Oceanographic drivers and mistiming processes shape breeding success in a seabird

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ABSTRACT

Understanding the processes driving seabirds' reproductive performance through trophic interactions requires the identification of seasonal pulses in marine productivity. We investigated the sequence of environmental and biological processes driving the reproductive phenology and performance of the storm petrel (*Hydrobates pelagicus*) in the Western Mediterranean. The enhanced light and nutrient availability at the onset of water stratification (late winter/early spring) resulted in annual consecutive peaks in relative abundance of phytoplankton, zooplankton and ichthyoplankton. The high energy-demanding period of egg production and chick rearing coincided with these successive pulses in food availability, pointing to a phenological adjustment to such seasonal patterns with important fitness consequences. Indeed, delayed reproduction with respect to the onset of water stratification resulted in both hatching and breeding failure. This pattern was observed at the population level, but also when confounding factors such as individuals' age or experience were also accounted for. We provide the first evidence of oceanographic drivers leading to the optimal time-window for reproduction in an inshore seabird at southern European latitudes, along with a suitable framework for assessing the impact of environmentally driven changes in marine productivity patterns in seabird performance.

INTRODUCTION

The breeding phenology of many species has been shaped by individual optimal decisions in response to predictable patterns of food availability in space and time. This is particularly true for those species inhabiting temperate areas, where breeding success depends on the ability to adjust reproductive timing to seasonal patterns in food availability [1,2]. As long as seasonal productivity patterns vary between years, the optimal timing of reproduction will also vary [3], with individuals breeding more successfully when energetic demands overlap extensively with peaks in food availability [4]. Our ability to identify those environmental features leading to seasonal patterns of food availability is essential for understanding environmental processes driving reproductive performance through trophic interactions.

Vertebrates with a long gestation or incubation period are expected to time their reproduction so that the short seasonal pulses in food availability coincide with the maximum food requirements for offspring [5]. As reproduction initiates much earlier than the brooding phase, suitable reproductive timing as an adaptation to climatic seasonality should result from the use of cues that are available when the decision is taken to initiate breeding, and informing on future nutritional conditions [6,7]. The onset of reproduction may be influenced by a species-specific combination of fixed (e.g. photoperiod) and/or variable (e.g. weather, food availability) environmental cues [8]. Terrestrial birds provide good examples of phenological adaptations in response to environmental cues driving seasonal peaks in food availability such as temperature or photoperiod [6,9]. However, mechanistic processes underlying optimal decisions in seabirds are poorly known.

The dynamics of marine productivity patterns are complex, particularly in inshore areas where drivers of marine productivity, such as river outflows, upwellings

or thermal stratification of the water column, operate at short temporal and spatial scales [10]. Coastal systems are, therefore, particularly prone to environmental changes causing disruptions between seabird phenology and seasonal patterns in food availability [2,7]. Previous works have suggested that mistiming, i.e. the temporal mismatching between resource availability and the energetic needs of birds, may be an important determinant of fitness in seabirds (e.g. [2,3,11]). However, few studies have focused on mistiming processes across multiple trophic levels within seabird food webs in low-latitude, temperate areas [12]. This is mostly because environmental patterns and phenological data at the appropriate temporal and spatial resolution are scarce [13]. This has prevented our understanding on the mechanisms underlying decision-making, thus impeding prospective analysis on the fitness consequences of mistiming processes.

Here we use continuous, high-temporal resolution environmental and biological data to investigate the chronological sequence of processes driving the breeding phenology and reproductive performance of a small, long-lived seabird, the Mediterranean storm petrel (*Hydrobates pelagicus melitensis*), during the last 22 years (1993-2014). Depth profiles of water temperature and light attenuation were selected as the physical drivers of seasonal patterns in food availability in the Western Mediterranean inshore areas where petrels forage while breeding [14,15]. In these coastal systems, out of the reach of river outflows and upwelling areas, the peak in marine primary productivity occurs in late winter/early spring with the increase in light penetration and temperature within a nutrient-rich column after winter mixing [14]. The initial phytoplankton bloom is followed by a trophic cascade reflected in delayed detectable peaks of higher trophic planktonic organisms, which develop concurrently with the onset of the thermocline in spring [15]. Storm petrels feed mainly on zooplankton and small-sized fish [16] with a low reliance on fishing discards [17] and,

therefore, depend mostly on natural patterns in marine productivity. Fish consumption is particularly acute during chick-rearing [16,18], the most energetically demanding phase of their annual cycle, and the most critical period for breeding success [19].

