



UvA-DARE (Digital Academic Repository)

Moving in concert: Social and migratory behaviour of dolphins and whales in the North Atlantic Ocean

Visser, F.

Publication date
2014

[Link to publication](#)

Citation for published version (APA):

Visser, F. (2014). *Moving in concert: Social and migratory behaviour of dolphins and whales in the North Atlantic Ocean*. [Thesis, fully internal, Universiteit van Amsterdam].

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, P.O. Box 19185, 1000 GD Amsterdam, The Netherlands. You will be contacted as soon as possible.

Chapter 6

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

...st
...d ph.
...h they
...wing a
...is the s
...int of rec
...oundscap
...ur focus to
...us far, the s
...ns have recel
...ocial structur
...ween individuals
...as pilot whal
...vital importan
...l are regulated
...een individua
...gain insight int
...eir social stru
...term stable so
...s? These ques
...ork analysis
...the Azores.
...rowing whalr
...lhães et al. ?
...ly strong in t'
...te-fidelity
...at individu
...and coul
...tge and b
...hese wh
...ore-bi
...ving k
...r, we al
...-tens

Chapter 6. Timing of migratory baleen whales at the Azores in relation to the North Atlantic spring bloom

Fleur Visser, Karin L Hartman, Graham J Pierce, Vasilis D Valavanis, Jef Huisman

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.

This chapter is based on the paper: Visser F, Hartman KL, Valavanis, Pierce GJ and Huisman J (2011). Timing of migratory baleen whales at the Azores in relation to the North Atlantic spring bloom. Marine Ecology Progress Series 440:267-279.

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 $\sim 35^\circ$ N, just north of the North Atlantic Subtropical Gyre (NASG), in December–January (Fig. 1). The bloom subsequently 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 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 counterexample). 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 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). 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.

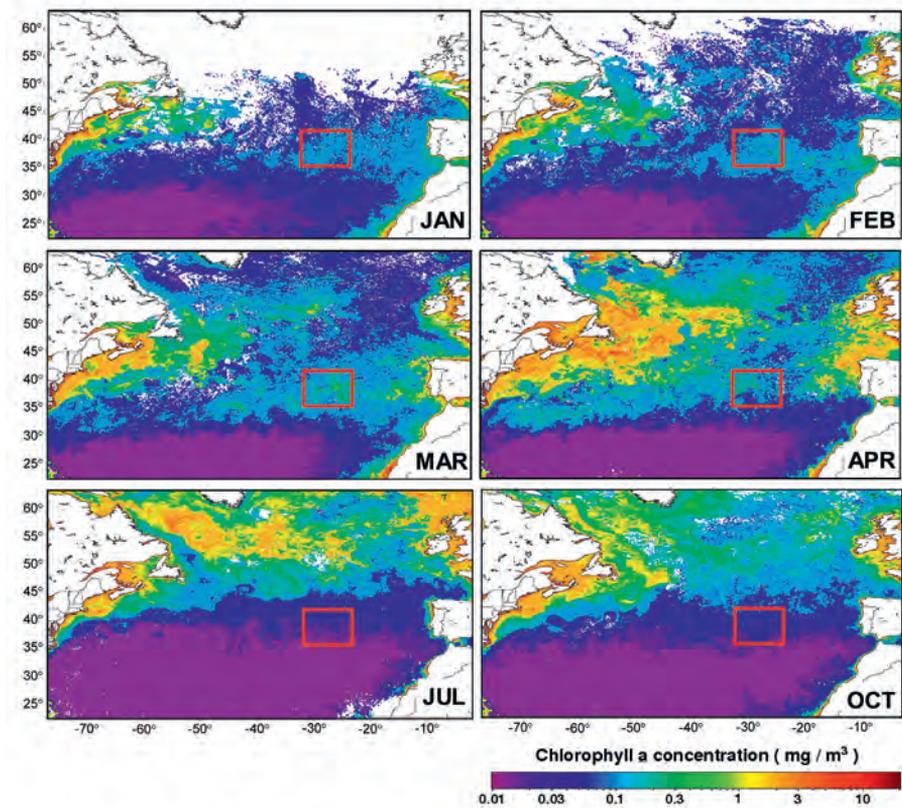


Figure 1. Annual variation in chlorophyll *a* concentration (chl *a*) in the North Atlantic Ocean. The location of the Azores is outlined by the red rectangle. The 6 panels represent mean monthly chl *a* values for January, February, March, April, July and October 2006. Data were retrieved from the NASA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

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 ($38^{\circ} 24' N$, $28^{\circ} 11' W$; 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).

