

# Timing of migratory baleen whales at the Azores in relation to the North Atlantic spring bloom

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**ABSTRACT:** Each year, a phytoplankton spring bloom starts just north of the North Atlantic Subtropical Gyre, and then expands northwards across the entire North Atlantic. Here, we investigate whether the timing of the spring migration of baleen whales is related to the timing of the phytoplankton spring bloom, using 4 yr of dedicated whale observations at the Azores in combination with satellite data on ocean chlorophyll concentration. Peak abundances of blue whale *Balaenoptera musculus*, fin whale *B. physalus*, humpback whale *Megaptera novaeangliae* and sei whale *B. borealis* were recorded in April–May. The timing of their presence tracked the onset of the spring bloom with mean time lags of 13, 15, 15 and 16 wk, respectively, and was more strongly related to the onset of the spring bloom than to the actual time of year. Baleen whales were actively feeding on northern krill *Meganyctiphanes norvegica* in the area, and some photo-identified individuals stayed in Azorean waters for at least 17 d. Baleen whales were not observed in this area in autumn, during their southward migration, consistent with low chlorophyll concentrations during summer and autumn. Our results support the hypothesis that baleen whales track the secondary production generated by the North Atlantic spring bloom, utilizing mid-latitude areas such as the Azores as foraging areas en route towards their summer feeding grounds.

**KEY WORDS:** Baleen whales · *Balaenopteridae* · Phytoplankton spring bloom · Whale migration · Feeding area · Satellite remote sensing · North Atlantic Ocean · Azores

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## INTRODUCTION

The phytoplankton spring bloom is one of the most important biological events in the North Atlantic Ocean (Siegel et al. 2002, Longhurst 2007). Following winter, increasing light conditions and ample nutrient availability lead to the onset of the spring bloom (Sverdrup 1953, Townsend et al. 1994, Huisman et al. 1999). The bloom starts at a latitude of ~35°N, just north of the North Atlantic Subtropical Gyre (NASG), in December–January (Fig. 1). The bloom subse-

quently develops across the North Atlantic throughout spring and summer, propagating northwards to Arctic waters in June (Siegel et al. 2002, Behrenfeld 2010). Concurrently, the stratified nutrient-depleted waters of the NASG also extend northwards, reaching the latitudes of the Azores in late spring to early summer. In summer and autumn, chlorophyll concentrations in the southern and central North Atlantic waters are very low (Fig. 1).

Migratory organisms whose reproductive success ultimately relies on marine primary production may