Accordingly, we used information on seasonal productivity for those links within the petrel food web to investigate the onset of the productivity cascade that initiates after water stratifications and sets the optimal time-window for their reproduction. We then assessed whether birds adjust the beginning of reproduction to match the subsequent peaks in food availability and explored the consequences, in terms of reproductive performance (hatching and breeding success), of mistiming between productivity patterns and breeding phenology. Importantly, reproductive consequences of mistiming processes were explored at the population level, but also within breeding pairs, thus accounting for alternative drivers of seabirds' reproductive performance different from feeding conditions, such as individuals' age or experience [20,21].

METHODS

Study area, model species, and field work

Individual-based data on laying date and breeding output were obtained as part of the long-term monitoring of the storm petrel at Benidorm Island (38°30' N, 0°07' W), off the southern Mediterranean coast of Spain (see more details in [22]). Individuals typically arrive at the colony in late March and early April [23]. Females lay a single egg, usually in May, and incubation and nestling periods last ca. 40 and 65 days, respectively [23]. Storm petrels are central-place foragers returning every 1-2 days to their nests to relay with the partner during incubation or to feed the offspring ([23], authors' own data).

Accessible nests (~ 400 nests per year) were monitored from 1993 to 2014 every one to two weeks from April to September to collect data on nest occupancy, laying

date and breeding performance (egg hatching and nestling survival until fledging). Near the end of the incubation and the beginning of the hatching period nests were visited on a daily basis for capture and identification of breeding birds (see details in [22,24]). When hatching date was known, we assumed that laying occurred 40 days before [23]; otherwise, we assumed that laying occurred in the middle of the inter-visits period before the egg was first seen, i.e. 3.5-7 days before.

Environmental variables

Water column stratification. Daily means for water temperature profiles (ºC) for the period 1993-2012, were provided by the Mediterranean Sea Physics Reanalysis model (MED REA), supplied by the Nucleus for European Modelling of the Ocean (NEMO, see details in Supporting Information). Depth profiles of temperature were obtained by averaging water temperature at each vertical level within what we considered a suitable foraging area for storm petrels (30km buffer area around the colony, Fig. S1). Depth for the 15ºC isotherm was considered a suitable proxy to the thermocline ([25]; Fig. S2) and used to describe inter-annual variations in water stratification.

Light penetration into the water column. The diffuse attenuation coefficient for downwelling irradiance at 490nm (hereafter KD490 in m^{-1}, years 1998 to 2014) was used as an index of light penetration into the water column (see details in Supporting Information). Eight-day composites for KD490 data were averaged within the storm petrel's assumed foraging range and interpolated daily using a non-parametric locally smoothing function (loess) to remove noise in the original eight-day composite signal [26].

The productivity cascade. Remote sensing-derived sea surface chlorophyll-a concentration (chl-a) is widely used as a proxy of phytoplankton biomass in marine

systems [27]. However, during the stratification period in the Mediterranean, optimal

conditions of light and nutrient availability occur associated with the thermocline rather

than at the sea surface, resulting in the well-described "deep chlorophyll-a maximum"

(DCM, [14]). Accordingly, satellite-observable chl-a values are poor predictors of

phytoplankton biomass (and to some extent, primary productivity) during the

stratification period in these marine systems. Instead of chl-a, we used daily information

on chlorophyte concentrations in the water column (mg·m^{-3}, 1998-2007), as a more

accurate proxy of phytoplankton biomass during this period (see Fig. S3 and details in

