Human activities have opposing impacts on Mediterranean Yellow-Legged Gull (*Larus michahellis*) breeding populations

by

Rachael Carlberg

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Thesis committee:
Dr. Johannes Foufopoulos, Chair
Dr. Georgios Karris
Dr. Manish Verma

Abstract

The islands of the Aegean Sea (Greece, NE Mediterranean Basin) are areas of high biodiversity and endemism, and harbor globally important seabird communities. Resident seabirds breed on offshore islands where they often form strong nesting colonies. Breeding seabirds are important determinants of island ecosystem function while also being subject to a plethora of human activities. Understanding how anthropogenic activities impact such colonies is not just essential for seabird conservation but is also critically important for the management of small insular ecosystems and the native species communities they support. This study aims to quantify the effect of relevant human activities on the size and locations of Yellow-legged Gull (*Larus michahellis*) colonies, a generalist gull species native to the western Palearctic that is the most abundant among resident seabirds.

We censused gull colonies from 152 islands located in the Cyclades and Sporades archipelagos. We also gathered data on variables suspected to influence seabird colonies, including physical islet characteristics, resource availability (e.g., open-air landfills and fisheries activity), and type and extent of human disturbance. Analyses were conducted on the local (islet) and on the regional (island cluster) levels to identify proximate and ultimate factors shaping the density and breeding population sizes of resident gull colonies.

Our results reveal divergent impacts of human activities in resident gull populations. On the local level we identify a clear negative effect of the presence of invasive rats (*Rattus* sp.) on gull nesting density. Similarly, presence of feral grazing mammals such as goats (*Capra hircus*) and rabbits (*Oryctolagus cuniculus*) had negative impacts on gull populations, an effect that appears to be primarily mediated through nest disturbance rather than through vegetation degradation. Access to landfills and fishing vessels both had positive impacts on gull nesting density. Presence of olive groves was also positively associated with the size of resident Yellow-legged Gull populations, highlighting the role of these anthropogenic food resources in local gull diets. Our results suggest approaches to manage Yellow-legged Gull populations in the Mediterranean Basin by taking into consideration the roles of introduced mammals and fishing activities on seabirds in the region.

Keywords: *Larus michahellis*, seabirds, island communities, introduced predators, PAFS (Predictable Anthropogenic Food Subsidies)

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Table of Contents

Introduction

Island ecosystems have emerged as critically important areas of conservation interest due to the high levels of biodiversity and endemism they harbor (Myers *et al.* 2000, Russell & Kueffer 2019). Because of their remoteness and isolation, such island ecosystems are often the only places where native wildlife can find refuge to reproduce and survive (Anderson *et al.* 2017). Nonetheless, human-induced changes such as the introduction of invasive species and disturbance by visitors, as well as climate change, are increasingly putting these areas at risk (Klöck & Fink 2019, Martin *et al.* 2000). In many parts of the world, proper functioning of small island ecosystems depends on the maintenance of local biodiversity, and especially of breeding seabird communities (Anderson *et al.* 2017). Seabirds therefore serve as globally significant island keystone taxa, largely due to the nutrients they deposit on land in the form of guano, food scraps, and carcasses, which ultimately serve to stimulate primary productivity (Anderson & Polis 1999, Wainright *et al.* 1998). For remote or very small islets, seabirds can be the sole link between terrestrial and marine ecosystems as they transfer nutrients to their nutrient-poor terrestrial breeding grounds. This activity makes them a critical component for the maintenance of endemic islet communities. Nutrient deposits benefit island flora as well as organisms of higher trophic levels like insects or small reptiles which depend on robust plant communities for their establishment (Croll *et al.* 2005, Sánchez-Piñero & Polis 2000). Seabirds also affect islands through nesting habits, which can change soil physical and chemical properties and impact the vegetation types present on an island (De La Peña-Lastra *et al.* 2021). Understanding the factors that shape seabird breeding presence on islands is therefore important not just for the conservation of these species, but also for the successful management of island ecosystems in general.

The Aegean lies at the biogeographic crossroads located at the vertex of three continents, and its high number of endemic species makes it an area of high environmental value (Medail & Quezel 1997). In regard to seabirds, the Aegean Sea has exceptional conservation importance as it harbors substantial breeding populations of several rare or otherwise not well-understood seabird species (Fric *et al.* 2012). Currently, thirty-nine species of waterbirds and seabirds can be found in Greece. Twelve of these use Greek territory as their breeding grounds (Fric *et al.* 2012). The region is characterized by the very large number of islands (>7500) of which only a small minority (<200) is inhabited by humans (Triantis & Mylonas 2009). The absence of permanent human presence on these islands has historically offered important refugia from human disturbance and unfavorable conditions for sensitive wildlife. Especially on smaller islands, species communities have evolved in the absence of terrestrial mammals and are not well adapted to herbivory or predation (Blumstein & Daniel 2005, Coblentz 1978). However, human activities have increasingly led to the introduction of non-native mammals such as rats, feral cats, goats, and rabbits, which have large impacts on native communities through changes in soil, vegetation, and predation pressure (Gizicki *et al.* 2018, Jones *et al.* 2008, Ruffino *et al.* 2009). The most populous and ecologically important seabird species native to the region is the Yellow-legged Gull (*Larus michahellis*) (Fric *et al.* 2012). The species was considered conspecific with the Herring Gull (*Larus argentatus*) or the Caspian Gull (*Larus cachinnans*) but since the 2000s has been treated with full specific status (Crochet *et al.* 2002). It is a generalist, colonial, ground-nesting seabird with a wide distribution across the western Palearctic (Harrison *et al.* 2021). Over the past several decades, large population increases have led to expansions of the range throughout Europe, despite concurrent increases in human populations and development (Vidal *et al.* 1998).

Like many other seabirds, Yellow-legged Gulls live in nesting colonies which can vary greatly in size and density. While some individuals exhibit migratory behavior, colonies in the Aegean can be found year-round (Fric *et al.* 2012, Keller *et al.* 2020). In this area, Yellow-legged Gulls typically nest on small, uninhabited islets and forage utilizing the resources of larger, human-inhabited nearby islands. Thus, their distributions are not only affected by the characteristics of the islets on which they nest, but also by the surrounding areas that supply the resources needed for reproduction. The birds exhibit high fidelity to their natal colonies, breeding each year at the same islet on which they were born (Arizaga *et al.* 2010). Egg-laying takes place from March to April, while the fledging period lasts 42 – 50 days (Harrison *et al.* 2021). The species has a foraging range up to 40-50 kilometers and is rarely found to travel any further from their colony sites, even as human development encroaches into current foraging ranges (Arizaga *et al.* 2010, Mendes *et al.* 2018).

Increasing development across the Mediterranean Basin has led to rising numbers of colonies dependent on human-derived resources, with human-gull interactions becoming progressively more common in populated areas (Soldatini *et al.* 2008). While Yellow-legged Gull colonies of the Aegean are located in uninhabited areas, the exact extent of human activity and reach to seabirds nesting on small unpopulated islets has yet to be determined. Since the species does not forage on breeding islets but rather feeds in the surrounding areas, it may compete with birds from other, nearby colonies, making it necessary to consider all colonies of a region as an aggregate for accurate biological interpretation. By combining small-scale analysis with regional-level investigation, this study elucidates for the first time the functional relationships driving seabird breeding occurrence at both scales (Figure 1). These relationships are particularly of interest in the Aegean, given the regional economy's dependence on fisheries as well as the common presence of open landfill sites for waste collection, both potential resources for seabirds (Egunez *et al.* 2018, Karris *et al.* 2018).

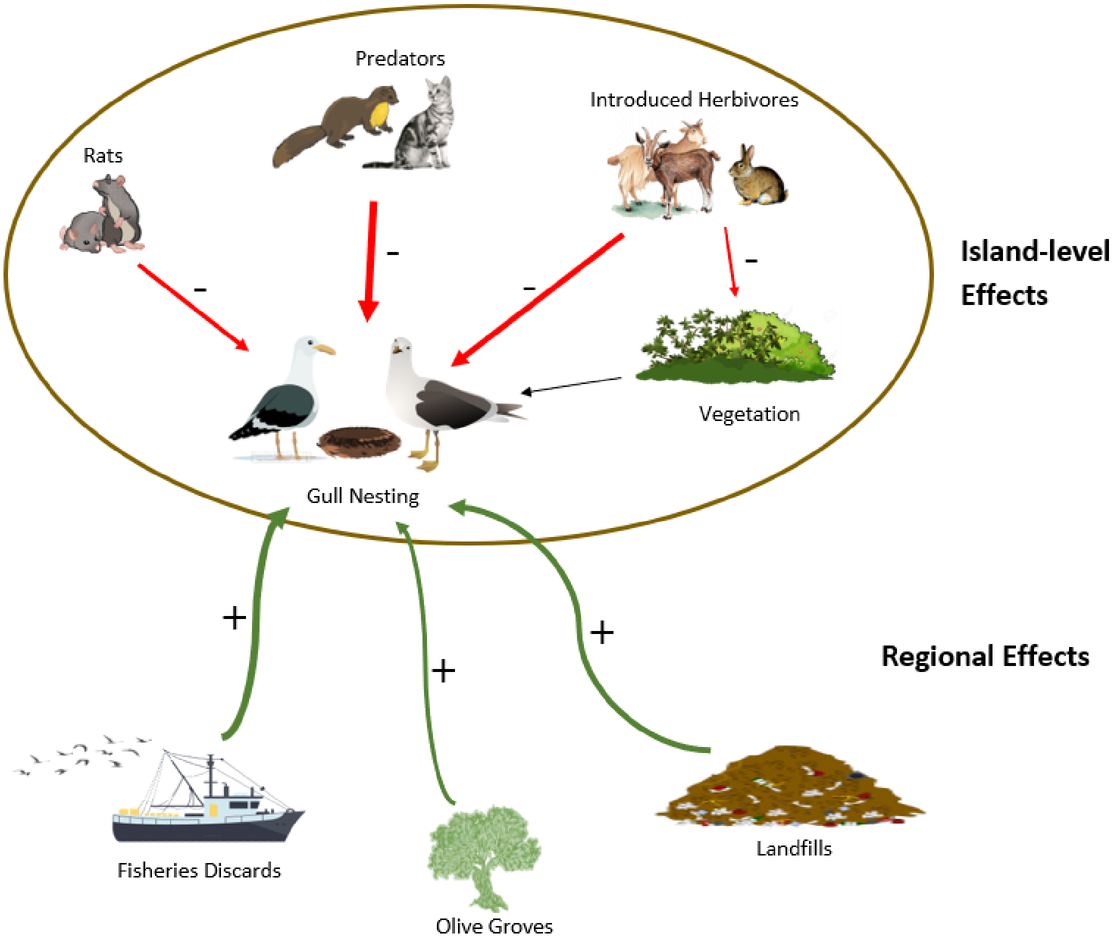

Figure 1. Conceptual diagram depicting functional interactions for a typical Yellow-legged Gull (*Larus michahellis*) colony in the Aegean, including both island-level and regional relationships with the potential to affect colony size and density. Red arrows represent expected negative effects to gull numbers, while green arrows suggest positive impacts.

