UNIVERSITAT DE BARCELONA

Influence of predictable anthropogenic food subsides on seabird´s breeding investment

Influencia de los recursos alimentarios predecibles de origen antropogénico en la inversión reproductiva de las aves marinas

Enric Real Garcia

Influence of predictable anthropogenic food subsidies on seabirds’ breeding investment

Enric Real Garcia

Thesis 2019

Cover photo: Scopoli’s shearwater by Victor París

Influence of predictable anthropogenic food subsidies on seabirds' breeding investment

Enric Real Garcia

Doctoral Thesis

Programa de Doctorado en Ecologia, Ciencias Ambientales y Fisiologia Vegetal

Influence of predictable anthropogenic food subsidies on seabirds' breeding investment

Influencia de los recursos alimentarios predecibles de origen antropogénico
en la inversión reproductiva de las aves marinas

Memoria presentada por Enric Real Garcia para optar al grado de doctor por
la Universitat de Barcelona

Enric Real Garcia

El codirector de la tesis	El codirector de la tesis	La tutora de la tesis
Dr. Giacomo Tavecchia	Dr. Daniel Oro de Rivas	Dra. Mª Isabel Muñoz Garcia
Instituto Mediterraneo de Estudios Avanzados (IMEDEA-UIB-CSIC)	Centro d'Estudios Avanzados de Blanes (CEAB-CSIC)	Universidad de Barcelona (UB)

A Inmaculada Castro Durán

Acknowledgments / Agradecimientos

En primer lugar, quiero agradecer a mis directores de tesis, Giacomo Tavecchia y Daniel Oro el haberme ofrecido esta oportunidad que tanto anhelaba en un momento en el que parecía del todo imposible. Gracias por confiar en mi, por transmitirme tan valiosas enseñanzas y por darme vuestro apoyo en todo momento. Gracias también por vuestra infinita paciencia y por haber sido tan buenos guias en este increíble viaje.

En segundo lugar, quiero agradecer al Ministerio de Economía y Empresa (anteriormente Ministerio de Economía y Competitividad) el soporte económico recibido a través de una beca de formación de personal investigador (FPI) (ref: CGL2013-42203-R). Sin esta beca, esta tesis literalmente no existiría.

También quiero dar las gracias a mi esposa Inma, quien ha vivido esta aventura en primera persona. Gracias por celebrar conmigo cada uno de los pequeños logros y alegrías que me ha dado esta tesis, pero también por apoyarme y darme ánimos en los momentos difíciles. Gracias por estar siempre a mi lado y por ser como eres.

Esta tesis no habría sido posible de no haber sido por la importantísima labor de monitoreo llevada a cabo por el Grupo de Ecología y Demografía Animal (GEDA), antiguamente Grupo de Ecología de Poblaciones (GEP). Gracias al trabajo de estos grupos, a dia de hoy disponemos de series temporales de datos de gran calidad, para algunas de las poblaciones de aves marinas más importantes del Mediterraneo Occidental. En este sentido también quiero destacar la profesionalidad y el magnifico trabajo llevado a cabo por los técnicos José Manuel Igual y Albert Bertolero con quienes he tenido el placer de compartir multitud de jornadas. Gracias Manolo y Albert por vuestros valiosísimos consejos y enseñanzas.

También quiero dar las gracias a todas las personas con la que he tenido el gusto de colaborar en los artículos que aparecen en esta tesis. Gracias Alejandro Martínez-Abraín, Meritxell Genovart, Marc Bosch, Ana Sanz, Ana Payo y Manuel Hidalgo. Os estoy infinitamente agradecido por vuestra ayuda, aportaciones y consejos. Sin duda esta tesis es de todos vosotros.

Y como no, al resto de compañeros de grupo con quienes también he compartido horas de trabajo de campo, reuniones y descansos en el Ágora. Gracias Ainara, Pilar (Bibi), Andreu, Noelia, Álvaro, María, Alfonso y Marga. Ha sido un autentico placer conoceros y poder compartir esta aventura con todos vosotros.

Gracias también a José Manuel Arcos, Víctor París, Mariano Cebolla y Miquel Gomila por haber cedido amablemente las fabulosas fotografías con las que he podido ilustrar esta tesis.

Moltíssimes gràcies a la Universitat de Barcelona, en especial, a Teresa Vegas per la seva labor de coordinació i a la meva tutora de tesis Mª Isabel Muñoz, així com a als membres de la comisió de seguiment Marisol Felip, Lluís Cardona i Jacob González.

I also want to thank to Steve Votier, Richard Sherley and the Environment and Sustainability Institute (Penryn Campus, University of Exeter) for their support during my stay in the UK.

Finalmente, quiero dar las gracias a todo el personal del Instituto Mediterráneo de Estudios Avanzados (IMEDEA), por su maravillosa acogida, y en especial, al personal de administración por su imprescindible labor.

A todos vosotros, ¡gracias!.

Synopsis

Recent policies on the ban of fishing discards and the closure of open-air landfills are expected to reduce amount of predictable anthropogenic food subsidies (PAFS) for seabirds. To forecast the ecological consequences of these policies, it is necessary to understand the influence that each of these resources has on ecological parameters and how this can be mediated by density-dependent mechanisms. Besides, for those species exploiting both types of resources, it is important to consider whether or not their effects act synergistically. Finally, it is also important to understand how the ecological interactions between seabirds and PAFS can be influenced by other potentially important environmental factors, such as for example, the abundance of natural prey or the one of foraging conditions.

In the first chapter of this thesis, I reviewed the current knowledge on the ecological interactions between seabirds and fishery discards, with the aim of identifying the main knowledge gaps and to propose new challenges to improve our understanding of the ecological role of PAFS availability to seabirds. In the second chapter, I assessed the relative role of fishery discards and open-air landfills in the breeding investment of a generalist seabird, investigating the possible interplay with density-dependent mechanisms. In the third chapter I collaborated to investigate the role of PAFS in buffering environmental stochasticity and disrupting the natural synchronous dynamics between two seabirds. Finally, in the last chapter, I assessed the importance of several environmental factors in the breeding investment of three seabirds with contrasting life-history strategies. In particular, I considered local environmental variables (food abundance, competition and sea state) during breeding as well as the influence of winter conditions summarized by a large-scale climatic index, the North Atlantic Oscillation (NAO). Considering these variables simultaneously allowed me to assess the relative importance of natural and anthropogenic food resources, intra- and inter-specific competition and foraging conditions in the form of detectability and accessibility of food.

This thesis shows that the main knowledge gaps on seabird-discard ecological interactions are related to survival, dispersal and reproduction, the resilience of their populations against perturbations and the role of individual specialization in the foraging process. Results showed that both fishery discards and open-air landfills can significantly increase seabirds' breeding investment. However, the landfill effect was weaker than the effect of fishing discards, probably due to the lower quality of waste as food resource. It is also shown that these effects can be masked by density-dependence processes. In addition, the thesis highlights the importance of considering the possible influence of socio-economic factors on the availability of these PAFS depending on the geographic area considered. I showed that PAFS can alter natural stochasticity, increasing the breeding investment of generalist species, which in turn, may alter the community structure. Finally, this thesis makes evident that foraging conditions in the form of detectability and accessibility of food can play a very important role in key demographic parameters such as breeding investment. This implies that in contrast to what is commonly assumed, food abundance does not directly translate into food intake. Finally, the results also suggest that the influence that the winter North Atlantic Oscillation has on breeding investment in some seabirds is limited to winter months and acts in spring as a '*carry-over*' effect of winter conditions.

Contents

General introduction

Predictable anthropogenic food subsidies in seabirds' diet

Since the appearance of the first human societies and especially after the industrial revolution, human activities have spilled into the ecosystems a great amount of food in the form of Predictable Anthropogenic Food Subsidies (hereafter PAFS; Oro *et al.* 2013). The high spatio-temporal predictability of PAFS makes them, in general, more easily accessible than natural food resources, which are often sparse and less predictable. The effect of PAFS can also be mirrored in the foraging strategy and dispersion of organisms (Bartumeus *et al.* 2010). Hence, PAFS can constitute an important part of the diet of many opportunistic animals, increasing the natural carrying capacity of their populations.

Recent studies on the role of PAFS in animal population dynamics point to a more complex ecological role for food subsidies. PAFS, for example, can increase the resilience of populations, reduce their temporal variability and decrease the diversity of communities (Oro *et al.* 2013). Moreover, PAFS may also reduce the influence of environmental stochasticity as well as disrupt or mask communal processes, i.e. population synchronies (Heino *et al.* 1997; Liebhold *et al.* 2004). Changes in the availability of PAFS can have direct effects on important ecological parameters of opportunistic species as, for example, body condition, survival and/or breeding performance (Oro *et al.* 2013). These changes may in turn alter population dynamics, community structure and ecosystem functioning.

Seabirds are among the main scavengers of PAFS, due to their relative abundance, their wide distribution and mobility range and their often generalist diet. Two of the most important PAFS in terms of consumption by seabirds are discards from fisheries and landfill refuse (Oro *et al.* 2013). The relative role of these two types of subsidies changes according to the species considered, but regardless, they influence seabirds' ecology and modify the spatio-temporal pattern of their populations. Considering that seabirds are declining worldwide (Paleczny *et al.* 2015), elucidating the role of PAFS is fundamental to

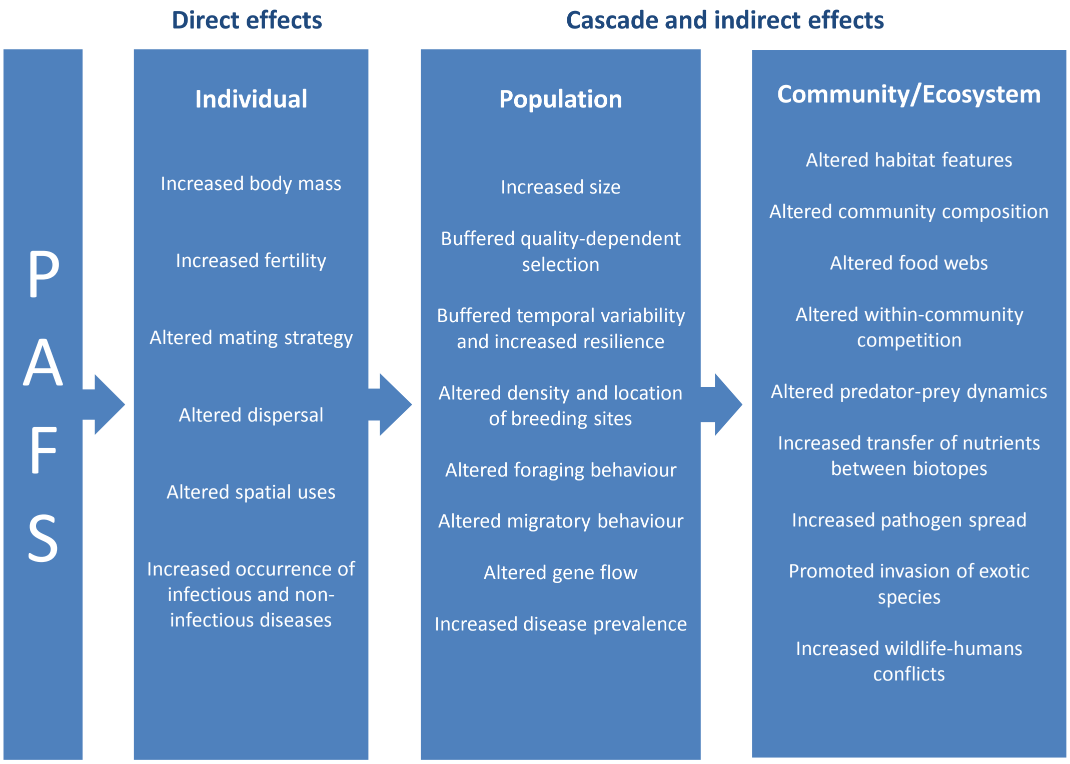

Figure 1. Effects of PAFS at individual, population, community and ecosystem levels. Adapted from Oro et al. 2013.

understanding their ecology and planning management actions, an important step towards achieving sustainability of human activities. However, measuring the impact of PAFS comes with serious challenges. Not only is the measure of the amount of subsidies available to birds difficult to calculate, but it is also challenging to determine its effect on seabird ecology because its influence can be indirect, i.e. through a change in the trophic chain or in the community, or through cryptic cascading effects, changing the phenotypic quality of individuals (Grémillet David *et al.* 2008; Steigerwald *et al.* 2015) or the changing population age-structure (Porter & Sealy 1982; Hamer *et al.* 1991).

Fishery discards

Discards generated by industrial fisheries are one of the main PAFS that are regularly incorporated into marine ecosystems and, in turn, made available to seabirds for consumption (Oro *et al.* 2013). Global discard generation has been estimated to be ca. 10

Figure 2. Selection by fishermen of marketable items and discard of those none marketable.

million t/year in recent decades with a peak of 19 million t/year in the late 1950's (Zeller *et al.* n.d.). In general, those fishing gears generating the most discards are also the least selective. In the western Mediterranean, trawl fisheries are known to be the most important fishing gear in terms of discard generation (around 40% of the total catch; Carbonell *et al.* 1998; Tsagarakis *et al.* 2014). In general, fishery discards are mainly composed of offal and organisms that are non-marketable given their low commercial interest, their poor state or because they do not meet the minimum legal size. In general, the most commonly discarded organisms are elasmobranchs, teleosts (both benthic and pelagic; Martínez-Abraín *et al.* 2002) and benthic invertebrates (Garthe et al. 1996). Discard practices have a great impact on populations of discarded species. In addition, it has been observed that trawls alter the structural complexity of submarine canyons, which may have consequences for the diversity of the community (Canals *et al.* 2006). These negative impacts are somehow counterbalanced by the positive effects that discards have for marine apical predators.

Fishery discards constitute an important food resource, especially for opportunistic species, including many seabirds (Votier *et al.* 2004; Cury *et al.* 2011; Bicknell *et al.* 2013). When discards are thrown into the sea, seabirds are usually the first organisms to intercept them. During the discard process, it has been observed that positions taken by different seabird species with respect to fishing vessels follow a particular pattern. For example, gulls usually stay very close to the stern of the vessel to intercept discards immediately after they are launched at sea, often even before they reach the water. Meanwhile, at a certain distance behind the vessels, shearwaters (the best divers) intercept those discards that have already begun to sink, and are therefore, now out of reach of gulls. This foraging strategy allows shearwaters to minimize kleptoparasitism (Oro 1996b; Arcos *et al.* 2001) and competition with other species, some of which are superabundant, e.g. larids (Abelló *et al.* 2003).

Seabirds are among the most important discard consumers at a global level. Three decades ago, it was estimated that in the North Sea alone, fishery discards were able to support ca. 6 million seabirds (Garthe et al. 1996). The high availability and predictability of this anthropogenic food resource, along with a decrease in the abundance of natural prey due to industrial fishing, makes seabirds increasingly dependent on fishery discards. For example, in some species discard availability is directly reflected in birds' reproductive parameters (Oro *et al.* 1995; Oro 1996a; Oro, D. *et al.* 1996). It has also been observed that a decrease in discard availability (e.g. due to a trawl moratorium) can cause seabirds to increase their interactions with other fishing gears such as longliners, which have associated high mortality rates due to bycatch (Laneri *et al.* 2010).

Open-air landfills receiving urban waste

Open-air landfills receiving urban waste can also constitute an important food resource for generalist seabirds. Among these landfills there are two types deserving special consideration: controlled and uncontrolled landfill sites. Controlled landfill sites are those especially designed and under legal regulations regarding their location, size, isolation

Figure 3. Examples of identification of controlled (left) and uncontrolled (right) deposits of urban solid waste through Google Earth.

capacity, etc.. At these sites, generally the type, the flux and the treatment of the waste processed is supervised. In contrast, uncontrolled landfill sites lack legal assets and supervision. In many countries, there are still several landfill sites that have seriously deficient infrastructure. Both controlled and uncontrolled deposits can be an important food source for some generalist seabirds. However, factors such as the size of the landfills, the amount of waste they receive periodically or the way they are managed can alter the way they influence the ecology of these birds.

The main characteristics of urban waste as a food resource for generalist species are: i) its high predictability spatially and temporally, ii) its high heterogeneity and iii) the high degree of insalubrity associated, which may potentially affect the health of individuals as well as their offspring. Compared to fishery discards, the number of seabird species attending landfill sites is small (species belonging to the family *Laridae* mainly). However, some of these species may be superabundant, increasing the level of competition for this resource. On the other hand, foraging at a landfill site is less costly than, for example, following fishing vessels and waiting for discards. The easier accessibility may favour survival of less competitive individuals (e.g. sick individuals, weaker or less experienced; see Genovart *et al.* 2010). The access to food resources for less competitive animals has probably been an important factor in the population increase of landfill foragers (Moulaï 2007; Duhem *et al.* 2008; Steigerwald *et al.* 2015), to the point that some countries have undergone management actions to reduce the population size (culling programs; see e.g. Bosch *et al.* 2000; Steigerwald *et al.* 2015). The effectiveness of these practices has been widely questioned and the best solution seem to be limiting the carrying capacity of the ecosystem through a progressive reduction of PAFS (Oro & Martínez-Abraín 2007).

Relative importance of fishery discards and open-air landfills as PAFS for generalist seabirds

Waste at landfills and especially fishing discards are present in the diet of many seabirds and as such, are an important driver of their ecology. Some seabirds, i.e. shearwaters, exploit fishery discards intensively but do not feed on landfill refuse, while others, i.e. gulls, exploit both types of PAFS. In addition to these main differences, there are also differences within the same species due to individual specialization in the use of food subsides. In order to forecast the ecological consequences arising from changes in the availability of these PAFS, it is important to understand the influence that each of these resources has on ecological parameters and how this can be mediated by density-dependent mechanisms. For those species exploiting both resources (fishery discards and open-air landfills), it is important to consider whether or not their effects act synergistically. Finally, it is also important to understand how the ecological interactions between seabirds and PAFS can be influenced by other potentially important environmental factors, such as for example, the abundance of natural prey or foraging conditions.

Current European policies: an ideal experimental scenario to assess the effects of PAFS on seabirds' ecology

In recent years, the European Union has progressively implemented new policies on the ban of fishery discards (e.g. European Comission 2008) and the closure of open-air landfills receiving urban waste (e.g. European Comission 1999). These policies are expected to have an important impact not only on seabirds' foraging ecology but also on their populations (Bicknell *et al.* 2013). Despite that some interactions between opportunistic species and PAFS have been previously reviewed (Tasker *et al.* 2000; Arcos *et al.* 2008; Wagner & Boersma 2011), the ecological and evolutionary implications of PAFS at a global level (Oro *et al.* 2013), as well as the potential impact of current EU directives, call for a revision of the existing information and the identification of the main knowledge gaps. On the other hand, these new policies offer an optimal BACI-type (Before-After-Control-Impact) scenario to assess the effects that changes on the availability and predictability of these PAFS (i.e. the carrying capacity) may have on the ecology of opportunistic organisms such as seabirds.

Egg volume as an indicator of food availability and breeding investment

It is known that the mean egg volume in a clutch (hereafter 'egg volume') is a suitable indicator of breeding investment and environmental conditions (e.g. food availability) reflecting the ecosystem's carrying capacity (Oro 1996b; Oro *et al.* 1996). Moreover, it plays an important role in chick size and survival, especially during their first days of life (Bolton 1991; Blomqvist *et al.* 1997; Risch & Rohwer 2000; Parsons *et al.* 2008). Therefore, considering the importance that PAFS may have for some generalist seabirds, changes in the availability of these resources should be reflected at least in part in the egg volume of these seabirds. However, changes in food availability can only explain a small part of the egg volume in birds. Indeed, egg volume can also respond to factors other than food availability, such as female size (Christians 2002), food quality (Batchelor & Ross 1984; Piatt & Anderson 1996; Grémillet David *et al.* 2008) as well as the age and experience of the individuals. (Cunningham & Russell 2000; Oro *et al.* 2014) .

A data collection challenge

Evaluating how the temporal variance of PAFS availability influences seabirds' breeding investment constitutes an important challenge. A first problem in using egg volume as a proxy of breeding investment is that seabirds (except those species that lay a single egg) can modulate breeding investment through egg number, i.e. the clutch size (Ruiz *et al.* 2000). Differences in the breeding investment among individuals can complicate its use as a proxy of environmental biotic and abiotic conditions. A way to limit this complication in multiparous species is to restrict the analysis to the egg volume of the modal clutch. A second complication is that the availability of food can only explain a small part of the egg volume variability (see above). Therefore, sufficiently large data sets are necessary to detect spatio-temporal differences and achieve a high enough statistical power to make inferences. In addition, detecting the effect of specific types of food (e.g. fishery discards or landfill refuse) on the egg volume can be especially difficult in species with a generalist diet. Another important challenge is that, in many cases, records on the amounts of urban waste available to birds at landfills are inaccurate or non-existent. In less developed countries, for example, many open-air landfills lack infrastructure and remain uncontrolled or cryptic. With regards to fishery discards, some European Union countries recently began to keep a record of the amounts of discards generated by fisheries; however, these data are also inaccurate and the time period covered is short.

General objectives

It is expected that current policies on the ban of fishery discards and the closure of open-air landfills that are being progressively implemented in several countries both inside and outside the European Union, will have important ecological consequences for seabirds. These policies also offer an ideal BACI-type scenario to assess the effects that a large-scale reduction in the carrying capacity may have on the ecology of populations, communities and ultimately on ecosystem functioning. I framed my work within the broad issue of the influence of PAFS on the ecology of seabirds. Within this framework, I dealt with several problems at different spatio-temporal scales, combining data collected in the field at individual and population levels with the information available in the literature.

In the first chapter of this thesis, I reviewed the current knowledge on the ecological interactions between seabirds and fishery discards (probably the most important PAFS that are being incorporated in marine ecosystems), with the aim of identifying the main knowledge gaps and to propose new challenges to improve our understanding of the ecological role of food availability to seabirds. It was a natural starting point, considering the large number of new studies on this issue, the increasing importance of PAFS in animal ecology and the new scenario established by the recent EU policies on PAFS management. In the second chapter, I assessed the relative role of fishery discards and open-air landfills in the breeding investment of a generalist seabird, investigating the possible interplay with density-dependent mechanisms. In the third chapter I collaborated to investigate the role of PAFS (in this case open-air landfills) in buffering environmental stochasticity and disrupting the natural synchronous dynamics between two seabirds. Finally, in the last chapter of the thesis, I assessed the importance of several environmental factors in the breeding investment of three seabirds with contrasting life-history strategies. In particular, I considered local environmental variables (food abundance, competition and foraging conditions) during the early breeding season as well as the influence of winter conditions summarized by a large-scale climatic index, the North Atlantic Oscillation (NAO). Considering these variables simultaneously allowed me to assess the relative importance of natural and anthropogenic food resources, intra- and inter-specific competition and foraging conditions in the form of detectability and accessibility of food. This thesis ends with a general discussion on the relevance of the findings in broad terms.

Introducción general

Recursos antropogénicos predecibles en la dieta de las aves marinas

Desde la aparición de las primeras sociedades humanas y en especial a partir de la segunda mitad del siglo XVIII, coincidiendo con la revolución industrial, los ecosistemas han venido recibiendo un importante flujo de subsidios alimentarios predecibles de origen antropogénico (en adelante PAFS; Oro *et al.* 2013). El elevado grado de predictibilidad tanto espacial como temporal de estos PAFS, hace que sean más fácilmente accesibles que muchas de sus presas naturales, a menudo más escasas y menos predecibles. De hecho se ha observado que los PAFS puede influir en la estrategia de forrajeo y en la dispersión de algunos organismos (Bartumeus *et al.* 2010). En la actualidad, los PAFS constituyen una parte importante de la dieta de muchos organismos oportunistas, lo cual ha hecho que se incremente la capacidad de carga natural de sus poblaciones. Además, algunos estudios recientes sobre el papel de los PAFS en la dinámica poblacional de los organismos sugieren que el papel ecológico de estos recursos todavía va más allá. De hecho se sabe que los PAFS pueden aumentar la resiliencia de las poblaciones, reducir su variabilidad temporal y disminuir la diversidad de la comunidad (Oro *et al.* 2013). Otros estudios también sugieren que los PAFS pueden aumentar la capacidad de los organismos de hacer frente a la estocasticidad ambiental, así como alterar o enmascarar procesos naturales de sincronización ecológica (Heino *et al.* 1997; Liebhold *et al.* 2004). En especies generalistas, los cambios en la disponibilidad de estos PAFS pueden tener una influencia directa en parámetros ecológicos importantes tales como la condición individual o el rendimiento reproductivo (Oro *et al.* 2013). A su vez, estos cambios pueden influir de forma indirecta en la dinámica poblacional, la estructura de las comunidades y el funcionamiento de los ecosistemas. Las aves marinas se encuentran entre los principales consumidores de PAFS a nivel global, debido a su abundancia, su elevada movilidad, su amplia distribución y a su dieta, a menudo generalista.

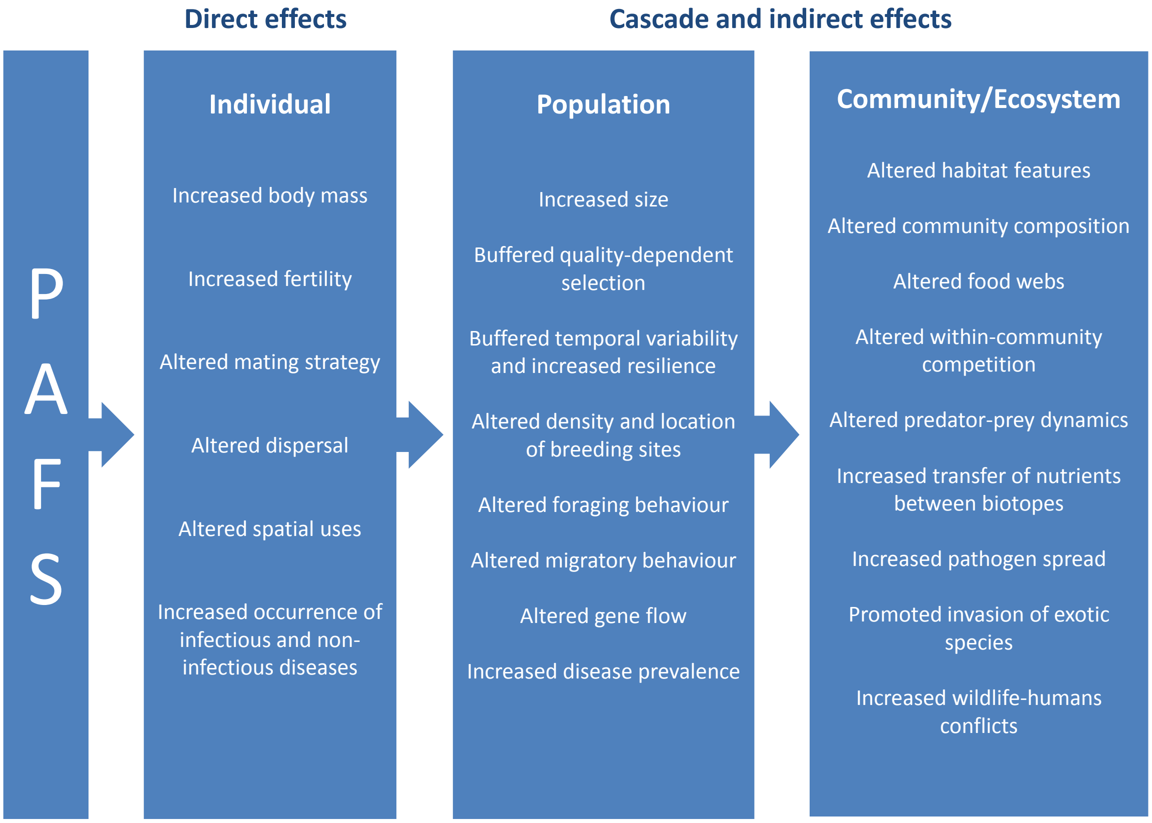

Figura 1. Efectos de los PAFS a nivel individual, de población, de comunidad y de ecosistema. Esquema adaptado a partir de Oro et al. 2013.

Dos de los PAFS más importantes en términos de consumo por parte de las aves marinas son los descartes de la pesca y la basura de los vertederos (Oro *et al.* 2013). El papel que juega cada uno de estos PAFS cambia en función de la especie considerada, sin embargo ambos recursos influyen en la ecología de las aves marinas y modifican los patrones de distribución espacio temporal de sus poblaciones. Teniendo en cuenta el declive que las aves marinas están experimentando a nivel global (Paleczny *et al.* 2015), entender cómo estos PAFS influyen en la ecología de estos organismos es de gran importancia para poder diseñar planes de gestión adecuados, lo cual supone además, un importante paso para hacer que las actividades humanas sean más sostenibles. Sin embargo, medir el impacto de estos PAFS presenta serias dificultades. Además de que el hecho de cuantificar la cantidad de estos recursos que están disponibles para las aves marinas puede ser una labor muy complicada *per se*, evaluar sus efectos en la ecología de las aves marinas también supone un importante desafío, dado que su influencia puede ser directa, indirecta (i.e. a través de cambios en la cadena trófica o en la comunidad), a través de efectos de cascada (i.e. alterando la calidad fenotípica de los individuos (Grémillet David *et al.* 2008; Steigerwald *et al.* 2015) o bien a través de cambios en la estructura de edad de la población (Porter & Sealy 1982; Hamer *et al.* 1991).

Descartes pesqueros

Los descartes generados por la pesca industrial constituyen uno de los principales PAFS que están siendo incorporados de forma regular en los ecosistemas marinos y que pasan a estar disponibles para las aves marinas (Oro *et al.* 2013). Se ha estimado que la generación de descartes a nivel global rondaba los 10 millones de toneladas anuales en las últimas décadas, con un pico de 19 millones de toneladas a finales de los años 50 (Zeller *et al.*

Figura 2. Proceso de selección y descarte de las capturas por parte de los pescadores.

2017). Por lo general, las modalidades de pesca que generan una mayor cantidad de descartes son también las menos selectivas. Se sabe que en el Mediterráneo Occidental el arrastre demersal es la modalidad de pesca más importante en términos generación de descartes (Alrededor del 40% de la captura total; Carbonell *et al.* 1998; Tsagarakis *et al.* 2014). En general, los descartes de la pesca se componen principalmente de vísceras y organismos no comercializables, ya sea por su bajo interés comercial, por no alcanzar la talla mínima legal o por su mal estado (p. ej. tras haber quedado aplastados en el copo etc.). En general, los organismos que constituyen los descartes suelen ser peces elasmobranquios, peces teleósteos e invertebrados bentónicos (Garthe et al. 1996). Entre los peces descartados se pueden diferenciar tanto especies bentónicas como pelágicas (Martínez-Abraín *et al.* 2002). Además del fuerte impacto que esta actividad tiene sobre las poblaciones de las especies que son objeto de descarte, también se ha observado que los aparejos de arrastre demersal alisan la superficie de los cañones submarinos, reduciendo la complejidad estructural de este hábitat y por tanto afectando a la diversidad de la comunidad (Canals et al. 2006). Estos impactos negativos quedan en cierto modo contrarrestados por los efectos positivos que los descartes pueden tener para algunos depredadores apicales marinos.

Los descartes de la pesca constituyen un recurso alimentario importante especialmente para especies oportunistas, entre las que se incluyen las aves marinas (Votier *et al.* 2004; Cury *et al.* 2011; Bicknell *et al.* 2013). Las aves marinas suelen ser los primeros organismos en interceptan los descartes cuando estos son arrojados al mar. Se ha observado que durante el proceso de descarte, la posición de las diferentes especies de aves marinas con respecto a los barcos de pesca sigue un patrón particular. Por ejemplo, las gaviotas tienden a posicionarse cerca de la popa del barco con el fin de interceptar los descartes a menudo incluso antes de que estos lleguen a tocar el agua. Por su parte, las pardelas (mejores buceadoras), a menudo se posicionan a cierta distancia por detrás del barco, a fin de interceptar los descartes que ya han empezado a hundirse quedando fuera del alcance de las gaviotas. Mediante esta estrategia de forrajeo, las pardelas consiguen minimizar la competencia con otras especies a menudo superabundantes (véase p. ej. Abelló *et al.*

2003) y/o cleptoparásitas (Oro 1996b; Arcos *et al.* 2001). Las aves marinas se encuentran entre los principales consumidores de descartes a nivel global. A finales de los años 90 se estimó que sólo en el Mar del Norte, los descartes de la pesca podían estar alimentando alrededor de 6 millones de aves marinas (Garthe et al. 1996). La elevada disponibilidad y predictibilidad de este recurso, junto con un incremento en la escasez de presas naturales asociado a la sobrepesca, ha provocado que las aves marinas dependan cada vez más de este recurso. Por ejemplo, en algunos casos se ha podido observar que los cambios en la disponibilidad de este recurso se pueden ver reflejados en parámetros demográficos de algunas especies (Oro *et al.* 1995; Oro 1996a; Oro, D. *et al.* 1996). También se ha observado que al disminuir la disponibilidad de descartes, p. ej. durante las moratorias de la pesca de arrastre, algunas aves marinas aumentan el nivel de interacción con otras modalidades de pesca como el palangre. Esto constituye un problema, ya que esta modalidad de pesca se asocia a una elevada tasa de mortalidad de aves marinas por captura accidental (bycatch; véase p.ej. Laneri *et al.* 2010).

Vertederos a cielo abierto de residuos sólidos urbanos

Los vertederos a cielo abierto de residuos sólidos urbanos (RSU) también constituyen una importante fuente de alimento para algunas aves marinas generalistas. En función de sus características, existen dos grandes tipos de vertederos de RSU que merecen una atención especial: los depósitos controlados y los depósitos no controlados. Los depósitos controlados son infraestructuras legalmente reguladas que han sido específicamente diseñadas para este fin cumpliendo con una serie de requisitos en cuanto a su localización, capacidad, impermeabilización, etc. y donde además se lleva a cabo un control tanto del flujo (tipo, la cantidad etc.) como del tratamiento de los residuos que se procesan. Por su parte, los depósitos no controlados, son todos aquellos vertederos de residuos sólidos urbanos que no cumplen con alguna/s de las características anteriores. A día de hoy, en muchos países todavía existen multitud de vertederos cuyas infraestructuras presentan serias deficiencias. Tanto los depósitos controlados como los no controlados pueden constituir una fuente de alimento importante para algunas aves marinas generalistas. Sin embargo, factores como el tamaño de los vertederos, la cantidad de residuos que reciben

Figura 3. Ejemplos de identificación de depósitos controlados (izquierda) y no controlados (derecha) de residuos sólidos urbanos a través de Google Earth.

periódicamente o el modo en que estos son gestionados pueden alterar su influencia en la ecología de estas aves.

Las principales características de la basura de los vertederos como recurso alimentario son: i) una elevada predictibilidad tanto espacial como temporal, ii) una gran heterogeneidad y iii) un elevado grado de insalubridad, lo cual puede repercutir negativamente en la salud de los individuos y de su descendencia. En comparación con los descartes de la pesca, el número de especies de aves marinas que se alimentan en los vertederos es reducido (en su mayoría especies de la familia *laridae*). Sin embargo, algunas de estas especies pueden ser superabundantes, por lo que el nivel de competencia por este recurso también puede ser muy elevado. Por otra parte, el coste energético asociado al proceso de forrajeo en los vertederos puede ser relativamente bajo si se compara por ejemplo, con la energía que requiere seguir a los barcos de pesca en busca de descartes. Esta mayor accesibilidad podría favorecer la supervivencia de individuos que presentan mayores limitaciones a la hora de obtener el alimento (enfermos, lisiados, menos experimentados etc. (véase Genovart *et al.* 2010). De hecho, se ha observado que la disponibilidad de este recurso favorece considerablemente el crecimiento poblacional en aves marinas generalistas (Moulaï 2007; Duhem *et al.* 2008; Steigerwald *et al.* 2015), hasta el punto de que en algunos casos se han llevado a cabo programas de de control de sus poblaciones (Bosch *et al.* 2000; Steigerwald *et al.* 2015). No obstante, la efectividad de estas prácticas ha sido bastante cuestionada ya que parece ser que en la mayoría de estos casos, la solución pasa por limitar la capacidad de carga del ecosistema a través de una reducción progresiva de estos recursos (Oro & Martínez-Abraín 2007).

Importancia relativa de los descartes de la pesca y de los vertederos como PAFS para las aves marinas generalistas

La basura de los vertederos y en especial los descartes de la pesca, forman parte de la dieta de muchas especies de aves marinas, lo que hace que estos recursos puedan influir de forma importante en la ecología de estos organismos. Algunas aves marinas como p.ej. algunas pardelas explotan intensivamente los descartes de la pesca, pero no la basura de los vertederos, mientras que otras, como p.ej. algunas gaviotas, explotan ambos PAFS. Sin embargo, también se dan diferencias dentro de una misma especie debido a la especialización individual en el uso de los subsidios alimentarios. De cara a poder pronosticar las consecuencias ecológicas de los cambios en la disponibilidad de estos PAFS, es importante entender la influencia por parte de cada uno de estos recursos, así como si esta influencia se ve mediada por mecanismos de densodependencia. Así mismo, en el caso de las especies que explotan ambos recursos (descartes y vertederos) también es importante evaluar la posibilidad de que sus efectos ecológicos puedan actuar de forma sinérgica. Finalmente, también es importante entender cómo las interacciones entre las aves marinas y los PAFS pueden verse afectadas por otros factores ambientales potencialmente importantes, como por ejemplo la abundancia de presas naturales o las condiciones de forrajeo.

Políticas europeas en materia de descartes y vertederos: un escenario experimental óptimo para evaluar los efectos de los PAFS en la ecología de las aves marinas

A lo largo de los últimos años, en la Unión Europea se están implementando progresivamente una serie de políticas en materia de prohibición de descartes (p. ej. European Comission 2008) y cierre de vertederos de RSU a cielo abierto (P. ej. European Comission 1999). Se espera que estas políticas tengan un impacto importante no sólo para la ecología de forrajeo de las aves marinas sino también en sus poblaciones (Bicknell *et al.*

2013). A pesar de que las interacciones entre especies oportunistas y PAFS han sido revisadas por algunos trabajos (Tasker *et al.* 2000; Arcos *et al.* 2008; Wagner & Boersma 2011), las implicaciones ecológicas y evolutivas de los PAFS a nivel global (Oro *et al.* 2013) así como el impacto que se espera que tengan las directivas europeas, plantean la necesidad de revisar el conocimiento existente sobre estas interacciones e identificar los principales vacíos de conocimiento (knowledge gaps). Por otra parte, estas nuevas políticas ofrecen un escenario experimental ideal de tipo BACI (Before-After-Control-Impact) de cara a estudiar los efectos que los cambios en la disponibilidad y la predictibilidad de estos PAFS (i. e. de la capacidad de carga) puede tener sobre los parámetros ecológicos de organismos oportunistas como es el caso de algunas aves marinas.

El volumen del huevo como indicador de la disponibilidad de alimento y la inversión en reproducción

Se sabe que el volumen medio del huevo en una puesta (en adelante 'volumen del huevo') es un buen indicador de la energía que las aves marinas invierten en la reproducción y de las condiciones ambientales (p.ej. de la disponibilidad de alimento) ya que en él se pueden ver reflejados la capacidad de carga del ecosistema (Oro 1996b; Oro *et al.* 1996). Además también se sabe que el tamaño del huevo está relacionado con el tamaño de los pollos así como en su supervivencia, especialmente durante los primeros días de vida (Bolton 1991; Blomqvist *et al.* 1997; Risch & Rohwer 2000; Parsons *et al.* 2008). Por tanto, se puede asumir que el volumen del huevo es un indicador espacio-temporal de la fitness o de la eficacia biológica de una población. Teniendo en cuenta la importancia que tienen los PAFS para algunas aves marinas generalistas, cabe esperar que los cambios en la disponibilidad de estos recursos se vean reflejados en el volumen del huevo de estas aves. Sin embargo, capturar este efecto puede ser bastante complejo, ya que por lo general, los cambios en la disponibilidad del alimento sólo reflejan una pequeña parte de la variabilidad del volumen del huevo en aves. Esto se debe a que el volumen del huevo también depende de otros factores diferentes de la disponibilidad de alimento *per se*, como son el tamaño de la hembra (Christians 2002), la calidad del alimento (Batchelor & Ross 1984; Piatt & Anderson

1996; Grémillet David *et al.* 2008) o la edad y la experiencia de los individuos (Cunningham & Russell 2000; Oro *et al.* 2014).

Un desafío de recopilación de datos

Evaluar cómo la variabilidad temporal en la disponibilidad de estos PAFS influye en la energía que las aves marinas invierten en la reproducción constituye un importante desafío. Un inconveniente de utilizar el volumen del huevo como indicador de la inversión en la reproducción es que las aves marinas (excepto en aquellas especies que ponen un solo huevo) pueden modular dicha inversión a través del tamaño de la puesta (Ruiz *et al.* 2000). Las diferencias entre individuos en la inversión en reproducción pueden complicar su uso como indicador de las condiciones bióticas y/o abióticas. Una forma de limitar el efecto de esta complicación en especies que ponen más de un huevo, consiste en considerar únicamente el volumen de huevo de la puesta modal. Otro inconveniente es que la disponibilidad de alimento únicamente explica una pequeña parte de la variabilidad del volumen del huevo (ver más arriba), lo cual implica que en general, para poder detectar estos efectos haya que trabajar con series datos que abarquen una escala espacio-temporal lo suficientemente grande. Además, detectar el efecto de un alimento concreto (p. ej. descartes pesqueros o basura de vertederos) en el volumen del huevo, puede ser especialmente difícil en especies que siguen una dieta generalista. Otra dificultad importante es que a menudo, no se dispone de registros de generación de PAFS lo suficientemente precisos o bien estos son inexistentes. De hecho, en algunos países, muchos vertederos de RSU ni siquiera disponen de infraestructura. Por lo que respecta a los descartes de la pesca, a día de hoy sólo unos pocos países han empezado a llevar un registro de los descartes generados, aunque las series de datos de las que se dispone son poco precisos y/o abarcan periodos de tiempo muy cortos.

Objetivos generales

Se espera que las actuales políticas en materia de prohibición de descartes y cierre de vertederos que están siendo progresivamente implementadas en diversos países, dentro y fuera de la Unión Europea, tengan consecuencias ecológicas importantes para las aves marinas. Por otro lado, estas políticas plantean un escenario ideal de tipo BACI que nos puede ayudar a entender mejor los efectos que una reducción de la capacidad de carga a gran escala pueden tener sobre la ecología de poblaciones y comunidades, así como para el funcionamiento de los ecosistemas. Mi trabajo se enmarca en investigar el papel de algunos de los PAFS más importantes en la inversión que algunas aves marinas hacen en la reproducción. Dentro de este marco de trabajo, he tratado diferentes problemáticas que abarcan diferentes escalas espacio-temporales, combinando el uso de datos de campo tanto a nivel de individuo como de población, con diversos tipos de variables ambientales. En el primer capítulo de esta tesis se revisa la literatura existente sobre las interacciones ecológicas que se dan entre las aves marinas y los descartes de la pesca (probablemente los PAFS más importantes que están siendo incorporados en los ecosistemas marinos), con el fin de identificar los principales vacíos de conocimiento existentes y plantear nuevos retos orientados a mejorar nuestra comprensión sobre el papel de la disponibilidad de alimento en la ecología de las aves marinas. Este era un punto de partida bastante natural teniendo en cuenta el elevado número de estudios que abordan este tema, la creciente importancia de los PAFS desde el punto de vista ecológico y el escenario que se deriva de las recientes políticas de la Unión Europea en relación a la gestión de estos PAFS. En el segundo capítulo evalué la importancia relativa de dos importantes PAFS, los descartes de la pesca y la basura de los vertederos, en la inversión que una ave marina generalista hace en la reproducción, teniendo también en cuenta su posible interacción con mecanismos de densodependencia. En el tercer capítulo colaboré en un estudio en el cual se investiga la capacidad que tienen algunos PAFS (en este caso un vertedero de RSU a cielo abierto) a la hora de amortiguar la estocasticidad ambiental y alterar la dinámica de la sincronía natural entre dos especies de aves marinas. Finalmente, en el último capítulo de la tesis, evalué el papel que juegan diversos factores ambientales en la inversión en reproducción de tres aves marinas que presentan diferentes estrategias de vida. En particular, consideré variables ambientales locales (abundancia de alimentos, competencia y condiciones de forrajeo) durante la época de cría así como la influencia de las condiciones invernales, resumidas a partir de un índice climático a gran escala, la Oscilación del Atlántico Norte (NAO). El considerar estas variables simultáneamente me permitió estimar la importancia relativa de los recursos alimentarios, tanto naturales como antropogénicos, la competencia (intra e interespecífica) y las condiciones de forrajeo (i.e. detectabilidad y accesibilidad del alimento). Esta tesis termina con la discusión general de la relevancia de los hallazgos en términos generales.

Supervisors' report

Dr. Daniel Oro de Rivas, Research professor at CEAB-CSIC and Dr. Giacomo Tavecchia, tenured researcher at IMEDEA-UIB-CSIC, as supervisors of the PhD. Thesis of Mr. Enric Real García entitled: *Influence of predictable anthropogenic food subsidies on seabirds' ecology*.

INFORM

That the present thesis is organized into four chapters corresponding to 2 published articles and 2 manuscripts under review. These publications and manuscripts are listed below, along with the name of the journal and the corresponding impact factor:

Enric Real, Giacomo Tavecchia, Meritxell Genovart, Ana Sanz-Aguilar, Ana Payo-Payo, Daniel Oro, 2018. Discard-ban policies can help improve our understanding of the ecological role of food availability to seabirds. Scientia Marina. 82S1 : 121-129.
Impact factor: 1,183.

Enric Real, Daniel Oro, Alejandro Martínez-Abraín, José Manuel Igual, Albert Bertolero, Marc Bosch and Giacomo Tavecchia, 2017. Predictable anthropogenic food subsidies, density-dependence and socio-economic factors influence breeding investment in a generalist seabird. Journal of Avian Biology 48: 1462–1470.
Impact factor: 2,488.

