Differential Waterbird Population Dynamics After Long-Term Protection: The Influence of Diet and Habitat Type

Authors: Martínez-Abraín, Alejandro, Jiménez, Juan, Gómez, Juan Antonio, and Oro, Daniel

Source: Ardeola, 63(1) : 79-101

Published By: Spanish Society of Ornithology

URL: https://doi.org/10.13157/arla.63.1.2016.rp4

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Ardeola on 16 Jul 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Ardeola 63(1), 2016, 79-101 DOI: 10.13157/arla.63.1.2016.rp4

DIFFERENTIAL WATERBIRD POPULATION DYNAMICS AFTER LONG-TERM PROTECTION: THE INFLUENCE OF DIET AND HABITAT TYPE

DIFERENTES GRUPOS TAXONÓMICOS DE AVES ACUÁTICAS RESPONDEN CON DINÁMICAS POBLACIONALES DIFERENTES A LA PROTECCIÓN A LARGO PLAZO: EL PAPEL DE LA DIETA Y EL TIPO DE HÁBITAT

Alejandro Martínez-Abraín[1, 2 *], Juan Jiménez[3],
Juan Antonio Gómez[3] and Daniel Oro[2]

Summary.—Using as a model system a long-term data set (1984-2014) of waterbird counts at nine large wetlands of Eastern Spain (Comunidad Valenciana), we explored the ecological drivers of population fluctuations, both during the wintering (34 species) and breeding (36 species) seasons. Most species showed increasing trends (80% during breeding, 62% in winter), including both initially common and rare species, suggesting a positive effect of site protection policies that were mainly applied in the 1980s. Specialised freshwater species such as diving ducks and coots did not show population recovery, most probably due to the characteristic tendency of shallow lagoons to remain eutrophic even after several decades of the implementation of sewage management and water purification. In fact re-introduction of a diet-specialist (red-knobbed coot) failed but that of a diet-generalist (purple swamphen) succeeded. Waterfowl hunting and the abandonment of rural practices also probably played a role in the lack of recovery by some species. Population trends of breeding species were more dependent on local conditions than trends of wintering populations. Body size could also have some influence on growth rates because some of the smallest species of shorebirds and Laridae (such as Kentish plovers, little terns and black-headed gulls) showed decreasing trends in one or both seasons. Finally, a few species were gained for the system as new wintering species, probably due to climate warming. Our results suggest that growth rates alone are poor descriptors of population fluctuations, especially for birds and other vagile taxa, and that it is more appropriate to interpret

---

[1] University of A Coruña, Evolutionary Biology Group (GIBE), Campus da Zapateira s/n, 15071 A Coruña, Spain.

[2] Mediterranean Institute of Advanced Studies (CSIC-UIB), Population Ecology Group, Miquel Marquès 21, 07190 Esporles, Mallorca, Spain.

[3] Wildlife Service, Generalitat Valenciana, Conselleria d'Agricultura, Medi Ambient, Canvi Climàtic i Desenvolupament Rural, Ciutat Administrativa 9 d'Octubre, Torre 1, 46018 Valencia, Spain.

* Corresponding author: a.abrain@udc.es

trends when considering natural regions spatially, and when growth rates are analysed within the time scale of the theoretical logistic curve.

Key words: ecological drivers, environmental stochasticity, logistic curve, long-term trends, protection policies, waterbird counts.

RESUMEN.—Empleando como modelo de estudio una base de datos de treinta y un años de conteos de aves acuáticas (1984-2014) en los nueve humedales principales de la Comunidad Valenciana (este de España), exploramos los determinantes ecológicos de las fluctuaciones poblacionales tanto en época reproductora (36 especies) como en la invernada (34 especies). La mayoría de las especies mostraron tendencias crecientes (80% durante la reproducción; 62% durante la invernada), incluyendo tanto especies inicialmente escasas como comunes, lo que sugiere un efecto positivo de las políticas de protección de espacios. Sin embargo, las especies dulceacuícolas especialistas, como los patos buceadores y las fochas, tuvieron las probabilidades más bajas de mostrar una tendencia positiva. Esto se debió probablemente a la tendencia característica de las lagunas someras de permanecer en un régimen eutrófico incluso muchas décadas después de que se hayan realizado grandes inversiones económicas en tratamiento de aguas residuales. De hecho, la reintroducción de una especie de dieta especializada (focha moruna) fracasó pero la reintroducción de un generalista (calamón) fue exitosa. Sugerimos que la caza de aves acuáticas y el abandono de las prácticas tradicionales jugaron también un papel en la tendencia negativa de algunas especies. Las tendencias en la abundancia de las especies reproductoras dependieron más de las condiciones locales que las de las aves invernantes. El tamaño corporal también pudo influenciar las tasas de crecimiento porque algunas de las especies más pequeñas de limícolas y láridos (como el chorlitejo patinegro, el charrancito y la gaviota reidora) mostraron tendencias decrecientes en alguna estación. Finalmente, el sistema ganó algunos taxones nuevos como invernantes probablemente debido al calentamiento climático. Nuestros resultados sugieren que las tasas de crecimiento usadas de manera aislada son malos descriptores de las fluctuaciones poblacionales, sobre todo en el caso de especies con alta movilidad, y es más adecuado interpretar las tendencias cuando se trabaja espacialmente con regiones naturales y cuando dichas tasas son analizadas dentro del marco temporal en el que se da la curva de crecimiento logístico.

Palabras clave: conteos de acuáticas, curva logística, determinantes ecológicos, estocasticidad ambiental, fluctuaciones a largo plazo, plasticidad ecológica, políticas de protección.

INTRODUCTION

The analysis of long-term population trends is a common tool to assess the conservation status of vertebrate species (see e.g. Galewski *et al*., 2011), and of waterbirds in particular (Böhning-Gaese and Bauer, 1996; Green *et al*., 2002; Rendón *et al*., 2008; González and Pérez-Aranda, 2011). Substantial efforts are devoted annually to counting waterbird numbers all over Europe, and waterbird time series are now available for longer periods than for most other vertebrate taxa. These time series allow us, among many other things, to assess whether all taxonomic groups respond similarly to general protection policies and help to adjust these policies accordingly. In Spain, the Spanish Ornithological Society (SEO/BirdLife) has coordinated the International Waterbird Census since 1967. This census today covers over 25,000 sites in more than 100 countries and involves more than 15,000 people. The data gathered has been used to identify Important Bird Areas (IBAs) and to declare Special Protection Areas for Birds (SPAs) (http://www.magrama.gob.es/es/biodiversidad/temas/espacios-protegidos/red-natura-2000/zepa_cvalenciana.aspx).

In addition, these data have been used to develop ecological studies. Specifically Pagel *et al*. (2014) recently analysed a subset of waterbird counts (1984-2011) corresponding to a political western Mediterranean region, Comunidad Valenciana, in order to study the effects of long-term site protection on changing diversity patterns of both wintering and breeding waterbirds. One of the major findings of that study was that most taxa were expanding their geographical ranges at the metacommunity level, with the exception of a few zoological groups: specifically most breeding shorebird species and most wintering duck species. These were not expanding despite all major wetlands in the region being legally protected and having been managed for conservation purposes since the mid-1980s.

Here we aimed to analyse the same dataset further, and adding three more years, in order to study whether abundance trends provide similar conclusions than diversity patterns (that responses to protection differ among bird groups), and to identify the main ecological drivers of such differences. We also intended to determine whether regional trends are dependent on trends at larger geographical scales and additionally we explore how the interpretation of population growth rates is not only influenced by spatial considerations, but also by time factors, specifically the stage of the theoretical logistic curve at which each species can be assigned. Our prior expectation is that many waterbird species should show a logistic pattern of growth after three decades of protection. Only species highly dependent on water quality are expected to have decreasing trends, because water quality is still not fully recovered from the effects of agricultural, urban and industrial pollution that took place mainly in the 60s, 70s and 80s of the XX century.

METHODS

The study system

Comunidad Valenciana is a southern European region extending over ca. 23,000 km^2 in eastern Spain. It became an autonomous region with a regional government (Generalitat Valenciana) and a regional environmental authority (Conselleria de Medi Ambient) in 1982. The main sites for breeding and wintering waterfowl (Cabanes, Albufera, Pego-Oliva, Santa-Pola, Torrevieja and El Hondo; fig. 1) were protected as natural parks during 1986-1988 or have since been protected as Special Protection Areas for birds (SPAs, 2007-2009) by the regional environmental authority.

Data set and field procedures

An official data set of bird counts for 31 consecutive years (1984-2014), coordinated by SEO/BirdLife and/or the regional authorities, was used. It consists of a collection of annual counts including 44 breeding and 67 wintering species at 18 wetlands. However, for the purposes of this study we have selected only those species that had full time series (i.e. series with no or just a few missing values), and also those corresponding to the most abundant species, so that our results have higher conservation value and may be of interest to a wider readership. Hence we have finally worked with 34 wintering species and 36 breeding species, and we have only considered the counts at the nine major wetland sites where censuses were carried out during the whole study period.