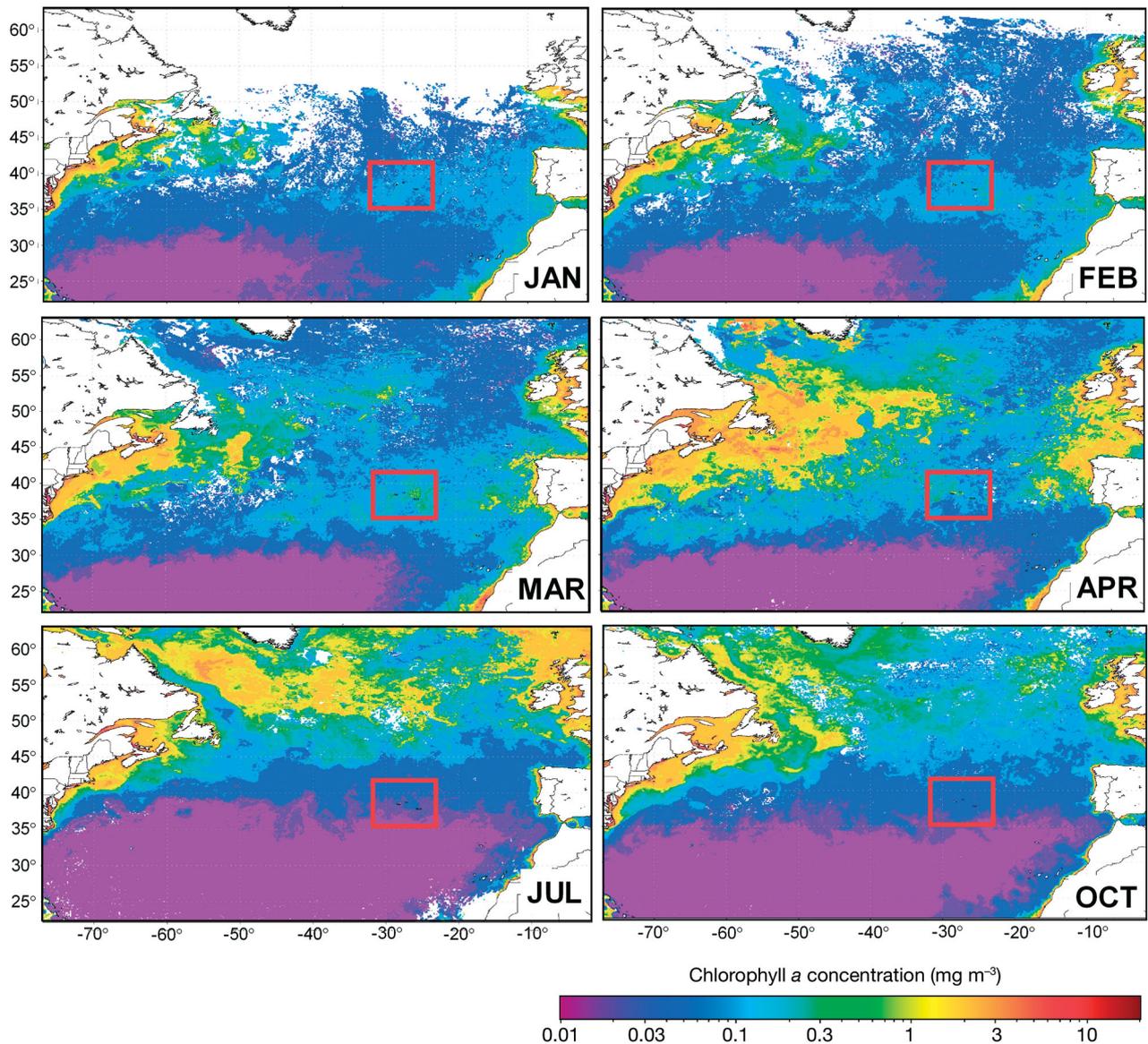


Fig. 1. Annual variation in chlorophyll *a* concentration (chl *a*) in the North Atlantic Ocean. The location of the Azores is outlined by the red rectangle. The 6 panels represent mean monthly chl *a* values for January, February, March, April, July, and October 2006. Data were retrieved from the NASA Ocean Color website (MODIS Aqua instrument; <http://oceancolor.gsfc.nasa.gov/>)

tune their migration to the timing of the North Atlantic spring bloom. Baleen whales need dense aggregations of krill or fish to enable efficient foraging (Whitehead & Carscadden 1985, Friedlaender et al. 2006, Goldbogen et al. 2011), and temporal synchrony with the presence of suitable prey is evident in these species. Most baleen whale species undertake extensive north-south migrations associated with feeding at mid- to high latitudes in summer and breeding in (sub)tropical regions during winter (Kellogg 1929, Norris 1967; but see Simon et al. 2010 for a counter-

example). Seasonal presence of baleen whales at the summer feeding grounds coincides with increased food availability in these waters. Nevertheless, migratory patterns over the North Atlantic are still largely unknown for most species of baleen whales.

The North Atlantic spring bloom could temporarily produce sufficient prey densities to induce foraging of baleen whales during their spring migration towards the high-latitude feeding grounds. This might particularly apply to areas where the phytoplankton spring bloom combines with physical factors to con-

concentrate prey. Physical conditions conducive to concentrating prey may include coastal zones, upwelling areas, fronts and seamounts. For example, offshore regions of high marine productivity have been documented as foraging areas during trans-Atlantic migration in a variety of taxa, including birds, turtles and sharks (e.g. Doyle et al. 2008, Gore et al. 2008, Egevang et al. 2010). Recently, association with offshore fronts and seamounts was found for migratory sei whales in the North Atlantic Ocean (Skov et al. 2008, Olsen et al. 2009).

Since baleen whales capitalize on enhanced secondary production, it is unlikely that the timing of whale migration will coincide with the timing of the phytoplankton spring bloom. Rather, zooplankton development often tracks the phytoplankton spring bloom with a time lag of several weeks to months (Longhurst 2007). For instance, a maturation time of several months is required for krill to reach sizes suitable for baleen whale feeding (Fiedler et al. 1998, Croll et al. 2005, Santora et al. 2010). This suggests the existence of a characteristic time lag between the phytoplankton spring bloom and the presence of foraging baleen whales. Indeed, monitoring studies in the North Pacific Ocean have shown that abundances of blue and fin whales typically lag behind maximum primary productivity by several weeks to months (Burtenshaw et al. 2004, Croll et al. 2005, Stafford et al. 2009).

The Azorean archipelago, situated on the Mid-Atlantic Ridge at the northern edge of the NASG, offers a potential foraging area for migratory baleen whales. The occurrence of an early phytoplankton spring bloom (Siegel et al. 2002) in combination with local upwellings, thermal fronts and eddies (Johnson & Stevens 2000) may result in enhanced ecosystem productivity and the aggregation of prey species in coastal waters of the Azorean islands (Santos et al. 1995). Several studies report observations of baleen whales at the Azores during spring and summer, including blue whale *Balaenoptera musculus*, fin whale *B. physalus*, sei whale *B. borealis*, humpback whale *Megaptera novaeangliae*, Bryde's whale *B. edeni* and minke whale *B. acutorostrata* (Chaves 1924, Gordon et al. 1990, 1995, Steiner et al. 2008). Satellite tracking of blue, fin and sei whales suggests use of the area during migration (Olsen et al. 2009; see also Great Whales Satellite Telemetry Program: [www.portulano.org/wkit/index.html](http://www.portulano.org/wkit/index.html)). However, there are no long-term records of seasonal variation in baleen whale abundances in the area, and it is not known whether the Azorean islands are used as a feeding area by migratory baleen whales.

Here, we present results of a dedicated 4 yr study of baleen whale abundances at the Azores, and compare these observations with interannual variation in local ocean chlorophyll concentrations obtained from satellite remote sensing. More specifically, we investigate: (1) whether there is an association between the timing of baleen whale presence at the Azores and the timing of the phytoplankton spring bloom at the Azores, and (2) whether baleen whales use the Azores as a feeding area.

## MATERIALS AND METHODS

### Research area

The Azorean archipelago is a group of 9 volcanic islands situated on the Mid-Atlantic Ridge (Fig. 2). Bottom topography of the archipelago is characterized by steep submarine walls and the presence of seamounts, ridges and submarine canyons. The local oceanography is influenced by the Azores Current, which is a relatively weak ocean current that flows in a southeastward direction from the Gulf Stream towards the Canary Current (Johnson & Stevens 2000), and by the Azores Front, a major source of eddies and meanders situated just south of the islands, producing localised patches of enhanced productivity in the coastal waters of the islands (Angel 1989, Santos et al. 1995).

Our research area is located off the south coast of Pico, one of the islands of the Azorean Central Group (38° 24' N, 28° 11' W; Fig. 2). Along this coastline, the ocean floor descends steeply to >1000 m depth within 3 km from shore. Except for waters within 100 m of the shore, the high clarity of the open ocean water in our study area, with Secchi depths ranging from 18 to 28 m, is representative of Case 1 water (Morel et al. 2007).

