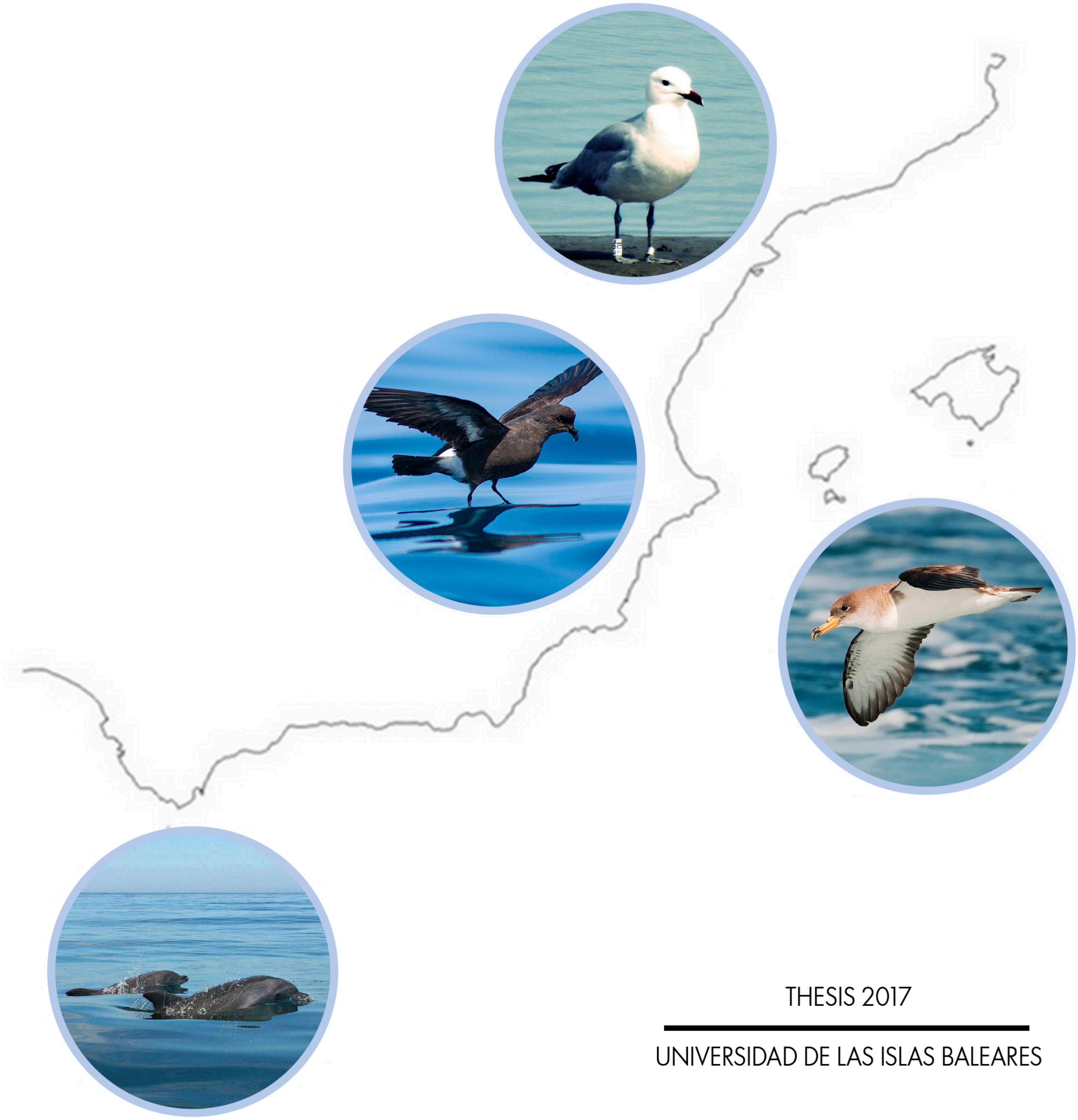
EFFECTS OF ENVIRONMENTAL STOCHASTICITY ON LIFE-HISTORY PARAMETERS OF MARINE TOP PREDATORS

Noelia Hernández Muñoz



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EFFECTS OF ENVIRONMENTAL STOCHASTICITY ON LIFE HISTORY PARAMETERS OF MARINE TOP PREDATORS

PhD Thesis

Noelia Hernández Muñoz

Palma de Mallorca, Mayo 2017

Diseño portada: Noelia Hernández
Foto *Ichthyaetus audouinii*: Noelia Hernández
Foto *Calonectris diomedea*: Pedro Trejo
Foto *Hydrobates pelagicus melitensis*: Juan Carlos Andrés
Foto *Tursiops truncatus*: Noelia Hernández

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EFFECTS OF ENVIRONMENTAL STOCHASTICITY ON LIFE HISTORY PARAMETERS OF MARINE TOP PREDATORS

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I DECLARE:

That the thesis titles

Effects of environmental stochasticity on life history parameters of marine top predators

presented by Noelia Hernández to obtain a doctoral degree, has been completed under my supervision.

For all intents and purposes, I hereby sign this document.

Signature

Palma de Mallorca, 25 mayo de 2017

A mi familia.

The Voice Of Nature

"Some call me Nature, others call me mother nature

I've been here for over four and a half billion years

Twenty-two thousand five hundred times longer than you

I don't really need people but people need me

Yes, your future depends on me

When I thrive, you thrive

When I falter, you falter or worse

But I've been here for aeons

I have fed species greater than you, and

I have starved species greater than you

My oceans, my soil, my flowing streams, my forests,

They all can take you or leave you

How you chose to live each day whether you regard or

disregard me, doesn't really matter to me

One way, or the other, your actions will determine your fate

not mine

I am nature

I will go on

I am prepared to evolve

Are you?"

Nature is Speaking by Conservation International

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AIC: Akaike information criterion.

Chla: Clorofila.

DEV: Deviance.

ENSO: Fenómeno de la Oscilación del Sur “El Niño”.

GHRSST: Group for High Resolution Sea Surface Temperature.

GLM: General Linear Model.

GLMM: Generalized Linear Mixed Model.

IUCN: International Union for Conservation of Nature.

JAGS: Just Another Gibbs Sampler.

LMM: Linear Mixed Model.

HDF: Hierarchical Data Format.

NAO: Indice de Oscilación Atlántico Norte.

NAOa: Oscilación Atlántico Norte anual.

NAOw: Oscilación Atlántico Norte invierno.

NOAA: National Oceanic and Atmospheric Administration.

SOI: Indice de Oscilación Sur.

SST: Temperatura superficial del agua de mar.

WeMO: Indice de Oscilación del Mediterráneo Occidental.

Publicaciones incluidas en la tesis doctoral

- Oro, D., Hernández, N., Jover, L., & Genovart, M. (2014). From recruitment to senescence: food shapes the age-dependent pattern of breeding performance in a long-lived bird. *Ecology*, *95*(2), 446-457.
  DOI: 10.1890/13-0331.1
  Impact factor: 4.733
  Journal quartile: Q1

- Hernández, N., Genovart, M., Igual, J. M., & Oro, D. (2015). The influence of environmental conditions on the age pattern in breeding performance in a transequatorial migratory seabird. *Frontiers in Ecology and Evolution*, *3*, 69.
  DOI: 10.3389/fevo.2015.00069

- Hernández, N., Oro, D., & Sanz-Aguilar, A. (2017). Environmental conditions, age, and senescence differentially influence survival and reproduction in the Storm Petrel. *Journal of Ornithology*, 1-11.
  DOI: 10.1007/s10336-016-1367-x
  Impact factor: 1.419
  Journal quartile: Q1

- Hernández, N., Tenan, S., Fearnbach, H., de Stephanis, R., Verborgh, P., & Oro, D. (2017). The influence of intense maritime traffic and whale-watching on survival, recruitment and population size in bottlenose dolphins. Under revision in *Aquatic Conservation: Marine and Freshwater Ecosystems.*
  Impact factor: 2.415
  Journal quartile: Q1

Resumen

Uno de los principales objetivos en ecología de poblaciones es conocer a que se deben las diferencias encontradas en los rasgos de vida entre individuos de una población y determinar cómo se relacionan con el entorno.

Para comprender mejor los parámetros de las historias de vida de los individuos (longevidad, senescencia, esfuerzo reproductor, frecuencia de la reproducción), son varios los estudios que han invertido un gran esfuerzo en investigar variables individuales o ambientales en distintos parámetros demográficos. Sin embargo, son menos los trabajos que han analizado ambos tipos de variables en un mismo estudio y especialmente escasos los que han estudiado las posibles interacciones entre los distintos tipos de variables. Debido a ello, el principal objetivo de esta tesis ha sido tratar de proporcionar una mejor base para la comprensión de como variables individuales y fluctuaciones de carácter ambiental, u antropogénico, pueden influenciar los rasgos de vida de los individuos. Para conseguirlo, se han realizado estudios a largo plazo basados en diferentes poblaciones de animales marinos longevos, y apicales en la cadena trófica (i.e. aves marinas y delfines). El objetivo central fue estudiar cómo la edad de los individuos (factor esencial que influencia los diferentes rasgos de una especie) y distintos tipos de fluctuaciones (las más importantes según cada población de estudio), podrían estar ejerciendo un efecto sobre diferentes parámetros demográficos (i.e. reproducción, supervivencia y reclutamiento).

En los tres primeros capítulos de la tesis se estudiaron diferentes poblaciones de aves marinas del Mediterráneo, evaluando distintos índices climáticos y/o condiciones ambientales (i.e. descartes pesqueros, Índice de Oscilación del Atlántico Norte, Índice de Oscilación Sur y temperatura superficial del agua de mar). Encontramos un claro efecto de la edad en todas las poblaciones y parámetros demográficos estudiados. En los estudios con *Ichthyaetus audouinii* (capítulo 1) *e Hydrobates pelagicus melitensis* (capítulo 3) se encontró un patrón cuadrático, indicando un mecanismo de senescencia en las últimas clases de edad, mientras que en el estudio con *Calonectris diomedea* (capítulo 2) no pudo encontrarse este patrón posiblemente debido a una falta de potencia de datos. Otro de los principales resultados, fue el efecto de la edad en interacción con las fluctuaciones ambientales encontrado en los parámetros reproductores (capítulo 1 y 2). Resultado no encontrado en la tercera población de estudio (capítulo 3) donde se encontró un efecto temporal en reproducción y ninguno en supervivencia. De manera inesperada, se descubrió heterogeneidad individual en todas las poblaciones estudiadas. Los resultados encontrados sugieren que ante condiciones ambientales adversas sólo individuos de mayor calidad fenotípica o con

mayor experiencia se reproducen, mientras otros evitarían la reproducción para no comprometer su supervivencia futura.

En el último capítulo, a diferencia de los anteriores donde el alimento podía ser el factor más limitante en las poblaciones, en esta población se evaluó el impacto antropogénico que causa el tráfico marítimo en la población de delfines mulares (*Tursiops truncatus*) del Estrecho de Gibraltar. En este trabajo, debido a una falta de crías y juveniles con marcas identificables, no fue posible analizar la edad. Los resultados obtenidos indicaron un efecto del número de ferries sobre la supervivencia, reclutamiento y tamaño de población, mientras que el efecto de los barcos dedicados al avistamiento de cetáceos fue casi despreciable. Los cambios detectados en estos parámetros se correlacionaron con la construcción de un nuevo puerto en la costa marroquí, el cual incrementó un 40% el tráfico de ferries en el Estrecho. La explicación más plausible sugiere que los individuos pueden estar migrando permanentemente a otras áreas más prístinas. Bajo nuestro conocimiento, este es el primer estudio que ha conseguido cuantificar el efecto de los ferries en una población de cetáceos.

Summary

One of the main objectives in population ecology is to know what causes the differences found in life history traits between individuals of the same population and to determine how they are related with the environment.

In order to better understand the life histories of individuals (longevity, senescence, reproductive effort, frequency of reproduction), several studies have invested great effort in researching individual or environmental variables in different demographic parameters. However, fewer studies have analyzed both types of variables in the same study, and even fewer have studied the possible interactions between the different types of variables. Thus, the main objective of this thesis was to attempt to provide a better basis for the understanding of how individual variables and environmental, or anthropogenic, fluctuations can influence individuals' life traits. To achieve this goal, long-term studies were carried out with different populations of marine top predators (i.e. seabirds and dolphins). The main objective was to study how the age of individuals (an essential factor that influences the different traits of a species) and different environmental conditions (the most important ones for each population studied) could be influencing different demographic parameters (i.e. reproduction, survival, and recruitment).

In the first three chapters of the thesis, different populations of Mediterranean seabirds were studied, evaluating distinct climate indices and/or environmental conditions (i.e. fishing discards, North Atlantic Oscillation Index, South Oscillation Index, and surface water temperature). A clear effect of age was found in all the populations and demographic parameters studied. In two of the three species studied, *Ichthyaetus audouinii* (Chapter 1) and *Hydrobates pelagicus melitensis* (Chapter 3), a quadratic age pattern was found, indicating a mechanism of senescence in the last age classes; whereas in the other species, *Calonectris diomedea* (Chapter 2), it was not possible to find this pattern, maybe due a lack of data power. Another of the main results found was the effect of age on interaction with environmental fluctuations upon reproductive parameters (Chapters 1 and 2); a result not found in the third population studied (Chapter 3) where a temporary effect was found in reproduction but none in survival. Unexpectedly, individual heterogeneity was found in all the populations studied. The results suggest that under adverse environmental conditions only the better quality individuals (phenotypically or those with the greatest experience) reproduce, while the worse quality individuals would avoid reproduction so as not to compromise their future survival.

In the last chapter, unlike the previous ones where food was the most likely limiting factor in populations, the anthropogenic impact caused by maritime traffic in the population of bottlenose dolphins (*Tursiops truncatus*) in the Strait of Gibraltar was assessed. In this study, due to a lack of calves and juveniles with identifiable marks, it was not possible to analyze age. The results obtained indicated an effect of the number of ferries on survival, recruitment, and population size, while the effect of whale-watching vessels was almost negligible. The changes detected in these parameters were correlated with the construction of a new port on the Moroccan coast, which increased ferry traffic in the Strait by 40%. The most plausible explanation suggests individuals may be permanently migrating to other more pristine areas. To our knowledge, this is the first study that has managed to quantify the effect of ferries on different demographic parameters in a cetacean population.

Resum

Un dels principals objectius en ecologia de poblacions és conèixer a què es deuen les diferències trobades en els trets de vida entre individus d'una mateixa població, i determinar com aquests es relacionen amb l'entorn.

Per comprendre millor les històries de vida dels individus (longevitat, senescència, esforç reproductor, freqüència de la reproducció), són diversos els estudis que al llarg dels últims anys han invertit un gran esforç en investigar variables individuals o ambientals en diferents paràmetres demogràfics. No obstant això, són menys els treballs que han analitzat els dos tipus de variables en un mateix estudi, i especialment escassos els que han estudiat les possibles interaccions entre els diferents tipus de variables. A causa d'això, el principal objectiu d'aquesta tesi ha estat tractar de proporcionar una millor base per a la comprensió de com variables individuals i fluctuacions ambientals, o antropogèniques, poden influenciar els trets de vida dels individus. Per aconseguir-ho, s'han realitzat estudis a llarg termini basats en diferents poblacions d'animals marins longeus, i apicals en la cadena tròfica (i.e. aus marines i dofins). L'objectiu central va ser estudiar com l'edat dels individus (factor essencial que influència els diferents trets d'una espècie) i diversos tipus de fluctuacions (les més importants segons cada població d'estudi), podrien estar exercint-hi un efecte sobre diferents paràmetres demogràfics (i.e reproducció, supervivència i reclutament).

En els tres primers capítols de la tesi es van estudiar diferents poblacions d'aus marines de la Mediterrània, avaluant diferents índexs climàtics i / o condicions ambientals (i.e descarts pesquers, Índex de Oscil·lació de l'Atlàntic Nord, Índex de Oscil·lació Sud i temperatura superficial de l'aigua de mar). Trobem un clar efecte de l'edat en totes les poblacions i paràmetres demogràfics estudiats. En els estudis amb *Ichthyaetus audouinii* (capítol 1) i *Hydrobates pelagicus melitensis* (capítol 3) es va trobar un patró quadràtic, indicant un mecanisme de senescència en les darreres classes d'edat, mentre que en l'estudi amb *Calonectris diomedea* (capítol 2) no es va trobar aquest patró, possiblement degut a la falta de potència de dades. Un altre dels principals resultats, va ser l'efecte de l'edat en interacció amb les fluctuacions ambientals trobat en els paràmetres reproductors (capítol 1 i 2). Resultat no trobat en la tercera població d'estudi (capítol 3) on es va trobar un efecte temporal en la reproducció i cap en la supervivència. De manera inesperada, es va descobrir en totes les poblacions estudiades, que l'heterogeneïtat individual mostrava una diferència de qualitat entre individus. Els resultats suggereixen que davant de condicions ambientals adverses, només individus de major qualitat fenotípica o amb més experiència es reprodueixen, mentre que d'altres evitarien la reproducció per no comprometre la seva supervivència futura.

En l'últim capítol, a diferència dels anteriors, on l'aliment podia ser el factor més limitant en les poblacions, es va avaluar l'impacte antropogènic que causa el trànsit marítim a la població de dofins mulars de l'Estret de Gibraltar. En aquest capítol, a causa d'una falta de cries i juvenils amb marques identificables, no va ser possible analitzar l'edat. Els resultats obtinguts van indicar un efecte del nombre de ferris sobre la supervivència, reclutament i grandària de la població, mentre que l'efecte dels vaixells dedicats a l'albirament de cetacis va ser gairebé menyspreable. Els canvis detectats en aquests paràmetres es van correlacionar amb la construcció d'un nou port a la costa marroquina, el qual va incrementar un 40% el trànsit de ferris a l'Estret. L'explicació més plausible suggereix que els individus poden estar migrant permanentment a altres àrees més prístines. Sota el nostre coneixement, aquest estudi és el primer que ha aconseguit quantificar l'efecte dels ferris en diferents paràmetres demogràfics d'una població de cetacis.

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I

PRÓLOGO

Introducción General

Ecología de poblaciones

Una de las definiciones más precisas sobre ecología la especifica como el estudio científico de las interacciones que determinan la distribución y abundancia de los organismos (Krebs, 2001). Para poder conocer donde se encuentran los organismos y cuantos hay, primero es necesario comprender las causas y efectos que rigen dichos parámetros, siendo uno de los principales objetivos y problemas a resolver en ecología. A la dificultad que implica llegar a conocer las causas, hay que añadir la complejidad que presentan algunos de sus efectos, debido a que estos no sólo pueden afectar a la distribución de las especies, sino también a la abundancia de los organismos (Krebs, 2001), llegando a generar efectos indirectos sobre otras variables y/o parámetros.

Cuando hablamos de ecología de poblaciones hacemos referencia al estudio de un grupo de individuos, pertenecientes a una misma especie, que coexisten en un espacio particular en un tiempo determinado (Begon et al., 1990; Krebs, 2001). Para comprender adecuadamente la dinámica de una población es necesario estudiar cuatro parámetros claves: natalidad, mortalidad, inmigración y emigración (Fig. 1.). Estos parámetros aportan información esencial para determinar si una población se mantiene estable o si por el contrario presenta alteraciones (Williams et al., 2002). Conociendo las causas o variables que pueden originar fluctuaciones, podremos comprender adecuadamente los cambios en la abundancia de una población y responder tanto a preguntas de ecología, como aportar información necesaria para realizar medidas efectivas de conservación.

De los cuatro parámetros claves para analizar la abundancia de una población, en esta tesis nos hemos centrado en dos de ellos, reproducción y supervivencia.

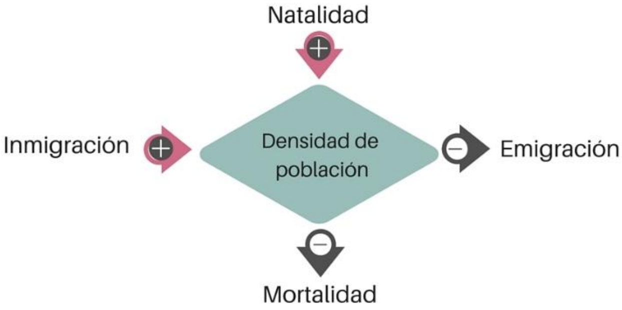

FIG.1. Esquema de como los principales parámetros demográficos de una población contribuyen a cambios en su densidad. Figura modificada de Krebs (2001).

Teoría de historia de vida

Con el objetivo de explicar las diferencias que presentan los individuos en los distintos rasgos de vida, en la década de 1990 se llegó a un consenso sobre una explicación plausible de las características generales que presentan las historias de vida de los organismos (Roff, 1992; S. C Stearns, 1992). En esta teoría se expone que las historias de vida están determinadas por la interacción entre factores extrínsecos e intrínsecos; siendo los factores extrínsecos los impactos ecológicos y los factores intrínsecos las compensaciones entre los rasgos de vida (S. C. Stearns, 1989). Estas compensaciones representan costes en la eficacia biológica de los organismos, beneficiando uno de los rasgos de vida en detrimento de otro (S. C. Stearns, 1989). No obstante, para comprender la dinámica de una población no sólo es necesario conocer que factores afectan a los organismos, sino también establecer una conexión entre los procesos individuales y los procesos poblacionales (Tuljapurkar & Caswell, 1997). Por ejemplo, en especies longevas con una baja tasa reproductiva (especies k-estrategas), el parámetro más importante es la supervivencia adulta, por lo tanto, invertir una elevada cantidad de energía con el fin de maximizar su éxito reproductor no sería una buena estrategia, debido a que la repercusión en la población sería mínima mientras su supervivencia sí se vería afectada (Nevoux et al., 2010; Sæther y Bakke, 2000). Por el contrario, especies con baja tasa de supervivencia y alta fecundidad (r- estrategas), los cambios en la fecundidad pueden tener una gran repercusión en la población (Sæther y Bakke, 2000) y un detrimento de la supervivencia a favor de la reproducción si puede ser compensatorio. Ante condiciones desfavorables, la estrategia o respuesta que van a llevar a cabo estos diferentes tipos de especies no va a ser la misma, por lo que es fundamental conocer la respuesta de los individuos al medio ambiente, así como la evolución de sus historias de vida. De esta forma podremos comprender la dinámica de una población desde un punto de vista ecológico y evolutivo (Williams et al., 2002).

Factores que influyen en la reproducción y supervivencia

Un gran número de estudios han centrado sus trabajos en comprender qué factores afectan a los diferentes parámetros demográficos, especialmente reproducción y supervivencia. Algunos de esos estudios han sido abordados analizando covariables individuales: la edad (Cam y Monnat, 2000; Jones et al., 2008; Martin y Festa-Bianchet, 2011); la experiencia (Desprez et al., 2011; Froy et al., 2013; Sanz-Aguilar et al., 2008) y/o el sexo (Nussey et al., 2009; Tavecchia et al., 2001). Por el contrario, otros se han centrado en factores ambientales como la disponibilidad de alimento (Durant, 2004; Durant et al., 2007; Frederiksen et al., 2004), cambios debido al clima (Sandvik et al., 2005; Winkler et al., 2002). Sin embargo, el número de estudios que han analizado ambas variables es bastante inferior (Bunce et al., 2005; Grosbois y Thompson, 2005; Lee, 2011; Oro et al., 2010;

Tavecchia et al., 2005) y especialmente escasos los que han estudiado cómo los patrones específicos de la edad pueden variar ante diferentes condiciones ambientales (Pardo et al., 2013).

Según las diferentes condiciones ambientales, la respuesta de los individuos puede venir determinada en función de la edad, la experiencia y/o la heterogeneidad individual, por este motivo el trabajo realizado en esta tesis se ha centrado en analizar la reproducción y la supervivencia teniendo en cuenta tanto covariables individuales como variables de carácter ambiental. Principalmente se ha estudiado en detalle el patrón específico de la edad teniendo en cuenta la estocasticidad del medio, lo que ha permitido comprender de una manera más completa y real como la reproducción y la supervivencia pueden variar no sólo en función de la edad de los individuos, sino también en un hábitat con condiciones favorables o adversas.

Variación específica de la edad

Cuando estudiamos la dinámica y evolución de una población salvaje, la edad es un factor esencial (Charlesworth, 1980) ya que puede tener efectos muy importantes en los rasgos fisiológicos, fenotípicos, de comportamiento y demográficos de una especie (Lecomte et al., 2010; Reid et al., 2003). Una de las cuestiones más importantes en ecología es conocer el patrón específico de la edad que presenta cada especie en los diferentes parámetros demográficos (Stearns, 1992). Conociendo el patrón se puede comprender cómo evolucionan los rasgos de vida y aplicarlo al estudio de la población (Morris y Doak, 2002). Por ejemplo, el éxito reproductivo y la supervivencia en los individuos iteróparos generalmente muestra una mejoría inicial con la edad, hasta alcanzar un valor máximo de éxito reproductivo o supervivencia (Pardo et al., 2013). En algunos organismos, tras alcanzar ese valor máximo, se puede observar un deterioro progresivo tanto en reproducción como supervivencia (Clutton-Brock, 1988; Monaghan et al., 2008), debido a una disminución de la función fisiológica de los individuos que causa el envejecimiento (Bronikowski y Flatt, 2010; Rose, 1991; Stearns, 2000).

Existen cuatro hipótesis, no excluyentes entre sí, que nos permiten explicar de manera conjunta las variaciones específicas en el éxito reproductor y en la supervivencia debida a la edad (ver revisión en Forslund & Part, 1995).

1) Hipótesis de selección (Curio, 1983; Nol y Smith, 1987). En ella se explica que las diferencias observadas en supervivencia y reproducción vienen dadas por la aparición o desaparición progresiva de fenotipos. Es decir, se espera que con el paso del tiempo los

individuos de cada cohorte sean de mayor calidad y estén mejor adaptados (Forslund y Part, 1995). Esta hipótesis tiene dos versiones. La primera de ellas consiste en la desaparición de fenotipos malos (también conocida como hipótesis de selección) donde se explica que el cese reproductivo es causado por una mayor mortalidad de los individuos de peor calidad fenotípica (Curio, 1983). La segunda hipótesis consiste en la incorporación tardía de fenotipos buenos, también llamada hipótesis de reproducción retrasada (Hutchings, 1993; Tuljapurkar, 1990).

2) Hipótesis de limitación (Curio, 1983). Sugiere que los individuos pueden tener limitaciones en la reproducción debido a su condición fisiológica, experiencia y/o habilidades. En esta hipótesis se plantea que los individuos con la edad adquieren capacidades que les permiten tener un mayor éxito reproductor, por tanto, individuos con más experiencia se reproducirán mejor que aquellos que no la tienen (Nol y Smith, 1987). Entre estas limitaciones destacan:

(a) Madurez fisiológica. El funcionamiento endocrino controla diferentes aspectos de la reproducción, como es la producción de gametos fértiles o incluso el desarrollo de los cuidados parentales (Wingfield y Farner, 1993). Por tanto, los procesos de maduración sexual en las clases de edad más jóvenes, así como el deterioro del sistema endocrino en ejemplares más veteranos, pueden ocasionar limitaciones e impedir la reproducción (Ottinger y Bakst, 1995).

(b) Habilidad de forrajeo. Si con la edad los individuos adquieren capacidades para una mayor eficiencia en la búsqueda, captura y manipulación del alimento, la aptitud de los individuos jóvenes para realizar con éxito la reproducción será menor que aquellos individuos más longevos que presentan mayor destreza para adquirir alimentos (Desrochers, 1992; Pärt, 2001). Incluso en el caso de que los individuos jóvenes muestran suficientes habilidades para adquirir alimento, la elección de la dieta y los requerimientos nutritivos pueden cambiar cuando se trata de sacar adelante la descendencia. La mejora en el éxito reproductivo con la edad, se explica probablemente por el aprendizaje de las habilidades asociadas con la búsqueda de alimento. Un estudio con skúas (Ratcliffe et al., 1998) encontró mejoras en la fecha y tamaño de puesta con la edad, asociadas al aprendizaje y adquisición de habilidades con la experiencia de la cría.

(c) Experiencia reproductiva. La eficacia en el desarrollo de actividades como el cortejo, la construcción del nido, incubación y sacar adelante a la descendencia, puede mejorar con la edad (Wheelwright y Schultz, 1994; Wiebe y Martin, 1998), obteniendo mayor éxito los ejemplares experimentados (generalmente de mayor edad) con respecto a reproductores jóvenes de menor experiencia (Weimerskirch, 2002). Esta hipótesis asume que la edad de la primera reproducción es independiente de la calidad fenotípica de los individuos. Si los ejemplares de peor calidad retrasan el inicio de la reproducción, el menor éxito reproductivo podría deberse a su peor calidad fenotípica y no a la falta de experiencia previa (Pärt, 1995).

(d) Acceso a los recursos. El mejor acceso a los recursos (no sólo en términos de alimentación) también puede influenciar en un mayor éxito reproductor de los ejemplares que presentan unas condiciones más óptimas (Reznick et al., 2000; Williams, 1966). En numerosas especies, estos individuos llegan más temprano a las áreas de cría o adquieren un estatus más dominante en la jerarquía social. Como resultado tienen prioridad en el acceso a los mejores territorios para nidificar, pudiendo aumentar de esta manera su éxito reproductor (Kokko, 1999; Møller, 1994; Wiggins et al., 1994).

3) La hipótesis de restricción (Pianka, 1976; Williams, 1966) predice que individuos sin experiencia mostrarán un mayor gasto en reproducirse según adelanten la edad de la primera reproducción (Forslund y Part, 1995). Propone que los individuos más jóvenes se abstienen de reproducirse o reducen su esfuerzo en reproducción para poder mejorar sus posibilidades de supervivencia y reproducción futura (Pugesek, 1981), mientras que los individuos de más edad realizan un mayor esfuerzo en reproducción debido a su menor esperanza de vida reproductiva.

4) Hipótesis de senescencia. A diferencia de las anteriores hipótesis (que explican un aumento de los parámetros demográficos con la edad), esta última hipótesis nos permite explicar la disminución en reproducción y supervivencia que se puede observar en edades más avanzadas (ver Nussey et al, 2013). Existen dos teorías principales que explican la senescencia (Hamilton, 1966). La primera de ellas es la hipótesis de acumulación de mutaciones (Medawar, 1952), donde se expone que la senescencia ocurre como consecuencia de una acumulación de genes con mutaciones débilmente dañinas las cuales actúan en una fase tardía de la vida. La segunda teoría responde a la hipótesis de pleiotropía antagonística (Williams, 1957). Esta teoría sugiere que los rasgos seleccionados mejoran la capacidad de reproducción en la fase más temprana de la vida, pero también tiene efectos perjudiciales en el futuro, cuando la selección es más débil. Según esta teoría, a pesar de los efectos negativos que pueda causar en los últimos años de vida, existe una selección positiva a favor de estos genes. Bajo esta hipótesis se espera que los individuos que fueron seleccionados para tener una primera reproducción a una edad temprana, también tengan un ritmo de senescencia mucho más rápido, que a su vez da lugar a una edad más anticipada de la última reproducción (Hamilton, 1966).

Debido a las diferentes respuestas que pueden tener individuos de distinta edad, es fundamental conocer el patrón específico de la edad. De esta manera podremos llegar a comprender las variaciones específicas que ocurren en los diferentes parámetros demográficos y conocer la dinámica de una población, así como la evolución de su historia de vida (Dugdale et al., 2011).

Estocasticidad ambiental

Para interpretar bien la historia de vida de un organismo es importante tener en cuenta covariables individuales como la edad, y conocer el patrón específico que presenta en los distintos casos de estudio. Sin embargo, para comprender la dinámica de una población no basta con conocer sólo el patrón de edad que presenta una especie, también es necesario conocer a que amenazas o limitaciones se enfrentan las especies. En la última década muchas especies marinas se encuentran en peligro crítico o son vulnerables (Lascelles et al., 2014; Paleczny et al., 2015), por lo tanto, es de gran importancia conocer la respuesta que van a presentar los individuos ante diferentes factores externos y como estos pueden afectar a sus rasgos de vida.

Las fluctuaciones medioambientales, ya sean por causas naturales o antropogénicas (características físico-químicas del medio, procesos climáticos, catástrofes, pesquerías, contaminación, etc.) pueden tener efecto de forma directa o indirectamente sobre los individuos de una población. Por ejemplo, unas condiciones climáticas adversas pueden tener efectos directos en la fisiología de los organismos, pero también pueden presentar un efecto indirecto mediante cambios en la cadena trófica (Durant et al., 2004). De hecho, una de las variables más importantes a la hora de estudiar la reproducción y la supervivencia es la disponibilidad de alimento (Martin, 1987). Esta variable puede variar tanto por causas naturales, ej. fluctuaciones en la producción primaria (Howarth, 1988), como por causas antropogénicas, ej. actividades de pesca. Sin embargo, para llegar a comprender bien cómo estas variables afectan a los depredadores, es necesario entender a qué escala espacial actúan los diferentes indicadores de disponibilidad de alimento y qué efectos temporales pueden llegar a tener (Stenseth et al. 2002).

a) Fluctuaciones naturales

Los océanos y la atmósfera están estrechamente vinculados, de tal manera que las condiciones climáticas (vientos, temperatura y presión atmosférica) afectan a la estructura y funcionamiento de los océanos (ej. corrientes marinas, afloramientos y estratificación de masas de agua; ver Stenseth et al. 2002). Cuando se producen fluctuaciones en las condiciones climáticas y/u oceanográficas, se generan cambios físicos en el medio marino que propician condiciones favorables, o desfavorables, para la producción primaria, así como alteraciones en la distribución y abundancia de zooplancton (Durant et al. 2004). Debido al control que se ejerce de abajo hacia arriba en la cadena trófica, fluctuaciones en los niveles más inferiores pueden desencadenar efectos en los superiores (Gordo et al. 2011) afectando a peces, aves marinas y cetáceos. No obstante, los mecanismos que controlan estas fluctuaciones son muy difíciles de llegar a determinar con exactitud. Hay que considerar que el efecto de algunas condiciones meteorológicas, o situaciones oceanográficas, pueden reducir o aumentar la disponibilidad de alimento de forma indirecta, incluso pueden causar un efecto no detectable hasta después de un tiempo determinado, que a veces pueden ser años (ver Durant et al. 2004). Además de influir en la disponibilidad de alimento, ciertas condiciones ambientales como huracanes, tormentas, etc. pueden propiciar situaciones adversas que afectan a la condición fisiológica del individuo y su supervivencia (Genovart et al., 2013)

Un aspecto muy importante a la hora de evaluar las condiciones ambientales, es tener en cuenta la escala temporal y espacial del estudio. Como se ha comentado anteriormente, las condiciones climáticas y oceanográficas pueden tener efectos directos o indirectos, y algunos de ellos sólo se pueden observar con el paso de los años, por lo que es necesario trabajar con la escala espacial y temporal adecuada para cada caso de estudio. En esta tesis hemos tratado la fluctuación medioambiental a dos escalas diferentes, escala local y escala global, explorando los índices climáticos más utilizados para analizar las diferentes fluctuaciones medioambientales en demografía (ver Oro, 2014). Estos índices son: índice de Oscilación Norte (NAO), índice de Oscilación Sur (SOI) y temperatura superficial del agua de mar (SST).

La Oscilación del Atlántico Norte (NAO) es la fluctuación de la masa atmosférica entre el centro de baja presión en Islandia y el de alta presión en Azores (Hurrell, 1995). Condiciona, en gran medida, la variabilidad invernal de muchas regiones, especialmente en Europa del Norte, ya que se correlaciona con la temperatura superficial del mar (SST) y la velocidad del viento (Hurrell et al., 2003). Durante el invierno, cuando el índice NAO es alto (valores positivos), la baja presión en Islandia y la alta presión en Azores producen vientos más fuertes de lo normal desde el Oeste hacia el norte de Europa, dando lugar a condiciones relativamente cálidas y húmedas, produciéndose un transporte de masas de aguas cálidas y ricas en zooplancton en el Mar de Barents, mientras que en el Mediterráneo se produce una situación de inviernos fríos y secos (Hurrell, 1995). Por el contrario, inviernos con valores negativos de NAO, los vientos del oeste se debilitan y su trayectoria es hacia el sur, lo que produce condiciones más cálidas y húmedas en el sur de Europa e inviernos más severos en el norte de Europa. La NAO, al estar definida como una diferencia de presión, no afecta directamente a las poblaciones animales, pero al influenciar la velocidad y dirección de los vientos (Hurrell, 1995) puede llegar a tener un efecto sobre los procesos oceanográficos (Ottersen et al., 2001) y biológicos (Stenseth et al., 2002) especialmente importantes a tener en cuenta en estudios de poblaciones marinas (Ottersen et al., 2004; Stenseth et al., 2002). Si la hidrodinámica de la columna de agua cambia, se produce un efecto sobre el plancton marino que a su vez afecta a la producción, distribución y abundancia de organismos marinos, teniendo un efecto cascada en niveles tróficos superiores (Durant et al., 2004).

Muchas aves marinas invernan en el sur (Egevang et al., 2010; González-Solís et al., 2007; Shaffer et al., 2006), donde la variabilidad en el océano se caracteriza por grandes fluctuaciones en la distribución y abundancia de zooplancton. Esta variabilidad viene determinada en gran medida por el Índice de Oscilación del Sur (SOI). El SOI es un índice estandarizado en base a las diferencias de presión observadas a nivel del mar entre Tahití (Polinesia francesa) y Darwin (Australia), determina las fluctuaciones entre la presión del aire que hay en el Pacífico tropical occidental y el oriental. Los periodos prolongados de valores negativos de SOI coinciden con aguas anormalmente cálidas en todo el Pacífico oriental tropical, dando lugar a episodios de El Niño (también llamado ENSO), mientras que valores positivos de SOI da lugar a aguas anormalmente frías y se denomina La Niña (Knutson et al., 2008). Es de gran importancia biológica conocer esta diferencia de presiones, ya que en situaciones normales hay episodios donde el agua cálida superficial es reemplazada por aguas frías y ricas en nutrientes procedentes del fondo marino. Este fenómeno es conocido como afloramiento y tiene implicaciones biológicas muy importantes, debido a que favorece un aumento de la producción primaria y como consecuencia un aumento en el stock de peces (Cury y Roy, 1989; Hilborn y Walters, 2013). Este índice también nos proporciona información asociada a la actividad de huracanes del Atlántico. Durante las fases positivas (La Niña) se registra una mayor actividad de huracanes, mientras que en fases negativas (El Niño) la actividad de huracanes es mucho menor (Hanley et al., 2003; Knutson et al., 2008).

En ecosistemas costeros y oceánicos, además de los índices climáticos, la temperatura superficial del agua de mar (SST) tiene un importante efecto sobre la producción primaria marina (Field et al., 1998; Gregg et al., 2003), particularmente en zonas de afloramiento. Ante situaciones de temperaturas superficiales frías y vientos intensos, la mezcla de las masas de agua ocurre a mayor profundidad y se produce un incremento de nutrientes en la zona más superficial, generando altas concentraciones de clorofila en primavera y verano, que son utilizados por el fitoplancton. Por el contrario, cuando la temperatura superficial del agua de mar es elevada y los vientos son leves, la mezcla de las masas de agua ocurre de manera más superficial y se reduce el número de nutrientes disponibles, generando una menor concentración de clorofila en primavera y verano (Daly y Smith, 1993). Varios estudios han encontrado que anomalías en la temperatura superficial del agua de mar tienen efectos sobre diferentes parámetros demográficos de aves marinas (Durant et al., 2003; Harris et al., 2005). Incluso puede ser utilizado para determinar potenciales áreas de invernada, como ocurre con el paíño europeo *(Hydrobates pelagicus melitensis*) en el Estrecho de Gibraltar (Soldatini et al., 2014).

b) Causas antropogénicas

Además de las fluctuaciones ambientales a las que se enfrentan los individuos, ciertas actividades antropogénicas suponen también una amenaza directa o indirecta para ciertas especies. Estudios recientes (ver Paleczny et al., 2015) han encontrado que el tamaño poblacional de algunas aves marinas, monitorizadas desde los años 50, han disminuido casi un 70% debido al deterioro que han sufrido los ecosistemas marinos en las últimas décadas. Gran parte de esta disminución se asocia a las actividades pesqueras, tanto a la sobreexplotación de niveles tróficos inferiores de los que depende la alimentación de aves marinas y cetáceos (IUCN 2015), como por causa de la captura incidental de individuos que mueren atrapados en los aparejos de pesca, caso del palangre (González-Solís et al., 2007; Seco Pon et al., 2007). No obstante, algunas artes de pesca como el arrastre de fondo proporcionan descartes que son un importante recurso trófico para algunas aves marinas (Louzao et al., 2011; Oro, 1999; Tasker et al., 2000). La disponibilidad de alimento procedente de los descartes, puede conllevar a una mejora en el éxito reproductor de los individuos. Mejora mediada por un aumento del tamaño de huevo y/o de la puesta, así como una mayor tasa de alimento a los pollos y un aumento en su supervivencia (Oro et al., 2004; Oro y Furness 2002; Oro et al., 1995). Por tanto, algunas actividades antropogénicas, como el caso de los descartes, también pueden afectar de manera positiva a la dinámica poblacional de algunas aves marinas oportunistas (Oro, 1999; Votier et al., 2004).

La degradación del hábitat, ya sea por contaminación o por destrucción física, es una de las principales causas que más afectan a la reproducción y supervivencia de muchas especies marinas (Aubry et al., 2013; Durant et al., 2004). Diferentes procesos antropogénicos como la quema de combustibles fósiles, la manufacturación de productos químicos, así como vertidos en el mar, han dado lugar a elevadas concentraciones de metales pesados en el océano y otros contaminantes (Dietz et al., 2009; Jepson et al., 2016). Estos metales se acumulan durante un largo periodo de tiempo en el mar (Bearhop et al., 2000; Burger, 2008) y pasan a incorporarse a la dieta de los organismos, produciéndose bioacumulación en los niveles tróficos superiores y ocasionando posibles daños a nivel fisiológico, comprometiendo la supervivencia y reproducción de los organismos (Goutte et al., 2014). Además de los contaminantes, y metales pesados, hay que destacar el problema provocado por la ingesta de plásticos en tortugas, aves y cetáceos (de Stephanis et al., 2013; Derraik, 2002; Laist, 1987; Wilcox et al., 2015) que puede ocasionar efectos perjudiciales en la reproducción y supervivencia de los individuos (Lavers et al., 2014; Tanaka et al., 2013), al igual que sucede con la contaminación lumínica y acústica, que pueden dar lugar a efectos negativos en aves marinas y cetáceos (Erbe, 2002; Francis et al., 2009; Gaston et al., 2014; Longcore y Rich, 2004).

Cabe destacar que la destrucción y alteración de los ecosistemas marinos (J. P. Croxall et al., 2012) está influenciada por la introducción de especies invasoras y/o depredadoras en las colonias de cría. Estas perturbaciones perduran durante largos periodos de tiempo y suponen una gran amenaza para poblaciones, perjudicando a los individuos.

Depredadores marinos apicales como especies de estudio

En biología de la conservación es de gran importancia estudiar especies que se encuentran en niveles tróficos superiores, debido al papel fundamental que tienen en el mantenimiento del ecosistema (Bowen, 1997). Estas especies ejercen un control (de arriba hacia abajo) sobre niveles inferiores de la cadena trófica (Baum y Worm, 2009; Frederiksen et al., 2006; Myers et al., 2007). Si se produce la eliminación de un depredador apical del sistema, como consecuencia se pueden producir alteraciones drásticas en la abundancia de las especies situadas en niveles inferiores (Heithaus et al., 2008; Worm y Duffy, 2003) y estas variaciones, a su vez, pueden llegar a ocasionar la degradación de un ecosistema entero (Jackson et al., 2001; Worm et al., 2006).

Debido a su importancia ecológica, los depredadores apicales han sido usados como especies clave para desarrollar iniciativas de conservación marina (ver Hooker y Gerber, 2004; Hoyt, 2012; Sergio et al., 2008). No obstante, la consideración de usar niveles tróficos superiores en iniciativas de conservación marina se ha centrado especialmente en especies que están en situación de peligro o presentan un valor económico comercial (Bowen, 1997). Debido a esto, es necesario conocer cómo estas especies responderán a las diferentes fluctuaciones ambientales que ocurren en el medio y comprender si estas respuestas están condicionadas por algún patrón específico, como puede ser la edad u otros factores.

Para abordar los objetivos de la tesis nos hemos centrado en el estudio de cuatro poblaciones diferentes de aves marinas y cetáceos, especies situadas en niveles superiores de la cadena trófica que en las últimas décadas han incrementado considerablemente su grado de amenaza (ver Paleczny et al., 2015; Springer et al., 2003). Además, son importantes como objeto de estudio ya que presentan un elevado valor ecológico como indicadores de la calidad de un ecosistema y permiten establecer la protección de una comunidad ecológica mucho más amplia.

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Objetivos de la tesis

Varios trabajos han centrado sus estudios en analizar cómo individuos de diferentes edades responden a factores limitantes, pero muchos de ellos fueron realizados mediante experimentos manipulados. En la mayoría de ocasiones estos experimentos se realizaron incrementando o disminuyendo la disponibilidad de alimento, pero en el medio natural no es viable manipular las diferentes variables ambientales, ni puede asumirse que sólo un factor está influenciando a la población. Debido a la falta de estudios, en poblaciones silvestres, que han analizado la edad y las fluctuaciones medioambientales simultáneamente en esta tesis hemos abordado el trabajo considerando ambas variables. El objetivo general fue conocer si la edad ejercía un papel significativo en la reproducción y supervivencia, determinar que patrón mostraba y saber si este patrón variaba en función de las condiciones ambientales. Se recopilaron datos de seguimiento individual sobre diferentes especies marinas y se procedió abordar los siguientes puntos:

- Obtener estimas temporales de diferentes parámetros demográficos como éxito reproductor, reclutamiento, supervivencia y tamaño poblacional.
- Conocer si la edad ejerce un papel significativo en dichos parámetros demográficos y hallar el patrón específico que presenta en cada caso, evaluando si existe senescencia en cada especie.
- Evaluar si existen fluctuaciones medioambientales o antropogénicas que tengan impacto en la demografía de la población y si estos factores responden a cambios en la disponibilidad de alimento.
- Conocer si existe interacción entre la edad y las fluctuaciones ambientales en supervivencia y reproducción.
- Estudiar la heterogeneidad individual y analizar las diferentes hipótesis que pueden explicar las variaciones específicas de la edad.

Para conseguir estos objetivos se utilizaron diferentes enfoques metodológicos y poblaciones de estudio.

En el capítulo 1, "From recruitment to senescence: food shapes the age-dependent pattern of breeding performance in a long-lived bird" analizamos 26 años de datos, de individuos de edad conocida, de la colonia de gaviota de Audouin (*Ichthyaetus audouinii*) situada en el Delta del Ebro. El objetivo en este capítulo fue evaluar el patrón específico de la edad en diferentes parámetros reproductores (fecha de puesta, tamaño de la puesta, volumen promedio del huevo y éxito de eclosión) y ante diferentes condiciones ambientales determinadas por la disponibilidad de alimento durante la reproducción. Modelamos la media y las varianzas de los diferentes parámetros de estudio para incorporar la heterogeneidad individual y analizar cómo el patrón específico de la edad podía variar ante diferentes condiciones ambientales.

En el capítulo 2, "The influence of environmental conditions on the age pattern in breeding performance in a transequatorial migratory seabird" analizamos 23 años de datos de hembras de pardela cenicienta *(Calonectris diomedea),* de edad conocida, pertenecientes a la colonia de la Isla de Pantaleu (Mallorca). Esta especie realiza grandes migraciones trans-equatoriales al hemisferio sur que nos permitieron analizar el efecto de la edad y las fluctuaciones ambientales a escala local (disponibilidad de alimento explicada mediante la oscilación del Atlántico Norte; NAO) durante los meses previos a la reproducción, así como las condiciones ambientales a escala global (Índice de Oscilación Sur; SOI) durante la migración. Además de la variabilidad explicada por la edad y los índices climáticos, analizamos la varianza explicada por el efecto *random* para precisar la importancia de la calidad individual en la reproducción.

En el capítulo 3, "Environmental conditions, age and senescence influence differentially survival and reproduction in the storm petrel" se usaron 22 años de datos de individuos de edad conocida del paíño europeo (*Hydrobates pelagicus melitensis)* de la colonia situada en Benidorm. Se estudió el patrón dependiente de la edad, las fluctuaciones medioambientales (Índice de Oscilación del Atlántico Norte (NAO) y temperatura superficial del agua del mar (SST)), así como la heterogeneidad individual tanto en éxito reproductor (dado por la edad de primera reproducción observada en la población) como en supervivencia.

