**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 Coruña, Campus da Zapateira s/n,
15008 Elviña, A Coruña, Spain. A. Bertolero, Associació Ornitològica Picapall 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.*

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.

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 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 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 (Figure 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 (see for example Gilbert et al. 2016). We also expected this association to change with population density, due to competition among individuals.

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 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 $V = 0.476 \cdot L \cdot W^2$ (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 a 100km 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.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: <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 1).

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).

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 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 (Figure 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 model included an additive effect of horsepower and landfill together with an interaction with population density (Model 1; Table 2; Figure 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 (Figure 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 (Figure 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 (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).

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-financed 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 N°. 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).

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Figure and table legends

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.

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 $1 \cdot 10^6$.

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).

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 (W_i). 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.

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 (W_i). 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.

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Figure 1

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Figure 2

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Figure 3a

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Figure 3b

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638 **Table 1.**

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	

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647 **Table 2.**

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

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