center. The Norcross Wildlife Foundation provided equipment. Hubbs Seaworld Research Institute and the National Marine Mammal Laboratory funded early work. Dozens of individuals have made substantial contributions to this multidecadal project. We are indebted to all of you. We would like to thank O. von Ziegeler, C. St. Amand, L. A. Holmes, L. Mazzuca, D. Maldini, and D. Olsen for data contributions. A. Gaylord assisted with GIS analysis. W. Perrin

and three reviewers made invaluable comments on the manuscript.

## Literature cited

- Allen, B. M., and R. P. Angliss.  
2010. Alaska marine mammal stock assessments, 2009. NOAA Tech. Memo. NMFS-AFSC-206, 276 p.
- Andrews, R. D., R. T. Pitman, and L. T. Balance.  
2008. Satellite tracking reveals distinct movement patterns for Type B and Type C killer whales in the southern Ross Sea, Antarctica. *Polar Biol.* 31:1461–1468.
- Barrett-Lennard, L. G.  
2000. Population structure and mating patterns of killer whales (*Orcinus orca*) as revealed by DNA analysis. Ph.D. diss., 97 p. Univ. British Columbia, Vancouver, B.C., Canada.
- Barrett-Lennard L. G., C. O. Matkin, J. W. Durban, E. L. Saulitis, and D. Ellifrit.  
2011. Predation of gray whales and prolonged feeding on submerged carcasses by transient killer whales at Unimak Island, Alaska. *Mar. Ecol. Prog. Ser.* 421:229–241.
- Brooks S. P., and A. Gelman  
1998. General methods for monitoring convergence of iterative simulations. *J. Comput. Graph. Stat.* 7:434–455.
- Carlin, B. P., A. E. Gelfand, and A. F. M. Smith.  
1992. Hierarchical Bayesian analysis of changepoint problems. *J. Appl. Stat.* 41:389–405.
- Dahlheim, M. E., and P. A. White.  
2010. Ecological aspects of transient killer whales *Orcinus orca* as predators in southeastern Alaska. *Wildl. Biol.* 16:308–322.
- DeMaster, D. P., A. W. Trites, P. Clapham, S. Mizroch, P. Wade, R. J. Small, and J. Ver Hoef.  
2006. The sequential megafaunal collapse hypothesis: testing with existing data. *Prog. Oceanogr.* 68:329–342.
- Durban, J., D. Ellifrit, M. Dahlheim, J. Waite, C. Matkin, L. Barrett-Lennard, G. Ellis, R. Pitman, R. Leduc, and P. Wade.  
2010. Photographic mark-recapture analysis of clustered mammal-eating killer whales around the Aleutian Islands and Gulf of Alaska. *Mar. Biol.* 157:1591–1604.
- Estes J. A., D. F. Doak, A. M. Springer, and T. M. Williams.  
2009. Causes and consequences of marine mammal population declines in southwest Alaska: a food-web perspective. *Phil. Trans. R. Soc. B.* 364:1647–1658.
- Estes, J., A., M. T. Tinker, T. M. Williams, and D. F. Doak.  
1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282:473–476.
- Ford, J. K. B., and G. M. Ellis.  
1999. Transients: mammal-hunting killer whales, 96 p. UBC Press, Vancouver, B.C., Canada.
- Ford, J. K. B., G. M. Ellis, L. G. Barrett-Lennard, A. B. Morton, and K. C. Balcomb.  
1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Can. J. Zool.* 76:1456–1471.
- Frost, K. J., L. F. Lowry, and J. M. VerHoef.  
1999. Monitoring the trend of harbor seals in Prince William Sound, Alaska. *Mar. Mamm. Sci.* 15:494–506.
- Gelfand A. E., and S. K. Ghosh.  
1998. Model choice: A minimum posterior predictive loss approach. *Biometrika* 85:1–11.



