Relative influence of climate variability and direct anthropogenic impact on a sub-tropical Pacific top predator, the Hawaiian monk seal

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ABSTRACT: Abundance trends of Hawaiian monk seals *Monachus schauinslandi* at 6 subpopulations throughout the Northwestern Hawaiian Islands (NWHI) have fluctuated considerably during the past 5 decades. Direct human impacts have been widely accepted as the primary cause of previous monk seal population declines and, consequently, much conservation effort has focused on minimizing these threats. Yet climate variability has been increasingly identified as a factor influencing monk seal demography. We endeavored to evaluate the relative influence of climate versus direct anthropogenic impacts on historic trends in monk seal populations. Periods of growth and decline in monk seal abundance at 4 subpopulations were associated with positive and negative phases, respectively, of the Pacific Decadal Oscillation (PDO). Moreover, PDO regime shifts were followed, after approximately 2 yr lags, by corresponding changes in monk seal abundance trajectories, especially in the absence confounding human impacts. We propose that the PDO is a proxy for varying productivity in the northern NWHI, the effects of which propagate vertically through the food web and are reflected in top predators such as the monk seal. Our results suggest that long-term dynamics of monk seal populations may have been driven as much, if not more, by climate–ocean variability as by direct human activity. In recent years, direct human impacts on monk seals have been virtually eliminated from the NWHI. As such, previous and continued detailed monitoring of Hawaiian monk seal demographics offer a unique opportunity to document and understand how future anticipated global climate change will affect marine ecosystems in the central North Pacific.

KEY WORDS: Pacific Decadal Oscillation · *Monachus schauinslandii* · Climate change · Northwestern Hawaiian Islands · Population dynamics · Anthropogenic disturbance

INTRODUCTION

Upper-trophic predators are highly vulnerable to impacts in both terrestrial and marine ecosystems, whether perturbations are directly anthropogenic (e.g. overexploitation, habitat fragmentation) or related to indirectly human-caused or natural change (e.g. climate variability) (Petchey et al. 1999, Purvis et al. 2000, Voigt et al. 2003, Pichegru et al. 2009). This sensitivity of top predators is partly why they are often considered surrogate species to be monitored for various aspects of ecosystem status (Sergio et al. 2008).

In marine ecosystems, large-bodied top predators consistently exhibit conspicuous response to fishing pressure (Pauly et al. 1998, Myers & Worm 2003, Polovina et al. 2009) and climate change (Regehr et al. 2007, Moore & Huntington 2008). Profound changes to the world's oceans are anticipated in the coming decades as the effects of global climate

change intensify (Overland & Wang 2007, Hoegh-Guldberg & Bruno 2010). Large-scale physical changes will alter marine biotic communities in ways that are difficult to predict (Brander 2007). Thus, clarifying the links between climate variability and top-predator population dynamics and, moreover, monitoring those populations into the future will likely be crucial for understanding impacts as climate change fully manifests in the oceans. However, for this process to be most informative, separating direct anthropogenic impacts from other factors, namely climate variability, is critical (Van Houtan & Halley 2011). Achieving this is difficult because of simultaneous occurrences of these influences, the possibility of non-independent effects, and typically incomplete data on the nature and magnitude of both natural and direct anthropogenic perturbations.

The Hawaiian monk seal *Monachus schauinslandi* is a long-lived, large-bodied predator with a range extending more than 2500 km throughout the Hawaiian Archipelago (Fig. 1). Because of its endangered status, the monk seal has been the subject of intensive study for 3 decades, with some survey data extending back to the late 1950s. Early on, researchers adopted the perspective that the monk seal's endangered status was largely the result of localized anthropogenic factors on the tiny islands and atolls of the Northwestern Hawaiian Islands (NWHI), where virtually all monk seals were located. This was a reasonable conclusion because compelling evidence argued that monk seals were reduced by hunting mostly in the 19th century and then subjected to harassment, persecution and exclusion from key terrestrial habitats during much of the 20th century (Kenyon 1972, Gerrodette & Gilmartin 1990, Ragen 1999). Thus, a primary goal of monk seal conservation has been to minimize direct human impacts.

Over time, several observations have eroded the concept that mere protection of the monk seal from direct anthropogenic insult would be sufficient to foster recovery. Beginning in the late 1980s at one site and spreading throughout the NWHI by the early 2000s, poor juvenile survival associated with food limitation was becoming chronic (Craig & Ragen 1999, Baker & Thompson 2007, Baker 2008). Such a trend could not be attributed to disturbance
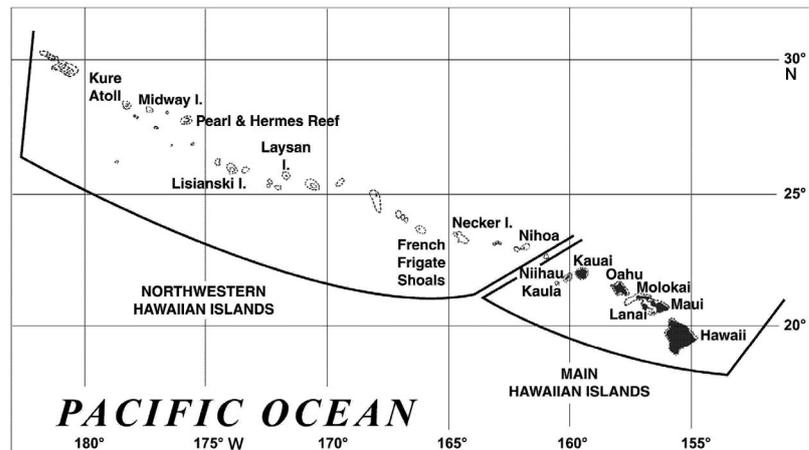

Fig. 1. The Hawaiian Archipelago, indicating the main Hawaiian Islands and the primary Northwestern Hawaiian Islands. Subpopulations of monk seals are found at French Frigate Shoals, Laysan Island, Lisianski Island, Pearl and Hermes Reef, Midway Atoll and Kure Atoll

or harassment on shore. Another surprising development was the apparent recolonization of the main Hawaiian Islands (MHI) by monk seals. Prior to the 1990s, sightings of seals were extremely rare in the MHI, but they subsequently became increasingly common, even in areas intensively used by people, and now make up a substantial and robustly growing population (Baker & Johanos 2004, Baker et al. 2011). Monk seals are thriving in the MHI, which are home to more than 1 million people and host to several million more tourists annually. This contradicts the notion that the seals cannot tolerate human presence.

Subsequently, researchers began investigating ecosystem factors that might be driving monk seal population dynamics. Hawaiian monk seals are generalist predators, feeding on a wide variety of demersal and benthic fish, cephalopods and crustaceans (Goodman-Lowe 1998, Longenecker 2010). Polovina et al. (1994, 1995) first reported that a large-scale North Pacific regime shift in the late 1980s, which resulted in lower primary productivity in the NWHI, was associated with declines in survival and productivity at higher trophic levels (lobsters, seabirds and monk seals) at one NWHI location, French Frigate Shoals. Antonelis et al. (2003) found that the weaning condition of monk seal offspring was improved in El Niño years, suggesting that short-term fluctuations in ocean conditions also influence monk seal development. Building on this foundation and based on data from 1984 to 2005, Baker et al. (2007) found a lagged relationship between the position of the transition zone chloro-

phyll front (TZCF) and juvenile monk seal survival in the northern portion of the NWHI. The TZCF is a large-scale oceanographic feature separating the vertically stratified, low-chlorophyll subtropical surface waters and the vertically mixed, cool, high-chlorophyll transition zone waters. The TZCF annually migrates more than 1000 km in latitude, and its southern extent in winter varies (Bograd et al. 2004). The frontal region is associated with surface convergence, thereby likely concentrating resources throughout the food chain (Polovina et al. 2001). Polovina et al. (2008) subsequently developed a lower-trophic ecosystem model coupled with an ocean circulation model, which demonstrates how a strong and dynamic physical, chemical and biological gradient, for which the TZCF is a proxy, influences variable productivity in the northern NWHI.