Ana Payo-Payo, José Manuel Igual, Ana Sanz-Aguilar, Enric Real, Meritxell Genovart, Meritxell, Daniel Oro, Giacomo Tavecchia. Predictable Anthropogenic Food Subsidies Decouple Inter-Specific Temporal Synchrony. Under review in Oikos.
Impact factor: 3,71

Enric Real, Albert Bertolero, José Manuel Igual, Daniel Oro, Ana Sanz-Aguilar, Meritxell Genovart, Manuel Hidalgo and Giacomo Tavecchia. Título: It's not all availability: carry-over

effects, detectability and accessibility to food also explain breeding investment in long-lived animals. Revista: Under review in Ecology.
Impact factor: 4,285.

CERTIFIES

That the participation of the student in the articles and manuscripts sent in co-authorship has always been relevant. In all the articles and manuscripts where the student is the first author, he has taken over the planning of the study, the analysis and the writing. In the article in which the student does not appear as the first author, he has participated in the planning the study and writing of the manuscript. Likewise, they also certify that none of the co-authors of the published or submitted manuscripts included in this thesis has used implicitly or explicitly these works for the preparation of any other doctoral thesis.

Esporles, July 6, 2019

Giacomo Tavecchia Daniel Oro de Rivas

Main chapters

Chapter 1

Discard-ban policies can help to improve our understanding on the ecological role of food availability to seabirds

---

Enric Real, Giacomo Tavecchia, Meritxell Genovart, Ana Sanz-Aguilar, Ana Payo-Payo and Daniel Oro (2018). Discard-ban policies can help to improve our understanding on the ecological role of food availability to seabirds. *Scientia Marina*. 82 (S1), 115-120.

Discard-ban policies can help to improve our understanding on the ecological role of food availability to seabirds

Enric Real, Giacomo Tavecchia, Meritxell Genovart, Ana Sanz-Aguilar, Ana Payo-Payo and Daniel Oro

E. Real (https://orcid.org/0000-0002-6190-6303)(ereal@imedea.uib-csic.es), G. Tavecchia, Ana Sanz-Aguilar and Ana Payo-Payo, Group of Ecology and Animal Demography, GEDA, IMEDEA (CSIC-UIB), C/Miquel Marquès 21, 07190, Esporles, Spain. Meritxell Genovart and Daniel Oro, CEAB (CSIC), Accés Cala Sant Francesc 14, 17300 Blanes, Spain and IMEDEA (CSIC-UIB), Miquel Marquès 21, 07190 Esporles, Spain.

1.1. Abstract

Discards from fisheries are the most important predictable anthropogenic food subsidies (PAFS) that are being incorporated into marine ecosystems. Changes on their availability and predictability can help to understand the role that food availability (i.e. an important indicator of the carrying capacity) plays at different ecological levels, from individual fitness to community dynamic and ecosystem's functioning. Seabirds constitute an excellent model to evaluate the ecological effects derived from a lack of discards for several reasons: seabirds are 1) one of the most important discard scavengers, 2) easy to monitor and 3) apical predators globally distributed, which makes them suitable ecosystem's health indicators. Here we review the existing information on seabirds-discards interactions to identify main knowledge gaps and to propose new challenges to improve our understanding on the general role of food availability. We conclude that the new policies on the ban of fishery discards that are being progressively implemented at the European

Union, Norway, Chile or New Zealand offer a suitable experimental scenario to improve our understanding on how a large decrease in the carrying capacity may alter demographic parameters such as survival, dispersal and reproduction, the resilience of populations against perturbations and the role of individual specialization in the foraging process.

Keywords: Food availability; fishery discards; seabirds; ecological interactions; discard policies.

1.2. Introduction

The large amount of discards in the form of offal that are daily generated by industrial and artisanal fisheries and thrown into the sea constitute one of the most important and predictable anthropogenic food subsidies (PAFS) that are being incorporated into marine ecosystems worldwide (Oro et al. 2013). Global discards generation in recent years have been estimated in ca. 10 million t/year, with a peak of 19 million t/year in the late 1950s (Zeller et al. 2017). The high abundance and predictability of this anthropogenic food resource together with a decrease on the natural prey availability due to industrial fisheries makes fishery discards to have important ecological implications at global level for marine scavengers, including seabirds (Votier et al. 2004, Cury et al. 2011, Bicknell et al. 2013, Oro et al. 2013). Garthe et al. (1996) for instance, estimated that 5.9 million seabirds were potentially supported by fishery discards in the North Sea.

Changes in the availability and predictability of fishery discards as PAFS can help to understand the ecological role that food availability (i.e. carrying capacity) have at multiple ecological levels, from individual fitness to community dynamic and ecosystem's functioning.

Seabirds constitute an excellent model to evaluate the ecological effects derived from a lack of PAFS for several reasons: seabirds are 1) one of the most important discard scavengers at global level, 2) easy to monitor (by the fact of breeding on land) and 3) apical predators globally distributed, which makes them suitable ecosystem's health

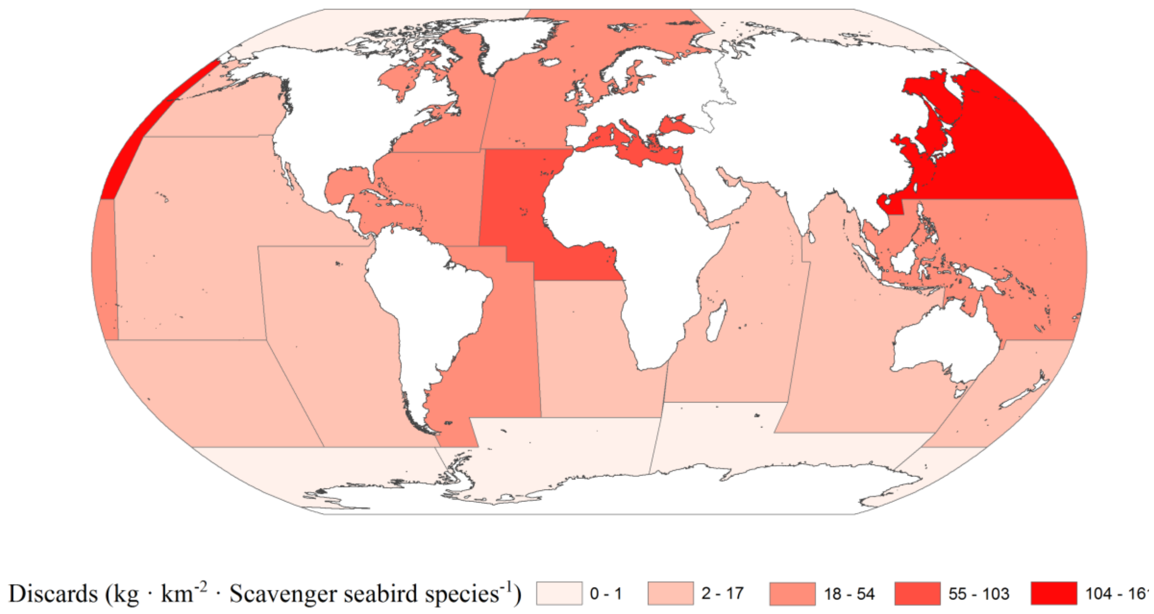

Figure 4. Global distribution of fishery discards availability for seabirds in different major FAO fishing areas considering amounts of discards available per unit area and number of scavenger seabird species converging in each area.

bioindicators. The link between seabirds and fishery discards has been reviewed in several studies (Tasker et al. 2000, Arcos et al. 2008, Wagner and Boersma 2011). However, the ecological and evolutionary implications that fishery discards have as PAFS at global level (Oro et al. 2013) as well as the current changes in fishery policies (see e.g. Borges et al. 2016) call for a new revision of the existing information and the identification of knowledge gaps.

Here we review the global current knowledge on the ecological interactions between seabirds and fishery discards with the aim to identify main knowledge gaps and to propose new challenges to improve our understanding on the ecological role that food availability have for populations, communities and ecosystems.

1.3. Methods

Table 1. Percentage of species (regarding the total number of species of each taxonomic family) for which different ecological effects derived from seabird-discard interactions were evaluated by reviewed studies (e.g. the effect of fishery discards on the diet was evaluated in 25% of species belonging to the taxonomic family Laridae). The total number of species belonging to each family was consulted in: https://www.itis.gov. Most common seabird families attending to fishing vessels are shown in the upper part whilst less common are shown in the lower part.

Family	Diet	Foraging Ecology	Energy requirements	Bycatch	Competition	Reproduction	Population dynamics	Body condition	Pollutants	Predatory interactions	Migration patterns	Parasitism	Survival	Ecosystem level	Resilience	Dispersal
Laridae (102 spp.)	25	12	13	11	15	4	9	3	6	3	0	4	1	0	2	1
Procellaridae (88 spp.)	11	6	3	14	1	1	0	0	2	1	0	0	0	1	0	0
Diomedeidae (21 spp.)	19	19	5	38	5	5	0	0	0	0	0	0	0	0	0	0
Sulidae (10 spp.)	50	20	20	20	20	10	20	20	0	0	0	0	0	0	0	0
Stercorariidae (7spp.)	29	29	14	14	14	14	0	14	14	14	14	0	0	0	0	0
Phalacrocoracidae (37spp.)	5	0	3	3	3	0	0	0	3	0	0	0	0	0	0	0
Hydrobatidae (25 spp.)	8	4	4	12	0	0	0	0	0	0	0	0	0	0	0	0
Fregatidae (5 spp.)	40	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0
Alcidae (24 spp.)	17	0	17	0	0	0	0	0	0	8	0	0	0	0	0	0
Spheniscidae (19 spp.)	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0
Chionidae (2 spp.)	0	0	0	50	0	0	0	0	0	0	0	0	0	0	0	0
Ardeidae (68 spp.)	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Cathartidae (7 spp.)	0	0	0	0	29	0	0	0	0	0	0	0	0	0	0	0
Pelecanidae (8 spp.)	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

We considered the information available on SCI journals (June 6th, 2017) on the Web of Science platform (WOS; Clarivate Analytics). We first selected articles with concomitant terms: *((Seabirds AND "Fishery Waste") OR (Seabirds AND Discard))* in title, abstract or keywords (Search field = Topic) as a representative sample of research focusing on the effects of discards on seabird's ecology. A second search with concomitant terms: *((Seabirds AND Ecosystem AND Discard) OR (Seabirds AND Ecosystem AND "Fishery Waste"))* (Search field = Topic) was conducted to find those studies focusing on the effects derived from seabirds-discards interactions at the ecosystem level. Then, the selected studies were classified according to: 1) the species and families of seabirds interacting with fishery discards, 2) the fishing gear used and 3) the ecological parameter or effect investigated. Additionally, in order to identify those areas where ecological interactions between seabirds and fishery discards are more likely to occur (e.g. with high discard availability or high presence of scavenger seabirds) we calculated: 1) the average amount of discards (in tons) for each major FAO fishing area (www.fao.org) from 2004 to 2014 (raw data from www.seaaroundus.org) and 2) the main distribution areas of seabird species (identified as discard-scavengers by reviewed studies)(data from www.iucn.org). We considered that the level of confluence of these species within each major FAO fishing area may vary throughout the year due to the large-scale movements of migratory species.

1.4. Results

A total of 166 studies addressing up to 15 different ecological effects derived from seabird-discard interactions were selected and subsequently reviewed (Tables 1, S1). Up to 107 seabird species (Table S1) belonging to 14 taxonomic families (Table 1) were identified as scavengers of fishery discards. Demersal trawlers were, by far, the main fishing gear involving seabird-discard interactions (98% of studies). According to their attendance to fishing vessels most common discard-scavengers were Laridae, Procellaridae and Diomedeidae (Table 1). Major FAO fishing areas presenting highest discard availability per scavenger seabird species were the Northwest Pacific, the Easter Central Atlantic and the Mediterranean and Black Sea (Figure 4).

In general a scarce number of studies quantified the effect of discards on seabird's ecology, while the majority of studies focused on the amount/type of fishing discard in seabird's diet and on species attendance rate (68% of studies). In particular, we found that for most important scavenger seabirds (Table 1) there was a lack of studies addressing potentially important ecological effects of discards in terms of food availability on: a) demographic parameters such as survival, dispersal and reproduction, b) resilience of populations against perturbations and c) individual foraging specialization (e.g. changes on predatory interactions, foraging and migratory patterns and the possible consequences of this heterogeneity for population dynamics. More specifically, the effect of discards on scavenging-seabird's survival has only been studied in the family Laridae, and only 1% of species belonging to this family have been considered (Table 1). The effect that fishery discards have on seabird's breeding success has been hardly studied in the species belonging to the families Procellariidae (only 1% of species studied) and Diomedeidae (only 5% of species studied) which are two of the most important seabird families in terms of discard scavenger species (Table 1).We only found three studies where individual differences in seabird foraging strategies were related to fishing practices (Matich et al. 2011, Wakefield et al. 2015, Votier et al. 2017). Finally, the role that fishery discards play on the resilience of populations remains unknown for 98% of seabirds identified as discards scavengers and for 99% of seabirds in general (Table1).

1.5. Discussion

Main knowledge gaps on seabird-discard interactions

The effect of discards on demographic parameters and population resilience

Fishery discards may have important ecological effects on demographic parameters as well as the resilience of scavenger's populations. However, these effects have never been evaluated for most of species scavenging on fishery discards. A few studies have shown that fishery discards, as other PAFS, can increase average individual survival and reproductive output in several scavenger species (Oro et al. 2013 and references therein), but they can also reduce adult survival by increasing bycatch of scavenger seabirds. Bycatch mortality might change over time according to the composition of the fishing fleet. Laneri et al. (2010) and Soriano-Redondo et al. (2016) observed a substantial increase on seabird's bycatch by longliners in the absence of discards, when trawling vessels were not operating. This suggests that a ban of fishery discards, which are mainly generated by trawling vessels, may increase the attendance of seabirds to longliners, increasing their mortality probabilities (Laneri et al. 2010, Bicknell et al. 2013).

The availability of fishery discards could have important effects on dispersal of several species among breeding colonies with potential consequences for the structure of communities and ecosystems. However, these effects remain unstudied for most of species directly and indirectly associated with fishery discards. Oro et al. (2004) for example, showed that fishery discards as PAFS can have a direct effect on the dispersal between breeding patches and the functioning of a spatially-structured population in a long-lived seabird. On the other hand, dispersal could also be indirectly affected by fishery discards through an increase on predatory interactions among sympatric species competing for food and breeding habitat when discards are not available (see González-Solís 2003). In addition, discards from fisheries and other PAFS (Real et al. 2017) could also be altering migration patterns of generalist species (Gilbert et al. 2016). Furness et al. (2006) for example, suggested that fishery discards may be affecting migration patterns of the Great skua (*Catharacta skua).*

Fishery discards may improve average breeding success in scavenger seabirds such as Larids (Oro et al. 1995, Oro 1996a, Oro et al. 1996, 1999), shearwaters (Louzao et al. 2006, Genovart et al. 2016) and albatrosses (Rolland et al. 2008). Contrarily, Pichegru et al. (2007) and Grémillet et al. (2008) observed that during periods of natural prey shortage and high energy requirements, fishery discards did not allow to compensate for the breeding needs on Cape gannets *Morus capensis*. Nevertheless, more studies are needed in order to have a global assessment of the role that fishery discards play on the reproductive output of scavenger seabirds and to predict the consequences of discard prohibitions.

Food availability is known to increase population resilience after perturbations (see e.g. Scheffers et al. 2017). Similarly, fishery discards have been shown to buffer natural food shortages reducing the long term variability of population fluctuations, especially in generalist species (Oro et al. 2013, Fondo et al. 2015). However, very little is known on the role that fishery discards play on the resilience of populations in most scavenger species. Yet, it is plausible to expect larger fluctuations of seabird populations after discard reduction, in those ecosystems more tightly linked to climate anomalies and extremes climate events (Hansen et al. 2012, National Academies of Sciences 2016).

Individual foraging specialization: a recent topic

Individual specialization in foraging strategies may have important ecological implications by altering the dynamics of populations and the structure of communities and ecosystems (Bolnick et al. 2003), especially in highly mobile marine top predators (Matich et al. 2011). Within scavenger seabird populations only certain individuals are fishery-discard scavengers but little is known about which individual features may influence this difference (e.g. age, sex, condition, behavior traits). It is likely that there is a large individual heterogeneity within populations in discard use and this may influence variance in demographic parameters and population dynamics. Navarro et al. (2010) showed that inexperienced, younger adults of Audouin's gulls (*Ichthyaetus audouinii*) consumed more discards and less small pelagics, the natural prey of the species. Differences in resource availability (e.g. due to a ban of discards) and intraspecific competition may increase individual specialization (Matich et al. 2011). For example, when food resources (including discards) become scarce, predatory (González-Solís 2003, Regehr and Montevecchi 1997, Votier et al. 2004) and kleptoparasite (Oro 1996b) interactions among individuals may increase. Specialization in certain foraging strategies such as bird predation may have important associated advantages for individuals (e.g. by improving individual survival or breeding success). This may in turn favor the learning of these strategies by other individuals sharing the same habitat (see e.g. Annett and Pierotti 1999), with potential consequences for the structure of communities. However, despite the potential ecological consequences that individual specialization may have for populations, communities and ecosystems, the available information is still scarce (but see Tuck et al. 2015).

Ecosystem level effects derived from scavenger-discard interactions

A reduction of fishery discards is expected to cause a population decrease of scavengers' marine organisms (including generalist seabirds), but they can also trigger cascading effects through a change in nutrients in the water column. The general lack of studies addressing the potential impacts of fishery discards at ecosystem level makes difficult to predict the real ecological consequences of a ban of discards. For example, a population decrease of scavenger seabirds would alter soil composition and the structure of animal and plant's communities in coastal regions (Vidal et al. 2000, Oro et al. 2013, Ellis 2005). Hawke (2006) found a decrease on the median soil N:P molar ratio of a Westland petrels (*Procellaria westlandica*) breeding colony when birds fed on fishery discards and Calvino-Cancela (2011) showed that Larids, a group characterized by a large use of fishery discards, may act as important seed dispersals in many different regions worldwide.

A chance for an experimental scenario for ecologists

There are several large areas of the world where interactions between discards from fisheries and marine scavengers could be potentially important, that have received little or no attention. Besides, most of important ecological effects that fishery discards have on marine ecosystems have been never or seldom studied. Considering this, the new policies on the ban of fishery discards, that are being progressively implemented at the European Union, Norway, Chile or New Zealand offer a suitable experimental scenario for improving our understanding on how food availability (e.g. carrying capacity) may alter the dynamics of populations as well as the structure of communities and ecosystems. The example given at the Ebro Delta (e.g. Oro et al. 2013), where a long-term trawling moratorium was established in the early 90’s during the breeding season of the seabird community breeding there, is illustrative of the potential that the discard banning offer to ecologists in their understanding of how food availability influences ecological processes and patterns. For instance we expect an increase of competition at intra- and inter-specific level with larger impacts on population densities for more opportunistic species, a decrease in the variance of the breeding performance within populations and a decrease in the resilient capacity of populations against anthropogenic impacts.

1.6. Acknowledgements

Funds for this study were supplied by the Spanish Ministry of Economy and co-funded by the European Social Fund (grant ref: CGL2013-42203-R). This research has also received funding from the European commission’s Horizon 2020 Research and Innovation Programme under Grant Agreement no. 634495 for the project Science, technology, and society initiative to minimize unwanted catches in European fisheries (MINOUW). MG and

ASA are supported by postdoctoral contracts co-funded by the Regional Government of the Balearic Islands and the European Social Fund. Two reviewers helped to improve the MS.

1.7. References

Annett C.A., Pierotti R. 1999. Long-Term Reproductive Output in Western Gulls: Consequences of Alternate Tactics in Diet Choice. Ecology. 80:288–297.

Arcos J., Louzao M., Oro D. 2008. Fisheries ecosystem impacts and management in the Mediterranean: seabirds point of view. In: Nielsen J., Dodson J.J., Friedland K., Hamon T.R., Musick J., Verspoor E. (eds) Reconciling Fisheries with Conservation. Am. Fish. Soc. Symp., Washington DC, 49:1471-1479.

Bicknell A.W.J., Oro D., Camphuysen K. (C. J.), Votier S.C.. 2013. Potential consequences of discard reform for seabird communities. J Appl. Ecol. 50:649–658.

Bolnick D.I., Svanbäck R., Fordyce J.A., Yang L.H., Davis J.M., Hulsey C.D., Forister M.L. 2003. The ecology of individuals: incidence and implications of individual specialization. Am. Nat. 161:1–28.

Borges L., Cocas L., Nielsen K.N. 2016. Discard ban and balanced harvest: a contradiction? ICES J. Mar. Sci. 73:1632–1639.

Calvino-Cancela M. 2011. Gulls (Laridae) as frugivores and seed dispersers. Plant. Ecol. 212:1149–1157.

Cury P.M., Boyd I.L., Bonhommeau S., Anker-Nilssen T., Crawford R.J.M., Furness R.W., Mills J.A., Murphy E.J., Österblom H., Paleczny M., et al. 2011. Global Seabird Response to Forage Fish Depletion—One-Third for the Birds. Science. 334: 1703–1706.

Ellis J.C. 2005. Marine birds on land: a review of plant biomass, species richness, and community composition in seabird colonies. Plant Ecology. 181: 227-241.

Fondo E.N., Chaloupka M., Heymans J.J., Skilleter G.A. 2015. Banning Fisheries Discards Abruptly Has a Negative Impact on the Population Dynamics of Charismatic Marine Megafauna. PLOS ONE. 10:e0144543.

Furness R.W., Crane J.E., Bearhop S., Garthe S., Käkelä A., Käkelä R., Kelly A., Kubetzki U., Votier S.C., Waldron S. 2006. Techniques to link individual migration patterns of seabirds with diet specialization, condition and breeding performance. Ardea. 94:631–638.

Garthe S., Camphuysen K., Furness R. 1996. Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. Mar. Ecol. Prog. Ser. 136:1–11.

Genovart M., Arcos J.M., Álvarez D., McMinn M., Meier R., B. Wynn R., Guilford T., Oro D. 2016. Demography of the critically endangered Balearic shearwater: the impact of fisheries and time to extinction. J. Appl. Ecol. 53:1158–1168.

Gilbert N.I., Correia R.A., Silva J.P., Pacheco C., Catry I., Atkinson P.W., Gill J.A., Franco A.M.A. 2016. Are white storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident white storks (*Ciconia ciconia*) from a partially migratory population. Mov. Ecol. 4:7.

González-Solís J. 2003. Impact of fisheries on activity, diet and predatory interactions between yellow-legged and Audouin's gulls breeding at the Chafarinas Islands. Sci. Mar. 67:83–88.

Grémillet D., Pichegru L., Kuntz G., Woakes A.G., Wilkinson S., Crawford R.J., Ryan P.G. 2008. A junk-food hypothesis for gannets feeding on fishery waste. Proc. R. Soc. B. Biol. Sci. 275:1149–1156.

Hansen J., Sato M., Ruedy R. 2012. Perception of climate change. Proc. Natl. Acad. Sci. 109:E2415–E2423.

Hawke D.J. 2006. Soil P in a forested seabird colony: inventories, parent material contributions, and N:P stoichiometry. Soil. Res. 43:957–962.

Laneri K., Louzao M., Martínez-Abraín A., Arcos J.M., Belda E.J., Guallart J., Sánchez A., Giménez M., Maestre R., Oro D. 2010. Trawling regime influences longline seabird bycatch in the Mediterranean: new insights from a small-scale fishery. Mar. Ecol. Prog. Ser. 420:241–252.

Louzao M., Igual J.M., McMinn M., Aguilar J.S., Triay R., Oro D. 2006. Small pelagic fish, trawling discards and breeding performance of the critically endangered Balearic shearwater: improving conservation diagnosis. Mar. Ecol. Prog. Ser. 318:247–254.

Matich P., Heithaus M.R., Layman C.A. 2011. Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. J. Anim. Ecol. 80:294–305.

National Academies of Sciences E. 2016. Attribution of Extreme Weather Events in the Context of Climate Change [Internet]. [place unknown]; [cited 2017 Dec 21]. Available from: https://www.nap.edu/catalog/21852/attribution-of-extreme-weather-events-in-the-context-of-climate-change.

Navarro J., Oro D., Bertolero A., Genovart M., Delgado A., Forero M.G., 2010. Age and sexual differences in the exploitation of two anthropogenic food resources for an opportunistic seabird. Mar. Biol. 157: 2453–2459.

Oro D. 1996a. Effects of trawler discard availability on egg laying and breeding success in the lesser black-backed gull *Larus fuscus* in the western Mediterranean. Mar. Ecol. Prog. Ser. 132:43–46.

Oro D. 1996b. Interspecific kleptoparasitism in Audouin's Gull *Larus audouinii* at the Ebro Delta, northeast Spain: a behavioural response to low food availability. Ibis. 138:218–221.

Oro D., Bosch M., Ruiz X. 1995. Effects of a trawling moratorium on the breeding success of the Yellow-legged Gull *Larus cachinnans*. Ibis. 137:547–549.

Oro D., Jover, L., Ruiz, X. 1996. Influence of trawling activity on the breeding ecology of a threatened seabird, Audouin's gull *Larus audouinii*. Mar. Ecol. Prog. Ser. 139:19–29.

Oro D., Pradel R., Lebreton J-D. 1999. Food availability and nest predation influence life history traits in Audouin's gull, *Larus audouinii*. Oecologia. 118:438–445.

Oro D., Cam E., Pradel R., Martínez-Abraín A. 2004. Influence of food availability on demography and local population dynamics in a long-lived seabird. Proc. R. Soc. Lond. B. Biol. Sci. 271:387–396.

Oro D., Genovart M., Tavecchia G., Fowler M.S., Martínez-Abraín A. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecol. Lett. 16:1501–1514.

Pichegru L., Ryan P.G., van der Lingen C.D., Coetzee J., Ropert-Coudert Y., Grémillet D. 2007. Foraging behaviour and energetics of Cape gannets *Morus capensis* feeding on live prey and fishery discards in the Benguela upwelling system. Mar. Ecol. Prog. Ser. 350:127–136.

Real E., Oro D., Martínez-Abraín A., Igual J.M., Bertolero A., Bosch M., Tavecchia G. 2017. Predictable anthropogenic food subsidies, density-dependence and socio-economic factors influence breeding investment in a generalist seabird. J. Avian Biol. 48:1462–1470.

Regehr H.M., Montevecchi W.A. 1997. Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: indirect effects of fisheries activities and implications for indicator species. Mar. Ecol. Prog. Ser. 155:249–260.

Rolland V., Barbraud C., Weimerskirch H. 2008. Combined Effects of Fisheries and Climate on a Migratory Long-Lived Marine Predator. J. Appl. Ecol. 45:4–13.

Scheffers B.R., Shoo L., Phillips B., Macdonald S.L., Anderson A., VanDerWal J., Storlie C., Gourret A., Williams SE. 2017. Vertical (arboreality) and horizontal (dispersal) movement increase the resilience of vertebrates to climatic instability. Glob. Ecol. Biogeogr. 26:787–798.

Soriano-Redondo A., Cortés V., Reyes-González J.M., Guallar S., Bécares J., Rodríguez B., Arcos J.M., González-Solís J. 2016. Relative abundance and distribution of fisheries influence risk of seabird bycatch. Sci. Rep. 6:37373.

Tasker M.L., Camphuysen C.J., Cooper J., Garthe S., Montevecchi W.A., Blaber S.J.M. 2000. The impacts of fishing on marine birds. ICES J. Mar. Sci. 57:531–547.

Tuck G.N., Thomson R.B., Barbraud C., Delord K., Louzao M., Herrera M., Weimerskirch H. 2015. An integrated assessment model of seabird population dynamics: can individual heterogeneity in susceptibility to fishing explain abundance trends in Crozet wandering albatross? J. Appl. Ecol. 52:950–959.

Vidal E., Médail F., Tatoni T., Bonnet V. 2000. Seabirds drive plant species turnover on small Mediterranean islands at the expense of native taxa. Oecologia. 122:427–434.

Votier S.C., Fayet A.L., Bearhop S., Bodey T.W., Clark B.L., Grecian J., Guilford T., Hamer K.C., Jeglinski J.W.E., Morgan G., et al. 2017. Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. Proc. R. Soc. B. Biol. Sci. 284(1859), 20171068. http://doi.org/10.1098/rspb.2017.1068.

Votier S.C., Furness R.W., Bearhop S., Crane J.E., Caldow R.W.G., Catry P., Ensor K., Hamer K.C., Hudson A.V., Kalmbach E., et al. 2004. Changes in fisheries discard rates and seabird communities. Nature. 427:727–730.

Wagner E.L., Boersma P.D. 2011. Effects of Fisheries on Seabird Community Ecology. Rev. Fish. Sci. 19:157–167.

Wakefield E.D., Cleasby I.R., Bearhop S., Bodey T.W., Davies R.D., Miller P.I., Newton J., Votier S.C., Hamer K.C. 2015. Long-term individual foraging site fidelity—why some gannets don't change their spots. Ecology. 96:3058–3074.

Zeller D., Cashion T., Palomares M., Pauly D. 2017. Global marine fisheries discards: A synthesis of reconstructed data. Fish Fish.:00:1-10. https://doi.org/10.1111/faf.12233.

1.8. Supporting information

Table S1. Seabird species identified as scavengers of fishery discards according to reviewed studies and number of studies considering each ecological effect derived from seabird-discard interactions.

Species	Diet	Foraging Ecology	Energy req.	Bycatch	Competition	Reproduction	Population dynamics	Body condition	Pollutants	Predatory interactions	Migration patterns	Parasitism	Survival	Ecosystem level	Resilience	Dispersal
Alca torda	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Alle alle	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anous minutus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Anous stoldius	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ardea alba	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ardenna gravis	1	5	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Ardenna grisea	2	4	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Ardenna tenuirostris	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calonectris borealis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calonectris diomedea	3	11	2	2	0	0	0	0	0	0	0	0	0	0	0	0
Catharacta antarctica	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Catharacta skua	12	7	3	0	2	1	0	1	1	1	0	0	0	0	0	0
Cathartes aura	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Chionis alba	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Chlidonias hybridus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Chlidonias niger	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Chroicocephalus cirrocephalus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chroicocephalus maculipennis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chroicocephalus novaehollandiae	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chroicocephalus ridibundus	4	8	3	0	2	0	0	0	0	0	0	1	0	0	0	0
Coragyps atratus	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Daption capense	1	4	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Diomedea dabbenena	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diomedea epomophora	0	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Diomedea exulans	2	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Diomedea sanfordi	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Egretta caerulea	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Egretta thula	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Fratercula arctica	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0
Fregata ariel	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fregata magnificens	0	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Fregata minor	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fregetta tropica	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fulmarus glacialis	10	6	6	1	4	0	0	0	0	1	0	0	0	0	0	0
Fulmarus glacialoides	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Gelochelidon nilotica	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0

Continuation Table S1

Species	Diet	Foraging Ecology	Energy req.	Bycatch	Competition	Reproduction	Population dynamics	Body condition	Pollutants	Predatory interactions	Migration patterns	Parasitism	Survival	Ecosystem level	Resilience	Dispersal
Hydrobates pelagicus	2	6	2	1	0	0	0	0	0	0	0	0	0	0	0	0
Hydroprogne caspia	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ichthyaetus audouinii	8	11	2	1	3	2	1	1	2	1	0	1	2	0	1	1
Ichthyaetus melanocephalus	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Larus argentatus	11	7	4	0	4	0	3	1	0	0	0	1	0	0	0	0
Larus atlanticus	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus canus	3	5	2	0	1	0	0	0	0	0	0	0	0	0	0	0
Larus dominicanus	4	10	0	7	2	0	0	0	0	0	0	0	0	0	0	0
Larus fuscus	11	13	3	1	3	1	0	0	0	0	0	0	0	0	0	0
Larus genei	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Larus hyperboreus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus marinus	4	6	2	0	3	0	2	1	0	0	0	0	0	0	0	0
Larus michahellis	6	8	2	1	3	1	0	0	1	1	0	1	0	0	0	0
Larus minutus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus pacificus	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus sabini	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leucocarbo atriceps	0	2	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Leucophaeus atricilla	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Macronectes giganteus	1	5	0	6	0	0	0	0	0	0	0	0	0	0	0	0
Macronectes halli	0	2	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Morus bassanus	10	12	2	1	3	0	0	1	0	0	1	0	0	0	0	0
Morus capensis	5	5	3	1	0	3	0	1	0	0	0	0	0	0	0	0
Morus serrator	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Oceanites oceanicus	1	3	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Oceanodroma leucorhoa	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onychoprion anaethetus	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Pachyptila belcheri	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pagodroma nivea	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pelecanus occidentalis	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phalacrocorax aristotelis	2	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Phalacrocorax brasilianus	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Phalacrocorax carbo	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phalacrocorax olivaceus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phoebetria palpebrata	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Procellaria aequinoctialis	0	7	0	6	0	0	0	0	1	0	0	0	0	0	0	0
Procellaria conspicillata	1	3	0	1	0	0	0	0	1	0	0	0	0	0	0	0

Continuation Table S1

Species	Diet	Foraging Ecology	Energy req.	Bycatch	Competition	Reproduction	Population dynamics	Body condition	Pollutants	Predatory interactions	Migration patterns	Parasitism	Survival	Ecosystem level	Resilience	Dispersal
Procellaria westlandica	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Pterodroma mollis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Puffinus assimilis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Puffinus mauretanicus	4	8	1	1	0	2	0	0	0	0	0	0	0	0	0	0
Puffinus puffinus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Puffinus Yelkouan	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pygoscelis antarcticus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pygoscelis papua	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rissa tridactyla	5	7	3	1	1	1	0	0	0	2	0	0	0	0	0	0
Spheniscus magellanicus	0	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Stercorarius parasiticus	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stercorarius pomarinus	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sterna dougallii	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sterna hirundinacea	0	6	0	5	2	0	0	0	0	0	0	0	0	0	0	0
Sterna hirundo	3	9	3	1	0	0	0	0	2	0	0	0	0	0	0	0
Sterna paradisaea	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sterna sumatrana	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Sterna vittata	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sternula alfibrons	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Sula dactylatra	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sula leucogaster	1	3	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Sula sula	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalassarche bulleri	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalassarche cauta	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Thalassarche chlororhynchos	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Thalassarche chrysostoma	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Thalassarche melanophrys	6	14	1	9	1	1	0	0	0	0	0	0	0	0	0	0
Thalassarche steadi	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalasseus bengalensis	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Thalasseus bergii	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Thalasseus eurygnathus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Thalasseus maximus	2	4	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Thalasseus sandvicensis	4	10	2	2	2	0	0	0	1	0	0	0	0	0	0	0
Uria aalge	4	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0
Uria lombia	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Chapter 2

Predictable anthropogenic food subsidies, density-dependence and socio-economic factors influence breeding investment in a generalist seabird

---

Enric Real, Daniel Oro, Alejandro Martínez-Abraín, José Manuel Igual, Albert Bertolero, Marc Bosch and Giacomo Tavecchia (2017). Predicable anthropogenic food subsidies, density-dependence and socio-economic factors influence breeding investment in a generalist seabird. *Journal of Avian Biology*, 48: 1462-1470.

Predictable anthropogenic food subsidies, density-dependence and socio-economic factors influence breeding investment in a generalist seabird

Enric Real, Daniel Oro, Alejandro Martínez-Abraín, José Manuel Igual, Albert Bertolero, Marc Bosch and Giacomo Tavecchia

E. Real (https://orcid.org/0000-0002-6190-6303)(ereal@imedea.uib-csic.es), D. Oro, J.M. Igual and G. Tavecchia, Population Ecology Group, IMEDEA (CSIC-UIB), C/Miquel Marquès 21, 07190, Esporles, Spain. A. Martínez-Abraín, Biology Department, Facultad de Ciencias, Universidade da Coruna, Campus da Zapateira s/n, 15008 Elviña, A Coruña, Spain. A. Bertolero, Associació Ornitològica Picampall de les Terres de l'Ebre, C/La Galera 53, 43870 Amposta, Spain. Marc Bosch, Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, Avda. Diagonal 645, E08028, Barcelona, Spain.

2.1. Abstract

Recent European policies on the ban of fishing discards and the closure of open-air landfills are expected to reduce predictable and abundant food resources for generalist seabirds. In order to forecast the consequences of this reduction on seabird breeding investment it is important to understand whether diverse anthropogenic foraging resources act synergistically or not and whether their influence is mediated by density-dependent mechanisms. To assess these effects at large spatio-temporal scale, we measured mean egg volume as a proxy of breeding investment in ca. 5,000 three-egg clutches of the Yellow-legged Gull (*Larus michahellis)* from 20 colonies of the Western Mediterranean, located both along European and African coasts. In European gull colonies, egg volume increased with the availability of fishing discards and landfills in the vicinity of the colony. However, the landfill effect was weaker than the effect of fishing discards, probably due to the lower quality of waste as food for gulls. In contrast, none of the anthropogenic food subsidies influenced egg volume in African colonies, likely due to socio-economic differences (i.e. a much lower availability and predictability of both discards and waste food. Finally, results showed that the positive association between fishing discards and open-air landfills on egg volume was mediated by negative density-dependent mechanisms probably related to an increase in competition for food.

2.2. Introduction

Predictable anthropogenic food subsidies (PAFS, see Oro et al. 2013) play an important role in the diet of generalist species with cascading effects on individual fitness, population growth rate, the structure of ecological communities and ultimately on the functioning of whole ecosystems (Oro et al. 1995; 1996, González-Solís et al. 1997a, 2003; Votier et al. 2004; Hobson et al. 2015). Fishing discards and open-air landfills are two of the most important PAFS exploited by several generalist seabirds. Recent European environmental policies promoting the closure of open air landfills (European Commission 1999) and the reduction and later ban of fishing discards (European Commission 2008), are expected to have an impact on scavenging seabird ecology and demography (Bicknell et al. 2013). The Yellow-legged Gull *Larus michahellis* (hereafter YLG), is a generalist species widely distributed throughout the Mediterranean region that makes large use of fishing discards (Oro et al. 1995; Martínez-Abraín et al. 2002; González-Solís 2003; Cama et al. 2012) and open-air landfills (Duhem et al. 2003; Ramos et al. 2006; 2011; Jordi et al. 2014). These predictable and abundant food resources are thought to be responsible for the proliferation of YLG populations. Large populations of YLGs have been often associated with negative effects on other syntopic bird species via predation, kleptoparasitism and

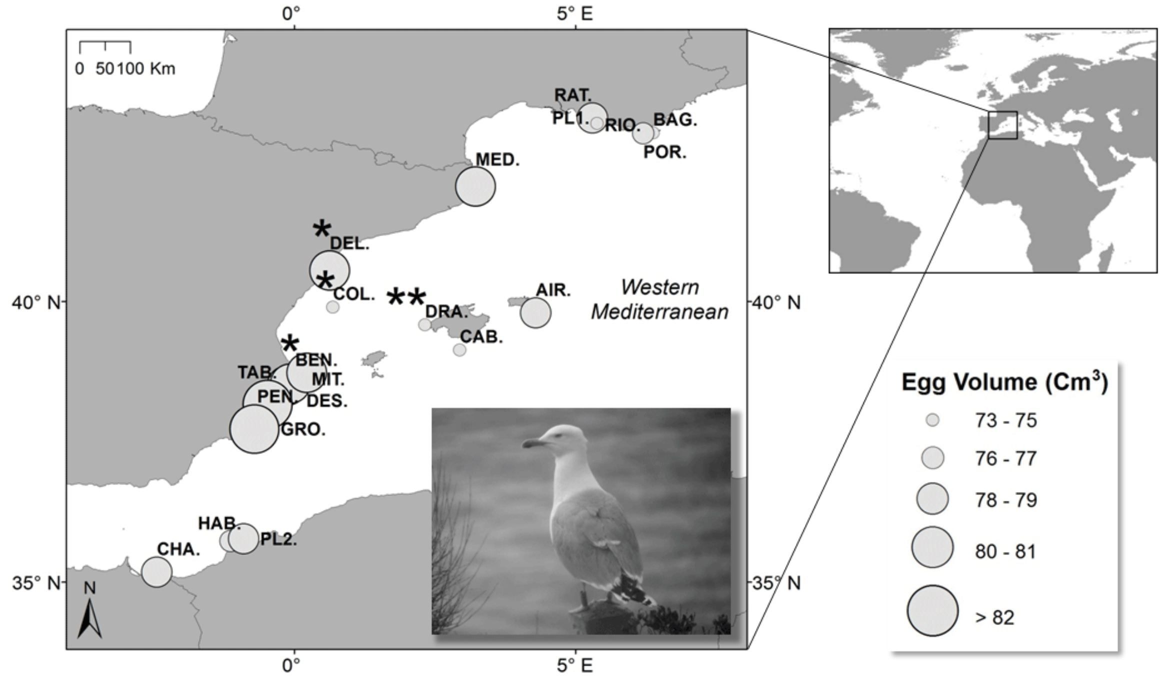

Figure 5. Study area with the distribution of the twenty Yellow-Legged Gull colonies throughout the Western Mediterranean where eggs were measured between 1992 and 2015. AIR: Aire, BAG: Bagaud, BEN: Benidorm, CAB: Cabrera, CHA: Chafarinas, COL: Columbretes, DEL: Delta, DES: Descubridor, DRA: Dragonera, GRO: Grossa, HAB: Habibas, MED: Medes, MIT: Mitjana, PEN: Penyal d'Ifach, PL1: Plane, PL2: Plana, POR: Porquerolles, RAT: Ratoneau-Pomegues, RIO: Riou, TAB: Tabarca. Circles represent the global mean egg volume per clutch for each gull colony. Colonies considered in the density-dependence analysis have been represented with an asterisk. Among these, those around which there were also subject to "no landfill" regime (due to the closure of landfill) have been represented with double asterisk.

competition for nesting places (Oro and Martínez-Abraín 2007; Paracuellos and Nevado 2010; Vidal et al. 1998). In addition, gull-human conflicts associated to their bold behavior and their role as a potential vector for human pathogens, such as *Escherichia coli*, might arise due to the usual vicinity of breeding sites to human settlements (Vergara et al 2017). These issues have raised concerns to the point that several countries have undergone management actions to reduce population size (Bosch et al. 2000; Steigerwald et al. 2015).

The efficient management of large gulls and other generalist species necessitates an assessment of the potential effects of PAFS reduction on gull population dynamics. However, the exact role of PAFS is difficult to measure in species with a diverse and

Table 2. Upper part: Linear Mixed-Effects Models explaining effects of trawling discards and refuse from open-air landfills on YLG egg volume (mean egg volume per clutch), deviance, Akaike Information Criterion values (AIC) and Akaike weights (Wi). The best explanatory model (model 1) is the one with the lowest AIC. Middle and lower parts: estimates and standard error of the three equivalent Linear Mixed-Effects Models (1, 2 and 3) and variance of random effects. In the notation, the star (*) indicates the presence of the main effects and their statistical interaction (A+B+A:B), while the colon (:) indicates the interaction term only. All models consider year and colony as random effects. Landfill variable corresponds to the number of landfills associated to colonies which has been transformed with the natural logarithm. Null model only considers factors year and colony as random effects. Hp corresponds to the main horsepower of bottom trawlers associated to colonies.

Model	**Notation**	**Deviance**	**AIC**	**ΔAIC**	**Wi**
1	Continent*(Hp+Landfill)	300.13	314.40	0.00	0.37211
2	Continent*Hp+Landfill	305.75	315.53	1.13	0.21149
3	Continent*Hp	302.69	315.68	1.28	0.19621
4	Continent*Hp*Landfill	299.96	316.84	2.44	0.10986
5	Continent*(Hp+LN.1LdfN.std)+Hp*Landfill	299.87	316.88	2.48	0.10768
6	Continent*Landfill	315.86	326.15	11.75	0.00105
7	Hp	316.80	327.08	12.68	0.00066
8	Hp+Landfill	315.85	328.51	14.11	0.00032
9	Continent	323.81	328.94	14.54	0.00026
10	Hp*Landfill	315.10	329.73	15.33	0.00017
11	Null model	324.21	330.89	16.49	0.00010
12	Landfill	322.04	331.24	16.84	0.00008
Estimates of fixed effects ± SE		**Model 1**	**Model 2**	**Model 3**	
Intercept		77.93 ± 1.46	77.81 ± 1.44	77.91 ± 1.45	
Continent Europe		0.60 ± 1.55	0.77 ± 1.53	0.73 ± 1.55	
MainPwr.		-1.73 ± 1.06	-2.20 ± 1.03	-1.81 ± 1.02	
LnLandfill		-0.09 ± 0.39	0.42 ± 0.24		
Continent Europe:MainPwr.		3.12 ± 1.12	3.62 ± 1.09	3.25 ± 1.08	
Continent Europe:LnLandfill		0.81 ± 0.49			
MainPwrN.std:LN.1LdfN.std					
ContinentFEurope:MainPwrN.std:LN.1LdfN.std					
Variance of random effects					
Intercept (Year:Colony)		1.34	1.38	1.41	
Intercept (Colony)		3.96	3.80	3.88	
Residual		31.16	31.17	31.17	

generalist diet, and little is known about whether these resources act synergistically or if they represent independent food resources. Mirroring what is known about the effect of natural food resources on population dynamics (Christians 2002), PAFS availability should

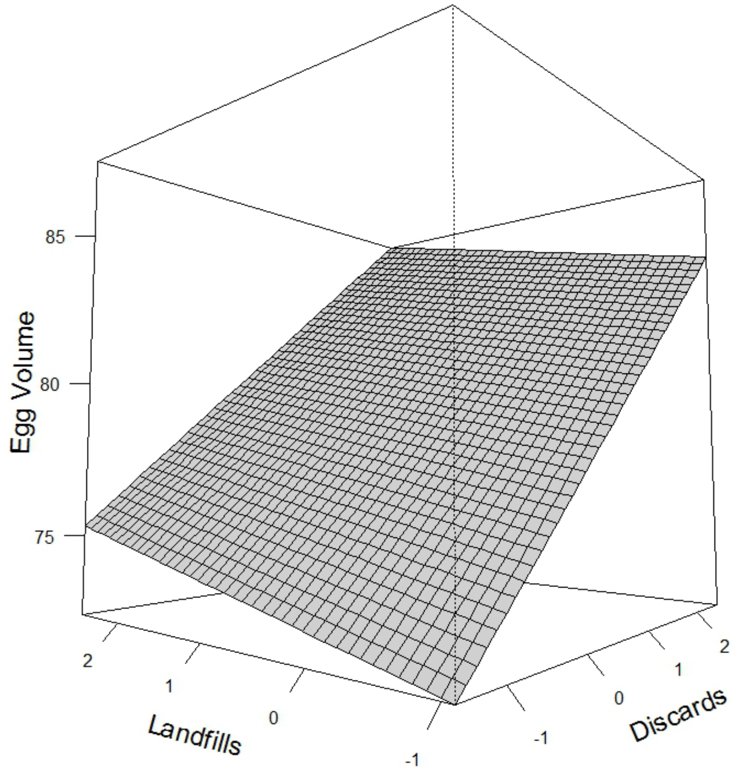

Figure 6. Resulting model explaining effects derived from trawl horsepower (as a proxy of trawling discards) and number of landfills (as a proxy of refuse from open-air landfills) on YLG egg volume (mean egg volume per clutch in cm3) in 17 European colonies from the Western Mediterranean. Covariate values were scaled dividing by $1{\cdot}10^6$.

be reflected in the variation of breeding investment and performance in generalist birds, e.g. clutch size and/or mean egg volume (Oro 1996; Oro et al. 1996). Additionally, egg volume is known to be a good predictor of chick size at hatching and later survival (Parsons 1970; Bolton 1991; Blomqvist et al. 1997; Risch and Rohwer 2000). However, measuring the effect of PAFS on egg volume is not straightforward. Changes in food availability generally explain a small part of egg size variability in birds that is highly influenced by maternal effects (genetics) (Christians 2002). Also, other factors such as density-dependence (Oro et al. 2006), food quality (Batchelor and Ross 1984; Piatt and Anderson 1996; Grémillet et al. 2008), individual investment and age (Cunningham and Russell 2000) or the presence of alternative food resources, among others, can make the association between PAFS and egg size difficult to ascertain. Most avian species (except those laying a

Table 3. Upper part: Linear Mixed-Effects Models explaining density-dependent effects on YLG egg volume (mean egg volume per clutch), deviance, Akaike Information Criterion values (AIC) and Akaike weights (Wi). The best explanatory model (model1) is the one with the lowest AIC. Middle and lower parts: estimates of the four equivalent Linear Mixed-Effects Models (models 1, 2, 3 and 4) and variance of random effects. In the notation, the star (*) indicates the presence of the main effects and their statistical interaction (A+B+A:B), while the colon (:) indicates the interaction term only. All models consider year and colony as random effects. Pop. size corresponds to the population size associated to colonies. Landfill variable corresponds to the number of landfills associated to colonies which has been transformed with the natural logarithm. Hp corresponds to the main horsepower of bottom trawlers associated to colonies. Null model only considers factors year and colony as random effects.