Winter counts were performed simultaneously at all wetlands each year during two weeks around the second weekend of January, in coordination with the International Waterbird Census (IWC) (for further details see http://www.wetlands.org/AfricanEurasianWaterbirdCensus/tabid/2788/Default.aspx). Wintering ducks, coots and grebes were counted through telescopes from fixed points every year. Other wintering bird groups, such as herons, gulls or shorebirds, were counted along fixed car routes with variable detection band widths depending

FIG. 1.—Location of the study wetlands in Comunidad Valenciana, Eastern Spain. Detailed information on locations and characteristics of the SPAs is available online at: http://www.docv.gva.es/datos/2009/06/09/pdf/2009_6699.pdf.
[Localización de los humedales de estudio en la Comunidad Valenciana, este de España. La información detallada sobre la localización y características de las ZEPA se puede consultar en: http://www.docv.gva.es/datos/2009/06/09/pdf/2009_6699.pdf.]

on the characteristics of each study site. Wintering marsh harriers *Circus aeruginosus* and herons were counted around sunset at communal roosts (Gómez *et al*., 2006; Bibby *et al*., 2000). Further information on winter and summer counts for the whole study region during 1984-2004 is available at http://www.cma.gva.es/webdoc/documento.ashx?id=164402.

Breeding season counts were not coordinated internationally and were mostly carried out by the staff of protected areas that regularly monitor study sites. Visits to each study area were carried out almost on a daily basis over the whole breeding season (March-August) to prevent overlooking important data as a result of the incomplete overlap in the breeding calendar of the study species. Counts were performed using specific and fixed methodologies for each species. Colonial species (i.e. herons, gulls, terns, shorebirds and the greater flamingo *Phoenicopterus roseus*) were counted by visiting breeding colonies and counting individual nests at the peak of their breeding period. Non-colonial species (i.e. ducks, coots, grebes) were detected by inspecting water masses by means of motor boats, counting nests, birds displaying breeding behaviour or adults in the company of chicks. Species of difficult detection (e.g. rallids and the little bittern *Ixobrychus minutus)* were monitored by looking for nests from boats propelled manually in shallow water areas. We assume that counts are comparable between years and sites, although the accuracy of the counts will vary between taxonomic groups. This assumption is based on the standardisation of count methods, which were carried out by roughly the same people across years and sites.

Statistical analyses

We fitted Generalized Additive Models (GAMs hereafter) to count data for each species studied during the winter and breeding seasons, to show graphically the population trends during the last 31 years. We did not fit linear models because we had no prior expectations on what the trend could be (e.g. linear, exponential, logarithmic, quadratic) for each species, and GAMs are flexible statistical tools that can be used to explore and obtain non-linear fits to any data structure (Wood, 2006). GAMs have been used in the past to aggregate large quantities of population trend data (see e.g. Collen *et al*., 2009), and are commonly used for the analysis of bird monitoring data (Atkinson *et al*., 2006; Fewster *et al*., 2000). Other alternative tools are available to obtain smoothed trends (e.g. TRIM; TrendSpotter; see e.g. Soldaat *et al*., 2007) but we opted to use the more general GAMs in the R environment (http://www.r-project.org/), assuming that alternative methods would provide the same answers.

In order to estimate annual population growth rates quantitatively we employed exponential growth state-space models (EGSS hereafter), a modelling approach that accounts both for process noise and observational error (Humbert *et al*., 2009). EGSS models are written as linear mixed models, and perform well even with half of the counts in the time series missing, as well as across a wide range of time series lengths and sources of variation. Other alternative tools for modelling trends with missing data that account for process and observational error exist, such as MARSS (Multivariate Autoregressive State-Space models) (see e.g. Paleczny *et al*., 2015).

Not all time series cover exactly the same time period because no counts were available for the first count (1984) in some cases. To prevent problems with zero values and the use of logarithms we transformed all zero counts to 1. We left the abundance value for a given year blank if any of the main sites for the species had not been counted, unless the overall count was of a similar magnitude to the preceding count, suggesting a possible transfer of individuals to other sites. The statistical significance of lambda (i.e. the annual growth rates) was assessed by testing whether the 95% confidence interval included the value of lambda = 1 or not. Our criterion for assigning a "stable" status was that lambda did not show a decrease/increase larger than 2% in relation to 1 and also that the confidence interval limits were not smaller than 0.95 or larger than 1.05.

The status of wintering species (i.e. increasing, decreasing or stable) in Spain was obtained from the most updated specific quantitative monograph (González and Pérez-Aranda, 2011). The status of breeding species in Spain was obtained from the most recent Spanish breeding bird atlas (Martí and del Moral, 2003).

Generalized linear mixed models, with the binomial family of errors together with the logit link, were used to relate the trend (lambda > 1 or lambda < 1) of wintering and breeding waterbirds to habitat type (i.e. freshwater/saline waters), diet (i.e. generalist/specialist). Diet was obtained from Cramp (1998)

TABLE 1

Geometric growth rate (lambda), and 95% confidence intervals (CI), for long-term A) wintering bird counts and B) breeding bird counts at Comunidad Valenciana (E Spain) wetlands, obtained by means of exponential growth state-space modelling (EGSS). SP = diet specialised on particular animal or plant groups; GE = generalist diet. Freshwater = preferentially wintering at freshwater sites; Saline = preferentially wintering at saline water sites. Status S = species status in Spain. Logistic = stage of the logistic curve (Initial = Initial slow phase; Exponential = exponential growth; Fitting = fitting the logistic curve; Dynamic = dynamic equilibrium).

[Tasa geométrica de crecimiento (lambda) e intervalos de confianza al 95% (CI) para A) conteos a largo plazo de aves invernantes y B) conteos de aves reproductoras en humedales de la Comunidad Valenciana (este de España), obtenidos mediante modelización "state-space" del crecimiento exponencial (EGSS). SP = dieta especializada en determinados grupos animales o vegetales; GE = dieta generalista. Freshwater = invernada preferencial en agua dulce; Saline = invernada preferencial en humedales de agua salada. S = status de la especie en España. Logistic = estado de la curva logística (Initial = fase lenta inicial; Exponential = crecimiento exponencial; Fitting = crecimiento que se ajusta a la curva logística; Dynamics = en fase de equilibrio dinámico).]

A)

Family	Species	Diet	Habitat	λ	Lower 95% CI	Upper 95% CI	Status S	Logistic
Podicipedidae	*Tachybaptus ruficollis*	SP	Freshwater	1.02	0.98	1.07	Increasing	Initial
	Podiceps cristatus	SP	Freshwater	0.97	0.89	1.06	Increasing	Dynamic
	Podiceps nigricollis	SP	Saline	0.98	0.68	1.41	Increasing	Dynamic
Phalacrocoracidae	*Phalacrocorax carbo*	GE	Freshwater	1.14	1.03	1.27	Increasing	Exponential
Ardeidae	*Bubulcus ibis*	GE	Freshwater	1.04	0.90	1.21	Increasing	Dynamic
	Egretta garzetta	GE	Freshwater	1.14	0.98	1.33	Increasing	Fitting
	Ardea cinerea	GE	Freshwater	1.04	1.03	1.05	Increasing	Fitting
Therskiornithidae	*Plegadis falcinellus*	GE	Freshwater	1.30	1.00	1.67	Increasing	Exponential
Phoenicopteridae	*Phoenicopterus roseus*	SP	Saline	1.06	0.98	1.14	Increasing	Initial
Anatidae	*Tadorna tadorna*	SP	Saline	1.14	1.12	1.17	Increasing	Exponential
	Anas penelope	SP	Freshwater	0.94	0.78	1.12	Decreasing	No pattern
	Anas crecca	SP	Freshwater	1.03	0.98	1.09	Increasing	Initial
	Anas platyrhynchos	GE	Freshwater	1.07	1.06	1.08	Increasing	Fitting
	Anas acuta	SP	Freshwater	0.98	0.90	1.06	Increasing	Decreasing
	Anas strepera	SP	Freshwater	1.02	0.92	1.12	Increasing	Dynamic
	Anas clypeata	SP	Freshwater	0.99	0.97	1.02	Increasing	No pattern
	Netta rufina	SP	Freshwater	0.97	0.92	1.02	Decreasing	Decreasing
	Aythya ferina	SP	Freshwater	0.95	0.93	0.97	Decreasing	Decreasing
	Aythya fuligula	SP	Freshwater	0.93	0.84	1.04	Decreasing	Decreasing
	Oxyura leucocephala	SP	Saline	1.17	0.85	1.61	Increasing	Dynamic

TABLE 1 (cont.)

A)

Family	Species	Diet	Habitat	λ	Lower 95% CI	Upper 95% CI	Status S	Logistic
Rallidae	*Porphyrio porphyrio*	GE	Freshwater	1.14	0.83	1.58	Unknown	Fitting
	Fulica atra	SP	Freshwater	0.93	0.83	1.04	Increasing	Dynamic
Recurvirostridae	*Himantopus himantopus*	GE	Freshwater	1.19	0.99	1.42	Increasing	Fitting
	Recurvirostra avosetta	SP	Saline	1.01	0.97	1.05	Increasing	No pattern
Charadriidae	*Charadrius alexandrinus*	SP	Saline	0.97	0.88	1.07	Increasing	Dynamic
	Pluvialis apricaria	GE	Freshwater	1.16	1.11	1.21	Unknown	Fitting
	Pluvialis squatarola	GE	Freshwater	1.02	0.94	1.11	Increasing	Dynamic
	Vanellus vanellus	GE	Freshwater	1.02	0.91	1.14	Unknown	Dynamic
Scolopacidae	*Calidris minuta*	GE	Saline	1.09	0.92	1.29	Increasing	Initial
	Calidris alpina	GE	Saline	1.03	0.94	1.13	Increasing	No pattern
	Limosa limosa	GE	Freshwater	0.99	0.96	1.03	Increasing	No pattern
Laridae	*Chroicocepalus ridibundus*	GE	Freshwater	0.99	0.94	1.04	Increasing	Dynamic
	Larus fuscus	GE	Freshwater	1.06	0.95	1.18	Increasing	Exponential
	Larus michahellis	GE	Freshwater	1.01	0.91	1.13	Increasing	Dynamic