These revelations about the influence of fluctuating large-scale climate patterns in the North Pacific on Hawaiian monk seal population dynamics raise doubt about the previously accepted wisdom that declines in monk seals during the latter half of the 20th century were primarily the result of direct human impacts. In this paper, we extend the investigation of climate and monk seal dynamics to several previous decades and evaluate the relative impacts of direct anthropogenic factors from the influence of climate. Because neither monk seal survival estimates nor sufficiently precise tracking of the TZCF were available prior to the 1980s, we examined alternative parameters that extended our observation period to over 5 decades.

Global warming is likely to have profound impacts on ecosystems in the central Pacific. Polovina et al. (2011) projected massive changes in the extent and productivity of temperate, subtropical and equatorial ecosystems over the remainder of this century. Among their predictions is that the boundary between the subtropical gyre and the temperate biome will shift northward by 5° to 10° latitude, likely reducing productivity in the NWHI. The Hawaiian monk seal is the subject of the longest-term, most detailed, and broadest spatially sampled demographic study for any species in the central Pacific. Originally, these data were collected to inform conservation efforts; however, they are now relevant in a broader context. Better characterization of previous dynamic relationships as conducted here, as well as continued monitoring in the future, represents a unique opportunity to document and clarify how global climate change will impact marine ecosystems in the central Pacific in coming decades.

MATERIALS AND METHODS

Beach count time series

A tally of the numbers of Hawaiian monk seals on shore at a specified location and time is referred to as a 'beach count'. Such counts were first conducted in the late 1950s and are the longest-running indicator of monk seal population trends. The proportion of seals in a population on shore at any given time is likely influenced by a number of factors, including weather, time of day, date, prey resources, habitat variables and individual age, and reproductive and health status. Nevertheless, beach counts, particularly mean counts within a year, provide a reliable indicator of long-term trends in abundance status (Eberhardt et al. 1999).

Most beach counts were conducted by walking the entire perimeter of all shorelines (including all islands within atolls) and systematically tallying all seals observed on land. Counts were sometimes conducted from small boats, for example, when landing on very small sand spits would disturb resting seals. Boat-based counts were only used in cases when all seals on shore were visible. Finally, aerial surveys with photographs were used to generate a small proportion of beach counts. Total counts at multiple-islet atolls (French Frigate Shoals, Pearl and Hermes Reef, Midway Atoll and Kure Atoll) were completed in 2 d or less, whereas counts at single-island subpopulations (Laysan and Lisianski Islands) were always completed within a single day.

The time series analyzed here consist of mean annual total beach counts subject to the following restrictions. Constructing the time series from all available beach count data involved balancing consistency in methods while retaining sufficient counts to adequately characterize long-term trends. Only documented complete counts were included. Any counts that were noted as approximate or which did not cover all shorelines within an atoll or island were excluded. Hiruki & Ragen's (1992) meticulous compilation of all historical Hawaiian monk seal count data was the primary source for beach counts conducted from the late 1950s until the early 1980s. Counts were conducted sporadically during these years; typically, at most, a few counts were available per year at a given site. No date restrictions were applied to these early data because the counts were sparse and conducted at various times of the year.

Far more data were available after the early 1980s, when a research program that used standardized protocols to monitor Hawaiian monk seal populations

at the 6 NWHI subpopulations, from French Frigate Shoals to Kure Atoll, was established. As part of that program, multiple beach counts each year were conducted nearly annually during field camps. These data are maintained by the US National Marine Fisheries Service. For the past 3 decades, research effort has focused on the spring–summer period, when the majority of pups are born (Johanos et al. 1994). To reduce within-site variability in beach count trends due to seasonal effects, data collected after the early 1980s were restricted by date. The range of dates used varied somewhat among sites reflecting each site's particular history of field effort, but restrictions were consistently applied within each site (Table 1). At Laysan Island, date restrictions were applied beginning in 1977 because consistent annual research was initiated there at that time. In contrast, field effort at Midway Atoll remained sporadic for a longer time than at other sites so date restrictions were not applied.

Because date restrictions were only imposed on counts conducted during more recent years (Table 1), we examined how the representation of beach count trends changed when site-specific date restrictions were applied to the earlier years as well.

Pacific Decadal Oscillation (PDO)

Monthly PDO values were downloaded from an FTP site maintained by N. Mantua (jisao.washington.edu/pdo/PDO.latest; Mantua et al. 1997). We annualized the time series by calculating the mean of monthly values for October through March and assigning the result to the year in which the October value occurred. For example, the mean of monthly values from October 1960 to March 1961 was assigned to 1960. We used October–March PDO for 2 reasons. First, because of the relationship between the latitudinal minimum of the TZCF and monk seal survival, our intent was to capture the TZCF dynam-

ics by using PDO values during those months when the TZCF migrates south. Further, year-to-year PDO fluctuations are most energetic during October through March (Mantua 2002).

The correlation between October–March PDO and the southernmost latitude of the TZCF was examined to evaluate whether these 2 indicators tend to express similar dynamics. Data for both time series were available from 1982 to 2010. Following Baker et al. (2007), we used Reynolds optimally interpolated sea surface temperature (SST) data to determine the southernmost latitude of the 18°C isotherm averaged between 180° and 160°W, a proxy for the TZCF. Because the front moves farther south in the first quarter of each year (Bograd et al. 2004), we lagged the TZCF time series back 1 yr, so that it coincided appropriately with the way we assigned October–March PDO to years.

Data analysis

Our analysis approach was informed by expectations of how our central hypothesis, if true, would likely manifest based on the available observational data. Positive or 'warm phase' PDO periods are associated with lower productivity in the northeastern Pacific and higher productivity in the central Pacific (Parrish et al. 2012). Conversely, negative ('cool phase') PDO is associated with lower central Pacific productivity. Thus, we expected the Hawaiian monk seals to fare better during periods of positive PDO and worse during periods of negative PDO. Because PDO is often characterized as a decadal scale phenomenon punctuated by more or less abrupt regime shifts (Mantua et al. 1997, Overland et al. 2008), we expected that any influence of PDO on monk seal populations would occur on similar (decadal) time scales rather than year-to-year fluctuations. Further, Baker et al. (2007) concluded that varying productivity significantly affected juvenile seal survival, whereas effects on older seals were relatively weak and equivocal. Juvenile age classes typically comprise only a small proportion of the total population, and adult monk seal survival has been shown to be fairly constant and high (Baker & Thompson 2007). Thus, changes in beach counts (an index of total abundance) driven by varying juvenile survival would be expected to manifest gradually, reflecting the inherent inertia in total population

Table 1. Date restrictions applied to Hawaiian monk seal beach count trend data

Location	No date restrictions	Date restrictions applied	Range within each year included
Kure Atoll	1957–1980	1981–2010	15 Apr to 31 Jul
Midway Atoll	1957–2010	None	1 Jan to 31 Dec
Pearl and Hermes Reef	1956–1982	1983–2010	15 Apr to 15 Sep
Lisianski Island	1957–1981	1982–2010	1 Apr to 31 Aug
Laysan Island	1957–1976	1977–2010	1 Apr to 30 Jun
French Frigate Shoals	1957–1984	1985–2010	15 Apr to 31 Jul

abundance. Finally, consistent with the results of Baker et al. (2007) regarding the influence of TZCF, we expected that PDO influences would likewise be stronger in the northern portion of the NWHI.