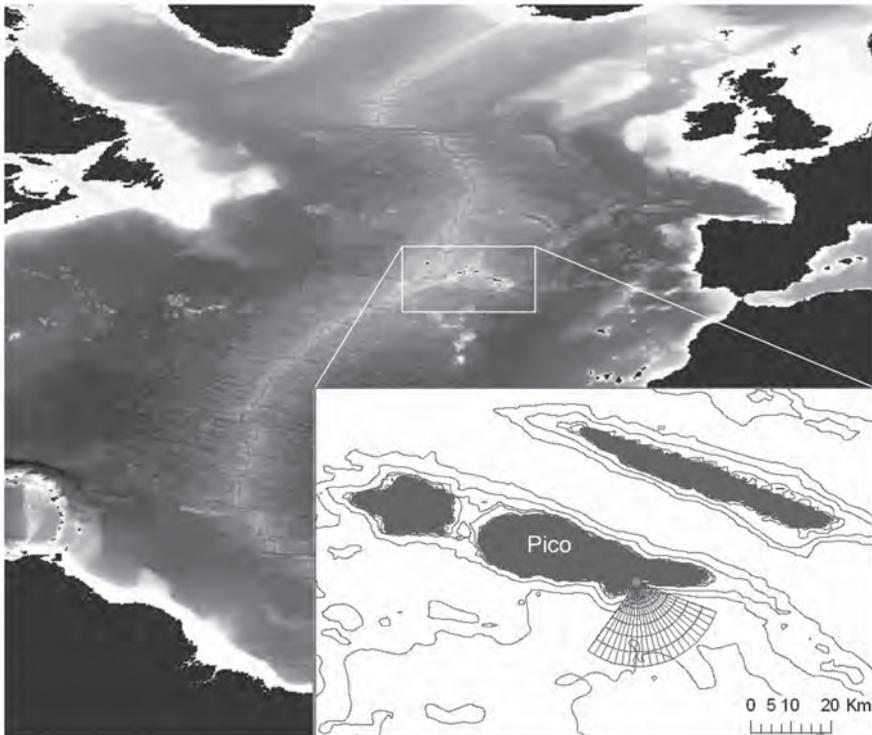


Figure 2. Location of the Azores and the research area south of Pico Island (inset). The observation grid outlines the range covered by the shore-based observations from our observation platform (*). Bathymetry map of the North Atlantic Ocean was reproduced from the GEBCO Digital Atlas (IOC IHO BODC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

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 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 × 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 km² 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× 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× 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 km² (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:

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

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 ± 3.1). Likewise, the timing of the peak of the bloom (Week 9.0 ± 3.2) and the duration of the bloom (14.0 ± 3.8 wk) were variable between years. The timing of the end of the bloom was fairly constant (Week 15.5 ± 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 mg m⁻³ (mean \pm SD = 0.48 ± 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 mg m⁻³ (mean \pm SD = 0.08 ± 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.

