

Humpback whale abundance in Hawai'i: Temporal trends and response to climatic drivers

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Funding information

Whale Tales

Abstract

In 2001, we began long-term monitoring using scan sampling methodology to study the relative abundance and distribution of humpback whales (*Megaptera novaeangliae*) on their Hawaiian breeding grounds. Samples were collected annually (2001–2019) from a shore site overlooking Kawaihae Bay, Hawai'i Island. Each sample included the number of whales, pod composition, and position. Whale numbers increased from 2001 to 2015, with increasing variability after 2010. Numbers then declined, including a precipitous 60% drop between 2015 and 2016. Crude birth rate fell from 6.5% in 2015 to 1.1% in 2016. We used generalized additive models, including predictor variables of year, date, observational conditions, and observer, to establish a base model. Climatic indices were individually added to base models, and their contributions were evaluated using Akaike information criteria. Models indicated that whale numbers and crude birth rate fell when climate indices reflected warmer water on high latitude feeding grounds in the North Pacific. Our results show that oceanographic conditions during prior feeding seasons correspond with the reproductive rate and the number of whales in Hawai'i. Continued long-term monitoring of whale populations is essential to documenting and understanding marine ecosystem responses to global climate change.

KEYWORDS

carrying capacity, climate change, crude birth rate, Hawai'i, humpback whale, long-term monitoring, population level, scan sample, theodolite

1 | INTRODUCTION

In the past decade, the effects of climate change on a wide variety of marine taxa have become increasingly apparent (Leaper et al., 2006; Macleod, 2009). Changes in the abundance of marine predators have been directly linked to changes in climate regimes (Becker et al., 2007; Champagnon et al., 2018; Mantua et al., 1997; Santora et al., 2020). We sought to use long-term monitoring data on the relative abundance, distribution, and population characteristics of humpback whales (*Megaptera novaeangliae*) to detect any changes over time and identify their potential drivers.

Humpback whales are commonly found in the near-shore waters of the Hawaiian islands between late fall and mid spring (November–May), with a peak in mid-winter (January–March) (Baker & Herman, 1981; Herman & Antinaja, 1977). Hawai'i and other low latitude waters are considered mating and calving areas. Most females are believed to mate in these waters and return the following year to calve (Dawbin, 1966). Aerial surveys conducted in 1992 on the leeward waters off Hawai'i Island indicated peak presence between mid-January and mid-March, with the highest numbers of whales sighted in the first week of March (Forestell & Brown, 1992). Whales primarily inhabit leeward coastal waters shallower than 100 fathoms (183 m), typically within 40 km of shore (Herman & Antinaja, 1977; Mobley et al., 1999). Whales are also found in deeper (>183 m) water near the islands (Frankel et al., 1995) and they move across the deep channels between islands (Cerchio et al., 1998).

Although exploitable prey resources may be available (Benoit-Bird et al., 2001), humpback whales rarely, if ever, feed in their tropical wintering grounds (Baraff et al., 1991; Gendron & Urbán R., 1993). Most of the whales seen in Hawai'i migrate to western, central, and southeastern Alaska, as well as northern British Columbia, to forage in the summer (Baker et al., 2013). These whales constitute the Hawaiian Distinct Population Segment (DPS) established under the revised Endangered Species Act (U.S. Federal Register, 2016).

Whale prey quality is dependent upon the physical environment. Physical forcing through mechanisms such as storms, Ekman transport, and upwelling can lead to increased levels of nutrients in the water column and enhanced productivity (Sverdrup, 1953) that may affect the zooplankton and forage fish that humpback whales eat (Nemoto, 1957; Witteveen et al., 2012). There are a variety of indices that describe ocean climate cycles and correlations with biological productivity (Litzow et al., 2020). One such index is the Pacific Decadal Oscillation (PDO), which is often described as a longer-lived El Niño-like pattern of Pacific Ocean climate variability (Zhang et al., 1997). Phases of the PDO can be described as warm or cool, as defined by ocean temperature anomalies in the northeast and tropical Pacific Ocean. Positive PDO values indicate warmer surface waters, whereas negative values indicate cooler surface waters from enhanced upwelling. The North Pacific Index (NPI) uses area-weighted sea level pressure over the region 30°N–65°N, 160°E–140°W to measure interannual to decadal variations in atmospheric circulation (Trenberth & Hurrell, 1994). Lower values of the NPI correspond with increased upwelling and resultant increased primary productivity. The North Pacific Gyre Oscillation (NPGO) is driven by fluctuations in wind-driven upwelling and horizontal advection of seawater. NPGO values are correlated with changes in salinity and nitrate levels and chlorophyll concentrations (Di Lorenzo et al., 2008). Understanding the potential relationships between humpback whale foraging success and oceanic indices may aid in interpreting population fluctuations in feeding and breeding areas.

In addition to oceanographic cycles, the largest marine heatwave ever recorded occurred in the Northeast Pacific Ocean over several years, starting in late 2013 (Di Lorenzo & Mantua, 2016). Several sources indicate that a prolonged period of ecological disruption occurred in response to the heatwave (Gabriele & Neilson, 2019; Jones et al., 2018; Piatt et al., 2020). Although the mechanisms by which these oceanographic changes directly or indirectly affect humpback whales are not well understood, there is evidence that these linkages exist (e.g., Cartwright et al., 2019; Kügler et al., 2020).

Shortly after the Hawai'i humpback DPS was removed from the U.S. Endangered Species List in 2016 (Muto et al., 2019), whale researchers and members of the public noted marked declines in the numbers and/or distribution of humpback whales in Alaska, Hawai'i, and elsewhere (Cornwall, 2019). Our working hypothesis is that, after decades of population growth, the Hawai'i population experienced a dramatic decline due to changes in the marine food web in their high-latitude feeding areas. In other words, if foraging conditions are poor in feeding areas, the number of whales observed at migratory destinations, including Hawai'i, could be affected. Here, we use a 19-year

