

# **Demographic parameters of seabirds in the North Atlantic along a marine productivity gradient**

Dissertação apresentada à Universidade de Coimbra para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Ecologia, realizada sob a orientação científica do Professor Doutor Jaime Albino Ramos (Universidade de Coimbra) e do Doutor Vítor Hugo Paiva (Universidade de Coimbra).

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Coimbra | 2016



# Agradecimentos

Quero agradecer primeiramente aos meus orientadores, o Dr. Jaime A. Ramos e o Dr. Vítor Hugo Paiva por toda a paciência e dedicação que tiveram comigo e na ajuda que me prestaram para a realização desta dissertação, sem eles tudo isto seria impossível.

Quero agradecer a toda a minha família por me terem apoiado durante estes seis anos que estive em Coimbra, em especial aos meus pais e ao meu irmão.

A todos os meus amigos em especial a Ana Filipa, Ana Coelho, Carlos Gonçalves, Carolina Magro, Joana Freitas, Rita Xoko, Sara Isidoro e ao Zé Pedro por terem sido uns amigos fantásticos, e que sei que o vão continuar a ser.

Ao meu futuro farmacêutico Gonçalo Bento por tudo aquilo que passamos juntos, foste sem dúvida uma pessoa importante nesta caminhada.

Ao Fenistil, Peixe e Aftaminas por estarem sempre prontos para sair à noite e aproveitar o que esta cidade tem de melhor, sem eles estes anos não tinham valido a pena.

Ao João Tabanez por ter sido o meu companheiro no apoio ao melhor clube do mundo.

A toda a minha família de praxe que foram como uma segunda família para mim em especial ao meu padrinho José Cerca que esteve sempre pronto para me ajudar nos estudos e à minha madrinha Gabi Nobre.

À minha farmacêutica preferida Joana Ferraz por teres sido uma pessoa que esteve sempre disponível para me ouvir e ajudar naquilo que podias.

À minha grande amiga Rita Alexandre que apesar de não termos feito a faculdade juntos fizeste e vais fazer sempre parte da minha vida.

Aos meus colegas de laboratório a Ana, Diana, Jorge e Zé pelas palhaçadas e risadas que me deram durante este último ano.

À Republica dos Galifões por todas as vivências que passei nela e por ter sido uma casa que significou muito nos últimos tempos, para vocês sai um GA... LI... e o resto vocês sabem.

*A todos o meu muito obrigado!*

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## ABSTRACT

It is well known that availability of food has an important role in explaining the breeding phenology of seabirds. This availability can be inferred from oceanographic conditions such as sea surface temperature (SST) and chlorophyll *a* concentration (CC), which are known to be proxies of marine productivity. Moreover, seabird species have the capacity to use these proxies as cues to start the breeding season.

We conducted a study to evaluate whether there is an adjustment of the breeding season of several species of seabirds (*Calonectris* sp., *Bulweria bulwerii*, *Hydrobates* sp., *Pterodroma* sp. and *Puffinus* sp.) with the oceanographic conditions around the archipelagos that constitute the Macaronesian region (Azores, Madeira, Canary and Cabo Verde), and also the Berlengas archipelago in the North Atlantic Ocean. In this region marine productivity broadly decreases from the Azores (temperate region) to Cabo Verde (tropical region).

The oceanographic conditions were assessed using remote sensing data from 2003-2015. Timing of breeding for all Procellariiform species was taken from the literature, and complemented with fieldwork in Cabo Verde. There was a clear seasonality pattern in oceanographic conditions, more marked in the temperate group (Azores, Berlenga, Madeira and Canary Islands) than the tropical group (Cabo Verde Islands), where the conditions were more stable throughout the year. We concluded that the species breed in several archipelagos along this temperate-tropical gradient (*Calonectris* sp. *Hydrobates* sp. and *Puffinus* sp.) lay eggs sooner in the northernmost archipelagos and later in the southernmost archipelagos where the peak of marine productivity (and likely prey availability) occur latter. Although there is some adjustment of the breeding season of these species with the oceanographic conditions in the different archipelagos, a direct relationship between the peak of laying and the peak in CC was not visible, partly because the difference between these two peaks differed greatly among archipelagos. Plus, the winter breeding species showed no apparent relationship with the prevailing oceanographic conditions.

We propose that in this region of the North Atlantic, the oceanographic conditions are not the sole reason explaining the seabirds' timing of breeding. Instead the competition for nesting sites may be even more relevant, given the little overlap in timing of breeding among species in the same location. This means that different species breed at a different time of the year, and winter breeding species may do so simply to avoid competition with the more numerous, larger and more competitive summer breeding species. Further studies are needed to support this hypothesis and help to understand the breeding phenology of the seabird species breeding on the Macaronesian region.

**Keywords:** Macaronesian, breeding season, adjustment, timing of breeding, Procellariiformes



## Resumo

A disponibilidade de alimento tem sido apontada como tendo um papel importante na fenologia da reprodução das aves marinhas. Esta disponibilidade pode ser inferida a partir de condições oceanográficas, tais como a temperatura da superfície do mar (SST) e a concentração de clorofila *a* (CC), que se sabe serem indicadores de produtividade marinha. Além disso, várias espécies de aves marinhas têm a capacidade de usar tais indicadores para iniciar a época de reprodução.

Realizou-se um estudo para avaliar se há um ajuste da época de reprodução de várias espécies de aves marinhas (*Calonectris* sp., *Bulweria bulwerii*, *Hydrobates* sp., *Pterodroma* sp. e *Puffinus* sp.) em relação às condições oceanográficas, em torno dos arquipélagos que constituem a região da Macaronésia (Açores, Madeira, Canárias e Cabo Verde), e também o arquipélago das Berlengas no Oceano Atlântico Norte. Nesta região a produtividade marinha em geral diminui a partir dos Açores (região temperada) para Cabo Verde (região tropical).

As condições oceanográficas foram avaliadas entre 2003-2015 utilizando dados de detecção remota. O tempo de reprodução para todas as espécies de Procelariiformes foi retirada a partir da literatura, e complementada com o trabalho de campo em Cabo Verde. Verificou-se um claro padrão de sazonalidade das condições oceanográficas, mais acentuado no grupo temperado do que no grupo tropical, onde as condições são mais estáveis ao longo do ano. Concluímos que as espécies que se reproduzem em vários arquipélagos ao longo deste gradiente temperado-tropical (*Calonectris* sp., *Hydrobates* sp. e *Puffinus* sp.) põem ovos mais cedo nos arquipélagos mais setentrionais e mais tarde nos arquipélagos meridionais, onde o pico de produtividade marinha é mais tarde. Embora haja algum ajuste da época de reprodução destas espécies com as condições oceanográficas nos diferentes arquipélagos, não se verificou uma relação directa entre o pico da postura e o pico em CC, em parte porque a diferença entre estes dois picos variaram muito entre os arquipélagos. Além disso, as espécies que se reproduzem no inverno

não mostraram nenhuma relação aparente com as condições oceanográficas prevalentes.

Propomos que nesta região do Atlântico Norte, as condições oceanográficas não deverão ser a razão principal para explicar a época de reprodução das aves marinhas. A competição por locais de nidificação pode ter um papel ainda mais importante, dada a pouca sobreposição no período de reprodução entre as espécies que se reproduzem no mesmo local. Isto significa que as diferentes espécies se reproduzem em alturas diferentes do ano, e as espécies que se reproduzem durante o inverno podem fazê-lo simplesmente para evitar a concorrência com as espécies mais numerosas, maiores e mais competitivas que se reproduzem no verão. Mais estudos são necessários para apoiar esta hipótese e para ajudar a compreender a fenologia de reprodução das espécies de aves marinhas que se reproduzem na região da Macaronésia.

**Palavras-chaves:** Macaronesia, época de reprodução, ajuste, período de reprodução, Procelariiformes

# INTRODUCTION

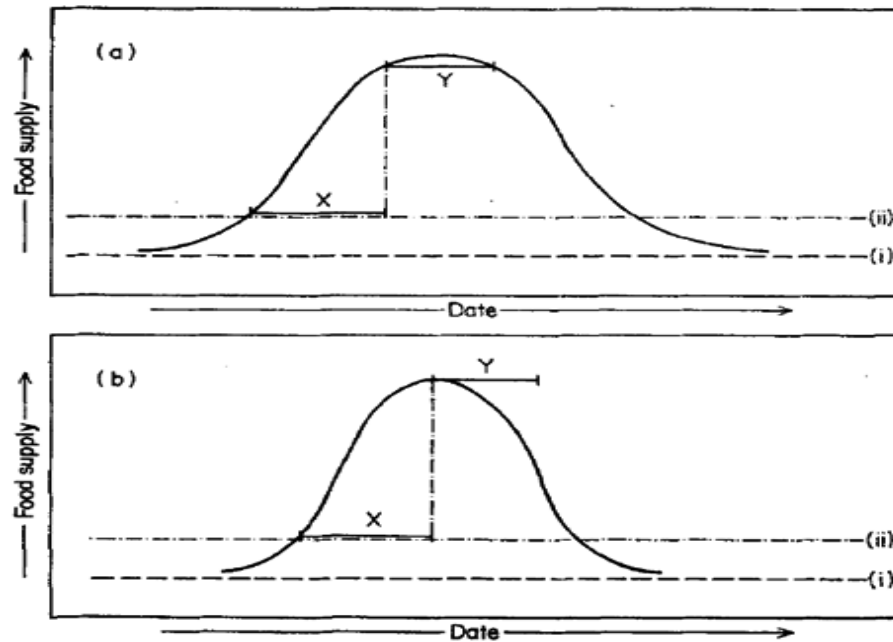
## *Timing of birds' breeding season*

The availability of food resources for top predators shows strong temporal variations and exerts a strong influence on the timing of their breeding season (Lack 1967). This difference in the temporal availability of food is more marked for temperate and polar regions because there is a well-defined seasonality than in tropical regions, where the conditions are normally more stable throughout the year (Ashmole 1971; Weimerskirch 2007; Mann and Lazier 2013). It is well established that animals will start the breeding season in order to match the period when chicks are in the nest with the timing when food availability is higher (Harris 1969; Perrins 1970; Cockrem 1995; Frederiksen *et al.* 2004; Verhulst & Nilsson 2008), so chicks have a greater probability of survival, leading to an overall increase of fitness. Top predators should commence breeding as quickly as possible because along the breeding season the availability of food tends to decline (Martin 1987), decreasing consequently the reproductive success (Verhulst & Nilsson 2008).

