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Ph.D. thesis

RESEARCH APPLIED TO THE CONSERVATION OF SEABIRDS BREEDING ON ISLANDS OF THE WESTERN MEDITERRANEAN

Investigación aplicada a la conservación de aves marinas nidificantes en islas del Mediterráneo occidental

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Memoria presentada por Alejandro Martínez Abraín para optar al título de Doctor en Ciencias Biológicas en el Departamento de Biología Animal (Vertebrados), Facultad de Biología, Universitat de Barcelona, bajo la dirección del Dr. Daniel Oro de Rivas.

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Agradecimientos

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The Mediterranean Sea in its history

In the upper Oligocene (25 million years B.P) the African plate first made contact with south-west Asia dividing the Tethys Sea into two parts, the southern one being the ancestor of the modern Mediterranean Sea. During the last phase of the Miocene era (ca. 6 million years B.P) Africa collided with the southwestern extreme of Eurasia closing the Mediterranean Sea at its western end. Owing to the prevailing warm climatic conditions, the Mediterranean seafloor dried up for 3 thousand years (5.6-5.3 million years B.P) and probably in less than a thousand years. Some 5.3 million years BP new tectonic movements broke open the land bridge between northern Africa and the Iberian Peninsula, allowing the Atlantic Ocean to surge through the Straits of Gibraltar. Present-day main characteristics of the Mediterranean basin (i.e. size, shape, physiography, geomorphology) were finally established approximately 5 million years B.P, at the beginning of the Pliocene (see Rodríguez 1982; Blondel and Aronson 1999).

Mediterranean-type climate was established some 3.2 million years ago. However, about 2.5 million years B.P (i.e. by the end of the Pliocene/begining of the Pleistocene) massive ice sheets started to grow in the Northern Hemisphere and major climatic oscillations occurred during most of the Pleistocene (Webb and Bartlein 1992). During the last glacial maxima (ca. 30 000 years B.P) the sea level dropped by some 100-150 m worldwide and many of the ca. 5 000 islands of the Mediterranean were only headlands within an enlarged Mediterranean area. However, most of the larger islands have been entirely disconnected from mainland since at least the Messinian Crisis (Blondel and Aronson 1999).

The Mediterranean Sea and the development of its modern seabird fauna

The days of splendour of seabirds in the Mediterranean (both in number of species and in abundance) occurred long ago. During the glacial episodes of the Pleistocene, seabirds breeding further north were forced southwards by the incoming ice sheet. Many islands and cliffs of the Mediterranean were then occupied by large colonies of seabirds, typical of the northern Atlantic Ocean. For example, fossil remains of the flightless great auk (*Pinguinus impenis*), as well as of guillemots (*Uria aalge*), are known from the upper Pleistocene of the Rock of Gibraltar (Sánchez 1996).

Many northern species moved back north once the last ice age was over. However, other Atlantic species stayed and gave rise to new species and subspecies. For example, all four petrel species (O. Procellariiformes) presently breeding in the Mediterranean probably colonised the Mediterranean basin during the last ice age (see Bretagnolle and Zotier 1998). Presumably *Puffinus* entered the Mediterranean first from the Atlantic Ocean, followed by *Calonectris* and *Hydrobates* (op.cit.). This chronological sequence of colonisation led to further differentiation of the genus *Puffinus*, now represented in the Mediterranean by two species, Mediterranean Shearwater *Puffinus yelkouan* and Balearic Shearwater *Puffinus mauretanicus*, endemic

to the Balearic islands (see Heidrich et al. 1998). *Calonectris* has differentiated so far at the subspecies level (*Calonectris diomedea diomedea*), Atlantic and Mediterranean subspecies being part of the same panmictic metapopulation (Randi et al. 1989). Finally, Mediterranean storm-petrels seem not to have differentiated yet from the Atlantic *Hydrobates pelagicus*, despite some authors defended their subspecific status a couple of decades ago (see Hemery and d'Elbee 1985). Hence, the present day seabird fauna of the Mediterranean is characterized by a paucity of species and a relatively high degree of endemism.

Humans and seabird population changes in the western Mediterranean

Pleistocene populations of western Mediterranean seabirds were for sure larger than present day populations, especially in large isolated islands with no terrestrial predators, like the Balearic islands (Alcover et al. 1981). However, the arrival of the Neolithic culture to this area, some 4-6 000 years ago, changed abruptly the *status quo* and initiated a seabird population decline that continues today. Although seabirds in the western Mediterranean are no longer captured for fat, flesh, feathers or bait nor their eggs are collected, human impact continues through overfishing, marine pollution, bycatch of birds in fishing gears, human presence in suitable breeding habitats and presence of human-associated fauna. Despite protection of colonies, it is likely that present human impact on seabirds (e.g. mortality in longline fisheries) is more threating than past uses. Adult mortality is especially dangerous for longlived birds characterized by low reproductive rates, and industrial fisheries are a non-selective cause of mortality that affect both adult and immature birds (see Belda and Sánchez 2001 and references therein). On the contrary old uses were mainly addressed to the collection of eggs and chicks within subsistence economies.

It is also true that fishing activities may have a positive influence on seabird population demography, mainly by providing abundant and highly predictable food (see Arcos 2001). Trawling and purse-seine fisheries somehow occupy the empoverished niche of large predator fish and cetaceans as food providers for commensal seabirds (Furness and Monaghan 1987). However, overfishing by these fishing fleets mortgage future availability of food resources and changing policies on fishing gears and fishing calendars, may have catastrophic consequences at the short run (Oro et al. 1996a; Oro et al. 1996b; Oro et al. 1997) and also at the long run if not implemented following appropriate biological criteria.

Accounting for seabird population dynamics

Conventionally, population change (see Croxall and Rothery 1991) is summarized by the equation:

Population change = (Recruitment + Immigration) – (Mortality + Emigration)

Changes in the demography of seabird species can be determined by a number of environmental factors (i.e food availability, breeding space, predation, disease), affecting the parameters of this equation. These factors may act either through density-

dependent (i.e. population regulation or balancing around an equilibrium) or density-independent processes (e.g. frequency of weather catastrophes) (see Begon and Mortimer 1986). Considering that seabird populations are organized as sets of local populations occupying habitat patches connected to one another by the movement of individuals (i.e. forming metapopulations), transfer processes (i.e. immigration/emigration processes) play a very important role in changes in population size, apart of born-death processes.

Human activities may affect negatively the terms of the equation typically by increasing mortality and fostering permanent emigration when changing food availability.

Background and focus of this thesis

This thesis was developed within the frame of a conservation project addressed to the protection of two western Mediterranean islands (i.e. Columbretes and Benidorm Islands). Research was directed to (a) take advantage of a relatively long series of data on seabird monitoring available for the Columbretes Islands and (b) fill in research gaps to explain population trends of the six insular species breeding in these two sites: shag *Phalacrocorax aristotelis*, Cory's shearwater *Calonectris diomedea diomedea*, European storm-petrel *Hydrobates pelagicus*, Audouin's gull *Larus audouinii*, yellow-legged gull *Larus cachinnans* and Eleonora's falcon *Falco eleonorae*, a raptor breeding exclusively on Mediterranean islands.

Despite having several insular species breeding on the same island, the aim of this thesis was not, however, to approach the structure of the seabird community (see Ballance et al. 1997). Interesting aspects of community organization (e.g. temporal succession on occupancy of the same breeding sites by different species) are certainly worth being explored in these small islands in the future. Nevertheless, work at the population level was more appropriate to obtain applied conclusions from the information cumulated so far (i.e. mainly data on population size and breeding success over more than a decade).

This thesis includes both works discussing the role of certain **biological factors (Section I)** on seabird population dynamics and assessing the effects of **human activities (Section II)** on population numbers. Each section is preceded by an introductory chapter dealing, in a more informal manner, with the topic approached by that section.

Section I approaches especifically the influence of immigration and environmental stochasticity on the population dynamics of shags (**Chapter 1**), the role of philopatry and conspecific atraction in breeding site selection in Audouin's gull (**Chapter 2**), the determinants of colony-site dynamics in Audouin's gull (**Chapter 3**), the movements of yellow-legged gulls from the Mediterranean to the Atlantic (**Chapter 4),** the presence of inmigrant Cory's shearwaters from Atlantic colonies in Mediterranean colonies (**Chapter 5**).

Section II includes works discussing the role of landfills in disease dispersal among yellow-legged gulls (**Chapter 6**), the role of discards of the trawling fishing fleet as a food source during the summer for gulls (**Chapter 7**), the role of fishing discards on the dynamics of a colony of Audouin's gull facing local extinction

(**Chapter 8**) and the impact of tourism on a small colony of the Eleonora's falcon (**Chapter 9**).

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Section I

Biological factors and seabird population dynamics

Introduction to Section I: Ecology and behavior of seabirds

Daniel Oro (IMEDEA) and Alejandro Martínez-Abraín (IMEDEA) (submitted as a book chapter to Marine Ecology, Enciclopedia of Life Support Systems, edited by Eolss Publishers-UNESCO, Oxford, UK, [http://www.eolss.net]).

Summary

Seabirds are marine predators and occupy the upper trophic level in marine food webs. They are present in all marine ecosystems and oceans of the world, from coastline to pelagic and open seas. Seabirds feed on a wide range of marine organisms, from zooplankton to relatively large fish and squid. They also use a wide variety of foraging techniques, from surface feeders to divers, which can feed at more than 200 m deep. Seabirds can forage near breeding colonies, not far from the coastline, or at very long distances during days or weeks out in the open ocean. Morphological and physiological adaptations for their marine life style are diverse. Seabirds comprise several different families of birds inhabiting marine ecosystems, and each group has its own ecological features. However, all seabirds share several life history traits: high adult survival, high mean generation time, progressive access to reproduction at relatively old ages, low reproductive rate and low number of predators. All these traits determine a rather k evolutionary strategy based on the high residual reproductive value established on the high number of reproductive chances in the life of an individual. Dynamics of seabird local population are not only determined by birth-death processes, but also by emigration-immigration processes, which connect populations at metapopulation scale. Seabirds compete with other marine predators, especially with human fisheries. The relationships between both groups are complex and represent a bulk of interactions, some of them beneficial and others detrimental for seabirds. Conservation of seabirds is essential and must be part of a well policy-oriented progress towards sustainable world development.

Consider a small Mediterranean archipelago by the beginning of March. The first Cory's Shearwaters of the season are homing from their wintering quarters in the waters of the Benguela Current off South Africa and Namibia, several thousand kilometers away. The old couples come to visit their old nesting tunnels as soon as it gets dark and some stay overnight and copulate protected by the darkness of their burrows. By the beginning of May, the birds that were present in their burrows during the day, start visiting the colony only at night, and during the second fortnight of the month almost all breeding birds in the colony lay one ovate white egg representing some 11% of the weight of the adult female. If the egg is lost, there will be no clutch replacement and the breeding season will end up unsuccessfully. As soon as the egg is laid, typically the female will begin incubating and the male will take up the task after a few uninterrupted days. This process goes on and on, day and night, for some fifty days until the egg hatches and a helpless brown-downed nestling comes to life by mid July. The chick will be brooded day and night by the adults during a few days, until homeothermy is attained. Afterwards, the nestling will be fed intermittently (mainly fish and squid) and only at night during three long months. Late in October they will leave their natal colony heading towards their Atlantic wintering quarters. These birds will not recruit as breeding adults until at least age seven. The same adult couple will return to breed next year, at the same colony and the same burrow, unless one of the members of the pair dies during wintertime and a new pair is formed. This cycle can go on and on for several decades…

We could describe the breeding cycle of many other seabird species and we would find some strikingly similar features in their ecology and behavior. Indeed, all marine birds are long-lived species, make small contributions to their populations every breeding season, albeit high effort is invested, take several years to reach maturity and have a high life expectancy. These life-history traits basically reveal the main life strategy of seabirds: maximizing life-time reproductive success. Seabirds (especially pelagic species) usually breed on islands, that is, environments typically free of predators and disease and these factors are selective pressures, which favor seabird species with long-lived individuals. In addition, the sea surrounding colonies is usually either an ecological desert or a rich source of food, but experimenting unpredictable ups and downs. In either case, the advantage is again for long-lived individuals since the currency in use is not how well you do in a given year (in terms of reproductive output) but how long you are able to survive and attempt reproduction annually. Hence, the longer you live the higher your fitness, if you are a seabird. Most seabirds are good examples of some evolutionary trade offs such as those between current reproduction and survival and current reproduction and future reproduction.

Taxonomy and distribution of seabirds

There are over 9,000 bird species on our planet of which only roughly three per cent are seabirds. One would say, after watching those figures, that becoming a seabird is not an easy evolutionary enterprise. However, we have to take into consideration that modern bird phylogenies, based on molecular techniques (DNA-DNA hybridization), place all (eight) seabird families (Laridae, Phaethontidae, Sulidae, Phalacrocoracidae, Pelecanidae, Fregatidae, Spheniscidae and Procellariidae) within the order Ciconiiformes, the youngest avian order only after Passeriformes (Table 1).

Table 1. Taxonomic groups of seabirds

Order	Suborder	Family	No. of species	Common names
Ciconiiformes	Charadrii	Laridae	130	jaegers, skuas / skimmers / gulls / terns / noddies / auks, murres, puffins
	Ciconii	Phaethontidae	3	tropicbirds
		Sulidae	9	bobbies, gannets
		Phalacrocoracidae	38	cormorants, shags
		Pelecanidae	9	pelicans / shoebill
		Fregatidae	5	frigatebirds
		Spheniscidae	17	penguins
		Procellariidae	116	petrels, shearwaters, diving-petrels / albatrosses / storm-petrels

In total, 327 species of seabirds are comprised, although certain other birds such as divers, seaducks, phalaropes and grebes are also sometimes classed as seabirds. Classical phylogenies include seabirds in at least four taxonomic orders: Sphenisciformes, Procellariiformes, Pelecaniformes and Charadriiformes and twelve families: Spheniscidae, Diomedeidae, Procellariidae, Hydrobatidae, Pelecanoididae, Phaethontidae, Pelecanidae, Phalacrocoracidae, Fregatidae, Stercoraridae, Laridae, Rynchopidae, Alcidae. These old phylogenies (still the most popular ones) based mostly on similarity of phenotypical traits (sharing of traits among related present-day species), used to place marine birds among the oldest bird groups (e.g. penguins were considered the oldest birds only after tinamous and giant flightless birds like kiwis, emus, cassowaries, rheas and ostrich).

Obviously, phylogenetic relationships derived from comparative anatomy can be very misleading since similarities could be due to adaptive convergence (analogous characters) and not to common ancestry (homologous characters). The analysis of similarity including ethological, physiological and biochemical clues strongly increases the chances of getting a right phylogenetic classification, albeit it does not remove completely the confounding effect of adaptive convergence. It seems clear however that some morphological characters used traditionally in bird systematics (e.g. relations established among toes by membranes) are not the most appropriate to avoid mistaking analogy and common ancestry. For example, traditional classifications include within Pelecaniformes all groups of seabirds with the four toes joined by membranes (totipalmate feet) whereas new classifications suggest that this feature has been acquired independently by the tropicbirds, the pelicans, the cormorants, darters and gannets and the frigatebirds.

We compare (see Table 2) the most widely accepted traditional classification of the Class Aves (that by Morony, Bock and Farrand published in 1975) with that from Sibley and Monroe based on modern molecular techniques and published in 1988.

Table 2. Classification of the Class Aves. Orders including seabird families are highlighted in bold type.

TRADITIONAL		MODERN	
ORDER	FAMILIES	ORDER	FAMILIES
Struthioniformes	5	Struthioniformes	4
Tinamiformes	1	Tinamiformes	1
Sphenisciformes	1	Craciformes	2
Gaviiformes	1	Galliformes	3
Podicipediformes	1	Anseriformes	4
Procellariiformes	4	Turniciformes	1
Pelecaniformes	6	Piciformes	5
Ciconiiformes	5	Galbuliformes	2
Phoenicopteriformes	1	Bucerotiformes	2
Anseriformes	2	Upupiformes	3
Falconiformes	4	Trogoniformes	1
Galliformes	4	Coraciiformes	9
Gruiformes	12	Coliiformes	1
Charadriiformes	16	Cuculiformes	6
Columbiformes	2	Psittaciformes	1
Psittaciformes	3	Apodiformes	2
Cuculiformes	2	Trochiliformes	1
Strigiformes	2	Musophagiformes	1
Caprimulgiformes	5	Strigiformes	9
Apodiformes	3	Columbiformes	1
Coliiformes	1	Gruiformes	9
Trogoniformes	1	**Ciconiiformes**	29
Coraciiformes	10	Passeriformes	46
Piciformes	6		
Passeriformes	60		

In fact if makes perfect sense that seabirds are not one of the oldest groups of birds since all marine vertebrate animals (e.g. sea turtles, dolphins, whales) come from terrestrial ancestors and have conquered the world seas necessarily late. Hence, the poor adaptive radiation of seabirds might

either be a consequence of the harshness of the marine environment or the youth of its evolutionary history. If the latter is the case, we should expect further diversification of seabird species during millennia to come.

Seabirds tend to be larger than landbirds and are generally much less colorful. Sexual dimorphism both in color and size is small compared to other families of birds.

Some seabird species have breeding populations distributed in wide geographical areas, comprising more than one biogeographical region, such as common tern, breeding in the Palearctic, the Nearctic and the Afrotropical regions, whereas some others have very minute distribution, like Heermann's gull, with only eight colonies known in the Nearctic region where they breed, or the Amsterdam albatross that only breed in Amsterdam Island in the Indian Ocean. There is normally an association between geographical range and abundance, and in turn conservation status, being once again the Amsterdam albatross a good example: only 5 pairs breed on average every year in Amsterdam Island, and the population is estimated at only ca. 44-63 birds (see **Life cycles and conservation of seabirds).**

World oceans cover 70% of the Earth surface. Hence, we should expect a wide distribution of seabird groups throughout the globe, from polar to equatorial regions. However, seabird distribution is influenced by a number of limiting factors. Penguins, for instance, only inhabit the Southern Hemisphere but they are not restricted to Antarctica as the Galapagos penguin lives on the equator. Actually, penguins need cold waters to forage and their distribution is thus determined by water temperature. Species living in warmer climates, like Humboldt penguins living along the coasts of Chile and Peru, are associated to cool marine currents, like the Humboldt current in western South America, or to local upwellings (as it is the case in the Galapagos Islands). These species (Humboldt and Galapagos penguins) among others are subjected to periodical variations in marine productivity. Complex oceanographic and atmospheric features like the El Niño-Southern Oscillation (ENSO) causes the inhibition of upwellings resulting in a paucity of phytoplankton and the depletion of the anchovy population on which many seabird species (as well as Peruvian fisheries) depend. Local and distant seabird colonies can suffer total breeding failures as well as slumps in adult numbers.

The distribution of land and water on the earth's surface is not uniform. In fact, the water-to-land ratio in the southern hemisphere is more than twice that in the northern hemisphere. This fact probably explains why seabirds are more diversified in the southern oceans. After all, pelagic seabirds only need a safe piece of land (a territory as large as an incubating bird can reach stretching its neck) during the breeding season, located as close as possible to food sources. Whole emblematic groups of seabirds like penguins occur only in the southern hemisphere and some authors believe that petrels may have evolved in the southern hemisphere like the penguins, although their fossil record (from the middle Oligocene on) is richer in the northern hemisphere, likely owing to better fossilization conditions. Migratory movements in the southern oceans may take place longitudinally, where seabirds may travel down the westerly winds.

Some seabird species generally feed in water not far from the colonies, such as terns, cormorants or most of the gulls, and are classed as "inshore feeders". They normally perform short feeding trips and chicks are fed frequently. Other species feed out of sight of land, and are called "offshore feeders", such as some penguins or some gulls. Among offshore feeders there are the so called "pelagic feeders", species which do not normally return to land outside of the breeding season and take several days to forage before feeding the chick (see **Feeding ecology of seabirds**)

Feeding ecology of seabirds

It is no surprise that seabirds, which spend most of their life at sea, feed mainly on marine organisms. Some terrestrial prey (invertebrates, small mammals, carcasses and garbage for scavenging species, olives and other fruits) may also be present for more opportunistic species, which are commonly inshore feeders, while this is not the case with offshore and especially pelagic species such as shearwaters or albatrosses. Size of prey is normally related to the species body size: while storm petrels (weighing ca. 30 g) feed on small zooplankton, albatrosses (weighing up to ca. 12 kg) feed mostly on large squids. The type of prey also influences the foraging behavior: small pelagic fish normally concentrate in shoals and attract flocks of surface feeders and plunge diver feeders like gulls or terns, whereas some other marine organisms like squid may be more solitary and are caught by more solitary feeders such as some albatrosses. When birds forage in flocks, both visual and auditory cues obtained from feeding individuals attract others (conspecifics or heterospecifics) to the same feeding spot. Foraging techniques and location can also affect seabird diets, which can even differ significantly between populations of the same species in nearby colonies due to different environmental features around breeding grounds. Seabirds mainly feed during the day, although there are several species that forage during the night since they have a vision adapted to darkness. Some larids (such as Audouin's gull or swallow-tailed gull), sulids and the black skimmer are partly or largely nocturnal foragers, whereas most "tubenoses" and some alcids attend young and excavate burrows only at night and some may forage at night.

Where large areas of comparatively shallow waters (called neritic waters) occur over the continental shelf, surface-shoaling fish are very important to seabirds, especially herrings, sardines, anchovies and sprats (Clupeidae), sandeels (Ammodytidae), and capelin (Osmeridae). In tropical regions, shoaling fish are less available and mostly when chased by predators such as dolphins or tunas. In these regions flying-fish and halfbeaks (Exocoetidae) are the main prey. Nevertheless, in Polar Regions fish are much less important to seabirds, being squid and crustaceans (especially the Antarctic krill) the main prey.

Whatever the cause of the poor adaptive radiation of seabirds, it is obvious that feeding and surviving out at sea is not a straightforward task. Remember the case study with which we opened this article. Cory's Shearwaters are equipped with a pair of long and narrow wings (high aspect ratio wings) and breed at latitudes where marine upwellings are nearly negligible. Shearwaters need those wings to spend days at sea searching for food. They either scavenge offal and fish discarded from fishing vessels or used as bait (the modern version of the old commensalism between seabirds and whales or schools of predatory fish) or capture squids at night, as they move upwards following the circadian vertical migrations of fish. Razorbills, puffins and guillemots on the contrary, have short wide wings (low aspect ratio wings) appropriate for long dives and short flies, what they need to take profit of the abundant resources present at high latitude upwellings. Here, food is extremely abundant, but only during short periods of time. For seabirds that normally catch prey sitting on the water (albatrosses, petrels), cephalopods usually constitute a large proportion of the diet. Most of those that use high energy techniques, like underwater diving (cormorants, auks), or hovering and diving (bobbies, terns), eat other than fish, which has a much higher energy content than cephalopods.

Feeding habitats for seabirds

Seabirds can be divided in two large sets, according to their feeding ecology: inshore feeders (e.g. gulls, terns, cormorants) and offshore feeders (e.g. albatrosses, shearwaters, petrels). The former breed mainly on mainland or islands located close to the mainland coast and feed within sight of land. The latter normally breed on oceanic islands and feed out of sight of land. Inshore feeding is usually associated with seabirds of small size, larger reproductive effort per season

(normally more than one egg per clutch), early maturity and shorter life spans. Somehow, a trade-off between present and future reproduction seems to occur so that an energetic fee is paid every time you reproduce and this cost accumulates over time and is paid as increased adult mortality. Inshore feeding would be closer to the r extreme of the r/K *continuum* of population ecology theory, whereas the opposite would be the case for offshore feeders. Inshore feeders inhabit less isolated environments where predation (by foxes, badgers, crows, etc) is an important selective pressure, making their breeding habitats more unpredictable in time. In fact one can tell, just by looking at the pigmentation of seabird eggs the extent to which they have evolved under the pressure of predation. Ground-nesting gull eggs imitate the background surrounding nests, just like the army camouflage clothing. However, the eggs of cliff-nesting gulls, like kittiwakes, are much less pigmented and hence more visible. The white coloration of the eggs of hypogeous species, like shearwaters or storm petrels, are the result of a trade-off between avoiding a less likely predation by aerial intruders like gulls and the need to become patent to adults coming into their burrows in complete darkness. In fact, nestlings of these species have dark plumages (that make them invisible to predators inside dark tunnels) because they do not have the need to advertise their presence by means of light colors, employing other clues like their characteristic strong odor and sound.

Inshore feeders not only have higher offspring mortality but also can get food more readily. That not only influences the number of eggs laid and the number of chicks reared per season but also the growth rate of the nestlings. Chicks of seabirds like terns and gulls have fairly rapid growth rates that can be sustained by a high number of feds a day. However, the only chick of oceanic seabirds needs to grow slowly (have a low metabolic rate) in order to make an optimum use of the eventual feds it can receive. In fact, chicks of petrels, albatrosses, shearwaters and other offshore feeders can accumulate large quantities of fat as an insurance against periods of food scarcity thanks to their slow growth rate (see **Life cycles and breeding behavior of seabirds**). Interestingly enough, this vital feature, extremely important for their ontogeny, has been one of the most significant causes of the recent decline of many seabird populations since chicks have been collected in big numbers by man (for feathers, down, flesh, fat and oil) until recently (see **Conservation of seabirds**).

The role of seabirds in marine ecosystems and nutrient cycling

Seabirds are predators of different marine organisms, mostly animal. Some species feed on zooplankton (which in turn depends on the availability of phytoplankton and nutrients), while some other feed on fish (both larval, juvenile and adult phases) and squid. Areas of high productivity resulting from oceanographic phenomenon such as upwellings, ocean currents or river mouths are rich in nutrients and trophic chains are enhanced. Seabirds, like some other marine organisms such as some dolphins, sharks or turtles, play the role of predators in the trophic chain, and some of them occupy actually the niche of top predators such as albatrosses, pelicans or shearwaters.

Many offshore feeders are night-dwelling seabirds. Seabirds not depending on nutrient-rich waters (like river deltas, marine fronts and oceanographic or orographic upwellings) are faced very often with a foraging ground resembling an ecological desert, punctuated here and there with patches of food fairly unpredictable in time and space. That is why many pelagic seabirds rely on the moon for foraging. Moonlight seems to attract phytoplankton to the surface which, in turn, is followed by zooplankton, zooplanktivorous fish species like sardines and fish-eating animals like squids. This piece of ecology is known by fishermen since ancient times. All fishing methods that employ more or less powerful lights at night to lure fish rely on this principle. Thus, full-moon nights are bad nights for purse-seine fishing since fish cannot be concentrated locally as the effect of light is very widespread. The fact that many marine creatures (e.g. many cephalopods) show bioluminescent properties may also help detecting prey at night. During daytime very often the most profitable option for seabirds is to follow fishing vessels and take advantage of offal and

discarded fish, just like fishermen used to employ seabirds as a cue for the location of fish schools prior to the times of the sonar and other modern technologies. Seabirds use visual cues to detect fishing boats but "tubenoses" (i.e. Procellariiformes) also seem to make use of olfactory cues. In fact their complex nostril is very likely an adaptation for a well-developed sense of smell.

Through their faeces, seabirds can increase the amounts of organic matter both in the soil of breeding colonies or in relatively closed marines areas such as bays, estuaries or mangles. This participation on nutrient cycles is of vital importance since some elements such a phosphorous or nitrogen can be injected back in the ecosystems. Nevertheless, when seabird local breeding populations increase dramatically as a consequence of the influence of human activities (refuse dumps, fisheries), the impact on local vegetation can be deleterious through physical disturbance (pulling-up, treading, collecting of nest materials), chemical disturbance (soil manuring, salt deposition) or alteration of competitive processes (dispersal of allochtonous seeds, expansion of annual or ruderal species).

Mechanisms of seabirds for obtaining food

Seabirds may search for food in a variety of ways. Foraging methods include surface seizing (e.g. albatrosses, storm petrels, prions), surface dipping (e.g. frigatebirds, petrels), pattering (e.g. storm petrels), active killing (e.g. jaegers, Audouin's gull), scavenging (e.g. giant petrels), kleptoparasitism (jaegers, frigatebirds), pursuit diving (e.g. shags, auks, penguins, diving petrels), plunge diving (e.g. gannets, boobies, terns, pelicans, tropicbirds), skimming (e.g. skimmers, storm petrels), hydroplaning and filtering (e.g. prions). All these techniques are not mutually exclusive; a given species may have a preferential foraging method but may occasionally employ other techniques (e.g. shearwaters and albatrosses are usually surface seizers but may also feed by shallow plunge diving or become kleptoparasitic when food is scarce). Likewise, within a given taxonomic group, it is possible to find all sorts of foraging techniques, depending on the morphological characteristics of each group.

Pursuit diving consists on the active pursuit of prey by diving at variable depths from the surface. Underwater feeding behavior is largely unknown but it includes a wide range of strategies. Some species employ their short wings as flippers to *fly* under the water (e.g. penguins, auks, some shearwaters) but other seabirds make use of their webbed feet as propellers under water (e.g. cormorants). Seabirds can pursuit dive collectively or individually (e.g. penguins may dive in flocks of even several hundred individuals, whereas auks are solitary feeders). The Emperor Penguin can reach over 260 m and auks may dive to 100 m or more. Some shearwaters dive from the air and only to very shallow depths, although some species may dive down to 30 m or more using their wings. When pursuit diving starts as a shallow plunge this is done obliquely. Penguins are so well adapted to diving under water that all species have lost the power of flight. Penguins can locate and pursuit prey in the darkness, at great depths or at night thanks to the bioluminescent properties of many fish, crustacean and cephalopod species.

Plunge diving consists on diving to a depth of several meters by plunging from the air. Typical plunge-diving seabirds are sulids, terns, tropicbirds and brown pelicans, which most often fish in groups. Plunge divers seem to select target fish from the air helped by their well-developed binocular vision and plunge almost at high angles with the sea surface to avoid refraction. Plunge-diving height depends upon the depth to which seabirds need to dive. Some species of gannets and boobies make use of their wings under water to avoid their positive buoyancy and dive up to 15-25 m. Some plunge-diving species (e.g. tropicbirds, terns) typically hover before plunging. Groups of seabirds foraging using this technique are highly visible and attract other seabirds from the distance. It seems that the confusion generated by a large number of predators results in more prey taken per individual. Pursuit divers can forage in multispecific flocks or even in association with plunge

divers like Jackass penguins and Cape gannets. Plunge diving in blue-footed and Peruvian boobies is done in a collaborative way. These species actually forage communally since they fly along in small groups and when one of the birds whistles all members of the group dive in as if they were one. Plunge-divers may collect their prey either on the way down (e.g. species plunging to shallow depths like terns) or on the way backs to the surface (e.g. species plunging deeper like sulids).

Surface seizing is the collection of food items with the bill while sitting on the water. This technique is typically practiced by albatrosses and petrels when feeding on offal discarded from commercial fishing ships or on scraps of food left by schools of cetaceans. It is typical of seabirds with reduced flying agility and it can be practiced by day or night.

Surface dipping is practiced by frigatebirds, foraging alone or in flocks. Once prey is sighted birds drift gradually down and snatch prey off the surface of the water, immersing the bill and occasionally the head.

Pattering is typically employed by storm petrels of the genus *Oceanites*. Most storm petrels feed on the wing with their legs dangling but Wilson's and Elliot's storm petrels patter on the surface of the water with their feet that have brightly colored webs. These webs may attract prey. In fact, storm petrels are commonly found with leg wounds or legs missing owing to predatory fish that mistake their webs for food. Storm petrels do not surface-seize while sitting on the water and rarely do shallow plunges or dives from the surface. Wilson's storm petrel use a number of variations of the pattering action like walking on the water and standing still, facing into the wind, with its feet into the water acting as anchors and its wings open.

Active killing is practiced, for example, by Audouin's gulls when breeding on islands where there is an important migratory flow of Passeriforms. Small passerines arrive on Mediterranean islands completely exhausted and become a very easy prey. They are probably a good source of protein when fish discarded from fishing activities is not available owing to moratorium periods. Larger seabirds may kill smaller seabird species, as it is the case of Yellow-legged gulls and storm petrels. Some large seabirds like jaegers and large gulls (e.g. great black-backed gull or Pacific gull) may feed on other seabirds. Jaegers can feed on small mammals and smaller birds like phalaropes. Jaegers take eggs, chicks and fledglings from nests and during periods of shortage they can kill chicks of its own species taken from other territories (cannibalism).

Scavenging consists on feeding on the carcasses of marine mammals and seabirds or any other carrion, fish offal from fishing boats, whale blubber, whale feces and garbage. Giant petrels feed largely near the coast where they find most of their food. They may gather in groups of several dozen birds and feed on carrion (just like vultures) for which they are well equipped with powerful bills. They can also walk well on land. Scavenging on discard from fishing vessels has been described for all oceans of the world and for several types of fishing fleets. For some seabird groups, offal and garbage are now among their most important food sources. In fact, the increased availability of these food sources is partly responsible for the spread and increase in the numbers of some seabird species (e.g. northern fulmars, yellow-legged gulls).

Kleptoparasitism consists on the opportunistic stealing of food from individuals of other species. Typically birds like frigatebirds or jaegers chase other birds until they drop or regurgitate their load. Kleptoparasitic species are well adapted to agile flying. Kleptoparasitism can be associated to periods of food shortage, especially for species with a wide foraging niche. Puffins, kittiwakes and terns are common victims of jaegers in the northern hemisphere. Birds carrying bigger prey are selectively parasitized.

