# Climate mediates the success of migration strategies in a marine predator

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LETTER

# Climate mediates the success of migration strategies in a marine predator

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**Abstract**

Individual behavioural specialisation has far-reaching effects on fitness and population persistence. Theory predicts that unconditional site fidelity, that is fidelity to a site independent of past outcome, provides a fitness advantage in unpredictable environments. However, the benefits of alternative site fidelity strategies driving intraspecific variation remain poorly understood and have not been evaluated in different environmental contexts. We show that contrary to expectation, strong and weak site fidelity strategies in migratory northern elephant seals performed similarly over 10 years, but the success of each strategy varied interannually and was strongly mediated by climate conditions. Strong fidelity facilitated stable energetic rewards and low risk, while weak fidelity facilitated high rewards and high risk. Weak fidelity outperformed strong fidelity in anomalous climate conditions, suggesting that the evolutionary benefits of site fidelity may be upended by increasing environmental variability. We highlight how individual behavioural specialisation may modulate the adaptive capacity of species to climate change.

**Keywords**

Behavioural strategy, climate variability, foraging ecology, habitat selection, individual specialisation, migration, *Mirounga angustirostris*, northern elephant seal, resource predictability, site fidelity.

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## INTRODUCTION

Animals face numerous tradeoffs when selecting habitats, and their selection strategies have broad implications for both individual fitness and a population's ability to cope with environmental change. Animals must balance the energy gained in high quality resource patches with travel costs, search times, and predation or competition risk in order to survive (Charnov 1976; Pyke 1984). In response to these trade-offs, individuals may specialise in their habitat selection and resource use (Bolnick *et al*. 2003; Dall *et al*. 2012). Variation in individual behaviour within the same species can have far-reaching effects on intraspecific competition, population persistence, community dynamics, and ultimately species diversity (Bolnick *et al*. 2003, 2011), and as a result, the causes and consequences of such variation are central to understanding ecological dynamics (Araújo *et al*. 2011; Dall *et al*. 2012; Farine *et al*. 2015; Spiegel *et al*. 2017). Moreover, as ecosystems experience unprecedented environmental change, research advancing understanding of the trade-offs of alternative behavioural strategies is an important component of anticipating species' responses to future change (Nagelkerken & Munday 2015).

Site fidelity, the tendency to revisit sites for foraging, breeding or shelter, is a widespread behavioural strategy expected to confer a fitness advantage in certain contexts (Switzer 1993; Schmidt 2004). While several empirical studies have documented indirect (Dyer 1996; Bradshaw *et al*. 2004; Arthur *et al*. 2015; Wakefield *et al*. 2015) and direct (Brown *et al*. 2008; Patrick & Weimerskirch 2017) fitness advantages of site fidelity, the ecological and evolutionary benefits driving intraspecific variation in site fidelity remain poorly understood. In particular, no empirical study has examined how individual performance is modulated by site fidelity under varying environmental regimes, nor the environmental and climatic contexts in which alternative site fidelity strategies are favoured. Such empirical research is challenging, requiring both performance data and movement data over sufficient time periods to observe space use patterns and changes in the environment. We approach these questions using a 10-year dataset on individual movement and energy gain in northern elephant seals, *Mirounga angustirostris*.

Site fidelity in unpredictable environments like the open ocean is theorised to confer an advantage when integrated over long timescales (Switzer 1993; Bradshaw *et al*. 2004; Arthur *et al*. 2015). When resources are distributed unpredictably, local knowledge gained via site familiarity may confer benefits such as increased foraging efficiency (Stamps 1995; Wolf *et al*. 2009; Piper 2011; Wakefield *et al*. 2015). Thus, for long-lived species, long-term site fidelity may be advantageous when outcomes are averaged over multiple years or an individual's lifetime, even if outcomes are not favourable in all

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years (Bradshaw *et al.* 2004). Conversely, strong site fidelity may be maladaptive in environments undergoing long-term change (Switzer 1993; Williams *et al.* 1993; Ganter & Cooke 1998; Faille *et al.* 2010). Changing environmental conditions can influence the relative benefits of strong or weak site fidelity strategies by altering forage abundance, community composition, and distribution (Durant *et al.* 2007; Fleming *et al.* 2015), thereby altering the profitability of familiar habitats. Increasing environmental variability associated with climate change (Sydeman *et al.* 2013) has the potential to favour lower site fidelity strategies that allow animals to better respond to changing conditions. Populations exhibiting strong site fidelity may also be more vulnerable to the effects of extreme climate events, making individual-level variation in behavioural strategies important for overall population persistence (Bolnick *et al.* 2003; Dall *et al.* 2012; Gallagher *et al.* 2015). Thus, both theoretically and from a conservation perspective, it is important to understand how environmental context influences the relative fitness-related benefits of individual site fidelity strategies, and how changing environmental conditions may affect these trade-offs.