Birds are not an exception to what is described above, as they also try to synchronize the breeding season with the time of the year when more food is available. However, for the females to lay eggs they need to form them first, which is a great energetic cost (Nager *et al.* 2001; Ramírez *et al.* 2016). Females form the eggs only when there is sufficient food to do it, without jeopardizing their own survival (Perrins 1970; Perrins 1996). Because the formation of the eggs is an expensive process, and given the fact that food availability is seasonal, females need to find these resources in the environment in a short time period (Perrins 1970). The only nutrient that apparently is stored in large quantities before the beginning of the breeding season is calcium (Sturkie 1965), most likely because of its importance in the formation of egg shells. Birds have a period before the chicks are in the nest, which is dependent on the time needed to develop the gonads, form, lay and incubate the eggs (Perrins 1970). Therefore the females need to initiate the breeding season when the abundance of food is not so high, so that when the eggs hatch the availability of food is at its highest (Perrins 1970; Monticelli *et al.* 2007). The

time that it takes to have the chicks on the nest varies from species to species, taking always a minimum of three weeks in the case of small passerines, like the European Robin *Erithacus rubecula* (Lack 1946), and more than eleven weeks in the case of the biggest albatrosses (Richdale 1952). It is because this timeline that birds need to adjust their breeding season to the best time possible, for the chicks to have higher food availability when they hatch. However the peak of food abundance generally varies from year to year, and from habitat to habitat so the birds need to adjust the breeding season according to temporal and spatial patterns of food availability (Dias & Blondel 1996; Frederiksen *et al.* 2004).

Perrins (1970) outlined two hypothetical situations of variation in food availability along the breeding season (the food necessary for body maintenance and needed to form the eggs is the same in both situations) differing in the speed and the time that food is available for female birds (Figure 1). In (a) the resources appear gradually in the environment (providing an opportunity for a better synchronization between food supply and reproduction), and birds can lay the eggs when food is not so abundant in order to raise their chicks when food availability reaches a peak. In (b) the resources appear suddenly and are available during a short period, so the synchronization between food supply and reproduction is poor: when females generate and incubate the egg the food supply is already at its maximum, consequently when the eggs hatch the food availability is already decreasing and by the end of the reproductive season the resources are scarce (Martin 1987).



**Figure 1** Two different scenarios for food availability in the environment: (a) the food appears gradually and is available during a longer time period; (b) the food appears suddenly and reaches the peak quickly. The period of time between the formation of the eggs and the hatching (X), and the hatching and the fledgling time (Y) are the same in both situations. The dashed lines represent the food necessary for body maintenance (i) and egg formation (ii). Figure reproduced from Perrins (1970).

Birds can have two different strategies in the breeding season. They can lay several eggs per clutch and adjust the quantity of eggs laid in relation to environmental conditions, laying more eggs when the food supply is higher and less when the conditions are not so favorable. Or they can lay only one egg per breeding season, and invest strong parental care in the only chick of the season; if the egg is lost they only can breed again in the next breeding season. This is the case of most seabird species of the order Procellariiformes. Normally, birds that lay only one egg and do not relay because the formation of the egg is very slow, so when the chick would hatch the environmental conditions would be so unfavorable that there would be no food to raise the replacement chick (Harris 1969). In these situations the adults opt to end the breeding season, in order not to jeopardize their own survival (Stearns 1992). This choice of not laying a second clutch is only profitable for long lived *K*-strategist species such as seabirds, because they will have more opportunities to breed in the future (Martin 1987). Studies with several species show that, in

these scenarios, the birds that start earlier the breeding season (when the food supply is already increasing) have more chances to raise their chick(s), because the reproductive success of birds that breed later is lower (Burger *et al.* 1996; Ramos 2001).

### ***Factors shaping the breeding season***

In the globe there are areas where the seasonality is well marked (polar and temperate regions) and other areas where this seasonality is not so noticeable (tropical regions). This difference is crucial when one thinks about matching the breeding season when food availability in the environment is higher. In temperate and polar regions to synchronize the breeding season with the peak of food availability is easier because the peak of food abundance is well defined (Baker 1938). Several studies showed that in predictable environments, particularly in polar and temperate regions, the seabird chick-rearing period is well synchronized with the period of maximum food availability (Schreiber 1980; Lormée *et al.* 2000; Le Corre 2001; Frederiksen *et al.* 2004). In the temperate regions, photoperiod and the temperature, which are connected, appear to play a major role in the breeding season (Baker 1938; Frederiksen *et al.* 2004) functioning as proximate factors for food availability (Cockrem 1995). In the tropics the environmental conditions are relatively constant throughout the year and several seabird species breed throughout the year (Baker 1938; Le Corre *et al.* 2003). Because food availability is very important for chick-rearing, tropical seabirds must rely on different signals to commence breeding.

Overall, food availability is a key factor that affects the reproductive success throughout the breeding season in both temperate and tropical areas (Harris 1969; Perrins 1970; Cockrem 1995; Frederiksen *et al.* 2004; Verhulst & Nilsson 2008). However, there is often also an increase of predation along the breeding season, which can explain a decrease in fledging success for many species. The abundance of some parasite species can also increase along the breeding season which leads to higher chick mortality. The cannibalism is other factor that increases along the breeding season. Because these effects also

increase along the breeding season, there is even more selective pressure to breed as soon as possible. However there are many reasons why breeding may be delayed: female age affects laying date; i.e. birds that breed for the first time have difficulties to breed at the best moment (Burger *et al.* 1996; Verhulst & Nilsson 2008), and although the difference may be only a few days, it can be enough to explain a lower reproductive success. In long lived species such as seabirds of the order procellariiformes, birds reproduce slightly earlier as they age, showing that reproductive success is also strongly linked with age (Ramos & Monticelli 2012). There are also studies showing that the date of laying may be, at least in part, a hereditary factor (Burger *et al.* 1996). Although most studies show that an early breeding season is advantageous, there are limits to this; as shown in Figure 1 there is a food limit required for females to form eggs, and this is a main factor to explain the annual variation in the onset of the breeding season.

### ***The breeding season of pelagic seabirds and food availability***

Similarly to terrestrial habitats, marine habitats also present seasonality in abundance of food therefore there are certain times of the year when it is more advantageous for marine animals to reproduce. Pelagic seabirds are animals that usually have high longevity and normally lay a clutch of only one egg, investing all the parental care in raising a single chick per breeding season. Many seabird species show annual reproductive cycles, therefore they should rely on some key-factor to initiate their breeding season. It is suggested by several authors that the breeding season is controlled by climatic signals such as sea surface temperature, which strongly modify the ocean conditions and lead to a favorable distribution of prey around breeding colonies (Brichetti *et al.* 2000; Jaquemet *et al.* 2007; Monticelli *et al.* 2007; Sandvik *et al.* 2008). Two factors have been used as surrogates of food abundance, and are strongly related with the initiation of breeding by seabirds, the sea surface temperature (SST) and the chlorophyll *a* concentration (CC) (Jaquemet *et al.* 2007; Monticelli *et al.* 2007; Sandvik *et al.* 2008). They are inversely related, in other words, when the SST is low CC is higher. The rapid variation of SST before the

beginning of the breeding season reflects a large environmental modification, favoring an increase in the marine productivity. This decrease in SST will lead to a bloom of phytoplankton (Jaquemet *et al.* 2007; Friedland *et al.* 2016) which overall represents a higher marine productivity, supporting the food webs at higher trophic levels (Monticelli *et al.* 2007). After the bloom of phytoplankton, which forms the base of the food chain, there will be the appearance of zooplankton followed by the appearance of pelagic fish, which are then predated by top predators such as cetaceans or seabirds. Records of fish abundance, which are the main food of seabirds, show that their breeding season is synchronized with such bloom of phytoplankton, which coincides with the best time for seabirds to reproduce (Brander & Hurley 1992; Frederiksen *et al.* 2006). For instance, Ramírez *et al.* (2016) found that the chick-rearing period of the European storm-petrel (*Hydrobates pelagicus*) in the Western Mediterranean coincided with the peak of abundance in ichthyoplankton species. When the seasonal variation in SST does not show a clear pattern the bloom of phytoplankton is smaller, which means that the birds cannot breed at the right time, failing the peak of food abundance. This principle appears to be identical in different oceans and has been well documented for several species of seabirds (Jaquemet *et al.* 2007; Monticelli *et al.* 2007; Fagundes *et al.* 2016). To have a correct match between the chick feeding period and the peak of food abundance there is usually an abrupt decrease in SST followed by a rapid increase in the abundance of phytoplankton. Jaquemet *et al.* (2007) studied the onset of the sooty tern (*Onychoprion fuscatus*) breeding season in the Indian Ocean in relation to oceanographic characteristics around four different islands and found that its timing of reproduction matched with the seasonal peaks of chlorophyll and with the variation of SST before this peak, in three of the four islands. The island without a seasonal breeding regime had stable oceanic conditions throughout the year, and therefore a greater unpredictability of the best time to breed.