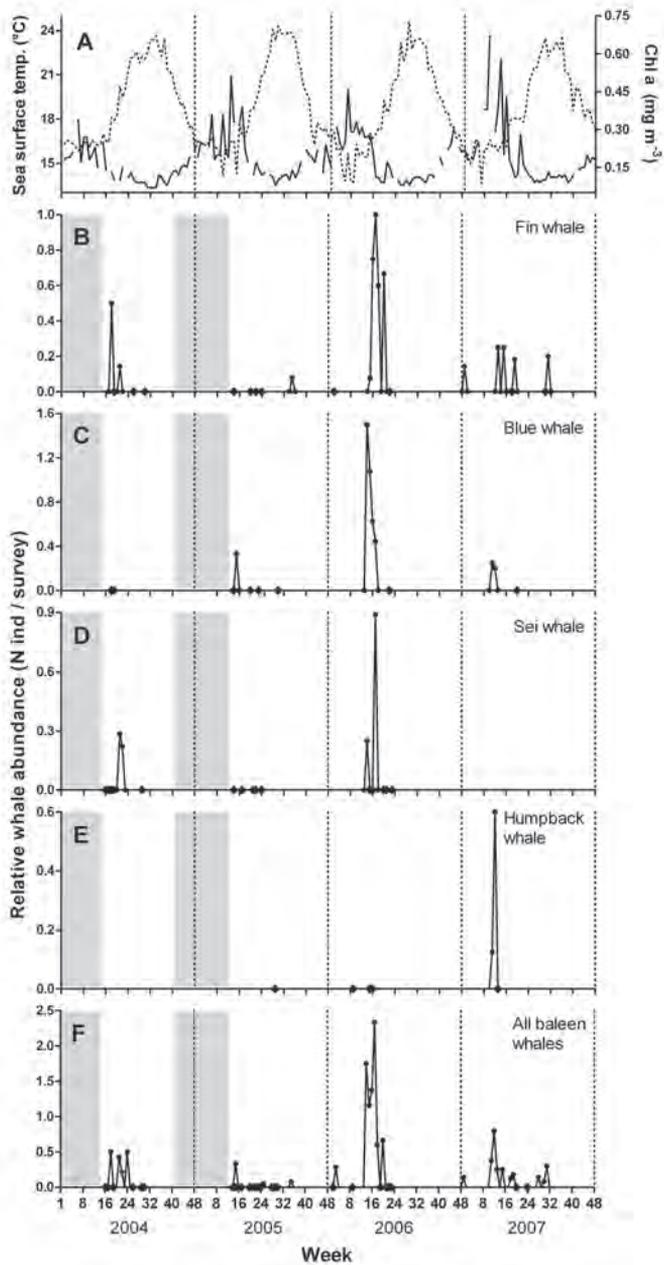


Figure 3. Relative abundance of baleen whales in relation to sea surface temperature (SST) and chlorophyll *a* (chl *a*) concentration. (A) Temporal variation in SST (dashed line) and chl *a* (solid line). (B-F) Temporal variation in relative abundance of fin whale, blue whale, sei whale, humpback whale, 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

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 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).

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.

	No. of focal follows			Relative abundance (ind. survey ⁻¹)	Minimum residence time		
	No. surveyed	(n)	(h)		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	-

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.

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
Fin whale ¹⁾				
2004	18	+14	+12	+3
2006	17	+14	+10	+3
2007	13	+16	+3	-3
Blue whale				
2005	15	+13	+2	-2
2006	14	+11	+7	0
2007	11	+14	+1	-5
Sei whale				
2004	21	+17	+15	+6
2006	17	+14	+10	+3
Humpback whale ²⁾				
2007	12	+15	+2	-4
<i>SD Fin whale (weeks)</i>	2.6	1.2	4.7	3.5
<i>SD Blue whale (weeks)</i>	2.1	1.5	3.2	2.5
<i>SD Sei whale (weeks)</i>	2.8	2.1	3.5	2.1
<i>SD all species (weeks)</i>	2.1	1.3	3.3	2.4

¹⁾In 2005, the number of fin whales in the surveys was too low to estimate the timing of their peak abundance.

²⁾SD of humpback whale could not be calculated, because its peak abundance could be determined for one year only.

Behaviour

The behavioural budgets of blue, fin, sei and hump back 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.