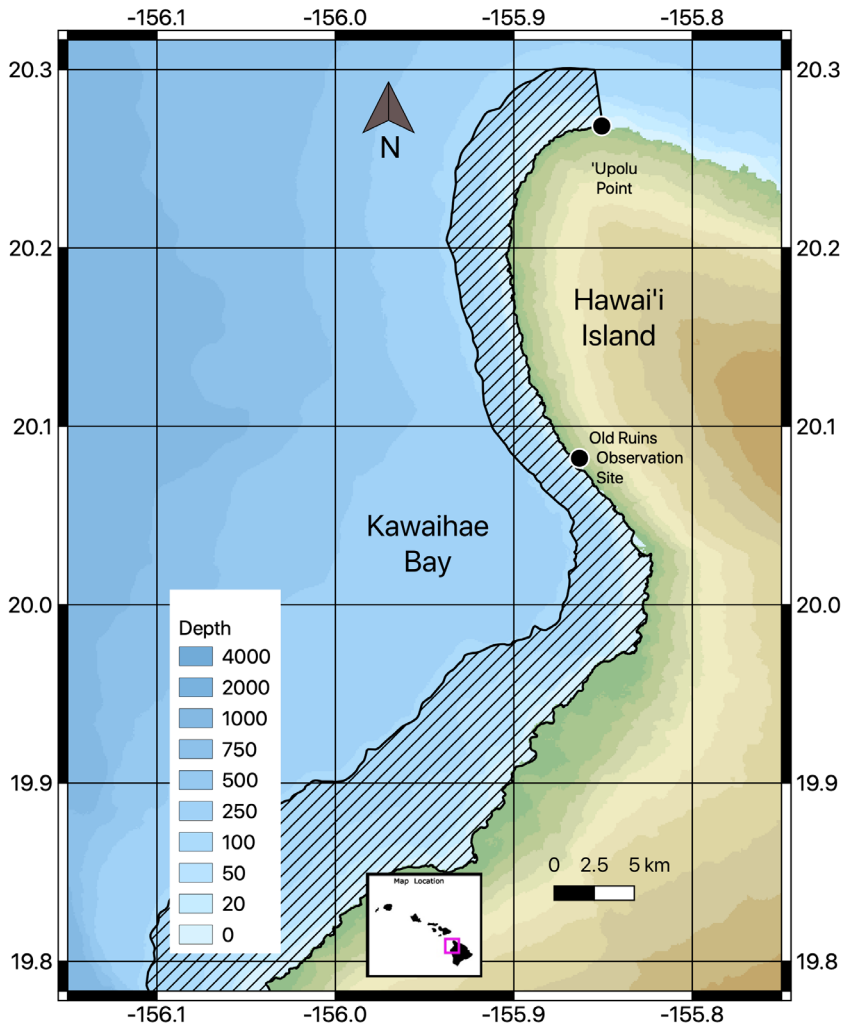


FIGURE 1 Study area on the northwest coast of Hawai'i Island. Depths are in meters. The hatched area represents the Hawaiian Islands Humpback Whale National Marine Sanctuary waters.

time series of systematic, shore-based humpback whale counts to describe the relative abundance, distribution, and population characteristics of whales in Kawaihae Bay, Hawai'i Island, to detect trends over time and investigate the drivers of those changes in numbers and distribution.

2 | METHODS

2.1 | Study area

The shore-based observation site is located on the northwest coast of Hawai'i Island at $20^{\circ}04.925'N$, $155^{\circ}51.795'W$, overlooking Kawaihae Bay at an elevation of 63.6 m (Figure 1). The site is known as "Old Ruins" because of the stone wall remnants of a Hawaiian village on nearby hillsides. The waters of Kawaihae Bay are steeply sloped, leeward waters, typical of volcanic islands like Hawai'i.

TABLE 1 Definitions of vessel type categories.

Vessel type	Definition
0	Nonmotorized (e.g., kayak, canoe, sailboat under sail)
1	Outboard engine(s) (typically <9 m length)
2	Inboard engine(s) (typically >9 m length)
3	All vessels >23 m length (e.g., tug and barge)

The waters between Keāhole Point and ‘Upolu Point (which encompass the study area), covering approximately 389 km² along the northwest coast, were designated as part of the Hawaiian Islands Humpback Whale National Marine Sanctuary in 1997. The Sanctuary encompasses approximately 3,626 km², comprised of five separate areas abutting six of the main Hawaiian islands.

2.2 | Scan samples

A three- or four-person team used scan sample methodology (Altmann, 1974) in timed, regimented counts of the number and location of humpback whales, vessels, and other marine mammals in the area. Data from each observation are referred to as a “scan sample.” Scan samples were conducted once per week in each of four time-blocks (0700–0900, 1000–1200, 1300–1500, and 1600–1800) to ensure that scans were conducted at various times during daylight hours to capture any diurnal trend. Data were collected between late January and late March from 2001 to 2019. Similar data were collected and presented by Helweg and Herman (1994).

The team included an observer who scanned the near-shore area from the coastline out to the horizon (~14 km), using compass-equipped 7 × 50 marine reticle binoculars and with the naked eye. To control for effort, only the observer called out new pods. A theodolite operator attempted to measure the position of all marine mammal pods relative to the shore station site. Using customized software, the computer operator collected theodolite location data or “fixes.” A notetaker was present to record binocular fixes and other information, such as comments on vessels, whale behavior, etc. Occasionally, the notetaker and computer operator was the same team member. The observer and theodolite operator roles were only filled by the authors, to reduce variability.

Environmental data included Beaufort sea state, swell height, and a qualitative assessment of visibility that incorporated haze, glare, and other factors that may have influenced the ability of the observers to detect marine mammals. Scans conducted when the Beaufort sea state was greater than four were excluded from the analysis.

A pod was defined as one or more whales within three adult whale-lengths of each other, moving in the same general direction and/or surfacing and diving in synchrony. The initial heading of each pod and whether it was surface active was also recorded. The composition of each pod was noted, including the presence or absence of a calf. Calves were identified by their small size and close, consistent association with an adult that was presumed to be their mother. Additional comments regarding whales with a distinctive physical appearance or behavior (e.g., a whale was moving very quickly) were noted on data sheets by the notetaker. These comments could be used later during data analysis.

To document changes in nearshore human use and provide an indication of the underwater sound environment, vessels were counted, and their initial location was fixed during a “vessel scan” of variable duration that occurred immediately prior to the timed “whale scan.” A description of each vessel and its “type” were recorded. Vessel types were based on engine power and vessel length (Table 1). Any additional vessels that entered the study area after the vessel scan and before the end of the whale scan, were also fixed when time allowed.

Scan samples in 2001–2002 were 15 min long. However, dramatic increases in whale numbers in 2003 made it difficult to count and acquire location data for all pods in the entire viewing area in 15 min. Therefore, the observation period was lengthened in 2003 and the study area was split into “south” and “north” regions of approximately

equal size, each of which was scanned for 15 min. A coin toss randomly determined which region to scan first. Other than scan duration, scan sampling methods were consistent throughout the entire study. After, each 15 min scan, there was a 10 min “grace period” to allow collection of any missing descriptive information (e.g., pod composition). Any whales that moved from one region to the next between scans were only counted once.

2.3 | Location measurement

Locations of vessels and whales were calculated from theodolite data (fixes) measured using a Sokkia DT500 theodolite with 5 s precision and 30-power magnification. Station height had been previously measured as 63.6 m (Frankel et al., 2009). Eye height (distance from the theodolite eye piece to the ground) was measured each day, added to the height of the shore station, and entered into the data file. The theodolite was linked to an Apple laptop computer running one of two data-collection programs, Aardvark (Mills, 1996) or Maka (Mills, 2014). Both programs recorded the declination and azimuth angles along with the time of each fix.

2.4 | Scan sample data processing

After data collection for a day was completed, each data file was opened in Aardvark and error-checked line by line. The analyst referred to the data sheets and computer file from the associated scan for any comments, and edited lines of data appropriately. All data files were processed by the same analyst (S.Y.) for consistency. If the data collection team had considered one pod likely to be a previously sighted pod during the scan, this was later evaluated using the Aardvark Viewer application, which converts theodolite angles to cartesian coordinates and calculates speeds. The data analyst examined these fixes and the speed necessary for a whale to move between fix locations, along with any comments from the data sheets and computer file. If the second designated pod could be the first pod (i.e., the speed was less than 15 km/hr), the behavioral observer and notetaker examined the data. If they both agreed that second location was a duplicate, then the second fix was deleted, and the total number of pods seen for that scan was decreased by one.