Based on the foregoing information, we predicted that periods of increasing beach counts would tend to occur during periods of generally positive PDO, and vice versa. Further, regime shifts evident in PDO were expected to be followed by corresponding alterations in beach count trends.

Our primary approach to evaluate the above predictions involved identifying periods of increasing and decreasing beach count trends at each site and then comparing PDO values during these same intervals. We did not simply model the annual beach counts as a function of PDO because, as noted above, we expect PDO effects to be manifest over multiple consecutive years rather than annually. Because the beach count data sometimes exhibited considerable annual variation, simply assessing visually the years at which trends changed from negative to positive (and vice versa) would have been subjective. Therefore, we fitted generalized additive models (GAMs) to beach count trends, using the default algorithm for determining the optimal degree of smoothing implemented in the MGCV package in program R (Wood 2006). An appealing feature of GAMs is that they do not assume a functional form for the fitted curve, thereby revealing underlying trends in the observed data. We examined the curves fitted by GAMs to objectively identify trend change points. Once the periods of decline and increase had been thus determined, simple log-linear regressions were fitted to the mean annual beach counts within each period to estimate the population growth rate. Mean October–March PDO for the same periods (lagged 1 yr prior) was then calculated. This lagging of PDO 1 yr previous to beach counts was consistent with the 1 to 2 yr lags previously detected in the relationship between TZCF and seal survival.

The data set derived as described above consisted of population growth rate estimates (during periods of increase and decline) paired with mean PDO during the same periods at all 6 subpopulations. Previous studies have concluded that various anthropogenic (and some natural) factors had strongly influenced NWHI monk seal population trends both positively and negatively (e.g. Gerodette & Gilmartin 1990, Polovina et al. 1994, Ragen 1999, Baker et al. 2007). We qualitatively characterized the most apparent of the human influences both temporally and spatially and created a binary variable indicating whether known direct negative anthropogenic fac-

tors occurred during each of the identified periods of population growth and decline. We then evaluated the relative influence of PDO and anthropogenic impacts on beach count trends using linear models.

A second approach to testing our predictions was to investigate the timing of PDO regime shifts and changes in seal population trajectories. We used a published regime shift-detection algorithm to objectively identify when climate regimes (PDO) changed phase (Rodionov 2004, 2006, Rodionov & Overland 2005) during 1950 to 2010. This algorithm is sensitive to the specified values of 3 parameters: a p-value for detecting differences in means between periods, the Huber parameter that affects weighting of outliers, and a parameter (l) that influences the length of periods between regime shifts. We chose 0.2 for the p-value, reasoning that our objective was to detect changes; more conservative values (such as 0.01 or 0.05, conventionally used for hypothesis testing) would likely mean that only extremely large shifts would be detected. We chose 2 for the Huber parameter, which meant that observations within 2 standard deviations of the mean would not be downweighted. Anticipating decadal scale variation in PDO, we ran the algorithm with l set at 10, 15, and 20 yr.

RESULTS

Pronounced trends in mean beach counts were evident at all monk seal subpopulations examined (Fig. 2). The 3 northernmost atolls (Kure Atoll, Midway Atoll, and Pearl and Hermes Reef) all exhibited a similar pattern of initial decline, partial recovery and then renewed decline, although the timing and slope of these trends varied among sites. Lisianski Island also exhibited a steep initial decline that eventually leveled off briefly, followed by a prolonged slow decline. Laysan Island beach counts exhibited marked annual variation until the late 1970s, but the overall trend was a decline from the late 1950s to 2010. With the exception of French Frigate Shoals, all subpopulations exhibited a steep decline from the late 1950s for roughly 2 decades. Trends at French Frigate Shoals differed markedly from all other locations in that counts began very low and grew rapidly until the late 1980s, followed by a prolonged crash.

The trends described were still apparent when date restrictions were applied to all years instead of including all counts in the early years (Table 1). The main difference was that 38 fewer years (all subpopulations combined) had counts within the prescribed
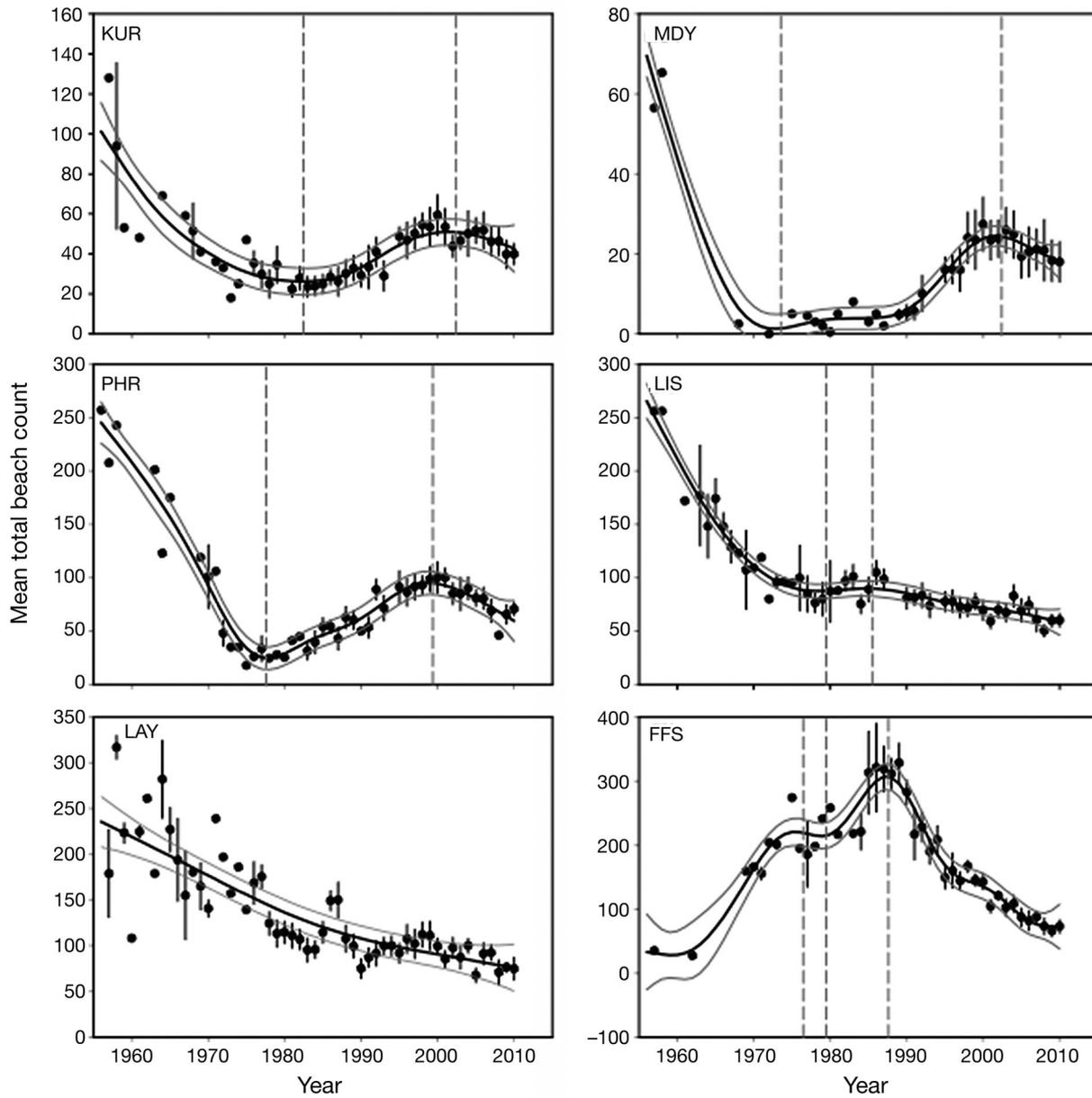
Fig. 2. *Monachus schauinslandi.* Trends in Hawaiian monk seal beach counts at 6 Northwestern Hawaiian Island subpopulations. Means of annual counts are shown (± 1SD when more than 1 count was available per year) and were fitted with curves from generalized additive models (GAMs) (solid black line) and 95% confidence limits (solid gray lines). Vertical dashed lines indicate change points between periods of increasing and decreasing trends in the fitted curves. KUR: Kure Atoll; MDY: Midway Atoll; PHR: Pearl and Hermes Reef; LIS: Lisianski Island; LAY: Laysan Island; FFS: French Frigate Shoals