As the SST is the environmental variable that is often more related with the onset of the seabirds' breeding season, changes in the SST values due to natural and anthropogenic causes will have profound effects in the breeding phenology of seabirds. The El Niño Southern Oscillation (ENSO) and the North



Atlantic Oscillation (NAO) are two worldwide phenomena that have a strong relationship with SST values. The ENSO is an atmospheric ocean phenomenon occurring every 3-7 years in the Pacific Ocean, but with effects on a global scale (Ramos *et al.* 2002; Monticelli *et al.* 2007). It consists of periods when there is a variation of SST, with two distinct phases, one phase in which there is warming of the ocean (El Niño), and a stage when the ocean is cooling (La Niña). El Niño begins in the central and eastern Pacific, and is related with a weakening of the trade winds, which causes a reduction of upwelling and consequently the collapse of food chains in the region (Brichetti *et al.* 2000). In relation to the NAO, there is also a relationship between SST of the region with NAO, causing a decrease in SST when the NAO values are positive and an increase when NAO values are negative. Years with a low extended winter NAO index are related with strong upwelling in the Portuguese and African coasts. This phenomenon causes a low abundance of pelagic prey because the larvae of fish and plankton are pushed away from the coast and die, which creates a spatial mismatch between plankton and fish larvae, pelagic prey and seabirds (Robinson 2004; Santos *et al.* 2004; Santos *et al.* 2007). Therefore, a very low NAO index leads to a low marine productivity and abundance of prey, which has consequences in delaying the breeding season of seabirds in southern Europe, more eggs are abandoned and chicks are in poor physical condition. In 2011 the North Atlantic region experienced one of the lowest NAO in the last 500 years, and Cory's shearwater (*Calonectris diomedea*) from Berlengas had a noticeable breeding failure, well visible in a lower hatching success; breeders in 2011 were lighter and had to travel great distances to find food than in years with a higher marine productivity (Paiva *et al.* 2013b). In contrast, years with a positive NAO are related with an increase in the CC along the Portuguese coast, and a higher breeding success of the Cory's Shearwater (Paiva *et al.* 2013b).

There can be strong intra- and inter-specific competition for nest sites (Ramos *et al.* 1997). Due to predators and human pressure, nest sites in predator-free islets and sea cliffs are now scarcer, so it is common to found different species sharing the same cavity (Monteiro *et al.* 1996a). This lead to a reduction in breeding success (Monteiro *et al.* 1996b) when birds are forced to

share the same nest site cavities. This competition for nest sites can also have an influence in the breeding phenology of the seabirds, leading to less competitive species having to breed when the conditions are not so favorable but the competition for nest sites and for food is smaller (Catry *et al.* 2009).

### ***Seasonal variation in productivity in the North Atlantic Ocean and the seabirds breeding season***

The Atlantic Ocean is the second largest ocean of the world, linking almost the two poles. For this reason along their extension the oceanographic conditions vary enormously. The oceanic circulation in the North Atlantic is characterized by an asymmetric, large scale gyre that flows from the subtropical areas (on the western side) to the north (the Gulf Stream), and after mixing with the cool waters of the Arctic Labrador current, divides into a multi-branch current system (Santos *et al.* 1995). One branch reaches the Azores archipelago and the other the Portuguese and African coast (Portugal/Canary currents) (Mann and Lazier 2013). Normally the center of the North Atlantic Gyre presents a low productivity pattern (Paiva *et al.* 2010a) but the productivity can rise locally due to the presence of seamounts, banks and canyons (Morato *et al.* 2008; Paiva *et al.* 2010a). Close to the coast of Portugal and Africa primary production is higher due to the presence of the upwelling that brings cooler and nutritious waters to the surface (Sousa *et al.* 2008). In the North Atlantic there is a noticeable productivity gradient, which decreases from north to south, along with a concomitant increase in SST (Paiva *et al.* 2010a). It is expected that this gradient will have an impact in the seabirds' breeding season, shaping their timing of reproduction in this region. SST should have an important role determining the timing of breeding because it influences marine primary productivity.

Among the species breeding in the Macaronesian (Azores, Madeira, Canaries and Cabo Verde) we have the genus *Calonectris* sp., with two closely related species, the Cory's shearwater (*Calonectris borealis*) which breeds during summer in Azores, Madeira, Canary and Berlengas islands (Granadeiro 1991; Granadeiro *et al.* 1998; Navarro *et al.* 2007; Giudici *et al.* 2010), and the

Cape Verde shearwater (*Calonectris edwardsii*) breeding only in Cabo Verde (Petry *et al.* 2000). The species Bulwer's petrel (*Bulweria bulwerii*) that breeds in all the macaronesian islands (Monteiro *et al.* 1996a; Monteiro *et al.* 1996b; Nunes 2000; Ramos *et al.* 2015) is also a summer breeder. The genus *Hydrobates* consisting of three species, the Madeiran storm-petrel (*Hydrobates castro*) breeding in Azores, Berlenga, Madeira and Canary archipelagos, and possibly Cabo Verde archipelago, is a winter breeder. While, the Monteiro's storm petrels (*Hydrobates monteiroi*) breeding in Azores (Monteiro *et al.* 1996a) and Cape Verde storm-petrels *Hydrobates jabejabe* breeding in Cabo Verde (Oliveira *et al.* 2013b) are summer breeders. The genus *Puffinus* composed of two species, the North Atlantic little shearwater (*Puffinus ilherminieri baroli*) breeding in Azores, Madeira and Canary islands and the Cape Verde little shearwater (*Puffinus ilherminieri boydi*) breeding only in Cabo Verde (Monteiro *et al.* 1996a; Monteiro *et al.* 1999) is a winter breeder. In relation to the genus *Pterodroma* there are three species in the Macaronesia: the Zino's petrel (*Pterodroma madeira*) and Desertas petrel (*Pterodroma deserta*) breeding in the madeira archipelago during summer (Monteiro *et al.* 1999; Ramírez *et al.* 2013; Ramírez *et al.* 2015), and the Fea's petrel (*Pterodroma feae*) breeding in Cabo Verde during the winter (Ramos *et al.* 2016).

The northern Atlantic region of the Macaronesia presents two peaks of productivity, a stronger peak in spring and other less marked peak in the autumn. The breeding season of the summer breeding seabirds follows the peak in chlorophyll *a* concentration (CC) in spring. In relation to the winter breeding species (Madeiran storm-petrel, North Atlantic little shearwater, Cape Verde little shearwater and Fea's petrel) it is not clear how their breeding season relates with the oceanic productivity, but all species began breeding after the autumn peak in CC. It is well know that there is a gradient of marine productivity in the Eastern North Atlantic, which decreases from high latitudes to low latitudes (Paiva *et al.* 2010a), so it expected that seabirds start to breed earlier in the Azores and Berlengas islands and gradually later when we approach Cabo Verde. The challenge is to see whether the different seabirds' species adjust their breeding season to the oceanographic conditions of the different archipelagos. To examine this question we compiled data from

published and unpublished literature with the information on the timing of breeding for the different species in the different archipelagos, and collected data for species breeding in the Cabo Verde archipelago. Then, we compared the time of breeding of the different seabirds with the peak of productivity in the different archipelagos, which is related with the SST and CC, to assess whether the different species adjust the breeding seasons with these peaks of productivity.

# METHODS

## ***Geographical and oceanographic characteristics of the study area***

### Azores

The Azores archipelago is situated in the mid-North Atlantic Ocean (36-39°N, 25-31°W) ca. 1500 km west of mainland Portugal. It is comprised of nine volcanic islands, forming three groups: western (Corvo and Flores), central (Faial, Pico, São Jorge, Graciosa and Terceira) and eastern (São Miguel and Santa Maria) and numerous small islets (0.1 to 10 ha), along a tectonic zone running about 600 km WNW-ESE (Monteiro *et al.* 1996a). It has a land surface of 2333 km<sup>2</sup> and about 780 km of rocky coastline with boulders shores, frequently with cliffs up to 100-300 m in height. The climate is subtropical and oceanic with low thermal amplitude, high precipitation and humidity (Santos *et al.* 1995). The oceanographic conditions in the Azores are strongly influenced by the Gulf Stream jet, which in the central North Atlantic has southern multi-branched current systems with many unstable meanders and eddies at the Azores front (Gould 1985). Oceanic waters are of low productivity, but that can be substantially elevated locally, due to upwellings at seamounts, island shelf breaks and thermal fronts (Colaço *et al.* 2013).

### Berlengas

The Berlengas archipelago is a group of small islands 10 to 15 km off the Portuguese coast (39° 24'N, 009° 30'W) (Ceia *et al.* 2014) formed by the Berlenga Grande island and the islets Estelas and Farilhões. The sea surface temperature varies between the 21-26 °C throughout the year. It is an area with high primary production due the upwelling along the Portuguese coast (Sousa *et al.* 2008).

### Madeira

The Madeira archipelago is constituted by six volcanic islands, Madeira and Porto Santo the two permanently inhabited islands, and the other four are in two distinct sub-archipelagos, Desertas islands formed by the islet Chão, Deserta Grande and Bugio, and Selvagens islands formed by Selvagem

Grande, Selvagem Pequena, Fora islet and others smaller islets. It is located in the African plate (30-33°N, 15-17°W) ca. 978 km south-west of Lisbon and about 700 km west of African coast (Borges *et al.* 2008). The climate varies from island to island; it is oceanic and Mediterranean in Madeira Island, semiarid in Porto Santo and Desertas islands and desert in Selvagens islands. The Gulf Stream jet has an important role in temperature of the oceanic waters surrounding the archipelago, with a mean of 24 °C in summer and 18 °C in winter (see Figure 3). The oceanic waters are of low productivity but the mixing of the hot water from Gulf Stream and the cool northern waters creates frontal zones increasing marine productivity (Paiva *et al.* 2010b).

