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Galápagos sperm whales (*Physeter macrocephalus*): waxing and waning over three decades

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Abstract: While population sizes and structures naturally fluctuate over time, rapid within-generation changes are usually driven by shifts in habitat quality and (or) abrupt mortality. We evaluate how sperm whales (*Physeter macrocephalus* L., 1758 = *Physeter catodon* L., 1758) responded to the dynamic habit off the Galápagos Islands over 30 years, relating it to variation in prey availability and whaling operations in the tropical Pacific. In the 1980s, males and females were commonly sighted foraging and socializing in the northwest of the archipelago. Sightings decreased during the 1990s; by the 2000s, they became very rare: occasional single foraging males were sighted and females abandoned the archipelago. In the 2010s, whales return to the southern waters, in large groups with apparently more breeding males and calves. The waxing and waning of Galápagos sperm whales are likely caused by environmental shifts together with ripple effects of whaling. Their patchy prey are influenced by variation in sea temperature and productivity, which drives movements of whales in and out of the archipelago. Whaling may have aggravated these movements by leaving an attractive surplus of prey in coastal waters depleted of whales. These findings highlight the magnitude of spatiotemporal scales used by sperm whales and the consequent challenges of assessing population dynamics of long-lived, mobile pelagic species.

Key words: El Niño, emigration, sperm whale, *Physeter macrocephalus*, whaling.

Résumé : Si la taille et la structure des populations fluctuent naturellement au fil du temps, les changements rapides en l'espace d'une génération sont généralement causés par des modifications de la qualité des habitats ou une mortalité soudaine. Nous évaluons la réaction de grands cachalots (*Physeter macrocephalus* L. 1758 = *Physeter catodon* L., 1758) aux conditions dynamiques de l'habitat au large des îles Galápagos sur une période de 30 ans, en reliant cette réaction aux variations de disponibilité de proies et des activités de chasse à la baleine dans le Pacifique tropical. Dans les années 1980, des mâles et des femelles s'alimentant ou socialisant étaient couramment observés dans le nord-ouest de l'archipel. Les observations étaient moins fréquentes durant les années 1990, devenant très rares dans les années 2000, alors que des mâles seuls s'alimentant étaient occasionnellement observés et que les femelles avaient abandonné l'archipel. Dans les années 2010, les cachalots sont revenus dans les eaux méridionales, en grands groupes comptant apparemment plus de mâles reproducteurs et de veaux. Les augmentations et baisses d'abondance des grands cachalots des îles Galápagos sont vraisemblablement le fait de changements environnementaux combinés à l'effet de la chasse. La distribution irrégulière de leurs proies est influencée par la température de la mer et la productivité, qui contrôlent les déplacements des cachalots vers l'archipel et hors de celui-ci. La chasse pourrait avoir accentué ces déplacements en produisant un surplus attrayant de proies dans des eaux côtières appauvries en baleines. Ces constatations font ressortir l'ampleur des échelles spatiotemporelles des déplacements des grands cachalots et les défis que cela présente pour l'évaluation de la dynamique de populations d'espèces pélagiques mobiles longévives. [Traduit par la Rédaction]

Mots-clés : El Niño, émigration, grand cachalot, *Physeter macrocephalus*, chasse à la baleine.

Introduction

Populations change over time. Their size and structure fluctuate as input (natality and immigration) is countered by output of individuals (mortality and emigration) (e.g., Wilson and Bossert 1971). This dynamic is influenced by extrinsic and intrinsic factors, as well as their interactions (Lack 1966; Sutherland 1996). Extrinsic factors principally concern environmental processes. For instance, a local increase in resource availability can promote population growth (e.g., Blake and Loiselle 1991; Adler 1998), while a disease outbreak (e.g., Daszak et al. 2003; Frick et al. 2010) or increase in predator density can result in population decline (e.g., Székely and Bamberger 1992). Intrinsic biological traits of the species determine how the population reacts to such external factors. For example, life-history parameters (e.g., reproduction rates, age of sexual maturity, life span, dispersal ability) and population structure (e.g., sex ratio, proportion of individuals in age groups) (Łomnicki 1988; Boyce et al. 2006) affect how and at what rate populations fluctuate with changes in habitat quality.

When environment changes, long-lived organisms usually experience relatively less variability in adult survival rates, but relatively more variability in reproduction and survival rates of young individuals, than short-lived organisms (Gaillard and Yoccoz 2003; Rotella et al. 2012). In such cases, adult survival of long-lived organisms is maintained by enduring external stressors (e.g., Bodmer 1990; Villegas-Amtmann et al. 2017) or by moving to more