Islets of the Aegean depend upon robust seabird communities for ecological functioning. Human activity throughout the Mediterranean, such as fishing and the introduction of feral mammals, has already impacted endemic species of the area (Coll *et al.* 2010, Gizicki *et al.* 2018). Given the ecological significance of the species it is important to understand the factors that drive occurrence and size of Yellow-legged Gull colonies. We hypothesize that human disturbances on the islet-level will constrain the density of breeding colonies by decreasing numbers of pairs; in contrast at a regional level, it is expected that the steadily increasing availability of Predictable Anthropogenic Food Subsidies (PAFS), particularly fisheries activity, will be a key factor in the increase in Yellow-legged Gull numbers of the eastern Mediterranean (Figure 1). To disentangle these potentially contradictory effects on gull presence, we perform two complementary approaches. To understand how proximate, islet-level factors affect the willingness of birds to nest on an island, we perform an analysis on small-scale effects impacting individual colony gull nesting density. On a larger, island-group scale, we complete exploratory visualizations and analyses to gain an understanding of how presence of PAFS may affect aggregate breeding population size on all colonies sharing the same main island resources. Ultimately the results of this study can be used to target and shape regional strategic conservation planning for wildlife. Therefore, our results have direct conservation implications for the region.

Methods

Study Area

This study focuses on the northeast Mediterranean Sea region with a particular emphasis on two large island clusters: the Cyclades cluster in the southern Aegean Sea and the Sporades cluster in the northern Aegean Sea. The marine ecosystem is oligotrophic and characterized by low concentrations of annual primary productivity (C 116 – 126 g/m^2year) (Bosc *et al.* 2004) and annual chlorophyll (chl-a 0.13 – 0.27 mg/m^3) (Gotsis-Skretas *et al.* 1999). Within each island cluster there are typically a few large islands inhabited by humans, each surrounded by multiple smaller islets, typically lacking any regular human presence, on which seabirds nest. Gull populations therefore will depend on the isolation of satellite islets for protection during the breeding period while foraging on resources from the surrounding sea and nearby large islands. The area experiences a typical Mediterranean maritime climate with modest annual precipitation levels, warm summers, and temperate winters (Gikas & Tchobanoglous 2009). Located in the Mediterranean Basin biodiversity hotspot, the region is home to a large number of island endemic flora and fauna species and is of high global conservation value (Myers *et al.* 2000). The islands are typically covered with aridity-adapted Mediterranean heath communities, with species which are often summer-deciduous, aromatic, and spinose.

Wildlife

The unique geographic position of the Aegean has led to the evolution of distinctive species communities. Due to the isolation of many islands and lack of large native mammals, island endemic taxa are not well-adapted to the conditions of grazing or heavy predation (Blumstein & Daniel 2005, Coblentz 1978). However, there are several invasive mammals in the region that have been introduced to many islands through human activities. Cats kept as pets are widespread on larger islands, and when not fed properly, will become feral and hunt wildlife to the point of impacting local populations (Krawczyk *et al*. 2019, Li *et al.* 2014, Medina *et al.* 2011). Releases of livestock (goats (*Capra hircus*) and less commonly, sheep (*Ovis aries*)) on islets, are timed to coincide with the annual spring flush of vegetation. While goat and sheep flocks are usually left on small islets only seasonally, the timing corresponds approximately with the Yellow-legged Gull breeding season and likely affects the nesting success of the birds (Gizicki *et al.* 2018). Rabbits (*Oryctolagus cuniculus*) are also released on islets for hunting purposes, where they reproduce and devastate vegetation not only through consumption of aboveground tissues, but also through digging of burrows, which destroys underground plant organs like tubers and roots and loosens soil leading to increased erosion.

Human Activity

Several human activities of Aegean communities have the potential to impact seabird populations. The expansion of human populations on large, inhabited islands, has led to key changes such as the increase in organized fishing over the past 50 years. Both the number of boats – mostly of a demersal type – operating, as well as the amount of gear deployed, increased steeply throughout the 1970s and 1980s (FAO 2006) and has remained relatively stable since then. Both individual fishermen and larger trawling vessels discard bycatch at sea, and resident gull populations can regularly be seen foraging behind boats on fishing refuse (Arcos *et al.* 2001, Cama *et al.* 2012). Urbanization and the introduction of more stringent hygienic standards has led to the establishment of substantial open-air landfill sites on almost every inhabited island of the Aegean. These sites are visited daily by large numbers of gulls using refuse as a food source—we therefore speculated that the distance to a landfill site is likely a factor determining nesting willingness in *L. michahellis* (see Bosch 1994, Duhem *et al.* 2003, Duhem *et al.* 2008). Lastly, olive groves are an important part of traditional agriculture on the larger islands, and gulls can be seen foraging in the fall in olive groves, and clusters of regurgitated olive pits can be found on breeding islets in the vicinity of gull nests (Battisti 2020, Oro 1996). As a result, we investigated whether presence and extent of olive groves has an impact on resident gull populations.

Data Collection

Between 2016 and 2021 we censused 152 islets for the presence of Yellow-legged Gulls. The islands were visited and assessed during the gull nesting period from May to June using standardized seabird quantification protocols (Hutchinson 1980). The small size of the nesting islets (ranging from 0.0004 to 15 km^2) and the often spatially delimited presence of gull colonies allowed for the completion of visual whole-colony counts of breeding pairs (Figure 2).

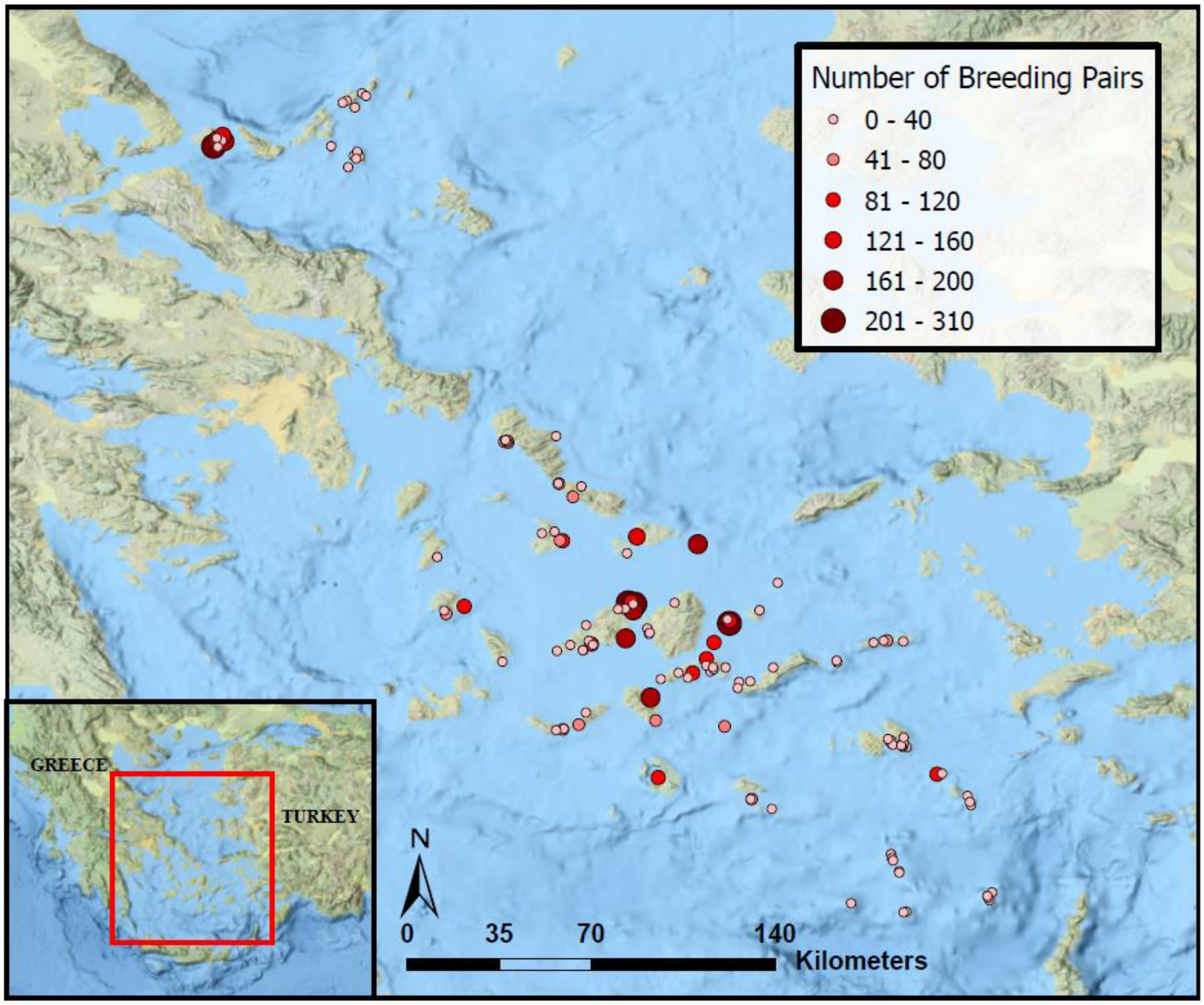

Figure 2. Locations and sizes (number of breeding pairs) of the sampled *Larus michahellis* colony sites located in the Aegean Sea of Greece. Base map sources: Esri, USGS, HERE, Garmin, FAO, NOAA, CGIAR

We also collected data for 14 selected variables that have the potential to influence Yellow-legged Gull colony size and distribution based on the literature and our own empirical assessment of gull biology. The variables include information on a) physical island characteristics, b) human populations, c) resource availability, and d) type of local anthropogenic activities (see supplemental materials for a full variables list). We categorized each variable as a local (islet-specific) or regional metric. Physical landscape characteristics such as islet area, coastline length, and distance to the nearest inhabited island and colony site were measured from aerial imagery. Information on human populations was retrieved from the Hellenic Statistical Authority 2011 Greek Census (ELSTAT 2011).

Number of introduced grazing species occurring on an islet (European rabbits, *Oryctolagus cuniculus*, and goats, *Capra hircus*; range of values 0-2) was determined either through direct identification of animals, or more rarely, through the presence of fresh sign, active burrows, or recent carcasses and confirmed through interviews with local shepherds and hunting associations. In addition, we quantified percent vegetation cover of an islet using randomized transects (see Gizicki *et al.* 2018 for detailed methods). The presence or absence of the two main invasive rat species of the area (*Rattus rattus* or more rarely *R. norvegicus*) was determined through a combination of literature review (Masseti 2012) and confirmed by detailed visual surveys for the presence of sign.

To determine resource availability for the islet colonies surrounding a larger, shared island, we created a 50-kilometer buffer around each colony based on the known foraging range of Yellow-legged Gulls (Arizaga *et al.* 2014). We examined the importance of landfills by measuring the distance from each colony site to the nearest landfill. We retrieved information from the United Nations Food and Agriculture Organization on registered fishing vessels to determine the number of vessels registered at each port (FAO 2020). We also measured each colony's distance to the nearest active fishing port. Lastly, we accessed landcover data from the CORINE Landcover Inventory to determine the area of olive groves falling within each region (European Union 2018). All spatial analysis was completed in ArcGIS Pro v2.7.1.

Statistical Analysis

Data analysis was completed on two levels to determine significant factors at the local islet-level scale, and at the regional level. To complete the regional analysis, we took advantage of the spatial clustering of the islands to aggregate data into biologically relevant units based on known gull behavior and established foraging ranges. Number of fishing vessels registered to a region was established by adding the number of vessels at each individual port in the region. Average distance to the nearest port and landfill were combined to obtain average regional values weighted by colony size. Other variables were only gathered at the regional scale (main island area, human population and density, and olive grove area). Regions without sufficient data were excluded from the regional analysis.

