ICES Journal of
Marine Science

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2020), 77(1), 109–118. doi:10.1093/icesjms/fsz251

Original Article

Humpback whales extend their stay in a breeding ground in the Tropical Eastern Pacific

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Avila, I. C., Dormann, C. F., García, C., Payán, L. F., and Zorrilla, M. X. Humpback whales extend their stay in a breeding ground in the Tropical Eastern Pacific. – ICES Journal of Marine Science, 77: 109–118.

Received 10 August 2019; revised 22 November 2019; accepted 29 November 2019; advance access publication 28 December 2019.

During the austral winter, G-stock humpback whales, *Megaptera novaeangliae*, migrate to the Tropical Eastern Pacific to breed. To analyse if the whale migration times have changed over time, we analysed 31 years (1988–2018) of arrival and departure times to Gorgona National Park, Colombia, an important breeding site. During this period, whales have significantly changed their arrival time, coming now earlier, but their departure time has not changed significantly. Hence, humpback whales now stay 1 month longer than 31 years ago. Humpbacks arrived in Gorgona at the earliest during the beginning of May and stayed at the most until late December. The change observed in the arrival time to breeding grounds could be related to ice sheet mass changes in autumn in Antarctica and increase in population size over the past decades but we were unable to determine which factor is more important in explaining the observed trend. Management decisions in Colombia need to account for a longer stay, specifically restricting anthropogenic activities from 1May to 31December. We urge other researchers to review their data, in case this shift is evident in other regions and management plans need to be updated.

Keywords: breeding site, Cetacea, Colombian Pacific, conservation, environmental changes, Gorgona National Park, G-stock, *Megaptera novaeangliae*, migration time

Introduction

Humpback whales, *Megaptera novaeangliae*, perform seasonal migrations between high-latitude summer feeding grounds and low-latitude winter breeding grounds (Dawbin, 1966). Humpbacks visit the Colombian Pacific, South America, in order to breed and rear their calves. Gorgona Natural Park (2°58′ N, 78°10′ W) is a key aggregation area (Avila *et al.*, 2013). The whales of Colombia comprise part of the eastern South Pacific breeding population, the G-stock, which is found during the austral winter from northern Peru to Ecuador, Colombia, Panama, and Costa Rica (Acevedo and Smultea, 1995; Best, 2008; Rasmussen *et al.*, 2007; Pacheco *et al.*, 2009). They migrate to three discrete summer feeding areas (Acevedo *et al.*, 2013) in the austral summer, including the waters off the western Antarctic Peninsula (63° S, 60° W; Mackintosh, 1965; Stone *et al.*, 1990; Caballero *et al.*, 2001), the Fueguian Archipelago in the Magellan Strait (54° S, 72° W; Gibbons *et al.*, 2003; Acevedo *et al.*, 2006, 2007) and Corcovado Gulf in the northern Patagonia (Hucke-Gaete *et al.*, 2013) in Chile. The main feeding area corresponds to the western Antarctic Peninsula, where they prey mostly on Antarctic krill (*Euphausia superba*; Friedlaender *et al.*, 2006; Nowacek *et al.*, 2011).

Migratory species that perform exceptionally long journeys, crossing multiple ecosystems with diverse environmental conditions (e.g. different temperatures, food availabilities), face several challenges. Environmental and oceanographic conditions have changed over the past decades (e.g. Turner *et al.*, 2005), and this affects how migratory species respond to environmental conditions. Some of the most significant changes include increasing ocean temperatures, changes in sea ice cover, rising sea levels and ocean acidification (e.g. Kawaguchi *et al.*, 2013). The Antarctic Peninsula, for example, has experienced an increase in both air and ocean temperatures, which have changed the extent and seasonality of sea ice over the last decades (Shepherd *et al.*, 2012; Constable *et al.*, 2014). Several studies have reported the importance of the ice sheet mass in the life cycle of Antarctic krill (e.g. Melbourne-Thomas *et al.*, 2016). Sea ice formation in autumn is crucial for juvenile krill, since the sooner ice mass is formed, the more algae biomass is incorporated into the ecosystem. These algae, in turn, represent the main food source for krill in winter (Fritsen *et al.*, 2008; Meyer, 2012). So, a mismatch between the accumulation of algae in autumn and the onset of sea ice formation will affect the development of krill during winter and, consequently, the stock of krill in the Antarctic Peninsula region (Meyer, 2012).

Marine mammals are likely to be impacted by oceanographic alterations related to climate change and to El Niño-Southern Oscillation (ENSO), either directly or indirectly through effects on prey availability or habitat availability (Ramírez and Urquizo, 1985; Tynan and DeMaster, 1997; Urbán *et al.*, 2003; Simmonds and Isaac, 2007; Salvadeo *et al.*, 2011).