Several whale variables were extracted from the data set. Whale abundance was represented by the total number of whales and calves for each scan sample. Crude birth rate (CBR) was defined as the number of calves per scan divided by the total number of whales per scan. Each pod location was used to determine the water depth at that location as well as the minimum distance from the shoreline. For comparison, these last two metrics were also calculated from GPS-measured locations taken during boat-based photographic identification efforts from 2004 to 2006 during the SPLASH study (Calambokidis et al., 2008), when an effort was made to survey areas uniformly. SPLASH (Structure of Populations, Levels of Abundance and Status of Humpbacks) was a large collaborative study of humpback whales in the North Pacific. We conducted boat-based surveys to collect data on distribution, locational data, identification images as well as tissue samples. Data from this time period provided a useful comparison to shore-based measurements.

2.5 | Data processing

2.5.1 | Environmental data

Environmental data were collected because they affect the observability of whales (Clarke, 1982). A principal components analysis (PCA) that included Beaufort sea state, sun glare, swell height, and a general visibility rating was conducted in JMP version 13 (SAS Institute, 2015). The first two principal components accounted for approximately 70% of the variability in environmental conditions. These two principal components were included in the base model analyses to control for variability in observation conditions.

2.5.2 | Climate index data

Climate indices were used as proxies for prey availability (e.g., Santora et al., 2020). Many potential climate indices were available for use. The ones selected here are focused on the North Pacific Ocean, where Hawaiian humpback whales forage in the summer. These include the PDO (Newman et al., 2016), NPGO (Di Lorenzo et al., 2008), and NPI (Trenberth & Hurrell, 1994). All of these indices have been used successfully to predict biological productivity at various trophic levels (Calambokidis et al., 2009; Fleming et al., 2016; Litzow et al., 2020; Wong et al., 1998). For each index, a “summer signal” was created by summing the index values over the months of May–September, a method devised by Mantua et al. (1997). Finally, sea surface temperature (SST) for Kawaihae Bay was extracted from the daytime MODIS 4 km data set (https://coastwatch.pfeg.noaa.gov/infog/MH1_sstMask_las.html) around the study area (19.5°–21°N and 155.75°–156.75°W). This data set has a temporal resolution of 8 days, and the mean SST for each period was calculated. SST values were assigned to scan observations using the value from the nearest date possible.

2.5.3 | Bathymetric data

Coastal relief model bathymetric data for the study area were downloaded with 3 s resolution from the National Geophysical Data Center (2005) and used to assess whale habitat use by water depth. Global self-consistent hierarchical high-resolution shoreline (GSHHS, Level 1) data (Wessel & Smith, 1996) were used as the reference dataset

TABLE 2 Number of scan samples collected in each time block in each year. Visibility encapsulates the other environmental variables (Beaufort sea state, swell, glare) so it is included here as an index of whale sightability.

Year	Mean visibility	0700–1000	1000–1300	1300–1600	1600–1900	Total
2001	2.9	4	6	6	5	21
2002	3.0	5	7	3	2	17
2003	3.2	4	4	6	2	16
2004	2.8	5	5	5	5	20
2005	2.6	5	5	5	5	20
2006	3.0	5	5	5	5	20
2007	2.8	5	4	4	4	17
2008	3.3	5	5	5	5	20
2009	3.4	5	5	5	5	20
2010	3.5	5	6	4	5	20
2011	2.9	5	5	5	5	20
2012	2.9	5	5	5	5	20
2013	3.1	4	5	4	3	16
2014	2.9	5	5	5	5	20
2015	2.9	5	5	4	5	19
2016	3.2	5	5	5	5	20
2017	3.0	5	5	5	5	20
2018	2.8	4	5	5	6	20
2019	2.3	19	1	0	0	20
Total	2.9	105	93	86	82	366

for calculating the offshore distances to whale locations using custom Matlab analysis scripts that incorporated appropriate mapping functions.

2.6 | Statistical analyses

The generalized additive model (GAM) analysis was conducted using the R package *mgcv* (Wood, 2017). The distribution and dispersion of the data were assessed to determine the appropriate distribution family to use for the GAM analyses. GAM outputs were evaluated with the *gam.check* function in the *mgcv* library (Wood, 2017). Graphical representations of the GAM output were created with the *visreg* function (Breheny & Burchett, 2012). These figures contain representations of the data, the model fit and the confidence limits around the fit.

A base statistical model for whale number was created using predictor variables of year, observer, time block, day of year (DOY), and the environmental principal components. The base model was tested to see if it could be improved by the addition of climatic indices. Because it is possible that climatic conditions from previous years may be more important than current conditions, the values of climate indices in this study were tested lagged between

TABLE 3 Principal components (PC) analysis results for observation environmental variables. These PCs were used to represent environmental conditions in the statistical analyses.

Parameter	Component 1	Component 2
Visibility	0.82322	-0.30641
Beaufort sea state	0.85676	-0.15512
Swell height	0.20422	0.88989
Sun glare	0.56619	0.35926

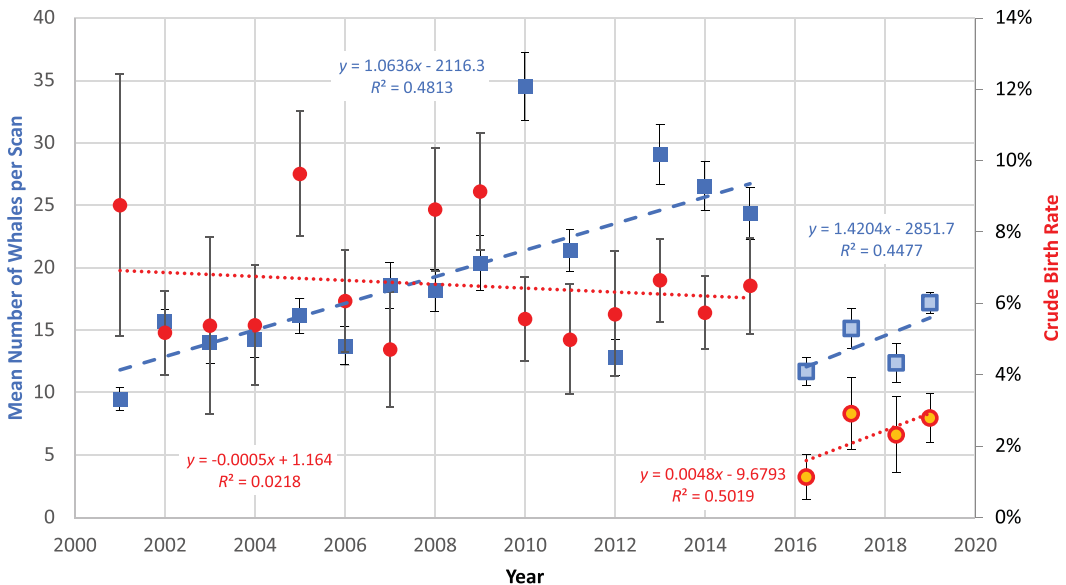


FIGURE 2 Mean number of whales per scan (blue squares) and the mean crude birth rate (red circles) across years. Separate linear fits have been applied to the data from 2001–2015 and 2016–2019. These fits show a strong linear growth in whale numbers over the years 2001–202015. CBR was essentially constant from 2001–2015. Both whale numbers and CBR dropped precipitously in 2016.

one and three years. Using the method of Meyer-Gutbrod et al. (2015), each climate index, paired with each temporal lag value, was added to the base model. The Akaike information criterion (AIC) for each model was then determined. The model with the best (lowest) AIC value was then chosen.