Migratory marine predators are a particularly sensitive guild to environmental change, and in particular to climate, due to the tight coupling between climate forcing and the availability of prey resources (Rahmstorf 2002; Perry *et al.* 2005; Pinsky *et al.* 2013; Stewart *et al.* 2014; Laidre *et al.* 2015). Northern elephant seals are a long-lived migratory marine predator that have strong natal site fidelity to their terrestrial breeding colonies, and display individual-level variation in site fidelity to foraging habitats in the North Pacific Ocean (Simmons 2008). Adult females perform a post-molting migration from June-January that is essential to survival and successful breeding, carrying them thousands of kilometres into productive pelagic waters (Robinson *et al.* 2012). During these migrations, northern elephant seals have been shown to have stable, individually-specialised site fidelity strategies over time (data up to 11 years), without switching strategies in response to poor performance (Simmons 2008; Costa *et al.* 2012). The amount of energy female northern elephant seals gain during these migrations, when pups are gestating, is tightly linked with reproductive success (Costa 1991; Robinson *et al.* 2012). Energy gained during migrations in female northern elephant seals is also strongly linked with climatic conditions. Sea surface temperature is a significant predictor of foraging areas, with females selecting cooler, more productive waters (Simmons *et al.* 2007). In addition, El Niño conditions have been shown to influence at-sea foraging performance (Le Boeuf & Reiter 1991; Crocker *et al.* 2006). Given their ecological importance as top predators, individual specialisation in site fidelity behaviour, and sensitivity to climate conditions, northern elephant seals are an ideal species with which to investigate the effects of environmental variability on the relationship between individual site fidelity strategies and performance.

We combined a 10-year satellite tracking dataset on female northern elephant seals, allowing precise quantification of individual-level site fidelity, with individual performance metrics to evaluate (1) the long-term benefits of site fidelity strategies, (2) the relative success of site fidelity strategies under different climate conditions, and (3) the spatial distribution and temporal variability in oceanographic conditions at foraging areas to help elucidate the mechanisms resulting in observed differences in performance. We developed a site fidelity index to quantify the spatial consistency of post-molting migration patterns for individuals tagged over multiple years to test three predictions: (1) integrated over long timescales (10 years), stronger site fidelity leads to better performance, as measured by mass gained during migrations, than lower site fidelity; (2) that the relative benefits of individual site fidelity strategies vary at an interannual timescale under different climatic conditions; and (3) that foraging areas used by individuals with higher site fidelity have greater long-term resource predictability than those used by individuals with lower site fidelity. Our study provides unique insight into the potential fitness consequences of individually-specialised behavioural strategies under different climatic regimes.

## MATERIALS AND METHODS

### Field site and data collection

As part of a long-term research program, 152 adult female northern elephant seals were randomly selected from the population at Año Nuevo State Park, California, USA (37°5′ N, 122°16′ W) between 2004 and 2014 and tagged with satellite tracking units prior to their post-molting migrations. A total of 30 repeat individuals were tagged for two ($N = 25$) or three ($N = 5$) post-molting migrations during this time period and included in our analyses, for a total of 65 trips (Appendix S1). Individuals were weighed using a digital scale mounted to a tripod (accuracy ± 1 kg) at time of tag deployment following a 1-month molting period on shore, and again at tag recovery following return to shore after migrating (Le Boeuf *et al.* 2000). A combination of GPS and ARGOS-linked technologies were used, both yielding hourly position estimates post-processing. For ARGOS tags, tracks were filtered for errors and smoothed using a state space model (*crawl* package (Johnson 2016) in R 3.1.1 (R Core Team 2016)). Details on tagging procedures, instrumentation and post-processing are provided by Robinson *et al.* 2012.