<u>Skimmering</u> is a foraging method only practiced by skimmers. These seabirds fly along ploughing the water with the lower mandibule (which is longer than the upper mandibule) to locate concentrations of fish and to grasp prey items by chance. This is an effective fishing method where prey density is high since it is mostly tactile. Skimmers may eat at night in complete darkness.

<u>Hydroplaning</u> is a technique only practiced by prions in which the birds rest on the water and uses its feet to skim rapidly over the surface, with its wings outstretched and the bill or the whole head submerged.

<u>Filtering</u> is also practiced by some prion species that have specialized bills with comb-like lamellae in the upper mandibule that act as filters. Water is forced through the lamellae and small food items are retained, in the way some dabbling duck species filter feed. Prions feed mostly on zooplankton (i.e. euphausiid crustaceans).

Seabird migration

The migration of birds, and of seabirds in particular, has caught the attention of man since ancient times. Many seabirds move southwards from high latitudes during winter time to run away the shortening of light days, because that reduces the number of foraging hours available, although the sea around breeding areas is often most productive during winter due to increased surge. No doubt, the most extreme case of all is the movement of arctic terns from their breeding grounds in Greenland and NE Canada to their wintering quarters in Antarctica, up to 20,000 km away. This way, arctic terns manage to live permanently in daylight. However, not all seabird species are highly migratory and many stay during the winter around upwelling zones or breeding grounds. Penguins are likely the extreme example of reduced dispersive habits around breeding grounds. Their complex morphological adaptations to diving prevents them from doing long movements and some species are even able to breed during the Antarctic winter, like the emperor penguin.

Nevertheless, migration patterns in seabirds include all possible combinations within and between hemispheres. Seabirds can move within polar regions or from polar regions to high latitude areas (e.g. fulmars, little auk, glaucous gull); from polar regions to tropical areas (e.g. Sabine's gull), from polar to polar regions (e.g. arctic terns); from high latitude areas to subtropical zones (e.g. kittiwakes, Atlantic puffins); from subtropical to subtropical areas (e.g. Manx shearwater, storm petrel, Leach's petrel, Cory's shearwater), from tropical or subtropical areas to low latitude zones (e.g. Madeira storm petrel, Bulwer's petrel, little shearwater); from subtropical zones to high latitude areas (e.g. great shearwater) or from high to high latitude areas (e.g. sooty shearwater, Wilson's storm petrel). Body size does not seem to be a trait associated to migration distance. It seems that wing aspect ratio is the most relevant limiting factor. Seabirds with low aspect ratio wings (auks, cormorants) are very well adapted to diving but pay the price of having low dispersal capabilities, whereas the more migratory species normally have long, narrow wings, as in shearwaters or terns, or are good soarers. Long-distance migratory movements are fast, with migrant birds feeding little on their way to their destination grounds.

Migration clearly represents a risk for seabirds. Long trips through oceanic waters probably increase the risk of gales or storms, presence of predators or other threats. Moreover, migrant birds, once arrived back to the breeding grounds, have to compete with resident species or individuals for space and mates. In some species (especially for those from northern regions), some individuals migrate whereas other stay not far from the breeding colonies; there is here a trade-off between current reproduction (which is normally better for resident individuals) and winter mortality (which can be lowered for migrant individuals). In tropical areas, where ecosystems are loosely structured and strongly seasonal (carrying capacities increase during winter and summer), most of the species

perform large migrations. Nevertheless, the fact that migration is widespread among several Families of seabirds suggests that there must be great advantages of being migratory.

Like breeding or molt, migration is subject to a genetically programmed, endogenous circannual rhythm, which is influenced by several proximate factors such as temperature, cloud cover or environmental features. Among these, food availability is probably one of the most important: it is known that some species of seabirds (e.g. lesser black-backed gull, Audouin's gull) that exploit food from human activities (garbage from refuse tips, discards from industrial fisheries) are becoming more sedentary. It is rather logical that migration is a type of behavior able to evolve quickly due to its high adaptive value. Some aspects of migration are still poorly known, such as the influence of age, sex or breeding effort in the distance covered, and the role of wintering grounds as information centers before the way back to the different breeding colonies.

Life cycles and breeding behavior of seabirds

Social breeding and mating systems

The vast majority of seabird species (98%) are social, that is, nest in colonies. Colony size is enormously variable, from only a few pairs to millions, as in the king penguin or the Guanay cormorant. Individuals prefer to nest in the center of the colonies where probabilities of being predated are normally lower than in the periphery. Until recently the coloniality conundrum has been approached as an economic balance between costs (e.g. increased risk of being detected by predators, increased transmission of diseases, increased intraspecific competition for food and mates) and benefits (e.g. collective mobbing of predators, enhanced food finding, access to extra-pair fertilization). However, it seems now clear that coloniality (and the loss of feeding territoriality) evolved before the passage to a marine life and hence that the conquest of the seas by seabirds was contingent on coloniality. It is not a marine life what forced species to become colonial but, quite the opposite, it was colonial breeding what allowed seabirds the exploitation of the patchy and unpredictable marine environment. Hence, many traditional benefits can only have favored secondarily the conquest of the seas.

Further evidence pointing out the difficulties associated to a marine life-style is the nature of mating systems. Almost all seabirds are monogamous, that is, males pair only with one female and vice versa. Incubation and chick rearing requires the co-operation of both parents to be successful. Besides, they are not only monogamous but show high mate fidelity, especially for some species. Once a seabird gets to pairs with a high quality individual, the bond tends to be maintained as long as possible and divorce will only happen if one of the members of the couple does not show the right capabilities to maximize breeding success or dies. Courtship feeding is one of the most common ways for females to assess whether their mates may be good food providers. Common Terns, for example, not only supply fish during displays but, once paired, males feed females until the first egg is laid when males begin to share incubation. Courtship feeding is not only important for pair bonding but most importantly for allowing adequate egg formation during the preincubation stage. Female terns may weight some 125 g and lay up to three eggs weighting 21 g each. This means that a three-eggs clutch comprise 50% of the body weight of the adult female, representing a tremendous reproductive investment, much larger than that of our oceanic Cory's Shearwater whose single-egg clutch represents a little over 11% of the weight of the female as we already mentioned in our introduction. Maybe the only exception to this rule, within the Procellariiformes, is that of storm petrels whose only egg represents some 25% of the weight of the female. Summarizing, terns and shearwaters are both monogamous although owing to very different causes. Terns are small sized, have a high juvenile mortality that needs to be compensated by a high productivity, breed in environments temporarily rich in food and their chicks have rapid growth rates. Shearwaters are relatively big, have a low productivity but also a low juvenile mortality, breed in environments

permanently poor in food and their nestlings have low growth rates. Terns invest more on quantity and shearwaters on quality, forced by the nature of the ecosystems where they have evolved. Although both systems are marine (littoral and oceanic zones) they are experimented very differently by both groups of seabirds and very different life strategies are favored. Some seabird species, such as colonial breeding auks, have ornamental crests or plumes and brightly colored bills, mouth linings, legs and feet, and breeding plumage can be very attractive. For these species, the facial and head ornaments, such as the large and colorful bills of puffins, may play an important role in pair formation and maintenance, courtship and agonistic behavior.

Within oceanic seabirds, there is a wide array of body sizes, from albatrosses to storm petrels. Although their life-history traits are basically very similar (small clutch size, long incubation period, slow growth rate of nestlings, delayed maturity, etc) size determines important differences. Smaller seabirds usually become nocturnal (on land) and hypogeous whereas larger seabirds can remain diurnal and breed above ground (e.g. albatrosses, giant petrels) or on sea cliffs (e.g. fulmars). It happens within penguins, where little penguins (the smallest penguin species) are the most nocturnal species with all activity on land carried out at night. Nevertheless, where predators are scarce or absent even medium-size birds may nest on the surface. Their complex morphological adaptations to the marine environment make seabirds (except for larger-size species that expend long periods of time on land owing to their long breeding cycles) very vulnerable on land.

Size is also important as a mechanism for decreasing competition for food among closely related species as well as for increasing the diversity of prey items supplied to nestlings. Congeneric species living simpatrically usually occur in a scale of body sizes and some species show sexual dimorphism. Nevertheless, differences between sexes are not usually very pronounced in seabirds (more accented in larger species like giant petrels), suggesting that their prey (species, class size, etc) are very abundant and that there is no need to diversify diets in order to prevent overexploitation of a given resource, as could be the case of forest raptors, where sexual dimorphism is particularly well stressed. Size is also related to the age at which first breeding is reached, being shorter for smaller species.

Breeding parameters of seabirds

The breeding season of seabirds starts when they occupy a breeding territory. A nest is build to protect the eggs and chicks from predation. Its efficiency depends heavily on its position. For most seabirds, nests are placed in sites like islands or cliffs, safe from predators. Many species (auks, shearwaters, petrels) use cavities in rocks or trees where the level of predation is lower than in the open. However, cavities have also some constraints such as precluding adults to escape or the low availability of suitable sites, which can limit the breeding portion of the total population. Most seabird species build very rude nests, sometimes simple scrapes in the ground or holes or ledges in cliffs where the eggs are laid.

Oceanic (pelagic) seabirds, either those species associated to upwellings like guillemots, razorbills, fulmars, puffins, boobies and gannets or those living in poorer environments typically lay one-egg clutches (occasionally two), whereas more terrestrial seabirds (littoral or inshore-feeding species) lay larger clutches. Hence, it seems likely that food is not the main factor influencing clutch size at the ultimate level, since food in upwelling areas is very abundant. However, both clutch and egg sizes are influenced by proximate factors, mainly food availability, suggesting that seabirds may somehow adjust their breeding effort depending on environmental conditions during the breeding season. This is easier for species laying more than one egg, being the species laying a single egg mainly determinate layers, that is, species unable to compensate for possible egg losses sustained during laying. Facts point out strongly toward larger clutches in littoral seabirds (terns and

gulls) as an insurance against low juvenile survival due to terrestrial predators. The number of eggs laid by a female is ultimately determined by the number of young that parents can provide with food, although the energetic demands of laying and incubating eggs can also affect parental fitness and in turn the clutch size. The Rapid Yolk Deposition RYD period in gulls seems related to female body size, ranging from 13 days in the great black-backed gulls to 6 days in mew gulls.

For seabirds laying one egg, most of the breeding failure normally occurs during the brooding period, when chicks are very few days old and are cared by parents, who have limited amount of time to forage. For species laying more than one egg, last eggs in a clutch produce fledglings only if environmental conditions (mainly food supply) are very high. Hatching asynchrony in clutches of two or more eggs enhances the different abilities of chicks to compete for food and ensure that at least the chicks hatched first have relatively high probabilities of surviving. The length of the incubation period depends on various factors, mainly egg size and the state of development in which the chick hatches. In most seabirds both sexes participate in incubation. The duration of stints is very variable depending on the species, lasting in Procellariiformes several days, and only a few hours in smaller species breeding in the open such as terns.

There is a remarkable dichotomy in seabirds regarding the development at hatching. Species breeding at ground in the open (terns, gulls) have normally more semi-precocial chicks (once they hatch they move leaving the nest although they are not able to find food for themselves) than species breeding on cliffs (some gulls or cormorants, alcids) or in burrows (shearwaters, petrels). The frequency of foraging trips varies greatly from one species to another, depending on the body size, type of food, the foraging technique and the number of chicks to attend. Once again there is a continuum between the strategies of seabirds such as terns, with several feedings every day to large albatrosses that may only bring food to chicks two or three times a week. Seabird chicks grow following typical sigmoid curves. In Procellariiformes chicks exceed the weight of adults at the end of the growing period due to an accumulation of fat that boosts the chances of its survival once leaving the nest.

Seabirds tend to attempt reproduction annually, although some species (generally the largest species but also medium and small-sized ones) breed only biennially, taking *sabbatical* years if reproduction was successful the previous year. Migratory species normally desert nestlings before they fledge. This behavior is in part motivated by the fact that chicks usually accumulate so much fat during the breeding season that they exceed the weight of adults and must shed weight before fledging. However, the ability of pelagic seabirds to withstand long periods of fasting and to find food at sea far from their usual feeding grounds give them a great potential for colonization.

Seabirds are k-selected species and show relatively low breeding success. Nevertheless, among seabirds, there are many intermediate situations between a small tern (recruiting at relatively young age, breeding every year, raising several chicks when environment is favorable) and a large albatross (recruiting at old ages, breeding not every year, raising only one chick at the maximum), which is also related to life history traits and the evolutionary trade-off between adult survival and breeding productivity. The largest species have no predators and they expectancy of life is higher than smaller species, which have to invest more in reproduction. At individual level, breeding success is influenced by age (which in turn is associated with foraging skills) and especially by genotypic quality: while some birds may raise several chicks even when conditions during a determinate season are bad, some others only succeed when environment is exceptionally good. Populations of red-billed gulls are maintained by a small number of productive individuals, but their productivity is not strongly inherited, nor is the frequency of breeding or laying date, factors which accounted for the greatest variability in lifetime reproduction. At senescence (which occurs in most seabirds with low adult mortality) it seems that breeding success lows down again as in youngest breeders, as it occurs with survival probability.

Seabird physiology

Physiologically, oceanic seabirds (petrels, penguins) are characterized by low body temperatures (averaging about 38º C, compared with 41º C for birds in general) a trait intimately linked to low basal metabolic rates and slow growth rates. This is thought to be an adaptation to periods of fasting, owing to the unpredictability of marine resources. One collateral consequence of having low body temperature could be having a richer energy budget available to be invested in maintaining their immune system. In fact, penguins and petrels are known to be free of blood microparasites *sensu lato*. The hypogeous habits of petrels, however, make them a perfect target for ectoparasites. Fleas, for example, find a very suitable place for completing their life cycles inside the burrows of shearwaters or rock crevices of storm petrels. More terrestrial species like gulls are known to be highly infected by blood parasites, probably because of higher chances of getting in contact with vectors but also because of a likely weaker immune system due to a higher energy budget devoted to keeping their body temperatures high and hence maintaining higher basal metabolic rates. Some authors however relate the prevalence of hemoparasites with the duration of the incubation period, since long periods of embryonic development could lead to a higher diversification of the immune system.

Population dynamics and regulation of seabird colonies

As any other organism, seabird local populations are regulated by two components: entries and exits. These two components of seabird demography can be in turn decomposed in other two: entries are a sum of local recruitment and immigration, and exits are a sum of mortality and emigration to other local populations. Other non-demographic factors related to environmental features can also play a role in population numbers, such as nest site availability or food supply, that can hamper some individuals to incorporate to the population. At the same time, proximal factors such as predators, food availability and stochastic and detrimental events can affect the breeding success of individuals and in turn affect one or more of the components of seabird population dynamics. It seems clear that seabird population are regulated by density-dependence trough the economic thresholds of food availability. The influence of man on seabird populations has been high even in remote polar regions. Man has depleted seabird population through harvesting for decades especially during the 19th century, and has been a major cause of seabird population decrease, since for some species the harvest represented a negative factor impossible to counterbalance. Yet, in largely inhabited regions such as in the Mediterranean, the decrease of suitable colony sites for seabirds by human urbanization and the introduction of predators such as rats, feral cats and dogs has probably limited the size of populations. Other threats imposed by man activities such as fishery catches depleting marine prey populations or causing by-catch adult mortality are also influencing seabird population dynamics (see **Conservation of seabirds**).

Recent development of mathematical tools such as capture-recapture models or Leslie matrices has allowed researchers to estimate more accurately several parameters that are crucial for seabird demography (survival by age and sex, recruitment probability, age at first reproduction, breeding probabilities, dispersal probabilities) and population dynamics. This has enhanced the study of metapopulation and the evolutionary trade-offs typical of these organisms, as well as the trends of seabird populations for the study of their evolution and management.

Seabirds have life-history traits, already described in this paper, which determine precise selective values of the different components of seabird populations. Generation time is high, related to delayed incorporation of individuals to the breeding population. For instance, generation time in a colony of Audouin's gull is estimated at 12 years. Local recruitment is relatively low, since productivity is low and they show delayed sexual maturity, whereas adult mortality is also low due

to the low number of predators and a conservative strategy when reproducing. Thus, local population growth of seabirds is very sensitive to changes in adult survival and a 3% decrease of this parameter can have a greater impact than a decrease of 30% in breeding success or other demographic parameters such as juvenile survival or probability of breeding. In St. Kilda (Outer Hebrides, Scotland) chicks of fulmars were harvested for centuries, with no detrimental effects on breeding numbers. Contrarily, mortality of adult albatrosses during foraging trip caused by long-line fisheries is nowadays greatly affecting breeding populations and marked decline in numbers. Adult survival rates are not constant and may vary among populations depending on environmental features influencing individuals. Cassin's auklets breeding in the north eastern Pacific show different adult survival probabilities depending on the local population, and differences are probably due to environmental conditions. For some of these local populations, survival rate below a threshold determines a population decline and thus a conservation concern. It has been suggested that a significant long-term decline in zooplankton production in the California current system has affected population dynamics of seabirds breeding there.

Although it has been stated that adult survival in seabirds is constant, some studies have demonstrated that environmental factors like food supply during breeding can affect survival probabilities: kittiwakes breeding in some colonies in the Shetland (the North Sea) showed in the last 20 years marked variations in adult survival ranging from 0.53 to 0.98. The influence of food availability is high not only for breeding success and breeding effort of kittiwakes, but also because potential predators such as jaegers are forced to shift their diet to adult kittiwakes when food (sandeel in this case) is in short supply. For some of those survival values, populations of a long-lived organism such as kittiwakes cannot be sustained and the threat of extinction can be high.

Apart of born-death processes, regulation of seabird populations occurs through processes of transfer of individuals, which are also involved in gene flow among populations to avoid endogamy. These dispersive individuals thus connect local populations within what is called a metapopulation. Emigration from a local population implies immigration to other, and this phenomenon is of great importance in many seabird species. Most seabirds are philopatric, that is, return to breed to their birthplaces, although transfer processes are very frequent in seabirds with relatively low philopatry, such as some gulls and terns, and are negatively associated with the spatio-temporal stability of the environment. For some unstable habitats, extinction-colonization turnover can be high, and species occupying these habitats have evolved to cope with this challenge. Local population dynamics of these species are very influenced by emigration-immigration processes and they can show great variation in breeding numbers from year to year. In a single colony of Audouin's gull in the western Mediterranean, immigration explains a population growth at an average rate of 44% per year since its establishment in 1981.

Individuals from other colonies within the metapopulation and even from more distant colonies emigrate to this patch when it was protected against human disturbances. Nowadays this colony holds 65% of the total world population of the species. A similar dramatic population increase has occurred in guano exploitations in Peru and southern Africa, where new suitable breeding sites (safe from predators and human disturbances) were set up to attract seabirds. In contrast, other species like cormorants, gannets or shearwaters normally occupy very stable habitats, and the acquisition of a good site in a colony is sometimes crucial for a successful reproduction. For these species, colonization of new patches is not a frequent phenomenon and normally involves few individuals and low population growth rates. However, man activities can force some of these species to colonize new patches, as it has been the case of Cape gannets in southern Africa after displacement by man due to guano harvesting in some colonies, or that of Cape cormorants in the same regions, probably as a result of overfishing.

Peruvian seabirds exploited for guano have shown marked fluctuations over the last 100 years, firstly unregulated due to its relatively low numbers, then regulated by nest site availability as a result of guano managers, and nowadays regulated by food supply and oceanographic events like El Niño. There is normally an inverse relationship between the population growth rate and population size, this probably being related to density-dependent factors like food availability. In a seabird community in the western Mediterranean, total seabird population has increased over the last 20 years when the habitat was protected and only when energy available *per capita* has approached the carrying capacity of the ecosystem the population growth has lowered down to stabilization.

At a larger geographical scale, colony sizes are influenced by the size of neighboring colonies, whose members can compete for food in shared foraging grounds. When density dependence is low, large colonies attract more individuals than small colonies, since size of colonies is probably showing the quality of the environment around the breeding grounds. Availability of both safe sites and food are probably the main factors influencing the quality of a patch and its attractiveness for individuals that decide to recruit into a breeding population as local recruits or immigrants coming from non-natal sites.

Little is known about the regulation of seabird breeding numbers by non-breeding individuals which are sexually mature but do not breed, because of the limitation of mates or breeding sites or because they cannot cope with the energetic requirements necessary to breed. It is known that for some species (alcids, Procellariiformes, some jaegers) there are non-breeding individuals at breeding grounds, some of them taking *sabbatical* years after high effort in previous breeding seasons, but some others not breeding for some unknown reasons. It has been suggested that in some cases these non-breeding populations act as a buffer against environmental stress at breeding colonies and can compensate detrimental stochastic events affecting breeding individuals.

Conservation of seabirds

The influence of man in nature and the environment has, as a general rule, favored organisms with an *r* strategy, in the case of seabirds, gulls rather than albatrosses. Competition has been reverted by man influences and pioneering and opportunistic species are nowadays favored in human-affected environments. A good example is that of some gulls or fulmars, which exploit food from human activities (discards from fisheries, garbage from refuse tips).

Relationships with man

No seabird populations can now be assumed to be unaffected by man activities, though their influences are often subtle and indirect. In some extreme cases, some species have been extinct by the harvesting of humans, as happened with the great auk in the 19th century. However, it seems also clear that some species occupying the highest position in trophic chains such as albatrosses have always been less abundant than other species such as terns or some gulls. Primitive man exploited birds for meat and eggs, and some of these activities persist nowadays in some areas where tradition or poverty precludes any effective protection of seabird populations.

Fisheries

It is not a surprise that seabirds have a strong relationship with human fisheries, since both act as marine predators and exploit the same resource. Thus, fisheries and seabirds compete for food and share fishing grounds; at ecosystems rich in nutrients such as upwelling areas large concentrations of seabird populations exist and in most of these areas commercial fleets also operate. There are two types of relationships between fisheries and seabirds: one represents a threat for seabirds through overexploitation of fish stocks, reducing the mean level or increasing

variability of recruitment, altering food-web structure and through direct mortality in long-lines; the other interaction represents a benefit for seabirds through large amounts of discards easily available.

The industrial fishery targeting on capelin stocks in the Barents Sea has collapsed several times during the 90's because of overexploitation and higher predation level from increased stocks of cod. Common guillemot numbers decreased by 80% in this region probably as a result of starvation leading to mortality of young and adults in winter. Similar declines were recorded in southern Africa in the Benguela Region, where collapse of the sardine stock triggered large decreases in some gannet colonies. However, small geographical areas can be somehow protected against fishing activities and some colonies still produce large number of fledglings. Moreover, high mobility of seabirds allows individuals to move to these areas where food is still highly available buffering the large-scale situation of short food supply.

Contrarily, discards from industrial fisheries have been exploited by scavenging seabirds and this has enhanced the recovery of some seabird populations from very low numbers, as it has been the case of the endangered Audouin's gull in the western Mediterranean. Exploitation of discards has been reported in many areas of the world: the North Sea, the northeastern Pacific, the southwestern Atlantic, the southwestern Pacific and the western Mediterranean. In some of these areas, timetables of vessels are so constant that discards represent a foraging resource very predictable in space and time. Nevertheless, in the long term this benefit can reverse and become a threat if fish stocks are overexploited.

Urbanization and introduced fauna

Man has occupied islands in temperate areas in recent times and tourism development has urbanized many of these areas where seabirds traditionally bred. As a result, many breeding grounds have disappeared as seabird fossil and sub-fossil records show clearly in some islands and coastlines, where seabirds had safe places to breed before the arrival of man. Moreover, mammalian predators have been deliberately or accidentally introduced to many seabird islands where they kill adults and disrupt or prevent breeding. This phenomenon is nowadays probably the main cause of seabird population extinction, and New Zealand native fauna is a good example. In some other areas such as in islands and islets of the Mediterranean, the North Sea or the northeastern Pacific (British Columbia), introduced carnivores are still a big threat especially for some Procellariiformes, gulls, terns or auks.

Other threats

Seabirds are very vulnerable to oil contact, and spills may kill large numbers. Pesticides may damage breeding performance and increase adult mortality. Heavy metals with potentially toxic effects are present in many seabird species, in their tissues and eggs, especially those feeding near industrial areas where these substances are thrown to marine ecosystems. Plastic particles are widespread in all oceans and can cause digestive blockage by ingestion.

Endangered species

Of the 1,186 globally threatened birds, 1,175 (99%) are at risk from human activities such as hunting, harvesting, agriculture or fisheries. Among seabirds the situation is also of big concern: 3 species of penguins are threatened from a total of 17 species (18%); 22 species of Procellariiformes (21% of 104 species), and 2 extinct species since 1600; 14 species of Pelecaniformes (22% of 63 species), 1 extinct since 1600; 12 species of Charadriiformes (9% of 127 species), 1 extinct since 1600. In total, 51 species of seabirds from a total of 311 (16%) are threatened in the world. Some of them such as Amsterdam albatross are really endangered due to the extremely small population (3-8

pairs) confined to a single breeding site in the southern Indian Ocean, as it happens with Madeira petrel: only 20 pairs breed in a single colony in the Madeira archipelago. Spectacled petrel is also critically endangered because it is confined to one tiny island (Inaccessible Island) when breeding and is likely to be declining because longline fishing vessels are catching large numbers. Current estimates are that some 700 individual birds are killed in longline fisheries each year from a total population estimated to be between 2,500 and 10,000 individuals. An extreme example is Chinese crested tern, which is virtually unknown and there are no records in the last century, although some recent information suggests that the species may survive in the Chinese Sea. All these endangered species share several characteristics: very limited breeding ranges, negative effects of man activities especially affecting adult survival and very conservative strategies that precludes adults to invest more in reproduction.

Policy challenges

Most seabird populations are nowadays protected from direct exploitation, although traditional hunting, egging and taking of young and adults persist in some areas throughout the world. In some areas present-day man activities still threat the stability of seabird populations, whereas in other cases such as in the western Pacific, where extremely large shearwater colonies persist, exploitation is managed and populations do not seem at risk. In relation to seabird mortality occurring in fishing gears, several conferences and agreements have been set up in recent times on this subject: the Kyoto Declaration (1995), The Rome Consensus on World Fisheries (1995), the Code of Conduct for Responsible Fisheries, United Nations Resolutions, Agenda 21 (UNCED). The FAO Code of Conduct for Responsible Fisheries, in article 7.6.9, promotes measures to minimise the catch of non-target, non-fish species. The International Pacific Halibut Commission introduced legislation to ensure that seabird mortality levels remain low. The Convention for the Conservation of the Southern Bluefin Tuna has established the Ecologically Related Species Working Group specifically to monitor the situation. In 1995 CCSBT adopted the recommendation relating to ecologically related species especially the incidental mortality of seabird by longline fishing which stipulate the policy on data and information collection, mitigation measures and education and information dissemination. The U.S. Government also adopted, by regulation, seabird bycatch reduction measures for its groundfish longline fisheries in the Bering Sea/Aleutian Islands and Gulf of Alaska in 1997, and is considering adopting regulations for its halibut and the Hawaiian pelagic longline fisheries. All these agreements set out principles and international standards of behavior for responsible practices with a view to ensuring the effective conservation, management and development of living aquatic resources, with due respect for the ecosystem and biodiversity.

Seabird as indicators of marine environments

Seabirds are upper trophic level consumers that can indicate marine productivity and biotic interactions. Seabirds can be useful in monitoring marine environmental changes. Planktonic species can indicate current systems and water masses. Analysis of seabird parameters of both behavior and ecology can help researchers to go beyond rudimentary associations of species and hydrography. It is not by chance that largest seabird concentrations mostly coincide with areas where fishery activities are important. Changes in fish stocks and their distribution can be tracked using seabird breeding and feeding performances, and even can be predicted using some seabird parameters. Levels of pollution or changes in marine ecosystems features can also be tracked using seabird physiology.

Conclusions

Seabirds are probably a recent, not yet well diversified group of birds, with a wide distribution around the planet, as it would be to expect from the large surface cover by the world's oceans and the movement capabilities of seabirds. Marine birds have long lives and complex breeding cycles, in most cases depending on locations especially rich in food but also on human activities. They are a unique zoological group, worth being known in more detail, which can be used as an effective indicator of the health of marine systems. Policy-oriented progress towards sustainable marine resources development must include seabird conservation, not only on its own right, but also on its usefulness for the role-played in oceanic functioning.

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A note on the potential role of philopatry and conspecific attraction as conservation tools in Audouin's Gull *Larus audouinii*

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Abstract

This short communication reports on the the first record of Audouin's Gulls *Larus audouinii* breeding in captivity and on the behaviour of some individuals released as fledglings. During the period 1995-2000 a hand-reared male returned to its natal place and responded, year after year, to the translocation of a captive group of Audouin's Gulls for nesting site selection. The potential role of philopatry and conspecific attraction as conservation tools for this vulnerable seabird after an eight year experiment are discussed.

Many seabirds are known to be relatively philopatric, that is, they recruit mainly to their natal site (see for example Bradley and Wooller 1991). This phenomenon has been commonly exploited for conservation purposes for other bird taxa (e.g. raptors) through hacking, the feeding of chicks within enclosures in the wild during the last stages of growth and their subsequent releasing so that on their subsequent release they become imprinted to their fledging site (e.g. Sherrod et al. 1982). However, similar attempts for seabird species are very scarce (see Kress 1997 for an example with Atlantic Puffins *Fratercula arctica* and Leach's Storm Petrels *Oceanodroma leucorhoa*).

At a finer spatial scale, birds reaching their fledging grounds get involved in a decision-making process to assess the quality of the breeding site. Nesting site selection is a crucial process since it can affect most components of fitness (Danchin et al. 1998). Conspecifics seem to provide key clues about habitat suitability and quality that prospecting birds use to decide whether and where they will establish a breeding territory (Reed and Dobson 1993; Smith and Peacock 1990).

Audouin's Gull *Larus audouinii* is an endemic seabird of the Mediterranean region, classified as globally Near-threatened (BirdLife International 2000). As part of a conservation program for the species, individuals have been kept in captivity at a recuperation center in eastern Spain, some taken in as adults and some hand-reared as chicks. Here we report the breeding behaviour of the captive gulls as well as that of

individuals released as fledglings, in relation to the potential role of philopatry and conspecific attraction for the conservation and management of Audouin's Gull colonies.

In 1992, five eggs from from the Columbretes archipelago colony (39º 51'N 0º 40' E) hatched at a recuperation centre (Centro de Protección y Estudio del Medio Natural) located at the Albufera de Valencia Nature Park. The chicks were hand-reared in captivity at the centre facilities (106 km south of the collection site) and subsequently released into the wild. All were ringed with darvic bands for individual field identification.

Table 1. Table 1. Main breeding parameters of captive and wild pairs of Audouin's Gull *Larus audouinii* at the Centro de Protección y estudio del Medio Natural, Albufera de Valencia Nature Park, Spain from 1995 to 2000.

	1995		1996		1997		1998		1999		2000	
	Captive [4]	Non-captive	Captive [6]	Non-captive	Captive [6]	Non-captive	Captive [5]	Non-captive	Captive [6]	Non-captive	Captive [2]	Non-captive
No of laid eggs	0	2	2	2	3	2	2	3	3	3	3	0
No of hatched eggs	0	0	2	2	3	0	2	2	1	3	0	0
No of fledged chicks	0	0	1 (a)	2	0 (b)	0 (c)	2	0 (d)	0 (e)	0 (f)	0	0
Date of first egg laid	-	9 May	1 May	9 May	29 April	8 May	4 May	24 April	28 April	20 April	30 April	-

Numbers in square parentheses are captive gulls in the enclosure. (a) A second chick was hand reared. (b) One chick died after ant attack and two chicks were hand reared. (c) Eggs were removed and chicks hand reared after a massive ant attack. (d) One egg was not fertile and two chicks were predated by dogs. (e) Two eggs failed hatching after ant attack; the only born chick died after ant attack. (f) Three eggs hatched but one chick died in a few days and two chicks were removed and hand-reared for hacking.

From 1995 to 2000 one of the released birds (a male determined by copulatory behavior) was observed breeding at the centre accompanied by an unringed wild female ("wild pair" hereafter). A second captive-reared chick, released in 1995, was also observed at the recuperation center three years after release, although it did not attempt breeding. There are no records of the other birds released in 1992. At the same time, a group of adult and subadult captive Audouin's Gulls (see Table 1) was experimentally translocated each year (see Fig. 1) in order to monitor the response of the wild pair to the presence of captive conspecifics.

Within this group, a breeding pair of captive birds ("captive pair" hereafter) was formed during the study period, the year after the wild pair started breeding. This pair comprised the same two individuals each year. Reproductive parameters (laying date, clutch size, hatching success and productivity) of the wild and captive pairs were recorded by daily visits during the breeding season (March-July).

Laying dates did not show a consistent pattern throughout the years between the two pairs (Table 1). Mean clutch size was similar for the wild and captive pairs (2.6 and 2.4 respectively) and although the average hatching success tended to be lower for the wild pair (53%) than for the captive pair (67%), significant differences were not detected (Fisher exact test combining data from all the years, $P = 0.312$).

This is the first record of Audouin's Gull breeding in captivity and it indicates the potentiality to breed endangered gull species in captivity for conservation purposes. Our observations also confirm that occasionally Audouin's Gulls can breed close to human settlements (see Oro 1998 and references therein).