Some previous studies described factors that might influence timing of migration of humpbacks (e.g. Dawbin, 1966; Ramírez and Urquizo, 1985; Ramp *et al.*, 2015). Ramp *et al.* (2015) determined that over a 26-year period (1984–2010) humpback and fin whales (*Balaenoptera physalus*) tended to arrive earlier to a summer feeding area in the North Atlantic. This change was likely related to warmer sea surface temperatures (SSTs) and earlier ice break-up, which in turn might bring about an earlier onset of heightened primary production and the occurrence of key prey (Ramp *et al.*, 2015). SSTs have been related to changes in whale presence and distribution in the Tropical Eastern Pacific Ocean. During El Niño events, number of blue whales (*Balaenoptera musculus*), fin whales (*B. physalus*), Bryde's whales (*Balaenoptera brydei*) and humpbacks from the north coast of Peru have decreased (Ramírez and Urquizo, 1985). Grey whales (*Eschrichtius robustus*) at Laguna San Ignacio, Mexico, showed a reduction in calf numbers and changes in occupation of the area (Urbán *et al.*, 2003). In a study conducted between 1988 and 2006 at La Paz Bay, Mexico, numbers of Bryde's whales increased during La Niña conditions but decreased during El Niño conditions, probably mediated by prey availability (Salvadeo *et al.*, 2011).

The G-stock population is estimated to have been depleted from a pre-whaling level of about 11 000 animals in the 1900s to a few hundred animals by the early 1960s (Johnston *et al.*, 2011). Since the end of humpback whaling in 1966, the population is estimated to have increased to about 6504 animals in 2006 (Félix *et al.*, 2011; Johnston *et al.*, 2011). Although humpback whales are classified as least concern by the International Union for Conservation of Nature and Natural Resources (Cooke, 2018), this species is currently the marine mammal with greatest risk exposure based on the distribution of worldwide threats (i.e. incidental catch, pollution, and traffic- and tourism-related threats; Avila *et al.*, 2018). Particularly in Colombian waters, the species is affected by entanglements in fisheries nets, ship collisions, unregulated tourism growth, the potential construction of mega-projects and acoustic prospecting, and exploration of oil and gas resources (Capella *et al.*, 2001; Avila *et al.*, 2013, 2015, 2017).

Understanding the temporal variation in the occurrence of humpback whales in the breeding ground of the Colombian Pacific improves the ecological understanding of the species, thus, supporting its strategic management. To support specific recommendations, the aim of this research was to review and update the arrival and departure times of humpbacks to Colombian waters using historical records data and to evaluate if the presence of humpback whales in Colombia has changed.

Material and methods

Data collection

Gorgona National Park (Figure 1) includes Gorgona Island (13.3 km^2) and a marine portion of 603.5 km^2, under a management regime that corresponds to an IUCN category II (García, 2010). It is located in the Southeast Pacific on the continental shelf of Colombia (2°47′–3°06N and 78°06′–78°18′W). Gorgona National Park is a breeding area where humpback whales carry out fundamental breeding activities, such as mating, calve rearing, socialization, and courtship (Flórez-González, 1991). As a protected area, the marine zone of the National Park is monitored regularly since 1985, including control patrols at least once a week.

Since 1988, the arrival date of the first humpback whales and the departure date of the last ones have been registered in the Park's official field logbook. All reported dates corresponded to direct sightings by rangers and researchers, who were trained in fauna and whale observations and have consistently written down these observations. These observations have been done daily from shore in El Poblado (Figure 1) and confirmed once a week from a boat, when conducting mandatory weekly patrols around the island, between 200 m and 2 km away from the shore. The arrival date of humpback whales was defined as the day when the first whale was sighted in the area followed by more sightings within the next 7 d. Departure date is the day when the last whale was sighted in the area, followed by no further sightings within the next 7 d. The observations also included the type of group sighted. Based on Baker *et al.* (1987) and Craig *et al.* (2003), group type was defined in this study according to the presence of adults (12–18 m length) and calves (4.0–7.0 m length); juveniles, which are smaller than adults, but too large to be calves, were not identified, because they were difficult to distinguish from adults. An adult that accompanies a calf was assumed to be its mother, and any additional adults travelling with the mother-calf pairs were deemed "escorts" (Herman and Antinoja, 1977).

Statistical analysis

We first analysed temporal trends in the arrival date, length of stay (defined as the time between the arrival and departure of whales each year), and departure date over the 31-year period from 1988 to 2018 using generalized additive models (GAM) with year as predictor, allowing for non-linear trends. Residuals were investigated for temporal autocorrelation, which was detected only for the length of stay. In this case, we added an AR1 model (i.e. with a 1-year lagged autoregressive term) to the GAM, which successfully removed the temporal autocorrelation in the residuals. Interestingly, the temporal autocorrelation was negative, indicating that a year of long stay was followed by a short stay ($\rho = -0.0787$). In addition, we employed the non-parametric Cox-and-Stuart-trend test, which tests for monotonic trends in