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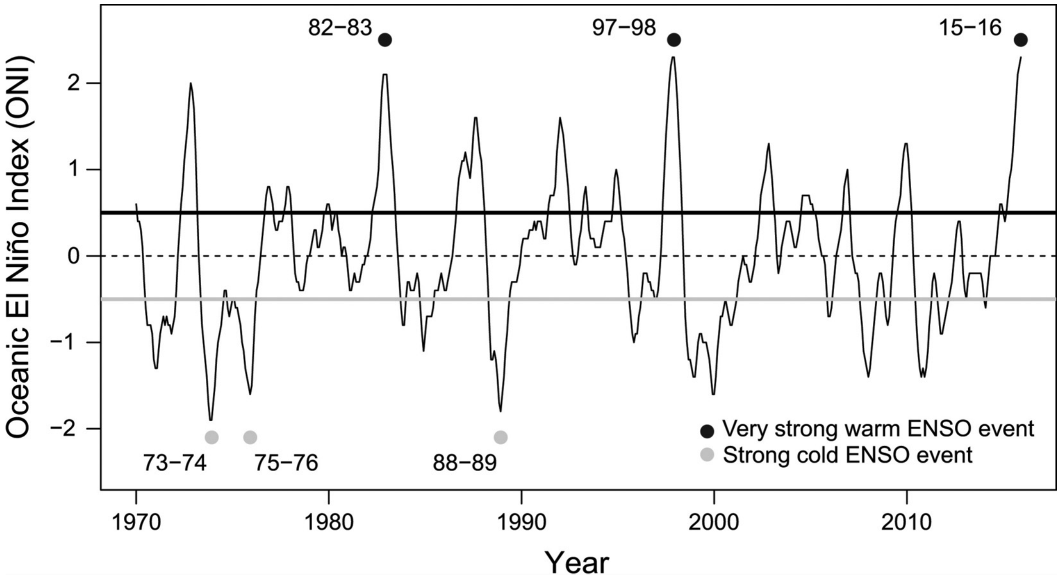
Fig. 1. Trimestral El Niño Southern Oscillation Index (ONI) between 1970 and 2015. Black and light grey straight lines indicate the +0.5 and −0.5 threshold for warm ENSO and cool ENSO events, respectively. Strong warm ENSO events (1982–1983, 1997–1998, and 2015–2016) are indicated by black circles and strong cool ENSO events (1973–1974, 1975–1976, and 1988–1989) are indicated by grey circles. Data from The Climate Prediction Center (NOAA 2016).



suitable habitats when local quality drops beyond a critical level (Fretwell and Lucas 1969; Moore 2005). By allocating resources to survival rather than reproductive rates, populations of long-lived organisms fluctuate less in response to natural environmental changes, but may take substantially longer to recover from drastic changes (Sinclair 1996; de Little et al. 2007).

A notable example of a long-lived species experiencing highly dynamic environments is the sperm whale (*Physeter macrocephalus* L., 1758 = *Physeter catodon* L., 1758). Deep-diving and widely distributed, they are key top predators of mesopelagic food webs (e.g., Paine 2006; Lavery et al. 2010; Roman et al. 2014). With few oceanographic barriers (Jaquet 1996), sperm whales move at various spatial scales (e.g., Whitehead et al. 2008) according to the distribution of their prey — the patchy, short-lived (1–2 years), and understudied deep-sea squids (Whitehead 1996; Nigmatullin et al. 2001; Mizroch and Rice 2013). The abundance and distribution of these squids is subjected to environmental shifts (e.g., Taipe et al. 2001; Markaida 2006), such as El Niño Southern Oscillations (ENSO) that radically affect primary productivity (e.g., Laurie and Brown 1990; Cai et al. 2014). In addition to environmental variability, until recently, sperm whale populations were exposed to an external pressure causing high mortality. Between 1712 and 1939, large numbers of sperm whales were killed for commerce, but in the 1950s, after the near extinction of most baleen whale stocks, they became the major target of the whaling efforts (Clapham and Baker 2002). Industrial and pirate whalers first concentrated on the large and sexually mature males, then aimed at females, decimating populations until the whaling moratorium in the 1980s (Whitehead 2002). The sperm whale sexes have widely different adult morphologies (males being about three times more massive), distributions (females using tropical and subtropical waters, with males largely at higher latitudes except when breeding), and behaviour (females being much more social); all of which have strongly affected our exploitation practices and attempts to understand the species (e.g., Best 1979; Whitehead 2003).

Long life cycles and wide geographical ranges challenge investigations into sperm whale population dynamics. Yet long-term studies can clarify how their distribution patterns and population structure interact with environmental variation and anthropogenic pressures. Our purpose was to evaluate how sperm whales responded to the dynamic environment of an important portion of their eastern tropical Pacific habitat over the last 30 years following the whaling moratorium. Here, we show how the occurrence of sperm whales fluctuated between 1985 and 2014 off the Galápagos Islands using measures that directly or indirectly indicate habitat use (sighting rates, feeding success, behavioural state, fine-scale distribution), population and social structure (sex ratio, cluster size, and group size), and reproductive success (proportion of breeding males and calves). Finally, we investigate variation in these parameters in light of changes in prey availability and the ripple effects of whaling in the tropical Pacific.

Materials and methods

Study area

The Galápagos Islands (00°40′S, 90°33′W; Supplementary Fig. S1[1]), Fn2 and more broadly the eastern tropical Pacific, are historically important concentration grounds for sperm whales (Shuster 1983; Whitehead et al. 1997; Smith et al. 2012). The archipelago is located in an upwelling zone that is productive but highly variable (e.g., Villegas-Amtmann et al. 2017). Specifically, it is strongly influenced by the multiannual ENSO cycles (Fig. 1). During its warm F1 phase, sea surface temperature rises and primary productivity decreases, affecting survival across all trophic levels (e.g., Barber and Chavez 1983; Strutton and Chavez 2000; Cai et al. 2014).