### Remote sensing data

We used remote sensing data of chlorophyll *a* concentration (chl *a*) to determine the timing of the phytoplankton spring bloom in our research area. In addition, we used remote sensing data of sea surface temperature (SST) as a simple indicator of seasonal variation in thermal stratification. During summer stratification, the supply of nutrients from deep water layers to the surface layer is strongly reduced, which suppresses phytoplankton growth (e.g. Behrenfeld et al. 2006, Huisman et al. 2006). Chl *a* and SST data

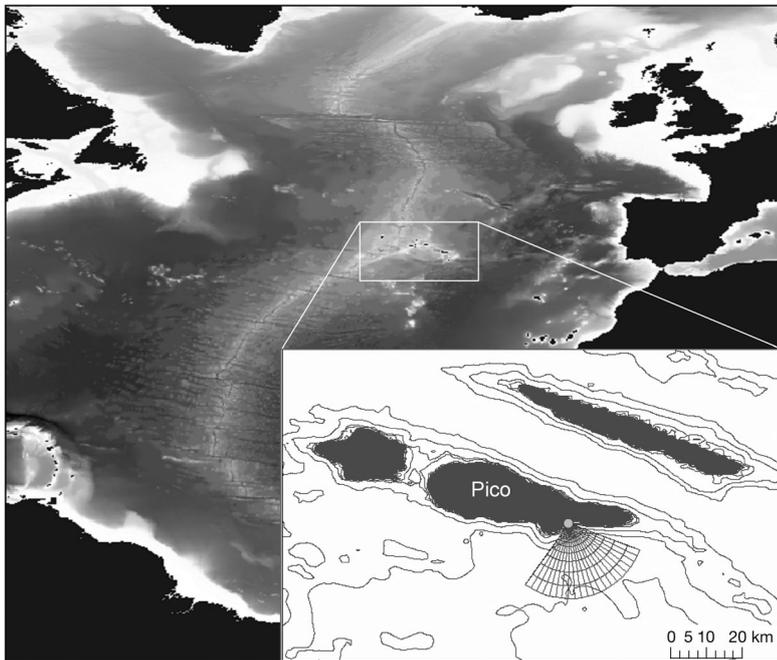


Fig. 2. Location of the Azores and the research area south of Pico Island (inset). The observation grid outlines the range covered by the shore-based observations from our observation platform (●). Bathymetry map of the North Atlantic Ocean was reproduced from the GEBCO Digital Atlas (IOC/IHO BODC 2003)

were obtained from the MODIS instrument (Moderate Resolution Imaging Spectroradiometer) aboard the Aqua satellite. We downloaded these data as Level 3 Standard Mapped Images from the NASA Ocean Color website (<http://oceancolor.gsfc.nasa.gov/>), at the finest spatial resolution available ( $4 \times 4$  km). The Aqua satellite scans the entire Earth's surface every 1 to 2 d, but cloud cover may prevent data collection. We therefore used composite images, where the data are binned in four 8 d 'weeks' for every month, totalling 48 'weeks' per year. Chl *a* and SST values for our study area of  $367 \text{ km}^2$  were calculated by averaging chl *a* and SST over all grid cells overlaying the study area (Valavanis 2002). Geographical mapping was conducted using ArcGIS version 9.2 (Environmental Systems Research Institute) with the Spatial Analyst Toolbox extension.

We defined 3 stages of spring bloom development: (1) Onset of the bloom; the first week at which chl *a* levels increased to more than  $3\times$  the lowest chl *a* level measured in the preceding summer or autumn; (2) peak of the bloom; the week with maximum levels of chl *a* for that year; and (3) end of the bloom; the week before the collapse of the spring bloom, visible as a strong decline in chl *a* concentration followed by

a prolonged period of low chl *a* levels. The duration of the bloom was calculated as the number of weeks from the onset to the end of the bloom.

### Relative whale abundances

To estimate relative whale abundances, we conducted standardized surveys from a fixed shore-based lookout 30 m above sea level using Steiner Observer binoculars (Steiner Binoculars) with  $25\times$  magnification and 80 mm objective lenses. The sighting range from our land-based lookout was determined empirically by recording the GPS locations of our research vessel at the limits of the sighting range. This showed that the sighting range from our lookout was 20 km offshore, encompassing a total research area of  $367 \text{ km}^2$  (Fig. 2; Visser et al. 2011). Sea state on the Beaufort scale (Bft), visibility and weather conditions were recorded at the start of each observation. The standardized surveys consisted of a scan of the research area, recording all baleen whales present. The area was scanned twice to account for individuals submerged or missed during the first scan. Surveys had a duration of 15 to 30 min and were spaced at least 2 h apart (Visser et al. 2011). Surveys were made on a nearly daily basis, during the periods April–October 2004 and April 2005–December 2007. Surveys at Bft  $>3$  or at limited visibility (no clear view of the horizon) were excluded from analysis.

Relative abundances of whale species were calculated as the mean number of individuals present per survey. We binned these relative abundances in four 8 d 'weeks' for every month, totalling 48 wk per year, to facilitate comparison with the chlorophyll data obtained from remote sensing. Peak whale abundance was defined as the maximum relative abundance of a whale species in a given year.

### Timing in relation to the spring bloom

To investigate whether the timing of migratory whales was associated with the timing of the phytoplankton spring bloom, we calculated the time lags (in wk) between the peak abundance of each whale

species and the 3 stages of spring bloom development. We also calculated the standard deviation (SD) of these time lags:

$$SD = \sqrt{\frac{\sum_{i,j} (x_{ij} - \bar{x}_i)^2}{n-1}}$$

where  $x_{ij}$  is the time lag between peak whale abundance and phytoplankton bloom development for whale species  $i$  in year  $j$ ,  $\bar{x}_i$  is the mean time lag for whale species  $i$  and  $n$  is the total number of time lags. This equation allows for differences in mean time lag between whale species, as some species may arrive earlier in the year than other species. As well as for all species combined, SD was also calculated for each whale species separately. Species for which peak abundance could be recorded in one year only were excluded from analysis.