For the local-level model, we calculated Pearson correlation coefficients to determine collinearity among continouous independent variables. Variables with high levels (>0.50) of collinearity were not included in the same model. Given the distribution of the count data and the overdisperson (the tendency of the variance of the dependent variable to be greater than the mean) a negative binomial model (link = log) where $\ln(y) = \beta_o + \beta_1 x_1 + \beta_2 x_2 \ldots$ was chosen. We used the natural logarithm of islet area as an offset in each tested model to account for the wide range in islet sizes in the dataset. We tested nested models, and the best model was selected by considering the Akaike Information Criterion (AIC). Due to the low sample size of the regional cluster units (n=19), we did not have enough statistical power to test multivariate models on a regional scale. Instead we present correlations between total cluster gull populations and the corresponding independent variables at the regional level, to explore the functional relationships between regional factors and gull breeding populations. All statistical analysis was completed in R 4.0.3 (R Core Team 2020). Packages 'MASS' (Venables & Ripley 2002) and 'ggplot2' (Wickham 2016) were used for analysis and data visualization.

Results

Local (Islet-level) Analysis

Number of breeding pairs on islets ranged from 0 to 310. After testing several nested models, the best model (AIC = 1203) included the variables of rat presence, presence of nonnative grazing species, percent vegetation cover, distance in kilometers to the nearest landfill, and number of fishing vessels registered to the nearest port (Table 1).

Model	**AIC**	**ΔAIC**
Gull Pairs ~ Rats + Grazers + Veg_cover + Dist_landfill + Fishing vessels	1203	
Gull Pairs ~ Rats + Grazers + Veg_cover + Dist_landfill	1205	2
Gull Pairs ~ Rats + Grazers + Veg_cover	1215	12
Gull Pairs ~ Rats + Grazers	1308	105
Gull Pairs ~ Rats	1317	114

Table 1. AIC and ΔAIC values for local models tested.

The output β-values of the model are related to the natural logarithm of breeding pair density. Therefore, to understand the effect size on breeding pair density, the β-value for each variable has been exponentiated and included in Table 2. The model results show a significant negative relationship between breeding colony density and presence of nonnative rats (β = -1.27, p = 0.00011), as well as presence of introduced grazing species (β = -0.74, p = 0.034 for one grazer present, β = -1.53, p = 0.0010 for two grazers present). Percent vegetation cover showed a positive, but nonsignificant, relationship with gull density (β = 0.50, p = 0.37). Distance to the nearest landfill showed a negative relationship with colony density (β = -0.034, p = 0.00023) while number of fishing vessels registered to the nearest port had a positive impact on gull density (β = 0.0075, p = 0.016).

Variable	**β**	**Effect size (e^{β})**	**SE**	**t**	**P-value**
Intercept	3.31	27.4	0.45	7.31	0.00000*
Islet Rats	-1.27	0.28	0.33	-3.87	0.00011*
Grazers1	-0.74	0.48	0.35	-2.12	0.034*
Grazers2	-1.53	0.22	0.47	-3.28	0.0010*
Veg_cover	0.50	1.65	0.55	0.89	0.37
Dist_landfill	-0.034	0.97	0.0092	-3.68	0.00023*
Fishing_vessels	0.0075	1.01	0.0031	2.41	0.016*

Table 2. Coefficients and error estimates for local-level gull density model. Those marked with an asterisk (*) are significant with a p-value less than 0.05.

Regional Analysis

The average total number of breeding pairs inhabiting a cluster was 256 (range from 7 to 836). At the regional (island group) level, the total number of Yellow-legged Gulls pairs inhabiting an island cluster was significantly related to the number of fishing vessels registered to that particular cluster (r=0.75, p = 0.00019) (Figure 3), and the total area of olive groves in the region (r=0.49, p = 0.03). There was also a marginally non-significant positive relationship between gull population and human population inhabiting the main island cluster (r=0.42, p=0.07). No other regional covariates were found to be significant (Table 3).

Variable	Correlation coefficient	P-value
Main (inhabited) island area	0.34	0.16
Human population	0.42	0.07
Total islet area	0.14	0.56
Fishing vessels	0.75	0.00019*
Olive grove area	0.49	0.03*
Average distance to nearest port	-0.14	0.56
Average distance to nearest landfill	-0.13	0.35

Table 3. Pearson's correlation coefficients between regional variables and the number of total nesting pairs in a region. Those marked with an asterisk (*) are significant with a p-value less than 0.05.

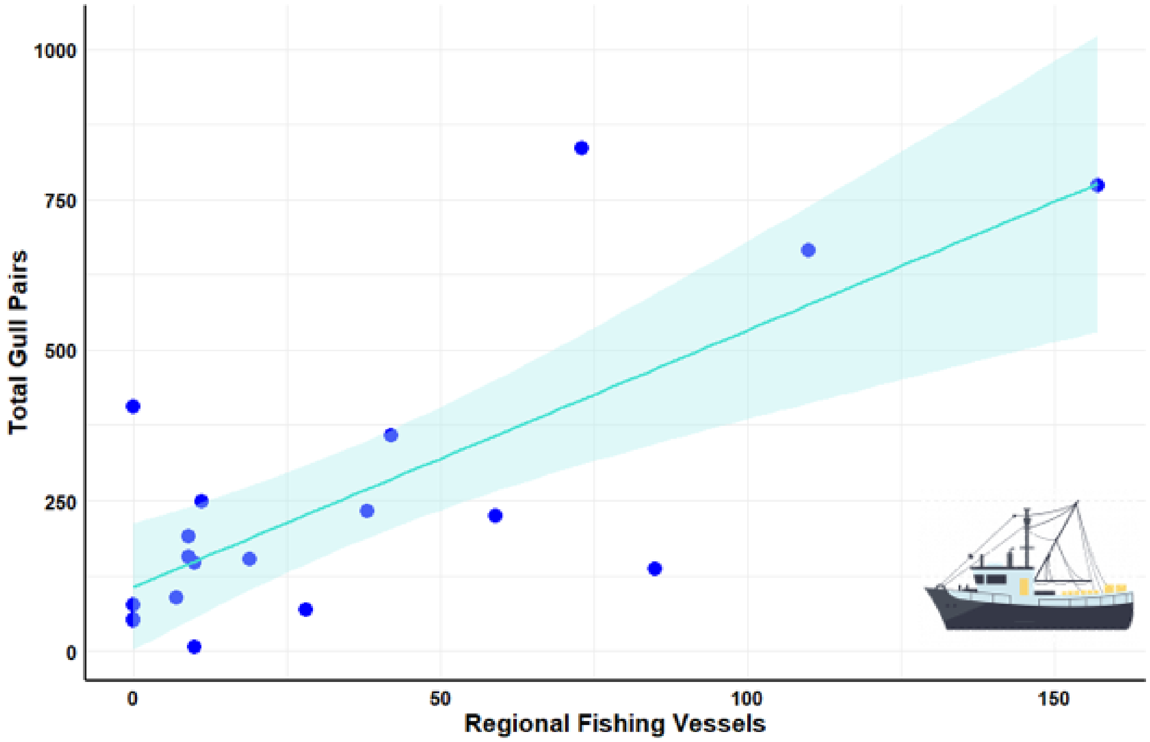

Figure 3. Plot illustrating the relationship between Registered Fishing Vessels per region versus the total number of Yellow-legged Gull pairs inhabiting the region.

Discussion

We conducted a two-tier analysis of *Larus michahellis* populations in the Aegean Sea in order to investigate both islet-specific and regional factors which influence the size of nesting colonies. The results demonstrate that humans have, through a diversity of direct and indirect ways, a strong effect on Yellow-legged Gull populations. As human presence continues to grow and development reaches new areas, Yellow-legged Gull populations show two divergent responses to the constellation of human-introduced changes.

At the islet level, the data revealed that gull breeding activity responds sensitively to the presence of a several other mammalian species occurring in the Aegean archipelago (Figure 4). On the broadest scale, presence of both humans and other mammal predators dramatically reduces the suitability of an island as a breeding site for Yellow-legged Gulls. Out of 152 islets visited, only 9 may harbor any mammal predators (other than rats), and gulls appear to potentially co-occur with mammal predators on only two sites, or about 1.3% of the sample colonies (Ano Fira (near Antiparos), and Kalo Livadi (off Kythnos)). The two main predators found in the region are one native species, the stone marten (*Martes foina*) and one human commensal, the feral cat (*Felis catus)*. Both predators live on large islands only, especially in the vicinity of agricultural areas and human settlements. They are essentially absent from small, uninhabited islets, both because such islets are too dry and too unproductive to support year-around terrestrial predator populations, and also because both taxa are very poor overwater dispersers (Masseti 2012). Cats occur in various stages of nutritional dependence to humans in the vicinity of permanent human settlements (Krawzcyk *et al.* 2019, Li *et al.* 2014), but can also be found – at least on the largest islands – at very low densities in a completely feral state away from humans (Cheke & Ashcroft 2017, Masseti 2012). While not explicitly included in this analysis due to the very low number of seabird islets which may also harbor mammal predators, these clear distributional patterns serve to illustrate the overwhelming influence that presence of mammalian predators have on colony site selection for seabirds (Medina *et al.* 2011). These patterns also argue that any reductions of feral cats, especially from smaller Mediterranean islands, will likely translate into important conservation gains in colony site dynamics as well as habitat use by wildlife in the region.

The islet-level analysis also revealed that the presence of exotic rats reduces the densities of breeding Yellow-legged Gull colonies. Our local model corroborates the previously documented negative impact that invasive rats have on seabirds, particularly ground-nesting species whose eggs and chicks are relatively easy prey (Jones *et al.* 2008). The impact of rats on various colonial seabirds has been the subject of extensive discussion in the island conservationist community. Whereas early investigations viewed rats as a harbinger of extinction for colonial seabirds, more recent studies have revealed more nuanced effects. Rat impacts depend not only on rat species identity but also on the type of seabird affected, with small-bodied species (e.g., *Hydrobates*) being more impacted by rats than large ones (Latorre *et al*. 2013). In the Mediterranean Basin in particular, a long history of co-occurrence of rats and seabirds appears to have allowed at least some seabird species to adapt to rat presence (Ruffino *et al.* 2009). Because Yellow-legged Gulls are a relatively large-bodied and aggressive species, rat presence may be an even larger deterrent to other native Aegean species. Completing population eradications of rats from smaller islands should therefore be a high conservation priority in the Mediterranean, as they have strong negative effects both on Yellow-legged Gulls as well as on smaller, less aggressive species such as Scopoli's shearwater (*Calonectris diomedea*) and Yelkouan shearwater (*Puffinus yelkouan*) (Igual *et al.* 2006, Lago *et al.* 2019).