Offshore surveys and data sampling

Between 1985 and 2014, we surveyed the deep waters (>1000 m) off the Galápagos archipelago during 2- to 3-week trips (Supplementary Table S1).[1] This time at sea was very largely divided into three survey modes as follows. During survey mode A (searching), we searched haphazardly for sperm whales during day and night, covering quasi-linear transects at a mean speed of 5 kn, listening for the whales every 30 min through omnidirectional hydrophone

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[1] Supplementary tables and figures are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2016-0266.

arrays (frequency responses: 6 Hz–10 kHz, ±3 dB; 1–10 kHz, ±3 dB). At the same time, we also conducted visual surveys with one to two observers at the deck (2 m above sea surface) and, weather permitting, also at the crows' nest (9 m). During survey mode B (female tracks), when a group of female sperm whales (sometimes including calves, juveniles, or breeding males) was encountered, we tracked visually and acoustically at ranges of about 0.1 to 8 km, for as long as possible. Encounters with groups of females typically lasted 1–3 days at time (minimum = 2 h; maximum = 12 days). During survey mode C (male encounters), when a single male or a small group of males was encountered, they were typically studied for a few hours before resuming searching (mode A).

In all three survey modes, we recorded the whales' position from the vessel approximately every 3 h with SAT-NAV between 1985 and 1991, with GPS every 15 min between 1995 and 1997, and every 1–5 min in 2013 and 2014. During daylight, in modes B and C, we slowly approached individuals from behind to photograph their flukes (tails) when they dived. We used the photographs to identify individual whales through patterns of natural marks on the trailing edge of the flukes, using a semi-automated photo-identification protocol (Whitehead 1990). We rated each photograph from poor to very high quality ($Q = 1$ to 5) based on focus, exposure, orientation, percent cover, and tilt of the fluke (see Whitehead 2003) and used only $Q \geq 3$ photographs.

We used body size and general behaviour to define age–sex classes (Whitehead 1996, 2003; Christal and Whitehead 1997): distinctively small animals (4–5.5 m in length) in close proximity with other larger individuals were considered calves; distinctively larger animals (>12 m long) were considered mature males; other animals (mostly 7.5–10.5 m in length) were considered bachelor males when consistently found alone or in small groups (2–4 individuals), or as adult females and immatures of both sexes when in large groups.

Population descriptors

We measured 10 direct and indirect descriptors of habitat use, social structure, and reproduction of the Galápagos population, defined as follows:

(a) Sighting rates

We calculated annual sighting rates as the number of female tracks (mode B) per total hours of acoustic and visual search (mode A) (Whitehead et al. 1997; Cantor et al. 2016*a*).

(b) Feeding success

We used defecation rates to infer feeding success in the previous 24 h (Whitehead et al. 1989). Whenever the vessel was suitably placed after the photo-identification attempt, we checked each "fluke-print" (a visible pattern on the water surface left by an individual whale after diving) to record whether or not it defecated (indicated by the presence of a brown patch in the water). We calculated defecation rate as the number of defecations observed divided by number of fluke-prints examined (during modes B and C).

(c) Behavioural ratio

For each daylight hour spent following a group of females (mode B) with sufficient observations, we classified its general behavioural state as foraging or socializing. These two states were defined using the empirical data from 1985 to 1987 based on cluster size (see below) and rate of long, deep dives ("fluking-up rate") as $B = (0.278{\cdot}c) - (2.030{\cdot}f)$, where c is mean cluster size and f is the fluking-up rate per whale in 5 min. If $B > 0.5$, then the whales were considered to be socializing, and foraging otherwise (in Whitehead and Weilgart 1991). Thus, foraging is defined by whales in small (1–3) clusters and performing long and deep dives; socializing is defined by whales in larger clusters and mostly found at the surface. Since after this analysis the two states became very distinctive, in subsequent years we recorded the general behaviour state at sea in real time during daylight hours (see Whitehead 1999). Here, we calculated the annual behavioural ratio as the proportion of hours spent foraging divided by the number of hours spent foraging or socializing (mode B).

(d) Cluster size

A cluster of whales is a temporary subset of a group composed of the individuals at the surface swimming in the same direction and speed, side by side in a coordinated manner a few body lengths or less apart usually for a matter of minutes (Whitehead 1999, 2003). To calculate annual mean cluster size, we used records of the number of adult individuals in each cluster that we photographed during mode B surveys. To avoid the confounding effect of males (mode C), we removed from this analysis the clusters with males only.