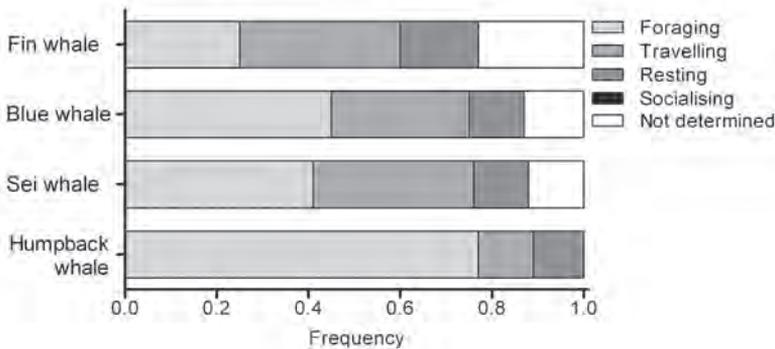


Figure 4. Behavioural budgets of fin, blue, sei and humpback whales

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 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 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) $>2\times$ 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^{-3} . 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 development 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 $>16\text{ mm}$ (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 (photo-period; 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 ($\sim 60^\circ\text{N}$; fin and sei whales), or up to the latitude of northern Spain ($\sim 42^\circ\text{N}$; blue whales) (Great Whales Satellite Telemetry Program: 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 associated 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 interannual 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 relative 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. Longterm 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.

Acknowledgements

We thank Enrico Villa for sharing his findings on foraging fin whales, and the reviewers for their helpful comments on our manuscript. We gratefully acknowledge support in GIS mapping by Kees den Hollander and Bert van den Broek of the Netherlands Organisation for Applied Scientific Research (TNO). The research of F.V. was supported by the 'ECOSUMMER' Marie Curie training site (MEST-CT-2005-020501) and the Prins Bernhard Cultuurfonds. G.J.P. was supported by the ANIMATE project (MEXCCT- 2006-042337) and J.H. by the STRATIPHYT project.

References

- Agler BA, Beard JA, Bowman RS, Corbett HD and others (1990) Finback whale, *Balaenoptera physalus*, photographic identification: methodology and preliminary results from the western North Atlantic. Rep Int Whaling Comm 12(Spec Issue): 349–357
- Alerstam T, Hedenström A, Åkesson S (2003) Long-distance migration: evolution and determinants. Oikos 103: 247–260
- Angel MV (1989) Vertical profiles on the pelagic communities in the vicinity of the Azores front and their implications to deep ocean ecology. Prog Oceanogr 22: 1–46
- Arnbom T (1987) Individual identification of sperm whales. Rep Int Whaling Comm 37: 201–204
- Astthorsson OS (1990) Ecology of the euphausiids *Thysanoessa raschi*, *T. inermis* and *Meganctiphanes norvegica* in Ísafjord-deep, northwest-Iceland. Mar Biol 107: 147–157
- Behrenfeld MJ (2010) Abandoning Sverdrup's critical depth hypothesis on phytoplankton blooms. Ecology 91: 977–989
- Behrenfeld MJ, O'Malley RT, Siegel DA, McClain CR and others (2006) Climate-driven trends in contemporary ocean productivity. Nature 444: 752–755
- Both C, Bijlsma RG, Visser ME (2005) Climatic effects on timing of spring migration and breeding in a longdistance migrant, the pied flycatcher, *Ficedula hypoleuca*. J Avian Biol 36: 368–373
- Burtenshaw JC, Oleson EM, Hildebrand JA, McDonald MA, Andrew RK, Howe BM, Mercer JA (2004) Acoustic and satellite remote sensing of blue whale seasonality and habitat in the Northeast Pacific. Deep-Sea Res II 51: 967–986