Fledging-site imprinting was probably responsible for bringing the hand-reared gulls back to their natal site year after year. However once there, nest site selection of the wild pair did not apparently occur at random nor was it based upon the nest site selected the previous year. On the contrary, this behavior seemed to be strongly influenced by the presence of captive conspecifics, except in 2000 after predation by a dog the year before. Although the behaviour of the captive and wild pairs is not necessarily representative of the species, these facts point towards a crucial role of philopatry and especially conspecific attraction for colony persistence and growth in ground-nesting gulls (e.g. Oro and Pradel 2000). Thus, painted decoys and sound recordings could be promising conservation tools for Audouin's Gull population reinforcement as they have been for several declining populations of other seabirds (Kress 1983; Kress 1997).

Acknowledgements
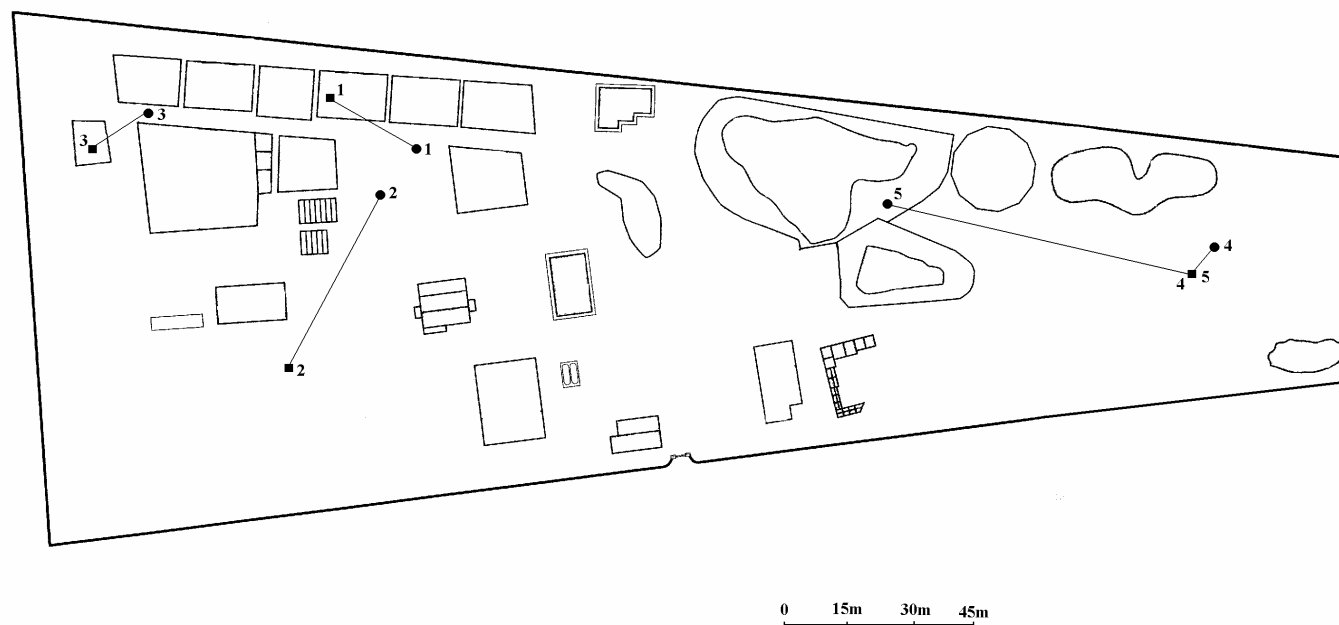
Figure 1. Experimental translocation of captive Audouin's Gulls *Larus audouinii* at a recuperation center located in eastern Spain and spontaneous response by non-captive gulls. 1 = 1995; 2 = 1996; 3 = 1997; 4 = 1998; 5 = 1999. Black squares represent nesting sites for captive gulls. Black circles represent nesting sites for non-captive gulls.

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Determinants of colony site dynamics in Audouin's Gull: a case study

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Abstract

We studied the determinants of colony dynamics in Audouin's gull *Larus audouinii*, breeding in a small archipelago of the western Mediterranean. Data on island occupation were available since colonization of the archipelago in 1973. Two group decisions were separately considered: whether to abandon or remain in an island previously occupied (patch abandonment or reoccupation) and whether to reoccupy or select a new island to establish a new colony (patch reoccupation or colonization). Generalized Linear Mixed Models (GLMMs) were used to identify the relative contribution of each of the explanatory variables. The average probability of island abandonment was very high (0.89) and the only variable among the 18 considered that influenced positively that probability was the change in number of pairs (realized growth rate λ) from time t_i to t_{i-1}. We suggest that island abandonment is a multi-step process where the first step (dispersal of a portion of the colony) takes place at random, as an evolutionary load typical of a species evolved in unstable habitats. The second step (a further loss of breeding pairs) is probably mediated by conspecific attraction to other patches. Finally a colony becomes extinct owing to some Allee effect. Island colonization seems to be only marginally and negatively affected by the presence of breeding yellow-legged gulls. According to our results, that show a high degree of movements of individuals among islands, protection of the vulnerable Audouin's gull requires protection not only of occupied islands but also of islands not occupied at present.

Introduction

Breeding dispersal in birds has recently received much attention (Clobert et al. 2001; Gunderssen et al. 2001; Serrano et al. 2001, Forero et al. 1999, 2002). In colonial species, individuals facing dispersal enter a two-fold decision process (e.g. Stamps 2001): first, they have to decide every breeding season whether to reoccupy or abandon they former colony, and secondly, individuals dispersing have to decide where to breed in the forthcoming season. These sets of decisions, influencing reoccupation, extinction and colonization of breeding patches, have important consequences on the structure and dynamics of local populations and metapopulations (Johst and Brandl 1997; Dieckmann et al. 1999). In long-lived birds such as seabirds, knowledge of factors conditioning dispersal is of crucial importance. Extinction-colonization processes (typical of metapopulation dynamics) occur by group dispersal (immigration-emigration) rather than by mortality and consequent extinction of some patches (Oro 2003).

A number of environmental cues have been proposed as proximate factors influencing the process of dispersal in colonial birds. However most approaches are individual based and only a few works have explored the causes and consequences of group

decisions as a whole (see e.g. Erwin et al. 1998; Serrano et al. 2001). Individuals tend to be more faithful with the familiarity to the breeding place due to the benefits reported from the previous knowledge of the area (Pärt 1995; Forero et al. 1999). In this way, several works have found a significant effect of breeding experience on dispersal decisions (Beletsky and Orians 1991; Pärt 1995). Previous reproductive performance of individuals has been also shown to affect breeding dispersal decisions (Switzer 1997; Forero et al. 1999), with those individuals or colonies having a higher breeding success being more philopatric to the breeding place. Some determinants of breeding success such as presence of predators (Cuthbert 1988; Erwin et al. 1991; 1998; Oro et al. 1999), food availability (Lurz et al. 1997), and other indicators of habitat quality have also been found to affect movement of individuals. In colonial birds, factors that determine abandonment and further selection of the colony site could also be related to colony characteristics, such as presence of conspecifics (Smith and Peacock 1990; Reed and Dobson 1993; Forbes and Kaiser 1994; Oro and Pradel 2000), colony size (Serrano et al. 2001) and other conspecific cues as breeding performance (Burger 1982; Danchin et al. 1998; Suryan and Irons 2001) or rates of change in colony size during previous years (Serrano com. pers.). On the other hand, most studies have addressed the study of the determinants of dispersal considering the isolated effect of different factors, but only a few have taken into account simultaneously the combined effect of several variables (e.g. Wiklund 1996; Forero et al. 1999; Serrano et al. 2001).

Here we aim to analyse the determinants of colony-site dynamics (i.e. colony site turnover) in a small local population of Audouin's gull *Larus audouinii* of the western Mediterranean. Nomadic behavior with a high frequency of change of breeding individuals among colonies has been previously described in Audouin's gull by Oro and Muntaner (2000) working at the small archipelago of Cabrera (Balearic Islands). Transfer processes between local populations as well as a high turnover rate of colony site occupancy (i.e. common colonization and extinction of islands within the archipelago) were found, although no cause was proposed to explain this behavior.

Our main objectives were, 1) to determine how frequent was the nomadic behavior (i.e. calculate a probability of island abandonment), 2) to identify what factors influenced group decision of abandoning or not the breeding patch from one year to the next, 3) to find out what cues were used by gulls to colonize a new island.

Methods

Study area and population

The study area were the Columbretes Islands, a small (ca. 19 ha) volcanic archipelago comprising four groups of islands, located ca. 57 km off the coast of Castellón (39º51'N, 0º40'E, northwestern Mediterranean), close to the edge of a wide continental shelf (see Figure 1). In addition to Audouin's gull four other seabird species breed on the Islands in small numbers: Yellow-legged gull *Larus cachinnans*, Cory's shearwater (*Calonectris diomedea*), European shag (*Phalacrocorax aristotelis*), Storm petrel

(*Hydrobates pelagicus*). The only non-seabird breeding species is Eleonora's Falcon (*Falco eleonorae*) and eventually the Peregrin Falcon (*Falco peregrinus*).
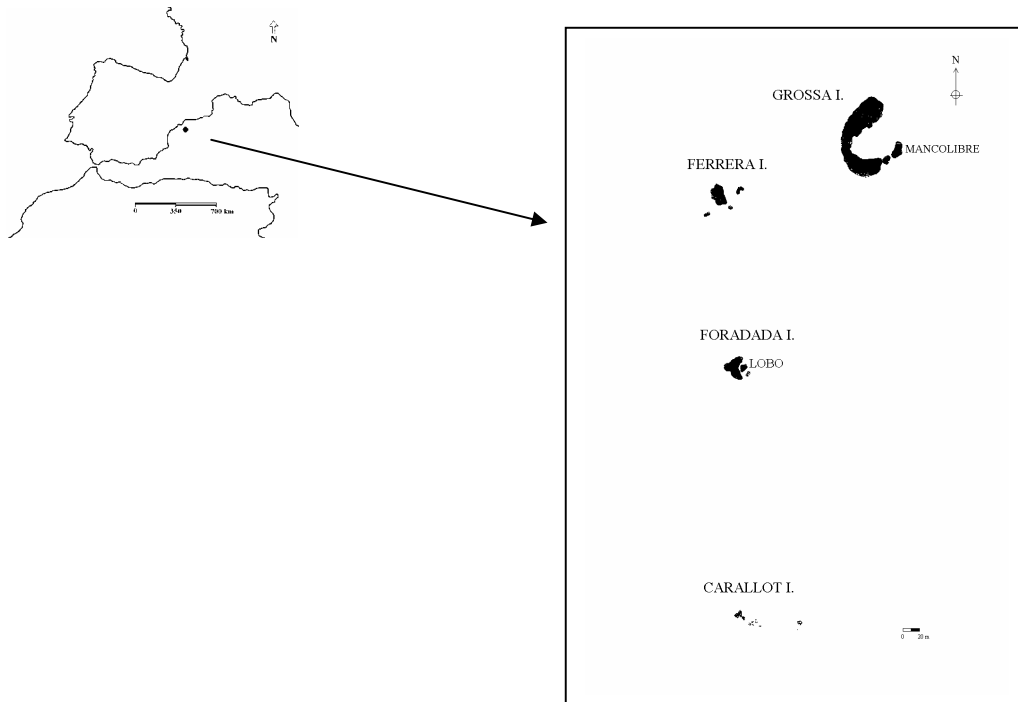
Figure 1. Map of the study area showing both the location of the Columbretes archipelago in the western Mediterranean and the islands within the archipelago where Audouin's gull breed.

Vegetation on the main island (Grossa) has been severely altered in the past by human activities (fires, agriculture, livestock) from a climax composed of *Pistacia lentiscus* (L.), *Chamaerops humilis* (L.), *Smilax aspera* (L.), *Lavatera arborea* (L.) and *Medicago citrina* (Bolòs & Vigo) to a number of small shrubby species like *Suaeda vera* (J. F. Gmelin), *Lycium intrincatum* (Boiss.) and *Asparagus horridus* (L.). Smaller islands (Ferrera, Foradada) have a weak vegetation cover but they still preserve remains of the climax. Data for Audouin's gull breeding in the Columbretes island come from unpublished reports of the Valencian regional government. Information extracted from these reports were mainly related to island occupancy, breeding numbers and breeding success. Data include information on occupancy of all 6 islets where the species has bred (i.e. Mancolibre, Ferrera, Foradada, Grossa, Bauzá and Lobo) during a period of 30 years (i.e. since first colonization of the archipelago in 1973 to 2002) except for 5 years for which data are missing. Data on occupancy of each islet was considered independently, although gulls may have occupied more than one islet in a given breeding season (see Table 1). The colony showed an increasing trend since its foundation in 1973 up to 1991, when a two-month trawling moratorium was established each year and reduced dramatically food availability, since this species makes an extensive use of fishing discards (Oro et al. 1996). From 1991 onwards the colony has decreased progressively (except for a "false" peak

during the mid nineties caused by immigration of hundreds of birds from the Ebro Delta after a predatory event) facing local extinction in 2002 (see Figure 2).

Table 1. Number of breeding pairs of Audouin's Gull *Larus audouinii* on each of the islands of the Columbretes archipelago (W Mediterranean) during the period 1973-2002. (*) In 1978 reports only indicate that the total number of pairs in Ferrera+Foradada were 130 pairs but we divided the total number of pairs between the two islands. Data for 1976, 1979, 1980, 1981 and 1982 are missing.

Year	Mancolibre	Ferrera	Foradada	Grossa	Bauza	Lobo
1973	20	0	0	0	0	0
1974	45	0	0	0	0	0
1975	105	0	0	0	0	0
1977	0	0	50	0	0	0
1978	0	65[*]	65[*]	0	0	0
1983	283	50	0	0	0	0
1984	0	0	0	300	0	0
1985	0	0	5	376	0	0
1986	0	0	0	300	0	0
1987	0	0	0	200	0	0
1988	0	0	0	225	0	0
1989	0	0	0	274	0	0
1990	50	2	0	378	0	0
1991	0	109	0	92	0	0
1992	0	169	0	0	0	0
1993	0	35	0	10	51	0
1994	0	0	0	273	0	0
1995	0	0	0	604	0	0
1996	0	0	0	502	0	0
1997	0	0	0	476	0	0
1998	0	158	0	14	15	0
1999	0	48	0	20	0	0
2000	0	0	64	10	0	6
2001	0	23	0	0	0	47
2002	0	0	13	0	0	7

Study species

Audouin's Gull is a middle size gull endemic of the Mediterranean Sea. At present it is considered a vulnerable species and its overall world population is ca. 20 000 pairs. It breeds on sandbars and islands and feeds on clupeoids mainly during the night, although discards from human fisheries are included in their diet when available (González-Solís et al. 1997; Oro 1998; González-Solís et al. 1999). It is a monogamous species with a modal clutch size of 3 eggs. Incubation is typically shared by the two sexes. Breeding failure can be caused by flooding of nests, predation by terrestrial mammals or yellow-legged gulls and

food shortage (Oro 1998). Kleptoparasitism by yellow-legged gulls is common especially when food is scarce and during the chick rearing period, although seemingly is not important (Oro and Martínez-Vilalta 1994; Martínez-Abraín et al. 2003). High nest density enhances protection against aerial predators (Oro 1998).
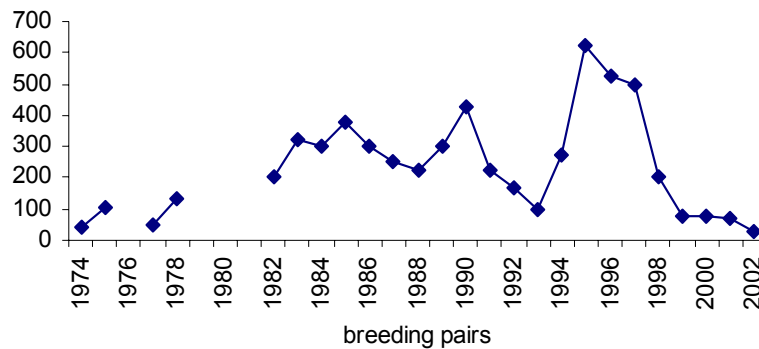
Figure 2. Number of breeding pairs of Audouin's gulls at the Columbretes archipelago since the foundation of the colony in 1973 up to 2001. Blanks appear when no data was available (1976 and 1979-1981).

Selected variables and statistical analyses

Information about the location and size of the colonies since first colonization in 1973 to 2002 (30 years) was obtained mainly from unpublished reports of the regional government (Table 1). We considered two different processes (i.e. two different response variables) for analyzing the nomadic behavior of this species: whether or not to abandon a breeding colony (extinction) and where to establish a new colony (colonization). We considered as explanatory variables those that evaluated the effect of the environment (e.g. food availability as availability of fishing discards), colony and population characteristics (e.g. colony size, realized changes in population size from time t_i to time t_{i-1}, λ), breeding success and presence of competitors (Tables 2 and 3). Data on island occupation were first treated as a series of zeros and ones, as when dealing with capture-recapture models, to select the appropriate cases to study colonization (0-1) and extinction (1-0) of islands. Colonization was defined as the occupation of an island after at least one year of non-occupation. Each island was considered as a colony (or patch) and the whole archipelago as a local population.

Colony-site dynamics was formerly studied by means of a "colony-site turnover index" (see Erwin et al. 1981). This approach was later substituted by modeling the presence and absence of colonies at particular sites as a function of local extinction and colonization probabilities. The use of general probabilistic models allows separate estimates of extinction and colonization probabilities and also testing effects of biotic or abiotic parameters (Erwin et al. 1998).

Table 2. Parameters used to analyze factors affecting group abandonment of an island by Audouin's Gull *Larus audouinii* at the Columbretes archipelago through GLM modeling.

- **1 response variable**: the permanence or abandonment of an island every year, Bernouilli distributed, with two possible values: 0 = permanence (if t_i =1 and t_{i+1} =1), 1 = extinction (if t_i =1 and t_{i+1} = 0).
- **The logit link function**: log $[\pi/(1-\pi)]$ where π is the probability of island extinction.
- **Explanatory variables**:
  1) The island, a factor with a different value for each island of the archipelago (1=Mancolibre, 2=Ferrera, 3=Foradada, 4=Grossa, 5=Bauzá, 6=Lobo). Introduced as random.
  2) Reproductive success on year t (0 = no chicks fledged the previous year, 1= some chicks fledged).
  3) Reproductive success on year t as a continuous variable, with actual productivity values (i.e. number of chicks fledged/pair).
  4) Number of years of continuous island occupation until t_{i-1} included.
  5) Presence of Yellow-legged Gull *Larus cachinnans* on year t (0 = absence, 1 = 1-50 pairs and 2 = 51-100 pairs).
  6) Effective protection (0 = absence of wardens on the island, 1 = permanent presence of wardens).
  7) Trawling fishing moratorium on year t (0 = moratorium not implemented, 1 = moratorium implemented).
  8) Vegetation cover (0 = low vegetation cover, a factor applied to all islands of small size and to Grossa I. only during the years before wild rabbits were removed from the island and also during those years in which the vegetation was mowed as a management practice and 1 = high vegetation cover).
  9) Period of fishing moratorium, a factor with a different value for each period of two-month moratorium.
  10) Number of breeding pairs of Audouin's Gull on year t_i.
  11) Density on year t_i (i.e. number of pairs/unit area). In Grossa I. we only considered half the island surface since it is the largest island and Audouin's Gull colonies have always used only on half of the whole island.
  12) Population change (λ) on every island from t_{i-1} to t_i. A factor with two values (0, when λ is equal to or less than 1, and 1 when λ is larger than 1).
  13) Population change (λ) on every island from t_{i-1} to t_i, introduced as a continuous variable with actual values.
  14) Population change (λ) from t_i to t_{i-1} at the local population level, as a continuous variable.
  15) Ratio Audouin's/Yellow-legged gulls (number of pairs) on year t_i for the whole archipelago.
  16) Change in productivity from t_{i-1} to t_i.
  17) Colonization (0 = the colony was colonized from t_{i-1} to t_i, 1 = the colony was already existent in t_{i-1}).
  18) Productivity change between t_{i-1} and t_i, as a continuous variable.

We used Generalized Linear Mixed Models (GLMMs; Littell et al. 1996) which represent an extension of Generalized Linear Models (McCullagh and Nelder 1993). GLMMs represent a multivariate approach appropriate to separate the potential effects of co-varying factors on the process of island abandonment and colonization. In addition GLMMs allow us to incorporate independent variables as random effects in the models. In our case, since during the study period a given island could present different stages of colonization and extinction, we fitted island as a random term in GLMMs using SAS Macro program GLIMMIX (Littell et al. 1996). GLIMMIX macro automatically adjusts extradispersion. We used scaled deviance to quantify the contribution of each variable to the change in the original deviance. Probability of island extinction or colonization was modeled as a binomial response variable (0=permanence, 1=extinction/colonization) using the logit link function. Explanatory variables and its interactions were fitted to the observed data following a stepwise forward procedure beginning with the random terms and testing each explanatory variable and its interactions separately (see Serrano et al. 2001). The variable best explaining variance in the response variable was incorporated to the model and the significance of the remaining variables tested again, until no additional variables significantly increased the fitting of the model. Parameter estimates of the final model were used to derive the predicted values for the probability that an island is abandoned in a given year, by means of the inverse link function.

Table 3. Parameters used to analyze factors affecting island colonization by groups of Audouin's Gull at the Columbretes archipelago.

- **1 response variable**: the permanence or colonization of an island every year, Bernouilli distributed, with two possible values: 0 = permanence (if $t_i = 1$ and $t_{i+1} = 1$), 1 = colonization (if $t_i = 0$ and $t_{i+1} = 1$).
- **The logit link function**: log $[\pi/(1-\pi)]$ where π is the probability of island colonization.
- **9 explanatory variables**:
  - The island, a factor with a different value for each island of the archipelago (1=Mancolibre, 2=Ferrera, 3=Foradada, 4=Grossa, 5=Bauzá, 6=Lobo). Introduced as random.
  - Management of the vegetation on time t_{i-1} (before the start of reproductive activities) with two values (0 = no vegetation management, 1 = vegetation mowing to facilitate colony establishment).
  - Presence of Yellow-legged Gull on time t_{i+1} (0 = absence, 1 = 1-50 pairs and 2 = 51-100 pairs).
  - Presence of Yellow-legged Gull on time t_{i+1} (0 = absence, 1 = presence).
  - Ratio Audouin's/Yellow-legged gulls (number of pairs) for the whole archipelago on time t_i.
  - Change in number of breeding pairs in the whole archipelago between t_i and t_{i+1}, a factor with two values (0 when λ equals to or less than 1, and 1 when λ less than 1).
  - Change in number of breeding pairs in the whole archipelago between t_i and t_{i+1} as a continuous variable.
  - Number of years of island occupation up to t_{i-1} included. This is the minimum number of years of occupation since we have no data for some years.
  - Number of years elapsed since first colonization of the island up to t_{i-1}, included.

Results

Causes of colony extinction

During the study period we recorded a total of 14 cases of colony extinction. The best significant GLMM obtained for the probability of colony extinction accounted for 38.6% of the original deviance (Table 4). Island identity did not enter significantly as random term in this model, showing that decisions of abandoning an island are typically independent of the island identity. The only explanatory variable retained significantly into the model was population change (λ) on every island from t_{i-1} to t_i, which was incorporated to the model as a factor with two values: 0, when λ was equal to or less than 1 (stable or declining trend respectively) and 1, when λ was larger than 1 (increasing trend in numbers) (Table 4). This model showed that the probability of abandonment of an island increased as the decrease in breeding pair numbers between years was larger. No other variables or interactions entered significantly into the model.

Table 4. GLMM model for probability of colony abandonment using binomial error and the logit link function. (0 means values of $\lambda \leq 1$ (stable or decreasing); 1 means values of $\lambda > 1$ (increasing numbers)). SE = standard error

Effect	Estimate	SE	F test	P
Intercept	-0.7308	1.0086		
Change in λ =0	2.7956	1.2571	4.95	0.03
Scaled deviance	39.49			

On the basis of the model obtained we calculated the probability of colony extinction. Values were very high with an average of 0.89 (0.76-1.00 95% CI). Although the final model showed that island identity had no effect on the probability of abandonment, the calculated probability was lower (0.78) for the largest island.

Causes of island colonization

A total of 11 cases of island colonization were recorded along the study period. A second GLMM was built to account for the probability of island colonization. No variable entered significantly into the model, suggesting that none of the variables considered had an effect on the decision of breeding in an island that was unoccupied the previous year. However, we found a marginal effect of the presence of yellow-legged gulls. Audouin's gulls tended to colonize preferentially islands where yellow-legged gulls were not present (F=3.05, P=0.06).

Discussion

The nature of the information used by individuals in decision-making processes like dispersal is poorly understood (Doligez et al. 2002) although it is of primary importance to know what factors drive it and whether they are density dependent or not (Hansson 1991; Doligez et al. 2003). Our analysis suggested that decisions on whether to abandon or remain in an island are based on different cues and constitute two independent processes. Only the change in population size influenced to the group to abandon the island and only the presence of yellow-legged gulls seemingly influenced colonization. These results underlie the importance of considering both decisions separately as meaningless results could have been obtained with a single analysis for both decisions combined.

Proximate and ultimate causes of colony extinction

Our results suggest that patch extinction is a multi-step process which involves a progressive loss of breeding pairs over a period of at least two years, as indicated by the significance of the realized change in number of breeding pairs (λ) from t_{i-2} to t_{i-1}. The first step of the process (i.e. abandonment of the island by some individuals –pioneers- of the colony) may take place at random as a demographic stochastic process affecting the probability of dispersal. This could be especially true in small local populations such as that of our study, much more prone to demographic stochasticity. In addition, this stochastic pattern of dispersal is to be found in species breeding in highly unpredictable habitats (Switzer 1993; Boulinier and Danchin 1997; Erwin et al. 1998; Ferrière et al. 2000; Doligez et al. 2003). However, the place were this study was carried out, the rocky islands of the Columbretes archipelago, cannot be considered as unstable habitats per se, although important fluctuations in food availability due to fisheries activities could exist. From a historical perspective, this gull species is probably occupying stable habitats only since recent times. In many cases human occupation and loss of littoral habitat positively selected by the species forced individuals to occupy these islands. Audouin's gulls are probably adapted to breed optimally in barrier islands and dune fields, as occurs presently at the Ebro Delta, where more than 60% of the total world population breeds. Barrier islands are indeed unstable habitats, subjected to the effect of wind and flooding and offer little protection against terrestrial predators. Species breeding in such unstable habitats can be unexpectedly affected by environmental changes (Beer 1966; Erwin et al. 1998) or predation events (Burger 1982; Southern et al. 1985; Oro et al. 1999), and are known to show low colony-site tenacity (McNicholl 1975; Beer 1966; Burger 1974; Montevecchi 1978; Burger 1982; Switzer 1993; Frederick et al. 1996; Oro 2002). These high extinction-colonization rates seem to occur under most ecological conditions (i.e. even when conditions are good and breeding success is high). According to Kharitonov and Siegel-Causey (1988) birds from the populations breeding in unstable habitats, under increased conditions of habitat stability, show a higher degree of colony-site tenacity, although a small proportion of adults typically continue to change sites. Hence, Audouin's gulls breeding today at Columbretes and showing a nomadic behaviour seem to be affected by a behavioral trait acquired during their evolutionary history, since the habitat where they breed now has a higher stability than that selected and occupied by the species in the past.

The second step of the process of island extinction, seemingly involves public information. Gulls detecting the dispersal of neighbors would perceive the decrease in number of birds as a loss of colony quality and would in turn decide to disperse. In the colonial lesser kestrel *Falco naumanni*, Serrano et al. (2001) found that the probability of colony change diminished the larger the colony of origin. This pattern of progressive loss of members probably goes on in an autocatalic manner so that colonies keep loosing members rapidly until extinction. The last step (i.e. loss of the last few pairs) is probably mediated by an Allee effect (i.e. inverse density dependence by intraspecific cooperation) (see Courchamp et al. 1999; Stephens and Sutherland 1999). Our inverse relationship between group dispersal and colony reduction suggests that (except for the first step of unconditional dispersal) colony extinction is a density-dependent process as described by Andreassen and Ims (2000) in a vole population, where dispersal was the main parameter behind patch extinction in small patches with few individuals.

As we found an overall strong positive correlation between number of pairs and breeding success (r_s=0.70, N=26, P<0.001) we suggest that gulls abandoning the colony during the second step perceive the loss of neighbours as an indication of a reduced chance to have a successful breeding season. Hence, despite the GLMM did not retain mean productivity in the patch as a factor with a significant effect it is likely that our results are at some degree in accordance with the performance-based conspecific attraction hypothesis (Boulinier and Danchin 1997; Danchin et al. 1998). Considering that productivity was obtained as an average for the whole patch (i.e. number of fledglings/number of breeding pairs) it is not possible to provide information on differences among individuals.

Interestingly, the probability of abandonment of an island was not influenced by its historical background of occupation, suggesting that triggers of nomadism in this species are stronger than familiarity to particular islands. Similarly, food shortage through fishing moratoria had no effect on the nomadic behaviour of gulls. In fact, prior to the establishment of the trawling moratorium in 1991, and hence with normal food availability and high breeding success, gulls already showed high colony-site turn over.

Proximate and ultimate causes of colonization

Little is known about the dynamics of colonization events. We cannot provide much information on how the first gulls dispersing from a colony choose a new one although the fact that gulls remaining on the same island than the previous year had a higher breeding success compared to gulls that did colonize a different island (U = 25.5, P = 0.011) supports the idea that the first step of island selection may also happen at random. The only factor marginally retained by the GLMM as influencing negatively the probability of island colonization was the presence of breeding yellow-legged gulls. Audouin's gulls choosing islands where yellow-legged gulls breed may have increased chances of breeding failure since the ratio yellow-legged/Audouin's gull will be less favorable in most cases to the small groups of colonizing gulls. In fact we have observed some cases of colonization followed by rapid an unexplained colony desertion once gulls had already completed clutches on islands with a small number of breeding yellow-legged gulls.

Additionally, it is likely that the presence of conspecifics plays an important role during the colonization process (Kharitonov and Siegel-Causey 1988; Smith and Peacock 1990). Audouin's gulls show no fidelity to particular breeding sites but cue on the presence of individuals of their own species for breeding patch selection (Martínez-Abraín et al. 2000; Oro and Pradel 2000). Similar patterns have been described for some tern species (McNicholl 1975; Renken and Smith 1995) coinciding with the important role of group adherence that is to be expected in species evolved in unstable habitats, according to Southern (1977).

Some predictions and suggestions

We would predict that a similar pattern should be found on subcolony formation and extinction in large colonies established on unstable environments.

We cannot provide information on the characteristics of gulls first abandoning colonies at random, since we have not collected information on individuals but only on groups, but it would be interesting to determine whether this population fraction is biased by sex, age, breeding experience or any other parameter. We suggest that the first individuals to abandon the colony are probably new breeders and that experienced individuals remain longer due to the benefits of familiarity with the breeding area. Typically, higher levels of group adherence are developed in older seabirds (Kharitonov and Siegel-Causey 1988). For example, Oro et al. (1999) showed that inexperienced breeders dispersed more than experienced breeders after a predatory event at the Ebro Delta colony.

We also predict that ectoparasites are not a trigger of dispersal in this gull species if its nomadism is certainly driven by their innate tendency to shift colony site together with conspecific attraction. Gull species from stable habitats, with higher colony-site tenacity, are more prone to be affected by ectoparasitism in their nests and show massive group dispersal because of this factor (Danchin 1992).

Conservation implications

The instinctive tendency of Audouin's gulls to move unpredictably indicates that nomadism between islands of a protected archipelago bears no relationship with the degree of effective protection of each island. This high nomadism in Audouin's gulls (shown by the average 0.89 probability of island abandonment) poses indeed a conservation problem (Crawford et al. 1994; Frederick et al. 1996) since protection cannot be limited to particular breeding sites but a wider conservation approach is needed instead. Although important exchange of individuals (i.e. emigration/immigration) between Columbretes and the large Ebro Delta colony has been well documented (Oro and Pradel 2000) the GLMM for the probability of island extinction did not retain the effect of change of lambda at the local population level. This fact suggests that nomadism is independent of the change of pairs at the scale of the whole archipelago and that it only depends on the change of pairs within islands of the archipelago. Nomadism in Audouin's gull will probably be a rule in all cases where suitable habitat is available at a short distance. However, it follows as a corollary conclusion from our results that placing decoys in a colony could reduce nomadism since it

could counteract the triggering effect that random dispersal has on non-dispersing gulls (Forbes and Kaiser 1994). Probably decoys could also foster the colonization of particular islands. These management measures could be useful in those cases where one particular site is safer for reproduction than others.

Acknowledgements

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Atlantic Cory's Shearwaters breeding in a colony of Mediterranean Cory's Shearwaters

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Abstract

We report on the breeding of several individuals of Atlantic Cory's Shearwater (*Calonectris diomedea borealis*) in a small colony of Mediterranean Cory's Shearwater (*C. d. diomedea*) in the western Mediterranean (Columbretes Islands, northeastern Spain). We briefly discuss the potential role of Atlantic Cory's shearwaters in gene flow at small and declining Mediterranean colonies.