En el capítulo 4, "The influence of maritime traffic and whale-watching on recruitment, survival and population size in bottlenose dolphins ", se analizó el impacto antropogénico ocasionado por el tráfico marítimo en la supervivencia, reclutamiento y tamaño de la población de delfines mulares (*Tursiops truncatus*) del Estrecho de Gibraltar. Para conseguir evaluar el impacto de los *ferries* y la actividad de empresas dedicadas al avistamiento de cetáceos se utilizaron 8 años de datos de identificación fotográfica individual. Las historias de encuentro fueron analizadas mediante modelización jerárquica, usando un enfoque bayesiano, teniendo en cuenta la heterogeneidad individual y el grado de marcaje de los individuos.

II

CAPÍTULOS PRINCIPALES

1

From recruitment to senescence: food shapes the age-dependent pattern of breeding performance in a long-lived bird.

Oro, D., Hernández, N., Jover, L., y Genovart, M. (2014). From recruitment to senescence: food shapes the age-dependent pattern of breeding performance in a long-lived bird. *Ecology*, *95*(2), 446-457.

Abstract

We used a long-term data set (26 years) from Audouin's Gull (*Larus audouinii*), a long-lived seabird, to address the relationship between the age-dependent pattern of reproductive performance and environmental conditions during breeding. Although theoretical models predict that the youngest and oldest breeders (due to inexperience and senescence, respectively) will perform less well than intermediate age classes, few empirical data exist regarding how this expected pattern varies with food availability. To assess the influence of age and food availability (corrected by population size of the main consumers to take into account density dependence) on a number of breeding parameters (laying dates, egg volume, clutch size, and hatching success), we modeled mean and variances of these parameters by incorporating heterogeneity into generalized linear models. All parameters varied with age and to different degrees, depending on food availability. As expected, performance improved with increased food supply, and the observed age pattern was quadratic, with poorer breeding performances occurring in extreme ages. For most parameters (except for laying dates, for which age and food did not interact), the pattern changed with food somewhat unexpectedly; the differences in performance between age classes were higher (i.e., the quadratic pattern was more noticeable) when food was more readily available than when food availability was lower. We suggest that, under poor environmental conditions, only high-quality individuals of the younger and older birds bred and that the differences in breeding performance between age classes were smaller. Although variances for egg volume were constant, variances for laying dates were highest for the youngest breeders and tended to decrease with age, either due to the selection of higher-quality individuals or to a greater frequency of birds skipping breeding with age, especially when food was in low supply. Our results show that mean and variances of breeding parameters changed with age, but that this pattern was different for each parameter and also varied according to food availability. It is likely that, other than food, certain additional factors (e.g., sex, cohort effects, density dependence) also influence changes in breeding performance with age, and this may preclude the finding of a common pattern among traits and among studies on different taxa.

Keywords: age pattern; Audouin's Gull; breeding performance; Ebro Delta, western Mediterranean; food availability; Larus audouinii; long-lived birds; selection hypothesis; variance analysis.

1.1 Introduction

It is a well-known phenomenon in nature that the reproductive performance of individuals improves with age (Bowen et al., 2006; Coulson et al., 2001; Forslund y Part, 1995; Trumbo, 2009). Younger breeders often perform badly and have lower reproductive capacity, which is related to their lack of experience in acquiring sufficient quality and quantity of resources, such as food, mates, and territories (Reid et al., 2003; Sanz-Aguilar et al., 2008). This lack of skills in first-time breeders compared to older individuals commonly translates into costs in successive breeding frequency or even in future survival (i.e., the survival–reproduction trade-off; see Stearns, 2000). In many long-lived animals, a similar pattern of lower breeding performance has been found in the oldest individuals, a phenomenon known as reproductive senescence (e.g., (Aubry et al., 2009; Jones et al., 2008; Rebke et al., 2010).

Three nonexclusive hypotheses exist to explain the poorer performance of younger breeders. The first is the constraint hypothesis (Curio 1983), which states that individuals gain experience and skills over the years (e.g., Nol and Smith 1987, Desrochers 1992, De Forest and Gaston 1996). On the other hand, the restraint hypothesis (Curio 1983) suggests that younger breeders that have higher residual reproductive value than older individuals should reduce their reproductive effort to avoid incurring high survival costs (e.g., Ericsson et al. 2001, Velando et al. 2006). Finally, the selection hypothesis advocates the existence of a selection filter, operating during the first breeding attempts, that leads to older age classes consisting only of individuals that reproduce well (Cam and Monnat 2000, Reid et al. 2003, Sanz-Aguilar et al. 2008).

Once established that the pattern of reproductive traits varies with age, it still remains to be seen whether this pattern is invariant in natural populations subject to stochastic environments. Life-history theory states that, apart from the intrinsic factors that shape the variation of breeding parameters with age (constrained by trade- offs), there are also extrinsic factors (i.e., environmental variation) that play an important and interactive role (e.g., Stearns 2000). Thus, it is to be expected that differences in environmental conditions, especially those related to the availability of food during breeding attempts, will cause variations in this pattern (see Fig. 2). Theoretical models (e.g., Stearns 1976) assume that when food is limited there is an increase in reproductive costs, which will be higher for younger breeders under these environmental conditions. Some of the few studies addressing the association between food supply (mostly estimated through proxies such as climate indexes or fisheries data), age, and breeding parameters have found that differences in breeding performance between age classes were highest when food was in short supply

(Boekelheide and Ainley 1989, Sydeman et al. 1991, Laaksonen et al. 2002, Bunce et al. 2005); see Fig. 2a. A second, unexpected pattern derived from theoretical expectations (see Fig. 2b) indicates that when food availability is high, breeding parameters are equally high for all age classes (Ratcliffe et al. 1998, Nevoux et al. 2007, Lee 2011). In a study of Great Skuas (Stercorarius skua), breeding success was found to vary with age under intermediate levels of food availability, but was rather constant when food supplies were either high or low (see Fig. 2c) (Ratcliffe et al. 1998). Finally, an additional unexpected pattern suggests that variability is irrespective of food supply (i.e., the only effect is that of age; Fig. 2d) (e.g., Vieyra et al. 2009, Pardo et al. 2013; see Appendix: Table A1 for supporting information).

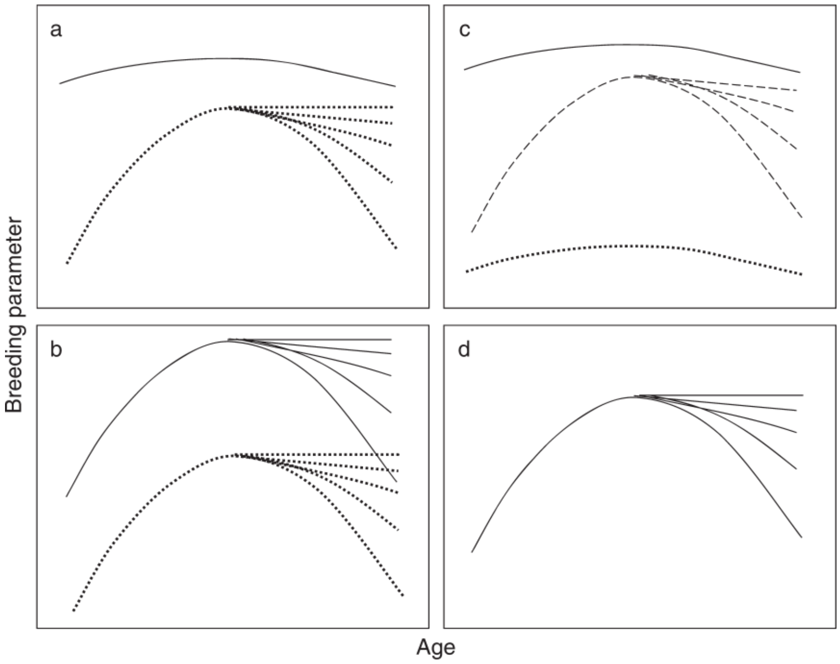


FIG. 2. The four alternative hypotheses built from the published literature (see Appendix: Table A1) to explain the variation in the breeding parameters with age in relation to the environment (see *Introduction* for explanation): high food availability (solid line), low food availability (dotted line), and intermediate food availability (dashed line, panel c). Panel (a) corresponds to the hypothesis that, under conditions with better food supply, the differences between age classes were less than when food availability was lower. In panel (b), differences between age classes were great but equal under all conditions of food availability; in panel (c), although differences between age classes were small but equal under conditions of higher and lower food availability, a more shaped quadratic pattern was found for intermediate food conditions. Panel (d) fits with the hypothesis that the age effect is independent of food availability. Note that the curves show the mean values for each age class and that the hypothesis with a large variation within classes encompasses different curves, depending on the strength of the senescence phase. For laying dates, the curves should be inverted (i.e., younger and older birds laying later in the season).

Here, we used long-term data from a 26-year study to assess how different levels of food availability affect the age-dependent pattern of variability in several breeding parameters of Audouin's Gull *Larus audouinii*, a long- lived colonial bird. Patterns of variability in breeding parameters between age classes are commonly analyzed without considering the variance structure of these parameters (e.g., Stearns and Kawecki 1994, Proaktor et al. 2007). However, variance heterogeneity may contain important ecological information and it is thus advisable to incorporate its analysis into the models (Zuur et al. 2009). Thus, we analyzed not only how age and food affected mean values of breeding parameters, but also how variance changed with age and food availability (Nakagawa and Schielzeth 2012, Violle et al. 2012, Pardo et al. 2013). In fact, the few empirical studies that have analyzed the changes in variance of demographic traits found that the greatest variance occurs in older individuals (Gaillard and Yoccoz 2003, Pardo et al. 2013). However, here we go beyond those findings and test how this variance changes not only with age but also with environmental conditions. For instance, we predict that the variance in clutch size of younger breeders will be larger due to heterogeneity in individual quality (i.e., some are able to perform better than others), and will decrease with environmental stress, i.e., lower food availability, because under these circumstances only good younger breeders will in fact breed.

1.2 Methods

The study was carried out in the Audouin's Gull colony at Punta de la Banya (Ebro Delta, western Mediterranean; 40°34'9.18" N, 0°39'7.86"E), which holds ~ 65% of the total world population of this gull (e.g., Tavecchia et al. 2007). The site lies on a 2500-ha peninsula of sandy dunes covered by halophilous vegetation, where the gulls build their nests. Audouin's Gulls are iteroparous and clutch size varies between 1 and 4 eggs (mode 3 eggs). Birds start to breed at three years old, and most recruitment in this colony occurs at 3–4 years and decreases sharply thereafter; annual adult survival probability is estimated at 0.91, and the mean life expectancy is ~14 years (Oro 1998), calculated as

$$\sum_{i_j}^{i_k} = -\frac{1}{\ln(\varphi_i)}$$

Where φ is survival, i is age, and j and k are pre-adult and adult ages.

PLATE 1. A group of Audouin's Gulls at Punta de la Banya in the western Mediterranean where the study was carried out. Some birds are banded; the second from the right holds the code A9N, and corresponds to a gull banded here as a chick in 1988. Photo credit: Carles Domingo

The banding program was initiated in 1985; by 2010, 27 914 chicks had been banded (annual median 1048, range 86–1792). Since 1988, chicks have also been marked with a plastic band with an individual alphanumeric code that can be read from a distance using a telescope (see Plate 1). For birds marked only with metal bands, incubating adults were detected using a telescope and were trapped at the nest following standard procedures (see Tavecchia et al. 2007). In the period 1994–2011, from the beginning of the laying period onward, nests were identified by searching for banded adults showing reproductive behavior. Once detected, nests were marked and monitored regularly (every 2 or 4 days). During these years, 1631 nests with at least one marked adult were monitored (annual median 101, range 13–143). We recorded the breeding phenology (laying date of the first egg as the number of days elapsed since 12 April (see Fig. 2b), that is, just before the start of laying), clutch size (the number of eggs laid), egg volume (length and maximum width of each egg measured with a digital caliper to ±0.1 mm; see Oro et al. 1996), and hatching success. Only the hatching success of non-abandoned or predated nests was considered. Nests abandoned or predated before the clutch was completed were considered only for laying dates, but not for the rest of parameters; when abandonment and predation occurred once the clutch was completed, these nests were considered also for egg volume and clutch size, but not for hatching success. Parameters related to eggs are an excellent indicator of environmental conditions during the breeding period; for instance, at the population level, egg volume and clutch size increase with improved food availability in the area around the colony (e.g., Oro et al. 1996). The visits (median seven visits for the laying and incubation period lasting ~30 days) allowed us to control for egg abandonment and predation; thus we were able to obtain unbiased estimates for clutch size. Once the clutch had been started, the laying date of these nests (except if they were predated) was estimated on the basis of the hatching date of the first egg (see Oro et al. 1996). Nests found when hatching was initiated or nests abandoned or predated before we could assess that the clutch was completed (i.e., once after three days—the maximum laying interval in Audouin's Gulls—since the last egg was recorded, except for clutches of four eggs) were not considered, in order to avoid overestimation of true hatching success. Furthermore, nests found once clutches were completed (i.e., consecutive visits did not record more eggs) did not underestimate clutch size or hatching success due to potential previous predation, because nests found on the laying date that suffered predation within the laying interval (i.e., before clutch was potentially completed) were always abandoned (own observations, N=37 nests). These filters, together with the fact that 87% of nests were found on the laying date, made apparent success a reasonable proxy of true hatching success. Because chicks abandon the nest just few days after hatching, breeding success could not be recorded. Given that Audouin's Gulls are ground- nesting birds and the large size of the colony (median number of breeding pairs: 11 300, range 9170–15 329), we only have transversal population data, i.e., most individuals could not be monitored in successive years. From the 1631 nests monitored over the study, 85% corresponded to individuals monitored only once, and 15% were monitored twice, the maximum number of replicated data from the same individual. Thus, we considered that pseudoreplication in our data was negligible. In many cases only one member of the pair was banded, so we checked assortative mating by age by using pairs in which both members were marked. The association between the ages of the two members was high (N=152, Spearman correlation r_s =0.736, $P<0.0001$, mean difference = 1.9 years, 95% CI: 1.5–2.3 years), so we were able to assume that the age of a non- banded partner was similar to that of the banded (known-age) bird.

The tons (1 metric ton = 1 Mg) of landings of the trawler fleet in La Rapita, the main fishing port near the colony (Oro and Ruiz 1997), were used as a proxy for annual food availability. In the study area, Audouin's Gulls overlap their foraging areas with the fishing grounds of the trawler fleet (Mañosa et al. 2004, Cama et al. 2012). Gulls exploit discards to a great extent (>75% of their diet; see Oro et al.

1997), and amounts of discards are highly correlated with trawler landings (Oro and Ruiz 1997); as a result, breeding success is correlated with fish landings (Fig. 3). When trawlers do not operate (e.g., during moratoria periods and weekends), gulls feed mainly on small pelagics and less importantly on secondary prey from rice fields (67% and 27% of the gull diet, respectively; Oro et al. 1997). Those landings were corrected for population size (i.e., food per capita, hereafter referred as food) by taking into consideration the number of both Audouin's and Yellow-legged Gulls L. michahellis breeding each year (see methods in Almaraz and Oro 2011)—the latter gull being a sympatric food-competing species—to account for the density dependence of the guild by interference competition recorded in the study colony (Tavecchia et al. 2007, Almaraz and Oro 2011). The availability of discards greatly influences the breeding parameters of the study colony (e.g., Oro et al. 1996; see Fig. 3). The variability in food supply was great and offered a wide range of environmental conditions. For instance, under severe food limitation when discard availability was at its lowest, the modal clutch size decreased to only two eggs, an exceptionally low value for this species (Oro et al. 1996).

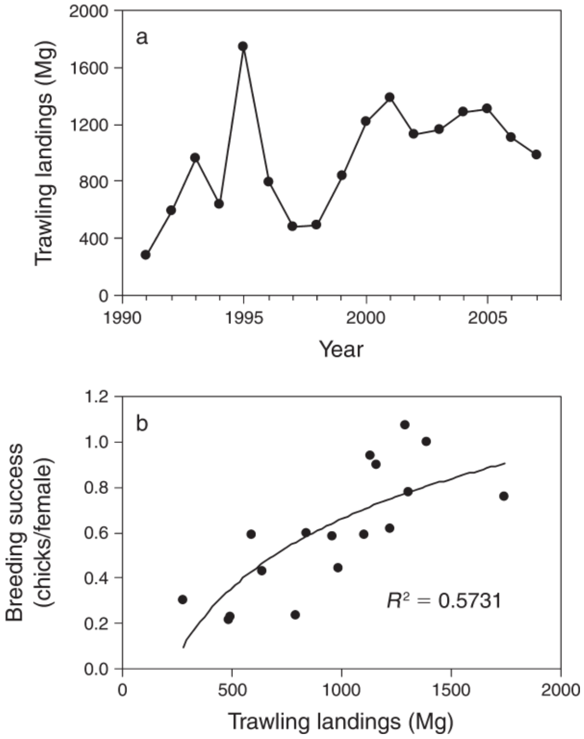


FIG. 3. (a) Variability of trawling landings (as a proxy for discard availability, expressed as metric tons [SI unit Mg] of catches from April to June, the whole breeding season) at the main fishing harbor close to the colony of Audouin's Gulls (*Larus audouinii*) at the Ebro Delta during the period 1991– 2007; and (b) association between breeding success (as mean number

of chicks per female) and trawling landings (the value of R^2 is calculated on a log relationship).

We analyzed data using generalized linear models (GLM) to assess the influence of age, food availability per capita (standardized), and their interaction on each breeding parameter. Breeding parameters were modeled as functions of continually valued age and food availability, with model error covariance matrices structured by group-specific error variances for age group and food availability. We used different error and link functions, depending on the distribution of the breeding parameter: Gaussian error and link identity function for average egg volume in a clutch, and laying date, binomial error, and logit link function for clutch size and hatching success. Owing to the fact that clutch size did not follow a Gaussian or a Poisson distribution (range 1–4), that one-egg clutches are rare (10%), and that most individuals lay three-egg clutches (the modal clutch size, corresponding to 55% of the clutches monitored), we treated that parameter as a binomial variable (i.e., laying or not laying a three-egg clutch).

Different models with additive fixed effects and their interactions were analyzed; age was introduced as linear, logarithmic, and quadratic to test for different patterns of age-dependent variation in the breeding parameter (see Fig. 2). Given that egg volume varies with clutch size (Oro et al. 1996), we also introduced clutch size as an explanatory factor for that parameter. We incorporated heterogeneity into the models to test for between- group heteroscedasticity, i.e., whether variances vary between age groups and food availability. We obtained the residual variances for each group directly from the GLM. Because hatching success and clutch size were treated as binomial variables, the heteroscedasticity procedure was not feasible because mean and variance are functionally linked. We used biologically meaningful categorizations of ages and food-availability classes; older age classes were pooled to ensure enough statistical power. Ages were categorized into a less constrained distribution (Age A, six classes: 3, 4, 5, 6, 7–14, and >14 years old) and two simpler, more constrained structures (Age B, four classes: 3, 4–5, 6–14, and >14 years old; Age C, three classes: 3, 4–6, and > 6 years old) (see Appendix: Table A2). Food availability per capita (as Mg of fish landed divided by the number of breeding pairs of Audouin's and Yellow-legged Gulls) was standardized through a standard normal transformation (by subtracting the mean and dividing the standard deviation) using categories in a single structure with three balanced groups: negative values (seven years with poor food supply per capita), values between 0 and 1 (five good years), and values higher than 1 (six very good years).The average egg volume in a clutch and mean laying date were fitted with the functions *gls* and *varIdent* from the *nlme* R package (Pinheiro et al. 2013); 95% confidence limits of the variances were obtained by utilizing the *intervals.gls* function from this package; clutch size and hatching success were fitted with the *glm* function, in all cases using R software (http://cran. r-project.org). Model selection was carried out using the AIC (Akaike information criterion) of each model (Burnham and Anderson 2002).

1.3 Results

Breeding ages ranged from three years old (first breeding age) to 25 years old. As usual in these types of data, larger standard errors of older birds are a result of the smaller sample of these ages (Fig. 4). All breeding parameters showed a trend of variation with age, that is, a general improvement in performance during the first attempts, followed by stabilization during intermediate ages (Fig. 4). A senescence pattern also seemed to emerge in all breeding parameters, most obviously for laying dates and less so for clutch size, egg volume, and hatching success (Fig. 4). Model selection showed that food and age played an important role in explaining variation in breeding parameters compared to the null models. Furthermore, these two effects in combination (either with or without interaction) appeared in the best models for all breeding parameters; likewise, age was always present quadratically (see selected models in Table 1 and Appendix: Table A2). Thus, all breeding parameters significantly increased as food availability improved and a quadratic effect with age appeared (younger and older individuals showing poorer performances; see Fig. 4).

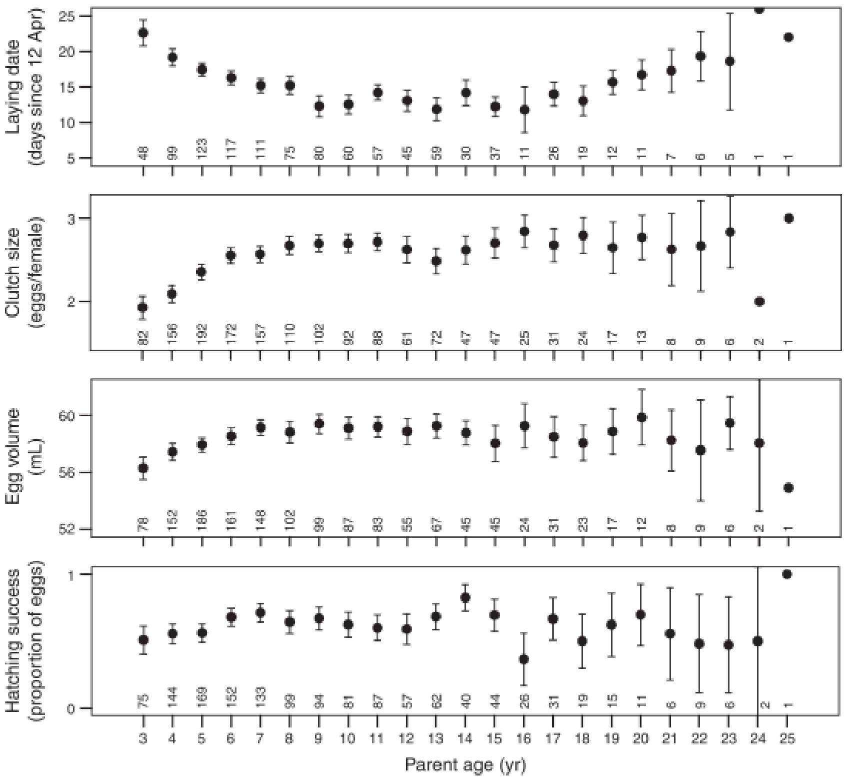


FIG. 4. Relationship between breeding parameters (laying dates, clutch size, egg volume, and hatching success) and age (mean values and 95% CI) in Audouin's Gulls. Note that the laying date is expressed as days elapsed since 12 April, the date on which females are about to lay their eggs. The numbers above the *x*-axis of each panel are the number of observations for each age class.

When food was in short supply, the pattern of variability in most breeding parameters with age was flatter (i.e., the difference between intermediate ages and both younger and older ages was less) than when food was readily available, an effect that increased the quadratic shape of the association (see Figs. 5 and 6). The exception was in laying dates when the selected model included food and age additively (i.e., without their interaction; see Table 1), which gave parallel quadratic curves and similar quadratic patterns, although all ages performed better when food was in good supply (Fig. 6).

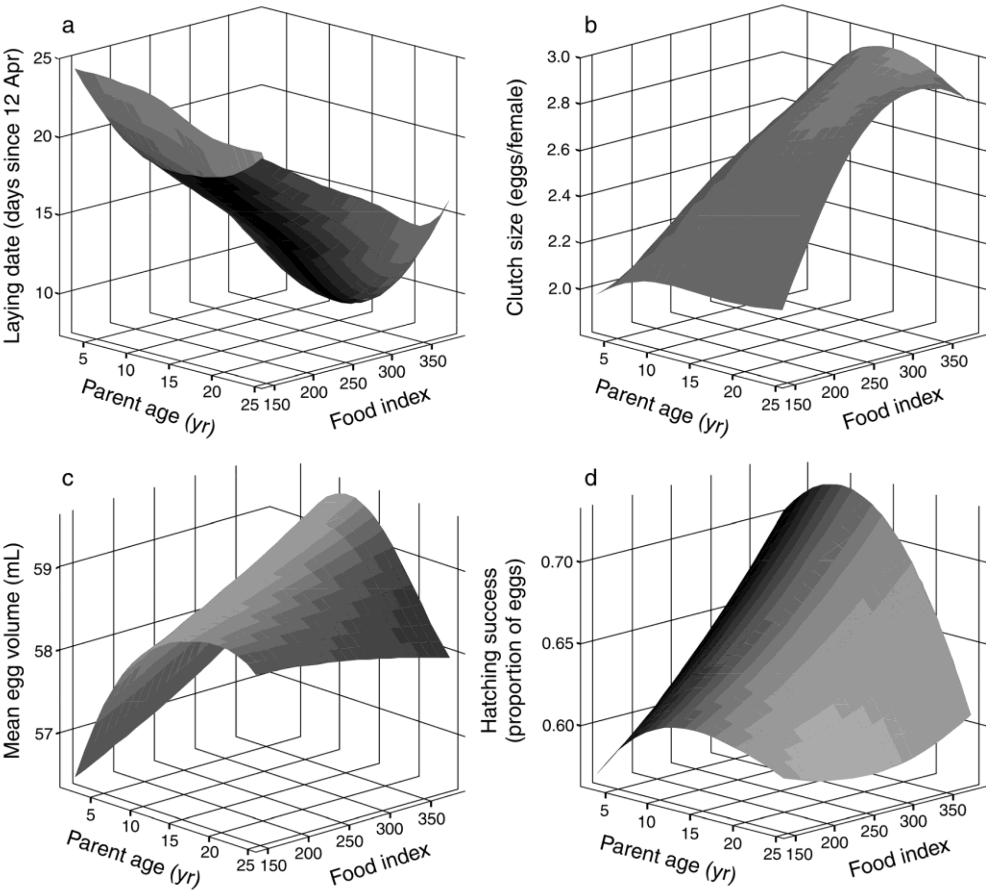


FIG. 5. Smoothing regression surfaces of the raw data, depicting the effects of age (ranging from 3 to 25 years of age) across all observed values of food availability (expressed as a food index of trawling discards per capita) on (a) laying dates, (b) clutch size, (c) average egg volume in three-egg clutches, and (d) hatching success of Audouin's Gulls in the Ebro Delta. The food index is a measure of density dependence because it reflects not the absolute amount of food available, but how much food is available for each individual (total trawling discards divided by the number of gulls).

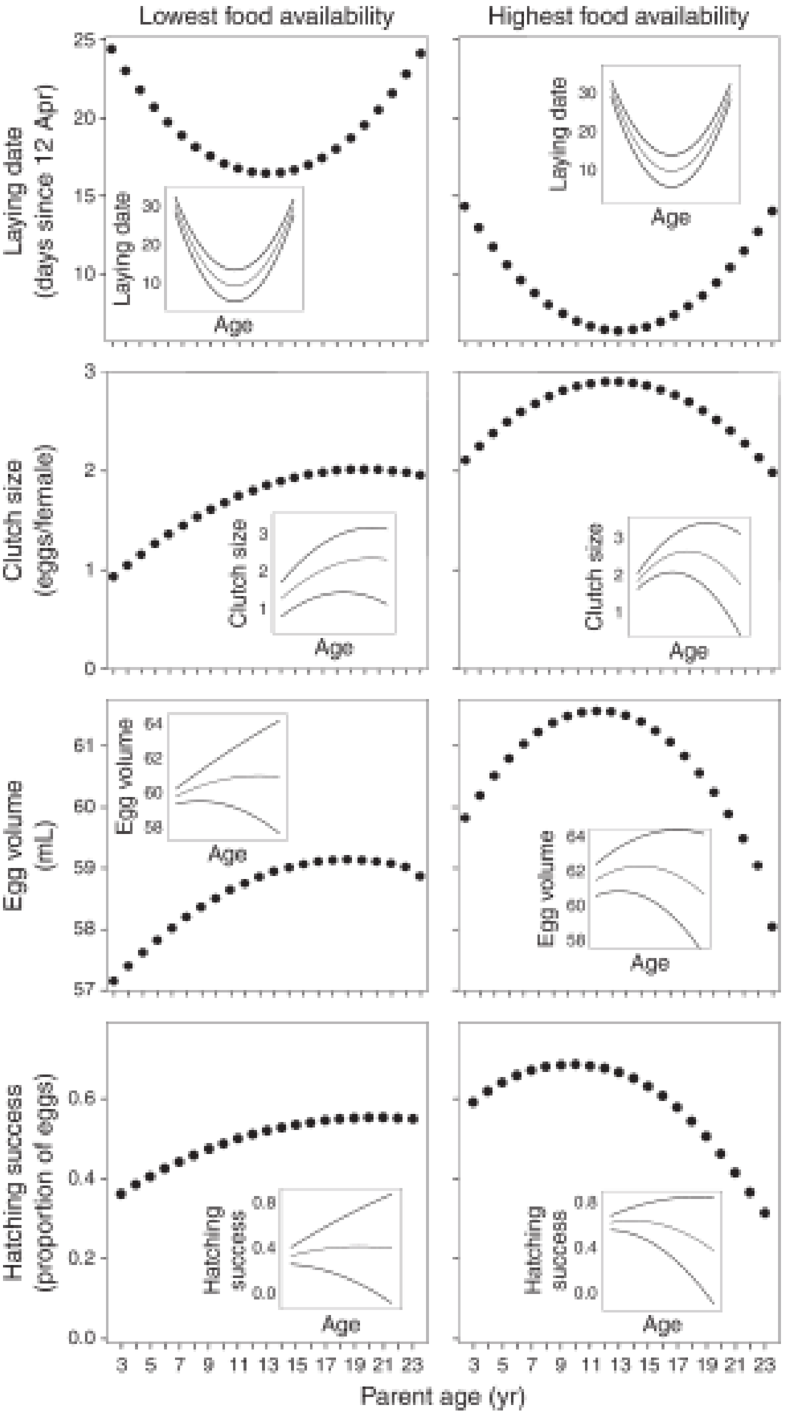
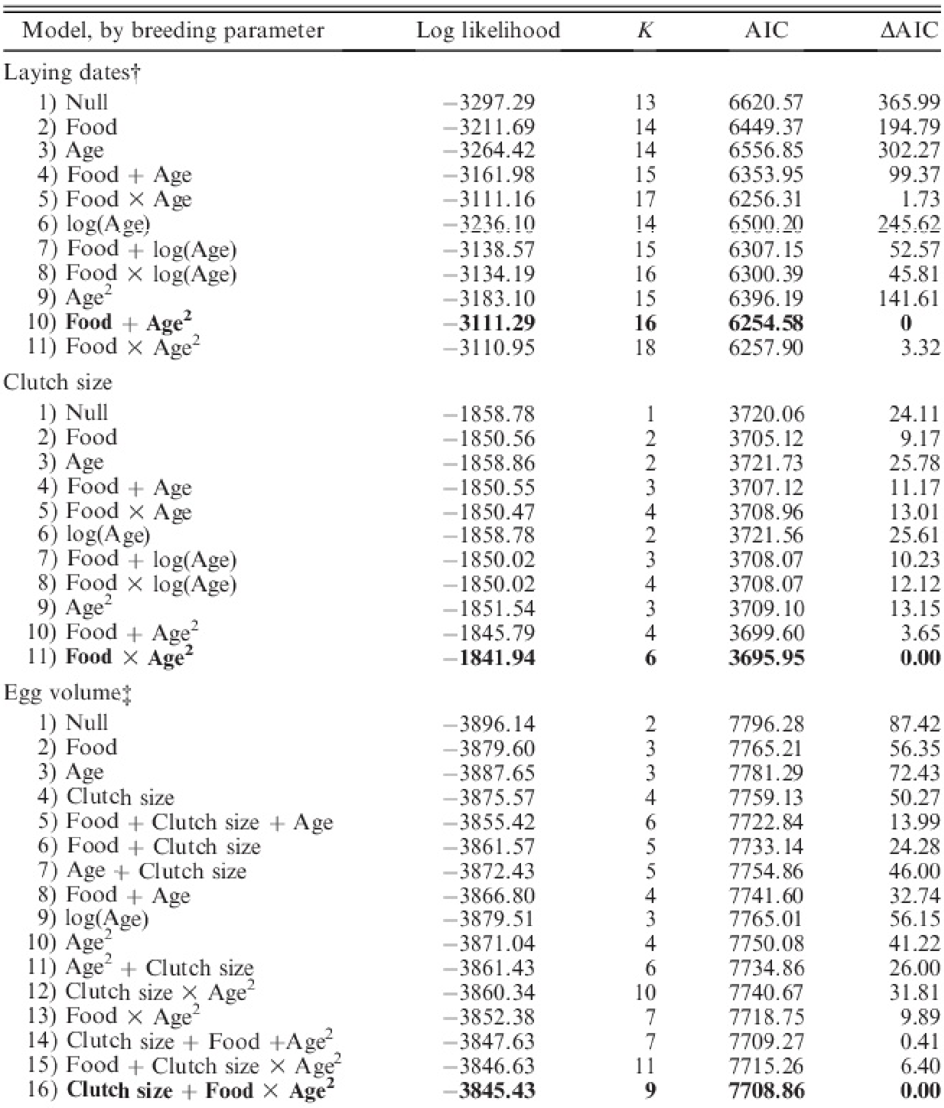
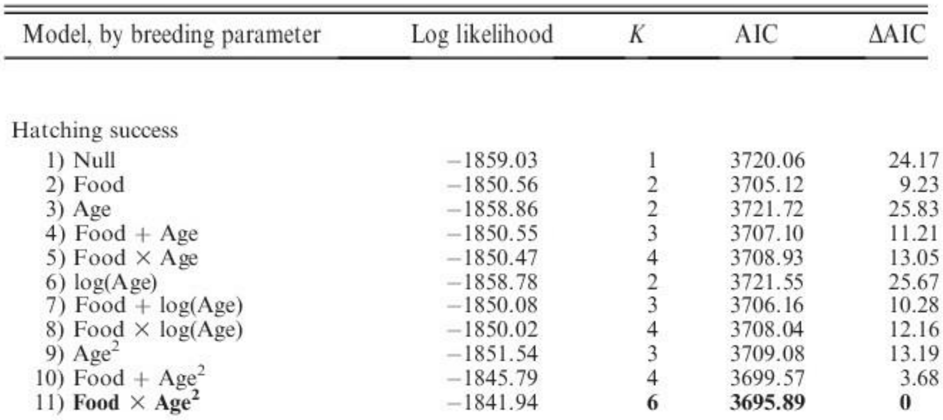


FIG. 6. Variation in the breeding parameters with age for the two extreme values of food availability per capita (years with lowest and highest values) to explore the two patterns of age variation under different food conditions. Solid circles show predicted mean values for each age estimated from the best model (see Table 1 and Appendix: Table A2). Inset figures show the mean values together with their 95% CI (same parameters as the respective axes in the main panels).

TABLE 1. Modeling the effects of age (mean and variance simultaneously) of Audouin's Gulls (*Larus audouinii*) on breeding parameters.



Model, by breeding parameter	Log likelihood	K	AIC	ΔAIC
Laying dates†				
1) Null	−3297.29	13	6620.57	365.99
2) Food	−3211.69	14	6449.37	194.79
3) Age	−3264.42	14	6556.85	302.27
4) Food + Age	−3161.98	15	6353.95	99.37
5) Food × Age	−3111.16	17	6256.31	1.73
6) log(Age)	−3236.10	14	6500.20	245.62
7) Food + log(Age)	−3138.57	15	6307.15	52.57
8) Food × log(Age)	−3134.19	16	6300.39	45.81
9) Age^2	−3183.10	15	6396.19	141.61
10) Food + $\mathbf{Age^2}$	**−3111.29**	**16**	**6254.58**	**0**
11) Food × Age^2	−3110.95	18	6257.90	3.32
Clutch size				
1) Null	−1858.78	1	3720.06	24.11
2) Food	−1850.56	2	3705.12	9.17
3) Age	−1858.86	2	3721.73	25.78
4) Food + Age	−1850.55	3	3707.12	11.17
5) Food × Age	−1850.47	4	3708.96	13.01
6) log(Age)	−1858.78	2	3721.56	25.61
7) Food + log(Age)	−1850.02	3	3708.07	10.23
8) Food × log(Age)	−1850.02	4	3708.07	12.12
9) Age^2	−1851.54	3	3709.10	13.15
10) Food + Age^2	−1845.79	4	3699.60	3.65
11) Food × $\mathbf{Age^2}$	**−1841.94**	**6**	**3695.95**	**0.00**
Egg volume‡				
1) Null	−3896.14	2	7796.28	87.42
2) Food	−3879.60	3	7765.21	56.35
3) Age	−3887.65	3	7781.29	72.43
4) Clutch size	−3875.57	4	7759.13	50.27
5) Food + Clutch size + Age	−3855.42	6	7722.84	13.99
6) Food + Clutch size	−3861.57	5	7733.14	24.28
7) Age + Clutch size	−3872.43	5	7754.86	46.00
8) Food + Age	−3866.80	4	7741.60	32.74
9) log(Age)	−3879.51	3	7765.01	56.15
10) Age^2	−3871.04	4	7750.08	41.22
11) Age^2 + Clutch size	−3861.43	6	7734.86	26.00
12) Clutch size × Age^2	−3860.34	10	7740.67	31.81
13) Food × Age^2	−3852.38	7	7718.75	9.89
14) Clutch size + Food +Age^2	−3847.63	7	7709.27	0.41
15) Food + Clutch size × Age^2	−3846.63	11	7715.26	6.40
16) Clutch size + Food × $\mathbf{Age^2}$	**−3845.43**	**9**	**7708.86**	**0.00**



Model, by breeding parameter	Log likelihood	K	AIC	ΔAIC
Hatching success				
1) Null	−1859.03	1	3720.06	24.17
2) Food	−1850.56	2	3705.12	9.23
3) Age	−1858.86	2	3721.72	25.83
4) Food + Age	−1850.55	3	3707.10	11.21
5) Food × Age	−1850.47	4	3708.93	13.05
6) log(Age)	−1858.78	2	3721.55	25.67
7) Food + log(Age)	−1850.08	3	3706.16	10.28
8) Food × log(Age)	−1850.02	4	3708.04	12.16
9) Age^2	−1851.54	3	3709.08	13.19
10) Food + Age^2	−1845.79	4	3699.57	3.68
11) **Food × Age^2**	−1841.94	**6**	**3695.89**	**0**

Notes: The best structure of variances (see Appendix: Table A2) was used for each parameter: for laying dates, food in interaction with age B structure; for clutch size, food in interaction with age C structure; and homoscedasticity for egg volume. Once the best variance structure was selected, we kept that structure for all models. Modeling followed a strategy of stepwise forward addition of parameters. We started with the null model with no effects, then single effects were tested, and finally interactions between these effects. Terms are: K, the number of identifiable parameters; AIC, Akaike's information criterion; DAIC, the difference in AIC value of the model with respect to the AIC value of the best model. The final selected model is in bold. Interaction between factors is denoted by "3" and "þ" indicates an additive effect between factors. Age^2 indicates a quadratic effect of age on the breeding parameter. Food is the availability of food per capita (see *Methods*).

† Twelve of the parameters (K) in all models corresponded to the variance structure (four age classes 3 three food classes).

‡ One of the parameters (K) in all models corresponded to a single variance value.

Effects of food supply on the variance of the age pattern

In tests for heteroscedasticity, the variances behaved differently for each breeding parameter, changing with age (four age classes) and food availability for laying dates, but remaining constant for egg volume (homogeneous variances for all ages and food classes); see Appendix: Table A2. For laying dates, the greatest variances occurred in 3-year and 4–5 year-old birds when food was in good supply, i.e., when individuals of different quality found suitable conditions to start breeding; the lowest variance occurred in the oldest birds (>14 years old) when food availability was highest (Fig. 7).

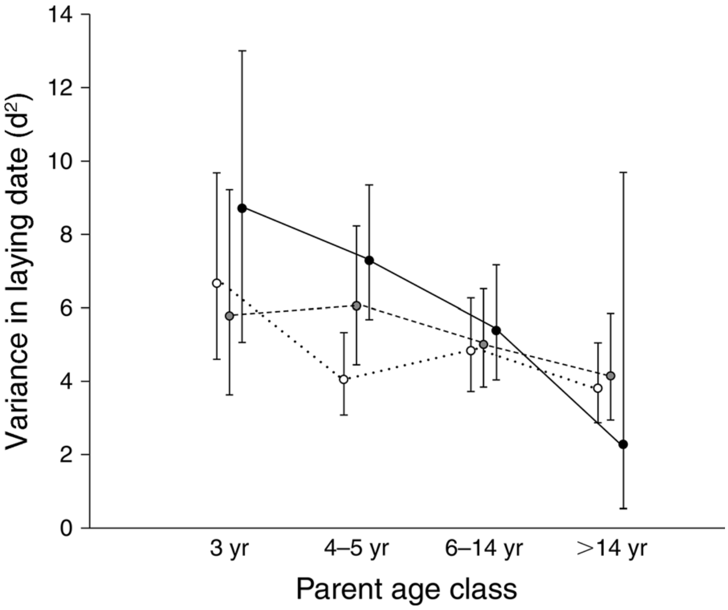


FIG. 7. Variances for each categorized age class (together with their 95% CI; see *Methods*) in laying dates of Audouin's Gulls in the Ebro Delta. Variance also varied with different categories of food availability: low (dotted line), intermediate (dashed line), and high (solid line).

1.4 Discussion

Age variation pattern

Our results show clear evidence of quadratic variation of age in several breeding parameters: younger and older birds laid later in the season (an indication of poorer acquisition of resources for reproduction), laid fewer eggs per clutch, laid smaller eggs, and hatched fewer eggs at the end of incubation. All studies dealing with multiple life-history and physiological traits report differences in the degree to which age influences each trait, ranging from no effect to a strong association, either linear or quadratic (e.g., Weimerskirch 1990, Blas et al. 2009, Lecomte et al. 2010, Pardo et al. 2013). Nevertheless, no common pattern in differences between and within traits across taxa has yet emerged, probably because additional factors other than age (e.g., sex, individual quality, experience, mate and site fidelity, cohort effects, age of the mate, density dependence, and stochastic fluctuations of food; see, for instance, Coulson et al. 2001) potentially influence the multi-trait pattern.

Even though an increase in breeding performance with age and experience has been widely reported in many iteroparous organisms (e.g., Berkeley et al. 2004, Bowen et al. 2006, Weladji et al. 2006, Trumbo 2009), the final decline in performance in older individuals has seldom been assessed (Monaghan et al. 2008) and has been recorded only in some but not all studied taxa (e.g., Vieyra et al. 2009, Rebke et al. 2010, Orzack et al. 2011, Pardo et al. 2013). In younger birds, poorer breeding performance is likely to indicate a lack of experience, especially when interference competition for resources with older (i.e., more experienced) birds occurs. Navarro et al. (2010) found that in Audouin's Gulls, younger breeders consumed lower quality prey in rice fields with lower energetic content, probably to avoid competition with the older birds that mainly consume lipid-rich fish. The decline in breeding performance observed in old gulls is the result of senescence, probably due to a deterioration of their functional abilities, particularly a lower foraging efficiency (e.g., Catry et al. 2006, Lecomte et al. 2010). This lower foraging efficiency in older birds would be more marked when food availability per capita decreased (i.e., when intra- and interspecific competition increased), determining a lower reproductive performance under such conditions. Although actuarial senescence (i.e., of survival) is a widespread phenomenon, reproductive senescence has been less studied and seems to be less common because it may also depend on food availability, on traits such as body size and migratory behavior, or on trade-offs between early- and late-life reproduction (Reed et al. 2008, Aubry et al. 2009, Berman et al. 2009).

Influence of food supply per capita on pattern in age variation

Once we had demonstrated the quadratic effect of age on all breeding parameters analyzed, the major chal- lenge of our study was to assess whether and how this common pattern in nature varies with food availability, the main environmental driver of breeding performance (in the absence of predation). As expected, performance improved with increased food supply in all parameters. In terms of laying dates, performance varied quadrat-ically with age and increased in parallel with food availability per capita: birds laying earlier were in better condition, and this was the only parameter in Audouin's Gulls that behaved like this (i.e., food did not alter the age pattern). Egg laying occurs at the beginning of the reproductive season and should be the breeding parameter less affected by environmental noise, which should accumulate across the season. This probably causes an increase in the effects of different conditions of food availability per capita for each age class, although the difference with other parameters and with laying dates in closely related organisms, e.g., Western Gulls L. occidentalis (Sydeman et al. 1991; see Appendix:

Table A1), remain poorly understood. For the rest of the reproductive parameters (clutch size, egg volume, and hatching success), the age pattern of breeding performance varied markedly with different levels of food availability and in an unexpected way. When food per capita was in short supply, the resulting quadratic age pattern was less marked (Fig. 6), even though most studies have found that differences in breeding performance between age classes decrease with improving feeding opportunities (see Appendix: Table A1). For instance, Ezard et al. (2006) report that young Common Terns (Sterna hirundo) performed well only in high-quality years, as is the case in Brandt's Cormorants (Phalacrocorax penicillatus) (Boekelheide and Ainley 1989). By contrast, our results show that the quadratic age pattern in Audouin's Gull for all parameters is more apparent under good conditions (except for laying dates; see Fig. 6), when middle-aged individuals greatly improve their breeding performance, thereby increasing differences in reproductive performance vis-à-vis older birds. Variances in laying dates decreased with age and under all conditions; higher variance differences within age classes in breeding performance were found in younger birds. These results suggest that heterogeneity in individual quality exists within young age classes. Heterogeneity within age classes has been invoked by many previous studies (e.g., Sydeman et al. 1991, Cam and Monnat 2000, Barbraud and Weimerskirch 2005, McCleery et al. 2008, Lescroël et al. 2009, Oro et al. 2010, Péron et al. 2010, Desprez et al. 2011) and is the basis for the selection hypothesis (e.g., Nevoux et al. 2007; but see Rebke et al. 2010). This hypothesis is also supported by the low variances in older age classes (Fig. 7), which suggest that heterogeneity in individual quality for these birds was low. The average individual quality should increase with age, once young breeders of lower quality are removed from the population due to the costs of reproduction (e.g., Sanz-Aguilar et al. 2008). Additionally, it remains to be understood whether skip breeding, a practice commonly recorded in many seabird species including other gulls (e.g., Cam and Monnat 2000, Pyle et al. 2001, Sanz-Aguilar et al. 2008, Goutte et al. 2011), also plays a role in the low variances recorded in older Audouin's Gulls.

To our knowledge, only Pardo et al. (2013) have ever analyzed how the variances of several demographic traits change with age; these authors found a U-shaped pattern in the Black-browed Albatrosses (*Thalassarche melanophrys*), with middle-aged individuals having the lowest variances. Thus, the patterns present in these two species coincide in the high variances for younger birds and the lower variances for middle-aged birds, whereas the least variance in Audouin's Gulls occurs in older individuals. The difference in the two species-specific patterns appears in older age classes, because variances in old Black-browed Albatrosses were high (and similar to variances of younger birds), whereas those in old Audouin's Gulls were the lowest. This is likely to be explained by the differences in life-history strategies between the two species: albatrosses are extremely long- lived birds, lay a single egg, and have sabbatical (nonbreeding) years, whereas Audouin's Gulls have a lower survival, lay 2–3 eggs, and are thus bet-hedgers, i.e., species that reduce the temporal variance in fitness at the expense of lowered arithmetic mean fitness. Our results suggest that a selection process takes place as the individual grows older, resulting in, at least for some parameters such as laying dates, progressively lower heterogeneity in quality and breeding performance. In other words, the average laying dates of younger and older Audouin's Gulls were later, and while variance in younger birds was high (suggesting a large degree of individual heterogeneity with some breeders performing well and others doing badly), variance in older and experienced breeders was low (suggesting that most old and experienced gulls performed similarly). Despite not analyzing how variances changed with age and environmental conditions, other studies have reported a similar pattern, i.e., an effect of selection on the best performing individuals and thus a progressive homogenization of performance with age (Daunt et al. 1999, Cam and Monnat 2000, Barbraud and Weimerskirch 2005, Nevoux et al. 2007).