3 | RESULTS

A total of 366 scan samples were collected between 2001 and 2019 (Table 2). Humpback whales were the only mysticete observed and spinner dolphins were the next most frequently sighted cetacean species. Thirteen scan samples that were collected with observers other than the three main observers (ASF, CMG, SHR) are shown in Table 2, but were omitted from statistical analyses to facilitate the inclusion of observer as a predictor variable with only three levels. Thus, the analyses were conducted on $n = 353$ scan samples. An analysis was conducted after the 2018 season to test for diurnal effect. Since no effect was detected, the protocol for 2019 removed the time-of-day requirement. Finally, whale abundance trends were examined with both the entire subset of “fixed” whales, i.e., those with a theodolite location measurement and only those whales that were fixed within 6.5 km.

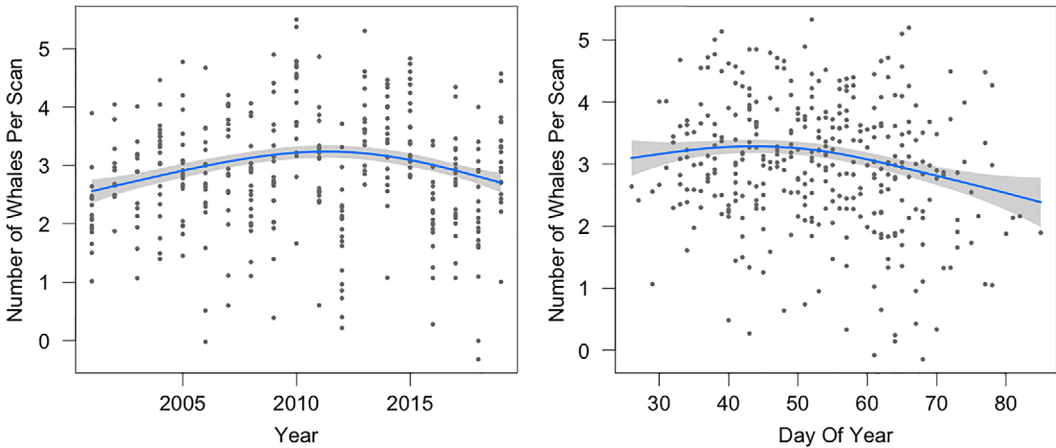


FIGURE 3 GAM smoothing functions are shown for the base model predicting the number of whales. The two significant predictors were year (left) and day of year (DOY) (right). Whale numbers appear to increase until about 2013 and then began to decline. The DOY plot shows the typical peak in local abundance around day 45. The y-axis values differ from Figure 2 because these curves are fit to adjusted modeled values that include the influence of the other predictor variables.

TABLE 4 Improvement (reduction) in AIC from the base model with different climate indices and temporal lags. The greatest improvement was observed with the PDO with a 1.5-year lag.

Model	Lag (years)		
	0.5	1.5	2.5
Base	0	0	0
Base+NPGO	56.639	31.783	29.925
Base+PDO	-12.052	-49.024	-10.805
Base+NPI	-8.793	-26.412	-27.251

The difference between these two trends was examined visually and was found to be negligible. Therefore, all whales detected by the observer were included in the analysis.

3.1 | Environmental variables

The principal components analysis loading matrix is reported in Table 3. Component 1 was dominated by Beaufort sea state and the overall visibility score. Component 2 was dominated by swell height. Components 1 and 2 were considered in the base model GAM analysis.

3.2 | Abundance

Across the entire study period, the mean number of whales per scan was 18.3 (range = 1–55). The annual mean number of whales per scan in 2001–2015 was 19.2 (range = 9.5–35.2). The 2016 season had an overt drop in whale numbers that remained low over the 2016–2019 period, with a mean of 13.1 (range = 11.7–15.2; Figure 2). In the early portion (2001–2009) of the study there was a relatively consistent increasing trend. Whale numbers peaked in 2010, with a mean count of 34 whales per scan, followed by a period of increased interannual variability lasting through 2015. Whale numbers dropped in 2016 to the lowest value since 2001 and remained low through 2019.

In 2001–2015, the annual mean crude birth rate (CBR) was 6.5% (range = 4.7–9.6; Figure 2), while in 2016–2019, it dropped to 2.1% (minimum 1.1, maximum 2.9). Taken alone, the 2016–2019 whale numbers and CBR both have a positive slope, but the values remain far lower than those from the 2001–2015 period. CBR has yet to recover to even the lowest value in the earlier period.

Using GAMs, we then investigated the effect of natural environmental variables that could explain changes in whale numbers and calf production. Since the standard deviation was greater than the mean, a negative binomial distribution and logarithmic link function were used. Base model predictors initially included year, day of year (DOY), time-block, scan observer, SST, and the environmental principal components. The base model was intended to

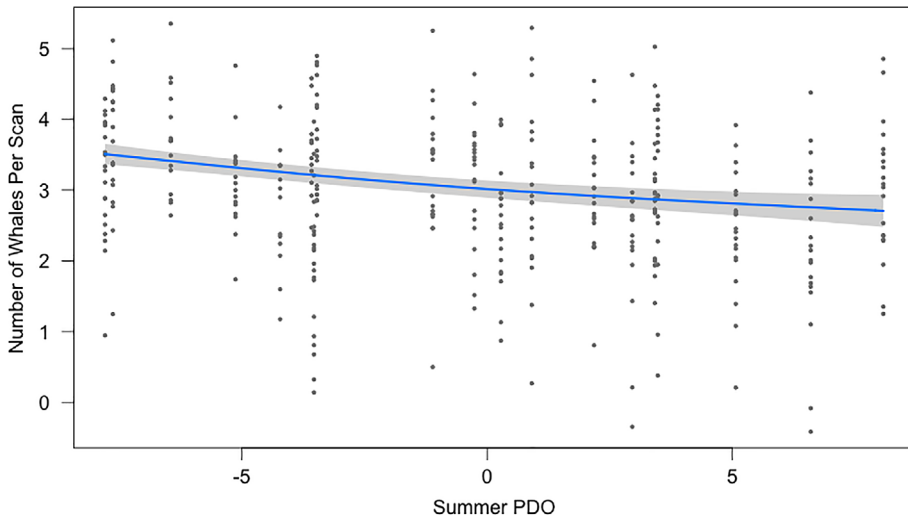


FIGURE 4 GAM smoothing functions are shown for PDO scores. The greatest number of whales is associated with a 1.5-year lagged PDO value of ~ -7.5 , which reflects the importance of the presence of cool, productive ocean water at high latitudes in prior years.