Cory's Shearwater (*Calonectris diomedea*) is a polytypic species. The nominate subspecies (*C.d.diomedea*) breeds in the Mediterranean whereas the Northeast Atlantic harbours a different subspecies (*C.d. borealis*). Shearwaters endemic to Cape Verde were traditionally considered a subspecies of Cory's Shearwaters, but are now regarded as a different species (*C. edwardsii*) (Thibault et al. 1997).
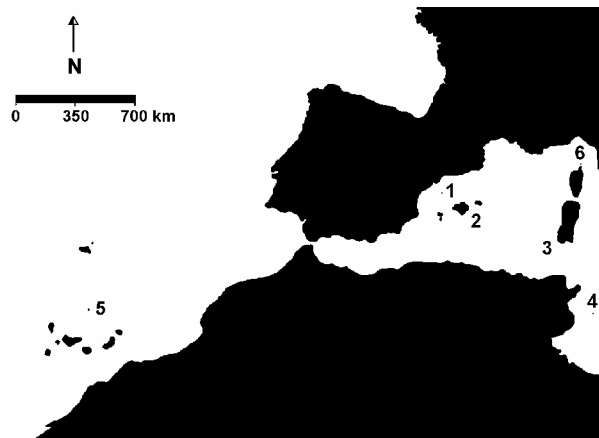
Figure 1. Main colonies of Cory's Shearwater (*Calonectris diomedea*) cited in the text. 1= Columbretes Island.; 2=Balearic Islands.; 3=Southwestern Sardinia; 4=Linosa; 5= Selvagens.

Since 1991, we have been monitoring intensively a colony of Mediterranean Cory's Shearwaters (ca. 100 pairs) located in a small volcanic archipelago (Columbretes Is., 39º 54'N, 0º 41' E, see Figure 1 and Table 1). During monitoring, adult birds were captured, measured and banded. We also determined sex by the size of the vent of birds at the begining of the laying period (Boersma and Davis 1987), reproductive status (breeding or non-breeding) and taxonomic identity (after Cramp and Simmons 1977; Granadeiro 1993; Sánchez and Castilla 1996; Thibault et al. 1997; Lo Valvo 2001 or checking the bands on birds marked as chicks). We have summarized in Table 2 the main monitoring parameters of the Columbretes colony during the last decade to give an idea of the effort invested in surveying.

The presence and verified breeding of Atlantic Cory's Shearwaters in Mediterranean colonies has been previously recorded (Lo Valvo and Massa 1988; Sánchez 1997; Thibault and Bretagnolle 1998). During the study period, we captured four Atlantic Cory's Shearwaters. The first two birds (a banded eleven year old male and a female determined by biometry: Bill length = 53.52 mm; Bill depth = 12.95 mm; Bill height = 19.8 mm; Wing length = 363 mm; Tarsus length = 58.39; Mass = 710 g) were paired and caught first in 1992. Both individuals belonged to the Atlantic subspecies (*C.d. borealis*). This couple successfully raised a chick, but in 1993 incubation failed after the male disappeared. The female was recaptured at the colony in 1994 but as a non-breeder, and was not recaptured in subsequent years. In 1999, a Mediterranean Cory's female, monitored as a breeder since 1993 and widowed in 1998 (A.S., unpub. data), was captured in a burrow with a banded seven year old male Atlantic Cory's Shearwater. This pair did not breed, but successfully raised a chick in the same burrow in the next year. In 2001, the female bred again in the same burrow, but with a male of the Mediterranean subspecies. A fourth Atlantic banded bird was captured in 1999 by the wardens of the Columbretes islands, but neither sex nor reproductive status were recorded. All four banded Atlantic birds where marked as chicks at the Selvagem Grande colony (Madeira, Portugal, 30º 09'N, 15º 52'W, see Figure 1) where thousands of birds have been banded during the last decades (J.P. Granadeiro, pers. comm.).

Despite Cory's Shearwaters show high philopatry, nest-site tenacity and mate fidelity (see Thibault *et al.* 1997 and references therein), colonies of Cory's Shearwaters are known to be connected by immigration/emigration processes, especially related to natal dispersal (e.g. Rodríguez *et al.* 2000), and are not genetically isolated (Randi et al. 1989). Whilst most shearwaters return to their natal colony to breed (Warham 1990; Thibault 1993 and 1994; Warham 1996; Sánchez 1997; Borg and Cachia-Zammit 1998; Rodríguez et al. 2000), results suggest that some birds disperse long distances, in a pattern previously recorded in other birds such as the Black-legged Kittiwakes (*Rissa tridactyla*) (Coulson and Nève de Mévergnies 1992). In fact, no neighboring Cory's Shearwaters from the large (ca. 12 000 pairs; Aguilar 1994) and well monitored Balearic archipelago colonies (more than 10,000 banded birds since 1973; F. Hernández pers. com.) have been recovered at Columbretes (Sánchez 1997; own data), where nevertheless Balearic birds commonly forage (Belda and Sánchez 2001).

Randi et al. (1989) suggested that colonies of the central Mediterranean (Linosa Is. and southwestern Sardinia) and the Azores formed a panmictic population, with an estimated 4-19 individuals being exchanged among colonies per generation time. Our results confirm this exchange rate, but only with Atlantic colonies (and suggest that northeast Atlantic and western and central Mediterranean colonies are patches of the same metapopulation. Gene flow from Atlantic birds could decrease the short-term probability of local extinction of small Mediterranean colonies (see Templeton and Read 1984) provided that this process takes place over a long time period, that offspring from mixed couples are fertile and that offspring usually recruit to its natal colony. This effect could be especially valuable in small island colonies like the Columbretes Is, theoretically prone to loss of variation by genetic drift (Hedrick and Miller 1992). Also, declining colonies, like Columbretes, may be more likely to be colonized by Atlantic birds, since chances to find vacant burrows or unpaired birds to breed with are higher. Thibault and Bretagnolle (1998) suggested that Atlantic birds recolonized the small Giraglia Island colony after its extinction.

Table 1. Comparison of morphometric data (mean ± SD; N) of Cory's Shearwater (*Calonectris diomedea*) from Columbretes, Linosa and Selvagens. After Sánchez and Castilla (1996), Lo Valvo (2001) and Granadeiro (1993).

	Columbretes		Linosa		Selvagens	
	Males	Females	Males	Females	Males	Females
Tarsus length (mm)	56.4 ± 6.52 (40)	53.6 ± 1.33 (44)	54.2 ± 2.67 (49)	52.8 ± 2.02 (49)	60.8 ± 1.61 (34)	58.2 ± 1.79 (40)
Wing length (mm)	360 ± 7.76 (38)	347 ± 7.21 (43)	357 ± 9.21 (49)	345 ± 9.86 (49)	376 ± 6.97 (38)	367 ± 7.57 (46)
Bill length (mm)	52.4 ± 6.62 (40)	48.1 ± 1.33 (44)	52.9 ± 1.84 (104)	49.6 ± 1.83 (107)	57.4 ± 2.33 (38)	53.7 ± 1.64 (46)
Bill depth (mm)	13.5 ± 6.52 (40)	11.9 ± 0.66 (44)	13.6 ± 0.61 (104)	12.1 ± 0.49 (107)	17.3 ± 0.59 (38)	15.5 ± 0.50 (46)
Mass (g)	738 ± 17.2 (36)	620 ± 75.6 (41)	668 ± 58.4 (317)	561 ± 40.6 (301)	947 ± 85.4 (38)	836 ± 69.2 (46)

It is likely that Atlantic birds enter the Mediterranean following Mediterranean birds on their way back to their natal colonies, since both subspecies share wintering quarters (Randi et al. 1989; Cramp and Simmons 1977; Warham 1990; Camphuysen and Van der Meer, in press). However, access to colonies probably happens only when colonies start declining.

Table 2. Main monitoring parameters of the Columbretes Is. colony of Mediterranean Cory's shearwaters (*Calonectris diomedea diomedea*) during the study period (1991-2000). Information comes from own data (A.S.) and unpublished reports of the regional government (Generalitat Valenciana). No data available for 1999.

Year	Occupied burrows	Adults+subadults banded	Adults+subadults recaptured
1991	84	29	43
1992	65	37	58
1993	86	49	98
1994	82	55	76
1995	113	45	122
1996	82	28	120
1997	54	29	102
1998	34	7	73
2000	63	6	48

Finally, the rate of exchange observed does not seem to be high enough to prevent further differentiation of birds of the Mediterranean subspecies over time (see Bretagnolle and Zotier 1998), since according to Randi et al. (1989) very low coefficients of selection are enough to counterbalance gene flow. However, genetic studies are needed to assess the implications resulting from the reproduction of Atlantic Cory's Shearwaters in Mediterranean colonies and to design proper management and conservation measurements.

Acknowledgements

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Movements of Yellow-legged Gulls *Larus [cachinnans] michahellis* from two small western Mediterranean colonies

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Abstract

In this study we analyse recoveries and resightings of ringed Yellow-legged Gulls *Larus michahellis* from two small colonies located along the E and SE Mediterranean Iberian coast. Results show that birds follow the same migratory routes as birds of other colonies of the western Mediterranean. Gulls move to the Atlantic coast of France and Iberia after fledging, where they summer and winter, although equally important numbers probably remain close to their natal colonies. Immature gulls (1y + 2y) seem to return and stay in the vicinity of their natal colonies during the spring. Long-range movements target Atlantic areas with a high primary-production during periods of food scarcity in the western Mediterranean. Adult gulls probably do shorter-term long-range dispersal movements than juveniles and immatures, owing to their larger experience on where to find alternative food sources.

Introduction

Yellow-legged Gulls *Larus [cachinnans] michahellis* have become increasingly common during the last 30 years due to protection of breeding sites, development of industrial fisheries and proliferation of open-air garbage dumps. Today, the western Mediterranean population numbers at least 120 000 breeding pairs (Vidal et al. 1998). It is important to know the location of wintering quarters to understand patterns of winter survival which influence the growth of colonies.

Yellow-legged Gulls from the Iberian Mediterranean were considered as sedentary in the past owing to the paucity of observations through the Gibraltar Straits during autumn and spring migrations (Tellería 1981). More recently, a N-NW movement was identified, albeit it was thought to be mere summer dispersal, corresponding with the period of complete moult (Carrera et al. 1993).

However, although Iberian Atlantic populations show non-migratory habits (Munilla 1997), it has been demonstrated that increasing numbers of western Mediterranean Yellow-legged Gulls undertake long summer migrations. Gulls fly overland to the Bay of Biscay, French Brittany, the English Channel, the southern North Sea and even to alpine lakes, following major river valleys (Yesou 1985; Le Mao and Yésou 1993; Carrera et al. 1993; Munilla 1997). Western Mediterranean birds known to migrate to the Atlantic and southern North Sea originate from Sardinia, colonies along the coast from the Hyères archipelago (France) to the Ebro Delta (Spain), the Balearic Islands and probably Corsica (Carrera et al. 1993).

The aim of this paper is to characterise the migration routes, phenology and age structure of gulls ringed at two small colonies of the Western Mediterranean and compare it with the information reported so far.

Methods

The study area includes the Columbretes archipelago and the island of Benidorm The Columbretes archipelago is a protected area consisting of a 19 ha. volcanic outcrop comprising four major islet groups, located ca. 57 km off the coast of Castellón (39º 54'N, 0º 41'E) close to the edge of a wide continental shelf. Gulls breed mainly on the largest of the islands, Grossa Island, with an area of about 13 ha. The number of breeding pairs, around 500 pairs, has not fluctuated much over the last 15 years (Table 1). A total of 1411 chicks have been marked during annual campaigns since 1993. Since 1998 most chicks (471 chicks, see Table 1) have been ringed with a yellow darvic band engraved with a black alphanumeric code (beginning either with 0 or 1) and with a metal ring. In 2001, gulls were only marked with darvic bands due to a lack of metal rings. The island of Benidorm is a 6.5 ha limestone outcrop located ca. 3 km off the coast of Benidorm (38º30'N, 0º08'E), 165 km to the south of the Columbretes Islands. The breeding population of Yellow-legged gulls has tripled during 1999-2001 (Table 1) and 231 gulls have been marked in that same period. Of these, 201 were also marked with the same type of darvic bands as used in Columbretes and again, in 2001 gulls were only marked with darvic bands due to a lack of metal rings. No resighting effort was done on the island. Resightings of engraved darvic rings (with an individual and unique alphanumeric code) and recoveries of metal rings were considered together. The frequencies used should be seen as an index, combining information on relative abundance, degree of permanence and degree of fidelity of marked gulls to a given site, since we pooled in our tables all sighting data and not only one record for each individual resighted (see North 1987). Four age classes were considered:

> 1y (juveniles in their first year of life)
> 2y (sub-adults in their second year of life)
> 3y (sub-adults in their third year of life)
> 4y (adults in their fourth year or older).

Ages of birds recovered are given to the nearest year (gulls recovered after 1 May were considered to belong to the next year age class). Juvenile birds found dead at the breeding colony one year after ringing were not considered for dispersal analysis to avoid confusion in dating recoveries of fledglings, which probably died before fledging (see Coulson and Wooller 1976; Møller 1981). Recoveries were grouped in three sets of months:

> March-June (breeding period)
> July-October (post-fledging dispersal)
> November-February (wintering)

Contingency tables together with the Chi-square statistic were used when appropriate. Yate's correction was applied to 2x2 contingency tables (Zar 1984).

Results

A total of 77 recoveries and sightings were reported up to the end of 2001, of which 73 (2 metal rings, 71 darvic bands) corresponded to 41 individuals ringed at the Columbretes archipelago. Of the 71 resightings of darvic bands, 14 corresponded to

sightings of gulls ringed at Columbretes as adults. These sightings corresponded to five individual birds controlled several times from March to October at their colony of origin. Only 4 resightings of gulls from Benidorm were reported, all on sites located further north from Benidorm where gulls from Columbretes were also recorded.

Young gulls performed large-scale movements. Juvenile birds seem to move north along the Mediterranean coast and once they reached the French border they moved west or northwest across the continent to reach French Brittany, the Bay of Biscay (Cantabria, Asturias) and up to the north coast of Portugal (Figure 1 and Table 2). Juvenile gulls seem to reach their long-distance dispersal quarters not earlier than September, since most sightings occur in November-February (Table 2) and provided that a constant effort between months is assumed. In contrast Carrera et al. (1993) reported that the bulk of Yellow-legged Gulls arrive to their summer quarters during the second half of July.

A contingency analysis revealed highly significant differences in the proportions of gulls resighted close (sectors A+B+C, see Figure 1) or far (D+E+F) from natal colonies within (March-June) or outside (July-February) the breeding season ($\chi^2_1=8.39$, p<0.01). Studentised residuals of the contingency table showed that the proportion of gulls resighted close to the Columbretes colony was higher during the breeding season whereas gulls outside the breeding season were equally frequently resighted close and far from the colonies.
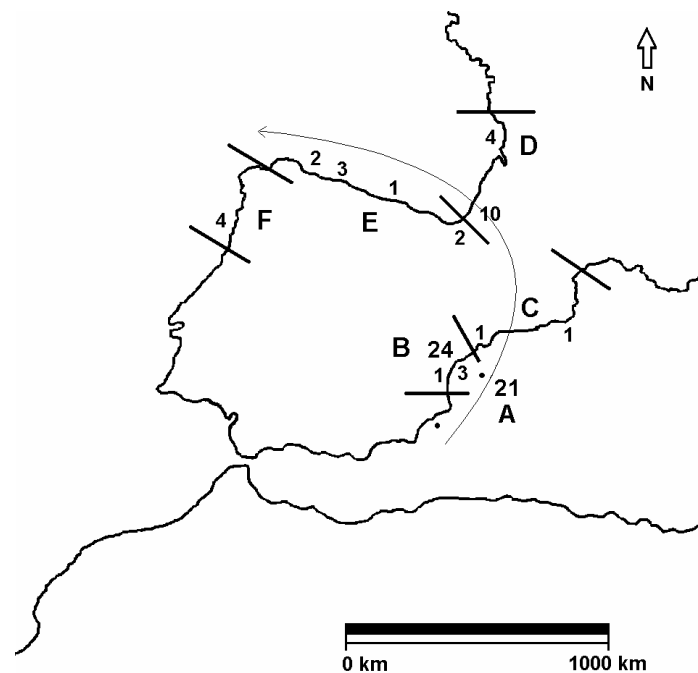
Figure 1. The number and approximate geographic location of recoveries and sightings of Yellow-legged gulls ringed at colonies of the Columbretes Islands and the Island of Benidorm. Solid dots show the location of both islands and the solid arrow the most likely overall migration route. Letters correspond to the geographical sectors used in the paper to study variations in migratory patterns in relation to age and season. (A=Columbretes archipelago; B=E Iberian Mediterranean coast; C=NE Iberian Mediterranean coast; D=French Atlantic; E=Cantabric Iberian coast; F=N Portugal).

Table 1. Yellow-legged Gulls ringed at the Columbretes and Benidorm Islands, which have been recovered or resighted from 1993-2001. B.P= Number of breeding pairs. Number of adults between brackets.

| | | COLUMBRETES | | | | | BENIDORM | | | |
| | | No.of gulls ringed | | No. of recoveries | | | No. of gulls ringed | | No. of recoveries | |
Year	B.P	Metal	Darvic	Metal	Darvic	B.P.	Metal	Darvic	Metal	Darvic
1993	425	165	0	0	0					
1994	425	135	0	0	0					
1995	475	102	0	0	0					
1996	675	88	0	0	0					
1997	650	96	0	0	0					
1998	500	160	141	0	2					
1999	530	40 (51)	16 (12)	2	28(1)	193	18 (1)	18 (1)	0	1
2000	400	154 (13)	154 (13)	0	30(13)	361	126 (26)	96 (26)	0	0
2001	420	0	160	0	13	652	0	87	0	3
Total		940 (64)	471 (25)	2	71(14)		144 (27)	201 (27)	0	4

Discussion

Migratory routes

The analysis of ringing recoveries suggests that birds of the two colonies under study follow the same migratory routes as those of other western Mediterranean colonies studied so far (i.e. move north and northwest after fledging; see Carrera et al. 1993, Le Mao and Yésou 1993). This is probably explained because Yellow-legged Gulls follow the shortest way, and because they can find food on mainland sources (e.g. following river valleys). Oceanic seabirds like Balearic Shearwaters (*Puffinus mauretanicus*) travel from the western Mediterranean to similar post-nuptial quarters but have to pass through the Gibraltar Straits and follow the Atlantic Iberian coast (Le Mao and Yésou 1993).

Age and movements of gulls.

According to our data, adult birds seem to be either sedentary or move north late in the season (November-February). The lack of observations of adult gulls during the winter months in northern locations could alternatively be interpreted as an artefact due to the low number of adults ringed. The chicks marked with darvic bands had not yet attained adult ages during our study. Munilla (1997) suggested that adult Yellow-legged Gulls ringed at Medes Islands (NW Mediterranean) performed long-range movements from July to February although Sol et al. (1995) found that adults from the Medes colony tend to stay closer to their natal colonies during the winter than juveniles. By direct observation of colonies outside the breeding season we know that a large number of adult and sub-adult gulls concentrate in both islands (Columbretes and Benidorm) in autumn (with decreasing numbers as winter begins) and that adult birds in colonies may start sexual displays and defence of territories as early as December (own data). However, if rough weather conditions prevail around colonies (e.g. during November-December), gulls may be deprived of one of their most important food sources (i.e. fisheries discards), since trawler boats cannot work out at sea (Arcos 2001) and hence some gulls might be forced to move. This may be especially so for the Columbretes Islands, located much farther from the mainland coast than Benidorm Island, and where access to alternative food sources on the mainland becomes more difficult.

Juveniles and immatures were involved in long-range movements, as it is the case in other gull species (Coulson and Butterfield 1986; Belant and Dolbeer 1993). Young Yellow-legged Gulls did not travel north only to summer, as reported so far (Carrera et al. 1993), but also to overwinter. Results suggest that during spring immature gulls (1y + 2y) move south to the vicinity of their natal colonies, when food availability is more favourable due to the oceanographic conditions.

Food abundance and movements

Oceanographic conditions of the Mediterranean are characterised by the development of a thermocline, which forces a decrease in primary productivity during the summer (Rodríguez 1982; Margalef 1985). On the contrary, the coast of the French Brittany and the Bay of Biscay are dominated by upwellings and large surfaces of tidal flats where food is abundant (Le Mao and Yésou 1993). These features probably explain why gulls move northwards to their summer and winter quarters. However, since the

ratio of adults to juveniles observed during the summer feeding behind trawler boats in the western Mediterranean is favourable to adults as a rule (Martínez-Abraín et al, 2002), it is likely that long-term long-range movements involve more juveniles and immatures than adults.

In fact, first-age classes of other gull species breeding in the Mediterranean, like Audouin's Gull (*Larus audouinii*) are linked to other upwelling systems (Oro and Martínez-Vilalta 1994), whereas subadults and adults are more independent of these sites. Hence, the interaction among age, time period and location in Mediterranean Yellow-legged Gulls is probably mediated by the experience acquired by gulls on where to find alternative food sources as refuse tips or fishing discards.

Acknowledgements

Table 2. Number of recoveries and sightings (number and proportion) of Yellow-legged Gulls ringed at Columbretes and Benidorm Islands by age and geographical sector (see Fig. 1).

	March-June				July-October				November-February			
	1y	2y	3y	4y	1y	2y	3y	4y	1y	2y	3y	4y
Columbretes	3 (15.8)	1 (9.1)	1 (100.0)	9 (100.0)	0	0	1 (100.0)	5 (100.0)	0	1 (16.7)	0	0
E Iberia	14 (73.7)	4 (36.4)	0	0	3 (50.0)	3 (100.0)	0	0	4 (25.0)	0	0	0
NE Iberia	1 (5.3)	0	0	0	0	0	0	0	0	1 (16.7)	0	0
French Atlantic	0	4 (36.4)	0	0	0	0	0	0	6 (37.5)	4 (66.7)	0	0
Cantabric	1 (5.3)	2 (18.2)	0	0	2 (33.3)	0	0	0	3 (18.8)	0	0	0
N Portugal	0	0	0	0	1 (16.7)	0	0	0	3 (18.8)	0	0	0
TOTAL	19	11	1	9	6	3	1	5	16	6	0	0
TOTAL	40				15				22			

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Section II

Human activities and seabird population dynamics
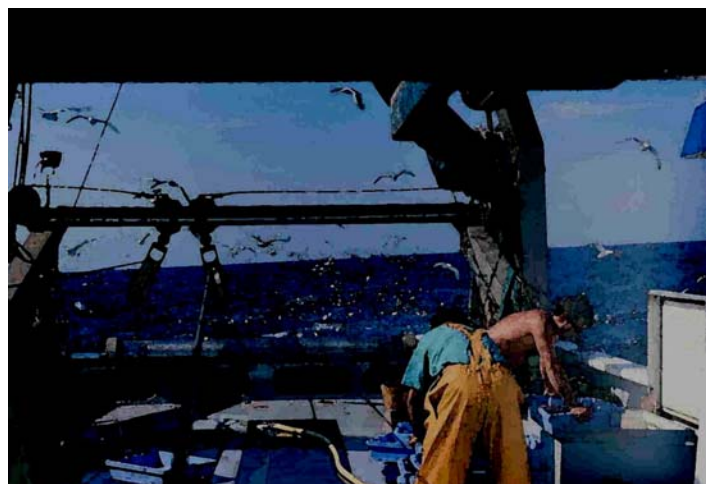
Conservación y explotación: el paradigma de la avifauna marina del Mediterráneo

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Conservation and exploitation: the paradigm of Mediterranean seabirds

Abstract

We present and discuss interactions between seabirds and fishing boats (trawlers, purse-seine vessels, long-lines and fix arts) in the western Mediterranean. Trawlers have the largest impact on seabird population dynamics. We conclude that seabirds are preadapted to the exploitation of fishing boats, that seabirds are good bioindicators of resource abundance and ecosystem health and finally that the best strategy for the conservation of seabirds is the right management of marine resources at the long run.

El Mediterráneo a vista de ave marina

Muchas especies de aves marinas están preadaptadas, en el sentido más Gouldiano del término, a la obtención de alimento en asociación con las embarcaciones de pesca. Ello es así porque una de las estrategias más comúnmente empleadas por la avifauna marina es asociarse a bancos de grandes peces pelágicos (atún, caballa, etc.) o a cetáceos, cuando estos empujan a la superficie a cardúmenes de peces o masas de invertebrados (*krill*) que constituyen sus presas (1). A fin de cuentas localizar y seguir a un rorcual a un traíña no parece muy diferente, especialmente si tenemos en cuenta que los grandes pelágicos y los cetáceos se han enrarecido, a la par que la flota pesquera ha ido aumentando en el curso de los últimos decenios.

Cualquier uso de los recursos naturales representa necesariamente una explotación de la naturaleza (2). Igual que el lago eutrófico se enriquece explotando los sistemas naturales de su cuenca hidrográfica, la actividad pesquera humana medra explotando el entorno marino, pudiendo llegar al empobrecimiento cuando existe sobrepesca. Sin embargo, este empobrecimiento no es simétrico en todas las direcciones del ecosistema marino: si bien las sardinas son cada vez más escasas, las gaviotas patiamarillas son cada vez más comunes. Por tanto la explotación humana del medio marino tiene, a primera vista, tanto efectos negativos (reducción de los *stocks* de presas tradicionales) como positivos (magnificación del efecto comensalismo) para la ornitofauna marina. Resulta curioso que no podamos incluir con facilidad a las especies beneficiadas y a las perjudicadas en grupos ecológicos bien definidos. Habitualmente las especies comensales del hombre son especies oportunistas, de hábitos alimenticios generalistas (como la rata o el gorrión). Sin embargo, los comensales orníticos de la actividad pesquera pueden pertenecer tanto a grupos propios de medios pioneros y cambiantes (p.ej. los charranes y las gaviotas) como a grupos de aves con estrategias de vida muy especializadas (p.ej. los petreles). Presumiblemente, la consecución de recursos tróficos en el mar es tan costosa (ya que el mar es como un gran desierto salpicado aquí y allá por parches ricos en alimento) que hace realmente atractivo a cualquier grupo (en términos de ahorro de energía) poder disponer de fuentes

predecibles de abundante comida, especialmente durante la época reproductora, cuando los requerimientos energéticos son máximos. Esto es aún más cierto, si cabe, en el marco del Mediterráneo, por ser éste un mar caracterizado por su pobreza de recursos y por la estratificación de sus aguas durante el estío (3). Y dentro del Mediterráneo, el aprovechamiento por parte de las aves marinas de los subproductos de la actividad pesquera (principalmente descartes de tallas o especies sin interés comercial) es particularmente significativo en su mitad occidental, donde se encuentran las flotas pesqueras no artesanales de mayor envergadura, reflejo tanto del poderío económico de los países ribereños de este extremo del Mediterráneo como de una mayor productividad marina, en gran medida provocada por la desembocadura de grandes ríos como el Ebro, el Ródano o el Po, y por los vertidos urbanos e industriales de las grandes concentraciones humanas de esta región geográfica.

Hemos dicho líneas arriba que el uso de los descartes pesqueros puede tener efectos positivos, si bien esto es cierto sólo desde la perspectiva de las especies beneficiadas, ya que el aumento desmedido de una especie puede suponer el decrecimiento de otras. Así, las deyecciones de la gaviota patiamarilla (que ha aumentado rápidamente en las últimas décadas) causa problemas a la flora adaptada a medios insulares pobres en nitrógeno y a otras aves marinas de menor talla y conducta menos agresiva, como la gaviota de Audouin o el paíño europeo (4). Además, los beneficios pueden tornarse catástrofe si el recurso que se consideraba seguro desaparece de la noche a la mañana. Para evitar el colapso de los stocks, se acuerdan moratorias de pesca temporales que suelen coincidir con la época de reproducción de las aves marinas, periodo en el que requieren de un alimento abundante y de buena calidad para sacar adelante a su progenie (5). Con lo dicho no queremos juzgar la bondad de los paros biológicos, sino únicamente relatar cómo se experimentan desde la perspectiva de especies concretas. De cualquier manera, es evidente que si se cumple el objetivo de las paradas biológicas, esto es, el aumento del stock pesquero, tanto las aves marinas como los pescadores saldrán beneficiados (6). No hay que olvidar que aunque pescadores y aves marinas compiten por un mismo recurso, la explotación razonable por parte del hombre (que no padece de fenómenos denso-dependientes reguladores de sus poblaciones) es fundamental para el futuro de la pesca, del estado de conservación del Mediterráneo, y finalmente del de las aves marinas que allí se reproducen y alimentan.

El arrastre y las gaviotas

Estudiemos el caso particular de la gaviota de Audouin en las islas Columbretes de Castellón. En la Tabla 1 se muestra la evolución temporal del número de parejas y de su productividad desde 1988 a 2000. Se puede observar con toda claridad como desde 1991 (año de establecimiento de una moratoria de pesca de arrastre de dos meses durante el periodo reproductor de la gaviota), el número medio de pollos producido por cada pareja cae desde valores muy altos situados entre uno y dos a valores próximos o iguales a cero. El número de parejas reproductoras tiene una caída después de 1991, recuperándose posteriormente (1995-1997) por razones ajenas a la dinámica de la colonia (entrada masiva de inmigrantes de la colonia del Delta del Ebro debida a la entrada de depredadores), para volver a caer en los últimos años hasta cotas que amenazan con la extinción de la colonia en pocos años.

Tabla 1. Número de parejas reproductoras y productividad de la gaviota de Audouin en las islas Columbretes desde 1988 a 2000. P.E= Número estimado de parejas reproductoras; E.R= Éxito reproductor (pollos/pareja). Datos de la Conselleria de Medio Ambiente.

	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
P.E	225	300	430	225	170	100	275	625	525	500	200	75	80
E.R	1.85	1.25	1.4	0.06	0.13	0	0.16	0.35	0.57	0	0	0	0.08

La gaviota de Audouin es una especie propia de hábitats costeros, como deltas de ríos, con amplias extensiones abiertas de barras de arena donde criar, abundante producción de pequeños pelágicos como la sardina y el boquerón (para cuya pesca esta gaviota muestra hábitos alimenticios nocturnos y relativamente pelágicos), presencia de recursos tróficos alternativos en tierra firme y presencia de otras especies orníticas a las que poder cleptoparasitar en caso de escasez de alimento. Obviamente, islas como las Columbretes, ubicadas lejos de recursos alternativos, de pequeña y abrupta superficie, con especies competidoras como la gaviota patiamarilla criando en una proporción desventajosa, no son el enclave más idóneo para esta gaviota. Su presencia en las Columbretes desde principios de la década de los 70 sólo se puede explicar por el aprovechamiento de los descartes realizados por los arrastreros que faenan en el límite de la plataforma continental (7, 8). Tan pronto esta condición desaparece, las Columbretes pierden todo su atractivo para la gaviota de Audouin y son principalmente aves que nacieron allí en años anteriores (con una fuerte fijación a su lugar natal) las que se obstinan en intentar la reproducción a pesar de las circunstancias adversas, a juzgar por el análisis de los marcajes realizados.

La gaviota patiamarilla de las Columbretes también ha notado el efecto de los paros biológicos desde 1991 aunque no de una manera tan dramática (ver Tabla 2), señalando que la dependencia de la pesca del arrastre de esta población local no es tan acentuada como en el caso de su congénere la gaviota de Audouin.

Tabla 2. Número de parejas reproductoras y productividad de la gaviota patiamarilla en las islas Columbretes desde 1989 a 2000. P.E= Número estimado de parejas reproductoras; E.R= Éxito reproductor (pollos/pareja). N.D= Información no disponible. Datos de la Conselleria de Medio Ambiente.

	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
P.E	200	275	318	300	425	425	475	675	650	500	530	400
E.R	1.10	1.50	1.08	0.50	0.84	0.85	0.93	N.D	0.33	0.6	0.6	0.88

No obstante, también parece evidente que las Columbretes no son un medio óptimo para esta especie ya que incluso cuando su éxito reproductor era alto, el número de parejas era bajo. Comparando con el caso de las Medas (unas islas que suman 20 ha., situadas a menos de 1 km de la costa del Ampurdán –Gerona- donde existe un gran vertedero de residuos sólidos y que llegaron a contar con más de 14.000 parejas antes de que se emprendiese el control por descaste de la colonia) se diría que los residuos de la pesca no son suficientes para permitir un crecimiento desmesurado de las poblaciones de esta especie, sino que es la presencia de basura la que determina una explosión demográfica (9). De hecho, en la isla de Benidorm cría aproximadamente el mismo número de parejas de gaviota patiamarilla que en Columbretes, si bien la isla de Benidorm cuenta con la mitad de superficie que la Columbrete Grande (donde se instala el grueso de las patiamarillas en Columbretes) y se encuentra situada tan sólo a tres

kilómetros de la costa, muy próxima a un gran vertedero de residuos sólidos, ahora recién clausurado. El papel del vertedero puede radicar en el incremento de la supervivencia invernal de las clases de edad más jóvenes, con menos bagaje "cultural" y una menor habilidad para el uso de los arrastreros como fuente de alimento. También es cierto que el paro biológico en Alicante se lleva a cabo tan sólo durante un mes y no durante dos consecutivos como es el caso en Castellón y Tarragona. En el Delta del Ebro (10, 11) la productividad de las gaviotas patiamarillas se redujo significativamente cuando la veda del arrastre coincidió con la fase de crecimiento de los pollos, comparado con las temporadas en las que la fase de pollo coincidió con actividad pesquera normal, lo cual sugiere que los descartes de la pesca del arrastre pueden ser un factor de control de la población, al reducir el éxito reproductor y por tanto el futuro reclutamiento local.