Supporting Information). Owing to the low spatial resolution of this variable, we

calculated the average value for the minimum spatial range around the colony that

included daily values of chlorophyte concentrations for the 1998-2007 period: 36.891°-

39.403° latitude, -1.068°-0.920° longitude. As in the case of KD490, the loess procedure

was used to remove excessive noise in the original signal. Additional information on the

average seasonal patterns in the availability of main zooplankton (ind·m^{-3}) and

ichthyoplankton species (ind·10m^{-3}) for the Western Mediterranean was extracted from

Fernández de Puelles et al. [28]. The data for zooplankton were obtained every ten days

from 1994 to 2003, and the data for ichthyoplankton came from monthly samples from

1994 to 1999 (see [28] for more details). Both series were obtained from a comparable

NW Mediterranean area (shelf area in the Mallorca channel, ca. 200km from the storm

petrel foraging area). The descriptive oceanographic patterns presented herein assume

that regions within nearby areas not directly affected by conspicuous mesoscale features

or local production mechanisms, such as river plumes, are comparable in general terms.

This holds true in many Mediterranean areas [15]. Although it is unknown if

ichthyoplankton are directly consumed by petrels, the unimodal ichthyoplankton peak

sets the stage for the later (about one month) appearance of pre-juvenile stages of

schooling fish (e.g. small pelagics) that have been identified in petrel's regurgitates ([16,18], authors' own data).

Statistical analysis

We firstly explored the potential role of water column stratification as a physical driver of the productivity cascade that leads to the optimal time-window for storm petrel reproduction. Smoothed data on KD490 and chlorophyte concentrations were decomposed into their trend, seasonality and irregular components by a time series additive model [29]. In this way, repeated patterns in annual peaks and troughs can emerge without the influence of potential confusing factors such as the long-term trends, allowing clearer descriptions of seasonal patterns. We considered the 15ºC isotherm depth as a reliable proxy to the thermocline formation ([25]; Fig. S2 and S4). Inter-annual variations on this variable were therefore used for describing stratification processes occurring at the water column and likely driving physical processes favoring primary production (i.e. light penetration) and seasonal patterns of marine productivity. Accordingly, we looked for a correlation between the depth of the 15ºC isotherm and detrended KD490 and chlorophyte concentration time series through a cross-correlation procedure. Coefficient values for these cross-correlations range from 0 (no correlation) to 1 or -1 (total direct of reversed correlation), as a function of daily time-lags.

The long-term patterns in the depth of the 15ºC isotherm were also explored in order to annually detect the start of the water stratification process (see Fig. S4). In particular, the first day within the annual cycle at which the 15ºC isotherm permanently deepened in the water column was considered as the breakpoint initiating the water stratification process and leading to the trophic cascade (from primary producers to higher trophic planktonic organisms) that would ultimately determine the optimal time-window for storm petrel reproduction. Accordingly, the time delay (in days) between

the start of water stratification and the onset of storm petrel reproduction (laying date) was considered as a measure of matching/mistiming between the seasonal pattern of productivity and the breeding phenology of this seabird.

Consequences in reproductive performance of potential mistiming were explored at the population level through the use of linear models in which the elapsed time between the onset of water stratification and the mean laying date was included as the explanatory variable. Complementary, Generalized Linear Mixed Models (GLMM) procedures with binomial error structure (hatching and breeding success or failure) and logit link function were used for exploring reproductive consequences of mistiming processes at the level of the breeding pairs. These models included derived estimates of the elapsed time between the start of water stratification and the laying date of each breeding pair as the explanatory variable of reproductive performance. The breeding pair (pair with male "x" and female "y" breeding n years, thus accounting for potential mate changes [30]) was included as a random factor in order to control for a range of intrinsic traits inherent to reproductive individuals such as age or experience, which are known to act as important drivers of reproductive performance in seabirds [22,24].

Statistical analyses were conducted in R version 3.0.2 (R Core Team 2013) with additional functions provided by the R packages MuMIn [31], lme4 [32] and arm [33].