(e) Group size

A group of whales was defined as a set of individuals that were photo-identified together, moving together in a coordinate manner for hours (Whitehead 1999, 2003). We estimated group sizes using high-quality individual photographic identification data ($Q > 3$) and the Lincoln–Petersen mark–recapture estimator, a closed-population abundance estimator that uses two capture occasions. Annual mean group size estimates were based on estimates for each day, calculated as $g = [(x_1 + 1)(x_2 + 1)/(x_{12} + 1)] - 1$, where x_1 are the whales identified in the first half of the photo-identifications on that day, x_2 in the second half, and x_{12} in both (Whitehead 1999). We calculated annual mean group sizes only for females (mode B), as males are found alone (sometimes in duos and trios) or in transit among female groups for short time periods (Whitehead 2003).

(f) Adult sex ratio

We inferred an annual adult sex ratio by calculating the number of individual adult males per female identified in high-quality photographs ($Q > 3$) while with groups of females (mode B) in each year.

(g) Calf proportion

We calculated calf sightings as the averaged proportion of calves per year observed in each cluster containing females approached for photo-identification (mode B). The clusters with only males were excluded from this analysis (mode C and males sighted during mode B).

(h) Breeding male proportion

We calculated proportion of breeding males as the number of clusters of females and immatures in which large males were observed in close proximity to them, divided by the total number of female and immature clusters approached for photo-identification (mode B). Since the abundance of breeding males off the Galápagos seems to vary seasonally (Whitehead 1993), we avoided potential biases by discarding data from months when males were scarcer.

(i) Female clusters

We calculated the total number of clusters of females photo-identified without breeding males (mode B).

(j) Fine-scale distribution

We created density maps to visualize annual and decadal spatial distribution of sperm whales. With geographic positions collected while searching and tracking groups of females (modes A and B), we calculate kernel density as a relative measure of the proportion of time spent in different areas around the archipelago. Kernel density creates a probability density function, which accounts for spatial auto-correlation, above each geographical point given a predetermined bandwidth; the resultant cell in a map is the sum of all the density functions that occur within that cell (e.g., Matthiopoulus 2003). To correct for the variation in sampling intervals across years (from 1 to 180 min), we subsampled positions every 3 h. We assigned 1 to positions that occurred while tracking groups of females and juveniles (mode B) and 0 when whales were being searched (mode A). We calculated the kernel density of presence points for each decade in ArcGIS version 10.2.2, using a 2 km × 2 km resolution and a bandwidth of 40 km. We chose this bandwidth based on the lower threshold of 24 h displacement of Eastern Pacific female and immature sperm whales (Whitehead 2003; Whitehead and Rendell 2004). We weighted density by effort so that weighted density (p_w) = p/d, where p is the raw kernel density of female and juvenile groups and d is the sampling effort. We measured sampling effort as the kernel density of all geographic positions (presences and absences) collected at a 2 km × 2 km cell and a 10 km bandwidth by year (or decade). The 10 km bandwidth reflected the range at which whales could be detected through hydrophones (7 km) plus the 3 km spread of groups of females and immatures (Whitehead 2003). We mapped the distribution of groups with only males (mode C) by using the first position of the encounter, instead of creating density maps because, in contrast with groups of females and juveniles (mode B), male groups were often abandoned soon after being found.

Trends in breeding male and calf presences

To infer potential changes after whaling in the sperm whale population using Galápagos, we tested whether two proxies of reproductive activity (presence of breeding males and calves) increased from 1985 to 2014. Using analysis of covariance (ANCOVA), we modeled the proportion of female clusters with large males and with calves, separately, as a function of years (linear predictor), calendar months (categorical predictor), and their interaction (Supplementary Table S2).[1] The proportion of breeding males was calculated as the total number of males divided by the total number of adults (females and males) per month during mode B surveys; similarly, the proportion of calves was calculated as the total number of calves divided by the total number females per month. We used months as units of analysis to avoid temporal correlation and ensure data independence.

Results

From 7842 high-quality photographs, we identified 1953 individual females and 138 individual males off the Galápagos Islands between 1985 and 2014 (Supplementary Table S1).[1] Sighting rates of sperm whales varied throughout this period. They were notably high in the 1980s, declined through the 1990s, dropped to zero in F2 the 2000s, and slightly rose again in the early 2010s (Fig. 2*a*). We found a larger proportion of males in the late 1990s and 2010s, and only males in the 2000s (Supplementary Fig. S2).[1] Feeding success was variable across the years (Fig. 2*b*). Particularly low defecation rates happened around El Niño years (e.g., 1987, 1997, 2014; Fig. 1), and particularly high rates in years when only males were found (e.g., 2002; Supplementary Fig. S2[1]). The proportion of time that females spent foraging compared with socializing decreased by about a third from the 1980s to the 1990s and, although data are few, it seemed to remain low after that (Fig. 2*c*).

Size of clusters of adults varied across years, with a decrease from the 1980s to the 1990s followed by a slight increase towards the 2010s (Fig. 2*d*). The mean group size of females and immatures peaked about 1990, and again in the 2010s (Fig. 2*e*). The sex ratio (number of identified males/females) was low in the 1980s (Fig. 2*f*), mirroring the large number of females found at the beginning of the study (Supplementary Fig. S2).[1] The sex ratio increased during the 1990s and early 2000s, as females left the area and more males arrived (Supplementary Fig. S2).[1] The males present in this period were mostly foraging because groups of females were nearly absent at the time (Fig. 2*i*). More recently, in the 2010s, the sex ratio decreased as large groups of females returned to the Islands (Fig. 2*e*).