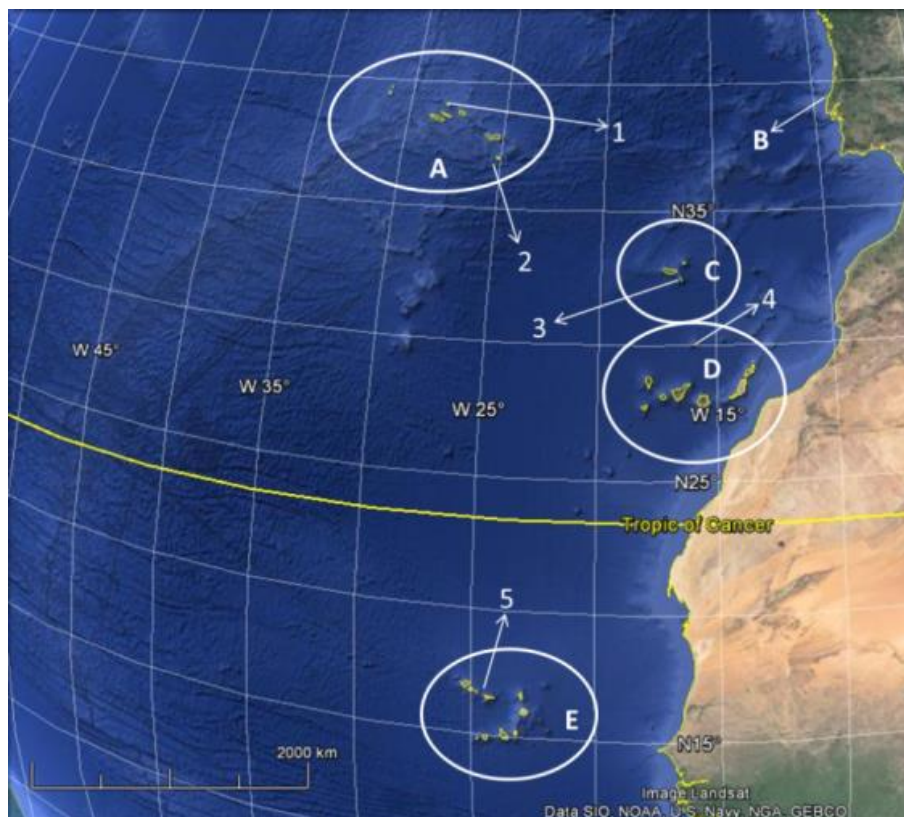
### Canary Islands

The Canary Islands are a Spanish archipelago located in eastern Central Atlantic, just off the southern coast of Marocco (27-29°N, 13-18°W) ca. 100 km west of its southern border (Dañobeitia & Canales 2000). Is formed by seven major volcanic islands (Tenerife, Fuerteventura, Gran Canaria, Lanzarote, La Palma, La Gomera and El Hierro) extended for almost 500 km, and also includes a number of smaller islands and islets (Delgado *et al.* 1988). The islands have a subtropical and desert climate, with long warm summers and moderately warm winters and the SST around the archipelago varies from 18°C to 22.5°C (Pérez & Barton 2001). The waters have low productivity but the cool waters of Canary Current and the upwelling of the African coast increase the productivity of the area (Pérez & Barton 2001).

Although Selvagens islands belong to the archipelago of Madeira, due to the fact they are closer to the Canary Islands (Faria 1998) and the conditions are more similar, in this study we consider the Selvagens islands as part of the Canary archipelago. Selvagem Grande is the largest island of the Portuguese sub-archipelago of the Selvagens and is classified as a Nature Reserve because of the fauna and flora (Granadeiro *et al.* 2006). The waters has low productivity due to high SST and consequently low chlorophyll *a* concentration (Paiva *et al.* 2010b; Alonso *et al.* 2012). Despite the low local productivity the island is 370 km away to the African coast which is under the influence of a strong upwelling (Paiva *et al.* 2010a).

## Cabo Verde

It is an island country formed by an archipelago of ten volcanic islands and several islets in the central Atlantic Ocean (17-14°N, 22-25°W) (Martins & Rebelo 2009) ca. 570 km off the coast of Western Africa, the islands cover a combined area of slightly over 4000 km<sup>2</sup>. The climate is arid or semiarid (Martins & Rebelo 2009) with an annual temperature between 20-25 °C. The water temperature varies from 22°C in February and 27°C in September (see Figure 3). The waters surrounding the Cabo Verde archipelago have a low productivity which is locally enhanced by intense and more nutritive currents between the islands and close to the seamounts present in the area (Paiva *et al.* 2015). Virtually all data on the breeding phenology of Cabo Verde seabirds was obtained from Razo Islet. Raso is included in the Integral Nature Reserve together with two other islets, Santa Luzia and Branco (Reservas Naturais, Decreto Lei 3/II/03 de 24 Fevereiro). In terms of biodiversity it is regarded as the most important seabird breeding site for Cabo Verde.



**Figure 2** Map of the Macaronesia region showing the 5 different study areas (A - Azores archipelago; B - Berlengas Island; C - Madeira archipelago; D - Canary archipelago and E - Cabo Verde archipelago) and the main seabird breeding sites (1 - Graciosa; 2 - Sta Maria; 3 - Desertas Islands; 4 - Selvagens Islands and 5 – Razo)

## **Study species**

### *Calonectris* sp.

Cory's shearwater (*Calonectris borealis*) is a species with a wide distribution in the Macaronesian islands breeding in practically all the archipelagos (Granadeiro *et al.* 1998; Meirinho *et al.* 2014), except Cabo Verde where other related species breeds (see below). The first birds arrive on the breeding area between February and March, lay a single egg from late-May to early-June, with an incubation period around 54 days, and the last juveniles leave the nest in early November (Granadeiro 1991; Monteiro *et al.* 1996b; Giudici *et al.* 2010). In the end of the breeding season birds travel to wintering areas in the South Atlantic (Monteiro *et al.* 1996b; Catry *et al.* 2011) and occasionally to the Indian Ocean. Cory's shearwater is the most abundant seabird species in the Macaronesian region, with an estimate of 500.000 mature individuals (BirdLife International 2016a). It is a pelagic species feeding mainly on small pelagic fishes (sardines, mackerel, horse mackerel) and cephalopods (Paiva *et al.* 2013a). The nests are located in cavities in rocks or in holes excavated by them, and it is rare to find exposed nests (Meirinho *et al.* 2014). Cape Verde shearwater (*Calonectris edwardsii*) is smaller compared with Cory's and breeds only in Cabo Verde archipelago in some restrict islets. Birds lay the egg in early-June, with an incubation period identical to Cory's shearwater, and the last juveniles leave the nest in early to mid-November. In the end of the breeding season they travel to South Atlantic to spend the winter (BirdLife International 2016b; Table 1).

### *Bulweria bulwerii*

Bulwer's petrel (*Bulweria bulwerii*) has a dark plumage with long, narrow wings and long tail. It is well distributed along the Macaronesian islands, breeding in all the archipelagos preferentially in islets (Nunes 2000). It lays one egg from late-May to early-June, with an incubation period of around 45 days (Nunes 2000), and the last juveniles leave the nest in September and early-October (Monteiro *et al.* 1996a). It is a pelagic solitary seabird that makes their nests among boulders or in cliffs (Monteiro *et al.* 1999). Their diet consists of



mesopelagic fishes, cephalopods and crustaceans (Monteiro *et al.* 1996b). They feed mainly at night taking advantage of vertical migration of mesopelagic prey (Meirinho *et al.* 2014; Table 1).

#### Hydrobates sp.

Madeiran storm-petrel (*Hydrobates castro*) is a dark seabird species with a white rump. It nests on islets and rocky cliffs in Azores, Madeira, Canary and Berlengas islands (Faria 1998; Oliveira *et al.* 2013a) and possibly in Cabo Verde archipelago. It is a winter breeder, laying one egg in late-September and early-October, with an incubation period around 42 days, and the last juveniles leave the nest in late-January and February (Monteiro *et al.* 1996b; Bolton *et al.* 2008). It is a pelagic seabird species (Faria 1998) feeding on planktonic crustaceans, small fishes and cephalopods (Monteiro *et al.* 1996b; Meirinho *et al.* 2014). Monteiro's storm-petrel (*Hydrobates monteiroi*) is very similar to Madeiran storm-petrel, breeds only in the Azores, and only recently it was separated taxonomically (Bolton *et al.* 2008). It is a summer breeder, laying one egg in May, with an incubation period of around 42 days, and the last juveniles leave the nest in September (Bolton *et al.* 2008). In the end of the breeding season they stay around the Azores archipelago (Meirinho *et al.* 2014). There are 250 to 999 mature individuals (BirdLife International 2016c). It feeds generally at higher trophic level prey than Madeiran storm-petrel during the non-breeding season. Nests in small cavities in undisturbed areas, and it readily occupy artificial nests (Oliveira *et al.* 2013a; Meirinho *et al.* 2014). Cape Verde storm-petrel (*Hydrobates jabejabe*) is very similar to the other two species describe above. Is an endemic species of Cabo Verde (Oliveira *et al.* 2013b). It is a summer breeder, laying one egg in May. Nests in cliffs many times in the company of other seabirds (Oliveira *et al.* 2013b). There is not information about the feeding habits (Table 1).