In addition to SDs of the time lags, we also calculated the SD of the actual time of the year (expressed as week number) at which the whales reached peak abundance. If the SD of the time lag between peak whale abundance and a given stage of bloom development were lower than the SD of the actual time of year at which whales reach peak abundance, then this would indicate that the timing of baleen whales visiting the Azores is more closely associated with the timing of the spring bloom than with the actual time of year. We therefore tested for significant differences between SDs using Levene's test for homogeneity of variance, followed by an  $F$ -test for pairwise comparisons to establish which SDs were different from which other SDs.

### Behavioural budget

We used focal follow observations to determine if whales were feeding in the research area. Focal follows were conducted from our shore-based lookout and from our research vessel (7.2 m Boston Whaler fitted with a Jetpac 150 hp diesel outboard waterjet engine). Most vessel-based focal follows were guided by an observer from land, who directed the vessel to known locations of whales. The research vessel kept a distance of at least 50 m from the whales, and in most cases a larger distance of 100 to 300 m was maintained to avoid disturbance of whale behaviour. We recorded group composition, group spacing, direction and speed of travel, surface display events and behavioural state using a standardized ethogram (Mann 1999). Group composition was determined by recording the number of

adults and sub-adults. Sub-adults, including calves and juveniles, were defined as all individuals that were less than half the size of their associates and strongly associated with an adult (Lockyer 1984, Panigada et al. 2005). Group spacing was determined by the distance (number of body lengths) between individuals. Speed was recorded in a qualitative manner, using 5 categories ranging from still to high speed. Four types of mutually exclusive behavioural states were defined: foraging, resting, socialising and travelling (Piatt et al. 1989, Johnston et al. 2005, Ingram et al. 2007). Foraging behaviour was defined as individuals moving in a non-directional path, displaying zigzag tracks (rapid turns up to 90 degrees), and lunge-feeding events at variable speeds and with variable group spacing (alternated joining and splitting of individuals). Resting was defined as individuals moving at low speed, displaying regular surfacing patterns, stable group spacing, short dives, and loggings (floating at or just below the surface). Socialising was defined as repeated interaction between 2 or more individuals, involving physical contact and surface display events. Travelling was defined as individuals moving steadily in a directional path at moderate to high speed, displaying regular surfacing patterns and stable group spacing. Behavioural parameters were recorded at intervals ranging from 1 to 10 min. Focal follows were conducted during the periods April–October 2003, April–October 2004, and April 2005–December 2007. Focal follows <15 min were excluded from our analysis of the behavioural budget. The behavioural budget was calculated from the cumulative time during which each behaviour was observed divided by the total effort (in h) of the focal follows.

### Individual residence time

Vessel-based observations were used for photo-identification of individuals (NIKON D70 digital SLR camera; 70/300 mm zoom lens). High-quality photo-identification pictures ( $Q \geq 3$ ; Arnbohm 1987) of the dorsal fin or hump and surrounding area, the fluke and/or the chevron pattern were used to assess (re)sightings of individuals (Agler et al. 1990, Katona & Beard 1990, Schilling et al. 1992, Sears et al. 2000). We created a catalogue of individual whales that was referenced by date observed. New whale photos were matched to this catalogue and used to calculate the minimum residence time (in d) of individual whales.

## RESULTS

### Phytoplankton spring bloom

Consistent with the large-scale picture of the North Atlantic spring bloom (Fig. 1), our study area off Pico Island showed a distinct annual phytoplankton spring bloom, starting in December–January and lasting up to April–May (Fig. 3A). The timing of the onset of the spring bloom varied between years (mean  $\pm$  SD: Week  $1.5 \pm 3.1$ ). Likewise, the timing of the peak of the bloom (Week  $9.0 \pm 3.2$ ) and the duration of the bloom ( $14.0 \pm 3.8$  wk) were variable between years. The timing of the end of the bloom was fairly constant (Week  $15.5 \pm 1.3$ ). Each year, the highest chl *a* concentrations were measured in the months February–April (Fig. 3A), when annual maximum chl *a* levels ranged between 0.34 and 0.64  $\text{mg m}^{-3}$  (mean  $\pm$  SD =  $0.48 \pm 0.13$ ). The lowest chl *a* concentrations were measured in the period June–October, when annual minimum chl *a* levels ranged between 0.07 and 0.10  $\text{mg m}^{-3}$  (mean  $\pm$  SD =  $0.08 \pm 0.01$ ). The low chlorophyll concentrations in summer were accompanied by high SST (Fig. 3A; Pearson's product-moment correlation of weekly chl *a* versus SST:  $r = -0.73$ ,  $n = 135$ ,  $p < 0.0001$ ), indicative of strongly stratified and nutrient-depleted surface waters throughout summer and early autumn.

### Baleen whale sightings and abundance

We conducted 1138 surveys during suitable environmental conditions and 98 focal follow observations. Surveys were conducted year-round, including 366 surveys in the period March–June (Weeks 11 to 24) when most baleen whales were observed. In total, 113 baleen whales were recorded during the surveys (Table 1), belonging to 5 different species: blue whale *Balaenoptera musculus*, fin whale *B. physalus*, sei whale *B. borealis*, humpback whale *Megaptera novaeangliae*, and minke whale *B. acutorostrata*. A total