Together with other factors such as sex, behavioral processes, and the varying costs of early reproduction, our results demonstrate that age and environmental conditions (in the form of food availability per capita) interact to shape differing aging patterns in an array of breeding parameters under natural conditions. These patterns vary from soft quadratic shapes in harsh environments (little effect of inexperience and senescence due to individual heterogeneity in quality and selection) to strongly quadratic patterns (important effect of inexperience and senescence) during good years when middle-aged individuals greatly improve their breeding performance. These two contrasting patterns, which are determined by food availability per capita (i.e., considering density dependence and thus competition; see Coulson et al. 2001), are rather unexpected because none of the studies analyzing the interaction between age and food conditions found that differences in breeding performance between age classes were lower when food was in shorter supply (see Fig. 2). The inclusion of the heterogeneity of variance in our analysis allowed us to shed some light on that particular pattern of the influence of food conditions and competition in the age pattern of breeding performance found in Audouin's Gulls. Variance variability between age classes suggests that important ecological processes, for example, the fact that selection decreases as individuals become older and their average quality increases, affects the patterns of age variation in breeding performance.

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The influence of environmental conditions on the age pattern in breeding performance in a transequatorial migratory seabird.

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Abstract

Several studies of marine top predators, above all of seabirds, have analyzed the effects of either individual age or environmental fluctuations on reproduction; nevertheless, little is known about the age patterns in breeding performance in a variable environment. To investigate the simultaneous influence of age and environmental conditions on laying dates and egg volumes, we tested different climate and food availability indices in a transequatorial migratory seabird using female data from a 23-year study. Our results show an improvement in breeding parameters with age (i.e., earlier laying dates and greater egg volumes) but no pattern of senescence in older age groups. The best models showed an interaction of time and age in breeding performance, i.e., the age pattern of breeding performance changed each year likely as a result of environmental variability. Nevertheless, climatic indexes used here explained part of that annual variability: NAO and SOI index accounted for 24 and 20% of deviances in laying dates and egg volume, respectively. Part of that unexplained variability might be related to other processes such as intermittent breeding and the individual quality of breeders, which were not assessed in our study.

Keywords: age pattern; breeding performance; Scopoli's Shearwaters; climatic index; food availability; migratory seabird.

2.1 Introduction

In marine ecosystems, climatic fluctuations and other physical oceanographic variables affect the population dynamics of organisms by exerting an influence on their vital rates. This influence is mediated by drivers such as food availability and environmental conditions during the breeding period or migration (Duffy-Anderson et al., 2005; Lee, 2011). For example, large-scale climatic phenomena and oceanographic processes produce changes in water temperatures and currents that generate spatio-temporal variation in the production, distribution, and abundance of the prey consumed by marine predators such as seabirds (Durant et al., 2004). Consequently, these processes may affect the foraging ecology of seabirds (Navarro and Gonzalez-Solís, 2009; Weimerskirch et al., 2012) and influence their survival, reproduction and population dynamics (Jenouvrier et al., 2005; Genovart et al., 2013).

Like environmental variability, individual covariates such as age and sex also influence vital rates (Stearns, 1992). Age-specific differences in breeding performance have been observed in several seabirds (Nevoux et al., 2007; Vieyra et al., 2009; Pardo et al., 2013). In most cases young individuals perform less well than older individuals (Martin, 1995), thereby indicating improvement in performance with age leading to a peak and then decline (i.e., senescence) (Clutton-Brock, 1988). Several non-exclusive hypotheses have been proposed to explain these age-related variations in breeding performance: a progressive appearance or disappearance of phenotypes, age- related improvements in the skills needed for reproducing, and an optimization of reproductive effort (Forslund and Pärt, 1995). Demographic parameters in wild populations are thus expected to be shaped by both individual covariates and environmental variability (e.g., Stearns, 2000; Nevoux et al., 2007; Oro et al., 2010). Despite this, few studies have ever examined at the same time how environmental conditions affect age patterns in breeding performance (Bunce et al., 2005; Pardo et al., 2013; Oro et al., 2014). Depending on environmental conditions, different age patterns can exist (see Oro et al., 2014): in most studies, either (a) differences among age classes in breeding performance were found to decrease under better environmental conditions (Sydeman et al., 1991; Laaksonen et al., 2002; Barbraud and Weimerskirch, 2005; Bunce et al., 2005) or (b) environmental conditions had no clear influence on breeding performance (Nevoux et al., 2007; Vieyra et al., 2009; Lee, 2011; Pardo et al., 2013); just one study found that differences between age-classes were greater under favorable environmental conditions (Oro et al., 2014).

Here we analyze 23 years of data from a population of Scopolis̈ Shearwater (*Calonectris diomedea*), a long-lived and highly monogamous seabird with extreme life-history traits that include high adult survival rates, low fecundity (females lay a single egg), intermittent breeding, and delayed sexual maturity (Thibault, 1994; Thibault et al., 1997). Shearwaters breed in the Mediterranean and, after reproducing, perform long trips to their Atlantic wintering grounds where there are important upwellings that provide abundant food resources (González-Solís et al., 2007). We tested the influence of environmental conditions at different spatial scales on two breeding parameters, laying date and egg volume, in individuals of different age classes. Our main aim was to test (a) whether breeding performance increased with age and (b) whether or not differences between age classes depend on environmental conditions at different spatial scales.

2.2 Methods

Population Monitoring

The study was conducted in the Scopoli's Shearwater colony on Pantaleu Islet in the Balearic Archipelago (30 ° 34′N, 2 ° 21′ E, Spain), where ca. 200 pairs breed in burrows under boulders or vegetation. In the period 1985–2010, a total of 1043 chicks were ringed with stainless-steel rings bearing unique numeric codes that allow individuals to be identified and aged. In 2001– 2013, accessible nests (ca. 150 each year) were marked and visited during the breeding period (May-September); nests with breeders of known ages were examined to record laying dates (with a maximum of 72 h between visits), and the size of the single egg (with the use of a digital caliper). Both breeding parameters have been shown to be related to fitness components as chick survival, or juvenile survival (see review in Krist, 2011). Birds were sexed when first captured using morphometric measures and calls. We gathered data from 87 different breeders and the total number of monitored nests during the study was 302 (annual median number of nests = 24: 11–32 nests; median of age = 12-year old, range: 5-23-year old) of which 98 cases are females of known age (annual median number of nests = 8, range: 212 nests; median of age = 11-year old, range: 5-23- year old). As in many cases we only had the age of one member of the pair, we first assessed the association between the ages of the two members in nine pairs for which the two members of the pair were of known age. In these nine breeding pairs, assortative mating was low ($n = 9$, Spearman correlation r_S=0.068, $p = 0.431$). Given that both laying dates and egg volumes in this species mainly depend on female body condition and their breeding capabilities (Jouanin et al., 2001), we only used data from females to be conservative. Nevertheless, since sample size of females was much lower than for males, and we could not confirm assortative mating, we also ran all models taking into account both sexes (Appendix B1 in Supplementary Material) to increase power by increasing sample size and check if the best model was the same as when taking only female data into account.

Environmental Variables

Previous studies have shown that Scopolis Shearwaters basically feed on fish (90%) during the breeding season (Granadeiro et al., 1998b). Like many other seabirds that breed in the study area, this species exploits fishing discards from the trawling fleet which fishes on the continental shelf off the Ebro Delta (Martínez- Abraín et al., 2002a). Thus, as an annual proxy of food availability, we used the total amount of trawling discards produced in March (when birds store energetic reserves before breeding) derived from statistics for trawling catches by a fishing guild in the Ebro Delta (Oro and Ruiz, 1997; Louzao et al., 2011). To obtain a proxy of food per-capita (i.e., correcting for density- dependence), we divided the total amount of available food by the total population size of all the scavenging seabirds—Audouins gulls (*Larus audouinii*), Yellow-legged gulls (*L. michahellis*), and Scopolis Shearwaters—that forage in the area (Oro and Ruiz, 1997).

As a proxy of an oceanic large-scale climatic index we used the Southern Oscillation Index (SOI), associated with Atlantic hurricane activity, which registers greater hurricane activity during positive phases (i.e., La Niña) and less in negative phases (i.e., El Niño) (Knutson et al., 2008). We used annual mean SOI values from January to December, obtained from http://www.cru.uea.ac.uk/cru/data/soi/soi.dat with a 1-year time lag to test the effect of environmental conditions in the Atlantic where birds winter before returning to their breeding areas.

To test the effect of local conditions during breeding we used another large-scale index, the North Atlantic Oscillation Index (NAO). This index affects water column hydrodynamics and may have a cascade effect at higher trophic levels (Gordo et al., 2011), thereby influencing the production, distribution and abundance of the organisms upon which birds feed (Durant et al., 2004). To test this effect we selected the extended annual winter NAO (i.e., December-March; NAO_W) with positive values related to windy and warmer conditions, and negative values to colder air and wetter conditions in the Mediterranean (Hurrell, 1995). We also checked to see if there was any effect of the previous years NAO value (NAO_a) since some fish have temperature-dependent gonadal development

(Ware and Tanasichuk, 1989) and may spawn and migrate earlier in warmer years (Sims et al., 2004). Data were obtained from https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based.

Data Analysis

To analyze the influence of environmental variability on age patterns in different breeding parameters, we built linear mixed models (LMMs) with the package lme4 and function lmer (Bates, 2010) using R software (http://www.R-project.org). We used laying date and egg volumes as dependent, normally distributed, variables. We included year as a fixed effect and female age as a continuous explanatory variable, either as a linear, quadratic or logarithmic function, and environmental variables as covariates of the year-dependent variations (see previous section). We also considered models including the statistical interactions between these effects. In all models we included individual identity as random effect (random intercept model) to avoid pseudo- replication and account for differences across individuals (see Bolker et al., 2009). We began by assessing the influence of age and determine the age pattern for each breeding parameter (i.e., linear, logarithmic or quadratic). Then we tested the influence of each environmental covariate (food availability, SOI, NAO_w, NAO_a) and progressively added complexity into the models, by including interactions term between the effects. We ranked the set of models using Akaike's information criterion with correction for small sample size (AICc; Anderson and Burnham, 2002) and selected the model with the lowest AICc value as the most parsimonious one, i.e., the best model for explaining our data using fewest parameters (Burnham and Anderson, 2002). When the difference between two models (i.e., 6AICc) was less than 2 we considered that the models explained the data equally well (Lebreton et al., 1992; Burnham and Anderson, 2002). We also computed the Akaike weights (*wi*; Burnham and Anderson, 2002), which provides a measure of the relative likelihood of a particular model given the models considered (Anderson et al., 2000). To assess the fit of the model, we estimated the coefficient of determination (R^2) between the fitted and observed values on selected models (Cameron and Windmeijer, 1996). We also estimated the R^2 using the method proposed by Nakagawa and Schielzeth (2013; r.squaredGLMM function in the MuMIn package for R), which gives the marginal R^2_m representing the variance explained by fixed factors, and the conditional R^2_c as the variance explained by both fixed and random factors (i.e., the entire model). Additionally, we also estimated the percentage of variation explained by each covariate (r^2) when tested alone as:

$$r^2 = \frac{Dev(M_{cnt}) - Dev\ (M_{cov})}{Dev(M_{cnt}) - Dev(M_t)}$$

where Dev(M_{cnt}) is the estimated deviance of the constant model, i.e., no effects considered, Dev(M_{cov}) is the deviance of the model with the climatic covariate considered and Dev(M_t) is the deviance of the time-dependent model.

To obtain the χ^2-values and the significance level of the different covariates, we performed a likelihood ratio test (LRT) comparing the null model with the different covariates for each breeding parameter (see Table 2). As random structure remained unchanged in all models tested, we can compare the LRT values of each case although the refitting model was run with ML and not with REML (see Zuur et al., 2009).

2.3 Results

We found a positive effect of age (log-transformed) on the breeding parameters analyzed (Table 2). Older individuals tend to lay earlier and to produce larger eggs than young birds (Table 2, Figure 8, and Appendix B2 in Supplementary Material). We found a large temporal variability in both parameters. In both cases, the retained model, i.e., the one with the lowest AICc value, assumed an effect of age, year and their statistical interaction, indicating that the strength of the relationship between breeding performance and age was changing across the years (Models 1 and 1; Table 2). The coefficient of determination (R^2) between the fitted and observed values of the selected models was 0.74 and 0.67 for laying date and egg volume analysis, respectively. Another important finding was that in both analyses the parameter accounting for across-individual variation was large. When we estimated the variance explained by Nakagawa and Schielzeth's (2013) method, we obtained R^2= 0.39 and R^2 = 0.64 for laying date (Model 1) and R^2= 0.28 and R^2 = 0.53 for egg volume analysis (Model 1). Thus, the variance explained by the random effect (i.e., the breeder) was 0.24 and 0.25 in laying date and egg volume, respectively. Environmental covariates were negatively associated with the parameters considered, but although this association was statistically significant, the covariates explained a relatively small part of the total temporal variability (NAO winter index explained about 24% of variance in laying date and SOI index 20% in egg volume; Table 3). For this reason none package for R), which gives the marginal R^2 representing the variance explained by fixed factors, and the conditional R^2 of the models that included climatic indexes were retained by the model selection procedure. Similarly, fishing discards taken as a proxy of food availability had a positive effect on both parameters, but the variance explained was low and this effect cannot be considered an important predictor of laying dates and egg volume. The year-by-age interaction term is indicating that differences between age classes were more marked under good environmental conditions (negative values of the climatic indexes; Figure 8).

TABLE 2. Modeling the effects of age and environmental conditions on the breeding parameters of Scopoli's Shearwater's using generalized linear mixed models.

N °	Laying date	np	dev	AICc	ΔAI	W_i
1	Year*Log	26	349.3	423.33	0.00	1.00
2	Year	14	425.4	458.99	35.66	0.00
3	Year+Log(Age)	15	422.6	459.03	35.70	0.00
4	NAOw	5	480.3	491.09	67.76	0.00
5	NAOw	4	483.2	491.68	68.35	0.00
6	NAOw	6	479.3	492.39	69.06	0.00
7	SOI*Log (Age)	6	493.2	506.21	82.88	0.00
8	Log(Age)	4	498.9	507.42	84.09	0.00
9	Null	3	501.3	507.62	84.29	0.00
10	NAOa	5	497.3	508.09	84.76	0.00
11	NAOa	4	499.8	508.27	84.94	0.00
12	Food*Log(Age)	6	495.6	508.63	85.30	0.00
13	NAOa	6	495.8	508.81	85.48	0.00
14	SOI+Log(Age)	5	498.2	508.91	85.58	0.00
15	SOI	4	500.6	509.09	85.76	0.00
16	Food +	5	498.6	509.36	86.03	0.00
17	Food	4	501.1	509.57	86.24	0.00
18	Age	4	504.0	512.54	89.21	0.00
19	Age^2	5	509.0	519.79	96.46	0.00

N °	Volume	np	dev	AICc	bAIC	W_i
1	Year*Log	26	378.0	451.96	0.00	1.00
2	Year+Log(Age)	15	446.0	482.44	30.48	0.00
3	Year	14	451.0	484.57	32.61	0.00
4	SOI*Log (Age)	6	481.8	494.84	42.88	0.00
5	SOI + Log(Age)	5	485.5	496.2	44.27	0.00
6	Food*Log(Age)	6	486.5	499.5	47.58	0.00
7	SOI	4	491.4	499.8	47.93	0.00
8	Food +	5	491.9	502.6	50.66	0.00
9	NAOw +	5	492.0	502.7	50.83	0.00
10	NAOw	4	495.1	503.5	51.62	0.00
11	NAOw	6	491.3	504.3	52.35	0.00
12	Food	4	496.7	505.1	53.23	0.00
13	Log(Age)	4	498.6	507.0	55.13	0.00
14	Null	3	501.6	507.9	55.95	0.00
15	NAOa +	5	500.3	511.0	59.10	0.00
16	NAOa	4	503.3	511.8	59.90	0.00
17	Age	4	503.7	512.2	60.27	0.00
18	NAOa	6	499.5	512.5	60.54	0.00
19	Age^2	5	508.5	519.2	67.25	0.00

Note that only the best models are shown. Notation: np, number of estimable parameters; dev, relative deviance; AIC, Akaike information criterion; ΔAICi, difference of AIC value of the model i with respect to the AIC value of the best model; Wi , weight of model i for the set of models tested. Model notation: Year, time effect; NAOw, NAO index in winter (see Materials and Methods); NAOa, annual NAO index effect with one-year time lag; SOI, SOI index effect with one-year time lag; Log(Age), logarithmic effect of age; Age, lineal effect of age; Age^2, *quadratic effect of age; Food, availability of food per capita (see Materials and Methods). The symbol "* " denotes interaction between factors and "+ " an additive effect between factors. The best model is shown in bold.*

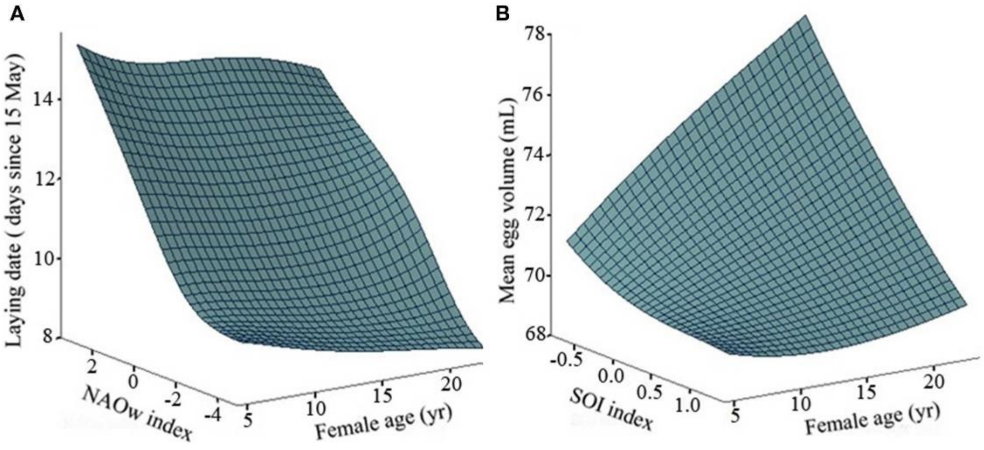

FIG. 8. Smoothing regression surfaces taking into account the effects of age and the climatic index that explain the greatest amount of variance for each breeding parameter. (A) NAOw index for laying date, (B) SOI index for egg volume.

TABLE 3. Percentages of variance explained by each environmental covariable for each breeding parameter and likelihood ratio test values (see Materials and Methods).

Variable	*df*	R^2		χ^2		*P-value*	
		LD	VOL	LD	VOL	LD	VOL
NAOw	4	23.9	12.9	19.6	8.6	< 0.001***	0.003**
SOI	4	1.0	20.2	0.0	9.7	0.957	0.002**
Food	4	0.3	9.7	0.0	5.2	0.923	0.023*

*Note: NAOw, NAO index in winter; SOI, SOI index effect with one-year time lag; Food, availability of food per capita; LD, laying date; VOL, egg volume. Significance level codes: *** (0); ** (0.001); * (0.01).*

2.4 Discussion

As has been previously reported in other long-lived animals (Clutton-Brock, 1988; Sæther, 1990; Forslund and Pärt, 1995) breeding performance in Scopoli's Shearwater increases with age; younger breeders have later laying dates and smaller egg volumes than older breeders. Since egg size and laying dates are positively associated with breeding success in several bird species and also in Scopoli's Shearwaters (e.g., Ramos et al., 2003), it is expected that fertility also increases with age. This increase in reproductive performance could be mediated by a gain in breeding skills over the years, which would enhance reproduction, or alternatively by the existence of a selection filter (the so-called "selection hypothesis"), whereby older age classes include a higher percentage of good breeders than younger age classes (Curio, 1983). In Storm petrel *Hydrobates pelagicus,* for example, individuals that survive their first breeding attempt should have a greater likelihood of breeding successfully the following year, probably due to the progressive selection of higher-quality individuals (e.g., Sanz-Aguilar et al., 2008). Furthermore, a previous study of Scopoli's Shearwater in our study colony (Genovart et al., 2013) detected that a large number first-time breeders do not return to the colony, either because they die (i.e., indicating thus the inherent costs of first reproduction) or permanently disperse to other breeding sites. Aside from the increase in breeding performance with age, several studies of long-lived animals have reported a decline in performance as a result of senescence (Vieyra et al., 2009; Pardo et al., 2013; Oro et al., 2014). We did not find a similar pattern, however the lack of senescence in our study may either be due to the small sample size (i.e., a lack of statistical power owing that there were only 4 individuals older than 20 years of age), to an increase of skip breeding with age, or to within-cohort phenotypic selection hiding senescence patterns (Cam et al., 2002).

Beside the clear and positive effect of age, we found that breeding performance varied across individuals and over the study period, the last probably reflecting environmental variability. We investigated whether the temporal variability was mirroring the fluctuations of large-scale climatic indices (namely NAOw and SOI) or the amount of fishing discards (a proxy for food availability just before the breeding season). NAOw and SOI are expected to influence breeding success of Scopoli's shearwater indirectly through their effects on marine productivity and oceanic conditions at the wintering grounds.

Their influence on breeding performances, however, can be complex as climatic conditions might affect birds' energetic reserves through for example adverse flying conditions (Knutson et al., 2008; Arizmendi-Mejía et al., 2013) or alternatively they might influence them indirectly by changing the availability of prey, i.e., water column mixing, increasing river run off, and primary productivity (Lloret et al., 2001; Ottersen et al., 2001). This complexity is reflected in the fact that environmental covariates alone, despite being significant, explained only up to 24% of the yearly variability in breeding performances. A stronger effect of environmental covariates has been found for other seabirds (e.g., Frederiksen et al., 2004; Tavecchia et al., 2007; Dunn and Winkler, 2010; Barbraud et al., 2011). Genovart et al. (2013) found that the NAO winter index explained up to 40% of the temporal variance in breeding success in Scopoli's shearwater, but they included birds of unknown age and also nests monitored in an additional colony of the western Mediterranean (Chafarinas Island). Here we have restricted the analysis to birds of known age because we were interested in investigating the age-dependent pattern of breeding performance and whether environmental variability might change that pattern each year. It is possible that the statistical signal is lost in a smaller data set.

Our results showed an important heterogeneity among individuals in both, egg volume and laying dates (approximately 25% of the total variance of the retained model). At present we do not know the reason for such heterogeneity. Human disturbance and terrestrial predators are known to trigger dispersal and determined breeding success in seabirds (Cam et al., 2004; Fernández-Chacón et al., 2013). The studied colony however is located in a protected site with no human disturbances or alien predators. We can thus exclude the influence of these factors as a potential cause for nest quality heterogeneity. Differences among individuals might be due to difference in body size, individual investment, or individual ability in exploiting anthropogenic food resources (i.e., fishing discards, Votier et al., 2010). This individual heterogeneity might explain part of the differences between age classes, a pattern that was more marked under good environmental conditions than during harsh years, as it has been recorded for Audouin's gull (Oro et al., 2014). Other process that might be involved in the differences between the two patterns (good vs. bad years) is intermittent breeding, which has been commonly found in the study species (Mougin et al., 1997; Genovart et al., 2013). Previous studies on other seabirds found that during harsh years, individuals in bad condition may skip breeding (Cam and Monnat, 2000; Pyle et al., 2001; Sanz-Aguilar et al., 2008) and therefore the differences between age classes in breeding performance might be more marked in good years. In Scopoli's shearwater, males do not feed females during courtship as other seabirds (Jouanin et al., 2001), therefore male quality does not affect females' body condition and can be ruled out as a possible explanation. However, female reproductive investment might depend on male quality (Cunningham and Russell, 2000), but we have not enough data to assess whether shearwaters exhibit assortative mating. Out of nine cases in which both members of the pair were of known age, only in one case, female and male had the same age. Nevertheless, when males were included in the data set, results did not change.

Our results show clearly that the interplay of environmental conditions and individual age influences the observed breeding performance of Scopoli's shearwaters. Neither a proxy of the local food availability nor the large-scale climatic indexes can explain the temporal variability in the age pattern of breeding performance. This complex pattern is further complicated by the potential effects of individual quality. Future research should focus on the role of local climatic indexes and direct measures of food availability as predictors of breeding performances in long-lived birds.

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3

Environmental conditions, age, and senescence differentially influence survival and reproduction in the Storm Petrel.

Hernández, N., Oro, D., & Sanz-Aguilar, A. (2017). Environmental conditions, age, and senescence differentially influence survival and reproduction in the Storm Petrel. *Journal of Ornithology*, 1-11.

Abstract

Demographic parameters in wild populations are expected to be shaped by individual covariates and environmental variability. Thus, the understanding of the effects of age and/or environmental conditions on variability in vital rates is of special importance in ecological and evolutionary studies. Early age-related improvements in survival and reproduction and later declines due to senescence are expected, above all in long-lived species. Survival in these species is predicted to be a more conservative parameter than reproduction, thereby giving rise to less temporal variability. We studied age-dependent patterns of survival and breeding success in a long-lived seabird, the Mediterranean Storm Petrel *Hydrobates pelagicus melitensis*, and the additive influence of individual heterogeneity and environmental climatic variables using 22 years of individual-based data (1993–2014). The North Atlantic Oscillation index (NAO) and sea surface temperature (SST) were selected as proxies of environmental conditions in both breeding and wintering areas. Our results show that vital rates improved with age for both survival and breeding success. A slow effect of senescence at older ages was detected for breeding success, whereas models did not disentangle the occurrence or the absence of actuarial senescence. Reproduction was also influenced by the age of first observed reproduction: at the same age, more experienced birds that recruited earlier had a higher breeding success than less experienced ones. Breeding success (but not survival) also showed great temporal variability in accordance with theoretical predictions. Neither the NAO nor the SST explained this variability, probably because petrels feed on lower trophic levels than most pelagic seabirds and other physical features such as river runoffs and winds may be involved, as well as other environmental stressors such as predation by sympatric gulls.

Keywords: Age pattern; Individual heterogeneity; Recruitment; age; Climatic index; Seabird; Hydrobates pelagicus melitensis; Aging; Long-lived species.

3.1 Introduction

In long-lived birds, survival and reproduction typically increase in early ages, reach their maximum values in intermediate ages, and then finally abate in later years as an expression of senescence (Forslund and Pärt 1995; Jones et al. 2008; Sergio et al. 2011; Oro et al. 2014). Several nonexclusive hypotheses attempt to explain this pattern of individual improvement (Curio 1983; Forslund and Pärt 1995; Dugdale et al. 2011). The ‘‘constraint hypothesis‘‘ links improvements to acquisition of experience and skills (Curio 1983; Sergio et al. 2014). The selection hypothesis predicts the progressive selective disappearance of lowquality phenotypes (Forslund and Pärt 1995; Sanz-Aguilar et al. 2008). However, in addition to selection, the progressive selective appearance (recruitment) of individuals differing in quality could mask age patterns at the population level (van de Pol and Verhulst 2006; Zhang et al. 2015). Finally, the hypothesis of the evolutionary trade-off between current reproduction and future survival (‘‘restraint hypothesis’’ in Curio 1983) makes the implicit assumptions that reproduction is costly (Tavecchia et al. 2001; Sanz-Aguilar et al. 2008) and that this cost is constant over time because, otherwise, a variable (unpredictable) cost would benefit those individuals that breed regardless of the survival payoff (Marrow et al. 1996). These three hypotheses are not mutually exclusive (Sergio et al. 2014), and their relative importance may change according to age and trait. For example, the early life improvement in survival and reproductive performances could be the result of both constraining and selection mechanisms (Dugdale et al. 2011; Sergio et al. 2014), even if these mechanisms cannot predict the emergence of senescence later in life, i.e., the decline in reproductive performance and/or survival (the latter also called actuarial senescence) that occurs with age (Flatt 2012). This decline is likely to be due to physiological deterioration, which can be attributed to two non-mutually exclusive evolutionary mechanisms: the damaging effects of mutation accumulation (Medawar 1952) and antagonistic pleiotropy, i.e., a selection of mutations with adverse effects late in life (Williams 1957). Hamilton (1966) postulated that the negative effects of senescence start to appear at the age of the first reproduction attempt owing to the action of natural selection.

On the other hand, both survival and reproductive performance might change over time as a response to environmental conditions, thereby adding a temporal dimension to variation in age-dependent vital rates (Durant et al. 2004; Oro 2014; Oro et al. 2014; Chantepie et al. 2015). However, in long-lived species adult survival is very high and is expected to vary little over time compared to reproductive success (Roff 1992; Gaillard and Yoccoz 2003; Oro 2014). An accurate description of the pattern of age-specific survival and reproductive performances is important for understanding individual life-history tactics and speciesspecific selective pressures. Moreover, environmental conditions can also be the driver of population dynamics through their effect on vital rates (Jenouvrier 2013; Oro 2014). Here, we analyze the age-dependent pattern of survival and reproductive success in a long-lived bird, the Mediterranean Storm Petrel *Hydrobates pelagicus melitensis*, using individual-based longitudinal data. We aimed to establish how fast vital rates increase with age (and breeding experience in the case of breeding success) and whether and when senescence appears. In addition, we investigated the potential influence of environmental variables and their variability as ecological predictors of both parameters.

3.2 Methods

Study area, individual and environmental data

The study was conducted on Benidorm Island in the western Mediterranean (38300 N, 080 E), where more than 400 pairs of Storm Petrels breed in colonies in two caves located 150 m apart. From 1993 to 2014 accessible nests in both colonies were inspected every 2 weeks during the breeding season (April–September) to capture/recapture breeding birds, record breeding success, and mark chicks (details in Sanz-Aguilar et al. 2008, 2009a). Individuals were classified as ‘‘unsuccessful’’ if their egg failed to hatch or the chick did not fledge, while the contrary were classified as successful. During this period, a total of 1741 chicks were marked before fledging with stainless steel rings and a unique alphanumeric code. Annual monitoring of the nests resulted in 454 recaptures of 165 known-age breeders (i.e., birds marked as chicks). In addition, 66 rings of birds of known age were recovered in pellets of YellowLegged Gulls *Larus michahellis*, the main predator of the petrels in this colony (Oro et al. 2005; Sanz-Aguilar et al. 2009b). This information allowed us to estimate the survival of pre-breeder individuals (i.e., survival below the age of 3 years, the age of their first breeding attempt; see Sanz-Aguilar et al. 2009a), since young birds are present and prospect the colony but are not captured during the standard nest monitoring of breeding birds. Given the limited sample size and the natal dispersal of some individuals within the study area, we chose to combine data from the two colonies. Mediterranean Storm Petrels are thought to stay in the Mediterranean Basin the whole year (see Soldatini et al. 2014), and currently no recoveries/observations of wintering birds have been made from any other site or region (own data). Information from regurgitates indicate that Storm Petrels in the studied colonies feed on Opossum Shrimps *Mysidacea spp.* and on small pelagic fish such as Anchovy *Engraulis encrasicolus* and Round Sardine *Sardinella aurita* (the authors, unpublished data). In addition, it is likely that birds also feed on other small pelagic fish, as described for the central Mediterranean populations (Albores-Barajas et al. 2011), and on Krill *Euphausiacea* and micro-zooplankton, as reported for the Atlantic populations of the closely related European Storm Petrel Hydrobates pelagicus pelagicus (D'Elbee and Hemery 1998). The production, distribution, and abundance of the Storm Petrel's foraging resources may be influenced by large-scale climatic and hydrographic processes (Durant et al. 2004; Lloret et al. 2004; Bellido et al. 2008), as well by local factors such as river outflows, upwelling, and sea temperature (Estrada 1996; Ramírez et al. 2016). Here, we focus on the potential effects that a large-scale climatic index, the North Atlantic Oscillation index (NAO), and a local climatic measure, the sea surface temperature (SST) in the Alboran Sea and Benidorm area, could have on age-dependent survival and reproduction. The NAO is a large-scale fluctuation linked to the speed and direction of the surface westerlies blowing across the Atlantic (Hurrell, 1995) that have cascading effects on oceanographic and biological processes (Stenseth et al. 2002). We considered the winter NAO (i.e., December–March; NAOw) and used data available at https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlan tic-oscillation-nao-index-station-based (last accessed May 2014). The Alboran Sea is located 392 km south of the breeding colony and has been identified as a potential wintering area for the species; its SST conditions have been shown to be negatively correlated with the annual survival of Storm Petrels breeding in the central Mediterranean (Soldatini et al. 2014). Data on winter SST (December– February) for the Alboran Sea (SSTalb) were obtained from the National Oceanic & Atmospheric Administration (NOAA; http://www.esrl.noaa.gov/psd/data/gridded/data. noaa.oisst.v2.html). The Alboran Sea has a complex water convection system (Vélez-Belchí et al. 2005) that gives rise to spatial heterogeneity in SST. We used the average SST of six points covering the whole Alboran Sea to reflect this variability. In addition, we used mean winter SST values for a 30-km buffer surrounding Benidorm Island (SSTben), since this represents a potential foraging area where high numbers of individual petrels are observed during the breeding season (Arcos et al. 2009). Sea surface temperatures (SST, C) were sourced online on a weekly basis in 1993–2014 from two different sites: (a) AVHRR Pathfinder Version 5.2, spatial resolution of 0.041667, obtained from the US National Oceanographic Data Center, and GHRSST (http://pathfinder.nodc.noaa.gov) for SST data (Casey et al. 2010); and (b) Aqua MODIS (http://oceancolor.gsfc.nasa. gov/), as level 3 Hierarchical Data Format (HDF) for SST products at a spatial resolution of 0.041667 (2002–2014). SST variables were processed and converted from HDF files to raster images using the Marine Geospatial Ecology Tools for ArcGIS10.1 (Roberts et al. 2010).

Statistical analysis

Multievent capture-recapture models were used to evaluate the effect of age and environmental conditions on survival probabilities (Pradel 2005), and individual random effects in both survival and recapture probabilities (Gimenez and Choquet 2010). The multievent framework distinguishes field observations (the events coded in the encounter histories) from the underlying inferred biological states of the individuals (Pradel 2005). The possible events were 0 (bird not observed on a particular occasion), 1 (bird captured as a chick or bird recaptured as a breeding adult), 2 (petrel recovered recently dead), while the underlying biological states were defined as A (alive), RD (recently dead), and LD (long dead). The probabilities of the transition between states (survival) and the probabilities of the states (recapture and recovery) (see details in Online Appendix 1) were estimated simultaneously by maximum likelihood using the program E-SURGE 1.6.3 (Choquet et al. 2009a, b). We first tested the goodness-of-fit (GOF) of the Cormack–Jolly–Seber model by cohort (i.e., to account for age effects and temporal effects) using the software U-CARE (Choquet et al. 2009a, b). Our starting model considered the following parameter constraints: (1) full variation in age survival (21 age classes); (2) recapture probabilities of 1- and 2-year-old birds fixed to zero (given that recruitment begins at 3 years; Sanz-Aguilar et al. 2009a); (3) recapture probabilities varying over time and with age (see details in Online Appendix 1); and (4) recovery probabilities varying over time and differing between 1-year-old and older birds (because most Storm Petrels spend their first year at sea and so recoveries of these birds are less probable, see details in Appendix 1). We first tested the effects of age (see below) and environmental covariates on survival. Once the best structure was selected, we tested the effects of individual heterogeneity on survival and recapture (Gimenez and Choquet 2010). The effect of age was tested using linear, quadratic, log, and quadratic log functions compared to full age and constant models. To further test for senescence, we compared models considering a linear age effect up to a particular threshold (from age 3 to age 8) that indicated age of stabilization (constant value) with models in which the threshold indicated the start age of senescence (linear age effect with a different intercept and slope). Model selection was based on Akaike's information criterion (AIC) and the model with the lowest AIC was selected as the most parsimonious (Burnham and Anderson 2002); specifically for survival analyses we use the AIC adjusted for the effective sample size (AICc). When the AIC difference between two models (DAIC) was at most 2, these models were considered to be equivalent (Burnham and Anderson 2002). For each model we calculated the Akaike weights (wi) as an index of relative plausibility (Burnham and Anderson 2002). As a result of the limited sample size of several age classes during certain years, the evaluation of interactions of environmental covariates with age was not possible. The significance of environmental covariates was evaluated using an analysis of deviance with a Fisher–Snedecor distribution (ANODEV; Skalski et al. 1993) calculated as

$$F\big(1, np(M_t) - np(M_{cov})\big) = \frac{Dev(M_{cnt}) - Dev\ (M_{cov})}{(Dev(M_{cov}) - Dev\ (M_t))/(np(M_t) - np\ (M_{cov}))}$$

To assess the influence of environmental covariates on vital rates, we estimated the percentage of variation explained by each covariate (R^2) as

$$r^2 = \frac{Dev(M_{cnt}) - Dev\ (M_{cov})}{Dev(M_{cnt}) - Dev(M_t)}$$

where $Dev(M_{cnt})$ is the deviance of the constant model (i.e., no effects considered), $Dev\ (M_{cov})$ is the deviance of the model with the covariate considered, and $Dev(M_t)$is the deviance of the time-dependent model. The effects of individual heterogeneity were evaluated by means of likelihood ratio test (LTR) between models with and without individual random effects (Gimenez and Choquet 2010). In our study population, successful and failed breeders have equal probabilities (Sanz-Aguilar et al. 2008). As modeling the effects of age, time, and environmental covariates while including individual random effects in a single analysis will lead to overparameterized models for our dataset, we analyzed breeding success separately using generalized linear mixed models (GLMMs). Before analysis, we investigated the extent of age-dependent assortative mating in the studied population to discard potential biases in the observed age-related breeding success that may arise from differential ages of partners. We used data from 18 breeding pairs for which the age of both partners was known. Assortative mating was assessed by a Spearman correlation test. We subsequently modeled the influence of age, the age of first observed breeding (i.e., recruitment age), and environmental covariates on breeding success by means of GLMMs using the glmmML package in R software (http://www.R-project.org). The age of first observed breeding was included to account for the selective appearance of individuals in the breeding population (van de Pol and Verhulst 2006). Individual identity was considered as a random effect to avoid pseudo-replication. Age was modeled as a factor (12 levels from age 3 to age 14) and as a continuous variable using different relationships (linear, quadratic, logarithmic, and quadratic logarithmic) to assess how breeding success varied with age. We limited our data to 14 age classes because of the very low number of observations of individuals at least 15 years old (N = 11) and their uneven temporal distribution (i.e., only observed during the final years of the study). The first step was testing the effects of age and individual recruitment age. Once we had found the best age curve describing changes in breeding success, we evaluated the temporal variation (i.e., year) and the additional potential influence of environmental covariates (NAOw and SST). Again, because of the limited sample size of several age classes during certain years, the evaluation of the effect of a potential interaction of environmental covariates with age was not possible to test (i.e., the likelihood of these models did not converge). Model selection was based on AIC (see above). To test the significant effect of each environmental covariate on breeding success, we used a likelihood ratio test (LRT) to compare the constant model with the model that included the covariate.

3.3 Results

Breeding success analysis

The association between the ages of the two members of the breeding pairs indicate the existence of assortative mating by age (N = 18, Spearman correlation Rs = 0.57, p = 0.05). Although females were slightly younger than males (mean difference = 1.94, SD = 2.41), we assumed that the age of partners was similar. The best model for breeding success (model 13, Table 4) had a quadratic age-dependent pattern of breeding success that increased until the age of eight and then decreased (Figs. 9a, 10a) and also a negative effect of recruitment age: individuals recruiting at young ages had a higher breeding success (at the same ages) than individuals recruiting later (Fig. 9a). Both the age of first observed reproduction and the quadratic individual age were statistically significant (p = 0.01 and p = 0.03, respectively, model 13). The models with only the quadratic age pattern (model 4, Table 4) or the age of first observed breeding (model 7, Table 4) were not strongly supported, they were close (ΔAIC≤2) to the constant model (model 1, Table 4). In addition to age effects, the effect of time (i.e., year) on breeding success was clearly supported (model 13, Table 4). However models with environmental covariates (models 14–16, Table 4) failed to explain the temporal variation in breeding success (Table 4). In fact, the environmental covariates (NAOw, SSTben, and SSTalb) explained only 10.4, 11.6, and 0 %, respectively, of temporal variability, thereby showing a positive relationship in all cases.

TABLE 4. Modelling the effects of age, individual heterogeneity and environmental conditions on breeding success using generalized linear mixed models. Notation: np = number of parameters; dev = relative deviance; AIC = Akaike information criterion; ΔAIC = AIC difference between the current model and the one with the lowest AIC value; W_i = Akaike weight; R^2 = variance explained by environmental covariates (*p-value<0.05). Model notation: Year = time effect; NAO_w = winter North Atlantic Oscillation index; SSTben = winter sea surface temperature around Benidorm Island (potential foraging area); SSTalb = winter sea surface temperature in the Alboran Sea (potential wintering area); Age = full differences among age classes; A = lineal effect of age; A^2 = quadratic effect of age; Log(A) = logarithmic effect of age; $Log(A)^2$ = quadratic natural logarithmic effect of age; RA= first observed reproduction.

Model	**Breeding success**	**np**	**dev**	**AIC**	**ΔAIC**	**W_i**	**R^2**
1	Constant	2	613.46	617.46	9.09	0.01	
2	Age	13	605.60	631.60	23.23	0.00	
3	A	3	612.46	618.46	10.09	0.00	
4	A^2	4	607.85	615.85	7.48	0.01	
5	Log(A)	3	611.46	617.46	9.09	0.01	
6	$Log(A)^2$	4	608.94	616.94	8.57	0.01	
7	RA	3	612.16	618.16	9.79	0.00	
8	Age+ RA	14	601.36	629.36	21.00	0.00	
9	A+RA	4	608.18	616.18	7.81	0.01	
10	A^2+RA	5	603.44	613.44	5.07	0.04	
11	Log(A)+RA	4	606.06	614.06	5.69	0.03	
12	$Log(A)^2$+RA	5	604.22	614.22	5.86	0.03	
13	**A^2+Year+RA**	**23**	**562.37**	**608.37**	**0.00**	**0.54**	
14	A^2 +NAO_w+RA	6	599.18	611.18	2.81	0.13	10.37
15	A^2 +SST_{ben}+RA	6	598.70	610.70	2.33	0.17	11.54
16	A^2 +SST_{alb}+RA	6	603.44	615.44	7.07	0.02	0.03

Survival analysis

The overall GOF of the Cormack–Jolly–Seber model by cohort was not statistically significant, thereby indicating a good fit to the data (v2 = 16.32, df = 58, p = 1). After modeling different age structures for recapture and recovery probabilities (see details in Online Appendix C, Table C1), we retained two and seven age classes for recovery and recapture probabilities, respectively. The effects of age and year were additive for recapture and in interaction for recovery (recoveries of 1-year-old individuals occurred in very few years, results not shown). We used this structure to model survival probability. When modeling age with linear, log, and quadratic functions (models 1–6, Table 5), the model including the quadratic effect of log-age on survival (model 6, Table 5) was retained as the best model: survival probabilities substantially increased early in life (at 1–4 years), reached a plateau, and then slowly decreased (Figs. 1b, 2b). However, when specifically testing for senescence, models with two linear functions accounting for a survival increase and a later decrease (models 7–11, Table 5) showed lower support than models including a survival stabilization after initial increase (models 12–16, Table 5). In fact, a model in which survival increased up to age 4 and then stabilized had only 0.24 AICc points more than the model including the quadratic effect of log-age (models 6 and 12, Table 5), indicating high uncertainty about the existence of actuarial senescence. We used the structure of model with the lowest AICc value for testing environmental covariate effects (model 6, Table 5). The model including temporal variation in survival was not retained (model 17, Table 5), indicating that there was little temporal variability. Models with covariate effects in age-dependent survival probabilities (models 18–20, Table 5) failed to explain the temporal variability of survival (Table 5). The model with an individual heterogeneity on recapture (model 22, Table 6) was clearly supported as the best model, with the individual random effect being statistically significant (LTR, $0.5*\chi2(0)+ 0.5*\chi2(1)=54.09$, $p<0.001$). Survival estimates from model 6 (Table 6), which did not account for individual heterogeneity in recapture, were not biased and were nearly identical to that of model 22 (Fig. 9b). The effect of individual heterogeneity on survival (model 21, Table 6) was not statistically significant (LTR,$0.5*\chi2(0)+ 0.5*\chi2(1)=1.05$, p=0.15).

TABLE 5. Modelling the effects of age and environmental conditions on storm petrel survival using multievent capture-recapture models. General notation as in Table 4, age classes considered are indicated between parentheses, AICc= Akaike information criterion corrected by small sample size. Models 7 to 16 are testing the existence of a threshold value from which survival decreased or remained stable.

Model	**Survival**	**np**	**dev**	**AICc**	**ΔAICc**	**Wi**	**R2**
1	Constant	62	3145.53	3273.05	79.06	0.00	
2	Age	82	3031.25	3201.44	7.45	0.01	
3	A	63	3092.30	3225.58	31.59	0.00	
4	A2	64	3072.90	3204.65	10.66	0.00	
5	Log(A)	63	3075.02	3204.66	10.67	0.00	
6	**Log(A)^2**	**64**	**3062.23**	**3193.99**	**0.00**	**0.37**	
7	A (≤3) + A(≥4)	65	3064.04	3197.91	4.68	0.04	
8	A (≤4) + A(≥5)	65	3061.62	3195.49	2.26	0.12	
9	A (≤5) + A(≥6)	65	3067.03	3200.90	7.67	0.01	
10	A (≤6) + A(≥7)	65	3067.19	3201.06	7.83	0.01	
11	A (≤7) + A(≥8)	65	3076.99	3210.86	17.63	0.00	
12	A (≤3) + constant (≥4)	63	3064.59	3194.23	0.24	0.23	
13	A (≤4) + constant (≥5)	63	3069.50	3199.14	5.15	0.02	
14	A (≤5) + constant (≥6)	63	3073.53	3203.16	9.17	0.00	
15	A (≤6) + constant (≥7)	63	3078.52	3208.16	14.17	0.00	
16	A (≤7) + constant (≥8)	63	3080.99	3210.62	16.63	0.00	
17	Log(A)^2+Year	84	3023.02	3197.52	3.53	0.06	
18	Log(A)^2 +NAOw	65	3062.20	3196.07	2.08	0.13	0
19	Log(A)^2 +SSTben	65	3062.22	3196.09	2.10	0.13	0
20	Log(A)^2 +SSTalb	65	3062.16	3196.03	2.04	0.13	0

TABLE 6. Modelling individual random effects on survival and recapture probabilities on storm petrel using multievent capture-recapture models. General notation as in Table 5, “h” = individual heterogeneity (i.e. individual random effect), p-value= statistical significance of individual random effect by means of LTR test.