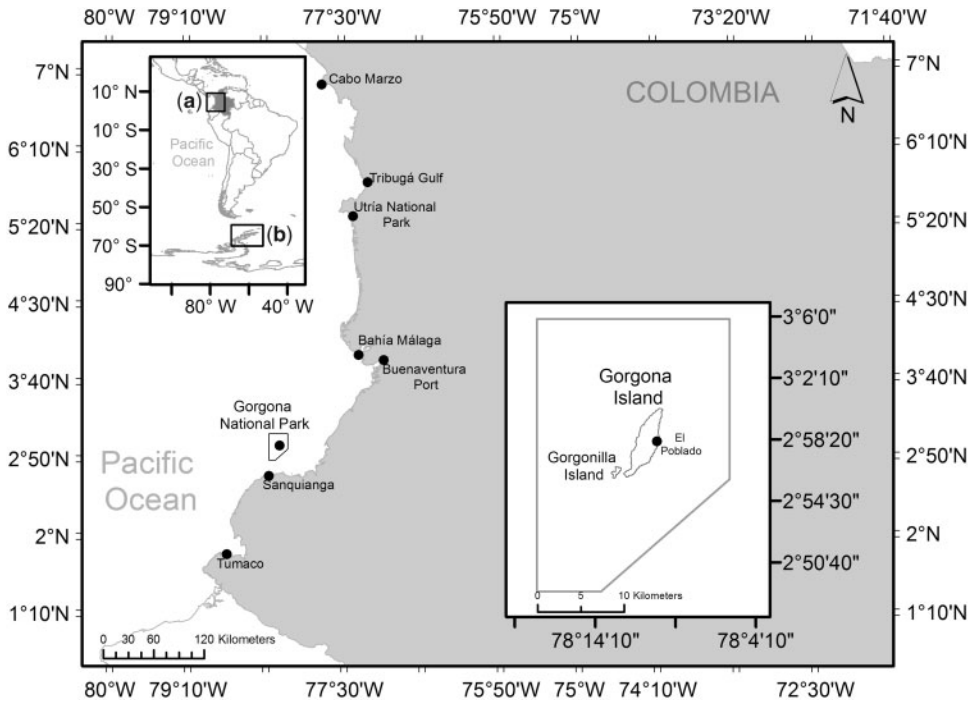

Figure 1. Geographical location of Gorgona National Park and areas were humpback whales have been recorded. In the inset to the right, Gorgona National Park ilustrating Gorgona and Gorgonilla Islands and the extension of the marine protected area. In the inset to the left, (a) breeding area in the Colombian Pacific and (b) feeding area in Antarctic Peninsula.

temporal data. We also analysed if there were differences between type of groups between arrival and departure sightings using a *t*-test to compare if the number of calves changed between arrival and departure groups.

Next, we explored the hypothesis that SSTs in the humpback whale's breeding grounds serve as cue for their migration to tropical waters, using a Pearson's correlation test. To analyse environmental conditions, we extracted data for the known main feeding area around the Antarctic Peninsula (indicated in Figure 1 box B). As SST source we used the National Center for Atmospheric Research's sea surface temperature and sea ice concentration (SSTICE) data (NCAR 2016; downloaded via ftp from ftp.cgd.ucar.edu/archive/SSTICE). The methodology behind these SST models is described in Hurrell *et al.* (2008). The NCDF files were queried for the monthly mean SST of the Antarctic summer location (at $1^\circ \times 1^\circ$ resolution) and for the months from February to June.

We explored if ENSO events drove the trends of arrival to Gorgona. For this purpose, we obtained estimates of NOAA's Oceanic Niño Index (ONI) as 3-month running means (http://ggweather.com/enso/oni.htm), which quantifies the strength of ENSO anomalies in the Pacific Equator. We used the data of the trimester that included June, July, or August, as this corresponded to the period when G-stock whales arrived to tropical waters.

Elevated chlorophyll *a* concentrations in spring and summer in the Antarctic Peninsula can be related to high densities of larval krill in autumn (Marrari *et al.*, 2008). We tried to use this information as a proxy for prey availability to relate this factor to time of arrival in Gorgona. However, the highest resolution data of chlorophyll *a* were only available since 2002 (NASA Goddard Space Flight Center, Ocean Biology Processing Group, 2014), so we were unable to make a robust analysis with this dataset.

As ice sheet mass change (IMC) is related to prey availability, we explored the relation between this factor and arrival of humpbacks to Colombian waters. Data of IMC in the Antarctic Peninsula were available for each year since 1992 (Shepherd *et al.*, 2012; https://imbie.org). We used the cumulative IMC for autumn (April and May) as an indirect factor to explore if reduced prey availability the following summer (December to March) was a cue for the northward migration of whales in winter. We analysed the correlation between autumn ice sheet formation and arrival times in Gorgona the following year. For this purpose, we used Pearson's correlation after confirming the data met the assumptions necessary (normal distribution and homoscedasticity).

Finally, we explored if population size could be affecting trends of arrival time to Gorgona waters. An increasing population of humpback whales could increase the probability of some whales arriving earlier and departing later. Larger number of whales could also make sightings in general more noticeable than for a small population. Reliable data for Colombia were not available, and data for the main feeding area (Antarctic Peninsula) of the G-stock population were insufficient (e.g. Branch, 2011). For this reason, we used data on an abundance projection obtained from the estimated trend of the G-stock population of Johnston *et al.*, (2011) using the reference case assessment. This estimation was based on a Bayesian approach using not only the estimated population size of 6504 individuals for Ecuador in 2006 (Félix *et al.*, 2011), but also Branch's (2011) IDCR/SOWER feeding ground relative abundance series.

Table 1. Arrival and departure dates of humpback whales to Gorgona Natural Park, Colombian Pacific from 1988 to 2018.