Model	Notation	Deviance	AIC	ΔAIC	Wi
1	Population size*(Hp+Landfill)	177.58	198.69	0.00	0.3028
2	Hp*Population size	183.23	199.50	0.80	0.2026
3	Population size*Hp*Landfill	176.12	199.74	1.05	0.1791
4	Population size*Hp+Landfill	180.89	199.96	1.27	0.1603
5	Population size*(Hp+Landfill)+Hp*Landfill	177.62	201.13	2.44	0.0895
6	Hp+Landfill	194.16	204.40	5.71	0.0174
7	Hp	194.91	205.08	6.38	0.0124
8	Landfill+Population size	196.24	205.15	6.46	0.0120
9	Landfill*Population size	195.34	206.00	7.31	0.0078
10	Landfill	198.80	206.30	7.60	0.0068
11	Hp+Population size	196.72	206.63	7.94	0.0057
12	Population size	201.75	208.16	9.47	0.0027
13	Null model	205.33	210.52	11.83	0.0008

Estimates for fixed effects ± SE	**Model 1**	**Model 2**	**Model 3**	**Model 4**
Intercept	78.69 ± 0.30	79.00 ± 0.26	78.76 ± 0.33	78.98 ± 0.26
Population size	-0.40 ± 0.29	-0.08 ± 0.27	-0.32 ± 0.30	-0.24 ± 0.29
Hp	1.22 ± 0.32	1.63 ± 0.28	1.56 ± 0.42	1.46 ± 0.30
Landfill	0.89 ± 0.38		1.07 ± 0.43	0.42 ± 0.28
Population size*Hp	-2.10 ± 0.53	-1.65 ± 0.50	-2.12 ± 0.74	-1.71 ± 0.50
Population size*Landfill	0.80 ± 0.46		1.13 ± 0.57	
Hp*Landfill			-0.60 ± 0.51	
Population size*Hp*Landfill			-1.27 ± 1.07	
Variance of random effects				
Intercept (Year:Colony)	1.50	1.73	1.54	1.66
Intercept (Colony)	0.00	0.00	0.00	0.00
Residual	29.29	29.29	29.29	29.29

single egg) can regulate breeding investment by adjusting not only egg volume but also clutch size. Finally, in many cases PAFS availability cannot be easily manipulated experimentally, so their potential effects on breeding investment are masked by optimal

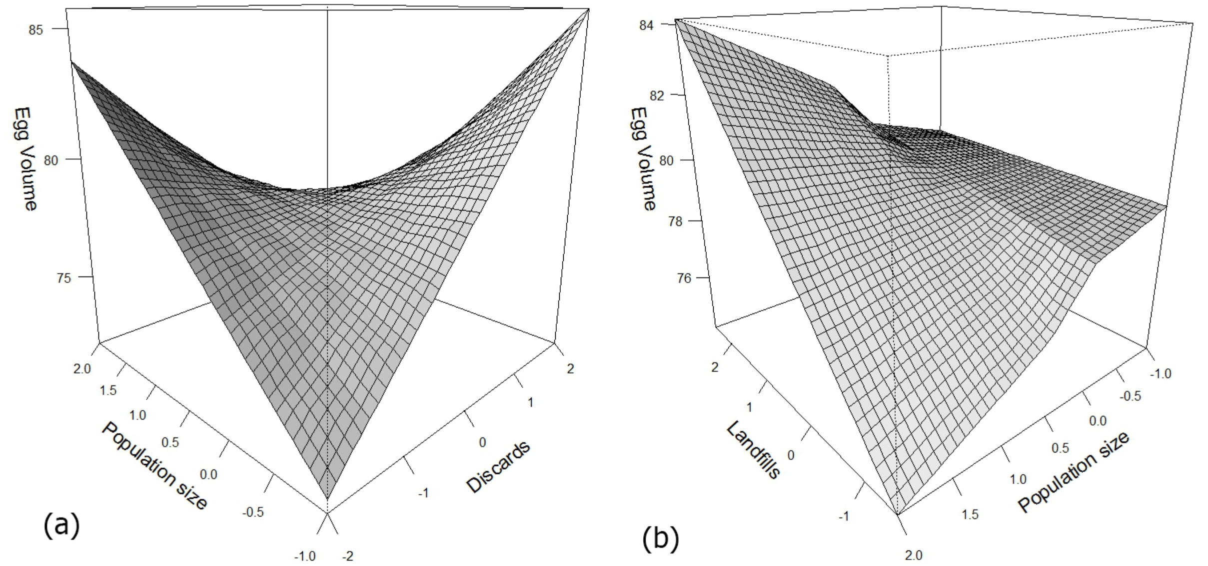

Figure 7. Regression surfaces of the influence of density-dependence on YLG egg volume (mean egg volume per clutch in cm3), where (a) represents the interaction between population size and horsepower (as a proxy of trawling discards) effects, and (b) represents the interaction between population size and landfill refuse effects. Data corresponds to four European colonies (Ebro Delta, Benidorm, Columbretes and Dragonera) from the Western Mediterranean (see Methods).

decisions of individuals. Therefore, it is necessary to obtain a large enough data set on PAFS, both temporally and spatially, to detect differences.

Here, we have gathered data on mean egg volume in three-egg clutches (hereafter "egg volume") of YLG breeding along the whole Western Mediterranean, as well as population size data of colonies with long monitoring periods (Figure 5). Our aim was to determine the relative influence of trawling discards and open-air landfills on the spatio-temporal variability of egg volume in the YLG, taking into account the possible existence of ecological synergies between these effects. A second goal was to assess the potential role played by density-dependent mechanisms. We expected the egg volume to increase along with PAFS availability, especially with fishing discards due to their intrinsic high quality compared to landfill waste (see for example Gilbert et al. 2016). We also expected this association to change with population density, due to competition among individuals.

2.3. Methods

Field data and study area

A total of 4,964 three-egg clutches (the modal clutch size for YLG) were measured between 1992 and 2015 from 20 different colonies distributed from southern France to Morocco (Figure 5). Data from French gull colonies were obtained from Duhem (2004). We only considered years with at least 15 clutches of 3 eggs measured. Eggs were measured with digital calipers to ±0.01mm and egg volume (V) was calculated in cm^3 according to the equation $V=0.476 \cdot L \cdot W^2$ (Harris 1964), where L=maximum egg length and W=maximum egg width. For our statistical analyses (see below) we used the mean egg volume in a clutch. In some of our study colonies we monitored a random sample of the nests in order to establish the peak of complete clutches. Considering that YLG is a long-lived seabird, which tends to breed in the same colony year after year, we assumed that the mean quality of individuals remained constant in the colonies during the study period.

Trawling discards

In the Western Mediterranean, the bottom trawling fleet is the fishery generating the highest amount of discards, compared to the other fisheries operating in the area (Carbonell et al. 1998; Tsagarakis et al. 2014). The distances that bottom trawlers are able to cover during the trawl phase as well as the size of the trawls are associated with trawler horsepower (Eigaard et al. 2011). Therefore, more powerful trawlers are able to cover greater areas with the trawl. Considering that discards constitute an important part of the total catch (Carbonell et al. 1998; Tsagarakis et al. 2014), we have assumed trawl horsepower to be positively related to the amount of discards generated. We used the main horsepower declared by European bottom trawlers on March 1st of each year (coinciding with the pre-laying period of the YLG) as a proxy of trawling discard availability. For African colonies only yearly estimates were available. Considering a foraging range around colonies of ca. 50km for the study species during the breeding season (Oro et al. 1995; Arizaga et al. 2014), we took the total main horsepower in the ports within a 100 km diameter area around each breeding site. Some of these foraging areas overlap so it is likely that individuals from close colonies are sharing the same resources. However, since several other species from the same guild can be foraging on the same resources, for practical reasons we decided not to take into account any kind of overlap, although we admit that this represents a simplification of a more complex situation. Data on main horsepower of three different types of bottom trawlers (bottom otter trawlers, bottom pair trawlers and beam trawlers) were obtained from the European Commission Fleet Register (European Commission 2015): http://ec.europa.eu/fisheries/fleet/index.cfm. For African fleets, we took the number of bottom trawlers operating per year and the mean horsepower per vessel (356HP). Thus, the total main horsepower was estimated by multiplying the annual number of bottom trawlers by the average horsepower per boat. Data from Moroccan and Algerian trawler fleets were obtained from CopeMed Group (FAO-CopeMed 2015). In the case of the Columbretes islands, a small archipelago of volcanic origin located some 50km offshore the eastern Spanish coasts, we used a100km diameter area from the closest mainland headland to the islands. This was done because bottom trawlers normally operate in the area located between mainland and the archipelago (Oro et al. 2004).

Landfills

We counted the number of active European landfills located within a 100km diameter area around each gull colony during each year. Based on the same reasoning regarding fisheries discards (see above), overlap between foraging areas was not considered. Only open-air landfills receiving urban waste during the study period were considered. European landfills were found thanks to the following agencies: European Pollutant Release and Transfer Register (European Environment Agency 2015): http://prtr.ec.europa.eu/, Registro Estatal de Emisiones y Fuentes Contaminantes (Ministerio de Agricultura, Alimentación y Medio Ambiente 2015): http://www.prtr-es.es/ and Registre Français des Émissions Polluantes (Ministère de l'Environnement, de l'Énergie et de la Mer 2015): http://www.pollutions-industrielles.ecologie.gouv.fr/IREP/.

Most information on years of activity for each landfill were obtained via these agencies, whilst some other information on active years, as well as location of African landfills, were confirmed through satellite imagery and aerial photography using Google Earth: https://www.google.es/intl/es/earth/. Infrastructures of African open-air landfills were identified by systematically inspecting images from areas around the main colonies. Thanks to the characteristic appearance presented by the garbage inside landfills (grey-violet color), we also were able to identify a second type of more rudimentary landfills with virtually no infrastructure.

Density-dependence

YLG is one of the largest species in the guild of marine scavengers in the Western Mediterranean and most competition that involves this species is intra-specific. Hence, in order to assess intra-specific food competition (i.e. a possible effect of per-capita food resources on mean egg volume), we used population density data from four European colonies for which long-term monitoring data were available: Ebro Delta, Benidorm Islet, Columbretes Islands and Dragonera Island, with 19, 10, 9 and 7 years of population monitoring respectively (Figure 5).

Data analysis

Covariates were scaled by dividing the values by $1 \cdot 10^6$ and standardized in order to equalize their means and standard deviations. We used egg volume variability as a dependent variable in Linear Mixed-Effects Models (library lme4 in software R [R Development team 2014]). Continent (two levels: Africa vs Europe), trawling discards, landfills and their statistical interactions were taken as fixed effects. Year and gull colony were modelled as random effects. The random component is meant to correct for pseudo-replication as well as for random spatial differences due to colony-specific features. Theoretical information theory based on AIC (Akaike Information Criterion; Burnham and Anderson 2002) was used to select the best explanatory model. Models having AIC differences (ΔAIC) ≤ 2 were considered to be equivalents (Burnham and Anderson 2004). We calculated two coefficients of determination for the Linear Mixed-Effects models (library MuMIn, R-project): the marginal coefficient, that represents the variance explained by the fixed part of the model, and the conditional coefficient that represents the variance explained by both, fixed and random factors (Nakagawa and Schielzeth 2013; Johnson 2014). The proportion of total spatio-temporal variance in egg volume explained by each covariate (i.e. trawling discards and open-air landfills) was calculated as [deviance (model constant) – deviance (model covariate)] / [deviance (model constant) – deviance (model with colony and time effects)]. The resulting statistics can be used as an equivalent of the coefficient of determination, r^2 (hereafter r^2, see Harris et al. 2005). Finally, we used model AIC-weight (*w*) to calculate the evidence ratio (w_i/w_j), i.e. the relative weight of model "i" compared to model "j", which allows for also evaluating the relative importance of each explanatory covariate or factor (Burnham and Anderson 2002).

2.4. Results

Effects on egg volume

Egg volume varied among colonies with no relationship to latitude (r = -0.009; 95% CI: -0.036, 0.018; Figure 5). However, egg volume was smaller in African colonies than in European ones ($F_{1/4962}$ = 23.75; P < 0.001). The model with the lowest AIC (Model 1; Table 2) included the interaction of continent (Europe vs. Africa) with the additive effect of horsepower and number of landfills (Figure 6; see Table 2 for estimates). According to this model, in European colonies both horsepower and landfill number had a positive effect on egg volume. The variability in egg volume explained by fixed and random effects (i.e. year and colony) of this model was r^2 = 0.05 and r^2 = 0.14, respectively. Models 2 and 3 (Table 2) were equivalent to model 1, and all three models included the interaction term between continent and horsepower. Moreover, the additive effect of landfills was retained in two of these models. Evidence ratios indicated that, models considering only the effects of horsepower and landfills, as well as the interaction between these two variables, had little support when compared to a null model (i.e. an only-intercept model) (Horsepower/Null Model, W_7/W_{11}=10.59; Landfill/Null Model, W_{12}/W_{11}=0.69; (Horsepower*Landfill)/Null

Model, W_{10}/W_{11} = 1.43). However, when the interaction continent*horsepower was considered, evidence ratios increased substantially ((Continent*Horsepower)/Null Model, W_2/W_{11}=3071.74). When continent interacted with landfill, the evidence ratio also improved ((Continent*Landfill)/Null Model, W_6/W_{11}=12.68), although to a much lesser extent than when considering horsepower. The percentage of the total spatio-temporal variance in the egg volume explained by horsepower and landfills in European colonies was 48%, and 2%, respectively. Both covariates when tested simultaneously explained 54%.

Density-dependence

When modelling egg volume in selected European colonies with long-term information on gull population size the best model included an additive effect of horsepower and landfill together with an interaction with population density (Model 1; Table 3; Figure 7). This model indicates that the positive increase that horsepower (i.e. fishing discards) and landfills had on egg volume was affected negatively by high gull densities (Figure 7a; see Table 3 for estimates). According to our estimates, the effect derived from the interaction between population size and the number of landfills on egg volume was positive (see Table 3 for estimates), although this trend was reversed when the number of available landfills was low (Figure 7b). The variability explained by fixed and random effects in this model was r^2 = 0.14 and r^2 = 0.18 respectively. Models 2, 3 and 4 (Table 3) were statistically equivalent to model 1 (see Table 3 for estimates). All of these models included the interaction between YLG population density and horsepower, while two of them included the additive effect of landfills. Only one of these models included an interaction between horsepower and landfills on egg volume. Evidence ratios showed that the relative weight of each effect was small for egg volume in general (population density/Null Model, W_{12}/W_{13} = 3.26; Horsepower/Null Model, W_7/W_{13} = 15.23; Landfill/Null Model, W_{10}/W_{13} = 8.27). Nevertheless, the interaction between population density and horsepower was relevant ((Population size*Horsepower)/Null model, W_2/W_{13} = 247.89), giving considerable support to models that include this interaction, whereas the interaction between population density and landfills was much less relevant ((Population density:Landfill)/Null Model, $W_9/W_{13} = 9.57$).

2.5. Discussion

According to our results, egg volume is not affected by latitude. Climatic differences derived from the latitudinal existing gradient (8º), do not seem to affect YLG egg volume. We found that availability of both trawling discards and landfills had a positive effect on egg volume of European YLGs in the Western Mediterranean, and that this effect was additive. This result shows that measuring complete egg clutches is proven to be a useful method to assess the relative importance of PAFS for seabirds.

While the fraction of fishing discards exploited by gulls is mainly composed by fish, food items taken on landfills are difficult to determine. Remains of processed foods, pieces of bread or offal from animals and fruits (e.g. olives) constitute some examples, although the high heterogeneity of this resource makes it very difficult to characterize it properly (see also Steigerwald et al. 2015). The effect of waste from open-air landfills on YLG egg volume was much weaker than that from trawler fishing discards, likely due to the lower nutritional quality of the former resource for egg-formation, a process that has considerable energetic costs (Robbins 1981; Oro et al. 1995; Oro et al. 1996; Williams 2005; Sanz-Aguilar et al. 2012). These results suggest a role for availability of discards and landfills on individual reproductive investment. Oro et al. (1995), for example, observed a 46% drop in YLG breeding success when discards were not available, and other studies reported a decrease in egg volume after landfill closure or a decrease in its availability (Pons 1992; Steigerwald et al. 2015). When both resources are available (landfill waste and trawling discards), it is expected that a decrease on the availability of trawling discards would result in an increase in the attendance of gulls to landfills, followed by a decrease in egg volume. The opposite might not be true so that a decrease of landfill availability may not necessarily result in more gulls attending trawlers. This is probably because refuse from landfills is a more accessible resource for gulls than fishing discards. Overall, the explanatory power of our best model was low (see Results), and this is in agreement with the variability in egg volume explained by food intake reported for several bird species, which usually ranges between 4-7% (Hiom et al. 1991; Wiebe and Bortolotti 1995; Ramsay and Houston 1997; Steigerwald et al. 2015 among others), while ca. 70% of this variability depends on intrinsic factors, such as individual investment or heritability (maternal effects) (Falconer 1960; Lessells and Boag 1987)). Although latitude did not have an effect continent did. The additive effect of fishing discards and landfills in our European study colonies explained 54% of the total spatio-temporal variability in egg volume. In contrast, we did not find a clear influence of discards and landfills on egg volume for African colonies. In Africa, since most fish is marketable, discards are much less available (Belhabib et al. 2012) and much less predictable than in European waters (see González-Solís et al. 1997a; Arcos and Oro, 2002). This lack of predictability in the availability of discards from trawlers is probably the reason why in African colonies YLGs usually attend purse seiners targeting small pelagics, although the amount of food that gulls can obtain from the former is small compared to European trawlers. On the contrary, it is rare to observe European YLGs attending purse seiners (González-Solís et al. 1997b; Arcos et al. 2001; González-Solís 2003). Therefore, it is clear that trawling discards play a much more relevant role in European colonies than in African ones. On the other hand, the lack of effect of African landfills on egg volume could be explained by the fact that waste production per capita is much higher in the European countries considered in this study than in African countries. Spanish and French waste generation rates are 1.61 and 1.07-1.48 (Kg capita-1 day-1) respectively, while in Morocco and Algeria these rates are 0.89 and 0.62 (Kg capita-1 day-1) respectively (ONEM 2001; Chantou et al. 2013). In addition, the number of people that inhabit areas near African colonies is generally less than near European colonies, and hence the total amount of waste available to gulls is also less. These socio-economic differences involving fishing and dumping practices can likely explain the smaller egg volume in African colonies. Density-dependence had a negative effect on egg volume of YLGs, presumably reducing the per capita availability of food. This effect was much more evident regarding trawling discards than regarding waste food. This result reinforces the idea that trawling discards are a high-quality foraging resource that plays an important role in YLG individual breeding performance (Oro et al. 1995) and probably on population fitness, compared to waste food from landfills in European colonies. Nevertheless, results showed a positive density-dependent association between egg volume and landfill number, suggesting that this resource does not limit breeding investment in YLG. It is possible that less competitive individuals (e.g. those in worse body condition, less skilled or sick; Genovart et al. 2010) are able to breed thanks to landfill waste (see Steigerwald et al. 2015). In fact, several studies on YLG in the western Mediterranean have shown the positive effect of the availability of waste food from landfills in population dynamics (Moulaï 2007; Duhem et al. 2008; Payo-Payo et al. 2015). This effect could act via an increase in adult winter survival. Waste food also promotes that a high number of individuals remain close to breeding sites rather than dispersing or migrating (Pons 1992; Sol et al. 1995; Arizaga et al. 2014), as it has been recorded for other generalist species such as the white stork *Ciconia ciconia* (Gilbert et al. 2016). This fact could also increase survival by removing the risks associated with dispersal and migration (Oro et al. 2008).

We have shown here that availability and quality of foraging resources mediated by density-dependence influences initial breeding investment in a generalist avian species. However, in multi-egg avian layers, breeding investment and performance can be regulated not only by modifying egg volume, but also clutch size, a parameter that has not been included in our study since we exclusively worked with modal clutches. When resources are scarce gulls first reduce egg volume and if this is not enough to prevent compromising female condition, clutch size is reduced afterwards (Martin 1987; Bolton 1991). Finally, our results suggest that a future regulation of fishing discards and the closure of open-air landfills within the European Union should trigger demographic changes not only for YLG but for the guild of generalist species exploiting these resources and competing for them (Oro et al. 2013). These changes may include an increase in dispersal, a decrease in survival, recruitment and breeding performance and a lowering of the carrying capacity of the marine environment for the whole community of generalist species, with a consequent decrease in their population numbers (see Payo-Payo et al. 2015).

2.6. Acknowledgements

We thank all the people who helped with fieldwork, especially J. Piccardo, B. Sarzo, M. Genovart, N. Pocino, M. Baena and M. Expósito. M. Calleja from GIS-IMEDEA kindly helped with maps. We are also grateful to OAPN, UB, NR Islas Columbretes, PN Serra Gelada, PN del Delta de l'Ebre, PN de Dragonera, PN de les Illes Medes, Iniciative PIM, Port Autònom de Barcelona, FAO and CSIC which kindly provided data and logistical support. We also want to thank A. Velando for providing interesting ideas. Funds were partially supplied by the Spanish Ministry of Economy and co-financiated by the European Social Fund (grant ref: CGL2013-42203-R) and by Generalitat Valenciana. This research has received funding from the European Commission's Horizon 2020 Research and Innovation Programme under Grant Agreement Nº. 634495 for the project Science, Technology, and Society Initiative to minimize Unwanted Catches in European Fisheries (MINOUW). A. Martínez-Abraín was supported by an Isidro Parga Pondal contract from Xunta de Galicia. Funding was also provided by Universidade da Coruña and Xunta de Galicia (reference GRC2014/050).

2.7. References

Arcos, J., Oro, D. and Sol, D. 2001. Competition between the yellow-legged gull *Larus cachinnans* and Audouin's gull *Larus audouinii* associated with commercial fishing vessels: the influence of season and fishing fleet. Mar. Biol. 139: 807–816.

Arcos, J. and Oro, D. 2002. Significance of nocturnal purse seine fisheries for seabirds: a case study off the Ebro Delta (NW Mediterranean). Mar. Biol. 141: 277–286.

Arizaga, J., Aldalur, A., Herrero, A., Cuadrado, J.F., Diez, E. and Crespo, A. 2014. Foraging distances of a resident yellow-legged gull (*Larus michahellis)* population in relation to refuse management on a local scale. Eur. J. Wildl. Res. 60: 171–175.

Batchelor, A.L. and Ross, G.J.B. 1984. The diet and Implications of dietary change of cape gannets on bird island, Algoa Bay. Ostrich 55: 45–63.

Belhabib, D., Pauly, D., Harper, S. and Zeller, D. 2012. Marine fisheries catches in West Africa, 1950-2010, part I. Fisheries Centre Research Reports. Fisheries Centre, University of British Columbia 20(3): 1–41.

Bicknell, A.W.J., Oro, D., Camphuysen, K. and Votier, S.C. 2013. Potential consequences of discard reform for seabird communities. J. Appl. Ecol. 50: 649–658.

Blomqvist, D., Johansson, O.C., and Götmark, F. 1997. Parental quality and egg size affect chick survival in a precocial bird, the lapwing *Vanellus vanellus*. Oecologia 110: 18–24.

Bolton, M. 1991. Determinants of chick survival in the lesser black-backed gull: relative contributions of egg size and parental quality. J. Anim. Ecol. 60: 949–960.

Bosch, M., Oro, D., Cantos, F.J. and Zabala, M. 2000. Short-term effects of culling on the ecology and population dynamics of the yellow-legged gull. J. Appl. Ecol., 37: 369–385.

Burnham, K.P. and Anderson, D.R. 2002. Model selection and multimodel inference: A practical information-theoretical approach. 2d ed. New York: Springer-Verlag, p.p. 60-115.

Burnham, K.P. and Anderson, D.R. 2004. Multimodel inference understanding AIC and BIC in Model Selection. Sociol. Methods Res. 33: 261–304.

Cama, A., Abellana, R., Christel, I., Ferrer, X. and Vieites, D. 2012. Living on predictability: modelling the density distribution of efficient foraging seabirds. Ecography 35: 912–921.

Carbonell, A., Martín, P. and Rainieri, S. 1998. Discards of the Western Mediterranean trawl fleets. Rapp. Comm. Int. Mer Médit. 35: 392-393.

Chantou, T., Feuillade-Cathalifaud, G., Bouzid, J. and Matejka, G. 2013. Seasonal and geographical characterizations of Municipal Solid Waste (MSW) in four Tunisian cities / comparison to French data. Eur. J. Sci. Res. 94: 501–512.

Christians, J.K. 2002. Avian egg size: variation within species and inflexibility within individuals. Biol. Rev. 77: 1–26.

Cunningham, E.J.A. and Russell, A.F. 2000. Egg investment is influenced by male attractiveness in the mallard. Nature 404: 74–77.

Duhem, C. 2004. Goelands surabondants et ressources alimentaires anthropiques: cas des colonies insulaires de Goélands leucophées du littoral provençal (doctoral thesis). Universite de droit, d'economie et des sciences - Aix-Marseille III, Français.

Duhem, C., Vidal, E., Legrand, G. and Tatoni, T. 2003. Opportunistic feeding responses of the Yellow-legged Gull *Larus michahellis* to accessibility of refuse dumps. Bird Study 50: 61–67.

Duhem, C., Roche, P., Vidal, E. and Tatoni, T. 2008. Effects of anthropogenic food resources on yellow-legged gull colony size on Mediterranean islands. Popul.Ecol. 50: 91–100.

Eigaard, O.R., Rihan, D., Graham, N., Sala, A. and Zachariassen, K. 2011. Improving fishing effort descriptors: Modelling engine power and gear-size relations of five European trawl fleets. Fish. Res. 110: 39–46.

European Commission 1999. European Council Directive 1999/31/EC of 26 April 1999 on the landfill of waste. Off. J. L, 282 (1999), pp. 1–19.

European Commission 2008. Directive 2008/56/EC of the European Parliament and of the Council. Establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). EC, Brussels.

European Commission (2016) Data from: Fleet Register on the Net. http://ec.europa.eu/fisheries/fleet/index.cfm.

European Environment Agency (2015) Data from: Release and Transfer Register of the European Environment Agency. http://prtr.ec.europa.eu/.

Falconer, D.S. 1960. Introduction to quantitative genetics. New York: The Ronald Press Company, p.p. 165-183.

FAO-CopeMed 2015. Report of the 4th meeting of CopeMed II Study Group on demersal stocks of interest to Algeria, Morocco and Spain in the Alboran Sea (GSAs 01, 02, 03 and 04). Malaga, Spain 3-6 November 2015. CopeMed II Technical Documents No40 (GCP/INT/028/SPA - GCP/INT/006/EC). Málaga, 2015. 60 pp.

Genovart, M., Negre, N., Tavecchia, G., Bistuer, A., Parpal, L. and Oro, D. 2010. The young, the weak and the sick: evidence of natural selection by predation. Plos One 5,5(3): e9774.

Gilbert, N.I., Correia, R.A., Silva, J.P., Pacheco, C., Catry, I., Atkinson, P.W., Gill, J.A. and Franco, A.M.A. 2016. Are white storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident white storks (*Ciconia ciconia*) from a partially migratory population. Mov. Ecol. 4:7.

González-Solís, J. 2003. Impact of fisheries on activity, diet and predatory interactions between yellow-legged and Audouin's gulls breeding at the Chafarinas Islands. Sci. Mar. 67: 83–88.

González-Solís, J., Ruiz, X. and Jover, L. 1997a. Influence of food availability on interactions between *Larus cachinnans* and *L. audouinii*. Can. J. Zool. 75: 719–724.

González-Solís, J., Oro, D., Jover, L., Ruiz, X. and Pedrocchi, V. 1997b. Trophic niche width and overlap of two sympatric gulls in the Southwestern Mediterranean. Oecologia 112: 75–80.

Grémillet, D., Pichegru, L., Kuntz ,G., Woakes, A.G., Wilkinson, S., Crawford, R.J.M. and Ryan, P.G. 2008. A junk-food hypothesis for gannets feeding on fishery waste. Proc. R. Soc. Lond. B Biol. Sci. 275: 1149–1156.

Harris, M.P. 1964. Aspects of the breeding biology of the gulls. Ibis 106: 432–456.

Harris, M.P., Anker-Nielssen, T., McCleery, R.H., Erikstad, K.E., Shaw, D.N. and Brosbois, V. 2005. Effect of wintering area and climate on the survival of adult Atlantic Puffins *Fratercula arctica* in the eastern Atlantic. Mar. Ecol. Prog. Ser. 297: 283-296.

Hiom, L., Bolton, M., Monaghan, P. and Worral, D. 1991. Experimental evidence for food limitation of egg production in gulls. Ornis Scand. 22: 94–97.

Hobson, K.A., Blight, L.K. and Arcese, P. 2015. Human-induced long-term shifts in gull diet from marine to terrestrial sources in North America’s coastal Pacific: more evidence from more isotopes (δ2H, δ34S). Environ. Sci. Technol. 49: 10834–10840.

Johnson, P.C. 2014. Extension of Nakagawa & Schielzeth’s R2GLMM to random slopes models. Methods Ecol. Evol. 5: 944–946.

Jordi, O., Herrero, A., Aldalur, A., Cuadrado, J.F. and Arizaga, J. 2014. The impact of non-local birds on yellow-legged gulls (*Larus michahellis*) in the Bay of Biscay: a dump-based assessment. Anim. Biodivers. Conserv.37: 183–190.

Lessells, C.M. and Boag, P.T. 1987. Unrepeatable repeatabilities: a common mistake. The Auk 104: 116–121.

Martin, T.E. 1987. Food as a limit on breeding birds: a life-history perspective. A. Rev. Ecol. Syst. 18: 453-487.

Ministère de l’Environnement, de l’Énergie et de la Mer (2015) Data from: Registre Français des Émissions Polluantes du Ministère de l’Environnement, de l’Énergie et de la Mer. http://www.pollutionsindustrielles.ecologie.gouv.fr/IREP/.

Ministerio de Agricultura, Alimentación y Medio Ambiente (2015) Data from: Registro Estatal de Emisiones y Fuentes Contaminantes del Ministerio de Agricultura,Alimentación y Medio Ambiente. http://www.prtr-es.es/.

Martínez-Abraín, A., Mestre, R. and Oro, D. 2002. Demersal trawling waste as a food source for Western Mediterranean seabirds during the summer. ICES J. Mar. Sci. J. Cons. 59: 529–537.

Moulaï, R. 2007. Fluctuation saisonnière des oiseaux de la décharge publique de la ville de Béjaia (Algérie), cas particulier du goéland leucophée (*Larus michahellis*). Ostrich 78: 527–531.

Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol.4: 133–142.

ONEM 2001. Environment state in Morocco. Chapter 4: wastes and urban areas. National Department of Environment, Morocco.

Oro, D. 1996. Effects of trawler discard availability on egg laying and breeding success in the lesser black-backed gull *Larus fuscus* in the western Mediterranean. Mar. Ecol. Prog. Ser. 132: 43–46.

Oro, D., Bosch, M. and Ruiz, X. 1995. Effects of a trawling moratorium on the breeding success of the Yellow-legged Gull *Larus cachinnans*. Ibis 137: 547–549.

Oro, D., Jover, L. and Ruiz, X. 1996. Influence of trawling activity on the breeding ecology of a threatened seabird, Audouin's gull *Larus audouinii*. Mar. Ecol. Prog. Ser. 139: 19–29.

Oro, D., Pradel, R. and Lebreton, J.D. 1999. Food availability and nest predation influence life history traits in Audouin's gull, *Larus audouinii*. Oecologia 118: 438–445.

Oro, D., Cam, E., Pradel, R. and Martínez-Abraín, A. 2004. Influence of food availability on demography and local population dynamics in a long-lived seabird. Proc. R. Soc. Lond. B Biol. Sci. 271: 387–396.

Oro, D., Martínez-Abraín, A., Paracuellos, M., Nevado, J.C. and Genovart, M. 2006. Influence of density dependence on predator-prey seabird interactions at large spatio-temporal scales. Proc. R. Soc. Lond. B Biol. Sci. 273: 379–383.

Oro, D. and Martínez-Abraín, A. 2007. Deconstructing myths on large gulls and their impact on threatened sympatric waterbirds. Animal Conservation, 10: 117–126.

Oro, D., Margalida, A., Carrete, M., Heredia, R. and Donázar, J.A. 2008. Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. Plos One 3 (12): e4084.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S. and Martínez-Abraín, A. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecol. Lett. 16: 1501–1514.

Paracuellos, M. and Nevado, J.C. 2010. Culling Yellow-legged Gulls *Larus michahellis* benefits Audouin's Gulls *Larus audouinii* at a small and remote colony. Bird Study. 57(1): 26-30.

Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in the herring gull (*Larus argentatus*). Nature 228: 1221–1222.

Payo-Payo, A., Oro, D., Igual, J.M., Jover, L., Sanpera, C. and Tavecchia, G. 2015. Population control of an overabundant species achieved through consecutive anthropogenic perturbations. Eccol. Appl. 25(8): 2228–2239.

Piatt, J.F. and Anderson, P. 1996. Response of common murres to the Exxon Valdez oil spill and long-term changes in the Gulf of Alaska marine ecosystem. Proc. Exxon Valdez Oil Spill Symp.

Pons, J.M. 1992. Effects of changes in the availability of human refuse on breeding parameters in a Herring Gull *Larus argentatus* population in Brittany, France. Ardea 80: 143-150.

Ramos, F.J., Ramirez, F., Sanpera, C., Jover, L. and Ruiz, X. 2006. Feeding ecology of Yellow-legged Gulls *Larus michahellis* in the Western Mediterranean: a comparative assessment using conventional and isotopic methods. Mar. Ecol. Prog. Ser. 377: 289–297.

Ramos, R., Ramírez, F., Carrasco, J.L. and Jover, L. 2011. Insights into the spatiotemporal component of feeding ecology: an isotopic approach for conservation management sciences. Divers. Distrib. 17: 338–349.

Ramsay, S.L. and Houston, D.C. 1997. Nutritional constraints on egg production in the blue tit: a supplementary feeding study. J. Anim. Ecol. 66: 649–657.

Risch, T.S. and Rohwer, F.C. 2000. Effects of parental quality and egg size on growth and survival of herring gull chicks. Can. J. Zool. 78: 967–973.

Robbins, C.T. 1981. Estimation of the relative protein cost of reproduction in birds. The Condor 83: 177–179.

Sanz-Aguilar, A., Minguez, E., Oro, D. 2012. Is laying a large egg expensive? female-biased cost of first reproduction in a petrel. The Auk 129: 510–516.

Sol, D., Arcos, J.M. and Senar, J.C. 1995. The influence of refuse tips on the winter distribution of Yellow-legged Gulls *Larus cachinnans*. Bird Study 42: 216–221.

Steigerwald, E.C., Igual, J.M., Payo-Payo, A. and Tavecchia, G. 2015. Effects of decreased anthropogenic food availability on an opportunistic gull: evidence for a size-mediated response in breeding females. Ibis 157, 439–448.

Tsagarakis, K., Palialexis, A. and Vassilopoulou, V. 2014. Mediterranean fishery discards: review of the existing knowledge. ICES J. Mar. Sci. J. Cons. 71: 1219–1234.

Vergara, A., Pitart, C., Montalvo, T., Roca, I., Sabaté, S., Hurtado, J.C., Planell, R., Marco, F., Ramirez, B., Peracho, V., de Simón, M. and Vila, J. 2017. Prevalence of extended-spectrum-β-lactamase- and /or carbapenemase-producing *Escherichia coli* isolated from yellow-legged gulls from Barcelona, Spain. Antimicrob Agents Chemother. 61: 1-5.

Vidal, E., Medail, F. and Tatoni, T. 1998. Is the yellow-legged gull a superabundant bird species in the Mediterranean? Impact on fauna and flora, conservation measures and research priorities. Biodivers. and Conserv. 7: 1013.

Votier, S.C., Furness, R.W., Bearhop, S., Crane, J.E.,Caldow, R.W.G., Catry, P., Ensor, K., Hamer, K.C., Hudson, A.V., Kalmbach, E., Klomp, N.I., Pfeiffer, S., Phillips, R.A., Prieto, I. and

Thompson, D.R. 2004. Changes in fisheries discard rates and seabird communities. Nature 427: 727–730.

Wiebe, K.L. and Bortolotti, G.R. 1995. Egg size and clutch size in the reproductive investment of American Kestrels. J. Zool. 237: 285–301.

Williams, T.D. 2005. Mechanisms underlying the costs of egg production. BioScience 55: 39–48.

Chapter 3

Predictable anthropogenic food subsidies decouple inter-specific temporal synchrony

Ana Payo-Payo, José-Manuel Igual, Ana Sanz-Aguilar, Enric Real, Meritxell Genovart, Daniel Oro and Giacomo Tavecchia (2019). Predictable anthropogenic food subsidies decouple inter-specific temporal synchrony. Under review in *OIKOS*.

Predictable anthropogenic food subsidies decouple inter-specific temporal synchrony

Ana Payo-Payo, José-Manuel Igual, Ana Sanz-Aguilar, Enric Real, Meritxell Genovart, Daniel Oro and Giacomo Tavecchia

A Payo-Payo (https://orcid.org/0000-0001-5482-242X)(anapayopayo@gmail.es), School of Biological Sciences, Zoology Building, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK. J.M. Igual, A. Sanz-Aguilar, E. Real and G. Tavecchia, Group of Ecology and Animal Demography, IMEDEA (CSIC-UIB), C/Miquel Marquès 21, 07190, Esporles, Spain. Meritxell Genovart and Daniel Oro, CEAB (CSIC), Accés Cala Sant Francesc 14, 17300 Blanes, Spain and IMEDEA (CSIC-UIB), Miquel Marquès 21, 07190 Esporles, Spain.

3.1. Abstract

Predictable anthropogenic food subsidies (PAFS) can buffer the influence of environmental stochasticity on animal populations. As a result, originally environmentally synchronized systems can become uncorrelated or *viceversa*. To investigate the role of PAFS on between species synchrony we analyzed the consequences of European policies implementation — i.e. termination of open landfilling — on interspecies temporal synchrony of two sympatric marine top predators with different foraging strategies. We considered data collected over 15 years on one marine specialist — the Scopoli's shearwater, and one generalist — the Yellow-legged gull. Using cross-correlation analysis and a state-based Markov chain modelling approach, we identified periods in which egg volume variations — as an indication of food availability at any given year — were synchronized. Our results show that perfect synchrony occurs after the disappearance of the largest local open-air landfill indicating that coupling is mediated by shared environmental signals and that PAFS can disrupt interspecific synchrony.

Keywords: Synchrony, predictable anthropogenic food subsidies, egg volume, seabird, cross-correlation, Markov Chain, fishing discards, human waste, wNAO, climate.

3.2. Introduction

Synchrony/asynchrony across and within species is a central issue in ecological theories (Moran 1953; Bjørnstad *et al.* 1999; McCarthy 2011). At large spatial scale the degree of spatio-temporal synchrony between systems should equal the degree of correlation between their environments (e.g. climate), the so called 'Moran's effect', Moran 1953; Ranta *et al.* 1995; Grenfell *et al.* 1998). At a small spatial scale, other climate-unrelated factors such as dispersal (Sutcliffe *et al.* 1996), parasites (Cattadori *et al.* 2005) or predation (Ims & Andreassen 2000, Tavecchia et al. 2008) can play an important role in driving population synchrony/asynchrony. Despite a relative large number of studies have solved numerical and conceptual difficulties (Vik *et al.* 2004), we still have identified only a limited number of factors that may cause or disrupt synchrony across populations (Liebhold *et al.* 2004; Tavecchia et al. 2008, Mortelliti *et al.* 2015). Here, we formulate a new testable hypothesis, the *anthropogenic mask of synchrony,* explaining synchrony disruption in natural systems. *This hypothesis* holds that the presence of predictable anthropogenic food subsidies (PAFS, Oro et al. 2013) helps buffer, or shield, a system from the impact of environmental stochasticity and therefore decouple the dynamics of its constituents (Figure 8). The removal of food subsidies is predicted to reveal the natural underlying dynamics, showing otherwise hidden patterns of synchrony across species. It has been seldom considered that the current pattern of population fluctuations might be altered by human activities that mask the environmental forcing, decoupling previously related dynamics (Oro *et al.* 2013; Payo-Payo *et al.* 2015). For instance, PAFS in the form of fishery discards or waste from human activities (Oro *et al.* 2013; Payo-Payo *et al.* 2015) produces profound changes in the ecology of the species associated with them. PAFS can change trophic niche, reduce the variance of demographic parameters and buffer the influence of environmental stochasticity (Lahoz-Monfort *et al.* 2013). Because not all species exploit anthropogenic subsidies in a similar way, PAFS are expected to influence the natural

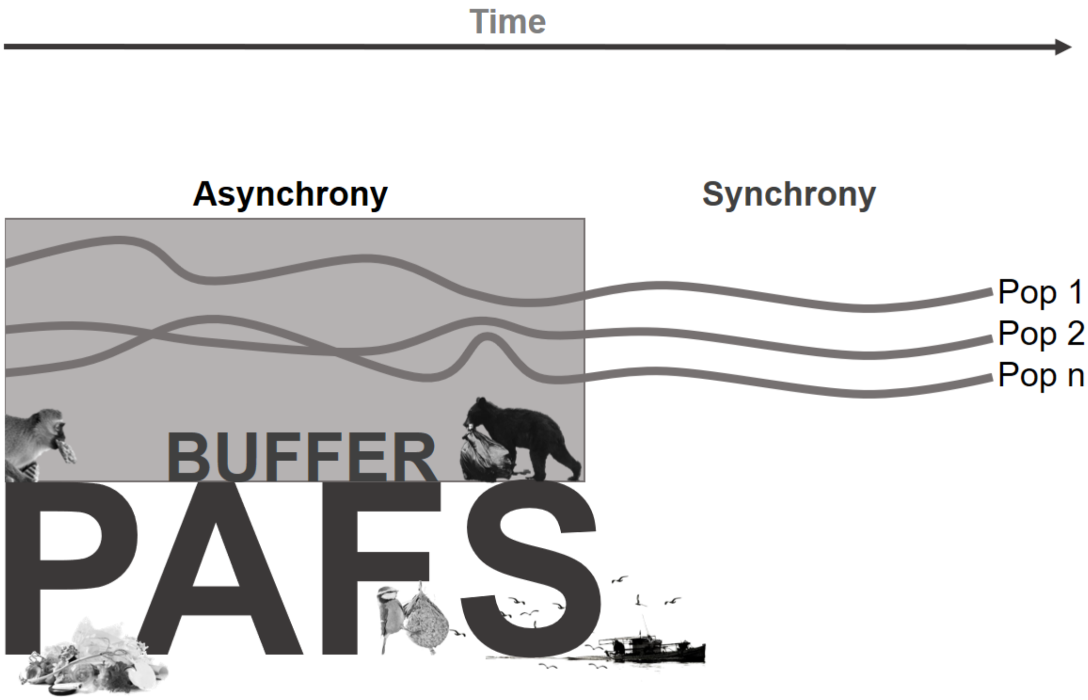

Figure 8. Schematic representation of the *buffering hypothesis*: changes in the availability of PAFS (Predictable Anthropogenic Food Subsidies) can decouple dynamics in natural systems through changes at different organization levels.

pattern of synchrony across populations of different species through effects on their vital rates, e.g. survival and reproductive parameters. We present a state-based approach (Box.1) by which our hypothesis can be tested and show a first prove of the 'anthropogenic mask of synchrony' hypothesis using real data. Finally, we identify opportunities in which this hypothesis can be further tested.