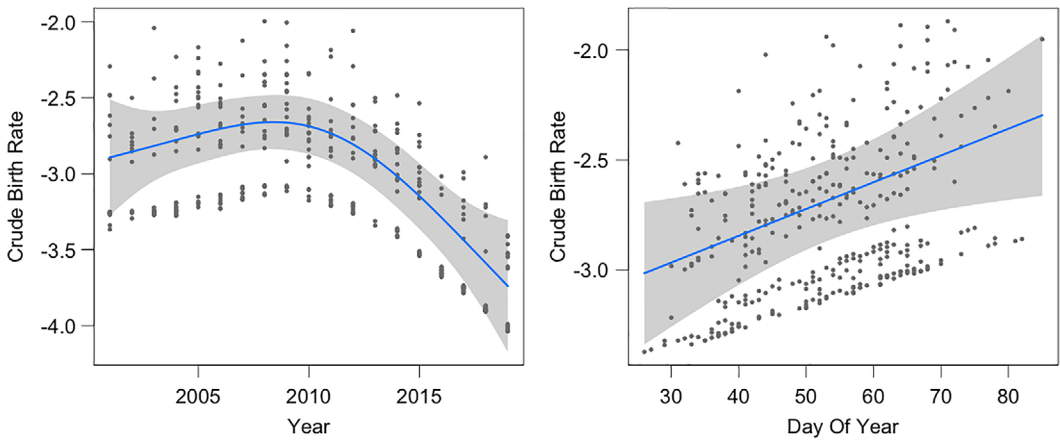


FIGURE 5 Crude birth rate GAM smoothing curves are shown for year and day of year (DOY). The curves show an increasing trend through 2010 and a major drop in 2016. The DOY curve shows an increase in crude birth rate (CBR) over the course of the season.

TABLE 5 Improvement (reduction) in AIC from the base model with different climate indices and temporal lags. The model with the best AIC score was base+NPI lagged 2.5 years, followed by base+NPGO lagged 0.5 years and base+PDO lagged 0.5 years.

Model	Lag (years)		
	0.5	1.5	2.5
Base	0		
Base+NPGO	-5.3099	-1.0447	0.1448
Base+PDO	-3.1965	-0.8832	1.5994
Base+NPI	1.6431	0.4061	-10.8184

account for local environmental and scan observer variability. We found no significant effect of environmental principal components and time-block on observed whale numbers, so these were removed from the base model. The remaining predictors in the base model included year and DOY. The smoothing functions of year and DOY are shown in Figure 3. They indicate a peak in whale abundance in 2013 and an annual peak in abundance around day 45 (mid-February).

Once the base model was established, the climate indices were added one by one, with each of three temporal lag values (0.5, 1.5, and 2.5 years). The model with the lowest AIC value was selected as the best model. Table 4 shows the change in AIC from the base model ($AIC = 2,310.7$) for the different climate variables and temporal lag values previously described. The most supported model (i.e., largest reduction in AIC) used PDO values lagged by 1.5 years ($r^2 = 0.409$; Table 4).

The smoothed curve fit to the PDO is shown in Figure 4. The PDO curve shows a peak in whale abundance at the lowest PDO value (~ 7.5). Low PDO values indicate cool, productive waters in the high latitude feeding grounds. Tables S1 and S2 show the detailed results of the GAM models. All predictors in the model were statistically significant. One potential issue with climate indices is the possibility of autocorrelation in the predictor variable values. Therefore, residual values and autocorrelation functions for both analyses were examined for any remaining temporal structure (chapter 6 in Zuur et al., 2009), but they indicated that none was present in the climate predictor variables.

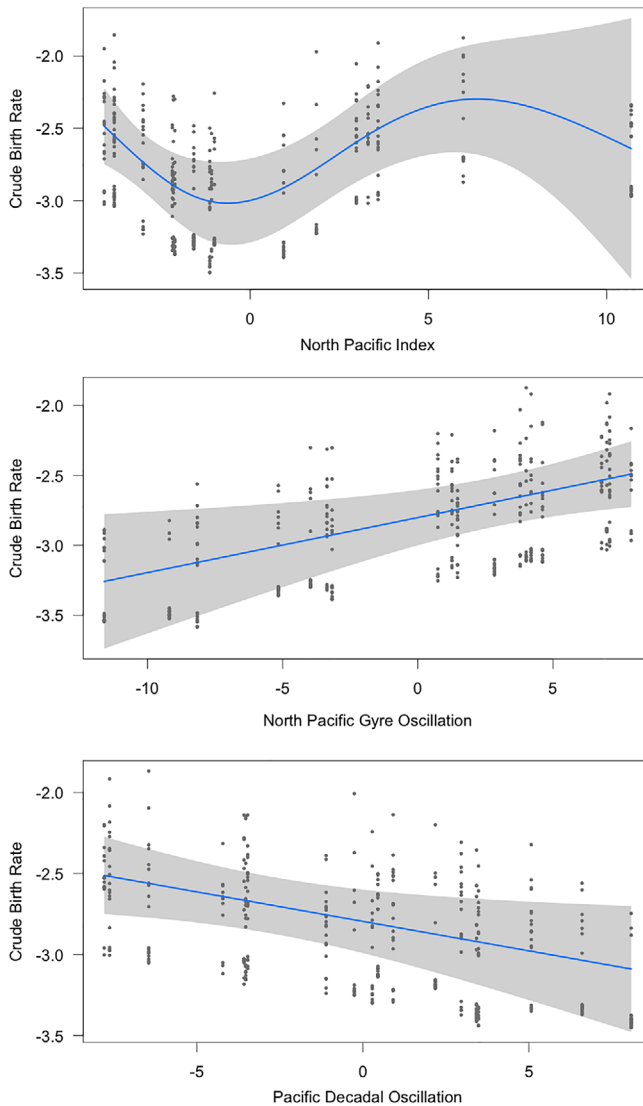


FIGURE 6 Crude birth rate GAM smoothing curves are shown for the North Pacific Index (lagged 2.5 years, top), North Pacific Gyre Oscillation (lagged 0.5 years, middle), and Pacific Decadal Oscillation (lagged 0.5 years, bottom). The NPI function (which was the best model according to improvement in AIC) does not describe a meaningful pattern. The second-best model was the NPGO (middle) with higher values indicating a higher CBR. The PDO model was the third best and is provided for comparison with the whale abundance function.

The CBR analysis used the same approach of creating a base model and examined the effect of climate predictors. Because the data were highly skewed toward zero, a Tweedie distribution with a logarithmic link function was used for the GAM. The base model retained year and DOY as significant predictors (Figure 5).

The same climate indices were added to the model one at a time with each of the three temporal lag values, with the changes in AIC shown in Table 5. The model with the greatest improvement in AIC was the NPI, lagged 2.5 years (Figure 6, top) that appears to indicate higher CBR would be predicted by high or low values 2.5 years prior ($r^2 = 0.106$). The second-best model is the NPGO lagged 0.5 years ($r^2 = 0.088$) and predicts that when the NPGO is high in summer, the CBR will increase in the subsequent winter. Higher NPGO values correspond to cooler waters in