Otro aspecto a tener en cuenta de la pesca del arrastre es no ya la cantidad de recurso alimenticio que genera sino su calidad. Los arrastreros capturan especies bentónicas (de fondo) que son grandes acumuladores de contaminantes, al entrar más en contacto con los sedimentos que las especies pelágicas. Las aves marinas capturan fundamentalmente pelágicos cuando se alimentan sin ayuda del hombre pero cuando se sirven de las embarcaciones, aún prefiriendo los pelágicos, ingieren también peces demersales. De esta manera, sustancias contaminantes que de otro modo quedarían fuera de su alcance, pasan a formar parte de sus tejidos, acumulándose con consecuencias aún desconocida (24).

El palangre y las pardelas

La pesca mediante palangre causa perjuicios mediante su actividad, no mediante el cese de la misma, como ocurría en el caso del arrastre. Desde una óptica más económica que ecológica se podría decir que la actividad de las aves marinas respecto al arrastre es inocua mientras que es dañina en el caso del palangre. Como puede verse en la Tabla 3 el número de parejas de pardela cenicienta que se reproducen en las Columbretes muestra un descenso sostenido en los últimos años, lo cual parece atribuible (en función de las anillas recuperadas por los propios pescadores) a la mortalidad de pardelas adultas por captura accidental en las embarcaciones palangreras que faenan en el entorno de las islas, al quedar enganchadas en los anzuelos cuando intentan capturar los peces empleados como cebo (12).

Tabla 3. Número estimado de parejas reproductoras y éxito reproductor de la pardela cenicienta (*Calonectris diomedea*) en las islas Columbretes desde 1993 a 2000. P.E= Parejas estimadas nidos; E.R= Éxito reproductor. N.D= Información no disponible. Datos de la Conselleria de Medio Ambiente.

	1993	1994	1995	1996	1997	1998	1999	2000
P.E	100	100	125-150	125	90	80	80	70
E.R	0.88	0.86	0.93	0.89	0.84	0.88	N.D	0.76

Las pardelas son aves marinas de larga vida, con un potencial reproductor por temporada muy bajo: ponen un solo huevo, lo incuban cerca de dos meses, cuidan del pollo durante tres y no alcanzan la madurez sexual como mínimo hasta los siete años. Por tanto su estrategia de vida consiste en invertir mucho esfuerzo para sacar adelante pocos propágulos por temporada pero tener muchos eventos reproductores a lo largo de su vida, por lo que su eficacia biológica (*fitness*) es muy dependiente de la supervivencia adulta. Así pues, que una colonia sufra molestias en una temporada dada

no supone un riesgo grave para la permanencia de la misma pero la muerte de individuos en edad reproductora o cercana a ésta representa la hipoteca de su futuro. La captura de pardelas en el palangre del entorno de Columbretes probablemente se incrementó desde que en 1991 se instaurara la veda del arrastre, ya que la pérdida de un recurso importante puede haber empujado a los animales a buscar otra fuente antrópica de alimento, dada la facilidad que representa frente a la obtención "natural" de presas. Es necesaria más investigación al respecto ya que la interacción podría incluso darse a tres bandas, dependiendo también de la presencia/ausencia de embarcaciones de cerco en la zona. La solución a la mortalidad en el palangre está bien estudiada, existiendo varios dispositivos que cumplen bien la función de espantar a las aves y evitar su captura accidental (23). No obstante el problema es más complejo ya que si las pardelas están acudiendo al palangre a la desesperada no basta con evitar que mueran enganchadas en los anzuelos (desde luego un objetivo muy necesario) sino que preocupa también restarles otra fuente de alimento. Es una visión personal del asunto pero cuanto más ahonda uno en la interacción entre pesquerías y aves marinas más patente resulta que la asociación no es solo una cuestión de cómodo aprovechamiento de un recurso sino de cierta dependencia para la supervivencia). Nuestro Mediterráneo es una especie de campo de arroz por el que faenan barcos en lugar de tractores. Igual que las garcillas bueyeras y las gaviotas reidoras tienen difícil alimentarse en algunas épocas si no es como comensales de las máquinas de labranza (como antaño lo eran de los grandes bóvidos) las aves marinas tienen cada vez más difícil subsistir sin aliarse a los tractores marinos que son las embarcaciones pesqueras.

Artes de enmalle y cormoranes

Los cormoranes moñudos obtienen su alimento buceando en las proximidades de los núcleos reproductores, dado que suelen utilizar sustratos sólidos para secar su plumaje tras cada sesión de inmersión. Los cormoranes no cuentan con un sistema de impermeabilización bien desarrollado, como adaptación para vencer la flotabilidad positiva durante el buceo. Para esta especie, el conflicto con la actividad pesquera ocurre sobre todo cuando se disponen artes fijos (trasmallos y también almadrabas, morunas, etc.) en las proximidades de las colonias, aunque cierta afección de los palangres de superficie también ha sido descrita (13). Este problema afecta sobre todo a las aves juveniles, ya que al parecer los adultos aprenden con rapidez a extraer peces atrapados en las redes sin enmallarse (14). Este conflicto ha sido estudiado en colonias cercanas a nuestro territorio (p.ej. Cabrera y Córcega) y también en las colonias atlánticas (15), si bien en el entorno del único núcleo de cría de cormoranes moñudos de la Comunidad Valenciana (las islas Columbretes) no se da tal conflicto ya que el entorno de las islas es una reserva marina (de más de 4.000 has. de superficie) donde está actividad pesquera está prohibida. En la Tabla 4 se puede observar como el número de parejas reproductoras (aunque bajo) ha ido en aumento desde la colonización del archipiélago (16). Igualmente la productividad de las parejas se ha mantenido más o menos constante con el tiempo, en torno a dos pollos volados por pareja, todo lo cual es reflejo de ausencia de conflicto de intereses con la actividad humana en la zona.

Tabla 4. Número estimado de parejas reproductoras de cormorán moñudo en las islas Columbretes desde 1991 a 2000 y evolución de la productividad en dicho periodo. P.E= Parejas estimadas. E.R= Éxito reproductor. N.D= Información no disponible. Datos de la Conselleria de Medio Ambiente.

	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
P.E	1	5	3	4	4	10	9	7	8	9
E.R	2	2.2	2	2.7	2	2.2	1.7	1.6	N.D	1.9

El cerco y las gaviotas

El cerco es principalmente un arte nocturno, especializado en la captura de sardinas, que no produce apenas descartes y (al menos en nuestra área de interés) poco predecible en el espacio, ya que acude allí donde se encuentran los cardúmenes de clupeidos, al parecer muy móviles. Estas características limitan mucho las posibilidades de explotación de las traíñas por parte de las aves marinas. Únicamente especies adaptadas a la predación nocturna (las sardinas ascienden a la superficie de noche siguiendo al zooplancton en su migración vertical circadiana), como la gaviota de Audouin, pueden aprovechar la concentración de presas que provocan las embarcaciones auxiliares (los botes de luz que imitan el efecto de la luna llena). En el Delta del Ebro parece que las gaviotas de Audouin hacen uso del cerco para obtener alimento aunque también parece igualmente probable que las gaviotas pesquen de noche sin ayuda de las embarcaciones ya que se ha observado que cuando la flota de cerco no faena el número de gaviotas que abandonan la colonia al atardecer es sólo ligeramente inferior que en el caso de que el cerco sí esté activo (17).

Si las traíñas faenan en caladeros muy próximos a colonias de gaviota patiamarilla, la ubicación de las barcas es fácilmente detectable (por las poderosas luces que emplean) y estas gaviotas pueden aprovechar también los cardúmenes que se concentran en la superficie, como ocurre en las islas Chafarinas (18). En las islas Columbretes la relevancia del cerco en la actividad trófica de las gaviotas patiamarillas reproductoras es presumiblemente muy esporádica ya que, aunque la flota de cerco de Castellón es importante y su actividad no está prohibida dentro de la reserva marina, tan sólo se aproximan traíñas al entorno de las Columbretes en épocas muy concretas (especialmente durante el verano, faenando lejos de la reserva marina) y en número y frecuencia impredecibles, mientras que las embarcaciones de arrastre tienen áreas de pesca mucho más constantes y son también más predecibles en el tiempo, lo que facilita su explotación por parte de las aves. El paro biológico del cerco tiene lugar durante los meses de diciembre y enero, por tanto fuera de la época de cría de las gaviotas, y parece que sus consecuencias sobre las aves marinas son nulas. Por ejemplo en Columbretes se ha observado que las gaviotas de Audouin no están presentes en tierra firme durante la noche, faenen o no las embarcaciones de cerco, lo que parece indicar que estas gaviotas realizan pesca activa nocturna al igual que sucede en el Delta del Ebro.

A diferencia del arrastre, la pesca de sardina y boquerón por la flota de cerco es una pesca muy selectiva (pues prácticamente sólo atrae a estas especies) y, por tanto, mucho menos agresiva con el medio.

También existe una flota de cerco especializada en la pesca de túnidos, compuesta por pocas embarcaciones pero de una relativa importancia en la dinámica de las pesquerías de esta región. El patrón de actividad de esta flota difiere en mucho de las

anteriormente mencionadas, pues son barcas que faenan durante semanas hasta llenar las bodegas de los atunes objeto de su explotación. En muchos mares del mundo es conocida la asociación de aves marinas con estas flotas, pues éstas utilizan los grandes bandos de aves marinas para localizar los bancos de atunes. A su vez es bien conocido el comensalismo de aves y atunes, al arrinconar estos a sus presas (mayoritariamente pequeños pelágicos como sardinas, boquerones o alachas) en cardúmenes compactos cerca de la superficie donde quedan a merced de la captura por parte de las aves. Aunque sabemos que las barcas atuneras de la zona utilizan sus radares para localizar a los bandos de aves marinas y por tanto a los atunes, aún desconocemos qué efectos puede tener esta interacción tanto para las aves como para la flota. La flota atunera está presente en el entorno de las Columbretes en primavera y sobre todo en otoño (octubre y noviembre), ya fuera de la época de reproducción.

Explotación de recursos marinos y conservación de aves marinas en el Mediterráneo

En octubre del año 2000 tuvo lugar en la ciudad de Benidorm el VI Simposio Mediterráneo MedMarAvis sobre Pesquerías, Productividad Marina y Conservación de Aves Marinas, al que acudieron oceanógrafos y ornitólogos marinos de todas las riberas del Mediterráneo y varios especialistas mundiales venidos de países no mediterráneos como el Reino Unido, Canadá o Sudáfrica. Las conclusiones de dicho Simposio apuntaron hacia la necesidad de realizar una correcta gestión de los recursos marinos como estrategia óptima para la conservación a largo plazo de las aves marinas. Los paros biológicos del arrastre, implementados desde 1991 de forma continua, han permitido (junto a condiciones ambientales favorables) que la biomasa del conjunto de especies comerciales y no comerciales de pequeños pelágicos se mantenga constante, si bien ello se ha debido fundamentalmente al aumento de las especies no comerciales (alacha, jurel, boga) ya que la sardina y el boquerón han descendido. El aumento desmesurado de las especies no comerciales no debe contemplarse como algo positivo ya que es señal de la existencia de desequilibrios que pueden derivar en mortalidades masivas al ser más probable la diseminación de enfermedades. Asimismo, los paros biológicos del cerco durante el invierno no han tenido el efecto positivo esperado sobre las poblaciones de boquerón ya que esta especie se reproduce en pleno verano (21). Este fracaso global de los paros biológicos se debe precisamente a que responden más a criterios de tipo economicista que puramente biológicos (19).

El hombre es hoy un elemento fundamental en el espacio marino. Las aves marinas no han evolucionado con la actividad pesquera humana, especialmente porque esta actividad tan sólo ha comenzado a desarrollarse a escala industrial durante la segunda mitad del siglo XX. Nuestras actividades de explotación de los recursos marinos y las actividades de explotación de las aves son a menudo complementarias, pero otras veces plenamente antagónicas. En estos últimos casos se deben buscar soluciones técnicas que eviten el conflicto entre aves y hombres y, en última instancia, trabajar por un mar en buen estado de conservación ya que si los recursos abundan habrá de sobra para ambas partes. A fin de cuentas la abundancia de aves marinas no es más que un fiel reflejo de la abundancia de recursos. Uno no puede evitar pensar (considerando al unísono la gran demanda actual, nuestra enorme capacidad de extracción y la limitada tasa de multiplicación de las especies) que la pesca, tal cual hoy la conocemos, quedará pronto relegada a una actividad minoritaria para paladares exquisitos (ver 22). La pesca se puede equiparar a la caza o la ganadería extensiva de

antaño. Nos guste o no la ganadería se vio forzada a la estabulación y la cría intensiva y al mar le llegará (le está llegando ya con la acuicultura, por ejemplo) su momento de reconversión. El futuro apunta hacia más granjas piscícolas de las que ahora empiezan a proliferar, hacia una reducción importante de la flota y hacia la explotación más racional de los recursos, minimizando la generación de descartes. Todo esto traerá, a corto plazo, una crisis en las poblaciones de aves marinas pero, a la larga veremos recuperarse el equilibrio perdido.

Cabe recordar también que la actividad pesquera del Mediterráneo no sólo tiene un claro efecto sobre las aves marinas que se reproducen en este mar (20) sino que puede afectar a la dinámica demográfica de colonias de aves marinas atlánticas, ya que el Mediterráneo es un importante lugar de invernada de aves marinas procedentes de latitudes más septentrionales para las cuales sobrevivir al invierno es tan fundamental como obtener alimento durante la temporada de reproducción.

Finalmente, es interesante destacar, desde el punto de vista de la ciencia aplicada a la conservación, que la actividad pesquera, con la alternancia de sus periodos de actividad e inactividad y la variación temporal de los periodos de inactividad, puede ser tomada como una serie de experimentos manipulativos (no planeados *ex profeso*) que proporcionan una información muy valiosa sobre las causas de variación de los parámetros reproductores vitales de las aves marinas, cuya comprensión es imprescindible para la correcta toma de medidas conservacionistas.

A modo de conclusiones

Existe una fuerte interacción entre la actividad pesquera en el Mediterráneo Occidental y la dinámica poblacional de las aves marinas. Las aves marinas están preadaptadas, por su ecología, a la explotación de las embarcaciones de pesca. La pesca de arrastre es la modalidad que tiene una mayor influencia, dado que produce gran cantidad de descartes que quedan al alcance de las aves marinas y además su actividad es altamente predecible en el espacio y en el tiempo. Esta modalidad de pesca está ligada al establecimiento, mantenimiento y crecimiento de colonias de aves marinas endémicas del Mediterráneo, como la Gaviota de Audouin y su importancia se puede comprobar durante los periodos de paro biológico. Además la pesca del arrastre pone en superficie, a disposición de las aves marinas, recursos bentónicos de otro modo no alcanzables por las aves. Estos recursos tienen cargas de contaminantes mucho más altas que sus presas pelágicas tradicionales. Una vez más, las aves marinas aparecen como unos excelentes indicadores de la salud ambiental de los ecosistemas marinos pues los humanos también consumimos pescado bentónico (todo el pescado plano del tipo de los lenguados), con toda su carga de contaminantes. La pesca del cerco juega un papel secundario como suministrador de recursos a las aves marinas dada su actividad nocturna, la baja generación de descartes y lo poco predecible que resulta en el espacio y en el tiempo. Por su parte, los artes fijos como el trasmallo entran en conflicto con aves buceadoras como los cormoranes, sobre todo juveniles, aunque esta problemática está ausente en la única colonia de cría de la especie en la Comunidad Valenciana gracias a la existencia de una reserva marina en su entorno. Los artes de anzuelo como el palangre tienen una importante interacción con algunos grupos de aves marinas como el de los petreles, pudiendo suponer una grave amenaza para la persistencia de pequeñas colonias como la de pardela cenicienta de las islas Columbretes, dada la vulnerabilidad que confiere a la especie la pérdida de aves adultas. Sin duda, la vía más eficaz para la

conservación a largo plazo de las aves marinas es la correcta gestión de los recursos pesqueros, lo cual dista mucho de ser la regla en el marco del Mediterráneo Occidental. A su vez, la abundancia de aves marinas es indicadora de abundancia de recursos marinos. Finalmente, la actividad pesquera del Mediterráneo también puede tener implicaciones en la dinámica poblacional de las aves atlánticas invernantes y, entendida como un experimento manipulativo natural, proporciona valiosa información sobre la biología de las aves marinas, indispensable para la efectiva protección de las mismas.

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Prevalence of blood parasites in two western-Mediterranean local populations of the Yellow-legged Gull *Larus cachinnans michahellis*

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Introduction

Historical information on haematozoan parasites of gulls is scarce. Peirce (1981a) reported on the absence of blood parasites in small samples of several gull species (Black-backed Gull *Larus fuscus*, Herring Gull *L. argentatus*, Great Black-backed Gull *L. marinus*, Common Gull *L. canus* and Kittiwake *Rissa tridactyla*) and a low prevalence of *Haemoproteus* sp. in the Black-headed Gull *Larus ridibundus* (1 individual out of 22 sampled). More recently Ruiz et al. (1995, 1998) reported on the prevalence of *Haemoproteus lari* in Audouin's Gull *Larus audouinii* and Yellow-legged Gull *Larus cachinnans michahellis* in the Ebro Delta and Chafarinas Islands colonies. Both host species had higher prevalences and intensities of parasitism at the Chafarinas Islands (4.5 km off the Moroccan Mediterranean coast) than at the Ebro Delta (on the mainland of eastern Spain), which was attributed to higher densities or activity of Haemoproteus vectors (ceratopogonid flies of the genus Culicoides) in the former location (op. cit.). Bosch et al. (1997) also found a high prevalence and a high intensity of a *H. lari* parasitemia in the Medes Islands, located 0.9 km off the coast (NE Spain).

Here we compare data on the prevalence and intensity of a *H. lari* parasitemia infecting the sedentary Yellow-legged gull, during one breeding season in two small colonies located at different distances from the Mediterranean coast of Spain.

Material and Methods

Study area

The Columbretes archipelago is formed by a 19 hectares volcanic outcrop (comprising 3 major islet groups) located *ca*. 57 km off the coast of Castellón (39º 54'N, 0º 41'E) close to the edge of the wide continental shelf of Castellón, eastern Spain. Gulls breed mainly on the largest of the islands (Columbrete Grande) with an area of about 13 ha. Mean annual rainfall is 265 mm and mean annual temperature is 16.8 ºC. The vegetation is mainly composed of small shrubby species like *Suaeda vera* (J. F. Gmelin), *Lycium intrincatum* (Boiss.) and *Asparagus horridus* (L.). On the main island, vegetation has been severely altered in the past by human activities (fires, agriculture, livestock) from a climax composed of *Pistacia lentiscus* (L.), *Chamaerops humilis* (L.), *Smilax aspera* (L.), *Lavatera arborea* (L.) and *Medicago citrina* (Bolòs and Vigo). The only sources of freshwater in the island are two water tanks which collect water from rainfall.

The island of Benidorm (6.5 ha.) is a limestone outcrop located approx. 3 km off the coast of Benidorm (38º30'N, 0º08'E), Alicante, 165 km South of the Columbretes Islands. Mean annual rainfall is approximately 300 mm and annual temperature fluctuates from 12 ºC in January-February to 27 ºC in July-August. The vegetation is dominated by small shrubs like *Lycium intrincatum* (L.), *Whitania frutescens* (L.), *Ephedra fragilis* (Desf.), *Salsola oppositifolia* (Desf.) and *Atriplex prostrata* (Boucher *ex* DC) with some scattered wild olives *Olea europaea* (L.) and abundant exotic vegetation like *Opuntia maxima* (Miller). There are no sources of freshwater in the island.

Parasite sampling procedure

All gulls were captured by placing traps on the nests. Traps were triggered by the gulls approaching their nests. Trapping took place during the incubation period of 2000. A total of 22 gulls were captured and sampled at the island of Benidorm and 13 gulls were trapped at the Columbretes Islands. In both cases the sex ratio of the captured birds was approximately 1:1. All gulls captured had fully developed adult plumage (i.e. they were all at least 4 years old).

For all captured birds measurements of the length of wing, tarsus, tail, head and bill as well as body mass were taken (Bosch 1996). Birds were immediately released after measurements and samples were taken. A drop of blood was obtained from the ulnar vein and immediately smeared, air dried and fixed in absolute ethanol for one minute within the next few hours. Samples were stained with Giemsa solution in the laboratory fifteen days after collection.

Parasite presence was established by inspecting 100 fields containing about 100 erythrocytes each. Intensity was established by counting the number of infected red cells in 40 fields, that is on the basis of approximately 4,000 red cells. All smears were scanned twice by one observer (A. Matínez-Abraín) and once by two other observers (S. Merino, B. Esparza). Blood parasites were screened microscopically using X1000 oil-immersion magnification. One of the observers (S. Merino) followed a different screening method (see Merino and Potti 1995; Merino et al. 1997) but results were consistent between methods.

Vector sampling procedure

During the first fortnigh of September 2000 vectors were sampled by means of light traps (CDC or Communicable Disease Center style) baited with carbonic ice (Reisen *et al*. 1999). Traps were placed at Columbretes (main island), Benidorm Island and the garbage dump of the city of Benidorm (during its final stage of sealing). One trap was placed at each location. Traps were active during three consecutive nights at Columbretes and during one night at the other two sampling sites.

Sex, body condition and mean egg volume

Sexing was done by using the table of mean body measurements for males and females compiled by Bosch (1996) for birds from the Medes Islands (NE, Spain). Body condition was estimated by using the residuals of a tarsus length on body mass as well as the ratio of body mass to tarsus length. Mean egg volume was calculated as the

arithmetic mean of the volume of all eggs in a clutch.

Clutch size

Mean clutch size could not be calculated from the overall census of the colonies at both study sites because dates for the Columbretes count were too late in the breeding season (20-25 April 2000) and many eggs had already hatched. Hence, we obtained mean clutch size from a random sample of nests (n = 51 at Benidorm and n = 22 at Columbretes) which were monitored throughtout the laying and incubation periods every 2-3 days. We used the information collected in both colonies on a date centered within the laying period (16 April 2000), when peak mean clutch size is reached (i.e. most nests have full clutches and hatching is about to start).

Statistics

The independence of prevalence and location was tested by means of a 2 x 2 contingency table with Yate´s correction. The relationships between body condition, mean egg volume and intensity of infection were tested using the Pearson correlation coefficient. The associations of intensity with sex and intensity with location as well as the association of body condition with locality were tested using the Mann-Whitney U test, two-tailed (Zar 1999). The relationship between distance to the coast and prevalence was analyzed by means of the non-parametric correlation coefficient.

Results

Two blood parasite species were found infecting gulls: *Haemoproteus lari* (Yakunin 1972) (see Peirce 1981b), and *Babesia bennetti* (Merino 1998). in Yellow-legged Gulls. *B. bennetti* was only detected infecting one bird from Benidorm Island. Overall prevalence (number of individuals infected by *Haemoproteus lari* over total number of individuals sampled) was 100% for Benidorm Island gulls and 38.5% for Columbretes gulls. Prevalence for Benidorm males (infected males/total number of gulls sampled) was 45.5% and 23.1% for Columbretes Islands males. Prevalence was 54.5% for Benidorm females (infected females/total number of gulls sampled) and 15.4% for Columbretes females. Data for both sexes were analyzed together as there were no significant differences between sexes in prevalence since all birds from Benidorm were infected (10 males and 12 females) as well as 3 males and 2 females from Columbretes Islands (χ^2_1=0.00, P = 1.00). Differences in intensity between sexes could not be tested for Columbretes gulls (intensities recorded were 1-2-2 infected cells/4.000 red cells for the three infected males and 3-2 for the two infected females) due to the small sample size but there were no significant differences in intensity of infection between sexes for Benidorm gulls (U = 58.5; ns, Table 1).

Table 1. Prevalence (individuals infected by *H. lari*/examined), intensity of infection (number of infected red cells in 40 fields) by *H. lari* and body condition (ratio of body mass to tarsus length) for Yellow-legged gulls from Benidorm and Columbretes Islands.

BENIDORM ISLAND

Sex	Prevalence	Intensity (SD)	Body Condition (SD)
Males	45.5%	22.8 (32.40)	15.41 (1.97)
Females	54.5%	42.0 (79.86)	14.62 (0.89)
Both	100%	33.3 (62.34)	14.98 (1.49)

COLUMBRETES ISLANDS

Sex	Prevalence	Intensity (SD)	Body Condition (SD)
Males	23.1%	1.7 (0.58)	14.93 (1.97)
Females	15.4%	2.5 (0.70)	15.95 (4.39)
Both	38.5%	2.0 (0.71)	15.34 (2.66)

Hence, a 2 x 2 contingency table was used to test the independence between status of infection (prevalence) and locality. The results of the contingency analysis show that gulls from Benidorm Islands had significantly higher prevalences than gulls from Columbretes Islands (Fisher's exact test, $\chi^2_1 = 14.2$, $P < 0.0001$). A similar result appeared for median intensities of infection, with Benidorm gulls showing much higher intensities than those from Columbretes ($U = 89.5$, $P < 0.05$).

Intensity of infection for birds from Benidorm was not correlated with body condition (males: $r_s = 0.12$; $P = 0.60$, females: $r_s = 0.06$; $P = 0.84$). Intensity was also not correlated with mean egg volume at Benidorm ($r_s = -0.10$, $P = 0.77$). The relationships between intensity and body condition and intensity and egg volume for Columbretes gulls could not be analyzed due to the small sample size. There were no differences in median body condition for gulls (infected + noninfected) from the two islands either using ratios ($U = 161$, $P = 0.83$, Table 1) or linear regression residuals ($U = 146$, $P = 0.51$) as a measure of body condition. Mean clutch size ($\pm$SD) was 2.50 $\pm$ 0.74 ($n = 22$) at Columbretes and 2.71 $\pm$ 0.54 ($n = 51$) at Benidorm. Differences in mean clutch size between islands were not significantly different ($U = 465$, $P = 0.162$). We found a strong inverse correlation between distance to the coast and prevalence after pooling our data from Columbretes and Benidorm with those from Chafarinas Islands (Ruiz et al. 1995, Ruiz et al. 1998) and Medes Islands (Bosch et al. 1997) ($r_s = -0.71$, $P < 0.001$). Data from Chafarinas and Medes Islands were collected during the breeding seasons (month of April) of 1994 and 1995. Data from the Ebro Delta were not included in the analysis because we restricted the comparison to sites with similar ecological features (western Mediterranean islands).

No Haemoproteus vector (*Culicoides*) was trapped neither at Columbretes nor at Benidorm (island and garbage dump). However, we collected three female *Phlebotomus*

papatasi and 1 female *Phlebotomus perniciosus* (Familiy Psychodidade) at the garbage dump of Benidorm, besides 5 *Culex pipiens* female mosquitoes. Phlebotoms are known to be the vectors of Leishmania (indicating a richer hematophagous diptera community at the dump than at both islands) and its role as possible vectors of Haemoproteus should be studied. We also trapped 7 female *Aedes mariae* (or *A. caspius*) at Benidorm Island. No haematophagous insect was trapped at Columbretes.

Discussion

Yellow-legged Gulls from Benidorm Island were more frequently parasitized and showed much higher parasite loads than gulls from Columbretes Islands Our results suggest differential prevalence and intensity of parasitemia of *Haemoproteus lari* between the two islands. In addition, another blood parasite, *Babesia bennetti,* was present in gulls from Benidorm Island (Merino 1998). At least two hypothesis may explain these differences.

First, parasitism may be linked to intrinsic factors such as breeding effort or physical condition, as previously shown for other bird species (see for example Apanius et al. 1994; Merino et al. 2000; Oppliger et al. 1995; Oppliger and Christe 1996; Siikamäki et al. 1997), probably implying an energetically based trade-off between prevalence and increased breeding effort. Our data on Yellow-legged Gulls do not support that hypothesis since birds from Benidorm and Columbretes differed in prevalence of blood parasites despite mean clutch size and body condition were similar between islands.

The fact that body condition or mean egg volume of infected females from Benidorm were not significantly correlated with intensity of parasitemia suggests that intensity of infection is not related to reproductive effort (but most likely to individual background of exposure to parasite vectors) although Bosch et al. (1997) found that more heavily infected females tended to lay smaller clutches and to be in leaner body condition at Medes Islands. Alternatively, the absence of a relationship between intensity and body condition also may be interpreted as Haemoproteus parasites having little effect on the health of gulls.

Secondly, prevalence may be determined by extrinsic factors like vector abundance. Recently, Sol et al. (2000) presented both observational and experimental evidence that vector abundance is the major influencing the spatial variation in prevalence of *Haemoproteus columbae* in pigeons. In fact, the general absence of haemoparasite infections in seabirds has been attributed to the lack of vectors in oceanic islands (Bennett et al. 1992). The abundance of vectors may be higher closer to the mainland (as our trapping results suggest) thus explaining the pattern found for Yellow-legged Gulls from Benidorm and Columbretes Islands and also the strong inverse relationship between distance to the coast and prevalence among the four islands analyzed. The proximity to the mainland may account for more frequently and more intensely infected gulls from Benidorm Island. Conversely, gulls from Columbretes may be less frequently and less intensely parasitized due to the long distance from the islands to the coast. In addition, gulls from Benidorm Island are known to frequently use the large garbage dump of the city of Benidorm as a feeding ground (own data), where vectors could find suitable places for reproduction, like wet sediments with high levels of organic matter and low salinity (Blackwell et al. 1994; Lardeux and

Ottenwaelder 1997). The same factor (absence of suitable places for vector breeding) may also explain the low prevalence reported by Ruiz et al. (1995) at the Ebro Delta, together with the fact that Yellow-legged gulls from the Ebro Delta do not make common use of refuse dumps since they can find abundant food in secondary foraging habitats (rice fields, sandy beaches) during periods of fishing moratorium (Bosch et al. 1994; Oro et al. 1995). Similarly, the high prevalence of gulls from the Medes Islands might be explained by the common use of nearby refuse tips as feeding grounds (Bosch et al. 1994, 1997). Finally, Yellow-legged Gulls from the Chafarinas are also known to exploit waste food from refuse tips when purse-seine fisheries do not operate (González-Solís et al. 1997 a, b).

Yellow-legged Gulls from Columbretes also visit garbage dumps on the mainland (probably during weekends and other periods during which the fishing trawler fleet is not active besides periods of dispersal) since some non-floating litter remains have been found scattered around the colony (authors, unpubl.). However, visits are considerably less frequent than in the case of gulls from Benidorm owing to the longer distance between Columbretes and the continental coast. Since intensity seem to be mostly influenced by individual background of exposure to parasites (see Allander and Bennett 1994), it is likely that the low intensities detected at Columbretes are explained by the fact that only older birds make use of resources from the mainland whereas all birds have an easy access to food resources at Benidorm.

Thus, prevalence of *Haemoproteus lari* in Yellow-legged gulls from the two colonies under study seems to depend on vector availability, which is influenced by distance to the coast.

The fact that neither prevalence nor intensity were associated with sex of Benidorm gulls indicates a similar degree of exposure to vectors, probably due to a similar time spent by males and females on the mainland.

Finally, we do not have any information on the presence and abundance of gull ticks (the supposed vectors of *Babesia*) at Columbretes. However, ticks are also common in other gulleries (Bosch and Figuerola 1999) and we have detected them infecting the brood patch of some adult gulls in Benidorm. A higher sample size might confirm the absence of this parasite in Columbretes, although the parasite may pass unnoticed, confounded with immature stages of infection by *H. lari*.

Acknowledgments

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Demersal trawling waste as a food source for western Mediterranean seabirds during the summer

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Abstract

We studied the use of demersal trawler discards by scavenging seabirds at one location of the western Mediterranean (Benidorm, SE Spain) from the end of June to the beginning of October 2000. Yellow-legged gull and Cory's shearwater were the most common species in the study area (52.35%, 35.49%) and behind boats (82.4%, 7.07%). Eight other seabird species were observed in much lower numbers following boats (Audouin's gull 2.6%, black-headed gull 2.3%, sandwich 1.5% , black 0.82% and common terns 0.97%, Balearic shearwaters 1.4%, storm-petrel 0.52% and shags 0.36%). Yellow-legged gulls were present behind trawlers in higher numbers than might have been expected by its abundance at sea, whereas Cory's shearwaters were less so.

The discarded fish ("discard") comprised mainly of sardine (22.4%), flatfish (19.1%) and horse-mackerel (17.3%) and included fish of a small size (median 10.5 cm) in the main. Yellow-legged gull made the largest use of discards, albeit lower than expected by its Presence Index. Average percentage consumption was about 54% of the edible discards, suggesting that yellow-legged gulls were not highly efficient at catching "discard". The average ratio of fish discarded over fish landed was ca. 65%, although the range was very variable (23-175%). Hence, there was no linear relationship between the amount of fish landed and discarded. Estimates of the energy requirements of yellow-legged gulls and energy availability from the ca. 8 tonnes of discard produced every fishing day, suggest that trawling waste was probably enough to support a local gull population four times larger than that present during the study period.