#### Pterodroma sp.

Zino's petrel (*Pterodroma madeira*) have a grey upper part with dark W-pattern, the under wing is almost entirely blackish and the upper tail is uniformly pale grey. It is endemic of Madeira island, nesting only in the eastern massif of

the island above the altitude of 1600m in ledges with native vegetation (Zino *et al.* 2001). The first birds arrive to the breeding grounds in late-March, start to lay in early-June, with an incubation period of around 52 days, and the last juveniles leave the nest in October. After the breeding season they travel to tropical and Oriental Atlantic Ocean where they spend the winter (Meirinho *et al.* 2014). The population is estimated at 90-110 mature individuals (BirdLife International 2016d). It feeds on cephalopods, fishes and crustaceans (Ramos *et al.* 2016). Desertas petrel (*Pterodroma deserta*) is very similar to Zino's petrel but slightly larger (Zino *et al.* 2008). It is endemic of Desertas islands in Madeira archipelago nesting specifically in Bugio Island (Ramírez *et al.* 2013). The first birds arrive in late-May to the breeding grounds, start to lay in mid-July, with an incubation period of around 52 days, and the last juveniles leave the nest in late-December and early-January. After the breeding season they travel to South and Western Atlantic. The breeding population is estimated at around 160-180 pairs (Menezes *et al.* 2010). It is essentially a pelagic seabird feeding on cephalopods, fish and crustaceans (Ramos *et al.* 2016). Fea's petrel (*Pterodroma feae*) is endemic of Cabo Verde breeding in small islets of the archipelago with reduced human disturbance (Ramos *et al.* 2016). It was recently separated taxonomically from Desertas petrel, it is phonologically similar to the other *Pterodromas* described above, and is very hard to distinguish at sea. A striking difference is in the breeding season, as this is a winter breeder (Ramos *et al.* 2016) laying one egg in mid-November, with an incubation period of around 52 days, and the last juveniles leave the nest in June. The population size and the diet are not known (Table 1).

### *Puffinus* sp.

North Atlantic little shearwater (*Puffinus lherminieri baroli*) is dark above and white below, the legs are bluish with black spots on tarsus. Is endemic of the Macaronesian islands breeding in all the Azores islands (excluding Terceira), Madeira and Canaries (Alauda 2006). It is a winter breeder laying one egg in late-January and early-February, with an incubation period around 45 days, and the last juveniles leave the nest in early-June (Monteiro *et al.* 1996b). After the breeding season this seabird stay close to the breeding area (Monteiro *et al.* 1996a). It is a pelagic seabird very difficult to observe on land. Their diet

consists of small cephalopods, fish and crustaceans (Monteiro *et al.* 1996b; Meirinho *et al.* 2014). Nests in cavities located in islets and coastal cliffs with difficult access (Beaman & Madge 2010). Cape Verde little shearwater (*Puffinus lherminieri boydi*) is very similar to North Atlantic little shearwater but breeds only in Cabo Verde (Alauda 2006). It is a winter breeder laying one egg in mid late-February, with an incubation period around 52-58 days, and the last juveniles leave the nest in June. Nests in cavities and burrows in islets and cliffs (Meirinho *et al.* 2014; Table 1).

In general the threats are similar for all the species: predation by introduced mammals (rodents, cats and mustelids), human disturbance (habitat loss, light pollution, oil spillages and fisheries), changes in natural vegetation and competition for nest sites between individuals of the same species or between different species (Monteiro *et al.* 1996a; Monteiro *et al.* 1996b; Ramos *et al.* 1997, Monteiro *et al.* 1999; Bolton *et al.* 2008; Meirinho *et al.* 2014).

**Table 1** Main characteristics of the different study species, highlighting the breeding season (summer/winter), the breeding area (Azores – Az; Berlengas – Ber; Madeira – Mad; Selvagens/Canaries – Can; Cabo Verde - CV), the incubation period in days, the fledging period, the length from the tip of bill to tip of tail, and wingspan from side to side of the wing.

Species	Common Name	Breeding Season	Breeding Area	Incubation Period (days)	Fledging time (days)	Length (cm)	Wingspan (cm)	References
<i>Calonectris borealis</i>	Cory's shearwater	Summer	Az, Ber, Mad, Can	52-55	95-100	45-56	112-126	Zino 1971 Cook & Yolden 1980 Granadeiro 1991 Ramos <i>et al.</i> 2003 2015 field data
<i>Calonectris edwardsii</i>	Cape Verde shearwater	Summer	CV	52-55	95-100	40-43	90-100	
<i>Bulweria bulwerii</i>	Bulwer's petrel	Summer	Az, Mad, Can, CV	42-46	61	25-29	67-73	Monteiro <i>et al.</i> 1996a Nunes 2000 Matias & Catry 2010
<i>Hydrobates castro</i>	Madeiran storm-petrel	Winter	Az, Ber, Mad, Can, CV	42	64-73	19-21	43-46	Delgado <i>et al.</i> 1988 Bolton 2007 Bolton <i>et al.</i> 2008 Menezes <i>et al.</i> 2010
<i>Hydrobates monteiroi</i>	Monteiro's storm-petrel	Summer	Az	42	64-73	16-19	-	Bolton <i>et al.</i> 2008
<i>Hydrobates jabejabe</i>	Cape Verde storm-petrel	Summer	CV	42	64-73	-	-	Oliveira <i>et al.</i> 2013b
<i>Pterodroma madeira</i>	Zino's petrel	Summer	Mad	52	85	32-34	80-84	Ramos <i>et al.</i> 2016
<i>Pterodroma deserta</i>	Deserta petrel	Summer	Mad	52	90	33-36	86-94	Ramos <i>et al.</i> 2016
<i>Pterodroma feae</i>	Fea's petrel	Winter	CV	51-54	90	33-36	88-94	Ramos <i>et al.</i> 2016
<i>Puffinus lherminieri baroli</i>	North Atlantic little shearwater	Winter	Az, Mad, Can	52-58	60	25-30	58-67	Monteiro <i>et al.</i> 1996a Alauda 2006 Menezes <i>et al.</i> 2010
<i>Puffinus lherminieri boydii</i>	Cape Verde little shearwater	Winter	CV	52-58	60	-	-	Alauda 2006

## **Data**

### Laying data

The laying data for the study species was collected from published articles (see references in Figure 4 and Figure 6), and the egg laying period was divided per blocks of ten days. This is because in most cases the data was not accurate in the precise day that the birds lay eggs, and only a time range was referred (e.g. early-May, mid-May, late-May); in such cases we assumed the late-May, for instance, as ranging from day 20 - 31 May. Specifically for the genus *Calonectris* sp. there is precise egg laying data, with a precision of one to three days, and field data was collected for Cabo Verde in 2015. When there was no data for egg laying, we used the hatching date, and subtracted the incubation period for each species (Table 1).

### Environmental variables

The environmental variables used (SST and CC) were extracted from Aqua-MODIS satellite (<http://oceancolor.gsfc.nasa.gov/cgi/l3>) with a range of 100km and 500km around the archipelagos for the period 2003-2015 and transformed in monthly anomalies values (using data for 100 km). Monthly raster images extracted from the abovementioned website were processed within the R-platform (R Core Team 2016) using diverse functions of the '*raster*' package (Hijmans 2015).

### Data analyses

The monthly anomalies values were obtained by subtracting the mean of each month from the annual mean, using the 12 years of data. The figures of the environmental variables were made in excel and the figures that combined the environmental variables and the peak laying period were made with the software R.

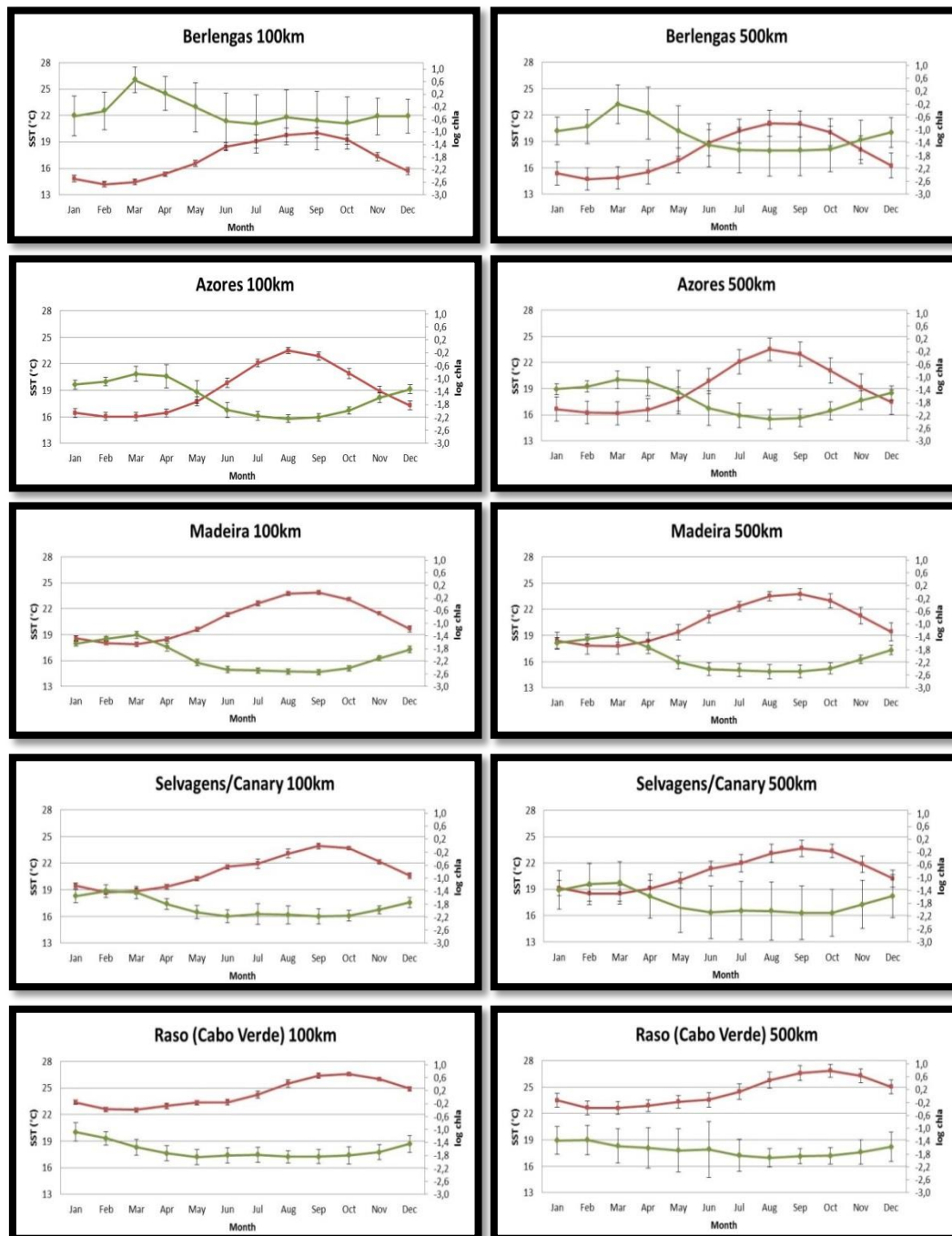
A one-way ANOVA was used to assess differences in SST and CC values among archipelagos. A one-way ANOVA was also used to test whether mean laying date of *Calonectris* sp. differed among archipelagos. All data was checked for homogeneity of variances (Levene test,  $F_{3,176}=1.59$ ,  $p=0.195$ ).