Model	Survival	Recapture	np	Dev	AICc	p-value
6	Log(A)^2	age (3,4,5,6,≥7)+t	64	3062.23	3193.99	
21	Log(A)^2+h	age (3,4,5,6,≥7)+t	65	3061.18	3191.18	0.15
22	Log(A)^2	[age (3,4,5,6,≥7)t]+h	65	3008.14	3138.14	<0.001

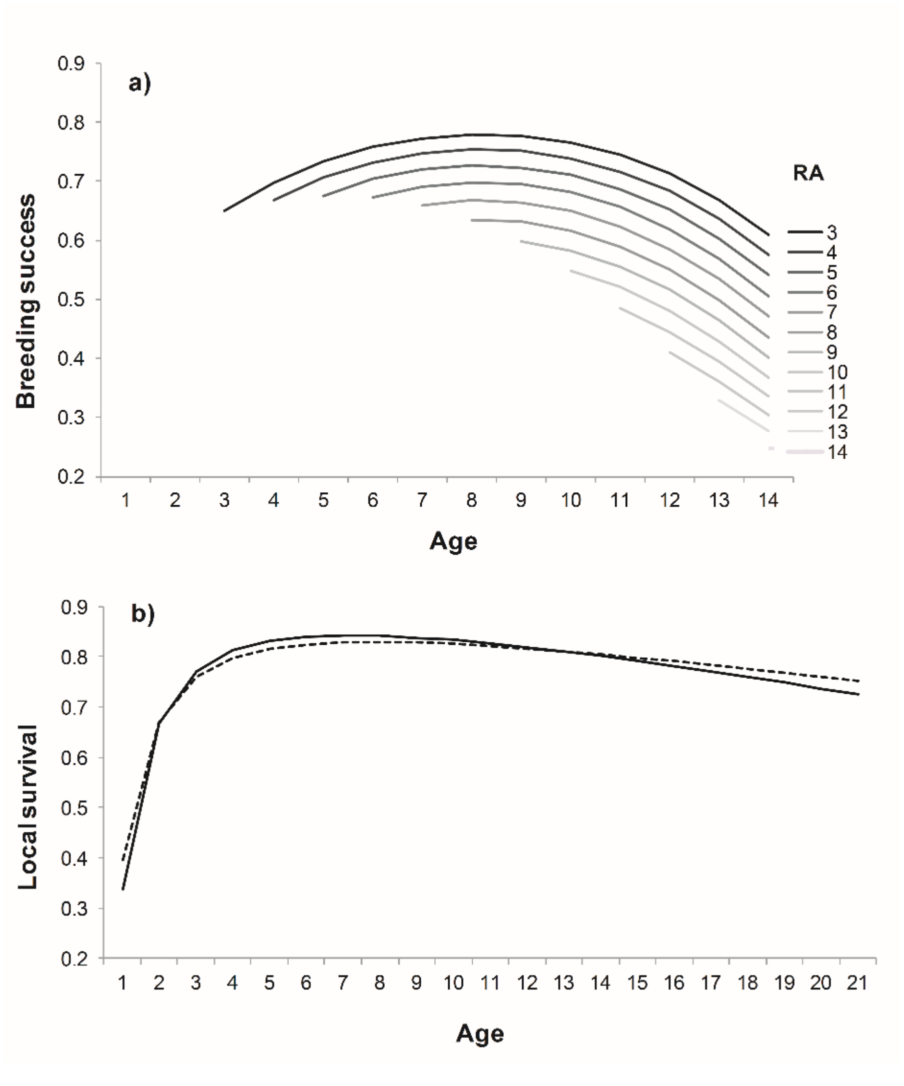

FIG. 9. Panel a) Variation in storm petrel breeding success with age and age of first observed reproduction (RA) estimated by model 10 (Table 4). Note that the first breeding attempt by storm petrels in Benidorm is at three years of age. Panel b) Variation in storm petrel survival with age estimated by model without individual random effect (dashed line; model 6; Table 5) and model with individual random effect in recapture (solid line; model 12; Table 6).

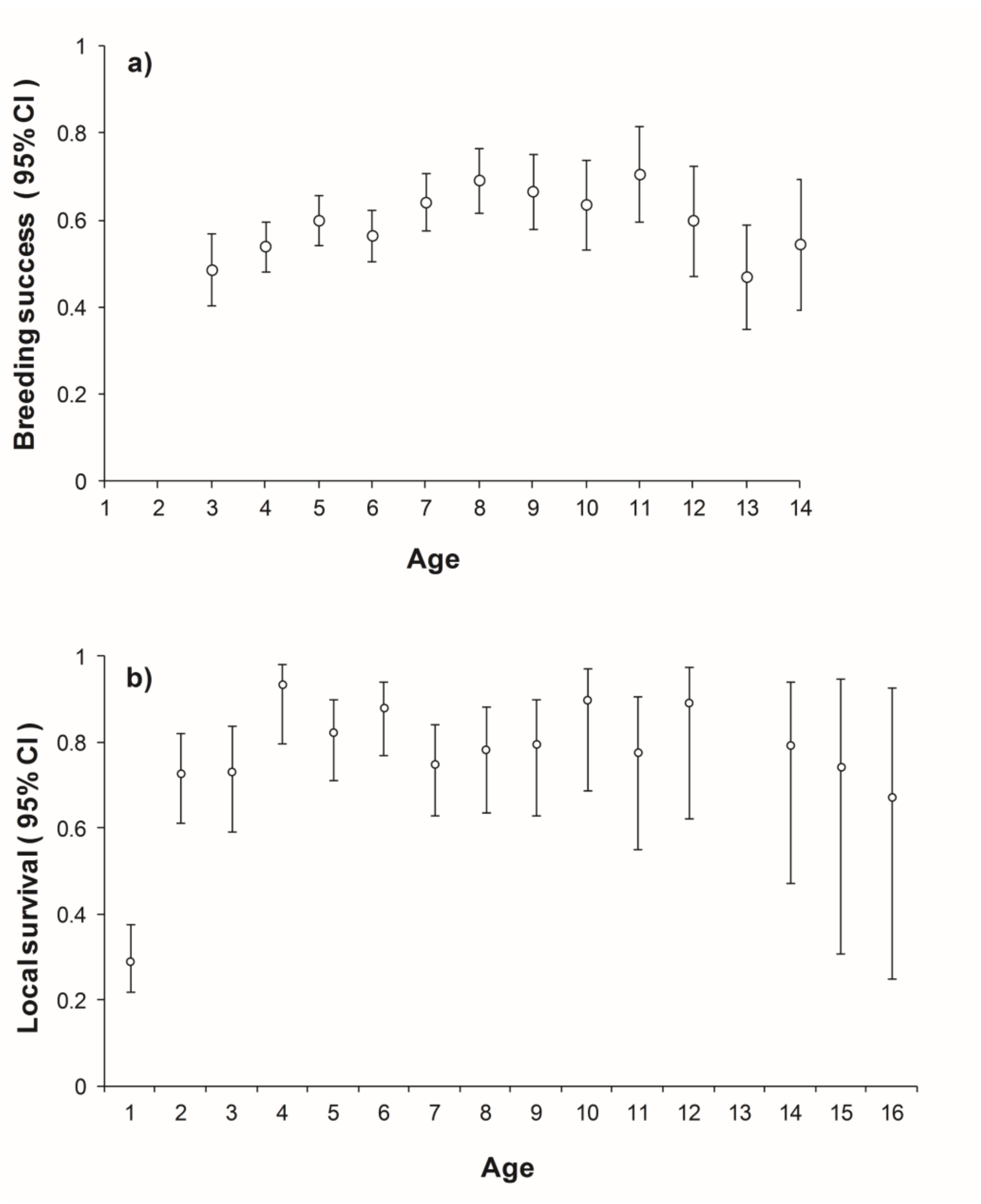

FIG. 10. Panel a) Full age-dependent estimates of breeding success and 95%CI (model 2, Table 4). Panel b) Full age-dependent estimates of survival and 95%CI (model 2, Table 5). Only identifiable estimates are shown.

3.4 Discussion

In long-lived species, survival and reproduction rates are expected to change with age (Stearns 1992). Long-term demographic studies (e.g., Pardo et al. 2012; Chantepie et al. 2015) predict an increase in breeding performance and survival at younger ages, a plateau of maximal values during adulthood, and finally a decrease at older ages (i.e., the evolutionary theory of senescence; Medawar 1952; Williams 1957). In our study, we found this age pattern in Storm Petrel breeding success and a clear increase at younger ages in survival. However, our results for survival should be interpreted with caution because the local survival rates estimated here for young Storm Petrels may in part be the result of permanent dispersal rather than true mortality (Ballerini et al. 2015). In birds, dispersal typically occurs before the first reproduction attempt (i.e., natal dispersal, Greenwood and Harvey 1982). Storm Petrels typically breed in inaccessible places, and monitoring programs are limited to just a few accessible areas and nests, making dispersal events difficult to detect. Consequently, we were unable to disentangle the proportion of the estimated mortality that corresponded to permanent emigration. However, we believe that the estimated curve reflects the real age-dependent changes of survival in this species. Young Storm Petrels prospect several colonies (including the natal colony) before attempting to breed and were impossible to capture during the monitoring of the breeding pairs. To overcome this limitation we used the recoveries of individuals killed by gulls, which are predicted to be a random sample of the petrels that prospect and breed on the island (Oro et al. 2005; Sanz-Aguilar et al. 2009b).

Contrary to Hamilton's theory (1966) that postulates that the negative effects of senescence start with the first breeding attempt, we found that senescence in our study began slowly and rather later in life, at around 8 years of age for reproduction. For actuarial senescence, results were uncertain because the model with no senescence and the one indicating a very slow senescence starting at age 8 were equally supported. We believe that if actuarial senescence was low, the model with no senescence should be favored in terms of AICc, given its lower number of parameters, so more data should be collected to disentangle the existence of a decrease of survival at older ages. A delayed senescence has been detected in many other studies conducted in a wide range of species (see reviews by Nussey et al. 2013; Jones et al. 2014), including other long-lived birds such as vultures, albatrosses, and gulls (Chantepie et al. 2015; Pardo et al. 2012; Oro et al. 2014). Several studies have found that body-mass declines and poorer physiological condition negatively affect the foraging behavior of older individuals (e.g., Catry et al. 2006; Lecomte et al. 2010). Poorer foraging efficiency may in turn provoke changes in the immune system, thereby affecting survival (see review by Palacios et al. 2011). Although we did not find evidence of individual heterogeneity in survival, we found a clear heterogeneity in recapture that did not bias survival estimates (as previously found for the Scopoli's Shearwater Calonectris diomedea by Choquet et al. 2013) and may respond to nest-specific catchability (Libois et al. 2012). Moreover, our results showed a negative influence of recruitment age (using the observed first age of reproduction as a proxy) on breeding success (see also Limmer and Becker 2010; Zhang et al. 2015). These results are in agreement with previous evidence on European Badgers Meles meles and Blue-Footed Boobies Sula nebouxii, in which an early recruitment was associated with higher reproductive success (Dugdale et al. 2011; Kim et al. 2011). On the contrary, other studies on long-lived birds associated an early recruitment with a lower reproductive success, lower egg volume, and/or delayed laying dates (van de Pol and Verhulst 2006; Limmer and Becker 2010). Our results may be explained by multiple and non-exclusive hypotheses. First, the constraint hypothesis (Curio 1983) which predicts a positive effect of breeding experience in breeding success, as we detected here (see also SanzAguilar et al. 2008). Also, individuals that recruit early in life may have the opportunity of gaining and improving parental skills (Desrochers 1992; Weimerskirch 1992) resulting in a higher breeding success later in life than less experienced individuals recruiting later. Selective disappearance of low quality individuals may also explain the increase in breeding performance and survival at younger ages (Forslund and Pärt 1995). A second side of the same coin is that some Storm Petrels able to breed at younger ages may be high quality individuals, as suggested by the negative relationship between recruitment age and breeding success found here. Further studies with additional data for a more reliable test of the interactions between age and recruitment and including their potential effects of last reproduction could provide additional insights into aging patters (van de Pol and Verhulst 2006; Dugdale et al. 2011; Zhang et al. 2015). Note that nearly half of the known-age breeders included in our study are still alive and reproducing. In long-lived species, greater temporal variability is to be expected in parameters to which population growth rate is less sensitive (e.g., fertility and juvenile survival) (Sæther and Bakke 2000). Procellariforms tend to limit reproductive effort independently of offspring requirements when environmental conditions are unfavorable in order to maximize survival expectations (Navarro and González-Solís 2007). Accordingly, we found that breeding success had greater temporal variation than survival. However, previous studies have found important temporal variation in survival probabilities in the Storm Petrels from Benidorm Island, especially in those individuals breeding in one of the two caves in particular (Sanz-Aguilar et al. 2008, 2010). Since 2004 a culling program on predatory gulls has been carried out to minimize the effect of predation on survival (Sanz-Aguilar et al. 2009b, own data). As most of the data used in this study was taken at the end of the study period, this fact may explain the lack of temporal variability in survival. Although breeding success was variable over time, none of the covariates we used explained its temporal variation satisfactorily. Several studies have shown that the NAO affects the Mediterranean climate

(Hurrell 1995) and marine environments (including fish abundance and predator–prey interactions, Ottersen et al. 2001; Palomera et al. 2007). However, variability in the Storm Petrel's breeding success was not related to the NAO index (or to the SST around the breeding colony or in the Alboran Sea). Despite the changes in the distribution and abundance of prey consumed by marine predators caused by climatic indices and oceanographic processes (Durant et al. 2004), there are different local features such as river runoffs and winds that influence the availability of small pelagic prey species in the Mediterranean (Lloret et al. 2001). In addition to the complex dynamics of marine systems, Storm Petrel prey species (anchovies and sardines) have different spawning seasons and exhibit different time lags in larval development and growth, and may compete for food and space (see Lloret et al. 2004; Sabatés et al. 2006). These complex relationships between oceanographic conditions and fish abundance hinder the selection of an appropriate oceanographic index as a proxy of food availability in Storm Petrels (see Oro 2014), also because we lack data on the spatial extent of Storm Petrels' foraging areas. Additionally, factors such as mistiming between Storm Petrel phenology and seasonal pulses of marine productivity (Ramıírez et al. 2016), or gull predation (Sanz-Aguilar et al. 2009a, b; Libois et al. 2012) not considered here, may also affect Storm Petrel reproduction and may add noise to the biological associations tested in this study. A previous study of the Storm Petrels breeding in the central Mediterranean found a relationship between Storm Petrel survival and SST in the Alboran Sea and reported that this area is a potential wintering area (Soldatini et al. 2014). The Alboran Sea is mainly characterized by two anticyclonic gyres (western and eastern) that undergo large variations on the surface and serious variations in time that modify the overall structure of the water mass (Vélez-Belchí et al. 2005). As the precise wintering area for the species is unknown, we used SST values from the whole Alboran Sea as a proxy of wintering conditions but found no relationship with demographic parameters. We speculate that Storm Petrels from the western Mediterranean (Benidorm Island) winter in a different area to central Mediterranean Storm Petrels (Soldatini et al. 2014). Finally, although thousands of Storm Petrels have been monitored over the last 22 years, the sample size of knownage breeders (especially the older age classes) is still small. This fact is linked to the complexity of the marine environment, while the lack of knowledge about the distribution of Storm Petrels at sea hampers the study of the relationships between age-dependent vital rates and environmental conditions (Oro 2014). Further long-term monitoring and detailed studies of this species' foraging ecology during breeding and wintering are thus still needed.

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4

The influence of intense maritime traffic and whale-watching on survival, recruitment and population size in bottlenose dolphins.

Hernández, N., Tenan, S., Fearnbach, H., de Stephanis, R., Verborgh, P., & Oro, D. (2017). The influence of intense maritime traffic and whale-watching on survival, recruitment and population size in bottlenose dolphins. Under review in *Aquatic Conservation: Marine and Freshwater Ecosystems.*

Abstract

The Strait of Gibraltar is an important habitat for cetaceans due to its high marine productivity, but is also the second most navigated channel in the world, subjecting cetaceans to a high level of vessel traffic, including an established whale-watch fleet. Both maritime traffic and whale-watching activities have been shown to impact the behaviour of cetacean populations, but little is known about their impact on demographic parameters and population dynamics. The aim of this study was to evaluate the impacts of both ferry traffic and whale-watching vessels on the local survival of a bottlenose dolphin (*Tursiops truncatus*) population that occurs in the Strait, as well as estimate their recruitment and evaluate demographic trends. A Bayesian hierarchical mark-recapture modelling approach was applied to 8 years of photo-identification data (2002-2009) and inferred that apparent survival was correlated with ferry traffic, whereas the influence of whale-watching was almost negligible on this parameter. The large unexplained variance in survival variability may have been due to permanent emigration outside of the study area, possibly to avoid the noise from intense maritime traffic, but real mortality from vessel collisions and other sources cannot be disregarded. Population size increased between 2002 and 2005, and then decreased between 2006 and 2009, while local per-capita recruitment decreased from 2004 until the end of the study period. These shifts correlated temporally with the construction of a large harbour on the Moroccan coast which increased maritime traffic significantly, including a 40% increase in ferry traffic that regularly transited the Strait.

The results suggest that anthropogenic activities related to maritime traffic likely had a negative impact on the demographic parameters and overall dynamics of this dolphin population. These results highlight the need to implement specific conservation regulations in this region to manage vessel traffic in areas of high cetacean occurrence.

Keywords: anthropogenic impact; capture-recapture; cetaceans; demography; anthropogenic impact; dolphins; maritime traffic; tourism.

4.1 Introduction

Estimating abundance and evaluating trends of animal populations provides information that is essential for their conservation and management of activities. It is necessary to have information about the size, recruitment and survival of a population in order to accurately assess its dynamics and understand the factors that influence these processes. As k-selected species, cetaceans maximize their fitness by having high and stable survival, despite environmental stochasticity. However, anthropogenic impacts often alter this life-history strategy by reducing survival and resilience.

Interactions between maritime traffic, whale-watching operations and wildlife are becoming an increasing concern to management and conservation agencies due to their global impact on a number of protected cetacean species. The commercial whale-watching industry has been increasing worldwide (i.e. at least in 119 countries in 2008; O'Connor et al., 2009), resulting in a number of studies investigating whether whale-watching activities negatively impact the behaviour and physiology of cetacean populations (see review New et al., 2015). Boat noise may cause stress to individuals, mask important acoustic signals and affect their behaviour. It has been also shown that some cetacean species perceive boats as a risk and individuals have been observed to react with anti-predatory tactics, such as spending less time at the surface and increasing both the depth and duration of dives, altering swim speed and direction, spending less time feeding and resting, and changing both the cohesiveness and size of their group (Arcangeli et al., 2009; Christiansen et al., 2013; Lusseau, Lusseau et al., 2006).

However, despite the large number of studies that have evaluated the effects of boat interactions on cetacean biology, no study, to our knowledge, has quantified the impact of boats on the survival or recruitment of cetacean populations. This analysis helps fill this key data gap. It was used bottlenose dolphin photo-identification data, collected in the Strait of Gibraltar (hereafter referred to as The Strait; Fig. 11) between 2002 and 2009, to evaluate the impact of ferry and whale watching traffic on the demographics trends of the local population. Due to its high marine productivity, the Strait is an important area for foraging and breeding for a number of cetacean species including long-finned pilot whales (*Globicephala melas*), bottlenose dolphins, common dolphins (*Delphinus* spp.), striped dolphins (*Stenella coereuleoalba*), killer whales (*Orcinus orca*), sperm whales (*Physeter microcephalus*) and fin whales (*Balaenoptera physalus)*, but is also exposed to high level of anthropogenic activity since it is the only connection between the Mediterranean Sea and Atlantic Ocean (De Stephanis et al., 2008).

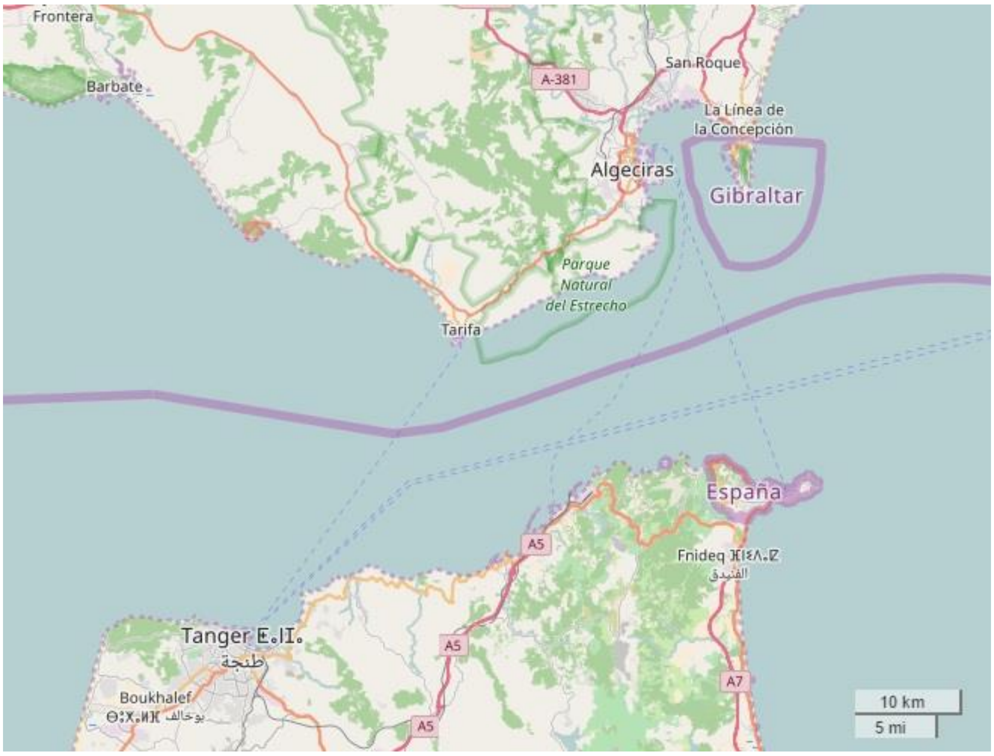

Fig. 11. The Strait of Gibraltar. The dashed lines show the maritime routes between Spain and Morocco. Made with marine traffic website.

Large maritime vessel traffic (including cargo ships and ferries) in the channel has been increasing over the past 10 years, with an increase of 41%, from 82,000 vessels in 2001 to 116,000 vessels in 2010. Ferry traffic saw an increase of 56%, changing from 25,000 to 39,000 vessels across the same time period (data provided by "Tarifa Tráfico" center). These numbers do not include smaller vessels (<50 m and 200 tons) such as local fishing, pleasure and whale watching boats. One of the primary causes of the observed increase in maritime traffic, especially ferries and fast ferries, was the construction of a new harbour in Tanger-Med, Morocco in 2007; additionally, the local whale-watching industry is one of the fastest growing economic sectors in the area, increasing from 172 excursions in 2002 to a peak of 461 excursions in 2008 (Fig. 12).

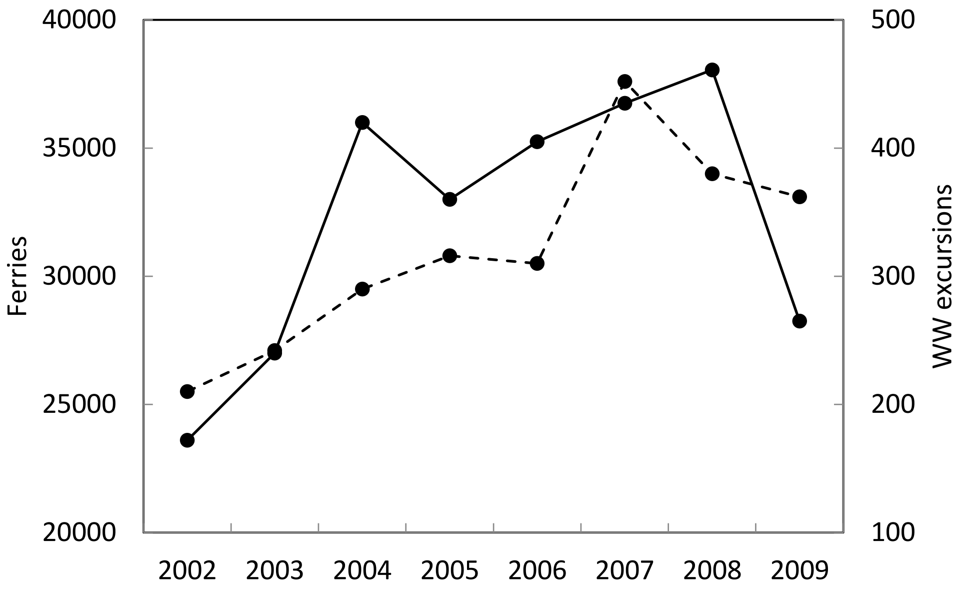

FIG. 12. Temporal changes in the number of ferries crossing the Gibraltar Strait (dashed line) and in the number of whale-watch excursions, per year, by all companies operating in Tarifa (solid line). Note that the number of ferries is ca. two orders of magnitude larger than the number of whale-watch excursions.

Here it is present the results from the analysis of the impact of vessel traffic (both ferry traffic and whale-watching boats) on the apparent survival, recruitment and population size of a local bottlenose dolphin population in The Strait. It was applied a Bayesian hierarchical state-space formulation of the Jolly-Seber model (Durban et al., 2010; Fearnbach, Durban, Parsons, & Claridge, 2012; Royle & Dorazio, 2008) to make inference on key variations in demography.

4.2 Methods

Species and study area

Bottlenose dolphins are listed in Annex II of the European Union (EU) Habitats Directive and are considered to be a priority species for conservation, requiring the creation of Special Areas of Conservation (SACs) in European waters. The study area of the Strait of Gibraltar includes all waters between 5ºW and 6ºW, except Moroccan waters (Fig. 11). It is an area that is characterized by a canyon that stretches from east to west, generating a complex system of water circulation that produces a high level of marine productivity (De Stephanis et al., 2008).

Data collection and analysis

Photo-identification data were collected during dedicated bottlenose dolphin surveys conducted on a research motorboat (see Verborgh et al., 2009; Wright et al., 2007). Individual dolphins can be identified based on both the pattern of naturally acquired nicks on their dorsal fin and dorsal fin shape (Scott, Wells, & Irvine, 1990; Wilson, Hammond, & Thompson, 1999). Attempts were made to photograph as many individuals as possible and all images were subsequently analysed following established photo-identification methods (Ottensmeyer & Whitehead, 2003; Wiirsig & Jefferson, 1990). From 2002 to 2004, a Canon EF100–400-mm lens with image stabilizer was used on a Canon EOS-3 camera. From 2004 onward, this lens was mounted on a Canon 10D digital camera. All the slides taken before 2004 were examined with an 8× magnifying eyepiece on a light table. Since 2004, digital pictures were examined on a computer screen. Identification numbers were assigned to all distinct individuals and a catalogue was created by comparing each dorsal fin image to all other individuals in the catalogue. An animal was assigned an existing identification number if a match was found, but was assigned a new identification number if the individual could not be matched to a catalogued animal. Sighting number, picture number, total number of individuals in the photo, number of the individual analysed on the picture (starting from the closet individual to the furthest, and from left to right if two animals are at the same distance), fin side (left or right), angle of the fin (the angle starts from 0°, when the animal is seen directly in front and goes around the animal every 30°), image quality, mark type and age class were recorded for all fin images. All data were subsequently imported into a database for analysis. Image quality (Q) was graded from zero to two (i.e. poor "Q0" to excellent "Q2") based on focus, size, orientation, exposure and the percentage of fin visible in the photo: Q0, unusable individual dorsal fin when its representation is blurred, too far away or if the angle is between 330 and 30° or 150° and 210°; Q1, medium quality representation of part of or the entire dorsal fin; Q2, high quality representation of the entire dorsal fin. Distinctiveness was assigned according to the number and size of marks (i.e. shape, notches and nicks) and ranged from 1 (few marks) to 3 (highly marked): M0, individuals without any marks on the dorsal fin but with a specific shape and a white fringe on the back; M1, individuals with small nicks that can only be seen on very high quality pictures; M2, individuals with medium size nicks or many small ones; M3, individuals with characteristic nicks (i.e. very deep or amputation of part or whole of the dorsal fin) which can be recognised on very low quality pictures. The individuals not included in the catalogue will be named unmarked, while the individuals in the catalogue (from M0 to M3) will be called marked individuals (M0 and M1, lightly marked; M2 and M3, well-marked individuals). Following Urian et al. (2015), only images of sufficient quality were included for the analysis, and used photos taken only of the left side of the fin “from 240º to 300º” and Quality 1 and 2.

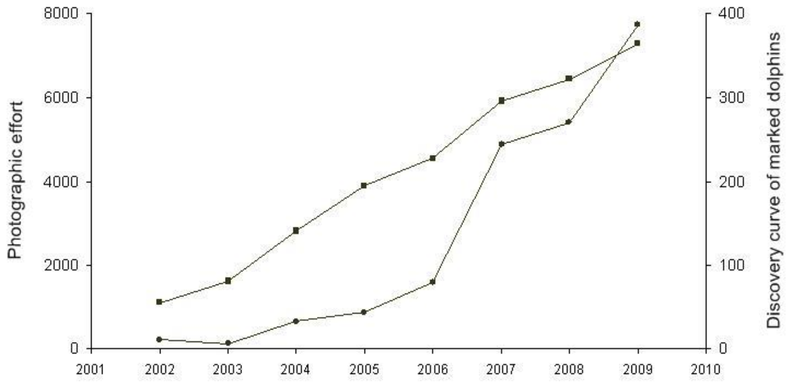

FIG. 13. Photographic effort made during May-August (left axis; circle markers) and discovery curve showing the cumulative number of newly identified individuals per year (right axis; square markers).

All maritime traffic have been required to report their presence in The Strait to “Tarifa Tráfico” (i.e. Centre of maritime area coordination in Tarifa, Spain) since 1997. Therefore, records of all ships that navigated the study area from Tarifa Tráfico were obtained and records of all whale-watch boat traffic data were collected from registers maintained by all companies operating in Tarifa. The number of whale-watch excursions conducted between May and August during the study period was used as an indicator of whale-watching impact intensity and the number of ferries (i.e. normal ferries and fast ferries together) as a proxy of marine traffic impact (Fig. 12).

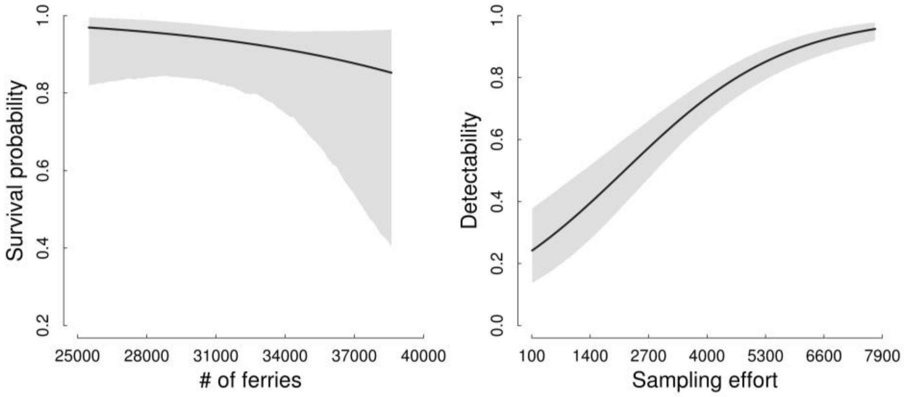

FIG. 14. Relationship between apparent survival probability of bottlenose dolphins at Gibraltar Strait and the number of ferries (a), and between detectability and sampling effort (b). The shaded areas indicate the 95% credible interval for the predicted relationships.

Model formulation

Individual encounter histories were analysed with the Jolly-Seber model, parameterized as a restricted dynamic occupancy model (Kéry & Schaub, 2012; Royle & Dorazio, 2008). The model uses the parameter-expanded data augmentation technique to overcome some technical challenges. Data augmentation technique implies the addition of a number of all-zero capture histories, which can be seen as potentially unobserved individuals, to the observed data of n individuals. This leads to an encounter matrix with dimension M x T, where $M >> N^s$, T is the number of sampling occasions, and N^s denotes the number of individuals ever alive during the study, the so-called superpopulation size. Part of the N^s individuals is already alive and in the population at the first sampling occasion, and the remaining portion of individuals has to enter the population by the end of the study. This method allows to estimate which of the $N^s - n$ individuals (rows of the augmented dataset) are members of the superpopulation (sampling zeros) or not (structural zeros).

In the state-space formulation, the observed encounter histories are the result of the observation process, which is conditional on the ecological (or state) process. For each observation $y_{i,t}$ of individual $i = 1,\dots,n$ at time $t = 1,\dots,T$, with T=8 years, the corresponding state variable $z_{i,t}$ indicates whether the individual is alive and present in the population ($z_{i,t} = 1$) or not ($z_{i,t} = 0$; i.e. it is either dead or has not yet entered the population). The entry and the survival processes constitute the unobserved or partially observed state process. At the first sampling occasion, the initial state of an individual is defined as $z_{i,1} \sim \text{Bernoulli}(\gamma_1)$, where γ_t is the probability that an available individual in M (i.e. with $z_{i,t-1} = 0$) enters the population. After the first sampling occasion individual state transitions are governed by survival (for individuals already alive and in the population) or by entry probability (for individuals not yet entered): $z_{i,t+1} \sim \text{Bernoulli}(z_{i,t}\, \varphi_{i,t} + \gamma_{t+1} \prod_{k=1}^{t} (1 - z_{i,k}))$, where $\varphi_{i,t}$ is the survival probability from t to t+1 for individual i. Parameter γ_t controls the number of addition to the population by referring to M, and thus it has no ecological meaning. The per-capita recruitment (Link & Barker, 2005) can be derived as $f_t = B_t / N_t$, where the number of newly entered individuals at time t is $B_t = \sum_{i=1}^{M} (1 - z_{i,t-1})\, z_{i,t}$, and population size $N_t = \sum_{i=1}^{M} z_{i,t}$. Note that population size estimates derived from the Jolly-Seber model (N_t) refer to identifiable individuals, i.e. individuals with recognizable marks on the dorsal fin. Superpopulation size can be derived as $N^s = \sum_{t=1}^{T} B_t$.

Parameter estimation

The models were fitted using a Bayesian formulation and the Markov chain Monte Carlo framework. Uniform (0,1) and Normal(0,1000) prior distributions were used for the intercepts and slopes (on the logit scale) respectively, of survival (φ), entry probability (γ) and detectability (p). For further details about prior specification of other model parameters see the model code (supporting information Appendix D). Posterior parameter distributions were assessed for prior sensitivity (e.g., (King, Morgan, Gimenez, & Brooks, 2009) by using a second set of priors with Uniform(-5,5) probabilities for the slopes. The two sets of priors yielded similar posterior parameter distributions, and estimates obtained under the first prior set were discussed. The encounter matrix was augmented by $500 - n$ individuals (Fig. 15). To assess the model adequacy, a goodness-of-fit test was conducted based on the posterior predictive distribution of the sum of absolute values of residuals, as measure of lack of fit. Bayesian p-value for the three models used to estimate the proportion of temporal variance explained by the two covariates ranged from 0.41 to 0.42, suggesting an adequate fit (i.e. p-values close to 0.5, and not close to 0 or 1; (Gelman, Meng, & Stern, 1996).

Summaries of the posterior distribution were calculated from three Markov chain initialized with random starting values, run 100000 times after a 100000 burn-in and re-sampling every 50 draws, resulting in 2000 posterior samples per chain. The Brooks-Gelman-Rubin convergence diagnostic (Brooks & Gelman, 1998) used to assess convergence was < 1.1 for all parameters. Models were implemented in program JAGS (Plummer, 2003), which were executed from R (“R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing,” 2012).

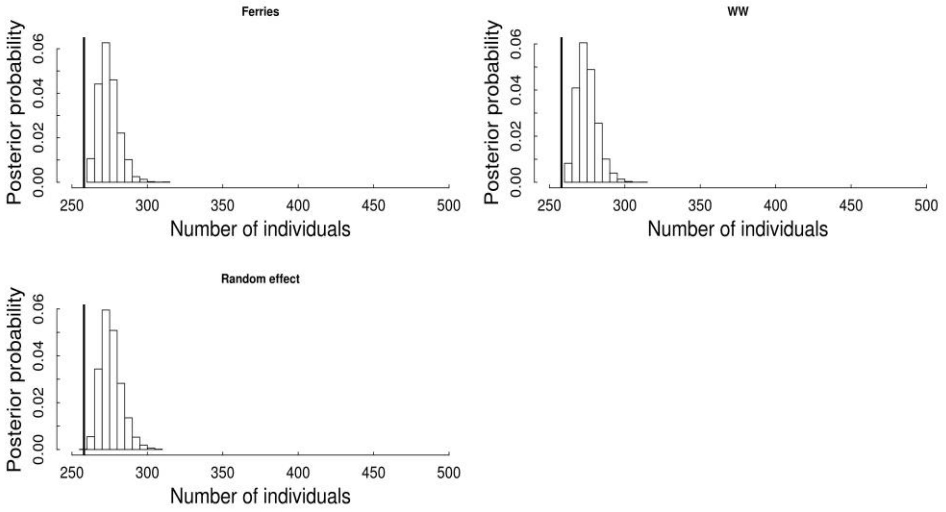

FIG.15. Posterior distribution of the superpopulation size N^s estimated using the different models with a logit-linear effect of the number of ferries ("Ferries") or whale-watching boats ("WW") on survival probability, or with a temporal random effect on survival ("Random effect"). The thick vertical lines indicate the observed number of individuals (n).

Impact of vessel traffic on survival

The effect of vessel traffic was measured on survival probability by separately modelling the demographic rate as a function of the number of ferry boats ("Ferries") and whale-watching boats ("WW"): $\text{logit}(\varphi_{i,t}) = \mu_\varphi + \beta_{\varphi,\text{traffic}}\ \text{traffic}_{i,t}$, where "traffic" indicates either "Ferries" or "WW" at year t. Both variables were not included in the linear predictor for survival in order to avoid collinearity (Pearson correlation; $r = 0.69$). In addition, the proportion of variance explained by the two covariates was derived, as $R^2_{var} = (\sigma^2_{\varphi,\text{tot}} - \sigma^2_{\varphi,\text{traffic}}) / \sigma^2_{\varphi,\text{tot}}$ (Grosbois et al., 2008). Total temporal variance ($\sigma^2_{\varphi,\text{tot}}$) was estimated from a model with survival characterized by a stochastic variation over years around the mean, i.e. $\text{logit}(\varphi_{i,t}) = \mu_\varphi + \varepsilon_{\varphi,t}$ where $\varepsilon_{\varphi,t} \sim \text{Normal}(0, \sigma^2_{\varphi,\text{tot}})$, whereas the unexplained temporal variance ($\sigma^2_{\varphi,\text{traffic}}$) was estimated from a model with the covariate effect and additional random time variation, i.e. $\text{logit}(\varphi_{i,t}) = \mu_\varphi + \beta_{\varphi,\text{traffic}}\ \text{traffic}_{i,t} + \varepsilon_{\varphi,t}$ where $\varepsilon_{\varphi,t} \sim \text{Normal}(0, \sigma^2_{\varphi,\text{traffic}})$.

Detectability was estimated by accounting for sampling effort in each year ("effort_t", expressed as fin images analysed in Q1 and Q2 per year, from May to August) and individual capture heterogeneity: $\text{logit}(p_{i,t}) = \mu_p + \beta_{p,\text{effort}}\ \text{effort}_t + \varepsilon_{p,i}$ where $\varepsilon_{p,i} \sim \text{Normal}(0, \sigma^2_p)$.

4.3 Results

A total of 33,552 photographs were collected between 2002 and 2009. From these, 27,147 photographs were deemed to be usable for individual identification and a total of 400 individuals were identified and catalogued. After quality and distinctiveness criteria and the sampling period (from May to August) were applied, 17,121 photographs and 258 individuals were included in analyses. The median number of survey days each year was 13.5 (range: 5-25), and the median number of dolphin sightings each year was 19 (range: 7-43). On average, individuals were seen between 2.2 (SD: 1.3) and 32.5 times (SD: 22.1) during the study period, while the number of times an individual was seen in a single season ranged between 1 and 130 times. From the 258 individuals identified, 50 of them (19%) were seen in only one year, and a median of 147 individuals were seen in each year (range: 45-185).

Mean apparent survival probability (φ) ranged from 0.918 and 0.924 in both models (supporting information Table 7), and apparent survival probability was, on average, negatively correlated with the number of ferries, β_φ = -0.492, (-1.480, 0.339) (Table 7, Figure 16a). A weaker negative effect on apparent survival was also detected in relation to the number of whale-watching boats, β_φ = -0.273 (-1.750, 1.368), with a larger portion of the 95% CRI > 0 reflecting a larger uncertainty (supporting information Table 7). Although 95% CRI for the slope estimates encompassed zero for both traffic covariates, the linear effect of the number of ferries accounted for more than 70% of temporal variation in survival, whereas almost no temporal variance was explained by the number of whale-watching boats. This indicates a moderate effect of the number of ferries on local survival. Detection probability ranged from 0.724 to 0.725 in both models (Table 7, Figure 16b). The probability of a negative effect of the number of ferries on survival ($Pr\ (\beta_\varphi < 0)$) was 0.93, whereas those of whale-watching boats was 0.74.

Population size ranged from a minimum of 123 individuals (range: 98 - 158) in 2002, to a maximum of 234 individuals (range: 207 – 265) in 2005 (median and 95% CRI; Figure 4a). Local per-capita recruitment was lowest in 2009 (0.006, 0.000-0.018; mean and 95% CRI) and highest in 2004 (0.361, 0.259-0.448; Table 7, Fig. 16b).

TABLE 7. Posterior estimates (mean, standard deviation, and percentiles) for demographic parameters of bottlenose dolphins at Gibraltar Strait obtained for the two models with different covariates for boat traffic (number of ferries, “Ferries”, or whale-watching boats, “WW”). Mean survival ($\bar{\phi}$) and detection ($\bar{p}$) probabilities are given on probability scale, i.e., $\bar{\phi} = expit(\mu_\phi)$ and $\bar{p} = expit(\mu_p)$ where *expit* is the inverse-logit function. The related βs and σs are on logit scale.

				Quantiles		
Model		Estimated Mean	SD	0.025	0.500	0.975
Ferries	$\bar{\phi}$	0.924	0.050	0.806	0.933	0.967
	β_ϕ	-0.492	0.485	-1.480	-0.467	0.339
	σ_ϕ	0.835	0.991	0.036	0.555	3.529
	$\bar{p}$	0.725	0.034	0.652	0.727	0.785
	β_p	1.232	0.175	0.898	1.228	1.579
	σ_p	1.089	0.243	0.583	1.103	1.543
WW	$\bar{\phi}$	0.918	0.065	0.717	0.935	0.975
	β_ϕ	-0.273	0.817	-1.750	-0.312	1.368
	σ_ϕ	1.279	1.253	0.120	0.911	5.055
	$\bar{p}$	0.724	0.034	0.655	0.726	0.783
	β_p	1.241	0.175	0.902	1.239	1.588
	σ_p	1.102	0.236	0.616	1.112	1.551

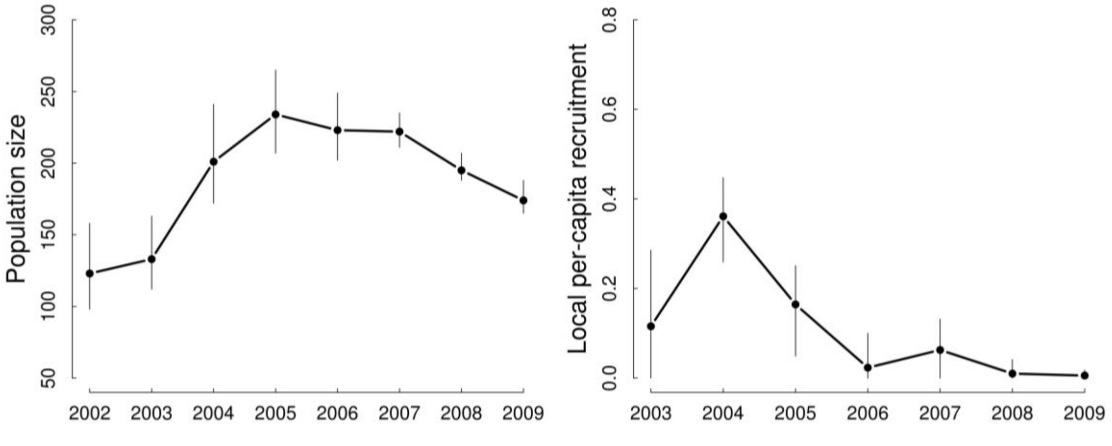

FIG.16. Posterior medians of population size (a) and per-capita recruitment (b) over the years of the study bottlenose dolphin population at Gibraltar Strait. The vertical lines indicate the 95% credible interval for the estimates.

4.4 Discussion

Most studies that have evaluated the impact of boat presence on cetaceans have focused on the behavioural responses of individuals within their study population. These studies have found that boats do impact individuals (Pirotta, Merchant, Thompson, Barton, & Lusseau, 2015), although the behavioural response varies with the number, type, and distance of boats to individuals, as well as the type of approach by the boat (Hodgson & Marsh, 2007; Lemon, Lynch, Cato, & Harcourt, 2006; Lundquist et al., 2013; Williams, Bain, Smith, & Lusseau, 2009; Williams, Trites, & Bain, 2002) and the activity state of the individuals during the interaction (Silvana Laura Dans, Degrati, Pedraza, & Crespo, 2012). Examples of behavioural response include a decrease in resting activity (Constantine et al. 2004; Lusseau, 2003) and either a disruption or total cessation of foraging activity (Li, Monclús, Maul, Jiang, & Blumstein, 2011; New et al., 2013), likely resulting in reduced foraging success and a negative impact on energy budget (Coscarella, Dans, Crespo, & Pedraza, 2003; Silvana L Dans, Crespo, Pedraza, Degrati, & Garaffo, 2008). There is an increased awareness about the cumulative exposure of cetaceans to non-lethal disturbances (Christiansen, Bertulli, Rasmussen, & Lusseau, 2015; Christiansen & Lusseau, 2015). The extra demand of energy caused by a response to boat traffic has been suggested to negatively impact the fitness of cetaceans and explain a decline in their vital rates (Pirotta et al., 2015) and population status.

In the present study, a moderate, negative correlation of ferry traffic was detected on the apparent survival of a local bottlenose dolphin population, whereas the effect of whale-watching boats was almost negligible. Whale-watching companies follow different guidelines (e.g., IWC, 1996), and the Spanish Royal Decree on the protection of cetaceans, which has been in effect since 2007, aims to reduce potential disturbance effects of boat presence on cetaceans, including maintaining a “safe” distance from all individuals (i.e., an approach distance of 500m, a restricted distance of 300m and an exclusion zone of 60m). In contrast, maritime traffic, including ferries, do not keep a safe distance, decrease speed or change the trajectory of the boat, which increases the probability of disturbance to and collisions with dolphins (Todd et al., 2014; Van Waerebeek et al., 2007). This is especially true for fast ferries which transit the Strait at high speed (ca. 30 knots). The documented increase in vessel traffic likely decreased quality habitat and the observed decline in population size, survival and reproductive output may be the result of some individuals permanently emigrating from the Strait to a less disturbed habitat, although data on this potential dispersal process are lack.

To our knowledge, this is the first study that has quantified a correlation between ferry traffic and local apparent survival, per-capita recruitment and population size of a cetacean population. The results show that an increase in ferry traffic in the area correlates with a decrease in the apparent survival of bottlenose dolphins in one of the most navigated marine regions of the world. The most plausible explanation of the lower survival with increased ferry traffic was dispersal to less impacted areas, although fatal casualties with ferries cannot be totally disregarded. For conservation purposes, it is important to assess if there is available habitat of the same quality in close areas where dolphins can avoid the impact of ferries. Since management actions such as stopping ferry traffic is not possible, detecting areas of suitable habitat quality in the nearby and protect them may be an alternative conservation measure to protect dolphins from that impact. The study highlights the need to implement specific management actions that focus on the potential impacts of vessel traffic on cetacean populations, as well as future research focus to deep and evaluate the impact of anthropogenic disturbances on cetacean populations.

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III

EPÍLOGO

Discusion General

Edad

Uno de los principales objetivos de la tesis era conocer si en animales marinos longevos, en concreto especies que están situadas en niveles superiores de la cadena trófica, la edad ejercía un papel significativo en reproducción y supervivencia. En el caso de encontrar un efecto de la edad, conocer que patrón mostraban y si este variaba ante diferentes tipos de fluctuaciones ambientales. Los resultados encontrados proporcionan un soporte concluyente de que la edad desempeña un papel clave en los diferentes parámetros demográficos. A excepción del trabajo realizado con delfines mulares (*Tursiops truncatus*), donde no fue posible analizar la edad debido a una falta de datos, en el resto de trabajos realizados con aves marinas *(Ichthyaetus audouinii, Calonectris diomedea e Hidrobates pelagicus melitensis)* encontramos una fuerte evidencia de que la edad siempre ejerce un papel fundamental en los diferentes parámetros estudiados.

Todos los resultados obtenidos mostraron un incremento de la capacidad reproductora con la edad hasta alcanzar valores máximos en edades intermedias. En los estudios realizados con la gaviota de audouin y el paíño europeo, no sólo encontramos una mejora progresiva en las primeras clases de edad, sino también una disminución en los últimos años de vida, observándose un patrón cuadrático en forma de U inversa, ocasionado por la senescencia (Monaghan et al., 2008; Nussey et al., 2008; Nussey et al., 2013; Rebke et al., 2010; Reed et al., 2008; Zhang et al., 2015). Estas variaciones específicas de la edad pueden responder a diferentes causas e hipótesis (selección, limitación, restricción y senescencia) no excluyentes entre sí.