- Chaves FA (1924) Cetáceos que aparecem nos mares dos Açores. *A Pesca Marítima* 15: 41–44
- Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, Tershy BR (2005) From wind to whales: trophic links in a coastal upwelling system. *Mar Ecol Prog Ser* 289: 117–130
- Dakos V, Benincà E, van Nes EH, Philippart CJM, Scheffer M, Huisman J (2009) Interannual variability in species composition explained as seasonally entrained chaos. *Proc Biol Sci* 276: 2871–2880
- Dalpadado P (2006) Distribution and reproduction strategies of krill (Euphausiacea) on the Norwegian shelf. *Polar Biol* 29: 849–859
- Doniol-Valcroze T, Berteaux D, Larouche P, Sears R (2007) Influence of thermal fronts on habitat selection by four baleen whale species in the Gulf of St. Lawrence. *Mar Ecol Prog Ser* 335: 207–216
- Doyle TK, Houghton JDR, O'Súilleabháin PF, Hobson VJ, Marnell F, Davenport J, Hays GC (2008) Leatherback turtles satellite-tagged in European waters. *Endang Species Res* 4: 23–31
- Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD (2010) Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proc Natl Acad Sci USA* 107: 2078–2081
- Fiedler PC, Reilly SB, Hewitt RP, Demer DA, and others (1998) Blue whale habitat and prey in the California Channel Islands. *Deep-Sea Res II* 45: 1781–1801
- Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ (2006) Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the western Antarctic Peninsula. *Mar Ecol Prog Ser* 317: 297–310
- Gaskin DE (1982) The ecology of whales and dolphins. Heinemann, London
- Goldbogen JA, Calambokidis J, Oleson E, Potvin J, Pyenson ND, Schorr G, Shadwick RE (2011) Mechanics, hydro - dynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. *J Exp Biol* 214: 131–146
- Gordon JCD, Steiner L, Gonçalves JM (1990) Sei whales (*Balaenoptera borealis*) encountered in the Azores: a new record for the region. *Arquipel Life Earth Sci* 8: 97–100
- Gordon JCD, Steiner L, Martins HR (1995) Observations of fin whales (*Balaenoptera physalus* L., 1758) around the central north Atlantic islands of the Azores and Madeira. *Arquipel Life Earth Sci* 13A: 79–84
- Gore MA, Rowat D, Hall J, Gell FR, Ormond RF (2008) Transatlantic migration and deep mid-ocean diving by basking shark. *Biol Lett* 4: 395–398
- Gwinner E (1996) Circannual clocks in avian reproduction and migration. *Ibis* 138: 47–63
- Hoelzel AR, Dorsey EM, Stern SJ (1989) The foraging specializations of individual minke whales. *Anim Behav* 38: 786–794
- Huisman J, van Oostveen P, Weissing FJ (1999) Critical depth and critical turbulence: two different mechanisms for the development of phytoplankton blooms. *Limnol Oceanogr* 44: 1781–1787
- Huisman J, Pham Thi NN, Karl DM, Sommeijer B (2006) Reduced mixing generates oscillations and chaos in the oceanic deep chlorophyll maximum. *Nature* 439: 322–325
- Ingram SN, Walshe L, Johnston D, Rogan E (2007) Habitat partitioning and the influence of benthic topography and oceanography on the distribution of fin and minke whales in the Bay of Fundy, Canada. *J Mar Biol Assoc UK* 87: 149–156
- IOC/IHO BODC (2003) Centenary Edition of the GEBCO Digital Atlas. Published on CD-ROM on behalf of the Intergovernmental Oceanographic Commission and the International Hydrographic Organization as part of the General Bathymetric Chart of the Oceans. British Oceanographic Data Centre, Liverpool
- Johnson J, Stevens I (2000) A fine resolution model of the eastern North Atlantic between the Azores, the Canary Islands and the Gibraltar Strait. *Deep-Sea Res I* 47: 875–899
- Johnston DW, Thorne LH, Read AJ (2005) Fin whales *Balaenoptera physalus* and minke whales *Balaenoptera acutorostrata* exploit a tidally driven island wake ecosystem in the Bay of Fundy. *Mar Ecol Prog Ser* 305: 287–295
- Katona SK, Beard JA (1990) Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. *Rep Int Whaling Comm* 12(Spec Issue): 295–305
- Kellogg R (1929) What is known on the migrations of some of the whalebone whales? Smithsonian Institution Annual Report No. 1928. U.S.G.P.O. Washington, DC, p 467–494
- Koeller P, Fuentes-Yaco C, Platt T, Sathyendranath S and others (2009) Basin-scale coherence in phenology of shrimps and phytoplankton in the North Atlantic Ocean. *Science* 324: 791–793
- Labat JPh, Cuzin-Roudy J (1996) Population dynamics of the krill *Meganyctiphanes norvegica* (M. Sars, 1857) (Crustacea: Euphausiacea) in the Ligurian Sea (NW Mediterranean Sea): size structure, growth and mortality modelling. *J Plankton Res* 18: 2295–2312