	Arrival		Departure		
Year	Arrival date	First group sighted	Departure date	Last group sighted	Length of stay (days)
1988	20 June	Mother and calf	12 November	Mother and calf	146
1989	30 June	3 adults	ND	ND	ND
1990	22 June	2 adults	16 December	Mother and calf	178
1991	03 June	1 adult	ND	ND	ND
1992	27 June	2 adults	13 November	1 adult	140
1993	17 May	1 adult (*)	20 November	1 adult	188
1994	27 June	2 adults	13 December	1 adult (*)	170
1995	ND	ND	ND	ND	ND
1996	17 June	1 adult (*)	3 December	Mother, calf, and 1 escort	170
1997	15 June	4 adults	ND	ND	ND
1998	19 June	1 adult	17 December	Mother and calf	182
1999	22 May	3 adults	4 December	1 adult	197
2000	ND	ND	ND	ND	ND
2001	13 June	1adult	20 December	1 adult (*)	202
2002	5 June	3 adults	30 November	Mother and calf	179
2003	17 May	1 adult (*)	4 December	1 adult (*)	202
2004	3 June	1 adult (*)	ND	ND	ND
2005	27 May	1 adult (*)	ND	ND	ND
2006	ND	ND	ND	ND	ND
2007	11 May	2 adults	14 November	Mother, calf, and 3 escorts	188
2008	11 May	1 adult (*)	25 November	2 adults	199
2009	6 May	1 adult	20 November	1 adult (*)	199
2010	1 June	2 adults	14 December	1 adult (*)	197
2011	21 May	Mother, calf and 1 escort	20 November	Mother, calf, and 3 escorts	184
2012	3 May	1 adult (*)	6 December	Mother and calf	218
2013	29 May	Mother and calf	25 November	Mother, calf, and 1 escort	181
2014	25 May	1 adult	20 November	1 adult (*)	180
2015	18 May	1 adult	18 November	Mother and calf	185
2016	27 May	1 adult	30 November	2 adults	188
2017	27 May	Mother and calf	5 December	Mother and calf	192
2018	20 May	3 adults	4 December	Mother and calf	204

For all of the sightings at least one adult was registered. The length of stay shows the amount of days that the humpback whales, as a population, stayed in the area. ND, no data; but whales were present in every year on record. Asterisk (*) indicates the presence at least one adult but type of group was not confirmed.

All analyses were carried out in R (version 3.6.0; R Core Team, 2019), with packages mgcv (Wood, 2017), ncdf4 (Pierce, 2017), nlme (Pinheiro *et al.*, 2017), and trend (Pohlert, 2017).

Results

From 1988 to 2018 humpback whales visited Gorgona between May and December. During these 31 years, the earliest day of arrival was 3 May in 2012 and the latest day of departure was 20 December in 2001. Humpback whales were observed in the area for 146 to 218 d (5–7 months), with a mean of 185 d (*i.e.* 6 months per year, *SD* = 17 d; Table 1). Of the identified group types across all years, when comparing presence of calves in arrival versus departure groups, only 15% of the first groups to be sighted (arrival) included calves, while as many as 52% of the last groups sighted at departure included calves ($t = -2.93$, $df = 39$, $p = 0.005$). However, results of group types should be taken cautiously because of the 31 groups that we should register in each period we have the certainty of 71% groups at arrival and only 55% groups at departure (Table 1).

Trend in arrival dates, length of stay, and departure dates at Gorgona National Park

The data display a clear 31-year trend towards earlier arrivals in the first 20 years, despite large inter-annual variability (Figure 2, top). Over the 20 years from 1988 until 2007, the arrival of humpbacks advanced by 31 d (one month), i.e. on average 1.5 d per year, based on GAM estimates. Since then, arrival time has stabilized at around 22 May (142nd day of year), albeit with substantial inter-annual fluctuations. Both GAM and Cox-and-Stuart-trend-test yielded significant effects of time ($p < 0.01$ and $p = 0.012$, respectively).

Length of stay has analogously increased over this period, from 160 to 185 d (GAM estimates—Figure 2, middle), starting to level off slightly earlier than arrival times, around 2005. Data of departure were more patchier, since departure dates for some years were not available. Again, the GAM detected a significant effect of time ($p < 0.001$), while the non-parametric trend test was not significant ($p = 0.054$). This inconsistency is explained by the fact that non-monotonic trends, in our case the levelling-off of length-of-stay in the last decade, cannot be accommodated by Cox-and-Stuart's monotonic trend test.

Departure dates varied substantially from 1 year to the next, and no trend in departure date could be detected (Figure 2, bottom; GAM: $p = 0.31$, trend test: $p = 0.809$). Thus, the main observation is the clear trend of humpback whales to arrive earlier, while leaving approximately at the same time, leading to a net longer stay around Gorgona.