- Gelman A., J. B. Carlin, H. S. Stern, and D. B. Rubin.  
1995. Bayesian data analysis, 685 p. Chapman and Hall, London.
- Hammond, P. S.  
1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. Rep. Int. Whal. Comm. Special Issue 8:253–282.  
1987. Techniques for estimating the size of whale populations. Symp. Zool. Soc. London 58:225–245.  
1990. Capturing whales on film – estimating cetacean population parameters from individual recognition data. Mamm. Rev. 20:17–22.
- Heise, K., L. Barrett-Lennard, E. Saulitis, C. Matkin, and D. Bain.  
2003. Examining the evidence for killer whale predation on Steller sea lions in British Columbia and Alaska. Aquat. Mamm. 29:325–334.
- Herman, D. P., D. G. Burrows, P. R. Wade, J. W. Durban, C. O. Matkin, R. G. LeDuc, L. G. Barrett-Lennard, and M. M. Krahn.  
2005. Feeding ecology of eastern North Pacific killer whales *Orcinus orca* from fatty acid, stable isotope, and organochlorine analyses of blubber biopsies. Mar. Ecol. Prog. Ser. 302:275–291.
- Kuo, L., and B. Mallick.  
1998. Variable selection for regression models. Sankhya, Series B 60:65–81.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson.  
1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol. Monogr. 62:67–118.
- Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter.  
2000. WinBUGS—a Bayesian modelling framework: concepts, structure and extensibility. Stat. Comput. 10:325–337.
- Maniscalco, J. M., C. O. Matkin, D. Maldini, D. G. Calkins, and S. Atkinson.  
2007. Assessing killer whale predation on Steller sea lions from field observations in Kenai Fjords, Alaska. Mar. Mamm. Sci. 23:306–321.
- Matkin, C. O., L. G. Barrett-Lennard, H. Yurk, D. Ellifrit, and A. W. Trites.  
2007a. Ecotypic variation and predatory behavior of killer whales (*Orcinus orca*) in the eastern Aleutian Islands, Alaska. Fish. Bull. 105:74–87.
- Matkin, C. O., G. M. Ellis, E. L. Saulitis, L. G. Barrett-Lennard, and D. Matkin.  
1999. Killer whales of southern Alaska, 96 p. North Gulf Oceanic Soc., Homer, AK.
- Matkin C. O., E. L. Saulitis, G. M. Ellis, P. Olesiuk, and S. D. Rice.  
2008. Ongoing population level impacts on killer whales following the 'Exxon Valdez' oil spill in Prince William Sound, Alaska. Mar. Ecol. Prog. Ser. 356:269–281.
- Matkin, D. R., J. M. Straley, and C. M. Gabriele.  
2007b. Killer whale feeding ecology and non-predatory interactions with other marine mammals in the Glacier Bay region of Alaska. In Proceedings of the fourth Glacier Bay science symposium, 2004 (J. F. Piatt and S. M. Gende, eds.), p. 155–158. U.S. Geological Survey, Anchorage, AK.
- Morin, P. A., F. I. Archer, A. D. Foote, J. Vilstrup, E. E. Allen, P. Wade, J. Durban, K. Parsons, R. Pitman, L. Li, P. Bouffard, S. C. Abel-Nielsen, M. Rasmussen, E. Willerslev, M. Thomas, P. Gilbert, and T. Harkins.  
2010. Complete mitochondrial genome phylogeographic analysis of killer whales (*Orcinus orca*) indicates multiple species. Genome Res. 20:908–916.
- Saulitis, E., C. O. Matkin, and F. H. Fay.  
2005. Vocal repertoire and acoustic behavior of the isolated AT1 killer whale subpopulation in Southern Alaska. Can. J. Zool. 83:1015–1029.
- Saulitis, E. L., C. O. Matkin, K. Heise, L. G. Barrett-Lennard, and G. M. Ellis.  
2000. Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. Mar. Mamm. Sci. 16:94–109.
- Scheel, D., C. Matkin, and E. Saulitis.  
2001. Distribution of killer whale pods in Prince William Sound, Alaska over a thirteen-year period, 1984–1996. Mar. Mamm. Sci. 17:555–569.
- Schofield, M. R., R. J. Barker, and D. MacKenzie.  
2009. Flexible hierarchical mark-recapture modeling for open populations using WinBUGS. Environ. Ecol. Stat. 16:369–387.
- Springer A. M., J. A. Estes, G. B. van Vliet, T. M. Williams, D. F. Doak, E. M. Danner, K. A. Forney, and B. Pfister.  
2003. Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? Proc. Natl. Acad. Sci. USA 100:12223–12228.
- Springer A. M., J. A. Estes, G. B. van Vliet, T. M. Williams, D. F. Doak, E. M. Danner, and B. Pfister.  
2008. Mammal-eating killer whales, industrial whaling, and the sequential megafaunal collapse in the North Pacific Ocean: a reply to critics of Springer et al., 2003. Mar. Mamm. Sci. 24:414–442.
- Wade P. R., V. N. Burkanov, M. E. Dahlheim, N. A. Friday, L. W. Fritz, T. R. Loughlin, S. A. Mizroch, M. M. Muto, D. W. Rice, L. G. Barrett-Lennard, N. A. Black, A. M. Burdin, J. Calambokidis, S. Cerchio, J. K. B. Ford, J. K. Jacobsen, C. O. Matkin, D. R. Matkin, A. V. Mehta, R. J. Small, J. M. Straley, S. M. McCluskey, and G. R. VanBlaricom.  
2007. Killer whales and marine mammal trends in the North Pacific—a re-examination of evidence for sequential megafauna collapse and the prey-switching hypothesis. Mar. Mamm. Sci. 23:766–802.
- Wade, P., J. Ver Hoef, and D. DeMaster.  
2009. Mammal eating killer whales and their prey—trend data for pinnipeds and sea otters in the North Pacific Ocean do not support the sequential megafaunal collapse hypothesis. Mar. Mamm. Sci. 25:737–747.
- Whitehead, H.  
1990. Mark-recapture estimates with emigration and re-immigration. Biometrics 46:473–479.
- Yurk, H., L. Barrett-Lennard, J. K. B. Ford, and C. O. Matkin.  
2002. Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. Anim. Behav. 63:1103–1119.
- Yurk, H., O. Filatova, C. O. Matkin, L. G. Barrett-Lennard, and M. Brittain.  
2010. Sequential habitat use by two resident killer whale (*Orcinus orca*) clans in Resurrection Bay, Alaska as determined by remote acoustic monitoring. Aquat. Mamm. 36:67–78.