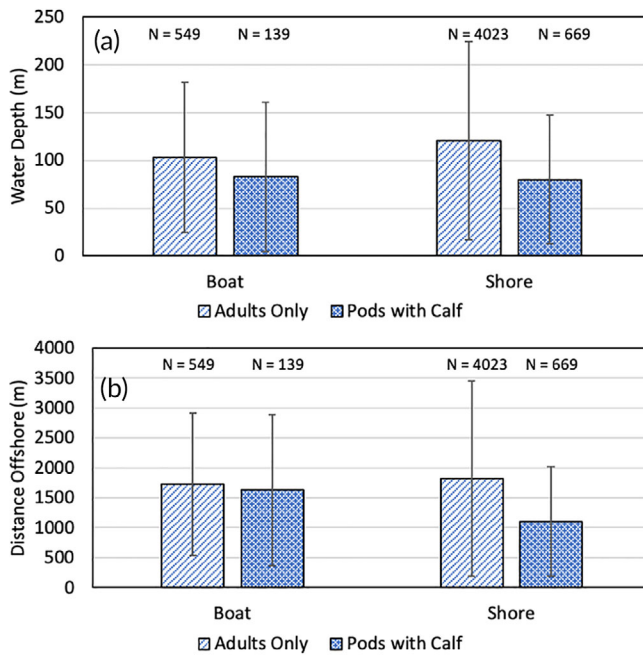


FIGURE 7 Mean water depth (a) and distance offshore (b) at locations of adult-only pods and pods with a calf, as observed from boat-based and shore-based observers. For shore-based scans, pods containing a calf were found significantly closer to shore and in shallower waters than pods composed solely of adults. In the boat-based data, pods with a calf were found significantly closer to shore than adult pods, but the difference in water depth for the two types of pods was not found to be statistically significant. Error bars are standard deviations.

central and southeast Alaska, where the majority of Hawaiian humpback whales forage in summer. For comparison with the overall whale abundance models presented earlier, the PDO ($r^2 = 0.078$) also shows a higher CBR with lower values (cooler waters).

3.3 | Spatial distribution

We calculated two quantitative metrics of distribution: distance offshore and water depth, for each whale pod. Mean values for both metrics were calculated for each scan sample. The same set of predictor variables (year, DOY, time block, observer) used for the abundance analyses as well as the number of vessels were incorporated into GAMs. There was no change in either of the whale distribution metrics as a function of year, number of vessels present, time block or observer.

Pods with a calf were closer to shore (1.1 versus 1.8 km, Kolmogorov–Smirnov $KS = 0.089$, $p < .0001$) and in shallower water than adult-only pods (80 versus 121 m, $KS = 0.074$, $p < .0001$). It is possible that calves were present offshore, and that the observation team missed them. To evaluate this possibility, the analysis was repeated using archived boat-based GPS pod locations. A subset of data from the SPLASH project (Calambokidis et al., 2008) was selected from years 2004–2006, when boat-based effort was consistent and directed toward documenting as many whales as possible. In the boat-based data, water depth was statistically significantly different for pods with or without a calf (83 versus 103 m, $KS = 0.090$, $p < .001$). Distance offshore showed the same trend (Figure 7) but was not found to be significant

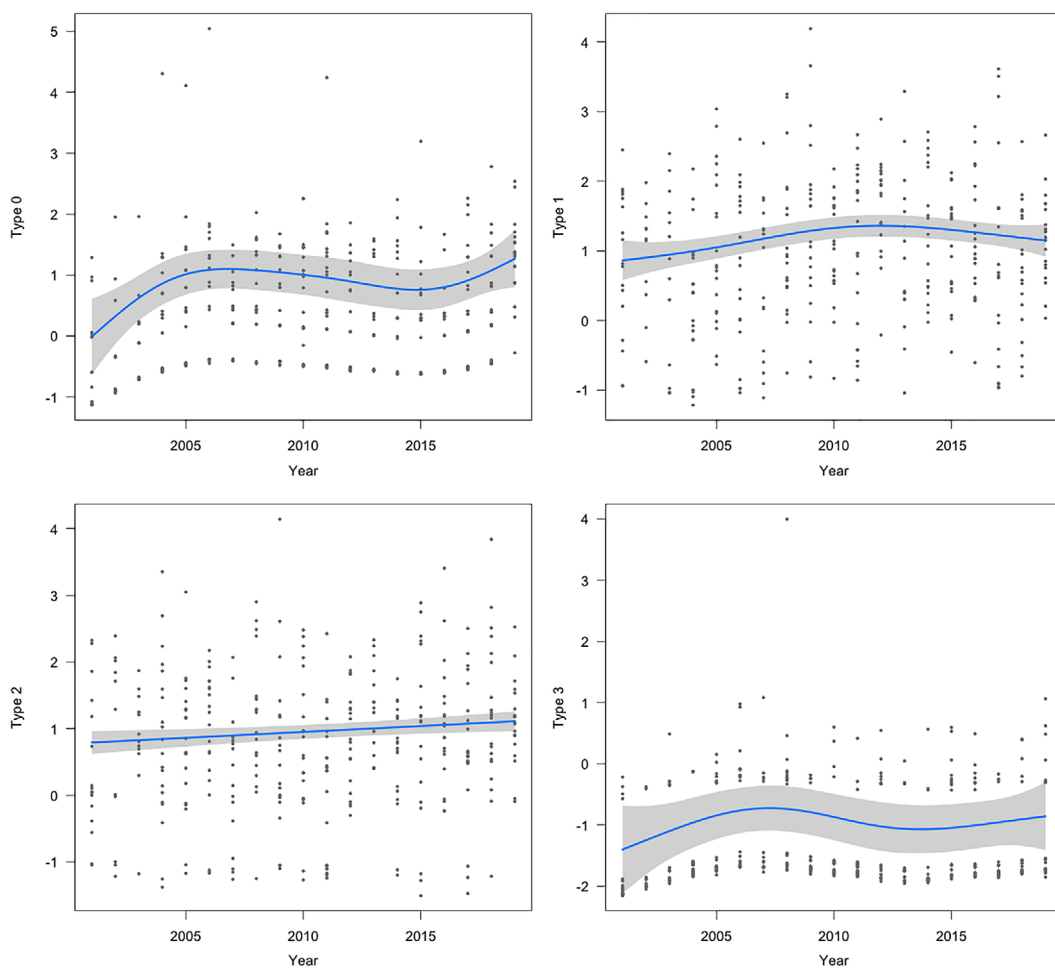


FIGURE 8 Number of vessels as a function of year. Type 0 = nonmotorized, Type 1 = vessel with outboard engine, <9 m, Type 2 = powered vessel >9 m, Type 3 = powered vessel >23 m.

(1.6 versus 1.7 km, $KS = 0.042$, $p = .081$). The boat-based calf pod location analysis supports our shore-based finding of water depth values for both shore and boat-based data sets, as shown in Figure 7.

3.4 | Human habitat usage: Observed vessel numbers

While whales respond to environmental factors, including some that are controlled at ocean-basin scales, local factors are also of interest, (e.g., vessel traffic and shoreline development) as anthropogenic influence has the potential to affect habitat quality (due to factors such as vessel noise and water quality degradation due to shoreline runoff). Mean counts of all vessel types increased from 5.2 vessels per scan in 2001 to 11.3 in 2019. Vessel counts during scans were analyzed with the same predictor variables (year, DOY, time block) that were applied to whale numbers, plus a weekday/weekend variable, because vessel traffic often increases during weekends (Martin & Popper, 2016). Counts of vessel types 0 (nonmotorized), 1 and 2, (small to medium powered vessels) showed general increases over time. Large type 3 vessel counts (tug and barges, or military vessels) fluctuated, but showed no significant trend over time (Figure 8).