### Quantifying site fidelity

We developed a site fidelity index representing the interannual consistency of migration patterns (Fig. 1). Following recent studies, we calculated interannual site fidelity as the overlap of each year's 95% kernel density utilisation distribution (UD) using Bhattacharyya's affinity (BA) metric (Arthur *et al.* 2015; Wakefield *et al.* 2015; McIntyre *et al.* 2017). Kernel density UDs quantify the intensity of use of a given location, in addition to mapping used and unused areas, and has reduced bias when the bandwidth, or smoothing parameter, of the kernel estimator is fixed (Seaman & Powell 1996). In estimating UDs, we specified a bivariate normal kernel, fixed bandwidth of 50 km, and a grid resolution of 25 km to match the spatial resolution of environmental variables (Wakefield *et al*. 2015). Given the likelihood of temporal autocorrelation between relocations, we also estimated UDs using a Brownian bridge kernel density estimator (Horne *et al*. 2007) with a motion variance parameter of 1 km/$\sqrt{s}$ (Appendix S2). Bhattacharyya's affinity ranges from 0 (no overlap) to 1 (perfect overlap), and is recommended by an extensive comparison of home-range overlap indices as a reliable method for quantifying similarity between UDs (Fieberg & Kochanny 2005). Site fidelity values were considered fixed individual traits given support for long-term individual specialisation in elephant seal site fidelity strategies (Bradshaw *et al*. 2004; Simmons 2008; Costa *et al*. 2012; McIntyre *et al*. 2017).

The greater part of our analyses retained site fidelity index as a continuous variable, but for purposes of comparing long-term performance of strategies we created a categorical variable of site fidelity. Based on the frequency distribution of BA values in the population (Appendix S2), we assigned individuals as either high (BA > 0.75) or low (BA < 0.75) site fidelity. We tested the sensitivity of our results to this cutoff by recalculating with cutoffs at 0.6, 0.65, 0.7 and 0.8, which did not alter the results (Appendix S2). To consider the potential role of transit periods from/to the colony in weighting our site fidelity index, we explored the sensitivity of our index to excluding the first and last 3 days, week, 2 weeks, and month of each trip (Appendix S3). No significant differences in results were observed, so all locations within each trip were retained for analysis. In addition, we checked for effects of individual age, initial body weight, and years between migration tracks on our site fidelity index. There was no effect of age (linear model slope = 0.005, intercept = 0.74, $P = 0.58$) nor initial body weight (linear model slope = 0.0003, intercept = 0.71, $P = 0.69$) on site fidelity, nor of years between tracks