B)

Family	Species	Diet	Habitat	λ	Lower 95% CI	Upper 95% CI	Status S	Logistic
Podicipedidae	*Tachybaptus ruficollis*	SP	Freshwater	1.04	0.98	1.11	Increasing	Fitting
	Podiceps cristatus	SP	Freshwater	1.01	0.92	1.11	Increasing	Dynamic
	Podiceps nigricollis	SP	Freshwater	1.19	0.78	1.82	Variable	Exponential
Ardeidae	*Ixobrychus minutus*	GE	Freshwater	1.00	0.95	1.06	Increasing	Dynamic
	Nycticorax nycticorax	GE	Freshwater	1.05	1.00	1.10	Increasing	Exponential
	Ardeola ralloides	GE	Freshwater	1.13	1.01	1.26	Increasing	Exponential
	Bubulcus ibis	GE	Freshwater	1.03	0.98	1.08	Decreasing	Fitting
	Egretta garzetta	GE	Freshwater	1.03	0.97	1.09	Decreasing	Fitting
	Ardea cinerea	GE	Freshwater	1.13	0.98	1.30	Increasing	Exponential
	Ardea purpurea	GE	Freshwater	1.01	1.00	1.02	Increasing	Dynamic
Therskiornithidae	*Plegadis falcinellus*	GE	Freshwater	1.23	1.04	1.45	Increasing	Exponential
Phoenicopteridae	*Phoenicopterus roseus*	SP	Saline	1.34	0.41	4.35	Increasing	No pattern

TABLE 1 (cont.)

B)

Family	Species	Diet	Habitat	λ	Lower 95% CI	Upper 95% CI	Status S	Logistic
Anatidae	*Tadorna tadorna*	SP	Saline	1.06	1.00	1.19	Increasing	Initial
	Anas strepera	SP	Freshwater	1.07	0.96	1.20	Increasing	Fitting
	Anas platyrhynchos	GE	Freshwater	1.04	0.92	1.19	Increasing	Dynamic
	Netta rufina	SP	Freshwater	0.97	0.90	1.05	Unknown	Dynamic
	Aythya ferina	SP	Freshwater	1.03	0.88	1.19	Increasing	Dynamic
	Marmaronetta angustirostris	SP	Freshwater	0.98	0.81	1.20	Decreasing	Dynamic
	Oxyura leucocephala	SP	Saline	1.17	0.90	1.51	Stable	Initial
Rallidae	*Porphyrio porphyrio*	GE	Freshwater	1.21	1.01	1.45	Decreasing	Fitting
	Fulica atra	SP	Freshwater	0.94	0.90	0.98	Unknown	Decreasing
	Fulica cristata	SP	Freshwater	1.04	0.89	1.21	Increasing	No pattern
Recurvirostridae	*Himantopus himantopus*	GE	Freshwater	1.07	0.98	1.17	Increasing	Initial
	Recurvirostra avosetta	SP	Saline	1.01	0.89	1.15	Increasing	No pattern
Glareolidae	*Glareola pratincola*	SP	Saline	1.05	1.01	1.09	Unknown	Fitting
Charadriidae	*Charadrius dubius*	SP	Freshwater	1.09	0.99	1.19	Unknown	Fitting
	Charadrius alexandrinus	SP	Saline	0.97	0.87	1.09	Stable	Dynamic
Laridae	*Chroicocephalus ridibundus*	GE	Freshwater	1.16	1.05	1.27	Increasing	Exponential
	Chroicocephalus genei	SP	Saline	1.25	0.95	1.64	Unknown	Exponential
	Larus melanocephalus	GE	Saline	1.27	1.06	1.52	Stable	Exponential
	Larus audouinii	GE	Saline	1.36	1.06	1.77	Increasing	Fitting
	Gelochelidon nilotica	GE	Saline	1.20	0.88	1.64	Increasing	Fitting
	Sterna sandvicensis	GE	Saline	1.24	0.95	1.62	Increasing	Fitting
	Sterna hirundo	GE	Saline	1.09	1.01	1.19	Stable	Fitting
	Sternula albifrons	GE	Saline	0.99	0.84	1.18	Stable	Dynamic
	Chlidonias hybrida	SP	Freshwater	1.05	0.96	1.14	Unknown	Fitting

and del Hoyo *et al*. (1992). We classified waters as "saline" if conductivity was higher than 5000 µS/cm, including both primarily saline and secondarily saline wetlands, following the terminology of Moss (1994). We considered taxonomic family, taken as a random variable, to account for possible phylogenetic effects (table 1). Probabilities of having an increasing trend as a function of diet and habitat type were obtained by means of the inverse logit function in R. Comparison of frequencies between seasons was performed by means of contingency tables together with the Chi-square statistic with Yate's correction.

Dynamic equilibrium

Most population fluctuations are non-stationary because variance changes over time, a fact that precludes a simple description of the trends. Moreover, measures of population fluctuation, such as the population growth rate, are poorly informative if taken alone because they are appropriate for discrete exponential growth curves and hence very sensitive to the initial and final population sizes (see fig. S1 in Supplementary Electronic Material, for a comparison of three time series, one that grows exponentially and two that do not, for which lambda takes the same value despite the series starting and ending with the same number of individuals). Furthermore, growth rates are expected to vary along the theoretical logistic population growth curve, from maximum values at medium population sizes (with exponential growth) to minimum or zero values at higher populations close to a more or less flat dynamic equilibrium (Krebs, 2009). Hence we assigned species abundance curves visually to one of four major classes that we arbitrarily named: a) initial slow phase of growth, b) exponential growth, c) dynamic equilibrium phase, and d) fitting the logistic curve (see fig. S2 in Supplementary Electronic Material). Species were assigned to these classes according to the shape of the GAM curves and the value of r^2 (adj) (see table S1 in Supplementary Electronic Material). Most species were clearly associated with one of those classes, whereas a few were more difficult to label because they shared features with more than one class. Hence our qualitative assessment may thus have some degree of error but we consider that this error is small and that most species were unequivocally assigned to the four major classes in a repeatable manner. When no pattern in the curve was evident, we assigned species to a “no-pattern” class. If species were decreasing (and hence it was not possible to assign any logistic curve stage to them) they were assigned to a “decreasing” class.

Water quality

Data on water quality for the largest freshwater study site (Albufera de Valencia; fig. 1) and one of the largest saline water sites (El Hondo, fig. 1) were provided by the regional environmental authorities (Generalitat Valenciana). Since information on water quality was not available for the beginning of our time series of waterbird counts we compared data on water quality from the mid part of the time series (1995-2000) with the end of it (2006-2011).

RESULTS

Population fluctuations

Most geometric growth rate (lambda) estimates in both seasons were not statistically significant (only 20% in winter and 25% during breeding), reflecting high uncertainty in the estimate of growth rates from the EGSS model fitted to our data. Hence, trends were later on modelled only in relation to their point estimates, which are highly coincident with the visual information provided by most of the GAM graphs.

During wintering 21 waterbird species (62%) showed an increasing trend, nine species (26%) a decreasing trend and only three species (ca. 1%) were stable. During breeding, 29 species (80%) increased, five species (14%) decreased and only two species (5%) were stable (table 1). Hence, most species in both seasons were increasing, a feature that can be probably attributed to protection policies applied to sites and species during recent decades. Only a few were already in equilibrium. We were unable to detect statistically significant differences between the percentage of species increasing vs. non-increasing during summer and winter ($\chi^2 = 2.17$, d.f. = 1, $p = 0.14$) so patterns of increase were fairly similar between seasons.

Grebes and ducks (mostly diving Anatidae, but also some dabbling ducks such as the Eurasian wigeon *Anas penelope* and northern pintail *A. acuta*) and coots *Fulica* spp. had the highest percentage (53%) of species with decreasing trends during winter. Grebes did not show decreasing trends during the breeding season. Herons, cormorants, shorebirds and Laridae (gulls and terns) showed increasing trends during wintering (table 1). Of all shorebird and Laridae species considered, only Kentish plovers *Charadrius alexandrinus* (both in winter and breeding), little terns *Sternula albifrons* (breeding only) and black-headed gulls *Chroicocephalus ridibundus* (winter only) showed decreasing trends.

Modelling results indicated a combined influence of diet and habitat type (ecological drivers) on species having increasing or

TABLE 2

Multiple generalized linear mixed model comparison and selection relating the trend (lambda) of a) wintering waterbirds and b) breeding waterbirds as a discrete variable (> 1 or < 1) in relation to habitat type and diet, controlling by taxonomic family as a random variable to account for phylogenetic effects. The best models are highlighted in bold. K = number of parameters; AICc = Akaike Information Criterion for small sample sizes; ΔAICc = difference in AICc value with the best model; w_i = weight of the model (see Burnham and Anderson, 2002).

[Comparación múltiple y selección de modelos lineales generalizados mixtos que relacionan la tendencia (lambda) de a) aves acuáticas invernantes y b) aves reproductoras como variable discreta (> 1, < 1) en relación con el tipo de hábitat y a la dieta, controlando por familia taxonómica como variable random para tener en cuenta efectos filogenéticos. Los mejores modelos se destacan en negrita. K = número de parámetros estimables; AICc: Criterio de Información de Akaike para bajo tamaño de muestra; ΔAICc = diferencia en valor de AICc del modelo en cuestión respecto al mejor modelo; w_i = peso de Akaike de cada modelo (véase Burnham y Anderson, 2002).]