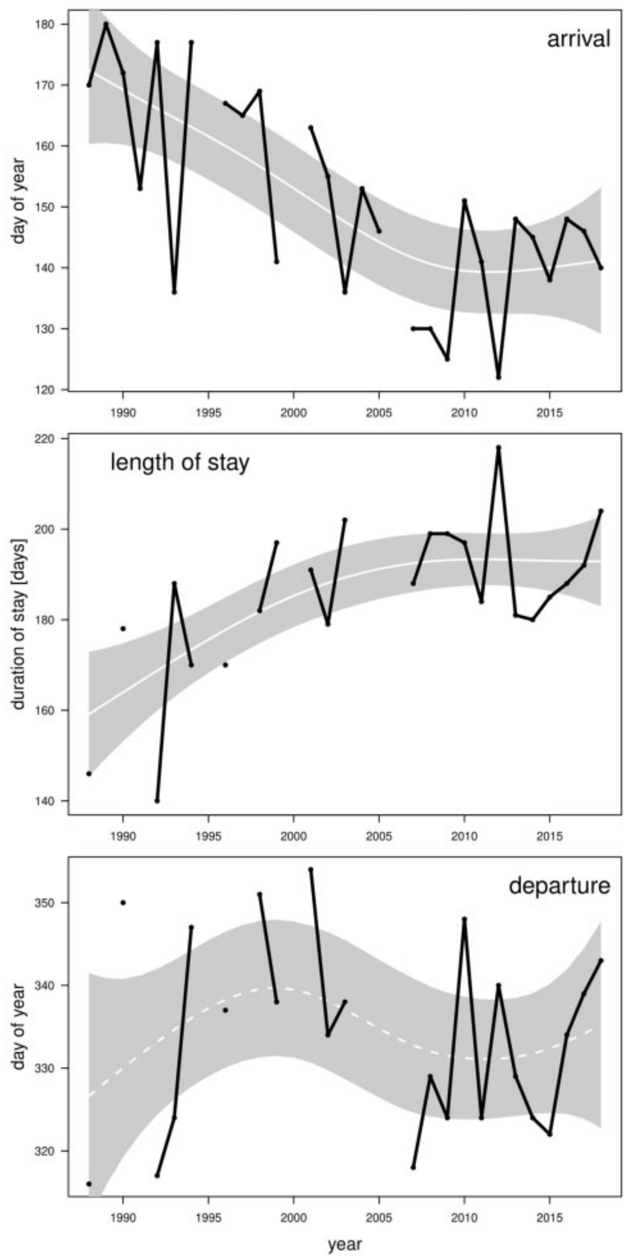

Figure 2. Arrival date, length of stay, and departure date for Gorgona National Park from 1988 to 2018. Shaded areas are 95% confidence intervals of GAM fits (white lines). Departure trends were not significant (dashed white line).

SST, ENSO, IMC at breeding grounds and population size versus arrival dates

We correlated SSTs off the Antarctic Peninsula from February to June each year with arrival times in Gorgona. Travel time from Antarctic Peninsula to Eastern Pacific breeding grounds is approximately 2 months (Félix and Guzmán, 2014), making SST around March the most likely candidate for a temperature cue. However, we found no substantial correlation between SST and arrival time for any month investigated, for either of the two breeding grounds. The strongest correlation ($r = -0.23$) was with SST in March (Figure 3a), but it was not significant ($p = 0.227$). Thus, we failed to confirm our expectation that breeding-ground SST serves as cue for onset of migration towards tropical waters.

We found no correlation between ONI and arrival time. The strongest correlation ($r = 0.067$) was for the trimester May–June–July (Figure 3c), but it was not significant ($p = 0.719$). Hence, we could not confirm that changes in the ocean environment driven by ENSO conditions in wintering grounds had an effect on arrival times.

We also evaluated if the IMC in the Antarctic Peninsula in autumn was correlated with arrival times in Gorgona the following year. IMBIE provides data on monthly cumulative ice sheet mass (Gt) changes per year for the Antarctic Peninsula (Shepherd *et al.*, 2012; https://imbie.org), so we used data for autumn (mean value between April and May), when the sea ice formation is crucial for the juvenile Antarctic krill (Fritsen *et al.*, 2008; Meyer, 2012). We found a near significant correlation between IMC and arrival time ($r = 0.40$, $p = 0.058$; Figure 3b). In addition, both GAM and Cox-and-Stuart-trend-test yielded significant effects of time on ice sheet mass trends ($p < 0.0001$ and $p = 0.004$). Therefore, we suggest that the change of annual ice sheet mass in autumn of the Antarctic Peninsula indirectly affects the migration timing to Colombian waters. In years with lower accumulation of ice in autumn, humpbacks arrived earlier to Gorgona the following year.

To explore if G-stock population size could be affecting arrival times to Gorgona waters, we extracted the abundance projections (number of individuals) per year provided by Johnston *et al.* (2011) and correlated them with arrival times in Gorgona the same year. Results showed a significant negative correlation between abundance projections and arrival time ($r = -0.68$, $p < 0.001$; Figure 3d). Both GAM and Cox-and-Stuart-trend-test yielded significant effects of time on population estimate trends ($p < 0.0001$ and $p = 0.0002$, respectively). As the G-stock population increased, whales arrived earlier to Gorgona.

Two models, one including IMC in autumn in Antarctica and another the G-stock population size explained satisfactorily the change in arrival times to Gorgona waters (41% and 57%, respectively). Both factors were highly correlated ($r = -0.94$, $p < 0.001$) and for this reason, we did not include them simultaneously in the fitted models. With the available data, we were unable to determine which factor is more important in explaining the observed trend.