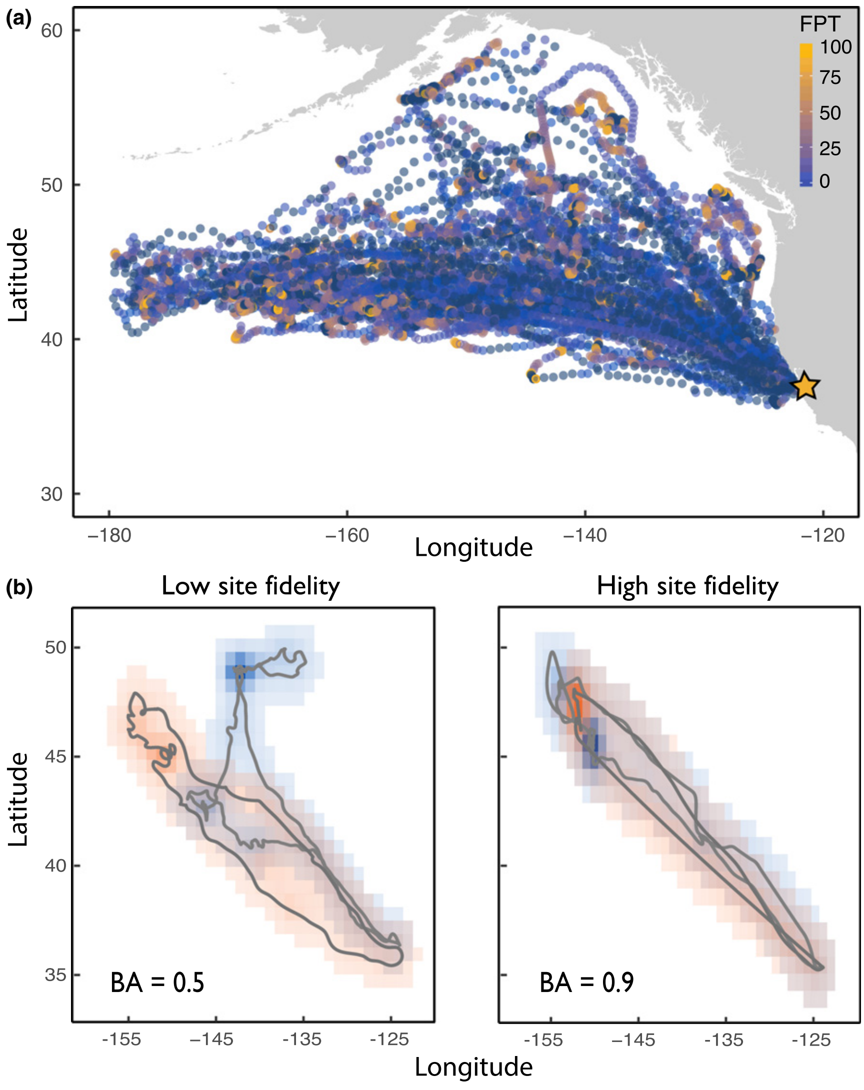


**Figure 1** (a) Tracking data of 30 adult female northern elephant seals performing 65 foraging migrations departing from Año Nuevo (star). Locations in the figure are subsampled to daily fixes and colour-coded by First Passage Time (FPT) values used to identify putative foraging areas. (b) Sample utilisation distributions from two satellite-tracked individuals used to calculate Bhattacharyya's affinity (BA) index for quantifying individual-level site fidelity. Blue and orange utilisation distributions for each individual represent space used during different years; darker colours represent areas of most intensive use.

upon removal of an outlier (intercept = 0.88, slope = −0.02, $P = 0.10$; Appendix S4). Home range and UD overlap analyses were conducted using the *adehabitatHR* package (Calenge 2013) in R 3.3.1 (R Core Team 2016).

### Evaluating performance under different climate conditions

Performance, the net energy balance of foraging success and travel costs, was measured as percent mass gained over the duration of the migration. Body mass of each individual was measured at the time of tag deployment and recovery. Mass gained was calculated as a percent of body weight at time of tag deployment to control for initial body size, and corrected for pup gestation for pregnant females (see Robinson *et al.* 2012 for details). We used linear regression to evaluate the influence of site fidelity on mass gained, while accounting for age and trip duration as covariates. To evaluate the variability in interannual performance as a function of site fidelity and differences in trip duration, we calculated the difference in mass gained between years for each individual, and used linear regression to relate variability in mass gained to site fidelity. As a second measure, we use maximum likelihood estimation to fit the following model:

$$Y \sim \mathrm{Normal}(\mu, \sigma = \exp(-\beta X))$$

where $Y$ is mass gain, $X$ is site fidelity index, and $\beta$ is the rate at which the standard deviation in mass gain changes with site fidelity. A positive $\beta$ value would indicate that variance in mass gain decreases with increasing site fidelity, whereas a negative $\beta$ would indicate that variance in mass gain increases with site fidelity.

The relationship between performance and site fidelity was evaluated under three climate conditions characterised by positive, neutral, and negative phases of the Pacific Decadal Oscillation (PDO), the leading mode of climate variability in the North Pacific (Mantua & Hare 2002; Peterson & Schwing 2003). The PDO is associated with shifts in sea surface temperature (SST) anomalies and positioning of the boundary between the sub-arctic and sub-tropical gyres (Latif & Barnett 1994; Di Lorenzo *et al.* 2013), where northern elephant seals are known to forage (Robinson *et al.* 2012). PDO indices between −0.5 and 0.5 were considered neutral phases, while positive and negative phases were considered above and below these values, respectively (Latif & Barnett 1996; Mantua *et al.* 1997). In the central North Pacific, positive PDO phases are associated with cool SST anomalies, and negative PDO phases are associated with warm SST anomalies (Di Lorenzo *et al.* 2013). Here, the PDO is also linked to fluctuations in the abundance of lower trophic level taxa, with positive phases seeing dramatic increases in salmon (Mantua *et al.* 1997), sardines (Chavez *et al.* 2003; Zwolinski & Demer 2012), and zooplankton (Di Lorenzo *et al.* 2013). While the PDO is associated with long-term climatic regimes, on the order of 20 years, over the last decade the PDO has been switching phases at intervals of 2–4 years (Fleming *et al.* 2015). For each year, we obtained 3-month running PDO means for August-October, the middle of the migration period, from the University of Washington Joint Institute for the Study of the Atmosphere and Ocean (http://research.jisao.washington.edu/pdo/).

### Characterising variability in oceanographic conditions in foraging areas

We identified probable foraging areas using First Passage Time (FPT) analysis to detect area-restricted search (ARS; Fauchald & Tveraa 2003). First passage time measures the length of time an animal spends within an circle of a given radius, and is considered to be a reliable predictor of pelagic foraging behaviour in elephant seals (Robinson *et al.* 2010; Pascoe *et al.* 2016). Given the spatial error associated with ARGOS tags, we investigated ARS behaviour between 20 and 50 km radii. A plot of the variance in FPT vs. spatial scale identified a characteristic scale of restricted search behaviour at a 30-km radius. First passage time values were henceforth calculated for circles with a 30-km radius (see Fauchald & Tveraa 2003 for methods). Locations corresponding to ARS were conservatively classified as those with FPT values > 48 h, consistent with published measurements of mean time spent in focal foraging areas by migrating females in the same population (Le Boeuf *et al.* 2000; Simmons *et al.* 2007). First passage time analysis was conducted using the *adehabitatLT* package (Calenge 2015) in R 3.3.1 (R Core Team 2016).