Introduction

The utilization of fishery waste by scavenging seabirds has been studied thoroughly during the last decade especially in the northern and southern Atlantic (e.g. Furness et al. 1992; Thompson 1992; Garthe and Hüppop 1994; Thompson and Riddy 1995; Garthe et al. 1996). The situation found in Mediterranean inshore trawling fisheries, on the othre hand, has seldom been studied (Carbonell et al. 1997, 1998) and in most cases information is available only in the form of grey publications (e.g. Salas, 1995). The use of fishery waste by seabirds in the western Mediterranean has been addressed only recently by a few researchers (see Oro, 1999 and references therein). In general, most studies deal with breeding gulls and little is known about the use that seabirds make of fishery waste outside the breeding season in the western Mediterranean (e.g. Sarà 1993). However, resource availability during this period can be crucial for winter survival (e.g. Harris and Wanless 1996; Harris et al. 1998; Marra et al. 1998) and recruitment (Spear et al. 1995).

In this paper we consider the utilization of fishery waste from bottom trawling as a food source for scavenging seabirds during the summer, when some seabird species

(gulls) have finished their breeding cycle and others (petrels) are completing their breeding season. We also evaluate the availability of fish waste and the energetic needs of seabirds in the study area in order to assess the potential importance of the fish waste to seabirds breeding there.

Study area and methods

The study area was within the foraging range of yellow-legged gulls (*Larus cachinnans*) breeding on the small islands of Benidorm (Alicante, Spain, 38º30'N, 0º08'E), a "Special Protection Area" for the conservation of the European storm-petrel (*Hydrobates pelagicus*). Data were obtained on 22 commercial trawler cruises representing 45 fishing operations on board vessels from Villajoyosa, a fishing port located a few kilometers south of Benidorm (Figure 1). Cruises were carried out during the months of June (2), July (5), August (8), September (8) and October (2) and each lasted lasted about 12 h (from 5-6 a.m. to 5-6 p.m.). To avoid a possible biasing of the results, sampling was performed on board five different commercial fishing vessels. Boat lengths ranged between 15-23 m, displacement between 10-65 gross registered tonnes and horse power between 82 and 430 hp.

Seventeen cruises took place aboard small boats (fishing range 54-90 m deep) and five aboard larger boats (90-115 m deep). The vessels did not have any specific target species, but the most valued catch was European hake (*Merluccius merluccius*). Trawlers fishing further than 45 km off the coast -mainly for commercial shrimp species at ≥300m deep- were not included in the study. There are 56 trawlers at the Villajoyosa port but only 35 operate in the study area daily, from Monday to Friday. However, 18 trawlers from Campello, Altea and Calpe also operate within the foraging range of the gulls breeding at Benidorm. All of these vessels operated within the limits of the Alicante continental shelf. This shelf has a mean width of 32 km, with a minimum of 23 km off Santa Pola and a maximum of 40 km off Altea. The edge of the shelf is located between 110-140 m deep and the sea-bed surface is predominantly sand and mud (Carbonell et al. 1997) (Figure 1).

Figure 1. Map of the study area showing the port from which trawler cruises began (Villajoyosa), the islands of Benidorm (solid black dots), the 200 m isobath and the approximate limits of the fishing grounds of the trawlers.
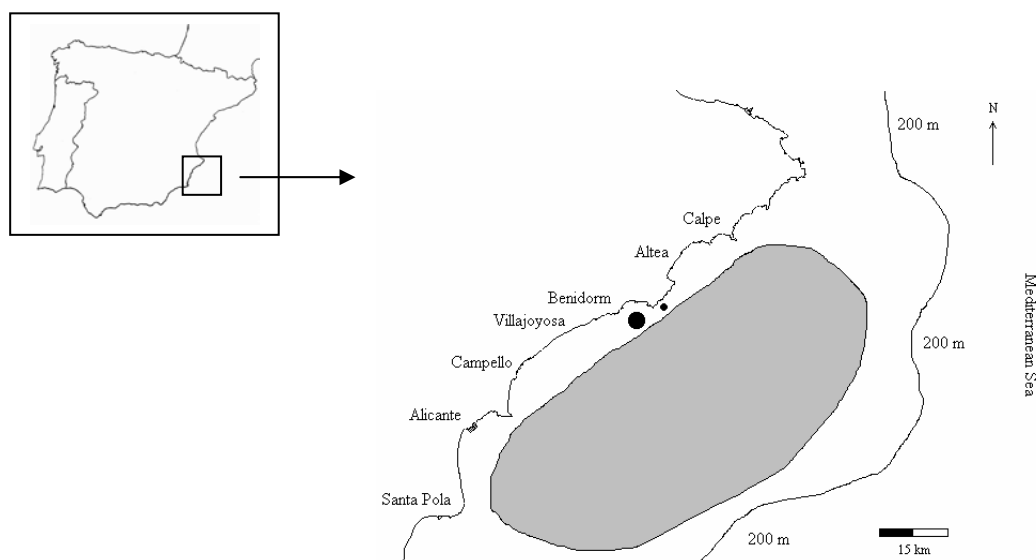
The only seabird species breeding in the study area were yellow-legged gulls and storm petrels. The number of breeding gulls for the two islands of Benidorm (used for the development of our energetic index) was estimated at 400 pairs (own data) and its productivity was calculated as the arithmetic mean of all data available in the literature combined with own data (1.0 fledglings pair^{-1}). The number of non-breeding gulls present around colonies was estimated as five times the number of breeding pairs, according to the ratio of immature-plumaged to adult-plumaged gulls we had observed in smaller colonies (e.g. Campello, Tabarca). The breeding season of yellow-legged gulls ranges from late March (start of egg laying) to late June (fledging period) and that of storm petrels from early May to mid August. Hence most of the information comes from late in or outside the breeding season for both species.

The species and number of seabirds observed in a transect line were recorded every 10 min for about one hour within a 250m-wide band during the first haul of the day, to obtain an index of seabird abundance (birds/km^2) in the area previous to discarding. The distance covered by the boat was calculated from the velocity of the boat and the duration of each haul. During the sorting and discarding phase following each haul (from net lifting to end of discarding) we recorded the species and number of seabirds following the boat every 15 minutes, after Tasker et al. (1984). However, when discarding was not done gradually but all at once at the end of the fish-sorting process, we recorded the number of seabirds present behind the boat at that precise moment taking advantage of the fact that seabirds watch boats from the distance until the first discard of the day has taken place. The age (adult or juvenile) of yellow-legged and Audouin's gulls was recorded both during transects and discarding phases.

The vessels made a varying number of consecutive hauls a day, ranging from three (large boats, fishing farther off the coast) to six (small boats, fishing inshore). Birds were recorded in a 180º scan around the boat, from one of the vessel's sides, during transect lines and from the stern of the boat during the census of seabirds associated to the trawler. The census of seabirds was continuous after first discarding, since "next hauling" started immediately after sorting and discarding of fish from the previous haul had ended. Final sorting ended when boats where close to their home port.

In order to assess whether there were seabird species making a greater use of discards than has to be expected from their abundance in the area, we tested the simple null hypothesis that the two most common seabird species followed boats proportionately to their abundance in the area before discarding as obtained from transect lines. A "Presence Index" was then computed (see for instance Oro and Ruiz 1997), assuming that all species were equally likely to follow a trawler. We used the average of the largest number of seabirds of each species present behind the boat in each discard operation and the mean of the largest density value of each species on the transect lines. This index was expressed by the residuals of the chi-square distribution obtained from the standardized difference between the observed and expected frequencies. Values below –2 or above +2 were considered to be significant (Zar 1999).

To estimate the amount of fish discarded we made use of all the fish sorted for discard by one of the fishermen. We estimated the amount of discard in each haul by counting the number of boxes that we were able to fill in with "discard" (each box ranges between 12-15 kg depending on fish species) and multiplying by the number of fishermen discarding. We divided our sample into four equal portions and then

estimated the weight of edible and unedible (shells, rocks, plant remains) "discard" in one of the four quarters. Each day a sub-sample of 3-4 kg of fish, from one of the hauls, was collected to classify and measure the length of all individuals in the laboratory. When this sub-sample was collected after the last haul, the fraction available or not available for seabird consumption was estimated from this smaller sample, rather than from one of the usual quarters. Overall, 2036 fish were measured and identified.

To measure feeding efficiency and prey-size selection by seabirds we took fish sorted out by the fishermen and threw single items overboard -close to the stern of the vessel but from one side, to avoid the turbulence generated by the engines- during sorting and discarding phase (after Hudson and Furness 1988). Fish were thrown while the fishermen themselves were discarding to avoid biasing our results (after Garthe et al. 1996). Overall, we experimentally threw 1187 fish overboard in 33 discard experiments. We noted the size classes and species of the fish captured as well as the seabird species involved. A Success Index was calculated based on the average numbers of seabirds observed behind the boat and the number of fish captured by each species. Our null hypothesis here was that the relative frequency of fish capture mirrored the relative frequency of species observed behind the boat, assuming that all species following the boat have an equal probability of obtaining fish (Camphuysen 1994). This index was also expressed via the residuals of the chi-square distribution obtained from the standardized difference between the observed and the expected frequencies. Manly's "Preference Index" (Krebs 1989) was used to determine the preference of seabirds for the class sizes of discarded fish
:

$$\alpha_j = \log p_j \Big/ \sum_{j=1}^{m} p_j$$

where α_j = Manly's alpha for the size class of fish j; m = number of fish size classes and p_j proportion of the size class of the fish that are not consumed at the end of the experiment (j = 1, 2, 3, …, m) = e_j/n_j [e_j = number of fish of size that are not consumed at the end of the experiment and n_j = initial number of fish of size j in the experiment]. The length of fish discarded was grouped into three categories: small (2-10 cm), medium (11-19 cm) and large (20-40 cm).

To test whether there was an association between the amount of fish discarded and the amount of fish landed we obtained the weight of fish landed in each cruise by consulting the catch statistics at Villajoyosa.

To design a rough index of food requirement over food availability for yellow-legged gulls during the study period, we assigned an average calorific value of 5 kJ g^{-1} to "discards" and a food assimilation efficiency of 75% (after Furness et al. 1988). The estimate of the basal metabolic rate for yellow-legged gulls was based on Bryant and Furness (1995), where BMR (kJ d^{-1}) = 2.3 (body mass), considering an average body mass of 1019 g, based on our own data on gulls captured on Benidorm island. BMR of yellow-legged gulls is probably overestimated since the equation used was developed for Atlantic birds. Since BMR only covers a part of the energy expenditure of seabirds we calculated the Field Metabolic Rate (FMR) as 2.5 BMR after Garthe et al. (1996).

Presence and success indices were obtained by means of chi-square goodness-of-fit tests. Contingency tables (together with the G statistic), Mann-Whitney U test and non-parametric analysis of variance (Kruskal-Wallis H-test) were performed when

appropriate. The correlation between fish landed and fish discarded was assessed by Spearman rank correlation. Species diversity of the community following the boats was calculated by means of the Shannon-Weaver index, and differences between indices were compared by means of the t test proposed by Hutcheson (Zar 1999). All statistical tests were two-tailed. Mean percentage consumption during "experimental discard" was estimated by weighting the consumption percentage for each fish species by its sample size (after Zar 1999) and considering only fish species with n>10.

Results

Yellow-legged gull and Cory's shearwater were the most abundant species in the area before the first discarding operation (first haul), representing 87.8% of the seabirds observed. All other six species recorded were present in lower densities (Table 1). The adult/juvenile ratio was 8.4 for yellow-legged gulls and 3.9 for Audouin's gulls.

After performing an analysis of mean abundance by months (July, August, and September) for the five most common species, we found that both Cory's shearwaters (Kruskall-Wallis test, χ^2=6.46, df=2, P=0.04) and Balearic shearwaters *Puffinus mauretanicus* (Kruskall-Wallis test, χ^2=6.31, df=2, P=0.04) were more abundant in the study area late in the summer, whereas all other species (yellow-legged gulls, Audouin's gulls *Larus audouinii* and black-headed gulls *Larus ridibundus*) were equally abundant in all three summer months.

To verify whether the composition of the seabird communities were similar regardless of distance from the coast, we measured species diversity of the two groups of boats considered -boats fishing not farther than 28 km off the coast and boats fishing between in the 28 and 47 km zone- and found there was not significant difference (Hutchenson Student's t statistic, v=19.72, t=-0.12, P>0.05).

We also tested whether there were differences in seabird abundance depending on the schedule of the cruises and found that there were no significant differences between early morning (0620am-0735 h; n=9), late morning (later than 0735 h; n=11) and afternoon cruises (later than 1500 h; n=2) (Kruskall-Wallis test, χ^2=1.3, df=2, p=0.53) consequently we pooled our data, regardless of distance to the coast or time of cruises.

Yellow-legged gull was the most common species (82.4%) following boats (Table 1). All other nine species were present in lower numbers. However, some species were present behind boats (Sandwich tern *Sterna sandvicensis* and black tern *Chlidonias niger*) which were not recorded on transect lines. The adult/juvenile ratio was 6.0 for yellow-legged gull and 4.5 for Audouin's gull.

We found that there were significant differences between observed and expected frequencies of the two most common seabird species following boats (χ^2=19.3, df=1, P<0.001). "Presence Indices" suggest that yellow-legged gull were seen behind boats more often than expected, whereas Cory's shearwater was seen less often than expected, from their respective abundance in the area.

Table 1. Relative abundance of seabirds in the study area (during first haul) and behind boats (during sorting and discarding). Data for "seabirds at sea" are the means (± sd) of the largest number of birds of each species in each line transect (n=22), standardized by the area covered in each transect. Data for "seabirds at boats" are means of the largest number of birds censused after each haul (n=45).

Seabird Species	Seabirds at sea (birds/km^2)	Seabirds at boats (birds)
	Mean ± sd	Mean ± sd
Yellow-legged gull	14.13±11.25	68.2 ± 55.81
Cory's shearwater	9.58 ± 19.15	5.85 ± 10.07
Audouin's gull	1.19 ± 1.69	2.18 ± 3.54
Black-headed gull	0.54±1.19	1.88 ± 7.86
Sandwich tern	0	1.27 ± 1.72
Balearic shearwater	0.60±1.63	1.15 ± 3.56
Common tern	0.16±0.33	0.80 ± 1.75
Black tern	0	0.68 ± 3.04
European storm petrel	0.21±0.49	0.43 ± 2.34
Shag	0.58±1.85	0.30 ± 0.90

Availability of fish waste

Discard composition included 32 taxonomic groups (Table 2). The richness of the "discard" observed in our study wass very similar to that observed at the Ebro Delta (29 categories) but much lower than that of Balearic waters (47 categories), according to Oro and Ruiz (1997). The most commonly discarded fish species were sardine *Sardina pilchardus* (22.4%), flatfish (19.1%) and horse mackerel *Trachurus* spp. (17.3%). All other groups recorded were present in lower numbers. These three species, comprising ca. 60% of all discards, were of small size (median 10.5 cm, range 8.5 – 10.7).

We ran a nonparametric correlation between the weight of fish landed and the weight of "discard" and found that there was no relationship (r_s=0.02, P=0.96, n=10). The ratio of fish discarded to fish landed was very variable and ranged from 23-175%.

The median percentage of the ratio was 64.8. The median weight of fish discarded was 145 kg (vessel d)$^{-1}$ and the median weight of fish landed was 209 kg (vessel d)$^{-1}$.

The trawlers operating in the study area generated an average of ca. 8 tonnes of discarded fish per day. Energy availability from these discards was enough to maintain four times the energetic requirements of the local population of yellow-legged gulls (see Table 3), assuming that the effect of other species on discard consumption in the area is negligible and that catching discarded pieces is a density-independent process so that percentage consumption-catching fish remains constant with increasing population size. Hence, trawling activity solely maintain a gull population four times larger (ca. 12 700 gulls) than that present during the study period.

Table 2. Number (n), percentage (% n) and length (Mean ±s.d) of fish discarded from samples collected at the trawlers. The median of the mean lengths is shown. Data come from samples (n=22) ranging 2-3 kg.

Fish species	N	% n	Length	Class size
Horse mackerel (*Trachurus* sp.)	353	17.3	10.3±0.12	Small
Spotted flounder (*Citharus linguatula*)	389	19.1	8.5±0.05	Small
Sardine (*Sardina pilchardus*)	456	22.4	10.7±0.11	Small
Boar fish (*Capros aper*)	13	0.6	8.7±0.24	Small
Bogue (*Boops boops*)	100	4.9	13.1±0.20	Medium
European hake (*Merluccius merluccius*)	33	1.6	11.5±0.34	Medium
Goby (*Gobius* sp)	53	2.6	6.4±0.52	Small
Seabream (*Pagellus* sp)	95	4.7	11.6±0.15	Medium
Imperial jerret (*Centracanthus cirrus*)	88	4.3	11.8±0.40	Medium
Triglidae	10	0.5	8.2±0.33	Small
Conger eel (*Conger conger*)	2	0.1	40±7.07	Large
Common sole (*Solea solea*)	12	0.6	8.8±0.46	Small
Trisopterus sp.	27	1.3	15.2±0.84	Medium
Roughfish (*Hoplostethus mediterraneus*)	15	0.7	9.4±0.42	Small
Myctophidae	54	2.6	11.9±0.50	Medium
Black mouthed dogfish (*Galeus melastomus*)	28	1.4	19.9±0.77	Medium
Mendole (*Spicara maena*)	21	1.0	12.9±0.42	Medium
Cusk eel (*Ophidion barbatum*)	11	0.5	14.7±0.28	Medium
Snipefish (*Macrorhamphosus scolopax*)	23	1.1	8.6±0.88	Small
Comber (*Serranus cabrilla*)	24	1.2	8.4±0.16	Small
Anchovy (*Engraulis encrasicholus*)	14	0.7	10.3±0.18	Small
Greater forkbeard (*Phycis blennoides*)	45	2.2	9.3±0.14	Small
Striped seabream (*Lithognatus mormyrus*)	4	0.2	7.5±0.910	Small
Boar fish (*Capros aper*)	9	0.4	7.4±0.83	Small
Red bandfish (*Cepola rubescens*)	4	0.2	18.7±0.59	Medium
Blue whiting (*Micromesistius poutassou*)	63	3.1	14.5±0.10	Medium
Twaite shad (*Alosa fallax*)	39	1.9	13.5±0.47	Medium
Brill (*Scophthalmus rombus*)	11	0.5	11.6±0.22	Medium
Scorpionfish (*Scorpaena* sp)	2	0.1	10.2±0.53	Small
Saddled seabream (*Oblada melanura*)	4	0.2	10.4±1.77	Small
Bluemouth (*Helicolenus dactylopterus*)	12	0.6	5.1±0.47	Small
Stargazer (*Uranoscopus scaber*)	17	0.8	16±1.18	Medium
Total	2 036		10.55	Small

Table 3. Energy requirements of yellow-legged gulls and energy equivalents of trawler "discards" in the study area (Benidorm, SE Spain). An index of energy required over energy available is shown (corrected by the average discard percentage consumption and food assimilation efficiency) after Garthe et al. (1996).

Population	Gull population (nº. individuals)	Energy Required (x 10^6 kJ d^{-1})	Energy available (x 10^6 kJ d^{-1})	Index (required/available)
Breeding adults + offspring	1 200	1.47	15.56	0.09
Breeding adults + offspring + non-breeding birds	3 200	3.9	15.56	0.25

Experimental discards

From all seabird species that were recorded following trawlers only yellow-legged gull, Audouin's gull, Cory's shearwater and common tern captured fish thrown during "experimental discards". Yellow-legged gulls ate 644 out of the 886 pieces thrown overboard (ca. 73%).

We tested whether seabirds caught fish items proportionally to their abundance behind boats and found that the observed frequencies of fish capture were significantly different compared to those expected from the birds relative abundance behind trawlers (χ^2=33.54, df=3, P<0.001). The values of the "success index" were only significant for yellow-legged gull and indicate that this species obtained less discards than expected from its abundance behind boats.

Seabird species showed no overall difference in the consumption of the three size classes considered (small: χ^2=1.7, df=8, p=0.99; medium: χ^2=2.3, df=11, p=0.99; large: χ^2=0.1, df=3, p=0.99). Mean percentage consumption of experimentally discarded fish (fish caught/fish thrown) was 58.5% for fish of small size, 49.4% for medium size fish and 46.6% for fish of large size (Table 4), differences among size classes being sligtly significant (G-test = 6.53, df = 4, P = 0.04). Overall percentage consumption in the experiment was 53.3%. When consumption was corrected taking into consideration the proportion of each species in the real "discard" composition, we found a very similar result (54.4%), indicating that fish thrown experimentally mirrored very closely the composition of actual "discard". Differences in the consumption of flatfish (spotted flounder) versus roundfish (sardine and horse-mackerel) in the experiments were not significant (χ^2 = 2.08, df = 2, P=0.35).

Discussion

Seabird species associated to trawlers

The abundance of yellow-legged gulls at boats during the summer may be explained by the presence of breeding colonies of the species on the islands of

Benidorm. It is known that gulls exploit "discards" mainly for chick rearing during the breeding season (see Furness et al. 1992; Oro et al. 1995). "Discards" are also commonly exploited in the study area by adults rather than by juveniles outside the breeding season, although the high adult/juvenile ratio observed could only reflect an earlier dispersal of juveniles compared to adults (e.g. Oro and Martínez-Vilalta 1994). European storm-petrels also breed locally, but do not make use of trawler waste during the summer probably because this is mostly composed of fish of unsuitable size and because almost no offal is generated by the fishery, contrary to what happens in fisheries elsewhere (see Furness et al. 1992; Thompson 1992; Thompson and Riddy 1995; Garthe et al. 1996). Storm petrels were rare at boats also in Majorca and the Ebro Delta (Oro and Ruiz 1997). The relative absence of Audouin's gulls on the transects and behind the boats was surprising considering that the largest colony in the world (10 189 pairs in 1999, own data) is located only 270 km further north and that thousands of migrant birds must cross the study area during the summer (Oro and Martínez-Vilalta 1994). It seems that Audouin's gulls migrate closer to the coast and do not exploit intensively trawling discards during their migration (Arcos et al. 2001). Cory's shearwaters were common in the area, and following boats, even though their colonies were located further away, at more than 100 km from the study area (see Oro and Ruiz 1997). Breeders can forage at large distances from colonies and it is impossible to assess whether birds at the study area were breeders or non-breeders on the basis of plumage, as this does not differ with age. The higher abundance of Cory's shearwaters in the study area late in the summer possibly reflects a higher presence of adults at sea during the chick-rearing stage *versus* the incubation stage. The low abundance of Balearic shearwaters in the area and following trawlers is also surprising (e.g. Sarà 1993; Conejero and Beaubrun 2000), especially at the beginning of our study when birds breeding on the Balearic Islands start to disperse and should be more numerous, given the records from neighboring areas (Arcos and Ruiz 1997). Some shags were observed following trawlers, indicating that this species can forage opportunistically, although there are very few previous records of seabirds of the genus Phalacrocorax following trawlers (Blaber and Wassenberg 1989). However, shags were present behind boats only when these were fishing closer to the coast (<28 km off the coast) suggesting either a low dependence on discards or a smaller foraging range than other species.

Discard features

Most fish discarded were suitable for seabird consumption because of their small size but only 54% of the fish discarded were consumed. This low percentage consumption contrasts with estimates from the Ebro Delta (72%) and Majorca (64%) (Oro and Ruiz 1997). The three most commonly discarded groups (sardines, flatfish and horse-mackerel) were swallowed with great efficiency at the Ebro Delta (100%, 94%, 93%) where Audouin's gull is the commonest species behind trawlers; however, percentages were lower at Majorca (50%, 78%, 87%) where yellow-legged gulls were the most common followers. Our overall (54%) and partial percentages (49%, 57%, 61%) resemble more closely data from Majorca than data from the Ebro Delta. These results suggest that Audouin's gull is more efficient than yellow-legged gull at catching this type of "discard", probably because of its more specialized fishing habits (e.g. Oro 1998; Arcos et al. 2001). Other studies also recorded differences in seabird species efficiency at feeding on "discards" (e.g. Furness et al. 1992; Camphuysen, 1995). Flatfish were consumed with the same success as roundfish, although flatfish species are typically considered to be less attractive for seabirds (Garthe et al. 1996). The high

consumption of flatfish in this study probably stems from the relatively small size of flatfish discarded (e.g. see Camphuysen 1994).

Table 4. Number of each size class of fish discarded experimentally. Small (2-10cm), Medium (11-19 cm), Large (20-40 cm). Percentage consumption of each species and size class is indicated between brackets.

Species	Small	Medium	Large	Total
Horse-mackerel (*Trachurus sp*.)	76 (67.1%)	95 (55.8%)	0	171 (60.8%)
Goby (*Gobius sp*.)	12 (41.7%)	3 (100%)	0	15 (53.3%)
Sardine (*Sardina pilchardus*)	87 (47.1%)	265 (49.1%)	4 (100%)	356 (49.2%)
European hake (*Merluccius merluccius*)	4 (75%)	9 (100%)	1 (100%)	14 (92.9%)
Seabream (*Pagellus sp*)	4 (50%)	46 (37.0%)	0	52 (36.6%)
Imperial jerret (*Centracanthus cirrus*)	4 (25%)	62 (48.4%)	12 (50%)	78 (47.4%)
Bogue (*Boops boops*)	7 (85.7%)	103 (60.2%)	0	110 (61.8%)
Spotted flounder (*Citharus linguatula*)	115 (65.2%)	51 (37.3%)	0	166 (56.6%)
Common pandora (*Pagellus erythrinus*)	0	6 (100%)	0	6 (100%)
Triglidae	3 (66.7%)	9 (100%)	0	12 (91.7%)
Conger eel (*Conger conger*)	0	2 (100%)	18 (44.4%)	20 (50%)
Common sole (*Solea solea*)	12 (25%)	0	0	13 (23.1%)
Mendole (*Spicara maena*)	2 (100%)	4 (100%)	2 (100%)	8 (100%)
Cusk eel (*Ophidion barbatum*)	3 (33.3%)	5 (80%)	1 (100%)	9 (66.7%)
Snipefish (*Macrorhamphosus scolopax*)	22 (36.4%)	0	0	22 (36.4%)
Paracentropistis sp	7 (85.7%)	0	0	7 (85.7%)
Dragonet (*Callionymus* sp)	0	2 (50%)	0	2 (50%)
Mackerel (*Scomber scombrus*)	0	0	1 (0%)	1 (0%)
Anchovy (*Engraulis encrasicholus*)	5 (20%)	4 (75%)	0	9 (44.4%)
Greater forkbeard (*Phycis blennoides*)	20 (85%)	56 (42.9%)	1 (100%)	77 (54.5%)
Striped seabream (*Lithognatus mormyrus*)	10 (70%)	0	0	10 (70%)

Marbled electric ray (*Torpedo marmorata*)	0	1 (100%)	0	1 (100%)
Boar fish (*Capros aper*)	0	3 (0%)	0	3 (0%)
Red bandfish (*Cepola rubens*)	0	0	2 (100%)	2 (100%)
Silver scabbard-fish (*Lepidopus caudatus*)	0	0	3 (33.3%)	3 (33.3%)
Blue whiting (*Micromesistius potassou*)	8 (37.5%)	5 (0%)	0	13 (23.1%)
Brill (*Scothphalmus rhombus*)	0	6 (100%)	0	6 (100%)
Greater weever (*Trachinus draco*)	0	1 (100%)	0	1 (100%)
Total	403 (58.3%)	739 (52.1%)	45 (57.8%)	1 187 (54.4%)

The absence of a significant correlation between fish landed and discarded indicates that "discard" percentage is highly unpredictable and that the amount of "discard" cannot readily be deduced from catch statistics. However, this finding is contrary to results previously reported for the western Mediterranean (Oro and Ruiz 1997). Differences between zones may arise owing to oceanographic factors (i.e. width of the shelf, nature of the bottom) or even to market factors, such as the price of fish in the market or the vigilance of fishermen especifically devoted to clupeoid fishing, if both types of fisheries are practiced by boats in the same port or region).

Acknowledgements

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Influence of food availability on demography and local population dynamics in a long-lived seabird

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Introduction

Population size is a state variable of central interest in many domains of ecology. Detailed demographic studies are required to address the processes underlying temporal variation in numbers (Yoccoz et al. 1998). This change is a function of births, deaths, immigration, and emigration (i.e., fitness components, or demographic parameters). A general result in demography is that the fitness components whose variations have the greatest influence on population growth rate depend on the life cycle (e.g. Stearns 1992; Caswell 2001). Life history theory predicts that selection should favour allocation of time and resources toward the stage at which survival or reproduction is least variable, all other things being equal (Roff 1992; Stearns 1992; McNamara and Houston 1996). In long-lived species, the population growth rate is more sensitive to variations in adult survival than in other components of the life cycle (e.g., Saether and Bakke 2002). In seabird species in particular, the population growth rate is less sensitive to changes in fecundity (Cairns 1992; Lebreton and Clobert 1991; Russell 1999), and more sensitive to variations in adult survival or permanent dispersal. Natural selection may minimize variation in those parameters to which population growth is most sensitive (Pfister 1998; Cooch et al. 2001), and observed variation in population growth may reflect changes in components to which the growth rate is less sensitive (e.g., recruitment or emigration; (Cooch et al. 2001; Oro and Ruxton 2001). One may thus expect that environmental factors have a greater influence on fitness components such as juvenile survival, recruitment, or reproduction than on adult survival or breeding dispersal.

In addition, the predictions made within the framework of life history theory concerning the relationship between population dynamics and changes in adult survival rely on changes in true mortality. Very few studies of seabirds have addressed true mortality (Spendelow et al. 1995). Any study conducted at a single site, or a subset of locations addresses *local* survival (i.e., (1-true mortality)*fidelity; (Nichols et al. 1992); (Brownie et al. 1993); (Spendelow et al. 1995; Joe and Pollock 2002); Spendelow et al. 2002). Decreased fidelity (i.e., increased rate of permanent emigration out of the study area) will translate into lower local survival. It is not clear whether previous results concerning the influence of "adult survival" on population dynamics reflect genuine effects of adult mortality, or the confounding influence of permanent emigration.

Several environmental factors may influence population dynamics. A factor commonly invoked as potentially important is food availability. Its influence on seabird population dynamics has often been highlighted (e.g. Birkhead and Furness 1985; Cairns 1992). It has been suggested that increased food supply resulting from human activities (e.g. industrial fisheries, refuse dumps) are responsible for the substantial increase in numbers in populations of several opportunistic seabird species in recent decades (e.g. (Furness et al. 1988; Croxall and Rothery 1991); Burger and Gochfeld 1996), although most of the studies have attributed this trend to the increase of

fecundity and not of adult survival or immigration. Similarly, fisheries have also been suspected to threaten seabird populations because human and birds compete for the same resource (e.g., fish, squid). Stock overexploitation may have a negative influence on seabird population dynamics in this situation (Furness and Monaghan 1987; Tasker et al. 2000; Oro 1999), although there is again a lack of empirical data on that.

To understand the process underlying the influence of food availability on variation in numbers in seabird populations, the demographic parameters covarying with resource availability have to be identified. Food availability may affect parental condition, annual productivity, and lifetime reproductive success. It has been shown that food availability influences different components of fecundity such as laying dates (e.g. (Safina et al. 1988; Oro et al. 1996b), clutch size (e.g. Oro et al. 1996b; Spendelow et al. 1996), egg size (e.g. (Hiom et al. 1991; Bolt*on et al.* 1992; Oro 1996; Ratcliffe et al. 1998) or breeding success (e.g. Springer et al. 1986; Monaghan et al. 1992; Oro et al. 1996b; Phillips and Caldow 1996; Gill 1999). Nevertheless, there is little evidence of an influence of food availability on demographic parameters other than reproductive rates. Some studies have shown that there is a relationship between resource availability and deferred breeding (e.g. Monaghan et al. 1992; Wernham and Bryant 1998), adult survival (Pons and Migot 1995; Harris et al. 1997; Oro et al. 1999; Oro and Furness 2002) or local recruitment rates (Boekelheide and Ainley 1989; Oro and Pradel 2000). Moreover, unless emigration and mortality are disentangled, decreased food availability may have indirect consequences translating into lower *local* survival. Indeed, it has been shown that breeding failure is associated with increased breeding dispersal probability (e.g. Danchin et al. 1998; Oro et al. 1999), which may lead to a decrease in the size of a local population.

Unequivocal evidence that food availability influences population growth in seabird populations is rare (Croxall and Rothery 1991), even though long-term data sets on both fish stock and seabird demographic parameters are becoming more available (Chapdelaine and Rail 1997; Harris et al. 1997; Crawford 1999; Oro and Furness 2002)). Simulations of population dynamics under different scenarios of food availability have rarely been used to assess the possible effect of human activities such as fisheries and discarding on seabird populations, or they were based on sets of parameters that were not estimated using empirical data (MacCall 1984; Cairns 1992). Here we addressed the influence of discards (i.e., an additional food source) from fisheries on the demographic parameters in a local population of Audouin's gulls (*Larus audouinii*), an endemic species breeding in the Mediterranean, and considered as vulnerable. We used an approach permitting distinction between adult survival and the probability of emigrating permanently out of the study area. We also used simulations to assess population viability on a local population of the species, considering several scenarios corresponding to situations with higher or lower food availability, and compared estimated population extinction risk.