A) Wintering waterbirds

Model	K	Deviance	AICc	ΔAICc	w_i
Diet + Habitat	**4**	**32.42**	**41.80**	**0**	**0.54**
Diet	**3**	**35.35**	**42.15**	**0.35**	**0.45**
Habitat	3	43.60	50.41	8.61	0.01

B) Breeding waterbirds

Model	K	Deviance	AICc	ΔAICc	w_i
Lambda ~ Diet	**3**	**26.79**	**33.54**	**0**	**0.61**
Lambda ~ Habitat	3	28.89	35.65	2.10	0.21
Lambda ~ Habitat + Diet	4	26.67	35.96	2.42	0.18

decreasing trends during wintering (table 2). Freshwater species performed worse in winter than saline-water species, especially if they were diet specialists (fig. 2). During breeding the probability of having an increasing trend only depended on diet specialisation regardless of habitat type (20% increase in probability of having a positive lambda when comparing generalists to specialists).

Water quality analyses suggest that freshwater sites have improved most of their key parameters indicative of hypertrophic waters in the past (table 3), assuming that data for the site that we analysed was representative for the whole regional wetland system, an assumption that seems acceptable because water purification policies have been applied across the study region as a whole. Mean total phosphorus levels in winter halved between 1995-2000 and 2006-2011; this led to a reduction of chlorophyll a, through algal decline, and hence to a decrease in dissolved oxygen. Suspended matter also decreased as algal biomass fell, although nitrates from agricultural sources increased. Despite this quality improvement, water quality parameters are still far from the original pre-pollution situation existing during the early decades of the 20th century (own data).

During wintering the regional status of our study species coincided in most cases with country-wide status (72% of species with available information). Discrepancies were always in the direction of positive trends in Spain for species that were decreasing or stable regionally (table 1), suggesting that most species were increasing regionally because their status at broader geographical scales was positive. Hence, regional decreases would most likely be due to causes acting locally and regionally. During breeding the status of most species at regional level also coincided with country-wide status (65% of the species with available information; table 1). Interestingly, during

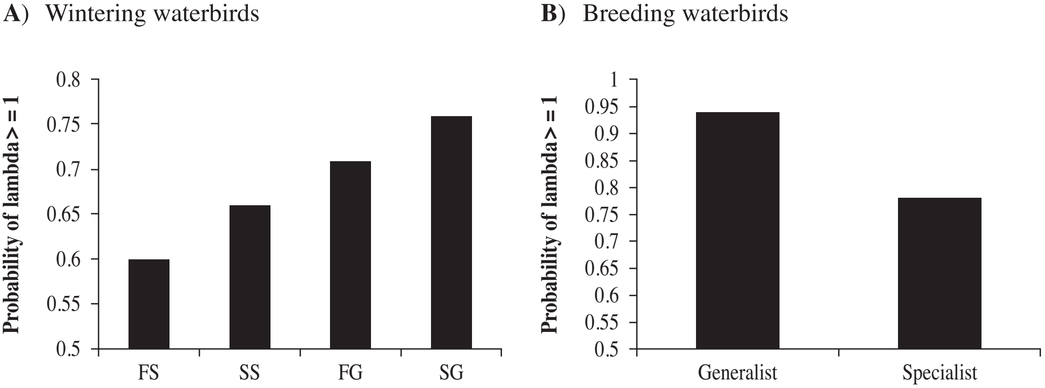

FIG. 2.—Probabilities of having a lambda value larger than or equal to 1 for A) wintering and B) breeding waterbird species as a function of diet and habitat. FG = freshwater generalist; FS = freshwater specialist; SG = saline-water generalist; SS = saline-water specialist. Probabilities come from the best models in table 2.

[Probabilidades frecuentistas de tener una "lambda" mayor o igual a 1 para A) aves acuáticas invernantes y B) aves acuáticas reproductoras en función de la dieta y el tipo de hábitat. FG = generalista de agua dulce; FS = especialista de agua dulce; SG = generalista de aguas saladas; SS = especialista de aguas saladas. Las probabilidades proceden de los mejores modelos de la tabla 2.]

breeding many of the discrepancies consisted of species showing either decreasing or stable status at country level but either increasing or decreasing status at regional level. This suggests that trends at local level during the breeding period are more independent of the broader geographical situation than wintering trends, and hence are more dependent on local features or conservation actions.

TABLE 3

Mean values (± standard deviation) of several basic water quality parameters associated with eutrophication obtained by the middle of our time series of counts of waterbirds (1995-2000) and by the end of it (2006-2011). Data refer to February for one of our main freshwater study sites (Albufera de Valencia). Source: Generalitat Valenciana.

[Media aritmética (± desviación típica) de varios parámetros básicos de calidad del agua asociados con la eutrofia, obtenidos hacia la mitad de nuestra serie de conteos de aves acuáticas (1995-2000) y hacia el final de la misma (2006-2011). Los datos se refieren al mes de febrero en uno de los principales humedales de agua dulce estudiados (Albufera de Valencia). Fuente: Generalitat Valenciana.]

	1995-2000	**2006-2011**
Dissolved oxygen	12.1 ± 3.40	9.18 ± 3.53
Phosphorous (total)	0.36 ± 0.05	0.16 ± 0.07
Chlorophyll a	102.8 ± 90.2	85.1 ± 40.1
pH	8.81 ± 0.59	8.47 ± 0.23
Suspended matter	68.2 ± 54.7	39.2 ± 11.5
Nitrates	7.78 ± 6.47	10.5 ± 4.80

Population fluctuations and the logistic curve

Breeding population trends of most species (58%) seemed to be either following a logistic pattern or at equilibrium (table 4; see some examples in fig. 3 and all species curves in fig. 3S of the electronic appendix). More specifically, the proportion of species according to classes were *Fitting the logistic curve > Dynamic equilibrium >> Exponential growth >> Initial phase = No trend >> Decreasing trend*. During wintering, 50% of the species were either at equilibrium or fitting the logistic curve and the overall frequency scheme was: *Dynamic equilibrium >> Fitting the logistic curve >> No trend >> Initial phase = Exponential growth = Decreasing trend* (table 4; see some examples in fig. 4 and all species curves in fig. 4S of the electronic appendix). The percentage of species at equilibrium + fitting the logistic curve was not found to be statistically different when comparing breeding and wintering seasons ($\chi^2 = 0.15$, d.f. = 1, $p = 0.69$). Ducks had the highest percentage of species fitting the logistic curve or at dynamic equilibrium during breeding (71%), followed by grebes and gulls. During wintering the taxon with the highest number of species fitting the logistic curve or at equilibrium was herons (75%), again followed by grebes and gulls.

Interaction between stages of the logistic growth curve and abundance trends

During breeding, four of the nine species classified within the dynamic equilibrium class (little bittern, purple heron *Ardea purpurea*, Kentish plover and little tern) had a stable quantitative trend. However, the other five species within equilibrium had either increasing or decreasing trends assigned (great-crested grebe *Podiceps cristatus*, mallard *A. platyrhynchos*, red-crested pochard

Netta rufina, common pochard *Aythya ferina* and marbled duck *Marmaronetta angustirostris*). For these latter five species (or at least some of them), their decreasing or increasing trends could actually be fluctuations within a more global pattern of stability, rather than true increases or decreases. Additionally the increasing trends of greater

TABLE 4

Species included in each of the logistic growth curve classes considered.
[Especies incluidas en cada una de las tipologías de la curva de crecimiento logístico consideradas.]

Class	Species	%
	Breeding period	
Initial slow growth	*Himantopus himantopus*, *Tadorna tadorna*, *Oxyura leucocephala*	8
Exponential growth	*Ardeola ralloides*, *Ardea cinerea*, *Plegadis falcinellus*, *Chroicocephalus ridibundus*, *Larus melanocephalus, Podiceps nigricollis, Nycticorax nycticorax, Chroicocephalus genei*	22
Fitting the curve	*Tachybaptus ruficollis*, *Bubulcus ibis*, *Egretta garzetta*, *Anas strepera*, *Porphyrio porphyrio*, *Glareola pratincola*, *Charadrius dubius*, *Larus audouinii*, *Sterna sandvicensis*, *Sterna hirundo*, *Chlydonias hybrida, Gelochelidon nilotica*	33
Dynamic equilibrium	*Podiceps cristatus*, *Ixobrychus minutus*, *Ardea purpurea*, *Marmaronetta angustirostris*, *Netta rufina*, *Aythya ferina*, *Charadrius alexandrinus*, *Sternula albifrons*, *Anas platyrynchos*	25
No pattern	*Phoenicopterus roseus*, *Fulica cristata*, *Recurvirostra avosetta*	8
Decreasing	*Fulica atra*	3
	Wintering period	
Initial slow phase	*Phoenicopterus roseus*, *Anas crecca*, *Calidris minuta*, *Tachybaptus ruficollis*	12
Exponential growth	*Phalacrocorax carbo*, *Tadorna tadorna*, *Plegadis falcinellus*, *Larus fuscus*	12
Fitting the curve	*Egretta garzetta*, *Ardea cinerea*, *Porphyrio porphyrio*, *Anas platyrhynchos*, *Himantopus himantopus*, *Pluvialis apricaria*	18
Dynamic equilibrium	*Podiceps cristatus*, *Podiceps nigricollis*, *Bubulcus ibis*, *Anas strepera*, *Oxyura leucocephala*, *Fulica atra*, *Charadrius alexandrinus*, *Pluvialis squatarola*, *Vanellus vanellus*, *Chroicocephalus ridibundus, Larus michahellis*	32
No pattern	*Anas penelope*, *Recurvirostra avosetta*, *Calidris alpina*, *Limosa limosa*, *Anas clypeata*	15
Decreasing	*Anas acuta*, *Netta rufina*, *Aythya ferina, Aythya fuligula*	12