The presence of large, mature males in close proximity to females was high in early 1980s and declined to zero in the early 2000s (as the females abandoned the area), and rose again in 2013 and 2014 (Figs. 2*h*, 2*i*). The trend in the proportion of calves in the clusters visually mirrored the proportion of breeding males' pattern (Fig. 2*g*). However, none of the six tested ANCOVA models suggested statistically significant increase in proportions of clusters with breeding males or calves per year or per month at the 5% level (Supplementary Table S2).[1]

The fine-scale distribution of whales around the archipelago also changed across decades (Figs. 3*a*–3*c*; Supplementary Figs. S3*a*–S3*h*[1]). F3 Groups of females and immatures were more often sighted off the northwestern portion of the archipelago in the 1980s (Fig. 3*a*), off the northern and northeastern portions in the 1990s (Fig. 3*b*), but switched to the southern and southwestern portions from the 2000s on (Fig. 3*c*). Solitary mature males, or small groups of 2–3 bachelor males (survey mode C), were sighted only in the 1990s and 2010s. In such years, while some male encounters occurred overlapping the distribution of female groups, foraging males were also found by themselves in other parts of the archipelago. This was particularly the case in 1997 when females were completely absent and males were found off north and northeast.

Discussion

The emerging picture from our three-decade offshore research is the waxing and waning of the sperm whale population in the waters off Galápagos Islands. Sperm whale occurrence was common in the 1980s, declined over the 1990s to a complete abandonment in the 2000s, and showed a modest increase in the 2010s. Furthermore, the two sexes showed somewhat different patterns. In what follows, we consider how the fluctuation of population descriptors combined may reflect the nomadic behaviour of sperm whales in response to environmental dynamics and whaling operations in the eastern tropical Pacific.

Decadal patterns

Sperm whales were relatively common off the Galápagos in the 1980s, following the end of commercial whaling in the eastern tropical Pacific in 1981 (Ramirez 1989). During this time, both males and females used Galápagos waters to forage and socialize, often forming large groups with a relatively high proportion of calves. They were mostly seen in the western and northwestern portion of the archipelago, where cold, upwelling waters are usually found (Palacios 2002; Schaeffer et al. 2008). This suggests that food availability may have attracted and sustained whales in the waters off Galápagos. In the 1990s, their numbers started to decrease, especially the groups of females with immatures and calves. Solitary, foraging males became more common, mostly in the northern portion of the archipelago, even without females (suggesting some degree of reproductive philopatry; see Mesnick et al. 2011). With fewer groups of females, single males experienced higher feeding success. This might be due to a reduction in resource competition or to a shift in the behavioural state of males from socializing to foraging, both consequences of the absence of groups of females in the area.

But by the late 1990s and early 2000s, sperm whales were practically gone. Sightings became rare: females were no longer seen, and males tended to disperse (see Alexander et al. 2016), except for occasional solitary large males or small groups of bachelors. In consequence, group and cluster sizes decreased along with calf sightings and socializing females. The nearly complete absence of females in our surveys, supported by a nearly complete absence of opportunistic whale sightings in the area (G. Merlen, personal observation), motivated us to survey other areas, such as Chile and the Sea of Cortez (see Whitehead et al. 2008; Cantor et al. 2016*b*). After this gap in our sampling effort off Galápagos in the late 2000s, whales started to return. In the 2010s, they were more concentrated in the southern and southwestern part of the archi-