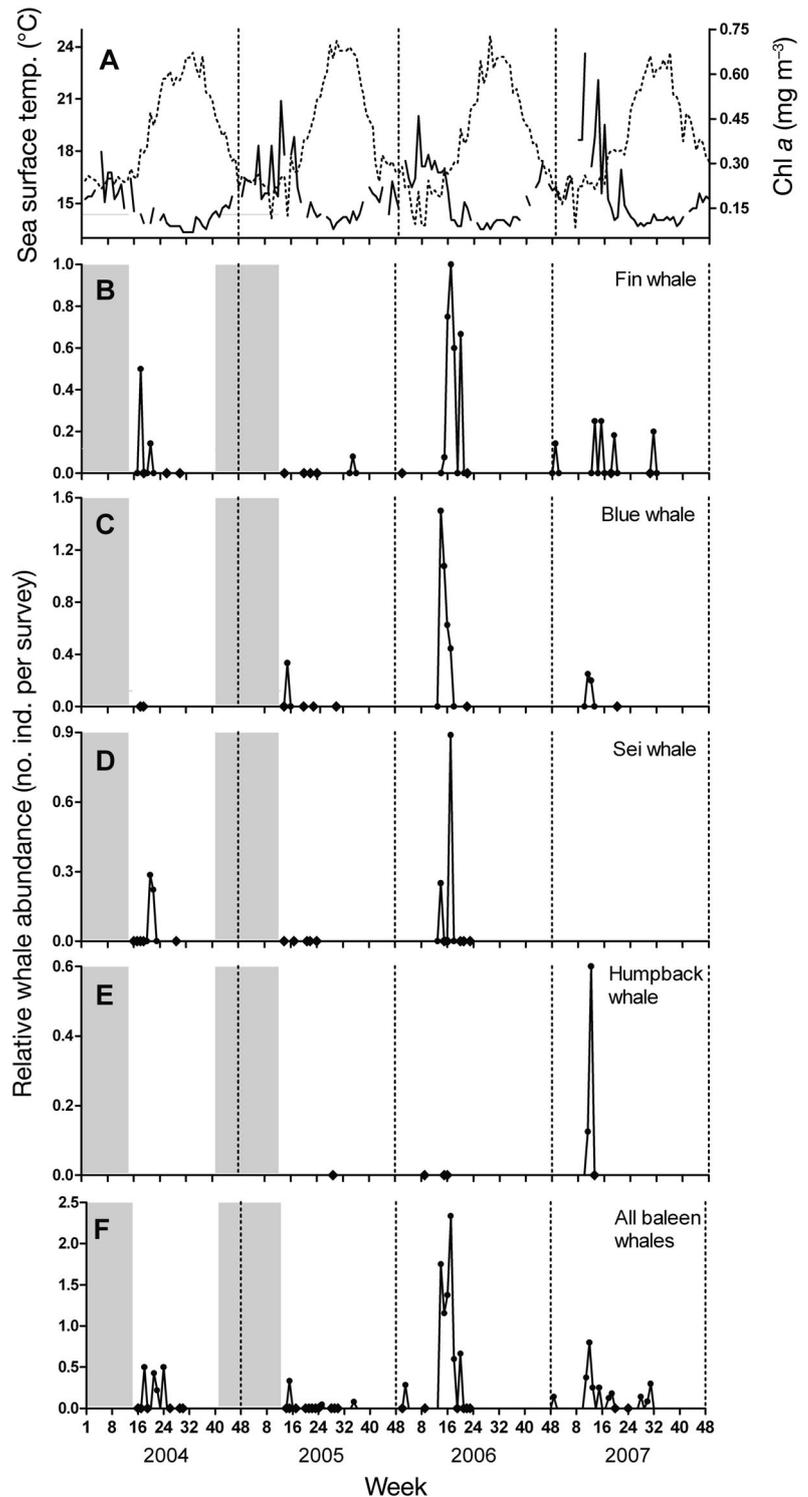


Fig. 3. Relative abundance of baleen whales in relation to sea surface temperature (SST) and chlorophyll *a* (chl *a*) concentration. (A) Temporal variation in SST (dashed line) and chl *a* (solid line). (B–F) Temporal variation in relative abundance of fin whale, blue whale, sei whale, humpback whale, and all baleen whales based on standardized survey observations. (♦) on x-axis indicate additional sightings of whales outside the surveys. Grey areas indicate periods without observation effort. Note the differences in scale between the graphs

Table 1. Sightings, relative abundance in spring (averaged over the period March–June, Weeks 11 to 24; covered by 366 surveys), and minimum residence time of fin whale *Balaenoptera physalus*, blue whale *B. musculus*, sei whale *B. borealis*, humpback whale *Megaptera novaeangliae*, and minke whale *B. acutorostrata* off Pico Island

Species	No. surveyed	No. of focal follows (n)	Relative abundance (ind. survey <sup>-1</sup> )	Minimum residence time			
				No. identified	No. of resightings	Days between resightings	
Fin whale	46	33	23.9	0.11	28	5	1–5
Blue whale	35	25	21.9	0.10	30	4	1–7
Sei whale	13	29	19	0.03	30	1	17
Humpback whale	7	9	9.5	0.02	5	2	1–13
Minke whale	6	2	0.8	0.01	0	0	–

of 6 of the 113 individuals could not be identified to species level. Blue and fin whales were observed during all years (2003–2007), sei and humpback whales during 4 years and minke whales during 3 years. Sub-adults (calves and juveniles) of fin whales ( $n = 18$ ), sei whales ( $n = 10$ ), and blue whales ( $n = 5$ ) were observed in 42, 31 and 20% of the focal follows, respectively.

The overall relative abundance of baleen whales during March–June was 0.28 individuals per survey. Blue and fin whales were more abundant than sei and humpback whales (Table 1). Minke whales were recorded at very low abundance and were excluded from further analysis. Baleen whale abundances varied between years. Blue whales were especially abundant in spring 2006; fin and sei whales were more abundant in 2004 and 2006, while humpback whales were present in higher numbers in 2007 than in the other years (Fig. 3).

