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Ph.D. thesis

FORAGING ECOLOGY OF SEABIRDS AT SEA: SIGNIFICANCE OF COMMERCIAL FISHERIES IN THE NW MEDITERRANEAN

Ecologia alimentària dels ocells marins en mar obert: importància de les pesqueres comercials al Mediterrani nord-occidental





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Introduction: seabird-fisheries interactions

Commercial fisheries have drastically developed and extended their range throughout the last century worldwide (e.g. Safina 1995). The pressure exerted by this human activity has resulted in serious changes not only affecting the targeted fish stocks, but also the entire marine ecosystems (see Bostford et al. 1997, Tegner & Dayton 1999, Gislason et al. 2000). Seabirds most often operate at high levels of marine food webs, being important consumers of densely-schooling small pelagic fish, squid, swarming crustaceans, and young demersal fish (e.g. Ashmole 1971, Croxall 1987, Furness & Monaghan 1987, Montevecchi 1993). As such, they are potential competitors with commercial fisheries (Furness 1982). Nevertheless, interactions between seabirds and fisheries are diverse, either direct or indirect, and most often complex and paradoxical. Moreover, environmental perturbations can exert an influence over these interactions, thus making even more difficult their understanding (e.g. Bourne 1983, Montevecchi 1993, Tasker et al. 2000). For simplification purposes, seabird-fisheries interactions can be viewed as positive, negative, or neutral, from the point of view of either man or seabirds (Duffy & Schneider 1994).

Seabird-fisheries interactions: man's point of view

Direct competition. The role of seabirds in the energy flow through marine ecosystems has often been considered as negligible. However, increasing number of studies demonstrate the importance of seabirds as marine top predators (cf. Furness 1982, Furness & Ainley 1984). Indeed, fish consumption by seabirds in some areas, particularly in highly productive systems with large populations of breeding seabirds, has been estimated at ca. 20-30% of annual fish production (e.g. Wiens & Scott 1975, Furness 1978, Furness & Cooper 1982, McCall 1984). This is a significant amount of fish, though lower than that captured by many pelagic fisheries (50-70% of annual fish production; Furness & Ainley 1984). This being so, competition could easily arise when both seabirds and fisheries would target the same fish species and age-classes. In any case, it is difficult to demonstrate direct competition events (Duffy & Schneider 1994), and these are most likely largely one-way (i.e. fisheries outcompeting seabirds; Furness & Monaghan 1987, Tasker et al. 2000). Only local and artisanal fisheries, operating in the vicinity of large seabird colonies, are likely to note the effects of seabird competition. At a greater scale the complexity of food webs would probably vanish the effects of seabirds consumption, so that the removal of seabirds and other top predators would not result in a net gain of fish equivalent to the amount that otherwise would be captured by these predators (see May et al. 1979, Duffy et al. 1987, Yodzis 1998).

Seabirds signalling fish. Fishermen have traditionally benefited of following seabirds, since the latter often signal concentrations of fish and mammals (e.g. Montevecchi 1993). With the increasing application of new technologies to fishing practices, such as echo-sounder and GPS, seabirds have lost this role for most fisheries. However, artisanal fisheries can still use seabirds as prey signallers, and even industrial tuna fisheries sometimes use the radar to detect seabird concentrations, which could signal tuna concentrations (e.g. Au & Pitman 1986).

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Seabirds as indicators of fish stocks. Seabirds present several features that make of them appropriate management tools (e.g. Furness & Camphuysen 1997): they are conspicuous, wide-ranging, surface-living marine animals, which most often breed in large colonies of relatively easy access. Seabirds also present long life spans, low reproductive rates, and delayed maturity, adults presenting diverse buffering strategies that allow them facing adverse environmental conditions (Cairns 1992a). These buffering (behavioural and ecological) strategies, rather than changes in population numbers, provide the most important opportunities to monitor environmental changes (Montevecchi 1993). Fisheries could take profit of seabird information to monitor marine prey stocks in several ways (see reviews in Cairns 1992b, Montevecchi 1993). For instance, since fisheries often target older fish age-classes than seabirds, detailed information of inter-annual changes in seabirds' diet could bring forward information on the abundance of fish cohorts before their recruitment into the fishable stock, thus making possible to establish management strategies in advance. Seabirds could also improve information on natural mortality, movements, and distribution of fish prey.

Seabird-fisheries interactions: seabirds' point of view

Direct mortality. Fisheries can cause direct mortality of seabirds in several ways: use of seabirds as bait (not an extended practice at present), entanglement of seabirds in lost gear, and by-catch of seabirds in gillnets and longlines (Duffy & Schneider 1994, Tasker et al. 2000). The last point is of special concern, longlines being considered as one of the major threats to pelagic seabirds nowadays (Brothers et al. 1999). Several thousands of seabirds, especially albatrosses and petrels in the Southern Hemisphere, die each year entangled in longline hooks, basically when the longline is set and seabirds are attracted by their bait. Given life-history traits of seabirds (see above; Cairns 1992a), this source of adult mortality is more serious than it could be regarded at first instance, since some seabird populations could be declining at a too fast rate (though difficult to detect) to be compensated through reproduction. Several mitigating measures have been proposed (and a few applied) in the last few years, but the problem of longliners is still of high concern. Since seabirds cause a negative effect for the fishery (lose of bait and hooks), a positive point is that fishermen are prone to apply these measures.

Competition. As previously exposed, competition between seabirds and fisheries is difficult to prove, but most likely affects seabirds in the first instance when it takes place. Most cases reporting direct competition between seabirds and fisheries refer to rich and simple ecosystems (upwellings), where the main prey is densely schooling small pelagic fish: Humboldt current (Schaefer 1970); Benguela current (Crawford et al. 1980, Furness & Cooper 1982, Duffy et al. 1987); California Bight (Andersson & Gress 1984). These ecosystems are subject to important environmental fluctuations, thus leading to fluctuations in fish abundance. Though seabirds in these regions are adapted to strong natural fluctuations (investing more in reproduction and less in survival than other seabirds), fisheries overexploitation of fish stocks can amplify natural fish mortality and drive stocks to very low levels (Furness & Monaghan 1987, Montevecchi 1993, Tasker et al. 2000). The

most widely known example is that of the anchoveta *Engraulis ringens* fishery off Peru. Populations of this fish species used to be extremely abundant in the rich waters of the Humboldt current, sustaining a seabird community of several million birds. Periodical (El Niño) warm water events used to cause crashes in both fish and seabird populations, but they often recovered quickly. Since the late fifties, the establishment of an industrial fishery for the anchoveta strongly affected seabirds, because overexploitation of fish made difficult the recovery of seabird populations after El Niño events. This way, seabird numbers decreased from 17 to 3-4 million birds after 1963 and 1965 En Niño events, and hardly recovered after that (not exceeding 5 million birds since then).

Reduction of seabirds' competitors. Seabirds are though to have benefited from fisheries targeting either their direct competitors or the competitors of their fish prey (e.g. Duffy & Schneider 1994, Tasker et al. 2000). For instance, over-fishing of whales in Antarctic waters resulted in a surplus of krill *Euphasia superba*, which could explain the parallel increase of seabirds, seals, and other krill consumers (May et al. 1979). Nevertheless, marine ecosystems are complex, and alterations in their structure are far from easy to predict (e.g. May et al. 1979, Kock & Shimadzu Y 1994, Lavigne 1996, Yodzis 1998).

Fishery waste. Demersal trawlers and other fisheries return large amounts of fishery waste to the sea, in the form of offal (intestines and other remains of gutted fish) and discards (fish either under the minimum legal landing size, of little commercial value, exceeding the quota established for individual vessels, or damaged during the fishing process). Seabirds largely consume this fishery waste, as several studies have reported for different regions (see Tasker et al. 2000 and references therein). This way, surface-feeding seabirds have easy access to prev otherwise unavailable (demersal fish), usually predictable in space and time, and provided in abundance. This anthropogenic food resource has been considered to be a key factor in the growth that some seabird populations experimented along the last century. However, this is a controversial assumption that still needs to be unequivocally proven (cf. Camphuysen & Garthe 1999), in spite of the increasing evidence demonstrating a link between breeding performance and discards availability for several seabird populations (e.g. Oro 1999 and references therein). On the other hand, demersal fisheries strongly affect marine ecosystems, and could cause direct and indirect reduction of natural seabirds' prey (Oro 1999), especially affecting diving species and other seabirds highly specialised in the capture of fish by their own. Moreover, differential influence of trawler discards on the biology of different species probably alters the structure and composition of seabird communities. Thus, what seems beneficial for seabirds in the short term could reverse in the long term, especially if the offer of fishery waste is reduced (as can be expected from incoming fishing policies; FAO 1995, Fluharty 2000) and seabird numbers result to be higher than those sustainable by marine ecosystems. In such a situation, opportunist seabirds could outcompete more specialised seabirds at capturing discards (e.g. Furness 1992, Garthe & Hüppop 1998). Moreover, large scavenger seabirds could compensate the lack of discards by turning to kleptoparasite and predate over smaller seabirds, as has been reported for yellow-legged gulls Larus cachinnans in the western Mediterranean (Oro & Martínez 1994, González-Solís et al. 1997a), and for great skuas Catharacta skua in Scotland (Phillips et al 1999, Oro & Furness in press).

Seabird-fisheries interactions in a confined sea: the Mediterranean case

The Mediterranean is a rather low productive sea, though heterogeneous (e.g. Margalef 1985, Estrada 1996), which sustains both modest fisheries and modest seabird populations. However, seabird-fisheries interactions exist, and should be considered of special concern given the high level of endemism presented by the Mediterranean seabird community (Zotier et al. 1999). Most fisheries are artisanal, and are not likely to exert a strong influence over seabirds. However, bottom trawler (demersal fishery with diurnal activity) and purse seine fleets (pelagic fishery with nocturnal activity) have notably developed in the western region along the last 40 years (Farrugio et al. 1993), becoming important enough to considerably affect seabirds.

So far, few studies have directly assessed any seabird-fishery interaction in the Mediterranean. Concerning artisanal fisheries, there is only evidence of seabird mortality caused by longlines, basically on shags *Phalacrocorax aristotelis desmarestii* (Guyot 1988) and Cory's shearwaters Calonectris diomedea diomedea (Sánchez & Belda 2000, Belda & Sánchez 2001). On turn, semi-industrial fisheries (trawlers and purse seiners) seem to strongly influence the feeding ecology of some seabird populations, but most evidence in this respect is indirect. Certainly, trawling moratoria established around the Ebro Delta (NW Mediterranean) allowed for the first time assessing with detail how a reduction of discards influence the breeding biology of discard-consuming seabirds (see review in Oro 1999). This was especially so for Audouin's gull Larus audouinii (e.g. Oro et al. 1996), the vellow-legged gull (Oro et al. 1995), and the lesser black-backed gull Larus fuscus (Oro 1996). All these gulls showed diverse buffering strategies compensating for the lack of discards during trawling moratoria, and their breeding performance was often negatively affected. Purse seiners appeared to provide feeding opportunities to Audouin's gulls during discard shortages, though there was not clear how the gulls take profit from this fishery (Oro 1995, Oro et al. 1997). Studies at the Chafarinas Isles reveal similar results than those reported from the Ebro Delta, for Audouin's gull and the yellow-legged gull (e.g. González-Solís et al. 1997b). In spite of all these evidence, very few studies have been conducted at sea to assess how seabirds interact with trawlers (Sarà 1993, Oro & Ruiz 1997) and purse-seiners (no studies at all) in the Mediterranean. It is important to fill this gap, addressing studies at sea to assess how seabirds take profit from fishing vessels, how they interfere, and what species are particularly affected. Moreover, seabird efficiency at capturing discards could allow estimating the energy obtained by different species from discards. The preceding information is also important for predicting potential changes in seabirds' community structure resulting from changes in fishing practices.

Focus of this thesis

This thesis was directed to go deeply into the significance of trawler and purse seine fisheries for seabirds in the NW Mediterranean, through direct studies at sea. Fieldwork was concentrated around the Ebro Delta area, as well as off Barcelona, and was conducted throughout the year (1996-2000). This area of study was selected for its high productivity within the Mediterranean context (Estrada 1996), and because it holds important fisheries and important seabird populations. Moreover, the well-studied seabird colonies at the Ebro

Delta, with outstanding information on how the availability of discards influence the breeding performance of seabirds there, provided a unique opportunity to interpret and complement our observations at sea.

The **first section** is directed to assess the relationship of seabirds with trawlers (**chapter 1**) and purse-seiners (**chapter 2**), reporting on fishing practices, seabird numbers and diversity attending fishing vessels, and behaviour of seabirds at capturing discards. In addition, both chapters present bioenergetic considerations on the profit that seabirds obtain from each fishery. The second chapter is particularly novel, since there are few previous studies reporting on the association of seabirds with nocturnal fisheries, and none at all dealing with the case of purse seiners. The **second section** reports on case studies concerning particular species and/or subjects. It begins with a study of competition at fishing vessels between Audouin's gull and the yellow-legged gull, two species of conservation/management concern (**chapter 3**). This chapter is followed by a comprehensive study directed to assess the significance of commercial fisheries for a threatened seabird endemic to the NW Mediterranean, the Balearic shearwater *Puffinus mauretanicus* (**chapter 4**). A final chapter studies the potential role of trawler discards (with a high proportion of demersal fish, not directly available to seabirds) as a source of mercury contamination for seabirds (**chapter 5**).

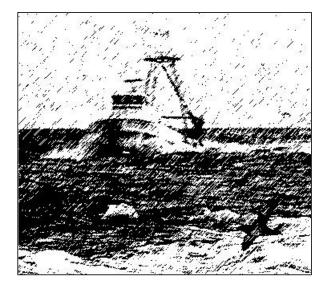
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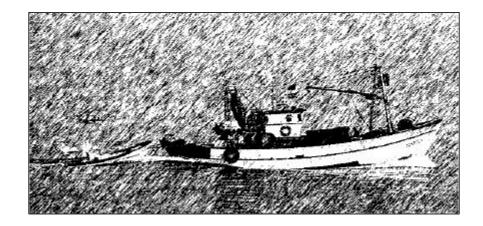
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Section I

The significance of commercial fisheries as a feeding resource for seabirds in the NW Mediterranean



Attendance to trawlers and consumption of discards by seabirds in two NW Mediterranean areas (Barcelona and Ebro Delta) throughout the year

Abstract. The present study was directed to assess the association of seabirds with fishing trawlers, as well as the significance of trawler discards for the former, in the NW Mediterranean. Fieldwork was conducted on board commercial fishing trawlers operating off Barcelona and off the Ebro Delta. During cruises at sea, we collected information on fishing practices, amounts of discards and discard composition, as well as on seabird numbers and behaviour at trawlers. In addition, we collected discard samples to determine their calorific value in the laboratory. We observed differences in fishing practices between the two study areas, related with their different topography. As a rule, trawlers generated more discards off Barcelona, though discard availability was high everywhere, discards being positively correlated with the amounts of marketable catches. Most fish in discards were of small size (< 200 mm), thus suitable to be captured by seabirds. Seabirds attended trawlers in large numbers everywhere and at any time of year. Differences between areas in the variety of seabirds attending trawlers were higher during the breeding season, and were in accord with the different seabird communities breeding close to each site. In average seabirds consumed 84% of fish discarded, this value being lower in the breeding season (79%) than outside this season (89%). Audouin's gull Larus audouinii was the most efficient species at capturing discards, followed by the yellow-legged gull Larus cachinnans and the lesser black-baked gull Larus fuscus; the latter two species were comparatively more opportunist than the former, often relying on kleptoparasitism. Surface feeding seabirds tended to select fish with some floatability, while the contrary was true for seabirds with diving abilities (i.e. shearwaters). Size selection also differed between species, but most fish in discards were suitable for the majority of seabird species. According to bioenergetic modelling, seabirds breeding at the Ebro delta would obtain in average 65.4% of their energetic requirements from discards, though this estimate was subject to strong variability (SD = \pm 29.8%). Audouin's gull was the most benefited from this resource (76.7% of its energetic requirements obtained from discards), whereas terns made little use of discards (19.0 and 1.4% respectively for the common Sterna hirundo and Sandwich terns Sterna sandvicensis). This resource also seems important for seabirds breeding outside the Ebro Delta (procellariforms from nearby archipelagos), as well as for migrating/wintering seabirds.

Introduction

Seabirds are known to make extensive use of fishery waste, which is especially generated by low-selective demersal fisheries such as trawlers (Tasker et al. 2000, and references therein). This phenomenon has been most often studied directly at sea, with work directed to understand the features of trawler fisheries and the behaviour of seabirds taking profit of them. However, this is not the case in the Mediterranean, where evidence of trawler discards utilisation by seabirds comes basically from indirect studies on seabirds'

breeding performance, activity budgets, and diet, conducted at breeding colonies (see Oro 1999, and references therein). These studies have been among the first to demonstrate a significant influence of discards on the dynamics of some seabird populations, as is the case for Audouin's gulls *Larus audouinii* breeding at the Ebro Delta (Oro 1999, Oro & Ruxton 2001). This being so, this is remarkable the generalised lack of studies conducted at sea in the Mediterranean, which should be necessary in order to have a better understanding of this phenomenon. Moreover, at the view of new fishing policies directed to reduce discarding practices (see Fluharty 2000), it is important to have a detailed knowledge of the use that seabirds make of discards, in order to predict potential changes in seabird communities (cf. Furness 1992, Oro & Furness 2002).

So far, studies at sea reporting on the interaction of seabirds and trawler fisheries are limited, in the Mediterranean, to the Sicilian Channel (Sarà 1993), the Balearic Islands, and the Ebro Delta (Oro & Ruiz 1997, Arcos et al. 2001). The study by Oro and Ruiz (1997) is the most comprehensive of them, and reports on the numbers and diversity of seabirds attending trawlers, as well as on some behavioural features, during the breeding season, off the Ebro Delta and Mallorca. In addition, these authors gave some information concerning trawler fisheries (relationship between catches and discards, discards composition), and attempted to model the energy obtained by breeding seabird communities from discards, in relation with their requirements. The aim of the present study is to go deeply into some of these subjects, in order to increase the existent base-line information on trawler fisheries and their potential profitability for seabirds in the NW Mediterranean. With this purpose, we first provide general information for two study areas (Ebro Delta and Barcelona), which differ in their topographical features and their fishing practices, comprising the whole year. The following points were specifically addressed:

- (1) Trawler fisheries features (fish species targeted, sea depths at which trawlers operate, relationship between discards and marketable catches, discards composition)
- (2) Seabird numbers and diversity
- (3) Behaviour of seabirds at fishing vessels: foraging efficiency, interactions, and fish selection.

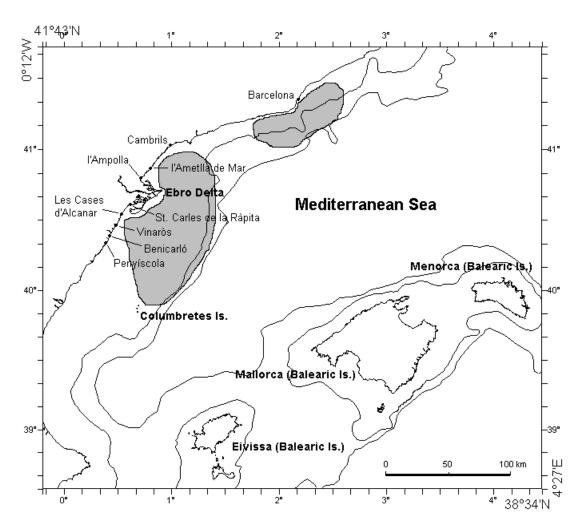
These data would allow modelling the profit that different seabird species obtain from discards, as well as predicting the effect of changes in fishing practices (resulting in different availability and composition of discards) in a close future. As an example, we estimated the current significance of discards, in terms of energy, for different seabird species breeding at the Ebro Delta, as well as for the breeding community as a whole. Detailed breeding numbers in this area makes this approach more interesting, and also allows comparing our results with those obtained by Oro and Ruiz (1997) for the whole community. In comparison with the preceding model, we improve the estimate by providing confidence intervals (following Stratoudakis 1999). Moreover, input parameters in the model are derived for a wider range of situations and larger sample size, thus making the estimate more confident.

Materials and methods

Study area, seabird communities, and fisheries

The study was carried out on board commercial trawlers operating in the NW Mediterranean, off Barcelona (Barcelona port) and off the Ebro Delta (ports of l'Ametlla the Mar, Sant Carles de la Ràpita, and Vinaròs; see Fig. 1). These two areas are separated by about 120 Km, and present different topographical features: the Barcelona area shows a rather narrow and irregular continental shelf, extending some 10-20 km offshore; off the Ebro Delta the continental shelf is swallow and extends up to 70 km offshore. The Ebro Delta area is considered of special productivity within a Mediterranean context (e.g. Estrada 1996, Salat 1996), as a result of the Ebro River runoff and the influence of the Liguro-Provençal-Catalan front at the continental slope, the latter also affecting the area off Barcelona.

Fig. 1. Map showing the two study areas (shadowed area) and nearby ports. The map also shows important geographical references, such as Columbretes Isles and the Balearics. 200- and 1000-m isobaths are also shown.



Within the study area, the most important breeding colonies of seabirds are located in the Ebro Delta (ca. 20000 breeding pairs of gulls and terns, cf. Oro 1999), while only a few hundreds of yellow-legged gulls *Larus cachinnans michaellis* breed close to the Barcelona area. In addition, shearwaters and European storm-petrels *Hydrobates pelagicus* breeding in the Balearic and the Columbretes archipelagos (Fig. 1) often visit the areas considered for study for foraging purposes (Abelló & Oro 1998, Abelló et al. 2000). Species of particular concern are the Balearic shearwater *Puffinus mauretanicus* (endemic to the Balearic Islands, with a breeding population of some 3300 pairs; Aguilar 1991) and Audouin's gull (with three quarters of its breeding population being concentrated in the Ebro Delta colony, 11500 pairs; Oro 1998). Out of the breeding season, seabirds breeding in the North Atlantic meet with some typical Mediterranean species in the two areas studied (e.g. Bourne 1991).

Although artisanal fleets are dominant in Mediterranean fisheries, bottom trawler (demersal) fleets are well developed in the two study areas and are considered of a semiindustrial type (e.g. Farrugio et al. 1993), representing the most important fishery in economic terms. There are ca. 25 vessels in Barcelona and ca. 200 vessels in the ports surrounding the Ebro Delta area (Penyíscola to Cambrils, Fig. 1), all of them having a timetable limited to diurnal hours.

Methods

We conducted a total of 87 one-day cruises on board commercial trawlers, 58 off Barcelona (1996-2000) and 29 off the Ebro Delta (1997-1998). Data collected during these cruises was complemented with observations conducted on board R/V Cornide de Saavedra in May 1999 and June 2000, when prospecting the Ebro Delta area (discard experiments, see below). Discards samples were examined both at sea and in the laboratory (composition of discards, determination of calorific value).

Analysis of discards: qualitative and quantitative composition, calorific value

As a rough simplification, we classified hauls into three categories, according to the sea depth and the type of fish targeted: shelf hauls (up to 150 m depth, and including a wide variety of fish species); upper-slope hauls (from 150 to ca. 300 m, mostly directed to catch hake *Merluccius merluccius* and blue whiting *Micromesistius poutassou*); and mid-slope hauls (from 300 to 800 m, directed to deep-water crustaceans and conducted over submarine canyons).

For each haul, we recorded the amounts of discards and marketable catches. When discards were thrown directly overboard, most frequently using plastic shovels, we counted how many times fishermen discarded fish with these shovels, and weighted the content of a representative number of them (usually 5-10) to obtain an average weight (cf. Oro & Ruiz 1997). In other cases fishermen first accumulated discards in boxes, that were directly weighted before being thrown overboard (the weight of these boxes was alternatively estimated, once we gained some experience). Marketable catches were either estimated for each haul with the help of fishermen, or we directly obtained the amounts of fish landed at port. From the previous data we established a ratio of fish discarded vs. marketable catches (discards ratio, DR = fish discarded/fish landed).

When possible, we collected sub-samples of discards for their analysis in the laboratory. We first estimated the proportion of discards (in weight) that were *a priori* consumable by seabirds (consumable fraction, CF = discards consumable/total discards), which included all fish species, as well as crustaceans and small cephalopods (the two last groups were little consumed by seabirds, but anyway these groups were usually scarce among discards). Other invertebrates, as well as vegetable and inorganic material, were considered as no consumable by seabirds. For the consumable fraction, each fish item was identified to the species/genera/family level, measured (to the nearest mm), and weighted (to the nearest g).

Samples of the most common fish species in the discards were stored frozen at -20°C short after arriving to port, in order to determine their calorific value subsequently. Samples consisting on 2-10 fish of the same species and similar size were homogenised and oven-dried at 60°C to constant weight. For each fish species we selected five different samples, trying to cover the range of sizes presented by the species in the discards. Once dried, the calorific value of the samples was determined through lipid extractions, considering a calorific value of 40 kJ g⁻¹ for lipids and of 24 kJ g⁻¹ for proteins (Peters 1983). Values for fish in discards were referred to fresh weight. A mean calorific value for discards was obtained by averaging the mean values of each fish group considered, weighting for their representation (% in weight) in the discards.

Association of seabirds with trawlers

Seabirds attending trawlers were counted at 15-min intervals, during the fishing process (from the hauling of the net through the whole process of discarding). During these counts we identified seabirds to the species level, and the maximum number of birds was recorded for each species and haul. Results are given as mean and maximum number of birds per haul, as well as percentage of presence (%P, proportion of hauls in which the species was recorded). Although the median would be more appropriate than the mean for this kind of data (departing from a normal distribution, see below), the former value was zero for many species, and the mean was considered to provide more information. Seabird counts were considered separately according to the season: breeding period (March-July for most species), post-breeding period (August-October), and winter (November-February).

Discard experiments: efficiency of seabirds at capturing discards, interactions, and selection of fish type and size

We conducted experiments to assess how seabirds take profit of discards: fish from the by-catch fraction were thrown overboard individually or in small numbers at a time, recording on tape fish species, length (classified according to 5-cm categories), and fate, either sunk or picked up by a seabird. In the latter case we recorded the seabird's species and age, and followed the bird in order to ascertain if the fish was swallowed, dropped, or lost to kleptoparasitism, and so on until its final fate. Although in three occasions these experiments were conducted on board a research vessel (one in May 1999 and two in June 2000), most often they were conducted on board commercial trawlers and coinciding with the fish processing on board, thus approaching the conditions of typical discarding by fishermen. This way we reduced some biases described for experiments on board research vessels (Garthe & Hüppop 1998a). However, some biases could still remain, especially when fishermen discard fish previously amounted in boxes (a practice more frequently occurring in Barcelona), as discussed by Oro and Ruiz (1997) and Arcos et al. (2001).