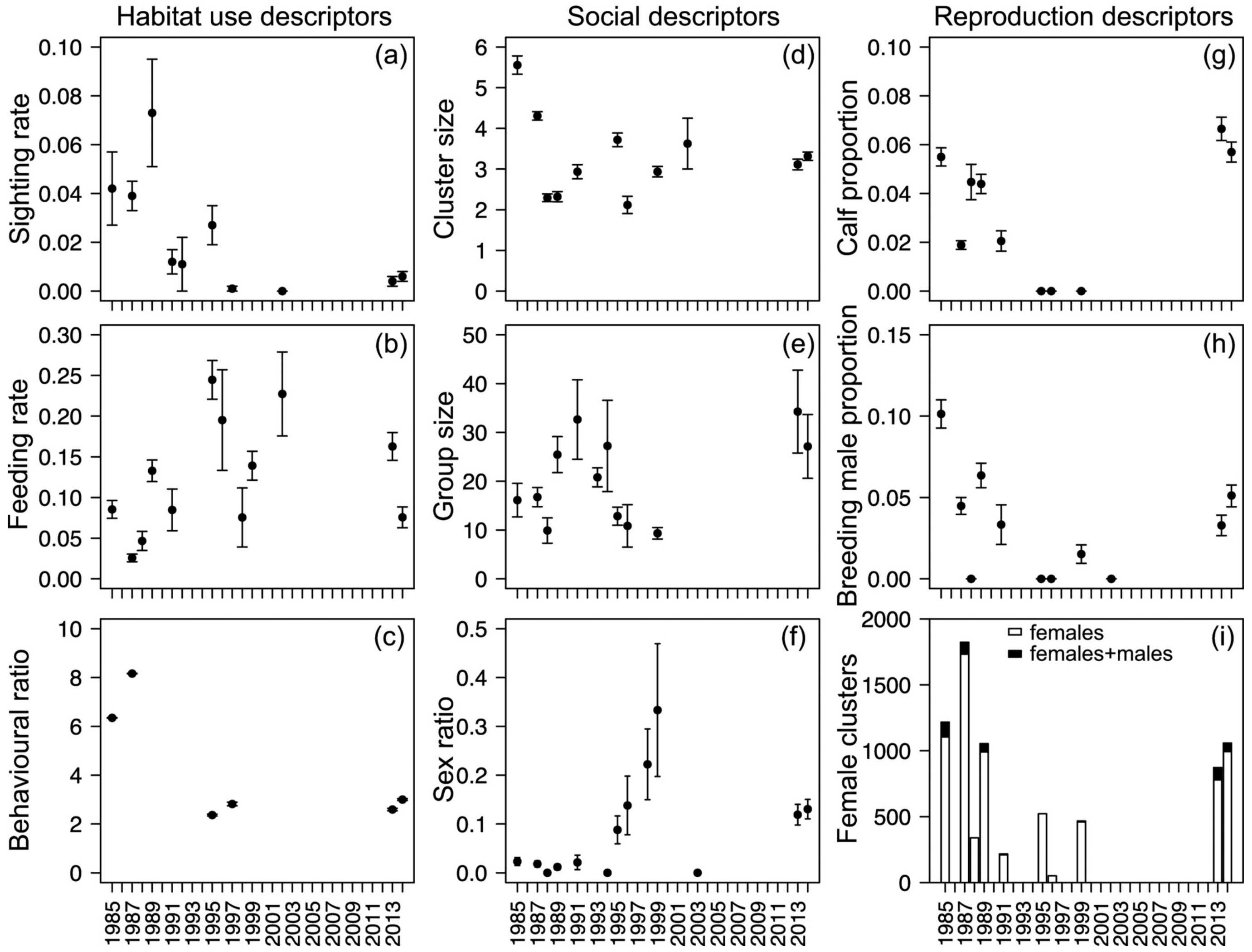


Fig. 2. Temporal distribution of nine descriptors of population dynamics of sperm whales (*Physeter macrocephalus*) off the Galápagos Islands for the years between 1985 and 2014, where data were available. Whiskers represent standard errors (SE). Letters within each plot match their definitions in the Materials and methods section: (*a*) sighting rates as number of encounters by total hours of searching; (*b*) feeding rate as proportion of defecation records; (*c*) behavioural ratio as number of hours females spent foraging by hours socializing; (*d*) cluster size as number of females and immatures in close proximity at the surface; (*e*) group size as number of females and immatures seen together over days; (*f*) sex ratio as number of photo-identified males per females; (*g*) calf proportion as number of clusters of females with calves; (*h*) breeding male proportion as number of clusters of females with mature males; (*i*) female clusters as number of clusters containing (black bars) or not (white bars) mature males.

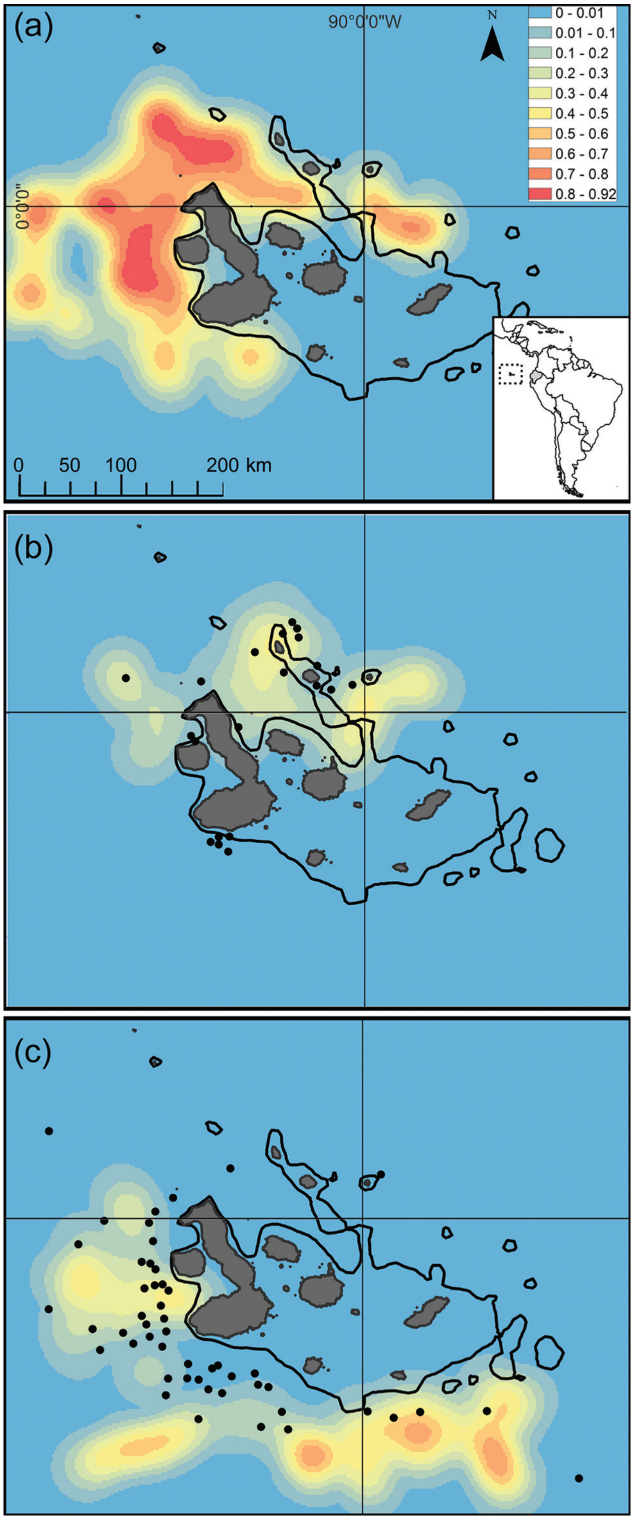
pelago, in larger groups of females with an apparent increased proportion of calves and mature males. Given few differences in prey size and diet composition (Ruiz-Cooley et al. 2004), largely discrete foraging distributions of males and females suggest strategies for reducing intraspecific competition (Christal et al. 1998). While at very larger scales sperm whales' movements are characterized by male-biased dispersal and female geographic and social group philopatry (see Alexander et al. 2016), prey availability is a major driver of their displacement over relatively smaller scales (Whitehead et al. 2008; Mizroch and Rice 2013). This aligns with the changes in overall patterns of occurrence that we observed off the Galápagos along the last three decades.