We also compiled the breeding phenology of the studied species that breeds in the same locations (Azores, Madeira, Selvagens/Canary and Cabo Verde) (Figure 8) in order to verify if the breeding season of these seabirds overlap in time.

# Results

## *Oceanographic conditions in the North Atlantic Ocean*

Figure 3 presents the monthly variation in the values of SST and CC for each studied archipelago in the North Atlantic, for the period 2003-2015.



**Figure 3** Monthly mean  $\pm$ SD sea surface temperature (SST, red dots) and the log of Chlorophyll a concentration (CC, green dots) around (100km and 500km) Berlengas, Azores, Madeira, Selvagens/Canary and Cabo Verde, over the 2003-2015 period.

The SST values show that there are two well-marked seasons, the coldest season during the winter, which comprises the months between December and March, and the warmer season during summer, which comprises the months between July and October. Obviously, the temperatures increased with the decreasing of latitude, and were higher for Cabo Verde than for Berlengas. When the SST was higher the CC had the lowest values for all archipelagos, and when the temperature decreased the CC began to increase.

When we analyzed the archipelagos separately we can see that Berlengas had higher values of CC than the oceanic archipelagos, presumably because it is a coastal zone within an upwelling area. The peak in CC in the northernmost archipelagos (Berlengas, Azores and Madeira) was in March, and it was earlier for the southernmost archipelagos: between February and March for the Selvagens/Canaries and January for Cabo Verde. As expected from its sub-tropical location Cabo Verde had relatively stable SST and CC values throughout the year. When comparing the values of 100km and 500km we see that there are no noticeable differences, therefore the values for 100km are used in further analysis.

The one-way ANOVA shows significant differences in the SST values among all archipelagos ( $F_{1,4}=242.9$ ;  $p<0.001$ ) except between Madeira and Selvagens/Canaries (pos-hoc Tukey test), as well as significant differences in the values of CC among all the archipelagos ( $F_{1,4}= 322.8$ ;  $p< 0.001$ ) except between Cabo Verde and Azores.

### ***Breeding phenology of the seabird species***

#### **Summer breeding species**

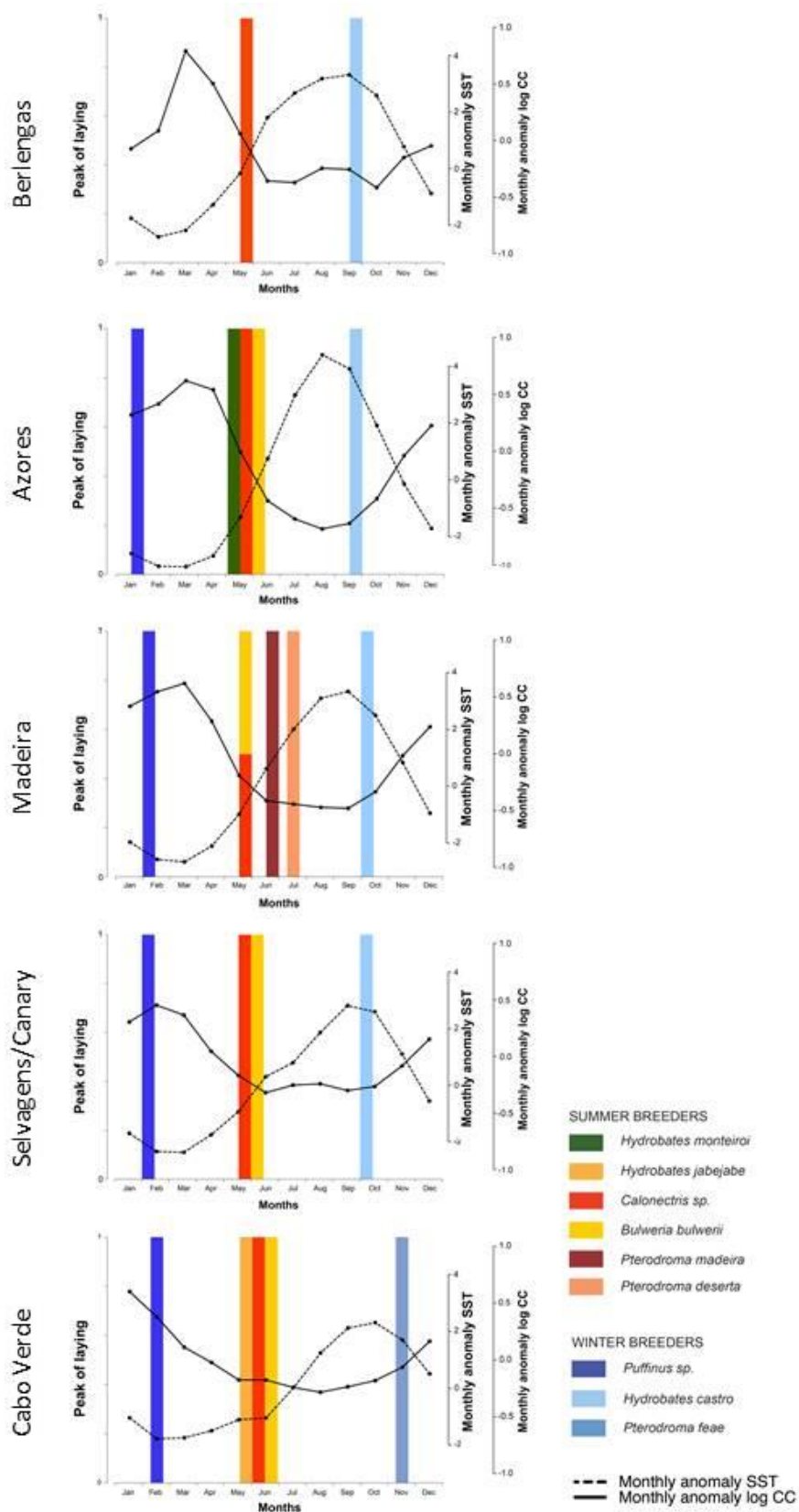
When we plotted the breeding phenology of the *Calonectris* sp. that breed in the different archipelagos of the North Atlantic (Figure 4) we can see that birds reproduce first at higher latitudes. *Bulweria bulwerii*, on the other hand, appears to reproduce first in Madeira than in the other archipelagos, although the difference was only about 10 days.



When comparing the peak of laying with the peak of CC (Figure 5) we can see that for *Calonectris* sp. in the Berlengas, Azores and Madeira the difference between the two peaks was approximately 71 days, in Selvagens/Canaries it was 99 day, and in Cabo Verde it was 141 days. For *Bulweria bulwerii* such difference for the Azores was 82 days, for Madeira it was 71 days, for Selvagens/Canaries it was 110 days, and for Cabo Verde it was 161 days. *Hydrobates monteiroi*, which breeds only in the Azores, laid eggs 51 days after the peak of CC, the *Pterodroma madeira* and *Pterodroma deserta* laid eggs respectively 102 and 122 days after the peak of CC (Table 2). Although data on Cape Verde storm-petrel *Hydrobates jabejabe* is very scarce, filed observations of birds in active incubation in early June 2015 and 2016 at Raso Islet (Cabo Verde), suggest birds should reach peak laying between mid to end of May (Figure 5).



**Figure 4** Breeding phenology of different summer breeder seabird species for each archipelago in the North Atlantic, from laying to hatching (green; incubation), from hatching to fledging (blue; chick-rearing) and during non-breeding (white). Each month was divided in three intervals, with 10 days each. Data for breeding phenology was taken from the literature: Azores (Monteiro *et al.* 1996a; Monteiro *et al.* 1996b; Bolton *et al.* 2008; Ramos *et al.* 2003), Berlengas (Granadeiro 1991), Madeira (Cook & Yalden 1980; Nunes 2000; Ramos *et al.* 2016; 2008 field data performed by Ivan Ramirez), Selvagens/Canary (Zino 1971; Giudici *et al.* 2010; Matias & Catry 2010) and Cabo Verde (2015 our own data).

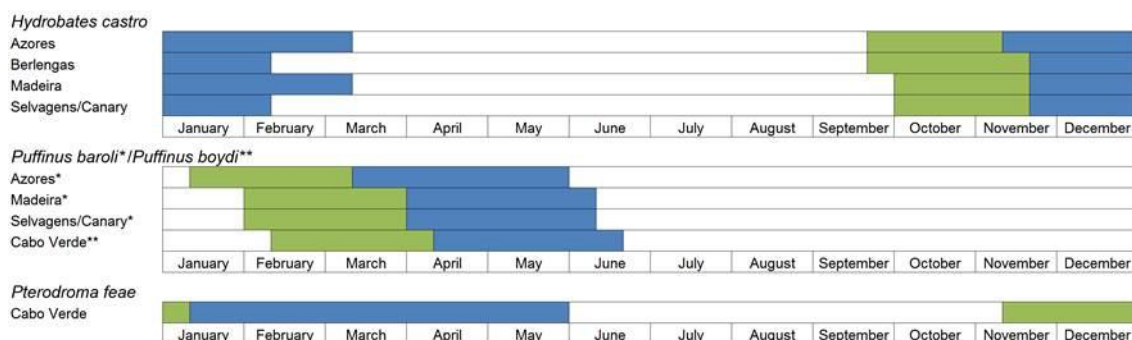


**Figure 5** Correlation between the peak of laying (histograms) and the monthly anomalies values of sea surface temperature (SST; dashed line) and chlorophyll a concentration (CC; solid line) over the period 2003-2015.