dates. Restricting the dates changed the mean beach count value in 21 cases, but not in a consistent direction; 12 counts were lower and 9 were higher than when no date restrictions were applied. Finally, 36 mean beach count values already met the date criteria and were thus unchanged. Beach count trends estimated using log-linear regression did not differ significantly during these earlier years when dates were restricted versus when all counts were in-

cluded. At all sites, the estimated annual rate of change in restricted-date beach counts differed from the all-inclusive count trend by an average of just 1.7% (range 0.3 to 2.8%), and the 95% confidence intervals overlapped in all cases.

Two or 3 regime shifts were detected in the 1950–2010 October–March PDO time series based on whether *l* was specified as 10, 15 or 20 yr (Fig. 3). In all cases, a distinct shift from negative to positive
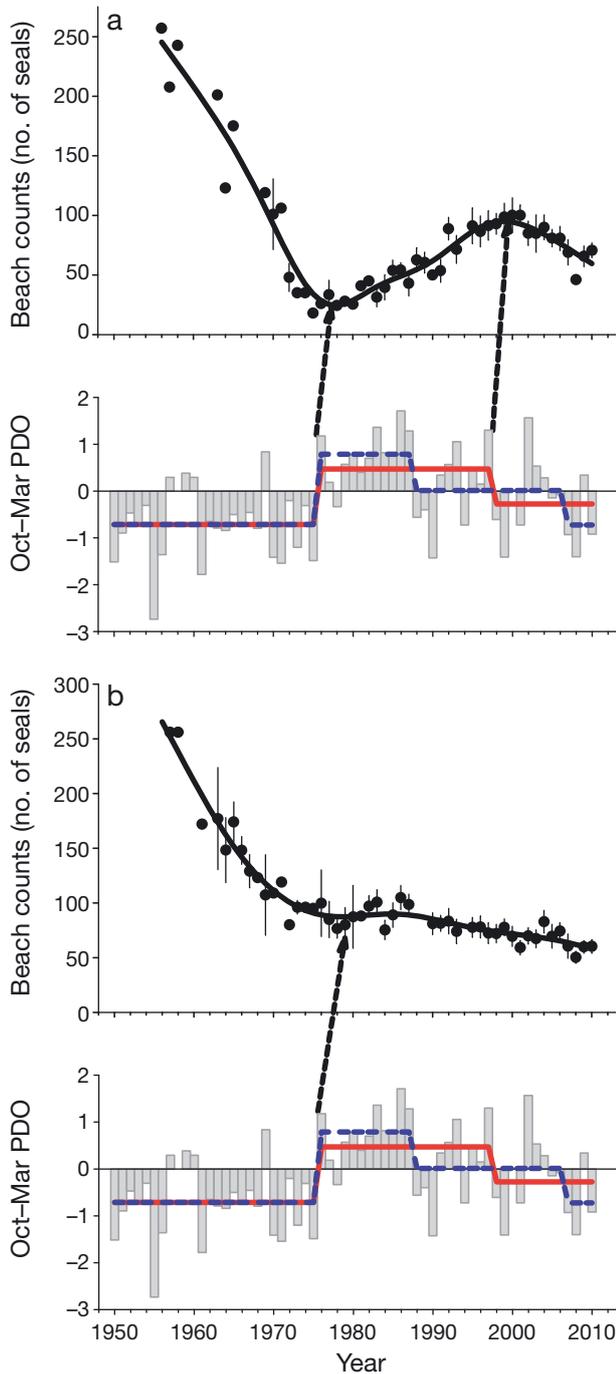
Fig. 3. *Monachus schauinslandi*. Association of trends in Hawaiian monk seal beach counts at (a) Pearl and Hermes Reef and (b) Lisianski Island with variability in October–March Pacific Decadal Oscillation (PDO), showing PDO regimes and shifts (blue line: regime shift parameters *l* = 10 or 20 yr, red line: *l* = 15 yr) and time lags (dashed black line) between regime shifts and subsequent changes in monk seal abundance trajectories

PDO was detected between 1975 and 1976. The subsequent positive phase lasted either 11 or 21 yr, followed by either 1 or 2 shifts to lower mean values.

October–March PDO was negatively correlated with the minimum latitude of the TZCF in winter (r = −0.56) during 1982 to 2010. Linear regression of the 2 time series was highly significant (p = 0.001), although the relationship was somewhat noisy (r^2 = 0.32, N = 29).

Periods of growth or decline in beach counts (defined using the fitted GAM curves) were positively associated with October–March PDO at sites from Kure Atoll southeast to Lisianski Island (Fig. 4). As mentioned above, the timing and slope of beach count trends somewhat differed among these subpopulations. At Laysan Island, no such relationship was evident; the population declined regardless of PDO regimes. Lastly, highly variable beach count trends at French Frigate Shoals exhibited no coherent relationship with PDO.

A total of 17 periods of increasing and decreasing seal counts were identified across the 6 subpopulations, and negative anthropogenic impacts occurred during 5 of the periods. We report model comparison results as small-sample corrected Akaike's information criterion (ΔAIC_c) values relative to a null model. We initially fitted 2 univariate linear models, one with PDO and the other with anthropogenic impact as the independent variable, and beach count growth rate as the dependent variable. Including PDO resulted in only a slight improvement compared to a null model (ΔAIC_c = −0.827), whereas a model with anthropogenic impact was less well supported (ΔAIC_c = 2.443). The TZCF was previously found to significantly influence juvenile seal survival at the 4 subpopulations from Kure Atoll southeast to Lisianski Island but not at Laysan Island nor French Frigate Shoals (Baker et al. 2007). We therefore fitted interaction models with PDO and a 2-level location factor. One level grouped the 4 subpopulations known to be influenced by TZCF, and the other level included French Frigate Shoals. The single observation from Laysan Island was alternately included with each of the 2 location levels in 2 separate models.