4 | DISCUSSION

Consistent, rigorous, long-term monitoring of natural systems enables scientists to discern and understand change over time. In this study, we used a 19-year monitoring data set to document the increasing trend of a whale population recovering from commercial whaling, and an abrupt disruption of that trend in the same timeframe as the strongest marine heatwave documented on our planet to date (Di Lorenzo & Mantua, 2016). Our analysis indicates that ocean-basin-scale oceanographic parameters strongly influence habitat use and calf production and highlights this population's vulnerability to warming oceans. The details of the findings are as illustrative as the general trends, and hint at the sensitive life history junctures for calf production.

4.1 | Abundance and calf production

Historical records (Herman & Antinaja, 1977) and the contemporary data presented here indicate that Kawaihae Bay continues to represent important humpback whale habitat. Winter whale abundance in Kawaihae Bay reached its highest values near mid-February (Figure 3), consistent with the pattern reported in aerial surveys in the early 1980s (Baker & Herman, 1981; Figure 4A). These data suggest that our observational efforts are well timed to document the peak in whale abundance, even though peak timing varies slightly each year. Whale numbers increased through 2015, regardless of the scan time of day (Figure 3). An earlier study using similar methodology also found no changes in whale numbers as a function of the time of day (Helweg & Herman, 1994). Smultea (1994) found that while the number of pods did not change with time, the distribution of pods with calves did change before and after noon.

The effect of environmental conditions on the sightability of animals is well established (e.g., Clarke, 1982). However, when the principal components representing Beaufort sea state, swell height, and glare were included in the base GAM model, these factors were not found to be significant, so they were removed from the base model. We conclude that our standard protocol of collecting data only when the Beaufort sea state was <5 (winds <17 knots) limited the range of environmental variability, which eliminated much of the importance of sea state as a predictor of whale count.

Humpback whale population growth documented in the North Pacific (Barlow et al., 2011; Mobley et al., 1999) is the most likely explanation for the overall increasing whale count trend in Kawaihae Bay through 2015. Fluctuations in the number of whales off the northwest coast of Hawai'i over the entire time period are also likely attributable to whales moving throughout the Hawaiian Island chain (Baker & Herman, 1981; Cerchio et al., 1998). Changes in the numbers of whales and calves over time that are seen in the raw data (Figure 2) are corroborated in the base model GAM analysis (Figure 3), that found the change in numbers over time to be statistically significant. Citizen science efforts corroborate an increasing whale population since 2000 off several of the main Hawaiian islands, according to summary data available from the National Marine Sanctuary Program's Ocean Count (unpublished data, <https://hawaiihumpbackwhale.noaa.gov/involved/ocean-count.html>).

During the period 2001–2015, the overall trend in whale numbers increased with relatively low interannual variation between 2001 and 2009. (Figure 2). The time period between 2010 and 2015 shows more variability. The highest mean count of 34 whales per scan was observed in 2010 and whale numbers were particularly low in 2012. The highest single count of 55 occurred in 2013. It is possible that these years reflect a temporary shift of whales within the Hawaiian Islands (Baker & Herman, 1981; Cerchio et al., 1998) or a shift in the proportion of whales migrating to Mexico instead of Hawai'i (Darling et al., 2019). Colleagues reported low numbers of humpback whales in other breeding areas, but we have limited information about numbers of whales in the feeding areas during winter.

The pattern of increasing whale numbers between 2010 and 2015 is not as clear as in the first portion of the data set. There are at least two scenarios which could be supported from these data. First, the overall population continued its near linear increase in numbers (Figure 2) from 2001 to 2015, albeit with increasing variability. This continued increase is supported by the nearly uniform CBR of about 6% through the study. Furthermore, the limited

scan data from 1988 (Helweg, 1989; mean whales per scan of 4.0 and a CBR of 7.9%) is consistent with the trends we report here. Both whale numbers and CBR declined precipitously in 2016, following the occurrence of the North-east Pacific marine heatwave and the ongoing elevated sea surface temperatures (Di Lorenzo & Mantua, 2016).

Alternatively, the variability in population growth in 2010–2015 may indicate that the population was approaching carrying capacity prior to the sharp ecological disruption probably caused by the marine heatwave (which became evident in our data set starting in 2016). However, increased numbers of emaciated whales (little fat behind the blowhole, protruding scapulas) were observed in our study area in 2016, concurrent with, rather than prior to, a drop in observed whale numbers. Sharply reduced numbers of whales in 2016–2018 were noted by both the general public and whale research community (Cartwright et al., 2019, Kügler et al., 2020; Loomis, 2016). It is also possible that both an approach to carrying capacity and prey supply disruption combined to produce the large drop in observed whale numbers in 2016. It could also be argued that the marine heatwave may have reduced the carrying capacity for humpback whales and other species.

Pairing our annual whale count data with oceanographic indices revealed that higher whale numbers in the winter breeding grounds were predicted by negative PDO scores lagged by 1.5 years. Negative PDO values indicate cooler, productive waters in high latitudes (Mantua & Hare, 2002). Thus, we suggest that differences in the wintering whale population are largely attributable to the influence of ocean conditions on prey availability in prior summers. Specifically, in the case of the 2014–2016 marine heatwave, reduced marine productivity and prey availability in the whales' high latitude feeding areas appear to have constrained the whales' likelihood to migrate and/or reproduce. There are numerous links between body condition and reproduction in mammals (e.g., Wade & Schneider, 1992; Williams et al., 2013). Lack of prey has been suggested as the underlying cause for increased mortality and decreased recruitment in gray whales (*Eschrichtius robustus*; Le Boeuf et al., 2000), southern right whales (*Eubalaena australis*; Seyboth et al., 2016) and humpback whales (Seyboth et al., 2021).

The pattern of lower overall whale numbers in the breeding grounds 18 months after an unfavorable feeding season (Figure 5) must include both adults and subadults. While migrations are staggered by age-sex class (Chittleborough, 1965; Craig & Herman, 1997; Dawbin, 1966; Gabriele, 1992), and not all whales migrate every winter (Straley et al., 2018), we do not know all the factors that influence humpback whale migration (Durban & Pitman, 2012). It is not unreasonable to presume that social as well as biological factors are important. If fewer females chose to migrate in a given year because of poor body condition, perhaps males may follow suit and be less likely to migrate to the wintering grounds. Staggered migration, led by females about to wean a calf, could give males an opportunity to make a migratory decision (based on availability of females) in real time. In a special case like the 2014–2016 marine heatwave, the abrupt decline in humpback whales in Hawaiian waters in 2016 and 2017 (Figure 2) appears to indicate that few whales of any age-sex class were in sufficiently good condition to migrate. For those whales that did migrate to Hawai'i in those two years, our boat-based observations noted numerous emaciated whales (unpublished data) who migrated despite their poor condition.

The effect of climate indices on crude birth rate (CBR) was not as straightforward. The base models between whale numbers and CBR are similar, but the amount of variation explained with the whale abundance model was 40%, whereas the crude birth rate models explained only 8%–10% of the variation. The AIC model selection criteria found that the most supported model for CBR was the NPI lagged 2.5 years, but the smoothing function does not show a meaningful pattern (Figure 6, top). The effect of ocean conditions 2.5 years before the birth of a calf are difficult to interpret in terms of whale physiology, although it may incorporate the females' favorable prey conditions as they restore their energy reserves after their previous calving and lactation. The next two “best” models were the effects of the NPGO and PDO, both lagged 6 months (Figure 6, middle and bottom). These two models indicate a much clearer trend, with CBR increasing in winters when there were cool waters in the feeding grounds the previous summer.