The anthorpogenic mask of synchrony

We evaluate changes in the egg volume over time of two long-lived marine top predators: the Scopoli's shearwater (*Calonectris diomedea, CD* hereafter) and the Yellow-legged gull (*Larus michahellis, LM* hereafter). The egg volume in birds correlates with chick size and survival (Risch & Rohwer 2000; Krist 2011). Moreover, for income breeders, egg volume is an indicator of parental foraging conditions just before the egg formation period (Oro 1996) and, as such, we expect to vary in parallel in species submitted to the same environmental forcing and/or exploiting a similar resources. The *CD* and the *LM* have different diets. The

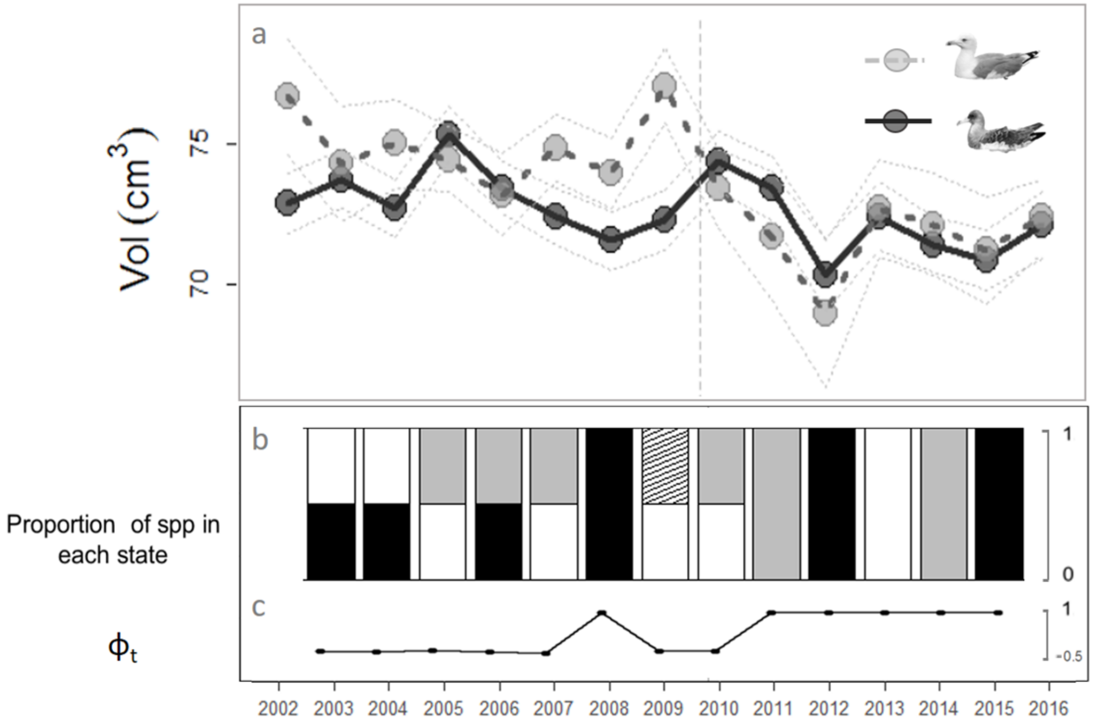

Figure 9. a) Mean egg volume (±1.96 SE, Vol) time series of the Scopoli's shearwater and the Yellow-legged gull breeding simpatrically at Balearic Islands (Spain) from 2002 to 2016. Vertical dashed line indicates the time at which landfill refuse was no longer available. b) Proportion of species that are in: state1 (trough state, black); 2 (increase state, grey stripped); 3 (peak state, white); and 4 (decrease state, grey). For example, in 2005 each one of the species was in a different state while in 2011 both species were in the same state. c) The line (solid circles) indicates synchrony measure (Φ_t), with perfect synchrony being Φ=1.

former is a marine opportunistic specialist, which mainly feeds on pelagic fish and on fishing discards. The latter is a generalist species with a broad dietary spectrum which, in the Mediterranean basin, includes natural prey (both terrestrial and aquatic), fishing discards and, in vast majority, human waste from landfills (Granadeiro *et al.* 1998; Payo-Payo *et al.* 2015). In our studied populations, the trophic segregation described above was compromised after 2010, when local authorities transformed the only open-landfill in Mallorca Island in an incinerator and forced *LM* to progressively shift their diet towards marine resources (Payo-Payo *et al.* 2015). This shift has necessary increased the diet overlapping of the two species. We hypothesize that PAFS availability damped and decoupled Yellow-legged gull breeding parameters from environmental stochasticity but

BOX 1. *Synchrony patterns through a state-based Markov chain*

Correlation and cross-correlation between time-series is a common method to measure synchrony; however, despite it considers the magnitude of the change, it does not necessary reflect coupled dynamics (Vik et al 2004). Consequently we used a complementary approach and identified coupling patterns through a state-based Markov chain modelling approach as in Haydon et al (2003) (Haydon *et al.* 2003). To validate the hypothesis and illustrate the approach, we considered two time series $\{X_{i,t}\}$ of *k* values of populations i (with i =1,2) at time t (with t=1, 2, .., *k,* see an example in the next paragraph). We were interested in the degree of synchrony, that is to say the extent to which fluctuations of the two series are aligned. Following Haydon et al. (2003), for each time-series we built a new one $\{Y_t\}$ of *k*-2 elements (with t = 2, 3, ..., *k*-1) where:

$Y_t = 1$ when $X_{t-1} > X_t \leq X_{t+1}$ (X_t is a trough in the time series)

$Y_t = 2$ when $X_{t-1} \leq X_t \leq X_{t+1}$ (X_t is the intermediate value of two consecutive increases)

$Y_t = 3$ when $X_{t-1} \leq X_t > X_{t+1}$ (X_t is a peak in the time series),

$Y_t = 4$ when $X_{t-1} > X_t > X_{t+1}$ (X_t is the intermediate value of two consecutive decrease years).

The series $\{Y_t\}$ describes the variable state at a given point in time in relation to the precedent and subsequent states. Considering the new series $\{Y_t\}$ as a first order Markov process, there is a 4 x 4 matrix, **T**, that describes the transition probabilities, $\tau_{(r,\ m)}$ from state r to state m. Let the elements, $s(j)_t$, of a row vector $\mathbf{s}_t$ be the proportion of time series in each state at time t, with j = 1, 2, …, 4 and t=2, 3, …, *k*-1. Note that with two series, s(j) can only take three values: 0, 0.5 and 1, but depending on the number of time-series it can take any value between 0 and 1. As a measure of state synchronization, we adopt the entropy, H_t. This measure is equivalent to the Shannon–Weaver diversity index (e.g. Ricklefs 1990) estimated as:

$$Ht = -\sum_{j=1}^{4} s(j)_t \ \ln(s(j)_t)\,.$$

Let H_{null} denote possible values of H_t under the hypothesis that the two-time series are stationary independent Markov chains, all associated with the transition matrix **T**. We approximate the distribution of H_{null} by simulation, noting that $\mathbf{s}_{t+1} = \mathbf{s}_t \mathbf{T}$, and using **T** as the estimate of the transition matrix to simulate the dynamic **s** of each of the n population treated as separate and independent as in Haydon *et al.* 2003. A useful measure of degree of synchronization is then the quantity $\Phi_t = 1 - \frac{H_t}{H_{null}}$ (where H_{null} is the expected value of H_{null}) which will be close to zero when the observed time-series are independent and close to one if the time-series are always all in the same state at the same time (i.e. fully synchronized).

once the food subside at landfill was no longer available, the species become susceptible to the same environmental stimuli than sympatric *CD*, potentially inducing synchrony among species.

Data of both species were collected between 2002 and 2016 at Dragonera Natural Park, a 380ha reserve off the western coast of Mallorca Island, Balearic archipelago, Spain. *CD* is a medium size seabird that feeds mainly on small epipelagic fish and squid (Granadeiro *et al.* 1998), yet discards from trawling fleets can represent an important percentage of its diet (Oro & Ruiz 1997; Martínez-Abraín *et al.* 2002). The species breeds in burrows under boulders or vegetation from May to October. *CD*s lay single egg-clutches, and their breeding population at the studied colony is estimated to be around 200 pairs (Sanz-Aguilar *et al.* 2016). It is a trans-equatorial migrant that leaves Mediterranean waters in October to move to more productive areas in the Atlantic Ocean (González-Solís *et al.* 2007) and they come back into the Mediterranean in February-March to breed. Dragonera Island hosts the largest *LM* colony of the Balearic archipelago (ca. 3000 pairs in 2015). *LM*s usually lay 2-3 eggs in March-April and after the breeding season birds show movements towards the northern coasts of Spain (Cantabric Sea) as well as along the coasts of France (Mediterranean) and Portugal (Atlantic Ocean) (own data). Gulls come back to the Balearic Islands in January, few weeks before *CD*. In the fifteen-year period of the study, we measured 1777 eggs of *CD* (1777 nests) and 1590 eggs of *LM* from 3-egg clutches (530 nests) to the nearest millimetre using a digital calliper. Egg volume (V), expressed in cm^3, was calculated as $V = \beta(L)(W)^2$ (Harris 1964; Hoyt 1979), where L and W are egg length and width, respectively, and β is a species-specific constant (here 0.000509 and 0.000476 for *CD* and *LM*, respectively).

The entropy analysis showed a synchronization measure (Φ_t) equal to 1 after 2009 pointing to a synchronous dynamics following the landfill closure in 2010, i.e. both time-series were in the same state despite oscillating over time consistently (Figure 9).

Hidden synchrony between sympatric species: implication for the mechanisms and further research

We showed how perfect synchronization of egg-size variations for two sympatric species arises after the disappearance of one PAF (i.e. landfill human waste). This indicates that egg volume variations responds to common drivers - at least for the seven-year period after PAFS cessation considered here. A first hypothesis is that synchrony between the two species arises from the increased overlap between their trophic niches. For example, Payo-Payo *et al.* 2015 showed a progressive shift of *LM* diet toward marine items after the landfill closure. This can be due by a change in gulls' foraging strategy or/and by the permanent dispersal of those individuals that previously exploited primarily human waste resources. A second hypothesis is that the two sympatric species have common drivers that indirectly, and possible through different paths, influence both species at the same time, e.g. food resources whose dynamics are coupled by environmental forcing (Robinson *et al.* 2013). In our case, this can be a plausible hypothesis as the For example, the breeding success in our *CD* population was associated by an external climatic stimulus: the winter North Atlantic Oscillation (wNAO; Genovart *et al.* 2018). Low wNAO values have been previously reported to increase water mixing due to low temperatures which promotes higher marine productivity in the Western Mediterranean (Fernández de Puelles & Molinero 2007; Martín *et al.* 2011). This would explain its direct association with *CD* egg volume, but it does not fully explain why the egg of should also depend on marine productivity *per se* given the broader diet of the species. Therefore, the synchrony should also be due to common environmental factors: for example, wNAO also influences the availability of terrestrial food items through precipitations (Stenseth *et al.* 2002) and it also may drive laying date in both species, which in turn would be associated with egg volume (Oro *et al.* 2014). A third possible explanation is that the perturbation enacted to the system by the landfill closure might have led to temporary synchrony among both populations (i.e. transient synchrony, Keitt 2008) due to the rapid change in *LM* population size (Payo-Payo *et al.* 2015; Klapwijk *et al.* 2018). Synchronized transient dynamics have been described in invertebrates in seasonal environments and they have been ascribed to a change in community composition. Changes in community composition can lead to changes in interspecific interactions such as temporal interspecific competition which can potentially enact as an underlying synchronization mechanism. It seems difficult that the same explanation holds in our system. If it was the case, we expect that present temporal pattern in egg size variation will be decoupled in the future. Although both correlations and state-based Markov chain modelling provided a clear evidence of the synchronization of egg volume of both species after landfill closure we are not able to pin-down unequivocally the factors responsible. We acknowledge that our time series is still short and that future studies should corroborate our findings, in particular about the transient nature of the dynamics. Despite, we believe that the hypothesis on the *anthropogenic mask of synchrony* lead to clear prediction on intraguild synchrony. Moreover, the European Union (EU) has recently implemented new environmental policies to manage PAFS availability to mitigate their effects on natural systems and human well-being (Landfill Waste Council Directive, LWCD – aiming termination of open landfilling or the Landing Obligation Directive, LO – enacting fisheries discard ban) (E.U. 2009; European Commission 2014). This provides an extraordinary opportunity to experimentally test the role of PAFS on the synchrony between sympatric species.

3.3. Conclusions

Most synchrony studies on the spatial and the temporal dimension of synchronous dynamics have focussed on the role of climate, dispersal, predation and/or parasite load (Grenfell *et al.* 1998; Cattadori *et al.* 2005; Abbott 2007; Crump *et al.* 2009; Angeler & Johnson 2012; Batchelder *et al.* 2012; Walter *et al.* 2017). We provide the first evidence showing that the termination of food subsides of anthropogenic origin can lead to synchronization of sympatric species, opening new questions for scientific exploration.

3.4. Acknowledgements

We would like to thank all people helping with the fieldwork. Marti Mayol and the staff of the Dragonera Natural Park help us with logistics. Thanks to Pablo Almaraz for fruitful discussions. Permits were provided by the OAPN (Spanish Ministry of the Environment) and

Balearic Regional Government. Funds were partially provided by the Balearic Government (FEDER Program), the Spanish Ministry of Education (ref. FPU2012-000869), the Spanish Ministry of Economy (IBISES-CGL2013-42203-R and RESET-CGL2017-85210-P) and EU project MINOW (H2020- 634495). ASA and MG are supported by a postdoctoral contract co-funded by the Regional Government of the Balearic Islands and the European Social Fund (ref. PD/003/2016 and PD/023/2015).

3.5. References

Abbott, K.C. 2007. Does the pattern of population synchrony through space reveal if the Moran effect is acting? *Oikos*, 116, 903–912.

Allan, R., Lindesay, J. & Parker, D. 1996. *El Nino: Southern Oscillation and Climatic Variability*.

Angeler, D.G. & Johnson, R.K. 2012. Patterns of temporal community turnover are spatially synchronous across boreal lakes. *Freshw. Biol.*, 57, 1782–1793.

Batchelder, H.P., Mackas, D.L. & O'Brien, T.D. 2012. Spatial–temporal scales of synchrony in marine zooplankton biomass and abundance patterns: A world-wide comparison. *Prog. Oceanogr.*, 97–100, 15–30.

Bjørnstad, null, Ims, null & Lambin, null. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends Ecol. Evol.*, 14, 427–432.

Calado, J.G., Matos, D.M., Ramos, J.A., Moniz, F., Ceia, F.R., Granadeiro, J.P., *et al.* 2017. "Seasonal and annual differences in the foraging ecology of two gull species breeding in sympatry and their use of fishery discards." *J. Avian Biol.*

Cattadori, I.M., Hydon, D.T. & Hudson, P.J. 2005. Parasites and climate synchronize red grouse populations. *Nature*, 433, 737–741.

Crump, B.C., Peterson, B.J., Raymond, P.A., Amon, R.M.W., Rinehart, A., McClelland, J.W., *et al.* 2009. Circumpolar synchrony in big river bacterioplankton. *Proc. Natl. Acad. Sci.*, 106, 21208–21212.

E.U. 2009. E.U.2009 emendation, 1999directive. council Directive on the Landfill of Waste.

European Commission. 2014. *Directive 1392/2014. Establishing a discard plan for certain small pelagic fisheries in the Mediterranean Sea* COMMISSION DELEGATED REGULATION EU. European Commission.

Fernández de Puelles, M.L. & Molinero, J.C. 2007. North Atlantic climate control on plankton variability in the Balearic Sea, western Mediterranean. *Geophys. Res. Lett.*, 34, L04608.

Genovart, M., Bécares, J., Igual, J.-M., Martínez-Abraín, A., Escandell, R., Sánchez, A., *et al.* 2018. Differential adult survival at close seabird colonies: The importance of spatial foraging segregation and bycatch risk during the breeding season. *Glob. Change Biol.*

González-Solís, J., Croxall, J.P., Oro, D. & Ruiz, X. 2007. Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Front. Ecol. Environ.*, 5, 297–301.

Granadeiro, J.P., Nunes, M., Silva, M. & Furness, R.W. 1998. Flexible foraging strategy of Cory’s shearwater,Calonectris diomedea, during the chick-rearing period. *Anim. Behav.*, 56, 1169–1176.

Grenfell, B.T., Wilson, K., Finkenstädt, B.F., Coulson, T.N., Murray, S., Albon, S.D., *et al.* 1998. Noise and determinism in synchronized sheep dynamics. *Nature*, 394, 674–677.

Harris, M.P. 1964. Aspects of the Breeding Biology of the Gulls. *Ibis*, 106, 432–456.

Hoyt, D.F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk*, 96, 73–77.

Hurrell, J.W., Kushnir, Y., Ottersen, G. & Visbeck, M. 2003. An Overview of the North Atlantic Oscillation. In: *The North Atlantic Oscillation: Climatic Significance and*

Environmental Impact eds. Hurrell, J.W., Kushnir, Y., Ottersen, G. & Visbeck, rtin. American Geophysical Union, pp. 1–35.

Ims, R.A. & Andreassen, H.P. 2000. Spatial synchronization of vole population dynamics by predatory birds. *Nature*, 408, 194–196.

Keitt, T.H. 2008. Coherent ecological dynamics induced by large-scale disturbance. *Nature*, 454, 331–334.

Klapwijk, M.J., Walter, J.A., Hirka, A., Csóka, G., Björkman, C. & Liebhold, A.M. 2018. Transient synchrony among populations of five foliage-feeding Lepidoptera. *J. Anim. Ecol.*, 87, 1058–1068.

Krist, M. 2011. Egg size and offspring quality: a meta-analysis in birds. *Biol. Rev.*, 86, 692–716.

Lahoz-Monfort, J.J., Morgan, B.J.T., Harris, M.P., Daunt, F., Wanless, S. & Freeman, S.N. 2013. Breeding together: modeling synchrony in productivity in a seabird community. *Ecology*, 94, 3–10.

Liebhold, A., Koenig, W.D. & Bjørnstad, O.N. 2004. Spatial Synchrony in Population Dynamics. *Annu. Rev. Ecol. Evol. Syst.*, 35, 467–490.

Martín, P., Sabatés, A., Lloret, J. & Martin-Vide, J. 2011. Climate modulation of fish populations: the role of the Western Mediterranean Oscillation WeMO in sardine Sardina pilchardus and anchovy Engraulis encrasicolus production in the north-western Mediterranean. *Clim. Change*, 110, 925–939.

Martínez-Abraín, A., Maestre, R. & Oro, D. 2002. Demersal trawling waste as a food source for Western Mediterranean seabirds during the summer. *ICES J. Mar. Sci. J. Cons.*, 59, 529–537.

McCarthy, M.A. 2011. Breathing some air into the single-species vacuum: multi-species responses to environmental change. *J. Anim. Ecol.*, 80, 1–3.

Moran, P. a. P. 1953. The statistical analysis of the Canadian Lynx cycle. *Aust. J. Zool.*, 1, 291–298.

Mortelliti, A., Westgate, M., Stein, J., Wood, J. & Lindenmayer, D.B. 2015. Ecological and spatial drivers of population synchrony in bird assemblages. *Basic Appl. Ecol.*, 16, 269–278.

Oro, D. 1996. Effects of trawler discard availability on egg laying and breeding success in the lesser black-backed gull Larus fuscus in the western Mediterranean. *Mar. Ecol. Prog. Ser.*, 132, 43–46.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S. & Martínez-Abraín, A. 2013. Ecological and evolutionary implications of food subsidies from humans. *Ecol. Lett.*, 16, 1501–1514.

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, 446–457.

Oro, D. & Ruiz, X. 1997. Exploitation of trawler discards by breeding seabirds in the north-western Mediterranean: differences between the Ebro Delta and the Balearic Islands areas. *ICES J. Mar. Sci. J. Cons.*, 54, 695–707.

Payo-Payo, A., Oro, D., Igual, J.M., Jover, L., Sanpera, C. & Tavecchia, G. 2015. Population control of an overabundant species achieved through consecutive anthropogenic perturbations. *Ecol. Appl. Publ. Ecol. Soc. Am.*, 25, 2228–2239.

Ranta, E., Lindström, J. & Lindén, H. 1995. Synchrony in Tetraonid Population Dynamics. *J. Anim. Ecol.*, 64, 767–776.

Risch, T.S. & Rohwer, F.C. 2000. Effects of parental quality and egg size on growth and survival of herring gull chicks. *Can. J. Zool.*, 78, 967–973.

Robinson, J.P.W., Dornelas, M. & Ojanguren, A.F. 2013. Interspecific synchrony of seabird population growth rate and breeding success. *Ecol. Evol.*, 3, 2013–2019.

Sanz-Aguilar, A., Igual, J.M., Oro, D., Genovart, M. & Tavecchia, G. 2016. Estimating recruitment and survival in partially monitored populations. *J. Appl. Ecol.*, 53, 73–82.

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S. & Lima, M. 2002. Ecological effects of climate fluctuations. *Science*, 297, 1292–1296.

Sutcliffe, O.L., Thomas, C.D. & Moss, D. 1996. Spatial Synchrony and Asynchrony in Butterfly Population Dynamics. *J. Anim. Ecol.*, 65, 85–95.

Tavecchia, G., Minguez, E., De León, A., Louzao, M. & Oro, D. 2008. Living close, doing differently: small-scale asynchrony in demography of two species of seabirds. *Ecology*, 89, 77–85.

Vik, J.O., Stenseth, N.C., Tavecchia, G., Mysterud, A. & Lingjærde, O.C. 2004. Living in synchrony on Greenland coasts? *Nature*, 427, 697–698.

Walter, J.A., Sheppard, L.W., Anderson, T.L., Kastens, J.H., Bjørnstad, O.N., Liebhold, A.M., *et al.* 2017. The geography of spatial synchrony. *Ecol. Lett.*, 20, 801–814.

Chapter 4

It’s not all availability: carry-over effects, detectability and accessibility to food also explain breeding investment in long-lived animals

---

Enric Real, Daniel Oro, Albert Bertolero, José Manuel Igual, Ana Sanz-Aguilar, Meritxell Genovart, Manuel Hidalgo and Giacomo Tavecchia (2019). It’s not all availability: carry-over effects, detectability and accessibility to food also explain breeding investment in long-lived animals. Under review in *Ecology*.

It's not all availability: carry-over effects, detectability and accessibility to food also explain breeding investment in long-lived animals

Enric Real, Daniel Oro, Albert Bertolero, José Manuel Igual, Ana Sanz-Aguilar, Meritxell Genovart, Manuel Hidalgo and Giacomo Tavecchia

E. Real (https://orcid.org/0000-0002-6190-6303)(ereal@imedea.uib-csic.es), J.M. Igual, A. Sanz-Agilar and G. Tavecchia, Group of Ecology and Animal Demography,GEDA, IMEDEA (CSIC-UIB), C/Miquel Marquès 21, 07190, Esporles, Spain. A. Bertolero, Associació Ornitològica Picampall de les Terres de l'Ebre, C/La Galera 53, 43870 Amposta, Spain. Meritxell Genovart and Daniel Oro, CEAB (CSIC), Accés Cala Sant Francesc 14, 17300 Blanes, Spain and IMEDEA (CSIC-UIB), Miquel Marquès 21, 07190 Esporles, Spain. Manuel Hidalgo, Instituto Español de Oceanografía, Centre Oceanográfico de Baleares, Ecosystem Oceanography Group (GRECO), Palma, 07015, Spain.

4.1. Abstract

Large-scale climate indices are extensively used as predictors of ecological processes. However, the spatio-temporal scale at which these climate indices influence these processes is often speculative. Here, we used long-term data on the average egg volume, taken as an indicator of individual breeding investment, measured on 10573 nests of three long-lived seabirds. We assessed the influence of local variables (food abundance, foraging conditions and competition) measured during breeding on egg volume, compared to the predicting power of a large-scale climate index (winter and spring values of the North Atlantic Oscillation). Although local and large-scale variables were not correlated, both had a high predictive power. The importance of the winter North Atlantic Oscillation suggested carry-over effects of winter conditions on subsequent breeding investment. Interestingly, for two out of the three species considered, the most important local variables were more associated with detectability and accessibility of food (foraging conditions) than with food abundance *per se*. This implies that, contrary to what is commonly assumed, food abundance does not directly translate into food intake and that detectability and accessibility of food should be considered in the study of food-related ecological processes.

Keywords: Climate index, Foraging conditions, Breeding investment, Egg volume, Competition, Food detectability, Food accessibility, Seabirds.

4.2. Introduction

An important challenge in the study of population fluctuations is revealing the link between demographic parameters and climatic variables (Oro *et al.* 2013; Jenouvrier *et al.* 2014; Tavecchia *et al.* 2016). It is difficult, however, to single out the effect of a single climatic variable on a given biological system because variables can act directly (e.g. Barbraud *et al.* 1999), indirectly through multiple paths (e.g. Bentz *et al.* 2010), alone (e.g. Fernández-Chacón *et al.* 2011) or in combination with others (e.g. Molinero *et al.* 2005). For this reason, large-scale climatic indices are often preferred as predictors of biological and ecological processes than local variables because they are able to integrate contrasting environmental processes over different temporal and spatial scales (Jonzén *et al.* 2002; Hallett *et al.* 2004; Stenseth & Mysterud 2005). The North Atlantic Oscillation (NAO) and the Southern Oscillation indexes (SOI), for example, have been used as predictors of ecological processes in both terrestrial and marine ecosystems (Ottersen *et al.* 2001; Stenseth *et al.* 2003 and references therein). However, in many cases, the mechanisms behind these relationships remain largely unexplained or speculative (Jonzén *et al.* 2002). It is often assumed that the influence of large-scale climatic indices on ecological processes occurs *via* the direct link to local climatic variables or *via* the indirect effects on local food abundance (e.g. Ottersen *et al.* 2001; Hallett *et al.* 2004; Genovart *et al.* 2013). In marine

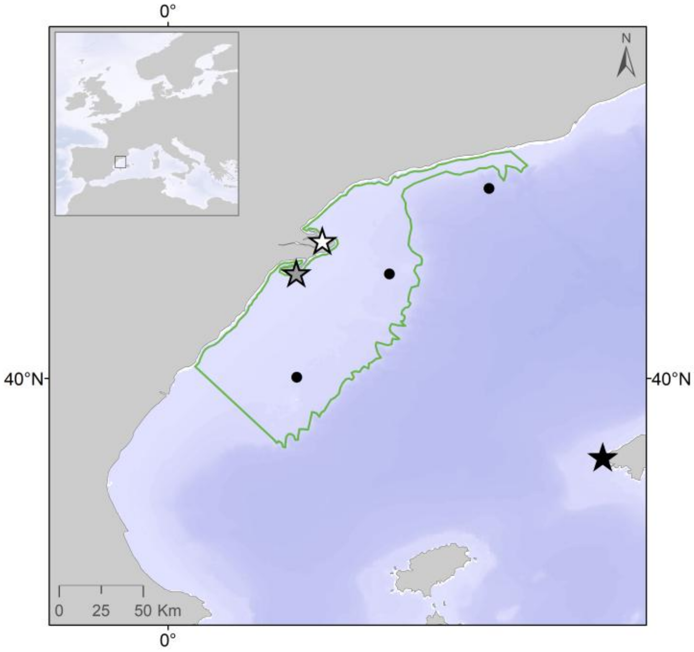

Figure 10. Common foraging area (delimitated by the green line) of studied populations during the breeding season within the Ebro Delta continental shelf (Western Mediterranean) and locations of breeding colonies of studied populations of the Scopoli's shearwater (black star), the Sandwich tern (grey star) and the Audouin's gull (white star).Black dots represents stations where local climatic and oceanographic variables (wind speed and direction, wave height and sea water turbidity) were measured to assess foraging conditions for studied populations during the early breeding season

ecosystems, the winter NAO (hereafter wNAO) is known to influence demographic parameters, such as reproductive success and survival of top predators like seabirds (see e.g. Frederiksen *et al.* 2004; Lewis *et al.* 2009; Genovart *et al.* 2013; Rodríguez *et al.* 2019). Here, we used long-term data on average egg volume of three long-lived colonial seabirds, the Scopoli's shearwater *Calonectris diomedea*, the Sandwich tern *Thalasseus sandvicensis* and the Audouin's gull *Ichthyaetus audouinii*, to assess the influence that both the wNAO and local variables (food abundance, competition and sea state), measured during breeding have on egg volume, taken as a proxy of breeding investment. Egg volume constitutes a reliable indicator of breeding investment and environmental conditions (e.g. density-dependence) in seabirds (Oro 1996; Oro *et al.* 1996) and it correlates with chick growth and survival (Parsons 1970; Bolton 1991; Blomqvist *et al.* 1997; Risch & Rohwer 2000). In the Western Mediterranean, these three species breed sympatrically and despite presenting different foraging strategies, the three species overlap in their foraging areas (Figure 10), especially when they feed on fishery discards (Martínez-Abraín *et al.* 2002). Before breeding, they also partially overlap their winter distribution, in particular along the western coasts of Africa (Figure 11). Moreover, we evaluated whether the influence of the wNAO was through its effect on winter conditions or through its effect few months later on local conditions at breeding areas. As potential predictor of realized breeding investment soon before laying, we considered food abundance, competition (i.e. population size), food detectability and accessibility at the moment of egg laying. By contrasting winter (large-scale index) and spring environmental conditions we aimed to elucidate the role of local variables vs winter carrying-over effects on breeding investment.

4.3. Methods

Field data and study area

The Sandwich tern and Audouin's gull colonies studied are located at the Delta de l'Ebre Natural Park (hereafter Ebro Delta, Lat. 40.58 Long. 0.68, decimal degrees) while the Scopoli's shearwater colony is located about 170 Km east, at Dragonera Natural Park (Balearic archipelago, Lat. 39.6, Long. 2.35; Figure 10). Previous studies based on observations and direct tracking of marked individuals indicate that adults of the three species forage actively within the Ebro Delta continental shelf (Bécares *et al.* 2016; Reyes-González *et al.* 2017); thus, we considered a marine area of 100Km radius centered on the Ebro Delta as representative of their common foraging area (Figure 1). The three species winter off the Atlantic coasts of Africa (Bécares *et al.* 2016; Reyes-González*et al.* 2017), but gulls are partial migrants, with part of their population remaining on the Western Mediterranean coast (Carrera & Garcia 1986; Bécares *et al.* 2016). For each species, we considered the annual mean volume of the modal clutch (hereafter, egg volume; N =10573 clutches in total) as an indicator of the energy reserves accumulated for breeding (see e.g. Oro 1996; Oro *et al.* 1996) (Scopoli's shearwater: 1440 one-egg clutches measured between 2001 and 2017; Sandwich tern: 425 two-egg modal clutches measured between 2000 and 2016; Audouin's gull: 8708 three-egg modal clutches measured between 2001

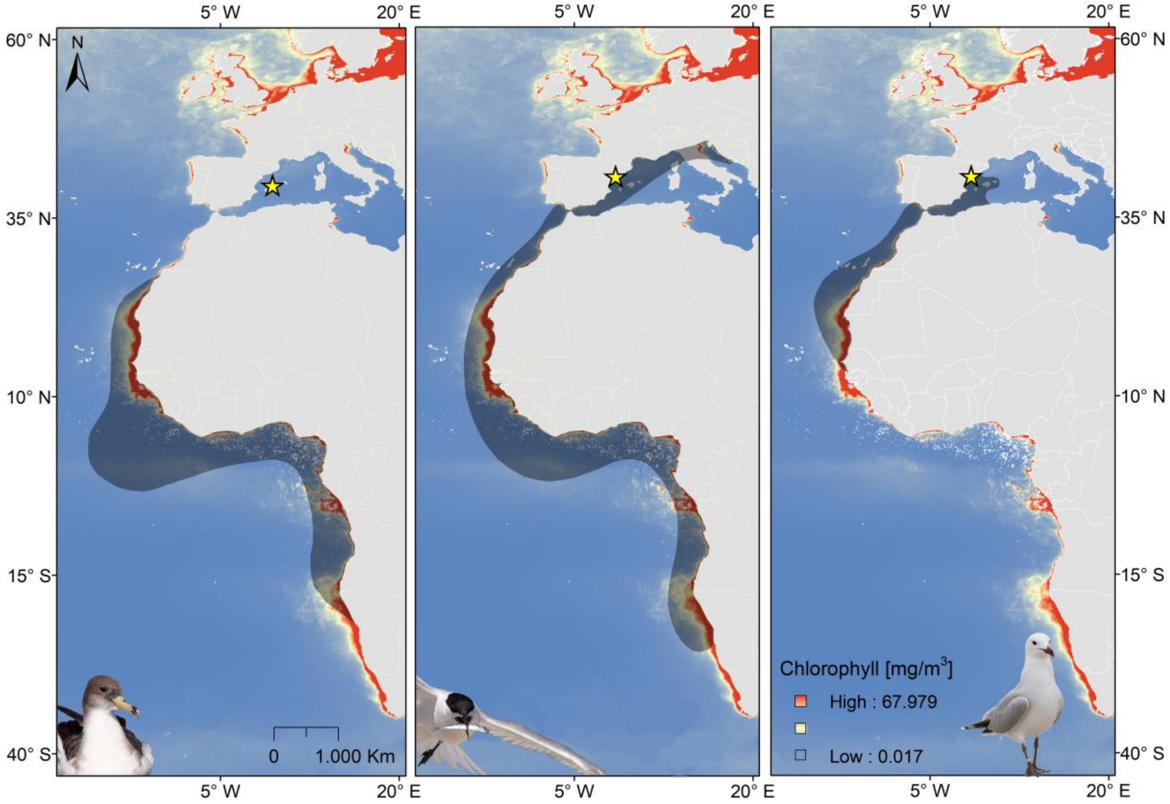

Figure 11. Wintering areas (shaded areas) of studied populations of the Scopoli's shearwater (left; data from Reyes-Gonález et al 2017), the Sandwich tern (center; data from: Institut Català d'Ornitologia) and the Audouin's gull (right; data from Bécares et al 2015). Yellow stars show the location of the breeding colonies where eggs were measured. Mean annual sea surface concentration of Chlorophyll-a for the period 2009-2013 is also shown (data obtained at: http://data.unep-wcmc.org/datasets/37).

and 2017). Eggs were measured with digital calipers to ± 0.01mm and egg volume (V) was calculated in cm^3 according to the equation $V = K \times L \times W^2$ (Hoyt 1979), where L = maximum egg length and W = maximum egg width and K is a species-specific constant value related to the shape of the egg (here 0.51×10^{-3}, 0.51×10^{-3} and 0.467×10^{-3} for shearwaters, terns and gulls respectively). Female body size was not available for all nests and despite being an important predictor of variation in egg volume across individuals (Christians 2002), we made the assumption that body size variation within a given colony is a random and additive component of the total variance.

Predictors of egg volume

Table 4. Generalized linear models explaining egg volume variability (mean egg volume in a clutch) of the Scopoli's shearwater based on Akaike information criterion values (AIC) and Akaike weights (Wi). The best explanatory model (Model 1) is the one with the lowest AIC. In the notation: Winter NAO = winter North Atlantic Oscillation, Spring NAO = Spring North Atlantic Oscillation during the species-specific pre-laying period, SS = Scopoli's shearwater, YLG = Yellow-legged Gull, AG = Audouin's Gull, PC= per capita, Wind1Q, 2Q, 3Q and 4Q = 1st ,2nd ,3rd and 4th quartile winds respectively, Discards = fishery discards, Null model is an only-intercept model. Discards PC and Sardine PC consider the number of individuals of YLG+AG+SS.

Model	Notation	Deviance	df	AIC	ΔAIC	Wi
1	Winter NAO + WaveHeight * DiscardsPC	40733,54	6	8911,61	0,00	0,85
2	Winter NAO + WaveHeight + DiscardsPC	40899,95	5	8915,48	3,87	0,12
3	Winter NAO + WaveHeight	41035,65	4	8918,25	6,64	0,03
4	Winter NAO	41331,38	3	8926,59	14,98	0,00
5	WaveHeight	41478,83	3	8931,72	20,11	0,00
6	Compet. by AG	41558,13	3	8934,47	22,86	0,00
7	Wind4Q	41602,25	3	8936,00	24,39	0,00
8	Discards PC	41635,50	3	8937,15	25,54	0,00
9	Wind3Q	41693,72	3	8939,16	27,55	0,00
10	Wind1Q	41734,33	3	8940,56	28,95	0,00

The large-scale climatic index

We used winter means (December to March) of the station-based North Atlantic Oscillation index, (wNAO) (https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based) to assess the relative importance that winter climate in year *i* (December *i*-1 to March *i*) has on predicting the egg volume of the following breeding season. Finally, spring means (considering the species-specific early breeding season; see Tables 6, S4) of the North Atlantic Oscillation (spNAO) were also used to assess the possible influence exerted by this climate index during spring months.

Local foraging conditions: detectability and accessibility of food resources

To assess how local climatic and oceanographic variables potentially affect detectability and accessibility of food, and influence the temporal variance of the egg volume of studied populations during the species-specific early breeding season (see Table S5), we used monthly means of i) wind speed and direction, ii) wave height and iii) sea water turbidity.

Table 5. Generalized linear models explaining egg volume variability (mean egg volume in a clutch) of the Sandwich tern based on Akaike information criterion values (AIC) and Akaike weights (Wi). The best explanatory model (Model 1) is the one with the lowest AIC. In the notation: Winter NAO = winter North Atlantic Oscillation, Spring NAO = Spring North Atlantic Oscillation during the species-specific pre-laying period, YLG = Yellow-legged Gull , PC= Per capita, Wind1Q, 2Q, 3Q and 4Q = 1st ,2nd ,3rd and 4th quartile winds respectively, Discards = fishery discards, Null model is an only-intercept model. Both, discards PC and anchovy PC consider the number of individuals of ST, YLG, AG and SS.

Model	Notation	Deviance	df	AIC	ΔAIC	Wi
1	Winter NAO + Wind3Q + Turbidity	1655,94	5	1787,71	0	0,23
2	Winter NAO + Wind3Q	1665,30	4	1788,10	0,39	0,19
3	Winter NAO + Wind3Q + Turbidity + Compet. by YLG	1650,57	6	1788,34	0,63	0,17
4	Winter NAO + Wind3Q + Compet. by YLG	1662,09	5	1789,28	1,57	0,10
5	Winter NAO + Wind3Q * Turbidity	1655,69	6	1789,65	1,94	0,09
6	Winter NAO + Wind3Q + AnchovyPC	1664,01	5	1789,77	2,06	0,08
7	Winter NAO + Wind3Q + Wind1Q	1664,41	5	1789,87	2,16	0,08
8	Winter NAO	1689,33	3	1792,16	4,45	0,02
9	Wind3Q	1690,22	3	1792,38	4,67	0,02
10	Spring NAO	1704,32	3	1795,893	8,18	0,00

Data on wind speed (m·s^{-1}), wind direction (degrees) and wave height (m) based on

numeric modeling data were obtained from the SIMAR dataset at: http://www.puertos.es/es-es/oceanografia/Paginas/portus.aspx. To account for a cumulative effect on foraging conditions, the number of days of winds blowing from each quartile (Q1: 0º-90º; Q2: 91º-180º; Q3: 181º-270º and Q4: 271º - 360º) were multiplied by the corresponding mean wind speed (days·m·s^{-1}). Finally, seawater turbidity was estimated by considering the diffuse attenuation coefficient of light at 490 nm (kd490) (1 Km^2 resolution) from multi-satellite observations (http://marine.copernicus.eu/services-portfolio/access-to-products/).

Intra- and inter-specific competition during the early breeding season

To assess the potential effect that intra-specific competition has on the temporal variance of the egg volume when species match spatially and during the foraging process we used annual estimates of breeding pair numbers for each studied species. For the Audouin's gull,

Table 6. Generalized linear models explaining egg volume variability (mean egg volume in a clutch) of the Audouin's gull based on Akaike information criterion values (AIC) and Akaike weights (Wi). The best explanatory model (Model 1) is the one with the lowest AIC. In the notation: Winter NAO = winter North Atlantic Oscillation, Spring NAO = Spring North Atlantic Oscillation during the species-specific pre-laying period, YLG = Yellow-legged Gull, AG= Audouin's Gull, SS= Scopoli's shearwater, PC= Per capita, Discards = fishery discards, Null model is an only-intercept model. Discards PC, Sardine PC and Anchovy PC consider the number of individuals of YLG+AG+SS.

Model	Notation	Deviance	df	AIC	ΔAIC	W
1	Winter NAO + Intrasp. compet. * Compet. by YLG	94498,10	6	45482,82	0,00	1,00
2	Winter NAO + Intrasp. compet. + Compet. by YLG	94640,28	5	45493,91	11,09	0,00
3	Winter NAO + AG pairs	94695,19	4	45496,96	14,14	0,00
4	Intrasp. compet.	95560,62	3	45574,18	91,36	0,00
5	Sardine PC	95790,58	3	45595,10	112,28	0,00
7	Discard PC	97288,69	3	45730,22	247,40	0,00
8	Anchovy PC	97531,97	3	45751,97	269,15	0,00
9	Wave height	97782,89	3	45774,34	291,52	0,00
10	Winter NAO	98076,86	3	45800,48	317,66	0,00

population size estimates were based on annual censuses from three different breeding colonies sharing the same foraging area (Ebro Delta, see coordinates above; Castellón, Lat. 39.96 Long. 0.01 and Tarragona, Lat. 41.09 Long. 1.22). Among all breeding colonies of the Scopoli's shearwater whose individuals are known to feed in the study area, the one considered here is the largest known (estimated to be c.200 pairs; Sanz-Aguilar *et al.* 2016) (Figure 10, Reyes-González*et al.* 2017). Population size estimates were based on the number of nests occupied in the studied colony each year. Finally, annual estimates of breeding pairs of Sandwich terns at the Ebro Delta Natural Park were obtained through direct censuses. The effect of inter-specific competition for food was assessed by considering the total number of breeding pairs of the three seabird species (See table S6) and the Yellow-legged gull *Larus michahellis*, an abundant generalist species competing for the same foraging resources (i.e. sardines, anchovies and trawling fishery discards) in the study area.

Per capita food abundance during the early breeding season

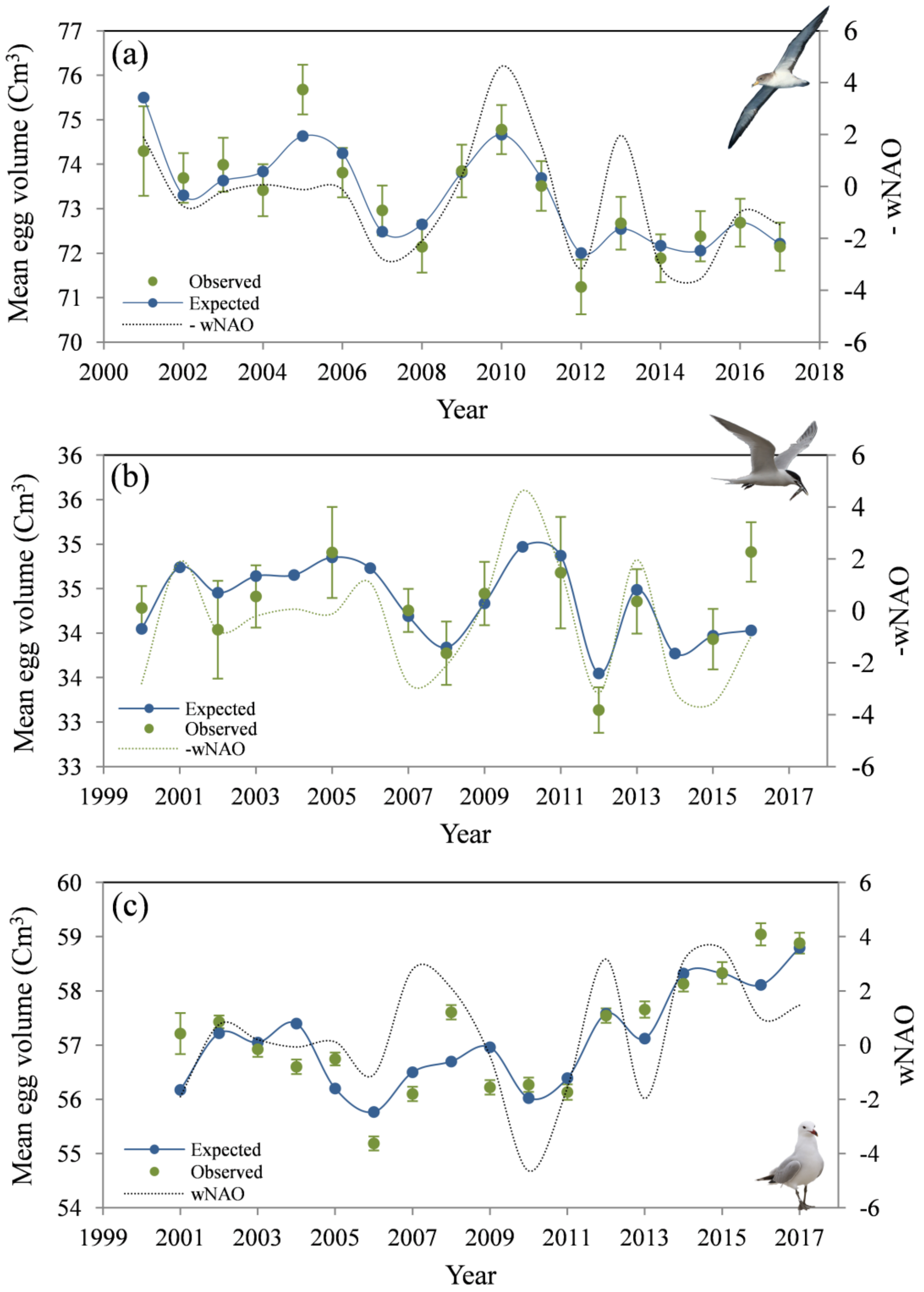

Figure 12. Time series with the mean egg volume observed (filled circles) ± s.e. and the mean egg volume expected (open circles) according to the best explanatory models in (a) the Scopoli's shearwater (Model1, Table S2), (b) the Sandwich tern (Model1, Table S3) and (c) the Audouin's gull (Model1, Table S4). wNAO values (multiplied by -1 for better appreciation in figures "a" and "b") are also shown (dotted line).