- Learmonth JA, MacLeod CD, Santos MB, Pierce GJ, Crick HQP, Robinson RA (2006) Potential effects of climate change on marine mammals. *Oceanogr Mar Biol Annu Rev* 44: 429–456
- Littaye A, Gannier A, Laran S, Wilson JPF (2004) The relationship between summer aggregation of fin whales and satellite-derived environmental conditions in the northwestern Mediterranean Sea. *Remote Sens Environ* 90: 44–52
- Lockyer C (1984) Review of baleen whale (Mysticeti) reproduction and implications for management. *Rep Int Whaling Comm* 6(Spec Issue): 27–50
- Longhurst AR (2007) *Ecological geography of the sea*. Academic Press, London
- Malcolm SB (1987) Monarch Butterfly migration in North America: controversy and conservation. *Trends Ecol Evol* 2: 135–138
- Mann J (1999) Behavioural sampling methods for cetaceans: a review and critique. *Mar Mamm Sci* 15: 102–122
- Morel A, Huot Y, Gentili B, Werdell PJ, Hooker SB, Franz BA (2007) Examining the consistency of products derived from various ocean color sensors in open ocean (Case 1) waters in the perspective of a multi-sensor approach. *Remote Sens Environ* 111: 69–88
- Nieukirk SL, Stafford KM, Mellinger DK, Dziak RP, Fox CG (2004) Low-frequency whale and seismic airgun sounds recorded in the mid-Atlantic Ocean. *J Acoust Soc Am* 115: 1832–1843
- Norris K (1967) Some observations on the migration and orientation of marine mammals. In: Storm RM (ed) *Animal orientation and navigation*. University of California Press, Berkeley, CA, p 320–380
- Olsen E, Budgell WP, Head E, Kleivane L and others (2009) First satellite-tracked long-distance movement of a sei whale (*Balaenoptera borealis*) in the North Atlantic. *Aquat Mamm* 35: 313–318
- Panigada S, Notobartolo Di Sciarra G, Zanardelli-Panigada M, Airoidi S, Borsani JF, Jahoda M (2005) Fin whales (*Balaenoptera physalus*) summering in the Ligurian Sea: distribution, encounter rate, mean group size and relation to physiographic variables. *J Cetacean Res Manag* 7: 137–145
- Pauly D, Trites AW, Capuli E, Christensen V (1998) Diet composition and trophic levels of marine mammals. *ICES J Mar Sci* 55: 467–481
- Pendleton DE, Pershing AJ, Brown MW, Mayo CA, Kenney RD, Record NR, Cole TVN (2009) Regional-scale mean copepod concentration indicates relative abundance of North Atlantic right whales. *Mar Ecol Prog Ser* 378: 211–225
- Piatt JF, Methven DA, Burger AE, McLagan RL, Mercer V, Creelman E (1989) Baleen whales and their prey in a coastal environment. *Can J Zool* 67: 1523–1530
- Polovina JJ, Howell EA, Abecassis M (2008) Ocean's least productive waters are expanding. *Geophys Res Lett* 35: L03618. doi: 10.1029/2007GL031745
- Santora JA, Reiss CS, Loeb VJ, Veit RR (2010) Spatial association between hotspots of baleen whales and demographic patterns of Antarctic krill *Euphausia superba* suggests size-dependent predation. *Mar Ecol Prog Ser* 405: 255–269
- Santos RS, Hawkins S, Monteiro LR, Alves M, Isidoro EJ (1995) Marine research, resources and conservation in the Azores. *Aquat Conserv Mar Freshwat Ecosys* 5: 311–354
- Sarmiento JL, Slater R, Barber R, Bopp L and others (2004) Response of ocean ecosystems to climate warming. *Global Biogeochem Cycles* 18: GB3003. doi: 10.1029/2003GB002134
- Schilling MR, Seipt I, Weinrich MT, Frohock SE, Kuhlberg AE, Clapham PJ (1992) Behavior of individually-identified sei whales *Balaenoptera borealis* during an episodic influx into the southern Gulf of Maine in 1986. *Fish Bull* 90: 749–755
- Sears R, Williamson JM, Wenzel FW, Bérubé M, Gendron D, Jones P (2000) Photographic identification of the blue whale (*Balaenoptera musculus*) in the Gulf of St. Lawrence, Canada. *Rep Int Whaling Comm* 12 (Spec Issue): 335–342
- Seebens H, Einsle U, Straille D (2009) Copepod life cycle adaptations and success in response to phytoplankton spring bloom phenology. *Glob Change Biol* 15: 1394–1404
- Siegel DA, Yoder SC, Yoder JA (2002) The North Atlantic spring phytoplankton bloom and Sverdrup's critical depth hypothesis. *Science* 296: 730–733
- Simon M, Stafford KM, Beedholm K, Lee CM, Madsen PT (2010) Singing behaviour of fin whales in the Davis Strait with implications for mating, migration and foraging. *J Acoust Soc Am* 128: 3200–3210
- Skov H, Gunnlaugsson T, Budgell WP, Horne J and others (2008) Small-scale spatial variability of sperm and sei whales in relation to oceanographic and topographic features along the Mid-Atlantic Ridge. *Deep-Sea Res II* 55: 254–268
- Stafford KM, Citta JJ, Moore SE, Daher MA, George JE (2009) Environmental correlates of blue whale and fin whale call detections in the North Pacific Ocean from 1997 to 2002. *Mar Ecol Prog Ser* 395: 37–53