RESULTS

The long-term data (1993-2012) on the depth of the 15ºC isotherm illustrated that the water column remained well-mixed during the winter, and stratification processes initiated in late winter/early spring and lasted to late fall/early winter (Fig. 1, S2 and S4). Concurrently with the start of water stratification, the capacity of light to penetrate into the water column increased as revealed by decreasing values in KD490 (Fig. 1a, S4 and S5b), thus providing the suitable conditions, i.e. enhanced light and

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nutrient availability, for phytoplankton blooming. The initiation of water stratification was revealed as a clear environmental precursor of primary productivity as evidenced by the strong, lagged correlation between the depth of the 15ºC isotherm and the concentration of chlorophytes, which peaked ca. 15 days after (Fig. 1b, S2 and S5a). This enhanced phytoplankton relative abundance was followed by delayed and consecutive peaks in the subsequent links of the storm petrel food web, with the mean relative abundance of main species of zooplankton and ichthyoplankton reaching maximum values ca. 50 and 110 days after the peak in marine productivity (Fig. 1b). The beginning of the chick-rearing period coincided with the maximum mean relative abundance of the main ichthyoplankton species (Fig. 1b).

Mean laying dates for storm petrels ranged from early to late May and were consistently delayed ca. two months after the onset of water stratification (Fig. 2a). Inter-annual variations in these temporal delays affected petrel reproductive performance, with increasing delays resulting in decreasing values of the mean hatching ($F_{1,19}$=7.206, p=0.015, R^2=0.286) and breeding success ($F_{1,19}$=10.44, p=0.005, R^2=0.367; Fig. 2). Reproductive consequences of mistiming processes were also observed at the level of the breeding pair, with lower reproductive performance in those years with more delayed reproduction relative to the onset of thermal stratification (χ^2=36.859, d.f.=1, p<0.001 and χ^2=39.77, d.f.=1, p<0.001, for the hatching and breeding success, respectively; Fig. 3 and Table S1).

DISCUSSION

Matching reproductive timing to variable seasonal patterns in food availability requires certain plasticity in an animal's phenology [34,35], along with a clear precursor signal informing on the optimal time-window for successful reproduction [3,36]. Regulation of breeding onset has been suggested to reflect the spatio-temporal scale at

which organisms perceive their environment [5]. While migrant species are expected to respond to large-scale climatic signals (e.g. NAO), resident species should be more affected by local conditions around the colony (e.g. local SST or air temperature; [5,11]). However, actual conditions at the breeding area cannot be predicted exactly from large-scale environmental cues [5]. A sequential adjustment of phenology would thus be expected, based on the progressive use of local cues as birds become more closely associated with the colony. This would allow for fine-tuning the onset of reproduction to inter-annual changes in seasonal productivity patterns [5]. At present, little is known about the wintering habits of Mediterranean storm petrels (but see [37]). Thus, we cannot rule out the role of large-scale environmental cues, or even cues at wintering quarters, in driving reproductive timing and/or constraining adaptive shifts in the onset of reproduction in response to local cues [37,38]. However, we provide evidence indicating environmental cues related to water stratification (e.g. a given threshold in the temperature at the sea surface where storm petrels forage) as the local environmental cue informing on inter-annual variations in local productivity patterns and allowing optimal-decision making (i.e., fine-tuning). Indeed, water stratification dynamics have been revealed as an oceanographic feature strongly linked to the trophic cascade upon which storm petrels set the onset of their reproduction.

Successful reproduction depends on a correct decision in springtime, as the high energetic demands of growing chicks at the beginning of the summer should overlap with the peak in food availability [19,23]. Our population approach revealed that the reproductive success of petrels decreased as breeding delayed with respect to the onset of water stratification. Differences in the parental capacities of early vs. late breeders [2,20,21], may hamper our ability to draw firm conclusions about the putative role of optimal decision-making in response to feeding conditions as a determinant of breeding

success [2]. However, seasonal declines in the breeding performance also occurred within breeding pairs and, therefore, when controlling for those intrinsic drivers of breeding performance such as age or experience [20,21]. Mistiming processes and seasonal deterioration in feeding conditions seem, therefore, a more plausible explanation for the observed decrease in reproductive success as the season progresses. This concurs with studies on parental-offspring conflict for Procellariforms suggesting that parents tend to limit effort in reproduction depending on feeding conditions, independently of reproductive requirements [39].