Fluctuation of prey availability

Sperm whale diet is mostly composed of deep-sea squids, such as histioteuthids and the Humboldt squid (*Dosidicus gigas* (D'Orbigny, 1835 in 1834–1847)) (Clarke 1977). Given the sperm whales' large food requirements (400–1000 kg/day; Clarke et al. 1993) and the patchiness, short life cycles and unpredictability of their prey, they move constantly at small and large scales (Whitehead and Rendell 2004; Whitehead et al. 2008), from areas of low to high feeding success (Whitehead 1996). The substantial fluctuations in fine-scale distribution, sighting rates, and feeding rates off Galápagos suggest major temporal and spatial variation in prey availability.

Sperm whales are often associated with thermal discontinuities and steep slopes (Jaquet 1996). These are usually up- or down-welling areas (Gulland 1974) where productivity, and hence cephalopod abundance, is enhanced (see Jaquet 1996). The Galápagos and western South American shelf break present such bathymetric (Supplementary Fig. S1)[1] and oceanographic features, and the Humboldt and other squid species are distributed throughout these waters (see Taipe et al. 2001; Ibáñez et al. 2009; Baque-Menoscal et al. 2012). However, the distribution and abundance of Humboldt squid throughout the Eastern Pacific fluctuate greatly in response to oceanic changes induced by ENSO. Warm ENSO events have strong negative impact (Taipe et al. 2001; Markaida 2006*a*; Waluda and Rodhouse 2006), whereas cool ENSO events intensify upwelling and phytoplankton productivity that impact Humboldt squid

Fig. 3. Decadal fine-scale distribution of groups of sperm whales (*Physeter macrocephalus*) off the Galápagos Islands. Color code (refer to color version online) indicates kernel densities for groups of females and immatures; black circles indicate first position of group sightings of small groups with only males (note that no such groups were found in the 1980s); dark grey shapes within the black contours represent the islands and black contours around them indicate 1000 m isobaths. The following years with enough spatial data were grouped by decades as (*a*) 1985, 1987, 1989; (*b*) 1991, 1995, 1997; and (*c*) 2013, 2014.



distribution and abundance positively, although not immediately (Markaida 2006*b*).

In years of mild warm ENSO events (e.g., 1987, 2014), the annual feeding rate of female sperm whales dropped significantly (see also Whitehead et al. 1989; Smith and Whitehead 1993) and their fine-scale distribution shifted away from the core productive region west of the Galápagos archipelago. During strong warm ENSO events, consequences were more drastic. For instance, in the 1997–1898 event, the Humboldt squid fisheries off Peru and the Gulf of California collapsed (Markaida 2006*b*; Taipe et al. 2001), and a similar sharp decrease in deep-sea squids may have happened around the Islands as suggested by the dramatic decreases in phytoplankton production and in the presence of seabirds and marine mammals (Wolff et al. 2012). During the cool ENSO event of 1988–1989, the sperm whale feeding rates were higher than in previous years, and they were sighted more often at the productive core of the Islands. This suggests high availability of prey associated to intensified upwelling during that period. However, during the 1999–2001 mild cool ENSO, sperm whales were absent from the archipelago and were rare in the area after over a decade. This is remarkable because they were present and abundant in 1985, only 2 years after the strongest warm ENSO event of the century (Trillmich and Limberger 1985).