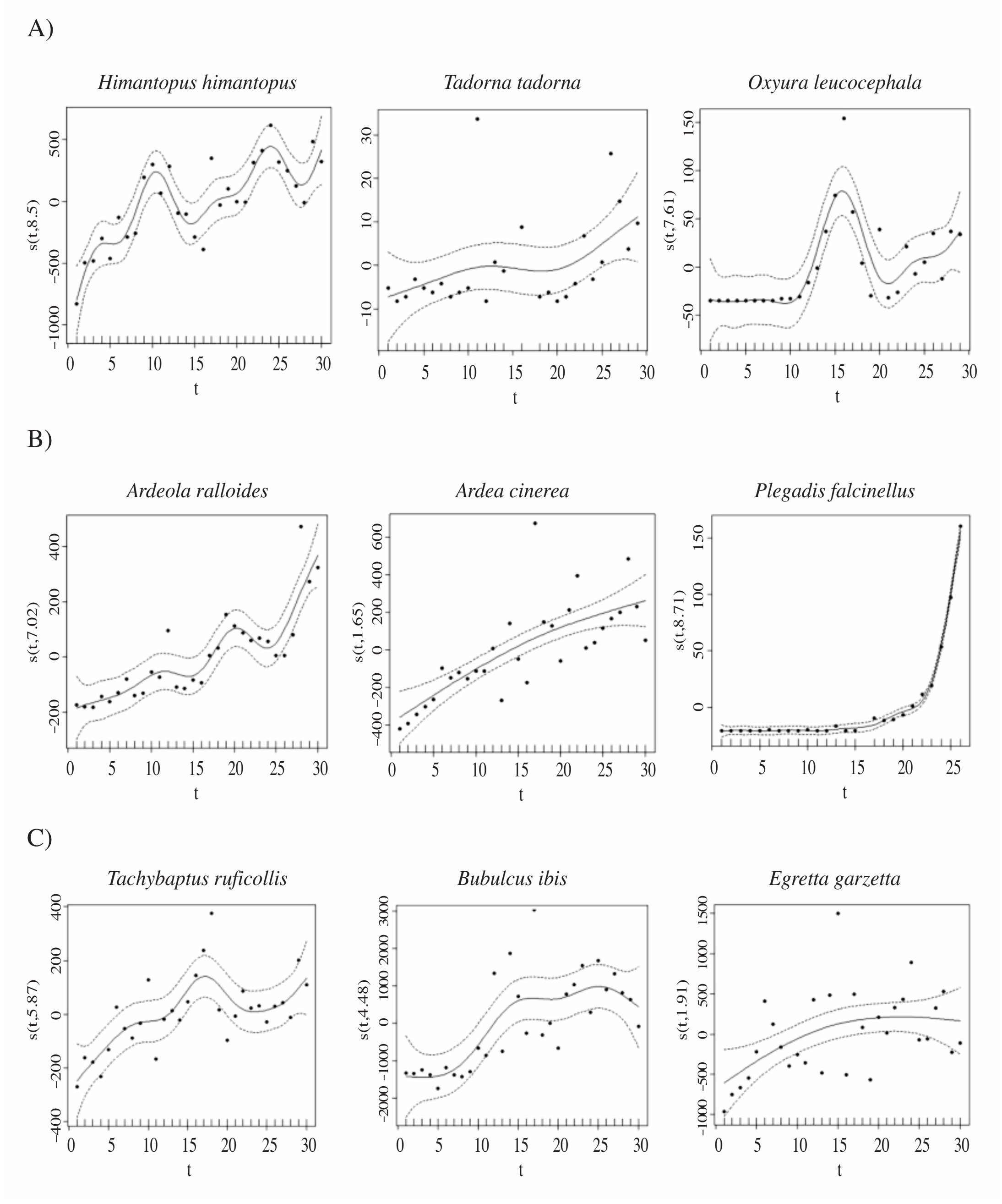

FIG. 3.—Examples of qualitative assignment of breeding waterbird species to the different stages of the logistic growth curve. A) Initial slow phase of growth; B) Exponential Growth; C) Fitting the logistic curve; D) Dynamic equilibrium; E) No trend; F) Decreasing. The y-axis represents standardized abundance units for the smoothing line from GAM models. Models for all species can be found in fig. S3 (supplementary electronic material).

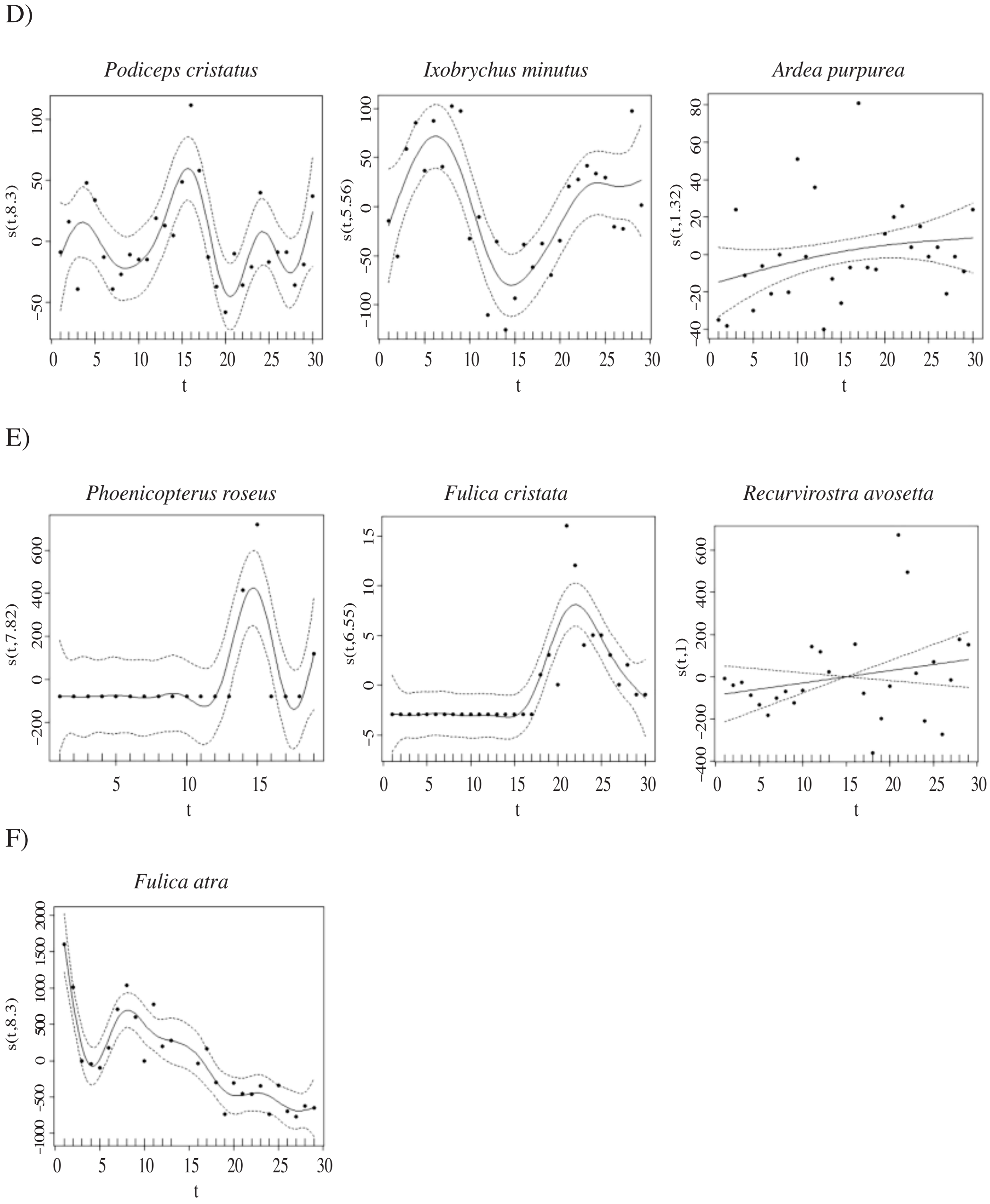

FIG. 3 (cont.).—*[Ejemplos de asignación cualitativa de las aves acuáticas reproductoras a los diferentes estadios de la curva de crecimiento logístico. A) Fase de lento crecimiento inicial; B) Crecimiento exponencial; C) Ajustándose a la curva de crecimiento logístico; D) Equilibrio dinámico; E) Sin patrón detectable; F) Decreciendo. El eje de coordenadas representa unidades de abundancia estandarizadas para la línea de suavizado obtenida a partir de los modelos GAM. Los modelos para todas las especies se pueden encontrar en la fig. S3 (material electrónico suplementario).]*