While the gestation period for a humpback whale is nearly a year long (Chittleborough, 1958), producing and rearing a calf is an even more prolonged energetic event when the mother's body condition is taken into account. The 18-month lag that our whale numbers models demonstrate (Figures 3 and 4), suggests that the female's

condition may affect whether she migrates to the winter grounds. Cool, productive ocean water at high latitudes during the feeding season during pregnancy predicted higher CBR 6 months later on the winter grounds (Figure 6). This line of reasoning may also help explain why the 2016–2019 data, taken on their own, suggest a moderate increase in whale numbers, with little to no recovery in crude birth rate (Figure 2). After several unfavorable feeding seasons, following the 2014–2016 marine heatwave (Cornwall, 2019), we surmise that mature females had not yet regained the physical reserves necessary to initiate and/or sustain a pregnancy but were still migrating to the breeding grounds. Conversely, once feeding conditions improve after a period of suppressed calving, an unusually high proportion of females will likely be available for mating (i.e., not be with a calf that year) and we may see a calf-production boom in subsequent seasons (e.g., Corkeron et al., 2018). The 2016 marked drop in abundance was observed statewide. Whale numbers in Kawaihae Bay remained low through 2019, while other areas within the state showed evidence of stronger recovery (Cartwright et al., 2019; Kügler et al., 2020).

4.2 | Distribution

Pods containing a calf were found closer to shore than adult-only pods, corroborating a similar finding from Hawai'i Island, 60 km south of the study area (Smultea, 1994). These observations lend credence to the hypotheses that a mother with a calf may stay near shore to avoid predators or large and boisterous competitive pods (Craig et al., 2014). In scan samples and boat-based surveys, calf pods were found in significantly shallower water than adult-only pods. Scans also found that calf pods were significantly closer to shore than adult-only pods. Boat-based data showed the same trend but were not significantly different. The overall distribution of whales has not apparently changed within the study area even as the number of whales increased between years. Mean values for metrics for water depth and distance offshore showed no correlation with year, day of year, time block, observer, or number of vessels. It has been suggested that increased vessel traffic may lead to mother and calf pods moving offshore (Cartwright et al., 2012). Our data do not support this, but it is worth noting that the number of vessels in Kawaihae Bay remain far lower than those off Maui where Cartwright and others conduct their research.

4.3 | Human habitat usage: Observed vessel numbers

The overall numbers of vessels increased throughout the entire 19-year study period (Figure 8). Nonmotorized vessels (e.g., kayaks and canoes) as well as small and medium-sized vessel types showed increases over the study period. The increase in small to medium-sized vessels may reflect increases in the local human population. Tug and barge and large military vessel numbers fluctuated but showed no net change over time (Figure 8). Trends shown in Figure 8 suggest a slow increase perhaps interrupted by the economic downturn of 2008–2009, with a renewed trend of increasing vessel numbers beginning about 2012.

4.4 | Conclusions

During the 2014–2016 marine heatwave, the value of our data time series became very apparent. Due to limited funding and other factors, few research groups can sustain long-term projects, but their value in contributing to a better understanding of changes in distribution and abundance of long-lived organisms is undeniable. Continued long-term monitoring of whale populations is essential to documenting and understanding marine ecosystem responses to global climate change. Preserving the habitat value of this breeding and calving area is essential to the overall health of whales in Hawaiian waters.

The increase in the number of humpback whales in Kawaihae Bay over the past 19 years is encouraging. Indeed, the recovery and removal of the central North Pacific population of humpback whales from the U.S. Endangered Species list is perceived as a conservation success story. Unfortunately, the sharp decline in adult whales and calves that started in 2016 highlights the population's continued vulnerability. Evidence of a mortality spike for multiple whale species in the Gulf of Alaska during the 2014–2016 marine heatwave (Savage, 2017) and the persistence of lower calf production in our study suggests an ecological disruption that affected whales from various North Pacific feeding areas. Numerous other marine predators appear to have experienced contemporaneous declines (Arimitsu et al., 2020; Cornwall, 2019; Piatt et al., 2020). Changes in migratory patterns between islands, and reductions in the amount of time spent at migratory termini could explain a portion of the observed changes in whale numbers. However, if whale numbers remain low over the next few years, a general population decline is the most likely hypothesis. Only time and systematic monitoring will tell. Consistent winter survey efforts in Alaskan waters would be needed to document whether the whales have begun to spend less time in the Hawaiian Islands and more time in their feeding grounds, presumably to meet their nutritional needs.

Because the 2016 decline in whale numbers was experienced throughout the main Hawaiian Islands, interisland movement seems unlikely to explain what we observed off Hawai'i Island during and after the 2014–2016 marine heatwave. The ability to distinguish future changes in whale distribution from population decline will require consistent population monitoring surveys at multiple sites in the Hawaiian Islands. And finally, ongoing ocean warming, and the associated habitat changes may cause these whales to move further north into the Northwest Hawaiian Islands. A collaborative acoustic monitoring network over this immense geographic area may be the most cost-effective way to detect broadscale distributional changes. Documenting individual whale movement may be part of the solution as well (Boyd & Punt, 2021), made easier by recent advances in automated photographic matching (e.g., Kierdorf et al., 2020). Employing some or all of these methods toward rigorous, long-term population monitoring will be an essential component of ongoing assessment of the health of the North Pacific humpback whale population.

ACKNOWLEDGMENTS

Our heartfelt thanks go to the many volunteers that have helped us conduct whale scans over the years, including our dear friend, the late Michael Hoffhines. Kimberly New deserves special mention as our most dedicated volunteer throughout the study, traveling from snowy Minnesota to work with us each winter since 2004. Harold Mills volunteered his time to produce a new software package, Maka, after hardware changes made the old program unusable for data collection. We gratefully acknowledge the State of Hawai'i Department of Land and Natural Resources, and the Hawaiian Islands Humpback Whale National Marine Sanctuary for critical funding that allowed the HMMC to get this study off the ground. Big mahalo to Whale Tales who funded data analysis that allowed us to complete this manuscript. We thank Daniel Palacios of Oregon State University for providing useful critique and commentary on the GAM analyses. Thanks to the anonymous reviewers whose comments improved the final paper. Boat-based data were collected under scientific research permit No. 782-1719 (NMML), 774-1714 (SWFSC) and State of Hawai'i DLNR Permits #SH2004-04, #SH2005-05 and #SH2006-06. The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

Christine Gabriele: Conceptualization; investigation; methodology; writing - original draft; writing-review & editing. **Suzanne Yin:** Conceptualization; data curation; formal analysis; investigation; methodology; project administration; resources; writing-review & editing. **Susan Rickards:** Data curation; investigation; project administration; writing-review & editing.

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SUPPORTING INFORMATION

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How to cite this article: Frankel, A. S., Gabriele, C. M., Yin, S., & Rickards, S. H. (2021). Humpback whale abundance in Hawai'i: Temporal trends and response to climatic drivers. *Marine Mammal Science*, 1–21. <https://doi.org/10.1111/mms.12856>