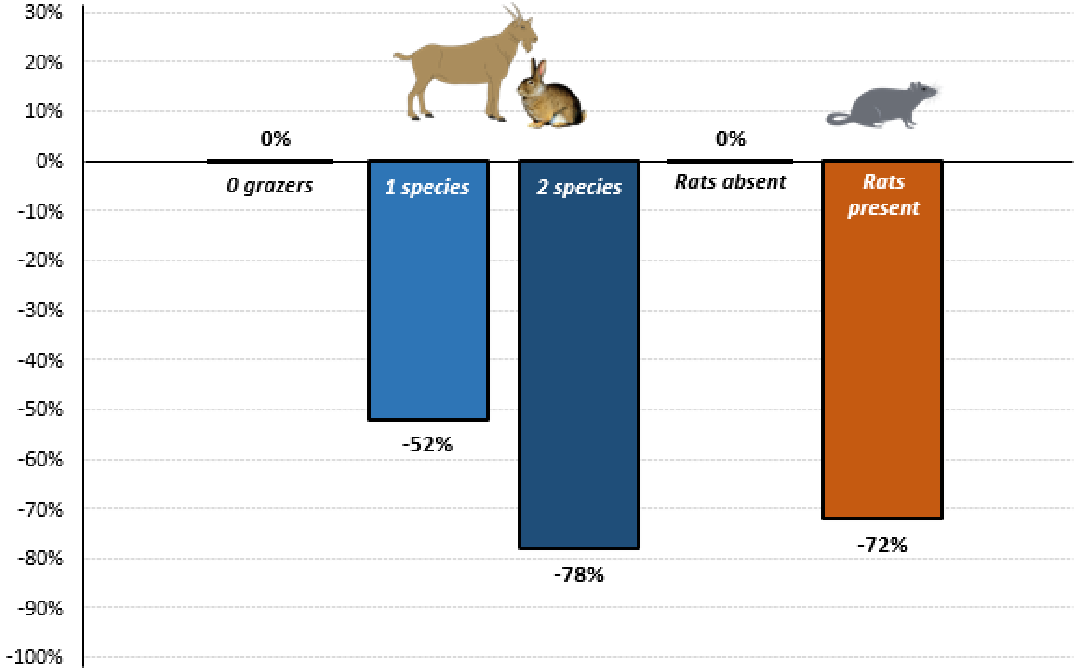

Figure 4. Changes in baseline density of islet breeding colonies based on disturbance type. 1 species = rabbits OR goats are present on an islet, 2 species = Rabbits AND Goats are present on the islet.

Beyond predation, we found that the introduction of non-native grazing species also had a clear-cut impact on Yellow-legged Gull colonies. Recent and ongoing research has shown the pervasive effects that introduced herbivores—whether seasonal like goats, or permanent like rabbits—have on Mediterranean islet ecosystems. These effects include dramatic declines in shrub vegetation cover and shifts in plant community composition towards grazing-resistant, generalist species, due to non-sustainable plant biomass removal (Gizicki *et al*. 2018). Soil disturbance through digging, trampling and burrowing leads to elevated levels of erosion, resulting in irreversible soil loss. Consequently, observed effects on nesting gulls are mediated either directly through trampling and disturbance at the nest, or indirectly, through soil damage and destruction of the vegetation beneficial for successful gull nesting (e.g., for shade) (Hata *et al*. 2018).

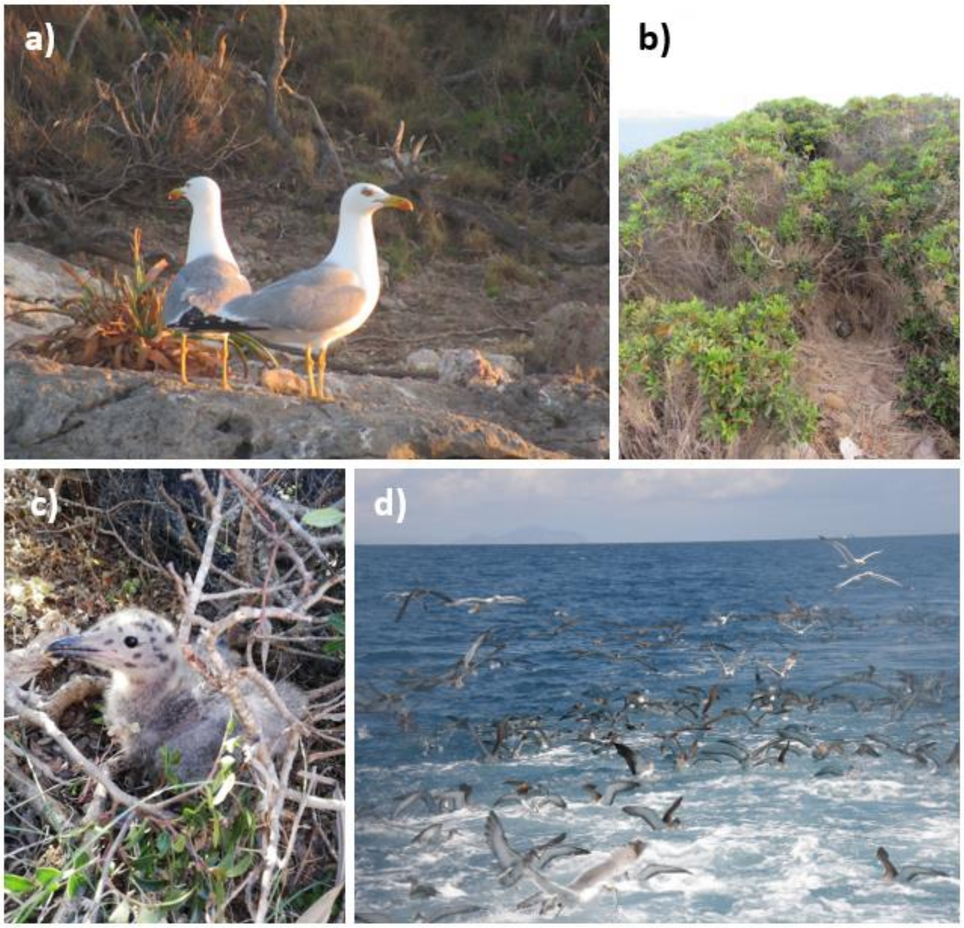

Figure 5. Photos of typical *Larus michahellis* activity: a) adult breeding pair, b) typical ground nest with egg, c) *L. michahellis* chick, d) mixed flock including *L. michahellis* foraging in the wake of a fishing vessel. Photos: Georgios Karris.

The data here argue more for effects through direct nest disturbance as gull nesting density was not significantly related to the extent of perennial vegetation cover. Field observations indicate that while Yellow-legged Gulls can successfully breed in the open (Figure 5), they do prefer the presence of shade; hence more research is needed to ascertain the relative importance of the two mechanisms (Figure 5). As shown in Figure 4, presence of a single grazing species (either rabbits or goats) reduces the baseline density of a colony by about 52%. The addition of a second grazing species further reduces the density of a colony to about 78% below the model baseline, indicating an additive effect of nonnative grazer presence. The reduction of gull numbers by grazers is likely ecologically significant for the region (Pafilis *et al.* 2013), as seabird presence and guano deposits on land are often depended upon for the recovery of overgrazed areas (Jones 2010). A decrease in seabird numbers likely lessens the chance of ecological recovery of endemic plant communities after the grazing species are moved or eradicated from an islet. Our results indicate an urgent need for policy prohibiting grazer releases to be put in place to avoid further reductions in seabird nesting, as well as the eradication of feral grazing individuals from small islets to restore potential nesting habitat.

Islet colony densities were also constrained by the distance to the nearest landfill site, with more dense colonies present closer to landfills, and colony density decreasing by 3% for each additional kilometer of distance from a landfill. In addition, the number of active fishing vessels registered to the nearest port of a colony increased colony density—each additional fishing vessel caused an approximately 1% increase in nesting population density. These results confirm our hypothesis that Yellow-legged Gulls utilize landfills and fisheries discards as food sources, and also indicate the importance of Predictable Anthropogenic Food Subsidies (PAFS) in the Aegean, which provide gulls with sources of stationary, relatively low-effort food year-round (Figure 5). Our results mirror those seen in other regions of the Yellow-legged Gull's range, highlighting once again the extensive and widespread impact of PAFS on seabirds (see Calado *et al.* 2017, Duhem *et al.* 2003, Duhem *et al.* 2008, Ramos *et al.* 2009, Real *et al.* 2017).

Because of the feeding ecology of Yellow-legged Gulls, it is important to examine not only colony-specific factors, but also regional variables impacting multiple colonies at once. At the regional scale, the most significant factor impacting aggregate gull population size was found to be the number of active registered fishing vessels in that region. The presence of fishing vessels acts as a stable, high-quality food source for gulls by providing bycatch and offal (Calado *et al.* 2017, Garthe & Scherp 2003). While trawlers are particularly important as food sources to seabirds in the Aegean Sea, all types of demersal fishing boats are utilized by Yellow-legged Gulls who do not hesitate to enter harbors to feed on refuse. We also found evidence for a relationship between gull populations and olive cultivation. Cultivation of olive trees varies greatly between islands, with olive groves being found extensively only on the larger and more productive islands. During the winter season when the fruit mature, olive groves are visited regularly by gulls so as to forage on this relatively inferior quality, but stable and predictable, food source. Consequently, substantial amounts of regurgitated olive pits can be found near nests on seabird islets. Although evidence of feeding on olive pits has been found in Yellow-legged Gull nests previously (Battisti 2020, Oro 1996), this is the first study that documents and quantifies a link between olive cultivation and gull populations.

The patterns shown by our data are important for Yellow-legged Gull population management, but also have implications for Aegean island species communities in general. The rapid population growth of Yellow-legged Gulls is a reflection of their ability to exploit a variety of available resources. Because of their behavioral flexibility, Yellow-legged Gulls are uniquely suited to take advantage of a diversity of PAFS including landfills, fishing discards, and olive groves. At the same time, Yellow-legged Gulls are known to exhibit high levels of aggression (Bracho Estévanez & Prats Aparicio 2019) and have also been shown to compete with other species for food sources and display kleptoparasitic behavior (Karris *et al.* 2018, Martínez-Abraín *et al.* 2003, Skórka & Martyka 2005). Their increasing populations exacerbate the effects of their behavioral dominance and is increasingly presenting a threat to other, rarer Aegean seabirds such as shearwaters and Audouin's Gulls (*Ichthyaetus audouinni*), which both lack their behavioral flexibility and are more susceptible to predation by rats. Another factor of concern is the link between use of PAFS, chemical contamination through ingestion of plastics, and disease spread, such as *Salmonella,* in seabirds (Malekian *et al.* 2021, Navarro *et al.* 2019). As individual gulls congregate in small areas to compete over food, there is a higher risk of disease transmission both at the food site and at colony islets, where other species will be impacted. As Yellow-legged Gulls reap the benefits of these food sources in the Aegean, their rising populations, aggressive behavior, and disease spread may become intense enough to outcompete and eventually eradicate other seabirds from nesting islets.

As human populations are expected to continue to increase in the future, the impacts of disturbances are expected to become more pronounced. By having a solid knowledge of the factors which constrain and increase Yellow-legged Gull numbers, their populations can be better monitored and controlled to avoid potential negative ecological outcomes. Past population control efforts for Yellow-legged Gulls such as culls have been unreliable (Baxter & Allan 2006, Bosch *et al.* 2000), indicating the need for different methods. Humans are responsible for the spread of rats, releases of grazers, and availability of fisheries discards and waste. Currently, there is no large-scale rat eradication effort in the Aegean, and the release of grazers onto small islets is largely unregulated. A comprehensive plan to control the spread of rats and designate where grazing species can be released could have benefits for the natural seabird communities of the area as well as endemic plants and invertebrates which are unadapted to grazing and depend upon seabird nutrients. Most importantly, policies on mitigation measures for fisheries bycatch and landfill waste, as well as the banning of fisheries discards by imposing an obligation to land unwanted catch (according to the Common Fishery Policy reform proposed by the European Commission in 2013) could help curb continual Yellow-legged Gull population increases, potentially allowing other seabird species to better compete for breeding territory in the region. We propose further research into the interactions between Yellow-legged Gulls and other native seabirds in the oligotrophic Aegean marine ecosystem to ascertain the impact that Yellow-legged Gull population expansions have on other species. It will also be particularly important to examine disease spread, since landfills and fisheries, both known vectors, are so relied upon by the gulls. This knowledge could further guide best practices to preserve healthy seabird communities and whole-island ecosystems.