Methods

Study area and the trawling moratorium

Data were collected from 1974 to 2001 in a colony located on the Columbretes Islands (western Mediterranean: 39º 51'N 0º 40' E, see Fig. 1). The study area is a volcanic outcrop (comprising 3 major islet groups) of 19 ha, located close to the edge of

the continental shelf, 60 km off the mainland coast. The width of the continental shelf is almost maximal in that location compared to the rest of the western Mediterranean. Breeding numbers fluctuated greatly during the study. The site was colonized in 1974 (40 pairs) and breeding numbers reached to 625 pairs in 1995. The study site is located in a Natural Reserve and is protected all year long. No terrestrial predator has been reported in the colony. Only Yellow-legged gulls *Larus cachinnans* regularly prey upon Audouin's gulls, especially on eggs and chicks (Martínez-Abraín et al. 2002).
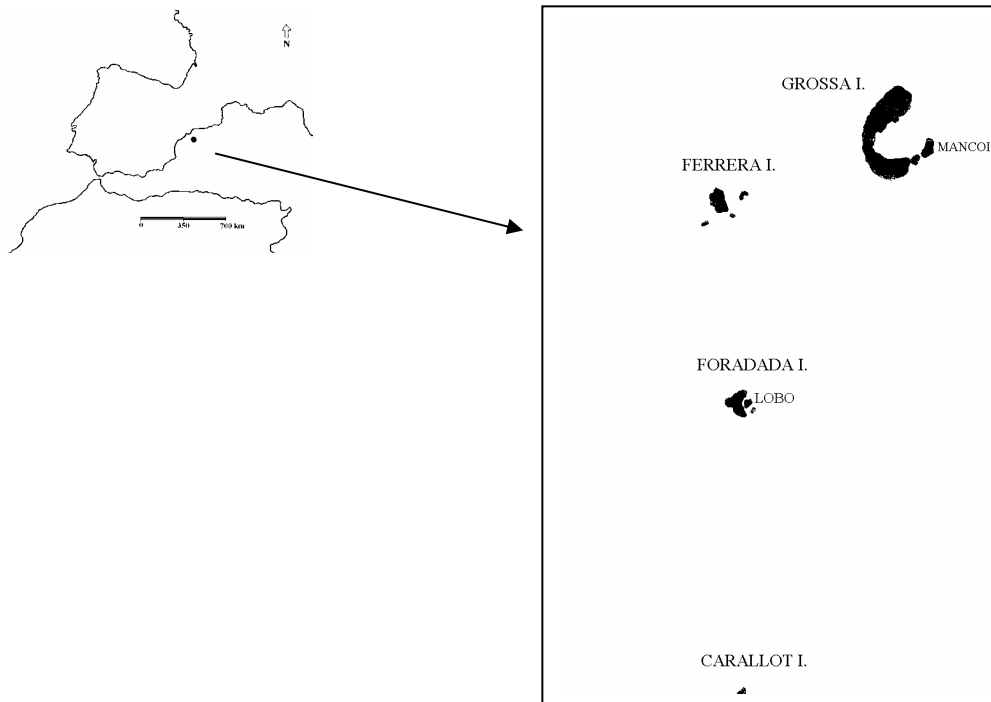
Figure 1. Map of the western Mediterranean and the study area at Columbretes islands.

A trawling moratorium was established from 1991 onwards to allow fish populations to recover from overfishing (Lostado et al. 1999). The moratorium concerned an area extending 220 km along the coast out to the limit of the continental shelf (ca. 60 km) (see Oro et al. 1996a for more details). The moratorium was effective for two months every year, and it always overlapped one of the following stages of the breeding season: the laying stage (April-May), the incubation period and first weeks of the chick rearing stage (May-June), or mainly the chick rearing stage (June-July). Discard availability was estimated using statistics of fish catches from fishermen's guild bulletins. The amount of fish discarded in this area is highly correlated with the size of commercial catches of trawlers (Oro and Ruiz 1997; Oro 1999; Oro and Pradel 1999).

Data collection

Individuals were marked as chicks before fledging from 1988 onwards using a plastic ring with a unique engraved three-digit code (e.g. Oro and Pradel 2000). Ringing was carried out as a part of the Spanish Ringing Programme for the species. From 1988 to 1996, 843 chicks were ringed at the colony (range = 0-208 a year, depending on chick productivity). Complete breeding failure occurred in 1993 and 1997. From 1992 to 2000 (except for 1994) marked gulls were resighted from a distance using a telescope in the colony during the breeding season (from March to July). The total number of

resightings was 1334. Only one resighting per individual and breeding season was retained for analysis. We also excluded immature birds (less than 3yrs old, the youngest age of first breeding reproduction estimated in Audouin's gull, see (Oro and Pradel 1999). We assumed that all observed adult birds were breeders. We realize that this assumption may have consequences on our results, as we may have retained individuals breeding in other locations, and therefore may have lower local survival. We eliminated resightings from birds also observed the same year in the neighbouring colony of the Ebro Delta and the Balearic Archipelago in order to minimize this possible bias. This was the best possible approach available, as for practical reasons, it is not possible to assess individual breeding status for every bird resighted in colonies. A total of 214 individuals were taken into account for analysis (Lebreton et al. 1992). To limit confusion between death and permanent emigration (i.e. birds leaving the colony permanently, which are indistinguishable from dead birds), the first resighting as a breeder at the Columbretes Islands was considered as its initial capture (Pradel et al. 1997).

The number of breeding pairs was estimated in every year of the study except 1980 and 1981. Population size was assessed using nest counts, a standard procedure for the species (e.g. Oro and Ruxton 2001). This approach provides fairly reliable estimates of population size, especially in such a small colony.

Adult survival and emigration out of the study area

Adult survival was estimated from mark-recapture data (Lebreton et al. 1992). Many standard capture-recapture models rely on the assumption that all marked individuals have the same survival probability, regardless of whether they were marked at the sample occasion immediately before the current resighting, or they were marked several years before and perhaps resighted several time before the current occasion (e.g., (Burnham et al. 1987); reviewed in Williams et al. 2002). Several sources of heterogeneity in survival probability among individuals lead to violations of the assumptions underlying capture-recapture models, one of which is the presence of transients. Transients (as opposed to residents) are individuals that leave the study area after first capture and thus have a local survival probability equal to 0 (Pradel et al. 1997). The presence of transients in the marked sample may bias estimation of survival. Comparisons between models including a residency parameter $(1-\tau) < 1$ (not all the individuals in the sample are residents) or equal to 1 (the marked sample includes residents only) addresses the presence of transients in the study population (Hines 1996)). Importantly, the presence of transients indicates emigration out of the study area. This parameter cannot be used to assess the importance of emigration *sensu stricto* because it is assessed relatively to the local survival probability of individuals recaptured several times (i.e., "residents"; Eq. (1) below). However, we cannot tell to what extent the local survival probability of individuals resighted several times reflects true survival (i.e., it may also incorporate permanent emigration out of the study area). The residency parameter assesses a "relative" probability of dispersing in newly marked birds compared to birds with a longer history in the marked sample. Nevertheless, the influence of environmental factors such as food availability on the residency parameter provides insight into the relationship between these factors and the probability of emigrating permanently out of the study area.

We started with the Cormack-Jolly-Seber (CJS) model (ϕ_t, p_t), where ϕ is the local survival rate and p is the recapture (or resighting) probability (e.g., (Pollock et al. 1990), Lebreton et al. 1992). This model had time-specific parameters. For model selection and assessment of the biological hypotheses guiding model development (Burnham and Anderson 1998), it is critical that the general model fit the data (Lebreton et al. 1992). Consequently, we first assessed the fit of the general model using the program U-Care (Choquet et al. 2000). The program provides insight into possible violations of the assumptions underlying the CJS model (see (Burnham et al. 1987; Pradel et al. 1997). The components of several tests (e.g., TEST2 and TEST3) address the effect of first capture on future capture probability (e.g., trap-dependence; individuals may tend to avoid capture after being captured once) or survival probability.

The initial CJS model did not fit the data (TEST2 + TEST3, see Results). TEST3.SR made the largest contribution to the test statistic. Consequently, we developed models accounting for the presence of transients in the marked sample (Pradel et al. 1997). $\tau(\omega, e)$ was the probability that an unmarked animal ω captured at time e was a transient. The estimator of τ has the following form:

$$\tau(\omega,e)=1-\frac{\phi^*(\omega,e)}{\phi(\omega,e)}, \qquad (1)$$

where $\phi^*(\omega, e)$ was the apparent survival rate of individuals newly observed in the colony, and $\phi(\omega, e)$ the survival probability of individuals resighted several times in the colony (in different years). Nevertheless, the parameter of interest was the proportion of transients in the whole population (denoted T_i) and not only among the individuals newly observed. This proportion can be modelled because T and τ are related by:

$$T_e = \frac{N_e}{N_e + m_e} \cdot \tau(\omega,e), \qquad (2)$$

where N_e is the number of birds first captured at time e, and
m_e the total number of birds captured at time e (see also (Pradel et al. 1997).

The relationship between T_e and $\phi(\omega, e)$ starts with equation (1):

$$\phi^*(\omega,e) = \phi(\omega,e) \cdot \tau(\omega,e) = \phi(\omega,e) \cdot \frac{T_e}{c_e} \qquad (3)$$

where c_e comes from equation (2),

$$c_e = \frac{N_e}{N_e + m_e}$$

We can finally use the log function instead of the logit function to link the parameters to a linear formula:
$\log \phi^*(\omega,\varepsilon) = \log \phi(\omega,\varepsilon) - \log(c_e) + \log(T_e)$

Several models with a transient effect [denoted ($\tau., \phi., p.$), see notation in (Pradel et al. 1997) were considered. We assessed several *a priori* ecological hypotheses based on factors that, in our view, could affect transience, survival or capture probabilities (Table 1). We investigated the influence of discard availability on survival probability and the transient parameter. Hypotheses concerning food availability were assessed

using ultrastructural models (e.g., Nichols and Kendall 1995; Lebreton et al. 1992). Data on the amount of fish landed (i.e. as an index of food availability in the study area, see (Oro et al. 1999) each month were available for every year. We addressed whether food supply influenced transient or survival probability in four different ways depending on the timing of the moratorium: (1) discards were available during the whole breeding season (March-July) (denoted by ε), (2) discards were available only during the egg-laying period (March-April) ($\varepsilon 1$), (3) discards were available only during the chick rearing period (June-July) ($\varepsilon 2$), (4) the trawling moratorium occurred during the chick rearing period (June-July) (denoted by ξ).

Table 1. Summary of the different (τ, ϕ, p) models built with SURGE to estimate the proportion of birds among unmarked that emigrated after the first resight (τ), survival probability (ϕ), and recapture probability (p) depending on the biological hypotheses tested.

Model notation	Biological hypothesis
Modeling τ	
τ	Constant
τ_a	2 age-classes dependent: $\leq$ 4y (3+4y) and older birds
τ_A	depending on true age (from 3y to 12y old)
τ_ε	depending on availability of trawler discards during the whole breeding season (March-July)
τ_β	depending on availability of trawler discards during the laying period (March-April)
τ_δ	depending on availability of trawler discards during the chick rearing period (June-July)
τ_ξ	depending on availability of trawler discards during the chick rearing period (June-July) as categorical (moratorium-not moratorium)
Modeling ϕ	
ϕ_t	survival varied with time (year)
ϕ	constant survival
ϕ_ε	survival is dependent on availability of trawler discards for the whole breeding season
ϕ_β	survival varied with the availability of trawler discards during the laying period (March-April)
ϕ_δ	depending on availability of trawler discards during the chick rearing period (June-July)
ϕ_ξ	depending on availability of trawler discards during the chick rearing period (June-July) as categorical (moratorium-not moratorium)
Modeling p	
p_t	recapture is time-dependent
p_A	recapture varied with true age (from 3y to 12y old)
p	recapture is constant
P_e	recapture is dependent on effort of resightings (no. of days sampled each year)

Models also included year and age (from 3y old to 12y old birds). Concerning age, two age-classes were considered to achieve a reasonable sample size in each category: animals resighted for the first time at 3 or 4 years old (age-class 1, named younger birds) and older individuals (up to 12 years old) (age-class 2, named older

birds). Concerning recapture probability, we also developed models where p varies with yearly resighting effort, measured as the number of days spent at the colony. We used the logit function for all the models. We systematically assessed linear, quadratic or logarithmic (log) effects of time and age on transient, survival and recapture rates. These models should provide insight into the existence of major trends across years. Linear trends with age were denoted A, the quadratic effects A^2 and the log effects $\breve{A}$. The trends were linear, quadratic or log on the logit scale. These different functions account for different possible relationships between survival and food availability. For example, with a linear relationship the increase (or decrease) in survival with food availability is always the same for an increase of one unit of resource. Quadratic relationships can account for accelerations or decelerations of changes in survival with food availability. Some models were successively fitted keeping transient probability constant beyond a given age (i.e. a plateau for different ages), considering that breeding experience may influence this parameter (see also (Oro et al. 1999; Oro and Pradel 2000). For instance, $(\tau_{\breve{A}5}, \phi, p_t)$ designated a model with a log trend in transient probability up to age 5, with constant survival and time-specific recapture probability.

Analyses were performed using software program SURGE 4.2 (Cooch et al. 1996). Model notation followed Lebreton et al. (1992). A model including two factors and their interaction was described using an asterisk. Additive models were described using a "+" symbol instead. For instance, $(\tau_{a*t}, \phi_{a*t}, p_{a*t})$ designated a model where transient, survival and recapture probabilities varied with age and time, with the effect of time potentially different in different age classes. The biological hypotheses underlying the structure of models were assessed using AIC (Akaike Information Criterion). Models with the lowest values of AIC were retained as good candidate models (Lebreton et al. 1992; Anderson and Burnham 1999b; Anderson and Burnham 1999a; Reboulet et al. 1999). Models with differences in AIC values lower than 2 were considered as "equivalent" (i.e., data were insufficient to lead to definitive conclusions concerning the process that gave rise to the data). Note that model selection procedures based on information theory permit consideration of a set of models whose structure reflects several not necessarily exclusive or alternative biological hypotheses about the processes that gave rise to the data (Burnham and Anderson 1998). Comparisons among models using information criteria allows us to assess the hypotheses in question, even whether the corresponding models have a different structure, which precludes use of test statistics such as likelihood ratio tests (Burnham and Anderson 1998).

Extinction probability

Extinction probability was estimated using a matrix population model accounting for demographic and environmental stochasticity (e.g., Caswell 2001). We considered demographic stochasticity because the small size of our study population in some years made it likely to be subject to that type of process (e.g.,Caswell 2001). Environmental stochasticity was considered to account for variation in environmental factors other than food availability (e.g., climate, etc.) We used a Monte-Carlo approach and simulated population numbers over time using different sets of parameters and sources of uncertainty. (Table 2). Monte-Carlo analysis incorporates uncertainty in both the estimation and analysis process and is considered as a powerful tool for assessing population viability (e.g. Caswell 2001).

Table 2. Demographic parameters used in the Monte-Carlo simulations depending on availability of food around the colony during the breeding season. Only mean values are shown.

Parameter	Estimate		References
	Higher food availability	Lower food availability	
Juvenile survival 1y	0.79		Oro 1998
	0.88		Oro 1998
Adult survival	0.94		This study
Proportion of emigrants[*]	0.45 - 0.19	0.58 - 0.31	This study
Proportion of breeders[§]	0.84 - 0.90		Oro and Pradel 2000
Fecundity[¥]	0.15-0.41-0.33-0.11	0.92- 0.07 - 0.01-0	Oro et al 1996; own data

[*] Only younger breeders (3y - 4y old birds) are considered

[§] Only 3y and 4y old birds are considered since proportion of breeders of birds older than 4y is 1

[¥] Empirically derived probability distribution of each female producing 0, 1, 2 or 3 fledglings

Model development was based on vital rates mainly estimated at the Columbretes colony: adult survival and emigration (this study), and fecundity (from literature). Other vital rates such as immature survival, age at first breeding and proportion of breeders arise from studies carried out at a neighbouring colony located at the Ebro Delta (Oro 1998; Oro et al. 1999; Oro and Pradel 2000). Since some first time breeders (especially 3- and 4-year old birds, see results below) from the Delta colony emigrated to other colonies (Oro et al. 1999), we also took immigration into account (see *Immigration from the Ebro Delta colony* below). We assumed a balanced sex ratio (Oro and Ruxton 2001). All parameters were drawn from probability distributions.

We considered two different scenarios: (1) the first scenario corresponds to a situation where trawlers operate normally around the colony during the breeding season (i.e., situation with higher food availability); (2) the second scenario corresponds to a situation where the trawling moratorium overlaps with the chick rearing period (i.e., situation with lower food availability). The only two parameters assumed to be affected by food were the proportion of emigrants (higher when food availability was lower; see results) and fecundity (positively associated with food availability; (e.g. Oro et al. 1996a). We know that adult survival was not affected by food availability (see Results) and assumed that immature survival and proportion of breeders were not affected either. We started simulations using numbers corresponding to year 1991, when the trawling moratorium was first established and 225 females bred (Oro 1998). We also considered the number of females breeding in the 3 previous years (i.e., 1998-1990) in order to take into account the offspring produced during that time period which started recruiting into the breeding segment of the population in 1991. Models include several sources of stochasticity. Consequently, different runs for the same parameter values can lead to different results. We therefore simulated 500 trajectories over a 100-year time interval. The proportion of extinct trajectories (when population size n at time t is 0) we used to estimate the extinction probability at time t_i. For each scenario, we ran one set of

simulations with demographic stochasticity, and one set with both demographic and environmental stochasticity. Simulations were visually compared with the observed trajectory of local population size during the period 1991-2001 (for which data on breeding numbers were available). Formal comparisons would be difficult because we did not only consider the mean trajectory, but also variability (Brook et al. 1997).

Immigration from the Ebro Delta colony

We estimated the proportion of immigrants from the nearest colony (the Ebro Delta; Fig. 1), where chicks were also marked since 1988 (6523 chicks through 1997). The number of individuals born in the Ebro Delta observed as breeders at the Columbretes Islands was 464 over the study period (1992-2000). The expected number N_i^t available to breed at the Columbretes Islands in year t (from 1992 to 2000) from the pool marked in year i at the Ebro Delta (from 1988 to 1997) is:

$$N_i^t = N_i \cdot \phi_j \cdot \phi^{t-i-3} \cdot b_{t-i} \quad \text{where}$$

N_i is the number of individuals marked in year i,
ϕ_j is the juvenile survival from birth to age 3 (age of first breeding),
ϕ is the adult survival probability,
b_{t-i} is the breeding propensity, i.e. the proportion of breeders among the survivors, at age $t-i$.

Let n_i^t be the number of individuals born in year i and resighted in year t. The ratio n_i^t / N_i^t estimates the probability of presence at the Columbretes colony times the probability of detecting a bird breeding in that location. We assume that the demographic parameters and detection probability do not depend on the origin of the birds (from the Columbretes Islands "C" or from the Ebro Delta "E"), nor on the year of ringing. Then relative presence (rp) of birds from the Ebro Delta colony at the Columbretes Islands can be estimated as follows: $(n_i^t / N_i^t)_E / (n_i^t / N_i^t)_C$, where the superscript "E" indicates that only birds marked at the Ebro Delta are considered for the numerator, and "C" indicates that only birds marked at the Columbretes Islands are considered for the denominator. Finally, if we assume that this quantity does not depend on i, the year the individual was marked, but only on t, the year the individual was resighted, then relative presence can be estimated using the following formula:

$$rp_t = (\sum_i (n_i^t / N_i)_E)/(\sum_i (n_i^t / N_i)_C)$$

An estimate of the variance of rp_t obtained by the delta method as:

$$\frac{\left\{\sum_i \dfrac{n_i^t\left(N_i - n_i^t\right)}{\left(N_i\right)^3}\right\}_E}{\left\{\left(\sum_i \dfrac{n_i^t}{N_i}\right)^2\right\}_C} + \left(rp_t\right)^2 \frac{\left\{\sum_i \dfrac{n_i^t\left(N_i - n_i^t\right)}{\left(N_i\right)^3}\right\}_C}{\left\{\left(\sum_i \dfrac{n_i^t}{N_i}\right)^2\right\}_C}$$

Finally, 95% confidence intervals (CI) were calculated to assess whether there were significant differences between the different values of rp_t (see also (Oro and Pradel 2000).

Results

The goodness of fit test showed that the CJS model (ϕ_t, p_t) did not fit our data (TEST2 + TEST3: $\chi^2_{18} = 33.44$, P = 0.015). All the deviations from expected values laid in TEST3.SR ($\chi^2_6 = 20.14$, P = 0.003). This indicates the presence of transient (or emigrating) individuals in the sample of individuals resighted in the colony for the first time. When TEST3.SR was ignored, the overall test did not indicate lack of fit (GOF test: $\chi^2_{12} = 13.20$, P > 0.50). We developed a model denoted as (τ_t, ϕ_t, p_t), which incorporates a residency parameter (to account for transients). This model was used as a starting point for further model selection. The first set of models assessed (Table 3) led to a candidate model ($\tau_{\bar{A}6}$, ϕ, p_t) where survival of resident birds did not vary with time, whereas residency probability varies with log(age) up to age 6. Models with recapture varying with time had lower AIC values than models with constant recapture or with an effect of resighting effort. We also addressed the hypothesis that emigration of newly marked birds was progressive and also influenced second resighting year [model denoted as (τ_ω, ϕ, p_t)]. We did not find evidence of such an effect (Table 3).

Table 3. Set of models starting from the initial model (τ_t, ϕ_t, p_t) and taking also into account the age effect (both the two age classes effect (*a*) and the true age effect (*A*), see text for explanations), and resight effort effect on recapture probabilities. For each model, we give the number of estimable parameters (*np*), its deviance (DEV) and the Akaike Information Criterion (AIC), which results from: (DEV+2·*np*). Model notation is according to Lebreton et al. (1992). Boldface denotes the provisionally selected model.

Model	*np*	DEV	AIC
(τ_t, ϕ_t, p_t)	22	918.119	962.119
(τ_t, ϕ_t, p)	16	951.382	983.382
(τ_t, ϕ, p_t)	17	921.128	955.128
(τ, ϕ, p_t)	10	928.582	948.582
(τ_a, ϕ, p_t)	11	925.255	947.255
(τ_A, ϕ_A, p_t)	10	935.980	955.980
(τ_{t+A}, ϕ_{t+A}, p_t)	21	928.130	970.130
(τ_{t+A}, ϕ_{t+A}, p_{t+A})	22	903.116	947.116
(τ, ϕ, p_e)	4	941.302	949.302
(τ_a, ϕ, p_e)	5	936.974	946.974

Model	np	DEV	AIC
$(\tau_a, \phi, p_\check{e})$	5	943.390	953.390
$(\tau_t, \phi_{A}^{2}, p_t)$	18	918.261	954.261
(τ_t, ϕ_A, p_t)	18	917.406	953.406
(τ_a, ϕ_A, p_t)	19	916.748	954.748
(τ_A, ϕ, p_t)	11	916.957	938.957
$(\tau_{\check{A}}, \phi, p_t)$	11	914.416	936.416
$(\tau_{\check{A}5}, \phi, p_t)$	11	913.197	935.197
$(\tau_{\check{A}6}, \phi, p_t)$	**11**	**912.932**	**934.932**
$(\tau_{\check{A}7}, \phi, p_t)$	11	913.438	935.438
(τ_ω, ϕ, p_t)	12	917.708	941.708

In the next step we considered models including an influence of discard availability. Most of the models had AIC values very close to that of the model selected in the previous step (Table 4). One model had a lower AIC value [denoted as $(\tau_{\check{A}6+\delta}, \phi, p_t)$]. In this model transient probability varies with food availability during the chick-rearing period (Table 4). This provides evidence discard availability influences the probability of emigrating permanently out of the Columbretes Islands. We also built a set of model where food availability during different stages of the breeding cycle influences survival in resident birds, but none of these models had lower AIC values than the previous one.

Table 4. Set of models starting from the provisionally selected model $(\tau_{\check{A}6}, \phi, p_t)$ and taking into account the effect of food availability as amounts of trawler discards (ε). For each model, the number of identifiable parameters (*np*), its deviance (DEV) and the Akaike Information Criterion (AIC) are shown. Boldface denotes the finally selected model.

Model	*np*	DEV	AIC
$(\tau_{\check{A}6}, \phi, p_t)$	11	912.932	934.932
$(\tau_{\check{A}6+\varepsilon}, \phi, p_t)$	12	911.261	935.261
$(\tau_{\check{A}6+\beta}, \phi, p_t)$	12	911.511	935.511
$(\tau_{\check{A}6+\delta}, \phi, p_t)$	**12**	**908.667**	**932.667**
$(\tau_{\check{A}6+\xi}, \phi, p_t)$	12	912.287	936.287
$(\tau_{\check{A}6+\delta}, \phi_\varepsilon, p_t)$	13	912.876	938.876
$(\tau_{\check{A}6+\delta}, \phi_\beta, p_t)$	13	912.217	938.217
$(\tau_{\check{A}6+\delta}, \phi_\delta, p_t)$	13	912.071	938.071
$(\tau_{\check{A}6+\delta}, \phi_\xi, p_t)$	13	912.254	938.254
(τ_δ, ϕ, p_t)	11	927.375	949.375

Finally, we assessed an *a posteriori* hypothesis based on the provisionally selected model in the first step (Table 3) and eliminated the influence of age on transient probability. The AIC of this model (Table 4) was higher than that of the model including age. Estimated adult survival was 0.941 (95% CI: 0.857-0.977) and recapture probabilities ranged from 0.187 (95% CI: 0.113 - 0.292) to 0.594 (95% CI: 0.458 - 0.718) (Fig. 2).
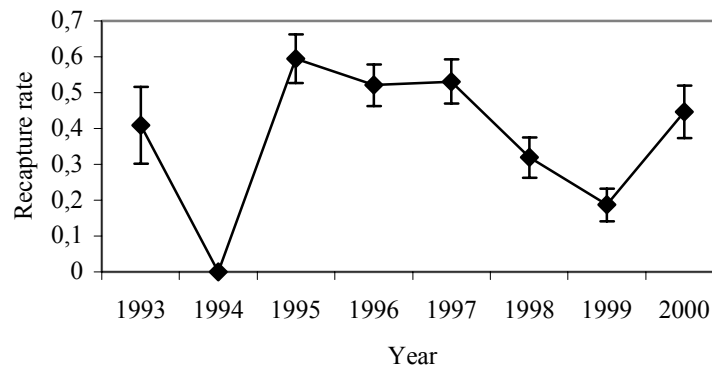
Figure 2. Recapture probabilities for Audouin's gulls at the Columbretes Islands during the study period (1992-2000), under the finally selected model (see Results). Bars show standard errors.

There is a negative influence of food availability during the chick-rearing period and age on the probability of emigrating out of the Columbretes colony (Figure 3). There are two extreme situations (years), with the trawling moratorium overlapping with the chick-rearing period (lower food availability), or with normal trawling moratorium (higher food availability). When food availability was lower, the proportion of younger breeders (birds of 3y old) that emigrated from the colony was high, ca. 60%. When food was highly available, this proportion was still high, but lower, ca. 45%. In both cases the proportion of dispersing birds decreased sharply with age, and it was lower than 10% for 5y old and older birds (Fig. 3).
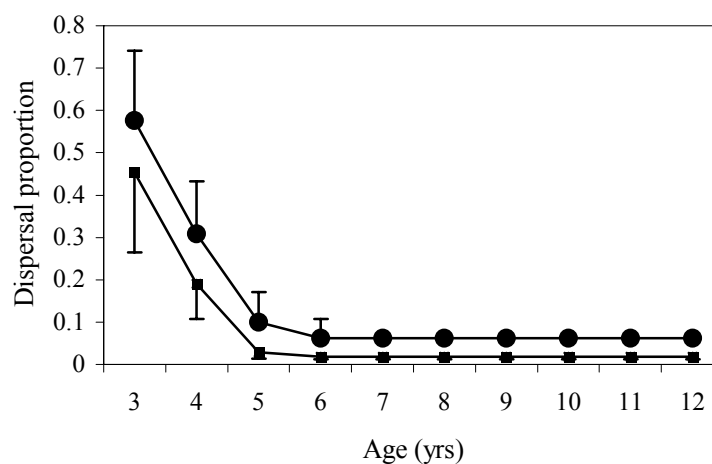
Figure 3. Proportion of transients depending on the age of individuals and food availability: solid dots represent a year with trawling moratorium overlapping with the chick rearing stage and solid squares a year with normal trawler activity, i.e. a year with higher food availability. Bars show standard errors.

Monte-Carlo simulations showed that extinction probability varied greatly with food availability during chick rearing. When demographic stochasticity was considered,

extinction probability increased with time, especially when the trawling moratorium overlapped with the chick rearing stage (Fig. 4). When environmental stochasticity was incorporated (Table 5), the difference in trend between the two situations regarding food availability was similar, but overall extinction probability was higher (Fig. 4).

Table 5. Demographic parameters of Audouin's Gull at the Columbretes islands with environmental stochasticity.

| Parameter	Mean value	SD
Juvenile survival 1y	0.79	0.30
Immature survival 2y	0.88	0.25
Adult survival	0.94	0.08
Breeding dispersal 3y	0.51	0.40
Breeding dispersal 4y	0.25	0.40
Proportion of breeders 3y	0.84	0.20
Proportion of breeders 4y	0.90	0.10
Fecundity bad year[1]	0.11	0.30
Fecundity good year[2]	1.10	0.20

[1] When trawling moratorium overlapped with the chick rearing stage (in chicks per pair)
[2] When trawler discards were normally available (in chicks per pair)
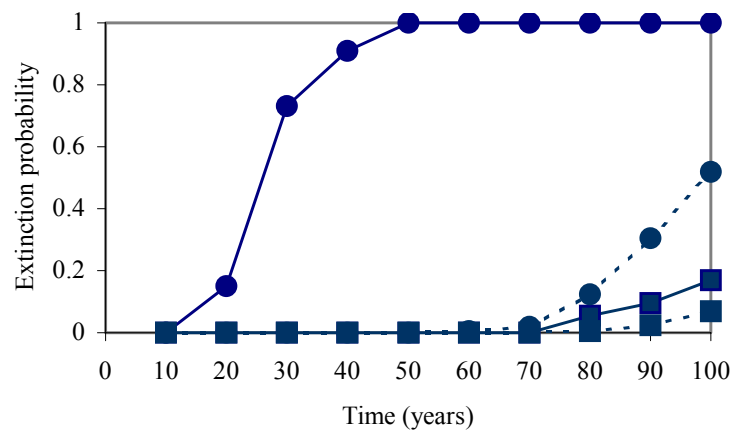
Figure 4. Probability of extinction estimated through Monte-Carlo simulations of the two different scenarios considered: when trawling moratorium coincided with the chick rearing stage (lower food availability) (shown by solid dots) and when trawler discards were normally available (higher food availability) (shown by solid squares). Solid lines show the simulations with demographic and environmental stochasticity and dashed lines the simulations with only demographic stochasticity.