The best fit model included PDO and an interaction between PDO and the location grouping with French Frigate Shoals segregated (ΔAIC_c = −3.167). That is, there was a positive relationship between PDO and beach count trend at all locations except French Frigate Shoals. Grouping Laysan Island with French Frigate Shoals instead degraded model support slightly (ΔAIC_c = −2.092), but given there was only a single observation from Laysan Island, this difference is equivocal. Finally, we added anthropogenic impact back into our best model, resulting in much lower support (ΔAIC_c = 0.676).
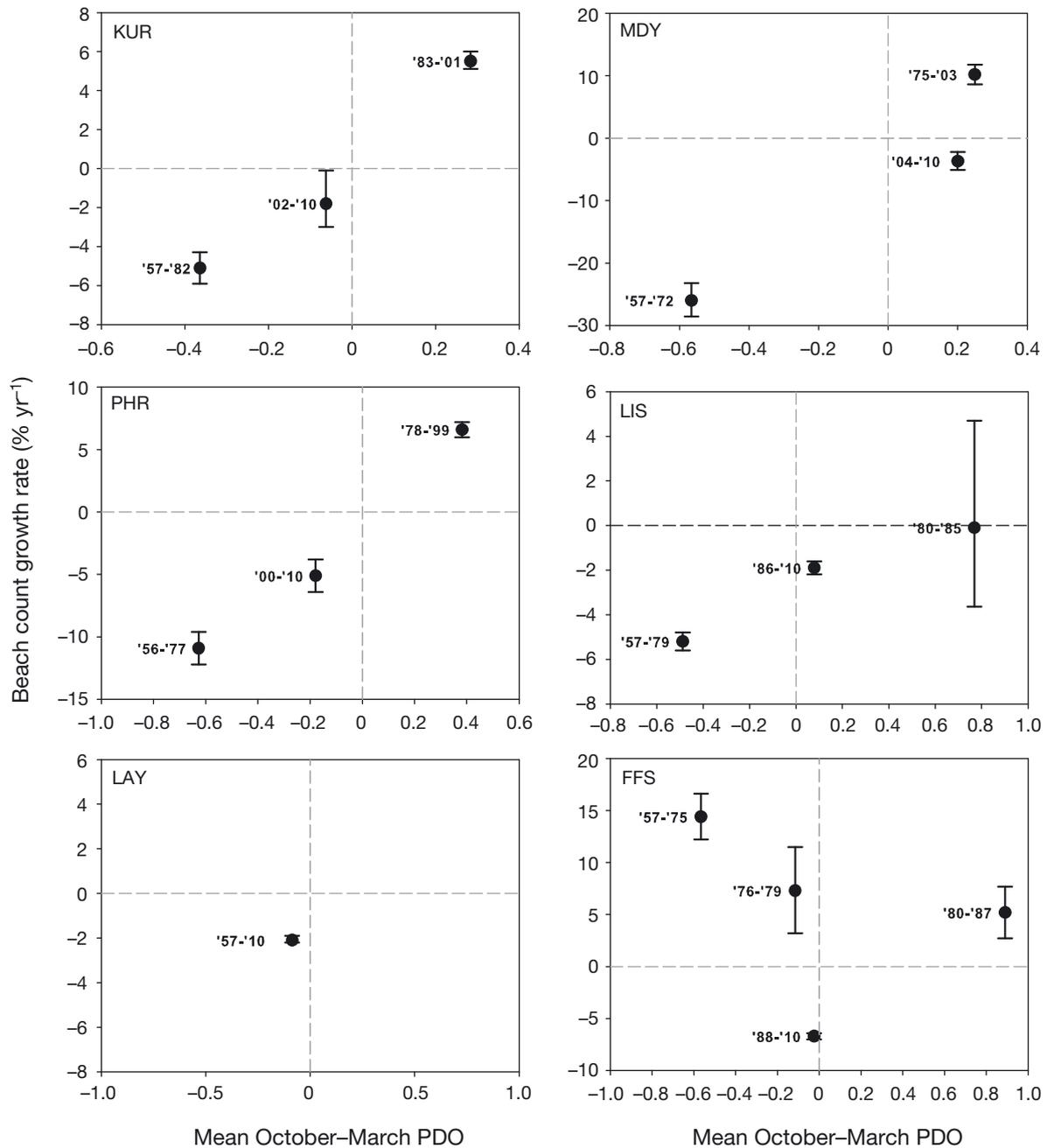
Fig. 4. *Monachus schauinslandi.* Relationship between October–March Pacific Decadal Oscillation (PDO) and annual growth rates of Hawaiian monk seal beach counts for 6 subpopulations. Estimated growth rates and 95% confidence intervals are shown with the associated years indicated to the left of each point. KUR: Kure Atoll; MDY: Midway Atoll; PHR: Pearl and Hermes Reef; LIS: Lisianski Island; LAY: Laysan Island; FFS: French Frigate Shoals

Although we did not detect significant effects on beach count trends of a binary variable indicating presence or absence of anthropogenic impact, others (e.g. Ragen 1999) make a compelling case that human effects historically have had profound impacts on Hawaiian monk seal populations. The temporal and spatial patterns in these impacts during most of the 20th century will be discussed further below. However, 2 sites, Pearl and Hermes Reef and Lisianski Island, were relatively free from direct anthropogenic influences during the period for which beach counts were available. From 1926 to 1931, a short-lived fishery rapidly depleted pearl oysters at Pearl and Hermes Reef (Keenan et al. 2006) but

ended almost 3 decades prior to the earliest beach counts. The suggestion has been made that occasional military operations were conducted at Pearl and Hermes Reef during the 1950s and 1960s (Ragen 1999). There is no indication that such activities, to the extent that they occurred, involved frequent or long-term impacts on monk seals. No such direct anthropogenic effects are known to have occurred at Lisianski Island after the early 1900s.

Because Lisianski Island and Pearl and Hermes Reef were uniquely isolated from direct human impacts or known natural perturbations, we expected that these sites would exhibit the clearest signal of any climate forcing associated with PDO. The positive relationship between observed growth rates at these locations and PDO were already noted (Fig. 4). In Fig. 3, we examine beach count trends and the timing of PDO regime shifts in greater detail. In both subpopulations, beach counts were steeply declining when research was initiated in the late 1950s and this corresponded to a prolonged period of negative PDO, which also preceded the first counts. At Pearl and Hermes Reef, counts ceased declining and began to increase about 2 yr after the strong positive regime shift in 1975 to 1976. At Lisianski Island the population stopped declining and became roughly stable approximately 2 to 3 yr after the regime shift. Subsequent correspondence between regime shifts and beach counts were suggestive but less compelling. One fit of the regime shift detection algorithm (red line, Fig. 3) found a downward shift in PDO in 1997 to 1998, which was followed 2 yr later by a shift from positive to negative growth of monk seal abundance at Pearl and Hermes Reef. Since 1980, however, the trend in counts at Lisianski Island altered only subtly without any compelling relationship to PDO regime shifts.