Discussion

Arrival times of humpback whales to Gorgona National Park have substantially shifted over the last 31 years and are now 1 month earlier than in the late 1980s. This is the result of a clear linear trend until around 2008, of whales arriving on average 1.5 d earlier each year. This trend has levelled off in the last decade, making the last week of May the best estimate for arrival in recent years. As departure dates have not changed significantly, humpback whales are now 1 month longer around Gorgona than 31 years ago, *i.e.* close to half of the year. It is important to note that this length of time refers to the species and not to individual animals. Individual animals stay in this area on average 18 d with a maximum stay of 55 d (Capella *et al.*, 1995).

Whale migration serves the purpose of providing warmer waters during calving. Humpback whale wintering breeding areas are found in warm (>25°C) coastal waters irrespective of latitude (Rasmussen *et al.*, 2007). Although whales and their calves could

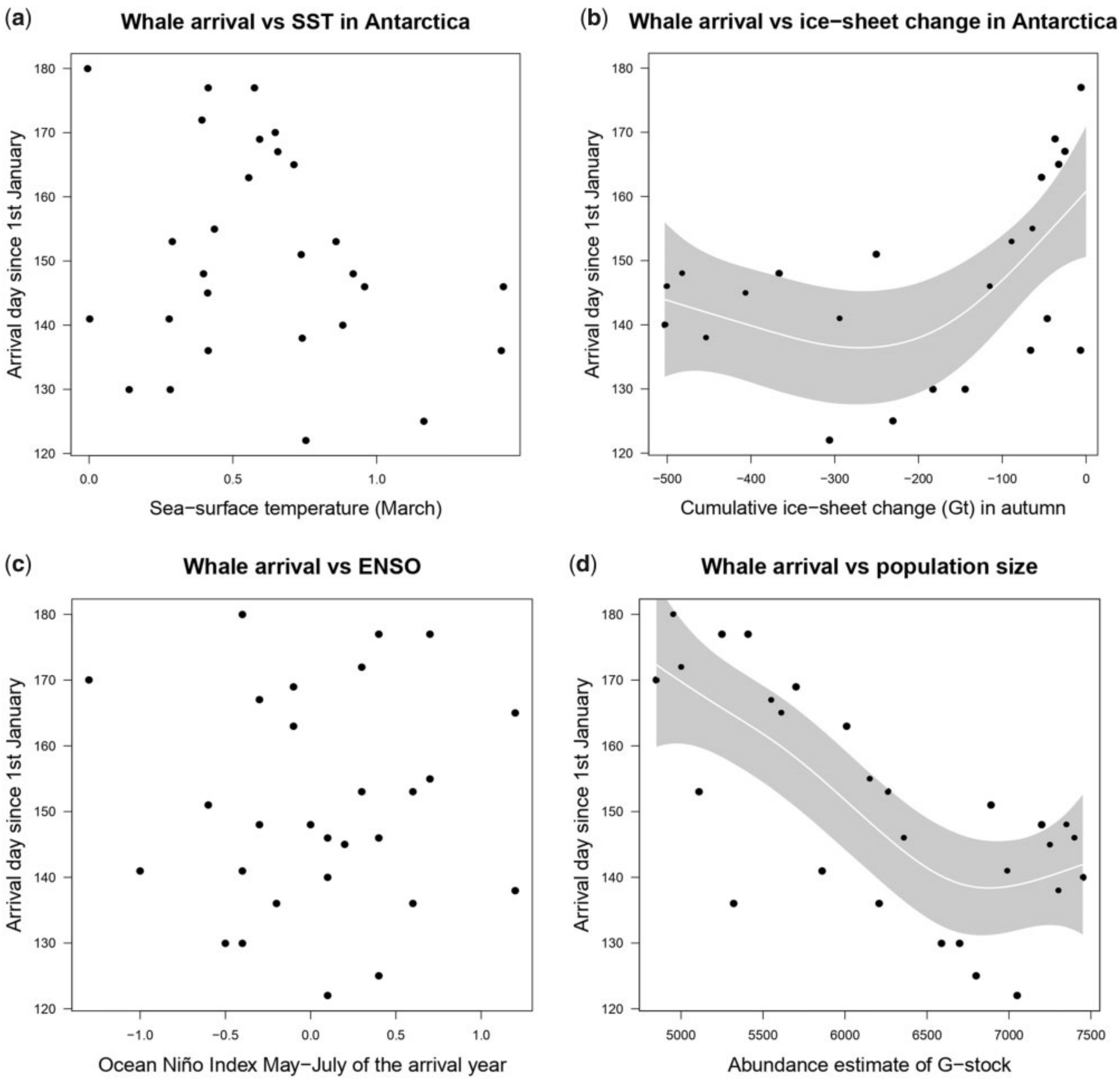

Figure 3. Whales' arrival date to Gorgona waters between 1988 and 2018 in relation to: (a) SST (°C) in March around the Peninsula Antarctica of the arrival year; (b) cumulative IMC (Gt) around the Peninsula Antarctica in the previous autumn (April and May) of the arrival year; (c) ONI values for May–June–July off Tropical waters of the arrival year; and (d) abundance estimate (number of individuals) of the humpback whale G-stock population of the arrival year. Day of arrival is counted from 1 January. For significant cases (b and d) shaded areas are 95% confidence intervals of GAM fits (white lines).

stay thermo-neutral in any ocean (Watts *et al.*, 1993), the migration of whales to warmer waters during calving can increase the survival chances of offspring by reducing the metabolic overhead of mother–calf pairs (Trillmich, 2009), and by reducing predation risks by orcas (*Orcinus orca*; Steiger *et al.*, 2008).