To assess how the abundance of natural and anthropogenic food resources influences the temporal variance of the egg volume, we used estimates of the per capita abundance of both natural prey and fishery discards during the species-specific early breeding season (Table S5). Temporal variability in the abundance of natural prey was approximated by using the catch per unit effort (hereafter 'CPUE') of sardines *Sardina pilchardus* and anchovies *Engraulis encrasicolus*, the most abundant small pelagic species in the study area (Morote *et al.* 2010; Tugores *et al.* 2010) and potential natural prey for the three studied species (Pedrocchi *et al.* 2002; Alonso *et al.* 2012, 2018; Gaglio *et al.* 2018). Considering this, we assumed that sardines are one of the main natural prey for the Scopoli's shearwater in the Western Mediterranean while anchovies should be the main prey for Sandwich terns, and both (sardines and anchovies) should be the main natural for the Audouin's gull and the Yellow-legged gull. CPUE was obtained by dividing the total landings (in Kg) of each species by the number of vessels of the main purse seine fleets in the area (Table S5). Data on landings and number of fishing vessels were facilitated by the Direcció General de Pesca I Afers Marítims of the Generalitat de Catalunya. We used the sum of the main horsepower declared by trawl fleets in the study area (Table S5) as a proxy of the abundance of fishery discards (see Real *et al.* 2017). Data on trawl horsepower were obtained from the European Commission Fleet Register at: http://ec.europa.eu/fisheries/fleet/index.cfm. Per capita abundance of natural prey and fishery discards were calculated dividing estimates of each resource type by the total number of breeding pairs of the main seabird species competing for each specific resource (See Table S6).

Data analysis

We analyzed factors affecting egg volume by means of general linear models in the software R (R- Development team 2014), with mean egg volume in a clutch as the dependent variable. Covariates were scaled by dividing by $1*10^3$ and standardized in order to equalize their means and obtained comparable standard deviations. We began the analysis by calculating the correlation coefficient across all covariates described above to avoid the simultaneous presence of highly correlated covariates (collinearity). Information theory based on Akaike Information Criterion (AIC, Burnham & Anderson 2002) was used to select the best explanatory models. Models with AIC differences ≤ 2 were considered equivalents (Burnham & Anderson 2002; 2004). The proportion of total temporal variance in egg volume explained by covariates was calculated as [deviance (model constant) – deviance (model with covariate)] / [deviance (model constant) – deviance (model time-dependent)]. The resulting statistics can be used as an equivalent of the coefficient of determination, R^2 (hereafter R^2; see Harris *et al.* 2005).

4.4. Results

Cross-correlations indicated a low level of co-linearity among the variables considered (Tables S6, S7 and S8).

Scopoli's shearwater

For the Scopoli's shearwater, the model with the lowest AIC value included the additive effect of the wNAO and the statistical interaction between the wave height and the per capita abundance of fishery discards (Model 1 in Tables 4, S2; Figure 12a). According to this model, high values of wave height had a negative effect on the egg volume, even when fishery discards per capita were abundant. The wNAO had a negative effect on the egg volume whilst the effect of fishery discards was positive. When assessing wNAO and local conditions separately, the percentage of the total temporal variance in the egg volume explained by the wNAO was 45%, while the model considering only local conditions (wave height and fishery discards) explained 66%. When tested simultaneously (wNAO, wave height and fishery discards), these covariates explained 79% of the total temporal variance of the egg volume (Model 1; Fig 1a). We did not find a significant effect of the number of potential competitors (Tables 4, S2) nor of the spNAO.

Sandwich terns

For the Sandwich tern, the best model suggested that egg volume was associated with the additive effect of the wNAO and food detectability and accessibility in the form of 3rd quartile winds and sea water turbidity (Model 1 in Tables 5, S3, Figure 12b). Assessed alone, the wNAO explained 28% of the total temporal variance while local conditions (3rd quartile winds and sea water turbidity) explained 27%. All three covariates exerted a negative effect on the egg volume. When these covariates where tested simultaneously (Model 1), they explained 59% of the total temporal variance. Models 2 to 5 including the additive effect of the interspecific competition exerted by Yellow-legged gulls, sea water turbidity or the statistical interaction with the 3rd quartile winds, had a similar explanatory power to Model 1 (i.e. ΔAIC values < 2; Tables 5, S3). However, both the interaction and the additive terms in these models act as pretending variables (Anderson 2008) and should not be considered further (Appendix B in Evans & Davis 2011).

Audouin's gulls

Model information theory indicated that Audouin's gull egg volume was influenced by the wNAO and the statistical interaction between the intra-specific and inter-specific competition (Model 1 in Tables 6, S4, Figure 12c). When tested individually, the percentage of the total temporal variance in the egg volume explained by the wNAO was 24%, while the effect of competition (intra- and inter-specific) explained 59%. Tested simultaneously (Model 1), these covariates explained 70% of temporal variance in the egg volume. Population density in this species was correlated with the abundance of natural prey, fishery discards and wave height (see Table S9). Therefore, to avoid collinearity these covariates were not considered together in our models. Contrary to the other species considered, the effect of the wNAO on the egg volume of the Audouin's gull was positive.

4.5. Discussion

The set of variables used to assess local conditions during the early breeding season were unrelated to the wNAO, probably due to the two- to three-month time-lag between winter and breeding. This highlights the importance of considering the correct spatio-temporal scale when assessing the mechanisms through which large-scale climatic indices influence ecological processes (Stenseth & Mysterud 2005). In fact, the breeding investment of all species considered was dependent on the additive effect of both the winter climate index and the local variables during breeding. This additive effect would indicate a carry-over effect (see Harrison *et al.* 2011; O'Connor *et al.* 2014) of winter conditions on individual breeding investment, especially important for shearwaters. Martínez-Asensio *et al.* (2016) found strong associations between this climate index and winter anomalies in wind speed and direction and the wave height in the Atlantic Ocean and the Mediterranean Sea. It is likely that high values of wNAO relate to adverse foraging conditions, and in turn, a poorer body condition when breeding. The wNAO has also been related to changes in the temporal and spatial distribution of natural prey (see e.g. Sims *et al.* 2001, 2004). However, these changes occur after the laying period and cannot be responsible for egg volume variation. The influence of wNAO on the egg volume of shearwaters and terns has the opposite relationship to that in the Audouin's gull. A plausible explanation for this is that many gulls remain in the Western Mediterranean during winter (see Figure 11; Bécares *et al.* 2016; Reyes-González*et al.* 2017), where positive values of the wNAO are associated with less stormy winters (see e.g. Hurrell & Deser 2010). This is in agreement with Jonzén *et al.* (2002), who found that bird species wintering in the Mediterranean area had different responses to the wNAO when compared to species wintering in northern Europe. Another non-exclusive explanation is that intra- and inter-specific competition has a far greater importance than other effects for Audouin's gulls. Finally, different responses to the wNAO could also be associated with differences in species-specific foraging strategies (e.g. terns and gulls can cope with adverse weather conditions by feeding in sheltered coastal areas, while shearwaters only feed offshore) and their different evolutionary life histories: terns and gulls are bet-hedgers whereas shearwaters lay a single egg.

Interestingly, in the absence of density-dependence, local variables related to food detectability and accessibility (oceanographic physical features; see e.g. Daunt *et al.* 2006) during the early breeding season (spring) were more important than food abundance (natural prey and fishery discards). This implies that food abundance *per se* does not necessarily translate into food intake by organisms and that the role played by detectability and accessibility of food in several ecological processes deserves more consideration.

Regarding climatic and oceanographic variables used to assess food detectability and accessibility, as expected, wind speed and wave height were strongly correlated. Their relative importance, however, changed with the species considered probably due to differences in the foraging strategies between shearwaters and terns (pursuit versus surface plunging and gliding versus flapping, respectively; see Ashmole 1971). Larger waves may drive natural prey to deeper waters affecting their detectability and accessibility to shearwaters (see Dunn 1973 and references therein). Wind may act in opposite ways and non-linearly (i.e. with threshold values) on fishing conditions depending on its intensity (Louzao *et al.* 2019). Strong winds may negatively affect terns' flying trajectories when they pounce on their prey during fishing (Dunn 1973; Taylor 1983), but favorable winds can result in important energy savings by seabirds on displacements (see e.g. González-Solís *et al.* 2009; Navarro & González-Solís 2009). Although weak, we also detected a negative effect of water turbidity on the egg volume of Sandwich terns, in agreement with previous studies of this species in the North Sea (Baptist & Leopold 2010).

The effect of competition was only retained for the Audouin`s gull. Initially, both intra- and inter-specific competition have a negative effect on the egg volume of this species. However, when the population density of Audouin's gulls increases, the effect arising from inter-specific competition (exerted by the Yellow-legged gull) decreases. Competition between the Audouin's gull and the Yellow-legged gull has been widely reported in the Western Mediterranean, especially for fishery discards (see e.g. González-Solís *et al.* 1997; Arcos*et al.* 2001). The important role of density-dependence for this species is not surprising considering that the study colony is the largest in the world (Pedrocchi *et al.* 2002; Genovart *et al.* 2018). When population size is over its carrying capacity, the breeding investment would be constrained by an increase on competition for food, making it difficult to assess the influence of other effects potentially important for breeding investment, such as winter climate (see Yalden & Pearce-Higgins 1997) or local oceanographic physical features driving foraging conditions in breeding grounds (see above). This result highlights the importance of considering density-dependence when assessing ecological processes. The effect of density-dependence was not retained for two of the three species considered (shearwaters and terns). Although the explanatory power of the resulting models was high, our estimates of population numbers of terns and shearwaters were not as accurate as for gulls. Hence, the presence in the study area of other terns and shearwaters coming from neighbouring colonies was probably underestimated for these species.

Conclusions

Our results provide new insights on the relative influence of large-scale climatic indices *vs* local variables on ecological processes. We showed that both large-scale climatic index and local variables influence breeding investment because they operate at different spatio-temporal scales (e.g. in the form of carry-over effects arising from winter conditions). We found that considering detectability and accessibility of food can considerably improve the predictive capacity when modeling ecological processes related to food resources. Finally, and in contrast to what is commonly assumed, food abundance does not necessarily translate into individual food intake. Large-scale climate indices present several advantages as indicators of regulating forces of ecosystems (Ottersen *et al.* 2001; 2003), but local variables may be more important. Therefore, further research should focus on clarifying the mechanisms through which local variables affect food intake, for example by coupling foraging activity with tracking data with sea-state variables.

4.6. Aknowledgments

We are grateful to everyone who helped with fieldwork, and provided data, images and logistic support, especially the staff of the Ebro Delta Natural Park. Funds were supplied by the Spanish Ministry of Economy and the European Union (grant ref.: CGL2013-42203-R and CGL2017-85210-P). The study also received funding from the European Commission's Horizon 2020 Research and Innovation Program under Grant Agreement no. 634495 for the project Science, Technology, and Society Initiative to Minimize Unwanted Catches in European Fisheries (MINOUW). MG and ASA were partially funded by Govern Balear. ASA was also supported by a Ramón y Cajal contract (RYC-2017- 22796).

4.7. References

Alonso, H., Granadeiro, J.P., Dias, M.P., Catry, T. & Catry, P. 2018. Fine-scale tracking and diet information of a marine predator reveals the origin and contrasting spatial distribution of prey. Prog. Oceanogr., 162, 1–12.

Alonso, H., Granadeiro, J.P., Paiva, V.H., Dias, A.S., Ramos, J.A. & Catry, P. 2012. Parent–offspring dietary segregation of Cory's shearwaters breeding in contrasting environments. Mar. Biol., 159, 1197–1207.

Anderson, D.R. 2008. Model Based Inference in the Life Sciences: A Primer on Evidence. Springer-Verlag, New York.

Arcos, J.M., Oro, D. & Sol, D. 2001. Competition between the yellow-legged gull Larus cachinnans and Audouin's gull Larus audouinii associated with commercial fishing vessels: the influence of season and fishing fleet. Mar. Biol., 139, 807–816.

Ashmole N.P. 1971. Seabird ecology and the marine environment. Farner D.S. & King J.R. editors. p.p. 224-286.

Baptist, M.J. & Leopold, M.F. 2010. Prey capture success of Sandwich Terns Sterna sandvicensis varies non-linearly with water transparency. Ibis, 152, 815–825.

Barbraud, C., Barbraud, J.-C. & Barbraud, M. 1999. Population dynamics of the White Stork Ciconia ciconia in western France. Ibis, 141, 469–479.

Bécares, J., Arcos, J.M. & Oro, D. 2016. Migración y Ecología Espacial de la gaviota de Audouin en el Mediterráneo Occidental y Noroeste Africano. Monografía n.o 1 del programa Migra.

Bentz, B.J., Regniere, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., et al. 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. Biosci. 608 602-613, 602–613.

Blomqvist, D., Johansson, O.C. & Götmark, F. 1997. Parental quality and egg size affect chick survival in a precocial bird, the lapwing Vanellus vanellus. Oecologia, 110, 18–24.

Bolton, M. 1991. Determinants of Chick Survival in the Lesser Black-Backed Gull: Relative Contributions of Egg Size and Parental Quality. J. Anim. Ecol., 60, 949–960.

Burnham, K.P. & Anderson, D.R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd edn. Springer-Verlag, New York.

Burnham, K.P. & Anderson, D.R. 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociol. Methods Res., 33, 261–304.

Carrera, E. & Garcia, J. 1986. The Importance of the Iberian Mediterranean Coast as a Wintering Area for Gulls and Terns. In: Mediterranean Marine Avifauna, NATO ASI Series. Springer Berlin Heidelberg, pp. 315–331.

Christians, J.K. 2002. Avian egg size: variation within species and inflexibility within individuals. Biol. Rev. Camb. Philos. Soc., 77, 1–26.

Daunt, F., Afanasyev, V., Silk, J.R.D. & Wanless, S. 2006. Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. Behav. Ecol. Sociobiol., 59, 381–388.

De los Reyes González, J.M., Zajková, Z., Virginia, Morera-Pujol, V., De Felipe, F., Militão, T., et al. 2017. Migración y ecología espacial de las poblaciones de Pardela Cenicienta.

Dunn, E.K. 1973. Changes in Fishing Ability of Terns associated with Windspeed and Sea Surface Conditions. Nature, 244, 520–521.

Evans, J.A. & Davis, A.S. 2011. Consequences of parameterization and structure of applied demographic models: a comment on Pardini et al. 2009. Ecol. Appl., 21, 608–613.

Fernández-Chacón, A., Bertolero, A., Amengual, A., Tavecchia, G., Homar, V. & Oro, D. 2011. Spatial heterogeneity in the effects of climate change on the population dynamics of a Mediterranean tortoise. Glob. Change Biol., 17, 3075–3088.

Frederiksen, M., Harris, M.P., Daunt, F., Rothery, P. & Wanless, S. 2004. Scale-dependent climate signals drive breeding phenology of three seabird species. Glob. Change Biol., 10, 1214–1221.

Gaglio, D., Cook, T.R., McInnes, A., Sherley, R.B. & Ryan, P.G. 2018. Foraging plasticity in seabirds: A non-invasive study of the diet of greater crested terns breeding in the Benguela region. PLOS ONE, 13, e0190444.

Genovart, M., Oro, D. & Tenan, S. 2018. Immature survival, fertility, and density dependence drive global population dynamics in a long-lived species. Ecology, 99, 2823–2832.

Genovart, M., Sanz-Aguilar, A., Fernández-Chacón, A., Igual, J.M., Pradel, R., Forero, M.G., et al. 2013. Contrasting effects of climatic variability on the demography of a trans-equatorial migratory seabird. J. Anim. Ecol., 82, 121–130.

González-Solís, J., Felicísimo, A., Fox, J.W., Afanasyev, V., Kolbeinsson, Y. & Muñoz, J. 2009. Influence of sea surface winds on shearwater migration detours. Mar. Ecol. Prog. Ser., 391, 221–230.

González-Solís, J., Oro, D., Jover, L., Ruiz, X. & Pedrocchi, V. 1997. Trophic Niche Width and Overlap of Two Sympatric Gulls in the Southwestern Mediterranean. Oecologia, 112, 75–80.

Hallett, T.B., Coulson, T., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M. & Grenfell, B.T. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. Nature, 430, 71–75.

Harris, M.P., Anker-Nilssen, T., McCleery, R.H., Erikstad, K.E., Shaw, D.N. & Grosbois, V. 2005. Effect of wintering area and climate on the survival of adult Atlantic puffins Fratercula arctica in the eastern Atlantic. Mar. Ecol. Prog. Ser., 297, 283–296.

Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R. & Bearhop, S. 2011. Carry-over effects as drivers of fitness differences in animals. J. Anim. Ecol., 80, 4–18.

Hoyt, D.F. 1979. Practical Methods of Estimating Volume and Fresh Weight of Bird Eggs. Auk Ornithol. Adv., 96, 73–77.

Hurrell, J.W. & Deser, C. 2010. North Atlantic climate variability: The role of the North Atlantic Oscillation. J. Mar. Syst., Impact of climate variability on marine ecosystems: A comparative approach, 79, 231–244.

Jenouvrier, S., Holland, M., Stroeve, J., Serreze, M., Barbraud, C., Weimerskirch, H., et al. 2014. Projected continent-wide declines of the emperor penguin under climate change. Nat. Clim. Change, 4, 715–718.

Jonzén, N., Hedenström, A., Hjort, C., Lindström, Å., Lundberg, P. & Andersson, A. 2002. Climate patterns and the stochastic dynamics of migratory birds. Oikos, 97, 329–336.

Lewis, S., Elston, D.A., Daunt, F., Cheney, B. & Thompson, P.M. 2009. Effects of extrinsic and intrinsic factors on breeding success in a long lived seabird. Oikos, 118, 521–528.

Louzao, M., Gallagher, R., García-Barón, I., Chust, G., Intxausti, I., Albisu, J., et al. 2019. Threshold responses in bird mortality driven by extreme wind events. Ecol. Indic., 99, 183–192.

Martínez-Abraín, A., Maestre, R. & Oro, D. 2002. Demersal trawling waste as a food source for Western Mediterranean seabirds during the summer. ICES J. Mar. Sci. J. Cons., 59, 529–537.

Martínez-Asensio, A., Tsimplis, M.N., Marcos, M., Feng, X., Gomis, D., Jordà, G., et al. 2016. Response of the North Atlantic wave climate to atmospheric modes of variability. Int. J. Climatol., 36, 1210–1225.

Molinero, J.C., Ibanez, F., Nival, P., Buecher, E. & Souissi, S. 2005. North Atlantic climate and northwestern Mediterranean plankton variability. Limnol. Oceanogr., 50, 1213–1220.

Morote, E., Olivar, M.P., Villate, F. & Uriarte, I. 2010. A comparison of anchovy Engraulis encrasicolus and sardine Sardina pilchardus larvae feeding in the Northwest Mediterranean: influence of prey availability and ontogeny. ICES J. Mar. Sci., 67, 897–908.

Navarro, J. & González-Solís, J. 2009. Environmental determinants of foraging strategies in Cory’s shearwaters Calonectris diomedea. Mar. Ecol. Prog. Ser., 378, 259–267.

O’Connor, C.M., Norris, D.R., Crossin, G.T. & Cooke, S.J. 2014. Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. Ecosphere, 5, art28.

Oro, D. 1996. Interspecific kleptoparasitism in Audouin’s Gull Lams audouinii at the Ebro Delta, northeast Spain: a behavioural response to low food availability. Ibis, 138, 218–221.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S. & Martínez-Abraín, A. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecol. Lett., 16, 1501–1514.

Oro, D., Genovart, X., Ruiz, X., Jiménez, J. & García-Gans, J. 1996. Differences in Diet, Population Size and Reproductive Performance between Two Colonies of Audouin’s Gull Larus audouinii Affected by a Trawling Moratorium. J. Avian Biol., 27, 245–251.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P.C. & Stenseth, N.C. 2001. Ecological effects of the North Atlantic Oscillation. Oecologia, 128, 1–14.

Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in the herring gull Larus argentatus. Nature, 228, 1221–1222.

Pedrocchi, V., Oro, D., González-Solís, J., Ruiz, X. & Jover, L. 2002. Differences in diet between the two largest breeding colonies of Audouin’s gulls: the effects of fishery activities. Sci. Mar., 66, 313–320.

Real, E., Oro, D., Martínez-Abraín, A., Igual, J.M., Bertolero, A., Bosch, M., et al. 2017. Predictable anthropogenic food subsidies, density-dependence and socio-economic factors influence breeding investment in a generalist seabird. J. Avian Biol., 48, 1462–1470.

Risch, T.S. & Rohwer, F.C. 2000. Effects of parental quality and egg size on growth and survival of herring gull chicks. Can. J. Zool., 78, 967–973.

Rodríguez, A., Arcos, J.M., Bretagnolle, V., Dias, M.P., Holmes, N.D., Louzao, M., et al. 2019. Future Directions in Conservation Research on Petrels and Shearwaters. Front. Mar. Sci., 6.

Sanz-Aguilar, A., Igual, J.M., Oro, D., Genovart, M. & Tavecchia, G. 2016. Estimating recruitment and survival in partially monitored populations. J. Appl. Ecol., 53, 73–82.

Sims, D.W., Genner, M.J., Southward, A.J. & Hawkins, S.J. 2001. Timing of squid migration reflects North Atlantic climate variability. Proc. R. Soc. Lond. B Biol. Sci., 268, 2607–2611.

Sims, D.W., Wearmouth, V.J., Genner, M.J., Southward, A.J. & Hawkins, S.J. 2004. Low-temperature-driven early spawning migration of a temperate marine fish. J. Anim. Ecol., 73, 333–341.

Stenseth, N.C. & Mysterud, A. 2005. Weather packages: finding the right scale and composition of climate in ecology. J. Anim. Ecol., 74, 1195–1198.

Stenseth, N.C., Ottersen, G., Hurrell, J.W., Mysterud, A., Lima, M., Chan, K.-S., et al. 2003. Review article. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. Proc. R. Soc. Lond. B Biol. Sci., 270, 2087–2096.

Tavecchia, G., Tenan, S., Pradel, R., Igual, J.-M., Genovart, M. & Oro, D. 2016. Climate-driven vital rates do not always mean climate-driven population. Glob. Change Biol., 22, 3960–3966.

Taylor, I.R. 1983. Effect of Wind on the Foraging Behaviour of Common and Sandwich Terns. Ornis Scand. Scand. J. Ornithol., 14, 90–96.

Tugores, M.P., Iglesias, M., Díaz, N., Oñate, D., Miquel, J. & Giráldez, A. 2010. Latitudinal and interannual distribution of the European anchovy Engraulis encrasicolus and sardine

Sardina pilchardus in the western Mediterranean, and sampling uncertainty in abundance estimates. ICES J. Mar. Sci., 67, 1574–1586.

Yalden, D.W. & Pearce-Higgins, J.W. 1997. Density-dependence and winter weather as factors affecting the size of a population of Golden Plovers Pluvialis apricaria. Bird Study, 44, 227–234.

4.8. Supporting information

Table S.2. Generalized linear models explaining egg volume variability (mean egg volume in a clutch) of the Scopoli's shearwater based on Akaike information criterion values (AIC) and Akaike weights (Wi). The best explanatory model (Model 1) is the one with the lowest AIC. In the notation: wNAO = winter North Atlantic Oscillation, SS = Scopoli's shearwater, YLG = Yellow-legged Gull, AG = Audouin's Gull, PC= per capita, Wind1Q, 2Q, 3Q and 4Q = 1st, 2nd, 3rd and 4th quartile winds, respectively, Discards = fishery discards, Null model is an intercept-only model. Discards PC and Sardine PC consider the number of individuals of YLG + AG + SS.

Model	Notation	Deviance	df	AIC	ΔAIC	Wi
1	WNAO + WaveHeight * DiscardsPC	40733,54	6	8911,61	0,00	0,85
2	WNAO + WaveHeight + DiscardsPC	40899,95	5	8915,48	3,87	0,12
3	WNAO + WaveHeight	41035,65	4	8918,25	6,64	0,03
4	WNAO	41331,38	3	8926,59	14,98	0,00
5	WaveHeight	41478,83	3	8931,72	20,11	0,00
6	Competition by AG	41558,13	3	8934,47	22,86	0,00
7	Wind4Q	41602,25	3	8936,00	24,39	0,00
8	Discards PC	41635,50	3	8937,15	25,54	0,00
9	Wind3Q	41693,72	3	8939,16	27,55	0,00
10	Wind1Q	41734,33	3	8940,56	28,95	0,00
11	Sardine PC	41754,58	3	8941,26	29,65	0,00
12	Wind2Q	41979,94	3	8949,01	37,40	0,00
13	Turbidity	42004,55	3	8949,86	38,25	0,00
14	Null Model	42112,58	2	8951,56	39,95	0,00
15	Intraspecific competition	42107,99	3	8953,40	41,79	0,00
16	Competition by YLG	42112,14	3	8953,54	41,93	0,00

Table S.3. Generalized linear models explaining egg volume variability (mean egg volume in a clutch) of the Sandwich tern based on Akaike information criterion values (AIC) and Akaike weights (Wi). The best explanatory model (Model 1) is the one with the lowest AIC. In the notation: wNAO = winter North Atlantic Oscillation, YLG = Yellow-legged Gull, PC= Per capita, Wind1Q, 2Q, 3Q and 4Q = 1st, 2nd, 3rd and 4th quartile winds respectively, Discards = fishery discards, Null model is an intercept-only model. Both discards PC and anchovy PC consider the number of individuals of ST, YLG, AG and SS.

Model	Notation	Deviance	df	AIC	ΔAIC	Wi
1	wNAO + Wind3Q + Turbidity	1655,94	5	1787,71	0	0,23
2	wNAO + Wind3Q	1665,30	4	1788,10	0,39	0,19
3	wNAO + Wind3Q + Turbidity + Competition by YLG	1650,57	6	1788,34	0,63	0,17
4	wNAO + Wind3Q + Competition by YLG	1662,09	5	1789,28	1,57	0,10
5	wNAO + Wind3Q * Turbidity	1655,69	6	1789,65	1,94	0,09
6	wNAO + Wind3Q + AnchovyPC	1664,01	5	1789,77	2,06	0,08
7	wNAO + Wind3Q + Wind1Q	1664,41	5	1789,87	2,16	0,08
8	wNAO	1689,33	3	1792,16	4,45	0,02
9	Wind3Q	1690,22	3	1792,38	4,67	0,02
10	Wave height	1708,91	3	1797,03	9,32	0,00
11	Wind1Q	1709,45	3	1797,16	9,45	0,00
12	Null model	1718,36	2	1797,36	9,65	0,00
13	Competition by YLG	1711,99	3	1797,79	9,65	0,00
14	Wind4Q	1713,32	3	1798,12	10,41	0,00
15	Discards PC	1713,65	3	1798,20	10,49	0,00
16	Anchovy PC	1712,60	3	1798,20	10,49	0,00
17	Turbidity	1715,30	3	1798,61	10,90	0,00
18	Intraspecific competition	1715,46	3	1798,65	10,94	0,00
19	Wind2Q	1718,35	3	1799,36	11,65	0,00

Table S.4. Generalized linear models explaining egg volume variability (mean egg volume in a clutch) of the Audouin's gull based on Akaike information criterion values (AIC) and Akaike weights (Wi). The best explanatory model (Model 1) is the one with the lowest AIC. In the notation: wNAO = winter North Atlantic Oscillation, YLG = Yellow-legged Gull, AG= Audouin's Gull, SS= Scopoli's shearwater, PC= Per capita, Wind1Q, 2Q, 3Q and 4Q = 1st, 2nd, 3rd and 4th quartile winds, respectively, Discards = fishery discards, Null model is an intercept-only model. Discards PC, Sardine PC and Anchovy PC consider the number of individuals of YLG+AG+SS.

Model	Notation	Deviance	df	AIC	ΔAIC	W
1	wNAO + Intraspecific competition * Competition by YLG	94498,10	6	45482,82	0,00	1,00
2	wNAO + Intraspecific competition + Competition by YLG	94640,28	5	45493,91	11,09	0,00
3	wNAO + AG pairs	94695,19	4	45496,96	14,14	0,00
4	Intraspecific competition	95560,62	3	45574,18	91,36	0,00
5	Sardine PC	95790,58	3	45595,10	112,28	0,00
7	Discard PC	97288,69	3	45730,22	247,40	0,00
8	Anchovy PC	97531,97	3	45751,97	269,15	0,00
9	Wave height	97782,89	3	45774,34	291,52	0,00
10	wNAO	98076,86	3	45800,48	317,66	0,00
11	4th q. winds	98114,50	3	45803,82	321,00	0,00
12	2nd q. winds	99288,54	3	45819,25	336,43	0,00
13	Competition by YLG	99061,17	3	45887,43	404,61	0,00
14	1st q. winds	99109,83	3	45891,70	408,88	0,00
15	3rd q. winds	99719,21	3	45945,07	462,25	0,00
16	Turbidity	99871,94	3	45958,40	475,58	0,00
17	Null	99945,84	2	45962,84	480,02	0,00
18	Competition by SS	99936,80	3	45964,05	481,23	0,00

Table S.5. Species-specific early breeding periods of studied population considering from the mean date of arrival to the breeding colony to the mean laying dates. Different fishing fleets considered to estimate abundances of fishery discards and natural prey (see methods in the main manuscript) varies according to the species-specific home range during the breeding season. Sca: Sant Carles, Tar: Tarragona, Ame: Ametlla de Mar, Amp: Amposta, Cal: Cases d'Alcanar, Del: Deltebre.

Species	Arrival to the breeding colony	Mean laying date	Home range during the breeding season	Fishing ports considered	Home range reference
Scopoli's shearwater	early March	end of May	150-200 Km	Ame, Amp, Cal, Del, Sca, Tar	Reyes-González et al 2017
Sandwich tern	early April	end of May	15 Km	Sca, Tar	Fassola 1990
Audouin's gull	early March	end of April	70 Km	Ame, Amp, Cal, Del, Sca, Tar	Bécares et al 2015

Table S.6. On the left side, species considered to compete for the same food resource types in the study area used to assess per capita food abundance (in this case, foraging strategies may be very different and individuals of different species do not necessarily match in space and time). On the right side, species considered when considering interspecific interactions during the foraging process (due to species-specific foraging strategies, individuals of different species can match in space and time and interspecific interactions such as kleptoparasitism can occur).

Species	Food resource type			Interspecific interactions during the foraging process		
	Sardines	Anchovies	Fishery discards	Scopoli's shearwater	Sandwich tern	Audouin's gull
Scopoli's shearwater	x		x	x		x
Sandwich tern		x			x	
Audouin's gull	x	x	x	x		x
Yellow-legged gull	x	x	x	x	x	x

Table S.7. Correlation matrix based on Pearson's correlations among all covariates considered for modeling the Scopoli's shearwater breeding investment. Used values correspond to March (when birds arrive to the breeding colony) to May (mean laying date) means except for climate indexes (December to March means) for the period 2001-2017 (n=17). Correlations where p-value < 2 are shown in bold.

	IA Pairs	LM pairs	CD pairs	wNAO	PC discards	PC Sardine	WaveHeight	1stQ.wind	2ndQ.wind	3rdQ.wind	4thQ.wind
LM pairs	0,27										
CD pairs	-0,01	-0,41									
wNAO	-0,23	0,01	0,04								
PC discards	0,45	-0,16	-0,31	-0,34							
PC Sardine	0,46	0,19	0,06	-0,17	0,03						
WaveHeight	**-0,49**	0,13	-0,33	0,34	-0,24	-0,22					
1stQ.wind	-0,38	0,13	-0,28	**0,57**	-0,44	-0,03	**0,62**				
2ndQ.wind	-0,43	-0,04	-0,3	0,22	-0,16	-0,13	**0,49**	0,35			
3rdQ.wind	-0,3	0,22	-0,01	-0,09	-0,05	-0,01	0,33	-0,33	0,28		
4thQ.wind	-0,47	0,01	0,07	0,33	-0,22	-0,32	**0,79**	0,22	0,3	0,57	
Turbidity	-0,06	-0,31	-0,18	-0,32	0,23	-0,01	0,25	0,06	0,01	-0,21	0,11

Table S.8. Correlation matrix based on Pearson's correlations among all covariates considered for modeling the Sandwich terns' breeding investment. Used values correspond to April (when birds arrive to the breeding colony) to May (mean laying date) means except for climate indexes (December to March means) for the period 2000-2016 (n=15). Correlations where p-value < 2 are shown in bold.

	TSPairs	wNAO	PCanchovy	PCdiscards	WaveHeight	1stQ.wind	2ndQ.wind	3rdQ.wind	4thQ.wind
wNAO	-0,2								
PCanchovy	0,05	0,09							
PCdiscards	-0,05	-0,17	**-0,64**						
WaveHeight	0,24	0,39	0,04	-0,3					
1stQ.wind	-0,39	**0,53**	-0,03	-0,24	0,4				
2ndQ.wind	0,14	0,47	0,11	-0,18	**0,67**	0,36			
3rdQ.wind	0,06	0,17	0,14	**-0,53**	**0,52**	-0,1	0,32		
4thQ.wind	0,4	0,18	0,25	-0,17	**0,8**	0,08	0,42	0,45	
Turbidity	0,21	-0,31	-0,2	0,3	0,3	0,13	0,16	-0,29	0,34

Table S.9. Correlation matrix based on Pearson’s correlations among all covariates considered for modeling the Audouin’s gull’s breeding investment. Used values correspond to March (when birds arrive to the breeding colony) to April (mean laying date) means except for climate indexes (December to March means) for the period 2001-2017 (n=17). Correlations where p-value < 2 are shown in bold.

	IA pairs	LM pairs	CD pairs	wNAO	PC Sardine	PC Anchovy	PC discards	WaveHeight	1stQ.wind	2ndQ.wind	3rdQ.wind	4thQ.wind
LM pairs	0,27											
CD pairs	-0,01	-0,42										
wNAO	-0,29	-0,01	0,03									
PC Sardine	**0,76**	-0,13	0,17	-0,33								
PC Anchovy	**-0,69**	-0,05	0,32	0,18	**-0,75**							
PC discards	**0,72**	-0,24	-0,12	-0,29	**0,83**	**-0,85**						
WaveHeight	**-0,5**	0,17	-0,38	0,35	**-0,53**	0,12	**-0,49**					
1stQ.wind	-0,4	0,24	-0,36	**0,49**	**-0,51**	0,26	**-0,48**	**0,71**				
2ndQ.wind	-0,36	-0,05	-0,22	0,22	**-0,56**	0,3	-0,39	**0,5**	0,35			
3rdQ.wind	-0,11	0,15	0,1	-0,1	-0,13	0,16	-0,2	0,02	-0,47	0,26		
4thQ.wind	-0,31	0,13	0,16	0,41	-0,21	0,08	-0,34	**0,51**	0,01	0,14	**0,59**	
Turbidity	-0,22	-0,31	-0,13	-0,22	-0,02	-0,04	0,04	0,33	0,11	-0,2	-0,33	-0,05

References

Bécares, J. et al ., (2015). Modelling Terrestrial and Marine Foraging Habitats in Breeding Audouin’s Gulls Larus audouini: Timing Maters. Plos One 10(4): e0120799. pmid:25875597.

Fasola, M. et al., (1990). Foraging Ranges of an Assemblage of Mediterranean Seabirds. Colonial Waterbirds, 13:1, 72-74.

Reyes-González et al 2017. Migración y Ecología Espacial de las Poblaciones Españolas de Pardela Cenicienta. Monografía nº3 del programa Migra. SEO/BirdLife. Madrid. https://doi.org/10.31170/0056.

Resúmenes por capítulos

Capítulo I

Las políticas sobre prohibición de descartes pueden ayudar a mejorar la comprensión sobre el papel ecológico de la disponibilidad de alimento en aves marinas

Enric Real, Giacomo Tavecchia, Meritxell Genovart, Ana Sanz-Aguilar, Ana Payo-Payo y Daniel Oro

Los descartes de la pesca constituyen el recurso alimentario predecible de origen antropogénico (PAFS) más importante que está siendo incorporado en los ecosistemas marinos. Cambios en su disponibilidad y predictibilidad pueden ayudar a entender mejor el papel ecológico de la disponibilidad de alimento (i.e. un importante indicador de la capacidad de carga) a diferentes niveles, desde la eficacia biológica individual hasta la dinámica de poblaciones o el funcionamiento de los ecosistemas. Las aves marinas constituyen un modelo excelente para estudiar los efectos ecológicos de la falta de descartes por múltiples razones: las aves marinas: 1) se encuentran entre los principales carroñeros de descartes, 2) son fáciles de monitorear y 3) son depredadores apicales globalmente distribuidos, lo que los convierte en buenos indicadores de la salud del ecosistema. En el presente estudio se revisa la información existente sobre las interacciones ecológicas que se dan entre las aves marinas y los descartes de la pesca, con el fin de identificar los principales vacíos de conocimiento y plantear retos futuros para mejorar nuestra comprensión sobre el papel ecológico de la disponibilidad de alimento. Concluimos que las políticas actuales en materia de prohibición de descartes que están siendo implementadas en la Unión Europea, Noruega, Chile o Nueva Zelanda, ofrecen un escenario ideal para mejorar nuestra comprensión sobre cómo una reducción en la capacidad de carga puede alterar parámetros demográficos tales como la supervivencia, la dispersión y la reproducción, la resiliencia de las poblaciones frente a las perturbaciones y el papel de la especialización individual en el proceso de forrajeo.

Capítulo II

Recursos alimentarios predecibles de origen antropogénico, densodependencia y factores socioeconómicos influyen en la inversión en reproducción de un ave marina generalista

Enric Real, Daniel Oro, Alejandro Martínez-Abraín, José Manuel Igual, Albert Bertolero, Marc Bosch and Giacomo Tavecchia.

Se espera que las recientes políticas de la Unión Europea en materia de prohibición de descartes y cierre de vertederos a cielo abierto, reduzcan la disponibilidad de una serie de recursos que a día de hoy son abundantes y altamente predecibles para las aves marinas. De cara a poder pronosticar las consecuencias de esta reducción para la inversión que las aves marinas hacen en la reproducción, es importante entender si se producen sinergias cuando se explotan varios de estos recursos, así como si su influencia puede verse afectada por mecanismos de densodependencia. Para tratar de evaluar estos efectos en una escala espacio-temporal grande, utilizamos el volumen medio de la puesta modal de la gaviota patiamarilla (*Larus michahellis)* como indicador de su inversión en la reproducción. Para ello medimos ca. de 5000 puestas de tres huevos, procedentes de 20 colonias distribuidas a lo largo de las costas europeas y africanas del Mediterráneo Occidental. En las colonias europeas, el volumen del huevo se incremento con la disponibilidad de descartes y vertederos en los alrededores de la colonia. Sin embargo, el efecto del vertedero fue más débil que el efecto de los descartes, probablemente debido a la menor calidad de la basura como alimento para las gaviotas en comparación con los descartes. Por el contrario, ninguno de los dos recursos influyó el volumen del huevo en las colonias africanas, probablemente debido a diferencias asociadas a factores socioeconómicos (p.ej. una menor disponibilidad y predictibilidad tanto del alimento en forma tanto de descartes como de basura de los vertederos. Finalmente, los resultados mostraron que el efecto positivo tanto de los descartes como de la basura de los vertederos en el volumen del

huevo estaba mediado por mecanismos de densodependencia negativos, probablemente asociados a un incremento en la competencia por el alimento.

Capítulo III

Predictable anthropogenic food subsidies decouple inter-specific temporal synchrony

Ana Payo-Payo, José-Manuel Igual, Ana Sanz-Aguilar, Enric Real, Meritxell Genovart, Daniel Oro and Giacomo Tavecchia

Los recursos alimentarios predecibles de origen antropogénico (PAFS) pueden amortiguar la influencia de la estocasticidad ambiental en poblaciones animales. Como resultado, sistemas originalmente sinconizados por factores ambientales pueden ver perder dicha sincronía o *viceversa*. Para investigar el papel que juegan los PAFS en la sincronía entre especies, se analizaron las consecuencias de las políticas europeas en materia de cierre de vertederos en la sincronía interespecifica entre dos depredadores apicales marinos que presentan diferentes estrategias de forrajeo. Se utilizaron datos recopilados a lo largo de 15 años de dos organismos marinos, uno especialista (la pardela cenicienta) y otro generalista (la gaviota patiamarilla). A través del análisis de correlaciones cruzadas y de un modelo de estado de cadenas de Markov, se identificaron periodos en los cuales las variaciones del volumen del huevo (como indicador de la disponibilidad de alimento para ambas especies en un año dado) se sincronizaban. Nuestros resultados muestran como se produce una sincronía perfecta tras el cierre del vertedero a cielo abierto más grande a nivel local, lo cual indica que el acoplamiento depende de estímulos ambientales compartidos y que dicha sincronía puede verse interrumpida por los PAFS.

Capítulo IV

La disponibilidad no lo es todo: efectos de tipo *carry-over*, la detectabilidad y la accesibilidad del alimento también explican la inversión en reproducción en organismos de larga vida

Enric Real, Daniel Oro, Albert Bertolero, José Manuel Igual, Ana Sanz-Aguilar, Meritxell Genovart, Manuel Hidalgo and Giacomo Tavecchia.

Los índices climáticos a gran escala son ampliamente utilizados como predictores de procesos ecológicos. Sin embargo, la escala espacio-temporal a través de la cual se cree que estos índices influyen en dichos procesos ecológicos, no está exenta de especulaciones. En el presente estudio utilizamos series temporales del volumen medio de la puesta, como indicador de la inversión en la reproducción. Para ello se han medido el volumen de la puesta en 10573 nidos de tres especies de aves marinas de larga vida. Se evalúa la influencia de las variables locales (abundancia de alimento, condiciones de forrajeo y competencia) medidas al principio del periodo de reproducción, para compararlas con el poder predictivo de un índice climático de gran escala (valores invernales y primaverales de la Oscilación del Atlántico Norte). A pesar de que las variables locales y el índice a gran escala no se correlacionaron, ambas demostraron tener un elevado poder predictivo. La importancia de los valores invernales de la Oscilación del Atlántico Norte sugiere que las condiciones invernales ejercen un efecto de tipo *carry-over* sobre la inversión en reproducción que tiene lugar unos meses después en primavera. Curiosamente, en dos de las tres especies consideradas, las variables locales que demostraron ser más importantes estaban más relacionadas con la detectabilidad y la accesibilidad del alimento (condiciones de forrajeo) que con la abundancia de alimento *per se*. Esto implica que al contrario de lo que comúnmente se asume, el hecho de que el alimento sea abundante, no se traduce necesariamente en ingesta por parte de los

organismos. Por tanto, factores como la detectabilidad y la accesibilidad deberían de ser tenidos en consideración en estudios en los que se abordan procesos ecológicos que dependen de la disponibilidad de alimento.

General discussion

There is no doubt that current EU policies that ban fishing discards and close open-air landfills receiving urban waste will have important consequences for seabird populations and communities (Bicknell *et al.* 2013; Oro *et al.* 2013). For example, fishing discards are, by far, the most important Predictable Anthropogenic Food Subsidy (PAFS) for seabirds. A better understanding of the interactions between seabirds and fishery discards would allow the forecasting of ecosystem effects of current policies. Therefore, a first goal of this thesis was to review the current knowledge on these interactions to identify the main knowledge gaps and set new challenges toward understanding the role of fishery discards in seabird ecology (Chapter I). Moreover, the reduction and subsequent ban of fishery discards arising from these policies offers an optimal BACI-type scenario (Before-After-Control-Impact) to evaluate the ecological consequences of a reduction in the availability of this food resource. Open-air landfills can also be an important food source for generalist seabird species, some of which have become superabundant during the last decades. PAFS increase the ecosystem's carrying capacity, altering the amount of energy that is available to seabirds for their survival and reproduction. Thus, another important goal of this thesis was to evaluate the relative role of these PAFS in influencing the breeding investment of an opportunistic seabird whose ecology is now tied to human activities, the yellow-legged gull *Larus michahellis* (Chapter II). This thesis also includes a collaborative study that shows how PAFS can potentially disrupt synchrony in the breeding investment of two sympatric species (Chapter III). Finally, this thesis explores the role played by other environmental factors that may potentially affect seabird breeding investment: i) the abundance of food of both natural and anthropogenic origin, ii) the level of competition (intra- and interspecific), iii) the foraging conditions during the pre-laying period (detectability and accessibility of food) and iv) climatic variations during winter, estimated through the winter North Atlantic Oscillation index (NAO) (Chapter IV).

Main knowledge gaps on the ecological interactions between seabirds and fishing discards

This thesis shows that, even today, there are important knowledge gaps on how ecological parameters of seabirds can be affected by changes in the availability of fishery discards. The identification of these knowledge gaps can facilitate the work of researchers when evaluating what we know and what (and where) remains to be investigated in seabird-fishery interactions. A clear result was that demersal-trawling fisheries are by far the most important fishing gear involving seabird-discards interactions (98% of reviewed studies). This is probably because, very often, this fishing gear generates the largest amount of discards (Carbonell *et al.* 1998; Tsagarakis *et al.* 2014). Most studies focus on: i) the attendance of seabirds at fishing vessels, ii) the role of discards in seabirds' diet in terms of composition and energy requirements, and iii) the influence of fishery discards on seabirds' bycatch. Only few studies address the role of discards in important demographic parameters related to survival, dispersal or reproduction. Even fewer deal with the effect of discards on communities and ecosystems. For example, while it is known that fishery discards constitute an important food resource for many seabird species, very little is known about how changes in the availability of this food resource influence seabird survival (but see: Oro *et al.* 1999, 2004). Moreover, hardly any evaluate the influence of these PAFS on seabird reproductive parameters, the resilience of populations to perturbations, as well as individual dispersal and specialization in relation to foraging strategy. This thesis provides a list, for the first time, of the extent to which each seabird species exploits fishery discards (up to 111 species). In addition, I also identified several FAO fishing areas where interactions between seabirds and fishery discards could be especially important. The identification of these knowledge gaps provides future directions for those researchers addressing the ecological interactions between seabirds and fishery discards. This large-scale overview is especially important considering the imminent scenario of a discard shortage arising from the current policies implemented both inside and outside the European Union (e.g., see discard policies in Chile, New Zealand, etc.).