### Winter breeding species

A similar analysis for winter breeding species (Figure 6) shows that *Puffinus* sp. and *Hydrobates castro* reproduce first at higher latitudes than at lower latitudes.

When comparing the peaks of laying with the peak of CC (Figure 5) we can see that *Puffinus* sp. in the Azores had the laying peak 49 days before the peak of CC, in Madeira the difference was 38 days, in Selvagens/Canaries of 10 days only, and in Cabo Verde it was 31 days after. *Hydrobates castro* apparently does not regulate laying with the peak of CC, but with the peak of SST, as it laid eggs always when the SST began to decrease. *Pterodroma feae* laid eggs 304 days after the peak of CC (Table 2).



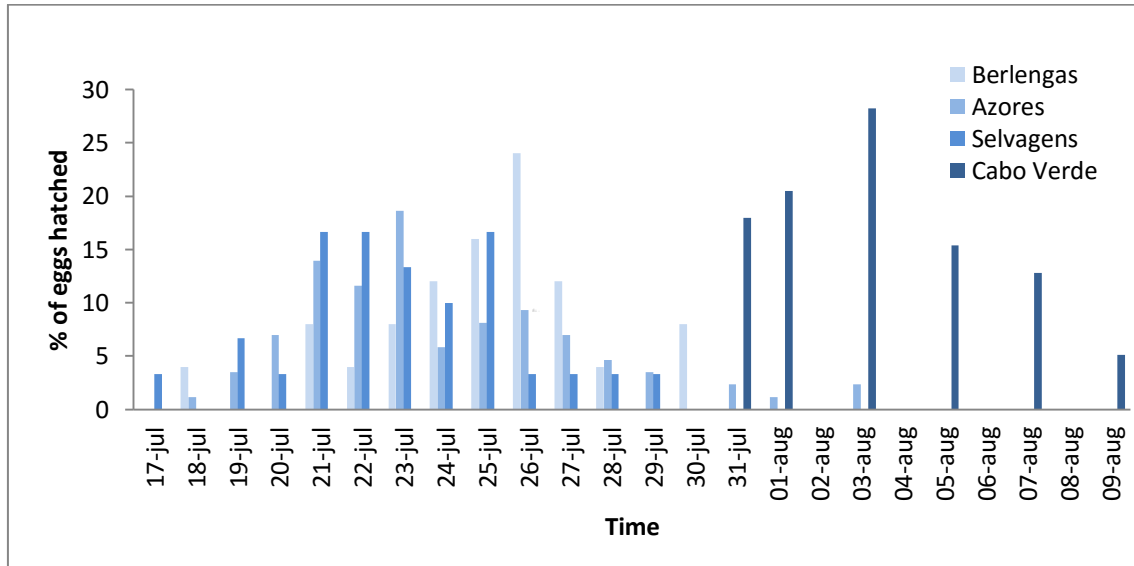
**Figure 6** Breeding phenology of different winter breeder seabird species for each archipelago in the North Atlantic, from laying to hatching (green; incubation), from hatching to fledging (blue; chick-rearing) and during non-breeding (white). Each month is divided in three intervals, with 10 days each. Data for breeding phenology was taken from the literature: Azores (Monteiro *et al.* 1996a; Monteiro *et al.* 1996b; Bolton *et al.* 2008), Berlengas (Oliveira *et al.* 2013a), Madeira (Menezes *et al.* 2010; Ramos *et al.* 2016), Selvagens/Canary (Delgado *et al.* 1988; Alauda 2006) and Cabo Verde (Ramos *et al.* 2016).

**Table 2** Difference between the peak of laying and the peak of chlorophyll a concentration (CC) for the summer and winter breeding species in the different North Atlantic archipelagos. Negative values indicate that the peak of laying is before the peak of CC.

<b>Summer breeding species</b>	<b>Archipelagos</b>	<b>Difference between the peak of laying and the peak of CC (in days)</b>
<i>Calonectris</i> sp.	Azores	71
	Berlengas	71
	Madeira	71
	Selvagens/Canary	99
	Cabo Verde	141
<i>Bulweria bulwerii</i>	Azores	82
	Madeira	71
	Selvagens/Canary	110
	Cabo Verde	161
<i>Hydrobates monteiroi</i>	Azores	51
<i>Hydrobates jabejabe</i>	Cabo Verde	130
<i>Pterodroma deserta</i>	Madeira	122
<i>Pterodroma madeira</i>	Madeira	102
<b>Winter breeding species</b>		
<i>Hydrobates castro</i>	Azores	194
	Berlengas	194
	Madeira	204
	Selvagens/Canary	232
<i>Puffinus</i> sp.	Azores	-49
	Madeira	-38
	Selvagens/Canary	-10
	Cabo Verde	31
<i>Pterodroma feae</i>	Cabo Verde	304

### Breeding phenology of *Calonectris* sp.

For the *Calonectris* sp. it is possible to obtain egg hatching data daily or every 2-3 days, allowing us to document detailed differences in laying date among archipelagos. For the Berlengas, Azores and Selvagens archipelagos, as shown in Figure 7, the chicks hatch at the same time (late-July), but in Cabo Verde they began to hatch about one week later.



**Figure 7** Timing of egg hatching for *Calonectris* sp. in the different archipelagos (Berlengas, Azores, Selvagens and Cabo Verde). The data from Berlengas are taken from Granadeiro 1991 (N=86), the data of Azores are from Ramos *et al.* 2003 (N=25), the data from Selvagens are taken from Zino 1971 (N=30) and data from Cabo Verde is field data in 2015 (N=39).

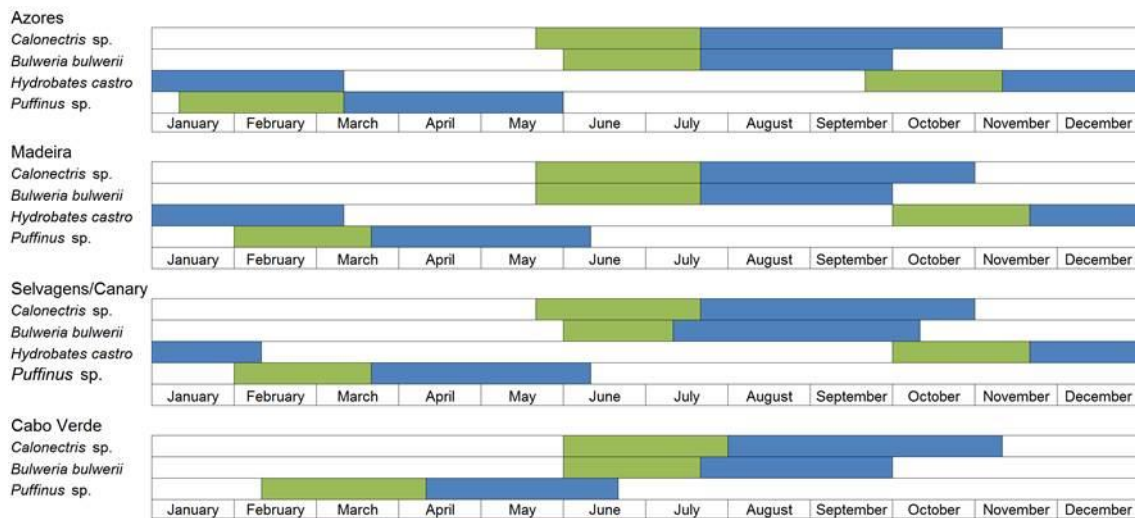
The mean hatching date differed significantly among archipelagos ( $F_{3,176}=117.9$ ;  $p<0.001$ ), and Tukey test showed that only Cabo Verde differed from the other archipelagos ( $p<0.001$ , Table 3). This means that there is a clear separation between the temperate archipelagos (Berlengas, Azores and Selvagens) and the tropical archipelago (Cabo Verde).

**Table 3** Mean laying date of *Calonectris* sp. in Berlengas, Azores, Selvagens and Cabo Verde.

Archipelagos	Mean laying date $\pm$ SD
Berlengas (n=86)	25 July $\pm$ 2.7 days
Azores (n=25)	24 July $\pm$ 3.4 days
Selvagens (n=30)	23 July $\pm$ 2.7 days
Cabo Verde (n=39)	3 August $\pm$ 2.7 days

## The interspecific competition hypothesis

We found a time lag among the summer breeders (*Calonectris* sp. and *Bulweria bulwerii*) and winter breeding species (*Hydrobates castro* and *Puffinus* sp.) in all the archipelagos. Therefore, when the summer breeders start to leave the nest is when *the Hydrobates castro* lay the eggs, and when they are already feeding the chicks, *Puffinus* sp. start their breeding season and end curiously when the summer breeders start again their breeding season.



**Figure 8** Breeding phenology of *Calonectris* sp., *Bulweria bulwerii*, *Hydrobates castro* and *Puffinus* sp. in Azores, Madeira, Selvagens/Canary and Cabo Verde archipelagos, from laying to hatching (green; incubation), from hatching to fledging (blue; chick-rearing) and during non-breeding (white). Each month was divided in three intervals, with 10 days each.

## Discussion

Our study shows that oceanographic conditions in the North Atlantic should have some influence in explaining the timing of breeding of the different seabird species that breed in this area. It is clear the distinction between the temperate (Berlengas, Azores, Madeira and Canary) and tropical group (Cabo Verde) with the majority of the birds breeding later in the tropical group, where the oceanographic conditions are more stable (Ashmole 1971; Jaquemet *et al.* 2007). Despite this distinction, in the statistical analyses, we do not find significant differences in the SST between Madeira and Selvagens/Canary and in CC between Azores and Cabo Verde. With respect to the SST this difference was not verified because both archipelagos are sub-tropical (Ramos *et al.* 2015) and close to each other. With respect to the CC, the non-significance of CC between Cabo Verde and Azores is misleading because when we observe the values of CC in these two archipelagos (Figure 3) we can see that they are very different: Azores has a well-marked seasonality and Cabo Verde is more stable along the year, but the higher and lowest values of CC in the Azores region cancel each other and for that reason the analysis did not show significant differences between these two archipelagos.