The whales' immediate responses to decreased food availability include changes in aggregation behaviour, diet composition, and short-scale movements (e.g., Flinn et al. 2002). But when food availability drops below a critical threshold, the benefits of undertaking large-scale movements towards a new habitat may outweigh the cost of staying in a lower quality habitat (Whitehead 2000). In 1982, for instance, sperm whales off Peru moved south to the more productive waters off Chile (Ramirez and Urquizo 1985). Such large-scale movements in response to low food availability may explain the complete absence of female and juvenile sperm whales in years following the 1997–1998 warm ENSO event because the Galápagos waters likely became not productive enough, unsuitable for such larger groups.

Therefore, we suggest that emigration and immigration, as opposed to changes in mortality and survival rates, are the most likely drivers of the fluctuation in sperm whale occurrence around the Galápagos Islands (see also Whitehead et al. 1997; Cantor et al. 2016*b*). There is no evidence for abnormally high mortality rates in the 1990s, after the cessation of the whaling industry (see Whitehead et al. 1997). Additionally, their long life cycles (e.g., Whitehead 2003) make 30 years too short of a period for a rapid population increase by abnormally high birth rates to be the cause of increased whale presence in the 2010s. Although it remains uncertain where the whales come from and go to, there have been a number of re-sightings of individuals moving 1000–2000 km from Galápagos to the coastal waters of Ecuador and Peru, as well as a few moving 4000 km to and from the Gulf of California and northern Chile (Dufault and Whitehead 1995; Whitehead et al. 2008; Cantor et al. 2016*b*). While such large-scale displacements seem normal sperm whale responses to fluctuation in prey availability, they were likely exacerbated in the period after whaling by artificially large disjunctions between resource availability and whale densities.

Ripple effects of whaling

Whaling operations have been targeting sperm whale population in the eastern tropical Pacific since the late 1790s. In the 19th century, whaling activities around the Galápagos Islands, particularly by U.S. whalers, targeted both male and female sperm whales (Hope and Whitehead 1991). Whaling from open boats with hand-held harpoons declined in the latter 19th Century, and sperm whales world-wide received something of a reprieve until modern commercial whaling with harpoon guns fired from diesel-powered catcher vessels began targeting sperm whales intensively in the 1950s (e.g., Whitehead 2002). In modern whaling, the preferred targets were large, mature males. This was particularly the case for the shore stations catching sperm whales off Peru and Chile (Ramirez 1989), as well as likely also true for pirate whalers working farther from shore. The coastal areas off western South America where once whales abounded were heavily depleted, especially of mature males (Ramirez 1989). In consequence, these productive areas became available for the fewer remaining whales.

Sperm whale distribution is, at least partially, determined by density-dependent habitat selection (Whitehead 2000). Therefore, opening such a niche in coastal waters may have further motivated the abandonment of the Galápagos waters just a little west of the prime whaling grounds (Whitehead et al. 1997). This potential eastward emigration to the more productive coastal waters agrees with the observed absence of female and juveniles off Galápagos in the late 1990s and 2000s. After the whaling moratorium, the population was expected to increase even if very slowly. If this were the case, then coastal waters would saturate over time, stimulating the repopulation of peripheral areas, perhaps being reflected in the return of sperm whales to Galápagos waters in the early 2010s. Our recent data suggest a very slight, although not significant, increase in the presence of large males and calves off Galápagos. An increased proportion of calves would be a consequence of the increased number of breeding males if their low numbers in the 1980s, following intense male-based whaling in the region (Ramirez 1989), reduced pregnancy rates (Whitehead et al. 1997).

Although it is possible that sperm whale populations are slowly recovering, even rigorous evaluation of recent and historical data on population dynamics leaves the question open for debate (e.g., Whitehead 2002; Baker and Clapham 2004). We emphasize that our three-decade study is a relatively short period in the sperm whale life span. Sperm whales are long-lived (>70 years old; Whitehead 2003) and slow-reproducing animals. They have late sexual maturity (females at about 9 years, males at about 20 years) and long reproductive cycle (14- to 16-month gestation period, e.g., Best et al. 1984), and very low calving rates (0.2 calf per mature female per year; Best et al. 1984). Therefore, detecting population recovery following the end of industrial whaling, if any, requires substantial amount of empirical data spanning multiple generations, which is particularly challenging to collect given the spatiotemporal scales used by sperm whales.

Conclusions

Our findings suggest the interaction between environmental processes affecting prey availability and anthropogenic pressure have driven substantial changes in occurrence of sperm whales off the Galápagos Islands. The local population fluctuation over the last 30 years reflects the large-scale movement of sperm whales from and to the Galápagos, as well as within the Galápagos region, likely in response to changes in prey availability. Additionally, these movements may include lagged responses to the end of the whaling industry at the onset of our research in the early 1980s. Our findings emphasize the magnitude of the spatiotemporal scales that are relevant for such a mobile, pelagic species. Affording a clearer picture of the population dynamics after the whaling era requires continuing research effort over wide areas and long periods of time.

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