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Supplemental Materials

1. *Islet-level data from all surveyed colony sites.*

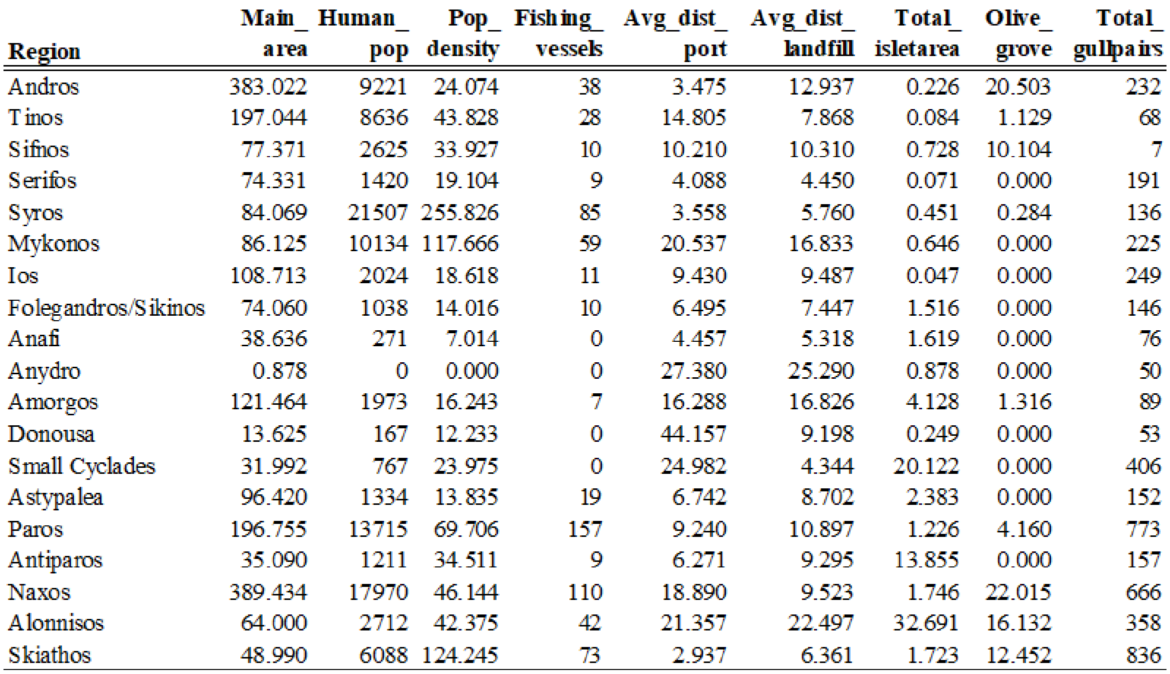
Islet	Region	Latitude	Longitude	Islet_ area	Veg_ cover	Islet_ coast	Coastarea_ ratio	Dist_ main	Dist_ colony	Grazers	Islet_ rats	Mammal_ pred	Fishing_ vessels	Dist_ landfill	Dist_ port	Gull_ pairs
Agios Petros	Alonnisos	39.322	24.055	0.608	0.45	0.299	49.128	8.570	1.380	0	1	0	42	24.73	25.56	1
Grammesa	Alonnisos	39.342	24.138	77.420	0.75	4.510	5.825	15.270	0.957	2	1	0	42	31.14	31.73	1
Korakas	Alonnisos	39.035	24.062	79.634	0.43	1.230	1.545	19.460	4.390	1	0	0	42	22.37	20.71	103
Melissa	Alonnisos	39.293	24.090	0.104	0.60	0.155	149.221	9.610	4.870	0	0	0	42	24.93	25.43	8
Mikros Adelphos	Alonnisos	39.126	23.988	30.773	0.51	3.110	10.106	7.860		2	1	0	42	11.63	10.44	21
Pappous	Alonnisos	39.354	24.121	57.092	0.83	1.030	1.804	15.110	0.957	0	0	0	42	31.19	31.9	30
Pelerissa	Alonnisos	39.313	24.038	13.978	0.24	1.650	11.804	6.580	1.380	0	1	0	42	22.81	23.66	10
Polemika	Alonnisos	39.102	24.100	6.258	0.61	1.210	19.336	17.820	0.516	2	1	0	42	21.75	20.55	55
Prassonissi	Alonnisos	39.072	24.096	20.621	0.45	2.560	12.415	19.030	0.293	0	1	0	42	22.59	21.18	107
Skantzoura	Alonnisos	39.081	24.110	561.000	0.93	20.840	3.715	18.460	0.293	1	1	0	42	22.31	21.07	1
Strongyllo	Alonnisos	39.083	24.086	0.649	0.98	0.332	51.184	17.850	1.240	1	1	0	42	21.52	20.17	23
Anydro	Amorgos	36.625	25.684	87.779	0.18	7.830	8.920	17.420	18.520	2	1	0	7	25.29	27.38	50
Glaros	Amorgos	36.986	26.326	12.185	0.35	2.400	19.696	23.090	2.940	0	0	0	7	44.81	44.25	10
Grambonissi	Amorgos	36.879	25.893	15.010	0.85	1.860	12.392	1.380	10.570	0	0	0	7	8.62	6.02	1
Gramvoussa	Amorgos	36.808	25.745	75.900	0.51	5.680	7.484	0.494	0.038	1	1	1	7	10.79	10.34	0
Kato Antikeri	Amorgos	36.842	25.666	105.100		6.010	5.718	6.890		2	0	0	7	11.82	16.87	0
Kato Mavra	Amorgos	36.995	26.383	7.117	0.50	2.420	34.004	28.150	0.076	1	0	0	7	47.75	49.32	42
Kinaros	Amorgos	36.980	26.289	456.100	0.40	17.180	3.767	18.480	0.953	1	1	0	7	40.23	39.63	0
Kisiri	Amorgos	36.791	25.740	1.200	0.23	0.750	62.461	0.108	2.740	0	0	0	7	11.83	11.81	12
Liadi	Amorgos	36.909	26.166	32.400	0.50	2.380	7.346	6.900	0.379	0	0	0	7	28.32	27.99	10
Pano Mavra	Amorgos	36.995	26.369	7.942	0.17	2.840	35.759	26.790	0.076	0	0	0	7	47.62	47.94	13
Petalidi	Amorgos	36.819	25.794	5.040	0.10	1.810	35.913	0.557	3.720	0	0	0	7	7.09	6.14	10
Plaka	Amorgos	36.901	26.170	5.741	0.90	1.190	20.728	7.280	0.379	0	0	0	7	28.51	28.26	21
Psalidi	Amorgos	36.816	25.746	2.480	0.08	1.150	46.371	2.110	2.740	0	0	0	7	11.26	10.49	35
Nikouria	Amorgos	36.886	25.908	275.000	0.90	11.110	4.040	0.273	0.229	2	1		7	9.29	6.77	0
Nisaki	Amorgos	36.991	26.454	0.646	0.70	0.558	86.345	34.250	5.860	0	0	0	7	48.47	55.42	1
Makria	Anafi	36.270	25.887	34.859	0.26	5.860	16.811	8.770	8.050	1	1	0	0	13.03	12.58	2
Megalo Fteno	Anafi	36.312	25.800	4.057	0.53	1.870	46.097	3.680	0.078	1	0	0	0	5.15	4.31	44
Mikro Fteno	Anafi	36.312	25.796	2.016	0.14	0.937	46.497	3.690	0.078	1	0	0	0	5.05	4.13	30
Pachia	Anafi	36.272	25.830	121.000	0.55	6.090	5.033	7.590	3.550	2	1	0	0	9.63	8.77	0
Andros Harbor Islet	Andros	37.841	24.944	0.290	0.90	0.440	151.729	0.010	4.090	0	1	1	38	10.09	18.84	0
Kapetidas	Andros	37.856	24.747	1.987	0.52	0.693	34.901	1.850	0.247	1	0	0	38	13.02	3.25	58
Lagonissi	Andros	37.852	24.735	2.773	0.95	1.320	47.609	2.490	0.625	0	0	0	38	13.5	3.57	77
Makedonos	Andros	37.853	24.746	0.557	0.82	0.459	82.477	2.770	0.247	0	0	0	38	12.87	3.65	22
Megalo	Andros	37.849	24.751	16.954	0.87	3.270	19.287	2.390	0.267	1	0	0	38	11.95	3.64	60
Prassonissi	Andros	37.859	24.739	0.048	0.70	0.325	671.870	2.030	0.607	0	0	0	38	13.77	2.94	15
Theotokos	Andros	37.876	24.958	0.540	0.84	0.437	80.922	0.134	4.090	0	0	0	38	13.8	19.4	56
Ano Fira	Antiparos	37.061	25.087	21.533	0.50	3.660	16.997	1.030	6.950	1	1	1	9	6.37	2.03	20