During the discard experiments seabirds associated to the vessel were counted and identified to the species level, and those censuses were recorded independently from the maximum number of seabirds observed during the whole haul. This allowed calculating a foraging success index for each species and experiment, based on the Ivlev's electivity index (Krebs 1989), in order to assess the relative efficiency of different species at capturing discards,

$$SI_j = \frac{O_j - E_j}{O_j + E_j}$$

where SI_i is the foraging success index for seabird species j, O_i is the observed number of items swallowed by this species, and E_i is the expected number of items swallowed, estimated from multiplying the total number of items offered by the representation (percentage) of the species behind the vessel. If this representation was observed to change substantially, the experiment was stopped. Only those experiments with at least 30 items discarded were considered in order to minimise biases resulting from small sample size (Garthe & Hüppop 1998a,b). Nevertheless, success indexes should be considered as mere approximations to the actual efficiency of seabirds at capturing discards, since they are subject to biases of different types. For instance, they do not account either for the time spent following the vessel by different species, or for individual differences in efficiency, or for differences in size and type selection which would result in differences in the energy obtained by picking up a fish, or for the energetic requirements of different species/individuals (cf. Garthe & Hüppop 1994, Camphuysen et al. 1995, Arcos et al. 2001). To reduce some of these biases, we also considered the percentage of discards captured by the different species at each experiment, considering size selection, and used this measure to estimate the energy obtained by different seabirds from attending trawlers (see bioenergetic model below).

Discard experiments allowed studying kleptoparasitic interactions between seabirds attending trawlers. We estimated a global kleptoparasitic rate as the percentage of fish discarded that were involved in any kleptoparasitic event. In addition, we recorded the number of attacks performed by each species (and their success rate, SR = proportion of successful attacks), as well as the number of attacks received by this species (and the proportion of these attacks that were successful for the kleptoparasite). Finally, we calculated a robbery index (RI_j) as the number of items stolen by species *j* divided by the number of items lost to kleptoparasitism by this species. To obtain symmetrical data, we offer the logarithm of this division as the actual RI (cf. Arcos et al. 2001).

Fish type selection was assessed considering nine groups of fish in discards (see below). For each seabird species (*j*) and fish group (*i*), a preference index (PI_{ij}) was calculated as $PI_{ij} = O_{ij}/E_{ij}$, where O_{ij} is the observed number of fish items *i* picked up by seabird species *j*, and E_{ij} is the corresponding expected value. This last value was computed for each experiment (considering the proportion of fish group *i* discarded and the total number of fish items picked up by seabird species *j*) and then summed up, thus avoiding biases resulting from differences in the representation of each fish group between experiments. To make figures more intuitive (symmetrical around zero), we represented

 $PI_{ij} = (PI_{ij} - 1)$. Size (i.e. length) selection was assessed similarly, although we assumed similar representation of each size category among discards and did not consider experiments separately. Thus, size preferences were expressed for each size category and seabird species as,

$$SP_{ij} = \frac{CS_{ij} / Of_i}{CS_j / Of}$$

where SP_{ij} is the preference index of seabird species *j* for fish size category *i*, CS_{ij} is the total number of fish size category *i* captured by seabird species *j*, Of_i is the total number of items of fish size category *i* offered during discard experiments, and CS_j and Of are equivalent parameters considering all fish size categories altogether. This way, we eliminated the effect of general efficiency at capturing discards, which allowed comparing relative preferences for any fish size category. To reduce biases when assessing fish selection (either type or size), we only considered those seabird species that captured at least 30 fish items.

Utilisation of discards by seabirds: bioenergetic considerations

We built a bioenergetic model to estimate the importance of discards for the breeding seabird community at the Ebro Delta, as well as for each breeding species separately. We first estimated the energy obtained from discards (ED) as,

$$ED = CC \times DR \times CF \times CR_W \times CAL \times AE$$

where CC is the total amount of commercial catches from the surrounding ports, DR is the ratio of discards vs. marketable catches, CF is the consumable fraction of discards, CR_W is the consumption rate of seabirds (% in weight of discards captured), CAL is the mean calorific value of fish in discards, and AE is the assimilation efficiency of seabirds. In the calculation of these parameters we only considered data corresponding to the Ebro Delta area for the period March-July (breeding season). The model includes all ports within 40 km around the Ebro Delta, since we considered that most of their vessels operate within the foraging range of the breeding seabirds (ca. 50 km; Fasola & Bogliani 1990, Oro & Ruiz 1997). These ports were: Cambrils (21 trawlers), l'Ametlla de Mar (27 trawlers), l'Ampolla (2 trawlers), Sant Carles de la Ràpita (59 trawlers), les Cases d'Alcanar (7 trawlers), Vinaròs (22 trawlers), Benicarló (29 trawlers), and Penyíscola (32 trawlers). Commercial catches were averaged from data on monthly catches statistics obtained at the three ports where we conducted cruises, considering the period 1994-1998. From these catches we estimated an average value of catches per vessel and month, and this value was extrapolated to all ports considered. The discards ratio (DR) and the consumable fraction of discards (CF) were estimated as described above. The consumption rate of discards was estimated for the seabird community as a whole, as well as for each species separately. This parameter was subject to considerable variability, which was partly reduced by gathering all experiments for each month and year, and calculating an average value from these partial results instead of doing that from each experiment. Since the consumption rate estimated at sea (CR_N) was the percentage in number of discards consumed by seabirds,

without accounting for the size (and hence the weight) of the discards consumed, we corrected this parameter in order to have a measure in terms of weight (CR_W) . This was achieved as follows:

$$CR_W = CR_N \times \sum_{i=1}^n (SP_i \times PW_i)$$

where SP_i is the size preference index of seabirds for fish size category *i*, and PW_i is the representation in weight of fish size category *i* in the discards. When considering each seabird species *j* separately, CR_{Wj} was estimated using specific values for CR_{Nj} and SP_{ij} . Moreover, in order to account only for breeding birds, we multiplied CR_{Wj} by the percentage of adults of *j* capturing fish. The mean calorific value of discards was calculated as explained above. Finally, the assimilation efficiency of seabirds was considered of 75%, following Furness et al. (1988).

Once estimated the energy obtained by seabirds from discards, we assessed the energetic requirements (ER) of the breeding community at the Ebro Delta. Although the breeding season was considered to include the whole period from March to July, we selected for each seabird species the three or four months that best fitted to their actual breeding performance. Bioenergetic estimates were restricted to species showing welldefined marine habits, at least by part of the population: Audouin's gull, the yellow-legged gull, the lesser black-backed gull Larus fuscus, Sandwich tern Sterna sandvicensis, and the common tern Sterna hirundo. Seabird species considered to feed preferentially in marsh habitats were not considered. Energetic requirements (ER) were estimated for each species *i* as the product of the field metabolic rate $(FMR_i; \text{ in } \text{kJ } \text{day}^{-1})$ by the number of breeding individuals in the colony (N_i) . In turn, FMR was considered to be 3.9 times the basal metabolic rate (BMR) for breeding birds (Garthe et al. 1996), and the latter parameter was estimated as BMR_i (kJ day⁻¹) = 2.30 (W_i)^{0.774}, where W is body mass (g), according to Bryant and Furness (1995). This last equation was estimated from North Atlantic seabirds and probably overestimates the BMR of Mediterranean seabirds, but latitudinal and associated climatic differences could not be as important as previously expected (cf. Bryant & Furness 1995). In order to have an estimate for the whole breeding community, mean body mass was estimated by averaging specific body masses, weighting for the representation in number of each species.

The significance of discards for breeding seabirds (*SD*, or proportion of the energetic requirements that is met through consuming discards) was finally estimated through dividing the energy obtained from discards (ED) by the energetic requirements of seabirds (ER). This was done for each breeding species of seabird as well as for the community as a whole. Since most of the parameters entering the above equations are subject to some variability, we also estimated 95% confidence intervals, after calculating a global coefficient of variation (CV) through the Delta method (see Stratoudakis 1999),

$$CV^{2} (SD) = CV^{2} (CC) + CV^{2} (DR) + CV^{2} (CF) + CV^{2} (CR_{W}) + CV^{2} (CAL) + CV^{2} (AE) + CV^{2} (W) + CV^{2} (SD) + CV^{2} (FMR) + CV^{2} (N)$$

These coefficients of variation were estimated either directly or making the appropriate transformations when data distributions departed from normality.

Statistical analysis

Data were first tested for normality using the Shapiro-Wilk test. In most cases there was a significant departure from normality, which was corrected using the appropriate transformations in order to employ parametric statistics; alternatively, data were treated using non-parametric procedures (Zar 1996).

Pseudoreplication for seabird's counts was partially avoided by considering only one count per haul (that of the maximum number of birds), while hauls performed in the same day were often well separated in time and space. When considering sets of tests directed to test similar events we employed the Bonferroni correction according to Rice (1989). Significance level was set at 0.05, although marginal values were also discussed following Stoehr (1999).

Results and discussion

Analysis of discards: qualitative and quantitative composition, calorific value

Trawler fisheries' generalities. Trawlers targeted a wide variety of demersal fish species, which differed according to the sea depth and the type of substrate. At the Ebro Delta area, where the continental shelf is wide and it takes vessels a long time to reach the continental slope, most trawlers operated strictly over the former (usually al depths not greater than 150 m), with few trawls conducted at the upper-slope. Shelf trawls were directed to catch several species of demersal whitefish. Off Barcelona trawlers regularly operated over the continental shelf too, exploiting a wider variety of substrates and prey than those at the Ebro Delta. However, the narrowness of the continental shelf off Barcelona limited the possibilities of exploiting shallow areas, and trawlers also frequently operated over the upper-slope (basically targeting hake and blue whiting) and the mid-slope (targeting Norway lobster *Nephrops norvegicus* and the deep-water shrimp *Aristeus antennatus*). Differences in the width of the continental shelf also led to differences in the frequency and duration of trawls, shelf trawls being more numerous and of shorter duration off Barcelona (3-5 trawls per day vs. 2-3 off the Ebro Delta).

Fish processing. Fish processing was similar in all cases. Catches were lowered on the stern deck, and directly classified either while the vessel was steaming towards a new fishing point or just after lowering the net again for a new trawl. Discards (i.e. fish rejected either because does not reach the minimum legal size, has little commercial value, exceeds the quota established for individual vessels, or has been damaged during the fishing process) were often directly thrown overboard, using the hands and small shovels; alternatively, fishermen stored discards in boxes (10-25 kg) and threw their content overboard once filled. Fishermen rarely gutted fish on board, with the exception of anglerfish (*Lophius piscatorius*) and, sometimes, dogfish, hake, and scabbard fish *Lepidopus caudatus*. Thus, offal was generated in negligible amounts (Table 1) compared to fisheries in other areas (cf. Oro & Ruiz 1997), such as SW Atlantic (Thompson & Riddy 1995) and the North Sea (Garthe et al. 1996).

| | | | Contine | ntal s | helf | | | Uppe | r-slope | | Mid | -slope |
|--------|----|-------|------------|--------|-------|-------------|----|-------|------------|----|------|--------------|
| | | Barce | elona | | Ebro | Delta | _ | | | | | |
| • | п | Mean | Range | п | Mean | Range | п | Mean | Range | п | Mean | Range |
| Catch. | 23 | 124.2 | 13 - 550 | 36 | 184.4 | 57-850 | 21 | 158.5 | 34-460 | 28 | 59.7 | 5 - 230 |
| Disc. | 31 | 174.8 | 20 - 1125 | 36 | 89.3 | 16 - 425 | 31 | 120.8 | 14 - 690 | 36 | 28.2 | 4 - 90 |
| Offal | 30 | 0.27 | 0 - 2 | 36 | 0.17 | 0 - 2 | 29 | 0.76 | 0 - 5 | 34 | 0.29 | 0 - 3 |
| DR (%) | 23 | 176.8 | 47.2 - 730 | 36 | 56.1 | 8.2 - 212.5 | 21 | 125.6 | 11.7 - 664 | 28 | 46.3 | 14.5 - 110.3 |
| CF (%) | 1 | 75.3 | - | 24 | 64.0 | 12.7 - 99.9 | 1 | 96.8 | - | 1 | 88.5 | - |

Table 1. Landed catches, discards, and offal per haul (in kg), according to the type of haul and the area (only in the case of continental shelf hauls). The ratio of discards vs. landed captures is also provided (DR), as well as the percentage of discards a priori consumable by seabirds (consumable fraction, CF). (n, number of hauls)

Relationship between discards and marketable catches. Catches and discards differed in both amounts and composition according to the sea depth/type of substrate, as well as to the area (only shelf hauls compared between areas; see Tables 1 and 2). The ratio of discards to marketable catches (DR) showed strong variation (mean = 93%, range 8-730%, Table 1), though there was a strong correlation between the two variables (Spearman's rank correlation, $r_s = 0.61$, n = 108, p < 0.0001). Nevertheless, DR showed significant differences both between depths/substrates (Kruskal-Wallis test, $H_{2,108} = 6.3$, p =0.04) and between areas (Mann-Whitney test, $U_{36,23} = 96.5$, p < 0.0001; Table 1). For the Ebro Delta area, discards represented in average slightly more than one third of total catches (36%, given the mean DR of 56%), agreeing with the previous estimate in this area of 15-45% (Oro & Ruiz 1997). Trawlers off Barcelona discarded a considerably higher proportion of the total catches, the amounts of discards exceeding in average those of marketable catches (i.e. DR > 100%, with exptreme values up to 730%). Trawls directed to catch crustaceans (mid-slope hauls) were the most selective, generating comparatively both low amounts (mean = 28 kg) and low proportion of discards (DR = 47%). This last result contrast with the low selectivity of fisheries targeting crustaceans in the North Sea and the British Isles (average DR of 900% for Brown shrimp Crangon crangon, and 200% for Norway lobster; see Walter & Becker 1994 and Furness et al. 1988, respectively).

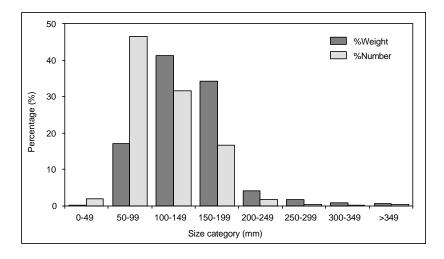
Composition of discards. The proportion of discards *a priori* consumable by seabirds (*CF*: fish, crustaceans and cephalopods) ranged between 12.7 and 99.9%, being in average of 66.5% (Table 1). Slope trawls apparently generated a higher proportion of consumable discards, though the limited sample size did not allow for any statistical comparisons. The composition of *CF* was quite variable and involved high diversity of fish species. Nine main groups of fish type were considered, according to their relative abundance and their ecological/phylogenetic affinities: dogfish and other small sharks (Chondrychthies), sardine *Sardina pilchardus*, anchovy *Engraulis encrasicolus*, bogue *Boops boops*, gadoids (Gadiformes), strictly mesopelagic fish (Stomiiformes, Aulopiformes, Myctophiformes), gobies and dragonets (Gobiidae and Callionymidae), flatfish (Pleuronectiformes), and remaining species ('others'). The representation of these groups in discards (% in number and % in weight) is shown in Table 2, differentiating

between types of haul. Most fish in discards were of small size, the majority below 200 mm in length (Table 4, Fig. 2), thus being suitable for most seabirds. In addition, fish over 200 mm were often snake-like fish (cf. Oro & Ruiz 1997), which was more suitable for seabirds' consumption than either roundfish or flatfish (e.g Forbes 1989). This situation differs from that described in other areas, such as the North Sea, where discards are considerably larger in average and this becomes a limiting factor for most seabird species (e.g. Furness 1992, Camphuysen 1994, Garthe & Hüppop 1998b).

Table 2. Representation in number (% N) and weight (%W) of the nine fish groups of fish considered, according to the type of haul: shelf hauls (n = 27), upper slope hauls (n = 2) and mid slope hauls (n = 1); nf = number of fish sampled. For each group, the mean legth (in mm) and weight (in g) of fish is also provided, as well as the percentage of fish consumed by seabirds in discard experiments (CR_N , %). (n, number of fish offered during experiments)

| | Shelf | | Upslo | ope | Mid-s | slope | | | |
|------------------------------------|--------|------|----------------|------|--------|-------|--------------|-----------------|-------------|
| _ | nf = 4 | 4015 | <i>nf</i> = 61 | 5 | nf = 2 | 215 | | | |
| Group | % N | % W | % N | % W | % N | % W | Length | Weight | $CR_N(n)$ |
| Chondricthies | 0.1 | 0.3 | 16.3 | 7.8 | 48.4 | 25.8 | 185 ± 49 | 20.8 ± 21.6 | 58.7 (92) |
| Sardine, Sardina pilchardus | 17.5 | 24.0 | 0.7 | ? | - | - | 148 ± 20 | 24.6 ± 9.1 | 91.8 (964) |
| Anchovy, Engraulis encrasicolus | 8.0 | 7.9 | 2.4 | ? | - | - | 123 ± 12 | 11.5 ± 3.1 | 79.2 (370) |
| Bogue, Boops poops | 8.0 | 16.0 | 0.7 | ? | - | - | 156 ± 28 | 35.3 ± 21.0 | 94.1 (579) |
| Gadiformes | 9.9 | 5.8 | 54.2 | 79.8 | 22.8 | 8.2 | 78 ± 24 | 6.6 ± 6.1 | 88.7 (630) |
| Mesopelagi fishs | 0.2 | 0.7 | 3.8 | 1.2 | 18.6 | 3.9 | 107 ± 83 | 7.0 ± 12.4 | 87.6 (170) |
| Gobiidae/Callionymidae | 19.5 | 6.4 | 2.0 | ? | - | - | 71 ± 15 | 3.1 ± 2.3 | 57.9 (95) |
| Pleuronectiformes | 20.5 | 14.9 | 1.0 | 2.6 | 0.9 | 0.3 | 89 ± 17 | 6.0 ± 3.5 | 68.5 (184) |
| Others | 16.5 | 23.5 | 33.5 | 8.7 | 9.3 | 17.8 | 118 ± 74 | 16.2 ± 17.5 | 85.2 (1018) |
| TOTAL | 100 | 100 | 100 | 100 | 100 | 100 | | | 86.1 (4102) |

Fig. 2. Percentage in number and percentage in weight of fish size categories among discards (n = 5080 fish, sampled at 30 hauls)



Energetic content of discards. The calorific value was determined for 15 fish species collected at the Ebro Delta area, being representative of discards from shelf hauls (only chondrychthies and mesopelagic fish were not represented). Specific mean values ranged from 4.81 kJ g⁻¹ in the black goby *Gobius niger* to 10.03 kJ g⁻¹ in the sardine (Table 3). The mean calorific value for discards (only considering the Ebro Delta area during the breeding season) was estimated at 7.06 \pm 0.09 kJ g⁻¹, which is slightly higher than that assumed by other studies (e.g. 5 kJ g⁻¹ in Furness et al. 1988, Oro & Ruiz 1997).

Table 3. Calorific value $(kJ g^{-1})$ of fish representative of trawler discards. Five samples were examined for each species, each sample resulting of pooling 2-10 fish of similar size. Results in boldface correspond to the seven fish type groups typical of discards from hauls over the continental shelf.

| Species/groups | п | Energetic content (kJ g^{-1} fw) |
|--|----|------------------------------------|
| Sardine, Sardina pilchardus | 5 | 10.03 ± 0.97 |
| Anchovy, Engraulis encrasicolus | 5 | 6.67 ± 0.44 |
| Bogue, Boops poops | 5 | 5.94 ± 0.23 |
| Gadiformes: | 20 | 5.81 ± 0.75 |
| Hake, Merluccius merluccius | 5 | 4.88 ± 0.43 |
| Blue whiting, Micromesistius poutassou | 5 | 5.98 ± 0.08 |
| Silvery pout, Gadiculus argenteus | 5 | 6.77 ± 0.27 |
| Poor cod, Trisopterus minutus | 5 | 5.59 ± 0.33 |
| Gobiidae/Callionymidae | 15 | 5.34 ± 0.47 |
| Black goby, Gobius niger | 5 | 4.81 ± 0.20 |
| Goby, Deltenosteus quadrimaculatus | 5 | 5.81 ± 0.15 |
| Dragonet, Callionymus phaeton | 5 | 5.38 ± 0.32 |
| Flatfish, Pleuronectiformes | 15 | 5.28 ± 0.42 |
| Citharus macrolepidotus | 5 | 4.92 ± 0.40 |
| Scoftalmiidae/Bothidae spp. | 5 | 5.33 ± 0.29 |
| Tongue sole, Symphurus nigrescens | 5 | 5.81 ± 0.33 |
| Others: | 15 | 7.60 ± 0.78 |
| Gurnard, Triglidae spp. | 5 | 8.45 ± 0.48 |
| Brown comber, Serranus hepatus | 5 | 7.43 ± 0.50 |
| Guilt sardine, Sardinella aurita | 5 | 6.91 ± 0.32 |

Association of seabirds with trawlers

All seabird species observed regularly during the study attended trawlers to some extent, often in large numbers, with auks being the most rarely attracted. In total, 29 seabird species were involved, of which 22 are shown in Table 4. The remaining seven species were either rare visitors to the study area, recorded occasionally (great shearwater *Puffinus*)

gravis, long-tailed skua Stercorarius longicaudus, common gull Larus canus, herring gull Larus argentatus, and white-winged black tern Chlidonias leucopterus), or coastal species rarely observed offshore, that sporadically attended trawlers in the vincinty of fishing ports (great cormorant Phalacrocorax carbo and little tern Sterna albifrons).

Breeding period. At this time of year, most seabirds attending trawlers off the Ebro Delta pertained to local breeding species, either at the Delta colonies (several larids; see Oro 1999) or at the relatively close archipelagos of Columbretes and the Balearics (basically procellariforms; e.g. Aguilar 1991, Belda & Sánchez 2001). Particularly important for their numbers were the yellow-legged gull (35% of all seabirds observed), Audouin's gull (23%), the Balearic shearwater (20%), and Cory's shearwater Calonectris diomedea diomedea (9%). Non-breeding or migrating species were very scarce in this area. Off Barcelona, the seabird community attending trawlers was clearly dominated by yellowlegged gulls (77% of total seabirds), the only species breeding nearby. However, the breeding population is small (from several ten to few hundred pairs), and most birds attending trawlers were probably non-breeders, as can be deduced from the high proportion of immatures observed (ca. 60%; authors, unpublished data). There was also a considerable diversity of species with low representation, either breeders from distant colonies (Cory's, Balearic, and Levantine shearwaters Puffinus yelkouan, storm-petrels, Audouin's gulls), wintering birds still remaining in the area as non-breeders or late migrants (e.g. Mediterranean gulls Larus melanocephalus and northern gannets Sula bassana), or strictly migrant species (e.g. Stercorarius skuas, little gull Larus minutus, and terns).

Non-breeding period. During the post-breeding period typical breeding species were still common, especially late breeders such as Cory's shearwater, and attended trawlers at the same time that several migrating species. The situation changed in winter, when the two areas presented more similar seabird communities. The yellow-legged gull became the most common seabird everywhere, with also high representation of wintering Mediterranean gulls (which were especially abundant offshore) and, to a lower extent, lesser black-backed gulls, black-headed gulls *Larus ridibundus* (which remained quite coastal), and others. There was also representation of wintering birds coming from northern latitudes, such as northern gannets, great skuas *Catharacta skua*, and kittiwakes *Rissa tricdactyla*.

Remarks. The previous results highlight the importance of discards as a feeding resource for many seabird species, at different stages of their annual cycle (breeding, migration, and wintering) and affecting different age categories (immatures, adults). However, the actual significance of discards for seabirds cannot be directly deduced from direct counts at fishing vessels, but require of more detailed data on seabird's behaviour and efficiency at capturing discards. The following section deal with more detail with these topics.