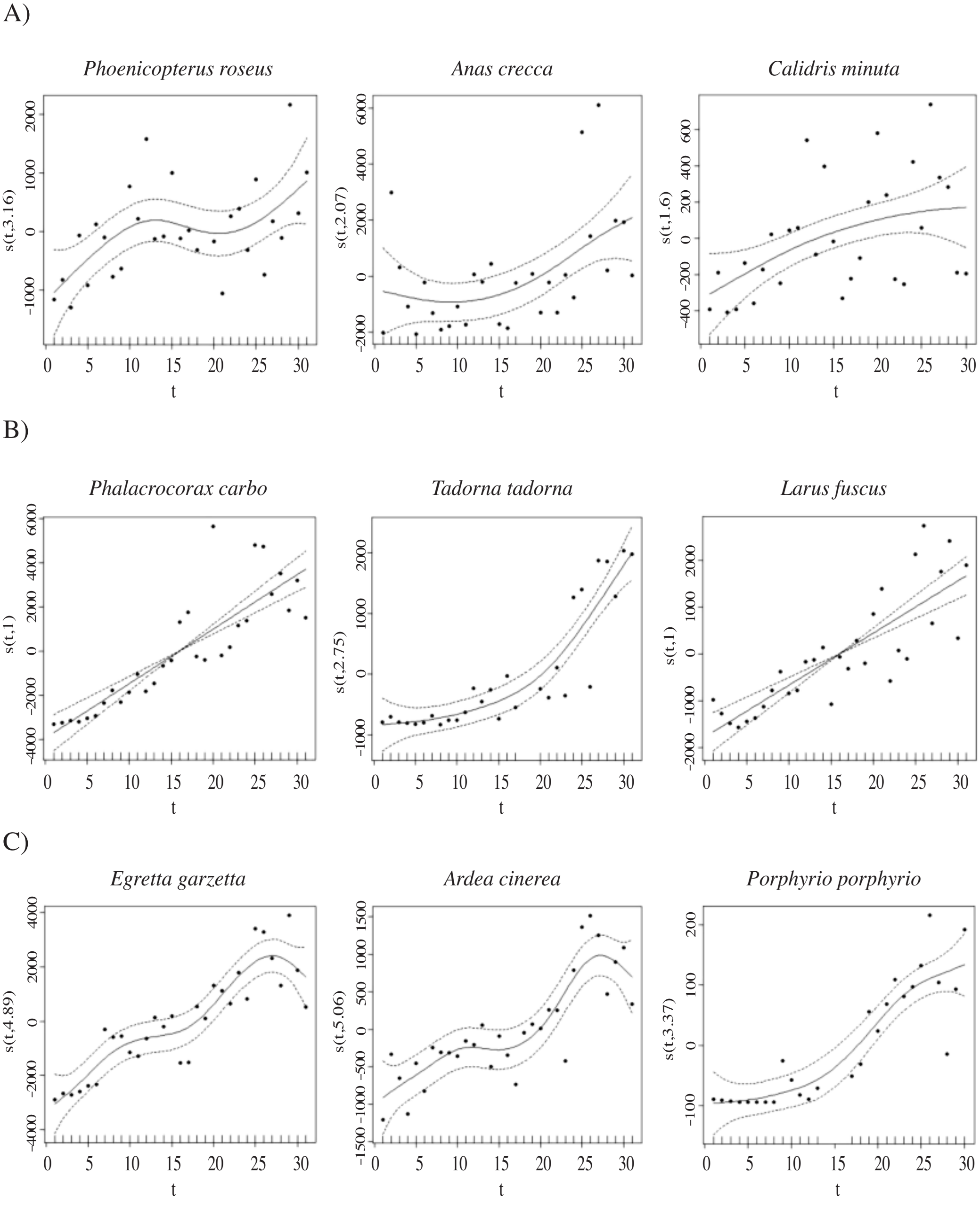

FIG. 4.—Examples of qualitative assignment of wintering waterbird species to different stages of the logistic growth curve. A) Initial slow phase; B) Exponential Growth; C) Fitting the logistic curve; D) Dynamic equilibrium; E) No trend; F) Decreasing. The y-axis represents standardized abundance units for the smoothing line from GAM models. Models for all species can be found in fig. S4 (supplementary electronic material).

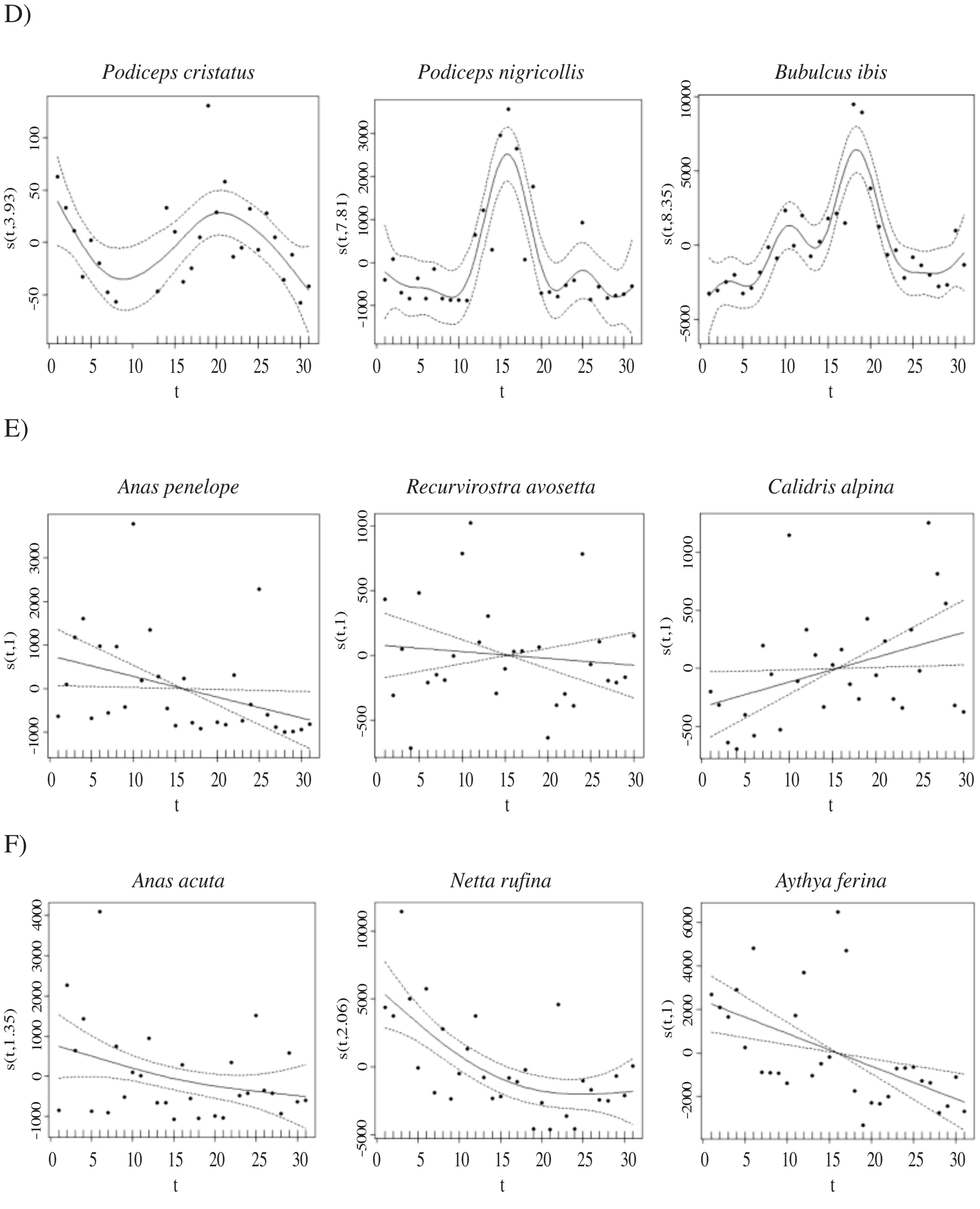

FIG. 4 (cont.).—*[Ejemplos de asignación cualitativa de las aves acuáticas invernantes a los diferentes estadios de la curva de crecimiento logístico. A) Fase de lento crecimiento inicial; B) Crecimiento exponencial; C) Ajustándose a la curva de crecimiento logístico; D) Equilibrio dinámico; E) Sin patrón detectable; F) Decreciendo. El eje de coordenadas representa unidades de abundancia estandarizadas para la línea de suavizado obtenida a partir de los modelos GAM. Los modelos para todas las especies se pueden encontrar en la fig. S4 (material electrónico suplementario).]*

flamingos, red-knobbed coots *Fulica cristata* and pied avocets *Recurvirostra avosetta* were also uncertain because these species could not be assigned to any particular stage of the logistic growth curve. Common coots *F. atra* had a decreasing trend according to their lambda value and were classified as decreasing as well according to their lack of match with the logistic curve, suggesting that common coots were unequivocally doing badly during breeding.

During wintering, all of the 11 species in dynamic equilibrium were found to have either increasing trends (great-crested grebe, cattle egret *Bubulcus ibis*, gadwall *Anas strepera*, white-headed duck *Oxyura leucocephala*, grey plover *Pluvialis squatarola*, northern lapwing *Vanellus vanellus* and yellow-legged gull *Larus michahellis*) or decreasing trends (black-necked grebe *Podiceps nigricollis*, common coot, Kentish plover and black-headed gull) according to their lambda values. Again, these patterns could just be fluctuations around dynamic equilibrium values rather than true declines or increases. Three of the five species with no logistic growth curve pattern assigned (northern shoveler *Anas clypeata,* pied avocet and black-tailed godwit *Limosa limosa*) showed a stable trend, one (dunlin *Calidris alpina*) showed an increasing trend and one (Eurasian wigeon) a decreasing trend. All these latter trends could be uncertain. However, some species (northern pintail, red-crested pochard, common pochard and tufted duck *Aythya fuligula*) found to have decreasing abundance trends in winter were also classified as decreasing when their abundance/time curves were matched to the logistic growth curves.

All species classified during wintering and breeding as showing initial slow growth, previous to an exponential phase, or fitting the logistic curve, were found to have increasing trends, suggesting that their abundance trends are most likely reliable.