De acuerdo a la hipótesis de selección (Curio, 1983; Forslund y Part, 1995); estas diferencias encontradas entre individuos de distintas edades podrían explicarse mediante una desaparición de fenotipos de baja calidad, que originaría una selección progresiva de animales de mayor calidad con la edad. Según la hipótesis de restricción y limitación (Curio, 1983), las diferencias encontradas entre los reproductores pueden atribuirse a la adquisición de habilidades y experiencia con los años (Desrochers, 1992; Limmer y Becker, 2010; Sanz-Aguilar et al. 2008; Tavecchia et al., 2001; Weimerskirch, 1992). Ciertas habilidades de los individuos se van adquiriendo con la edad, como el conocimiento de los predadores, competidores, parejas, territorios y rutas migratorias (Greenwood y Harvey, 1982). Además de la experiencia adquirida con los años, estudios de procesos dispersivos exponen que en numerosas especies las aves jóvenes quedan relegadas a los peores territorios, y con la edad se establecen en otros lugares de mayor calidad (Greenwood y Harvey, 1982). Otra explicación es que los individuos pueden llevar a cabo una táctica de compensación entre reproducción y supervivencia (Curio, 1983). Debido al elevado coste que tiene la reproducción, algunos individuos decidirían no invertir en reproducción para no perjudicar su supervivencia futura (Erikstad et al., 1998; Sanz-Aguilar et al., 2017; Sergio et al., 2014; Tavecchia et al., 2001). Por el contrario, la disminución en la tasa reproductiva con la edad no es posible distinguir si es debido a un descenso en la capacidad reproductora o es debido a un incremento progresivo de la tasa de mortalidad (Flatt, 2012). Hay que destacar que una limitación en el tamaño muestral de las últimas clases de edad podría dificultar encontrar un patrón cuadrático que indique senescencia. Aspecto relevante a considerar en el estudio con pardela cenicienta y el paíño europeo en el análisis de supervivencia. En estos estudios el tamaño muestral en las últimas clases de edad era muy pequeño y podría haber limitado encontrar un claro efecto de senescencia en ambas especies. Especialmente en el caso del paíño europeo, donde en el éxito reproductor si se encontró un patrón cuadrático marcado, pero en supervivencia el patrón encontrado fue una curva logarítmica cuadrada con un descenso muy sutil. Estos resultados deben ser interpretados con cautela, ya que no puede descartarse un efecto de senescencia en ambas especies de estudio, efecto encontrado en diferentes estudios con aves marinas tanto en reproducción como en supervivencia (Berman et al., 2009; Kim et al., 2011; Nussey et al., 2008; Rebke et al., 2010; Reed et al., 2008; Weimerskirch et al., 2005).

Estocasticidad Ambiental

Aunque a lo largo de la tesis se han obtenidos diferentes resultados respecto a las condiciones ambientales, queda demostrado el efecto que tiene la estocasticidad ambiental en la demografía de depredadores marinos apicales.

Los resultados encontrados demuestran que las fluctuaciones en los recursos pueden ser un factor crítico a la hora de determinar el éxito reproductor de los individuos (Cairns, 1988; Oro, 1999) siendo la disponibilidad de alimento el factor que probablemente proporcione un mayor límite del número total de aves marinas que se reproducen (Croxall y Rothery, 1991; Furness y Birkhead, 1984; Lewis et al., 2001). Estos resultados coinciden con hallazgos encontrados en estudios previos (Erikstad et al., 1998; Rindorf et al., 2000; Vincenzi et al., 2013) donde obtuvieron que el éxito reproductor de las aves marinas dependía de la disponibilidad de alimento, por ejemplo debido a una disminución de las presas por la pesca (Furness, 2002, 2003; Tasker et al., 2000) o por subsidios alimentarios de origen antropogénico (Bicknell et al. 2013; Oro et al., 2013; Votier et al., 2004) podría afectar al rendimiento reproductivo de las aves. Resultados acordes a los obtenidos en el trabajo realizado con la gaviota de Audouin, donde la disponibilidad de alimento procedente de los descartes pesqueros es una importante fuente de alimento que influencia los diferentes parámetros reproductores (Oro et al., 2004; Oro et al., 1996; Soriano-Redondo et al., 2016). En animales de vida larga, como son las especies estudiadas en esta tesis, normalmente la época de reproducción es el ciclo de vida energéticamente más exigente (Williams, 1966) y un resultado exitoso dependerá en gran medida de la disponibilidad y calidad de alimento en las primeras etapas de la reproducción (Martin, 1987; Oro, 1996; Wanless et al., 2005). Estos resultados, reflejan no sólo la necesidad de testar fluctuaciones ambientales, sino también de considerar las interacciones que presentan estos animales con la pesca y otras actividades antropogénicas.

Un aspecto adicional a considerar, es que bajo condiciones de reducida disponibilidad de alimento los reproductores presentan mayor dificultad para encontrar suficiente alimento para ellos y su descendencia, así que necesitan invertir más tiempo en su búsqueda. Como consecuencia de incrementar el esfuerzo de forrajeo, necesitan una mayor demanda energética y por tanto realizar un mayor esfuerzo. Esto puede tener consecuencias a nivel fisiológico del reproductor y también problemas con escasez de alimento para sacar adelante la descendencia (Navarro y González-Solís, 2007; Ricklefs, 1983; Weimerskirch et al., 1994).

En los estudios realizados con pardela cenicienta y el paíño europeo, a diferencia del trabajo realizado con la gaviota de audouin, encontramos un efecto temporal en los parámetros reproductores. Ninguna de las covariables testadas como indicador ambiental explicaba satisfactoriamente la variabilidad en los parámetros de estudio. Contrario a lo esperado, tampoco encontramos ningún efecto debido a fluctuaciones ambientales en el estudio de la supervivencia del paíño europeo. A pesar de no encontrar un indicador local o índice climático que explique gran variabilidad en la reproducción de estas dos especies, en el caso de la pardela cenicienta encontramos una asociación estadísticamente significativa, donde el índice NAO explicaba cerca de un 24% de la varianza en la fecha de puesta, mientras que el índice SOI lo hacía en un 20% para el volumen del huevo. Existen varias explicaciones posibles para estos resultados. Una de ellas radica en la dificultad de conocer bien como afectan los procesos oceanográficos a nivel biológico. Se conoce que la oceanografía tiene un gran impacto en la distribución de la vida marina (Mann y Lazier, 2013; Stenseth et al., 2002), pero se requiere de una alta comprensión en las interacciones que ocurren en el medio marino (Winder & Schindler, 2004), a grande y pequeña escala, para poder comprender adecuadamente como las condiciones físicas influencian la producción primaria y esta a su vez la disponibilidad de alimento (Durant et al., 2007). Durante el afloramiento primaveral, la producción primaria proporciona alimento a las poblaciones de zooplancton (Howarth, 1988) que son la principal fuente de alimento de pequeños pelágicos y estos a su vez de las aves marinas de nuestro estudio. No obstante, el tiempo, la duración y magnitud de la floración son factores potencialmente importantes para poder determinar la disponibilidad final de alimento (Platt et al., 2003; Sommer y Lengfellner, 2008). Por ejemplo, en el caso del paíño resulta muy difícil conocer la disponibilidad de alimento a la que podrán tener acceso los individuos. El paíño se alimenta de larvas de peces, pero una vez que eclosionan los huevos, las larvas pueden moverse por advección hacia otros lugares, variable en el espacio-tiempo, dependiendo de la velocidad y dirección del viento, así como la rapidez con que las larvas alcanzan la capacidad de hacer migraciones verticales (Cury y Roy, 1989; Scheltema, 1986). Además, se conoce que pequeñas fluctuaciones en el medio marino pueden originar grandes cambios, incluso a largo plazo sobre la cadena trófica (ver Durant et al. 2004) pero estos cambios resultan muy difíciles de predecir y evaluar con exactitud, lo que hace especialmente sensibles a determinadas especies marinas. A pesar de todas estas dificultades, varios estudios han demostrado que el índice NAO puede explicar la variación en algunas variables ecológicas en ciertas especies (Sandvik et al., 2012).

Además de los fenómenos ocasionados por índices climáticos de larga escala, procesos oceanográficos locales pueden producir cambios en la temperatura del agua y las corrientes marinas, generando variaciones espacio-temporales en la producción, distribución y abundancia de los recursos tróficos disponibles para los depredadores (Bellido et al., 2008; Durant, 2004; Lloret, et al., 2004). Adicionalmente, la escorrentía de ríos y actividades antropogénicas, como pesquerías y contaminación también pueden causar efectos sobre la disponibilidad de alimento en el mar, haciendo que varíe de manera irregular e imprevisible. Las complejas interacciones ecológicas que pueden ocurrir entre las poblaciones de peces a través de la competencia y por medio de las relaciones depredador-presa hacen que la predicción de la disponibilidad de alimento para nuestras especies de estudio sea difícil de cuantificar (Bascompte et al., 2005; Bruno y O'Connor, 2005; Hixon y Jones, 2005). Estas variaciones hidrográficas, pesqueras y oceanográficas pueden impulsar también agregaciones y/o migraciones de especies pelágicas (ver Cury et al., 2000; Lloret et al., 2001) que son presa para las aves reproductoras. Como consecuencia, estos procesos podrían afectar el forrajeo de las aves marinas (Navarro y Gonzalez-Solís, 2009; Weimerskirch et al., 2012) e influenciar su supervivencia, reprodución, así como la dinámica de la población (Genovart et al., 2013; Jenouvrieret al., 2005). En el caso de la gaviota de audouin se testaron directamente los descartes, ya que se conoce que las gaviotas aprovechan el pescado que se tira por la borda para alimentarse (Oro et al., 1996). En el caso de la pardela cenicienta también se testaron los descartes, pero no fue un buen indicador de la disponibilidad de alimento, posiblemente otras condiciones locales estén influenciando más a las pardelas cenicientas de la Isla de Pantaleu. En el caso del paiño europeo, testamos la temperatura superficial del agua de mar (SST) en el mar de Alborán, ya que estudios previos con paiño (Soldatini et al., 2014) comunicaban el Mar de Alborán como potencial área de invernada. En nuestro caso no encontramos un efecto de SST ni en reproducción, ni supervivencia, pero una posible explicación es que los individuos de nuestra población tengan otra área de invernada y sean diferentes índices climáticos y/o condiciones ambientales las que tengan un efecto sobre sus historias de vida (ver Ramírez et al., 2016). No obstante, es necesario considerar que no sólo la temperatura superficial del agua de mar explica el pico de abundancia de pequeñas larvas de peces. Una zona puede tener aguas no muy frías, pero si hay una elevada productividad primaria las larvas de peces sobrevivirían bien. En casos como el Mar de Alborán, donde se producen afloramientos, tendría sentido que condiciones de baja SST no esté asociado a una baja disponibilidad de alimento para el paiño. Otro posible motivo de porque no encontramos un índice climático, que explique gran variabilidad en el paiño europeo y la pardela cenicienta, es que testamos el índice NAO como índice local para testar las condiciones ambientales del noroeste mediterráneo, mientras que hay estudios (Gonzalez-Hidalgo et al., 2009) que confirman que es más apropiado testar el Índice de Oscilación del Mediterráneo Oeste (WeMO) (ver limitaciones) antes que NAO para esta zona (Gonzalez-Hidalgo et al., 2009). Esta explicación concuerda con resultados obtenidos en estudios de pequeños pelágicos, donde encuentran una correlación significativa entre el índice WeMO y las capturas de sardina y anchoa en el oeste mediterráneo (Martín et al. 2012). Esto muestra la dificultad de encontrar una sola variable local, o global, que pueda explicar un mayor porcentaje de variabilidad en el éxito reproductor que el efecto temporal.

A la dificultad que conlleva seleccionar un índice climático como indicador de las condiciones ambientales, hay que tener en cuenta que es muy importante tener una base de datos muy potente para poder analizar algunos modelos y más trabajando con individuos de edad conocida. Esto es otra de los posibles motivos en la diferencia de resultados encontrados entre las poblaciones estudiadas en la presente tesis. La base de datos de la población de audouin era mucho más potente que las otras, lo que permitió poder analizar los modelos con más detalle y robustez.

Fluctuaciones por acción antropogénica

La estocasticidad ambiental puede ser crucial para que un individuo se reproduzca y sobreviva con éxito, pero son las perturbaciones humanas y la degradación del hábitat las principales amenazas en la dinámica de una población (IUCN 2015). Causa más frecuente por la cual una especie entra en la categoría de amenazada (Hoffmann, 2010; Myers et al., 2000; Pimm y Raven, 2000).

En el caso de las aves marinas, según la IUCN, las principales amenazas antropogénicas actuales en el mar son las pesquerías comerciales (Pauly et al., 2002) y la contaminación por derrames de petróleo (Kingston, 2002), plásticos (Derraik, 2002) y en general desechos marinos (Laist, 1997), mientras que en tierra la mayor amenaza es la depredación por invasores (Croxall et al., 2012). La explotación pesquera puede suponer una competencia para las aves marinas (Furness, 1982), aunque actualmente es de mayor preocupación su muerte a través de capturas accidentales en pesquerías de palangre y redes de enmalle (Croxall et al., 2012; Lewison et al., 2014). Sin embargo, por otro lado, los descartes procedentes de este tipo de pesquerías suponen un importante recurso para algunas poblaciones de aves marinas (Arcos y Oro, 2002; Bartumeus et al., 2010; Bicknell et al., 2013; Garthe et al., 1996; Votier et al., 2004); entre las que se encuentran las poblaciones estudiadas de audouin y pardela cenicienta. No obstante, hay estudios que demuestran que las aves marinas prefieren capturar presas de forma natural y recurren a los descartes sólo cuando sus principales presas escasean (Tew Kai et al., 2013).

En el caso de los delfines que viven en zonas costeras, están expuestos a una gran variedad de amenazas, entre las de mayor preocupación se encuentra la exposición a tóxicos de químicos xenobióticos (ej. PCBs), reducción de la disponibilidad de presas causada por la degradación ambiental y la sobrepesca (Jackson et al., 2001), construcción/demolición de infraestructuras marinas, destrucción y degradación del hábitat, incluido el ruido antropogénico y hostigamiento directo e indirecto (ej. tráfico marítimo y actividades comerciales de observación y/o interacción con cetáceos) (ver IUCN 2015). Estas amenazas son técnicamente difíciles de cuantificar y su impacto acumulativo es probable que origine declives de la población. No obstante, son varias las amenazas que pueden estar derivando del tráfico marítimo: con el aumento del número de barcos, incrementa el ruido acústico por debajo de la superficie del mar, lo que puede potencialmente reducir la comunicación entre los delfines (Codarin et al., 2009) y afectar a su comportamiento, incluyendo la capacidad de forrajeo (Todd et al., 2014; Wright et al., 2007) y aumentando la posibilidad de enfermar (Perrings et al., 2009). Hay estudios que afirman que un incremento del ruido puede afectar también a la presa de los delfines, como son los cefalópodos (Mooney et al., 2010) lo que puede ocasionar una migración permanente de los delfines en búsqueda de comida a otras áreas (Rako et al., 2013). Por otro lado, la creación del nuevo puerto Tanger Med implicó la realización de dragados y otras actividades que podrían haber incrementado la contaminación, afectando a la salud y fisiología de los delfines (ver Todd et al., 2014). La falta de datos históricos ha dificultado la comprensión de las tendencias a largo plazo de la población, por lo que la contribución de nuestro estudio en delfines mulares supone un punto de partida y una información muy valiosa para el estudio de factores antropogénicos sobre la supervivencia de delfines mulares.

Interacción entre edad y estocasticidad ambiental

Otro de los principales objetivos de la tesis era analizar en detalle la interacción entre las condiciones ambientales y el patrón de edad específico encontrado en cada especie. En el caso de la gaviota de audouin y la pardela cenicienta se encontró que la capacidad reproductora no sólo depende de la edad de los individuos y las condiciones ambientales, sino que dicho patrón puede variar ante las diferentes condiciones ambientales.

En el estudio de la gaviota de Audouin, contrario a lo que esperábamos, se encontró que el patrón de la edad era más marcado bajo un escenario de óptimas condiciones ambientales que ante condiciones adversas, es decir, en años de malas condiciones ambientales las diferencias encontradas entre individuos de distintas edades eran menores que en años con buenas condiciones. Los resultados muestran que ante condiciones desfavorables, sólo los individuos que poseen una buena condición corporal y/o presentan una mayor calidad intrínseca deciden reproducirse (Cubaynes et al. 2011; Jenouvrier, 2013). Estos resultados son acordes a investigaciones previas, donde exponen que algunos individuos no se reproducen en años donde la disponibilidad de presas es baja (Monaghan, 1992; Navarro y González-Solís, 2007). Esto podría explicarse por la compensación entre reproducción y supervivencia, donde individuos de peor calidad fenotípica o con menos habilidades de forrajeo evitarían llevar a cabo la reproducción para no perjudicar su supervivencia futura, mientras que otros individuos ajustarían la búsqueda de alimento y/o cambiarían de presa (Martin, 1989) mostrando una mayor calidad individual.

En el análisis de la gaviota de audouin, al disponer de una base de datos potente se pudo realizar un análisis de heterocedasticidad de los datos analizando la edad. Bajo nuestro conocimiento, este tipo de análisis sólo ha sido realizado anteriormente por Pardo et al. (2013). Obtuvimos que las varianzas de los parámetros estudiados cambian con la edad, siendo mayor en individuos jóvenes y disminuyendo según envejecen los reproductores. Estos resultados muestran que existe una heterogeneidad entre las clases de edad (Barbraud y Weimerskirch, 2005; Cam y Monnat, 2000; Oro et al., 2010; Pardo et al., 2013), sugiriendo que ocurre un proceso de selección de individuos de mayor calidad (Nevoux et al., 2007; Rebke et al., 2010; Sanz-Aguilar et al., 2008) donde sus diferencias, en la capacidad de reproducirse, disminuyen progresivamente con la edad.

En Pardela Cenicienta, debido a una falta de potencia, no fue posible analizar la heterocedasticidad de los datos cómo se realizó en audouin, pero encontramos igualmente un fuerte efecto de la calidad individual en la reproducción (el factor individuo explicaba un 25% de la variabilidad). Lo mismo con Paiño europeo, donde no se encontró interacción entre el patrón de la edad y los índices testados, pero si se observó que el éxito reproductor no sólo venía determinado por el patrón cuadrático de la edad, sino que además influía el año y la edad de reclutamiento. Aquellos individuos que habían reclutado antes en la población tenían un mayor éxito reproductor en comparación con individuos de la misma edad. A pesar de no encontrar un efecto individual en supervivencia, sí que encontramos dicho efecto en la probabilidad de recaptura de los individuos.

En el estudio de delfines mulares no se pudo analizar el efecto de la edad, pero se realizaron análisis teniendo en cuenta diferentes niveles de marcaje de los individuos (ver apéndice D) y se obtuvo que la fracción estimada de la varianza temporal, en supervivencia, era mayor cuando se analizaban todos los individuos marcados que cuando se excluían del análisis los individuos poco marcados (marcas de nivel 1) (ver apéndice D). Una posible explicación sería debido a la pérdida y adquisición de nuevas marcas durante el periodo de estudio. Pero otra posible explicación, hipótesis especulativa, sería debido a que el efecto del tráfico marítimo tiene un mayor efecto sobre individuos jóvenes y crías que adultos. Los individuos poco marcados (M1: micromarcas) son la gran mayoría animales de menor edad, ya que los delfines adquieren marcas con el paso de los años, por lo tanto, estos resultados podrían indicar que ante condiciones desfavorables los efectos del tráfico marítimo serían mayores en juveniles y crías que en adultos. Hay estudios que demuestran que las hembras con crías son más sensibles a la interacción con barcos en comparación al resto de la población (Stamation et al. 2010; Stensland y Berggren, 2007), lo que explicaría que un elevado número de delfines pudiesen estar emigrando del Estrecho a otros hábitats más prístinos.

En el inicio de la tesis, estudiar la calidad individual de los individuos no era uno de los objetivos, pero al estudiar el patrón de la edad en interacción con las condiciones ambientales surgieron estos hallazgos que muestran que existen variaciones específicas incluso entre individuos de la misma edad y que pueden ser significativas en la demografía de una población.

Depredadores marinos apicales

De forma general, el número de animales en una población natural puede ser limitada de tres maneras (Andrewartha y Birch, 1954 y 1986): (1) por limitación de los recursos disponibles, como alimentos o sitios para reproducirse; (2) inaccesibilidad a esos recursos debido a las capacidades de los individuos para dispersar y buscarlos; (3) por fluctuaciones en la tasa de incremento poblacional, causadas por el tiempo, depredadores o cualquier otro componente medioambiental. Teniendo en cuenta estas limitaciones y que el hábitat es un medio en constante cambio, comprender la demografía de poblaciones situadas en los niveles tróficos superiores es una información muy valiosa y necesaria para poder conocer un ecosistema y realizar medidas de gestión en el caso de que sean necesarias. Debido a las limitaciones comentadas anteriormente, un gran aumento o disminución de una especie tendrá un efecto cascada sobre otras especies situadas en diferentes niveles, pudiendo llegar a ocasionar una importante pérdida de biodiversidad en algunos ecosistemas (ver Camphuysen, 2006; Sergio et al., 2006).

Los estudios en depredadores marinos apicales, además de ser útiles para su conservación, también pueden usarse como bioindicadores del sistema marino, mejorando la comprensión de los efectos biológicos ante cambios oceanográficos y anticipar cambios en la dinámica de la cadena alimentaria (Camphuysen, 2006; Wanless et al., 2007). Las especies de estudio en esta tesis son consideradas especies paraguas, mediante su conservación y gestión del ecosistema que habitan también se protegen otras especies marinas que pueden tener problemas de conservación. Además, algunas de ellas son consideradas especies carismáticas (especies bandera), que a menudo sirven para conseguir apoyo financiero e implementar programas de conservación y/o fomentar la conciencia ambiental, incluso se puede conseguir proteger áreas donde habitan (ver Sergio et al., 2005).

Según importantes estudios con depredadores apicales (Sergio et al., 2005), los sitios habitados por estos animales están constantemente asociados con una alta biodiversidad, en comparación con sitios seleccionados al azar o sitios habitados por especies situadas en niveles inferiores de la pirámide trófica. Sus resultados indican que la conservación centrada en los depredadores superiores puede ser justificada desde un punto de vista ecológico y que ofrece beneficios más amplios para la biodiversidad.

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Futuras líneas de investigación

- Algunos de los resultados encontrados generaron más preguntas y futuras oportunidades de investigación. No obstante, se requiere seguir continuando con los seguimientos de las poblaciones de estudio y aumentar el número de individuos de edad conocida para confirmar los resultados y patrones encontrados, realizar modelos que requieren de una mayor potencia de datos y poder abordar nuevas investigaciones con mayor número de individuos, especialmente seniles, así como testar la interacción de la edad con diferentes tipos de variables ambientales y antropogénicas.

- En muchas especies de aves marinas se han podido marcar los individuos con diferentes tipos de emisores y conocer sus rutas migratorias, pero en el caso del paíño europeo su peso corporal (~26gr) no permite marcarlo con ciertos emisores y obtener este tipo de información. Esta limitación impide, a día de hoy, conocer sus áreas de invernada y comprender qué condiciones ambientales pueden estar afectando a la población. Se necesita que la tecnología avance lo suficiente para poder incorporar emisores al paíño europeo, así como investigar nuevas variables y posibles áreas donde podrían migrar los individuos de la colonia de Benidorm. De este modo conseguiríamos testar índices climáticos y variables oceanográficas más adecuadas para el estudio de sus parámetros demográficos, especialmente supervivencia.

- Una de las mayores limitaciones en la presente tesis fue realizar un estudio de la edad en delfines mulares. Por lo que futuras investigaciones deberían encaminarse a intentar solucionar este problema y analizar si ante diferentes tipos de fluctuaciones los individuos jóvenes y adultos muestran diferencias en su reproducción y supervivencia, así como evaluar diferentes variables que puedan influenciar en su dinámica poblacional como son las condiciones oceanográficas que suceden en el Estrecho de Gibraltar: afloramientos, anomalías de la temperatura superficial del agua de mar y otros indicadores de las condiciones ambientales del hábitat.

- En aves marinas, algunos de los resultados obtenidos indican que podría estar ocurriendo una estrategia de optimización entre el esfuerzo reproductor y la supervivencia, por lo que se sugiere estudiar en detalle la compensación entre reproducción y supervivencia de las especies que no ha sido estudiando antes y considerar la edad de los individuos y fluctuaciones ambientales del medio. Para ello, como se comentó anteriormente, se requiere de un número muy elevado de datos.

- Por último, una futura línea de investigación sería realizar un estudio de heterocedasticidad de los datos en individuos de edad conocida, del paíño europeo y pardela cenicienta, así como modelos de reproducción y supervivencia usando el Índice de Oscilación del Oeste Mediterráneo (WeMO). Índice poco estudiado en la actualidad, pero con estudios relevantes que indican que es mejor indicador de la disponibilidad de pequeños pelágicos en el Mediterráneo que el Índice Oscilación del Atlántico Norte (NAO).

Conclusiones

1) A lo largo de esta tesis se demuestra la importancia de conseguir datos individuales que permitan estimar diferentes parámetros demográficos y responder a preguntas de ecología poblacional. La escala espacio-temporal a la que se trabaja en dinámica de poblaciones, así como las limitaciones encontradas, resaltan la importancia de realizar estudios a largo plazo de manera continuada y conseguir un gran número de datos de la mayor calidad posible. Esto permitirá realizar modelos complejos y responder a las preguntas planteadas evitando problemas analíticos y de fiabilidad.

2) Debido a las diferentes estrategias de vida que presentan cada especie, se enfatiza en conseguir y utilizar datos individuales de edad conocida. Con estos datos se podrá estudiar en detalle el patrón específico y saber cómo se comportan los individuos durante diferentes fases de su vida. Es de especial interés estudiar si existe un mecanismo de senescencia, como se detectó en la gaviota de audouin y el paíño europeo, y conocer a partir de que edades puede aparecer.

3) Los resultados obtenidos demuestran que la estocasticidad ambiental del medio, producida tanto por causas naturales como perturbaciones de origen antropogénico, tienen un efecto importante sobre la dinámica de las poblaciones. Es necesario, por tanto, comprender que variables pueden estar causando fluctuaciones en el hábitat de cada población y conocer cómo responden los individuos ante las diferentes fuentes de estocasticidad.

4) Uno de los hallazgos más importantes fue la respuesta heterogénea de los individuos ante las distintas condiciones ambientales. En condiciones óptimas se encontró que las diferencias entre individuos de distintas edades eran mayores que ante condiciones ambientales desfavorables, mostrando los individuos una diferente calidad. Estos resultados sugieren que bajo condiciones adversas los individuos de peor calidad optan por no reproducirse para no comprometer su supervivencia futura.

5) Las diferencias de calidad entre individuos podrían enmascarar ciertos patrones de edad, por lo que se llevó a cabo un estudio de heterocedasticidad de los datos, en la gaviota de audouin, para estudiar las varianzas encontradas entre las distintas edades. Se encontró que en individuos jóvenes las varianzas eran mayores que en individuos adultos, siendo estos, en promedio, reproductores de mayor calidad. Estas diferencias pueden explicarse por adquisición de habilidades con los años, experiencia y/o una selección progresiva de individuos de mayor calidad fenotípica. Estos resultados fueron

secundados por la heterogeneidad individual encontrada en la pardela cenicienta y la importancia de la primera edad de reclutamiento en el paíño europeo.

6) Encontramos un claro resultado de las fluctuaciones ambientales testadas como disponibilidad de alimento en el estudio de audouin, mientras que en el estudio con pardela cenicienta y el paíño europeo la variabilidad no fue explicada por los índices climáticos, sino por la variabilidad temporal. No obstante, el Índice de Oscilación Atlántico Norte explicaba un 24% de la fecha de puesta en pardela cenicienta, mientras el Índice de Oscilación Sur lo hacía en un 21% en el volumen del huevo. En el paíño europeo, las diferentes variables testadas no llegaron a explicar más del 12% de variabilidad. A la posible falta de potencia en estos dos últimos estudios, se suma la complejidad de predecir la disponibilidad de alimentos a partir de un índice climático en un sistema tan complejo como es el medio marino.

7) La falta de conocimiento de las áreas de invernada en la población de paíño europeo podría estar dificultando encontrar el efecto de un índice climático adecuado que explique las condiciones ambientales a las que están sometidos los individuos. En futuras líneas de investigación se sugiere profundizar en este tema y poder realizar modelos más adecuados y específicos para la población de paíños de la Isla de Benidorm.

8) La disminución del tamaño de población, reclutamiento y supervivencia de delfines mulares, en el Estrecho de Gibraltar, se correlaciona con la actividad antropogénica ocasionada por el tráfico marítimo debido a los ferries. Los cambios detectados en estos parámetros se correlacionaron con la construcción de un nuevo puerto en la costa marroquí, el cual incrementó un 40% el tráfico de ferries en el Estrecho. La explicación más plausible sugiere que los individuos pueden estar migrando permanentemente a otras áreas más prístinas.

9) Debido al número de datos tan reducido de crías y juveniles de delfines mulares, no fue posible realizar un análisis de la edad. Para poder conseguir una mayor comprensión en las historias de vida de esta especie, se enfatiza la necesidad de seguir realizando monitoreos cada año y disponer de un mayor número de datos para intentar analizar la edad, así como continuar evaluando el efecto del tráfico marítimo con más años de estudio y respaldo analítico.

10) En especies con marcas naturales se recomienda utilizar animales altamente distinguibles, con marcas lo suficientemente grandes o moderadas, para evitar la incertidumbre que puede producirse utilizando datos de individuos levemente marcados.

11) La presente tesis pone de manifiesto la importancia de estudiar la edad en diferentes especies marinas que están influenciados por diferentes fuentes de estocasticidad ambiental u antropogénica, así como las posibles interacciones entre las variables, para comprender bien los rasgos de vida de una especie y poder responder a preguntas de ecología y/o aportar información necesaria para la gestión de su conservación.

IV

MATERIAL SUPLEMENTARIO

APÉNDICE A

CAPÍTULO 1

Table A1. List of published studies in which the association of breeding parameters was tested with age under different environmental conditions (food availability or proxies such as climatic indexes). N/A = not analyzed; FA = food availability.

Laying date	**Clutch size**	**Clutch volume**	**Fertility**	**Hypotheses supported (see Fig. 1)**	**Reference and taxa**
N/A	N/A	N/A	Older birds fledged equivalent numbers of young in both good and moderate years, whereas youngest birds fledged young in good years only. In poor years, few birds of any age attempted to breed and they failed.	c?	Boekelheide and Ainley 1989 (Brandt's Cormorants, *Phalacrocorax penicillatus*)
Differences between young and mature birds were most apparent during years when food availability was reduced	N/A	N/A	Differences between young and mature birds were most apparent during years when food availability was reduced	a	Sydeman et al. 1991 (Western gulls, *Larus occidentalis*)
N/A	N/A	N/A	Differences in reproductive performance with age were not a result of environmental effects	d	Daunt et al. 1999 (Shags, *Phalacrocorax aristotelis*)
No effects	No effects	No effects	Low for all age classes at low FA; increase with age with higher FA; high for all age classes with high FA	a,b?,c	Ratcliffe et al. 1998 (Great skuas, *Stercorarius skua*)
Differences appeared to emerge more clearly in poor/ intermediate food conditions	Differences appeared to emerge more clearly in poor/ intermediate food conditions	N/A	N/A	a	Laaksonen et al. 2002 (Tengmalm’s owls, *Aegolius funereus*)
N/A	N/A	N/A	When food was not limited, both young and experienced parents were equally capable of	a	Bunce et al. 2005

Laying date	Clutch size	Clutch volume	Fertility	Hypotheses supported (see Fig. 1)	Reference and taxa
			rearing chicks and had similar levels of breeding success		(Australasian gannets, *Morus serrator)*
N/A	N/A	N/A	Young adults performed well only when FA was high	a	Ezard et al. 2006 (Common tern, *Sterna hirundo*)
N/A	N/A	N/A	The reproductive success of inexperienced individuals was lower but affected by climatic fluctuations in the same way as the experienced ones	b (but age has only two values)	Nevoux et al. 2007 (Black browed albatross, *Thalassarche melanophrys*)
N/A	Only an effect of age	N/A	Increases with age and similarly under any environmental conditions	d	Vieyra et al. 2009 (Heermann's Gull, *Larus heermanni*)
N/A	N/A	N/A	Similar under environmental stress	b (but age has only two values)	Lee 2011 (Northern elephant seals, *Mirounga angustirostris*)
Older birds bred earlier in years when food availability was greater, but younger birds did not do so	N/A	N/A	N/A	c?	Ramos and Monticelli 2012 (Roseate tern, *Sterna dougallii*)
N/A	N/A	N/A	Only an effect of age	d	Pardo et al. 2012 (Black browed albatross, *Thalassarche melanophrys*)

Table A2. Modeling the effects of age (mean and variances simultaneously) in Audouin's gulls on breeding parameters except for hatching success (see text for explanation). Ages were categorized either with a less constrained distribution (Age A, 6 classes: 3y, 4y, 5y, 6y, 7y-14y, and >14) or with simpler, more constrained age structures (Age B, 4 classes: 3y, 4y-5y, 6y-14y, and >14y; Age C, 3 classes: 3y, 4y-6y, and >6y). Modeling followed the strategy of stepwise forward addition of parameters. We started with the null model with no effects; then single effects were tested and finally interactions between these effects. The finally selected model is shown in bold. "*" denotes interaction between factors and "+" an additive effect between factors. Age^2 indicates a quadratic effect of age on the breeding parameter. Food is the availability of food per capita (see Methods). Only AIC values are shown for simplicity. The finally selected model is in bold.

		Structure of variances							
Parameter	Model	Homoscedasticity of variances	Food	Age A	Age B	Age C	Food*Age A	Food*Age B	Food*Age C
Laying dates									
1	Null	413.177	397.828	365.543	370.569	379.284	363.805	365.992	363.482
2	Food	263.616	251.505	190.316	201.073	206.341	NA	197.031	201.565
3	Age	340.817	316.094	324.984	328.438	327.959	307.170	302.267	303.664
4	Food+Age	143.231	130.627	106.312	113.944	113.426	100.192	99.370	103.773
5	Food*Age	113.132	20.304	10.740	13.307	23.824	4.993	85.63	14.473
6	Log(Age)	282.555	256.014	279.689	280.922	279.757	252.958	245.615	250.098
7	Food+Log(Age)	80.356	69.170	62.192	66.470	66.404	54.870	52.566	57.519
8	Food*Log(Age)	64.037	57.285	49.700	53.461	55.441	49.020	45.806	50.307
9	Age^2	194.593	167.599	174.219	174.445	193.117	149.102	141.608	159.950
10	**Food+Age^2**	31.461	18.318	8.742	11.307	21.842	3.436	**0**	12.493
11	Food*Age^2	31.781	20.460	11.793	14.268	24.363	6.733	3.316	15.900

Parameter	Model	Structure of variances							
		Homoscedasticity of variances	Food	Age A	Age B	Age C	Food*Age A	Food*Age B	Food*Age C
Clutch size									
1	Null	203.134	201.508	163.752	164.045	168.627	172.004	166.379	168.699
2	Food	188.754	184.912	148.661	149.339	156.037	145.362	140.370	148.203
3	Age	108.224	108.686	99.848	97.754	96.318	113.202	104.739	100.167
4	Food+Age	76.844	71.720	69.625	67.089	66.940	64.203	55.690	60.030
5	Food*Age	76.244	12.887	17.792	14.778	13.305	NA	NA	60.492
6	Log(Age)	58.364	58.544	57.045	54.732	51.910	68.916	60.515	54.370
7	Food+Log(Age)	28.814	22.270	28.034	24.990	23.563	22.398	12.976	15.602
8	Food*Log(Age)	30.594	23.758	29.933	26.880	25.429	NA	NA	17.522
9	Age^2	43.304	42.842	42.166	39.942	37.028	50.881	43.323	37.331
10	Food+Age^2	24.464	18.194	24.104	21.142	19.348	20.707	11.189	12.029
11	**Food*Age^2**	14.844	6.464	14.799	11.799	10.101	10.438	1.103	**0**

Parameter	Model	Homoscedasticity of variances	Food	Age A	Age B	Age C	Food*Age A	Food*Age B	Food*Age C
Egg volume									
1	Null	87.423	90.507	91.006	89.449	86.843	100.787	94.02	94.082
2	Food	56.347	59.793	59.383	57.375	55.064	73.598	65.76	64.593
3	Age	72.435	75.13	78.443	76.605	74.751	NA	NA	82.477
4	Clutch size	50.273	52.877	56.708	54.571	52.168	NA	NA	60.215
5	Food+Clutch size+Age	13.986	17.13	21.24	18.628	16.667	37.817	29.491	26.464
6	Food+Clutch size	24.28	27.25	30.444	27.947	25.641	45.277	37.187	35.072
7	Age+Clutch size	45.999	48.44	52.981	50.821	48.83	65.99	58.387	57.064
8	Food+Age	32.736	36.286	39.206	36.78	34.943	56.131	47.915	44.947
9	Log(Age)	56.152	58.742	62.934	61.033	59.552	75.698	68.595	67.701
10	Age^2	41.222	43.971	48.348	46.517	44.629	53.308	60.487	53.099
11	Age^2+Clutch size	26.004	28.54	33.404	31.359	29.402	46.709	38.885	38.033
12	Clutch size*Age^2	31.811	34.422	39.125	37.122	35.181	51.505	43.815	43.713
13	Food*Age^2	9.892	13.524	17.193	14.879	13.314	NA	NA	23.044
14	Food+Clutch size+Age^2	0.406	3.654	8.116	5.572	3.815	24.498	16.095	13.717
15	Food+Clutch size*Age^2	6.400	9.677	14.052	11.543	9.822	29.793	21.616	19.507
16	**Clutch size+Food*Age^2**	**0**	3.283	7.603	5.152	3.402	NA	NA	12.996

APÉNDICE B

CAPÍTULO 2

APPENDIX B1

Table B1. Modelling the effects of age and environmental conditions on laying date and egg volume of Scopoli's Shearwater using data from both females and males of known age. Notation: np = number of estimable parameters; dev = relative deviance; AIC = Akaike information criterion; ΔAIC_i = difference of AIC value of the model *i* with respect to the AIC value of the best model; W_i = weight of model *i* for the set of models tested. Model notation: Year = time effect, NAO_w = NAO index in winter (see Methods), NAO_a = annual NAO index effect with one-year time lag, SOI= SOI index effect with one-year time lag, Log(Age)= logarithmic effect of age, Age= lineal effect of age, Age^2= quadratic effect of age, Food = availability of food per capita (see Methods). The symbol "*" denotes interaction between factors and "+" an additive effect between factors. The best model is shown in bold.

Nº Model	Laying date models	np	dev	AIC	ΔAIC	*W*
1	**Year*Log (Age)**	**28**	**1384.10**	**1440.10**	**0.00**	**1.00**
2	Year	15	1440.83	1470.83	30.73	0.00
3	Year+Log(Age)	16	1439.12	1471.12	31.01	0.00
4	NAO_w	4	1517.73	1525.73	85.62	0.00
5	NAO_w +Log(Age)	5	1516.46	1526.46	86.35	0.00
6	NAO_w *Log(Age)	6	1516.75	1528.75	88.65	0.00
7	NAOa	4	1590.18	1598.18	158.07	0.00
8	NAOa +Log(Age)	5	1588.70	1598.70	158.59	0.00
9	NAOa *Log(Age)	6	1588.37	1600.37	160.27	0.00
10	SOI*Log (Age)	6	1588.67	1600.67	160.57	0.00
11	Food+Log(Age)	5	1593.33	1603.33	163.22	0.00
12	Food*Log(Age)	6	1591.46	1603.46	163.36	0.00
13	Food	4	1595.84	1603.84	163.74	0.00
14	SOI+Log(Age)	5	1594.30	1604.30	164.20	0.00
15	SOI	4	1596.50	1604.50	164.39	0.00
16	Null	3	1602.64	1608.64	168.54	0.00
17	Log(Age)	4	1601.02	1609.02	168.92	0.00
18	Age	4	1606.26	1614.26	174.16	0.00
19	Age^2	5	1608.47	1618.47	178.37	0.00

Nº Model	Volume models	np	dev	AIC	ΔAIC	*W*
1	**Year*Log (Age)**	**28**	**1675.27**	**1731.27**	**0.00**	**1.00**
2	Year+Log(Age)	16	1748.16	1780.16	48.89	0.00
3	Year	15	1750.72	1780.72	49.46	0.00
4	Food*Log(Age)	6	1788.89	1800.89	69.62	0.00
5	SOI*Log (Age)	6	1792.75	1804.75	73.48	0.00
6	SOI+Log(Age)	5	1795.26	1805.26	73.99	0.00
7	SOI	4	1797.35	1805.35	74.08	0.00
8	NAOw +Log(Age)	5	1797.43	1807.43	76.17	0.00
9	Food+Log(Age)	5	1798.01	1808.01	76.74	0.00
10	Food	4	1800.05	1808.05	76.79	0.00
11	NAOw *Log(Age)	6	1796.94	1808.94	77.67	0.00
12	NAOw	4	1800.97	1808.97	77.70	0.00
13	Log(Age)	4	1807.82	1815.82	84.55	0.00
14	Null	3	1810.40	1816.40	85.13	0.00
15	NAOa +Log(Age)	5	1809.69	1819.69	88.43	0.00
16	NAOa	4	1812.16	1820.16	88.90	0.00
17	Age	4	1812.31	1820.31	89.04	0.00
18	NAOa *Log(Age)	6	1808.73	1820.73	89.46	0.00
19	Age^2	5	1816.50	1826.50	95.24	0.00

APPENDIX B2

Estimates of the best models for laying date (Model 1, Table 4) and egg volume (Model 1, Table 5).

Table 4. Estimates model: Laying date ~ Year *Age(Log)

Random effects	Variance	SD
Individual effect	3.6	1.9
Residual	6.51	2.55

Fixed effects	Estimate	SE
(Intercept)	30.05	39.21
Year 2002	-29.23	41.23
Year 2003	38.24	43.34
Year 2004	-20.68	39.87
Year 2005	-27.63	40.19
Year 2006	-24.34	39.97
Year 2007	-10.83	39.61
Year 2008	-18.62	39.37
Year 2009	-28.10	39.48
Year 2010	12.71	80.27
Year 2011	-19.64	39.55
Year 2012	-23.71	39.82
Year 2013	-17.81	41.57
Age(Log)	-8.57	17.89
Year 2002: Age(Log)	14.91	18.71
Year 2003:Age(Log)	-15.54	19.60
Year 2004:Age(Log)	10.27	18.14
Year 2005:Age(Log)	10.89	18.20
Year 2006:Age(Log)	10.61	18.13

Year 2007:Age(Log)	7.23	18.03
Year 2008:Age(Log)	8.86	17.90
Year 2009:Age(Log)	12.72	17.92
Year 2010:Age(Log)	-5.80	34.72
Year 2011:Age(Log)	8.15	17.92
Year 2012:Age(Log)	11.52	17.97
Year 2013:Age(Log)	7.76	18.59

Table 5. Estimates model: Volume ~ Year *Age(Log)

Random effects	Variance	SD
Individual effect	7.15	2.67
Residual	10.10	3.18

Fixed effects	Estimate	SE
(Intercept)	67.45	49.23
Year 2002	-9.41	51.94
Year 2003	-33.46	54.59
Year 2004	-6.68	49.94
Year 2005	2.30	51.21
Year 2006	-21.60	50.64
Year 2007	1.69	50.03
Year 2008	5.94	49.41
Year 2009	3.08	49.56
Year 2010	11.98	49.39
Year 2011	3.59	49.53
Year 2012	2.13	49.89

Year 2013	-29.62	52.03
Age(Log)	1.25	22.46
Year 2002: Age(Log)	5.10	23.58
Year 2003:Age(Log)	15.34	24.69
Year 2004:Age(Log)	4.17	22.73
Year 2005:Age(Log)	0.96	23.15
Year 2006:Age(Log)	9.50	22.96
Year 2007:Age(Log)	-0.84	22.76
Year 2008:Age(Log)	-2.93	22.44
Year 2009:Age(Log)	-0.93	22.48
Year 2010:Age(Log)	-3.70	22.41
Year 2011:Age(Log)	-1.72	22.44
Year 2012:Age(Log)	-1.36	22.51
Year 2013:Age(Log)	11.94	23.27

APÉNDICE C

CAPÍTULO 3

APPENDIX C

Specification of the multievent modelling approach.

The multievent framework distinguishes the events, coded in the capture histories, from the states, which must be inferred. For the analyses performed, the events were:

0- bird not observed in a particular occasion
1- bird encountered alive
2- bird recovered dead

and the underlying biological states were:

A- alive

RD- bird recently dead

LD- bird long dead

A multievent model use three kinds of parameters: the initial state probabilities, the transition probabilities and the event probabilities (conditional on the underlying states).

The initial state probabilities correspond in our model to the proportions of newly encountered individuals belonging to the states A and RD. In this model all the individuals were alive (A) at the time of marking.

$$\text{Initial state} = \begin{array}{cc} \text{A} & \text{RD} \\ (1 & 0) \end{array}$$

The transition between the state probabilities corresponds to the survival (Φ) and mortality (1-Φ) probabilities.

$$\text{Survival} = \begin{array}{c|ccc} & \text{A} & \text{RD} & \text{LD} \\ \text{A} & \Phi & 1-\Phi & 0 \\ \text{RD} & 0 & 0 & 1 \\ \text{LD} & 0 & 0 & 1 \end{array}$$

The event probabilities relate the observations coded in the capture histories to the underlying biological states. Here the probability of recapture (ρ) of live birds and the probability of recovery (τ) of dead individuals were estimated.

$$\text{Recapture and recovery} = \begin{array}{c} \\ A \\ RD \\ LD \end{array} \begin{array}{c} \begin{array}{ccc} 0 & 1 & 2 \end{array} \\ \begin{pmatrix} 1-\rho & \rho & 0 \\ 1-\iota & 0 & \tau \\ 1 & 0 & 0 \end{pmatrix} \end{array}$$

Table C1. Selection of the best age structure for recapture and recovery probabilities and testing individual random effect. The first step was modelling the age structure of recovery, once selected the best structure in this step we modelled the age structure of recapture. With the best age structure for both parameters we modelled different time effects. Also, were tested individual random effect in survival and recapture. The asterisk denotes problems of parameter identifiability: (*) denotes one parameter non identifiable and (**) two parameters non identifiables.

Modelling age structure of recovery

Model	Survival	Recovery	Recapture	np	Dev	AICc	Notes
1	age	age (1,2,3,4,5,6,≥7)	age (3,4,5,6,≥7)	31	3240.15	3303.03	**
2	age	age (1,2,3,4,5,≥6)	age (3,4,5,6,≥7)	30	3242.13	3302.95	**
3	age	age (1,2,3,4,≥5)	age (3,4,5,6,≥7)	29	3242.25	3301.03	**
4	age	age (1,2,3,≥4)	age (3,4,5,6,≥7)	28	3242.73	3299.45	**
5	age	age (1,2,≥3)	age (3,4,5,6,≥7)	28	3242.73	3299.45	*
6	**age**	**age (1,≥2)**	**age (3,4,5,6,≥7)**	**28**	**3242.73**	**3299.45**	
7	age	Constant	age (3,4,5,6,≥7)	27	3291.62	3346.29	

Modelling age structure of recapture

10	age	age (1,≥2)	age (3,4,5,6,7,≥8)	29	3241.20	3299.98
6	**age**	**age (1,≥2)**	**age (3,4,5,6,≥7)**	**28**	**3242.73**	**3299.45**
8	age	age (1,≥2)	age (3,4,5,≥6)	27	3246.84	3301.51
9	age	age (1,≥2)	age (3,4,≥5)	26	3256.35	3308.98
11		age (1,≥2)	age (3,≥4)	25	3276.34	3326.92
12		age (1,≥2)	constant	24	3366.06	3414.59

Modelling time effects on recovery and recapture

13	age	age (1,≥2)*t	age (3,4,5,6,≥7)*t	132	2980.38	3260.71
14	age	age (1,≥2)+t	age (3,4,5,6,≥7)+t	48	3154.41	3252.52
15	age	age (1,≥2)+t	age (3,4,5,6,≥7),t	121	2958.49	3214.16
16	**age**	**age (1,≥2)*t**	**age (3,4,5,6,≥7)+t**	**82**	**3031.25**	**3201.44**

Testing other age stuctures

17		age (1,≥2)*t	age (3,4,5,≥6)+t	81	3075.56	3243.60
18		age (1,≥2)*t	age (3,4,5,6,7,≥8)+t	83	3067.43	3239.78
19		**age (1,2,≥3)*t**	**age (3,4,5,6,≥7)+t**	**90**	**3014.69**	**3202.17**
20		t	age (3,4,5,6,≥7)*t	67	3077.93	3216.05

Testing individual random effect

16	**age**	**age (1,≥2)*t**	**age (3,4,5,6,≥7)+t**	**82**	**3031.25**	**3201.44**
	Log(A)2	age (1,≥2)*t	age (3,4,5,6,≥7)+t	64	3062.23	3193.99
	Log(A)2 +ind	age (1,≥2)*t	age (3,4,5,6,≥7)+t	65	3061.18	3191.18
	Log(A)2	age (1,≥2)*t	{age (3,4,5,6,≥7)+t}+ind	65	3008.14	3138.14

APÉNDICE D

CAPÍTULO 4

APPENDIX D1

Table D1. Posterior estimates (mean, standard deviation, and percentiles) for demographic parameters obtained from the two data sets (M123, M23) and the two models with different covariate for boat traffic (number of ferries, "Ferries", or whale-watching boats, "WW"). Mean survival ($\bar{\phi}$) and detection ($\bar{p}$) probabilities are given on probability scale, i.e., $\bar{\phi} = expit(\mu_\phi)$ and $\bar{p} = expit(\mu_p)$ where *expit* is the inverse-logit function. The related βs and σs are on logit scale.