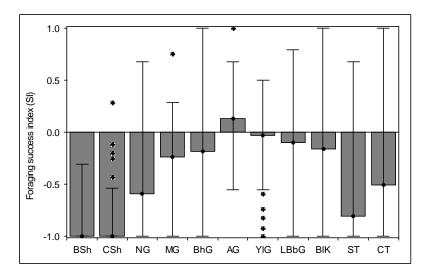
| auls attended by a given species of seabird vs. total hauls recorded) and number (mean and maximum) of the different species | ig to the study site (Ebro Delta and Barcelona) and the season (breeding period, March-July, post-breeding period, August- | $\langle n, number of hauls \rangle$. |
|--|--|--|
| Table 4. Percentage of presence (%P, hauls attended by a given specie | | October, winter, November-February). (n, number of hauls). |

| | | | | | Barcelona | | | | | | | | Ð | Ebro Delta | e, | | | |
|--|------|--------------------|-------------|----------|-------------------------|----------|-------|--------------------|----------|---------|--------------------|-----|-------------------------|------------|-------|------|--------------------|-------|
| | Bree | Breeding (MarJul.) | (Iul. | Post-bre | Post-breeding (AugOct.) | (-0 ct.) | Winte | Winter (N ovF eb.) | eb.) | Breedin | Breeding (MarJul.) | | Post-breeding (AugOct.) | g(Aug. | Oct.) | Win | Winter (N ovF eb.) | Feb.) |
| | | (n = 110) | | ű. | (n= 42) | | | (n = 28) | | 0 | (n= 36) | | (n = 11) | ~ | | | (n= 14) | |
| | %P | Mean | Max. | %P | Mean | Max. | %P | Mean | Max. | %P | Mean Max | ex. | %P | Mean | Max. | %P | Mean | Max. |
| Balearic shearwater Puffivrus mauretavicus | 58.2 | 3.53 | 38 | 33.3 | 0.50 | 4 | 60.7 | 2.79 | 27 | 77.8 | 35.83 5: | 550 | 54.5 | 2.27 | 9 | 92.9 | 8.43 | 33 |
| Levantine shearwater Puffixus yelkouan | 37.3 | 1.94 | 89 | 59.5 | 0.88 | 9 | 21.4 | 0.36 | б | 13.9 | 0.28 | 5 | 9.1 | 0.09 | 1 | ł, | | 8 |
| Cory's shearwater Calonectris diomedea | 63.6 | 5.61 | 90 | 92.9 | 13.00 | 130 | 20 | 89 | <u>.</u> | 77.8 | 16.64 1(| 104 | 72.7 | 30.09 | 153 | 21.4 | 0.43 | m |
| European storm-petrel <i>Hydr obates pelagicus</i> | 22.7 | 0.48 | 9 | 7.1 | 0.07 | | э | э | 2 | 55.6 | 2.14 1 | 16 | 27.3 | 2.91 | 27 | ì | 55 | æ |
| N orthern gannet <i>Sula bassana</i> | 31.8 | 0.45 | σ | 33.3 | 0.76 | ~ | 64.3 | 2.50 | 17 | 5.6 | 0.11 | ~1 | 18.2 | 0.18 | 1 | 71.4 | 6.71 | 30 |
| Shag Phalacrocor ax aristotelis | 6.0 | 0.01 | H | 13 | e | T. | • | R. | 5 | 2.8 | 0.03 | - | ł. | 12 | e. | ł. | 18 | 5 |
| Great skua <i>Catharacta skua</i> | 18.2 | 0.25 | 4 | 4.8 | 0.05 | 1 | 50.0 | 0.68 | ব | 36.1 | 0.39 | ~1 | • | 32 | 2 | 21.4 | 0.21 | - |
| Pomarine skua Stercor arius pomarinus | 9.1 | 0.09 | - | э | ы | э | э | э | | 11.1 | 0.28 | 10 | ł | э | a | ì | 52 | æ |
| Arctic skua Stercorænus parasiticus | 8.2 | 0.11 | 4 | 90 | , | 30 | 7.1 | 0.07 | - | 83 | 0.08 | - | | × | × | 42.9 | 0.50 | 7 |
| Mediterranean gull Larus melævocephalus | 50.0 | 6.04 | 95 | 81.0 | 5.60 | 28 | 100 | 48.86 | 220 | 11.1 | 0.44 | ~ | 18.2 | 0.18 | 1 | 100 | 82.86 | 330 |
| Little gull Larus miratus | 17.3 | 1.58 | 37 | 7.1 | 0.10 | 6 | 10.7 | 0.14 | 5 | 5.6 | 0.06 | 1.0 | • | 32 | 2 | 6 | 22 | 2 |
| Black-headed gull Larus r <i>idibundus</i> | 18.2 | 1.43 | 40 | 50.0 | 5.79 | 28 | 42.9 | 2.39 | 21 | 36.1 | 4.89 3 | 38 | 63.6 | 14.45 | 84 | 78.6 | 30.00 | 160 |
| Slender-billed gull Larus genei | a. | æ | a | a. | | a. | æ | × | | 33.3 | 1.03 1 | 12 | 18.2 | 0.27 | 2 | i | <u>.</u> | |
| Audouiri's gull Larus audouinii | 50.9 | 1.49 | 12 | 15 | E. | T. | 28.6 | 0.32 | 7 | 100 | 41.89 10 | 107 | 72.7 | 3.36 | 17 | 85.7 | 3.07 | 13 |
| Y ellow-legge d gull Larus cachimnans | 97.3 | 80.33 | 600 | 100 | 146.67 | 510 | 100 | 106.32 | 500 | 100 | 63.14 4 | 450 | 100 | 51.45 | 250 | 100 | 201.43 | 950 |
| Lesser black-backed gull <i>Larus fuscus</i> | 20.9 | 0.47 | 20 | 52.4 | 0.76 | Ś | 89.3 | 2.04 | 9 | 77.8 | 4.78 7 | 72 | 90.9 | 2.36 | 10 | 100 | 9.71 | 75 |
| Kittiwake Rissa tridactyla | 3.6 | 0.05 | 2 | æ | | 90 | 60.7 | 1.07 | ব | 83 | 0.17 4 | ব | ł. | æ | a. | 35.7 | 0.71 | ব |
| Sandwich tern Sterna savávicensis | 9.1 | 0.18 | 4 | 16.7 | 0.36 | 5 | 7.1 | 0.07 | - | 47.2 | 1.00 | 5 | 63.6 | 0.91 | ы | 143 | 0.21 | 7 |
| Common tern Sterves hirundo | 19.1 | 0.23 | 7 | 28.6 | 0.71 | 5 | 29 | 29 | 2 | 77.8 | 7.19 3 | 5 | 81.8 | 13.00 | 36 | | 2 | 2 |
| Black tern Chlidonias niger | 8.2 | 0.13 | ŝ | 14.3 | 0.29 | ব | э | э | 2 | 36.1 | 1.72 3 | 35 | 36.4 | 0.55 | ы | 1 | 55 | æ |
| Razorbill Alca torda | 30 | æ | <u>(</u> 1) | 90 | | 90 | 7.1 | 0.07 | | i. | ł. | | | a. | , | • | œ | 20 |
| Puffin Fratercula arctica | 60 | 0.01 | I | 13 | e | r: | • | ю | 5 | ł, | 6 | 12 | | 12 | r. | ł. | 18 | E. |
| TOTAL | 100 | 104.4 | 648 | 100 | 175.5 | 540 | 100 | 167.7 | 564 | 100 | 182.4 92 | 927 | 100 | 122.1 | 346 | 100 | 344 4 | 1177 |

Discard experiments: efficiency of seabirds at capturing discards, interactions, and selection of fish type and size

Seabird's efficiency at capturing discards. Seabirds showed a high efficiency at capturing discards (consumable fraction) in discard experiments, obtaining in average 83.9% of the items offered (range 16.1-100%). This efficiency did not statistically differ between areas (84.0% in Barcelona vs. 83.9% in the Ebro Delta; Mann-Whitney test, $U_{37,17}$ = 308.0, p = 0.9), but showed seasonal differences (79.4% during the breeding season vs. 89.2% outside this season; $U_{29.25} = 237.5$, p = 0.03). Seabird's efficiency could be overestimated since items in discard experiments were offered either singly or in small numbers, while fishermen often discarded fish in larger amounts at a time (for further discussion, see the Methods section). In any case, our results lay within the range estimated by Berghahn and Rösner (1992) in the North Sea (68-90% of fish captured by seabirds); these authors used a presumably better approach, consisting in the use of a stow-net to recatch not-consumed discards behind the vessel. When only considering the breeding period, at the Ebro Delta, our estimate was slightly higher than the obtained previously in this area (81% vs. 72%; see Oro & Ruiz 1997). The higher efficiency observed outside the breeding season, combined with the lower energetic requirements of seabirds (e.g. Rickleffs 1983), suggests that a considerably higher number of seabirds could be sustained at this time of year.

Fig. 3. Seabird species' foraging success indexes (*SI*) at capturing fish during discard experiments. The figure shows the median (columns), non-outlier range (whiskers), and outliers and extremes (asterisks). Seabird species are: Balearic shearwater (BSh), Cory's shearwater (CSh), Northern gannet (NG), Mediterranean gull (MG), black-headed gull (LR), Audouin's gull (AG), yellow-legged gull (YIG), lesser black-backed gull (LBbG), black-legged kittiwake (BIK), Sandwich tern (ST), and common tern (CT).



Interspecific differences in foraging efficiency. When considering different seabird species, Audouin's gull was the most efficient at capturing discards (i.e. presented the highest *SI*), followed by the yellow-legged gull, while shearwaters showed the lowest efficiencies; however, there was strong variation between experiments (Fig. 3; Table 5). When considering different periods and areas, there were some intraspecific differences in foraging efficiency, probably related with differences in the relative abundance of seabird

species (see Table 5). This was the case of shearwaters, which were relatively more efficient in those periods (breeding season) and areas (Ebro Delta) where they were present in larger numbers. However, this trend was not clear for all seabirds, and some species were little affected by either their relative or absolute numbers; Audouin's gull, for instance, showed the highest *SI* in all situations, despite strong variation in both its relative and absolute numbers (cf. Arcos et al. 2001).

Table 5. Foraging success index of seabirds according to the season and the study area. (*n*, number of experiments performed; only those experiments with at least 30 items offered were considered here)

| | | Barcelona | | | Ebro Delta | |
|--------------------------|----------------|-----------------|---------|----------|-----------------|----------|
| | Breed. | Post-breed. | Winter | Breed. | Post-breed. | Winter |
| | (<i>n</i> =6) | (<i>n</i> = 2) | (n = 9) | (n = 23) | (<i>n</i> = 4) | (n = 10) |
| Balearic shearwater | -0.93 | - | -1.00 | -0.74 | -0.72 | -0.89 |
| Cory's shearwater | -0.88 | -0.36 | - | -0.88 | -0.45 | - |
| Northern gannet | 0.08 | - | -0.66 | -0.16 | - | -0.53 |
| Mediterranean gull | -0.52 | 0.75 | -0.41 | -1.00 | - | -0.31 |
| Black-headed gull | - | 0.15 | 0.08 | -0.48 | -0.30 | -0.27 |
| Audouin's gull | 0.66 | - | - | 0.06 | 0.34 | 0.18 |
| Yellow-legged gull | 0.03 | -0.05 | 0.00 | -0.25 | 0.01 | 0.00 |
| Lesser black-backed gull | -0.29 | 0.12 | -0.04 | -0.52 | -0.36 | -0.11 |
| Black-legged kittiwake | - | - | 0.13 | - | - | -0.33 |
| Sandwich tern | - | - | -0.20 | -0.59 | -0.55 | - |
| Common tern | - | -1.00 | - | -0.23 | -0.50 | - |

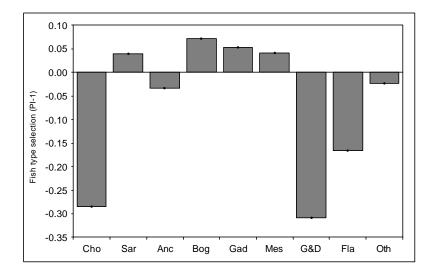
Significance of kleptoparasitism. Kleptoparasitic interactions frequently occurred between seabirds attending trawlers, with a mean rate of 13.4% (range 0-37.5%). This rate statistically differed when considering the area (higher rate in Barcelona) and the season (higher rate out of the breeding season; Kruskal-Wallis test, $H_{3.54} = 10.2$, p = 0.17). Only vellow-legged gulls and lesser black-backed gulls benefited from kleptoparasitism (positive robbery index, RI), while this behaviour was detrimental for most species (Table 6). Differences in the intensity of kleptoparasitism between areas and periods seem to be ultimately related to the abundance of the latter two species, which were more numerous in Barcelona than in the Ebro Delta, and increased in number out of the breeding season everywhere. This is interesting to note that species efficient as kleptoparasites were not the most efficient at capturing discards, acting as opportunists rather than as specialists. The lesser black-backed gull is often regarded as a seabird species specialised in the capture of fish at sea, with comparable fishing abilities to those of Audouin's gull (e.g. Noordhuis & Spaans 1992, Camphuysen 1995, Camphuysen pers. com.). However, this is clear that Audouin's gull behaved in a more specialised way here, being more efficient at capturing discards though usually avoiding kleptoparasitism (cf. Arcos et al. 2001). The comparison between the two species could be more appropriate in the case of the nominate form Larus

fuscus fuscus, not recorded in the study area, which seems to present higher flying abilities (Strann & Vader 1992).

Table 6. Percentage of attacks performed and received by different seabird species in relation with the number of attempts directed to capture fish. The proportion of successful chases (from the point of view of the kleptoparasite) is also shown (success rate, SR), as well as the robbery index (RI). The latter was only computed for species being involved in at least 20 kleptoparasitic events

| | | Attacks perform | ned | Attacks receive | ed | |
|--------------------------|----------|-----------------|--------|-----------------|--------|-------|
| Species | Attempts | Incidence (%) | SR (%) | Incidence (%) | SR (%) | RI |
| Balearic shearwater | 46 | 0 | - | 6.5 | 33.0 | - |
| Cory's shearwater | 154 | 9.7 | 26.7 | 31.2 | 47.9 | -0.76 |
| Northern gannet | 28 | 0 | - | 0 | - | - |
| Mediterranean gull | 645 | 4.5 | 13.8 | 11.5 | 20.3 | -0.57 |
| Black-headed gull | 233 | 10.3 | 16.7 | 21.5 | 32.0 | -0.60 |
| Audouin's gull | 891 | 2.0 | 27.8 | 7.5 | 34.3 | -0.66 |
| Yellow-legged gull | 1876 | 21.0 | 22.1 | 14.1 | 18.2 | 0.26 |
| Lesser black-backed gull | 145 | 17.2 | 32.0 | 9.0 | 46.2 | 0.12 |
| Kittiwake | 16 | 6.3 | 6.7 | 12.5 | 0 | - |
| Sandwich tern | 11 | 9.1 | 0 | 9.1 | 0 | - |
| Common tern | 106 | 0.9 | 0 | 16.0 | 23.5 | - |

Fig. 4. Fish type selection (PI_i) by seabirds (considered altogether). Fish groups are: chondrychthies (Cho), sardine (Sar), anchovy (Anc), bogue (bog), gadiforms (Gad), mesopelagic fish (Mes), gobies & dragonets (G&D), flatfish (Fla), and 'others' (Oth)



Fish type selection. Seabirds showed clear differences in their preference for different fish type groups ($c_8^2 = 24.7$, p = 0.002): sardine, bogue, gadiforms, and

mesopelagic fish were preferentially captured by most seabirds, while anchovy, chondrychthies, gobids and dragonets, and flatfish were usually selected negatively (Fig. 4). This was true for seabirds considered altogether, but some species showed a slight departure from this pattern (Table 7). With more detail, the previously described pattern reflect quite well the preference of surface feeding seabirds, since fish type groups selected positively were those that often floated for a while before sinking. Moreover, fish remaining in the surface for long time, as was especially the case for bogues and some gadiforms, could be captured some time after being discarded, their consumption being thus underestimated in discard experiments. On the other hand, species with diving abilities such as Cory's shearwater and, especially, the Balearic shearwater, showed a higher preference for fish type groups that tend to sink quickly, as is the case for the anchovy. In this case, the efficiency of these species could be underestimated if discard items assumed to be sunk were eventually captured underwater.

Table 7. Fish type selection (PI_{ij}) by different seabird species. Fish groups are: chondrychthies (Cho), sardine (Sar), anchovy (Anc), bogue (bog), gadiforms (Gad), mesopelagic fish (Mes), gobies & dragonets (G&D), flatfish (Fla), and 'others' (Oth). (*n*, number of fish picked up by each seabird species)

| | n | Cho | Sar | Anc | Bog | Gad | Mes | G&D | Fla | Oth |
|----------------------|------|------|------|------|------|------|------|------|------|------|
| Balearic shearwater | 39 | 0.00 | 1.48 | 2.31 | 0.13 | 1.54 | 0.00 | 0.64 | 1.36 | 0.56 |
| Cory's shearwater | 114 | 0.00 | 1.37 | 1.07 | 0.58 | 1.00 | 1.06 | 0.00 | 0.80 | 0.94 |
| Mediterranean gull | 567 | 0.32 | 1.00 | 0.96 | 1.13 | 1.42 | 1.11 | 0.74 | 0.42 | 0.82 |
| Black-headed gull | 173 | 0.00 | 1.13 | 0.89 | 0.94 | 1.42 | - | 0.42 | 1.10 | 0.92 |
| Audouin's gull | 826 | 0.00 | 1.06 | 0.99 | 1.18 | 1.02 | 0.68 | 0.74 | 0.88 | 0.95 |
| Yellow-legged gull | 1648 | 0.88 | 1.03 | 0.91 | 1.09 | 0.95 | 0.98 | 0.50 | 0.80 | 1.04 |
| Lesser black-b. gull | 118 | 1.75 | 0.97 | 0.50 | 1.17 | 0.95 | 1.27 | 0.95 | 0.68 | 1.00 |
| Common tern | 53 | - | 0.96 | 0.90 | 0.00 | 1.90 | 0.00 | 2.97 | 1.43 | 0.82 |

Fish size selection. All seabird species showed significant differences in the selection of different fish size (i.e. length) categories, even when applying the Bonferroni correction (chi-square contingency table, p < 0.05 in all cases). Size preferences are shown in Fig. 5 as a percentage, considering five size categories (which were determined according to their relative abundance in discards, see above). As a rule, the smallest seabird species showed preference for small fish, as would be expected from their size (e.g. Forbes et al. 1989), and also because small fish were less often kleptoparasitised (Hudson & Furness 1988, Arcos et al. 2001). On turn, the largest seabird species (yellow-legged and lesser black-backed gulls) selected preferentially the largest fish items. Nevertheless, most fish was of suitable size to be swallowed by any seabird species, rarely exceeding 200 mm in length (see above). Fish larger than this size and captured by small seabird species most often corresponded to snake-like fish, which would be more easily swallowed than either roundfish or flatfish.

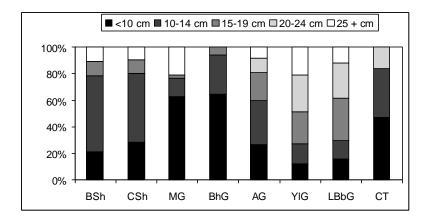


Fig. 5. Seabird's preferences (%) for different fish size categories, according to the seabird species

Utilisation of discards by seabirds: bioenergetic considerations

Seabird community approach. According to our model, seabirds obtain 7.87 x 10^9 kJ from discards during the breeding season off the Ebro Delta (ED), a value slightly higher that the 8.28 x 10^9 kJ required by the local breeding community (*ER*). Thus, assuming that all seabirds consuming discards were local breeders, in average they would obtain the 91.1% of their energetic requirements from discards (SD), although this estimate is subject to strong variability (95% CI: 9.7-172.6%). Moreover, since the breeding period for any particular species does not last more than 3-4 months (though the period for the whole community is of five months or longer), the energetic requirements of the community are probably lower than those estimated, and could be met exclusively by discards. Indeed, if we consider four months in the model, the energetic requirements descend to $6.30 \times 10^9 \text{ kJ}$, and the breeding community would obtain 114% of its energetic requirements from discards. Obviously, this is an overestimation, since seabirds consuming discards off the Ebro Delta during the breeding season are not only breeders at the Delta colonies. On the contrary, these birds share the resource with breeders from other colonies (mostly procellariforms from the Balearics, as well as Audouin's and yellow-legged gulls from Columbretes), non-breeding birds (especially immature yellow-legged gulls; see below), and migrating species. Therefore, discards could support the whole breeding seabird community at the Ebro Delta in the hypothetical case that any other birds were present, which is not the case. Nevertheless, this resource seems highly important for the community.

Oro and Ruiz (1997) made a similar approach to the above exposed, although they estimated that discards available could support twice the breeding community at the Ebro Delta. This seems a somewhat optimistic value, which almost double our present estimate, though Oro (1999) suggested that this overabundance of discards was decreasing and approaching to 100%. Differences between the two studies could result from different assumptions regarding the models, as well as differences in the estimated parameters. Concerning this last point, the present model is supported by a larger sample size and considers a wider spectrum of situations, probably presenting a better view of the actual

state. One important point differing between models is the consideration in the present of the percentage of discards actually suitable for seabirds (consumable fraction, *CF*), which reduces considerably the actual availability of discards to seabirds.

Table 8. General input parameters used in the model to estimate the importance of discards for the breeding seabird community at the Ebro Delta. The model is restricted to the breeding season (March-July), and all data was estimated for this period at the Ebro Delta. (n, sample size; CV, coefficient of variation)

| | Mean | п | Transformation | CV (%) |
|---|-------------------------------|----|----------------|--------|
| Commercial catches (CC, kg) | 838742 | 14 | Square root | 8.4 |
| Discards ratio (DR, %) | 56.09 | 19 | Square root | 19.3 |
| Consumable fraction (CF, %) | 66.64 | 14 | Arcsine | 34.3 |
| Consumption rate (CR_W , % in weight) | 86.44 | 9 | Arcsine | 12.1 |
| Calorific value (CAL, kJ g-1 fw) | 7.06 | 80 | Square root | 4.1 |
| Assimilation efficiency (AE, %) | 75 | - | - | - |
| Energy obtained from discards (ED, kJ) | 7.18 x 10 ⁹ | | | |
| Body mass (W, g) | 618.0 | 5 | - | 12.0 |
| Field metabolic rate (<i>FMR</i> , kJ d ⁻¹ bird ⁻¹) | 1297.2 | 14 | - | 12.3 |
| Number of breeding seabirds (N) | 42530 | - | - | - |
| Energetic requirements (ER, kJ) | 8.28 x 10 ⁹ | | | |

Species approach. We also made a second approach to estimate the actual importance of discards for each seabird species breeding at the Ebro Delta, directly estimating the proportion of discards consumed by adult (presumably breeding) birds of each species (see Table 9). This approach is subject to higher variability, since specific consumption rates (CR_{Wi}) varied considerably between experiments. However, the general picture obtained seems more realistic, and is in agreement with previous studies conducted in this area (cf. Oro 1999, and references therein). Indeed, discards availability is considered to most influence the breeding performance (Oro et al. 1996a,b), activity budgets (Oro 1995, Castilla & Pérez 1995), and diet (Ruiz et al. 1996, Oro et al. 1997) of Audouin's gulls breeding at the Ebro Delta and Columbretes colonies, and this species showed to make use of discards in a high proportion (76.7% of their energetic requirements obtained from this resource). Yellow-legged gulls at the Ebro Delta colony are also known to exploit discards extensively (Oro et al. 1995), which was confirmed by our results (significance of discards, SD = 57.7%). Lesser black-backed gulls showed less interest for discards (SD = 18.4%), despite this resource being of importance for this species according to Oro (1996). However, the local breeding population of lesser black-backed gulls is very small, and the proportion of discards consumed by this species could have been easily underestimated. Common terns showed a lower use of discards than the large gulls, obtaining 19.0% of their energetic requirements from this resource, while Sandwich terns almost ignored discards (SD = 1.4%). Results for terns agree with those of Oro (1999), who reported 23% and 4% of discard items in the diet of breeding common and Sandwich terns, respectively. Considering all species together, we estimated that the breeding seabird

community at the Ebro Delta would actually obtain 3.90 x 10^9 kJ from discards, which represents the more realistic *SD* value of 65.4%.

Table 9. Specific input parameters in the model directed to estimate to which extent different seabird species breeding at the Ebro Delta make use of discards: specific consumption rate (CR_{Wj} , % in weight), percentage of discards captured by adults (%Ads_{*i*}), body mass (W_j , g), field metabolic rate (FMR_j , kJ d⁻¹ bird⁻¹), and number of breeding individuals (N_j). The breeding period for each seabird species is also provided. Parameters not differing from those used in the general model for the whole breeding community are not shown here (see Table 5). The significance of discards for each species (SD_j) is also shown, and results of dividing the energy obtained from discards by each species (ED_j) by the energetic requirements of the breeding population (ER_j). (*n*, sample size; CV, coefficient of variation; CI, 95% confidence interval)

| | CR_W (% | %) | | _ | $W^{*}(g)$ | | | | | ED/ER | (%) |
|----------------------|-----------|----|-------|------|------------|-------|------|--------|----------|-------|-----------|
| Period | Mean | n | CV | %Ads | Mean | n | CV | FMR | N^{**} | Mean | CI |
| Audouin's gull Ap-Jl | 44.53 | 8 | 35.4 | 91.9 | 604.3 | 264.0 | 13.0 | 1274.9 | 23176 | 76.67 | 0 - 168.8 |
| Yellow-l. gull Mr-Jn | 23.90 | 7 | 49.6 | 71.0 | 1049.0 | 127.0 | 13.8 | 1953.8 | 8332 | 57.68 | 0 - 133.0 |
| Lesser b-b. g. My-Jl | 0.21 | 6 | 161.4 | 76.9 | 875.0 | - | 13.0 | 1697.9 | 286 | 18.4 | 0 - 78.7 |
| Sandwich tern My-Jl | 0.11 | 6 | 155.9 | 100 | 207.5 | - | 8.0 | 557.4 | 3778 | 1.43 | 0 - 6.0 |
| Common tern My-Jl | 0.96 | 6 | 133.3 | 93.3 | 124.1 | 124.1 | 8.0 | 374.4 | 6958 | 18.95 | 0 - 71.0 |

 W_j was obtained either from direct measurements at the Ebro Delta colonies (Audouin's gull, yellow-legged gull, and common tern; D. Oro & A. Hernández, unpublished data) or from the bibliography (del Hoyo et al. 1996).

 N_i correspond to the 1997 census (PN Delta de l'Ebre)

Effect of trawling moratoria. The previous results highlight the importance of discards as a feeding resource for seabirds breeding at the Ebro delta. However, none of our approaches has considered the effect of trawling moratoria. These temporal closures of the trawler fishery take place during two months each year in spring (see Oro 1995), the exact period varying from year to year but always overlapping with some stage of the breeding performance of seabirds. In recent years there have been some differences in the period of closure between ports, resulting in a total absence of discards for only one month. In any case, trawling moratoria would reduce the above estimates, and probably affect the breeding biology of most species here considered, as reported by several previous studies (Oro 1999, and references therein).

Concluding remarks

The present study confirms the importance of trawler discards as a feeding resource for breeding larids in the NW Mediterranean, as shown by our bioenergetic model. In addition to seabirds breeding at the Ebro Delta, the large numbers of shearwaters attending vessels during the breeding season suggest that this resource is also important for this group of seabirds. Moreover, large numbers of seabirds outside the breeding period, as well as their high efficiency at capturing discards, suggest that the resource is important at any time of year. Special attention should be directed to two endemic and threatened Mediterranean seabirds, which seem particularly influenced by discards: Audouin's gull (Oro 1998) and the Balearic shearwater (Mayol et al. 2000). In addition to trawlers, other fisheries are likely to provide discards/feeding opportunities to seabirds, as is the case of several artisanal fleets (which would particularly affect coastal species such as terns), as well as of purse-seiners (cf. Arcos et al. 2000). This is necessary to address studies in order to ascertain the actual importance of these fisheries for seabirds. Moreover, this is important to predict how changes in fishing policies, resulting from an emerging ecosistem-based approach to fisheries management (e.g. FAO 1995, Gislason et al. 2000) would affect seabirds. Data provided here could help to predict some of these changes, for instance when affecting discards composition (cf. Fluharty 2000).

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Significance of nocturnal purse seine fisheries for seabirds: a case study off the Ebro Delta (NW Mediterranean)¹

Abstract. Seabirds are known to make extensive use of fishery waste, a phenomenon that has been particularly well studied in relation with demersal fisheries, especially when operating during daylight hours. Contrarily, very little is known about the importance of predominantly nocturnal fisheries in providing feeding opportunities to seabirds. We considered the particular case of purse seining for small pelagic fish, which takes place basically at night, and assessed the significance of this fishing practice for seabirds off the Ebro Delta (NW Mediterranean). Fieldwork was conducted on board commercial purse seiners (nocturnal activity) in 1997-1998, and was complemented with observations performed on board both commercial trawlers (diurnal activity; 1997-1998) and a research vessel (1999-2000). The purse seine fleet targets small Clupeoids, which are attracted and concentrated by the light of a powerful lamp, and then captured using an encircling net. Purse seiners showed to be quite unpredictable, since frequently changed of fishing area, presented very irregular catches, and were strongly influenced by the weather. This made the fishery little attractive to most seabird species, which basically attended purse seiners during the discarding process. This process took place during the way back to port with daylight and was quite irregular, thus attracting lower numbers of seabirds than did trawlers. The threatened Audouin's Gull Larus audouinii was the only species attending purse seiners regularly at night, capturing live fish concentrated at the sea surface during the hauling process. Although this species seems specialised in the capture of epipelagic fish at night, purse seiners strongly facilitate this feeding strategy. Indeed, the vessels would favour the direct capture of fish (illumination of the sea surface, concentration of the fish), as well as the location of the shoals (light signalling). The purse seining fishery was especially important for Audouin's gull during trawling moratoria (when trawling discards were not available) and out of the breeding season. A simple bioenergetic model estimated that individual Audouin's Gulls could obtain a mean of 669 kJ per haul, which would represent far more than a half of the daily energy requirements of breeding birds. Provided that Audouin's gulls feeding in a given area could attend more than one haul in a short time, birds attending purse seiners at night could easily meet their energy requirements. However, there was strong variability in our estimate (from 0 to 1659 kJ per haul and bird, 95% CI), and feeding at purse seiners could be not worth enough to Audouin's gulls in some occasions. Purse seine fisheries could be of importance for other nocturnal seabirds in other regions such as the SE Pacific, and this deserves further research. It is important to note that purse seiners could also be detrimental for many seabirds, through direct competition and eventual depletion of fish stocks.