The influence of fishery discards and open-air landfills on seabird breeding investment

Reproduction is a process with high associated energetic costs (Robbins 1981; Oro *et al.* 1995; Oro, D. *et al.* 1996; Williams 2005; Sanz-Aguilar *et al.* 2012). This thesis shows that both fishery discards and open-air landfills can significantly increase the carrying capacity of generalist seabirds and consequently, the amount of energy that is available for breeding. It is also shown that food subsides can alter natural stochasticity, increasing the breeding investment of generalist species, which in turn, may alter the community structure. However, not all subsidized food is the same or has the same impact on seabird ecology. For example, it is shown here that the influence exerted by fishery discards on breeding investment is greater than that exerted by open-air landfills. This difference is probably due to a higher quality of discards as a food resource compared to landfill refuse. In agreement with other studies, it is shown that the abundance of landfill refuse is positively related to the population size of some generalist species (Moulaï 2007), as well as the amount of energy invested by these birds in reproduction. This positive density-dependence effect between landfill refuse and breeding investment suggests that this food resource is often not limiting. Therefore, it follows that the availability of this food resource increases the carrying capacity and seabird population probably through an increase in survival and immigration (see e.g.: Moulaï 2007; Payo-Payo *et al.* 2015; Steigerwald *et al.* 2015). However, there results a complex interplay between population level and food availability. Indeed, for a given amount of discards, the number of birds in the population can negatively influence breeding investment. This is probably because discards constitute a much less abundant and, therefore, more limiting resource, compared to landfill refuse. Moreover, in contrast with landfill refuse, discards are only available to seabirds before they begin to sink deep into the ocean. In some cases, the effect of bird density can overwhelm (and mask) that of PAFS. This is the case, for example, of the Audouin's gull *Ichtyaetus audouinii* in the eastern Iberian Peninsula where its population constitutes the largest concentration of individuals of this species globally (Pedrocchi *et al.* 2002; Genovart *et al.* 2018). In other cases, there is a lack of clear density-dependence effects on breeding investment (e.g. shearwaters and terns) suggesting the absence of limiting factors. This result, however, must be considered with caution, as population estimates for these species are not as accurate and the contribution of individuals belonging to colonies other than those considered might be underestimated. Another important aspect that should be taken into consideration is that each system has specific characteristics and dynamics that can influence the way seabirds exploit these PAFS. For example, despite the abundance in fishery discards in the Western Mediterranean, the sandwich terns *Thalasseus sandvicensis* in this region make a fairly modest use of this food resource (≈10% of its diet, unpublished data). This is not the case in other parts of the world where fishery discards can constitute up to 35% of the diet in this species (see e.g. Liechty *et al.* 2016).

The importance of foraging conditions: food detectability and accessibility

Some studies have shown that climatic and oceanographic variables such as wind speed, wave height (Dunn 1973) and seawater turbidity (Baptist & Leopold 2010) can influence seabird foraging success. Birkhead, T.R. 1976 for example have shown that the feeding ratio of chicks in the common guillemots (*Uria aalgae*) decreased when marine conditions were adverse. These studies suggest that food intake not only depends on the abundance of food resources, but also on environmental factors influencing the ability of birds to detect and access these resources. Therefore, the temporal variability of environmental factors should be mirrored in some ecological parameters related to food intake (e.g. survival, reproductive parameters etc.).

Taking this into account, this thesis has considered these variables (wind speed, wave height and water turbidity) to assess how detectability and accessibility of food resources of both natural and anthropogenic origin can influence the breeding investment of some seabirds. Results showed that foraging conditions rather than resource abundance have an important influence on the breeding investment of seabirds. Results also showed that the influence of these factors may change according to the species considered, probably due to differences in foraging strategy (e.g. wind speed and seawater turbidity are important for terns while wave height is important for shearwaters). Foraging conditions were in some cases more important than the abundance of food *per se* of both natural (prey abundance) and anthropogenic origin (fishing discards). This finding shifts the interest from food availability to food accessibility, suggesting that food abundance is not always a limiting factor of breeding investment. Food abundance does not necessarily translate to food intake (i.e. food abundance ≠ food availability); therefore, considering detectability and accessibility of food can significantly improve our predictive power when modeling food-dependent demographic parameters.

Other environmental factors potentially affecting seabird breeding investment

Large-scale climatic indices, such as the winter North Atlantic Oscillation (winter NAO), have been related to demographic parameters of seabirds (see e.g. Frederiksen *et al.* 2004; Lewis *et al.* 2009; Genovart *et al.* 2013; Rodríguez *et al.* 2019). However, the mechanisms behind this relationship remain in many cases speculative. For example, it is unknown whether the influence of these climatic indices occurs through local conditions at breeding grounds (in spring) or if on the contrary, its influence is limited to winter months. Therefore, I first evaluated the influence that this climatic index has on the breeding investment of three seabird species, the Scopoli's shearwater *Calonectris diomedea*, the sandwich tern and the Audouin's gull. Secondly, to rule out the possibility that wNAO influences spring conditions, I investigated the possible link between this climatic index and local conditions at breeding grounds during the pre-laying period (spring). Local conditions were described as i) abundance of natural prey (specific for each species considered), ii) diverse climatic and oceanographic variables potentially affecting foraging conditions (see above) and iii) population size. In all species considered, the winter NAO had a strong influence on the breeding investment. However, no relationship was found between this climatic index and local conditions at the breeding grounds during spring. This suggests that, at least in the studied populations, the influence that winter NAO has on the breeding investment only occurs during winter months (i.e. through winter conditions in wintering areas). Therefore, winter conditions would have a 'carry-over' effect on the energy invested in reproduction.

Egg volume as a proxy of seabird breeding investment

Seabirds have two main strategies to modulate the amount of energy to invest in reproduction: i) through clutch size and ii) through egg size (i.e. the egg volume). In species laying more than one egg per clutch, using clutch size as a proxy of breeding investment is not recommended, because the number of eggs observed may differ from the true clutch size. For example, clutches might be incomplete or may have been predated at the time of observation. Hence, to minimize this error, it is recommended to consider the mean volume of the modal clutch only. This thesis showed how egg volume can reflect the influence of fishery discards and open-air landfills. However, assessing these effects is not always straightforward and in some cases can be a major challenge. On the one hand, the high mobility of these long-lived birds makes it necessary to gather datasets considering large spatio-temporal scales. Moreover, detecting the effect of these resources on egg volume can be especially complicated in those species that have a more generalist diet. For example, one of the time-series used to assess the breeding investment of the yellow-legged gull was based on c.a. 5,000 three-egg clutches measured from 20 different colonies distributed throughout the Western Mediterranean. Similarly, the time scale considered ranged from 15 to 20 years. Results showed that the breeding investment of yellow-legged gulls and Scopoli’s shearwater is affected by changes in the availability of PAFS. However, this thesis also showed that these effects can be masked by density-dependence processes, as for example in studied populations of the Audouins' gull (see above). Finally, it is also shown that the temporal variance in egg volume not only reflects the pre-laying period conditions (between the arrival to breeding colonies and the laying of the clutch), but also what occurred a few months earlier at the wintering areas (carry-over effect of winter conditions).

Estimates of the abundance of fishery discards and landfill refuse

Estimating how changes in the availability of PAFS influence ecological parameters can also constitute an important challenge. Data on the amounts of discards generated by fisheries or the amounts of urban waste received by open-air landfills are often inaccurate (i.e. due to low periodicity) or in many cases, non-existent (e.g. in less developed countries). Moreover, for those studies considering a very wide spatial scale, e.g. when the study area encompasses several countries or continents, gathering accurate data on PAFS can be even more complicated, as each country has different monitoring protocols. Hence, in these cases, the best alternative is to use appropriate proxies that mirror the availability of food subsidies.

Demersal trawling is by far the most important fishing gear **involving interactions between seabirds and fishery discards at a global level** (see above). Both the distances that these boats are able to cover during the trawl phase, as well as the size of their trawls are associated with the with the motor horsepower of these vessels (Eigaard *et al.* 2011). Taking this into account, the proxies used in this thesis to estimate the temporal variance of the availability of these PAFS were the horsepower declared each year by the demersal trawling fleet (as a proxy of the availability of fishery discards) and the number of open-air landfills receiving urban waste (as a proxy of landfill refuse availability). Since the recent application of the European policies on fishery discards and open-air landfills, several management actions have been implemented to reduce these PAFS. Some of the most important measures have consisted of a progressive reduction in the fishing fleet as well as the number of open-air landfills. As a result of the application of these measures, the availability of these PAFS in several countries of the European Union has experienced an important decrease over the last 15-20 years. This has meant an important reduction in the carrying capacity for some populations of generalist seabirds, which can be seen mirrored in their breeding investment.

The influence of socio-economic factors

This thesis also highlights the importance of considering the possible influence of socio-economic factors on the availability of these PAFS depending on the geographic area considered. More specifically, in European coastal areas fishery discards and landfill refuse influenced the breeding investment of a generalist seabird. However, in the African coastal areas, neither of these two resources had a clear influence on the reproductive investment of the species. This is probably because in some African countries practically all fish caught are commercialized, with nearly no or few discards generated (Belhabib, et al. 2012). Similarly, the amounts of urban waste generated *per capita* in these countries are also much lower than those generated in the European Union (ONEM 2001; Chantou et al. 2013); therefore, the amount of organic matter available in these landfills is also much lower. This suggests that the European populations of this species would be overfed due to the higher availability of these PAFS. The greater availability of resources would also explain in part why some generalist species are superabundant in some regions of the European Union (see e.g. Vidal *et al.* 1998; Moulaï 2007; Duhem *et al.* 2008; Payo-Payo *et al.* 2015).

Future research directions

Recent policies that ban discards and close open-air landfills have been progressively implemented in several countries. This offers an ideal BACI-type scenario to investigate the ecological consequences associated with a drastic reduction in the availability of these PAFS. More specifically, these policies offer a good opportunity to better understand how a reduction in the carrying capacity can influence important ecological parameters such as survival, dispersion, reproduction, the resilience of populations to perturbations as well as the role played by individual specialization in foraging processes. The expected short-term effects of these policies will be a reduction in the carrying capacity followed by an increase in competition for food, for example in the form of predatory interactions, kleptoparasitism, etc. In the medium-long term, we expect an increase in dispersal, a decrease in reproductive performance, a lower resilience of populations to perturbations, i.e. a lower capacity to face the effect of environmental stochasticity, and a decrease in survival, especially in those species highly dependent on these PAFS. This will probably result in a decrease in the proportion of generalist species in the community, which may benefit other species. The results of this thesis show that foraging conditions can play an important role in key demographic parameters such as breeding investment. Finally, the results also suggest that the influence that winter NAO has on breeding investment in some seabirds is limited to winter months and acts in spring as a '*carry-over*' effect of winter conditions. The combined use of remote-tracking data in seabirds with data on foraging conditions during winter months poses an interesting possibility for further research to improve our understanding of the mechanisms through which these large-scale climatic indices influence seabird ecology.

General conclusions

1. The main knowledge gaps on seabird-discard ecological interactions are related to survival, dispersal and reproduction, the resilience of their populations against perturbations and the role of individual specialization in the foraging process.
2. Demersal trawlers are by far the most important fishing gear involving interactions between seabirds and fishery discards at a global level.
3. Both fishery discards and open-air landfills can influence breeding investment in generalist seabirds; however, results suggest a weaker effect of landfills, probably due to the lower quality of waste as a food resource.
4. PAFS can buffer environmental stochasticity and disrupt the natural synchronous dynamics between species.
5. Socio-economic factors and density dependence processes can influence the ecological effects of PAFS on generalist seabirds.
6. Of around 300 known seabird species, we now know that at least 111 interact with fishery discards to a greater or lesser extent.
7. Both large-scale climate indexes and local variables influence seabird breeding investment because they operate at different spatio-temporal scales.
8. Considering detectability and accessibility of food can substantially improve our predictive capacity when modeling ecological processes related to food availability.
9. Further research is needed to clarify the mechanisms through which local variables affect food intake, for example by coupling direct tracking of foraging activity with foraging conditions.
10. More monitoring programs are needed to provide suitable data on demographic parameters and natural and anthropogenic factors influencing the ecology of seabirds.

Discusión general

No cabe duda de que las actuales políticas de la Unión Europea en materia de prohibición de descartes y de clausura de vertederos a cielo abierto de residuos sólidos urbanos (RSU) que están siendo progresivamente implementadas, van a tener importantes consecuencias para las poblaciones y comunidades de aves marinas (Bicknell et al., 2013; Oro et al., 2013). Por ejemplo, los descartes de la pesca son, con diferencia, los recursos antropogénicos predecibles (PAFS) que afectan a un mayor número de especies de aves marinas. Entender mejor las interacciones ecológicas que se dan entre las aves marinas y los descartes de la pesca permitiría pronosticar los efectos de estas políticas sobre el ecosistema. Por tanto, un primer objetivo de esta tesis consistía en revisar el conocimiento actual sobre estas interacciones a fin de identificar los principales vacíos de conocimiento, de cara a poder plantear nuevos retos orientados a mejorar nuestra comprensión sobre el papel que juegan estos PAFS en la ecología de las aves marinas (Capítulo I). Además, la reducción y posterior prohibición de los descartes que se deriva de estas políticas, ofrece un escenario experimental de tipo BACI (Before-After-Control-impact) ideal para evaluar las consecuencias ecológicas derivadas de una reducción progresiva en la disponibilidad de este recurso. Por otra parte, los vertederos de RSU a cielo abierto, a pesar de afectar a un menor número de especies de aves marinas, también constituyen una importante fuente de recursos para algunas especies que presentan una dieta más generalista, algunas de las cuales se han convertido en superabundantes a lo largo de las últimas décadas. Los PAFS incrementan la capacidad de carga del ecosistema, alterando la cantidad energía que las aves tienen disponible tanto para su propia supervivencia como para la reproducción. En consecuencia, otro importante objetivo de esta tesis consistía en evaluar el papel que juega cada uno de estos PAFS para la inversión en la reproducción de una ave marina oportunista, cuya ecología se encuentra muy ligada a las actividades humanas, la gaviota patiamarilla *Larus michahellis* (Capítulo II). En esta tesis también se incluye una colaboración en un estudio donde se muestra cómo los PAFS pueden alterar sincronías en la inversión que dos especies simpátricas hacen en la reproducción (Capítulo III).

Finalmente, esta tesis también explora la influencia por parte de otros factores ambientales que potencialmente pueden afectar a la inversión en reproducción de las aves marinas, como son: i) la abundancia de alimento, tanto de origen natural como antropogénico, ii) el nivel de competencia intra e interespecífica, iii) las condiciones de forrajeo durante el periodo de prepuesta (detectabilidad y accesibilidad al alimento) y iv) las variaciones climáticas que se dan durante el invierno, las cuales se resumen a través del índice invernal de la Oscilación del Atlántico Norte Winter (NAO)(Capítulo IV).

Principales vacíos de conocimiento en relación a las interacciones ecológicas entre las aves marinas y los descartes de la pesca

En esta tesis se pone de manifiesto que a día de hoy, todavía existen importantes vacíos de conocimiento acerca de cómo algunos parámetros ecológicos importantes de las aves marinas pueden verse afectados por los cambios en la disponibilidad de los descartes de la pesca. La identificación de estos vacíos de conocimiento facilitaría la labor de los investigadores a la hora de evaluar tanto lo que ya se ha investigado, como lo que todavía queda por investigar en relación a las interacciones que se dan entre las aves marinas y los descartes. En este sentido, también se ha tenido en cuenta que la forma en que los descartes de la pesquería influyen en estos parámetros ecológicos puede cambiar según la especie considerada. Un resultado evidente fue que la pesca de arrastre demersal es con diferencia, la modalidad de pesca que más se asocia con el consumo de descartes por parte de las aves marinas a nivel global (98% de los estudios revisados). Esto probablemente se deba a que a menudo, esta modalidad es también la que genera mayores cantidades de descartes (Carbonell et al., 1998; Tsagarakis et al., 2014). También se ha podido ver que la mayoría de estudios revisados en los cuales se abordan interacciones entre las aves marinas y descartes, se centran principalmente en: i) la identificación y cuantificación de especies que siguen a los barcos de pesca, ii) el papel de los descartes en la dieta en términos de composición y requerimientos energéticos, y iii) la influencia de los descartes en la captura accidental de aves marinas (bycatch). Sin embargo, sólo unos pocos estudios tratan la influencia de los descartes en parámetros demográficos importantes relacionados con la supervivencia, la dispersión o la reproducción. También, se ha identificado una clara falta de estudios en los que se evalúen los efectos que pueden tener los descartes a nivel de comunidades y ecosistemas. Por ejemplo, a pesar de que se sabe que los descartes constituyen un importante recurso alimentario para muchas especies de aves marinas, se sabe muy poco acerca de cómo los cambios en su disponibilidad pueden influir en la supervivencia de las aves marinas (pero véase: Oro et al., 1999, 2004). Además, prácticamente no existen estudios en los que se evalúe cómo estos PAFS afectan a parámetros relacionados con la reproducción de las aves marinas, la resiliencia de sus poblaciones frente a perturbaciones así como con la dispersión y la especialización individual en relación con la estrategia de forrajeo. Esta tesis también recoge por primera vez un listado con las principales especies de aves marinas que se ha podido constatar que interaccionan con los descartes de la pesca (hasta 111 especies). Así mismo, también se han identificado diversas áreas de pesca de la FAO donde las interacciones entre las aves marinas y los descartes de la pesca podrían ser especialmente importantes. Esta perspectiva a gran escala es especialmente importante teniendo en cuenta la importante reducción en la disponibilidad de estos PAFS que está teniendo lugar en diversos países, dentro y fuera de la Unión Europea (véase p. ej. también políticas en materia de descartes en Chile, Nueva Zelanda, etc.).

Influencia de los descartes y los vertederos en la energía que las aves marinas invierten en la reproducción

La reproducción es un proceso que tiene asociado un importante coste energético (Oro et al., 1995; Oro, D. et al., 1996; Robbins, 1981; Sanz-Aguilar et al., 2012; Williams, 2005). En esta tesis se ha podido constatar que tanto los descartes de la pesca como la basura de los vertederos pueden incrementar considerablemente la capacidad de carga en poblaciones de aves marinas generalistas, y por tanto, la energía que estas aves invierten en la reproducción. También se muestra que los subsidios alimentarios pueden alterar la estocasticidad natural incrementando la inversión en la reproducción por parte de especies generalistas, lo cual a su vez, puede alterar la estructura de la comunidad. Sin embargo, no todos los PAFS tienen el mismo impacto en la ecología de las aves marinas. Por ejemplo, se ha podido observar que los descartes ejercen una mayor influencia sobre este parámetro reproductivo que la basura de los vertederos. Esta diferencia probablemente se deba a una mayor calidad de los descartes como alimento en comparación con la basura de los vertederos. En concordancia con los resultados de otros trabajos, también se ha podido ver que el incremento poblacional de algunas especies generalistas se relaciona positivamente con la disponibilidad de basura de los vertederos (Moulaï, 2007), así como con la energía que estas aves invierten en la reproducción. Este efecto de densodependencia positiva entre la inversión en reproducción y el número de vertederos sugiere que este recurso a menudo no es limitante. Probablemente, la disponibilidad de este recurso incrementa la capacidad de carga de estas aves, favoreciendo el crecimiento de la población, a través de un incremento de la supervivencia y de la inmigración (véase por ej. Moulaï, 2007; Payo-Payo et al., 2015; Steigerwald et al., 2015). Sin embargo, también se ha visto que para una cantidad dada de descartes, el número de individuos puede tener un efecto negativo en la inversión en reproducción (efecto de densodependencia negagivo). Esto probablemente se deba a que los descartes constituyen un recurso mucho menos abundante y por tanto, más limitante, en comparación con la basura de los vertederos. Además, al contrario de lo que ocurre con la basura de los vertederos, las aves marinas disponen de un tiempo mucho más limitado para hacerse con los descartes a partir del momento en que estos son arrojados al mar, i.e. antes de que estos se hundan quedando fuera de su alcance. También se ha podido observar que el efecto de la denso-dependencia en la inversión en la reproducción puede superar (y enmascarar) el efecto de estos PAFS. Este es el caso por ejemplo de las colonias de gaviota de audouin *Ichtyaetus audouinii* del levante de la Península Ibérica consideradas en esta tesis, las cuales albergan la mayor concentración de individuos de esta especie de todo el mundo (Genovart et al., 2018; Pedrocchi et al., 2002). En otros casos existe una clara falta de densodependencia en la inversión en reproducción (como es el caso de las pardelas y de los charranes). Sin embargo, este resultado debe ser considerado con cautela, ya que para estas especies, las estimas poblacionales no eran tan precisas como en el caso de las gaviotas. De hecho, es muy probable que hayamos subestimado la competencia por estos PAFS, por parte de individuos pertenecientes a otras colonias. Otro aspecto a tener en cuenta es que cada ecosistema tiene unas características y una dinámica particulares, lo cual puede influir en la forma en la que las aves marinas explotan estos PAFS. Por ejemplo, a pesar de que en el Mediterráneo Occidental los descartes de la pesca son abundantes, el charrán patinegro *Thalasseus sandvicensis* hace un uso bastante modesto de este recurso (≈10% de su dieta; datos propios sin publicar. Sin embargo, en otras partes del mundo este recurso puede constituir hasta el 35% de la dieta de esta especie (véase p. ej. Liechty et al., 2016).

La importancia de las condiciones de forrajeo: detectabilidad y accesibilidad del alimento

Algunos estudios han demostrado que variables climáticas y oceanográficas como la velocidad del viento, la altura de las olas (Dunn, 1973) o la turbidez del agua (Baptist and Leopold, 2010) pueden influir en el éxito de forrajeo de algunas aves marinas. Birkhead, T.R., 1976 por ejemplo, demostró que el ratio de alimentación de los pollos de Arao común (*Uria aalgae*) disminuía cuando las condiciones marinas eran adversas. En definitiva, estos estudios sugieren que la ingesta de alimento no sólo depende de la abundancia de recursos *per se*, sino que también depende de una serie de factores ambientales que influyen en la capacidad de las aves para detectar y acceder al alimento. Por tanto, la variabilidad temporal de estos factores ambientales también debería de verse reflejada en parámetros ecológicos que dependen de la disponibilidad de alimento (p. ej. dieta, parámetros reproductivos etc.). Teniendo esto en cuenta, en esta tesis se han utilizado estas variables (velocidad del viento, altura del oleaje y turbidez del agua) para evaluar cómo la detectabilidad y la accesibilidad a los recursos, tanto de origen natural como antropogénico, puede influir en la inversión que algunas aves marinas hacen en la reproducción. Los resultados muestran que las condiciones de forrajeo afectan de forma muy importante a la inversión que algunas aves marinas hacen en la reproducción. También se puede ver que la influencia por parte de estos efectos es diferente en función de la especie considerada, probablemente debido a las diferencias en la estrategia de forrajeo (p. ej. velocidad del viento y turbidez del agua en charranes vs. altura del oleaje en pardelas). En algunos casos, las condiciones de forrajeo han jugado un papel más importante para la inversión en la reproducción que la propia abundancia de alimento *per se*, tanto de origen natural (presas naturales) como de origen antropogénico (descartes).

Este hallazgo sugiere que la abundancia de alimento no siempre es un factor limitante para la inversión en la reproducción. Por tanto, si la abundancia de alimento no se traduce necesariamente en ingesta de alimento (i.e. abundancia ≠ disponibilidad), considerar la detectabilidad y la accesibilidad del alimento puede mejorar de forma significativa nuestro poder predictivo a la hora de modelar los parámetros demográficos que dependen de la disponibilidad de alimento.

Influencia por parte de otros factores ambientales en la energía que las aves marinas invierten en la reproducción

Algunos índices climáticos de gran escala como es el caso de los promedios invernales de la Oscilación del Atlántico Norte (winter NAO), se han relacionado con parámetros demográficos de las aves marinas (véase p. ej. Frederiksen et al., 2004; Genovart et al., 2013; Lewis et al., 2009; Rodríguez et al., 2019). Sin embargo, los mecanismos que subyacen detrás de esta relación, en muchos casos son especulativos. Por ejemplo, se desconoce si la influencia que estos índices climáticos tienen sobre estos parámetros ecológicos tiene lugar a través de las condiciones locales de las áreas de reproducción (en primavera) o si en cambio su influencia únicamente tiene lugar en las áreas de hibernada. Por tanto, en primer lugar se evaluó la influencia que este índice climático tiene sobre la inversión en la reproducción de tres especies de aves marinas, la pardela cenicienta *Calonectris diomedea*, el charrán patinegro y la gaviota de audouin. En segundo lugar, de cara a poder descartar que la influencia del Winter NAO tuviera lugar en los meses de primavera, se investigó la posible relación entre este índice climático y las condiciones locales en las áreas de cría durante la época de prepuesta (en primavera). Para estimar las condiciones locales se utilizaron estimas de: i) abundancia de presas naturales (específicas para cada especie de ave marina considerada), ii) diversas variables climáticas y oceanográficas que potencialmente pueden afectar las condiciones de forrajeo (ver más arriba) y iii) del tamaño poblacional. En todas las especies consideradas, el winter NAO tuvo una influencia muy marcada en la inversión que estas aves marinas hacen en la reproducción. Sin embargo, no se encontró ninguna relación entre este índice climático y las condiciones locales en las áreas de cría durante la temporada de reproducción. Esto sugiere que, al menos en las poblaciones estudiadas, la influencia que el winter NAO tiene sobre la inversión en reproducción se produce sólo durante los meses de invierno (es decir, a través de las condiciones que se dan en las áreas de invernada). Por tanto, las condiciones invernales tendrían un efecto de tipo '*carry-over*' sobre la energía que estas aves invierten en la reproducción en primavera.

Volumen del huevo como indicador de la inversión en reproducción

Las aves marinas disponen principalmente de dos mecanismos a la hora de modular la energía que invierten en la reproducción: i) a través del tamaño de la puesta (en el caso de las especies multíparas) y ii) a través del tamaño del huevo (i.e. el volumen del huevo). En especies cuya puesta se puede estar formada por más de un huevo, utilizar el tamaño de la puesta como indicador de la inversión en reproducción es poco recomendable ya que se pueden dar diversas situaciones que pueden hacer que el número de huevos observados no se correspondan con el tamaño real de la puesta. Por ejemplo, en algunos casos se pueden contar como completas puestas que en realidad no lo son debido a que la hembra todavía no ha terminado de poner todos los huevos o bien por haber sido depredadas. Por tanto, para tratar de minimizar este error, es mucho más recomendable considerar únicamente el volumen de la puesta modal. Esta tesis muestra como el volumen del huevo puede reflejar cómo los descartes de la pesca y la basura de los vertederos influyen en la energía que algunas aves marinas invierten en la reproducción. Sin embargo, evaluar estos efectos no siempre es fácil y en algunos casos puede constituir un importante desafío. Por un lado la elevada movilidad de estas aves a menudo obliga a tener que trabajar con escalas espacio temporales muy grandes. Además, detectar el efecto de estos recursos en el volumen del huevo puede ser especialmente complicado en aquellas especies que siguen una dieta más generalista. Por ejemplo, la serie temporal utilizada para estimar la inversión en reproducción de la gaviota patiamarilla se basaba en cerca de 5000 puestas medidas en 20 colonias diferentes distribuidas a lo largo de todo el Mediterráneo Occidental. De forma similar, la escala temporal considerada oscilaba entre 15 y 20 años. Los resultados mostraron que la inversión que algunas aves marinas como la gaviota patiamarilla o la pardela cenicienta hacen en la reproducción se ve claramente afectada por los cambios en la disponibilidad de estos PAFS. Sin embargo, esta tesis también muestra que estos efectos también pueden verse enmascarados por proceso de densodependencia, como por ejemplo en el caso de las poblaciones de gaviota de audouin aquí estudiadas (ver más arriba). Por último, también se muestra que la variación temporal del volumen del huevo no sólo refleja lo que ocurre durante el periodo de prepuesta (periodo que transcurre desde la llegada de las aves a las colonias de cría hasta el momento de la puesta), sino también lo que ocurre algunos meses antes en las áreas de hibernada (ver más arriba efecto de tipo '*carry-over'* de las condiciones invernales).

Estimas de la abundancia de descartes de la pesca y basura de vertederos

Estimar el efecto que tiene la variación temporal de la abundancia de algunos PAFS en parámetros ecológicos puede ser sumamente complicado. A menudo, los datos de generación de descartes y de gestión de RSU en vertederos no son lo suficientemente precisos (p.ej. debido a su baja periodicidad) para evaluar esto tipo de efectos y en muchos casos son incluso inexistentes (p. ej. en países menos desarrollados). Si además se trabaja a una escala espacial grande, e.g. en un área geográfica que englobe diversos países o continentes, recopilar datos precisos de generación de estos PAFS puede resultar todavía más complicado si cabe, ya que cada país establece sus propios protocolos de monitoreo. Por tanto, en estos casos, la solución pasa por utilizar proxies adecuados que reflejen lo más fielmente posible los cambios en la disponibilidad de estos recursos. El arrastre demersal es con diferencia, la modalidad de pesca que genera una mayor cantidad de descartes a nivel global (ver más arriba). La distancia que estos barcos son capaces de cubrir durante la fase de arrastre, así como el tamaño de sus aparejos están relacionados con la potencia motora de estos barcos (Eigaard et al., 2011). Teniendo esto en cuenta, los proxies que se han utilizado en esta tesis para estimar los cambios en la disponibilidad de estos PAFS han sido por un lado, la potencia declarada cada año por la flota de arrastre demersal (como proxie de la disponibilidad de descartes) y por otro el número de vertederos operativos de RSU a cielo abierto (como proxie de la disponibilidad de basura de los vertederos). A raíz de las políticas europeas en materia de descartes y vertederos se han implantado una serie de medidas orientadas a una reducción progresiva de la disponibilidad de estos PAFS. Algunas de las medidas más relevantes en este sentido, han sido llevar a cabo una reducción progresiva del tamaño de la flota pesquera así como del número de vertederos de RSU a cielo abierto. Estas medidas han supuesto que la disponibilidad de estos PAFS se haya visto reducida de forma muy considerable a lo largo de los últimos 15-20 años en algunos países de la Unión Europea. Esto ha supuesto una disminución de la capacidad de carga para las poblaciones de algunas aves marinas generalistas, lo cual se ha podido ver reflejado en la energía que estas aves invierten cada año en la reproducción.

Influencia por parte de factores socioeconómicos

La presente tesis también pone de manifiesto la importancia de considerar la posible influencia por parte de factores socioeconómicos en la disponibilidad de estos PAFS en función del área geográfica considerada. Más especificamente, se pudo observar que en las costas Europeas , tanto los descartes de la pesca como la basura de los vertederos influyeron de forma importante en en la inversión en la reproducción de una ave marina generalista. Sin embargo, en las costas africanas, ninguno de estos dos recursos influyó de forma clara en la inversión en la reproducción de esta especie. Esto probablemente se debe a que en algunos países del norte de África prácticamente todo el pescado capturado se comercializa, por lo que apenas se generan descartes (Belhabib, et al., 2012). Se forma similar, la cantidad de residuos sólidos urbanos generados *per cápita* en estos países también es muy inferior a los generados en la Unión Europea (ONEM 2001; Chantou et al. 2013), por tanto, la cantidad de materia orgánica disponible en estos vertederos también es mucho menor. La principal consecuencia de estas diferencias espaciales en la cantidad de subsidios fue que las gaviotas que criaban alrededor de las costas europeas pusieron huevos más grandes en comparación con las que criaban en las costas africanas. Esto sugiere que las poblaciones Europeas de esta especie estarían sobrealimentadas debido a una mayor disponibilidad de estos PAFS. Esta mayor disponibilidad de recursos también explicaría en parte que algunas especies generalistas sean superabundantes en algunas regiones de la Unión Europea (Duhem et al., 2008; Moulaï, 2007; Payo-Payo et al., 2015; véase p.ej. Vidal et al., 1998).

Retos de cara a investigaciones futuras

Las políticas en materia de descartes y vertederos que están siendo progresivamente implementadas en diversos países, ofrecen un escenario de tipo BACI ideal para investigar las consecuencias ecológicas asociadas a una drástica reducción de la disponibilidad de estos PAFS. Más específicamente, estas políticas ofrecen una muy buena oportunidad para entender mejor los efectos que una reducción de la capacidad de carga puede tener sobre parámetros demográficos importantes como la supervivencia, la dispersión, la reproducción, la resiliencia de las poblaciones frente a perturbaciones o el papel de la especialización individual en el proceso de forrajeo. Los efectos que cabría esperar a corto plazo a raíz de estas políticas son una reducción de la capacidad de carga seguido de un incremento en la competencia por el alimento, por ejemplo en forma de interacciones predatorias, cleptoparasitismo, etc. A medio-largo plazo, cabría esperar un aumento de la dispersión, una disminución del rendimiento reproductivo, una menor resiliencia de las poblaciones frente a perturbaciones (i.e. una menor capacidad de amortiguación del efecto de la estocasticidad ambiental) y una disminución de la supervivencia, principalmente en aquellas especies que presentan una mayor dependencia de estos PAFS. Esto probablemente tendrá como consecuencia una disminución en la proporción de especies más generalistas en la comunidad, lo cual puede resultar en beneficio de otras especies. Los resultados de esta tesis muestran que las condiciones de forrajeo pueden influir de forma importante en parámetros demográficos importantes, como es el caso p.ej. de la energía que algunos organismos invierten en la reproducción. Finalmente, los resultados también sugieren que la influencia que tiene el winter NAO sobre este parámetro reproductivo en algunas aves marinas parece ser estrictamente invernal (i.e. *carry-over effect* de las condiciones invernales). Teniendo esto en cuenta, el uso combinado de datos de seguimiento remoto de las aves (remote tracking data), con datos de las condiciones de forrajeo durante los meses de invierno, plantea un interesante reto de cara a entender mejor los mecanismos a través de los cuales estos índices climáticos influyen en la ecología de las aves marinas.

Conclusiones generales

1. Los vacíos de conocimiento más importantes en relación a las interacciones ecológicas entre las aves marinas y los descartes hacen referencia a la supervivencia, la dispersión, la reproducción, la resistencia de sus poblaciones frente a las perturbaciones y el papel de la especialización individual en el proceso de forrajeo.
2. El arrastre demersal es, con diferencia la modalidad de pesca más importante por lo que respecta a las interacciones que se dan entre las aves marinas y los descartes.
3. Tanto los descartes de la pesca como la basura de los vertederos pueden influir en la cantidad de energía que algunas aves marinas generalistas invierten en la reproducción. Sin embargo, los resultados sugieren un efecto más débil por parte de los vertederos, probablemente debido a la menor calidad de la basura como recurso alimentario.
4. Los PAFS pueden amortiguar el efecto de la estocasticidad ambiental y alterar la dinámica de la sincronía natural entre especies.
5. Los factores socioeconómicos y los procesos de densodependencia pueden afectar al modo en que los PAFS influyen en la ecología de las aves marinas.
6. De las más de 300 especies de aves marinas conocidas, sabemos que al menos 111 interaccionan con los descartes de la pesca en mayor o menor medida.
7. Tanto los índices a gran escala como las variables locales influyen en la inversión en reproducción de las aves marinas, ya que a menudo operan en diferentes escalas espacio-temporales.
8. Considerar la detectabilidad y la accesibilidad al alimento puede mejorar considerablemente el poder predictivo en la modelización de procesos ecológicos relacionados con la disponibilidad de alimento.
9. Hacen falta más estudios que permitan entender mejor los mecanismos a través de los cuales las variables locales afectan a la ingesta de alimento, por ejemplo combinando el uso datos de seguimiento remoto de aves (tracking data) con las condiciones de forrajeo.

10. Se necesitan más programas de monitoreo que proporcionen datos adecuados tanto de parámetros demográficos como de factores naturales y antropogénicos que influyen en la ecología de las aves marinas.

References

Abelló, P., Arcos, J.M., and Sola, L.G. 2003. Geographical patterns of seabird attendance to a research trawler along the Iberian Mediterranean coast. Scientia Marina *67*, 69–75.

Arcos, J., Louzao, M., and Oro, D. 2008. Fisheries ecosystem impacts and management in the Mediterranean: seabirds point of view. American Fisheries Society Symposium *49*, 1471–1479.

Arcos, J.M., Oro, D., and Sol, D. 2001. Competition between the Yellow-Legged gull *Larus cachinnans* and Audouin's gull *Larus audouinii* associated with commercial fishing vessels: The influence of season and fishing fleet. Marine Biology *139*, 807-816.

Baptist, M.J., and Leopold, M.F. 2010. Prey capture success of Sandwich Terns *Sterna sandvicensis* varies non-linearly with water transparency. Ibis *152*, 815–825.

Bartumeus, F., Giuggioli, L., Louzao, M., Bretagnolle, V., Oro, D., and Levin, S.A. 2010. Fishery discards impact on seabird movement patterns at regional scales. Current Biology *20*, 215–222.

Batchelor, A.L., and Ross, G.J.B. 1984. The Diet and Implications of dietary change of Cape gannets on Bird Island, Algoa Bay. Ostrich *55*, 45–63.

Belhabib, et al. 2012. Reconstruction of marine fisheries catches for Morocco North, central and South, 1950-2010. In: Belhabib, D., Zeller, D., Harper, S., and Pauly, D. eds., Marine fisheries catches in West Africa, 1950-2010, part I. Fisheries Centre Research Reports 20 3. Fisheries Centre, University of British Columbia, Canada [ISSN 1198-6727].

Bicknell, A.W.J., Oro, D., Camphuysen, K. C. J., and Votier, S.C. 2013. Potential consequences of discard reform for seabird communities. Journal of Applied Ecology *50*, 649–658.

Birkhead, T.R. 1976. Effects of sea conditions on rates at which Guillemots feed chicks. British Birds *69*, 490-492.

Blomqvist, D., Johansson, O.C., and Götmark, F. 1997. Parental quality and egg size affect chick survival in a precocial bird, the Lapwing *Vanellus vanellus*. Oecologia *110*, 18–24.

Bolton, M. 1991. Determinants of chick survival in the Lesser Black-Backed gull: relative contributions of egg size and parental quality. Journal of Animal Ecology *60*, 949–960.

Bosch, M., Oro, D., Cantos, F.J., and Zabala, M. 2000. Short-term effects of culling on the ecology and population dynamics of the Yellow-Legged gull. Journal of Applied Ecology *37*, 369–385.

Canals, M., Puig, P., Madron, X.D. de, Heussner, S., Palanques, A., and Fabres, J. 2006. Flushing submarine canyons. Nature *444*, 354.

Carbonell, A., Martín, P., Ranieri, S., and Team, W. 1998. Discards of the Western Mediterranean trawl fleets. Rapports et procès-verbaux des réunions - Commission internationale pour l'exploration scientifique de la mer Méditerranée. 35: 392–393.

Christians, J.K. 2002. Avian egg size: variation within species and inflexibility within individuals. Biological Reviews *77*, 1–26.

Cunningham, E.J.A., and Russell, A.F. 2000. Egg investment is influenced by male attractiveness in the mallard. Nature *404*, 74.

Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J.M., Furness, R.W., Mills, J.A., Murphy, E.J., Österblom, H., Paleczny, M., et al. 2011. Global seabird response to forage fish depletion—one-third for the birds. Science *334*, 1703–1706.

Duhem, C., Roche, P., Vidal, E., and Tatoni, T. 2008. Effects of anthropogenic food resources on Yellow-Legged gull colony size on Mediterranean islands. Population Ecology *50*, 91–100.

Dunn, E.K. 1973. Changes in fishing ability of terns associated with wind speed and sea surface conditions. Nature *244*, 520–521.

Eigaard, O.R., Rihan, D., Graham, N., Sala, A., and Zachariassen, K. 2011. Improving fishing effort descriptors: Modelling engine power and gear-size relations of five European trawl fleets. Fisheries Research *110*, 39–46.

Frederiksen, M., Harris, M.P., Daunt, F., Rothery, P., and Wanless, S. 2004. Scale-dependent climate signals drive breeding phenology of three seabird species. Global Change Biology *10*, 1214–1221.

Garthe, S., Camphuysen, K., and Furness, R. 1996. Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. Marine Ecology Progress Series *136*, 1–11.

Genovart, M., Negre, N., Tavecchia, G., Bistuer, A., Parpal, L., and Oro, D. 2010. The young, the weak and the sick: evidence of natural selection by predation. Plos One *5*, e9774.

Genovart, M., Sanz-Aguilar, A., Fernández-Chacón, A., Igual, J.M., Pradel, R., Forero, M.G., and Oro, D. 2013. Contrasting effects of climatic variability on the demography of a trans-equatorial migratory seabird. Journal of Animal Ecology *82*, 121–130.

Genovart, M., Oro, D., and Tenan, S. 2018. Immature survival, fertility, and density dependence drive global population dynamics in a long-lived species. Ecology *99*, 2823–2832.

Grémillet David, Pichegru Lorien, Kuntz Grégoire, Woakes Anthony G, Wilkinson Sarah, Crawford Robert J.M, and Ryan Peter G 2008. A junk-food hypothesis for gannets feeding on fishery waste. Proceedings of the Royal Society B: Biological Sciences *275*, 1149–1156.

Hamer, K.C., Furness, R.W., and Caldow, R.W.G. 1991. The effects of changes in food availability on the breeding ecology of Great skuas *Catharacta skua* in Shetland. Journal of Zoology *223*, 175–188.

Heino Mikko, Kaitala Veijo, Ranta Esa, and Lindström Jan 1997. Synchronous dynamics and rates of extinction in spatially structured populations. Proceedings of the Royal Society of London. Series B: Biological Sciences *264*, 481–486.

Laneri, K., Louzao, M., Martínez-Abraín, A., Arcos, J.M., Belda, E.J., Guallart, J., Sánchez, A., Giménez, M., Maestre, R., and Oro, D. 2010. Trawling regime influences longline seabird bycatch in the Mediterranean: new insights from a small-scale fishery. Marine Ecology Progress Series *420*, 241–252.

Lewis, S., Elston, D.A., Daunt, F., Cheney, B., and Thompson, P.M. 2009. Effects of extrinsic and intrinsic factors on breeding success in a long lived seabird. Oikos *118*, 521–528.

Liebhold, A., Koenig, W.D., and Bjørnstad, O.N. 2004. Spatial synchrony in population dynamics. Annual Review of Ecology, Evolution, and Systematics *35*, 467–490.

Liechty, J.S., Fontenot, Q.C., and Pierce, A.R. 2016. Diet composition of Royal tern *Thalasseus maximus* and Sandwich tern *Thalasseus sandvicensis* at Isles Dernieres Barrier Island Refuge, Louisiana, USA. Cowa *39*, 58–68.

Martínez-Abraín, A., Maestre, R., and Oro, D. 2002. Demersal trawling waste as a food source for Western Mediterranean seabirds during the summer. ICES Journal of Marine Science *59*, 529–537.

Moulaï, R. 2007. Fluctuation saisonnière des oiseaux de la décharge publique de la ville de Béjaia Algérie, cas particulier du goéland leucophée *Larus michahellis*. Ostrich *78*, 527–531.

ONEM 2001. Environment state in Morocco. Chapter 4: waste and urban areas. Natl Dept of Environment, Morocco.

Oro, D. 1996a. Interspecific kleptoparasitism in Audouin's Gull *Larus audouinii* at the Ebro Delta, Northeast Spain: a behavioural response to low food availability. Ibis *138*, 218–221.

Oro, D. 1996b. Effects of trawler discard availability on egg laying and breeding success in the lesser black-backed gull *Larus fuscus* in the Western Mediterranean. Marine Ecology Progress Series *132*, 43–46.

Oro, D., and Martínez-Abraín, A. 2007. Deconstructing myths on large gulls and their impact on threatened sympatric waterbirds. Animal Conservation *10*, 117–126.

Oro, D., Bosch, M., and Ruiz, X. 1995. Effects of a trawling moratorium on the breeding success of the Yellow-Legged gull *Larus cachinnans*. Ibis *137*, 547–549.

Oro, D., Genovart, M., Ruiz, X., Jiménez, J., and García-Gans, J. 1996. Differences in diet, population size and reproductive performance between two colonies of Audouin's Gull *Larus audouinii* affected by a trawling moratorium. Journal of Avian Biology *27*, 245–251.

Oro, D., Pradel, R., and Lebreton, J.-D. 1999. Food availability and nest predation influence life history traits in Audouin's gull *Larus audouinii*. Oecologia *118*, 438–445.

Oro, D., Cam, E., Pradel, R., and Martínez-Abraín, A. 2004. Influence of food availability on demography and local population dynamics in a long-lived seabird. Proceedings of the Royal Society of London B: Biological Sciences *271*, 387–396.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S., and Martínez-Abraín, A. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters *16*, 1501–1514.

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

Oro, D., Jover, L., and Ruiz, X. 1996. Influence of trawling activity on the breeding ecology of a threatened seabird, Audouin's gull *Larus audouinii*. Marine Ecology Progress Series *139*, 19–29.

Paleczny, M., Hammill, E., Karpouzi, V., and Pauly, D. 2015. Population trend of the world's monitored seabirds, 1950-2010. Plos One *10*, e0129342.

Parsons, M., Mitchell, I., Butler, A., Ratcliffe, N., Frederiksen, M., Foster, S., and Reid, J.B. 2008. Seabirds as indicators of the marine environment. ICES Journal of Marine Science *65*, 1520–1526.

Payo-Payo, A., Oro, D., Igual, J.M., Jover, L., Sanpera, C., and Tavecchia, G. 2015. Population control of an overabundant species achieved through consecutive anthropogenic perturbations. Ecological Applications *25*, 2228–2239.

Pedrocchi, V., Oro, D., González-Solís, J., Ruiz, X., and Jover, L. 2002. Differences in diet between the two largest breeding colonies of Audouin's gulls: the effects of fishery activities. Scientia Marina *66*, 313–320.

Piatt, J.F., and Anderson, P. 1996. Response of Common murres to the Exxon Valdez oil spill and long-term changes in the Gulf of Alaska marine ecosystem. American Fisheries Society Symposium *18*, 720-737.

Porter, J.M., and Sealy, S.G. 1982. Dynamics of seabird multispecies feeding flocks: Age-Related Feeding Behaviour. Behaviour *81*, 91–109.

Risch, T.S., and Rohwer, F.C. 2000. Effects of parental quality and egg size on growth and survival of herring gull chicks. Canadian Journal of Zoology. *78*, 967–973.

Robbins, C.T. 1981. Estimation of the relative protein cost of reproduction in birds. The Condor *83*, 177–179.

Rodríguez, A., Arcos, J.M., Bretagnolle, V., Dias, M.P., Holmes, N.D., Louzao, M., Provencher, J., Raine, A.F., Ramírez, F., Rodríguez, B., et al. 2019. Future directions in conservation research on petrels and shearwaters. Frontirs in Marine Science *6*.

Ruiz, X., Jover, L., Pedrocchi, V., Oro, D., and González-Solís, J. 2000. How costly is clutch formation in the Audouin's gull *Larus audouinii*? Journal of Avian Biology *31*, 567–575.