Our results showed that ice sheet mass change in autumn in Antarctica was related to the earlier arrival of whales to Gorgona. In the summer feeding grounds, the distribution and occurrence patterns of humpback whales in Antarctic waters relate primarily to prey abundance (Nowacek *et al.*, 2011). The annual advance and retreat of the Antarctic sea ice influences the abundance of krill and is likely to play a major role in determining the timing of the whales' annual migration (Johnston *et al.*, 2012), similar to reports from northern feeding grounds (e.g. Ramp *et al.*, 2015). The formation of sea ice sheet in autumn is critical for the food supply for juvenile krill and thus their development and survival in winter and abundance in summer (Fritsen *et al.*, 2008; Meyer, 2012). When the autumn ice sheet has a larger mass, more krill can find food in winter and the following summer whales would have more prey available. In such years, humpbacks are arriving later to Gorgona. If some of the whales use low prey availability as a cue to initiate their migration to wintering grounds, this could explain why some whales arrived earlier to Gorgona when krill abundance was lower than usual.

Substantial foraging on krill is primarily conducted in cold productive waters, and whales lose weight in the tropics, especially adult females during their calving spell, due to migratory and lactation energy demands (e.g. Curtice *et al.*, 2015). Therefore, groups with calves possibly arrive later in the season to Gorgona because they need to forage for longer before migrating. Our results suggest that some whales could stay longer in Antarctica when there is more food there. To improve the interpretation of our results, it would be necessary to analyse arrival and departure dates of individual whales at several wintering grounds and correlate these data to abundance of krill in specific feeding grounds.

Previous studies in breeding areas reported that the proportion of groups with calves increased as the season advanced, e.g. in Hawaii (Smultea, 1994), Abrolhos, Brazil (Morete *et al.*, 2007), and Bahía Málaga, Colombia (Avila *et al.*, 2017). Craig *et al.* (2003) reported that migratory timing in Hawaii varied as a function of age, sex, and reproductive status and documented that juveniles arrived and departed earlier from breeding grounds while females with calves arrived and departed later. Similar temporal fluctuation was confirmed by our observations, as we recorded fewer groups with calves when whales arrived, than when whales left.

In other locations, humpback abundance changed throughout the season (e.g. Dawbin, 1966; Morete *et al.*, 2003). We could not evaluate if this was the case in Gorgona, as time-series data of abundance in Gorgona are not available. But using the estimated trend of the G-stock population (Johnston *et al.*, 2011), our results showed that as the population increased, whales started to arrive earlier to Gorgona. However, whales are not departing later. So, the relationship between population size and arrival time might be linked to an increase in a specific section of the population or specific individual roles, rather than to an absolute number of whales. Craig *et al.* (2003) registered that humpback whale juveniles migrated first to the breeding grounds. In Gorgona, groups without calves arrived earlier and we believe some of those might have been juveniles. Pallin *et al.* (2018) registered an increase in the pregnancy rates for humpback whales in Antarctica (from 2010 to 2014), so more calves would be expected. These calves, in turn, become juveniles in following years, temporarily changing the structure of the population. If juveniles became more abundant once the population started to recover (Clapham and Mayo, 1987), this could explain earlier arrival of whales to tropical areas but not departure time. If this was the case, as the population matures, we might see a new shift of arrival time in the future. Consequently, the increase in length of stay in Gorgona waters could be the result of some individuals that are starting the migration earlier, giving the impression that the breeding season is expanding for the population but this is not necessarily true.

Neither SSTs in the Antarctic feeding ground nor changes in the breeding grounds driven by ENSO conditions appear to explain the earlier arrival to Gorgona breeding ground. Given the general absence of feeding of adult humpbacks on breeding grounds (Dawbin, 1966), the availability of food in high latitudes, indirectly related to the balance of ice sheet mass in autumn, seems to play a main role in determining if and when whales migrate to low latitudes. Availability of food is likely a key factor behind an increasing population. However, as we found that both factors, ice sheet mass and population size, are highly correlated, we cannot determine which one is the most important factor behind the northward migration of whales in winter. As Craig *et al.* (2003) mentioned, the initiation of migration in individual whales can be determined by a complex interaction of several factors, like hormonal state, body condition, photoperiod, and food availability. Factors other than those measured in this study are possibly influencing the observed change in arrival times and length of stay.