Model		Estimated Mean	SD	*Quantiles* 0.025	0.500	0.975
M123						
Ferries	$\bar{\phi}$	0.927	0.038	0.845	0.932	0.972
	β_ϕ	-0.645	0.581	-2.089	-0.553	0.159
	σ_ϕ	0.817	0.990	0.026	0.528	3.429
	$\bar{p}$	0.656	0.050	0.546	0.660	0.740
	β_p	1.182	0.168	0.865	1.176	1.524
	σ_p	1.519	0.247	1.056	1.510	2.044
WW	$\bar{\phi}$	0.928	0.051	0.795	0.938	0.982
	β_ϕ	-0.524	0.874	-2.305	-0.528	1.308
	σ_ϕ	1.275	1.236	0.129	0.912	4.793
	$\bar{p}$	0.652	0.050	0.546	0.656	0.738
	β_p	1.198	0.171	0.869	1.194	1.536
	σ_p	1.541	0.238	1.094	1.536	2.028
M23						
Ferries	$\bar{\phi}$	0.924	0.050	0.806	0.933	0.967
	β_ϕ	-0.492	0.485	-1.480	-0.467	0.339
	σ_ϕ	0.835	0.991	0.036	0.555	3.529
	$\bar{p}$	0.725	0.034	0.652	0.727	0.785
	β_p	1.232	0.175	0.898	1.228	1.579
	σ_p	1.089	0.243	0.583	1.103	1.543
WW	$\bar{\phi}$	0.918	0.065	0.717	0.935	0.975
	β_ϕ	-0.273	0.817	-1.750	-0.312	1.368
	σ_ϕ	1.279	1.253	0.120	0.911	5.055
	$\bar{p}$	0.724	0.034	0.655	0.726	0.783
	β_p	1.241	0.175	0.902	1.239	1.588
	σ_p	1.102	0.236	0.616	1.112	1.551

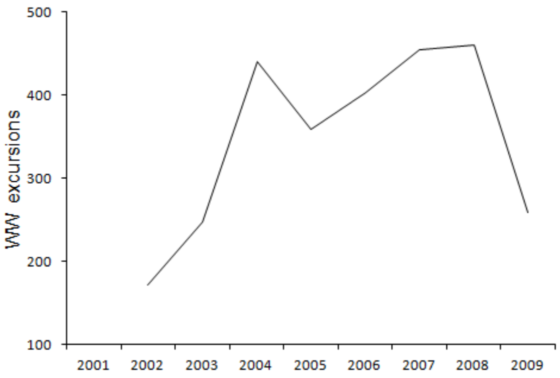

Figure D1. Number of whale-watch excursions, per year, by all companies operating in Tarifa.

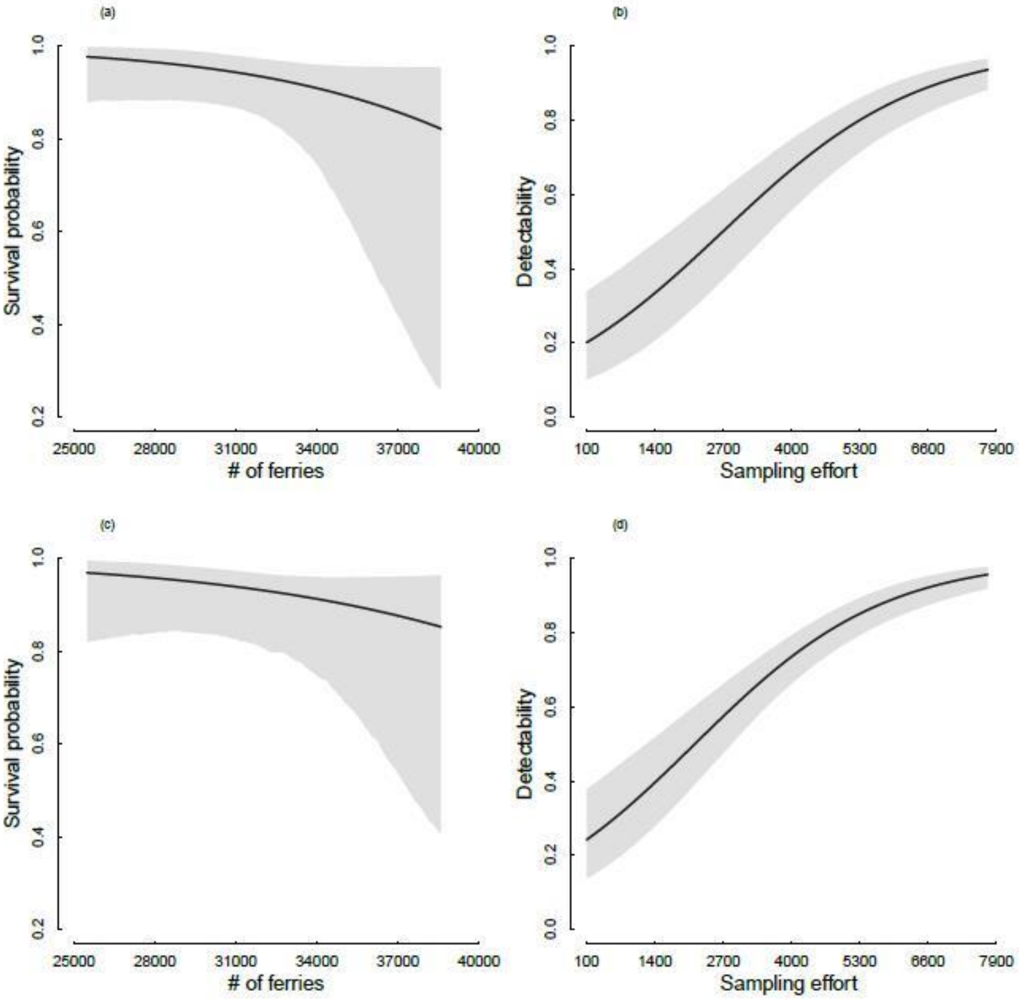

Figure D2. Relationship between survival probability and the number of ferries, and between detectability and sampling effort, under the two data set, M123 (a) and (b), M23 (c) and (d). The shaded areas indicate the 95% credible interval for the predicted relationships.

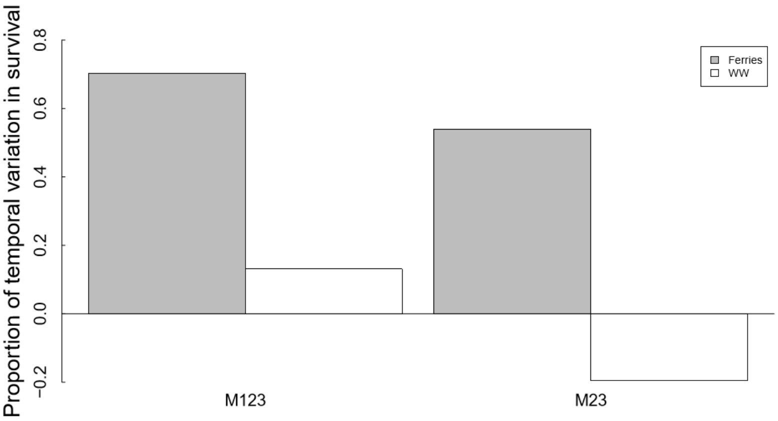

Figure D3. Estimated fraction of temporal variance in survival probability explained by the number of ferries (“Ferries”) and whale-watching boats (“WW”), for the two data sets (M123, M23).

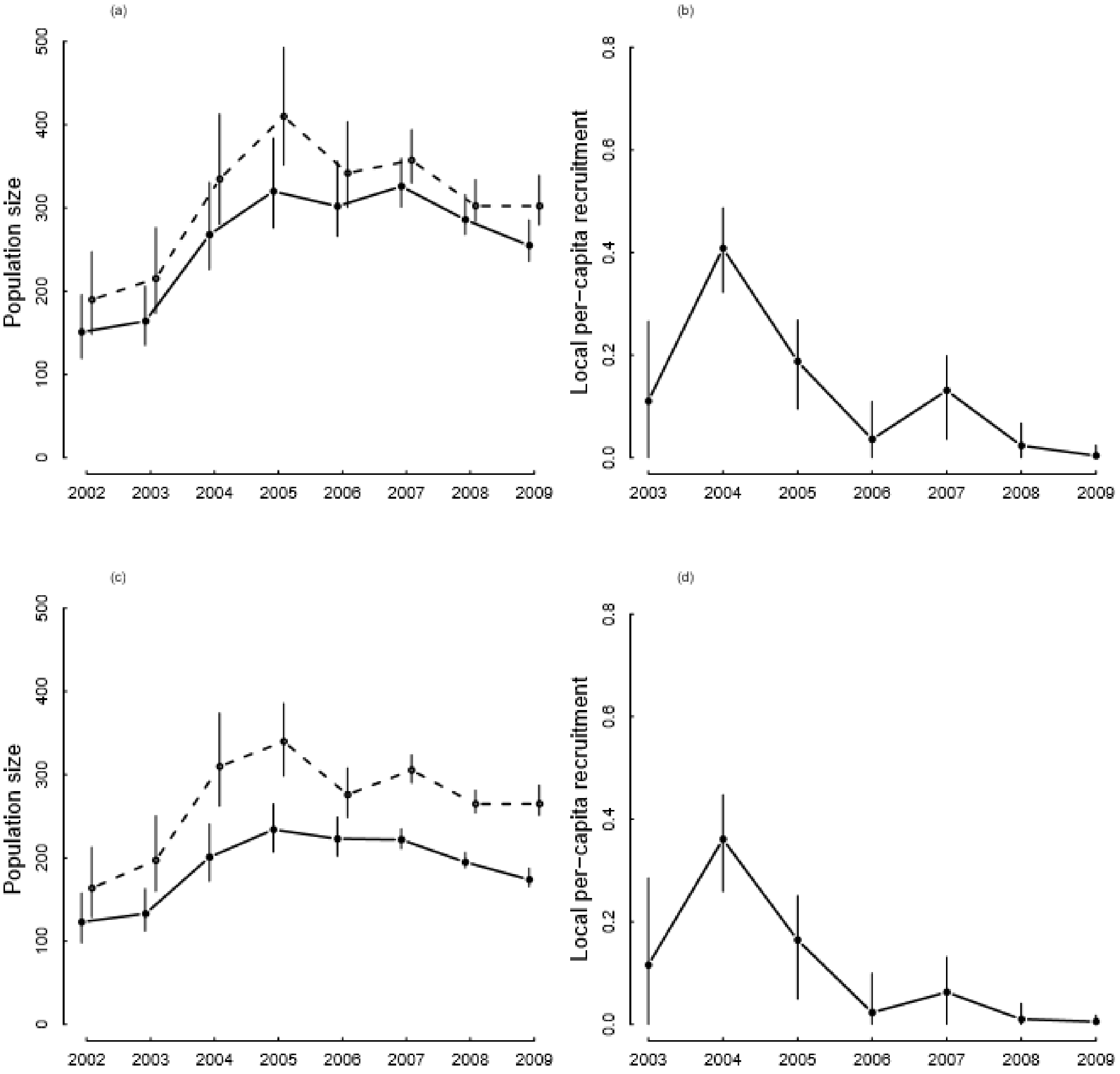

Figure D4. Posterior medians of population size and per-capita recruitment estimated for the two data set, M123 (a,b), M23 (c,d). Population size derived from the model, and thus referred to identifiable individuals (i.e. with nicks on the dorsal fin), is indicated by the solid line, total population size (including individuals without nicks) is indicated by the dashed line. Per-capita recruitment is referred to identifiable individuals. The vertical lines indicate the 95% credible interval for the estimates.

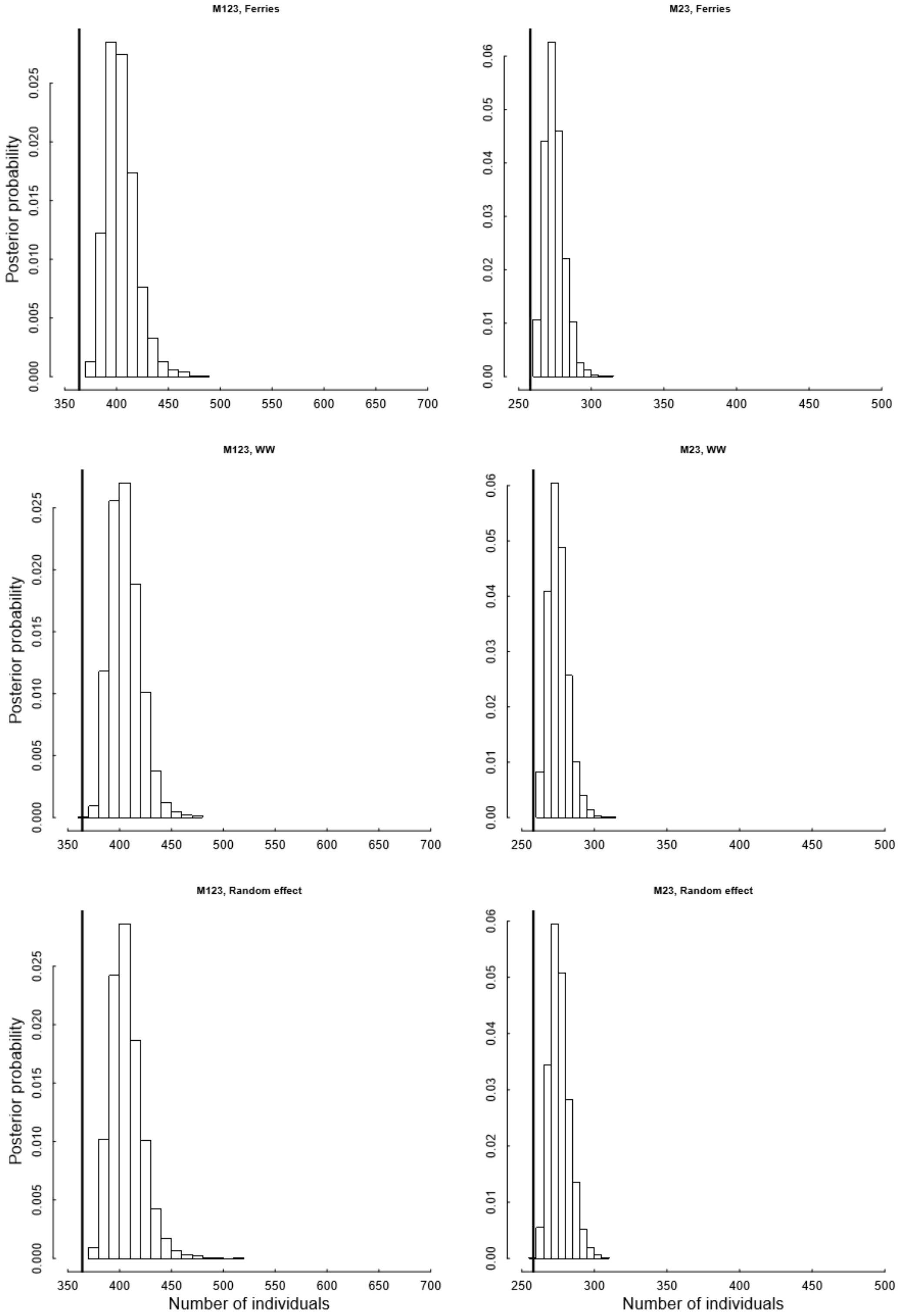

Figure D5. Posterior distribution of the superpopulation size N^s estimated using the two data sets (M123 and M23) and the different models with a logit-linear effect of the number of ferries ("Ferries") or whale-watching boats ("WW") on survival probability, or with a temporal random effect on survival ("Random effect"). The thick vertical lines indicate the observed number of individuals (n).

Parameter estimation

We fit the models using a Bayesian formulation and the Markov chain Monte Carlo framework. We used Uniform(0,1) and Normal(0,1000) prior distributions for the intercepts and slopes (on the logit scale) respectively, of survival (φ), entry probability (γ) and detectability (p). For further details about prior specification of other model parameters see the supplementary model code (Appendix D2). Posterior parameter distributions were assessed for prior sensitivity (e.g., (King et al., 2009) by using a second set of priors with Uniform(-5,5) probabilities for the slopes. The two sets of priors yielded similar posterior parameter distributions and we thus discussed estimates obtained under the first prior set. Encounter matrices for all sets of data were augmented by $700 - n$ individuals for M123 data, and by $500 - n$ for M23 (Appendix D, Fig. D5). To assess the model adequacy, we conducted a goodness-of-fit test based on the posterior predictive distribution of the sum of absolute values of residuals, as measure of lack of fit. For all models, Bayesian P-values ranged from 0.26 to 0.42 suggesting an adequate fit (i.e. P-values close to 0.5, and not close to 0 or 1; (Gelman et al., 1996)).

Summaries of the posterior distribution were calculated from three Markov chain initialized with random starting values, run 100000 times after a 100000 burn-in and re-sampling every 50 draws, resulting in 2000 posterior samples per chain. The Brooks-Gelman-Rubin convergence diagnostic (Brooks & Gelman, 1998) used to assess convergence was < 1.1 for all parameters. Models were implemented in program JAGS (Plummer, 2003), that we executed from R («R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing», 2012).

APPENDIX D2.1

```
####################################################
##############################################

# R and BUGS code for the model with the effect of the number of ferries on survival probability

####################################################
##############################################


# Capture histories structure

head(y)

#      T1 T2 T3 T4 T5 T6 T7 T8

#[1,]  0  0  0  0  0  0  0  1

#[2,]  0  0  0  1  1  0  0  0

#[3,]  1  0  0  0  0  0  0  0

#[4,]  0  0  0  1  1  1  1  1

#[5,]  0  0  1  1  1  1  1  1

#[6,]  0  1  1  1  1  1  0  0


# Covariates for boat traffic

covar

#  year  WW Ferrys_EAV

#1 2002 172       25494

#2 2003 248       27849

#3 2004 441       29825

#4 2005 359       30978

#5 2006 403       30456

#6 2007 455       38600

#7 2008 461       33634

#8 2009 259       32807
```

```
# augment dataset
M <- 500
yaug <- rbind(y, matrix(0, nrow=(M-dim(y)[1]), ncol=dim(y)[2]))

# effort, Q1 and Q2 (May-Agost)
effort <- c(226,109,647,875,1596,4879,5405,7736)
st_effort <- (effort-mean(effort))/sd(effort)

# Model specified as a restricted dynamic occupancy model (Kery and Schaub 2012, Royle and
Dorazio 2008)
sink("model_EAV_RE_indP.txt")
cat("
model{

##### Priors
for(t in 1:n.occasions-1){
    logit(phi[t]) <- mu.phi + beta.phi * EAV[t] + eps.phi[t]
    eps.phi[t] ~ dnorm(0, tau.phi)T(-16,16)
}
mu.phi <- log(mean.phi / (1-mean.phi))
mean.phi ~ dunif(0, 1)

beta.phi ~ dnorm(0,0.001)


for(t in 1:n.occasions){
    logit(gamma[t]) <- mu.gamma + eps.gamma[t]
    eps.gamma[t] ~ dnorm(0, tau.gamma)
}
```

```
mu.gamma <- log(mean.gamma / (1-mean.gamma))
mean.gamma ~ dunif(0, 1)

for (i in 1:M){
    for(t in 1:n.occasions){
        logit(p[i,t]) <- mu.p + beta.p * st_effort[t] + eps.p[i]
    }
eps.p[i] ~ dnorm(0, tau.p)T(-16,16)
}
mu.p <- log(mean.p / (1-mean.p))
mean.p ~ dunif(0, 1)

beta.p ~ dnorm(0,0.001)

tau.gamma <- 1/(sd.gamma*sd.gamma)
sd.gamma ~ dunif(0,10)

tau.phi <- 1/(sd.phi*sd.phi)
sd.phi ~ dunif(0,10)

tau.p <- 1/(sd.p*sd.p)
sd.p ~ dunif(0,10)

##### Likelihood
for (i in 1:M){
# First occasion
    # State process
    z[i,1] ~ dbern(gamma[1])
```

```
    recruitable[i,1]<-1
    # Observation process
    mu.y[i,1]<-p[i,1]*z[i,1]
    y[i,1] ~ dbern(mu.y[i,1])

# later years
    for(t in 2:n.occasions){
        # State process
        recruitable[i,t] <- recruitable[i,t-1]*(1-z[i,t-1])
        survived[i,t] <- z[i,t-1]*phi[t-1]
        mu.z[i,t] <- survived[i,t] + gamma[t]*recruitable[i,t]  #gamma is the removal entry probability
        z[i,t] ~ dbern(mu.z[i,t])
        # Observation process
        mu.y[i,t] <- p[i,t]*z[i,t]
        y[i,t] ~ dbern(mu.y[i,t])
    } #t
} #i



###### Calculate derived population parameters
for (t in 1:n.occasions){
    qgamma[t] <- 1-gamma[t]
}
cprob[1] <- gamma[1]
for (t in 2:n.occasions){
    cprob[t] <- gamma[t] * prod(qgamma[1:(t-1)])
} #t
psi <- sum(cprob[])              # Inclusion probability
```

```
for (t in 1:n.occasions){
    b[t] <- cprob[t] / psi       # Entry probability
} #t
for (i in 1:M){
    recruit[i,1] <- z[i,1]
    for (t in 2:n.occasions){
        recruit[i,t] <- (1-z[i,t-1]) * z[i,t]
    } #t
} #i
for (t in 1:n.occasions){
    N[t] <- sum(z[1:M,t])          # Actual population size
    B[t] <- sum(recruit[1:M,t])  # Number of entries
} #t
for (i in 1:M){
    Nind[i] <- sum(z[i,1:n.occasions])
    Nalive[i] <- 1-equals(Nind[i], 0)
} #i
Nsuper <- sum(Nalive[])          # Superpopulation size


##### Posterior predictive checking
for (i in 1:M){
    Zpred[i,1]~dbern(gamma[1])
    for(t in 2:n.occasions){
        Zpred[i,t] ~ dbern(mu.z[i,t])
    }
}
```

```
for (i in 1:n){
    for (t in 1:n.occasions){
        #generate predicted data from the model
        y.rep[i,t] ~ dbern(mu.y[i,t])
        #for predictive model selection
        error[i,t] <- y.rep[i,t]-y[i,t]
        pe[i,t]<-pow(error[i,t],2)
        # for predictive goodness of fit
        residual.rep[i,t] <- abs(y.rep[i,t]-mu.y[i,t])
        residual[i,t] <- abs(y[i,t]-mu.y[i,t])
    }
}

for(t in 1:n.occasions){
    rr[t] <- sum(residual[1:n,t])
    rr.rep[t] <- sum(residual.rep[1:n,t])
}

Disc <- sum(rr[])
Disc.rep <- sum(rr.rep[])
pvalue <- step(Disc.rep - Disc)


}
",fill=TRUE)
sink()

# Bundle data
jags.data <- list(y = yaug, n.occasions=dim(yaug)[2], n=dim(y)[1], M=M,
```

```
                EAV=(covar[,"Ferrys_EAV"]-
mean(covar[,"Ferrys_EAV"]))/sd(covar[,"Ferrys_EAV"]),
                st_effort=st_effort)


# Initial values
z.init <- yaug
z.init[z.init==0] <- 1
inits <- function(){list(mean.p = runif(1, 0.5, 1), mean.phi = runif(1, 0.5, 1), mean.gamma =
runif(1, 0.05, 0.08),
                      sd.p = runif(1, 1, 2), sd.phi = runif(1, 1, 2), sd.gamma = runif(1, 1, 2),
                      beta.phi = runif(1, -2, 2), beta.p = runif(1, -2, 2),
                      z = z.init
                      )}


# Parameters monitored
parameters <- c("gamma", "mean.gamma", "mean.p", "mean.phi", "sd.gamma", "beta.p", "beta.phi",
"sd.p", "sd.phi",
              "psi","b","Nsuper","N","B","pvalue")


library(snow)
library(rjags)
library(dclone)


n.adapt <- 2000     #pre-burnin
n.update <- 100000#burnin
n.iter <- 100000#iterations post-burnin
thin <- 50
chains<-3


# run the model
```

```
cl <- makeCluster(3, type = "SOCK")
start.time = Sys.time()
out <- jags.parfit(cl, data = jags.data,
                   params = parameters,
                   model = "model_EAV_RE_indP.txt",
                   inits = inits,
                   n.adapt = n.adapt,
                   n.update = n.update,
                   n.iter = n.iter,
                   thin = thin, n.chains = chains)
end.time = Sys.time()
elapsed.time = difftime(end.time, start.time, units='mins')
cat(paste(paste('Posterior computed in ', elapsed.time, sep=''), ' minutes\n', sep=''))
stopCluster(cl)
```

APPENDIX D2.2

```
###################################################
#############################################
# R and BUGS code for the model with the effect of the number of ferries on survival probability,
# under the full data set (M123)
###################################################
#############################################


# Capture histories structure
str(y)
# int [1:364, 1:8] 0 0 1 0 0 0 0 0 0 1 ...
# - attr(*, "dimnames")=List of 2
#  ..$ : NULL
#  ..$ : chr [1:8] "T1" "T2" "T3" "T4" ...
```

```
head(y)
#      T1 T2 T3 T4 T5 T6 T7 T8
#[1,]  0  0  0  0  0  0  0  1
#[2,]  0  0  0  1  1  0  0  0
#[3,]  1  0  0  0  0  0  0  0
#[4,]  0  0  0  1  1  1  1  1
#[5,]  0  0  1  1  1  1  1  1
#[6,]  0  1  1  1  1  1  0  0

# Covariates for boat traffic
covar
#  year  WW Ferrys_EAV
#1 2002 172      25494
#2 2003 248      27849
#3 2004 441      29825
#4 2005 359      30978
#5 2006 403      30456
#6 2007 455      38600
#7 2008 461      33634
#8 2009 259      32807

# augment dataset
M <- 700
yaug <- rbind(y, matrix(0, nrow=(M-dim(y)[1]), ncol=dim(y)[2]))

# effort, Q1 and Q2 (May-Agost)
effort <- c(226,109,647,875,1596,4879,5405,7736)
st_effort <- (effort-mean(effort))/sd(effort)
```

```
# Data use to rescale for non-distinctive individuals
# total number of fin images with nicks (M123) for each encounter in each year
head(enc_M123)
#      [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8]
# [1,]   31   73   15  130  158   39  130   29
# [2,]    2   25   35  161   28   67  262   51
# [3,]    9   NA   97   58    6  128  361  175
# [4,]    5   NA   17    9  186  124  462  263
# [5,]  126   NA   66   45   35  160  368  297
# [6,]   35   NA   18    1   90   53  340  615

# total number of fin images (both with and without nicks) for each encounter in each year
(M123)
head(enc_tot)
#      [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8]
# [1,]   36   95   16  139  187   50  135   43
# [2,]    3   33   41  204   36   91  277   57
# [3,]   12   NA  108   63    9  153  364  236
# [4,]    6   NA   34   15  201  139  490  354
# [5,]  161   NA   70   82   40  172  400  384
# [6,]   43   NA   22    4   97   66  358  729


# Model specified as a restricted dynamic occupancy model (Kery and Schaub 2012, Royle and
Dorazio 2008)
sink("model_EAV_RE_indP.txt")
cat("
model{
```

```
##### Priors
for(t in 1:n.occasions-1){
    logit(phi[t]) <- mu.phi + beta.phi * EAV[t] + eps.phi[t]
    eps.phi[t] ~ dnorm(0, tau.phi)T(-16,16)
}
mu.phi <- log(mean.phi / (1-mean.phi))
mean.phi ~ dunif(0, 1)

beta.phi ~ dnorm(0,0.001)



for(t in 1:n.occasions){
    logit(gamma[t]) <- mu.gamma + eps.gamma[t]
    eps.gamma[t] ~ dnorm(0, tau.gamma)
}
mu.gamma <- log(mean.gamma / (1-mean.gamma))
mean.gamma ~ dunif(0, 1)

for (i in 1:M){
    for(t in 1:n.occasions){
        logit(p[i,t]) <- mu.p + beta.p * st_effort[t] + eps.p[i]
    }
eps.p[i] ~ dnorm(0, tau.p)T(-16,16)
}
mu.p <- log(mean.p / (1-mean.p))
mean.p ~ dunif(0, 1)
```

```
beta.p ~ dnorm(0,0.001)

tau.gamma <- 1/(sd.gamma*sd.gamma)
sd.gamma ~ dunif(0,10)

tau.phi <- 1/(sd.phi*sd.phi)
sd.phi ~ dunif(0,10)

tau.p <- 1/(sd.p*sd.p)
sd.p ~ dunif(0,10)

##### Likelihood
for (i in 1:M){
# First occasion
    # State process
    z[i,1] ~ dbern(gamma[1])
    recruitable[i,1]<-1
    # Observation process
    mu.y[i,1]<-p[i,1]*z[i,1]
    y[i,1] ~ dbern(mu.y[i,1])

# later years
    for(t in 2:n.occasions){
        # State process
        recruitable[i,t] <- recruitable[i,t-1]*(1-z[i,t-1])
        survived[i,t] <- z[i,t-1]*phi[t-1]
        mu.z[i,t] <- survived[i,t] + gamma[t]*recruitable[i,t] #gamma is the removal entry
probability
        z[i,t] ~ dbern(mu.z[i,t])
```

```
        # Observation process
        mu.y[i,t] <- p[i,t]*z[i,t]
        y[i,t] ~ dbern(mu.y[i,t])
    } #t
} #i


###### Calculate derived population parameters
for (t in 1:n.occasions){
    qgamma[t] <- 1-gamma[t]
}
cprob[1] <- gamma[1]
for (t in 2:n.occasions){
    cprob[t] <- gamma[t] * prod(qgamma[1:(t-1)])
} #t
psi <- sum(cprob[])             # Inclusion probability
for (t in 1:n.occasions){
    b[t] <- cprob[t] / psi      # Entry probability
} #t
for (i in 1:M){
    recruit[i,1] <- z[i,1]
    for (t in 2:n.occasions){
        recruit[i,t] <- (1-z[i,t-1]) * z[i,t]
    } #t
} #i
for (t in 1:n.occasions){
    N[t] <- sum(z[1:M,t])         # Actual population size
    B[t] <- sum(recruit[1:M,t])  # Number of entries
```

```
} #t
for (i in 1:M){
    Nind[i] <- sum(z[i,1:n.occasions])
    Nalive[i] <- 1-equals(Nind[i], 0)
} #i
Nsuper <- sum(Nalive[])          # Superpopulation size



##### Posterior predictive checking
for (i in 1:M){
    Zpred[i,1]~dbern(gamma[1])
    for(t in 2:n.occasions){
        Zpred[i,t] ~ dbern(mu.z[i,t])
    }
}

for (i in 1:n){
    for (t in 1:n.occasions){
        #generate predicted data from the model
        y.rep[i,t] ~ dbern(mu.y[i,t])
        #for predictive model selection
        error[i,t] <- y.rep[i,t]-y[i,t]
        pe[i,t]<-pow(error[i,t],2)
        # for predictive goodness of fit
        residual.rep[i,t] <- abs(y.rep[i,t]-mu.y[i,t])
        residual[i,t] <- abs(y[i,t]-mu.y[i,t])
    }
}
```

```
for(t in 1:n.occasions){
    rr[t] <- sum(residual[1:n,t])
    rr.rep[t] <- sum(residual.rep[1:n,t])
}

Disc <- sum(rr[])
Disc.rep <- sum(rr.rep[])
pvalue <- step(Disc.rep - Disc)

##### derive total population size
for (t in 1:n.occasions){
    Ntot1[t] <- N[t]/nobs_prop[t]
    nobs_prop[t] ~ dunif(0, 1)
}
for (t in 1:n.occasions){
    for (i in 1:n.encounters[t]){
        nobs_nicks[i,t] ~ dbin(nobs_prop[t], nobs_tot[i,t])
    }
}

}
",fill=TRUE)
sink()

# vector for the number of encounters
get.last <- function(x) max(which(is.na(x)==FALSE))
n.encounters <- apply(enc_tot,2,get.last)
```

```
# Bundle data
jags.data <- list(y = yaug, n.occasions=dim(yaug)[2], n=dim(y)[1], M=M,
                  EAV=(covar[,"Ferrys_EAV"]-
mean(covar[,"Ferrys_EAV"]))/sd(covar[,"Ferrys_EAV"]),

st_effort=st_effort,n.encounters=n.encounters,nobs_tot=enc_tot,nobs_nicks=enc_M123)


# Initial values
z.init <- yaug
z.init[z.init==0] <- 1
inits <- function(){list(mean.p = runif(1, 0.5, 1), mean.phi = runif(1, 0.5, 1), mean.gamma =
runif(1, 0.05, 0.08),
                         sd.p = runif(1, 1, 2), sd.phi = runif(1, 1, 2), sd.gamma = runif(1, 1, 2),
                         beta.phi = runif(1, -2, 2), beta.p = runif(1, -2, 2),
                         z = z.init,
                         nobs_prop = runif(dim(yaug)[2], 0.7, 0.9)
                         )}


# Parameters monitored
parameters <- c("gamma", "mean.gamma", "mean.p", "mean.phi", "sd.gamma", "beta.p", "beta.phi",
"sd.p", "sd.phi",
                "psi","b","Nsuper","N","B","pvalue","Ntot","Ntot1","nobs_prop")


library(snow)
library(rjags)
library(dclone)


n.adapt <- 2000     #pre-burnin
n.update <- 100000#burnin
```

```
n.iter <- 100000 #iterations post-burnin

thin <- 50

chains<-3


# run the model

cl <- makeCluster(3, type = "SOCK")

start.time = Sys.time()

out <- jags.parfit(cl, data = jags.data,

                   params = parameters,

                   model = "model_EAV_RE_indP.txt",

                   inits = inits,

                   n.adapt = n.adapt,

                   n.update = n.update,

                   n.iter = n.iter,

                   thin = thin, n.chains = chains)

end.time = Sys.time()

elapsed.time = difftime(end.time, start.time, units='mins')

cat(paste(paste('Posterior computed in ', elapsed.time, sep=''), ' minutes\n', sep=''))

stopCluster(cl)
```

APÉNDICE E

PUBLICACIONES

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From recruitment to senescence: food shapes the age-dependent pattern of breeding performance in a long-lived bird

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Abstract. We used a long-term data set (26 years) from Audouin's Gull (*Larus audouinii*), a long-lived seabird, to address the relationship between the age-dependent pattern of reproductive performance and environmental conditions during breeding. Although theoretical models predict that the youngest and oldest breeders (due to inexperience and senescence, respectively) will perform less well than intermediate age classes, few empirical data exist regarding how this expected pattern varies with food availability. To assess the influence of age and food availability (corrected by population size of the main consumers to take into account density dependence) on a number of breeding parameters (laying dates, egg volume, clutch size, and hatching success), we modeled mean and variances of these parameters by incorporating heterogeneity into generalized linear models. All parameters varied with age and to different degrees, depending on food availability. As expected, performance improved with increased food supply, and the observed age pattern was quadratic, with poorer breeding performances occurring in extreme ages. For most parameters (except for laying dates, for which age and food did not interact), the pattern changed with food somewhat unexpectedly; the differences in performance between age classes were higher (i.e., the quadratic pattern was more noticeable) when food was more readily available than when food availability was lower. We suggest that, under poor environmental conditions, only high-quality individuals of the younger and older birds bred and that the differences in breeding performance between age classes were smaller. Although variances for egg volume were constant, variances for laying dates were highest for the youngest breeders and tended to decrease with age, either due to the selection of higher-quality individuals or to a greater frequency of birds skipping breeding with age, especially when food was in low supply. Our results show that mean and variances of breeding parameters changed with age, but that this pattern was different for each parameter and also varied according to food availability. It is likely that, other than food, certain additional factors (e.g., sex, cohort effects, density dependence) also influence changes in breeding performance with age, and this may preclude the finding of a common pattern among traits and among studies on different taxa.

Key words: age pattern; Audouin's Gull; breeding performance; Ebro Delta, western Mediterranean; food availability; Larus audouinii; *long-lived birds; selection hypothesis; variance analysis.*

INTRODUCTION

It is a well-known phenomenon in nature that the reproductive performance of individuals improves with age (Forslund and Pärt 1995, Coulson et al. 2001, Bowen et al. 2006, Trumbo 2009). Younger breeders often perform badly and have lower reproductive capacity, which is related to their lack of experience in acquiring sufficient quality and quantity of resources, such as food, mates, and territories (Reid et al. 2003, Sanz-Aguilar et al. 2008). This lack of skills in first-time breeders compared to older individuals commonly translates into costs in successive breeding frequency or even in future survival (i.e., the survival–reproduction trade-off; see Stearns 2000). In many long-lived animals, a similar pattern of lower breeding performance has been found in the oldest individuals, a phenomenon known as reproductive senescence (e.g., Jones et al. 2008, Aubry et al. 2009, Rebke et al. 2010).

Three nonexclusive hypotheses exist to explain the poorer performance of younger breeders. The first is the constraint hypothesis (Curio 1983), which states that individuals gain experience and skills over the years (e.g., Nol and Smith 1987, Desrochers 1992, De Forest and Gaston 1996). On the other hand, the restraint hypothesis (Curio 1983) suggests that younger breeders that have higher residual reproductive value than older individuals should reduce their reproductive effort to avoid incurring high survival costs (e.g., Ericsson et al. 2001, Velando et al. 2006). Finally, the selection hypothesis advocates the existence of a selection filter,

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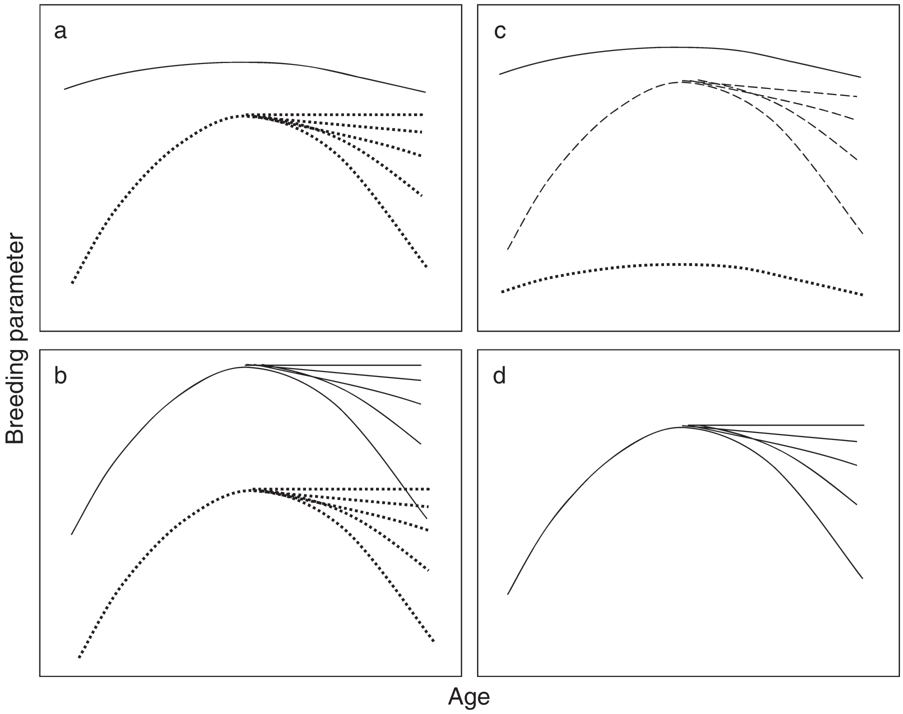

FIG. 1. The four alternative hypotheses built from the published literature (see Appendix: Table A1) to explain the variation in the breeding parameters with age in relation to the environment (see *Introduction* for explanation): high food availability (solid line), low food availability (dotted line), and intermediate food availability (dashed line, panel c). Panel (a) corresponds to the hypothesis that, under conditions with better food supply, the differences between age classes were less than when food availability was lower. In panel (b), differences between age classes were great but equal under all conditions of food availability; in panel (c), although differences between age classes were small but equal under conditions of higher and lower food availability, a more shaped quadratic pattern was found for intermediate food conditions. Panel (d) fits with the hypothesis that the age effect is independent of food availability. Note that the curves show the mean values for each age class and that the hypothesis with a large variation within classes encompasses different curves, depending on the strength of the senescence phase. For laying dates, the curves should be inverted (i.e., younger and older birds laying later in the season).

operating during the first breeding attempts, that leads to older age classes consisting only of individuals that reproduce well (Cam and Monnat 2000, Reid et al. 2003, Sanz-Aguilar et al. 2008).

Once established that the pattern of reproductive traits varies with age, it still remains to be seen whether this pattern is invariant in natural populations subject to stochastic environments. Life-history theory states that, apart from the intrinsic factors that shape the variation of breeding parameters with age (constrained by trade-offs), there are also extrinsic factors (i.e., environmental variation) that play an important and interactive role (e.g., Stearns 2000). Thus, it is to be expected that differences in environmental conditions, especially those related to the availability of food during breeding attempts, will cause variations in this pattern (see Fig. 1). Theoretical models (e.g., Stearns 1976) assume that when food is limited there is an increase in reproductive costs, which will be higher for younger breeders under these environmental conditions. Some of the few studies addressing the association between food supply (mostly estimated through proxies such as climate indexes or fisheries data), age, and breeding parameters have found that differences in breeding performance between age classes were highest when food was in short supply (Boekelheide and Ainley 1989, Sydeman et al. 1991, Laaksonen et al. 2002, Bunce et al. 2005); see Fig. 1a. A second, unexpected pattern derived from theoretical expectations (see Fig. 1b) indicates that when food availability is high, breeding parameters are equally high for all age classes (Ratcliffe et al. 1998, Nevoux et al. 2007, Lee 2011). In a study of Great Skuas (*Stercorarius skua*), breeding success was found to vary with age under intermediate levels of food availability, but was rather constant when food supplies were either high or low (see Fig. 1c) (Ratcliffe et al. 1998). Finally, an additional unexpected pattern suggests that variability is irrespective of food supply (i.e., the only effect is that of age; Fig. 1d) (e.g., Vieyra et al. 2009, Pardo et al. 2013; see Appendix: Table A1 for supporting information).

Here, we used long-term data from a 26-year study to assess how different levels of food availability affect the age-dependent pattern of variability in several breeding parameters of Audouin's Gull *Larus audouinii*, a long-lived colonial bird. Patterns of variability in breeding parameters between age classes are commonly analyzed without considering the variance structure of these parameters (e.g., Stearns and Kawecki 1994, Proaktor et al. 2007). However, variance heterogeneity may contain important ecological information and it is thus advisable to incorporate its analysis into the models (Zuur et al. 2009). Thus, we analyzed not only how age and food affected mean values of breeding parameters, but also how variance changed with age and food availability (Nakagawa and Schielzeth 2012, Violle et al. 2012, Pardo et al. 2013). In fact, the few empirical studies that have analyzed the changes in variance of demographic traits found that the greatest variance occurs in older individuals (Gaillard and Yoccoz 2003, Pardo et al. 2013). However, here we go beyond those findings and test how this variance changes not only with age but also with environmental conditions. For instance, we predict that the variance in clutch size of younger breeders will be larger due to heterogeneity in individual quality (i.e., some are able to perform better than others), and will decrease with environmental stress, i.e., lower food availability, because under these circumstances only good younger breeders will in fact breed.

METHODS

The study was carried out in the Audouin's Gull colony at Punta de la Banya (Ebro Delta, western Mediterranean; 40°34′9.18″ N, 0°39′7.86″ E), which holds ~65% of the total world population of this gull (e.g., Tavecchia et al. 2007). The site lies on a 2500-ha peninsula of sandy dunes covered by halophilous vegetation, where the gulls build their nests. Audouin's Gulls are iteroparous and clutch size varies between 1 and 4 eggs (mode 3 eggs). Birds start to breed at three years old, and most recruitment in this colony occurs at 3–4 years and decreases sharply thereafter; annual adult survival probability is estimated at 0.91, and the mean life expectancy is ~14 years (Oro 1998), calculated as

$$\sum_{i_j}^{i_k} = -\frac{1}{\ln(\varphi_i)}$$

where ϕ is survival, i is age, and j and k are pre-adult and adult ages.

The banding program was initiated in 1985; by 2010, 27 914 chicks had been banded (annual median 1048, range 86–1792). Since 1988, chicks have also been marked with a plastic band with an individual alphanumeric code that can be read from a distance using a telescope (see Plate 1). For birds marked only with metal bands, incubating adults were detected using a telescope and were trapped at the nest following standard procedures (see Tavecchia et al. 2007). In the period 1994–2011, from the beginning of the laying period onward, nests were identified by searching for banded adults showing reproductive behavior. Once detected, nests were marked and monitored regularly (every 2 or 4 days). During these years, 1631 nests with at least one marked adult were monitored (annual median 101, range 13–143). We recorded the breeding phenology (laying date of the first egg as the number of days elapsed since 12 April (see Fig. 1b), that is, just before the start of laying), clutch size (the number of eggs laid), egg volume (length and maximum width of each egg measured with a digital caliper to ±0.1 mm; see Oro et al. 1996), and hatching success. Only the hatching success of non-abandoned or predated nests was considered. Nests abandoned or predated before the clutch was completed were considered only for laying dates, but not for the rest of parameters; when abandonment and predation occurred once the clutch was completed, these nests were considered also for egg volume and clutch size, but not for hatching success. Parameters related to eggs are an excellent indicator of environmental conditions during the breeding period; for instance, at the population level, egg volume and clutch size increase with improved food availability in the area around the colony (e.g., Oro et al. 1996). The visits (median seven visits for the laying and incubation period lasting ~30 days) allowed us to control for egg abandonment and predation; thus we were able to obtain unbiased estimates for clutch size. Once the clutch had been started, the laying date of these nests (except if they were predated) was estimated on the basis of the hatching date of the first egg (see Oro et al. 1996). Nests found when hatching was initiated or nests abandoned or predated before we could assess that the clutch was completed (i.e., once after three days—the maximum laying interval in Audouin's Gulls—since the last egg was recorded, except for clutches of four eggs) were not considered, in order to avoid overestimation of true hatching success. Furthermore, nests found once clutches were completed (i.e., consecutive visits did not record more eggs) did not underestimate clutch size or hatching success due to potential previous predation, because nests found on the laying date that suffered predation within the laying interval (i.e., before clutch was potentially completed) were always abandoned (own observations, $N = 37$ nests). These filters, together with the fact that 87% of nests were found on the laying date, made apparent success a reasonable proxy of true hatching success. Because chicks abandon the nest just few days after hatching, breeding success could not be recorded. Given that Audouin's Gulls are ground-nesting birds and the large size of the colony (median number of breeding pairs: 11 300, range 9170–15 329), we only have transversal population data, i.e., most individuals could not be monitored in successive years. From the 1631 nests monitored over the study, 85% corresponded to individuals monitored only once, and 15% were monitored twice, the maximum number of replicated data from the same individual. Thus, we considered that pseudoreplication in our data was negligible.