We investigated the long-term variability in sea surface temperature (SST) and surface Chlorophyll-$\alpha$ concentration in foraging locations. Though northern elephant seals primarily prey on mesopelagic squid and forage fish species (Antonelis *et al.* 1994), these surface parameters are significantly associated with northern elephant seal foraging habitat selection (Crocker *et al.* 2006; Simmons *et al.* 2007; Robinson *et al.* 2012). Long-term persistence in the physical environment has been shown to be a better predictor of pelagic foraging locations in pinnipeds and seabirds than their instantaneous measurements (Bradshaw *et al.* 2004; Suryan *et al.* 2012; Scales *et al.* 2014; Arthur *et al.* 2015), and is theoretically linked with the emergence of site fidelity (Switzer 1993). Monthly SST climatologies were obtained from GHRSST Level 4 Global Sea Surface Temperature (25 km spatial resolution; https://podaac.jpl.nasa.gov). Monthly Chlorophyll-$\alpha$ climatologies were obtained from Aqua MODIS Chlorophyll Concentration (25 km spatial resolution; https://neo.sci.gsfc.nasa.gov). For each variable, long-term variability for each grid cell was measured as the standard deviation in monthly values over the 10-year study period. Chlorophyll-$\alpha$ and SST standard deviation values were extracted for each foraging location. After log-transforming values for normality, we compared these characteristics for high and low site fidelity individuals using mixed effects logistic regression with individual seal as a random effect.

## RESULTS

### Effects of site fidelity and climate on performance

During their post-molting migrations, individuals were at-sea for 7.3 ± 1 months (Appendix S1). According to our protocol for quantifying interannual site fidelity, site fidelity index values ranged between 0.23 and 0.97, with a large skew towards high index values (Appendix S1). Averaged across a 10-year period, there was no significant difference in percent mass gain between individuals considered as having high vs. low site fidelity (mean High = 0.95 ± 0.22%, mean Low = 0.89 ± 0.20%; Welch's *t*-test, $P = 0.4$; Appendix S2). However, results of a linear model indicated that in average climate conditions (neutral PDO phases), increased site fidelity was correlated with increased mass gain (Fig. 2; slope = 0.76, SE = 0.31, $P < 0.05$). In positive PDO phases, the opposite pattern appeared, where increased site fidelity was correlated with lower mass gain (slope = −0.46, SE = 0.16, $P < 0.05$). There was no significant relationship between percent mass gain and site fidelity in negative PDO years ($P = 0.9$).

#### Variability in oceanographic conditions and performance

Elephant seals exhibiting high site fidelity used foraging areas with significantly lower long-term variability in chlorophyll-α (logistic regression estimate = −4.74, SE = 0.78, $P < 0.001$) and sea surface temperature (estimate = −5.46, SE = 1.1, $P < 0.001$) than low site fidelity individuals (Fig. 3a and b). There was no difference in the instantaneous oceanographic measurements between the two groups (high site fidelity: chlorophyll-α = 0.36 ± 0.36 mg/m$^3$ (mean ± SD), SST = 14.3 ± 2.7 °C; low site fidelity: chlorophyll-α = 0.53 ± 1.03 mg/m$^3$, SST = 14.8 ± 2.4 °C). Individuals with stronger site fidelity also had lower variability in mass gain between years (Fig. 3c; linear model slope = −0.34, SE = 0.15, $P < 0.05$; maximum likelihood parameter estimation $\mu = 0.93$, $\beta = 1.86$, $P < 0.001$). Our site fidelity index explained 68% of the variation observed in interannual mass gain variability.

## DISCUSSION

Our findings reveal that ocean-scale climate conditions mediate the success of individually-specialised habitat selection strategies in a migratory marine predator. Satellite tracking of northern elephant seals conducted over multiple years, coupled with remote sensing and mass gain measurements, allowed us to quantify spatially-explicit migration patterns, characterise habitat associations, and link these patterns to energetic outcomes under different environmental conditions. Individuals that had a high degree of site fidelity in their migration patterns used areas with relatively stable resources over time, and had lower interannual variation in their mass gain. These individuals also performed best under neutral climate conditions, outperforming those that were more plastic in their movements, though this pattern was reversed during positive phases of the Pacific Decadal Oscillation. Together, our findings suggest that strong individual-level site fidelity is adaptive by yielding relatively reliable energy gain across years, but this strategic advantage may decline under continued long-term environmental change.