¹Arcos JM & Oro D, submitted ms

Introduction

Seabirds interact in a variety of ways with human fisheries, as a consequence of exploiting the same or interconnected prey (e.g. Cairns 1992). These interactions can be either positive or negative for both seabirds and fisheries, depending on their nature (Duffy and Schneider 1994; Tasker et al. 2000). Among the interactions considered to be positive for seabirds, the consumption of fishery waste is the most widely studied, and seems to play an important role in

the feeding ecology of several seabird populations (e.g. Furness 1999; Oro 1999). This phenomenon has received special attention in relation with demersal fisheries (basically trawlers), which provide large amounts of discards and offal otherwise unavailable to the seabirds (e.g. Camphuysen et al. 1995). However, the role of other fisheries in providing feeding opportunities to seabirds has received less attention, as is the case for purse seiners (González-Solís et al. 1999). Furthermore, most studies on the consumption of fishery waste by seabirds have been performed under daylight conditions, with very few studies reporting on the association of seabirds with fishing vessels at night (e.g. Blaber & Wassenberg 1989; Garthe and Hüppop 1993, 1996), excluding those addressed to assess the incidental mortality of seabirds in long-line fisheries (e.g. Tasker et al. 2000). In spite of that, many seabirds have nocturnal activity in a varying degree (McNeil et al. 1993 and references therein), and several fisheries usually operate during the night. Hence, nocturnal fisheries could play an important role in the feeding ecology of some seabirds.

The present study was directed to assess the significance of pelagic purse seine fisheries (which usually target on small shoaling fish at night) for seabirds, considering the particular case of the Ebro Delta region (NW Mediterranean). In this area recent research work has shown the extensive use of trawling discards by many seabird species breeding nearby (Oro and Ruiz 1997; Arcos et al. 2001). Furthermore, the absence of discards caused by trawling moratoria strongly affected several biological parameters of species such as Audouin's Larus audouinii, the yellowlegged Larus cachinnans, and the lesser black-backed gulls Larus fuscus, which demonstrates the importance of this extra food supply (see Oro 1999 and references therein). Contrarily, the purse seine fleet seems to play a minor role on the feeding ecology of seabirds breeding in the Ebro Delta, although the existing evidence is limited to indirect studies of daily activity and diet of breeding Audouin's gulls (Oro 1995 and Oro et al. 1997, respectively). These studies suggest that Audouin's gull take profit from purse seiners to a limited extent, and that this could be especially important during trawling moratoria. Indeed, Oro (1995) found a higher proportion of birds leaving their colony at sunset when trawlers did not operate, and this difference was slightly higher when purse-seiners operated at night (vs. any fishing activity in the area). Similarly, the proportion of Clupeoids in the diet of Audouin's gull was highest when purse seiners operated coinciding with trawling moratoria (73%), and this proportion decreased when any fishery was operating (47%), thus suggesting that purse seiners facilitated the capture of Clupeoids to this species (Oro et al. 1997). Nevertheless, there is no direct evidence of seabirds associating with purse seiners, either off the Ebro Delta or in other regions. Purse seiners are known to provide little amounts of discards (e.g. Oro 1995), and it is not clear how seabirds take profit from these vessels. Here, we addressed this topic through fieldwork conducted on board a commercial purse seiner. The main goals of the study were:

- (1) To describe some features of the purse seine fishery relevant to understand its significance for seabirds, given the lack of information on this subject.
- (2) To ascertain how seabirds take advantage of purse seiners, as well as what seabird species are involved in our study area.
- (3) To assess the effect of some factors considered to potentially influence the association of seabirds with purse seiners, such as the fishing regime (trawling activity vs. trawling moratoria) and the season (breeding vs. non-breeding).
- (4) To assess the potential benefit that some seabirds obtain from purse seiners, through simple bioenergetic estimations.

Complementary observations were performed on board commercial trawlers to compare the numbers of seabirds attracted by each fishery. Moreover, observations on the behaviour and

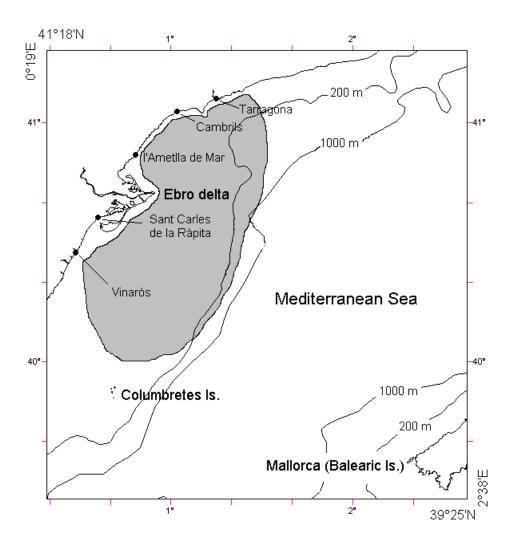
efficiency of seabirds feeding at night in association with non-fishing vessels were used to make comparisons with those observed at purse seiners.

Materials and methods

Study area and commercial fisheries

The study was carried out at sea off the Ebro Delta (NW Mediterranean), between 39° 55'N and 41° 05'N latitude, and 0° 35'E and 1° 30'E longitude (Fig. 1). The continental shelf off the Delta is broad, extending up to 70 km offshore. This area is highly productive as a result of the Ebro River runoff and the influence of a shelf-slope front (e.g. Salat 1996). Given these features, the Ebro Delta region is considered one of the most important spawning areas for Clupeoids in the western Mediterranean (Palomera 1992). It is therefore no coincidence that the area supports one of the most important seabird communities of the Mediterranean (e.g. Oro 1999), as well as very important fisheries within the context of this sea (Irzaola et al. 1996).

Figure 1. Map of the study area (in grey), showing the most important fishing ports and geographical references. The isobaths of 200 and 1000 m are also shown.



Two semi-industrial fishing fleets are of special importance in the study area: bottom trawlers and purse seiners (Irzaola et al. 1996; Pertierra and Lleonart 1996). The closest fishing ports to the area considered for study (Tarragona to Vinaròs; see Fig. 1) account for ca. 215 trawlers and 40 purse seiners. However, purse seiners are allowed to operate at long distances from their ports of base, thus varying in number within the study area (from a few vessels when most of the local fleet is away from their ports of base, to up to 100 or more vessels when foreign vessels are present, the latter situation being more frequent). The trawler fleet captures a wide variety of demersal and benthic fish and generates important amounts of discards; contrarily, the purse seine fleet is much more selective, targeting on Clupeoids and generating few discards (Pertierra and Lleonart 1996). Both fleets operate five days per week, with restricted timetables: trawlers by day and purse seiners by night (see Oro, 1995). In addition, fishing moratoria are established for trawlers (in spring) and purse seiners (in winter) during two months each year.

Methods

Fieldwork was conducted along 29 one-day cruises on board a commercial purse seiner from l'Ametlla de Mar (see Fig. 1), from May 1997 to December 1998. We also considered data from 29 one-day cruises on board bottom trawlers, carried out during the same period and area (ports of l'Ametlla de Mar, Sant Carles de la Ràpita and Vinaròs; Fig. 1), to make comparisons with the results obtained at purse seiners. Finally, we performed observations of seabirds feeding at night attracted by the lights of a non-fishing vessel (R/V 'Cornide de Saavedra''), in spring 1999 and 2000.

During our cruises on board the purse seiner, we collected information concerning the fishing process and estimated the amount of fish discarded by counting the number of boxes of known average weight that were thrown overboard. In addition, fishermen allowed us to consult the vessel's notebook for the years 1997 and 1998, where we found valuable information concerning our vessel (captures, days of activity, etc.). This information was considered useful since it can reflect the performance of the whole fleet, especially considering that environmental factors (weather, availability of fish) usually influence all vessels in the same way.

Data were treated regarding three different situations, with respect to the fishing regime (trawlers operating vs. trawling moratorium periods) and the season (breeding vs. non-breeding): (1) breeding season (March-July), trawlers operating; (2) breeding season, trawling moratorium; (3) non-breeding season, trawlers operating. Trawling moratoria affecting all ports within the study area at the same time took place from 15th May to 30th June 1997 and from 1st June to 15th July 1998. Comparisons were usually performed between any two of the above situations: trawling moratoria vs. trawlers operating (only considering the breeding season, when both situations took place) and breeding vs. non-breeding season (excluding trawling moratorium periods, since these only occurred in the breeding season).

Seabirds were counted, and identified to the species level, at 15-min intervals during the fishing process of the purse seiner. These counts were classified with respect to different activities of the vessel: (1) attraction of the fish to the sea surface; (2) encircling of the fish; (3) hauling of the seine; (4) discarding activity (separated from the haul, usually in the way back to port after sunrise). The maximum number of birds was recorded for each haul according to these activities, in order to make comparisons of the different use of purse seiners by the different seabird species. At trawlers, censuses were also conducted at 15-min intervals, but only maximum numbers of birds per haul are presented here.

Factors thought to potentially influence the attendance of seabirds to purse seiners were considered for each haul: minimum distance to the coast and to the colony (Punta de la Banya, in the Ebro Delta); catches (kg); number of purse seiners in the same fishing aggregation; and lunar

phase (moonlight, including the three nights before and after the night of moonlight, vs. other phases).

The efficiency of seabirds at capturing fish was assessed during the operation of hauling, when they picked up fish directly from the sea surface. Only Audouin's gull was considered here, since this was the only species regularly attending purse seiners at night. In order to do that, we recorded on tape the number of attempts to capture fish performed by Audouin's gulls at controlled intervals of time, relative to the number of individuals present at the vessel (attempts rate, AR, expressed as attempts per bird and minute). We also assessed the rate of success of these attempts (SR, percentage of successful vs. total attempts), thus obtaining the number of fish captured per individual and minute. Then we estimated the total time that the gulls spent picking up fish from the sea surface (T, in minutes), and obtained the mean number of fish captured per seabird at each haul. A similar procedure was employed to assess the efficiency of Audouin's gulls capturing fish when attracted by the light of the research vessel, when no fishing activity was conducted. For purse seiners, we tried to estimate this efficiency in terms of energy, through building a simple model. We first estimated the mean representation of sardine and anchovy within the captures landed (PS and PA, other prey were disregarded due to their scarcity), assuming that the fish landed by the vessels was representative of the fish available to (and captured by) the seabirds. These percentages were obtained in biomass, but were considered to be similar to those in number since anchovy and sardine presented very similar mean weights (see results). After that, we estimated the mean weight of each of these fish species (WS and WA), through analysing sub-samples of the captures landed by the vessel (n = 10 sub-samples)involving 614 fish). We then transformed these data into an energetic value (ES and EA, in kJ g ¹), considering data from lipid extractions conducted at the laboratory (J.M. Arcos, D. Oro and X. Ruiz, unpublished data) and following Peters (1983). Five samples were analysed for each fish species, each sample being the result of pooling and homogenising five fish of similar size. Considering an assimilation efficiency (AE) of 75% (Furness et al. 1988), the energy obtained by each gull when attending a haul (*EH*, in kJ bird⁻¹ haul⁻¹) was then calculated as:

 $EH = T \times AR \times SR \times ((PS \times WS \times ES) + (PA \times WA \times EA)) \times AE$

Given the variability of the parameters involved, we estimated a coefficient of variation (CV) of *EH* as a precision measure, using the Delta method (Stratoudakis 1999):

$$CV^{2}(EH) = CV^{2}(T) + CV^{2}(AR) + CV^{2}(SR) + CV^{2}(P) + CV^{2}(W) + CV^{2}(E)$$

Statistical analysis

Data were first tested for normality, using the Shapiro-Wilk test. When this assumption was violated, we either made the appropriate transformations (input data in the model) or used non-parametric statistics, following Zar (1996). Wilcoxon matched-pairs test (two samples) and Friedman two-way analysis of variance (three or more samples) were used to compare the numbers of seabirds associated to the vessel in different stages of the fishing process, given the interdependence of data. The effect of the different factors considered to potentially influence the attendance of seabirds to the vessel was assessed using either the Mann-Whitnney U-test or the Spearman's rank correlation. The Bonferroni correction (Rice, 1989) was considered when assessing the effect of these factors. Nevertheless, results were discussed without the restriction imposed by this correction, given that: (1) sample size was relatively small; and (2) we employed the more restrictive two-tailed test in all cases, although for several factors we expected defined

tendencies and the one-tailed test could have been employed. Other conventional tests were used when appropriate, following Zar (1996).

The significance level was held at 0.05, although marginal values were also discussed (see Stoehr, 1999). Although consecutive censuses of seabirds following fishing vessels may not accomplish independence of data, pseudoreplication was partially avoided by considering only one census (maximum number of seabirds) per haul and activity. Moreover, the vessel rarely performed more than one haul per night, and never more than two hauls when we were on board.

Results

Description of the purse seine fishery

Purse seiners targeted small shoaling fish, basically Clupeoids, which were captured at night. The fishery operated throughout the whole continental shelf, except for depths lower than 30 m and distances of less than 300 m from the coast due to regulatory restrictions. The vessels tended to concentrate in areas where fishable aggregations occurred, with concentrations well over 50 vessels often being observed. Fish were detected at first by means of acoustical methods (eco-sounder), although the concentration behaviour of the vessels also facilitated the detection of fishable shoals. The process of capture involved the main vessel and a small boat provided with a powerful lamp. Shoals were first attracted to the sea surface and concentrated around the boat by the light of the lamp. After that, the main vessel lowered the purse seine, encircling the fish gathered around the boat. The seine was then hauled, the whole process of capture lasting a median of 50 minutes (range 40-60 minutes, n = 23 hauls). In most cases the vessel only performed one haul per night, this value ranging from 0 to 3 (mean = 0.81, n = 340 cruises). Since the process of locating, attracting, and capturing fish took some time, most often hauls were performed short before dawn. The main prey of the purse seine fishery were the sardine Sardina pilchardus (88.4% of the total catches by biomass, n = 340 fishing days) and the anchovy Engraulis encrasicholus (10.8%). When the catches were completed, the vessel returned to port, usually at dawn (i.e. with a variable extent of daylight). At this stage, usually few discards (basically fish damaged during the hauling of the net) were thrown overboard (median = 15 kg, interquartilic range 5-25 kg, n = 19 operations). However, in a few occasions (15.8% of the observed cases, n = 19) the vessel discarded high amounts of fish, up to an estimated of 5600 kg in a single trip. This was due to the capture of shoals of gilt sardine Sardinella aurita, a species with low economic value that was usually rejected.

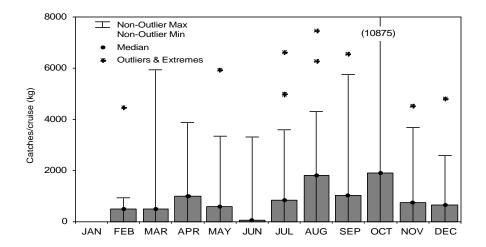
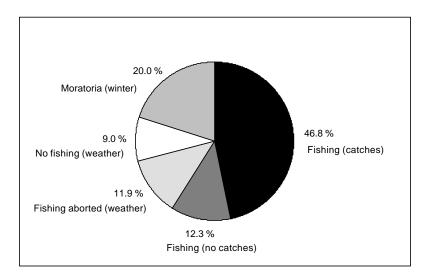


Figure 2. Daily catches (median and range) by a single purse seiner off the Ebro Delta, in 1997 and 1998, separated by months. Only those days when the vessel operated were considered (n = 340)

A purse seining moratorium was established during two months each year in mid winter (usually from mid-December to mid-February), coinciding with the recruitment period for the anchovy. The rest of the year catches of the purse seiner were found to be quite irregular (Fig. 2), and especially subject to weather conditions (Fig. 3). Indeed, the weather strongly influenced the capture of fish, since windy and rough-sea conditions made the process of encircling and hauling of the net difficult, if possible. Furthermore, fish probably stayed at greater depths during these conditions, making even more difficult their capture. Sometimes the cruise was aborted after a few hours of sailing due to bad weather, and in some cases the vessel remained at port the whole night (Fig. 3). Under good weather conditions the vessels also returned without fish in some occasions (12%), probably due to several reasons (fish not concentrated enough, or not attracted by the lamp; capture of shoals of non-commercial species, such as gilt sardine; breakdown of either the vessel or the seine; etc). Most often the whole fleet behaved in the same way, especially when it was affected by environmental factors (especially by the weather).

Figure 3. Percentage of weekdays when the studied purse seiner: (1) operated with normality and landed some fish; (2) operated with normality and returned without fish; (3) operated but aborted the cruise due to bad weather; (4) did not operate due to bad weather; and (5) did not operate due to a purse seine moratorium (mid-winter) during the study (information from 1997 and 1998; n = 479 weekdays)



Association between seabirds and purse seiners

Seabirds took advantage from purse seine vessels in two different ways: (1) direct capture of live fish concentrated near the surface by the light of the lamp and the encircling seine, during the night; and (2) capture of discards, with daylight. The first strategy was only important for Audouin's gull, which was present in the 91.3% of the hauls (n = 23) and accounted for the 86.2% of the seabirds observed during this process. Contrarily, several species of seabirds regularly attended purse seiners during the discarding process, although in lower numbers than those observed at trawlers (Fig. 4).

The number of Audouin's gulls significantly varied in accordance with the activity of the vessel (Friedman test, $\chi^2_r = 33.2$, P < 0.0001; Fig. 5). The first gulls appeared when the lamp was turned on, thus starting to attract fish towards the sea surface. At this stage, that sometimes lasted more than two hours, prey density (usually juvenile fish and adults of a few pelagic species,

mainly garpike, Belonidae) was usually very low near the surface, and Audouin's gulls only performed occasional captures (picking up fish by both surface seizing and surface plunging). In accordance with that, very few individuals attended the vessel during this period. The number of Audouin's gulls increased when the vessel started to encircle the boat with the purse seine, reaching their maximum during the operation of hauling. Only then, when the circle was completely closed and the fish was concentrated at high density close to the sea surface, Audouin's gulls started to pick up fish actively. This situation was observed in most but not in all hauls (82.6 % of the cases, n = 23), and lasted a median of 15 minutes (range 5-25 minutes) when it occurred. During the discarding process, usually separated in time from the last haul, the median number of Audouin's gulls was similar to that observed during the hauling of the net (Wilcoxon matched-pairs test, $T_{19} = 72$, P = 0.56).

Figure 4. Numbers (median and interquartilic range) of the most common seabirds associated to fishing vessels: (1) purse seiners, hauling (nocturnal); (2) purse seiners, discarding (daylight); and (3) trawlers, discarding (daylight). Results are presented separately for the breeding (4a) and the non-breeding seasons (4b). The species considered are the Balearic shearwater (BSh), Cory's shearwater (CSh), Audouin's gull (AG), the yellow-legged gull (YIG), the black-headed gull *Larus ridibundus* (BhG), the Mediterranean gull *Larus melanocephalus* (MG), the lesser Black-backed gull (LBbG), and the common tern (CT)

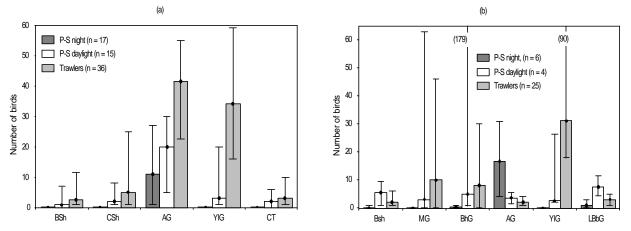
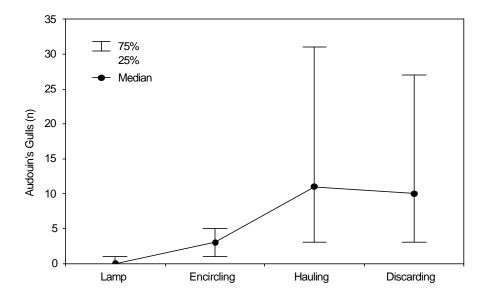


Figure 5. Numbers of Audouin's gull (median and interquartilic range) in accordance with the activity of the purse seiner (n = 18 complete operations).



Factors influencing the attendance of seabirds to purse seiners

Of the factors considered to potentially influence the attendance of Audouin's gulls to purse seiners (Table 1), we found a significant effect of the following: (1) fishing regime (higher numbers of gulls during trawling moratoria; Fig. 6); (2) season (higher numbers out of the breeding season; Fig. 6); (3) number of vessels in the same area (more gulls as the number of vessels increase); and (4) distance to the coast (more gulls at longer distances). Neither the distance to the colony, the lunar phase, or the amount of fish captured appeared to influence the number of Audouin's gulls attending purse seiners during the hauling process. If we apply the Bonferroni correction only the effect of the trawling moratorium is marginally significant (P = 0.06). However, sample size was relatively low (n = 23 hauls), and the effect of the season, the distance to the coast and the number of vessels in the area is probably important in determining the attendance of Audouin's gulls to purse seiners at night.

Table 1. Effect of the factors considered to potentially influence the attendance of Audouin's gulls to purse seiners during the hauling process (*n* number of hauls, n.s. not significant)

| Factor | п | Statistic | Р | Effect |
|-------------------------------------|----|-------------------|-------|---|
| Trawling moratorium [*] | 17 | $U_{9,8} = 9.0$ | 0.009 | Higher numbers of Audouin's gull during trawling moratoria. |
| Season ^{**} | 15 | $U_{9,6} = 9.5$ | 0.039 | Higher numbers of Audouin's gull out of the breeding season. |
| Number of vessels | 23 | rs = 0.51 | 0.013 | Higher numbers of Audouin's gull at higher number of vessels. |
| Distance to the coast | 23 | rs = 0.51 | 0.013 | Higher numbers of Audouin's gull at longer distance from the coast. |
| Distance to the colony [*] | 17 | rs = 0.40 | 0.11 | n.s. |
| Catches | 23 | rs = 0.17 | 0.44 | n.s. |
| Lunar phase | | $U_{15,8} = 59.0$ | 0.94 | n.s. |

^{*} Only those censuses performed during the breeding season were considered

^{*} Only those censuses performed under comparable fishing regime (i.e. trawlers operating) were considered

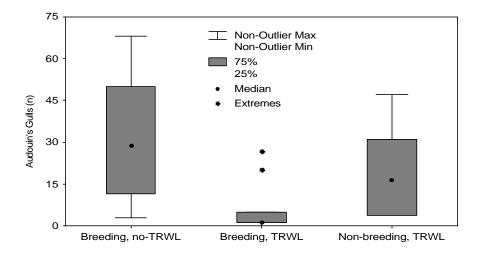


Figure 6. Numbers of Audouin's gull associated to the purse seiner during the hauling activity, with respect to the season and the fishing regime: (1) breeding season, Trawling moratorium (n =8); (2) breeding trawlers season, operating (n = 9); and (3) nontrawlers breeding season, operating (n = 6).

For the discarding period, we assessed the influence of the fishing regime (only considering the breeding period) on the number of the different seabird species attending the purse seiner. Audouin's gulls showed again to be influenced by trawling moratoria, being present in higher numbers at purse seiners when trawlers did not operate ($U_{8,7} = 4.0$, P = 0.005). The same tendency was true for Balearic Shearwaters *Puffinus mauretanicus* ($U_{8,7} = 10.5$, P = 0.04), while Cory's shearwaters *Calonectris diomedea*, yellow-legged gulls and common terns *Sterna hirundo* did not show any significant differences in accordance with the fishing regime.

Efficiency of Audouin's gull at capturing fish, and bioenergetic considerations

During the hauling of the seine, when most of the feeding activity of Audouin's gulls took place, we estimated that each gull captured a median of 0.18 fish per minute (Table 2). The type of fish captured at this stage did not apparently differ from that captured by the fishermen, which presented mean lengths of 141.6 ± 9.8 SE mm in the case of the sardine (n = 515), and 141.3 ± 11.9 SE mm in the case of the anchovy (n = 99) (see weights in Table 3). In terms of energy, from the parameters shown in Table 2, we estimated that any single bird could obtain from 0 to 1658.6 kJ at each haul (95% confidence interval), with a mean value of 669.2 kJ.

Table 2. Efficiency of individual Audouin's Gulls at capturing fish in association with purse seiners (hauling process) and with non-fishing vessels (illumination of the sea surface). The number of hauls or observations (n) and the total time spent observing the capture rate of the gulls (t, in minutes) are also shown

| | | | Attempts | rate (%) | Items min ⁻¹ bird ⁻¹ | | | |
|---------------------|----|------|----------|-----------|--|----------|--------|-----------|
| | n | t | Median | Range | Median | Range | Median | Range |
| Purse seiners | 19 | 86.8 | 0.38 | 0.06-1.69 | 66.7 | 31.3-100 | 0.18 | 0.03-1.60 |
| Non-fishing vessels | 3 | 19.4 | 0.17 | 0.04-1.33 | 62.5 | 0.0-63.0 | 0.10 | 0.00-0.84 |

Table 3. Specific input parameters used to estimate the energy obtained by individual Audouin's gulls at each haul of purse-seiners. (CV coefficient of variation, calculated from either absolute or transformed data; *n* number of cases)

| | | п | Mean | Transformation | CV (%) |
|---|-------------|-----|-------|----------------|--------|
| Time of activity, T (min) | | 23 | 12.07 | Logarithmic | 22.7 |
| Attempts rate, AR Attempts bird ⁻¹ min ⁻¹ | I | 18 | 49.1 | Square root | 22.5 |
| Success rate, SR (%) | | 17 | 71.8 | Arcsine | 35.1 |
| Percentage, $P(\%)$ | Sardine, PS | 232 | 92.7 | Arcsine | 37.0 |
| | Anxovy, PA | 232 | 7.3 | | |
| Weight, $W(g)$ | Sardine, WS | 515 | 21.59 | No | 23.4 |
| | Anxovy, WA | 99 | 18.67 | | |
| Energy, E (KJ g ⁻¹) | Sardine, ES | 5 | 10.03 | No | 22.9 |
| | Anxovy, EA | 5 | 6.67 | | |

The attendance of Audouin's gulls to non-fishing vessels, presumably attracted by their illumination of the sea surface, was similar to that observed when the boat of the purse seiner turned on the lamp. In these cases, Audouin's gulls were observed to pick up mainly juvenile fish (roughly averaged 3-5 cm long), and sometimes adults of garpike and other pelagic species. In

three occasions, during the spring, we observed relatively important numbers of Audouin's gulls, from 12 to 30 birds, when prey seemed to be in relatively high densities. In these situations Audouin's gulls approached the efficiency observed at purse seiners during the hauling process, with no significant differences when comparing the capture rate (items captured per bird and minute) in both situations ($U_{17.3} = 18.0$, P = 0.43; Table 2).