DISCUSSION

The fact that most species showed increasing trends suggests that site protection policies implemented during recent decades have been effective, even though we lack data from the years before protection, when other conservation measures were applied. Most likely many waterbird groups (such as gulls, terns or herons) were doing badly simply because of a lack of high-quality sites. Interestingly both initially rare (e.g. glossy ibis *Plegadis falcinellus*) and common species (e.g. mallard) were found to have positive trends. Our results coincide with those of previous analysis of the same waterbird assemblage, when analysed from the perspective of diversity (Pagel *et al*., 2014). On the other hand many species were found to be fitting the logistic curve, as expected *a priori*, suggesting that their populations were in a critical situation at the beginning of the study after severe degradation of Mediterranean wetlands, and that recovery to attain the carrying capacity of the study system has taken some three decades. Some species have taken a long time to start their exponential growth probably because they have had to colonise over a long distance across the western Palearctic (glossy ibis or Mediterranean gull *Larus melanocephalus*) or they needed better environmental conditions (squacco heron *Ardeola ralloides* or wintering common shelduck *Tadorna tadorna*).

Only a few species have not shown signs of recovery, including diving ducks (common pochard, tufted duck or red-crested pochard) and coots, associated with freshwater sites. Similar results were found by Rendón *et al.* (2008) at the Doñana National Park marshes in Southern Spain, i.e. herbivorous wintering species showed negative trends relative to resident carnivorous/omnivorous species. These species forage mostly on submerged vegetation, and this type of vegetation in turn depends on high-quality waters. Although water quality has improved during recent decades, key parameters are still far from the pre-pollution oligotrophic state in freshwater sites, due to the high asymmetry between the speeds of perturbation (mainly by anthropogenic eutrophication) and recovery pathways in wetlands (Villena and Romo, 2003; Romo *et al*., 2005; Kagalou *et al*., 2008). The mechanisms for recovery are multiple and involve the whole food web in shallow lagoons, from phytoplankton to macrophytes, invertebrates, fish and waterbirds, as well as physical drivers (e.g. water quality and quantity, wind mixing). Even the presence of herbivorous waterbirds may delay the recovery of macrophytes and the positive cascading effects enabling the total recovery of the original regime, confirming that such resurgences take a very long time in this type of ecosystem (Scheffer, 2009). Despite the large investment in water purification systems so far (1,328 million € invested in sewage management during the period 1993-2015; Generalitat Valenciana, unpublished data), further effort is needed to enable the full recovery of submerged macrophytes. It is a cause for concern that water supplies are becoming even scarcer and that wetlands are increasingly forced to subsist on low-quality agricultural runoff waters, slowing the recovery of the study wetlands. The decrease in water availability comes from the combined effect of unpredictable periods of low rainfall, together with water overexploitation in the upper and middle stretches of the basins, since most study wetlands are located at the lower end of their hydrographic basins (see fig. 1). In fact, re-introduction projects were successful for a generalist species, the purple swamphen *Porphyrio porphyrio*, which thrives in eutrophic waters, whereas they failed in the case of the red-knobbed coot, a freshwater dietary specialist that needs mesotrophic waters.

However, although suitable water quality and quantity are a major determinant of the population dynamics of diving ducks and coots (see e.g. Lehikoinen *et al*., 2016), this factor cannot explain this dynamics completely since *Aythya* species can potentially eat benthic invertebrates as well and survive in highly eutrophicated sites (Marsden and Bellamy, 2000). We think that there are two additional factors to consider. One is the abandonment of traditional rural practices, such as the burning, grazing or cutting of reedbeds. This leads directly to a reduction of open water that is detrimental to diving ducks and coots, even at sites where water quality is high. The second factor is waterfowl hunting. This human activity is still allowed at many protected sites and can be regarded as a weakness of protection policies. Hunting has some relevant indirect positive effects on wintering waterbirds at some major sites because large areas are flooded every winter mostly for duck hunting, providing high-quality additional habitat (see Martínez-Abraín and Jiménez, 2016) and large quantities of supplementary food for ducks and also for many other waterbird species (Oro *et al*., 2013). However, excessive hunting has been identified, for example, as one of the major causes for the declining trend of breeding coots in the region and for the low success of the red-knobbed coot re-introduction programme (Martínez-Abraín *et al*., 2007, 2011, 2013; Tavecchia *et al*., 2009).

Saline water sites have experienced higher levels of eutrophication, but also of salination. Conductivity has increased in summer from an average of 10,101 µS/cm to an average of 15,190 µS/cm from the period 1996-2000 to 2006-2011 in El Hondo (fig. 1). This salination process could be providing animal or/and plant food for saline-water specialists despite eutrophication. This could explain the classification of the marbled duck (a species of high conservation concern in Europe) within the dynamic equilibrium stage typology, despite its decreasing trend according to lambda. It is important to remark that the marbled duck (and many other species at dynamic equilibrium or close to it) showed wide fluctuations in abundance. This is most likely due to frequent changes in flooding levels that are sometimes due to unpredictable drivers such as climate but in other cases (e.g. at the "El Hondo" semi-natural reservoirs) are due to inadequate management of water levels. The high variability in abundance of wintering species may also involve their response to unpredictable variation in flooding levels outside the study region, which may involve long-distance dispersal to other regions, rather than a true decline.

Our finding that some of the species showing decreasing trends, within shorebirds and Laridae (little tern, Kentish plover, black-headed gull), were those with smaller body size suggests that this factor can also have some influence on their growth rates (see e.g. Oro *et al*., 2009). Since in the Mediterranean region, many of the study species breed in similar habitats, and in multi-species colonies habitat competition by interference can be high (see also Fasola and Canova, 1992), body size can be a handicap. However, confirming the influence of this variable would require specific modelling that we have not performed here.

Finally, climate warming has been probably responsible for the increase in the wintering numbers of some species, such as the little bittern or black-winged stilt *Himantopus himantopus*, which were regarded as summer visitors just a couple of decades ago (own data).

Overall, our findings were coincident with the general recovery of wetland vertebrates detected by Galewski *et al*. (2011) for the period 1970-2008 in 27 different Mediterranean countries, and with the end of the direct persecution wildlife in southern Europe identified by Martínez-Abraín *et al*. (2009, 2013). However, the wide fluctuations caused by stochastic drivers, acting upon populations already reduced by non-random causes, could jeopardise the long-term population persistence of a few diet-specialists. This is in accordance with Tavecchia *et al*. (2007) who concluded that stochastic (density-independent) factors are as relevant as density-dependent factors for open populations of waterbird species. Our results highlight the major strengths and weaknesses of the current protection policies and offer pointers to the major management actions required to improve the resilience of the few species that do not have true positive growth rates despite long-term protection.

Methodological considerations

The fact that many lambda estimates were not statistically significant could be due in part to the high population variability. This component of variability is, to a large extent, due to the nature of count data consisting of single counts instead of repeated counts providing an average and an estimate of sampling error. This important limitation has to be acknowledged.

From a methodological point of view, we have shown that it is helpful to assign abundance curves to particular regions of the logistic growth curve in order to interpret lambda values properly. For example a lambda value assigned to a species showing a logistic curve will be necessarily an underestimate because it is a composite of a higher lambda for the exponential phase and a lower lambda for the equilibrium phase. Lambda values, as well as other measures of population growth rates, can be useful for conservation guidelines, but for many bird species (and particularly among waterbirds) they can sometimes provide poor information. This is because population size variability (process variance) in these species is very high over time, due to environmental variability (particularly high in Mediterranean wetlands), and high dispersal between patches over moderate distances. This variability is not well recorded by lambda that is highly dependent on the initial and final stages of the abundance time series. Our qualitative procedure of assignment of abundance curves to logistic stages should be developed as a quantitative procedure to make the assignment more repeatable and transparent. However, for many species it is difficult to carry out that exercise because of several confounding factors. First, many waterbird populations are structured spatially and hence the true unit of habitat/resource saturation is the wider population rather than each individual local population. Our study works at quite a large geographical scale, and this is a clear advantage, but the scale is probably not large enough. Waterbirds are highly vagile and hence spatially structured populations can be larger than the political borders where we carried out our study. In our case birds from nearby regions could be part of the same population. Indeed Bernis (1964) was already aware of the limitation of political frontiers when analysing duck and coot trends in Iberia, and wisely employed a map divided into "natural regions", an approach that is largely overlooked nowadays in many publications of waterbird trends promoted by autonomous regional governments. On the other hand, breeding counts usually consist of reproductive individuals, whereas large numbers of non-breeders remain uncounted. The logistic growth curve, however, is most likely better achieved when including both the breeding and non-breeding fractions of populations, the latter varying over time and increasing with detrimental environmental conditions. Finally, covering a sufficient temporal scale is also important to include most of the variability inherent to biological systems, as well as the natural and anthropogenic non-linear responses of species after disturbances. For instance, shortening our time series to 20 years (a relatively long temporal window for a wildlife time-series) would have depicted quite a different situation for many of the study species. Despite the high value of any counting information, decision-making based only on data consisting of single counts, ignoring all these limitations, could be highly biased or wrong and hence extreme care needs to be applied when using this type of data for decision-making.

ACKNOWLEDGEMENTS.—We are grateful to all people involved in the winter and breeding season counts of waterbirds in the Comunidad Valenciana during the last thirty years, especially to the Spanish Ornithological Society (SEO/BirdLife). We are also thankful to María Sahuquillo (Generalitat Valenciana) for providing data on water quality, and to Catherine Andrés for drafting fig. 1. AMA was supported by a post-doctoral Isidro Parga-Pondal contract from the Xunta de Galicia. We are grateful also to "Programa de Investigación Competitiva del Sistema Universitario Gallego", reference GRC2014/050, from the Xunta de Galicia for financing our project "Grupo de Investigación en Biología Evolutiva (GIBE) de la Universidade da Coruña". An anonymous reviewer and Mario Díaz provided helpful comments for improving earlier versions of the manuscript.