In many cases only one member of the pair was banded, so we checked assortative mating by age by using pairs in which both members were marked. The association between the ages of the two members was high ($N = 152$, Spearman correlation $r_S = 0.736$, $P < 0.0001$, mean difference = 1.9 years, 95% CI: 1.5–2.3 years), so we were able to assume that the age of a non-banded partner was similar to that of the banded (known-age) bird.

The tons (1 metric ton = 1 Mg) of landings of the trawler fleet in La Rapita, the main fishing port near the colony (Oro and Ruiz 1997), were used as a proxy for annual food availability. In the study area, Audouin's Gulls overlap their foraging areas with the fishing grounds of the trawler fleet (Mañosa et al. 2004, Cama et al. 2012). Gulls exploit discards to a great extent (>75% of their diet; see Oro et al. 1997), and amounts of discards are highly correlated with trawler landings (Oro and Ruiz 1997); as a result, breeding success is correlated with fish landings (Fig. 2). When trawlers do not operate (e.g., during moratoria periods and weekends), gulls feed mainly on small pelagics and less importantly on secondary prey from rice fields (67% and 27% of the gull diet, respectively; Oro et al. 1997). Those landings were corrected for population size (i.e., food per capita, hereafter referred as food) by taking into consideration the number of both Audouin's and Yellow-legged Gulls *L. michahellis* breeding each year (see methods in Almaraz and Oro 2011)—the latter gull being a sympatric food-competing species—to account for the density dependence of the guild by interference competition recorded in the study colony (Tavecchia et al. 2007, Almaraz and Oro 2011). The availability of discards greatly influences the breeding parameters of the study colony (e.g., Oro et al. 1996; see Fig. 2). The variability in food supply was great and offered a wide range of environmental conditions. For instance, under severe food limitation when discard availability was at its lowest, the modal clutch size decreased to only two eggs, an exceptionally low value for this species (Oro et al. 1996).

We analyzed data using generalized linear models (GLM) to assess the influence of age, food availability per capita (standardized), and their interaction on each breeding parameter. Breeding parameters were modeled as functions of continually valued age and food availability, with model error covariance matrices structured by group-specific error variances for age group and food availability. We used different error and link functions, depending on the distribution of the breeding parameter: Gaussian error and link identity function for average egg volume in a clutch, and laying date, binomial error, and logit link function for clutch size and hatching success. Owing to the fact that clutch size did not follow a Gaussian or a Poisson distribution (range 1–4), that one-egg clutches are rare (10%), and that most individuals lay three-egg clutches (the modal clutch size, corresponding to 55% of the clutches monitored), we treated that parameter as a binomial variable (i.e., laying or not laying a three-egg clutch). Different models with additive fixed effects and their interactions were analyzed; age was introduced as linear, logarithmic, and quadratic to test for different patterns of age-dependent variation in the breeding parameter (see Fig. 1). Given that egg volume varies with clutch size (Oro et al. 1996), we also introduced clutch size as an explanatory factor for that parameter. We incorporated heterogeneity into the models to test for between-group heteroscedasticity, i.e., whether variances vary between age groups and food availability. We obtained the residual variances for each group directly from the GLM. Because hatching success and clutch size were treated as binomial variables, the heteroscedasticity procedure was not feasible because mean and variance are functionally linked. We used biologically meaningful categorizations of ages and food-availability classes; older age classes were pooled to ensure enough statistical power. Ages were categorized into a less constrained distribution (Age A, six classes: 3, 4, 5, 6, 7–14, and >14 years old) and two simpler, more constrained structures (Age B, four classes: 3, 4–5, 6–14, and >14 years old; Age C, three classes: 3, 4–6, and >6 years old) (see Appendix: Table A2). Food availability per capita (as Mg of fish landed divided by the number of breeding

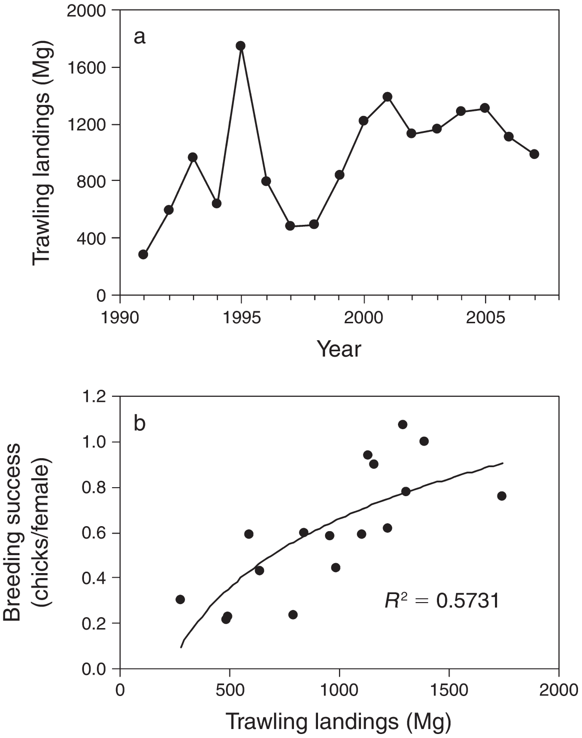

FIG. 2. (a) Variability of trawling landings (as a proxy for discard availability, expressed as metric tons [SI unit Mg] of catches from April to June, the whole breeding season) at the main fishing harbor close to the colony of Audouin's Gulls (*Larus audouinii*) at the Ebro Delta during the period 1991–2007; and (b) association between breeding success (as mean number of chicks per female) and trawling landings (the value of R^2 is calculated on a log relationship).

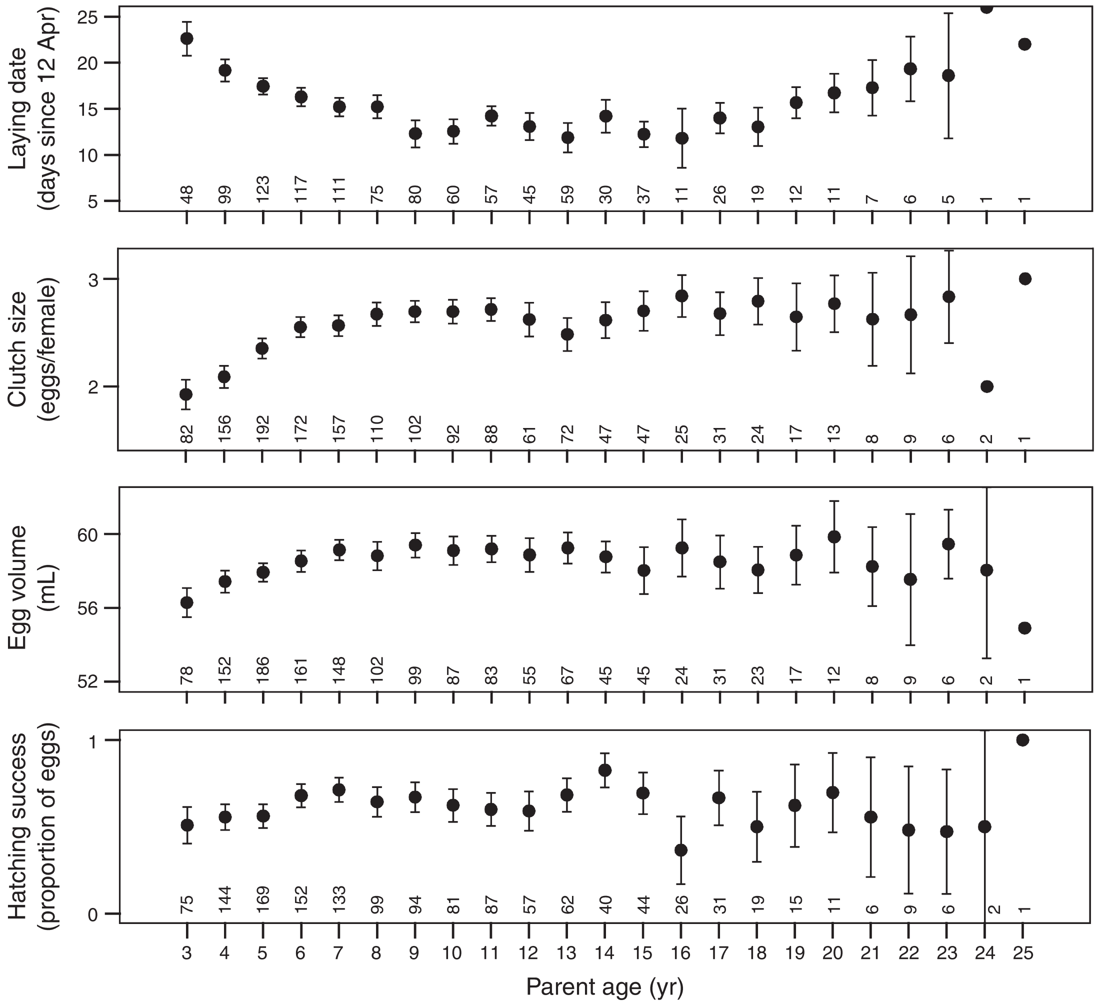

FIG. 3. Relationship between breeding parameters (laying dates, clutch size, egg volume, and hatching success) and age (mean values and 95% CI) in Audouin's Gulls. Note that the laying date is expressed as days elapsed since 12 April, the date on which females are about to lay their eggs. The numbers above the *x*-axis of each panel are the number of observations for each age class.

pairs of Audouin's and Yellow-legged Gulls) was standardized through a standard normal transformation (by subtracting the mean and dividing the standard deviation) using categories in a single structure with three balanced groups: negative values (seven years with poor food supply per capita), values between 0 and 1 (five good years), and values higher than 1 (six very good years).

The average egg volume in a clutch and mean laying date were fitted with the functions *gls* and *varIdent* from the *nlme* R package (Pinheiro et al. 2013); 95% confidence limits of the variances were obtained by utilizing the *intervals.gls* function from this package; clutch size and hatching success were fitted with the *glm* function, in all cases using R software (http://cran.r-project.org). Model selection was carried out using the AIC (Akaike information criterion) of each model (Burnham and Anderson 2002).

RESULTS

Breeding ages ranged from three years old (first breeding age) to 25 years old. As usual in these types of data, larger standard errors of older birds are a result of the smaller sample of these ages (Fig. 3). All breeding parameters showed a trend of variation with age, that is, a general improvement in performance during the first attempts, followed by stabilization during intermediate ages (Fig. 3). A senescence pattern also seemed to emerge in all breeding parameters, most obviously for laying dates and less so for clutch size, egg volume, and hatching success (Fig. 3). Model selection showed that food and age played an important role in explaining variation in breeding parameters compared to the null models. Furthermore, these two effects in combination (either with or without interaction) appeared in the best models for all breeding parameters; likewise, age was always present quadratically (see selected models in

PLATE 1. A group of Audouin's Gulls at Punta de la Banya in the western Mediterranean where the study was carried out. Some birds are banded; the second from the right holds the code A9N, and corresponds to a gull banded here as a chick in 1988. Photo credit: Carles Domingo.

Table 1 and Appendix: Table A2). Thus, all breeding parameters significantly increased as food availability improved and a quadratic effect with age appeared (younger and older individuals showing poorer performances; see Fig. 3). When food was in short supply, the pattern of variability in most breeding parameters with age was flatter (i.e., the difference between intermediate ages and both younger and older ages was less) than when food was readily available, an effect that increased the quadratic shape of the association (see Figs. 4 and 5). The exception was in laying dates when the selected model included food and age additively (i.e., without their interaction; see Table 1), which gave parallel quadratic curves and similar quadratic patterns, although all ages performed better when food was in good supply (Fig. 5).

Effects of food supply on the variance of the age pattern

In tests for heteroscedasticity, the variances behaved differently for each breeding parameter, changing with age (four age classes) and food availability for laying dates, but remaining constant for egg volume (homogeneous variances for all ages and food classes); see Appendix: Table A2. For laying dates, the greatest variances occurred in 3-year and 4–5 year-old birds when food was in good supply, i.e., when individuals of different quality found suitable conditions to start breeding; the lowest variance occurred in the oldest birds (>14 years old) when food availability was highest (Fig. 6).

DISCUSSION

Age variation pattern

Our results show clear evidence of quadratic variation of age in several breeding parameters: younger and older birds laid later in the season (an indication of poorer acquisition of resources for reproduction), laid fewer eggs per clutch, laid smaller eggs, and hatched fewer eggs at the end of incubation. All studies dealing with multiple life-history and physiological traits report differences in the degree to which age influences each trait, ranging from no effect to a strong association, either linear or quadratic (e.g., Weimerskirch 1990, Blas et al. 2009, Lecomte et al. 2010, Pardo et al. 2013). Nevertheless, no common pattern in differences between and within traits across taxa has yet emerged, probably because additional factors other than age (e.g., sex, individual quality, experience, mate and site fidelity, cohort effects, age of the mate, density dependence, and stochastic fluctuations of food; see, for instance, Coulson et al. 2001) potentially influence the multi-trait pattern.

Even though an increase in breeding performance with age and experience has been widely reported in many iteroparous organisms (e.g., Berkeley et al. 2004, Bowen et al. 2006, Weladji et al. 2006, Trumbo 2009), the final decline in performance in older individuals has seldom been assessed (Monaghan et al. 2008) and has been recorded only in some but not all studied taxa (e.g., Vieyra et al. 2009, Rebke et al. 2010, Orzack et al. 2011, Pardo et al. 2013). In younger birds, poorer breeding

TABLE 1. Modeling the effects of age (mean and variance simultaneously) of Audouin's Gulls (*Larus audouinii*) on breeding parameters.

Model, by breeding parameter	Log likelihood	K	AIC	ΔAIC
Laying dates†				
1) Null	−3297.29	13	6620.57	365.99
2) Food	−3211.69	14	6449.37	194.79
3) Age	−3264.42	14	6556.85	302.27
4) Food + Age	−3161.98	15	6353.95	99.37
5) Food × Age	−3111.16	17	6256.31	1.73
6) log(Age)	−3236.10	14	6500.20	245.62
7) Food + log(Age)	−3138.57	15	6307.15	52.57
8) Food × log(Age)	−3134.19	16	6300.39	45.81
9) Age^2	−3183.10	15	6396.19	141.61
10) **Food + Age^2**	**−3111.29**	**16**	**6254.58**	**0**
11) Food × Age^2	−3110.95	18	6257.90	3.32
Clutch size				
1) Null	−1858.78	1	3720.06	24.11
2) Food	−1850.56	2	3705.12	9.17
3) Age	−1858.86	2	3721.73	25.78
4) Food + Age	−1850.55	3	3707.12	11.17
5) Food × Age	−1850.47	4	3708.96	13.01
6) log(Age)	−1858.78	2	3721.56	25.61
7) Food + log(Age)	−1850.02	3	3708.07	10.23
8) Food × log(Age)	−1850.02	4	3708.07	12.12
9) Age^2	−1851.54	3	3709.10	13.15
10) Food + Age^2	−1845.79	4	3699.60	3.65
11) **Food × Age^2**	**−1841.94**	**6**	**3695.95**	**0.00**
Egg volume‡				
1) Null	−3896.14	2	7796.28	87.42
2) Food	−3879.60	3	7765.21	56.35
3) Age	−3887.65	3	7781.29	72.43
4) Clutch size	−3875.57	4	7759.13	50.27
5) Food + Clutch size + Age	−3855.42	6	7722.84	13.99
6) Food + Clutch size	−3861.57	5	7733.14	24.28
7) Age + Clutch size	−3872.43	5	7754.86	46.00
8) Food + Age	−3866.80	4	7741.60	32.74
9) log(Age)	−3879.51	3	7765.01	56.15
10) Age^2	−3871.04	4	7750.08	41.22
11) Age^2 + Clutch size	−3861.43	6	7734.86	26.00
12) Clutch size × Age^2	−3860.34	10	7740.67	31.81
13) Food × Age^2	−3852.38	7	7718.75	9.89
14) Clutch size + Food +Age^2	−3847.63	7	7709.27	0.41
15) Food + Clutch size × Age^2	−3846.63	11	7715.26	6.40
16) **Clutch size + Food × Age^2**	**−3845.43**	**9**	**7708.86**	**0.00**
Hatching success				
1) Null	−1859.03	1	3720.06	24.17
2) Food	−1850.56	2	3705.12	9.23
3) Age	−1858.86	2	3721.72	25.83
4) Food + Age	−1850.55	3	3707.10	11.21
5) Food × Age	−1850.47	4	3708.93	13.05
6) log(Age)	−1858.78	2	3721.55	25.67
7) Food + log(Age)	−1850.08	3	3706.16	10.28
8) Food × log(Age)	−1850.02	4	3708.04	12.16
9) Age^2	−1851.54	3	3709.08	13.19
10) Food + Age^2	−1845.79	4	3699.57	3.68
11) **Food × Age^2**	−1841.94	**6**	**3695.89**	**0**

Notes: The best structure of variances (see Appendix: Table A2) was used for each parameter: for laying dates, food in interaction with age B structure; for clutch size, food in interaction with age C structure; and homoscedasticity for egg volume. Once the best variance structure was selected, we kept that structure for all models. Modeling followed a strategy of stepwise forward addition of parameters. We started with the null model with no effects, then single effects were tested, and finally interactions between these effects. Terms are: K, the number of identifiable parameters; AIC, Akaike's information criterion; ΔAIC, the difference in AIC value of the model with respect to the AIC value of the best model. The final selected model is in bold. Interaction between factors is denoted by "×" and "+" indicates an additive effect between factors. Age^2 indicates a quadratic effect of age on the breeding parameter. Food is the availability of food per capita (see *Methods*).

† Twelve of the parameters (K) in all models corresponded to the variance structure (four age classes × three food classes).

‡ One of the parameters (K) in all models corresponded to a single variance value.

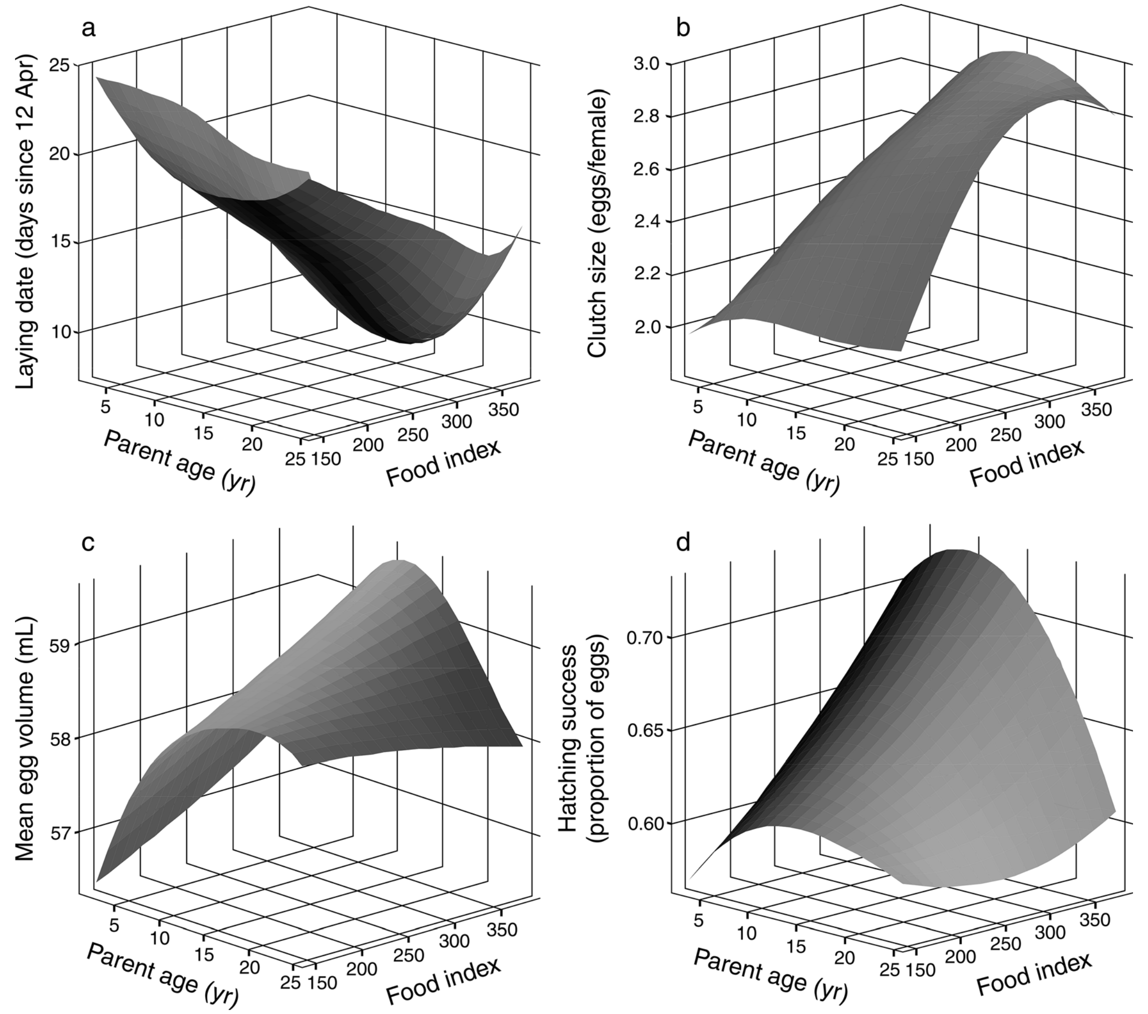

FIG. 4. Smoothing regression surfaces of the raw data, depicting the effects of age (ranging from 3 to 25 years of age) across all observed values of food availability (expressed as a food index of trawling discards per capita) on (a) laying dates, (b) clutch size, (c) average egg volume in three-egg clutches, and (d) hatching success of Audouin's Gulls in the Ebro Delta. The food index is a measure of density dependence because it reflects not the absolute amount of food available, but how much food is available for each individual (total trawling discards divided by the number of gulls).

performance is likely to indicate a lack of experience, especially when interference competition for resources with older (i.e., more experienced) birds occurs. Navarro et al. (2010) found that in Audouin's Gulls, younger breeders consumed lower quality prey in rice fields with lower energetic content, probably to avoid competition with the older birds that mainly consume lipid-rich fish. The decline in breeding performance observed in old gulls is the result of senescence, probably due to a deterioration of their functional abilities, particularly a lower foraging efficiency (e.g., Catry et al. 2006, Lecomte et al. 2010). This lower foraging efficiency in older birds would be more marked when food availability per capita decreased (i.e., when intra- and interspecific competition increased), determining a lower reproductive performance under such conditions. Although actuarial senescence (i.e., of survival) is a widespread phenomenon, reproductive senescence has been less studied and seems to be less common because it may also depend on food availability, on traits such as body size and migratory behavior, or on trade-offs between early- and late-life reproduction (Reed et al. 2008, Aubry et al. 2009, Berman et al. 2009).

Influence of food supply per capita on pattern in age variation

Once we had demonstrated the quadratic effect of age on all breeding parameters analyzed, the major challenge of our study was to assess whether and how this common pattern in nature varies with food availability, the main environmental driver of breeding performance (in the absence of predation). As expected, performance improved with increased food supply in all parameters. In terms of laying dates, performance varied quadrat-

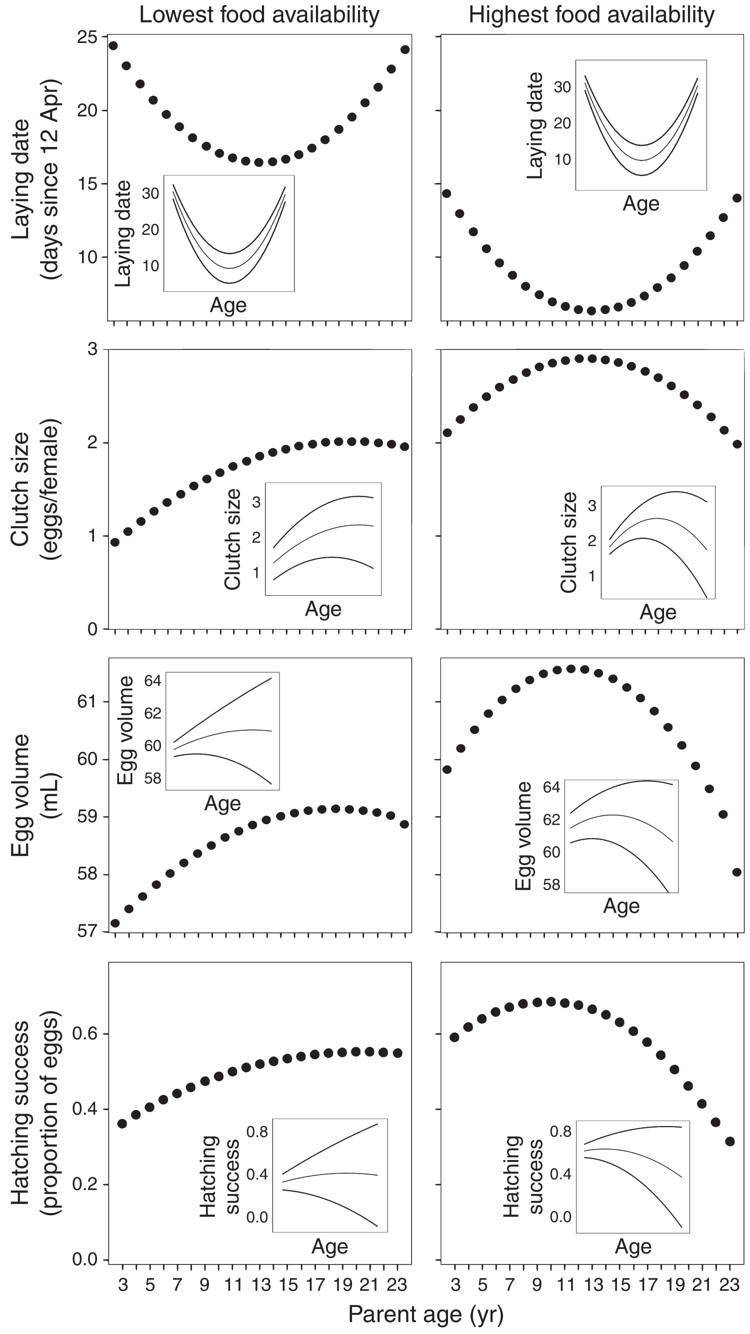

FIG. 5. Variation in the breeding parameters with age for the two extreme values of food availability per capita (years with lowest and highest values) to explore the two patterns of age variation under different food conditions. Solid circles show predicted mean values for each age estimated from the best model (see Table 1 and Appendix: Table A2). Inset figures show the mean values together with their 95% CI (same parameters as the respective axes in the main panels).

ically with age and increased in parallel with food availability per capita: birds laying earlier were in better condition, and this was the only parameter in Audouin's Gulls that behaved like this (i.e., food did not alter the age pattern). Egg laying occurs at the beginning of the reproductive season and should be the breeding parameter less affected by environmental noise, which should accumulate across the season. This probably causes an increase in the effects of different conditions of food availability per capita for each age class, although the difference with other parameters and with laying dates in closely related organisms, e.g., Western Gulls *L. occidentalis* (Sydeman et al. 1991; see Appendix: Table A1), remain poorly understood. For the rest of the reproductive parameters (clutch size, egg volume, and hatching success), the age pattern of breeding performance varied markedly with different levels of food availability and in an unexpected way. When food per capita was in short supply, the resulting quadratic age pattern was less marked (Fig. 5), even though most studies have found that differences in breeding performance between age classes decrease with improving feeding opportunities (see Appendix: Table A1). For instance, Ezard et al. (2006) report that young Common Terns (*Sterna hirundo*) performed well only in high-quality years, as is the case in Brandt's Cormorants (*Phalacrocorax penicillatus*) (Boekelheide and Ainley 1989). By contrast, our results show that the quadratic age pattern in Audouin's Gull for all parameters is more apparent under good conditions (except for laying dates; see Fig. 5), when middle-aged individuals greatly improve their breeding performance, thereby increasing differences in reproductive performance vis-à-vis older birds.

Variances in laying dates decreased with age and under all conditions; higher variance differences within age classes in breeding performance were found in younger birds. These results suggest that heterogeneity in individual quality exists within young age classes. Heterogeneity within age classes has been invoked by many previous studies (e.g., Sydeman et al. 1991, Cam and Monnat 2000, Barbraud and Weimerskirch 2005, McCleery et al. 2008, Lescroël et al. 2009, Oro et al. 2010, Péron et al. 2010, Desprez et al. 2011) and is the basis for the selection hypothesis (e.g., Nevoux et al. 2007; but see Rebke et al. 2010). This hypothesis is also supported by the low variances in older age classes (Fig. 6), which suggest that heterogeneity in individual quality for these birds was low. The average individual quality should increase with age, once young breeders of lower quality are removed from the population due to the costs of reproduction (e.g., Sanz-Aguilar et al. 2008). Additionally, it remains to be understood whether skip breeding, a practice commonly recorded in many seabird species including other gulls (e.g., Cam and Monnat 2000, Pyle et al. 2001, Sanz-Aguilar et al. 2008, Goutte et al. 2011), also plays a role in the low variances recorded in older Audouin's Gulls.

To our knowledge, only Pardo et al. (2013) have ever analyzed how the variances of several demographic traits change with age; these authors found a U-shaped pattern in the Black-browed Albatrosses (*Thalassarche melanophrys*), with middle-aged individuals having the lowest variances. Thus, the patterns present in these two species coincide in the high variances for younger birds and the lower variances for middle-aged birds, whereas the least variance in Audouin's Gulls occurs in older individuals. The difference in the two species-specific patterns appears in older age classes, because variances in old Black-browed Albatrosses were high (and similar to variances of younger birds), whereas those in old Audouin's Gulls were the lowest. This is likely to be explained by the differences in life-history strategies between the two species: albatrosses are extremely long-lived birds, lay a single egg, and have sabbatical (nonbreeding) years, whereas Audouin's Gulls have a lower survival, lay 2–3 eggs, and are thus bet-hedgers, i.e., species that reduce the temporal variance in fitness at the expense of lowered arithmetic mean fitness. Our results suggest that a selection process takes place as the individual grows older, resulting in, at least for some parameters such as laying dates, progressively lower heterogeneity in quality and breeding performance. In other words, the average laying dates of younger and older Audouin's Gulls were later, and while variance in younger birds was high (suggesting a large degree of individual heterogeneity with some breeders performing well and others doing badly), variance in older and experienced breeders was low (suggesting that most old and experienced gulls performed similarly). Despite not analyzing how variances changed with age and environmental conditions, other studies have reported a similar pattern, i.e., an effect of selection on the best performing individuals and thus a progressive homogenization of performance with age (Daunt et al. 1999, Cam and Monnat 2000, Barbraud and Weimerskirch 2005, Nevoux et al. 2007).

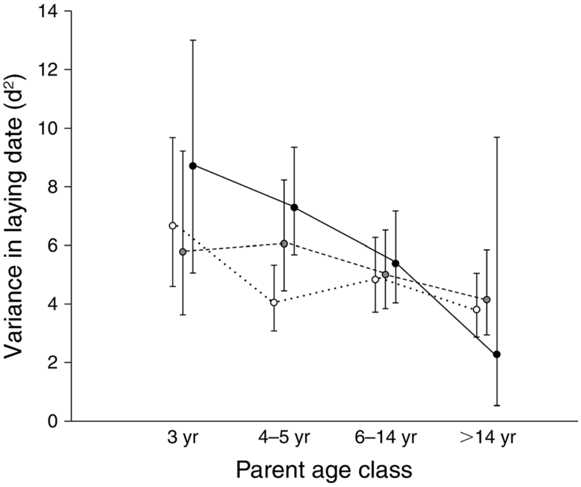

FIG. 6. Variances for each categorized age class (together with their 95% CI; see *Methods*) in laying dates of Audouin's Gulls in the Ebro Delta. Variance also varied with different categories of food availability: low (dotted line), intermediate (dashed line), and high (solid line).

CONCLUSION

Together with other factors such as sex, behavioral processes, and the varying costs of early reproduction, our results demonstrate that age and environmental conditions (in the form of food availability per capita) interact to shape differing aging patterns in an array of breeding parameters under natural conditions. These patterns vary from soft quadratic shapes in harsh environments (little effect of inexperience and senescence due to individual heterogeneity in quality and selection) to strongly quadratic patterns (important effect of inexperience and senescence) during good years when middle-aged individuals greatly improve their breeding performance. These two contrasting patterns, which are determined by food availability per capita (i.e., considering density dependence and thus competition; see Coulson et al. 2001), are rather unexpected because none of the studies analyzing the interaction between age and food conditions found that differences in breeding performance between age classes were lower when food was in shorter supply (see Fig. 1). The inclusion of the heterogeneity of variance in our analysis allowed us to shed some light on that particular pattern of the influence of food conditions and competition in the age pattern of breeding performance found in Audouin's Gulls. Variance variability between age classes suggests that important ecological processes, for example, the fact that selection decreases as individuals become older and their average quality increases, affects the patterns of age variation in breeding performance.

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SUPPLEMENTAL MATERIAL

Appendix

A list of papers testing the effects of age, together with environmental drivers and a table with all models tested for laying dates and egg volume (*Ecological Archives* E095-039-A1).

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The influence of environmental conditions on the age pattern in breeding performance in a transequatorial migratory seabird

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Several studies of marine top predators, above all of seabirds, have analyzed the effects of either individual age or environmental fluctuations on reproduction; nevertheless, little is known about the age patterns in breeding performance in a variable environment. To investigate the simultaneous influence of age and environmental conditions on laying dates and egg volumes, we tested different climate and food availability indices in a transequatorial migratory seabird using female data from a 23-year study. Our results show an improvement in breeding parameters with age (i.e., earlier laying dates and greater egg volumes) but no pattern of senescence in older age groups. The best models showed an interaction of time and age in breeding performance, i.e., the age pattern of breeding performance changed each year likely as a result of environmental variability. Nevertheless, climatic indexes used here explained part of that annual variability: NAO and SOI index accounted for 24 and 20% of deviances in laying dates and egg volume, respectively. Part of that unexplained variability might be related to other processes such as intermittent breeding and the individual quality of breeders, which were not assessed in our study.

Keywords: age pattern, breeding performance, Scopoli's Shearwaters, climatic index, food availability, migratory seabird

Introduction

In marine ecosystems, climatic fluctuations and other physical oceanographic variables affect the population dynamics of organisms by exerting an influence on their vital rates. This influence is mediated by drivers such as food availability and environmental conditions during the breeding period or migration (Duffy-Anderson et al., 2005; Lee, 2011). For example, large-scale climatic phenomena and oceanographic processes produce changes in water temperatures and currents that generate spatio-temporal variation in the production, distribution, and abundance of the prey consumed by marine predators such as seabirds (Durant et al., 2004). Consequently, these processes may affect the foraging ecology of seabirds (Navarro and Gonzalez-Solís, 2009; Weimerskirch et al., 2012) and influence their survival, reproduction and population dynamics (Jenouvrier et al., 2005; Genovart et al., 2013).

Like environmental variability, individual covariates such as age and sex also influence vital rates (Stearns, 1992). Age-specific differences in breeding performance have been observed in several seabirds (Nevoux et al., 2007; Vieyra et al., 2009; Pardo et al., 2013). In most cases young individuals perform less well than older individuals (Martin, 1995), thereby indicating improvement in performance with age leading to a peak and then decline (i.e., senescence) (Clutton-Brock, 1988). Several non-exclusive hypotheses have been proposed to explain these age-related variations in breeding performance: a progressive appearance or disappearance of phenotypes, age-related improvements in the skills needed for reproducing, and an optimization of reproductive effort (Forslund and Pärt, 1995).

Demographic parameters in wild populations are thus expected to be shaped by both individual covariates and environmental variability (e.g., Stearns, 2000; Nevoux et al., 2007; Oro et al., 2010). Despite this, few studies have ever examined at the same time how environmental conditions affect age patterns in breeding performance (Bunce et al., 2005; Pardo et al., 2013; Oro et al., 2014). Depending on environmental conditions, different age patterns can exist (see Oro et al., 2014): in most studies, either (a) differences among age classes in breeding performance were found to decrease under better environmental conditions (Sydeman et al., 1991; Laaksonen et al., 2002; Barbraud and Weimerskirch, 2005; Bunce et al., 2005) or (b) environmental conditions had no clear influence on breeding performance (Nevoux et al., 2007; Vieyra et al., 2009; Lee, 2011; Pardo et al., 2013); just one study found that differences between age-classes were greater under favorable environmental conditions (Oro et al., 2014).

Here we analyze 23 years of data from a population of Scopoli's Shearwater (*Calonectris diomedea*), a long-lived and highly monogamous seabird with extreme life-history traits that include high adult survival rates, low fecundity (females lay a single egg), intermittent breeding, and delayed sexual maturity (Thibault, 1994; Thibault et al., 1997). Shearwaters breed in the Mediterranean and, after reproducing, perform long trips to their Atlantic wintering grounds where there are important upwellings that provide abundant food resources (González-Solís et al., 2007). We tested the influence of environmental conditions at different spatial scales on two breeding parameters, laying date and egg volume, in individuals of different age classes. Our main aim was to test (a) whether breeding performance increased with age and (b) whether or not differences between age classes depend on environmental conditions at different spatial scales.

Materials and Methods

Ethics Statement

All animals were handled in strict accordance with good animal practice as defined by the current European legislation and the animal work was approved by the regional committee (Govern Balear, Balearic Is., Spain).

Population Monitoring

The study was conducted in the Scopoli's Shearwater colony on Pantaleu Islet in the Balearic Archipelago (30° 34′N, 2° 21′ E, Spain), where ca. 200 pairs breed in burrows under boulders or vegetation. In the period 1985–2010, a total of 1043 chicks were ringed with stainless-steel rings bearing unique numeric codes that allow individuals to be identified and aged. In 2001–2013, accessible nests (ca. 150 each year) were marked and visited during the breeding period (May–September); nests with breeders of known ages were examined to record laying dates (with a maximum of 72 h between visits), and the size of the single egg (with the use of a digital caliper). Both breeding parameters have been shown to be related to fitness components as chick survival, or juvenile survival (see review in Krist, 2011). Birds were sexed when first captured using morphometric measures and calls. We gathered data from 87 different breeders and the total number of monitored nests during the study was 302 (annual median number of nests = 24: 11–32 nests; median of age = 12-year old, range: 5–23-year old) of which 98 cases are females of known age (annual median number of nests = 8, range: 212 nests; median of age = 11-year old, range: 5–23-year old). As in many cases we only had the age of one member of the pair, we first assessed the association between the ages of the two members in nine pairs for which the two members of the pair were of known age. In these nine breeding pairs, assortative mating was low ($n = 9$, Spearman correlation $r_s = 0.068$, $p = 0.431$). Given that both laying dates and egg volumes in this species mainly depend on female body condition and their breeding capabilities (Jouanin et al., 2001), we only used data from females to be conservative. Nevertheless, since sample size of females was much lower than for males, and we could not confirm assortative mating, we also ran all models taking into account both sexes (Appendix A in Supplementary Material) to increase power by increasing sample size and check if the best model was the same as when taking only female data into account.

Environmental Variables

Previous studies have shown that Scopoli's Shearwaters basically feed on fish (90%) during the breeding season (Granadeiro et al., 1998b). Like many other seabirds that breed in the study area, this species exploits fishing discards from the trawling fleet which fishes on the continental shelf off the Ebro Delta (Martínez-Abraín et al., 2002a). Thus, as an annual proxy of food availability, we used the total amount of trawling discards produced in March (when birds store energetic reserves before breeding) derived from statistics for trawling catches by a fishing guild in the Ebro Delta (Oro and Ruiz, 1997; Louzao et al., 2011). To obtain a proxy of food per-capita (i.e., correcting for density-dependence), we divided the total amount of available food by the total population size of all the scavenging seabirds—Audouin's gulls (*Larus audouinii*), Yellow-legged gulls (*L. michahellis*), and Scopoli's Shearwaters—that forage in the area (Oro and Ruiz, 1997).

As a proxy of an oceanic large-scale climatic index we used the Southern Oscillation Index (SOI), associated with Atlantic hurricane activity, which registers greater hurricane activity during positive phases (i.e., La Niña) and less in negative phases (i.e., El Niño) (Knutson et al., 2008). We used annual mean SOI values from January to December, obtained from http://www.cru.uea.ac.uk/cru/data/soi/soi.dat with a 1-year time lag to test the effect of environmental conditions in the Atlantic where birds winter before returning to their breeding areas.

To test the effect of local conditions during breeding we used another large-scale index, the North Atlantic Oscillation Index (NAO). This index affects water column hydrodynamics and may have a cascade effect at higher trophic levels (Gordo et al., 2011), thereby influencing the production, distribution and abundance of the organisms upon which birds feed (Durant et al., 2004). To test this effect we selected the extended annual winter NAO (i.e., December–March; NAO_w) with positive values related to windy and warmer conditions, and negative values to colder air and wetter conditions in the Mediterranean (Hurrell, 1995). We also checked to see if there was any effect of the previous year's NAO value (NAO_a) since some fish have temperature-dependent gonadal development (Ware and Tanasichuk, 1989) and may spawn and migrate earlier in warmer years (Sims et al., 2004). Data were obtained from https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based.

Data Analysis

To analyze the influence of environmental variability on age patterns in different breeding parameters, we built linear mixed models (LMMs) with the package lme4 and function lmer (Bates, 2010) using R software (http://www.R-project.org). We used laying date and egg volumes as dependent, normally distributed, variables. We included year as a fixed effect and female age as a continuous explanatory variable, either as a linear, quadratic or logarithmic function, and environmental variables as covariates of the year-dependent variations (see previous section). We also considered models including the statistical interactions between these effects. In all models we included individual identity as random effect (random intercept model) to avoid pseudo-replication and account for differences across individuals (see Bolker et al., 2009).

We began by assessing the influence of age and determine the age pattern for each breeding parameter (i.e., linear, logarithmic or quadratic). Then we tested the influence of each environmental covariate (food availability, SOI, NAO_w, NAO_a) and progressively added complexity into the models, by including interactions term between the effects. We ranked the set of models using Akaike's information criterion with correction for small sample size (AICc; Anderson and Burnham, 2002) and selected the model with the lowest AICc value as the most parsimonious one, i.e., the best model for explaining our data using fewest parameters (Burnham and Anderson, 2002). When the difference between two models (i.e., ΔAICc) was less than 2 we considered that the models explained the data equally well (Lebreton et al., 1992; Burnham and Anderson, 2002). We also computed the Akaike weights (w_i; Burnham and Anderson, 2002), which provides a measure of the relative likelihood of a particular model given the models considered (Anderson et al., 2000). To assess the fit of the model, we estimated the coefficient of determination (R^2) between the fitted and observed values on selected models (Cameron and Windmeijer, 1996). We also estimated the R^2 using the method proposed by Nakagawa and Schielzeth (2013; r.squaredGLMM function in the MuMIn package for R), which gives the marginal R^2_{m} representing the variance explained by fixed factors, and the conditional R^2_{c} as the variance explained by both fixed and random factors (i.e., the entire model). Additionally, we also estimated the percentage of variation explained by each covariate (r^2) when tested alone as:

$$r^2 = \frac{Dev\,(M_{cnt}) - Dev\,(M_{cov})}{Dev\,(M_{cnt}) - Dev\,(M_t)}$$

where $\mathrm{Dev}(M_{cnt})$ is the estimated deviance of the constant model, i.e., no effects considered, $\mathrm{Dev}(M_{cov})$ is the deviance of the model with the climatic covariate considered and $\mathrm{Dev}(M_t)$ is the deviance of the time-dependent model.

To obtain the χ^2-values and the significance level of the different covariates, we performed a likelihood ratio test (LRT) comparing the null model with the different covariates for each breeding parameter (see **Table 2**). As random structure remained unchanged in all models tested, we can compare the LRT values of each case although the refitting model was run with ML and not with REML (see Zuur et al., 2009).

Results

We found a positive effect of age (log-transformed) on the breeding parameters analyzed (**Table 1**). Older individuals tend to lay earlier and to produce larger eggs than young birds (**Table 1**, **Figure 1**, and Appendix B in Supplementary Material). We found a large temporal variability in both parameters. In both cases, the retained model, i.e., the one with the lowest AICc value, assumed an effect of age, year and their statistical interaction, indicating that the strength of the relationship between breeding performance and age was changing across the years (Models 1 and 1; **Table 1**). The coefficient of determination (R^2) between the fitted and observed values of the selected models was 0.74 and 0.67 for laying date and egg volume analysis, respectively. Another important finding was that in both analyses the parameter accounting for across-individual variation was large. When we estimated the variance explained by Nakagawa and Schielzeth's (2013) method, we obtained $R^2_{\mathrm{m}} = 0.39$ and $R^2_{\mathrm{c}} = 0.64$ for laying date (Model 1) and $R^2_{\mathrm{m}} = 0.28$ and $R^2_{\mathrm{c}} = 0.53$ for egg volume analysis (Model 1). Thus, the variance explained by the random effect (i.e., the breeder) was 0.24 and 0.25 in laying date and egg volume, respectively. Environmental covariates were negatively associated with the parameters considered, but although this association was statistically significant, the covariates explained a relatively small part of the total temporal variability (NAO winter index explained about 24% of variance in laying date and SOI index 20% in egg volume; **Table 2**). For this reason none of the models that included climatic indexes were retained by the model selection procedure. Similarly, fishing discards taken as a proxy of food availability had a positive effect on both parameters, but the variance explained was low and this effect cannot be considered an important predictor of laying dates and egg volume. The year-by-age interaction term is indicating that differences between age classes were more marked under good environmental conditions (negative values of the climatic indexes; **Figure 1**).

TABLE 1 | Modeling the effects of age and environmental conditions on the breeding parameters of Scopoli's Shearwater's using generalized linear mixed models.

N° model	**Laying date**	**np**	**dev**	**AICc**	**ΔAICc**	W_i
1	**Year*Log (Age)**	26	349.39	423.33	0.00	1.00
2	Year	14	425.46	458.99	35.66	0.00
3	Year+Log(Age)	15	422.63	459.03	35.70	0.00
4	NAOw +Log(Age)	5	480.38	491.09	67.76	0.00
5	NAOw	4	483.21	491.68	68.35	0.00
6	NAOw *Log(Age)	6	479.39	492.39	69.06	0.00
7	SOI*Log (Age)	6	493.21	506.21	82.88	0.00
8	Log(Age)	4	498.95	507.42	84.09	0.00
9	Null	3	501.34	507.62	84.29	0.00
10	NAOa +Log(Age)	5	497.38	508.09	84.76	0.00
11	NAOa	4	499.80	508.27	84.94	0.00
12	Food*Log(Age)	6	495.63	508.63	85.30	0.00
13	NAOa *Log(Age)	6	495.81	508.81	85.48	0.00
14	SOI+Log(Age)	5	498.20	508.91	85.58	0.00
15	SOI	4	500.62	509.09	85.76	0.00
16	Food + Log(Age)	5	498.65	509.36	86.03	0.00
17	Food	4	501.10	509.57	86.24	0.00
18	Age	4	504.07	512.54	89.21	0.00
19	Age^2	5	509.08	519.79	96.46	0.00

N° model	**Volume**	**np**	**dev**	**AICc**	**ΔAICc**	W_i
1	**Year*Log (Age)**	26	378.02	451.96	0.00	1.00
2	Year+Log(Age)	15	446.04	482.44	30.48	0.00
3	Year	14	451.04	484.57	32.61	0.00
4	SOI*Log (Age)	6	481.84	494.84	42.88	0.00
5	SOI + Log(Age)	5	485.52	496.23	44.27	0.00
6	Food*Log(Age)	6	486.54	499.54	47.58	0.00
7	SOI	4	491.42	499.89	47.93	0.00
8	Food + Log(Age)	5	491.91	502.62	50.66	0.00
9	NAOw + Log(Age)	5	492.08	502.79	50.83	0.00
10	NAOw	4	495.11	503.58	51.62	0.00
11	NAOw *Log(Age)	6	491.31	504.31	52.35	0.00
12	Food	4	496.72	505.19	53.23	0.00
13	Log(Age)	4	498.62	507.09	55.13	0.00
14	Null	3	501.63	507.91	55.95	0.00
15	NAOa + Log(Age)	5	500.35	511.06	59.10	0.00
16	NAOa	4	503.39	511.86	59.90	0.00
17	Age	4	503.76	512.23	60.27	0.00
18	NAOa *Log(Age)	6	499.50	512.50	60.54	0.00
19	Age^2	5	508.50	519.21	67.25	0.00

Note that only the best models are shown. Notation: np, number of estimable parameters; dev, relative deviance; AIC, Akaike information criterion; ΔAIC_i*, difference of AIC value of the model i with respect to the AIC value of the best model;* W_i*, weight of model i for the set of models tested. Model notation: Year, time effect;* NAO_w*, NAO index in winter (see Materials and Methods);* NAO_a*, annual NAO index effect with one-year time lag; SOI, SOI index effect with one-year time lag; Log(Age), logarithmic effect of age; Age, lineal effect of age; Age*^{2}*, quadratic effect of age; Food, availability of food per capita (see Materials and Methods). The symbol "*" denotes interaction between factors and "+" an additive effect between factors. The best model is shown in bold.*

Discussion

As has been previously reported in other long-lived animals (Clutton-Brock, 1988; Sæther, 1990; Forslund and Pärt, 1995) breeding performance in Scopoli's Shearwater increases with age; younger breeders have later laying dates and smaller egg volumes than older breeders. Since egg size and laying dates are positively associated with breeding success in several bird species and also in Scopoli's Shearwaters (e.g., Ramos et al., 2003), it is expected that fertility also increases with age. This increase in reproductive performance could be mediated by a gain in breeding skills over the years, which would enhance

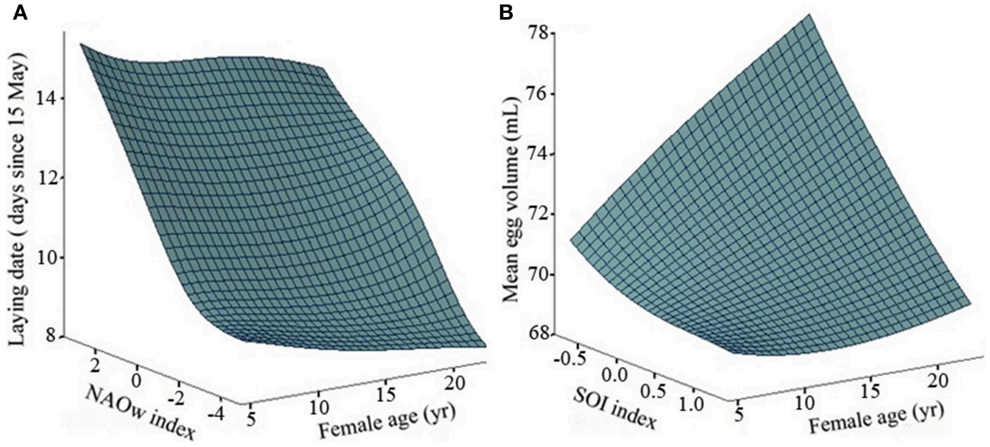

FIGURE 1 | Smoothing regression surfaces taking into account the effects of age and the climatic index that explain the greatest amount of variance for each breeding parameter. (A) NAO$_W$ index for laying date, **(B)** SOI index for egg volume.