Egg production is also an energetically expensive activity that requires additional nutrient acquisition [40]. This is particularly true for seabirds, such as storm petrels, laying a proportionally large egg, ca. 25% with respect to adult body mass [41]. Consequently, the onset of breeding itself is often dependent upon food availability, meaning that laying date is (by-and-large) correlated with concurrent, and not only future (i.e. at the brooding phase), feeding conditions [9].

Accordingly, our results indicated that mistiming processes may not only affect offspring survival, but also have important consequences in hatching success. This also indicates that feeding conditions during the egg production and incubation periods are important drivers of overall breeding performance. Egg production and brooding phases in petrels apparently coincide with successive peaks in food availability. In particular, the peak in the relative abundance of the main zooplankton species (ca. 50 days after water stratification) temporally matched with egg production (a ca. 12 day period before laying in yellow-legged gulls *Larus michahellis*, [42]), whereas chick rearing occurred concurrently with the summer peak in larval fish species [28]. Petrel regurgitates have been reported to be mainly composed of zooplankton and small fish around 2-4 cm, including both mesopelagic and small epipelagic fish ([16,18], authors' own data).

Coastal night-feeding has also been reported [16]. If this feeding pattern holds true for the study area, petrel breeding milestones would match with both the nocturnal ascent, to surface levels, of zooplankton and with grown postlarvae of schooling pelagic fish (e.g. anchovy *Engraulis encrasicolus*, round sardine *Sardinella aurita* found in regurgitate samples), plus small mesopelagic fish [43,44]. We therefore speculate that life-history traits other than breeding onset, such as the duration of incubation, may also respond to seasonal patterns in trophic cascades within seabirds' food webs.

Studies on mismatch consequences in seabirds are relatively common in northern latitudes (e.g. [13,45]), but they remain scarce at southern European latitudes. Here, we provide the first evidence pointing to water stratification of western Mediterranean waters as a driver of marine productivity, leading to the optimal time-window for reproduction in an inshore seabird. The novelty of the current work lies in the use of high-temporal resolution environmental and detailed longitudinal biological data to explore the relationships between environmental and phenological processes. Additionally, we described the reproductive consequences of mistiming when accounting for alternative drivers of seabirds' reproductive performance such as individuals' age or experience. We therefore provide a suitable framework to conduct exploratory assessments on the potential impact of environmental changes affecting productivity patterns and cues used for decision-making by seabirds in general, and petrels in particular [2,7,46]. Indeed, climate fluctuations are known to result in phenological shifts, sometimes differently across species and trophic levels in marine food webs [13]. This may lead to mismatches between functionally different components of marine ecosystems (e.g. food and consumer), with important effects on their structure and functioning [13]. Identification of factors driving the onset of breeding, the timing of peak food availability, and constraining potential adjustments

(e.g. phenotypic plasticity) are therefore crucial for understanding the actual impact of global change on seabird populations.