While high site fidelity individuals had relatively consistent mass gain between years, we found that the success of low site fidelity individuals was more variable (Fig. 3c), performed well in positive PDO phases and very poorly in neutral phases (Fig. 2). This variation is mirrored by the variability in oceanographic conditions characterising foraging areas (Fig. 3a and b). Individuals with strong site fidelity appear to select regions with greater long-term habitat stability than their low site fidelity counterparts, potentially enabling them to acquire consistently accessible or profitable resources each year. Selection for oceanic regions with long-term predictability in productivity has been demonstrated for other pinnipeds exhibiting strong site fidelity (Bradshaw *et al.* 2004; Arthur *et al.* 2015), though this was not compared with habitat selection of individuals with lower site fidelity. While there was variation within each assigned group, our results reveal two diverging habitat selection strategies within the population: a higher site fidelity strategy facilitating moderate rewards and low risk, alongside a lower site fidelity strategy encompassing potentially high rewards, but with high risk.

Unexpectedly, there was no difference in the overall performance between the two strategies when averaged over our 10-year study period (Appendix S2). However, when we separated by climate phase, strong and opposing patterns

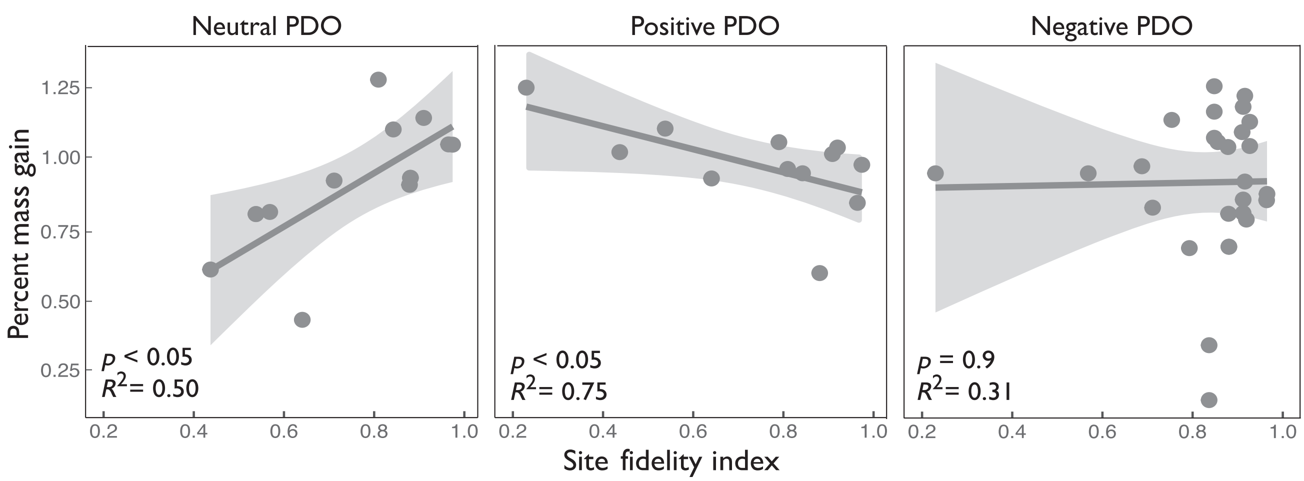


**Figure 2** Percent of mass gained during migration as related to an individual's level of site fidelity in neutral, positive and negative phases of the Pacific Decadal Oscillation (PDO). Each point represents a different migration trip for $N = 30$ adult females. In neutral PDO years, increasing site fidelity is correlated with higher mass gain (linear model slope = 0.76 ± 0.31; $P < 0.05$). In positive PDO years, corresponding to cooler pelagic waters, increasing site fidelity is correlated with lower mass gain (slope = −0.46 ± 0.16; $P < 0.05$). There is no significant relationship between percent mass gain and site fidelity in negative PDO years.