Islet	Region	Latitude	Longitude	Islet_ area	Veg_ cover	Islet_ coast	Coastarea_ ratio	Dist_ main	Dist_ colony	Grazers	Islet_ rats	Mammal_ pred	Fishing_ vessels	Dist_ landfill	Dist_ port	Gull_ pairs
Despotiko	Antiparos	36.962	25.002	717.000		18.900	2.636	0.780	0.818	2	1	1	9	14.84	9.59	0
Fira	Antiparos	37.055	25.082	72.800	0.51	4.590	6.305	0.140	0.026	2	1	1	9	6.49	1.13	0
Kydoni	Antiparos	36.953	25.072	0.088	0.35	0.210	238.277	0.099	0.219	0	1	0	9	13.35	9.69	2
Petalida	Antiparos	36.953	25.076	0.573	0.22	0.411	71.806	0.402	0.219	0	1	0	9	13.19	9.68	4
Strongyllo	Antiparos	36.950	24.962	578.000	0.95	6.540	1.131	5.390	4.740	1	1	0	9	20.01	13.85	6
Tsimintiri	Antiparos	36.976	25.019	5.558	0.50	1.390	25.008	0.263	4.740	0	1	0	9	14.97	9.13	5
Agia Kyriaki	Astypalea	36.549	26.404	21.465	0.54	2.720	12.672	2.030	0.011	1	0	0	19	5.79	4.22	21
Agios Fokas	Astypalea	36.578	26.455	1.397	0.25	0.915	65.474	0.042	2.350	0	1	0	19	10.3	9.43	3
Chondro	Astypalea	36.565	26.402	34.885	0.62	2.850	8.170	0.358	0.230	1	1	0	19	5.28	4.39	14
Chondropoulo	Astypalea	36.536	26.452	0.629	0.45	0.513	81.454	4.630	0.449	1	0	0	19	10.58	8.8	25
Fteno	Astypalea	36.541	26.451	1.621	0.55	0.629	38.813	4.080	0.465	1	0	0	19	10.3	8.59	13
Glyno	Astypalea	36.562	26.393	18.329	0.24	4.610	25.151	0.330	0.204	1	1	0	19	4.56	3.69	10
Kormo	Astypalea	36.546	26.408	1.402	0.03	0.805	57.424	2.500	0.011	1	0	0	19	6.48	4.74	8
Kounoupa	Astypalea	36.535	26.468	115.401	0.35	9.420	8.163	3.890	0.681	1	0	0	19	11.13	7.49	35
Koutsomyti	Astypalea	36.551	26.449	36.583	0.33	5.190	14.187	2.620	0.043	1		0	19	9.18	7.65	10
Megalo Diapori	Astypalea	36.571	26.387	0.255	0.30	0.285	111.842	0.110	0.204	1	1	0	19	4.37	3.91	2
Mikro Koutsomyti	Astypalea	36.556	26.455	0.131	0.45	0.308	235.763	2.510	0.043	0	0	0	19	10.41	9.02	4
Moni	Astypalea	36.544	26.444	0.657	0.24	0.627	95.425	3.870	0.331	1	0	0	19	9.69	8.04	3
Tigani	Astypalea	36.547	26.449	5.535	0.28	1.240	22.402	3.390	0.098	1	0	0	19	9.9	8.31	4
Agia Paraskevi	Dhonoussa	37.080	25.706	27.000	0.50	2.760	10.222	7.480	0.092	1	1	0	0	8.31	29.34	91
Chtenia	Dhonoussa	37.244	25.912	0.800	0.70	1.247	155.875	14.200	14.700	0	0	0	0	18.5	50.01	20
Skoulonissi	Dhonoussa	37.125	25.834	24.100	0.60	2.070	8.589	0.200	11.900	1	1	0	0	3.56	40.61	33
Strongyllo	Dhonoussa	37.069	25.705	36.000	0.30	2.810	7.806	8.020	0.516	1	1	0	0	8.98	29.34	215
Agios Ioannis	Folegandros	36.609	24.958	3.316	0.20	0.757	22.833	0.201	2.400	1	1	0	10	1.91	0.97834	1
Megalos Adelfos	Folegandros	36.612	24.987	3.942	0.15	0.907	23.013	2.450	0.093	0	0	0	10	4.41	3.31	50
Mikros Adelfos	Folegandros	36.615	24.991	3.033	0.05	0.863	28.454	2.790	0.093	0	0	0	10	4.69	3.58	7
Psathonissi	Ios	36.749	25.364	4.299		1.080	25.124	0.036	11.020	1	1	0	11	8.09	8.56	200
N Varvaronissi	Ios	36.650	25.387	0.374		0.550	147.016	0.186	11.020			0	11	15.19	12.98	49
Megalo Avelas	Iraklia	36.829	25.409	7.000	0.90	0.998	14.255	0.463	7.040	0	1	0	0	5.67	16.77	25
Venetiko	Iraklia	36.856	25.485	11.000	0.40	1.390	12.636	0.392	4.030	1	1	0	0	1.51	23.96	2
Astakida	Karpathos	35.886	26.820	86.879	0.63	5.420	6.239	31.790	0.103	1	0	0	54	50.83	54.29	10
Astakidopoulo	Karpathos	35.876	26.825	7.809	0.21	1.840	23.564	31.300	0.302	0	0	0	54	50.2	53.63	17
Cheli	Karpathos	35.894	26.816	1.056	0.03	0.543	51.352	32.890	0.103	0	0	0	54	52.87	55.83	2
Fokia	Karpathos	35.910	26.836	1.533	0.74	0.645	42.089	31.790	1.990	0	0	0	54	52.44	56.05	25
Daskalio	Koufonisi	36.888	25.604	1.760	0.75	0.626	35.550	4.630	2.370	0	1	0	0	6.64	23.95	5
Glaronissi	Koufonisi	36.917	25.605	15.600	0.10	2.920	18.718	1.090	2.610	2	1	0	0	3.18	24.85	90
Kato Koufonisi	Koufonisi	36.912	25.578	354.000	0.27	17.160	4.847	0.446	0.565	2	1		0	2.47	25.75	0
Keros	Koufonisi	36.892	25.648	1505.000	0.70	27.660	1.838	3.510	0.105	2	1	1	0	5.83	17.01	0

Islet	Region	Latitude	Longitude	Islet_ area	Veg_ cover	Islet_ coast	Coastarea_ ratio	Dist_ main	Dist_ colony	Grazers	Islet_ rats	Mammal_ pred	Fishing_ vessels	Dist_ landfill	Dist_ port	Gull_ pairs
Kopria	Koufonisi	36.987	25.638	13.500	0.03	1.530	11.333	4.290	7.820	2	0	0	0	5.36	26.5	99
Lazaros	Koufonisi	36.871	25.623	1.370	0.29	0.640	46.726	6.590	0.626	0	0	0	0	8.45	21.88	22
Lumbudiaris	Koufonisi	36.871	25.637	9.600	0.39	2.100	21.875	6.800	0.711	2	1	0	7	9	20.61	11
Megali Plaka	Koufonisi	36.878	25.627	3.080	0.15	0.811	26.345	5.870	0.515	2	1	0	0	8.07	21.96	0
Mikri Plaka	Koufonisi	36.879	25.634	1.206		0.565	46.831	5.930	0.711	1	1	0	0	8.14	21.17	4
Vulgaris	Koufonisi	36.879	25.688	9.200	0.15	1.520	16.522	8.560	4.110	1	1	0	0	10.93	16.4	7
Kalo Livadi	Kythnos	37.355	24.445	0.075	0.58	0.402	536.363	0.019	25.440	0	1	1	12	6.69	5.69	2
Baos	Mykonos	37.443	25.306	5.219	0.01	1.130	21.652	0.155	6.270	1	1	0	59	5.22	2.89	155
Choironissi	Mykonos	37.371	25.263	4.590	0.25	1.540	33.551	4.910	26.330	0	1	0	59	11.9	11.47	25
Chtapodia	Mykonos	37.411	25.568	45.200		5.050	11.173	9.750	26.330	1	1	0	59	17.45	21.67	200
Megalo Revmatiaris	Mykonos	37.395	25.261	9.600	0.61	1.670	17.396	3.860	2.290	2	1	0	59	10.53	9.21	0
Agia Nikolaos	Naxos	37.086	25.696	89.000	0.40	8.270	9.292	6.740	0.092	1	1	0	110	8.7	27.43	10
Aspronissi	Naxos	37.047	25.351	1.020	1.00	0.493	48.305	1.370	2.090	0	0	0	110	9.09	6.81	20
Chilies Vryses	Naxos	37.158	25.468	0.060	0.05	0.249	413.101	0.137	14.970	0		0	110	7.1	10.17	6
Mando	Naxos	37.089	25.362	2.500	0.51	0.839	33.574	0.075	7.230	1	1	0	110	4.85	1.95	0
Mikri Bigla	Naxos	37.023	25.358	0.200	0.40	0.298	148.860	0.495	0.601	0	0	0	110	11.12	9.24	14
Parthenos	Naxos	37.029	25.361	0.440	1.00	0.464	105.364	0.334	0.601	0	0	0	110	10.43	8.59	12
Agia Kali	Paros	37.130	25.225	0.966	0.52	0.503	52.019	0.267	0.167	0	0	0	157	10.43	8.08	1
Agios Artemios	Paros	37.131	25.227	0.416	0.57	0.397	95.581	0.462	0.167	0	0	0	157	10.69	8.35	14
Filitzi	Paros	37.125	25.290	14.366		1.780	12.391	0.172	2.620	1	1	0	157	10.23	7.42	175
Fonisses	Paros	37.152	25.290	0.620	0.25	0.881	142.033	0.461	0.333	0	0	0	157	11.17	8.91	25
Gaiduronisi	Paros	37.157	25.268	13.300	0.28	1.760	13.233	0.493	1.860	2	1	0	157	13.12	10.8	262
Galiatsos	Paros	37.131	25.246	0.573	0.37	0.444	77.445	0.212	0.646	1	1	0	157	11.59	9.69	2
Glarombi	Paros	36.979	25.110	19.465	0.40	1.900	9.761	1.410	0.099	1	0	0	157	8.93	6.74	120
Kambana	Paros	36.994	25.098	0.520	0.60	0.345	66.377	1.510	0.067	0	0	0	157	8.37	5.25	12
Makronisi	Paros	37.005	25.258	3.900	0.59	1.240	31.795	1.040	9.060	1		0	157	9.74	13.09	200
Mavronisi North	Paros	37.133	25.255	0.165	0.58	0.310	187.790	0.556	0.005	0	0	0	157	12.38	10.58	2
Mavronisi South	Paros	37.132	25.254	0.400	0.53	0.416	103.985	0.482	0.005	0	0	0	157	12.24	10.45	2
Ovriokastro	Paros	37.152	25.297	22.000	0.30	1.490	6.773	0.789	0.333	2	1	0	157	10.54	8.42	248
Panterionissi	Paros	36.971	25.119	43.722	0.50	3.100	7.090	2.010	0.101	1	1	0	157	9.26	7.7	0
Preza	Paros	36.989	25.101	1.459	0.13	0.528	36.176	1.390	0.493	0	0	0	157	8.55	5.78	35
Tigani	Paros	36.977	25.116	6.370	0.60	1.320	20.724	1.540	0.099	0	1	0	157	8.98	7.31	9
Tourlos	Paros	37.161	25.281	2.679	0.95	0.863	32.212	1.350	0.067	0	1	0	157	8.22	4.94	84
Chamili	S Aegean	35.863	26.229	31.026	0.28	4.880	15.729	60.370	19.710	0	1	0	0	68.34	67.47	35
Katsika	S Aegean	36.326	26.730	1.052		0.473	44.958	36.370	2.530	0	0	0	0	43.94	41.36	14
Megalo Divouni	S Aegean	35.826	26.465	19.965	0.23	3.270	16.379	57.890	0.286	0	1	0	0	82.62	75.87	12
Megalo Karavonissi	S Aegean	36.001	26.435	1.365	0.05	0.530	38.827	57.030	0.572	0	0	0	0	63.21	61.17	10
Megalo Sofrano	S Aegean	36.074	26.401	108.000	0.27	8.590	7.954	47.440	0.717	2	1	0	0	53.77	51.82	7