Sánchez, P., Sartor, P., Recasens, L., Ligas, A., Martin, J., Ranieri, S.D., and Demestre, M. 2007. Trawl catch composition during different fishing intensity periods in two Mediterranean demersal fishing grounds. Scientia Marina *71*, 765–773.

Sanz-Aguilar, A., Mínguez, E., and Oro, D. 2012. Is laying a large egg expensive? female-biased cost of first reproduction in a petrel. Auk *129*, 510–516.

Steigerwald, E.C., Igual, J.-M., Payo-Payo, A., and Tavecchia, G. 2015. Effects of decreased anthropogenic food availability on an opportunistic gull: evidence for a size-mediated response in breeding females. Ibis *157*, 439–448.

Tasker, M.L., Camphuysen, C.J., Cooper, J., Garthe, S., Montevecchi, W.A., and Blaber, S.J.M. 2000. The impacts of fishing on marine birds. ICES Journal of Marine Science *57*, 531–547.

Tsagarakis, K., Palialexis, A., and Vassilopoulou, V. 2014. Mediterranean fishery discards: review of the existing knowledge. ICES Journal of Marine Science *71*, 1219–1234.

Vidal, E., Medail, F., and Tatoni, T. 1998. Is the Yellow-legged gull a superabundant bird species in the Mediterranean? Impact on fauna and flora, conservation measures and research priorities. Biodiversity and Conservation *7*, 1013–1026.

Votier, S.C., Furness, R.W., Bearhop, S., Crane, J.E., Caldow, R.W.G., Catry, P., Ensor, K., Hamer, K.C., Hudson, A.V., Kalmbach, E., et al. 2004. Changes in fisheries discard rates and seabird communities. Nature *427*, 727–730.

Wagner, E.L., and Boersma, P.D. 2011. Effects of fisheries on seabird community ecology. Reviews in Fisheries Science *19*, 157–167.

Williams, T.D. 2005. Mechanisms underlying the costs of egg production. BioScience *55*, 39–48.

Zeller, D., Cashion, T., Palomares, M., and Pauly, D. Global marine fisheries discards: a synthesis of reconstructed data. Fish and Fisheries *19*, 30-39.

Resumen global

Se espera que las políticas recientes en materia de prohibición de descartes y cierre de vertederos a cielo abierto, tengan como consecuencia una importante reducción de la disponibilidad de los recursos antropogénicos predecibles (PAFS) para las aves marinas. De cara a poder pronosticar las consecuencias ecológicas que se derivan de los cambios en la disponibilidad de estos PAFS, es necesario entender el papel que juega cada uno de estos recursos en parámetros ecológicos importantes, así como la posible influencia por parte de mecanismos de densodependencia. Además, en especies que explotan ambos recursos, también es importante evaluar si estos efectos actúan de forma sinérgica o no. Así mismo, también es importante entender cómo las interacciones ecológicas que se dan entre las aves marinas y los PAFS pueden verse afectadas por otros factores potencialmente importantes, como por ejemplo, la abundancia de presas naturales o las condiciones de forrajeo.

En el primer capítulo de esta tesis he revisado el conocimiento actual sobre las interacciones ecológicas que se dan entre las aves marinas y los descartes de la pesca (probablemente los PAFS más importantes para las aves marinas), con el objetivo de identificar los principales vacíos de conocimiento y proponer nuevos retos de cara a entender mejor el papel de los PAFS en la ecología de las aves marinas. En el segundo capítulo, evalué la importancia relativa de los descartes de la pesca y la basura de los vertederos en la inversión que una ave marina generalista hace en la reproducción, así como la posible influencia por parte de mecanismos de densodependencia. En el tercer capítulo, colaboré en la investigación del papel de los PAFS a la hora de amortiguar la estocasticidad ambiental y alterar la dinámica de la sincronía natural que se da entre dos aves marinas. Finalmente, en el último capítulo, evalué la importancia de diversos factores ambientales en la inversión que tres aves marinas con diferentes estrategias de vida hacen en la reproducción. En particular, consideré variables ambientales locales (abundancia de alimento, competencia y estado del mar) al inicio del periodo de reproducción, así como la influencia por parte de las condiciones invernales, estimadas a partir de un índice climático a gran escala, la Oscilación del Atlántico Norte (NAO). Considerar estas variables de forma simultánea me permitió evaluar la importancia relativa de fuentes de alimento, tanto de origen natural como antropogénico, la competencia intra e interespecífica y las condiciones de forrajeo en forma de variables que afectan a la detectabilidad y accesibilidad del alimento por parte de las aves.

Los resultados de esta tesis ponen de manifiesto que los vacíos de conocimiento más importantes en relación a las interacciones ecológicas entre las aves marinas y los descartes de la pesca, hacen referencia a la supervivencia, la dispersión, la reproducción, la resiliencia de sus poblaciones frente a las perturbaciones y el papel de la especialización individual en el proceso de forrajeo. Los resultados mostraron que tanto los descartes de la pesca como la basura de los vertederos pueden incrementar la inversión que las aves marinas hacen en la reproducción. Sin embargo, este efecto fue menos marcado en los vertederos que en los descartes, probablemente debido a una menor calidad de la basura como recurso alimentario. Además, también se muestra cómo estos efectos pueden quedar enmascarados por procesos de densodependencia. La tesis también realza la importancia de considerar la posible influencia por parte de factores socioeconómicos en la disponibilidad de los PAFS, dependiendo del área geográfica considerada. También se muestra que los PAFS pueden alterar la estocasticidad natural, incrementando la inversión en reproducción en especies generalistas, lo que a su vez, puede producir alteraciones en la estructura de la comunidad. Esta tesis también pone de manifiesto que los factores ambientales que condicionan la detectabilidad y accesibilidad del alimento por parte de las aves, pueden jugar un papel muy importante en parámetros clave como por ejemplo la inversión en la reproducción. Esto implica que, al contrario de lo que comúnmente se asume, el hecho de que el alimento sea abundante, no implica que este alimento esté disponible (detectable i/o accesible) para los organismos. Finalmente, los resultados también sugieren que la influencia que la Oscilación del Atlántico Norte tiene en la inversión en la reproducción de algunas aves marinas, se limita a los meses de invierno y se manifiesta en primavera en forma de efecto de tipo *carry-over*.

Appendix Chapter 1

Discards regulation vs Mediterranean fisheries sustainability
M. Demestre and F. Maynou (eds)

Scientia Marina 82S1
December 2018, 115-120, Barcelona (Spain)
ISSN-L: 0214-8358
https://doi.org/10.3989/scimar.04746.10A

Discard-ban policies can help improve our understanding of the ecological role of food availability to seabirds

Enric Real [1], Giacomo Tavecchia [1], Meritxell Genovart [2,3], Ana Sanz-Aguilar [1],
Ana Payo-Payo [1], Daniel Oro [2,3]

[1] Grupo de Ecología y Demografía Animal, IMEDEA, CSIC-UIB, Miquel Marquès 21, 07190 Esporles, Spain.
(ER) (Corresponding author) E-mail: ereal@imedea.uib-csic.es. ORCID-iD: https://orcid.org/0000-0002-6190-6303
(GT) E-mail: g.tavecchia@uib.es. ORCID-iD: https://orcid.org/0000-0001-5435-2691
(AS-A) E-mail: asanz@imedea.uib-csic.es. ORCID-iD: https://orcid.org/0000-0002-4177-9749
(AP-P) E-mail: anapayopayo@gmail.com.ORCID-iD: https://orcid.org/0000-0001-5482-242X
[2] IMEDEA, CSIC-UIB, Miquel Marquès 21, 07190 Esporles, Spain.
(MG) E-mail: m.genovart@csic.es. ORCID-iD: https://orcid.org/0000-0003-2919-1288
(DO) E-mail: d.oro@csic.es. ORCID-iD: https://orcid.org/0000-0003-4782-3007
[3] Centre d'Estudis Avançats de Blanes, CSIC, Accés Cala Sant Francesc 14, 17300 Blanes, Spain.

Summary: Discards from fisheries are the most important predictable anthropogenic food subsidies (PAFS) that are being incorporated into marine ecosystems. Changes on their availability and predictability can help us to understand the role that food availability (i.e. an important indicator of the carrying capacity) plays at different ecological levels, from individual fitness to community dynamic and ecosystem functioning. For several reasons, seabirds are an excellent model for evaluating the ecological effects arising from a lack of discards: 1) they are one of the most important discard scavengers, 2) they are easy to monitor and 3) they are apical predators are globally distributed, which makes them suitable health indicators of ecosystems. Here we review the existing information on seabird-discard interactions to identify the main knowledge gaps and propose new challenges for improving our understanding of the general role of food availability. We conclude that the new policies on the ban of fishery discards that are being progressively implemented in the European Union, Norway, Chile and New Zealand offer a suitable experimental scenario for improving our understanding of how a large decrease in the carrying capacity may alter demographic parameters such as survival, dispersal and reproduction, the resilience of populations against perturbations and the role of individual specialization in the foraging process.

Keywords: food availability; fishery discards; seabirds; ecological interactions; discard policies.

Las políticas sobre prohibición de descartes pueden ayudar a mejorar la comprensión sobre el papel ecológico de la disponibilidad de alimento en aves marinas

Resumen: Los descartes pesqueros constituyen el recurso antropogénico predecible (PAFS) más importante que está siendo incorporado en los ecosistemas marinos. Cambios en su disponibilidad y predictibilidad pueden ayudar a entender mejor el papel ecológico de la disponibilidad de alimento (i.e. un importante indicador de la capacidad de carga) a diferentes niveles, desde la eficacia biológica individual hasta la dinámica de poblaciones o el funcionamiento de los ecosistemas. Las aves marinas constituyen un modelo excelente para estudiar los efectos ecológicos derivados de la falta de descartes por diversas razones: las aves marinas: 1) se encuentran entre los principales carroñeros de descartes, 2) son fáciles de monitorear y 3) son depredadores apicales globalmente distribuidos, lo cual las convierte en buenas indicadoras de la salud del ecosistema. En el presente estudio revisamos la información existente sobre las interacciones ecológicas entre las aves marinas y los descartes de la pesca, con el fin de identificar los principales vacíos de conocimiento y plantear retos futuros de cara a mejorar nuestra comprensión sobre el papel ecológico que tiene la disponibilidad de alimento. Concluimos que las políticas actuales en materia de prohibición de descartes que están siendo implementadas en la Unión Europea, Noruega, Chile o Nueva Zelanda, ofrecen un escenario ideal para mejorar nuestra comprensión sobre cómo una reducción de la capacidad de carga puede alterar parámetros demográficos tales como la supervivencia, la dispersión y la reproducción, la resiliencia de las poblaciones frente a perturbaciones y el papel de la especialización individual en el proceso de forrajeo.

Palabras clave: disponibilidad de alimento; descartes pesqueros; aves marinas; interacciones ecológicas; políticas de descartes.

Citation/Cómo citar este artículo: Real E., Tavecchia G., Genovart M., Sanz-Aguilar A., Payo-Payo A., Oro D. 2018. Discard-ban policies can help improve our understanding of the ecological role of food availability to seabirds. Sci. Mar. 82S1: 115-120. https://doi.org/10.3989/scimar.04746.10A

Editor: F. Maynou.

Received: December 22, 2017. **Accepted:** June 21, 2018. **Published:** July 25, 2018.

INTRODUCTION

The large amount of discards in the form of offal that are generated daily by industrial and artisanal fisheries and thrown into the sea constitutes one of the most important and predictable anthropogenic food subsidies (PAFS) that are being incorporated into marine ecosystems worldwide (Oro et al. 2013). Global discards generation in recent years has been estimated to be *ca*. 10 million t/year, with a peak of 19 million t/year in the late 1950s (Zeller et al. 2017). As a result of the high abundance and predictability of this anthropogenic food resource, together with a decrease in the natural prey availability due to industrial fisheries, fishery discards have important ecological implications at a global level for marine scavengers, including seabirds (Votier et al. 2004, Cury et al. 2011, Bicknell et al. 2013, Oro et al. 2013). Garthe et al. (1996), for instance, estimated that 5.9 million seabirds were potentially supported by fishery discards in the North Sea.

Changes in the availability and predictability of fishery discards as PAFS can help to understand the ecological role that food availability (i.e. carrying capacity) have at multiple ecological levels, including individual fitness, community dynamics and ecosystem functioning.

Seabirds constitute an excellent model for evaluating the ecological effects arising from a lack of PAFS for several reasons: seabirds are 1) one of the most important discard scavengers at a global level, 2) easy to monitor (because they breed on land) and 3) apical predators with a global distribution, which makes them suitable bioindicators of ecosystem health. The link between seabirds and fishery discards has been reviewed in several studies (Tasker et al. 2000, Arcos et al. 2008, Wagner and Boersma 2011). However, the ecological and evolutionary implications that fishery discards have as PAFS at a global level (Oro et al. 2013), as well as the current changes in fishery policies (see e.g. Borges et al. 2016), call for a new revision of the existing information and the identification of knowledge gaps.

Here we review current knowledge on the global ecological interactions between seabirds and fishery discards in order to identify the main knowledge gaps and propose new challenges for improving our understanding of the ecological role that food availability has for populations, communities and ecosystems.

METHODS

We considered the information available in SCI journals (6 June 2017) on the Web of Science platform (WOS; Clarivate Analytics). We first selected articles with concomitant terms: [(*Seabirds AND "Fishery Waste"*) *OR* (*Seabirds AND Discard*)] in title, abstract or keywords (Search field = Topic) as a representative sample of research focusing on the effects of discards on seabirds' ecology. A second search with concomitant terms: [(*Seabirds AND Ecosystem AND Discard*) *OR* (*Seabirds AND Ecosystem AND "Fishery Waste*")] (Search field = Topic) was conducted to find studies focusing on the effects arising from seabird-discard interactions at the ecosystem level. Then, the selected studies were classified according to: 1) the species and families of seabirds interacting with fishery discards, 2) the fishing gear used and 3) the ecological parameter or effect investigated. Additionally, in order to identify the areas where ecological interactions between seabirds and fishery discards are more likely to occur (e.g. with high discard availability or high presence of scavenger seabirds) we calculated: 1) the average amount of discards (in metric tons) for each major FAO fishing area (www.fao.org) from 2004 to 2014 (raw data from www.seaaroundus.org) and 2) the main distribution areas of seabird species (identified as discard scavengers by reviewed studies)(data from www.iucn.org). We considered that the level of confluence of these species within each major FAO fishing area may vary throughout the year due to the large-scale movements of migratory species.

RESULTS

A total of 166 studies addressing up to 15 different ecological effects arising from seabird-discard interactions were selected and subsequently reviewed (Table 1, Supplementary Material Table S1). A total of 111 seabird species (Table S1) belonging to 14 taxonomic families (Table 1) were identified as scavengers of fishery discards. Demersal trawlers were by far the main fishing gear involving seabird-discard interactions (98% of studies). According to their attendance at fishing vessels, the most common discard scavengers were Laridae, Procellaridae and Diomedeidae (Table 1). The major FAO fishing areas with the highest discard availability per scavenger seabird species were the Northwest Pacific, the Eastern Central Atlantic and the Mediterranean and Black seas (Fig. 1).

Few studies quantified the effect of discards on seabirds' ecology, and most (68%) focused on the amount/type of fishing discard in seabirds' diet and on species attendance rate. In particular, we found that for the most important scavenger seabirds (Table 1) there was a lack of studies addressing potentially important ecological effects of discards in terms of food availability on: a) demographic parameters such as survival, dispersal and reproduction, b) resilience of populations against perturbations and c) individual foraging specialization (e.g. changes of predatory interactions, foraging and migratory patterns and the possible consequences of this heterogeneity for population dynamics). More specifically, the effect of discards on scavenging seabirds' survival has only been studied in the family Laridae, and only 1% of species belonging to this family have been considered (Table 1). The effect

Table 1. – Percentage of species (regarding the total number of species of each taxonomic family) for which different ecological effects arising from seabird-discard interactions were evaluated by reviewed studies (e.g. the effect of fishery discards on the diet was evaluated in 25% of species belonging to the taxonomic family Laridae). The total number of species belonging to each family was consulted in https://www.itis.gov. The most common seabird families attending fishing vessels are shown in the upper part and less common ones in the lower part.

Family	Diet	Foraging Ecology	Energy requirements	Bycatch	Competition	Reproduction	Population dynanmics	Body condition	Pollutants	Predatory interactions	Migration patterns	Parasitism	Survival	Ecosystem level	Resilience	Dispersal
Laridae (102 spp.)	25	12	13	11	15	4	9	3	6	3	0	4	1	0	2	1
Procellaridae (88 spp.)	11	6	3	14	1	1	0	0	2	1	0	0	0	1	0	0
Diomedeidae (21 spp.)	19	19	5	38	5	5	0	0	0	0	0	0	0	0	0	0
Sulidae (10 spp.)	50	20	20	20	20	10	20	20	0	0	0	0	0	0	0	0
Stercorariidae (7 spp.)	29	29	14	14	14	14	0	14	14	14	14	0	0	0	0	0
Phalacrocoracidae (37 spp.)	5	0	3	3	3	0	0	0	3	0	0	0	0	0	0	0
Hydrobatidae (25 spp.)	8	4	4	12	0	0	0	0	0	0	0	0	0	0	0	0
Fregatidae (5 spp.)	40	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0
Alcidae (24 spp.)	17	0	17	0	0	0	0	0	0	8	0	0	0	0	0	0
Spheniscidae (19 spp.)	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0
Chionidae (2 spp.)	0	0	0	50	0	0	0	0	0	0	0	0	0	0	0	0
Ardeidae (68 spp.)	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Cathartidae (7 spp.)	0	0	0	0	29	0	0	0	0	0	0	0	0	0	0	0
Pelecanidae (8 spp.)	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

that fishery discards have on seabirds' breeding success has been hardly studied in the species belonging to the families Procellariidae (only 1% of species studied) and Diomedeidae (only 5% of species studied), which are two of the most important seabird families in terms of discard scavenger species (Table 1). We only found three studies in which individual differences in seabird foraging strategies were related to fishing practices (Matich et al. 2011, Wakefield et al. 2015, Votier et al. 2017). Finally, the role that fishery discards play in the resilience of populations remains unknown for 98% of seabirds identified as discards scavengers and for 99% of seabirds in general (Table 1).

DISCUSSION

Main knowledge gaps in seabird-discard interactions

The effect of discards on demographic parameters and population resilience

Fishery discards may have important ecological effects on demographic parameters and on the resilience of scavenger populations. However, these effects have never been evaluated for most of species scavenging on fishery discards. A few studies have shown that

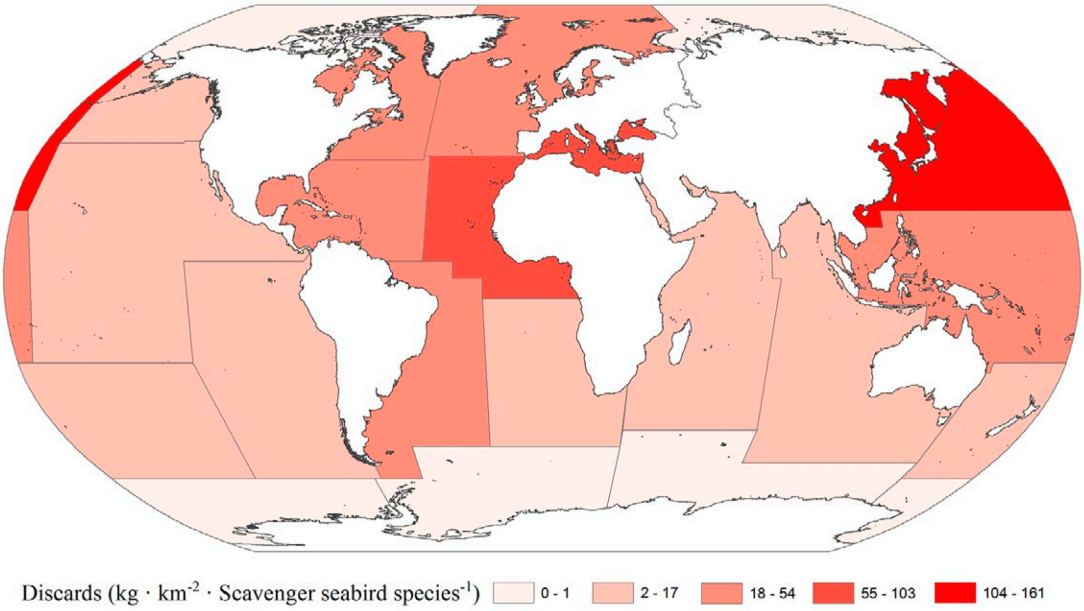

Fig. 1. – Global distribution of fishery discards availability for seabirds in different major FAO fishing areas considering amounts of discards available per unit area and number of scavenger seabird species converging in each area.

fishery discards, like other PAFS, can increase average individual survival and reproductive output in several scavenger species (Oro et al. 2013 and references therein), but they can also reduce adult survival by increasing bycatch of scavenger seabirds. Bycatch mortality might change over time according to the composition of the fishing fleet. Laneri et al. (2010) and Soriano-Redondo et al. (2016) observed a substantial increase in seabird bycatch by longliners in the absence of discards, when trawling vessels were not operating. This suggests that a ban of fishery discards, which are mainly generated by trawling vessels, may increase the attendance of seabirds at longliners, increasing their likelihood of mortality (Laneri et al. 2010, Bicknell et al. 2013).

The availability of fishery discards could have important effects on dispersal of several species among breeding colonies, with potential consequences for the structure of communities and ecosystems. However, these effects remain unstudied for most species directly and indirectly associated with fishery discards. Oro et al. (2004), for example, showed that fishery discards such as PAFS can have a direct effect on the dispersal between breeding patches and the functioning of a spatially structured population in a long-lived seabird. Dispersal could also be indirectly affected by fishery discards through an increase on predatory interactions among sympatric species competing for food and breeding habitats when discards are not available (see González-Solís 2003). In addition, discards from fisheries and other PAFS (Real et al. 2017) could also be altering migration patterns of generalist species (Gilbert et al. 2016). Furness et al. (2006), for example, suggested that fishery discards may be affecting migration patterns of the great skua (*Catharacta skua*).

Fishery discards may improve average breeding success in scavenger seabirds such as Larids (Oro et al. 1995, Oro 1996a, Oro et al. 1996, 1999), shearwaters (Louzao et al. 2006, Genovart et al. 2016) and albatrosses (Rolland et al. 2008). By contrast, Pichegru et al. (2007) and Grémillet et al. (2008) observed that during periods of natural prey shortage and high energy requirements, fishery discards did not compensate for the breeding needs in Cape gannets (*Morus capensis*). However, more studies are needed in order to obtain a global assessment of the role that fishery discards play on the reproductive output of scavenger seabirds and to predict the consequences of discard prohibitions.

Food availability is known to increase population resilience after perturbations (see e.g. Scheffers et al. 2017). Similarly, fishery discards have been shown to buffer natural food shortages, reducing the long-term variability of population fluctuations, especially in generalist species (Oro et al. 2013, Fondo et al. 2015). However, very little is known on the role that fishery discards play in the resilience of populations in most scavenger species. Nevertheless, it is plausible to expect larger fluctuations of seabird populations after discard reduction in those ecosystems that are more tightly linked to climate anomalies and extreme climate events (Hansen et al. 2012, National Academies of Sciences 2016).

Individual foraging specialization: a recent topic

Individual specialization in foraging strategies may have important ecological implications by altering the dynamics of populations and the structure of communities and ecosystems (Bolnick et al. 2003), especially in highly mobile marine top predators (Matich et al. 2011). Within scavenger seabird populations, only certain individuals are fishery-discard scavengers, but little is known about which individual features (e.g. age, sex, condition, behaviour traits) may influence this difference. It is likely that there is a large individual heterogeneity within populations in discard use, and this may influence variance in demographic parameters and population dynamics. Navarro et al. (2010) showed that inexperienced, younger adults of Audouin's gulls (*Ichthyaetus audouinii*) consumed more discards and fewer small pelagics, the natural prey of the species. Differences in resource availability (e.g. due to a ban of discards) and intraspecific competition may increase individual specialization (Matich et al. 2011). For example, when food resources (including discards) become scarce, predatory (González-Solís 2003, Regehr and Montevecchi 1997, Votier et al. 2004) and kleptoparasite (Oro 1996b) interactions among individuals may increase. Specialization in certain foraging strategies such as bird predation may have important associated advantages for individuals (e.g. by improving individual survival or breeding success). This may in turn favour the learning of these strategies by other individuals sharing the same habitat (see e.g. Annett and Pierotti 1999), with potential consequences for the structure of communities. However, despite the potential ecological consequences that individual specialization may have for populations, communities and ecosystems, little information is as yet available (but see Tuck et al. 2015).

Ecosystem level effects arising from scavenger-discard interactions

A reduction in fishery discards is expected to cause a population decrease of marine scavenger organisms (including generalist seabirds), but they can also trigger cascading effects through a change in nutrients in the water column. The general lack of studies addressing the potential impacts of fishery discards at an ecosystem level makes it difficult to predict the real ecological consequences of a ban of discards. For example, a population decrease of scavenger seabirds would alter the soil composition and the structure of animal and plant communities in coastal regions (Vidal et al. 2000, Oro et al. 2013, Ellis 2005). Hawke (2006) found a decrease in the median soil N:P molar ratio at a Westland petrel (*Procellaria westlandica*) breeding colony when the birds fed on fishery discards, and Calvino-Cancela (2011) showed that Larids, a group characterized by a large use of fishery discards, may act as important seed dispersers in many regions worldwide.

A chance for an experimental scenario for ecologists

Several large areas of the world where interactions between discards from fisheries and marine scavengers could be potentially important have received little or no attention. Furthermore, most important ecological effects that fishery discards have on marine ecosystems have never or seldom been studied. Considering this, the new policies on the ban of fishery discards, which are being progressively implemented in the European Union, Norway, Chile and New Zealand, offer a suitable experimental scenario for improving our understanding of how food availability (e.g. carrying capacity) can alter the dynamics of populations and the structure of communities and ecosystems. The example given at the Ebro Delta (e.g. Oro et al. 2013), where a long-term trawling moratorium was established in the early 1990s during the breeding season of the seabird community breeding there, is illustrative of the potential that discard banning offers to ecologists in their understanding of how food availability influences ecological processes and patterns. For instance, we expect an increase in competition at intra- and interspecific level, with larger impacts on population densities for more opportunistic species, a decrease in the variance of breeding performance within populations and a decrease in the resilience of populations against anthropogenic impacts.

ACKNOWLEDGEMENTS

Funds for this study were supplied by the Spanish Ministry of Economy and by the European Social Fund (grant ref.: CGL2013-42203-R). The study also received funding from the European Commission's Horizon 2020 Research and Innovation Programme under Grant Agreement no. 634495 for the project Science, Technology, and Society Initiative to Minimize Unwanted Catches in European Fisheries (MINOUW). MG and ASA are supported by postdoctoral contracts co-funded by the Regional Government of the Balearic Islands and the European Social Fund. Two reviewers helped to improve the manuscript.

REFERENCES

Annett C.A., Pierotti R. 1999. Long-Term Reproductive Output in Western Gulls: Consequences of Alternate Tactics in Diet Choice. Ecology 80: 288-297.
https://doi.org/10.1890/0012-9658(1999)080[0288:LTROIW]2.0.CO;2

Arcos J., Louzao M., Oro D. 2008. Fisheries ecosystem impacts and management in the Mediterranean: seabirds point of view. In: Nielsen J., Dodson J.J., Friedland K., et al. (eds) Reconciling Fisheries with Conservation. Washington DC. Am. Fish. Soc. Symp. 49: 1471-1479.

Bicknell A.W.J., Oro D., Camphuysen K. et al. 2013. Potential consequences of discard reform for seabird communities. J. Appl. Ecol. 50: 649-658.
https://doi.org/10.1111/1365-2664.12072

Bolnick D.I., Svanbäck R., Fordyce J.A., et al. 2003. The ecology of individuals: incidence and implications of individual specialization. Am. Nat. 161: 1-28.
https://doi.org/10.1086/343878

Borges L., Cocas L., Nielsen K.N. 2016. Discard ban and balanced harvest: a contradiction? ICES J. Mar. Sci. 73: 1632-1639.
https://doi.org/10.1093/icesjms/fsw065

Calvino-Cancela M. 2011. Gulls (Laridae) as frugivores and seed dispersers. Plant. Ecol. 212: 1149-1157.
https://doi.org/10.1007/s11258-011-9894-2

Cury P.M., Boyd I.L., Bonhommeau S., et al. 2011. Global Seabird Response to Forage Fish Depletion—One-Third for the Birds. Science 334: 1703-1706.
https://doi.org/10.1126/science.1212928

Ellis J.C. 2005. Marine birds on land: a review of plant biomass, species richness, and community composition in seabird colonies. Plant Ecol. 181: 227-241.
https://doi.org/10.1007/s11258-005-7147-y

Fondo E.N., Chaloupka M., Heymans J.J., et al. 2015. Banning Fisheries Discards Abruptly Has a Negative Impact on the Population Dynamics of Charismatic Marine Megafauna. PLoS ONE 10: e0144543.
https://doi.org/10.1371/journal.pone.0144543

Furness R.W., Crane J.E., Bearhop S., et al. 2006. Techniques to link individual migration patterns of seabirds with diet specialization, condition and breeding performance. Ardea 94: 631-638.

Garthe S., Camphuysen K., Furness R. 1996. Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. Mar. Ecol. Prog. Ser. 136: 1-11.
https://doi.org/10.3354/meps136001

Genovart M., Arcos J.M., Álvarez D., et al. 2016. Demography of the critically endangered Balearic shearwater: the impact of fisheries and time to extinction. J. Appl. Ecol. 53: 1158-1168.
https://doi.org/10.1111/1365-2664.12622

Gilbert N.I., Correia R.A., Silva J.P., et al. 2016. Are white storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident white storks (*Ciconia ciconia*) from a partially migratory population. Mov. Ecol. 4: 7.
https://doi.org/10.1186/s40462-016-0070-0

González-Solís J. 2003. Impact of fisheries on activity, diet and predatory interactions between yellow-legged and Audouin's gulls breeding at the Chafarinas Islands. Sci. Mar. 67: 83-88.
https://doi.org/10.3989/scimar.2003.67s283

Grémillet D., Pichegru L., Kuntz G., et al. 2008. A junk-food hypothesis for gannets feeding on fishery waste. Proc. R. Soc. B. Biol. Sci. 275: 1149-1156.
https://doi.org/10.1098/rspb.2007.1763

Hansen J., Sato M., Ruedy R. 2012. Perception of climate change. Proc. Natl. Acad. Sci. 109: E2415–E2423.
https://doi.org/10.1073/pnas.1205276109

Hawke D.J. 2006. Soil P in a forested seabird colony: inventories, parent material contributions, and N:P stoichiometry. Soil. Res. 43: 957-962.
https://doi.org/10.1071/SR05075

Laneri K., Louzao M., Martínez-Abraín A., et al. 2010. Trawling regime influences longline seabird bycatch in the Mediterranean: new insights from a small-scale fishery. Mar. Ecol. Prog. Ser. 420: 241-252.
https://doi.org/10.3354/meps08847

Louzao M., Igual J.M., McMinn M., et al. 2006. Small pelagic fish, trawling discards and breeding performance of the critically endangered Balearic shearwater: improving conservation diagnosis. Mar. Ecol. Prog. Ser. 318: 247-254.
https://doi.org/10.3354/meps318247

Matich P., Heithaus M.R., Layman C.A. 2011. Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. J. Anim. Ecol. 80: 294-305.
https://doi.org/10.1111/j.1365-2656.2010.01753.x

National Academies of Sciences, Engineering, and Medicine. 2016. Attribution of Extreme Weather Events in the Context of Climate Change. The National Academies Press, Washington, DC. 186 pp.
https://www.nap.edu/catalog/21852/attribution-of-extreme-weather-events-in-the-context-of-climate-change

Navarro J., Oro D., Bertolero A., et al. 2010. Age and sexual differences in the exploitation of two anthropogenic food resources for an opportunistic seabird. Mar. Biol. 157: 2453-2459.
https://doi.org/10.1007/s00227-010-1509-2

Oro D. 1996a. Effects of trawler discard availability on egg laying and breeding success in the lesser black-backed gull *Larus fuscus* in the western Mediterranean. Mar. Ecol. Prog. Ser. 132: 43-46.
https://doi.org/10.3354/meps132043

Oro D. 1996b. Interspecific kleptoparasitism in Audouin's Gull *Larus audouinii* at the Ebro Delta, northeast Spain: a behavioural response to low food availability. Ibis 138: 218-221. https://doi.org/10.1111/j.1474-919X.1996.tb04331.x

Oro D., Bosch M., Ruiz X. 1995. Effects of a trawling moratorium on the breeding success of the Yellow-legged Gull *Larus cachinnans*. Ibis 137: 547-549. https://doi.org/10.1111/j.1474-919X.1995.tb03265.x

Oro D., Jover L., Ruiz X. 1996. Influence of trawling activity on the breeding ecology of a threatened seabird, Audouin's gull *Larus audouinii*. Mar. Ecol. Prog. Ser. 139: 19-29. https://doi.org/10.3354/meps139019

Oro D., Pradel R., Lebreton J-D. 1999. Food availability and nest predation influence life history traits in Audouin's gull, *Larus audouinii*. Oecologia 118: 438-445. https://doi.org/10.1007/s004420050746

Oro D., Cam E., Pradel R., et al. 2004. Influence of food availability on demography and local population dynamics in a long-lived seabird. Proc. R. Soc. Lond. B. Biol. Sci. 271: 387-396. https://doi.org/10.1098/rspb.2003.2609

Oro D., Genovart M., Tavecchia G., et al. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecol. Lett. 16: 1501-1514. https://doi.org/10.1111/ele.12187

Pichegru L., Ryan P.G., van der Lingen C.D., et al. 2007. Foraging behaviour and energetics of Cape gannets *Morus capensis* feeding on live prey and fishery discards in the Benguela upwelling system. Mar. Ecol. Prog. Ser. 350: 127-136. https://doi.org/10.3354/meps07128

Real E., Oro D., Martínez-Abraín A., et al. 2017. Predictable anthropogenic food subsidies, density-dependence and socioeconomic factors influence breeding investment in a generalist seabird. J. Avian Biol. 48: 1462-1470. https://doi.org/10.1111/jav.01454

Regehr H.M., Montevecchi W.A. 1997. Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: indirect effects of fisheries activities and implications for indicator species. Mar. Ecol. Prog. Ser. 155: 249-260. https://doi.org/10.3354/meps155249

Rolland V., Barbraud C., Weimerskirch H. 2008. Combined Effects of Fisheries and Climate on a Migratory Long-Lived Marine Predator. J. Appl. Ecol. 45: 4-13. https://doi.org/10.1111/j.1365-2664.2007.01360.x

Scheffers B.R., Shoo L., Phillips B., et al. 2017. Vertical (arboreality) and horizontal (dispersal) movement increase the resilience of vertebrates to climatic instability. Glob. Ecol. Biogeogr. 26: 787-798. https://doi.org/10.1111/geb.12585

Soriano-Redondo A., Cortés V., Reyes-González J.M., et al. 2016. Relative abundance and distribution of fisheries influence risk of seabird bycatch. Sci. Rep. 6: 37373. https://doi.org/10.1038/srep37373

Tasker M.L., Camphuysen C.J., Cooper J., et al. 2000. The impacts of fishing on marine birds. ICES J. Mar. Sci. 57: 531-547. https://doi.org/10.1006/jmsc.2000.0714

Tuck G.N., Thomson R.B., Barbraud C., et al. 2015. An integrated assessment model of seabird population dynamics: can individual heterogeneity in susceptibility to fishing explain abundance trends in Crozet wandering albatross? J. Appl. Ecol. 52: 950-959. https://doi.org/10.1111/1365-2664.12462

Vidal E., Médail F., Tatoni T., et al. 2000. Seabirds drive plant species turnover on small Mediterranean islands at the expense of native taxa. Oecologia 122: 427-434. https://doi.org/10.1007/s004420050049

Votier S.C., Furness R.W., Bearhop S., et al. 2004. Changes in fisheries discard rates and seabird communities. Nature 427: 727-730. https://doi.org/10.1038/nature02315

Votier S.C., Fayet A.L., Bearhop S., et al. 2017. Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. Proc. R. Soc. B. Biol. Sci. 284: 20171068. https://doi.org/10.1098/rspb.2017.1068

Wagner E.L., Boersma P.D. 2011. Effects of Fisheries on Seabird Community Ecology. Rev. Fish. Sci. 19: 157–167. https://doi.org/10.1080/10641262.2011.562568

Wakefield E.D., Cleasby I.R., Bearhop S., et al. 2015. Long-term individual foraging site fidelity—why some gannets don't change their spots. Ecology 96: 3058-3074. https://doi.org/10.1890/14-1300.1

Zeller D., Cashion T., Palomares M., et al. 2017. Global marine fisheries discards: A synthesis of reconstructed data. Fish Fish. 19: 30-39. https://doi.org/10.1111/faf.12233

SUPPLEMENTARY MATERIAL

The following supplementary material is available through the online version of this article and at the following link:
http://scimar.icm.csic.es/scimar/supplm/sm04746esm.pdf

Table S1. – Seabird species identified as scavengers of fishery discards according to reviewed studies and number of studies considering each ecological effect derived from seabird-discard interactions.

Discards regulation vs Mediterranean fisheries sustainability
M. Demestre and F. Maynou (eds)

Scientia Marina 82S1
December 2018, S1-S3, Barcelona (Spain)
ISSN-L: 0214-8358

Discard-ban policies can help improve our understanding of the ecological role of food availability to seabirds

Enric Real, Giacomo Tavecchia, Meritxell Genovart, Ana Sanz-Aguilar,
Ana Payo-Payo, Daniel Oro

Supplementary material

Table S1. – Seabird species identified as scavengers of fishery discards according to reviewed studies and number of studies considering each ecological effect derived from seabird-discard interactions.

Species	Diet	Foraging Ecology	Energy req.	Bycatch	Competition	Reproduction	Population dynamics	Body condition	Pollutants	Predatory interactions	Migration patterns	Parasitism	Survival	Ecosystem level	Resilience	Dispersal
Alca torda	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Alle alle	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anous minutus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Anous stoldius	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ardea alba	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ardenna gravis	1	5	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Ardenna grisea	2	4	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Ardenna tenuirostris	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calonectris borealis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calonectris diomedea	3	11	2	2	0	0	0	0	0	0	0	0	0	0	0	0
Catharacta antarctica	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Catharacta skua	12	7	3	0	2	1	0	1	1	1	0	0	0	0	0	0
Cathartes aura	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Chionis alba	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Chlidonias hybridus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Chlidonias niger	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Chroicocephalus cirrocephalus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chroicocephalus maculipennis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chroicocephalus novaehollandiae	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chroicocephalus ridibundus	4	8	3	0	2	0	0	0	0	0	0	1	0	0	0	0
Coragyps atratus	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Daption capense	1	4	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Diomedea amsterdamensis	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Diomedea dabbenena	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diomedea epomophora	0	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Diomedea exulans	2	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Diomedea sanfordi	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Egretta caerulea	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Egretta thula	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Fratercula arctica	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0
Fregata ariel	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fregata magnificens	0	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Fregata minor	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fregetta tropica	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fulmarus glacialis	10	6	6	1	4	0	0	0	0	1	0	0	0	0	0	0
Fulmarus glacialoides	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Gelochelidon nilotica	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Halobaena caerulea	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Hydrobates pelagicus	2	6	2	1	0	0	0	0	0	0	0	0	0	0	0	0
Hydroprogne caspia	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ichthyaetus audouinii	8	11	2	1	3	2	1	1	2	1	0	1	2	0	1	1
Ichthyaetus melanocephalus	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Larus argentatus	11	7	4	0	4	0	3	1	0	0	0	1	0	0	0	0
Larus atlanticus	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus canus	3	5	2	0	1	0	0	0	0	0	0	0	0	0	0	0
Larus dominicanus	4	10	0	7	2	0	0	0	0	0	0	0	0	0	0	0
Larus fuscus	11	13	3	1	3	1	0	0	0	0	0	0	0	0	0	0
Larus genei	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Larus hyperboreus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus marinus	4	6	2	0	3	0	2	1	0	0	0	0	0	0	0	0
Larus michahellis	6	8	2	1	3	1	0	0	1	1	0	1	0	0	0	0
Larus minutus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus pacificus	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus sabini	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leucocarbo atriceps	0	2	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Leucophaeus atricilla	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Macronectes giganteus	1	5	0	6	0	0	0	0	0	0	0	0	0	0	0	0
Macronectes halli	0	2	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Morus bassanus	10	12	2	1	3	0	0	1	0	0	1	0	0	0	0	0
Morus capensis	5	5	3	1	0	3	0	1	0	0	0	0	0	0	0	0
Morus serrator	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Oceanites oceanicus	1	3	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Oceanodroma leucorhoa	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onychoprion anaethetus	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Pachyptila belcheri	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pagodroma nivea	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pelecanus occidentalis	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phalacrocorax aristotelis	2	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0

Table S1 (Cont.). – Seabird species identified as scavengers of fishery discards according to reviewed studies and number of studies considering each ecological effect derived from seabird-discard interactions.

Species	Diet	ForagingEcology	Energyreq.	Bycatch	Competition	Reproduction	Populationdynamics	Bodycondition	Pollutants	Predatoryinteractions	Migrationpatterns	Parasitism	Survival	Ecosystemlevel	Resilience	Dispersal
Phalacrocorax brasilianus	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Phalacrocorax carbo	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phalacrocorax olivaceus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phoebetria fusca	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Phoebetria palpebrata	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Procellaria aequinoctialis	0	7	0	6	0	0	0	0	1	0	0	0	0	0	0	0
Procellaria conspicillata	1	3	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Procellaria westlandica	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Pterodroma macroptera	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pterodroma mollis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Puffinus assimilis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Puffinus mauretanicus	4	8	1	1	0	2	0	0	0	0	0	0	0	0	0	0
Puffinus puffinus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Puffinus yelkouan	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pygoscelis antarcticus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pygoscelis papua	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rissa tridactyla	5	7	3	1	1	1	0	0	0	2	0	0	0	0	0	0
Spheniscus magellanicus	0	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Stercorarius parasiticus	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stercorarius pomarinus	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sterna dougallii	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sterna hirundinacea	0	6	0	5	2	0	0	0	0	0	0	0	0	0	0	0
Sterna hirundo	3	9	3	1	0	0	0	0	2	0	0	0	0	0	0	0
Sterna paradisaea	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sterna sumatrana	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Sterna vittata	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sternula alfibrons	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Sula dactylatra	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sula leucogaster	1	3	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Sula sula	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalassarche bulleri	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalassarche cauta	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Thalassarche chlororhynchos	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Thalassarche chrysostoma	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Thalassarche melanophrys	6	14	1	9	1	1	0	0	0	0	0	0	0	0	0	0
Thalassarche steadi	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalasseus acuflavidus	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Thalasseus bengalensis	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Thalasseus bergii	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Thalasseus maximus	2	4	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Thalasseus sandvicensis	4	10	2	2	2	0	0	0	1	0	0	0	0	0	0	0
Uria aalge	4	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0
Uria lombia	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix Chapter 2

Journal of Avian Biology 48: 1462–1470, 2017
doi: 10.1111/jav.01454

Subject Editor: Samantha Patrick. Editor-in-Chief: Thomas Alerstam. Accepted 29 July 2017

Predictable anthropogenic food subsidies, density-dependence and socio-economic factors influence breeding investment in a generalist seabird

Enric Real, Daniel Oro, Alejandro Martínez-Abraín, José Manuel Igual, Albert Bertolero, Marc Bosch and Giacomo Tavecchia

E. Real (https://orcid.org/0000-0002-6190-6303) (ereal@imedea.uib-csic.es), D. Oro, J. M. Igual and G. Tavecchia, Population Ecology Group, IMEDEA (CSIC-UIB), Esporles, Spain. – A. Martínez-Abraín, Biology Dept, Facultad de Ciencias, Univ. da Coruna, Campus da Zapateira s/n, A Coruña, Spain. – A. Bertolero, Associació Ornitològica Picampall de les Terres de l'Ebre, Amposta, Spain. – M. Bosch, Dept de Biologia Evolutiva, Ecologia i Ciències Ambientals, Univ. de Barcelona, Barcelona, Spain.

Recent European policies on the ban of fishing discards and the closure of open-air landfills are expected to reduce predictable and abundant food resources for generalist seabirds. In order to forecast the consequences of this reduction on seabird breeding investment it is important to understand whether diverse anthropogenic foraging resources act synergistically or not and whether their influence is mediated by density-dependent mechanisms. To assess these effects at large spatio-temporal scale, we measured mean egg volume as a proxy of breeding investment in ca 5000 three-egg clutches of the yellow-legged gull *Larus michahellis* from 20 colonies of the Western Mediterranean, located both along European and African coasts. In European gull colonies, egg volume increased with the availability of fishing discards and landfills in the vicinity of the colony. However, the landfill effect was weaker than the effect of fishing discards, probably due to the lower quality of waste as food for gulls. In contrast, none of the anthropogenic food subsidies influenced egg volume in African colonies, likely due to socio-economic differences (i.e. a much lower availability and predictability of both discards and waste food. Finally, results showed that the positive association between fishing discards and open-air landfills on egg volume was mediated by negative density-dependent mechanisms probably related to an increase in competition for food.

Predictable anthropogenic food subsidies (PAFS, Oro et al. 2013) play an important role in the diet of generalist species with cascading effects on individual fitness, population growth rate, the structure of ecological communities and ultimately on the functioning of whole ecosystems (Oro et al. 1995, 1996, González-Solís et al. 1997a, González-Solís 2003, Votier et al. 2004, Hobson et al. 2015). Fishing discards and open-air landfills are two of the most important PAFS exploited by several generalist seabirds. Recent European environmental policies promoting the closure of open air landfills (European Commission 1999) and the reduction and later ban of fishing discards (European Commission 2008), are expected to have an impact on scavenging seabird ecology and demography (Bicknell et al. 2013). The yellow-legged gull *Larus michahellis* (hereafter YLG), is a generalist species widely distributed throughout the Mediterranean region that makes large use of fishing discards (Oro et al. 1995, Martínez-Abraín et al. 2002, González-Solís 2003, Cama et al. 2012) and open-air landfills (Duhem et al. 2003, Ramos et al. 2006, 2011, Jordi et al. 2014). These predictable and abundant food resources are thought to be responsible for the proliferation of YLG populations. Large populations of YLGs have been often associated with negative effects on other syntopic bird species via predation, kleptoparasitism and competition for nesting places (Vidal et al. 1998, Oro and Martínez-Abraín 2007, Paracuellos and Nevado 2010). In addition, gull-human conflicts associated to their bold behavior and their role as a potential vector for human pathogens, such as *Escherichia coli*, might arise due to the usual vicinity of breeding sites to human settlements (Vergara et al 2017). These issues have raised concerns to the point that several countries have undergone management actions to reduce population size (Bosch et al. 2000, Steigerwald et al. 2015).