Discussion

Association between seabirds and purse seiners

The way in which seabirds made use of purse seiners strongly differed between species in the study area. Although more than ten seabird species are common off the Ebro Delta during the breeding season, and the same is true out of this period (e.g. Paterson 1997; Oro 1999), only Audouin's Gull showed regular attendance to purse seiners at night. This is in accordance with the specialisation of this gull in the capture of epipelagic and mesopelagic fish at night (see Oro 1998 and references therein), when these prey ascend to the sea surface following diel vertical migrations (Blaxter and Hunter 1982). Cory's shearwater, which also presents nocturnal foraging activity (Klomp and Furness 1992), was also observed regularly at night, although rarely attended purse seiners during the hauling process. The scarcity of other seabird species attending purse seiners at night could be partly explained by their more diurnal habits and their consequently lower adaptation to nocturnal foraging. However, typically diurnal seabirds have been reported to frequently attend trawlers looking for discards in other regions helped by the lights of these vessels (e.g. Blaber & Wassenberg 1989; Garthe & Hüppop 1993, 1996; although see García-Rodríguez 1972), thus suggesting that purse seiners present other disadvantages for most seabirds in addition to their timetable. Firstly, seabirds attending purse seiners at night mostly obtained fish by capturing them alive at the sea surface, which required some specialisation, and this probably prevented the generalised attendance to these vessels of opportunist species such as the yellow-legged gull (e.g. Oro et al. 1995). Secondly, the purse seine fleet was quite mobile compared to the trawler fleet, thus making difficult its location to the seabirds. Moreover, seabirds with restricted foraging ranges would have problems to attend purse seiners when the fleet operated far away from the colony. Thirdly, fish captured by purse seiners (assumed to be the same available to the seabirds) did not present strong variation in size (as is the case for trawler discards), and could be too large to be suitable for small seabird species (cf. Oro and Ruiz 1997). Finally, purse seiners were strongly influenced by environmental conditions (mostly the weather) and catches were consequently very irregular (null catches often occurring), the resource thus being little predictable for seabirds.

During the discarding process, conducted with daylight during the way back to port, the number and diversity of seabirds attending purse seiners increased substantially. However, censuses at this stage showed lower numbers of birds than those performed at trawlers also during the discarding activity. This was probably due to the unpredictability of the fishery, which was also reflected by the irregular (and most frequently small) amounts of fish discarded. Off the Chafarinas Islands (western Mediterranean) purse seiners appear to be more predictable than trawlers, and the feeding ecology of the larids breeding in the archipelago (Audouin's gull and the yellow-legged gull) seems more influenced by the former (González-Solís et al. 1997, 1999). However, direct observations on board purse seiners are lacking, and it is not clear if the birds obtain their prey in the form of discards or directly capture them at the sea surface during the hauling process of these vessels.

Audouin's Gull could find several advantages of attending purse seiners, despite the relative unpredictability of the fishery for most seabirds. Firstly, the aggregation behaviour of the vessels and the use of powerful lamps would signal important concentrations of fish to the gulls. Secondly, the illumination of the sea surface seems to facilitate the detection of fish. Thirdly, the high concentration of fish near the surface, due to the combined effect of light attraction and net encircling, would facilitate the capture of fish to the gulls. Finally, the concentration of several vessels in the same area, usually hauling at different times, could also provide favourable feeding opportunities during considerable periods to the seabirds, which would move from one vessel to another. The relatively large foraging range of Audouin's gull (Arcos and Oro 1996, Oro 1998) would facilitate the attendance to purse-seiners at long distances from the colony, thus reducing the problem of the high mobility of the fleet.

Factors influencing the attendance of seabirds to purse seiners

The number of Audouin's gulls attending purse seiners varied between nights. Among the factors considered to potentially influence this attendance, the fishing regime was found to be the most important. Indeed, during the breeding season the largest concentrations of Audouin's gulls at purse seiners occurred during trawling moratoria, whereas few birds turned up at these vessels when trawlers operated in the area. The same was true for the discarding process of purse seiners. This result suggests that most Audouin's gulls attended purse seiners as a buffering strategy in order to meet their energy requirements, especially when the most frequently used feeding resource (i.e. trawler discards) was not available in the study area (cf. Oro 1995; Oro et al. 1997; Arcos et al. 2001). The Balearic Shearwater could be in the same situation, since this species only occurred in important numbers at purse seiners (discarding process) when trawlers did not operate. This suggests that the feeding ecology of this rare shearwater could be more influenced by discards than previously considered (Mayol et al. 2000).

Audouin's gulls also associated with purse seiners in higher numbers at longer distances from the coast, in accordance with their more pelagic habits and relatively large foraging range (Arcos and Oro 1996, Oro 1998), and coinciding with the observed at trawlers (Arcos et al. 2001). The number of Audouin's gulls also increased in relation with the number of vessels aggregated. This was to be expected, since feeding opportunities would increase with the number of vessels concentrated in the same area, at the same time that a large number of vessels would indicate important fish aggregations. Finally, seasonal differences were also clear for Audouin's gull, with higher numbers at night out of the breeding season, when comparing periods of trawling activity. This result is of interest, considering that Audouin's Gull is far scarcer in the study area out of the breeding season (Oro 1998). In addition, the number of Audouin's gulls attending trawlers strongly decreased at this time of the year. A possible explanation would be that Audouin's gulls avoid trawlers out of the breeding season in order to avoid direct competition with the more aggressive and opportunistic yellow-legged gull, given the large numbers of the latter at these vessels (Arcos et al. 2001).

Efficiency of Audouin's gull at capturing fish, and bioenergetic considerations

The field metabolic rate (FMR) of Audouin's Gulls has been estimated at around 710 kJ day⁻¹, and this parameter would increase to slightly over 1000 kJ day⁻¹ for breeding adult birds (Ruiz et al. 2000). Therefore, our model estimate (mean of 669.2 kJ bird⁻¹ haul⁻¹) suggest that breeding Audouin's Gulls attending a single haul of purse seiners would obtain in average more than half of their daily energy requirements. Considering that Audouin's gulls also picked up prey from time to time during the attraction of the fish, and presumably attended more than one

vessel during the hauling process in a given fishing area, we suggest that individuals attending purse seiners could satisfy their daily energy requirements in this way. However, our estimate is subject to strong variability, which probably reflects the unpredictability of the fishery and explains why trawlers are preferentially attended. Several data on the diet of focal breeding pairs suggest that some Audouin's Gulls are more specialised than others in the capture of fish at night, thus attending purse seiners preferentially to trawlers (D. Oro, unpublished data). These birds could satisfy their energy requirements through fishing at night during most of the year (with the exception of adverse environmental conditions), which seems plausible according to our model.

Audouin's gulls were also observed to associate with non-fishing vessels at night, probably attracted by their lights. In these cases the vessels presumably only helped to detect fish, since they were sometimes steaming when the gulls turned up, thus precluding the attraction of fish to the surface. When fish density was high, Audouin's gulls associated with the non-fishing vessel approached the capture rate observed at purse seiners. However, the typical prey was juvenile fish of small size, thus making necessary the capture of a considerable higher number of fish in order to satisfy the daily energy requirements of the gulls. In situations of low prey density, and especially in absence of any light to help, the situation would be even less suitable. Therefore, in spite of the presumed specialisation of Audouin's gull in the capture of epipelagic fish at night, the association with purse seiners seems to greatly improve its efficiency. Seabirds with better adaptations to forage at night (basically better nocturnal vision), as could be the case of Cory's Shearwater, could find less advantageous to attend purse-seiners, although the lights of these vessels could help them to locate important aggregations of fish at long distances.

Nocturnal fisheries and seabirds: general considerations

Purse seine fisheries targeting small shoaling fish operate in several regions of the world, predominantly at night and using light attraction (e.g. Coello 1988; Camphuysen et al. 1995; Potier et al. 1997). Although the use of these fisheries by seabirds has been previously disregarded, it could be of special importance at least for some nocturnal species, as the present study demonstrates for Audouin's Gull in the Mediterranean. For instance, the rare swallowtailed Larus furcatus and sooty gulls Larus modestus show strong nocturnal habits (McNeil et al. 1993) and could obtain a substantial profit of exploiting purse seiners, especially considering the important purse seine fisheries operating within their distribution range (central and SE Pacific; e.g. Coello 1988; Anonymous 1991; Hart 1995). The ring-billed gull Larus delawarensis has been recorded capturing fish attracted to the sea surface by artificial lights at night (McNeil et al. 1993), and could also take profit of purse seine fisheries. It is worth to note, however, that purse seiners target the same prey than most seabirds do in a natural way, the former being a much more important source of mortality for these prey (e.g. Furness and Monaghan 1987). Thus, purse seine fisheries could be favouring some seabird species in the short term through facilitating them the capture of fish, but would exert a negative effect in the long term through direct competition and the eventual depletion of the targeted fish stocks. Moreover, the powerful lights used to attract fish could revert in the direct mortality of seabirds through dazzling them and causing strikes, as recorded for a lobster fishery off Tristan da Cunha Islands (Ryan 1991), although this phenomenon was not observed during our study. Other fisheries that often operate at night are longliners, which are considered a real threat to several seabird populations (see Tasker et al. 2000 and references therein). The mortality of seabirds entangled in longlines seems to be more important during daylight hours (e.g. Barnes et al. 1997; Belda and Sánchez 2001), but artificial lights also seem to increase the mortality of these fisheries when operating at night (Cherel et al. 1996). In the case of the western Mediterranean, the threatened Audouin's Gull could be especially vulnerable to longline mortality at night, given the observed tendency of this gull to associate with vessels presenting artificial lights.

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Section II

Seabird-fisheries interactions and conservation: case studies



Competition between the yellow-legged gull *Larus cachinnans* and Audouin's gull *Larus audouinii* associated to commercial fishing vessels: the influence of season and fishing fleet¹

Abstract. Competition between the yellow-legged gull Larus cachinnans and Audouin's gull Larus audouinii while foraging at commercial fishing vessels off the Ebro Delta (NW Mediterranean), was assessed in 1997 and 1998. Observations were performed onboard two kinds of fishing vessels with different timetables: bottom trawlers (diurnal activity) and purse seiners (nocturnal activity). Three situations were distinguished with respect to the season and the fishing regime: (1) breeding season, both fleets operating; (2) breeding season, only purse seiners operating due to a trawling moratorium; (3) non-breeding season, both fleets operating. Overall, the yellow-legged gull behaved as an opportunist species and exerted pressure over Audouin's gull through kleptoparasitism and agonistic interactions (i.e. contest competition). Despite this, Audouin's gull was more efficient at capturing discards through scramble competition and was able to take profit from fishing vessels when the capture of fish required high skills, in accordance with its higher specialisation. Competition varied in intensity according to the fishing fleet and the season. Indeed, Audouin's and the yellow-legged gulls only interfered at trawlers, since only Audouin's gull attended purse seiners. During the breeding season competition at trawlers was not severe and Audouin's gull preferentially attended these vessels. Purse seiners acted as a secondary food resource, and only attracted important numbers of Audouin's gulls during trawling moratoriums. Out of the breeding season the number of Audouin's gulls strongly declined in the area. Furthermore, the intensity of kleptoparasitism increased at trawlers, and the average size of the fish discarded was larger and less suitable. In parallel with these changes, Audouin's gull shifted to attend purse seiners preferentially, thus avoiding the high levels of competition at the trawlers. The lower representation of Audouin's gull in other breeding areas in the Mediterranean, as well as the less important fishing fleets in these areas, would probably reduce the attractiveness of trawlers for this species, even during the breeding season. Moreover, changes in fishing policies aimed to reduce discarding practices would lead to a globally less favourable situation for Audouin's gull.

Key words: Discards \cdot kleptoparasitism \cdot Mediterranean \cdot seabird-fisheries interactions \cdot trawling moratorium

¹Arcos JM, Oro D & Sol D (2001), Marine Biology (*in press*)

Introduction

Over the last century, the increasing offer of discards and offal provided by nonselective fisheries has led to an extensive use of this anthropogenic food resource by many seabird populations throughout the world (e.g. Tasker et al. 2000 and references therein). Some scavenging species have particularly benefited from attending fishing vessels (especially trawlers), and are thought to have increased in numbers mainly due to this foraging strategy (e.g. Oro 1999; Oro and Ruxton 2001). However, small and specialised species could find difficulties in feeding at fishing vessels if competition there was strong, as suggested by some authors (e.g. Furness et al. 1988; Garthe and Hüppop 1998a). Indeed, fishing vessels are patchily distributed and attract high numbers of birds (e.g. Garthe and Hüppop 1998a), thus increasing the chance of competition (cf. Milinski and Parker 1991). In addition, the size of fish selected by seabirds from discards usually broadly overlaps, and kleptoparasitic and agonistic interactions reported at fishing vessels support the view that competition is strong (Hudson and Furness 1988; Garthe and Hüppop 1998a). In spite of this, very few studies have specifically addressed the topic of competition between seabirds when attending fishing vessels (e.g. Camphuysen 1995; Garthe and Hüppop 1998a).

In the Mediterranean, the yellow-legged gull *Larus cachinnans* and Audouin's gull *L. audouinii* are amongst the species most influenced by trawling discards (e.g. Oro et al. 1995 and Oro et al. 1996b, respectively). The yellow-legged gull is a superabundant and generalist species with predominantly diurnal habits, typical of the south-western Palearctic, and has often been treated as a pest (e.g. Bosch et al. 2000). In contrast, Audouin's gull is a scarce species of conservation concern, endemic to the Mediterranean and specialised in the capture of epipelagic fish by night (see Oro 1998). Both species are considered potential competitors (González-Solís et al. 1997; Oro 1998), and some studies conducted at colony sites point to the yellow-legged gull as one of the main threats to Audouin's gull (e.g. Tucker and Heath 1995). Therefore, the study of the interactions between the two species when feeding at sea should be a subject of special concern.

In the present study, we examined competition between Audouin's and yellowlegged gulls while exploiting commercial fishing vessels in the Ebro Delta area (northwestern Mediterranean). We addressed three main questions:

- (1) Is there any evidence of competition between Audouin's and yellow-legged gulls when attending fishing vessels and, if so, how do they interfere?
- (2) Is the yellow-legged gull a threat to Audouin's gull when both species forage at fishing vessels?
- (3) Does the more specialised and vulnerable species (Audouin's gull) use any strategy to reduce competition?

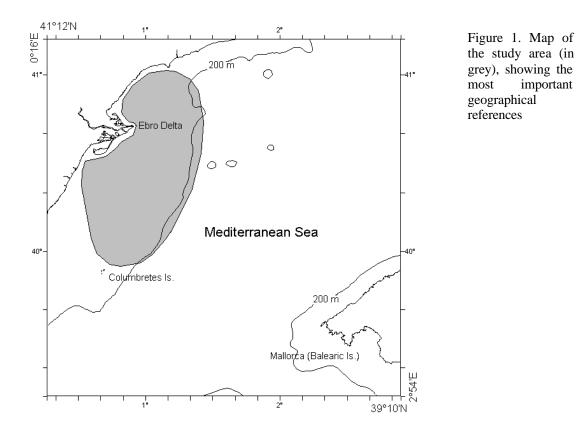
We considered two fishing fleets, trawlers and purse seiners, with different timetables (diurnal and nocturnal, respectively). This allowed us to assess potential differences in the temporal exploitation of fishing vessels by the two species, as a possible consequence of competition (see Schoener 1974). Furthermore, the establishment of trawling moratoriums overlapping with the breeding season of the gulls provided an exceptional opportunity to assess changes in the foraging behaviour of the two gulls depending on different conditions of food availability (cf. Oro 1999). Based on previous knowledge, we made some a priori predictions. Firstly, we predicted the existence of competition when both species attended fishing vessels together, in the form of both scramble and contest interactions (sensu Milinski and Parker 1991). Secondly, although the yellow-legged gull has been described as the dominant species in colonies, the specialisation of Audouin's gull in the capture of fish was expected to compensate for the greater aggressiveness of the former, when both species were feeding at sea (cf. Garthe and Hüppop 1998a). Finally, we expected to find some kind of segregation between the two

species as a result of competition (e.g. Schoener 1974). This segregation was predicted at several levels: (1) patterns of attendance to trawlers in accordance with their activity, with Audouin's gull concentrating in moments that required specialisation and therefore were not worthwhile to the yellow-legged gull; (2) spatial distribution, with Audouin's gull attending fishing vessels at higher distances from the colony and the coast, given its higher foraging range (Arcos and Oro 1996; Abelló and Oro 1998); (3) attendance to nocturnal (purse seiners) and diurnal fleets (trawlers), with Audouin's gull having a preference for purse seiners, since these vessels involve less competition but require higher specialisation; (4) size of the fish selected, with Audouin's gull targeting smaller fish due to its smaller size (cf. Forbes 1989).

Materials and methods

Study area, seabird species and commercial fisheries

The study was carried out on board commercial fishing vessels operating off the Ebro Delta (NW Mediterranean), between 39° 50'N and 41° 00'N, and 0° 35'E and 1° 30'E (Fig. 1). The continental shelf is wide (up to 70 km) and shallow (up to ca. 200 m deep) in this area, with a high productivity resulting from the abundance of sediments and nutrients carried by the Ebro River and the mixing effect of the Liguro-Provençal-Catalan front at the continental slope (e.g. Palomera 1992). This is considered to be one of the most important spawning areas for Clupeiforms in the western Mediterranean (Palomera 1992), and supports both large seabird populations and an important commercial fishery.



Seabirds feeding in the study area during the breeding season (March-July) mainly come from the Ebro Delta (20000 pairs of gulls and terns in 1997) and the Columbretes Archipelago colonies (1200 pairs of gulls, shearwaters and storm-petrels in 1997, e.g. Oro 1999; see Fig. 1). The breeding population of Audouin's gull (12000 pairs) outnumbers that of the yellow-legged gull (4500 pairs) in the area. Important numbers of the Balearic shearwater Puffinus mauretanicus, an endemic species of the Balearic Islands (over 115 km away from the study area), also feed extensively off the Ebro Delta (Abelló and Oro 1998; Arcos et al. 2000). Furthermore, the area also supports numbers of non-breeding (immature) individuals of gulls and other seabirds during the breeding season (J.M. Arcos and D. Oro, unpublished data). Out of the breeding season, some of the breeding species depart from the area either completely (e.g. Cory's shearwater Calonectris diomedea, Sánchez-Codoñer and Castilla 1997) or in part (e.g. Audouin's gull, Oro 1998), while others increase their numbers with the arrival of wintering birds (e.g. the yellow-legged gull, Sol and Arcos 1992). In addition, species such as the Mediterranean gull Larus melanocephalus arrive in high numbers to the area during the autumn and winter (e.g. Paterson 1997).

Two major commercial fishing fleets operate around the Ebro Delta, bottom trawlers (referred to as trawlers hereafter; ca. 215 vessels) and purse seiners (ca. 40 vessels; Irzaola et al. 1996). Both fleets have restricted timetables, trawlers operating by day and purse seiners by night (e.g. Oro 1995). Trawlers have low selectivity, capturing several species of demersal and benthic fish, as well as small pelagic fish (mainly Clupeiforms), and generating high amounts of discards. Seabirds associate with these vessels from the moment that the net is hauled, during all the process of classification and while the by-catch is discarded (Oro and Ruiz 1997). In contrast to trawlers, purse seiners are highly selective, targeting small shoaling fish (mainly Clupeiforms) and generating few discards. These vessels mainly attract seabirds during the encircling of the fish and the hauling of the net, whereas the discarding process, carried out on the way back to port, seems of little importance (J.M. Arcos and D. Oro, unpublished data). Since 1991, a fishing moratorium affects the trawler fleet during two months in spring, overlapping each year with different stages of the breeding season of the seabirds (e.g. Oro 1998 and references therein).

Methods

We carried out a total of 58 daily cruises onboard commercial fishing vessels, both trawlers (n = 29) and purse seiners (n = 29), between March and December of 1997 and 1998. Whenever possible, two factors were considered in the analyses since they were likely to influence results: season (breeding and non-breeding) and fishing regime (trawling moratorium and trawling activity periods). Taking this into account, three different situations were considered: (1) breeding season (March-July), with both fleets operating; (2) breeding season, when only purse seiners operated due to a trawling moratorium; and (3) non-breeding season (August-February), with both fleets operating.

Bird censuses

At both trawlers and purse seiners, counts of the different seabirds associated with the vessel were performed every 15 minutes during the fishing activity (during the hauling and, in the case of trawlers, also during the discarding process), and the maximum number of birds was recorded for each haul.

In addition to the absolute numbers of Audouin's and yellow-legged gulls, we also calculated their ratio, for each haul, as follows,

Ratio AG/YIG =
$$\log \frac{AG + 0.5}{YIG + 0.5}$$

where AG is Audouin's gull (birds/haul) and YlG is yellow-legged gull (birds/haul). The values obtained were thus symmetrical, and the problem of null data was avoided by adding 0.5 to the maximum count for each species.

Since the number of Audouin's gulls present in the area strongly differs between seasons (breeding vs. non-breeding; e g. Oro 1998), we calculated an index of attendance to fishing vessels that took into account such differences to compare the relative use of each fleet between seasons. This attendance index was calculated as the division of the number of Audouin's gulls at each haul by the estimated total number of birds of this species in the study area, and then multiplied by 1000. The estimated number of Audouin's gulls was 25000 birds for the breeding season (over 24000 breeding adults between the Ebro Delta and the Columbretes Islands, plus ca. 5% of immatures; Oro 1998; J.M. Arcos and D. Oro unpublished data), and 1500 birds for the non-breeding season (Oro 1998). This index was not computed for the yellow-legged gull because winter numbers in the area are unknown, and its association with nocturnal vessels was rare (see results), thus not allowing any comparisons of the use of the different fleets between seasons.

To assess differences in the patterns of attendance of yellow-legged and Audouin's gulls to trawlers, depending on their activity, each 15-minute count was classified as: (1) net on the sea surface (while being either hauled or lowered), when some fish is available directly from the net; (2) normal discarding, either while the vessel is steaming to a new station or towing; (3) moments of low or null offer of discards, while fishermen are classifying the captures, before all the by-catch has been discarded. The mean number of each species was calculated for each activity and haul. These comparisons were only performed during the breeding season, when both Audouin's and the yellow-legged gulls commonly attended trawlers. At purse seiners seabirds mainly attended the vessel when the fish were concentrated near the surface by the encircling net (J.M. Arcos and D. Oro unpublished data), and hence we only considered this stage of fishing activity.

At each haul we determined the minimum distance to the nearest colony and to the mainland coast. Hauls were then grouped according to three categories of distance: 0-9; 10-19; and 20-29 nautical miles, both when considering the distance to the colony and to the coast. We then looked for differences in the ratio AG/YIG in accord with these distance categories, to assess any spatial segregation. These comparisons were only performed during the breeding season.

Discard experiments: efficiency at capturing discards, kleptoparasitism, and fish size preference

At trawlers, experimental discarding was performed during the normal discarding activity. Subsamples of the by-catch fraction were discarded individually, and each item

was identified to the species level and classified according to its length into six size classes (<5 cm; 5-9 cm; 10-14 cm; 15-19 cm; 20-24 cm; and $\ge 25 \text{ cm}$). For each discarded item, we recorded on tape whether it sank or was picked up by a seabird; in the latter case, we recorded the seabird species and whether it was swallowed, lost or kleptoparasitised by another seabird. Each experiment finished when the food item sunk or was swallowed. Discard experiments have been considered to give a rough approximation of the real efficiency of seabirds feeding on discards at commercial fishing vessels, with a number of associated biases (Garthe and Hüppop 1998b). However, in the present study we were able to minimise the most important of the biases noted by these authors. Firstly, we worked on board commercial fishing vessels, while most studies performing discard experiments have been carried out on board research vessels. Secondly, we performed the experiments while fishermen were discarding, thus having a close approximation to real discarding. Finally, fishermen usually discard fish in small amounts and at a constant rate in the Ebro Delta area, a situation quite similar to that of the experiments (cf. Oro and Ruiz 1997).

During each discarding experiment the number of seabirds following the vessel was estimated carefully, independently of the maximum number obtained for the whole haul. From these counts, and to assess the efficiency of seabirds at capturing discards, we calculated a foraging success index (SI) for each species and experiment, based on the Ivlev's electivity index (Krebs 1989),

$$SI_i = \frac{O_i - E_i}{O_i + E_i}$$

where SI_i is the foraging success index for species *i*, O_i is the observed number of items swallowed by this species, and E_i is the expected number of items swallowed, estimated from multiplying the total number of items offered by the representation (percentage) of the species behind the vessel. If this representation was observed to change substantially, the experiment was stopped. Only those experiments with more than 30 items discarded were considered, to minimise biases resulting from low sample size (Garthe and Hüppop 1998a,b). Success indices should be considered with caution, since they do not account for a number of variables that could be of biological importance (Garthe and Hüppop 1994; Camphuysen et al. 1995). Firstly, success indices give an idea of the food intake rate at the species level, with no individual information. Secondly, the energy requirements and the size selection of each species are not taken into account, and different species showing similar indices could be obtaining different profits from following a vessel. Finally, the time spent by the different species behind a vessel is not considered, and differences in this respect could compensate for differences in their success indices.

To assess the influence of the relative and the absolute numbers of yellow-legged and Audouin's gulls on their efficiency at capturing discards, we compared the SI of each species with the ratio AG/YIG, as well as with the absolute number of each species. These comparisons were only performed during the breeding season, when both Audouin's and yellow-legged gulls commonly attended trawlers.

The rate of kleptoparasitism at trawlers was estimated for each haul as a percentage, comparing the number of discarded items that involved kleptoparasitic events with the total number of items offered. Then we assessed the relationship between the absolute numbers of each species, as well as their success index, and this measure of the incidence of

kleptoparasitism. The efficiency of kleptoparasitism for the studied species was assessed by way of a Robbery Index (RI), resulting from dividing the number of items stolen by a species by the number of items stolen from this species (Camphuysen et al. 1995). To obtain symmetrical data, we give the logarithm of that division as the actual RI. We also assessed the directionality and efficiency (success rate) of those kleptoparasitic chases that only involved Audouin's and yellow-legged gulls. Finally, the probability of an item being kleptoparasitised was also considered with respect to the size class of the fish offered.

We also studied the size preference for the items discarded, to assess the degree of overlap in the selection of discards between yellow-legged and Audouin's gulls. The representation of each size class in the captures of each species of gull was estimated using two approaches. In the first case, we estimated the direct percentage of fish, of each size class, captured by each species of gull. In the second case, the offer of each size class was relativised, thus calculating a percentage that would give a better idea of the real preferences of each gull. This estimation was performed using the Manly's preference index (Krebs 1989),

$$\boldsymbol{a} = \frac{\log p_i}{\sum_{j=1}^n \log p_j}$$

where α_i is the Manly's preference index for the size category *i*, *n* is the number of size categories, and p_i and p_j are the proportions of fish of categories *i* and *j* that have been not consumed by the species considered at the end of the experiment.

The degree of overlap between the two gull species studied was then estimated, for the two approaches, using an overlap index (from Horn 1966),

$$C = 2 \cdot \frac{\sum_{i=1}^{n} (x_i \cdot y_i)}{\sum_{i=1}^{n} x_i^2 + \sum_{i=1}^{n} y_i^2}$$

where C is the overlap index between the two gull species, n is the number of size categories of fish considered, and x_i and y_i are the proportion of fish of category i consumed by the two species of gulls. Again, comparisons of the fish selected by yellow-legged and Audouin's gulls were only performed during the breeding season, when both species commonly attended trawlers.