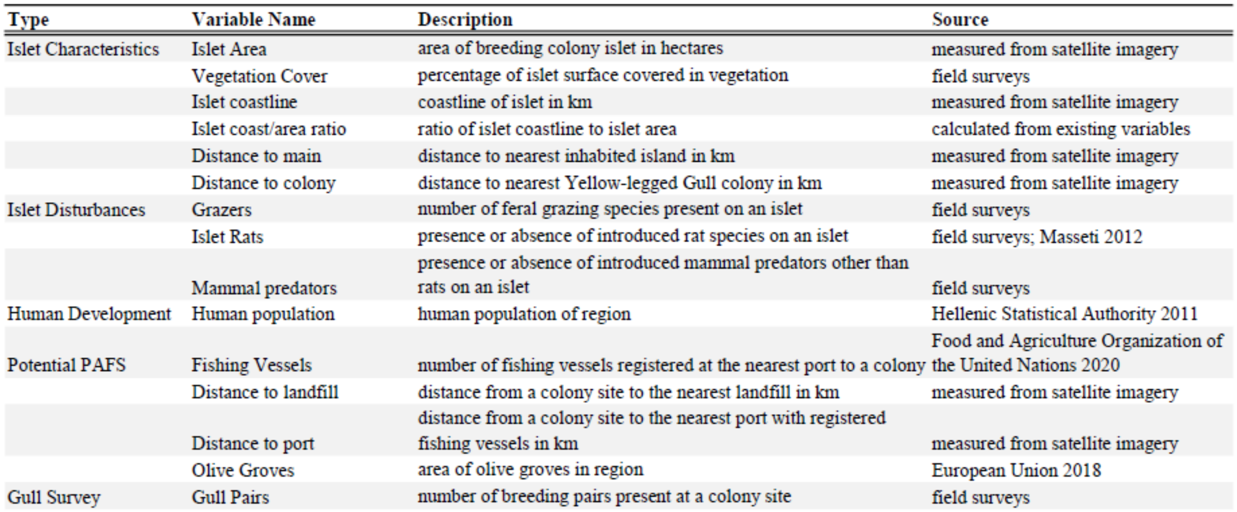
Islet	Region	Latitude	Longitude	Islet_ area	Veg_ cover	Islet_ coast	Coastarea_ ratio	Dist_ main	Dist_ colony	Grazers	Islet_ rats	Mammal_ pred	Fishing_ vessels	Dist_ landfill	Dist_ port	Gull_ pairs
Megalos Adelfos	S Aegean	36.422	26.621	17.541	0.19	2.240	12.770	21.670	1.280	1		0	0	29.42	27.27	17
Mesonissi	S Aegean	36.300	26.740	38.003	0.21	3.170	8.342	38.880	0.396	2	0	0	0	46.14	43.88	3
Mikro Divouni	S Aegean	35.824	26.454	15.442	0.23	1.950	12.628	57.560	0.286	0	1	0	0	82.75	76.79	5
Mikro Karavonissi	S Aegean	35.994	26.436	0.115	0.03	0.284	246.580	57.770	0.572	0	0	0	0	63.96	61.92	2
Mikro Sofrano	S Aegean	36.047	26.409	7.184	0.20	1.800	25.056	51.230	0.755	2	1	0	0	57.45	55.47	5
Mikros Adelfos	S Aegean	36.419	26.599	9.870		1.600	16.210	20.980	1.280	1		0	0	28.19	25.93	100
Plakida	S Aegean	36.285	26.745	46.199	0.25	4.330	9.372	40.270	0.396	1	0	0	0	47.33	45.06	20
Sochas	S Aegean	36.057	26.405	2.011	0.12	0.747	37.131	50.390	0.717	0	0	0	0	56.63	54.64	5
Syrina	S Aegean	36.347	26.676	696.000	0.33	20.290	2.915	29.670	3.640	2	1	0	0	36.74	34.21	0
Nea Kammeni	Santorini	36.405	25.397	333.000	0.10	11.940	3.586	1.480	0.294	0	1	0	124	1.93	7.23	100
Agriloussa	Schinoussa	36.835	25.525	8.400	0.54	1.620	19.286	1.690	2.520	1	1	0	0	2.74	25.58	20
Andreas	Schinoussa	36.862	25.622	4.500	0.22	1.120	24.889	6.970	0.626	0	0	0	0	8.28	21.67	22
Aspronissi	Schinoussa	36.856	25.546	3.800	0.80	0.971	25.556	0.214	2.520	0	1	0	0	1.67	28.28	99
Fidussa	Schinoussa	36.845	25.522	63.200	0.25	5.300	8.386	0.067	0.423	2	1		0	1.26	25.4	0
Garmbia	Serifos	37.110	24.484	0.321	0.20	0.384	119.575	0.115	1.690	0		0	9	1.11	4.61	56
Glaronissi	Serifos	37.124	24.475	0.059	0.15	0.230	386.962	0.041	1.690	0	0	0	9	2.12	4.23	17
Vous	Serifos	37.143	24.562	6.729	0.72	1.750	26.006	1.790	7.480	1	0	0	9	6.37	3.82	118
Kitriani	Sifnos	36.904	24.726	72.768	0.53	6.210	8.534	0.365	19.880	2	1	0	10	10.31	10.21	7
Avoladonisi	Sikinos	36.685	25.086	0.468	0.05	0.409	87.533	0.286	6.170	0		0	0	4.65	5.24	10
Kalogeros	Sikinos	36.633	25.055	7.361	0.67	1.740	23.638	0.393	5.870	1		0	0	10.07	9.03	78
Kardiotissa	Sikinos	36.630	25.018	133.530	0.30	7.320	5.482	2.640	1.750	1	1	0	0	6.38	5.29	0
Arkos	Skiathos	39.150	23.518	33.166	0.98	3.800	11.458	0.806	0.428	1	1	0	73	6.78	2.12	9
Aspronissi	Skiathos	39.171	23.521	14.589	0.84	1.840	12.612	0.405	1.430	1	1	0	73	7.14	2.44	160
Daskalio	Skiathos	39.161	23.495	0.088	0.90	0.143	161.854	0.296	0.963	0	0	0	73	5.08	0.29956	6
Maragos	Skiathos	39.151	23.500	7.133	0.83	1.430	20.047	0.411	0.950	1	0	0	73	5.57	1.25	185
Repi	Skiathos	39.147	23.528	2.424	0.77	0.981	40.489	2.110	0.428	1	1	0	73	8	3.41	165
Tsugria	Skiathos	39.123	23.500	109.000	0.87	5.350	4.908	2.530	0.898	2	1	0	73	6.37	3.57	1
Tsugriaki	Skiathos	39.125	23.482	5.928	0.71	1.410	23.785	1.320	0.898	1	0	0	73	5.57	4.02	310
Agathopes	Syros	37.387	24.876	2.167	0.70	0.807	37.219	0.039	7.920	1	1	1	85	10.85	7.59	0
Ambelos	Syros	37.385	24.951	0.130	0.21	0.496	381.431	0.010	4.730	0	1	1	85	9.4	5.51	0
Delfini	Syros	37.457	24.896	0.114		0.202	176.853	0.163	4.790	0	0	0	85	4.21	4.46	3
Didymi	Syros	37.427	24.974	38.519	0.75	4.960	12.877	1.060	0.216	1	1	0	85	5.09	2.56	43
Kommeno	Syros	37.465	24.951	0.170	0.78	0.351	206.229	0.054	4.140	0	1	0	85	0.95031	3.47	1
Strongyllo	Syros	37.425	24.985	3.978	0.87	1.100	27.652	1.890	0.216	0	0	0	85	6.19	4.01	89
Apokofto	Tinos	37.614	25.030	0.383		0.424	110.483	0.014	5.640	0	1		28	7.74	14.49	53
Dysvato	Tinos	37.672	24.967	0.670	0.00	0.360	53.683	0.560	0.111	0	0	0	28	15.07	22.62	24
Kalogeros	Tinos	37.671	24.970	2.263	0.72	0.750	33.157	0.140	0.111	0	0	0	28	15.21	21.97	64
Planitis	Tinos	37.659	25.067	5.077	0.17	1.690	33.290	0.159	5.640	1	1		28	8.32	15.92	15

2. *Regional aggregate data.*



Region	Main_ area	Human_ pop	Pop_ density	Fishing_ vessels	Avg_dist_ port	Avg_dist_ landfill	Total_ isletarea	Olive_ grove	Total_ gullpairs
Andros	383.022	9221	24.074	38	3.475	12.937	0.226	20.503	232
Tinos	197.044	8636	43.828	28	14.805	7.868	0.084	1.129	68
Sifnos	77.371	2625	33.927	10	10.210	10.310	0.728	10.104	7
Serifos	74.331	1420	19.104	9	4.088	4.450	0.071	0.000	191
Syros	84.069	21507	255.826	85	3.558	5.760	0.451	0.284	136
Mykonos	86.125	10134	117.666	59	20.537	16.833	0.646	0.000	225
Ios	108.713	2024	18.618	11	9.430	9.487	0.047	0.000	249
Folegandros/Sikinos	74.060	1038	14.016	10	6.495	7.447	1.516	0.000	146
Anafi	38.636	271	7.014	0	4.457	5.318	1.619	0.000	76
Anydro	0.878	0	0.000	0	27.380	25.290	0.878	0.000	50
Amorgos	121.464	1973	16.243	7	16.288	16.826	4.128	1.316	89
Donousa	13.625	167	12.233	0	44.157	9.198	0.249	0.000	53
Small Cyclades	31.992	767	23.975	0	24.982	4.344	20.122	0.000	406
Astypalea	96.420	1334	13.835	19	6.742	8.702	2.383	0.000	152
Paros	196.755	13715	69.706	157	9.240	10.897	1.226	4.160	773
Antiparos	35.090	1211	34.511	9	6.271	9.295	13.855	0.000	157
Naxos	389.434	17970	46.144	110	18.890	9.523	1.746	22.015	666
Alonnisos	64.000	2712	42.375	42	21.357	22.497	32.691	16.132	358
Skiathos	48.990	6088	124.245	73	2.937	6.361	1.723	12.452	836

3. *Name, description, and source of all variables tested.*

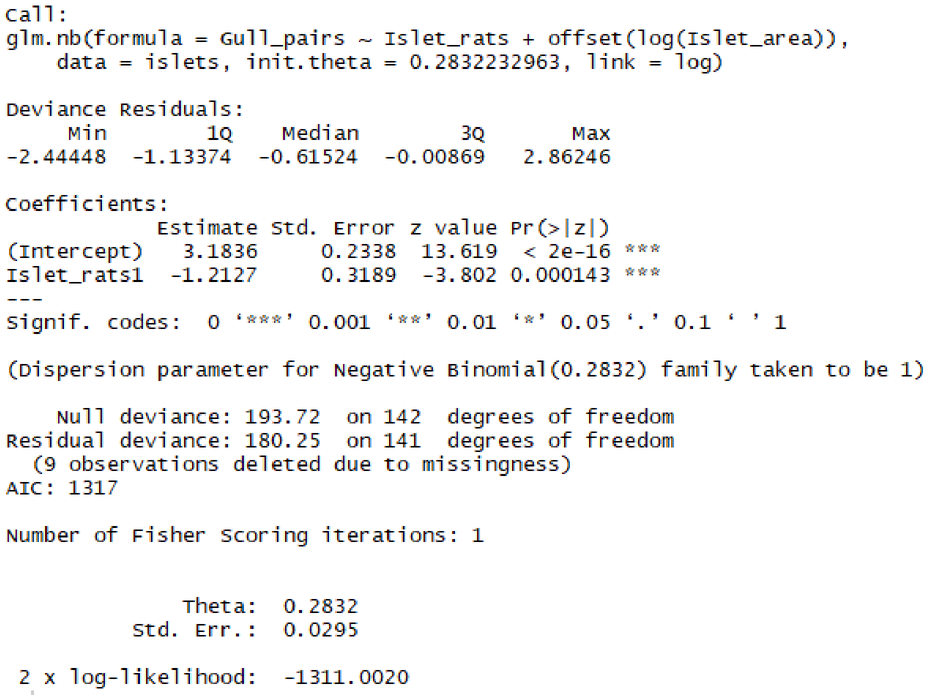


Type	Variable Name	Description	Source
Islet Characteristics	Islet Area	area of breeding colony islet in hectares	measured from satellite imagery
	Vegetation Cover	percentage of islet surface covered in vegetation	field surveys
	Islet coastline	coastline of islet in km	measured from satellite imagery
	Islet coast/area ratio	ratio of islet coastline to islet area	calculated from existing variables
	Distance to main	distance to nearest inhabited island in km	measured from satellite imagery
	Distance to colony	distance to nearest Yellow-legged Gull colony in km	measured from satellite imagery
Islet Disturbances	Grazers	number of feral grazing species present on an islet	field surveys
	Islet Rats	presence or absence of introduced rat species on an islet	field surveys; Masseti 2012
	Mammal predators	presence or absence of introduced mammal predators other than rats on an islet	field surveys
Human Development	Human population	human population of region	Hellenic Statistical Authority 2011
Potential PAFS	Fishing Vessels	number of fishing vessels registered at the nearest port to a colony	Food and Agriculture Organization of the United Nations 2020
	Distance to landfill	distance from a colony site to the nearest landfill in km	measured from satellite imagery
	Distance to port	distance from a colony site to the nearest port with registered fishing vessels in km	measured from satellite imagery
	Olive Groves	area of olive groves in region	European Union 2018
Gull Survey	Gull Pairs	number of breeding pairs present at a colony site	field surveys