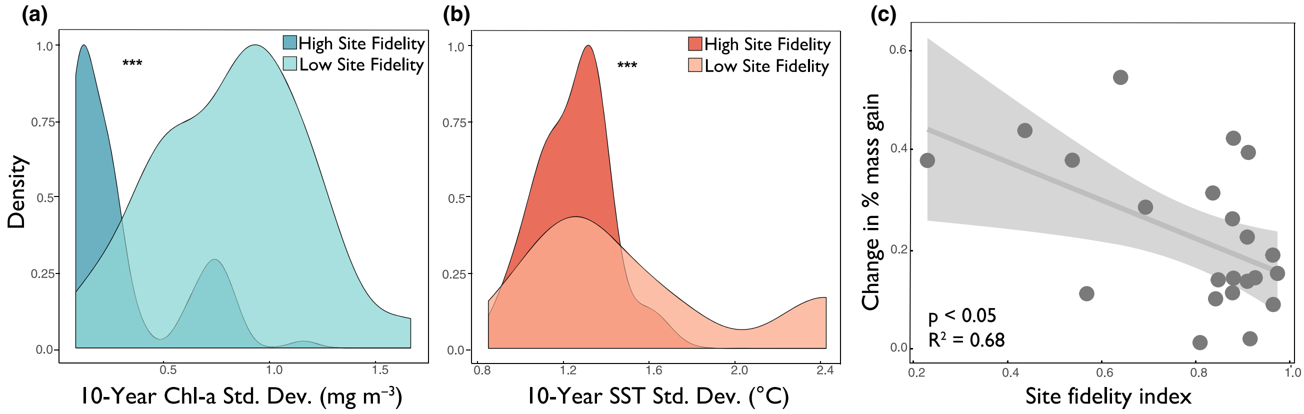


**Figure 3** (a and b) Distributions of temporal variability between 2004 and 2014 in (a) chlorophyll-a concentrations and (b) sea surface temperature characterising northern elephant seal putative foraging locations. High site fidelity is associated with significantly lower variability in chlorophyll-a (logistic regression estimate = $-4.74 \pm 0.78$, $P < 0.001$) and sea surface temperature ($-5.46 \pm 1.1$, $P < 0.001$). (c) Observed and predicted relationship between site fidelity and differences in percent mass gained between years, accounting for differences in trip duration. Each point represents a different individual. Individuals with higher site fidelity have lower variability in mass gain between years (linear model slope = $-0.34 \pm 0.15$, $P < 0.05$). *** is a standard notation of statistical significance, indicating a p-value < 0.001.

emerged. Individuals with stronger fidelity performed significantly better than those with lower fidelity under average climate conditions (Fig. 2), consistent with the hypothesis that site fidelity confers benefits via site familiarity (Wolf *et al.* 2009; Piper 2011). We observed no appreciable difference in performance among the strategies during negative PDO phases corresponding to warmer waters, during which there appears to be a great deal of variation in mass gained. In contrast, individuals with lower site fidelity had greater success during positive phases of the PDO, characterised by cooler and more productive pelagic waters, possibly because those individuals were better able to track high quality resources. This hypothesis is supported by another study examining northern elephant seal foraging success during El Niño events (Crocker *et al.* 2006), which also produce cool sea surface temperature anomalies in the central North Pacific (Di Lorenzo *et al.* 2013). That study reported dramatically reduced mass gain during a strong El Niño event compared to typical years, yet the individuals that had the greatest success were those that tracked the significant latitudinal movement of the highly productive Transition Zone Chlorophyll Front (TZCF; Crocker *et al.* 2006), a sharp surface chlorophyll gradient in the North Pacific Basin (Polovina *et al.* 2015). It is possible that lower site fidelity individuals are better able to follow the interannual migrations of the TZCF, which typically extends further south during positive PDO phases and further north during negative phases (Bograd *et al.* 2004; Howell *et al.* 2012). In addition, a recent study showed that PDO phase had a significant food-web-mediated effect on reproductive success in sea lions in the coastal eastern Pacific Ocean (Samhouri *et al.* 2017). Unfortunately these linkages cannot be tested for pelagic regions of the central Pacific as similar food web data are not available. Our findings support the hypothesis that behavioural plasticity is likely an important ecological response for coping with anomalous environmental conditions (Colles *et al.* 2009).

Owing to data limitations, our assessment of site fidelity relied on two or three repeat migrations per individual, with one individual exhibiting the same foraging pattern 11 years later (Costa *et al.*2012). While strong support exists for long-term individual specialisation in site fidelity strategies, independent of past performance, among northern and southern elephant seals (Bradshaw *et al.* 2004; Simmons 2008; Costa *et al.* 2012; McIntyre *et al.* 2017), lending confidence to our treatment of site fidelity as a fixed trait, additional repeat migrations would strengthen our classifications. Our analysis of site fidelity was also based on horizontal migratory movements, while for marine species, site fidelity in vertical movements may be altogether different. For example, while an individual may be consistent in foraging in a given horizontal area, it may vary its dive depth, dive shape, or target species (Kuhn *et al.* 2009; Le Bras *et al.* 2016). Recent research indicates elephant seals also display fidelity to three-dimensional habitats (McIntyre *et al.* 2017), and future research should continue to integrate movements over three dimensions (Bestley *et al.* 2015) to investigate the linkages between horizontal and vertical site fidelity. Finally, while our 10-year tracking dataset is unique in its length, the true evolutionary benefits of site fidelity strategies can only be observed over generations.