TABLE 2 | Percentages of variance explained by each environmental covariable for each breeding parameter and likelihood ratio test values (see Materials and Methods).

Variable	*df*	R^2		χ^2		*P-value*	
		LD	VOL	LD	VOL	LD	VOL
NAOw	4	23.9	12.9	19.6	8.6	< 0.001***	0.003**
SOI	4	1.0	20.2	0.0	9.7	0.957	0.002**
Food	4	0.3	9.7	0.0	5.2	0.923	0.023*

*NAO$_W$, NAO index in winter; SOI, SOI index effect with one-year time lag; Food, availability of food per capita; LD, laying date; VOL, egg volume. Significance level codes: *** (0); ** (0.001); * (0.01).*

reproduction, or alternatively by the existence of a selection filter (the so-called "selection hypothesis"), whereby older age classes include a higher percentage of good breeders than younger age classes (Curio, 1983). In Storm petrel *Hydrobates pelagicus,* for example, individuals that survive their first breeding attempt should have a greater likelihood of breeding successfully the following year, probably due to the progressive selection of higher-quality individuals (e.g., Sanz-Aguilar et al., 2008). Furthermore, a previous study of Scopoli's Shearwater in our study colony (Genovart et al., 2013) detected that a large number first-time breeders do not return to the colony, either because they die (i.e., indicating thus the inherent costs of first reproduction) or permanently disperse to other breeding sites. Aside from the increase in breeding performance with age, several studies of long-lived animals have reported a decline in performance as a result of senescence (Vieyra et al., 2009; Pardo et al., 2013; Oro et al., 2014). We did not find a similar pattern, however the lack of senescence in our study may either be due to the small sample size (i.e., a lack of statistical power owing that there were only 4 individuals older than 20 years of age), to an increase of skip breeding with age, or to within-cohort phenotypic selection hiding senescence patterns (Cam et al., 2002).

Beside the clear and positive effect of age, we found that breeding performance varied across individuals and over the study period, the last probably reflecting environmental variability. We investigated whether the temporal variability was mirroring the fluctuations of large-scale climatic indices (namely NAOw and SOI) or the amount of fishing discards (a proxy for food availability just before the breeding season). NAOw and SOI are expected to influence breeding success of Scopoli's shearwater indirectly through their effects on marine productivity and oceanic conditions at the wintering grounds. Their influence on breeding performances, however, can be complex as climatic conditions might affect birds' energetic reserves through for example adverse flying conditions (Knutson et al., 2008; Arizmendi-Mejía et al., 2013) or alternatively they might influence them indirectly by changing the availability of prey, i.e., water column mixing, increasing river run off, and primary productivity (Lloret et al., 2001; Ottersen et al., 2001). This complexity is reflected in the fact that environmental covariates alone, despite being significant, explained only up to 24% of the yearly variability in breeding performances. A stronger effect of environmental covariates has been found for other seabirds (e.g., Frederiksen et al., 2004; Tavecchia et al., 2007; Dunn and Winkler, 2010; Barbraud et al., 2011). Genovart et al. (2013) found that the NAO winter index explained up to 40% of the temporal variance in breeding success in Scopoli's shearwater, but they included birds of unknown age and also nests monitored in an additional colony of the western Mediterranean (Chafarinas Island). Here we have restricted the analysis to birds of known age because we were interested in investigating the age-dependent pattern of breeding performance and whether environmental variability might change that pattern each year. It is possible that the statistical signal is lost in a smaller data set.

Our results showed an important heterogeneity among individuals in both, egg volume and laying dates (approximately 25% of the total variance of the retained model). At present we do not know the reason for such heterogeneity. Human disturbance and terrestrial predators are known to trigger dispersal and determined breeding success in seabirds (Cam et al., 2004; Fernández-Chacón et al., 2013). The studied colony however is located in a protected site with no human disturbances or alien predators. We can thus exclude the influence of these factors as a potential cause for nest quality heterogeneity. Differences among individuals might be due to difference in body size, individual investment, or individual ability in exploiting anthropogenic food resources (i.e., fishing discards, Votier et al., 2010). This individual heterogeneity might explain part of the differences between age classes, a pattern that was more marked under good environmental conditions than during harsh years, as it has been recorded for Audouin's gull (Oro et al., 2014). Other process that might be involved in the differences between the two patterns (good vs. bad years) is intermittent breeding, which has been commonly found in the study species (Mougin et al., 1997; Genovart et al., 2013). Previous studies on other seabirds found that during harsh years, individuals in bad condition may skip breeding (Cam and Monnat, 2000; Pyle et al., 2001; Sanz-Aguilar et al., 2008) and therefore the differences between age classes in breeding performance might be more marked in good years. In Scopoli's shearwater, males do not feed females during courtship as other seabirds (Jouanin et al., 2001), therefore male quality does not affect females' body condition and can be ruled out as a possible explanation. However, female reproductive investment might depend on male quality (Cunningham and Russell, 2000), but we have not enough data to assess whether shearwaters exhibit assortative mating. Out of nine cases in which both members of the pair were of known age, only in one case, female and male had the same age. Nevertheless, when males were included in the data set, results did not change.

Our results show clearly that the interplay of environmental conditions and individual age influences the observed breeding performance of Scopoli's shearwaters. Neither a proxy of the local food availability nor the large-scale climatic indexes can explain the temporal variability in the age pattern of breeding performance. This complex pattern is further complicated by the potential effects of individual quality. Future research should focus on the role of local climatic indexes and direct measures of food availability as predictors of breeding performances in long-lived birds.

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Supplementary Material

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fevo.2015.00069

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ORIGINAL ARTICLE

Environmental conditions, age, and senescence differentially influence survival and reproduction in the Storm Petrel

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Abstract Demographic parameters in wild populations are expected to be shaped by individual covariates and environmental variability. Thus, the understanding of the effects of age and/or environmental conditions on variability in vital rates is of special importance in ecological and evolutionary studies. Early age-related improvements in survival and reproduction and later declines due to senescence are expected, above all in long-lived species. Survival in these species is predicted to be a more conservative parameter than reproduction, thereby giving rise to less temporal variability. We studied age-dependent patterns of survival and breeding success in a long-lived seabird, the Mediterranean Storm Petrel *Hydrobates pelagicus melitensis*, and the additive influence of individual heterogeneity and environmental climatic variables using 22 years of individual-based data (1993–2014). The North Atlantic Oscillation index (NAO) and sea surface temperature (SST) were selected as proxies of environmental conditions in both breeding and wintering areas. Our results show that vital rates improved with age for both survival and breeding success. A slow effect of senescence at older ages was detected for breeding success, whereas models did not disentangle the occurrence or the absence of actuarial senescence. Reproduction was also influenced by the age of first observed reproduction: at the same age, more experienced birds that recruited earlier had a higher breeding success than less experienced ones. Breeding success (but not survival) also showed great temporal variability in accordance with theoretical predictions. Neither the NAO nor the SST explained this variability, probably because petrels feed on lower trophic levels than most pelagic seabirds and other physical features such as river runoffs and winds may be involved, as well as other environmental stressors such as predation by sympatric gulls.

Keywords Age pattern · Individual heterogeneity · Recruitment age · Climatic index · Seabird · *Hydrobates pelagicus melitensis* · Aging · Long-lived species

Zusammenfassung

Umweltbedingungen, Alter und Seneszenz beeinflussen bei Sturmschwalben Überlebensrate und Fortpflanzung in unterschiedlicher Weise

Es ist davon auszugehen, dass demografische Parameter bei Freilandpopulationen von individuellen Kovariablen und veränderlichen Umweltbedingungen geprägt werden. Daher ist das Verständnis der Auswirkungen von Alter und/oder Umweltbedingungen auf die Variabilität demografischer Parameter (Vitalraten) von besonderer Bedeutung für Studien zu Ökologie und Evolution. Frühe altersbedingte Steigerungen der Überlebensrate und des Bruterfolges sowie spätere Abnahmen aufgrund von Seneszenz sind zu erwarten, ganz besonders bei langlebigen Arten. Es ist anzunehmen, dass die Überlebensrate bei

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diesen Arten einen konservativeren Parameter darstellt als der Bruterfolg, was somit weniger zeitliche Variabilität zur Folge hat. An der Mittelmeer-Sturmschwalbe *Hydrobates pelagicus melitensis*, einem langlebigen Seevogel, untersuchten wir auf der Grundlage individuenbasierter Daten aus 22 Jahren (1993–2014) altersabhängige Muster bei Überlebensraten und Bruterfolg sowie den zusätzlichen Einfluss individueller Heterogenität und klimatischer Umweltvariablen. Wir wählten den Nordatlantischen Oszillationsindex (NAO; North Atlantic Oscillation) und die Meeresoberflächentemperatur (SST; sea surface temperature) stellvertretend für die Umweltbedingungen in den Brut- sowie in den Überwinterungsgebieten. Unsere Ergebnisse zeigen, dass sich die Vitalraten mit zunehmendem Alter sowohl für das Überleben als auch für den Bruterfolg verbesserten. Beim Bruterfolg war ein allmählicher Effekt der Seneszenz zu beobachten, wohingegen die Modelle das Auftreten oder Fehlen altersbedingt erhöhter Mortalität nicht entschlüsseln konnte. Die Fortpflanzung wurde ebenfalls vom Alter der ersten beobachteten Reproduktion beeinflusst: Erfahrenere Vögel, welche sich schon früh am Brutgeschehen beteiligt hatten, wiesen einen höheren Bruterfolg auf als weniger erfahrene. Der Bruterfolg (aber nicht die Überlebensrate) zeigte, in Übereinstimmung mit theoretischen Vorhersagen, ebenfalls eine starke zeitliche Variabilität. Weder der NAO noch die SST konnten diese Variabilität erklären, vermutlich weil die Sturmschwalben auf niedrigeren Trophieebenen nach Nahrung suchen als die meisten pelagischen Seevögel; außerdem könnten noch andere physikalische Faktoren eine Rolle spielen, wie zum Beispiel Zuflüsse oder Wind, wie auch andere umweltbedingte Stressfaktoren, darunter Prädation durch sympatrisch vorkommende Möwenarten.

Introduction

In long-lived birds, survival and reproduction typically increase in early ages, reach their maximum values in intermediate ages, and then finally abate in later years as an expression of senescence (Forslund and Pärt 1995; Jones et al. 2008; Sergio et al. 2011; Oro et al. 2014). Several non-exclusive hypotheses attempt to explain this pattern of individual improvement (Curio 1983; Forslund and Pärt 1995; Dugdale et al. 2011). The “constraint hypothesis“ links improvements to acquisition of experience and skills (Curio 1983; Sergio et al. 2014). The selection hypothesis predicts the progressive selective disappearance of low-quality phenotypes (Forslund and Pärt 1995; Sanz-Aguilar et al. 2008). However, in addition to selection, the progressive selective appearance (recruitment) of individuals differing in quality could mask age patterns at the population level (van de Pol and Verhulst 2006; Zhang et al. 2015). Finally, the hypothesis of the evolutionary trade-off between current reproduction and future survival (“restraint hypothesis” in Curio 1983) makes the implicit assumptions that reproduction is costly (Tavecchia et al. 2001; Sanz-Aguilar et al. 2008) and that this cost is constant over time because, otherwise, a variable (unpredictable) cost would benefit those individuals that breed regardless of the survival payoff (Marrow et al. 1996). These three hypotheses are not mutually exclusive (Sergio et al. 2014), and their relative importance may change according to age and trait. For example, the early life improvement in survival and reproductive performances could be the result of both constraining and selection mechanisms (Dugdale et al. 2011; Sergio et al. 2014), even if these mechanisms cannot predict the emergence of senescence later in life, i.e., the decline in reproductive performance and/or survival (the latter also called actuarial senescence) that occurs with age (Flatt 2012). This decline is likely to be due to physiological deterioration, which can be attributed to two non-mutually exclusive evolutionary mechanisms: the damaging effects of mutation accumulation (Medawar 1952) and antagonistic pleiotropy, i.e., a selection of mutations with adverse effects late in life (Williams 1957). Hamilton (1966) postulated that the negative effects of senescence start to appear at the age of the first reproduction attempt owing to the action of natural selection.

On the other hand, both survival and reproductive performance might change over time as a response to environmental conditions, thereby adding a temporal dimension to variation in age-dependent vital rates (Durant et al. 2004; Oro 2014; Oro et al. 2014; Chantepie et al. 2015). However, in long-lived species adult survival is very high and is expected to vary little over time compared to reproductive success (Roff 1992; Gaillard and Yoccoz 2003; Oro 2014).

An accurate description of the pattern of age-specific survival and reproductive performances is important for understanding individual life-history tactics and species-specific selective pressures. Moreover, environmental conditions can also be the driver of population dynamics through their effect on vital rates (Jenouvrier 2013; Oro 2014). Here, we analyze the age-dependent pattern of survival and reproductive success in a long-lived bird, the Mediterranean Storm Petrel *Hydrobates pelagicus melitensis*, using individual-based longitudinal data. We aimed to establish how fast vital rates increase with age (and breeding experience in the case of breeding success) and whether and when senescence appears. In addition, we investigated the potential influence of environmental variables and their variability as ecological predictors of both parameters.

Methods

Study area, individual and environmental data

The study was conducted on Benidorm Island in the western Mediterranean (38°30′N, 0°8′E), where more than 400 pairs of Storm Petrels breed in colonies in two caves located 150 m apart. From 1993 to 2014 accessible nests in both colonies were inspected every 2 weeks during the breeding season (April–September) to capture/recapture breeding birds, record breeding success, and mark chicks (details in Sanz-Aguilar et al. 2008, 2009a). Individuals were classified as "unsuccessful" if their egg failed to hatch or the chick did not fledge, while the contrary were classified as successful. During this period, a total of 1741 chicks were marked before fledging with stainless steel rings and a unique alphanumeric code. Annual monitoring of the nests resulted in 454 recaptures of 165 known-age breeders (i.e., birds marked as chicks). In addition, 66 rings of birds of known age were recovered in pellets of Yellow-Legged Gulls *Larus michahellis*, the main predator of the petrels in this colony (Oro et al. 2005; Sanz-Aguilar et al. 2009b). This information allowed us to estimate the survival of pre-breeder individuals (i.e., survival below the age of 3 years, the age of their first breeding attempt; see Sanz-Aguilar et al. 2009a), since young birds are present and prospect the colony but are not captured during the standard nest monitoring of breeding birds. Given the limited sample size and the natal dispersal of some individuals within the study area, we chose to combine data from the two colonies.

Mediterranean Storm Petrels are thought to stay in the Mediterranean Basin the whole year (see Soldatini et al. 2014), and currently no recoveries/observations of wintering birds have been made from any other site or region (own data). Information from regurgitates indicate that Storm Petrels in the studied colonies feed on Opossum Shrimps *Mysidacea* spp. and on small pelagic fish such as Anchovy *Engraulis encrasicolus* and Round Sardine *Sardinella aurita* (the authors, unpublished data). In addition, it is likely that birds also feed on other small pelagic fish, as described for the central Mediterranean populations (Albores-Barajas et al. 2011), and on Krill *Euphausiacea* and micro-zooplankton, as reported for the Atlantic populations of the closely related European Storm Petrel *Hydrobates pelagicus pelagicus* (D'Elbee and Hemery 1998).

The production, distribution, and abundance of the Storm Petrel's foraging resources may be influenced by large-scale climatic and hydrographic processes (Durant et al. 2004; Lloret et al. 2004; Bellido et al. 2008), as well by local factors such as river outflows, upwelling, and sea temperature (Estrada 1996; Ramírez et al. 2016). Here, we focus on the potential effects that a large-scale climatic index, the North Atlantic Oscillation index (NAO), and a local climatic measure, the sea surface temperature (SST) in the Alboran Sea and Benidorm area, could have on age-dependent survival and reproduction. The NAO is a large-scale fluctuation linked to the speed and direction of the surface westerlies blowing across the Atlantic (Hurrell, 1995) that have cascading effects on oceanographic and biological processes (Stenseth et al. 2002). We considered the winter NAO (i.e., December–March; $\mathrm{NAO_w}$) and used data available at https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based (last accessed May 2014). The Alboran Sea is located 392 km south of the breeding colony and has been identified as a potential wintering area for the species; its SST conditions have been shown to be negatively correlated with the annual survival of Storm Petrels breeding in the central Mediterranean (Soldatini et al. 2014). Data on winter SST (December–February) for the Alboran Sea ($\mathrm{SST_{alb}}$) were obtained from the National Oceanic & Atmospheric Administration (NOAA; http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html). The Alboran Sea has a complex water convection system (Vélez-Belchí et al. 2005) that gives rise to spatial heterogeneity in SST. We used the average SST of six points covering the whole Alboran Sea to reflect this variability. In addition, we used mean winter SST values for a 30-km buffer surrounding Benidorm Island ($\mathrm{SST_{ben}}$), since this represents a potential foraging area where high numbers of individual petrels are observed during the breeding season (Arcos et al. 2009). Sea surface temperatures (SST, °C) were sourced online on a weekly basis in 1993–2014 from two different sites: (a) AVHRR Pathfinder Version 5.2, spatial resolution of 0.041667°, obtained from the US National Oceanographic Data Center, and GHRSST (http://pathfinder.nodc.noaa.gov) for SST data (Casey et al. 2010); and (b) Aqua MODIS (http://oceancolor.gsfc.nasa.gov/), as level 3 Hierarchical Data Format (HDF) for SST products at a spatial resolution of 0.041667° (2002–2014). SST variables were processed and converted from HDF files to raster images using the Marine Geospatial Ecology Tools for ArcGIS10.1 (Roberts et al. 2010).

Statistical analysis

Multievent capture-recapture models were used to evaluate the effect of age and environmental conditions on survival probabilities (Pradel 2005), and individual random effects in both survival and recapture probabilities (Gimenez and Choquet 2010). The multievent framework distinguishes field observations (the events coded in the encounter histories) from the underlying inferred biological states of the individuals (Pradel 2005). The possible events were 0 (bird not observed on a particular occasion), 1 (bird captured as a chick or bird recaptured as a breeding adult), 2 (petrel recovered recently dead), while the underlying biological states were defined as A (alive), RD (recently dead), and LD (long dead). The probabilities of the transition between states (survival) and the probabilities of the states (recapture and recovery) (see details in Online Appendix 1) were estimated simultaneously by maximum likelihood using the program E-SURGE 1.6.3 (Choquet et al. 2009a, b). We first tested the goodness-of-fit (GOF) of the Cormack–Jolly–Seber model by cohort (i.e., to account for age effects and temporal effects) using the software U-CARE (Choquet et al. 2009a, b). Our starting model considered the following parameter constraints: (1) full variation in age survival (21 age classes); (2) recapture probabilities of 1- and 2-year-old birds fixed to zero (given that recruitment begins at 3 years; Sanz-Aguilar et al. 2009a); (3) recapture probabilities varying over time and with age (see details in Online Appendix 1); and (4) recovery probabilities varying over time and differing between 1-year-old and older birds (because most Storm Petrels spend their first year at sea and so recoveries of these birds are less probable, see details in Online Appendix 1). We first tested the effects of age (see below) and environmental covariates on survival. Once the best structure was selected, we tested the effects of individual heterogeneity on survival and recapture (Gimenez and Choquet 2010). The effect of age was tested using linear, quadratic, log, and quadratic log functions compared to full age and constant models. To further test for senescence, we compared models considering a linear age effect up to a particular threshold (from age 3 to age 8) that indicated age of stabilization (constant value) with models in which the threshold indicated the start age of senescence (linear age effect with a different intercept and slope).

Model selection was based on Akaike's information criterion (AIC) and the model with the lowest AIC was selected as the most parsimonious (Burnham and Anderson 2002); specifically for survival analyses we use the AIC adjusted for the effective sample size ($\mathrm{AIC_c}$). When the AIC difference between two models (ΔAIC) was at most 2, these models were considered to be equivalent (Burnham and Anderson 2002). For each model we calculated the Akaike weights (w_i) as an index of relative plausibility (Burnham and Anderson 2002). As a result of the limited sample size of several age classes during certain years, the evaluation of interactions of environmental covariates with age was not possible. The significance of environmental covariates was evaluated using an analysis of deviance with a Fisher–Snedecor distribution (ANODEV; Skalski et al. 1993) calculated as

$$F(1, \mathrm{np}(M_t) - \mathrm{np}(M_{\mathrm{cov}})) = \frac{\mathrm{Dev}(M_{\mathrm{cnt}}) - \mathrm{Dev}(M_{\mathrm{cov}})}{(\mathrm{Dev}(M_{\mathrm{cov}}) - \mathrm{Dev}(M_t))/(\mathrm{np}(M_t) - \mathrm{np}(M_{\mathrm{cov}}))}.$$

To assess the influence of environmental covariates on vital rates, we estimated the percentage of variation explained by each covariate (R^2) as

$$R^2 = \frac{\mathrm{Dev}(M_{\mathrm{cnt}}) - \mathrm{Dev}(M_{\mathrm{cov}})}{\mathrm{Dev}(M_{\mathrm{cnt}}) - \mathrm{Dev}(M_t)}$$

where $\mathrm{Dev}(M_{\mathrm{cnt}})$ is the deviance of the constant model (i.e., no effects considered), $\mathrm{Dev}(M_{\mathrm{cov}})$ is the deviance of the model with the covariate considered, and $\mathrm{Dev}(M_t)$ is the deviance of the time-dependent model.

The effects of individual heterogeneity were evaluated by means of likelihood ratio test (LTR) between models with and without individual random effects (Gimenez and Choquet 2010).

In our study population, successful and failed breeders have equal probabilities (Sanz-Aguilar et al. 2008). As modeling the effects of age, time, and environmental covariates while including individual random effects in a single analysis will lead to overparameterized models for our dataset, we analyzed breeding success separately using generalized linear mixed models (GLMMs). Before analysis, we investigated the extent of age-dependent assortative mating in the studied population to discard potential biases in the observed age-related breeding success that may arise from differential ages of partners. We used data from 18 breeding pairs for which the age of both partners was known. Assortative mating was assessed by a Spearman correlation test. We subsequently modeled the influence of age, the age of first observed breeding (i.e., recruitment age), and environmental covariates on breeding success by means of GLMMs using the glmmML package in R software (http://www.R-project.org). The age of first observed breeding was included to account for the selective appearance of individuals in the breeding population (van de Pol and Verhulst 2006). Individual identity was considered as a random effect to avoid pseudo-replication. Age was modeled as a factor (12 levels from age 3 to age 14) and as a continuous variable using different relationships (linear, quadratic, logarithmic, and quadratic logarithmic) to assess how breeding success varied with age. We limited our data to 14 age classes because of the very low number of observations of individuals at least 15 years old ($N = 11$) and their uneven temporal distribution (i.e., only observed during the final years of the study). The first step was testing the effects of age and individual recruitment age. Once we had found the best age curve describing changes in breeding success, we evaluated the temporal variation (i.e., year) and the additional potential influence of environmental covariates ($\mathrm{NAO_w}$ and SST). Again, because of the limited sample size of several age classes during certain years, the evaluation of the effect of a potential interaction of environmental covariates with age was not possible to test (i.e., the likelihood of these models did not converge). Model selection was based on AIC (see above).

To test the significant effect of each environmental covariate on breeding success, we used a likelihood ratio test (LRT) to compare the constant model with the model that included the covariate.

Results

Survival analysis

The overall GOF of the Cormack–Jolly–Seber model by cohort was not statistically significant, thereby indicating a good fit to the data ($\chi^2 = 16.32$, $df = 58$, $p = 1$). After modeling different age structures for recapture and recovery probabilities (see details in Online Appendix 1, Table A1), we retained two and seven age classes for recovery and recapture probabilities, respectively. The effects of age and year were additive for recapture and in interaction for recovery (recoveries of 1-year-old individuals occurred in very few years, results not shown). We used this structure to model survival probability. When modeling age with linear, log, and quadratic functions (models 1–6, Table 2), the model including the quadratic effect of log-age on survival (model 6, Table 2) was retained as the best model: survival probabilities substantially increased early in life (at 1–4 years), reached a plateau, and then slowly decreased (Figs. 1b, 2b). However, when specifically testing for senescence, models with two linear functions accounting for a survival increase and a later decrease (models 7–11, Table 2) showed lower support than models including a survival stabilization after initial increase (models 12–16, Table 2). In fact, a model in which survival increased up to age 4 and then stabilized had only 0.24 $\mathrm{AIC_c}$ points more than the model including the quadratic effect of log-age (models 6 and 12, Table 2), indicating high uncertainty about the existence of actuarial senescence. We used the structure of model with the lowest $\mathrm{AIC_c}$ value for testing environmental covariate effects (model 6, Table 2). The model including temporal variation in survival was not retained (model 17, Table 2), indicating that there was little temporal variability. Models with covariate effects in age-dependent survival probabilities (models 18–20, Table 2) failed to explain the temporal variability of survival (Table 2). The model with an individual heterogeneity on recapture (model 22, Table 3) was clearly supported as the best model, with the individual random effect being statistically significant (LTR, $0.5 \times \chi^2(0) + 0.5 \times \chi^2(1) = 54.09$, $p < 0.001$). Survival estimates from model 6 (Table 2), which did not account for individual heterogeneity in recapture, were not biased and were nearly identical to that of model 22 (Fig. 1b). The effect of individual heterogeneity on survival (model 21, Table 3) was not statistically significant (LTR, $0.5 \times \chi^2(0) + 0.5 \times \chi^2(1) = 1.05$, $p = 0.15$).

Breeding success analysis

The association between the ages of the two members of the breeding pairs indicate the existence of assortative mating by age ($N = 18$, Spearman correlation $R_s = 0.57$, $p = 0.05$). Although females were slightly younger than males (mean difference = 1.94, SD = 2.41), we assumed that the age of partners was similar.

The best model for breeding success (model 13, Table 1) had a quadratic age-dependent pattern of breeding success that increased until the age of eight and then decreased (Figs. 1a, 2a) and also a negative effect of recruitment age: individuals recruiting at young ages had a higher breeding success (at the same ages) than individuals recruiting later (Fig. 1a). Both the age of first observed reproduction and the quadratic individual age were statistically significant ($p = 0.01$ and $p = 0.03$, respectively, model 13). The models with only the quadratic age pattern (model 4, Table 1) or the age of first observed breeding (model 7, Table 1) were not strongly supported, they were close ($\Delta\mathrm{AIC} \leq 2$) to the constant model (model 1, Table 1). In addition to age effects, the effect of time (i.e., year) on breeding success was clearly supported (model 13, Table 1). However models with environmental covariates (models 14–16, Table 1) failed to explain the temporal variation in breeding success (Table 1). In fact, the environmental covariates ($\mathrm{NAO_w}$, $\mathrm{SST_{ben}}$, and $\mathrm{SST_{alb}}$) explained only 10.4, 11.6, and 0 %, respectively, of temporal variability, thereby showing a positive relationship in all cases.

Discussion

In long-lived species, survival and reproduction rates are expected to change with age (Stearns 1992). Long-term demographic studies (e.g., Pardo et al. 2012; Chantepie et al. 2015) predict an increase in breeding performance and survival at younger ages, a plateau of maximal values during adulthood, and finally a decrease at older ages (i.e., the evolutionary theory of senescence; Medawar 1952; Williams 1957). In our study, we found this age pattern in Storm Petrel breeding success and a clear increase at younger ages in survival. However, our results for survival should be interpreted with caution because the local

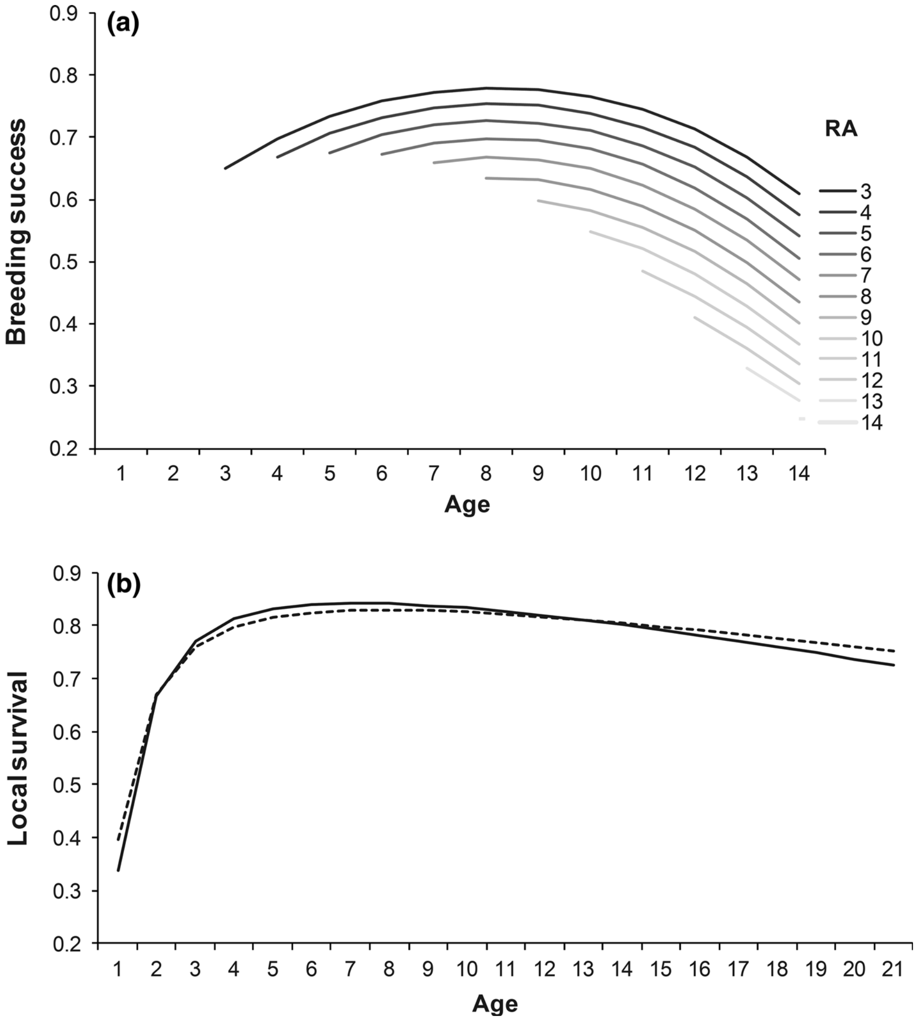

Fig. 1 **a** Variation in Storm Petrel breeding success with age and age of first observed reproduction (RA) estimated by model 10 (Table 1). Note that the first breeding attempt by Storm Petrels in Benidorm is at 3 years of age. **b** Variation in Storm Petrel survival with age estimated by model without individual random effect (*dashed line*; model 6, Table 2) and model with individual random effect in recapture (*solid line*; model 22, Table 3)

survival rates estimated here for young Storm Petrels may in part be the result of permanent dispersal rather than true mortality (Ballerini et al. 2015). In birds, dispersal typically occurs before the first reproduction attempt (i.e., natal dispersal, Greenwood and Harvey 1982). Storm Petrels typically breed in inaccessible places, and monitoring programs are limited to just a few accessible areas and nests, making dispersal events difficult to detect. Consequently, we were unable to disentangle the proportion of the estimated mortality that corresponded to permanent emigration. However, we believe that the estimated curve reflects the real age-dependent changes of survival in this species. Young Storm Petrels prospect several colonies (including the natal colony) before attempting to breed and were impossible to capture during the monitoring of the breeding pairs. To overcome this limitation we used the recoveries of individuals killed by gulls, which are predicted to be a random sample of the petrels that prospect and breed on the island (Oro et al. 2005; Sanz-Aguilar et al. 2009b).

Contrary to Hamilton's theory (1966) that postulates that the negative effects of senescence start with the first breeding attempt, we found that senescence in our study began slowly and rather later in life, at around 8 years of age for reproduction. For actuarial senescence, results were uncertain because the model with no senescence and the one indicating a very slow senescence starting at age 8 were equally supported. We believe that if actuarial senescence was low, the model with no senescence should be favored in terms of AIC$_c$, given its lower number of parameters, so more data should be collected to disentangle the existence of a decrease of survival at older ages. A delayed senescence has been detected in many other studies conducted in a wide range of species (see reviews by Nussey et al. 2013; Jones et al. 2014), including other long-lived birds such as vultures, albatrosses, and gulls (Chantepie et al. 2015; Pardo et al. 2012; Oro et al. 2014). Several studies have found that body-mass declines and poorer physiological condition negatively affect the foraging behavior of older individuals (e.g., Catry et al. 2006;

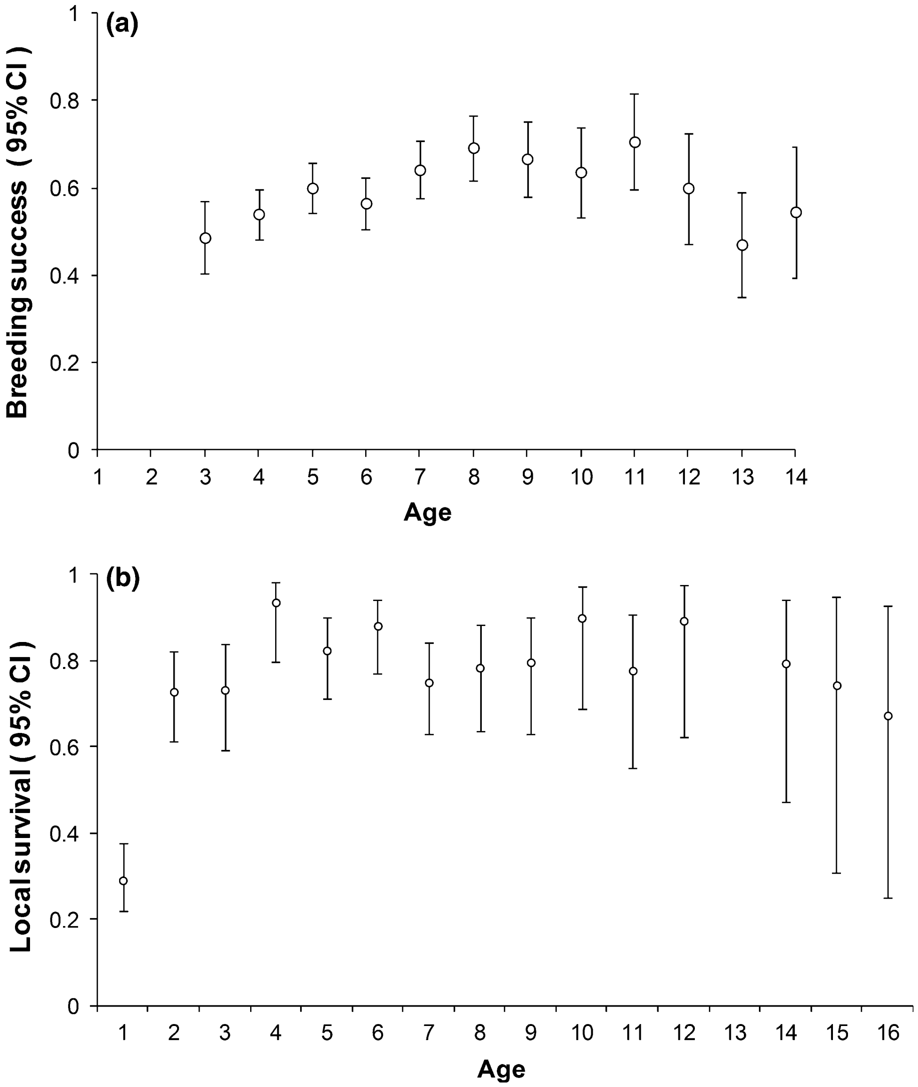

Fig. 2 Full age-dependent estimates of **a** breeding success and **b** survival and 95 % CI (model 2, Table 2). Only identifiable estimates are shown

Lecomte et al. 2010). Poorer foraging efficiency may in turn provoke changes in the immune system, thereby affecting survival (see review by Palacios et al. 2011).

Although we did not find evidence of individual heterogeneity in survival, we found a clear heterogeneity in recapture that did not bias survival estimates (as previously found for the Scopoli's Shearwater *Calonectris diomedea* by Choquet et al. 2013) and may respond to nest-specific catchability (Libois et al. 2012). Moreover, our results showed a negative influence of recruitment age (using the observed first age of reproduction as a proxy) on breeding success (see also Limmer and Becker 2010; Zhang et al. 2015). These results are in agreement with previous evidence on European Badgers *Meles meles* and Blue-Footed Boobies *Sula nebouxii*, in which an early recruitment was associated with higher reproductive success (Dugdale et al. 2011; Kim et al. 2011). On the contrary, other studies on long-lived birds associated an early recruitment with a lower reproductive success, lower egg volume, and/or delayed laying dates (van de Pol and Verhulst 2006; Limmer and Becker 2010). Our results may be explained by multiple and non-exclusive hypotheses. First, the constraint hypothesis (Curio 1983) which predicts a positive effect of breeding experience in breeding success, as we detected here (see also Sanz-Aguilar et al. 2008). Also, individuals that recruit early in life may have the opportunity of gaining and improving parental skills (Desrochers 1992; Weimerskirch 1992) resulting in a higher breeding success later in life than less experienced individuals recruiting later. Selective disappearance of low quality individuals may also explain the increase in breeding performance and survival at younger ages (Forslund and Pärt 1995). A second side of the same coin is that some Storm Petrels able to breed at younger ages may be high quality individuals, as suggested by the negative relationship between recruitment age and

Table 1 Modeling the effects of age, individual heterogeneity, and environmental conditions on breeding success using generalized linear mixed models

Model	Breeding success	np	Dev	AIC	ΔAIC	W_i	R^2
1	Constant	2	613.46	617.46	9.09	0.01	
2	Age	13	605.60	631.60	23.23	0.00	
3	A	3	612.46	618.46	10.09	0.00	
4	A^2	4	607.85	615.85	7.48	0.01	
5	Log(A)	3	611.46	617.46	9.09	0.01	
6	Log(A)^2	4	608.94	616.94	8.57	0.01	
7	RA	3	612.16	618.16	9.79	0.00	
8	Age + RA	14	601.36	629.36	21.00	0.00	
9	A + RA	4	608.18	616.18	7.81	0.01	
10	A^2 + RA	5	603.44	613.44	5.07	0.04	
11	Log(A) + RA	4	606.06	614.06	5.69	0.03	
12	Log(A)^2 + RA	5	604.22	614.22	5.86	0.03	
13	A^2 + year + RA	23	562.37	608.37	0.00	0.54	
14	A^2 + NAO_w + RA	6	599.18	611.18	2.81	0.13	10.37
15	A^2 + SST_ben + RA	6	598.70	610.70	2.33	0.17	11.54
16	A^2 + SST_alb + RA	6	603.44	615.44	7.07	0.02	0.03

np number of parameters, *Dev* relative deviance, *AIC* Akaike information criterion, *ΔAIC* AIC difference between the current model and the one with the lowest AIC value, W_i Akaike weight, R^2 variance explained by environmental covariates (* $p < 0.05$). Model notation: *Year* time effect, NAO_w winter North Atlantic Oscillation index, SST_{ben} winter sea surface temperature around Benidorm Island (potential foraging area), SST_{alb} winter sea surface temperature in the Alboran Sea (potential wintering area), *Age* full differences among age classes, *A* lineal effect of age, A^2 quadratic effect of age, *Log(A)* logarithmic effect of age, *Log(A)*^{2} quadratic natural logarithmic effect of age, *RA* first observed reproduction

breeding success found here. Further studies with additional data for a more reliable test of the interactions between age and recruitment and including their potential effects of last reproduction could provide additional insights into aging patters (van de Pol and Verhulst 2006; Dugdale et al. 2011; Zhang et al. 2015). Note that nearly half of the known-age breeders included in our study are still alive and reproducing.

In long-lived species, greater temporal variability is to be expected in parameters to which population growth rate is less sensitive (e.g., fertility and juvenile survival) (Sæther and Bakke 2000). Procellariforms tend to limit reproductive effort independently of offspring requirements when environmental conditions are unfavorable in order to maximize survival expectations (Navarro and González-Solís 2007). Accordingly, we found that breeding success had greater temporal variation than survival. However, previous studies have found important temporal variation in survival probabilities in the Storm Petrels from Benidorm Island, especially in those individuals breeding in one of the two caves in particular (Sanz-Aguilar et al. 2008, 2010). Since 2004 a culling program on predatory gulls has been carried out to minimize the effect of predation on survival (Sanz-Aguilar et al. 2009b, own data). As most of the data used in this study was taken at the end of the study period, this fact may explain the lack of temporal variability in survival.

Although breeding success was variable over time, none of the covariates we used explained its temporal variation satisfactorily. Several studies have shown that the NAO affects the Mediterranean climate (Hurrell 1995) and marine environments (including fish abundance and predator–prey interactions, Ottersen et al. 2001; Palomera et al. 2007). However, variability in the Storm Petrel's breeding success was not related to the NAO index (or to the SST around the breeding colony or in the Alboran Sea). Despite the changes in the distribution and abundance of prey consumed by marine predators caused by climatic indices and oceanographic processes (Durant et al. 2004), there are different local features such as river runoffs and winds that influence the availability of small pelagic prey species in the Mediterranean (Lloret et al. 2001). In addition to the complex dynamics of marine systems, Storm Petrel prey species (anchovies and sardines) have different spawning seasons and exhibit different time lags in larval development and growth, and may compete for food and space (see Lloret et al. 2004; Sabatés et al. 2006). These complex relationships between oceanographic conditions and fish abundance hinder the selection of an appropriate oceanographic index as a proxy of food availability in Storm Petrels (see Oro 2014), also because we lack data on the spatial extent of Storm Petrels' foraging areas. Additionally, factors such as mistiming between Storm Petrel phenology and seasonal pulses of marine productivity

Table 2 Modeling the effects of age and environmental conditions on Storm Petrel survival using multievent capture-recapture models

Model	Survival	np	Dev	AIC$_c$	ΔAIC$_c$	W_i	R^2
1	Constant	62	3145.53	3273.05	79.06	0.00	
2	Age	82	3031.25	3201.44	7.45	0.01	
3	A	63	3092.30	3225.58	31.59	0.00	
4	A^2	64	3072.90	3204.65	10.66	0.00	
5	Log(A)	63	3075.02	3204.66	10.67	0.00	
6	Log(A)^2	64	3062.23	3193.99	0.00	0.37	
7	A (≤3) + A (≥4)	65	3064.04	3197.91	4.68	0.04	
8	A (≤4) + A (≥5)	65	3061.62	3195.49	2.26	0.12	
9	A (≤5) + A (≥6)	65	3067.03	3200.90	7.67	0.01	
10	A (≤6) + A (≥7)	65	3067.19	3201.06	7.83	0.01	
11	A (≤7) + A (≥8)	65	3076.99	3210.86	17.63	0.00	
12	A (≤3) + constant (≥4)	63	3064.59	3194.23	0.24	0.23	
13	A (≤4) + constant (≥5)	63	3069.50	3199.14	5.15	0.02	
14	A (≤ 5) + constant (≥ 6)	63	3073.53	3203.16	9.17	0.00	
15	A (≤6) + constant (≥7)	63	3078.52	3208.16	14.17	0.00	
16	A (≤7) + constant (≥8)	63	3080.99	3210.62	16.63	0.00	
17	Log(A)^2 + year	84	3023.02	3197.52	3.53	0.06	
18	Log(A)^2 + NAO$_w$	65	3062.20	3196.07	2.08	0.13	0
19	Log(A)^2 + SST$_{ben}$	65	3062.22	3196.09	2.10	0.13	0
20	Log(A)^2 + SST$_{alb}$	65	3062.16	3196.03	2.04	0.13	0

General notation as in Table 1. Age classes considered are indicated between parentheses. *AIC$_c$* Akaike information criterion corrected by small sample size. Models 7–16 test the existence of a threshold value from which survival decreased or remained stable

Table 3 Modeling individual random effects on survival and recapture probabilities on Storm Petrel using multievent capture-recapture models

Model	Survival	Recapture	np	Dev	AIC$_c$	p value
6	Log(A)^2	Age (3, 4, 5, 6, ≥7) + t	64	3062.23	3193.99	
21	Log(A)^2 + h	age (3, 4, 5, 6, ≥7) + t	65	3061.18	3191.18	0.15
22	Log(A)^2	[age (3, 4, 5, 6, ≥7)t] + h	65	3008.14	3138.14	<0.001

General notation as in Table 2. h = individual heterogeneity (i.e., individual random effect), p value = statistical significance of individual random effect by means of LTR test

(Ramírez et al. 2016), or gull predation (Sanz-Aguilar et al. 2009a, b; Libois et al. 2012) not considered here, may also affect Storm Petrel reproduction and may add noise to the biological associations tested in this study.

A previous study of the Storm Petrels breeding in the central Mediterranean found a relationship between Storm Petrel survival and SST in the Alboran Sea and reported that this area is a potential wintering area (Soldatini et al. 2014). The Alboran Sea is mainly characterized by two anticyclonic gyres (western and eastern) that undergo large variations on the surface and serious variations in time that modify the overall structure of the water mass (Vélez-Belchí et al. 2005). As the precise wintering area for the species is unknown, we used SST values from the whole Alboran Sea as a proxy of wintering conditions but found no relationship with demographic parameters. We speculate that Storm Petrels from the western Mediterranean (Benidorm Island) winter in a different area to central Mediterranean Storm Petrels (Soldatini et al. 2014). Finally, although thousands of Storm Petrels have been monitored over the last 22 years, the sample size of known-age breeders (especially the older age classes) is still small. This fact is linked to the complexity of the marine environment, while the lack of knowledge about the distribution of Storm Petrels at sea hampers the study of the relationships between age-dependent vital rates and environmental conditions (Oro 2014). Further long-term monitoring and detailed studies of this species' foraging ecology during breeding and wintering are thus still needed.

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