#### Timing of baleen whales in relation to the spring bloom

Blue, fin, sei and humpback whale observations were highly seasonal: presence was largely confined to the spring months (March–June), with a limited number of observations extending into summer (July–September) (Fig. 3). Fin whales were also observed 3 times during winter, in January. Humpback whales visited the area almost every spring, but for a shorter period than blue, fin, and sei whales (Fig. 3). In contrast, minke whales were observed several times in summer (August–September), and occasionally in winter (January) and late spring (May–June). None of the baleen whale species were observed during autumn (October–December).

The majority of baleen whale sightings occurred towards the end of the spring bloom, associated with

increasing values of SST (Fig. 3). More specifically, peak whale abundance was observed in Weeks 11 to 21, depending on the species (Table 2). The data suggest that peak abundances of blue whales preceded peak abundances of fin and sei whales by 2 to 3 wk. Depending on the species, peak whale abundance showed a time lag of 11 to 17 wk with respect to the onset of the spring bloom, a time lag of 1 to 15 wk with respect to the maximum of the spring bloom and a time lag of 5 wk before to 6 wk after the end of the spring bloom (Table 2). The timings of peak abundances of blue, fin and sei whales all consistently showed the lowest SD with respect to the onset of the spring bloom (Table 2). Although our small data set provides insufficient statistical power to compare the SDs at the species level, we also calculated SDs aggregated over all 3 whale species. This showed that the SDs of the 4 predictors listed in Table 2 differed significantly (Levene's statistic = 4.65,  $df = 3, 28$ ,  $p = 0.009$ ). More specifically, the SD of the time lag between peak whale abundance and the onset of the spring bloom ( $SD = 1.3$  wk) was significantly lower than the SDs of the 3 other predictors ( $F_{7,23} = 3.85$ ,  $p = 0.037$ ). In other words, the timing of peak whale abundance was more strongly associated with the onset of the spring bloom than with the 2 other stages of bloom development and the actual time of the year.

#### Behaviour

The behavioural budgets of blue, fin, sei and humpback whales were composed largely of foraging and travelling behaviour (Fig. 4). Foraging comprised 25, 45, 41 and 77% of the behavioural budget of fin, blue, sei and humpback whale, respectively. Humpback whale individuals were observed several times producing bubbles during foraging bouts.

Table 2. Timing of maximum whale abundance (expressed as week number), and its time lag after 3 stages of bloom development (in wk). Time lags marked with + indicate that peak whale abundance followed the given stage of bloom development; time lags marked with – indicate that peak whale abundance preceded the given stage of bloom development. We also calculated the standard deviation (SD) of the time lags, for each species separately and for all species combined. A low SD indicates that the timing of maximum whale abundance is closely associated with the actual time of year or the given stage of bloom development

Species	Week of maximum whale abundance	Time lag with bloom development (wk)		
		Onset of bloom	Maximum of bloom	End of bloom
<b>Fin whale<sup>a</sup></b>				
2004	18	+14	+12	+3
2006	17	+14	+10	+3
2007	13	+16	+3	–3
<b>Blue whale</b>				
2005	15	+13	+2	–2
2006	14	+11	+7	0
2007	11	+14	+1	–5
<b>Sei whale</b>				
2004	21	+17	+15	+6
2006	17	+14	+10	+3
<b>Humpback whale<sup>b</sup></b>				
2007	12	+15	+2	–4
SD fin whale (wk)	2.6	1.2	4.7	3.5
SD blue whale (wk)	2.1	1.5	3.2	2.5
SD sei whale (wk)	2.8	2.1	3.5	2.1
SD all species (wk)	2.1	1.3	3.3	2.4

<sup>a</sup>In 2005 the number of fin whales in the surveys was too low to estimate the timing of their peak abundance  
<sup>b</sup>SD of humpback whale could not be calculated, because its peak abundance could be determined for one year only

span ranging from a few days up to 2.5 wk (Table 1). Overall average time between re-sightings was 5 to 6 d (Table 1). These 12 individuals included fin, blue, sei and humpback whales. No re-sightings were made between years.

## DISCUSSION

### Migratory baleen whales and the North Atlantic spring bloom

The phytoplankton spring bloom at the Azores started to develop during winter (December–January) and was maintained into early spring (April), preceding the onset of the North Atlantic spring bloom at higher latitudes (Fig. 1). This large-scale pattern was reflected by the seasonal variation in chl *a* concentration within our local research area, which showed an annually recurring phytoplankton spring bloom during the months December–April (Fig. 3A). Four species of baleen whales (blue, fin, sei and humpback whales) visited the research area in spring, during a few weeks in the period March–June. The timing of the peak abundances of

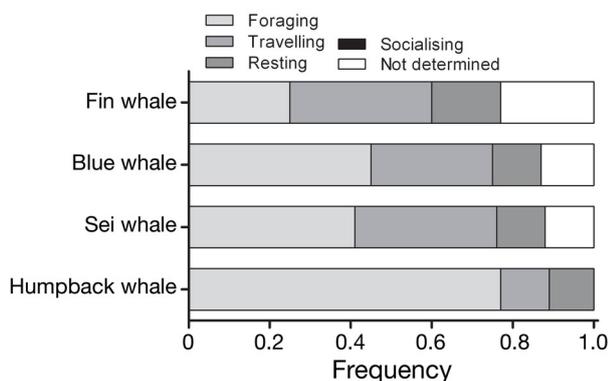


Fig. 4. Behavioural budgets of fin, blue, sei and humpback whales

### Individual residence time

During vessel-based focal follows, a total of 93 baleen whale individuals were photo-identified. Twelve individuals were sighted twice, within a time

the different species varied somewhat between years, and could be linked to the timing of the onset of the spring bloom. More specifically, peak abundances of blue, fin, humpback and sei whale were recorded with a mean time lag of 13, 15, 15 and 16 wk (3 to 4 mo), respectively, after the onset of the spring bloom. This corresponds well with studies of Burtenshaw et al. (2004) and Croll et al. (2005), which reported time lags of 3 to 4 mo between enhanced primary and secondary production, on which the whales capitalise, at the feeding grounds of blue whales in the North Pacific.