At the remaining 4 sites, evaluating the influence of North Pacific climate regimes is greatly complicated by a host of other known impacts (both negative and positive) on the monk seal populations. Here, and in Fig. 5, we summarized these impacts temporally and spatially to help clarify the potential composite effects of all putative factors driving monk seal population trends. In some cases, consideration of events that occurred prior to the late 1950s is illustrative.

Kure Atoll

In 1960, a US Coast Guard Loran (Long-range Navigation) base was established on Green Island, the primary land area at Kure Atoll. Frequent and sustained harassment of seals by people and dogs was responsi-ble for driving seals away from Green Island, most notably causing females to give birth on suboptimal habitat (Kenyon 1972, Gerrodette & Gilmartin 1990). In 1976 or 1977, disturbance was reduced to some degree by the removal of dogs and restrictions on vehicle use and beach access (Gilmartin et al. 2011a). The Loran station closed in 1992. Two Hawaiian monk seal enhancement programs were conducted at Kure Atoll. From 1981 to 1992, during the 'Headstart' Program, weaned female pups were temporarily held in shoreline pens with the intention of protecting them from natural sources of early mortality (e.g. shark predation and aggressive male seals). Male pups were allowed to range freely after weaning. During this program, both female and male juvenile survival increased equally, resulting in the conclusion that the temporary captivity itself was not beneficial but that the program resulted in a change in Coast Guard personnel behavior such that seal disturbance was greatly reduced (Gilmartin et al. 2011a). The other program involved captive care and rehabilitation of young seals (primarily animals in poor health collected from French Frigate Shoals) and subsequent release at Kure Atoll. During 1985 to 1995, Kure Atoll was thus supplemented with 56 young female seals, contributing to the growth of this subpopulation.

Midway Atoll

This atoll was arguably subject to the greatest human occupation and anthropogenic impact of all the NWHI. By the late 1800s, monk seals had been extirpated from Midway by sealers, shipwrecked crews, and others (Ragen 1999). In 1903, the Commercial Pacific Cable Company established operations at Midway Atoll with the permanent presence of humans. From 1935 to 1941, the Pan American Clipper aircraft used Midway as a stopover on their trans-Pacific air service. In 1940, construction of a US naval air station began and the base was in operation from 1941 to 1993. In 1942, the pivotal Battle of Midway occurred, during which Midway was bombed by the Japanese military. Subsequently, during the Vietnam War, some 5000 people were living on Sand Island, 1 of 2 primary land areas at Midway Atoll. In 1978, the base was downgraded to a naval air facility and the human population was reduced. In 1996, the Navy transferred Midway Atoll to the US Fish and Wildlife Service and nearly all beaches were subsequently off limits to most human access. As part of the aforementioned program, 18 juvenile female seals that had been collected at French Frigate
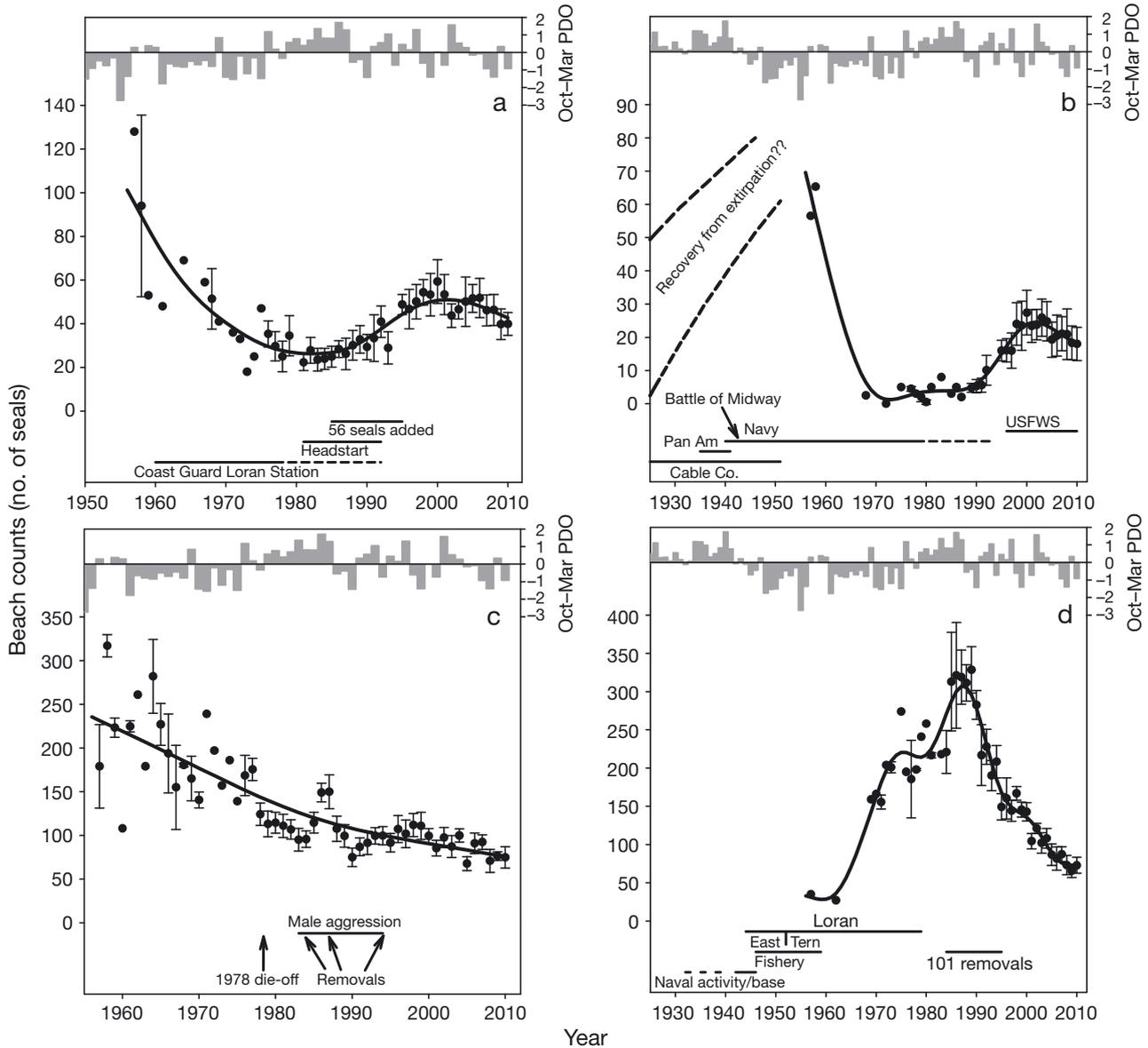
Fig. 5. *Monachus schauinslandi*. Time series of October–March Pacific Decadal Oscillation (PDO) (gray bars), mean ± SD Hawaiian monk seal beach counts (black dots) and trends (black curves), and both putative (dashed black line) and known (solid black line) human and natural impacts on Hawaiian monk seal populations at (a) Kure Atoll, (b) Midway Atoll, (c) Laysan Island and (d) French Frigate Shoals. USFWS: US Fish and Wildlife Service; Loran: Long-range navigation

Shoals were released at Midway Atoll during 1991 to 1993, mostly after only partial rehabilitation. Unlike at Kure, however, these seals did not fare well after release and only 3 survived for 1 yr (Gilmartin et al. 2011b). This effort did not significantly supplement the Midway seal population.