To have a better idea of the real discard offer in the different seasons, we collected sub-samples of discards for each fishing day. From these samples, we classified each item and measured it to the nearest millimetre.

Statistical analysis

To avoid pseudoreplication, we recorded data for a maximum of two hauls per day. It should also be noted that the intake rates were not calculated at the individual level but at the species level.

Data on censuses, ratio, success indices, and kleptoparasitic rates were first tested for normality. In the case of censuses, success indices, and kleptoparasitic rates, there was a significant departure from normality in most cases, even after the appropriate transformations, and these data were treated with non-parametric procedures. Only the ratio AG/YIG fitted well to a normal distribution, both in the breeding (Shapiro-Wilk test, W = 0.98, P < 0.86) and the non-breeding seasons (W = 0.95, P < 0.30), and was consequently treated with parametric statistics.

Comparisons of the number of birds associated with trawlers according to the activity of the vessel were performed grouping censuses for each haul (matched-data), by means of the Friedman's two-way analysis of variance (ANOVA) (in the case of censuses) and the repeated measures ANOVA (ratio). Post-hoc comparisons were then performed with the Wilcoxon matched-pairs test and the Schaeffer test, respectively. We also employed the Wilcoxon and Friedman tests for other comparisons of two or more variables, respectively, when the data was not completely independent. In the other cases, Mann-Whitney U and the Kruskal-Wallis tests were employed, as well as the t-test and the oneway ANOVA. Chi-square contingency tables were also used when appropriate. Comparisons between the success indices and the numbers of Audouin's and yellow-legged gulls, as well as their ratio, were performed using Spearman rank correlations. The same procedure was employed when assessing the relationship between the rate of kleptoparasitism and the absolute numbers of Audouin's and yellow-legged gulls, as well as with their success indices. Since the number of correlations with the same dependent variable was high, the Bonferroni correction was applied according to Rice (1989). Spearman correlations were also used when assessing the relationship between the kleptoparasitic and success rates and the size class of the fish. Significance level was held at 0.05, although marginal values are also discussed following Stoehr (1999).

Results

Bird censuses

Trawlers attracted high numbers of seabirds during both periods (Table 1). In the breeding season, Audouin's and the yellow-legged gulls were the most common species associated with these vessels, and presented similar abundances (Wilcoxon matched-pairs test, z = 0.86, P = 0.39). Other species commonly attending trawlers at this time of the year were shearwaters, both the Balearic and Cory's. Out of the breeding season, the yellow-legged gull was the most common seabird, reaching figures of almost 1 000 birds in a single haul. Other common species were the Mediterranean and the black-headed gulls *Larus ridibundus*. On the other hand, Audouin's gull almost disappeared from trawlers at this time of year. This was partially explained by the low numbers of this species wintering

in the study area, and there were no significant seasonal differences in its attendance index to trawlers (Mann-Whitney test, $U_{36,25} = 445$, P = 0.94; Table 2).

Table 1. Number of the most common seabirds (median, range, and percentage of the total number of seabirds observed) associated with trawlers (hauling and discarding) and purse seines (hauling) off the Ebro Delta, in accord with the season: breeding (March-July, $N_{\text{trawlers}} = 36$ hauls, $N_{\text{purse seiners}} = 17$ hauls) and non-breeding (August-February, $N_{\text{trawlers}} = 25$ hauls, $N_{\text{purse seiners}} = 5$ hauls)

| | | Ň | umber o | f birds/haul | | |
|---------------------|--------|-------------|---------|--------------|-----------|------|
| | Bre | eding seaso | on | Non-l | son | |
| | Median | Range | % | Median | Range | % |
| Trawlers | | | | | | |
| yellow-legged gull | 34 | 2 - 450 | 34.8 | 31 | 1 - 950 | 55.2 |
| Audouin's gull | 41.5 | 3 - 107 | 23.1 | 2 | 0 - 17 | 1.3 |
| balearic shearwater | 2.5 | 0 - 550 | 19.8 | 2 | 0 - 33 | 2.3 |
| Cory's shearwater | 5 | 0 - 104 | 9.2 | 0 | 0 - 153 | 5.5 |
| mediterranean gull | 0 | 0 - 8 | 0.3 | 10 | 0 - 330 | 19.0 |
| black-headed gull | 0 | 0 - 38 | 2.7 | 8 | 0 - 160 | 9.5 |
| Total seabirds | 118 | 29 - 927 | 100 | 108 | 20 - 1142 | 100 |
| Purse seines | | | | | | |
| Audouin's gull | 11 | 0 - 68 | 95.3 | 27 | 4 - 47 | 66.7 |
| yellow-legged gull | 0 | 0 - 1 | 0.5 | 0 | 0 - 12 | 7.0 |
| Total seabirds | 11 | 0 - 68 | 100 | 35 | 7 - 54 | 100 |

Table 2. Audouin's Gull's Index of attendance to fishing vessels (i.e. number of gulls at vessels in relation to their total numbers in the study area and multiplyed by 1000) according to the fleet (trawlers and purse seiners) and the season (breeding and non-breeding). Results are given as medians, and the inter-quantile (IQ) ranges (lower and upper quartiles) are also provided (n number of hauls)

| | | Attendance Indices | | | | | | | | |
|---------------|--------------|--------------------|---------------------|-----------------------|--|--|--|--|--|--|
| Vacal | Breeding sea | ison | Non-breeding season | | | | | | | |
| Vessel | Median | IQ-Range (n) | Median | IQ-Range (<i>n</i>) | | | | | | |
| Trawlers | 1.66 | 0.90-2.20 (36) | 1.33 | 0.67-2.67 (25) | | | | | | |
| Purse seiners | 0.44 | 0.00-2.72 (17) | 18.00 | 3.33-20.67 (5) | | | | | | |

At night, only Audouin's gull associated regularly with purse seiners (see Table 1), whereas the yellow-legged gull rarely attended these vessels except on the way back to port, with daylight, when some fish were often discarded. In the breeding season, the number of Audouin's gulls associated with purse seiners was significantly higher when the trawling moratorium was established ($U_{9,8} = 6.8$, P = 0.009; 100% of attendance vs. 66.7% during periods of trawling activity). When only considering periods of trawling activity,

there were also seasonal differences in the use of purse seiners (comparison of attendance indices, $U_{17,5} = 1.0$, P = 0.001; Table 2): during the breeding season, Audouin's gull preferentially attended trawlers over purse seiners ($U_{9,36} = 24.5$, P < 0.0001), whereas during the non-breeding season the contrary was true ($U_{5,25} = 10.0$, P = 0.003).

The number of birds attending trawlers varied significantly with the activity of these vessels, for both Audouin's (Friedman's test, $\chi^2_r = 14.8$, P < 0.0001) and the yellow-legged gulls ($\chi^2_r = 28.1$, P < 0.0001) (Table 3). The ratio AG/YIG also varied with the activity of trawlers (repeated measures ANOVA, F = 16.4, P < 0.0001, Fig. 2), indicating that the two species of gulls presented different patterns of attendance to these vessels. Post-hoc analyses showed that the yellow-legged gull mainly attended trawlers during the discarding activity, when moderate to high amounts of discards were easily available. On the other hand, Audouin's gull presented high numbers during the moments of high discard and also when the net was on the sea surface, with no significant differences between these situations. During the latter fishing activity some fish were available directly from the net, but their capture required some skill.

Table 3. Audouin's gull (AG) and yellow-legged gull (YIG) numbers [median and inter-quartile (IQ) range] associated with trawlers, during the breeding season, according to the activity of the vessel (n = 36 hauls)

| | Net in | the surface | Di | scards | Few/r | no discards |
|--------------------|--------|--------------|--------|---------------|--------|---------------|
| - | Median | IQ-Range | Median | IQ-Range | Median | IQ-Range |
| Audouin's gull | 14.0 | 5.3 to 32.5 | 16.1 | 8.2 to 28.2 | 7.3 | 2.0 to 14.0 |
| yellow-legged gull | 5.0 | 1.0 to 8.5 | 23.6 | 10.2 to 31.3 | 4.0 | 2.0 to 8.5 |
| Ratio AG/YlG | 0.53 | 0.10 to 0.91 | -0.04 | -0.41 to 0.15 | 0.24 | -0.43 to 0.56 |

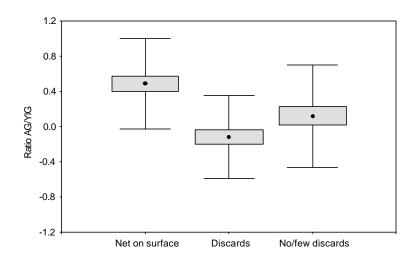
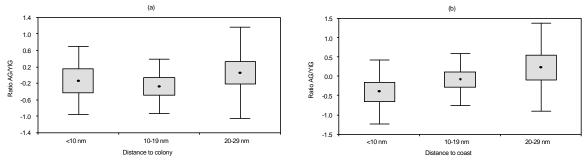


Figure 2. Ratio of Audouin's to yellow-legged gulls according to the activity of trawlers. Values given are the mean, standard error (boxes) and standard deviation (whiskers)

No clear differences in the ratio AG/YIG were observed with respect to the categories of distance, neither when considering the distance to the closest colony (one-way ANOVA, $F_{2,33} = 0.4$, P = 0.67) nor when considering the distance to the coast ($F_{2,33} = 1.5$, P = 0.24). However, there was a slight tendency of the ratio to increase with the distance to

the coast (Fig. 3), suggesting that Audouin's gull preferentially foraged farther away from the coast than did the yellow-legged gull.

Figure 3. Ratio of Audouin's to yellow-legged gulls in accord with the distance (categorised, *nm* nautical miles) to the nearest colony (a) and to the mainland coast (b), during the breeding season. Results are expressed as the mean, standard error (boxes) and standard deviation (whiskers)



Discard experiments: efficiency at capturing discards, kleptoparasitism and fish size preference

During the breeding season, Audouin's and the yellow-legged gulls did not present significant differences in their success indices (Wilcoxon matched-pairs test, z = 1.6, P = 0.11), although the former species tended to be more efficient at capturing discards (Table 4) and showed a more constant index (variance ratio test, $F_{18,18} = 2.79$, P < 0.05). From all the correlations tested, only the success index of yellow-legged gulls was significantly and negatively correlated with the ratio AG/YIG and positively correlated with their own numbers (Table 4). Outside of the breeding season, neither the yellow-legged ($U_{19,13} = 86$, P = 0.15) nor Audouin's gulls ($U_{19,13} = 86$, P = 0.15) showed significant changes in their success indices (see Table 4), in spite of the change in their relative numbers.

Table 4. Audouin's gull (AG) and yellow-legged gull (YIG) success indices [SIs; median and inter-quartile (IQ) range] at capturing fish during experimental discarding. The table also presents the results of the Spearman rank correlations between SIs and the number of each of the two species of gull, as well as with their ratio. Correlations were not carried out for the non-breeding season because of the low number of Audouin's gulls following trawlers. (*n* number of experiments; n.s. not significant)

| | | | | Corre | lation | 8 | | | |
|----------------------|----|---------------|--------------|--------|--------|---------|------|-------|------|
| | | Success Index | | Nb. AG | | Nb. Ylg | | Ratio | |
| | п | Median | IQ-Range | rs | р | rs | р | rs | р |
| Breeding season: | | | | | | | | | |
| Audouin's gull | 19 | 0.113 | -0.10 - 0.22 | 0.35 | n.s. | 0.30 | n.s. | 0.17 | n.s. |
| yellow-legged gull | 19 | -0.109 | -0.59 - 0.12 | -0.29 | n.s. | 0.61 | * | -0.74 | ** |
| Non-breeding season: | | | | | | | | | |
| Audouin's gull | 7 | 0.131 | 0.00 - 0.55 | | | | | | |
| Yellow-legged gull | 13 | 0.028 | 0.00 - 0.15 | | | | | | |

* significant at alpha < 0.05; ** = significant at alpha < 0.001, after Bonferroni correction

Kleptoparasitic events occurred frequently while seabirds attempted to capture discards. During the breeding season, the median incidence of kleptoparasitism was 5.7%, ranging from 0 to 21.7% (N = 19 experiments). The yellow-legged gull relied on this behaviour significantly more (17.1% of the attempts to capture discards being through kleptoparasitism, n = 533) than Audouin's gull (1.1%, n = 765; Yates $\chi^2_1 = 109.4$, P < 1000.0001). Moreover, Audouin's gull mainly kleptoparasitised conspecifics (n = 7 chases, 42.8% successful) and never chased any yellow-legged gull, while the latter species directed most of the chases towards Audouin's gulls (n = 44, 34.1% successful), with a lower incidence and lower success rate of conspecific chases (n = 35, 20.0% successful). In concordance with these results, the robbery indices showed a high kleptoparasitic efficiency for the yellow-legged gull (RI = 0.81), while kleptoparasitism was detrimental for Audouin's gull (RI = -0.87). Furthermore, the incidence of kleptoparasitism tended to be positively correlated with both the numbers (Spearman rank correlation, $r_s = 0.46$, n = 19, P = 0.05) and the success index of the yellow-legged gull ($r_s = 0.39$, n = 19, P = 0.09). On the other hand, the kleptoparasitic rate did not appear to influence either the numbers ($r_s = -$ 0.01, n = 19, P = 0.97) or the success index of Audouin's gull ($r_s = 0.04$, n = 19, P = 0.86). Although these tendencies seemed clear for the yellow-legged gull, none of the previous correlations was significant when we applied the Bonferroni correction.

Out of the breeding season, the general incidence of kleptoparasitism was more than double that that of the breeding season, with a median rate of 13.3% (range 4.7 - 37.5%; N = 13 experiments). This increase was statistically significant ($U_{19,13} = 68.0$, P = 0.03). Although the main reason for this increase was probably the parallel increase in the proportion of yellow-legged gulls at this time of the year (see above), both the yellow-legged (19.3% of incidence, n = 1257) and Audouin's gull (8.3%, n = 24) slightly increased their reliance on this behaviour. This increase was only significant for Audouin's gull (Yates $\chi^2_1 = 4.25$, P = 0.04), with no statistical differences for the yellow-legged gull (Yates $\chi^2_1 = 1.11$, P = 0.29).

When considering the size class of the fish, there was a significant increase of both the rate of kleptoparasitism and the proportion of successful chases as the size of the fish discarded increased (Spearman correlations, $r_s = 1.0$, n = 6, P < 0.01 in both cases; Figure 4).

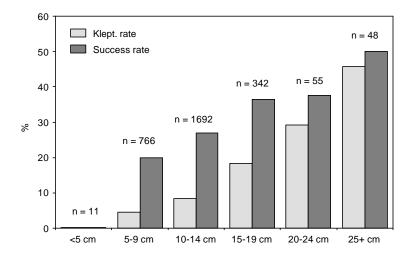
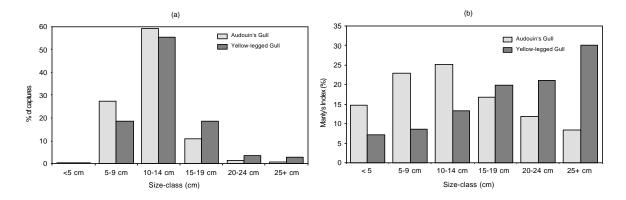


Figure 4. Rate of kleptoparasitism (in %) and percentage of successful chases for seabirds following trawlers. according to the size class of the fish offered. The number of items of each size class is shown over the respective column (*n*)

Audouin's and the yellow-legged gulls exhibited significant differences in the size of the fish selected (contingency table, $\chi^{2}_{5} = 35.7$, P < 0.001, n = 1129). As shown by the Manly's Index, Audouin's gull tended to select medium to small fish classes, while the yellow-legged gull selected preferentially the largest fish classes available from the discarded fraction (Fig. 5). However, there was still an important overlap in size preferences (C = 75.2%). This overlap became almost complete (C = 98.0%) when we did not consider Manly's correction, since the most extreme size categories were scarce among discards, and both gulls relied on medium-sized fish. Indeed, medium-sized items formed the main fraction of discards during the breeding season, with a mean length ± SD of 107 ± 44 mm (n = 3545 items). Out of the breeding season, the mean length of the fish discarded increased significantly (mean ± SD = 115 ± 44 mm, n = 1292; t-test, t = 11.5, P < 0.0001).

Figure 5. Percentage of fish selected by Audouin's and the yellow-legged gulls, during the breeding season, according to the size class: (a) Real percentage observed, given the relative offer of the different size classes of fish; (b) Manly's Index (%), which eliminates the effect of differential offer of size classes. The total number of fish offered was of 1510 items, of which Audouin's gull captured 699 items and the yellow-legged gull 430 items



Discussion

Our most important results may be summarised in five points: (1) competition exists between Audouin's and the yellow-legged gull when exploiting fishing vessels; (2) this varies in intensity according to the fishing fleet (trawlers, diurnal, vs. purse seiners, nocturnal) and the season (breeding vs. non-breeding); (3) Audouin's gulls are more competitive in scramble competition, while yellow-legged gulls are clearly superior in contest competition (kleptoparasitism); (4) the better skills of Audouin's gull in the capture of fish compensate in part for the greater aggressiveness of the yellow-legged gull; and (5) competition with yellow-legged gulls is partially avoided by Audouin's gulls by using a wide range of foraging techniques, selecting preys of smaller size, and adopting nocturnal foraging.

Direct competition during the breeding season

Direct evidence of competition was basically gathered at trawlers during the breeding season, since only under this situation did both species occur in important

numbers at the same time (see also Oro and Ruiz 1997). The larger and more aggressive yellow-legged gull behaved as an opportunist, mainly attending trawlers when high amounts of discards were offered and fish were easily captured. Moreover, this species relied to a great extent on kleptoparasitism and other agonistic interactions (i.e. contest competition), which is typical of opportunistic species (e.g. Furness 1987). In accordance with this, yellow-legged gulls showed considerable variability in their success index, which was correlated with the number of conspecifics associated to the trawler, as well as with the incidence of kleptoparasitism. A similar situation was observed in the North Sea for the close relative herring gull *Larus argentatus*, which was more efficient at capturing discards when present in high densities (Furness et al. 1992).

Audouin's gull proved to be the most proficient in the direct capture of discards (i.e. in scramble competition), as shown by its comparatively high and less variable success index, as well as by its wider range of foraging techniques. Although yellow-legged gulls often kleptoparasitised Audouin's gulls, the success index of the latter was not significantly influenced by the numbers of the former, nor by the rate of kleptoparasitism at trawlers. This suggests that the pressure exerted by the yellow-legged gull through contest competition was not severe for Audouin's gull during the breeding season. In agreement with this, Audouin's gull did not strongly avoid direct interference with the yellow-legged gull. However, we observed a series of strategies used by Audouin's Gull, which are in agreement with its higher specialisation (e.g. Oro 1998), that could help to reduce the degree of competition to some extent (e.g. Schoener 1974). Firstly, when considering the activity of trawlers, both species reached their peak in numbers during the discarding process, which suggests that that is the most rewarding period despite competition reaching its maximum. However, Audouin's gulls were also present in high numbers when the net was on the surface, which may be interpreted as a partial temporal segregation in order to reduce competition. Secondly, although the limited range of distances at which the trawlers operated probably did not allow for a clear spatial segregation, there was a slight increase of the relative numbers of Audouin's gull in relation to the distance to the coast. This agrees with the larger foraging range and the more pelagic habits of Audouin's gull (Arcos and Oro 1996; Abelló and Oro 1998), and could help to reduce the degree of competition with the yellow-legged gull. Thirdly, although there was a high overlap between Audouin's and the yellow-legged gulls in the size classes of the fish selected, given the limited offer of size classes among the discards, the former species tended to select smaller fish. This was to be expected given the smaller size of Audouin's gull (e.g. Forbes 1989), but also because smaller fish were less often kleptoparasitised (cf. Hudson and Furness 1988; Camphuysen 1994), and consequently their selection by Audouin's gull would reduce the pressure exerted by the yellow-legged gull through kleptoparasitism.

Only Audouin's gull attended purse seiners regularly, thus precluding competition with the yellow-legged gull. However, Audouin's gull still showed a preference for trawlers, which suggests again that competition with the yellow-legged gull was not severe at these vessels. In this situation purse seiners seemed to act as a secondary food resource, being important only when trawling discards were not available in the area (i.e. during trawling moratoriums, cf. Oro 1995; Oro et al. 1997).

Unfavourable conditions for Audouin's gull in the non-breeding season

Out of the breeding season the results changed substantially. The situation at trawlers appeared to become less attractive to Audouin's gull, as a combined effect of several factors. Firstly, the ratio of Audouin's to yellow-legged gulls reversed in the study area, becoming clearly favourable to the yellow-legged gull. This was due to the migration of the most important fraction of the local population of Audouin's gull out of the Ebro Delta area (Oro 1998, and references therein), as well as to the arrival of important numbers of the yellow-legged gull after the breeding season (Sol and Arcos 1992). Secondly, in association with the increase in numbers of the yellow-legged gull there was a significant increase in the incidence of kleptoparasitism at trawlers, reaching similar levels to those observed and considered high in the North Sea (Hudson and Furness 1988). Thirdly, fish discarded were, on average, of larger size during the non-breeding season, thus being less favourable for Audouin's gull, especially given the higher risk of losing the largest fish to kleptoparasitism.

All these changes presumably led to a higher intensity of competition at trawlers, to the disadvantage of Audouin's gull. Thus, the adoption of more nocturnal habits by this species, preferentially attending purse seiners out of the breeding season, could be interpreted as a strategy to avoid direct interference with the yellow-legged gull when competition was intense. The fact that Audouin's gull made use of purse seiners only as a secondary food resource when competition at trawlers was less severe (i.e. during the breeding season) supports this interpretation. Similarly, in the North Sea, fulmars *fulmarus glacialis* and herring gulls avoided trawlers when high numbers of competitors (herring gulls and Gannets *Sula bassana*, respectively) concentrated behind these vessels (Camphuysen and Garthe 1997; Furness et al. 1992).

Competition, fishing fleets, and implications for conservation

It is important to remark that the Ebro Delta area presents some particular features that could make trawlers especially attractive to Audouin's gulls and other seabirds, especially during the breeding season, in comparison with other areas in the Mediterranean. This area holds one of the most important trawling fleets in the western Mediterranean (e.g. Irzaola et al. 1996), and trawling discards are enough to meet the energy requirements of the local breeding community (Oro and Ruiz 1997; Oro 1999). This situation is probably exceptional, and discards are presumably limited in other breeding areas, as demonstrated for the Mallorca area (Oro and Ruiz 1997). Besides, in the Ebro Delta area trawlers have a very restricted timetable and well-established fishing grounds, discards being predictable in both time and space. Finally, this is the only colony where the breeding local population of Audouin's gull largely outnumbers that of the yellow-legged gull. Thus, the unfavourable situation at trawlers observed in the study area during the non-breeding season could be the equivalent of that occurring in other areas during the breeding season. This actually appears to be the case at the Chafarinas Islands, where Audouin's gulls mainly attended purse seiners (González-Solís et al. 1999). The relatively high numbers of breeding yellowlegged gulls, as well as the unpredictability of the trawling fleet, could explain this preference for purse seiners around these islands (González-Solís et al. 1999). The fact that attendance to trawlers by Audouin's gull has been only rarely recorded in the central and eastern Mediterranean (e.g. Oro 1998) could also reflect the low attractiveness of these

vessels for Audouin's gull, due in part to the very low numbers of this species compared to those of the yellow-legged gull. Indeed, it has been shown that interference at breeding sites (predation and kleptoparasitism) decreases with the ratio of Audouin's to yellow-legged gulls (Oro *et al.* 1996a; A. Martínez-Abraín, pers. com.).

Changes in fishing policies are occurring as a result of overexploitation of fish stocks throughout the world. The understanding and subsequent reduction of discards is one of the target subjects of these new fishing policies (e.g. Tegner and Dayton 1999; Fluharty 2000). This reduction would be mediated by several measures: increase of the mesh size for reducing the quantity of incidental captures (increasing at the same time mean discard length), creation of new markets for less appreciated fish, and reductions in the power, number and timetables of vessels. This situation will probably increase the competition at trawlers and the appearance of density-dependence regulation through food availability, and some species (smaller or with lower abilities) could be more affected than others (e.g. Furness 1999; Oro 1999; Tasker et al. 2000; Moore and Jennings 2000). Furthermore, larger and more predatory species could increase the predation rates on smaller seabird species as a result of the decrease in discard availability, as has been recorded in several areas such as the Shetland, Newfoundland or the Ebro Delta (e.g. Phillips et al. 1999; Regher and Montevecchi 1997; Oro and Martínez 1994, respectively). Our results suggest that Audouin's gull would be more affected than the yellow-legged gull by these changes, in spite of its higher specialisation and its ability to reduce competition to some extent. Smaller species of conservation concern, such as the Balearic shearwater, could become even more affected by this reduction of discards. Further research is necessary to understand how this future situation will affect the population dynamics of all the species influenced by discards.

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Feeding ecology and significance of fisheries discards for a threatened seabird endemic to the western Mediterranean: the Balearic shearwater *Puffinus mauretanicus*¹

Abstract. The Balearic Shearwater Puffinus mauretanicus is the rarest and most threatened Mediterranean seabird. The biology of this shearwater is still little understood, and its study should be the main goal of any conservation initiative. We studied the feeding ecology of the Balearic shearwater at sea in the western Mediterranean (1996-2000), focusing on the importance of fisheries discards for this species. Fieldwork was conducted on board commercial bottom trawlers (demersal fishery with diurnal activity) and purse seiners (pelagic fishery with nocturnal activity), as well as during experimental trawling surveys. The shearwaters made extensive use of discards, mostly those from trawlers. This was especially so during the late breeding season, which could be related with the general impoverishment of Mediterranean surface waters. The typical foraging range for breeding birds comprised the eastern Iberian coast and the Balearic Archipelago, with the largest concentrations occurring off the Ebro Delta. This distribution seems determined by favourable local hydrographic conditions and by the presence of important trawling fisheries. Balearic shearwaters captured discards through dives at some distance behind fishing vessels, thus reducing interactions with other seabirds. A bioenergetic model estimated that the 40.8% of the energy obtained by the Balearic shearwater population comes from trawler discards during the breeding season, although this value was subject to strong variability (±36.2% SD). In addition to the capture of discards (38% of the feeding instances observed), Balearic shearwaters also obtained food by capturing fish under floating drifting objects (33%), associating with sub-surface predators (10%), capturing small shoaling fish (10%), and feeding upon plankton (10%). The latter behaviour was observed in crepuscular hours, but the shearwaters did not appear to feed during the night. In winter, Balearic shearwaters attended fishing vessels to a lower extent, and seemed to mostly feed upon fish schools in shallow coastal waters. Incoming fishing policies could affect Balearic shearwaters in the short term through reduction of discards, although a good design of some management strategies (such as trawling moratoria) could help to reduce their negative effect.