4. *Pearson's correlation coefficients for local-level continuous independent variables. Those marked with an asterisk (*) are significant with a p-value less than 0.05.*

	Islet Area	**Vegetation Cover**	**Islet Coastline**	**Islet Coast/Area ratio**	**Distance to main**	**Distance to colony**	**Distance to landfill**	**Distance to port**	**Fishing Vessels**
Islet Area		0.08	0.89*	-0.17*	0.01	0.22*	0.1	0.11	-0.07
Vegetation Cover	0.08		0.04	-0.01	-0.23*	0.05	-0.17*	-0.21*	0.20*
Islet Coastline	0.89*	0.04		-0.27*	0.09	0.14	0.16	0.18*	-0.16
Islet Coast/Area ratio	-0.17*	-0.01	-0.27		-0.13	0.15	-0.11	-0.17*	0.12
Distance to main	0.01	-0.23	0.09*	-0.13		-0.06	0.94*	0.88*	-0.29*
Distance to colony	0.22*	0.05	0.14	0.15	-0.06		-0.01	0.04	-0.07
Distance to landfill	0.10	-0.17	0.16*	-0.11	0.94*	-0.01		0.89*	-0.22*
Distance to port	0.11	-0.21	0.18*	-0.17*	0.88*	0.04	0.89*		-0.34*
Fishing Vessels	-0.07	0.2	-0.16*	0.12	-0.29*	-0.07	-0.22*	-0.34*	

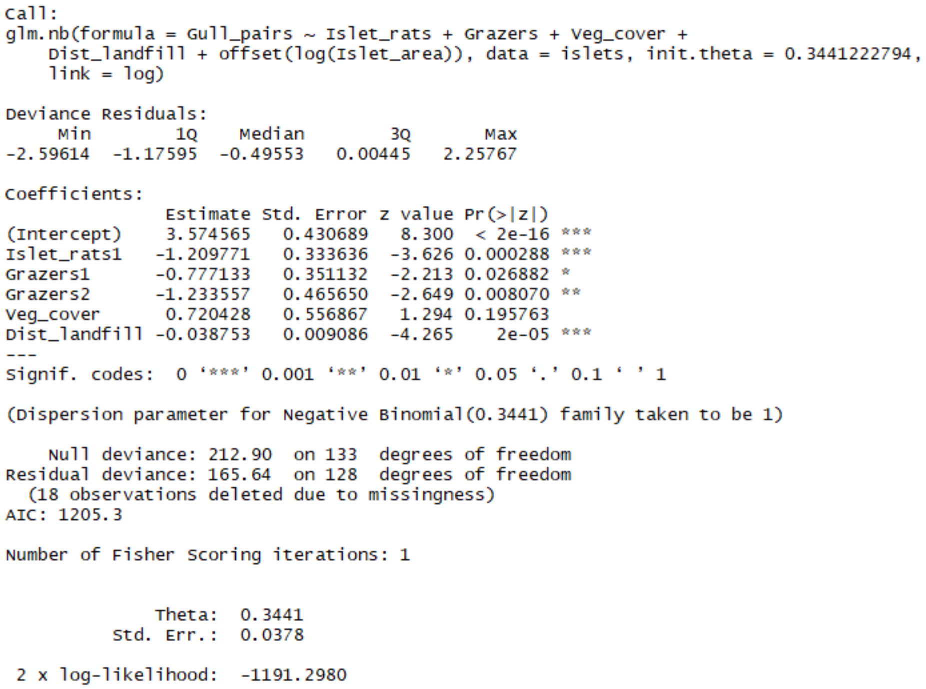
6. *R output for all local models tested.*



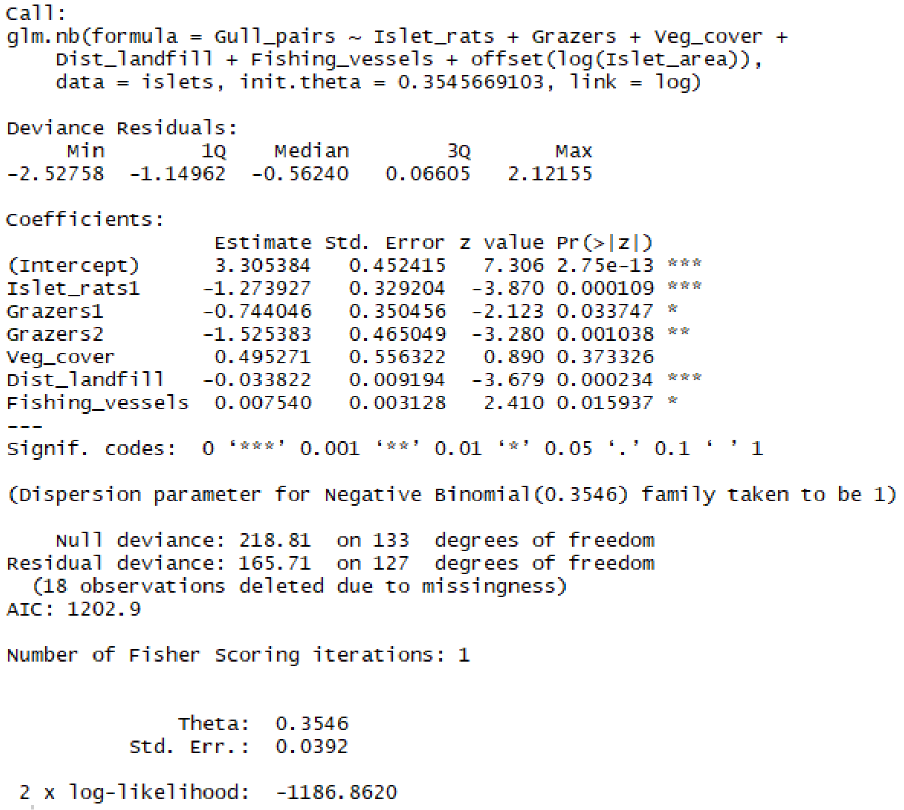
```
Call:
glm.nb(formula = Gull_pairs ~ Islet_rats + offset(log(Islet_area)),
    data = islets, init.theta = 0.2832232963, link = log)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-2.44448  -1.13374  -0.61524  -0.00869   2.86246

Coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)   3.1836     0.2338  13.619  < 2e-16 ***
Islet_rats1  -1.2127     0.3189  -3.802 0.000143 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.2832) family taken to be 1)

    Null deviance: 193.72  on 142  degrees of freedom
Residual deviance: 180.25  on 141  degrees of freedom
  (9 observations deleted due to missingness)
AIC: 1317

Number of Fisher Scoring iterations: 1


              Theta:  0.2832
          Std. Err.:  0.0295

 2 x log-likelihood:  -1311.0020
```

```
Call:
glm.nb(formula = Gull_pairs ~ Islet_rats + Grazers + offset(log(Islet_area)),
    data = islets, init.theta = 0.3033643263, link = log)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-2.36885  -1.19515  -0.58933  -0.02975   1.99670

Coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)   3.3699     0.2531  13.312  < 2e-16 ***
Islet_rats1  -0.6716     0.3388  -1.982   0.0475 *
Grazers1     -0.7743     0.3553  -2.179   0.0293 *
Grazers2     -1.9591     0.4679  -4.187 2.83e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.3034) family taken to be 1)

    Null deviance: 206.40  on 142  degrees of freedom
Residual deviance: 178.23  on 139  degrees of freedom
  (9 observations deleted due to missingness)
AIC: 1307.6

Number of Fisher Scoring iterations: 1


              Theta:  0.3034
          Std. Err.:  0.0318

 2 x log-likelihood:  -1297.6020
```

```
Call:
glm.nb(formula = Gull_pairs ~ Islet_rats + Grazers + Veg_cover +
    offset(log(Islet_area)), data = islets, init.theta = 0.3202519179,
    link = log)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-2.47202  -1.18529  -0.58761  -0.04055   2.34064

Coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)   2.9532     0.3638   8.118 4.72e-16 ***
Islet_rats1  -1.1910     0.3447  -3.455  0.00055 ***
Grazers1     -0.5600     0.3562  -1.572  0.11588
Grazers2     -1.1919     0.4813  -2.476  0.01327 *
Veg_cover     0.7361     0.5647   1.303  0.19241
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.3203) family taken to be 1)

    Null deviance: 199.3  on 133  degrees of freedom
Residual deviance: 166.8  on 129  degrees of freedom
  (18 observations deleted due to missingness)
AIC: 1215.4

Number of Fisher Scoring iterations: 1


              Theta:  0.3203
          Std. Err.:  0.0348

 2 x log-likelihood:  -1203.4070
```



```
Call:
glm.nb(formula = Gull_pairs ~ Islet_rats + Grazers + Veg_cover + 
    Dist_landfill + offset(log(Islet_area)), data = islets, init.theta = 0.3441222794, 
    link = log)

Deviance Residuals: 
     Min        1Q    Median        3Q       Max  
-2.59614  -1.17595  -0.49553   0.00445   2.25767  

Coefficients:
               Estimate Std. Error z value Pr(>|z|)    
(Intercept)    3.574565   0.430689   8.300  < 2e-16 ***
Islet_rats1   -1.209771   0.333636  -3.626 0.000288 ***
Grazers1      -0.777133   0.351132  -2.213 0.026882 *  
Grazers2      -1.233557   0.465650  -2.649 0.008070 ** 
Veg_cover      0.720428   0.556867   1.294 0.195763    
Dist_landfill -0.038753   0.009086  -4.265    2e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.3441) family taken to be 1)

    Null deviance: 212.90  on 133  degrees of freedom
Residual deviance: 165.64  on 128  degrees of freedom
  (18 observations deleted due to missingness)
AIC: 1205.3

Number of Fisher Scoring iterations: 1


              Theta:  0.3441 
          Std. Err.:  0.0378 

 2 x log-likelihood:  -1191.2980 
```



```
Call:
glm.nb(formula = Gull_pairs ~ Islet_rats + Grazers + Veg_cover + 
    Dist_landfill + Fishing_vessels + offset(log(Islet_area)), 
    data = islets, init.theta = 0.3545669103, link = log)

Deviance Residuals: 
     Min        1Q    Median        3Q       Max  
-2.52758  -1.14962  -0.56240   0.06605   2.12155  

Coefficients:
                 Estimate Std. Error z value Pr(>|z|)    
(Intercept)      3.305384   0.452415   7.306 2.75e-13 ***
Islet_rats1     -1.273927   0.329204  -3.870 0.000109 ***
Grazers1        -0.744046   0.350456  -2.123 0.033747 *  
Grazers2        -1.525383   0.465049  -3.280 0.001038 ** 
Veg_cover        0.495271   0.556322   0.890 0.373326    
Dist_landfill   -0.033822   0.009194  -3.679 0.000234 ***
Fishing_vessels  0.007540   0.003128   2.410 0.015937 *  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.3546) family taken to be 1)

    Null deviance: 218.81  on 133  degrees of freedom
Residual deviance: 165.71  on 127  degrees of freedom
  (18 observations deleted due to missingness)
AIC: 1202.9

Number of Fisher Scoring iterations: 1


              Theta:  0.3546 
          Std. Err.:  0.0392 

 2 x log-likelihood:  -1186.8620 
```