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Fig. 1. Environmental cycles and reproductive phenology. Averaged annual cycles for environmental features leading to the optimal time-window for the reproduction of Mediterranean storm petrels. (a) Daily-averaged (1993-2012) depths for the 15ºC isotherm (solid red line) in the water column have been used as a proxy to the thermocline. Daily-averaged (1998-2014) detrended data for the "diffuse attenuation coefficient -KD- for downwelling irradiance at 490nm" (KD490, solid blue line) were used as an indicator of the capacity of light to penetrate into the water column. (b) Daily-averaged (1998-2007) detrended data for chlorophyte concentration (solid green line) was considered as a reliable proxy to phytoplankton biomass. Monthly data on seasonal patterns for the subsequent links of the storm petrel food web, i.e. main species of zooplankton and ichthyoplankton (solid and dotted bars, respectively) were extracted from Fernandez de Puelles et al. (2007). For comparisons between environmental cycles and storm petrel breeding phenology, mean laying/hatching and fledging dates (1993-2014) were also represented in the top graph.
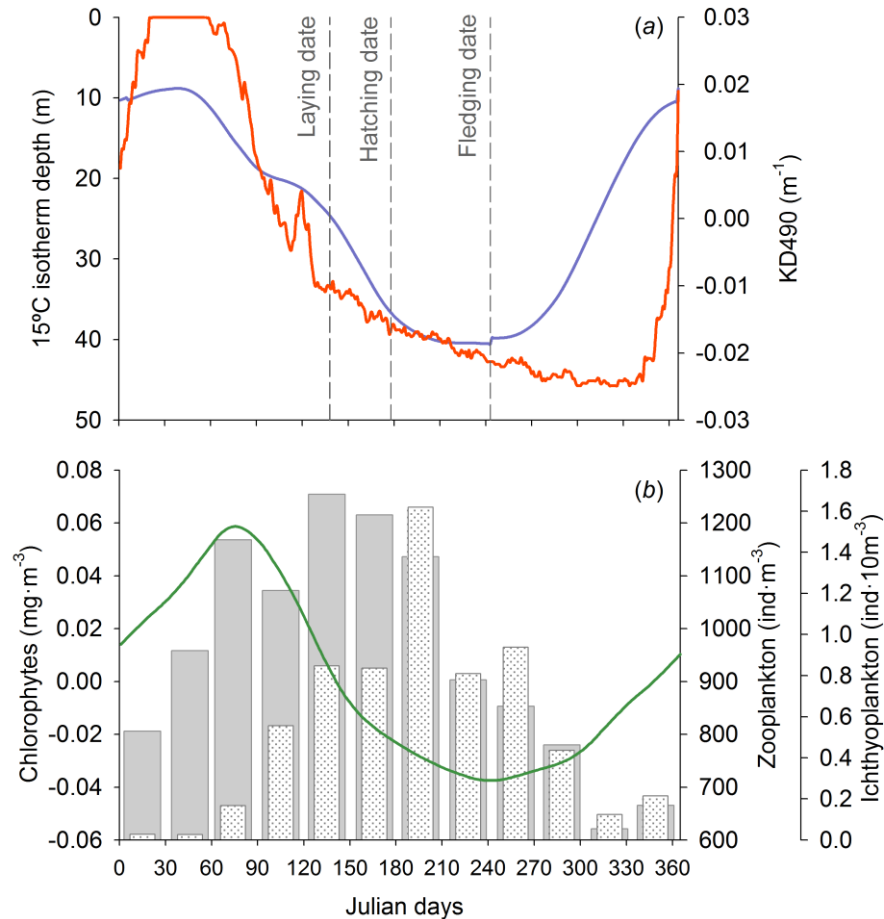