Although the link between prey availability and baleen whale presence has been well-documented for the feeding grounds, our study is one of the first to point out that prey availability could play a key role in the timing of spring migration of baleen whales in the North Atlantic Ocean (see also Olsen et al. 2009, Pendleton et al. 2009). Baleen whales visiting the Azores spent a substantial part of their time feeding (25 to 77%; Fig. 4). A few times we actually observed

humpback and blue whales foraging in close vicinity of large patches of krill, and we found several blue whale faeces filled with exoskeletons of krill (F. Visser & K. L. Hartman, pers. obs.). Another recent study observed feeding on krill and red-stained faeces of blue, fin and humpback whales at the Azores in April and May of 2010, and identified the prey species as northern krill *Meganyctiphanes norvegica* (Villa et al. 2011). Similarly, fin whales have been observed feeding on swarms of northern krill near the island of Madeira in May of 1990 (Gordon et al. 1995). Sub-adults of blue, fin and sei whales were recorded frequently in our research area, indicating extensive use of the waters as foraging area for females with calves and juveniles. Our re-sightings indicate that several individuals remained in Azorean waters for a few days to at least 2.5 wk. Similarly, Villa et al. (2011) reported that one fin whale was re-sighted 4 times over 20 d between 20 April and 10 May 2010.

Interestingly, our analysis indicates that the timing of peak whale abundances was associated more strongly with the timing of the onset of the phytoplankton spring bloom than with later stages of bloom development or the actual time of the year. Our observations covered only 4 yr, which restricts the statistical power of our analysis and hence requires caution in the interpretation of our data. We defined the onset of the spring bloom as the first week during which chl *a* concentrations increased to more than 3× the lowest chl *a* concentration measured in the preceding summer or autumn. To investigate the robustness of our finding, we tested 3 alternative definitions for the onset of the spring bloom, such as the first week during which chl *a* concentrations increased to (1) >2× the lowest chl *a* concentration of the preceding summer or autumn, (2) >5% above the median chl *a* concentration of the preceding summer or autumn (following Siegel et al. 2002), and (3) above a threshold value of 0.18 mg m<sup>-3</sup>. For these 3 definitions, the SDs (for all species) of the time lag between the onset of the spring bloom and the timing of peak whale abundance ranged from 1.5 to 1.8 wk. Hence, comparison against the SDs (for all species) of the other predictors in Table 2 shows that, irrespective of its exact definition, the onset of the spring bloom was a better predictor for the timing of peak whale abundances than the actual time of year.

Several zooplankton species are known to fine-tune their life-cycle to the onset of the spring bloom (e.g. Koeller et al. 2009, Seebens et al. 2009). In particular, there is increasing evidence that egg devel-

opment and spawning of northern krill *Meganyctiphanes norvegica* is initiated by the onset of the phytoplankton spring bloom (Astthorsson 1990, Tarling & Cuzin-Roudy 2003, Dalpadado 2006, Tarling 2010). This ensures that larval and juvenile krill can benefit from good feeding conditions provided by a thriving phytoplankton population, and may thus explain why the onset of the spring bloom provided a better predictor for the timing of peak whale abundances than the maximum of the spring bloom.

Implicit in the above discussion is the assumption of a consistent time lag between the onset of the spring bloom and the timing of suitable prey availability for foraging baleen whales. Data from Monterey Bay, California, and the California Channel Islands, indicate preferential feeding of blue whales on krill sizes >16 mm (Fiedler et al. 1998, Croll et al. 2005). Growth rates of krill individuals depend on temperature and feeding conditions, and data on growth rates of northern krill in the subtropical North Atlantic are lacking. However, demographic studies of the growth trajectory of northern krill in the Mediterranean Sea and Clyde Sea (Scotland) indicate that about 3 mo after spawning juveniles reached a size class suitable for foraging baleen whales (Labat & Cuzin-Roudy 1996, Tarling & Cuzin-Roudy 2003, Tarling 2010). Indeed, fin whales have been observed aggregating in those areas in the Mediterranean Sea where spring production had peaked a few months earlier and subsequently generated krill recruitment (Littaye et al. 2004). Extrapolating these findings to the Azores, assuming that spawning at the Azores is triggered by the early onset of the phytoplankton spring bloom, this could result in size classes of northern krill suitable for foraging baleen whales being present at the Azores in April–May. Indeed, Villa et al. (2011) reported sizes of 16 to 22 mm for northern krill individuals sampled near feeding fin whales at the Azores. Hence, the growth trajectory of northern krill might explain the consistent time lag of 3 to 4 mo between the onset of the phytoplankton spring bloom and peak whale abundances observed in our study area. Clearly, however, there is a need for detailed studies of the size structure of euphausiids and the diet composition of baleen whales at the Azores to investigate the validity of these ideas.

Taken together, our findings support the hypothesis that the Azores represent a mid-latitude feeding site for migratory baleen whales, where the timing of baleen whale visits is tuned to the timing of high prey abundance tracking the annual development of the phytoplankton spring bloom. This hypothesis is also

consistent with the lack of observations of baleen whales in our research area in autumn, during their southward migration to the low-latitude breeding grounds. Chl *a* levels at the Azores remain very low throughout summer and autumn, and are unlikely to sustain high abundances of krill and fish during that period. The Azores thus provide poor feeding conditions for baleen whales in autumn.