Laysan Island

As at Midway Atoll, Laysan Island seals were extirpated by the late 1800s, and they remained virtually

absent at least until guano mining operations ceased in 1910 (Ragen 1999). Subsequently, direct human influences abated whereas natural factors caused significant impacts in the latter part of the 20th century. In 1978, at least 50 seals (likely more) at Laysan Island died from an undetermined disease (Johnson & Johnson 1981). Subsequently, and possibly as a result of the 1978 mortality, the adult sex ratio at Laysan was highly male biased. Consequently, multiple male aggression, whereby several males attempt to mate with a female seal simultaneously, became a significant source of injury and mortality. During

1983 to 1994, an average of 4.1% of adult female seals at Laysan Island died each year from male aggression (Johanos et al. 2010). This situation was successfully mitigated by removing 37 adult males to rebalance the sex ratio (Johanos et al. 2010).

French Frigate Shoals

A variety of human activities occurred at French Frigate Shoals throughout much of the 20th century. US Navy training exercises were conducted in the 1930s, and a naval air station was in operation from 1942 to 1946. In 1944, a Loran station was established at East Island and was then moved to Tern Island in 1952 where it remained until 1979. Additionally, shore-based commercial fishing occurred from 1946 to 1959. A total of 101 female seals were removed from French Frigate Shoals from 1984 to 1995 (Gilmartin et al. 2011b). However, primarily undersized weaned pups and starving juveniles with poor survival prospects were removed for rehabilitation. Consequently, simulation modeling indicated that the removals likely only lowered the total population by a small amount (Gilmartin et al. 2011b).

DISCUSSION

We found a statistically significant positive relationship between PDO and Hawaiian monk seal abundance trends from Kure Atoll southeast at least to Lisianski Island (Fig. 4). Most prominent was the very rapid decline in monk seal counts from the late 1950s to the late 1970s, which corresponded to a prolonged period of strongly negative PDO. The regime shifts we detected in October–March PDO are well known and have been reported previously (e.g. Overland et al. 2008). The abrupt shift to a positive PDO regime in 1975 to 1976, especially, has been associated with a host of physical and biological changes in the North Pacific (Francis & Hare 1994, Polovina et al. 1995, Hare & Mantua 2000). The timing of this shift, followed a few years later by a cessation of the steep declines in beach counts at Pearl and Hermes Reef and Lisianski Island (sites with minimal confounding anthropogenic impacts), is compelling evidence that PDO strongly influenced monk seal population trajectories (Fig. 3).

Our results are entirely consistent with the hypothesis that large-scale oceanographic variability manifested in PDO drives ecosystem dynamics in the central subtropical Pacific. The direction of the rela-

tionship is as hypothesized; that is, positive PDO is associated with more favorable conditions for top predators such as monk seals. We expected that this relationship would be stronger in the northern portion of the NWHI, which is precisely what we observed. Finally, we anticipated a time lag between major oceanographic regime shifts and resulting expression in monk seal trends, which was also observed (Fig. 3).

The relationship between PDO and monk seal beach counts is similar to that proposed by Baker et al. (2007) regarding a link between the TZCF and monk seal juvenile survival. This study extends observation of this relationship farther back in time but makes use of different time series to represent the physical and biological components, because neither reliable characterization of the TZCF nor monk seal survival estimates are available prior to the early 1980s. The significant relationship between October–March PDO and the southernmost latitude of the TZCF in winter during 1982 to 2010 suggests that these 2 oceanographic time series reflect similar dynamics.

We propose that the following scenario underlies the observed relationships. Negative PDO is associated with warmer, less-productive waters in the central Pacific, and vice versa. When there is a shift to a negative PDO regime, lower primary productivity propagates up the ecosystem's food web, ultimately resulting in reduced prey for top predators (such as monk seals). Previous studies have shown that juvenile monk seal survival is most variable (Baker & Thompson 2007) and responds to changes in productivity (Baker et al. 2007). In contrast, adult survival rates tend to be high and relatively invariant (Baker & Thompson 2007). Therefore, productivity changes represented by PDO are likely to mediate monk seal population dynamics primarily through effects on juvenile survival. Beach counts include all age classes so that a given change in juvenile survival will be more gradually expressed in beach counts as a result of the dampening effect of the older seals in a population. A persistent oceanographic regime would result in progressively larger effects on seal abundance over time as a greater proportion of the age structure will have been affected. Prolonged periods of low productivity could also act on beach count trends through lowered fecundity. Harting et al. (2007) found that age-specific reproductive rates varied between monk seal populations in a manner coherent with abundance trends. That is, females in a rapidly declining subpopulation (French Frigate Shoals) began reproducing later and at a lower rate than did females in stable or less steeply declining populations (Laysan and Lisianski Islands). Finally,

changes in beach counts may reflect altered foraging behavior of monk seals as well as altered abundance. If prey becomes more scarce and seals respond by spending more time at sea foraging relative to resting on land, then beach counts could decline even if abundance were unchanged. Whether Hawaiian monk seals increase their proportion of time at sea when prey becomes more scarce is not known, but this trend has been observed in other pinniped species (Feldkamp et al. 1991, Boyd 1999). This behavioral mechanism would act in concert with coincident changes in seal abundance but would probably account for only a limited proportion of the long-term periods of decline and increase in beach counts observed (Fig. 2).

A prevalent perspective reflected in the scientific literature and among researchers and resource managers is that human activity has been the primary determinant of historic Hawaiian monk seal population trends (Kenyon 1972, Gerrodette & Gilmartin 1990, Ragen 1999). Certainly, unrestricted killing of monk seals for food and skins in the 19th century decimated populations and apparently caused at least 2 local extinctions. Additionally, compelling evidence shows that prolonged human disturbance (and harassment by dogs) led to seal population declines, and a cessation of such disturbance is believed to lead to recovery (Gerrodette & Gilmartin 1990). In contrast, our analysis did not find that the presence of direct human impacts significantly influenced beach count growth. One possible explanation for these contradictory findings could be that our simple characterization of anthropogenic impacts as present or absent may have been too coarse to reveal influences on population growth. Unfortunately, any attempt to more finely parse actual levels of human impact on seals at particular sites over time would have been highly speculative.

Our results suggest that long-term dynamics of monk seal abundance may have been driven as much, if not more, by climate–ocean variability as by direct human activity. Some significant declines in seal abundance have occurred in the absence of human disturbance and, conversely, rapid seal population growth has occurred despite intensive human activity. Graphically overlying trends in PDO and timelines of other known factors (positive and negative, natural and anthropogenic), along with beach count trends, provides insights suggesting that the timing of monk seal population trends may reflect both oceanographic variability and other site-specific factors (Fig. 5).

For example, steep declines in the monk seal populations occurred at both Kure and Midway Atolls from the late 1950s to at least the late 1980s, while a variety of human activities were ongoing at both sites. The declines have thus been largely attributed to human disturbance (Kenyon 1972, Gerrodette & Gilmartin 1990, Ragen 1999). Yet, inconsistencies undermine this conclusion. As noted previously, by the end of the 19th century, monk seals had been virtually extirpated from Midway Atoll; while there are no counts to characterize the subsequent trajectory, the population had rebounded to its historic highest level by the late 1950s. This impressive recovery occurred during a period of intensive human activity, including aerial bombardment during the battle of Midway. Notably, a strongly positive PDO regime prevailed from 1921 to 1941 while the Midway seal population was apparently growing.