The strong dependence of performance on climate phase implies that the relative long-term performance of each strategy is contingent on the frequency of alternate PDO phases throughout the study period. Our random sample of thirty individuals indicates that the incidence of strong site fidelity in the population is very high. This suggests that the population may have evolved to past climate conditions that were more stable and favourable for high site fidelity. There is clear evidence that over the last thirty years variance in North Pacific climate indices has increased significantly, explaining increased variability in the demography of salmon and seabird populations (Sydeman *et al.* 2013). Increased climate variability may favour greater behavioural plasticity (Dingemanse & Wolf 2013; Snell-Rood 2013); moreover, changes in habitats and their predictability have been posited to reduce the evolved fitness benefits of strong site fidelity (Switzer 1993). If changing environmental conditions favour lower site fidelity the frequency of strong site fidelity individuals in populations may shift. The implications of whether the loss of strong site fidelity would coincide with the loss of linked behavioural specialisations (Dall *et al.* 2012) is not understood. Monitoring the degree of site fidelity in a population over long timescales may serve as an indicator of a population's response to environmental change, with implications for a species' evolutionary ecology (Garamszegi & Møller 2017). Moreover, our results suggest that the behavioural responses of individuals to climate shifts may be masked if responses are averaged over the population, since individuals with strong site fidelity may not exhibit a spatial response. It is therefore important to consider the strength of individual variation in site fidelity in a population when investigating behavioural responses to environmental change.

It has been suggested that modern climate change may alter the ecological basis of migration (Middleton *et al.* 2013). Our study asks whether such adaptation may be occurring in additional ecological phenomena like long-term individual-level site fidelity. If site fidelity is heritable, it may be under selection by indirectly influencing reproductive success (Patrick & Weimerskirch 2017). Mass gained during the post-molting migration is a strong predictor of natality in northern elephant seal females (Robinson *et al.* 2012). In a closely related species, the southern elephant seal (*Mirounga leonina*), a longitudinal study demonstrated that energy gain in adult females was the largest determinant of pup survival in their first year (McMahon & Burton 2005). As migration performance is directly linked with reproductive success in elephant seals, long-term environmental change may influence the evolutionary underpinnings of site fidelity in the species. Understanding the functional links between environmental conditions, individual specialisation in habitat selection strategies, performance, and reproductive success enables predictions of population responses and the persistence of behavioural phenomena in future climate scenarios.

In the North Pacific, climate change is expected to precipitate a number of biophysical changes over the next century that are likely to affect marine predator populations (Woodworth-Jefcoats *et al.* 2016). The Transition Zone Chlorophyll Front is a highly productive region where many predator species concentrate foraging (Kappes *et al.* 2010; Block *et al.* 2011; Polovina *et al.* 2015; Thorne *et al.* 2015). These include not only charismatic species like northern elephant seals and albatross, but also those of great economic significance, namely, salmon and bluefin tuna (Block *et al.* 2011). Under the IPCC 'business-as-usual' emissions scenario, this major oceanographic feature is expected to shift northward *c.* 1000 kilometres over the next 100 years, coupled with a *c.* 38% decline in total primary production in the region (Bograd *et al.* 2004; Polovina *et al.* 2008, 2011). Whether predator species' ranges are able to track such environmental changes is a pressing question in ecology and conservation biology (Bellard *et al.* 2012; Hazen *et al.* 2012; Schloss *et al.* 2012; Pinsky *et al.* 2013), and underscores the importance of individual behavioural variation within a population (Bolnick *et al.* 2003; Araújo *et al.* 2011; Dall *et al.* 2012; Nicotra *et al.* 2015). Our study highlights the role of environmental conditions in mediating the success of individually-specialised behavioural strategies, and offers a window into how intraspecific behavioural variation may modulate the adaptive capacity of species to climate change.

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## AUTHORSHIP

BA performed analyses and wrote the manuscript with input from all authors. BA, EH, SB, JB, KS and DPC developed the work. PR and DEC collected and processed the data.

## DATA ACCESSIBILITY

Data supporting our results are publicly accessible on Movebank.org.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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