Under a scenario with lower food availability (trawling moratorium effective), all trajectories were extinct at time 100 (i.e. 100% probability of extinction), and mean extinction time was 26.9 years (SE = 0.8) (Fig. 5a). When food availability was higher (i.e. when discards were available), extinction probability dropped to 20%, and mean extinction time increased to 61.4 years (SE = 2.2) (Fig. 5a).

a)

b)

c)
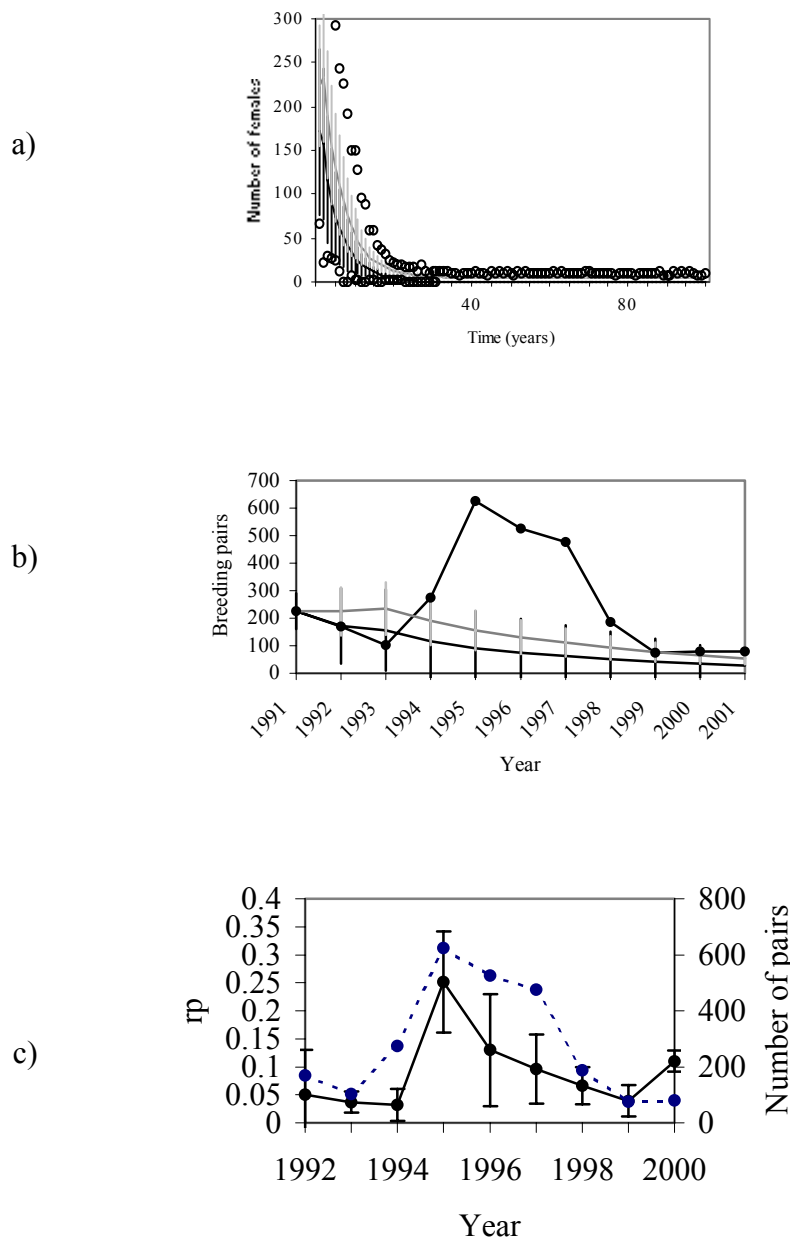
Figure 5. a) Number of female breeders at Columbretes islands from the Monte-Carlo simulated trajectories after a 100-y interval and taking into account demographic and environmental stochasticity. The two scenarios considered are: with lower food availability (when trawling moratorium was established, solid line) and with higher food availability (when trawlers discards were available, dashed line). Lines shows the mean trajectory over the different runs, bars show the standard error and dots the lowest (of the lower food scenario) and highest (of the higher food scenario) values of the different trajectories at each time interval. b) Population size estimates at the colony since the establishment of the trawling moratorium (solid line and dots), and simulated trajectories for the same period of time under the two scenarios (same legends). c) breeding dispersal of Audouin's gulls born in the Ebro Delta to the Columbretes Islands during 1992-2000 expressed as a relative presence (*rp*, see methods) probability (± 95%CI); a dashed line shows the population size estimates at the colony throughout this

period (see text).Breeding numbers fluctuated greatly from 75 to 625 pairs (Fig. 6) since the establishment of the trawling moratorium in 1991. When the two simulated trajectories were compared with observed population dynamics during these years (Fig. 5b), both scenarios led to projected numbers consistent with observed numbers in early and last years of the study period. However, for period 1995-1997, the observed population size was substantially larger, even larger than simulated trajectories taking into account higher food availability from discards (Fig. 5b). With regard to breeding immigration rates, we observed a substantial increase in numbers from the Ebro Delta in 1995 (Fig. 5c), which coincided with the increase in population size at the Columbretes colony. There was a positive correlation between the relative presence of females dispersing from the Ebro Delta to the Columbretes in a given year and the number of females breeding at the later colony (r = 0.76, n = 9, P = 0.017).
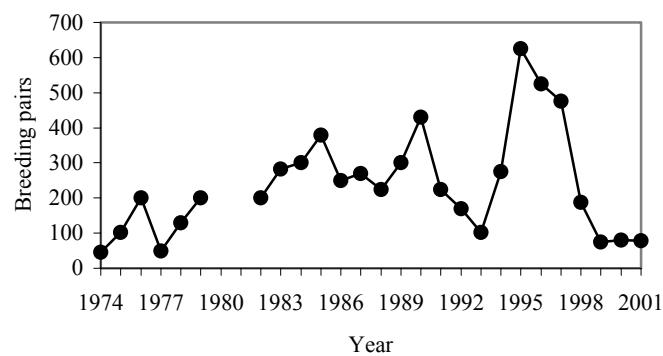
Figure 6. Annual population size (as number of breeding pairs) of Audouin's Gull at the Columbretes islands. Estimates are from the colonization of the site until 2001, except for the period 1980-1981.

Discussion

Our results provide unambiguous evidence that food availability influences the demography of a seabird local population. Importantly, we found evidence that food availability influences the probability of emigrating permanently out of the study area, but not survival. This is consistent with the hypothesis stating that natural selection may minimize variation in the demographic rates to which population growth is most sensitive (i.e., adult survival in long-lived species) (Pfister 1998; Caswell 2001; Cooch et al. 2001)). It has also been suggested that observed variation in population growth may reflect changes in rates to which the growth rate is less sensitive (Pfister 1998; Caswell 2001; Cooch et al. 2001). Variation in emigration probability with food availability may not necessarily be consistent with the latter hypothesis. Indeed, the sensitivity of population growth rate to emigration has seldom been thoroughly addressed, and populations have often been explicitly or implicitly considered as "isolated" in empirical studies. Indeed, *local* survival is often interpreted as *true* survival, and emigration ignored, or considered as negligible (see Boulinier et al. 1997 for discussion of this topic). However, breeding dispersal (emigration of breeders), corresponds to loss of individuals in the critical stage with regard to population growth in long lived species (e.g., Saether and Bakke 2000), and is somewhat equivalent to mortality in local populations. From that viewpoint, emigration may substantially

influence population growth (e.g., Cooch et al. 2001), even though our prospective demographic analysis identified adult survival as the most sensitive life history trait.

Dispersal, along with births and deaths, is one of the two main demographic processes governing changes in numbers. However, as emphasized by (MacDonald and Johnson 2001), "there remains an almost complete absence of empirical data on dispersal and other relevant behavioural parameters in recent population extinction studies" despite the remarkable number of models of dispersal evolution (Johnson and Gaines 1990). Th design of the present study is not appropriate to draw inferences about variation in the actual proportion of individuals leaving the Columbretes colony: this will require a multisite study or use of combined data sources (e.g., Hestbeck et al. 1991; Nichols et al. 1992; Clobert 1995; Nichols and Kendall 1995; Spendelow et al. 1995; Bennetts et al. 2001; Williams et al. 2002). Our approach is a first step towards quantification of emigration probability. Variation in the residency parameter should be interpreted as evidence of changes in the relative probability of emigrating out of the study area; the reference group corresponds to individuals resighted in several occasions (years) on the colony. Our results provided evidence that the probability of emigrating increases when food availability decreases during the chick rearing period. It can be hypothesized that this type of dispersal strategy is consistent with what has been identified as "conditional" dispersal (i.e. phenotypic plasticity in dispersal probability) ((Ims and Hjermann 2001; Ronce et al. 2001). The detailed mechanism underlying the decrease in fidelity to the breeding site is not known in the present case, but there is extensive evidence in the literature that breeding failure is associated with increased probability of dispersing (e.g., Danchin et al. 1998; Oro et al. 1999). The decrease in the probability of dispersing with age was already found in Audouin's gull (Oro et al. 1999) and may reflect a positive influence of age on breeding success (e.g., Curio 1983; Pärt and Forslund 1995). Identification of the cues animals rely on to make dispersal decisions is important to understand selective pressures involved in the evolution of dispersal (Danchin et al. 2001; Greene and Stamps 2001; Ronce et al. 2001). Our study area comprises two local populations, individuals attempting to recruit at the Ebro Delta, where number of conspecifics and their breeding success is normally much higher than at the Columbretes Islands (Oro et al. 1996a; Oro and Pradel 1999; Oro and Ruxton 2001). The dynamics of the Columbretes local population is influenced not only by dispersal to other sites, but also by immigration from the outside, mainly the Ebro Delta. These transfer processes are crucial in the dynamics of metapopulations and the extinction-colonisation events (Hanski 1999), which have been rarely addressed in long-lived organisms (Oro and Ruxton 2001; Cooch et al. 2001).
Our simulations also suggest that fisheries are likely to influence the dynamics of that population; the most likely mechanism underlying this influence is that birds depend on resources supplied by humans to reproduce on the Columbretes islands.

Acknowledgements

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Is growing tourist activity affecting the distribution and number of breeding pairs in a small colony of the Eleonora's Falcon?

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Abstract

Human disturbance is a common threat for species of conservation concern such as the Eleonora's Falcon. This paper shows that the rise in tourist presence from 1992 to 2000 has not affected the overall number of breeding pairs or their productivity in a small archipelago of the western Mediterranean (Columbretes Islands). However, the increasing tourist activity has coincided with a shift in the degree of occupancy on two islands within the archipelago, favouring that with a lower human presence close to colonies. Several conservation actions are reported and suggested, aimed at both testing and preventing the role of human presence as a factor influencing long-term colony persistence and growth.

Introduction

The Eleonora's Falcon (*Falco eleonorae*) is a highly migratory species which breeds on Mediterranean islands and winters in the Indian Ocean (Walter 1979). It is presently considered to have an unfavourable conservation status in Europe (Tucker and Heath 1994). This species has evolved a late breeding calendar as an adaptation to feeding chicks, taking advantage of the pulse of migrant birds moving southwards late in the summer over the Mediterranean basin (Walter 1979). Human disturbance is presently considered one of the major threats to birds and other vertebrates (Tucker and Heath 1994; Hill et al. 1997; Ristow 1999). Hence, Eleonora's Falcons are prone to suffer from human presence since tourist visits to colonies commonly peak during the breeding period.

This paper presents the effects of the increasing number of tourist boats on Eleonora's Falcons breeding on a small archipelago of the western Mediterranean, following a long period of monitoring their breeding performance.

Material and methods

The study took place on the Columbretes Islands (39º 51'N 0º 40' E), a 19 ha volcanic outcrop (comprising four major islet groups: Carallot, Ferrera, Foradada-Lobo and Grossa) located close to the edge of the wide continental shelf of Castellón, E Spain (Fig.1).

The Columbretes archipelago has been a nature reserve since 1988 and a marine reserve since 1990. The total area of the marine reserve is 4 400 ha. Two of the islands (the largest and the smallest, Grossa and Carallot) have a special protection regime (integral reserve).

Figure 1. Map of the study area showing the location of Eleonora's Falcons (*Falco eleonorae*) nests in 2001 and the approximate location of buoys for tourist boats in Grossa Island (dotted circle).
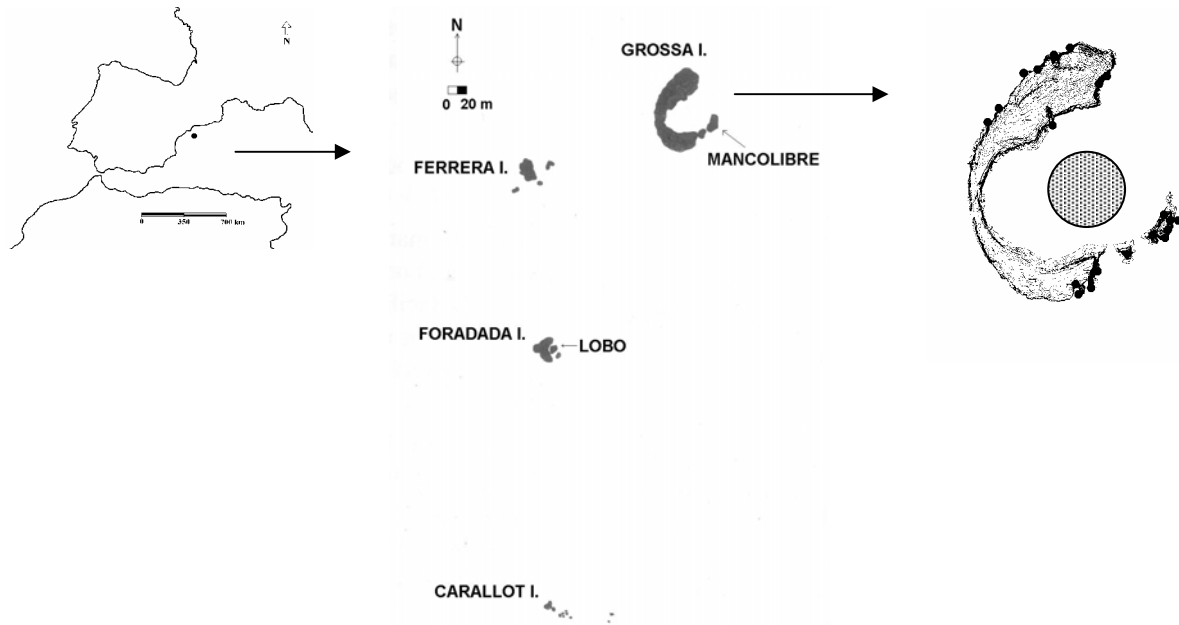
Our main prediction is that changes in distribution or number of breeding pairs on these two islands would be small whereas changes in both parameters on Ferrera and Foradada-Lobo whould be larger.

Data regarding public use of the islands and breeding performance of Eleonora's Falcons were obtained from unpublished reports (Reserva Natural Islas Columbretes 1988-2001) supplied by the regional government from 1988 to 2001. Human presence was measured as the number of boat licence plates recorded daily (boats-day hereafter).

Boats were tied up to the buoys located around the islands and the team of three wardens living on the main island counted them daily by means of a terrestrial telescope.

The monitoring of boats was constant throughout the study period. The number of breeding pairs was also determined by knowledgeable wardens of the reserve by inspecting the islands from a boat early in the breeding season to locate and count breeding pairs and by double-checking the existence of nests from the mainland.

Productivity (i.e. number of fledglings per nest) was estimated from the content of nests when visited for chick ringing by mid September, using field procedures developed by two members of the study team (AM, DO).

Monitoring and ringing of falcons was approximately constant throughout the study period. In 1999 the overall number of breeding pairs was not estimated due to lack of an appropriate boat to visit all the islands, but productivity was estimated from nests located on Grossa Island and Mancolibre (Fig. 1).

Results

Inter-annual variation in the number of boats-day is shown in Table 1. The overall trend was a progressive increase of human presence on the islands (r_s=0.97, n=13, p<0.001). Monthly variations in the number of boats-day are shown in Figure 2. Boats-day clearly peaked in July and August precisely the time when falcons are laying and incubating their eggs (Dolz and Dies 1987).

Table 1. Number of nests and productivity of Eleonora's Falcons (*Falco eleonorae*) detected on each island of the Columbretes archipelago during the period 1988-2000. Source: Reserva Natural Islas Columbretes (1988-2001). In brackets number of boats-day.

| Year	Carallot	Foradada-Lobo	Ferrera	Grossa	Productivity	Total
1988	1	6	5	11		23 (184)
1989					1.37	22 (242)
1990					1.73	28 (374)
1991					1.41	27 (509)
1992	0 (2)	8 (31)	4 (11)	15 (592)	1.53	27 (636)
1993	1 (12)	3 (65)	7 (31)	15 (537)	1.66	26 (645)
1994	1 (19)	4 (131)	5 (36)	14 (606)	1.0	24 (792)
1995	0 (33)	5 (86)	8 (40)	13 (493)	1.61	26 (652)
1996	1 (106)	3 (107)	6 (38)	13 (481)	1.89	23 (732)
1997	1 (0)	3 (94)	6 (66)	13 (695)	1.35	23 (855)
1998	1 (0)	3 (93)	8 (45)	15 (715)	2.0	27 (853)
1999	1 (0)	(75)	(66)	12 (804)	2.0	(945)
2000	1 (0)	1 (86)	9 (51)	14 (758)	1.6	25 (895)
2001	1	4	10	15	2.17	30

However, the number of breeding pairs, remained approximately constant through the years (26 ± 2.16 pairs, mean ± SD, n=13) as did their productivity (1.64 ± 0.33, mean ± SD, n=13) (table 1). In fact, correlations between years and number of pairs (r_s=0.18, n=13, p>0.05) and productivity (r_s=0.50, n=13, p>0.05) were not significant.

No significant correlation was found either between overall numbers of boats-day during the breeding period (July-September) and numbers of breeding pairs (r_s= -0.14, n=12, p=0.66,) or between overall number of boats-day during the breeding period and productivity (r_s= 0.23, n=12, p=0.46). Inter-annual variation in the use of the various islands by breeding falcons and tourist boats is shown in Table 1.

The percentage of falcons breeding at Ferrera (in relation to the total breeding pairs of Ferrera + Foradada-Lobo) increased over time (Table 1). Indeed, a non-parametric correlation run to check whether this percentage had changed over with time showed a significant strong correlation (r_s=0.78, p=0.014), although correlations

between annual numbers of breeding pairs and annual numbers of boats-day at Ferrera and Foradada (considering both the number of boat-days at years t_i and t_{i-1}, to test for any influence of tourist presence the year before) were all not significant.

Figure 2. Monthly variation in the number of boats-day at the Columbretes Islands during the period 1997-2000.
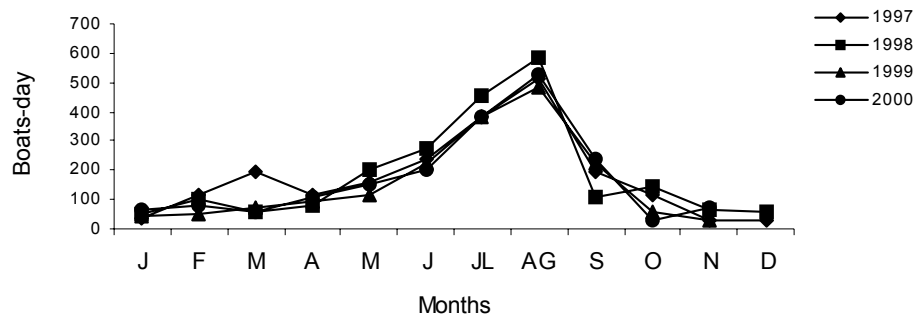
Discussion

Shifts in island use by Eleonora's falcons seem to have affected only the colonies on Ferrera and Foradada, the two islands with no special protection regime. Anchoring of boats around Carallot is not permitted as the distance from Grossa makes it difficult to keep activities carried out within the restricted area under control. Nevertheless, tourist activities such as scuba-diving are allowed on Grossa, where the island wardens, who have a permanent base on this island, can more easily monitor the activities of visitor; boats must be tied up to buoys in the bay, thereby remaining far from falcon nests which are mostly located in the outer cliffs of the island (see Fig. 1).

We are not aware of any factor (e.g. food, nest-site availability, competing species, ectoparasites) other than human presence that may have influenced the change in the distribution of breeding pairs, albeit the exact way in which human presence may have affected falcons remains unknown. However, the fact that scuba-divers prefer Foradada as compared to Ferrera, because of the existence of submerged archs (S. Sales, com. pers.) may have played some role.

Our data indicates that high tourist presence coincided with a loss of pairs at Foradada-Lobo and that low tourist presence coincided with an increase in the number of pairs at Ferrera, and that there were no changes in the overall number of breeding pairs (i.e. the colony remains stable and hence increases and decreases in the number of falcon pairs in each island are only rearrangements within the archipelago). However, only experimental manipulation of the number of boats-day could unequivocally demonstrate a cause-effect relationship. We predict that any marked decrease in the number of boats around Foradada-Lobo would be paralleled by an increase in the number of falcon breeding pairs.

These spatial changes may not be dangerous for short-term colony persistence. The clumping of breeding pairs in social species, such as the Eleonora's Falcon, can

have positive consequences for breeding performance; one possible short-term conservation option would be to increase protection of Ferrera (where the level of human presence is quickly approaching that of Foradada-Lobo) allowing only Foradada-Lobo as a tourist destination. However, given the reduced size of the archipelago, high protection on Foradada-Lobo should also be attained in the future not to threaten long-term colony persistence and growth (e.g. banning the presence of boats within a buffer zone around the island).

Tourism affecting Eleonora's Falcons in the Columbretes Islands was previously reported in 1997, when a marked decrease in breeding pairs occurred in a small rocky islet located beside the main island (Mancolibre, see Fig. 1). This reduction was probably caused by excessive presence of scuba divers according to Sánchez (1997). The environmental authorities experimentally removed a buoy placed close to the isle, and banned the transit of boats around the islet. This sub-colony quickly recovered its usual number of breeding pairs in 1998. Hence, conservation measures addressed to reduce human presence around the colonies of Eleonora's Falcons can give positive results and should be further employed to determine the role of human presence on the patterns of island use by falcons.

Acknowledgements

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Resumen y conclusiones

La dinámica de las colonias de aves marinas puede verse influenciada por factores de índole biológica y por factores ligados a la actividad humana ya sea en el medio marino o en el terrestre. Esta tesis ha abordado el estudio de ambos tipos de factores sobre colonias pequeñas de aves marinas ubicadas en islas del Mediterráneo occidental (Archipiélago de las Columbretes e Isla de Benidorm) dentro del marco de un proyecto de conservación. Los trabajos realizados (un total de nueve artículos y dos capítulos de libro) han ido dirigidos a aplicar el método científico a la solución de preguntas cuya respuesta era necesaria para una mejor protección de las distintas especies estudiadas (un total de cinco: Gaviota de Audouin, Gaviota Patiamarilla, Cormorán Moñudo, Pardela Cenicienta y Halcón de Eleonor, una especie que aún no siendo un ave marina vive ligada a los espacios insulares). Es por tanto ésta una tesis de ciencia aplicada y, más concretamente, una tesis de biología de la conservación. De manera un tanto pionera en el estado español, esta tesis ha sido financiada desde la administración autonómica (Generalitat Valenciana) y europea (Unión Europea) con el objeto de acercar la investigación a la toma de decisiones. Es éste un nicho *quasi* vacante que conviene ir rellenando en lo sucesivo.

Por lo que respecta a los factores biológicos que determinan la dinámica de las poblaciones en esta tesis se analiza el papel de la inmigración y la estocasticidad demográfica en el crecimiento de una colonia de cormorán moñudo durante sus diez primeros años de historia (**Capítulo 1**); el papel de la filopatria y la atracción conespecífica para la selección del lugar de nidificación en la Gaviota de Audouin (**Capítulo 2**); los factores que determinan la dinámica del recambio en el uso de las islas de un archipiélago para el establecimiento de colonias de Gaviota de Audouin (**Capítulo 3**); el papel de los inmigrantes de origen atlántico en una colonia mediterránea de Pardela Cenicienta (**Capítulo 4**) y finalmente el papel de la migración desde el Mediterráneo al Atlántico en la dinámica de una colonia de Gaviota Patiamarilla (**Capítulo 5**).

Por lo que respecta a los factores ligados a la actividad humana se ha estudiado indirectamente el papel de los vertederos de residuos como focos de infección para la Gaviota Patiamarilla (**Capítulo 6**); el papel de los descartes de la pesca del arrastre sobre como fuente de alimento de distintas especies de aves marinas (**Capítulo 7**); el papel de la disponibilidad de dichos descartes sobre la demografía y dinámica de una colonia de Gaviota de Audouin (**Capítulo 8**) y el papel de la actividad turística sobre la dinámica espacial de una colonia de Halcón de Eleonor (**Capítulo 9**).

Las **conclusiones** de mayor relevancia que se han obtenido de dichos estudios (siete publicados y dos enviados a publicación) se resumen a continuación:

1.- El reclutamiento de aves propias no explica el crecimiento observado en la colonia de cormoranes moñudos de las islas Columbretes durante sus diez primeros años de historia. La simulación que mejor se ajustó a lo observado incorporaba dos episodios de inmigración además de estocasticidad demográfica. Las aves inmigrantes posiblemente procedieron de una gran colonia ubicada en la isla de Mallorca que tuvo un fuerte declive coincidiendo con la fundación de la colonia de estudio. Un análisis de sensitividad y elasticidad mostró que los cambios en la supervivencia de las aves de

cuatro o más años fue el parámetro con mayor influencia sobre la tasa de crecimiento geométrico de la colonia.

2.- Tras un experimento de traslocación llevado a cabo durante ocho años en las instalaciones del centro de recuperación de fauna de Valencia se concluyó que las gaviotas de Audouin no son fieles al lugar de cría del año anterior sino que la elección del lugar de nidificación se lleva a cabo teniendo en cuenta la presencia de individuos de su propia especie en las cercanías. Esta conclusión da un importante papel a la colocación de señuelos en programas de conservación cuya meta sea la implantación de nuevas colonias de esta especie vulnerable en lugares donde antes no había criado. El trabajo demuestra además que las gaviotas de Audouin pueden criar en cautividad y también cerca de instalaciones humanas.

3.- Las gaviotas de Audouin muestran una gran tendencia a cambiar de isla para la instalación de colonias de cría, siendo la probabilidad media de abandono de una isla dada de 0.89. El abandono de una isla parece ser un proceso que se da en varios pasos. El primer paso, la dispersión de una porción de la colonia, parece suceder al azar como tendencia innata de una especie que ha evolucionado en medios inestables. La dispersión de una parte de la colonia desencadena la dispersión en grupo de más aves probablemente porque la pérdida de vecinos se percibe en la colonia como una pérdida de calidad de la misma. Finalmente sólo un grupo pequeño de aves (probablemente las más viejas) puede intentar de nuevo la reproducción aunque acabará fracasando debido a los problemas que se derivan de la falta de atractivo y protección de las colonias con pocos individuos. Asimismo, la colonización de nuevas islas (el segundo componente de la dispersión) parece estar influido únicamente por la presencia de gaviotas patiamarillas, aún en pequeño número, probablemente por la posibilidad de sufrir kleptoparasitismo o depredación por parte de una especie que se reproduce antes. La conservación de una especie nómada como la Gaviota de Audouin requiere una estrategia global en la que se conserven también las islas donde la especie no cría en la actualidad.

4.- Aunque la pardela cenicienta se considera una especie muy filopátrica (los machos siendo más fieles a su lugar natal que las hembras) esta regla parece tener sus excepciones. En la colonia de las islas Columbretes no se ha detectado ni un solo individuo adulto que no hubiera nacido en dicha colonia, en toda la historia de su seguimiento detallado, que ya se extiende más de diez años. Existen diversas recuperaciones de aves marcadas en varias de las islas Baleares (Mallorca, Cabrera, Menorca) pero todas ellas provienen de aves capturadas en el mar en el entorno de las Columbretes. Sin embargo, se han detectado en la colonia cuatro pardelas procedentes de las islas Salvajes (Madeira), pertenecientes a la subespecie atlántica. Dado que las aves atlánticas llegan a reproducirse con las mediterráneas, el flujo genético que se genera podría ser de importancia en colonias pequeñas del Mediterráneo susceptibles de pérdida de variabilidad por deriva genética y por tanto con un riego de extinción a corto plazo mayor que las colonias numerosas. No parece, por el contrario, que la tasa de intercambio observada sea lo suficientemente grande como para evitar una mayor diferenciación futura de las aves mediterráneas respecto a las atlánticas de las que históricamente provienen o para eliminar adaptaciones al medio local.

5.- El crecimiento de una colonia de aves marinas no depende solo de la fecundidad de las aves en dicha colonia sino también, de manera muy importante, de la

supervivencia de las aves adultas y de su descendencia. El marcaje mediante marcas de lectura a distancia de pollos de gaviota patiamarilla en las islas Columbretes y la isla de Benidorm ha permitido demostrar que las aves jóvenes realizan largos desplazamientos hacia el norte después de la cría para pasar el verano y el invierno en las costas del Golfo de Vizcaya, desde la región francesa de Landes hasta el norte de Portugal. Estos desplazamientos parecen estar motivados por la baja disponibilidad de alimento en el Mediterráneo en comparación con riqueza de las zonas de afloramiento y de marismas dejadas al descubierto durante los cambios de marea en el Atlántico. Sin duda este patrón migratorio (que probablemente no es válido para las aves adultas, con mayor experiencia para encontrar fuentes de alimento en el Mediterráneo) ha de tener una repercusión importante sobre las tasas de supervivencia de los juveniles y a larga sobre el reclutamiento y la dinámica de sus colonias de origen.

6.- Las gaviotas patiamarillas de Columbretes no parecen hacer un uso muy elevado de los vertederos de residuos sólidos situados sobre el continente, en comparación con las aves de la colonia de la isla de Benidorm. Ello se deduce a partir de las distintas prevalencias (38.5% en Columbretes y 100% en Benidorm) de un hematozoo (*Haemoproteus lari*) cuyo vector se reproduce óptimamente en suelos húmedos no salinos y ricos en materia orgánica. Las islas Columbretes se encuentran demasiado lejos de la costa (57 km frente a los 3 de la isla de Benidorm) como para que sea rentable energéticamente desplazarse hasta allí en busca de comida. Probablemente el no tener acceso fácil a esta fuente de comida explica porqué la colonia de Columbretes permanece más o menos estable mientras que la de Benidorm se ha triplicado en los últimos años, en cuanto la isla ha disfrutado de protección. Las grandes explosiones demográficas de esta especie posiblemente solo se pueden dar en colonias próximas a grandes vertederos o que dispongan a la vez de desechos pesqueros y basura.

7.- El aprovechamiento de los descartes de la pesca del arrastre por parte de las aves marinas es un aspecto bien conocido en el Atlántico y, más recientemente, en el Mediterráneo. No obstante, los trabajos realizados hasta la fecha en el Mediterráneo se han centrado sobre todo en la época reproductora. Mediante el estudio de los arrastreros en el entorno de la isla de Benidorm durante los meses de junio a octubre se encontró que diez especies de aves marinas: gaviota patiamarilla, pardela cenicienta, gaviota de Audouin, gaviota reidora, charrán patinegro, charrán común, fumarel común, paíño europeo y cormorán moñudo, seguían a los barcos de pesca. De éstas solo la primera especie fue observada siguiendo a los barcos en número mayor de lo esperado por su abundancia en el medio. De hecho las gaviotas patiamarillas fueron las que hicieron mayor uso del descarte, aunque menor de lo esperado en relación a su presencia detrás de los barcos. En conjunto, tan sólo el 54% de los descartes comestibles fue aprovechado por las aves. Todo ello parece indicar que las gaviotas patiamarillas hacen un uso poco eficiente del descarte, que estuvo compuesto mayoritariamente de sardina (22.4%), peces planos de fondo (19.1%) y jureles (17.3%). Las estimas realizadas de los requerimientos energéticos de las gaviotas patiamarillas y de la disponibilidad energética en el medio, a partir de las aproximadamente ocho toneladas de peces descartados cada jornada de pesca en la zona, indican que los descartes podrían mantener una población local de gaviotas cuatro veces superior a la presente durante el periodo de estudio. Por tanto, a pesar de que el vertedero de residuos sólidos de Benidorm ha sido recientemente clausurado, las gaviotas patiamarillas de Benidorm disponen de una buena fuente de recursos tróficos fuera del periodo reproductor. Esto

sin duda ha de tener implicaciones sobre la dispersión de las aves y sobre su supervivencia invernal.

8.- De hecho en las islas Columbretes se halló que la escasez de alimento desde el establecimiento de la veda bimensual en la pesca del arrastre ha afectado de manera muy importante a la tasa de dispersión permanente de las gaviotas. De hecho, el abrupto declive de la colonia desde el establecimiento de los paros biológicos de 1991 no se explica por una mayor mortalidad adulta (la supervivencia es elevada, en torno a 0.94) sino por el abandono masivo del archipiélago por parte de las gaviotas que no encuentran otras fuentes alternativas de alimentación en la zona. Bajo un escenario de escasez de alimento las simulaciones indican que la colonia se extinguirá en un horizonte de 27 años, tras 30 años de presencia ininterrumpida en el archipiélago. La aparente recuperación de la colonia a mediados de los años 90 no guarda relación con la dinámica propia de la colonia sino que se debe a la entrada de inmigrantes de la cercana colonia del delta del Ebro, tras un episodio de depredación por parte de mamíferos terrestres. Por tanto, la demografía y dinámica de esta colonia lejana a la costa son totalmente dependientes de la actividad humana.

9.- La actividad humana sin embargo no parece estar afectando de manera importante a la colonia de Halcón de Eleonor de las islas Columbretes. El marcado ascenso del turismo en los últimos años no parece influir negativamente al número de parejas reproductoras ni a su productividad, aunque sí parece guardar relación con un cambio observado en el uso de las islas. Aunque el número global de parejas del archipiélago permanece estable en torno a las 30 parejas, una de las islas está ganando parejas en detrimento de otra y este cambio coincide con una mayor frecuentación turística de la isla que pierde parejas reproductoras. Experiencias previas de manejo en las Columbretes sugieren que los halcones reaccionan con mucha rapidez a los cambios en el grado de presencia humana, de modo que pueden reocupar sus zonas tradicionales de cría en cuanto detectan una reducción de la molestias.

Al margen de estos estudios publicados en revistas científicas, se ha tratado de no descuidar la necesaria labor divulgativa, lo cual queda patente en las dos introducciones a las secciones I y II, que son sendos capítulos de libros. Asimismo, se han realizado diversas contribuciones en revistas de estudio y conservación de la naturaleza (*Quercus* 195: 14-20; *Quercus* 200: 16; *Quercus* 204, in press).

Diversos trabajos han quedado fuera de estas tesis ya que requerirán más trabajo de campo del previsto, a desarrollar en próximas temporadas, junto con otros autores, como el estudio del impacto del turismo sobre la colonia de gaviota patiamarilla de la isla de Benidorm. También se han excluido trabajos que quedaban un tanto fuera de la tónica general de esta tesis (trabajos con aplicación directa a la conservación) como por ejemplo, el estudio de la inmunocompetencia de paíños y gaviotas patiamarillas de dicha isla o el estudio de los hemoparásitos en pollos de Halcón de Eleonor. Finalmente, no se han incluido trabajos en los que el autor de la tesis ha participado de manera menos relevante que el resto de los coautores, caso del trabajo sobre kleptoparasitismo y predación de gaviota patiamarilla sobre gaviota de Audouin en las islas Columbretes, Chafarinas y delta del Ebro.