Despite the relative absence of human activity, the monk seal population on nearby Pearl and Hermes Atoll declined precipitously from the late 1950s to the late 1970s (while PDO was strongly negative) and began to grow soon after the PDO regime shifted to positive. Sustained growth at Kure did not begin until approximately 1983. Recovery of this already very diminished population may have been delayed by human harassment on the atoll's prime pupping habitat and only grew after disturbance was abated (Gilmartin et al. 2011a). The population was further supplemented by a subsequent infusion of rehabilitated young female seals (Gilmartin et al. 2011b). Midway's seal population had fallen to near zero, and very slow recovery began sometime in the latter 1970s. Yet the population only began to grow rapidly following the closure of the naval air station and associated restriction of beach access (Fig. 5b). Much of this growth was likely attributed to immigration from Kure Atoll and Pearl and Hermes Reef. Considerable natural movement occurs among these subpopulations (Schultz et al. 2011), and the protections provided following the closure of the base are likely to have made Midway beaches more appealing to seals. Finally, we note that despite minimal human disturbance at all 3 sites, all seal counts at Kure, Midway and Pearl and Hermes Reef began to decline in the early 2000s, a few years following a trend towards more negative PDO. Baker et al. (2007) investigated this more directly as a decline in juvenile seal survival at these sites following a northerly shift in the TZCF.

The situations at Laysan Island and French Frigate Shoals are more difficult to interpret. At Laysan Island, early counts were variable from year to year, but a downward trend occurred after the late 1950s. This may have been influenced by the same negative PDO regime that appears to have driven declines at

the 4 monk seal subpopulations to the northwest. However, no recovery ensued following the 1975–1976 regime shift. The 1978 disease-caused mass mortality at Laysan and subsequent chronic mortality caused by adult male seals perhaps outweighed any favorable conditions that may have been related to positive PDO.

At French Frigate Shoals, the seal population was very small when counts began to be collected in the late 1950s. This followed several decades of human activities. Unlike all other NWHI subpopulations examined, the French Frigate Shoals seal population grew very rapidly during the 1960s and through the 1980s until beach counts at this atoll exceeded the combined total of all 5 other sites. Gerrodette & Gilmartin (1990) suggested that this recovery may have been facilitated by the transfer of the Loran station from East Island (important seal pupping habitat) to Tern Island (historically not an important pupping site) in 1952. Notably, the seal population grew unabated during both negative and positive PDO regimes before and after the 1975–1976 shift. Since 1989, the French Frigate Shoals seal population has been declining rapidly as a result of prolonged poor juvenile survival (Craig & Ragen 1999, Baker & Thompson 2007). Craig & Ragen (1999) concluded that the population exceeded carrying capacity and that prey resources also seem to have declined. One set of results from the regime shift detection algorithm suggests a drop in PDO occurred in 1987 to 1988, preceding the population crash by about 2 yr. Despite this coincidence of trends, linear modeling demonstrated that the statistically significant relationship between PDO and beach counts apparent elsewhere in the NWHI was absent from French Frigate Shoals during the past 5 decades. Similarly, Baker et al. (2007) did not detect a relationship between the TZCF and French Frigate Shoals juvenile survival since the mid-1980s.

The lack of consistent and compelling evidence to support a link between PDO and monk seal population trends at Laysan Island and French Frigate Shoals suggests that either the link is weak or nonexistent or that it exists but was obscured by more influential local factors, both anthropogenic and natural. The former conclusion is consistent with Baker et al.'s (2007) findings and hypothesis that fluctuating productivity associated with TZCF is less important farther south in the Hawaiian Archipelago. In contrast, Parrish et al. (2012) found that including PDO in an ECOPATH model of French Frigate Shoals improved the fit of model predictions to observed trends in monk seal biomass. The reason for this discrepancy may be related to 2 distinctions. The present analysis covers a much broader temporal scale (1957 to 2010) compared to Parrish et al. (2012) (1998 to 2009), encompassing a greater range of variability in both PDO and monk seal trends. Further, the latter study focuses on detailed trophic dynamics rather than the abundance index investigated here.

Implications for monk seal conservation

The Hawaiian monk seal is highly endangered and various efforts to promote recovery of the species have been ongoing for about 3 decades. The results of this study may profoundly shape the understanding of the context in which conservation measures have occurred and will be operating in the future. For example, many early monk seal conservation efforts focused on reducing disturbance and harassment of seals, as this was viewed as the primary threat to recovery. Other measures have focused on direct threats to survival, such as entanglement in marine debris, male seal aggression and, more recently, shark predation (Donohue et al. 2001, Henderson 2001, Gobush 2010, Johanos et al. 2010). The underlying perspective, quite reasonably, has been that if threats were identified and mitigated, populations should recover. Certainly, the suite of interventions that have been conducted have improved the status of the species compared to what it otherwise would have been (A. L. Harting et al. unpubl. data). Despite these efforts, however, the status of the species overall has declined in recent years. This study suggests that extrinsic factors, namely climate–ocean variability leading to variable productivity in the central North Pacific, significantly influence whether conditions are favorable for monk seal population growth at least across a large portion of the NWHI. When conditions are unfavorable, it may well be that no amount of intervention will result in population growth, but conservation efforts can substantially reduce the magnitude of population declines. Under favorable conditions, however, there may be great potential for population recovery provided that known threats are minimized. This suggests the perspective that conservation efforts should seek to minimize degradation of populations during unfavorable conditions and maximize growth during favorable periods. The range of conservation actions may be unchanged by this perspective. However, the timing, spatial distribution, and intensity of applied efforts may be tailored to achieve maximal results by considering the prevailing oceanographic regime.

Monk seals as a central Pacific climate-change indicator

The Hawaiian monk seal demographic data have been collected for the express purposes of monitoring and managing that species. Fortuitously, these data also appear to reveal a link between NWHI ecosystems and large-scale climate–ocean variability. Detecting such relationships when the physical changes (such as reflected in PDO) vary on a decadal scale requires long-term biological time series. Such data sets are rare, especially in the central North Pacific, where there is no other biological time series that has been collected as regularly and consistently over as broad a geographic area as the monk seal information. Beach counts have been obtained for more than 50 yr, and detailed demographic data are available for approximately the past 30 yr at 6 sites spanning the NWHI. The factors that drive monk seal population trends at Laysan Island and French Frigate Shoals remain unclear but, if discovered, may reveal other influential climate processes in the region. A recently reestablished population of monk seals is growing robustly in the main Hawaiian Islands (despite high human density and frequent disturbance), counter to the overall trends in the NWHI (Baker et al. 2011). Demographic monitoring of this population has been initiated, thereby extending the geographic range of surveillance of the species and the ecosystems it represents to more than 2500 km.

Another rare feature of the monk seal data is the extent to which direct anthropogenic factors can be distinguished from climate impacts. Because of the protection now afforded to NWHI, direct anthropogenic impacts are minimal and those that may occur are likely to be well documented. As such, monk seal demographic trends in the NWHI will likely more directly reflect changes in climate.

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