BIBLIOGRAPHY

ALMARAZ, P. and ORO, D. 2011. Size-mediated non-trophic interactions and stochastic predation drive assembly and dynamics in a seabird community. *Ecology*, 92: 1948-1958.

ATKINSON, P. W., AUSTIN, G. E., REHFISCH, M. M., BAKER, H., CRANSWICK, P., KERSHAW, M., ROBINSON, J., LANGSTON, R. H. W., STROUD, D. A., TURNHOUT, C. V. and MACLEAN, I. M. D. 2006. Identifying declines in waterbirds: The effects of missing data, population variability and count period on the interpretation of long-term survey data. *Biological Conservation*, 130: 549-559.

BERNIS, F. 1964. *Información española sobre anátidas y fochas (época invernal)*. Sociedad Española de Ornitología. Madrid.

BIBBY, C. J., BURGUESS, N. D., HILL, D. A. and MUSTOE, S. 2000. *Bird Census Techniques*. Academic Press. London.

BÖHNING-GAESE, K. and BAUER, H.-G. 1996. Changes in species abundance, distribution, and diversity in a central European bird community. *Conservation Biology*, 10: 175-187.

BURNHAM, K. P. and ANDERSON, D. R. 2002. *Model Selection and multimodel inference: A practical information-theoretic approach*. Springer Science & Business Media. New York.

COLLEN, B., LOH, J., WHITMEE, S., MCRAE, L., AMIN, R. and BAILLIE, J. E. M. 2009. Monitoring change in vertebrate abundance: the living planet index. *Conservation Biology*, 23: 317-327.

CRAMP, S. 1998. *The Complete Birds of the Western Palearctic on CD-ROM*. Oxford Univ. Press. Oxford.

DEL HOYO, J., ELLIOT, A. and SARGATAL, J. 1992. *Handbook of the Birds of the World*. Lynx Edicions. Barcelona.

FASOLA, M. and CANOVA, L. 1992. Nest Habitat selection by eight syntopic species of Mediterranean Gulls and Terns. *Colonial Waterbirds*, 15: 169-291.

FEWSTER, R. M., BUCKLAND, S. T., SIRIWARDENA, G. M., BAILLIE, S. R. and WILSON, J. D. 2000. Analysis of population trends for farmland birds using generalized additive models. *Ecology*, 81: 1970-1984.

GALEWSKI, T., COLLEN, B., MCRAE, L., LOH, J., GRILLAS, P., GAUTHIER-CLERC, M. and DEVICTOR, V. 2011. Long-term trends in the abundance of Mediterranean wetland vertebrates: From global recovery to localized declines. *Biological Conservation*, 144: 1392-1399.

GÓMEZ LÓPEZ, J. A., DIES JAMBRINO, J. I., VILALTA VILANOVA, M. and BARTOLOMÉ, M. A. 2006. *Las aves acuáticas de la Comunitat Valenciana: censos y evolución de las poblaciones (1984-2004)*. Conselleria de Territori i Habitatge. Valencia.

GONZÁLEZ, R. and PÉREZ-ARANDA, D. 2011. *Las Aves Acuáticas en España, 1980-2009*. SEO/BirdLife. Madrid.

GREEN, A. J., EL HAMZAOUI, M., EL AGBANI, M. A. and FRANCHIMONT, J. 2002. The conservation status of Moroccan wetlands with particular reference to waterbirds and to changes since 1978. *Biological Conservation*, 104: 71-82.

HUMBERT, J.-Y., SCOTT MILLS, L., HORNE, J. S. and DENNIS, B. 2009. A better way to estimate population trends. *Oikos*, 118: 1940-1946.

KAGALOU, I., PAPASTERGIADOU, E. and LEONARDOS, I. 2008. Long term changes in the eutrophication process in a shallow Mediterranean lake ecosystem of W. Greece: Response after the reduction of external load. *Journal of Environmental Management*, 87: 497-506.

KREBS, C. J. 2009. *Ecology: The Experimental Analysis of Distribution and Abundance*. Benjamin Cummings. San Francisco.

LEHIKOINEN, A., RINTALA, J., LAMMI, E. and PÖYSÄ, H. 2016. Habitat-specific population trajectories in boreal waterbirds: alarming trends and bioindicators for wetlands. *Animal Conservation*, 19: 88-95.

MARSDEN, S. J. and BELLAMY, G. S. 2000. Microhabitat characteristics of feeding sites used by diving ducks *Aythya* wintering on the grossly polluted Manchester Ship Canal, UK. *Environmental Conservation*, 27: 278-283.

MARTÍ, R. and DEL MORAL, J. C. 2003. *Atlas de las Aves Reproductoras de España*. Dirección General de Conservación de la Naturaleza-Sociedad Española de Ornitología. Madrid.

MARTÍNEZ-ABRAÍN, A. and JIMÉNEZ, J. 2016. Anthropogenic areas as incidental substitutes for original habitat. *Conservation Biology* (in press). DOI:10.1111/cobi.12644

MARTÍNEZ-ABRAÍN, A., VIEDMA, C., BARTOLOMÉ, M. A., GÓMEZ, J. A. and ORO, D. 2007. Hunting sites as ecological traps for coots in southern Europe: implications for the conservation of a threatened species. *Endangered Species Research*, 3: 69-76.

MARTÍNEZ-ABRAÍN, A., CRESPO, J., JIMÉNEZ, J., GÓMEZ, J. A. and ORO, D. 2009. Is the historical war against wildlife over in southern Europe? *Animal Conservation*, 12: 204-208.

MARTÍNEZ-ABRAÍN, A., REGAN, H. M., VIEDMA, C., VILLUENDAS, E., BARTOLOMÉ, M. A., GÓMEZ, J. A. and ORO, D. 2011. Cost-effectiveness of translocation options for a threatened waterbird. *Conservation Biology*, 25: 726-735.

MARTÍNEZ-ABRAÍN, A., VIEDMA, C., GÓMEZ, J. A., BARTOLOMÉ, M. A., JIMÉNEZ, J., GENOVART, M. and TENAN, S. 2013. Assessing the effectiveness of a hunting moratorium on target and non-target species. *Biological Conservation*, 165: 171-178.

MOSS, B. 1994. Brackish and freshwater shallow lakes: different systems or variations of the same theme? *Hydrobiologia*, 275/276: 1-14.

ORO, D., PÉREZ-RODRÍGUEZ, A., MARTÍNEZ-VILALTA, A., BERTOLERO, A., VIDAL, F. and GENOVART, M. 2009. Interference competition in a threatened seabird community: A paradox for a successful conservation. *Biological Conservation*, 142: 1830-1835.

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.

PAGEL, J., MARTÍNEZ-ABRAÍN, A., GÓMEZ, J. A., JIMÉNEZ, J. and ORO, D. 2014. A long-term macroecological analysis of the recovery of a waterbird metacommunity after site protection. *PLoS ONE*, 9: e105202.

PALECZNY, M., HAMMILL, E., KARPOUZI, V. and PAULY, D. 2015. Population trend of the world's monitored seabirds, 1950-2010. *PLoS ONE*, 10: e0129342.

RENDÓN, M. A., GREEN, A. J., AGUILERA, E. and ALMARAZ, P. 2008. Status, distribution and long-term changes in the waterbird community wintering in Doñana, south-west Spain. *Biological Conservation*, 141: 1371-1388.

ROMO, S., VILLENA, M. J., SAHUQUILLO, M., SORIA, J. M., GIMÉNEZ, M., ALFONSO, T., DEVICENTE, E. and MIRACLE, R. 2005. Response of a shallow Mediterranean lake to nutrient diversion: does it follow similar patterns as in northern shallow lakes? *Freshwater Biology*, 50: 1706-1717.

SCHEFFER, M. 2009. *Critical Transitions in Nature and Society*. Princeton University Press. Oxford.

SOLDAAT, L., VISSER, H., VAN ROOMEN, M. and VAN STRIEN, A. 2007. Smoothing and trend detection in waterbird monitoring data using structural time-series analysis and the Kalman filter. *Journal of Ornithology*, 148: 351-357.

TAVECCHIA, G., PRADEL, R., GENOVART, M. and ORO, D. 2007. Density-dependent parameters and demographic equilibrium in open populations. *Oikos*, 116: 1481-1492.

TAVECCHIA, G., VIEDMA, C., MARTÍNEZ-ABRAÍN, A., BARTOLOMÉ, M. A., GÓMEZ, J. A. and ORO, D. 2009. Maximizing re-introduction success: Assessing the immediate cost of release in a threatened waterfowl. *Biological Conservation*, 142: 3005-3012.

VILLENA, M. J. and ROMO, S. 2003. Phytoplankton changes in a shallow Mediterranean lake (Albufera of Valencia, Spain) after sewage diversion. *Hydrobiologia*, 506: 281-287.

WOOD, S. N. 2006. *Generalized Additive Models: An Introduction with R*. Chapman & Hall/CRC. Boca Raton.

SUPPLEMENTARY ELECTRONIC MATERIAL

Additional supporting information may be found in the on-line version of this article. See volume 63(1) on www.ardeola.org

Fig. S1: A comparison of three hypothetical series of counts (N) over time.

Fig. S2: Schematic representation of the different stages of the theoretical logistic growth curve used to assign waterbird abundance curves to different typologies.

Fig. S3: Qualitative assignment of breeding waterbird species to the different stages of the logistic growth curve.

Fig. S4: Qualitative assignment of wintering waterbird species to different stages of the logistic growth curve.

Table S1: Degree of fit and deviance explained by the GAM models fitted to abundance data of our study waterbirds during breeding and wintering.

Editor: Mario Díaz