The efficient management of large gulls and other generalist species necessitates an assessment of the potential effects of PAFS reduction on gull population dynamics. However, the exact role of PAFS is difficult to measure in species with a diverse and generalist diet, and little is known about whether these resources act synergistically or if they represent independent food resources. Mirroring what is known about the effect of natural food resources on population dynamics (Christians 2002), PAFS availability should be reflected in the variation of breeding investment and performance in generalist birds, e.g. clutch size and/or mean egg volume (Oro 1996, Oro et al. 1996). Additionally, egg volume is known to be a good predictor of chick size at hatching and later survival (Parsons 1970, Bolton 1991, Blomqvist et al. 1997, Risch and Rohwer 2000). However, measuring the effect of PAFS on egg volume is not straightforward. Changes in food availability generally explain a small part of egg size variability in birds that is highly influenced by maternal effects (genetics) (Christians 2002). Also, other factors such as density-dependence (Oro et al. 2006), food quality (Batchelor and Ross 1984, Piatt and Anderson 1996, Grémillet et al. 2008), individual investment and age (Cunningham and Russell 2000) or the presence of alternative food resources, among others, can make the association between PAFS and egg size difficult to ascertain. Most avian species (except those laying a single egg) can regulate breeding investment by adjusting not only egg volume but also clutch size. Finally, in many cases PAFS availability cannot be easily manipulated experimentally, so their potential effects on breeding investment are masked by optimal decisions of individuals. Therefore, it is necessary to obtain a large enough data set on PAFS, both temporally and spatially, to detect differences.

Here, we have gathered data on mean egg volume in three-egg clutches (hereafter ‘egg volume’) of YLG breeding along the whole western Mediterranean, as well as population size data of colonies with long monitoring periods (Fig. 1). Our aim was to determine the relative influence of trawling discards and open-air landfills on the spatio-temporal variability of egg volume in the YLG, taking into account the possible existence of ecological synergies between these effects. A second goal was to assess the potential role played by density-dependent mechanisms. We expected the egg volume to increase along with PAFS availability, especially with fishing discards due to their intrinsic high quality compared to landfill waste (Gilbert et al. 2016). We also expected this association to change with population density, due to competition among individuals.

Material and methods

Field data and study area

A total of 4964 three-egg clutches (the modal clutch size for YLG) were measured between 1992 and 2015 from 20 different colonies distributed from southern France to Morocco (Fig. 1). Data from French gull colonies were obtained from Duhem (2004). We only considered years with at least 15 clutches of 3 eggs measured. Eggs were measured with digital calipers to ± 0.01 mm and egg volume (V) was calculated in cm^3 according to the equation $V = 0.476 \times L \times W^2$ (Harris 1964), where L = maximum egg length and W = maximum egg width. For our statistical analyses (see below) we used the mean egg volume in a clutch. In some of our study colonies we monitored a random sample of the nests in order

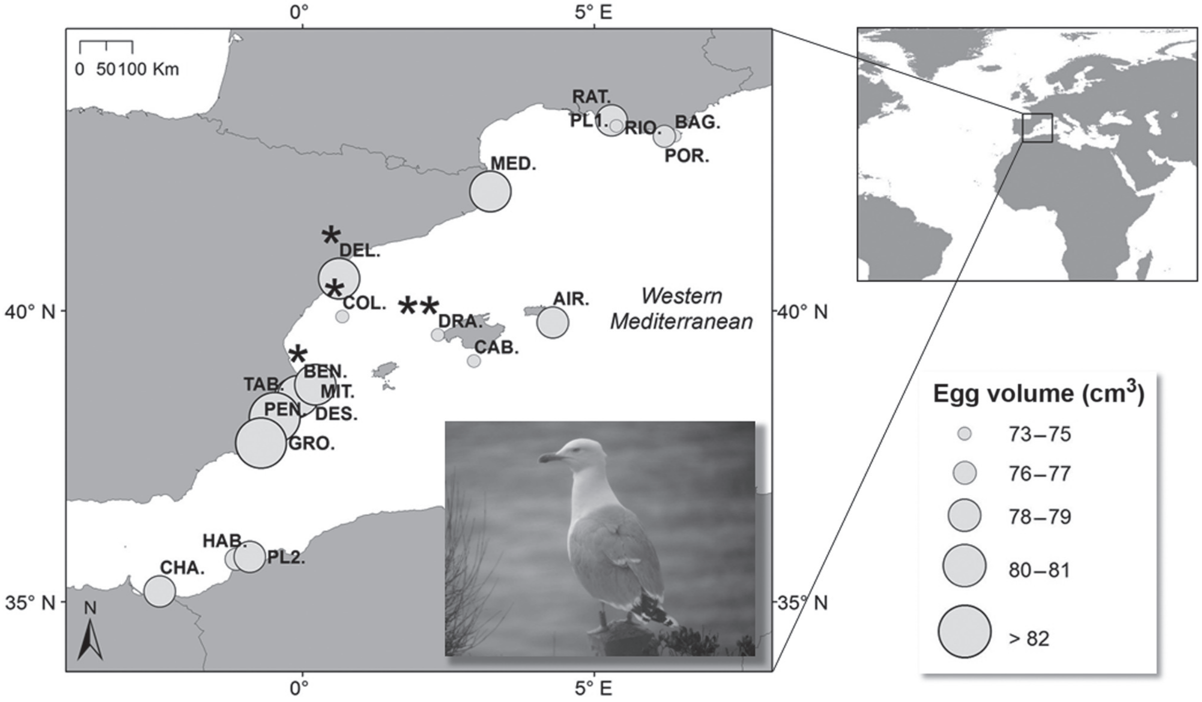

Figure 1. Study area with the distribution of the twenty yellow-legged gull colonies throughout the western Mediterranean where eggs were measured between 1992 and 2015. AIR: Aire, BAG: Bagaud, BEN: Benidorm, CAB: Cabrera, CHA: Chafarinas, COL: Columbretes, DEL: Delta, DES: Descubridor, DRA: Dragonera, GRO: Grossa, HAB: Habibas, MED: Medes, MIT: Mitjana, PEN: Penyal d’Ifach, PL1: Plane, PL2: Plana, POR: Porquerolles, RAT: Ratoneau-Pomegues, RIO: Riou, TAB: Tabarca. Circles represent the global mean egg volume per clutch for each gull colony. Colonies considered in the density-dependence analysis have been represented with an asterisk. Among these, those around which there were also subject to ‘no landfill’ regime (due to the closure of landfill) have been represented with double asterisk.

to establish the peak of complete clutches. Considering that YLG is a long-lived seabird, which tends to breed in the same colony year after year, we assumed that the mean quality of individuals remained constant in the colonies during the study period.

Trawling discards

In the western Mediterranean, the bottom trawling fleet is the fishery generating the highest amount of discards, compared to the other fisheries operating in the area (Carbonell et al. 1998, Tsagarakis et al. 2014). The distances that bottom trawlers are able to cover during the trawl phase as well as the size of the trawls are associated with trawler horsepower (Eigaard et al. 2011). Therefore, more powerful trawlers are able to cover greater areas with the trawl. Considering that discards constitute an important part of the total catch (Carbonell et al. 1998, Tsagarakis et al. 2014), we have assumed trawl horsepower to be positively related to the amount of discards generated. We used the main horsepower declared by European bottom trawlers on March 1st of each year (coinciding with the pre-laying period of the YLG) as a proxy of trawling discard availability. For African colonies only yearly estimates were available. Considering a foraging range around colonies of ca 50 km for the study species during the breeding season (Oro et al. 1995, Arizaga et al. 2014), we took the total main horsepower in the ports within a 100 km diameter area around each breeding site. Some of these foraging areas overlap so it is likely that individuals from close colonies are sharing the same resources. However, since several other species from the same guild can be foraging on the same resources, for practical reasons we decided not to take into account any kind of overlap, although we admit that this represents a simplification of a more complex situation. Data on main horsepower of three different types of bottom trawlers (bottom otter trawlers, bottom pair trawlers and beam trawlers) were obtained from the European commission fleet register (European Commission 2016): <http://ec.europa.eu/fisheries/fleet/index.cfm>. For African fleets, we took the number of bottom trawlers operating per year and the mean horsepower per vessel (356HP). Thus, the total main horsepower was estimated by multiplying the annual number of bottom trawlers by the average horsepower per boat. Data from Moroccan and Algerian trawler fleets were obtained from CopeMed Group (FAO-CopeMed 2015). In the case of the Columbretes islands, a small archipelago of volcanic origin located some 50 km offshore the eastern Spanish coasts, we used a100 km diameter area from the closest mainland headland to the islands. This was done because bottom trawlers normally operate in the area located between mainland and the archipelago (Oro et al. 2004).

Landfills

We counted the number of active European landfills located within a 100 km diameter area around each gull colony during each year. Based on the same reasoning regarding fisheries discards (see above), overlap between foraging areas was not considered. Only open-air landfills receiving urban waste during the study period were considered. European landfills were found thanks to the following agencies: European pollutant release and transfer register (European environment agency 2015): <http://prtr.ec.europa.eu/>, registro estatal de emisiones y fuentes contaminantes (ministerio de agricultura, alimentación y medio ambiente 2015): <www.prtr-es.es/> and registre français des émissions polluantes (ministère de l'environnement, de l'énergie et de la mer 2015): <www.pollutionsindustrielles.ecologie.gouv.fr/IREP/>. Most information on years of activity for each landfill were obtained via these agencies, whilst some other information on active years, as well as location of African landfills, were confirmed through satellite imagery and aerial photography using Google Earth: <www.google.es/intl/es/earth/>. Infrastructures of African open-air landfills were identified by systematically inspecting images from areas around the main colonies. Thanks to the characteristic appearance presented by the garbage inside landfills (grey-violet color), we also were able to identify a second type of more rudimentary landfills with virtually no infrastructure.

Density-dependence

YLG is one of the largest species in the guild of marine scavengers in the western Mediterranean and most competition that involves this species is intra-specific. Hence, in order to assess intra-specific food competition (i.e. a possible effect of per-capita food resources on mean egg volume), we used population density data from four European colonies for which long-term monitoring data were available: Ebro Delta, Benidorm Islet, Columbretes Islands and Dragonera Island, with 19, 10, 9 and 7 years of population monitoring respectively (Fig. 1).

Data analysis

Covariates were scaled by dividing the values by 1×10^6 and standardized in order to equalize their means and standard deviations. We used egg volume variability as a dependent variable in linear mixed-effects models (library lme4 in software R, R Core Team). Continent (two levels: Africa vs Europe), trawling discards, landfills and their statistical interactions were taken as fixed effects. Year and gull colony were modelled as random effects. The random component is meant to correct for pseudo-replication as well as for random spatial differences due to colony-specific features. Theoretical information theory based on AIC (Akaike information criterion; Burnham and Anderson 2002) was used to select the best explanatory model. Models having AIC differences (ΔAIC) ≤ 2 were considered to be equivalents (Burnham and Anderson 2004). We calculated two coefficients of determination for the linear mixed-effects models (library MuMIn, R-project): the marginal coefficient, that represents the variance explained by the fixed part of the model, and the conditional coefficient that represents the variance explained by both, fixed and random factors (Nakagawa and Schielzeth 2013, Johnson 2014). The proportion of total spatio-temporal variance in egg volume explained by each covariate (i.e. trawling discards and open-air landfills) was calculated as [deviance (model constant) – deviance (model covariate)]/[deviance (model constant) – deviance (model with colony and time effects)]. The resulting statistics can be used as an equivalent of the coefficient of determination, r^2 (hereafter r^2, see Harris et al. 2005). Finally, we used model AIC-weight (*w*) to calculate the evidence ratio (w_i/w_j), i.e. the relative weight of model 'i' compared to model 'j', which allows for also evaluating the relative importance of each explanatory covariate or factor (Burnham and Anderson 2002).

Data deposition

Data available from: <http://cedai.imedea.uib-csic.es/geonetwork/srv/es/main.home>.

Results

Effects on egg volume

Egg volume varied among colonies with no relationship to latitude (r = –0.009; 95% CI: –0.036, 0.018; Fig. 1). However, egg volume was smaller in African colonies than in European ones ($F_{1/4962} = 23.75$, $p < 0.001$). The model with the lowest AIC (model 1; Table 1) included the interaction of continent (Europe vs Africa) with the additive effect of horsepower and number of landfills (Fig. 2; see Table 1 for estimates). According to this model, in European colonies both horsepower and landfill number had a positive effect on egg volume. The variability in egg volume explained by fixed and random effects (i.e. year and colony) of this model was $r^2 = 0.05$ and $r^2 = 0.14$, respectively. models 2 and 3 (Table 1) were equivalent to model 1, and all three models included the interaction term between continent and horsepower. Moreover, the additive effect of landfills was retained in two of these models. Evidence ratios indicated that, models considering only the effects of horsepower and landfills, as well as the interaction between these two variables, had little support when compared to a null model (i.e. an only-intercept model) (horsepower/null model, $w_7/w_{11} = 10.59$; landfill/null model, $w_{12}/w_{11} = 0.69$; (horsepower × landfill)/null model, $w_{10}/w_{11} = 1.43$). However, when the interaction continent × horsepower was considered, evidence ratios increased substantially ((continent × horsepower)/null model, $w_2/w_{11} = 3071.74$). When continent interacted with landfill, the evidence ratio also improved ((continent × landfill)/null model, $w_6/w_{11} = 12.68$), although to a much lesser extent than when considering horsepower. The percentage of the total spatio-temporal variance in the egg volume explained by horsepower and landfills in European colonies was 48% and 2%, respectively. Both covariates when tested simultaneously explained 54%.

Density-dependence

When modelling egg volume in selected European colonies with long-term information on gull population size the best

Table 1. Upper part: linear mixed-effects models explaining effects of trawling discards and refuse from open-air landfills on YLG egg volume (mean egg volume per clutch), deviance, Akaike information criterion values (AIC) and Akaike weights (Wi). The best explanatory model (model 1) is the one with the lowest AIC. Middle and lower parts: estimates and standard error of the three equivalent linear mixed-effects models (1, 2 and 3) and variance of random effects. In the notation, the star (*) indicates the presence of the main effects and their statistical interaction (A + B + A:B), while the colon (:) indicates the interaction term only. All models consider year and colony as random effects. Landfill variable, which has been transformed with the natural logarithm, corresponds to the number of landfills associated to colonies. Null model only considers factors year and colony as random effects. Hp corresponds to the main horsepower of bottom trawlers associated to colonies.

Model	Notation	Deviance	AIC	ΔAIC	Wi
1	Continent*(Hp+ Landfill)	300.13	314.40	0.00	0.37211
2	Continent*Hp+ Landfill	305.75	315.53	1.13	0.21149
3	Continent*Hp	302.69	315.68	1.28	0.19621
4	Continent*Hp*Landfill	299.96	316.84	2.44	0.10986
5	Continent*(Hp+ LN.1LdfN.std)+ Hp*Landfill	299.87	316.88	2.48	0.10768
6	Continent*Landfill	315.86	326.15	11.75	0.00105
7	Hp	316.80	327.08	12.68	0.00066
8	Hp+ Landfill	315.85	328.51	14.11	0.00032
9	Continent	323.81	328.94	14.54	0.00026
10	Hp*Landfill	315.10	329.73	15.33	0.00017
11	Null model	324.21	330.89	16.49	0.00010
12	Landfill	322.04	331.24	16.84	0.00008
Estimates of fixed effects ± SE		Model 1	Model 2	Model 3	
Intercept		77.93 ± 1.46	77.81 ± 1.44	77.91 ± 1.45	
Continent Europe		0.60 ± 1.55	0.77 ± 1.53	0.73 ± 1.55	
MainPwr.		–1.73 ± 1.06	–2.20 ± 1.03	–1.81 ± 1.02	
LnLandfill		–0.09 ± 0.39	0.42 ± 0.24		
Continent Europe:MainPwr.		3.12 ± 1.12	3.62 ± 1.09	3.25 ± 1.08	
Continent Europe:LnLandfill		0.81 ± 0.49			
MainPwrN.std:LN.1LdfN.std					
ContinentFEurope:MainPwrN.std:LN.1LdfN.std					
Variance of random effects					
Intercept (Year:Colony)		1.34	1.38	1.41	
Intercept (Colony)		3.96	3.80	3.88	
Residual		31.16	31.17	31.17	

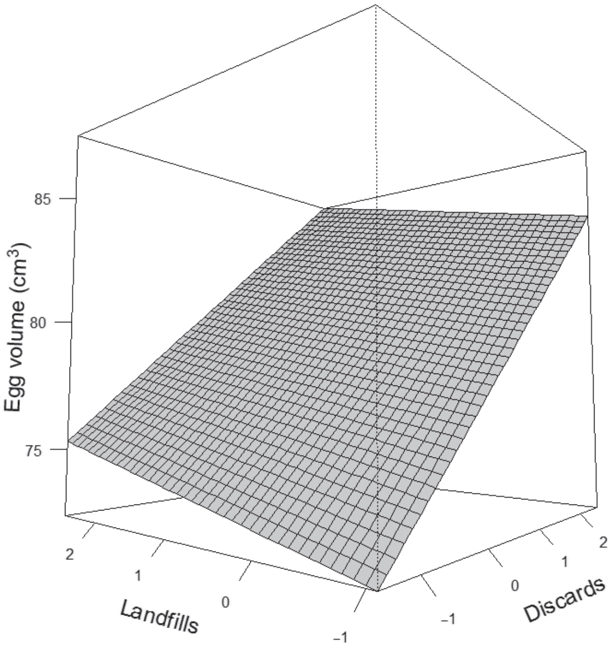

Figure 2. Resulting model explaining effects derived from trawl horsepower (as a proxy of trawling discards) and number of landfills (as a proxy of refuse from open-air landfills) on YLG egg volume (mean egg volume per clutch in cm^3) in 17 European colonies from the western Mediterranean. Covariate values were scaled dividing by 1×10^6.

model included an additive effect of horsepower and landfill together with an interaction with population density (model 1; Table 2; Fig. 3). This model indicates that the positive increase that horsepower (i.e. fishing discards) and landfills had on egg volume was affected negatively by high gull densities (Fig. 3a; see Table 2 for estimates). According to our estimates, the effect derived from the interaction between population size and the number of landfills on egg volume was positive (see Table 2 for estimates), although this trend was reversed when the number of available landfills was low (Fig. 3b). The variability explained by fixed and random effects in this model was $r^2 = 0.14$ and $r^2 = 0.18$ respectively. models 2, 3 and 4 (Table 2) were statistically equivalent to model 1 (see Table 2 for estimates). All of these models included the interaction between YLG population density and horsepower, while two of them included the additive effect of landfills. Only one of these models included an interaction between horsepower and landfills on egg volume. Evidence ratios showed that the relative weight of each effect was small for egg volume in general (population density/null model, $w_{12}/w_{13} = 3.26$; horsepower/null model, $w_7/w_{13} = 15.23$; landfill/null model, $w_{10}/w_{13} = 8.27$). Nevertheless, the interaction between population density and horsepower was relevant ((population size × horsepower)/null model, $w_2/w_{13} = 247.89$), giving considerable support to models that include this interaction, whereas the interaction between population density and landfills was much less relevant ((population density:landfill)/null model, $w_9/w_{13} = 9.57$).

Discussion

According to our results, egg volume is not affected by latitude. Climatic differences derived from the latitudinal existing gradient (8°), do not seem to affect YLG egg volume. We found that availability of both trawling discards and landfills had a positive effect on egg volume of European YLGs in the western Mediterranean, and that this effect was additive. This result shows that measuring complete egg clutches is proven to be a useful method to assess the relative importance of PAFS for seabirds.

While the fraction of fishing discards exploited by gulls is mainly composed by fish, food items taken on landfills are difficult to determine. Remains of processed foods, pieces of bread or offal from animals and fruits (e.g. olives) constitute some examples, although the high heterogeneity of this resource makes it very difficult to characterize it properly (Steigerwald et al. 2015). The effect of waste from open-air landfills on YLG egg volume was much weaker than that from trawler fishing discards, likely due to the lower nutritional quality of the former resource for egg-formation, a process that has considerable energetic costs (Robbins 1981, Oro et al. 1995, 1996, Williams 2005, Sanz-Aguilar et al. 2012). These results suggest a role for availability of discards and landfills on individual reproductive investment. Oro et al. (1995), for example, observed a 46% drop in YLG breeding success when discards were not available, and other studies reported a decrease in egg volume after landfill closure or a decrease in its availability (Pons 1992, Steigerwald et al. 2015). When both resources are available (landfill waste and trawling discards), it is expected that a decrease on the availability of trawling discards would result in an increase in the attendance of gulls to landfills, followed by a decrease in egg volume. The opposite might not be true so that a decrease of landfill availability may not necessarily result in more gulls attending trawlers. This is probably because refuse from landfills is a more accessible resource for gulls than fishing discards. Overall, the explanatory power of our best model was low (see Results), and this is in agreement with the variability in egg volume explained by food intake reported for several bird species, which usually ranges between 4–7% (Hiom et al. 1991, Wiebe and Bortolotti 1995, Ramsay and Houston 1997, Steigerwald et al. 2015), while ca 70% of this variability depends on intrinsic factors, such as individual investment or heritability (maternal effects) (Falconer 1960, Lessells and Boag 1987). Although latitude did not have an effect continent did. The additive effect of fishing discards and landfills in our European study colonies explained 54% of the total spatio-temporal variability in egg volume. In contrast, we did not find a clear influence of discards and landfills on egg volume for African colonies. In Africa, since most fish is marketable, discards are much less available (Belhabib et al. 2012) and much less predictable than in European waters (González-Solís et al. 1997a, Arcos and Oro 2002). This lack of predictability in the availability of discards from trawlers is probably the reason why in African colonies YLGs usually attend purse seiners targeting small pelagics, although the amount of food that gulls can obtain

Table 2. Upper part: linear mixed-effects models explaining density-dependent effects on YLG egg volume (mean egg volume per clutch), deviance, Akaike information criterion values (AIC) and Akaike weights (Wi). The best explanatory model (model1) is the one with the lowest AIC. Middle and lower parts: estimates of the four equivalent linear mixed-effects models (models 1, 2, 3 and 4) and variance of random effects. In the notation, the star (*) indicates the presence of the main effects and their statistical interaction (A + B + A:B), while the colon (:) indicates the interaction term only. All models consider year and colony as random effects. Population size corresponds to the population size associated to colonies. Landfill variable, which has been transformed with the natural logarithm, corresponds to the number of landfills associated to colonies. Hp corresponds to the main horsepower of bottom trawlers associated to colonies. Null model only considers factors year and colony as random effects.

Model	Notation	Deviance	AIC	ΔAIC	Wi
1	Population size*(Hp+ Landfill)	177.58	198.69	0.00	0.3028
2	Hp*Population size	183.23	199.50	0.80	0.2026
3	Population size*Hp*Landfill	176.12	199.74	1.05	0.1791
4	Population size*Hp+ Landfill	180.89	199.96	1.27	0.1603
5	Population size*(Hp+ Landfill)+ Hp*Landfill	177.62	201.13	2.44	0.0895
6	Hp+ Landfill	194.16	204.40	5.71	0.0174
7	Hp	194.91	205.08	6.38	0.0124
8	Landfill+ Population size	196.24	205.15	6.46	0.0120
9	Landfill*Population size	195.34	206.00	7.31	0.0078
10	Landfill	198.80	206.30	7.60	0.0068
11	Hp+ Population size	196.72	206.63	7.94	0.0057
12	Population size	201.75	208.16	9.47	0.0027
13	Null model	205.33	210.52	11.83	0.0008

Estimates for fixed effects ± SE	Model 1	Model 2	Model 3	Model 4
Intercept	78.69 ± 0.30	79.00 ± 0.26	78.76 ± 0.33	78.98 ± 0.26
Population size	–0.40 ± 0.29	–0.08 ± 0.27	–0.32 ± 0.30	–0.24 ± 0.29
Hp	1.22 ± 0.32	1.63 ± 0.28	1.56 ± 0.42	1.46 ± 0.30
Landfill	0.89 ± 0.38		1.07 ± 0.43	0.42 ± 0.28
Population size*Hp	–2.10 ± 0.53	–1.65 ± 0.50	–2.12 ± 0.74	–1.71 ± 0.50
Population size*Landfill	0.80 ± 0.46		1.13 ± 0.57	
Hp*Landfill			–0.60 ± 0.51	
Population size*Hp*Landfill			–1.27 ± 1.07	
Variance of random effects				
Intercept (Year:Colony)	1.50	1.73	1.54	1.66
Intercept (Colony)	0.00	0.00	0.00	0.00
Residual	29.29	29.29	29.29	29.29

from the former is small compared to European trawlers. On the contrary, it is rare to observe European YLGs attending purse seiners (González-Solís et al. 1997b, Arcos et al. 2001, González-Solís 2003). Therefore, it is clear that trawling discards play a much more relevant role in European colonies than in African ones. On the other hand, the lack of effect

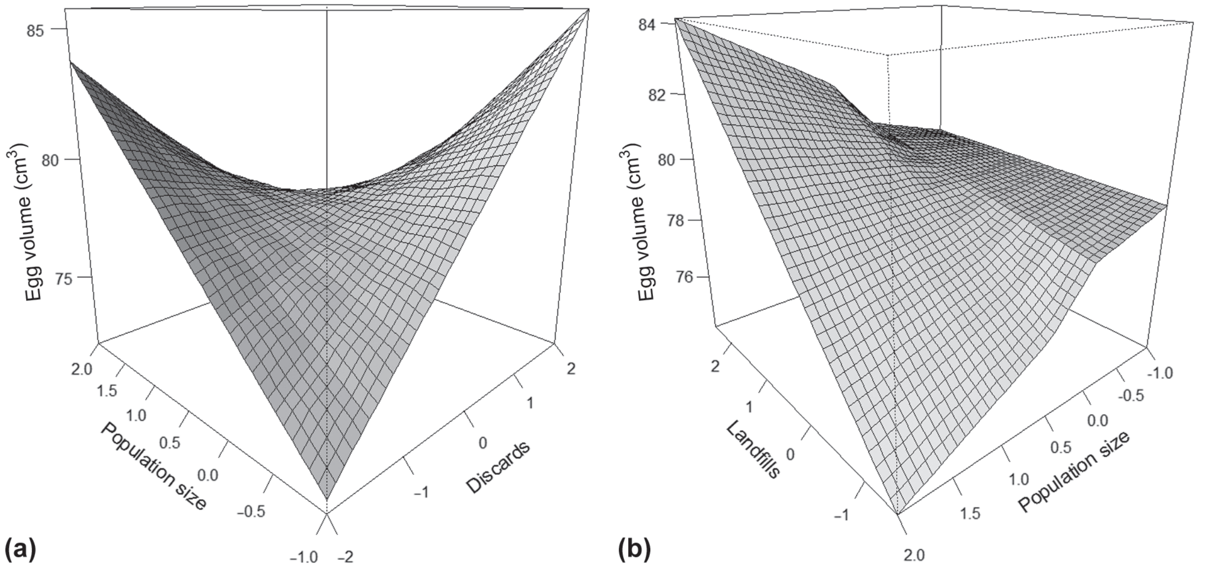

Figure 3. Regression surfaces of the influence of density-dependence on YLG egg volume (mean egg volume per clutch in cm^3), where (a) represents the interaction between population size and horsepower (as a proxy of trawling discards) effects, and (b) represents the interaction between population size and landfill refuse effects. Data corresponds to four European colonies (Ebro Delta, Benidorm, Columbretes and Dragonera) from the western Mediterranean (see Methods).

of African landfills on egg volume could be explained by the fact that waste production per capita is much higher in the European countries considered in this study than in African countries. Spanish and French waste generation rates are 1.61 and 1.07–1.48 (kg capita^{-1} day^{-1}) respectively, while in Morocco and Algeria these rates are 0.89 and 0.62 (kg capita^{-1} day^{-1}) respectively (ONEM 2001; Chantou et al. 2013). In addition, the number of people that inhabit areas near African colonies is generally less than near European colonies, and hence the total amount of waste available to gulls is also less. These socio-economic differences involving fishing and dumping practices can likely explain the smaller egg volume in African colonies. Density-dependence had a negative effect on egg volume of YLGs, presumably reducing the per capita availability of food. This effect was much more evident regarding trawling discards than regarding waste food. This result reinforces the idea that trawling discards are a high-quality foraging resource that plays an important role in YLG individual breeding performance (Oro et al. 1995) and probably on population fitness, compared to waste food from landfills in European colonies. Nevertheless, results showed a positive density-dependent association between egg volume and landfill number, suggesting that this resource does not limit breeding investment in YLG. It is possible that less competitive individuals (e.g. those in worse body condition, less skilled or sick; Genovart et al. 2010) are able to breed thanks to landfill waste (Steigerwald et al. 2015). In fact, several studies on YLG in the western Mediterranean have shown the positive effect of the availability of waste food from landfills in population dynamics (Moulaï 2007, Duhem et al. 2008, Payo-Payo et al. 2015). This effect could act via an increase in adult winter survival. Waste food also promotes that a high number of individuals remain close to breeding sites rather than dispersing or migrating (Pons 1992, Sol et al. 1995, Arizaga et al. 2014), as it has been recorded for other generalist species such as the white stork *Ciconia ciconia* (Gilbert et al. 2016). This fact could also increase survival by removing the risks associated with dispersal and migration (Oro et al. 2008).

We have shown here that availability and quality of foraging resources mediated by density-dependence influences initial breeding investment in a generalist avian species. However, in multi-egg avian layers, breeding investment and performance can be regulated not only by modifying egg volume, but also clutch size, a parameter that has not been included in our study since we exclusively worked with modal clutches. When resources are scarce gulls first reduce egg volume and if this is not enough to prevent compromising female condition, clutch size is reduced afterwards (Martin 1987, Bolton 1991).

Finally, our results suggest that a future regulation of fishing discards and the closure of open-air landfills within the European Union should trigger demographic changes not only for YLG but for the guild of generalist species exploiting these resources and competing for them (Oro et al. 2013). These changes may include an increase in dispersal, a decrease in survival, recruitment and breeding performance and a lowering of the carrying capacity of the marine environment for the whole community of generalist species, with a consequent decrease in their population numbers (Payo-Payo et al. 2015).

Acknowledgements – We thank all the people who helped with fieldwork, especially J. Piccardo, B. Sarzo, M. Genovart, N. Pocino, M. Baena and M. Expósito. M. Calleja from GIS-IMEDEA kindly helped with maps. We are also grateful to OAPN, UB, NR Islas Columbretes, PN Serra Gelada, PN del Delta de l'Ebre, PN de Dragonera, PN de les Illes Medes, Iniciative PIM, Port Autònom de Barcelona, FAO and CSIC which kindly provided data and logistical support. We also want to thank A. Velando for providing interesting ideas.

Funding – Funds were partially supplied by the Spanish Ministry of Economy and co-financiated by the European Social Fund (grant ref: CGL2013-42203-R) and by Generalitat Valenciana. This research has received funding from the European commission's Horizon 2020 research and innovation programme under grant agreement no. 634495 for the project science, technology, and society initiative to minimize unwanted catches in European fisheries (MINOUW). A. Martínez-Abraín was supported by an Isidro Parga Pondal contract from Xunta de Galicia. Funding was also provided by Univ. da Coruña and Xunta de Galicia (reference GRC2014/050).

References

Arcos, J., Oro, D. and Sol, D. 2001. Competition between the yellow-legged gull *Larus cachinnans* and Audouin's gull *Larus audouinii* associated with commercial fishing vessels: the influence of season and fishing fleet. – Mar. Biol. 139: 807–816.

Arcos, J. and Oro, D. 2002. Significance of nocturnal purse seine fisheries for seabirds: a case study off the Ebro Delta (NW Mediterranean). – Mar. Biol. 141: 277–286.

Arizaga, J., Aldalur, A., Herrero, A., Cuadrado, J. F., Diez, E. and Crespo, A. 2014. Foraging distances of a resident yellow-legged gull (*Larus michahellis)* population in relation to refuse management on a local scale. – Eur. J. Wildl. Res. 60: 171–175.

Batchelor, A. L. and Ross, G. J. B. 1984. The diet and implications of dietary change of cape gannets on bird island, Algoa Bay. – Ostrich 55: 45–63.

Belhabib, D., Pauly, D., Harper, S. and Zeller, D. 2012. Marine fisheries catches in West Africa, 1950–2010, part I. – Fisheries Centre Research Reports. Fisheries Centre, Univ. of British Columbia 20: 1–41.

Bicknell, A. W. J., Oro, D., Camphuysen, K. and Votier, S. C. 2013. Potential consequences of discard reform for seabird communities. – J. Appl. Ecol. 50: 649–658.

Blomqvist, D., Johansson, O. C., and Götmark, F. 1997. Parental quality and egg size affect chick survival in a precocial bird, the lapwing *Vanellus vanellus*. – Oecologia 110: 18–24.

Bolton, M. 1991. Determinants of chick survival in the lesser black-backed gull: relative contributions of egg size and parental quality. – J. Anim. Ecol. 60: 949–960.

Bosch, M., Oro, D., Cantos, F. J. and Zabala, M. 2000. Short-term effects of culling on the ecology and population dynamics of the yellow-legged gull. – J. Appl. Ecol., 37: 369–385.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretical approach. 2nd ed. – Springer, pp. 60–115.

Burnham, K. P. and Anderson, D. R. 2004. Multimodel inference understanding AIC and BIC in model selection. – Sociol. Methods Res. 33: 261–304.

Cama, A., Abellana, R., Christel, I., Ferrer, X. and Vieites, D. 2012. Living on predictability: modelling the density distribution of efficient foraging seabirds. – Ecography 35: 912–921.

Carbonell, A., Martín, P. and Rainieri, S. 1998. Discards of the Western Mediterranean trawl fleets. Rapp. – Comm. Int. Mer Médit. 35: 392–393.

Chantou, T., Feuillade-Cathalifaud, G., Bouzid, J. and Matejka, G. 2013. Seasonal and geographical characterizations of municipal solid waste (MSW) in four Tunisian cities/ comparison to French data. – Eur. J. Sci. Res. 94: 501–512.

Christians, J. K. 2002. Avian egg size: variation within species and inflexibility within individuals. – Biol. Rev. 77: 1–26.

Cunningham, E. J. A. and Russell, A. F. 2000. Egg investment is influenced by male attractiveness in the mallard. – Nature 404: 74–77.

Duhem, C. 2004. Goelands surabondants et ressources alimentaires anthropiques: cas des colonies insulaires de Goélands leucophées du littoral provençal. – PhD thesis, Univ. de droit, d'economie et des sciences – Aix-Marseille III, Français.

Duhem, C., Vidal, E., Legrand, G. and Tatoni, T. 2003. Opportunistic feeding responses of the yellow-legged gull *Larus michahellis* to accessibility of refuse dumps. – Bird Study 50: 61–67.

Duhem, C., Roche, P., Vidal, E. and Tatoni, T. 2008. Effects of anthropogenic food resources on yellow-legged gull colony size on Mediterranean islands. – Popul. Ecol. 50: 91–100.

Eigaard, O. R., Rihan, D., Graham, N., Sala, A. and Zachariassen, K. 2011. Improving fishing effort descriptors: modelling engine power and gear-size relations of five European trawl fleets. – Fish. Res. 110: 39–46.

European Commission 1999. European council directive 1999/31/ EC of 26 April 1999 on the landfill of waste. – Official J. L182, pp. 1–19.

European Commission 2008. Directive 2008/56/EC of the European parliament and of the council. Establishing a framework for community action in the field of marine environmental policy (marine strategy framework directive). – EC, Brussels.

European Commission 2016. Data from: Fleet Register on the Net. – <http://ec.europa.eu/fisheries/fleet/index.cfm>.

European Environment Agency 2015. Data from: Release and transfer register of the European environment agency. – <http://prtr.ec.europa.eu/>.

Falconer, D. S. 1960. Introduction to quantitative genetics. – The Ronald Press Company, pp. 165–183.

FAO-CopeMed 2015. Report of the 4th meeting of CopeMed II study group on demersal stocks of interest to Algeria, Morocco and Spain in the Alboran Sea (GSAs 01, 02, 03 and 04). Malaga, Spain 3–6 November 2015. – CopeMed II technical documents No. 40 (GCP/INT/028/SPA – GCP/INT/006/ EC). Málaga, 2015. 60 pp.

Genovart, M., Negre, N., Tavecchia, G., Bistuer, A., Parpal, L. and Oro, D. 2010. The young, the weak and the sick: evidence of natural selection by predation. – PloS One 5: e9774.

Gilbert, N. I., Correia, R. A., Silva, J. P., Pacheco, C., Catry, I., Atkinson, P. W., Gill, J. A. and Franco, A. M. A. 2016. Are white storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident white storks (*Ciconia ciconia*) from a partially migratory population. – Mov. Ecol. 4:7.

González-Solís, J. 2003. Impact of fisheries on activity, diet and predatory interactions between yellow-legged and Audouin's gulls breeding at the Chafarinas Islands. – Sci. Mar. 67: 83–88.

González-Solís, J., Ruiz, X. and Jover, L. 1997a. Influence of food availability on interactions between *Larus cachinnans* and *L. audouinii*. – Can. J. Zool. 75: 719–724.

González-Solís, J., Oro, D., Jover, L., Ruiz, X. and Pedrocchi, V. 1997b. Trophic niche width and overlap of two sympatric gulls in the southwestern Mediterranean. – Oecologia 112: 75–80.

Grémillet, D., Pichegru, L., Kuntz, G., Woakes, A. G., Wilkinson, S., Crawford, R. J. M. and Ryan, P. G. 2008. A junk-food hypothesis for gannets feeding on fishery waste. – Proc. R. Soc. B 275: 1149–1156.

Harris, M. P. 1964. Aspects of the breeding biology of the gulls. – Ibis 106: 432–456.

Harris, M. P., Anker-Nielssen, T., McCleery, R. H., Erikstad, K. E., Shaw, D. N. and Brosbois, V. 2005. Effect of wintering area and climate on the survival of adult Atlantic Puffins *Fratercula arctica* in the eastern Atlantic. – Mar. Ecol. Prog. Ser. 297: 283–296.

Hiom, L., Bolton, M., Monaghan, P. and Worral, D. 1991. Experimental evidence for food limitation of egg production in gulls. – Ornis Scand. 22: 94–97.

Hobson, K. A., Blight, L. K. and Arcese, P. 2015. Human-induced long-term shifts in gull diet from marine to terrestrial sources in North America's coastal Pacific: more evidence from more isotopes (δ2H, δ34S). – Environ. Sci. Technol. 49: 10834–10840.

Johnson, P. C. 2014. Extension of Nakagawa and Schielzeth's R2GLMM to random slopes models. – Methods Ecol. Evol. 5: 944–946.

Jordi, O., Herrero, A., Aldalur, A., Cuadrado, J. F. and Arizaga, J. 2014. The impact of non-local birds on yellow-legged gulls (*Larus michahellis*) in the Bay of Biscay: a dump-based assessment. – Anim. Biodivers. Conserv. 37: 183–190.

Lessells, C. M. and Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. Auk 104: 116–121.

Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. – Annu. Rev. Ecol. Syst. 18: 453–487.

Martínez-Abraín, A., Mestre, R. and Oro, D. 2002. Demersal trawling waste as a food source for western Mediterranean seabirds during the summer. – ICES J. Mar. Sci. 59: 529–537.

Ministère de l'environnement, de l'énergie et de la mer 2015. Data from: Registre français des émissions polluantes du ministère de l'environnement, de l'énergie et de la mer. – <http://www.pollutionsindustrielles.ecologie.gouv.fr/IREP/>.

Ministerio de Agricultura, Alimentación y Medio Ambiente 2015. Data from: Registro estatal de emisiones y fuentes contaminantes del ministerio de agricultura, alimentación y medio ambiente. – <http://www.prtr-es.es/>.

Moulaï, R. 2007. Fluctuation saisonnière des oiseaux de la décharge publique de la ville de Béjaia (Algérie), cas particulier du goéland leucophée (*Larus michahellis*). – Ostrich 78: 527–531.

Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. – Methods Ecol. Evol.4: 133–142.

ONEM 2001. Environment state in Morocco. Chapter 4: waste and urban areas. – Natl Dept of Environment, Morocco.

Oro, D. 1996. Effects of trawler discard availability on egg laying and breeding success in the lesser black-backed gull *Larus fuscus* in the western Mediterranean. – Mar. Ecol. Prog. Ser. 132: 43–46.

Oro, D. and Martínez-Abraín, A. 2007. Deconstructing myths on large gulls and their impact on threatened sympatric waterbirds. – Anim. Conserv. 10: 117–126.

Oro, D., Bosch, M. and Ruiz, X. 1995. Effects of a trawling moratorium on the breeding success of the yellow-legged gull *Larus cachinnans*. – Ibis 137: 547–549.

Oro, D., Jover, L. and Ruiz, X. 1996. Influence of trawling activity on the breeding ecology of a threatened seabird, Audouin's gull *Larus audouinii*. – Mar. Ecol. Prog. Ser. 139: 19–29.

Oro, D., Cam, E., Pradel, R. and Martínez-Abraín, A. 2004. Influence of food availability on demography and local population dynamics in a long-lived seabird. – Proc. R. Soc. B 271: 387–396.

Oro, D., Martínez-Abraín, A., Paracuellos, M., Nevado, J. C. and Genovart, M. 2006. Influence of density dependence on predator-prey seabird interactions at large spatio-temporal scales. – Proc. R. Soc. B 273: 379–383.

Oro, D., Margalida, A., Carrete, M., Heredia, R. and Donázar, J. A. 2008. Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. – PloS One 3: e4084.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M. S. and Martínez-Abraín, A. 2013. Ecological and evolutionary implications of food subsidies from humans. – Ecol. Lett. 16: 1501–1514.

Paracuellos, M. and Nevado, J. C. 2010. Culling yellow-legged gulls *Larus michahellis* benefits Audouin's Gulls *Larus audouinii* at a small and remote colony. – Bird Study 57: 26–30.

Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in the herring gull (*Larus argentatus*). – Nature 228: 1221–1222.

Payo-Payo, A., Oro, D., Igual, J. M., Jover, L., Sanpera, C. and Tavecchia, G. 2015. Population control of an overabundant species achieved through consecutive anthropogenic perturbations. – Ecol. Appl. 25: 2228–2239.

Piatt, J. F. and Anderson, P. 1996. Response of common murres to the Exxon Valdez oil spill and long-term changes in the Gulf of Alaska marine ecosystem. – Proc. Exxon Valdez Oil Spill Symp.

Pons, J. M. 1992. Effects of changes in the availability of human refuse on breeding parameters in a herring gull *Larus argentatus* population in Brittany, France. – Ardea 80: 143–150.

Ramos, F. J., Ramirez, F., Sanpera, C., Jover, L. and Ruiz, X. 2006. Feeding ecology of yellow-legged gulls *Larus michahellis* in the western Mediterranean: a comparative assessment using conventional and isotopic methods. – Mar. Ecol. Prog. Ser. 377: 289–297.

Ramos, R., Ramírez, F., Carrasco, J. L. and Jover, L. 2011. Insights into the spatiotemporal component of feeding ecology: an isotopic approach for conservation management sciences. – Divers. Distrib. 17: 338–349.

Ramsay, S. L. and Houston, D. C. 1997. Nutritional constraints on egg production in the blue tit: a supplementary feeding study. – J. Anim. Ecol. 66: 649–657.

Risch, T. S. and Rohwer, F. C. 2000. Effects of parental quality and egg size on growth and survival of herring gull chicks. – Can. J. Zool. 78: 967–973.

Robbins, C. T. 1981. Estimation of the relative protein cost of reproduction in birds. – Condor 83: 177–179.

Sanz-Aguilar, A., Minguez, E., Oro, D. 2012. Is laying a large egg expensive? Female-biased cost of first reproduction in a petrel. – Auk 129: 510–516.

Sol, D., Arcos, J. M. and Senar, J. C. 1995. The influence of refuse tips on the winter distribution of yellow-legged gulls *Larus cachinnans*. – Bird Study 42: 216–221.

Steigerwald, E. C., Igual, J. M., Payo-Payo, A. and Tavecchia, G. 2015. Effects of decreased anthropogenic food availability on an opportunistic gull: evidence for a size-mediated response in breeding females. – Ibis 157: 439–448.

Tsagarakis, K., Palialexis, A. and Vassilopoulou, V. 2014. Mediterranean fishery discards: review of the existing knowledge. – ICES J. Mar. Sci. 71: 1219–1234.

Vergara, A., Pitart, C., Montalvo, T., Roca, I., Sabaté, S., Hurtado, J. C., Planell, R., Marco, F., Ramirez, B., Peracho, V., de Simón, M. and Vila, J. 2017. Prevalence of extended-spectrum-β-lactamase- and /or carbapenemase-producing *Escherichia coli* isolated from yellow-legged gulls from Barcelona, Spain. – Antimicrob. Agents Chemother. 61: 1–5.

Vidal, E., Medail, F. and Tatoni, T. 1998. Is the yellow-legged gull a superabundant bird species in the Mediterranean? Impact on fauna and flora, conservation measures and research priorities. – Biodivers. Conserv. 7: 1013.

Votier, S. C., Furness, R. W., Bearhop, S., Crane, J. E., Caldow, R. W. G., Catry, P., Ensor, K., Hamer, K. C., Hudson, A. V., Kalmbach, E., Klomp, N. I., Pfeiffer, S., Phillips, R. A., Prieto, I. and Thompson, D. R. 2004. Changes in fisheries discard rates and seabird communities. – Nature 427: 727–730.

Wiebe, K. L. and Bortolotti, G. R. 1995. Egg size and clutch size in the reproductive investment of American Kestrels. – J. Zool. 237: 285–301.

Williams, T. D. 2005. Mechanisms underlying the costs of egg production. – BioScience 55: 39–48.