Key words: conservation; feeding ecology; purse seiners; trawlers; Procellariforms; seabird-fisheries interactions

¹Arcos JM & Oro D, submitted ms

Introduction

The Mediterranean basin holds a breeding seabird community characterised by a high level of endemism, with several subspecies and even a few species breeding only there (Zotier et al. 1999). This is the case of the Balearic shearwater *Puffinus mauretanicus*, the

rarest and most threatened Mediterranean seabird, with an estimated breeding population of 3300 pairs (Aguilar 1991) restricted to the Balearic Archipelago (western Mediterranean). The taxonomy of this shearwater received considerable attention in the last century, first being considered as a subspecies of the Manx Shearwater *Puffinus puffinus* (Lowe 1921), and later of the Yelkouan Shearwater *Puffinus yelkouan* (sharing specific identity with the nominate form, the Levantine Shearwater; Bourne et al. 1988). Only recently this shearwater has been widely accepted as a distinct species (e.g. Snow & Perrins 1998), at the light of increasing palaeontological (e.g. Walker et al. 1990) and molecular evidence (Heidrich et al. 1998), combined with the reconsideration of several morphological, ecological, and behavioural traits (e.g. Mayol et al. 2000). Most of the research efforts conducted on the species have focused on this uncertain taxonomy, while its general ecology has been little studied. As a distinct species, the lack of general knowledge about this rare shearwater is especially alarming, since a good understanding of its biology will be essential for the success of any conservation initiative.

The feeding ecology of the Balearic shearwater is particularly little known, and is partly confounded by extrapolations made on its better studied closest relatives, the Manx and the Levantine Shearwaters (cf. Le Mao & Yésou 1993), which mostly forage in flocks upon small shoaling fish (e.g. Brooke 1990). This behaviour seems also common for the Balearic shearwater (Araujo et al. 1977, Rebassa et al. 1998), but other feeding strategies have been also described. Indeed, Balearic shearwaters have been reported capturing discards behind fishing vessels (Le Mao & Yésou 1993, Oro & Ruiz 1997, Arcos et al. 2001), feeding in association with sub-surface predators (Oro 1995, Arcos et al. 2000a), capturing fish under floating drifting objects (Arcos et al. 2000a), and feeding upon planktonic organisms on the sea surface (Le Mao & Yésou 1993, Arcos et al. 2000a). Although these alternative feeding strategies have been often disregarded or considered of little importance (e.g. Snow & Perrins 1998), they could play an important role in the feeding ecology of the Balearic shearwater, at least in some periods of the year. Special interest should be focused on the case of fisheries discards, an anthropogenic food resource that has strongly influenced the ecology of several gulls and terns in the NW Mediterranean (see Oro 1999 and references therein), although is considered of rather little importance for the shearwaters (e.g. Mayol et al. 2000).

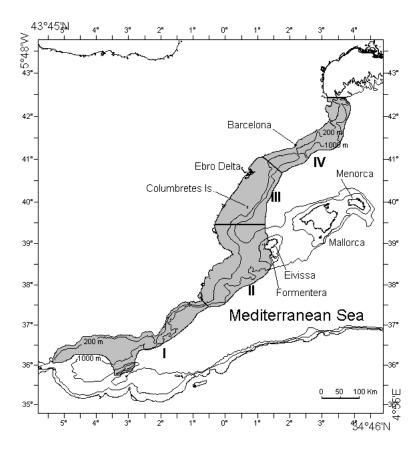
This study was directed to assess the significance of fisheries discards for the Balearic shearwater, as well as to ascertain what other feeding strategies are important for this species. Seasonal and geographical variations in the use of discards were assessed off the Mediterranean side of the Iberian Peninsula and the Balearic Archipelago, through cruises on board commercial fishing vessels (bottom trawlers and purse seiners) and experimental trawling surveys. We also recorded the behaviour of the shearwaters when attending fishing vessels, as well as their efficiency at capturing discards. A simple bioenergetic model allowed us to estimate to which extent Balearic shearwaters make use of trawler discards during the breeding season, when the resource seemed more important for this species. Other feeding strategies were also recorded and quantified during this season. Detailed information on the use of fisheries discards by Balearic shearwaters, as well as on the significance of alternative feeding strategies, could help to predict the effect of incoming changes in fishing practices for this threatened seabird.

Study area and methods

Study area

The study area comprised the entire Mediterranean region off the Iberian Peninsula, as well as the southern Isles of the Balearic Archipelago (Eivissa and Formentera; Fig. 1). We differentiated four areas according to their topographic and hydrographic features (see Salat 1996, Estrada 1996): Alboran Sea-Vera Gulf; Alacant-Eivissa; Ebro Delta-Columbretes Islands; and central-north Catalunya. The Alboran Sea and the Vera Gulf are characterised by a narrow continental shelf, as well as by the direct influence of surface Atlantic waters, which lead to local areas of high productivity. The continental shelf broadens in the Alacant - Eivissa area, where surface inflowing (modified) Atlantic and outflowing Mediterranean waters meet around the Eivissa sill. Around the Ebro Delta and the Columbretes Islands the continental shelf is widest (up to 70 km), and the area is highly productive as a combined effect of the Liguro-Provençal-Catalan front at the continental shelf becomes narrow again, with the Liguro-Provençal-Catalan front flowing south-westwards along the continental slope.

Figure 1. Map of the study area, showing the most important geographical references. The area where fieldwork was conducted at sea is shown in grey. The four sectors considered were: Alboran Sea-Vera Gulf (I), Alacant-Eivissa (II), Ebro Delta-Columbretes (III); and central-north Catalonia (IV). The latter three sectors and the remaining isles of the Balearic Archipelago (Mallorca and Menorca) were considered to represent the typical foraging range of the Balearic shearwater during the breeding season



Two commercial fisheries were selected for study given their importance in the western Mediterranean: bottom trawlers (diurnal activity) and purse-seiners (nocturnal activity). The former target on a wide variety of demersal species, generating large amounts of discards, while the latter mostly capture small pelagic fish, being more selective and usually generating few discards. In the Spanish Mediterranean, the official census is of ca. 1175 trawlers, while the number of purse-seiners is lower and more difficult to determine with confidence (Irzaola et al. 1996, Lostado 1997). Since 1991, an increasing number of ports (though still not all), have conducted trawling moratoria of two months during the spring, coinciding with some stage of the breeding period of the Balearic shearwater (i.e. March-June; Mayol 2000). Purse-seiners are also subject to moratoria in some areas, during the winter.

Cruises on board commercial fishing vessels were conducted in two specific zones: off the Ebro Delta and off Barcelona. The former area was selected due to its high productivity (e.g. Estrada 1996), and because it was assumed that an important fraction of the breeding population of the Balearic shearwater usually feeds there (e.g. Abelló & Oro 1998). The latter area was selected basically due to the high concentrations of Balearic shearwaters recorded in winter (Gutiérrez & Figuerola 1995).

Methods

A total of 114 one-day cruises were performed on board commercial fishing vessels, 58 off the Ebro Delta (29 on board trawlers and 29 on board purse-seiners, 1997-1998) and 58 off Barcelona (all on board trawlers, 1996-2000). Data were also collected during experimental trawling surveys conducted on board the R/V "Cornide de Saavedra", during the late spring of 1999 (4.V-4.VI) and 2000 (22.V-22.VI), throughout the study area considered. Data collected on board commercial fishing vessels were considered separately for different seasons, defined according to the annual cycle of the Balearic shearwater: breeding period (March-June); post-breeding/moulting period (July-October); and wintering period (November-February).

Censuses of birds attending fishing vessels. Seabirds attending fishing vessels were counted and identified to the species level at 15-min intervals during the fishing activity (from the hauling of the net through the whole discarding process). Then, the maximum number of birds per haul was recorded. In the case of experimental trawling surveys, only one count was performed for each haul, short after the hauling of the net.

To assess differences in the numbers of Balearic shearwaters attending commercial trawlers, depending on the activity of these vessels, each 15-minute count was classified as: (1) net on the sea surface (while being either hauled or lowered); (2) normal discarding; (3) moments of low or null offer of discards, before all the by-catch has been discarded (for more details, see Arcos et al. 2001). The mean number of shearwaters was then calculated for each activity and haul. At purse-seiners, we differentiated between the hauling of the net (when seabirds capture fish concentrated near the sea surface, usually at night); and the discarding activity (usually of little importance and separated in time, performed during the way back to port, with daylight; Arcos et al. 2000b).

Discard experiments. At trawlers, discard experiments were conducted when possible, coinciding with the discarding activity of the fishermen. Fish from the discard

fraction were thrown overboard individually or in low numbers at a time, after being identified to the species level and classified according to their length into six size classes (here regrouped into three classes: 0-9 cm, 10-19 cm, and ≥ 20 cm). Each discarded item was followed until its final fate, either sunk or picked up by any seabird. In the latter case we recorded the seabird species, and if the item was swallowed, lost, or kleptoparasitised by other seabird.

Counts of seabirds following the trawler were performed regularly during the discard experiments, and were recorded independently of the maximum number of seabirds censused during the whole haul. These counts allowed to calculate a foraging success index, based on the Ivlev's electivity index (Krebs 1989), in order to assess the efficiency of the shearwaters at capturing discards,

$$SI = \frac{O - E}{O + E}$$

where SI is the foraging success index of Balearic shearwaters, O is the observed number of items swallowed by the shearwaters, and E is the expected number of items swallowed, estimated from multiplying the total number of items offered by the representation (percentage) of the species behind the vessel. If this representation was observed to change substantially, the experiment was stopped. Only those experiments with more than 30 items discarded were considered, in order to minimise biases resulting from small sample size (Garthe and Hüppop 1998a).

Table 1. Fish-type species/groups selected according to their representation in the discards. The table shows the values of the three variables considered to estimate a mean calorific value of the discards (*CAL*, see text) obtained by shearwaters from of each these groups: preference index for each group (*Pl_i*), representation in weight of each group in discards (W_i , %), and specific calorific value (*CAL_i*, in kJ g⁻¹). (SD standard deviation)

| | | | CAL_i (kJ g ⁻¹) | | |
|---------------------------------|--------|-----------|-------------------------------|------|--|
| | PI_i | $W_i(\%)$ | Mean | SD | |
| Sardine, Sardina pilchardus | 1.45 | 18.61 | 10.03 | 0.97 | |
| Anchovy, Engraulis encrasicolus | 2.31 | 6.71 | 6.67 | 0.44 | |
| Bogue, Boops poops | 0.13 | 18.16 | 5.94 | 0.23 | |
| Gadiformes | 1.39 | 21.43 | 5.81 | 0.75 | |
| Gobiidae/Callionymidae | 1.50 | 14.59 | 5.34 | 0.47 | |
| Pleuronectiformes | 0.64 | 7.67 | 5.28 | 0.42 | |
| Others | 0.54 | 12.83 | 7.60 | 0.78 | |

We assessed fish size selection by Balearic shearwaters comparing the offer and the capture of fish of each size class. A similar procedure was performed to assess fish type selection, considering seven main classes of fish species/groups (see Table 1). These groups were determined after examining sub-samples of discards during the breeding season of the Balearic shearwater, when the resource seems more important in its diet (see Results; n =

11 hauls, 2453 fish and 24.9 kg examined). We estimated the number of items of each group expected to be captured by the shearwaters in each experiment, taking into account the total number of items actually captured during the experiment and the relative offer of each group. Then, we summed this value for all the experiments and the resulting value was compared with the actual number of items of each group captured by the shearwaters. A preference index (*PI*) was then calculated for each fish-type group as the division of the number of items swallowed by the number of items expected to be swallowed by the shearwaters.

Strip-transect counts. During the experimental trawling surveys we performed strip-transect counts to estimate seabird densities (birds km²), when the vessel was steaming between trawling stations. These counts were performed either 90° or 180° forward, depending on the conditions of light, considering a strip of 300 m wide (at each side when counting at 180° forward), which was determined according to Heinemann (1981). Flying birds were counted using snapshots, following Tasker et al. (1984). Birds observed out of the strip were also recorded, although they were not included in the estimates of seabird densities. The units of census were 10-min counts, although data were later gathered for longer periods (transects), provided that the counts were continuous and performed under similar conditions. In total, we conducted 972 ten-minute counts, which were regrouped into 282 transects, covering an area of 1400 km². For each transect we recorded the mean sea depth (categorised as 0-99; 100-199; and \geq 200 m), and the mean distance to the mainland coast (0-9; 10-19; and \geq 20 nautical miles). During transect counts, we recorded all instances of active feeding behaviour which involved Balearic shearwaters. In these occasions, we noted the foraging strategy and the number of shearwaters involved.

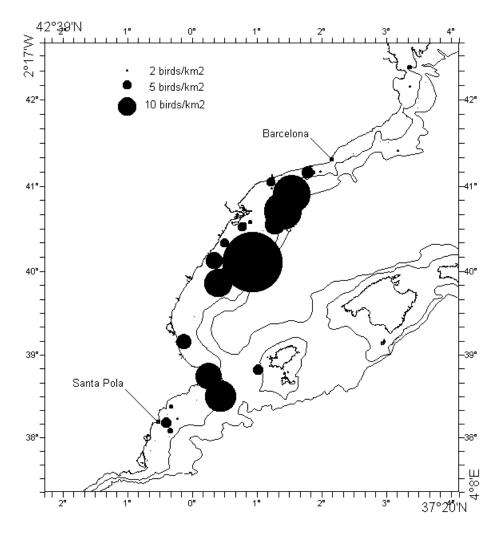
Bioenergetic model for Balearic shearwaters. A bioenergetic model was built to estimate to which extent the population of Balearic shearwaters (adults plus immatures) exploits trawler discards during the breeding season (March-June). Since several aspects of the feeding ecology (such as foraging ranges) and demography (such as survival rates or proportion of non-breeders) are little know or simply unknown, many inputs of the model had to be set from the literature published on similar species or estimated from data collected from few individuals. The significance of discards (*SD*, in terms of energy) was estimated by dividing the energy obtained from discards (*ED*) by the energetic requirements of the shearwaters population (*ER*). In turn, the energy provided by discards was obtained by multiplying several variables: amounts of commercial catches (*CC*), ratio of fish discarded to commercial catch (*DR*), consumable fraction of discards (*CF*), discard fraction consumed by shearwaters (*CR*), calorific value (*CAL*) and assimilation efficiency (*AE*). The energetic requirements were obtained by multiplying the field metabolic rate (*FMR*, estimated from body mass *BM*) by the number of shearwaters (*N*_S):

$$SD = \frac{ED}{ER} = \frac{CC \times DR \times CF \times CR \times CAL \times AE}{FMR \times Ns}$$

Since most of these variables have some variability, a coefficient of variation (CV) of *SD* was also estimated as a precision measure through the Delta method (Stratoudakis 1999):

$$CV^{2}(SD) = CV^{2}(CC) + CV^{2}(DR) + CV^{2}(CF) + CV^{2}(CR) + CV^{2}(CAL) + CV^{2}(AE) + CV^{2}(FMR) + CV^{2}(BM) + CV^{2}(N_{S})$$

Fig. 2. Balearic shearwater densities in the eastern Iberian shelf, recorded during May-June of 1999 and 2000. The area considered for the bioenergetic model, where most birds were detected, laid between Barcelona and Santa Pola



Energy obtained from discards (ED): Values obtained for the different variables directed to estimate the total energy that Balearic Shearwaters secure from discards are shown in Table 2. The area where most individuals may forage during the breeding season was defined according to our observations, as well as to data from satellite-tracked individuals (SEO/BirdLife, unpublished). This area comprised most of the Iberian Shelf (Barcelona to Santa Pola, see Fig. 2), and holds 576 trawlers. Commercial catches in this areas were estimated from multiplying the number of trawlers by the average amount of fish landed by each vessel, which in turn was estimated from data obtained at four ports (135 vessels) for the period 1994-1998 (March-June). This allowed estimating the amounts

of discards available to seabirds, by applying to the model the ratio of discards to commercial catches (DR) and the fraction of discards *a priori* consumable by seabirds (CF). We then considered the percentage of (consumable) discards captured by Balearic shearwaters (CR) to know the total amount of discards consumed by these seabirds. Since CR was estimated as a numeric percentage (% of fish items captured by shearwaters), and we were interested in a percentage in weight (and ultimately in energy), we estimated a calorific value of discards (CAL) that solved this problem, in the following way:

$$CAL = \sum_{i=1}^{7} W_i \times PI_i \times CAL_i$$

where Wi is the representation in weight of fish type *i* in the discards, PI_i is the preference of shearwaters for this fish type, and CAL_i is the calorific value of *i* (see Table 1). PI_i values slightly differ from those presented in Table 1 (PI_i , which results from the calculation explained above), since the former were weighted to average 1. Fish size was not considered here, since the shearwaters did not show clear preferences for any size class (see results) within the range of fish lengths discarded (most fish not exceeding 15-20 cm in length; authors, unpublished data). All data were obtained from samples collected on board or analysed at the laboratory during the study (see Table 1). The energetic equivalent for each group of fish was obtained through lipid extractions of 15 fish species, totalling 80 samples (J. M. Arcos, D. Oro & X. Ruiz, unpublished data), following Peters (1983). We assumed an assimilation efficiency of 75% following Furness et al. (1988) and measured without error (Stratoudakis 1999).

Energetic requirements for shearwaters (ER): The energetic requirements of the Balearic shearwater population were estimated from multiplying the field metabolic rate (FMR) by the number of shearwaters in the population (N_S) . In turn, FMR was considered as 3.9 times the basal metabolic rate (BMR) for breeders and 2.5 times BMR for nonbreeders, following Garthe et al. (1996). Finally, BMR (kJ day⁻¹) was estimated as 2.30(BM)^{0.774} according to Bryant and Furness (1995). BM is body mass (g), and was estimated from individuals caught at colonies (M. McMinn, unpublished data). Variability of metabolic estimates was obtained from Furness and Bryant (1996). Although these data came from a study on breeding Fulmars (larger than Balearic shearwaters and living in much higher latitudes), we were only interested in the coefficient of variation, which we assumed was independent of the species, its weight or environmental features. The total breeding population of Balearic Shearwaters was estimated at 3300 pairs (Aguilar 1991). We also estimated a number of immatures (sum of first, second and third year old individuals) considering a breeding success of 0.65 chicks per pair (M. McMinn, unpublished data), a first year survival of 0.70 and a second and third year survival of 0.80, and considering the sum of individuals surviving from the three previous cohorts. Since we have no data about the proportion of adults physiologically mature but that do not reproduce, we did not take this parameter into account.

| Parameter | Mean | п | Transf. | CV (%) | |
|--|---|--------|----------------|-------------|------|
| Energy consumed | | | | | |
| Commercial catches (CC, kg v | essel ⁻¹ month ⁻¹) | 4486.4 | 4 | Square root | 12.1 |
| Discard ratio (DR, %) | | 83.45 | 34 Square root | | 34.1 |
| Consumable fraction of discard | ds (<i>CF</i> , %) | 69.52 | 27 | Arcsine | 29.8 |
| Consumption rate (CR, %) | | 1.63 | 20 | 20 Arcsine | |
| Calorific value (<i>CAL</i> , kJ g^{-1}) | | 6.65 | 80 No | | 4.17 |
| Assimilation efficiency (AE, % |) | 75 | - | - | 0 |
| Energetic requirements | | | | | |
| Field metabolic rate | breeders | 1095.3 | 14 | No | 12.3 |
| $(FMR, kJ d^{-1} bird^{-1})$ | non-breeders | 702.1 | | | |
| Body mass (BM, g) | | 496.64 | 448 | No | 9.0 |
| Number of breeders (NS) | | 6600 | - | - | 0 |
| Number of immatures | | 3863 | - | - | 0 |

Table 2. Specific input parameters for model estimating total energy available from discards to shearwaters. All data correspond to March-June (i.e. breeding period). The table also indicates when estimates were performed using data transformation, and which transformation was employed. (*n* sample size; CV coefficient of variation, calculated from absolute or transformed data)

Statistical analysis. Data were first tested for normality, using the Shapiro-Wilk test. When this assumption was violated, we either made the appropriate transformations (input data in the model) or used non-parametric statistics, following Zar (1996).

Comparisons of the number of birds associated with fishing vessels according to their activity were performed grouping censuses for each haul (matched-data), by means of the Friedman two-way analysis of variance (ANOVA), given the interdependence of the data. Post-hoc comparisons were then performed with the Wilcoxon matched-pairs test. In the other cases, Mann-Whitney U and the Kruskall-Wallis tests were employed. Chi-square goodness of fit test and contingency tables were also used when appropriate, as well as the Speraman's rank correlation.

Significance level was held at 0.05, although marginal values are also discussed following Stoehr (1999). The problem of pseudoreplication was partially avoided by considering only one count per haul (that of the maximum number of birds). In addition, hauls were usually well separated in time and space. In the case of strip-transect counts, we regrouped the 10-min counts in longer periods (transects).

Results

Censuses of birds attending fishing vessels. Balearic shearwaters attended commercial trawlers regularly, especially during their breeding season (March-June; see Table 3). The maximum numbers of shearwaters associated with these vessels were

observed off the Ebro Delta, with the largest concentrations occurring in May (Fig. 3). Experimental trawling surveys conducted during the late spring confirmed the attendance of Balearic shearwaters to this fishing practice throughout the study area, and again showed the largest concentrations in the Ebro Delta-Columbretes area, with lower importance of the Alacant-Eivissa and the central-north Catalunya areas, and very few birds in the Alboran Sea- Vera Gulf area (Kruskall-Wallis test, $H_{5,229} = 82.3$, p < 0.0001; Fig. 4). Post-hoc analysis showed significant differences between all these areas, with the exception of Alacant-Eivissa and central-north Catalunya. The shearwaters did not attend trawlers off their main colonies (Formentera-Eivissa), although several birds were observed there flying towards or from the Iberian shelf.

Table 3. Numbers of Balearic shearwaters attending fishing vessels (TRWL = trawlers, PS = Purse seiners) off Barcelona (BCN) and off the Ebro Delta (DELT), according to the season (breeding: March-June; post-breeding/moulting: July-October; wintering: November-February). The median and the mean values are given along with the range. The percentage of hauls with presence of the species (P) and the representation in number with respect to the total seabirds censused behind the vessel (%n) are also provided. (*n* number of hauls)

| | | Breeding | | | | | Post-breeding/Moulting | | | | Wintering | | | | | |
|------|------------|----------|------------|-----|------------------|---------------|------------------------|--------------|-----|------------------|------------|---------|-------------|-----|------------------|--------------|
| | | п | Р | %n | Median/ Mean | Range | п | Р | %n | Median /Mean | Range | п | Р | %n | Median /Mean | Range |
| BCN | TRWL | 77 | 72.7 | 5.5 | 2/4.9 | 0-38 | 75 | 29.3 | 0.3 | 0/0.4 | 0-4 | 28 | 60.7 | 1.7 | 1/2.8 | 0-27 |
| DELT | TRWL PS | | 95.7 80 | | 10/55.4 4/6.3 | 0-550 0-21 | 24 7 | 50.0 28.6 | | 0.5/1.7 0/0.4 | 0-9 0-2 | 14 2 | 92.9 100 | | 4/8.4 9.5/9.5 | 0-33 9-10 |

Fig. 3. Monthly numbers of Balearic Shearwaters (median and non-outlier range) associated with trawlers off the Ebro Delta (a) and off Barcelona (b). January and February were not sampled (NS) off the Ebro Delta, while trawling moratoria always included June during the years of fieldwork at this site

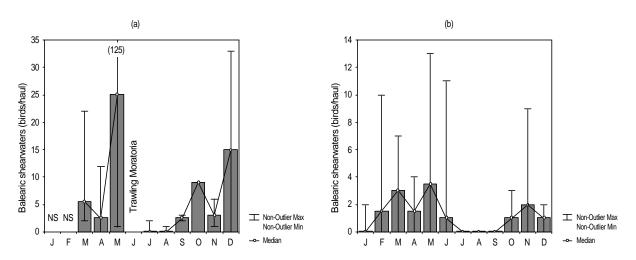
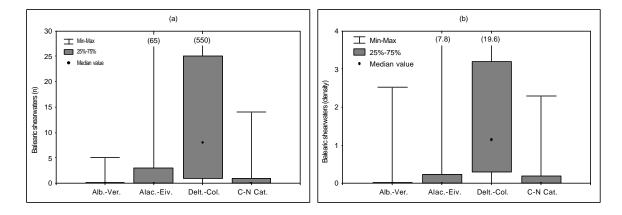


Fig. 4. Numbers of Balearic Shearwaters (median and range) recorded during experimental trawling surveys in May-June of 1999 and 2000, according to the geographical area (Alboran-Vera Gulf; Alacant-Eivissa; Ebro Delta-Columbretes; central-north Catalunya). Data presented are the number of birds associated to the trawler during the hauling of the net and the discarding activity (a), and the density (birds km⁻²) recorded during band transect counts (b)



Purse-seiners also attracted Balearic shearwaters off the Ebro Delta, although usually in lower numbers than did trawlers (Table 3). This occurred basically during the discarding process, at dawn (data presented in Table 3); contrarily, the presence of Balearic shearwaters at night, during the hauling of the net, was only occasionally detected (mean = 0.2 birds/haul, 10.5% of presence, n = 19 hauls; Wilcoxon matched-pairs test, $T_{18} = 2.0$, p < 0.005). The highest numbers of shearwaters attending purse-seiners occurred during the breeding season and in winter. During the breeding season, the number of shearwaters at these vessels tended to be higher coinciding with local trawling moratoria, although the difference was not statistically significant (Mann-Whitney test, $U_{3,7} = 3.0$, p = 0.09).

At trawlers, Balearic shearwaters reached their highest numbers in those moments of maximum offer of discards, with lower attendance when the net was being hauled, and even lower when very few discards were thrown overboard (Friedman's test, $\chi^2_r = 44.7$, p < 0.0001). The shearwaters usually followed trawlers at some distance, mostly capturing those discards that had sunk through plunge-dives and surface-dives. Less often Balearic shearwaters approximated to the vessel and captured discards short after being thrown overboard (but also sunken), a behaviour that mostly occurred when the shearwaters were present in high numbers.

Discard experiments. The efficiency of Balearic shearwaters at capturing discards was very low according to their success index (mean = -0.85, ranging from -0.31 to -1, n = 36 experiments). Despite that, the shearwaters could capture far more discards than observed, since their diving behaviour would allow them to capture items assumed to be sunk, at considerable distances from the vessel. This interpretation is supported by the fact that the success index was highest when high numbers of shearwaters attended the trawler (Spearman's correlation, r = 0.60, p < 0.0001), since in these cases the birds usually aproximated to the vessel and were more easily detected when capturing fish. Alternatively, the high representation of the sherawaters could increase their success index since they would be less vulnerable to competitors and kleptoparasites. Kleptoparasitic events involving Balearic shearwaters (always as hosts) were recorded in three occasions (6.5% of

the attempts to capture discards by the shearwaters, n = 46). These attacks were performed by yellow-legged gulls *Larus cachinnans* (n = 2) and Audouin's gulls *Larus audouinii* (n = 1), and were successful only in one occasion.