Seasonal variation in prey availability is one of the driving forces of long-distance migration in many species (Alerstam et al. 2003), and fine-tuning of the timing of migration to seasonally enhanced prey abundance is often critical (Both et al. 2005). However, our data do not indicate the mechanism by which baleen whales synchronize their migration to the phytoplankton spring bloom. Perhaps baleen whales respond to the same abiotic factors that trigger the spring bloom (e.g. light, temperature; Sverdrup 1953, Siegel et al. 2002). Abiotic cues triggering long-distance migration have been observed in several migratory taxa, including birds (photoperiod; Gwinner 1996) and insects (photoperiod, temperature; e.g. Malcolm 1987). Alternatively, baleen whales might just track large-scale gradients in prey abundance. Baleen whales visiting the Azores in spring may originate from southerly wintering grounds. Blue and fin whale sounds were recorded south of the Azores (26 to 35° N), along the Mid-Atlantic Ridge, from November to March (Nieukirk et al. 2004). The timing of krill spawning varies with latitude, being initiated progressively later from south to north (Tarling 2010). Hence, after their visit to the Azores, baleen whales may follow the spring bloom northward, and benefit from other areas of locally enhanced productivity (e.g. the Faraday Seamounts and the Charlie Gibbs Fracture Zone; Skov et al. 2008, Olsen et al. 2009). The North Atlantic spring bloom can thus be envisioned as a northward propagating wave of high productivity, which may create a consecutive series of feeding areas en route that ultimately lead the whales to their summer feeding grounds. Satellite tracks of baleen whales tagged at the Azores during spring show that these individuals migrated to northerly feeding grounds off Greenland (~60° N; fin and sei whales), or up to the latitude of northern Spain (~42° N; blue whales) (Great Whales Satellite Telemetry Program: [www.portulano.org/wkit/index.html](http://www.portulano.org/wkit/index.html)). A similar tracking of seasonal variation in SST and the phytoplankton spring bloom has been documented for blue and fin whales in the North Pacific (Burtenshaw et al. 2004, Stafford et al. 2009).

### Species-specific patterns of habitat use

Baleen whale species differed in the timing of their visits to the area. On average, peak abundances of blue whales were recorded 2 to 3 wk earlier in spring than peak abundances of fin and sei whales (Table 2). In contrast, minke whales were mainly observed in summer. This interspecific variation could be related to differences in diet, avoidance of competition, or other constraints on the timing of migration. Blue whale diet consists almost entirely of euphausiids (krill; Yochem & Leatherwood 1985, Pauly et al. 1998). Fin and sei whales feed on krill and copepods as well, but their diet also includes other prey types such as schooling fish and squid (Gaskin 1982, Pauly et al. 1998). In addition, baleen whale species may target different species and size classes of krill (Fiedler et al. 1998, Croll et al. 2005, Santora et al. 2010). Hence, while the timing and duration of blue whale presence may be synchronised to high densities of euphausiids, fin and sei whales may benefit from feeding at various trophic levels during a more prolonged period. Similar differences in the timing of migration were found for blue and fin whales in the subarctic North Pacific, where blue whales were subassociated with SST with a time lag of 1 to 2 mo, while fin whales showed a time lag of 3 to 4 mo to SST (Stafford et al. 2009). A comparable spatial pattern was found in the Gulf of St. Lawrence, where blue whales were more strongly associated to thermal fronts, which can concentrate patches of krill, than fin and humpback whales (Doniol-Valcroze et al. 2007). Interestingly, minke whales in the Gulf of St. Lawrence were not associated to thermal fronts (Doniol-Valcroze et al. 2007), and it is suggested that this species uses different foraging techniques than the other species of baleen whales (Hoelzel et al. 1989). Their limited dependency on dense zooplankton aggregations may explain the summer observations of minke whales at the Azores.

Our standardized surveys point to substantial inter-annual variation in the relative abundances of the different whale species (Fig. 3B–F), even though the phytoplankton spring bloom is an annually recurring event (Fig. 3A). This may be due to interannual variability in migratory patterns of individual whales. Another potential explanation could be the local patchiness of suitable prey. In some years, the whales might be feeding ‘just around the corner’, in other areas within the Azorean archipelago that provided higher prey abundance than our research area. It might also be that the species composition and rela-

tive abundances of the zooplankton show considerable variation between years (Valdés et al. 2007, Dakos et al. 2009), resulting in interannual differences in prey availability for baleen whales. If there is suitable prey available at the Azores, baleen whales may stay for a week or two; if not, the whales continue their migratory journey northwards. Long-term monitoring studies of the zooplankton community and other prey species at the Azores would be most desirable, as this may help to resolve this missing link between the phytoplankton spring bloom and the presence of migratory baleen whales.

### Possible implications of climate change

Although our study is limited to only 4 yr, the observed association between the timing of whale migration and the North Atlantic spring bloom suggests possible implications of climate change for migratory baleen whales. Warming of ocean waters tends to enhance thermal stratification, which suppresses the supply of nutrients into the surface layer and reduces phytoplankton growth (Sarmiento et al. 2004, Behrenfeld et al. 2006, Huisman et al. 2006). At present, Azorean waters are sufficiently destratified in winter to permit an early spring bloom, while high sea surface temperatures are accompanied by low chl *a* concentrations in summer. However, the Azores are situated just at the northern edge of the permanently stratified and extremely oligotrophic NASG (purple area in Fig. 1). Climate models predict an expansion of the NASG of 4 % by 2050 (Sarmiento et al. 2004), and remote sensing studies indicate an even faster expansion (Polovina et al. 2008). Incorporation of the Azores in the expanding zone of the NASG would suppress the spring bloom, thereby strongly reducing the productivity of the Azorean waters. If so, this might result in the loss of a foraging area at the early stages of spring migration. In this case, baleen whales would have to adjust their spring migration to avoid a mismatch with the availability of suitable prey (Learmonth et al. 2006).

In conclusion, our findings support the hypothesis that baleen whales track the North Atlantic spring bloom, and utilize mid-latitude areas such as the Azores as feeding areas en route towards their summer feeding grounds. In view of anticipated changes in ocean stratification and phytoplankton growth (Sarmiento et al. 2004, Behrenfeld et al. 2006, Polovina et al. 2008), further monitoring of the migratory patterns of baleen whales in relation to phytoplankton bloom development is of high importance.

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