Whales integrate a multitude of environmental signals into their migratory decisions (e.g. Dawbin, 1966; Ramp *et al.*, 2015). Without data on when specific whales leave the feeding grounds, and the trajectories of their migration, it will be very difficult to understand individual decisions. For instance, a previous study reported that in 2009 some humpbacks remained in an Antarctic feeding ground until 1 June, before beginning their migrations to the waters off Central and South America, Australia, and southern Africa (Johnston *et al.*, 2012). In the same year, we recorded whales arriving to Gorgona already on 6 May. Similarly, other studies report humpbacks in the Patagonian channels between December and June (Gibbons *et al.*, 1998, 2003). Perhaps several strategies are available, with some whales choosing to remain longer, feeding in Antarctic waters (e.g. Johnston *et al.*, 2012). Previous studies of Southern humpback whale populations showed that there is significant individual variation in migration patterns between feeding grounds and breeding areas (e.g. Zerbini *et al.*, 2006; Dalla Rosa *et al.*, 2008; Félix and Guzmán, 2014). Also, migratory timing of individual females varies across years depending on whether or not they have a calf (Craig *et al.*, 2003). In addition, dates of arrival and extension of the occurrence of humpback whales in the Gorgona area may be biased by individuals who may be transiting across Gorgona to or from northernmost reproductive areas (i.e. northern Colombia, Panama, and Costa Rica). Whales that occupy northernmost breeding areas could be migrating earlier than animals that mostly use the central area (such as Gorgona) and south of the breeding area (*i.e.* Ecuador). As timing of migration could be flexible for individual whales, further studies should include individual identification, individual tracking, as well as age/body size estimation, to understand the migratory timing pattern.

We are keenly aware of the limitations of this study, as it relies on opportunistic sightings from researches and rangers, even if they have consistently written down this information for over 31 years. Using migration data from a systematic study would be more informative, but these data are not available. Scientific studies in Colombia started in 1986, but lack of funding during multiple seasons has prevented a consistent longitudinal dataset. Moreover, these studies have been conducted haphazardly at peak months of whale migration —July to October—, but rarely covered the beginning or the end of the season (e.g. Stone *et al.*, 1990; Flórez-González, 1991; Flórez-González *et al.*, 1998; Capella *et al.*, 2001; Acevedo *et al.*, 2017). Regardless of limitations, we believe the length of time rarely seen in other whale studies, and the fact that trained researches and rangers have consistently written down these observations throughout the years, provide validity to the study. The key point of this study was to demonstrate that whale migrations are changing. We made some analysis to explore key variables that could explain this change, but we could not give a definitive answer as to why this is happening.

In Colombia, previous studies reported that humpback whales stay in Gorgona almost 5 months, from June to November (Flórez-González *et al.*, 2009; Capella *et al.*, 2014). Our study, which is the first long-term study compiling data about arrival and departure of humpbacks in the Colombian Pacific, complements previous studies and reveals that the humpback whales are present in Gorgona from May to December, staying up to 7 months. Although waters around Gorgona National Park are protected, whales are exposed to various threats within and outside protected areas (*e.g.* collision with vessels, Avila *et al.*, 2017, and bycatch, Capella *et al.*, 2001). Besides, whales may be negatively affected by noise pollution of acoustic prospection (Avila *et al.*, 2013). Seismic waves can have harmful effects on humpback whales, including changes in behaviour and distribution, hearing damage and strandings (Gordon *et al.*, 2003; Weir, 2008). Knowing the dates when humpback whales arrive and depart from the area contributes to the current development of a local and regional conservation action plan for the Southeast Pacific population and provides scientific evidence to support decisions of the Colombian Ministry of Environment and Sustainable Development regarding current and future permits for activities that may negatively affect whales. Such information should be incorporated in the planning of seismic cruises for oil and gas exploration, fisheries activities, and to regulate boat traffic/presence in the area.

Conclusions

Migration changes of humpback whales to Gorgona breeding area demonstrated in this study have implications for management and protection. Although the peak of the humpback whale breeding season is from July to October, following the precautionary principle, adopted by the Colombian government in 1993 (Law 1333 of 1993), we recommend establishing an official 8-month humpback whale season in Colombia from 1 May to 31 December. During this period, fishing activities and vessel traffic in the area should be minimized to reduce the probabilities of vessel collisions and incidental entanglements. Also, marine seismic explorations should be suspended during this time or have enough marine mammal observers on board to allow for reasonable observation shifts. Given the importance of Gorgona as a calving and breeding ground for the Southeast Pacific population, as well as its importance as a protected area, this study will underpin further improvements of preventive measures. It demonstrates the importance of long-term monitoring and contributes to the understanding of whale ecology in the Pacific region. Finally, we invite other scientists working with whales to explore what is happening in their study areas, in case a shift in whale migration time is registered. We recommend updating this in the management plans of their regions.

Acknowledgements

We thank Fundación Yubarta for data collection training. To staff members of Gorgona National Park, researchers, rangers, residents, divers, and visitors who recorded or helped to record data in the field book of the Park; especially to Pablo Montoya, Diego Aguiño, Héctor Montaño, Ever Solis, Simeón Yesquén, Corazón Aguiño, Paola Rojas, Héctor Chirimia, Elizabeth Hernández, Lilián Flórez-González, German Soler, Alejandro Suárez, Adolfo Salinas, Jaime Vasquez, Luis Jiménez, Jorge Lobatón, Yiyo Aguiño, and Manuel Vidal. We thank the Cetacean Society International (CSI) for the financial support of I.C.A. to travel to Gorgona to review the park's field book. To Andrew Shepherd, for facilitating data about the IMC for Antarctic Peninsula. We also thank Chris Parsons, Pia Anderwald, Alexandre Zerbini, Justin Cook, Milton Marcondes, Daniel Palacios, Anita Gilles, and two anonymous reviewers for valuable comments to improve the manuscript.

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Handling editor: Anita Gilles