As expected, summer breeding seabird species lay about 2-2.5 months after the peak in chlorophyll concentration and chicks hatch about 3.5-4 months after the peak in chlorophyll concentration. Other studies have shown the peak in chlorophyll usually occurs about 3 months before the main foraging distribution of seabird predators (Louzao *et al.* 2009), which should be a reflex of an increase in availability of prey. However, considering the whole seabird community breeding in the islands of the North Atlantic Ocean from the Azores to Cabo Verde, which includes summer and wintering breeding species it is apparent that oceanographic conditions are not the main factor in explaining the breeding season of the seabird species that breed in these archipelagos. Below we outline the limitations of our study and discuss the implications of our study to understanding the timing of breeding for the seabird communities in the sub-tropical North Atlantic Ocean.

## **Limitations**

For all species apart from Cory's shearwater there is no detailed data on timing of breeding, i.e. we obtain only the month or the period of the month (early, mid or late period) when a particular species lays eggs. Little information is known about the reproductive biology of some species (Monteiro *et al.* 1996b) such as the *Puffinus* and *Pterodroma*, often due to the difficulty in monitoring their nests because they reproduce frequently in inaccessible cliffs (Monteiro *et al.* 1999; Beaman & Madge 2010; Meirinho *et al.* 2014), making it difficult to find accurate information about the exact timing of egg laying. Since the oceanographic conditions vary between years, it would be important to have detailed data for each year, in order to examine the influence of environmental conditions on the timing of breeding. This prevents to examine a fine tuning relationship with oceanographic data. However, there is substantial information about the period of laying for all the study species, which enabled us to examine the broad relationships between oceanographic conditions and timing of breeding along the temperate sub-tropical gradient of the North Atlantic.

## **Timing of seabirds breeding season in the North Atlantic and oceanographic conditions**

The oceanographic condition of the study sites show a strong variation throughout the year, with a strong peak of chlorophyll at higher latitudes (Berlengas, Azores), which decreases in strength and is more temporally restricted as we approach the tropics. The Berlengas have the higher peak of chlorophyll of all the archipelagos due to the strong upwelling along the Portuguese coast (Sousa *et al.* 2008).

When we compared the time of breeding of the species that breed in several archipelagos (*Calonectris* sp., *Bulweria bulwerii*, *Hydrobates castro* and *Puffinus* sp.) we can see some adjustments according to the archipelagos. At the higher latitudes *Calonectris* sp., *Puffinus* sp. and *Hydrobates castro* lay the eggs firstly than at the lower latitudes. Despite this adjustment of the breeding season in the different archipelagos, is not visible a relationship between the



peak of chlorophyll and the peak of egg laying of the different species, i.e. the difference among these two peaks was very irregular in relation to the decrease in marine productivity from the Azores to Cabo Verde (Table 2). In other studies it appears that birds use oceanographic conditions as a cue to start laying: Jaquemet *et al.* (2007) did a study in a tropical area, where they evaluated the influence of SST and CC around four different colonies of breeding Sooty Terns (*Onychoprion fuscatus*). They concluded that the timing of reproduction of this species matches with the seasonal peaks of CC, except in one island, and they suggest that the breeding phenology is related to the strong modification of the SST that aggregates prey around the colonies. Also a study with the species Roseate tern (*Sterna dougallii*) in the western Indian Ocean (Monticelli *et al.* 2007) show that breeding season is correlated with CC. Years of a marked phytoplankton bloom results in greater reproductive success, in contrast to years when the phytoplankton bloom was less obvious and the reproductive success was lower. When the environmental conditions were poor terns lay the eggs latter compared with good years. They also hypothesize that SST is the cue to females start the breeding season because a decrease in SST is related with an increase in marine productivity and thus in food abundance. However, in our study area that does not seem to be the case because:

- a) *Bulweria bulwerii* does not have a set pattern of reproduction, breeding first in Madeira and later in the remaining archipelagos, although the difference was only a few days.
- b) The *Hydrobates castro* breeding in Berlengas, Azores, Madeira and Canaries appears to adjust the breeding season to the SST because they began to lay the eggs when the SST start to decrease, which is known to be related with a great change in the productivity of the oceans and an aggregation of prey (Robinson 2004; Jaquemet *et al.* 2007; Monticelli *et al.* 2007).
- c) For *Calonectris* sp. and *Bulweria bulwerii* the peak of laying was always after the peak of chlorophyll, which means that chicks should hatch during the peak of abundance of small pelagic fish (Monticelli *et al.* 2007, Louzao *et al.* 2009). However, the difference between the

peak of CC and the peak of laying was not the same for all the archipelagos, so these species appear to present some adjustment of the breeding season to the oceanographic conditions in the different archipelagos. However, we were unable to detect a consistent pattern in such adjustment.

- d) For *Puffinus* sp. data is even more mismatched. In the Azores, Madeira and Selvagens/Canary this species laid eggs before the peak of chlorophyll but in Cabo Verde the laying was after the peak, so we cannot conclude that CC is important to explain laying time for this species.

Previous studies (Frederiksen *et al.* 2004) with European shag (*Phalacrocorax aristotelis*) in the North Sea show that laying dates were correlated with local SST. They conclude that shags adjust the date of egg laying with the availability of prey. Also Gjerdrum *et al.* (2003) show the effect of SST in the reproductive success of Tufted puffin (*Fratercula cirrhata*) in the North Pacific. This species adjust the breeding season with the local SST. When the SST started to increase progressively over several years the puffin also started breeding earlier. The zooplankton peak also began earlier which in turn may have influenced the availability of prey. This study demonstrated a clear link among SST and the hatching date, chick growth and fledging success of this species and they conclude that when the SST exceeds a certain limit this species is not able to breed due to migration of its main prey, the sand lance (*Ammodytes hexapterus*).

### ***Explaining the timing of breeding of the seabirds in the North Atlantic***

Although the oceanographic conditions can influence the breeding season of several seabirds in various areas of the world (Ramos *et al.* 2002; Gjerdrum *et al.* 2003; Abraham & Sydeman 2004; Frederiksen *et al.* 2004; Jaquemet *et al.* 2007; Monticelli *et al.* 2007) in our study this assumption was not verified in the sense that no consistent patterns between oceanographic

conditions and timing of breeding was detected. Presumably resources are relatively superabundant in this area and oceanographic conditions play a relatively little role in explaining timing of breeding of the different seabird species. In some cases the availability of food may be so great that seabirds prefer to breed in the worst season to avoid predation or competition (see below) (Monteiro & Furness 1998). This may not be the case in tropical areas given the unpredictability and lower abundance of food resources, so birds must respond strongly to changing environmental conditions (Jaquemet *et al.* 2007; Monticelli *et al.* 2007).

Despite the fact that food availability is an important factor defining the breeding season of the seabirds, and its directly relation with oceanographic conditions, it does not appear to be the only cause that sets the breeding season. Meteorological conditions such as storms and heavy rainfall can contribute to explain the breeding phenology of some seabird populations (Harrison *et al.* 1983). In seabirds that nest in mixed colonies on the ground the defense of the nest from aggressive species may also be important (Dorward 1963), although this is not the case in our study because all the study species nest in fairly protected and deep cavities (Monteiro *et al.* 1999; Bolton 2007; Meirinho *et al.* 2014). One explanation for the timing of breeding in our study site is the intra and inter competition for nest cavities (Monteiro & Furness 1998; Bolton *et al.* 2008). As Ramos *et al.* (1997) showed for the Azores archipelago, the species Cory's shearwater, North Atlantic little shearwater, Bulwer's petrel and Madeira storm-petrel appear to compete for nest cavities and in some cases they share the same nests, because they are temporally segregated in their breeding season. Cory's shearwater are much larger and aggressive than small petrels, which tend to avoid nest cavities occupied by this species, and when they do not have a choice and decide to breed in large nest cavities their breeding success decreases (Monteiro *et al.* 1996b). When we look at the overlap of the breeding season of this four species in the Macaronesia region (Figure 8) we can see that they do not entirely overlap, except Cory's shearwater and Bulwer's petrel, which breed exactly at the same time (Monteiro *et al.* 1996a, this study). The Madeira storm-petrel starts to breed when Cory's shearwater is finishing, and the breeding season of the North Atlantic little

shearwater is completely temporally segregated from that of the Cory's shearwater. This may be the reason why smaller species, like North Atlantic little shearwater and Madeira storm-petrel decided to breed in winter, when the conditions are not so favorable but the competition for nesting sites and for food is reduced (Monteiro *et al.* 1996b; Catry *et al.* 2009). Also, the White tern (*Gygis alba*), in the Indian Ocean, prefer to nest when marine productivity is lower (Catry *et al.* 2009), presumably to avoid foraging interspecific competition with other very abundant seabird species.

We suggest that intra and inter competition for nest sites should exert a strong influence in the breeding phenology of the different seabird species in our study area, but further studies are needed. Such competition may be the reason why the current wintering breeders decided to reproduce at a less favorable time but avoiding competition from more competitive species like Cory's shearwater (Ramos *et al.* 1997; Monteiro & Furness 1998). With habitat loss and consequently the reduction of nesting sites (Monteiro *et al.* 1996a) this competition may become ever stronger. Some studies show that the construction of artificial nests can be a good solution to reduce the competition (Bolton *et al.* 2008; Oliveira *et al.* 2013a) since they can be adapted for different species and increases the availability of nesting sites for many species of seabirds.

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