- Steiner L, Silva MA, Zereba J, Leal MJ (2008) Bryde's whales, *Balaenoptera edeni*, observed in the Azores: a new species record for the region. *J Mar Biol Assoc UK Marine Biodiversity Records* 1: e66
- Sverdrup HU (1953) On conditions for the vernal blooming of phytoplankton. *J Cons Int Explor Mer* 18: 287–295
- Tarling GA (2010) Population dynamics of Northern krill (*Meganyctiphanes norvegica* Sars). *Adv Mar Biol* 57: 59–90
- Tarling GA, Cuzin-Roudy J (2003) Synchronization in the molting and spawning activity of northern krill (*Meganyctiphanes norvegica*) and its effect on recruitment. *Limnol Oceanogr* 48: 2020–2033
- Townsend DW, Cammen LM, Holligan PM, Campbell DE, Pettigrew NR (1994) Causes and consequences of variability in the timing of spring phytoplankton blooms. *Deep-Sea Res I* 41: 747–765
- Valavanis VD (2002) Geographic information systems in oceanography and fisheries. Taylor & Francis, London
- Valdés L, López-Urrutia A, Cabal J, Alvarez-Ossorio M and others (2007) A decade of sampling in the Bay of Biscay: what are the zooplankton time series telling us? *Prog Oceanogr* 74: 98–114
- Villa D, Hart JD, de Baker AC, Rossin V (2011) Fin whales feeding on Northern krill off Pico Island (Azores) during spring migration. Abstract at 25th Annual Conference of the European Cetacean Society, March 20–23, 2011, Cadiz, Spain
- Visser F, Hartman KL, Rood EJJ, Hendriks AJE and others (2011) Risso's dolphins alter daily resting pattern in response to whale watching at the Azores. *Mar Mamm Sci* 27: 366–381
- Whitehead H, Carscadden JE (1985) Predicting inshore whale abundance—whales and capelin off the Newfoundland coast. *Can J Fish Aquat Sci* 42: 976–981
- Yochem PK, Leatherwood S (1985) Blue whales *Balaenoptera musculus* (Linnaeus, 1758). In: Ridgway SH, Harrison RJ (eds) *Handbook of marine mammals, Vol. 3. The sirenians and baleen whales*. Academic Press, London, p 193–240