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Fig. 2. Inter-annual trends in environmental drivers and breeding performance. (a) Inter-annual variations in the time delay between onset of the water stratification and the breeding period (mean laying date) for storm petrels. (b,c) Resulting consequences, in terms of average hatching/breeding success (1993-2014), of observed delays in the mean laying date with respect to the timing of water column stratification (as revealed by the 15ºC isotherm). Black lines represent the output of the simple linear regression linking delays in reproduction with population reproductive performance. Inner grey lines represent the 95% confidence intervals and outer grey lines the predictor bands.
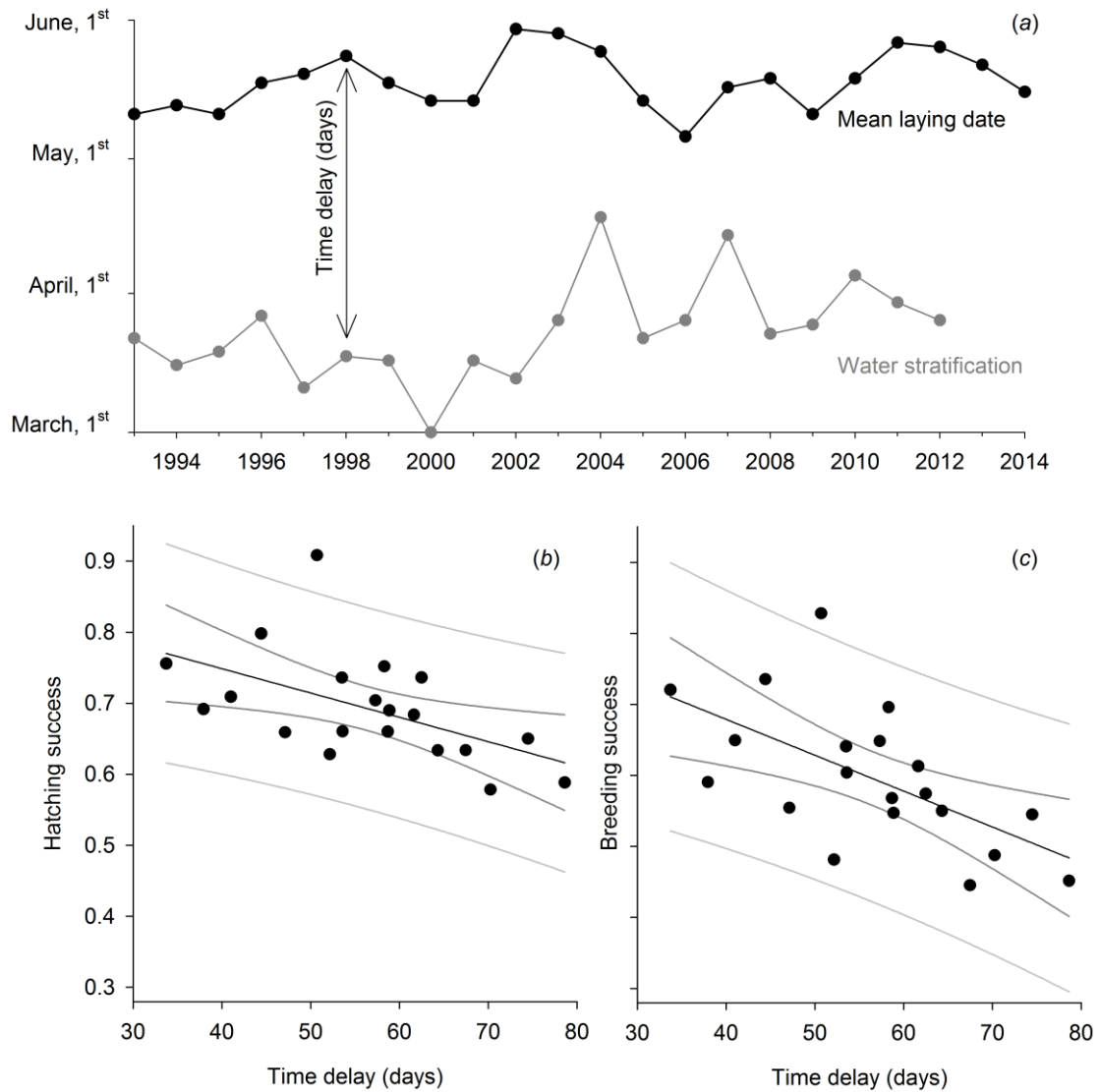
Fig. 3. Consequences of delayed breeding onset. Observed consequences, in terms of hatching and breeding success, of a temporal delay in the laying date with respect to the timing of water column stratification (as revealed by the 15ºC isotherm). Dots represent the hatching/breeding success of all breeding pairs controlled for during the 1993-2014 period and the solid line the outputs of the Generalized Linear Mixed Models that included the breeding pair as a random factor to control for individuals' age and experience.