Balearic shearwaters showed significant differences in the selection of different groups of fish (chi-square goodness of fit test, $\chi_6^2 = 15.7$, p = 0.02, n = 2786 items offered and 40 items swallowed; see *PI* in Table 1). Clupeoids (anchovy *Engraulis encrasicolus* and sardine *Sardina pilchardus*), gadoids, and flatfish were captured more often than expected, while the bogue *Boops boops*, the gobies and dragonets (Gobiidae and Callionymidae), and the remaining species (grouped as 'others') were captured less often. When considering the size of the fish, there were not significant differences in the selection of the different size-classes considered (contingency table, $\chi_2^2 = 0.55$, p = 0.8). However, discarded items longer than 20 cm captured by the shearwaters were in all cases snake-like fish, more easily swallowed, whereas any round-fish nor flatfish of this size class was captured.

Strip-transect counts. A total of 1194 birds were recorded during transect counts, with a mean density of 0.58 birds km⁻². Although higher densities of shearwaters were detected in 1999, when the survey took place in May (0.77 birds km^{-2}), than in 2000, when the survey was carried out mostly in June (0.29 birds km^{-2}), differences in the density of shearwaters between years were not significant (Mann-Whitney test, $U_{168,114} = 9020.5$, p = 0.4). Transect counts revealed the same geographical pattern than that obtained from censuses of birds attending experimental trawling, with the highest densities in the Ebro-Delta-Columbretes area, lower representation in the Alacant-Eivissa and the central-north Catalunya areas, and very low densities in the Alboran Sea- Vera Gulf area (Kruskal-Wallis test, $H_{3,282} = 102.8$, p < 0.0001; Figs. 2 and 4). When considering the sea depth and the distance to the coast, the density of shearwaters was highest in areas lower than 100 m depth (Kruskal-Wallis test, $H_{2,282} = 62.3$, p < 0.0001), while this parameter increased with the distance to the coast (kruskal-Wallis test, $H_{2,282} = 7.2$, p = 0.03). However, these differences were in part the result of different topographic features between areas differing in their average densities of shearwaters, and the effect of either the sea depth or the distance to the coast was not significant in any case when considering each of the four areas separately.

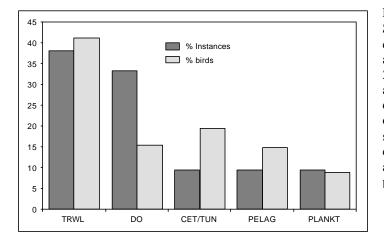


Fig. 5. Feeding strategies by Balearic Shearwaters observed during transect counts: percentage of instances (N = 21) and percentage of birds involved (n = 245). The strategies observed were the association with trawlers (TRWL); the capture of fish under floating drifting objects (DO); the association with subsurface predators (CET/TUN); the direct capture of small pelagic fish (PELAG); and the association with masses of plankton (PLANKT)

During transect counts we observed Balearic shearwaters feeding actively on 21 occasions, which involved 245 birds (Fig. 5). The most frequent foraging strategy was the capture of discards behind trawlers, which was observed in eight occasions and involved 101 birds. The capture of fish under floating drifting objects was also frequent during daylight hours, although involved fewer birds (7 instances, 38 birds). Other foraging strategies were less frequently observed and included the association of shearwaters with sub-surface predators (striped dolphins *Stenella coeruleoalba*), the direct capture of small pelagic fish close to the sea surface, and the capture of planktonic organisms where occurring in high densities. The latter behaviour was only observed in hours of low light levels (late evening).

Bioenergetic model for Balearic shearwaters. According to our model, 40.8% of the energetic requirements of the Balearic shearwater population would be obtained from discards during the breeding season (March-June), though this estimate was subject to strong variability (CV = 88.7%, $SD = \pm 36.2\%$; 95% CI: 0-111.9%). This average value would be traduced in 4272 that could meet their energetic requirements by solely feeding on discards. Considering numbers of breeders and non-breeders and the different energetic requirements of the two groups, breeders would obtain in average 35.4% of their energetic requirement from trawler discards, whereas the estimate for non-breeders would be of 55.3%. Finally, in case that only adults were present within the area considered in the model, they would obtain 56.2% of their energy requirements from discards.

Discussion

Breeding season, extensive use of discards

This study confirms the extensive use of trawler discards by Balearic shearwaters, which seem especially important during the late breeding season (May-June). At this time of the year the productivity of the Mediterranean decreases due to the stratification of water masses, which reduces the availability of nutrients in the photic zone and leads to a general impoverishment of the surface layers (e.g. Margalef 1985, Salat 1996). Trawlers could be then of special importance, since they provide demersal prey (discards) otherwise unavailable to the shearwaters, just when the energetic requirements of these seabirds are the highest (i.e. chick rearing) and pelagic prey is less available (cf. Le Mao & Yésou 1993). In concordance, the distribution of the shearwaters at sea coincides with the main grounds of trawling fisheries in the western Mediterranean, which are especially important off the Ebro Delta (Irzaola et al. 1996, Lostado 1997). Hydrographic features, however, could also explain this distribution. Indeed, despite the general impoverishment of the surface waters, several mechanisms of fertilisation can still operate and be important at a local scale during the spring-summer, such as shelf-slope fronts and river runoff (Estrada 1996, Salat 1996). This is the case of the area under consideration, influenced in its whole by the Liguro-Provençal-Catalan front, and more locally by the Ebro River runoff. Associated to this high fertility, anchovies spawn in this area mostly during June and July

(Palomera 1992), and probably represent another important reason for the shearwaters to forage there.

Balearic shearwaters concentrated behind trawlers when high amounts of discards were thrown overboard, usually capturing them at considerable distances from the vessel, most often once sunken. This was possible given the diving abilities of the shearwaters, which are able to reach depths of almost 30 m (Mayol et al. 2000). This behaviour considerably differed from that of gulls and terns attending trawlers (Oro & Ruiz 1997), thus reducing direct competition (e.g. Furness et al. 1992, Garthe & Hüppop 1998b, Arcos et al. 2001), although the shearwaters occasionally received kleptoparasitic chases. Purseseiners also attracted Balearic shearwaters during the discarding activity, although in lower numbers than did trawlers. Balearic shearwaters showed a special preference for Clupeoids among trawler discards, while purse seiners basically discarded this kind of fish. This should be taken into account when assessing the importance of discards through dietary studies, since Clupeoids are also the typical prey assumed to be captured by the shearwaters when feeding by their own (Snow & Perrins 1998).

According to the bioenergetic model, trawler discards supply ca. 40% of the energy requirements of the population of Balearic shearwaters during the breeding season, though this estimate is subject to strong variability and should be considered with caution. For several reasons, it seems likely that the actual importance of discards for Balearic shearwaters is even higher than the estimate above mentioned. Firstly, the rate of capture of discards behind trawlers was probably underestimated. Indeed, the particular strategy of Balearic shearwaters behind fishing vessels makes difficult to detect their captures, and items considered to be sunken could be actually swallowed by these birds. Moreover, fish in discard experiments is often offered in small amounts, thus being easily captured by gulls and terns that keep close to the vessel. When fishermen discard fish in large amounts at a time the proportion of fish captured by gulls and terns decreases, since the discards often sink quickly, thus increasing the availability of fish for the shearwaters (cf. Berghahn & Rösner 1992, Garthe & Hüppop 1998a). Secondly, fisheries statistics tend to underestimate the actual amount of catches (e.g. Irzaola et al. 1996), thus leading to an undervalue of the amounts of discards available from trawlers. Thirdly, we did not consider purse seiners in the model, given the unpredictability of their discards (Arcos et al. 2000b) and their relative low number. Fourthly, we considered that the whole population of the Balearic shearwater was within the area considered for the model, representative of most of the foraging range for the breeding birds. However, immature birds could forage in other areas during the breeding season, as suggest the observations of hundreds of birds leaving the Mediterranean through Gibraltar as early as in May (e.g. Bourne et al. 1988). This effect could be partly counterbalanced by having not considered non-breeding adults in the model, given the lack of information about the importance of these birds. Finally, the model considers all the breeding season as a whole, but it seems probable that the relative importance of discards increases as this season progresses. Thus, the representation of discards in May-June would be higher than the average value estimated for the whole breeding season. The establishment of trawling moratoria in spring-early summer could partly counterbalance the factors previously exposed, since they would reduce the availability of discards within the foraging range of the shearwaters. However, these moratoria do not affect all ports, nor are conducted at the same time by different ports, thus not completely precluding the consumption of discards by the shearwaters at any time. Moreover, purse seiners partly compensate for the lack of trawling discards, as shearwaters

appeared to attend these vessels in higher numbers during trawling moratoria. In any case, this is important to obtain better estimates of some of the parameters employed in our model, such as consumption rate, commercial catches, and relationship between commercial catches and discards. Meanwhile, our present estimate seems enough to confirm the importance that discards play on the feeding ecology of Balearic shearwaters, at least during their breeding season.

During transect counts, Balearic shearwaters were observed conducting several feeding strategies. In hours of high light levels, these strategies were related with processes that drive or keep prey close to the surface, since most pelagic organisms perform diel vertical migrations and are not available from the surface at these hours (e.g. Estrada et al. 1985). The shearwaters most frequently fed on trawler discards (38% of the feeding instances observed and 41% of the birds involved; which approximates and supports our energetic estimate). Floating drifting objects were also often prospected (33% of the feeding instances observed, although few birds were involved), since they usually present associated communities of fish (Arcos et al. 2000a). The shearwaters also associated with Striped Dolphins, which can drive prey towards the sea surface (see Oro 1995). In two occasions we observed Balearic shearwaters directly preving upon small shoals of pelagic fish, but these could have been also driven to the surface by sub-surface predators. Nocturnal foraging did not seem important (cf. Mayol et al. 2000), since only occasionally Balearic shearwaters were observed at night during the cruises on board purse-seiners. However, we recorded Balearic shearwaters feeding upon plankton in hours of low light levels, and this could be a common strategy in crepuscular hours (i.e. at late evening and at dawn), when these prey are closest to the surface (Estrada et al. 1985), especially in areas of anchovy spawning (Palomera 1991).

Significance of discards out of the breeding season

After the breeding season, the main fraction of the Balearic shearwater's population migrate to the French Atlantic coast (Bourne et al. 1988, Le Mao & Yésou 1993), where the hydrographic conditions seem more suitable than those in the Mediterranean in summer and early autumn (e.g. Koutsikopoulos & Le Cann 1996). During this period very few Balearic shearwaters were observed in the study area, but those birds remaining there attended fishing vessels regularly. The shearwaters were common again from late September onwards, although the numbers observed behind trawlers were lower than in the breeding season. Apparently, trawling discards are of little importance during the winter, when the shearwaters concentrate in high numbers in coastal and shallow waters off the NE Iberian Peninsula (Gutiérrez & Figuerola 1995, Arcos 2001), presumably feeding upon schools of sardine (cf. Bas et al. 1985, I. Palomera pers. com.).

Contrarily to trawlers, that attracted the highest numbers of shearwaters during the breeding season, purse seiners appeared to be more important for this species in winter, although our sample size was small. This coincides with the pattern observed for Audouin's gulls, which apparently preferred purse seiners to trawlers in winter because of the high competition levels reached at the latter (Arcos et al. 2001).

Balearic shearwaters, fisheries, and conservation

In the last decades there has been increasing consciousness of the impact of human fisheries over the entire marine ecosystems (e.g. Bostford et al. 1997, Tegner & Dayton 1999, Gislason et al. 2000). This point of view makes necessary the development of new fishing policies, based on a precautionary and ecosystem-based approach (see FAO 1995). One goal of these policies is to reduce discards, which could be partly accomplished through the development of more selective gears (increasing at the same time the size of the fish discarded; e.g. Fluharty 2000). This situation would first affect those species more sensible to competition and relying on the smallest discarded items (e.g. Furness 1992, Arcos et al. 2001, Oro & Furness 2002). An increase in the mean length of discards would probably affect Balearic shearwaters, since these birds were not observed to consume any roundfish nor flatfish larger than 20 cm. An increase of direct competition with other seabirds would probably be less important, given the particular behaviour of the shearwaters at capturing discards. Temporal moratoria are also promoted by the new fishing policies, and are currently applied in our study area. Although moratoria could be unfavourable to Balearic shearwaters in the short term, the associated recovery of the marine ecosystem should be considered a preferential target, and would probably benefit them in the long term. However, the accurate design of trawling moratoria could help to reduce their impact over the shearwaters and other seabirds of conservation concern, such as Audouin's gull. So far, local moratoria established in 1991 have been based on preliminary results obtained during the 60's in the same geographical area (Suau 1979, Lostado et al. 1999), although very little is known about their effects (e.g. Martín 1995). If not detrimental for marine ecosystems, the possibility of establishing moratoria out of the breeding season of the shearwaters, or in the early stages of that season, would probably reduce the effect of these management measures on the feeding ecology of these seabirds.

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Mercury levels in seabirds and their fish prey at the Ebro Delta (NW Mediterranean): the role of trawler discards as a source of contamination¹

Abstract. We determined mercury levels in internal tissues and feathers from corpses of Audouin's Larus audouinii and Yellow-legged gulls L. cachinnans michaellis, common terns Sterna hirundo and European shags Phalacrocorax aristotelis desmarestii, as well as from fish representative of trawler discards, collected at the Ebro Delta (NW Mediterranean) in March-July (seabird's breeding season) of 1997-1999. The levels of mercury were significantly lower in epipelagic (Clupeiforms) than in demersal fish. When representation of each species in the discards is taken into account, the mean mercury concentration from this resource is more than double that of epipelagic fish (the main natural prey for most seabirds in the area). The shag was the only species with direct access to benthic fish, as it can dive to the seabed, and shags presented high levels of mercury even though they do not feed on discards. The other seabirds showed mercury levels in accordance with their seasonal use of discards. Audouin's Gull, which exploits discards extensively during the breeding season, had the highest levels in those tissues reflecting mercury intake during the breeding season (i.e. liver and first primary feathers). In contrast, the common tern makes little use of discards and presented the lowest levels of mercury. For those samples reflecting the intake of mercury during the winter (i.e. mantle feathers), when only the yellow-legged gull exploits discards extensively, this species presented the highest values. Audouin's Gull and the common tern showed similarly low concentrations of mercury for this period. We conclude that consumption of discarded demersal fish strongly influenced mercury contamination of surface-feeding seabirds.

Key words: Biomonitoring; diet; heavy metals; Mediterranean; seabird-fisheries interactions

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Introduction

Mercury is a highly toxic, nonessential heavy metal, which is released to the environment by natural sources such as volcanic emissions, continental particulate and volatile matter, and fluxes from the marine environment (Nriagu 1989). In addition, anthropogenic emissions (e.g. from fossil fuel combustion, waste incineration, and chemical production processes) have increased over the last two centuries, contributing twice the amount of mercury released by natural sources at present (Nriagu 1989, Thompson 1996, Cossa et al. 1997, Monteiro et al. 1999). This metal is of special concern for aquatic ecosystems, where inorganic mercury is efficiently biotransformed into organic forms (methylmercury) and accumulates in biota (Bryan 1979, Lindqvist 1991). Moreover, mercury increases in concentration up aquatic food chains, a process termed

biomagnification (Bryan 1979, Walsh 1990, Bearhop 2000a). In the oceans, methylation processes are especially important in subthermocline waters (mesopelagic environments), where inorganic mercury arrives mainly through atmospheric deposition (Mason & Fitzgerald 1990, Cossa et al. 1994). As a consequence, mesopelagic organisms exhibit particularly high levels of mercury (Monteiro et al. 1996, 1998), and appear to have elevated tolerance to this metal (e.g. Thompson 1996). Mercury levels in these organisms are not directly related to acute human pollution events, and are quite constant at very broad scales (Monteiro et al. 1999). In contrast, coastal and estuarine areas seem to play a minor role in the global cycle of mercury. However, these areas can exhibit locally high levels of mercury directly resulting from human pollution, often associated with riverine inputs (Luoma 1990). In coastal polluted zones, mercury is readily deposited in sediments and is less bioavailable than in the open oceans (e.g. Nisbet 1994, Cossa et al. 1997), but is still incorporated into local food chains in a significant degree (e.g. Mikac & Picer 1985, Braune 1987, Furness et al. 1995). Moreover, coastal organisms tend to have lower tolerance to mercury than those in mesopelagic environments since the background levels of mercury in coastal waters are usually much lower (e.g. Thompson 1996).

The high toxicity of mercury and the increase of this metal in the environment resulting from human activities have emphasised the necessity of monitoring its levels, both spatially and temporally (e.g. Scheuhammer 1987, Furness 1993). In aquatic ecosystems this has often been done using live organisms as monitoring tools, given the complex behaviour of mercury in these environments (which includes several biologically-mediated processes), as well as its property of biomagnification. In this respect, seabirds are appropriate for several reasons, such as high trophic position (thus reflecting integrated mercury levels over the whole food chains), and relatively well known biology (Walsh 1990, Furness 1993). In addition, increasing knowledge of mercury dynamics in seabirds allows the interpretation of their mercury levels with some confidence (e.g. Monteiro et al. 1998). Mercury dynamics includes assimilation from the diet, accumulation in internal tissues (mainly the liver) and redistribution during moult periods to the growing feathers (Furness et al. 1986, Honda et al. 1986, Braune & Gaskin 1987, Monteiro and Furness 2001). Hence, mercury levels in the different seabird tissues are considered to ultimately reflect dietary input (e.g. Leonzio et al. 1986, Braune 1987, Monteiro et al. 1998, Bearhop 2000a). However, factors such as the moult pattern and the migratory habits of the different seabird species often obscure this relationship and should be taken into account, with considerations varying in accordance with the tissue selected (Walsh 1990, Furness 1993). Since the body pool of mercury is excreted into the growing feathers during moults, internal tissues would reflect mercury levels accumulated from the end of the last moult to the moment of collection. In turn, feathers would reflect levels of mercury accumulated between moults, with feathers grown in different moults reflecting different periods.

Given the importance of the diet in explaining inter- and intraspecific differences in mercury levels of seabirds, research efforts should be directed at ascertaining the content of mercury both in diet samples and in a wide range of prey (cf. Monteiro et al. 1998). In addition, it is important to assess the feeding ecology of the seabird species selected for study (e.g. Monteiro et al. 1999). Within this context, the increasing use of fishery waste by several seabird populations through the last century (e.g. Furness et al. 1992, Garthe et al. 1996, Oro 1999, Tasker et al. 2000) should be considered as a potential extra source of mercury in some cases, since this has led to important changes in their diets. Indeed, seabirds exploiting discards and offal have access to species otherwise unavailable to them

(Furness et al. 1988), which could expose them to higher levels of mercury than those found in their natural prey. This would be the case when discards are composed of either demersal fish (unavailable to surface-feeding seabirds) or mesopelagic fish (unavailable to both inshore and diurnal species, in the latter case because mesopelagic organisms are subject to diel vertical migrations and are available from the surface only at night; e.g. Whitehead et al. 1986). In the present study, we tested the hypothesis that trawler discards can provide extra mercury to some seabird species. In order to do this, we determined mercury levels in seabird tissue samples (feathers, liver, kidney) and discards collected off the Ebro Delta (NW Mediterranean) during the seabirds' breeding season. Four seabird species were selected for analysis, differing in both their feeding ecology and their relative use of discards: Audouin's Larus audouinii and the yellow-legged gulls L. cachinnans michaellis, the common tern Sterna hirundo and the shag Phalacrocorax aristotelis desmarestii. By sampling soft tissues and feathers grown at particular times of year we were able to investigate seasonal changes in mercury contamination that might relate to seasonal changes in diet. In the case of fish, fifteen species representative of discards were selected, including the typical natural prey for most of the seabirds (i.e. epipelagic fish). We predicted that: (1) demersal fish would have higher levels of mercury than epipelagic fish; (2) discards would have higher levels of mercury than typical fish prey of surface-feeding seabirds; (3) seabirds typically feeding upon discards would present higher levels of mercury than those more strictly feeding on epipelagic fish; (4) seasonal differences in the diet and the feeding habits of the seabirds would lead to differences in the levels of mercury accumulated during different periods, and hence in the different feather or soft tissue samples that reflect intake over particular periods. Soft tissues would reflect mercury levels accumulated shortly before their collection (i.e. the breeding season), while feathers would reflect the mercury accumulated either during the winter (when replaced during the prebreeding moult) or during the breeding season of the preceding year (when replaced during the post-breeding moult).

Materials and methods

Study area. The Ebro Delta (40° 43' N, 0° 55' E; NW Mediterranean) is surrounded by a wide continental shelf, with a high biological productivity resulting from the nutrients provided by the Ebro River and the mixing effect of the Liguro-proveçal-catalan front at the continental slope (Salat 1996). This area sustains one of the most important commercial fisheries of the Western Mediterranean, with both bottom trawler (demersal) and purse seine (pelagic) fishing fleets (Irzaola et al. 1996). At the same time, the area is home to one of the most important seabird communities of the Mediterranean, with several species taking advantage of the discards provided by the local fisheries (Oro & Ruiz 1997).

Samples. Between March and July of 1997 and 1998, fish samples were collected from the by-catch fraction of commercial trawlers operating off the Ebro Delta. After determining the composition of trawler discards (n = 14 hauls, 36 kg examined, 3000 fish measured and weighed) we selected 15 fish species, which accounted for 91.4% in weight of the total fraction of discards consumable by seabirds and were considered representative of this fraction (see Table 1). These species were classified into two categories according to

their distribution in the water column, their general ecology (Whitehead et al. 1986), and ultimately their natural availability to surface-feeding seabirds: epipelagic and nonepipelagic (demersal) fish. Epipelagic species comprised Clupeiforms, which feed mostly on plankton and spend an important fraction of the day close to the sea surface. These fish are considered to constitute the main natural prey for most seabird species in the study area, which basically are surface-feeders (Oro 1999). Demersal fish tend to occupy higher trophic levels than epipelagic fish and inhabit greater mean daytime depths. Although rarely captured in a natural way by surface-feeding seabirds, trawler discards make these fish available to some species. Mesopelagic fish species only occasionally occurred in the discards and were not considered in the present study, since trawlers off the Ebro Delta rarely operate at depths greater than 200 m. Each fish sample for mercury analysis was prepared by homogenising 2-10 fish of similar size. For each species, five samples were examined, trying to cover the range of sizes present in discards. Mercury concentrations were averaged for each fish species, and also for trawler discards as a whole. The average concentration for discards ([Hg]_D) was calculated as follows:

$$[Hg]_{D} = \sum_{i=1}^{n} \left([Hg]_{i} \times \frac{P_{i}}{\sum_{j=1}^{n} P_{j}} \right)$$

where [Hg]i is the mean concentration for species *i*, and P_i and P_j the representation (%) by weight of species *i* and *j* in the discards (values shown in Table 1). Since the 15 fish species selected for analysis did not represent 100% of discards, we referred the average concentration of mercury in discards to this sub-fraction by dividing each P_i by the sum of all P_j . This way, we assumed that the species selected for analyses were representative of the mercury concentration of the whole fraction of discards. Mercury concentrations were also averaged for epipelagic fish, following the above equation. In this case, P_i reflected the relative abundance (%) of each epipelagic species at sea, estimated from data of catches collected on board pelagic purse seiners (see Table 1; J.M. Arcos & D. Oro, unpublished data).

Seabird samples were obtained from corpses found dead at the Ebro Delta during spring-summers 1997-1999. Four seabird species were considered: Audouin's and the yellow-legged gulls, the common tern, and the European shag. The first two make extensive use of discards (Oro & Ruiz 1997), while the latter two species were selected for their low attendance at trawlers. The samples selected for analysis were internal tissues (liver and kidney) and feathers (mantle and primary feathers). Mantle feathers were collected from all specimens (from the upper mantle region, close to the neck), while primary feathers where only analysed in Audouin's and yellow-legged gulls (first - innermost- primary) and the common tern (first and seventh primaries). Since the gulls here considered perform a partial pre-breeding moult (body feathers and some coverts) and a complete post-breeding moult (including flight feathers; Grant 1986), we expected the individuals collected to have moulted the upper mantle feathers before the breeding season (thus reflecting winter levels of mercury) and the primaries after the preceding breeding season (thus reflecting mercury levels accumulated during the breeding period). The common tern is unusual among seabirds, since it moults its innermost primaries twice a

year (Olsen & Larsson 1995), and so when it reaches the breeding grounds it exhibits two generations of primaries. In this case, we expected the first primary (recently moulted) to reflect winter levels and the seventh primary (the innermost primary of the old generation) to reflect levels accumulated during the previous breeding season.

Juvenile birds were excluded from this study, since they usually show significantly lower mercury values than adults (Furness 1993). Starved individuals were also removed when considering internal tissues, since unusually high soft tissue concentrations of mercury can occur due to weight loss (Thompson 1996). Birds considered to have died of starvation were identified directly (e.g. unusually low weight either of internal tissues or for the whole bird) or through lipid extractions of liver tissue (with those birds exhibiting a particularly low proportion of extracted lipids being considered as starved).

Both fish and seabird samples were stored frozen at -20° C, immediately after their collection. Before mercury analysis, samples were homogenised and oven-dried at 60°C to constant weight.

Mercury analysis. All samples were analysed for total mercury by atomic fluorescence spectrophotometry, following standard digestion (for details, see Bearhop et al. 2000a). Mercury concentrations are given on a dry weight basis as ng g⁻¹ (equivalent to ppb) for fish and $\mu g g^{-1}$ (ppm) for seabirds, in order to facilitate their interpretation and their comparison with other studies. Detection limits on a typical run (10 ng g⁻¹ calibration) were less than 0.1 ng g⁻¹, which is an order of magnitude lower than the lowest concentrations measured in the study. Precision and accuracy of the method were tested using standard reference materials (TORT-2 lobster hepatopancreas \pm 95% CI = 0.26 \pm 0.03, n = 17, certified value = 0.27 \pm 0.06) and replicate samples.

Statistics. Mercury concentrations of both fish and seabirds were tested for normality using the Shapiro-Wilk test (see Zar 1996). Normality was violated in several cases, which could be due in part to low sample size, as well as to the typical skewness of the distributions of mercury levels (Walsh 1990). Thus, we adopted the more conservative non-parametric statistics in most cases, following Zar (1996). The significance level was held at 0.05, although marginal values are also discussed following Stoehr (1999).

Results

Mercury levels of the fish species examined are given in Table 1, along with the mean length of the individuals sampled in each case. As a rule, epipelagic fish showed lower levels of mercury than demersal fish (Mann-Whitney test, $U_{60,15} = 263$, p = 0.01; Fig. 1). Taking into account the contribution by weight of each fish species to the discards (Table 1), we estimated a mean mercury concentration of 228 ng g^{-1} in this source of food for seabirds. In the case of epipelagic fish this value was lower, 96 ng g^{-1} when considering the relative abundance of each species at sea.

At the species level, the concentration of mercury increased with the length of the fish, although for most species this relationship was not statistically significant (Spearman's correlation), probably due to low sample sizes. However, correlation

coefficients were high and in all cases positive (median = 0.66, range = 0.19 - 0.90), which suggests that this trend was consistent.

Table 1. Mercury concentrations (ng g^{-1} dry wt) in fish species occurring in trawler discards in the Ebro Delta area. Five samples were examined for each species, each sample resulting of pooling 2-10 fish of similar size. The total length of the fish analysed (mean \pm SD) is provided. The table also shows the percentage in weight of the different fish species with respect to total discards and, in the case of epipelagic fish, also considering their relative abundance in the environment estimated from purse-seine captures

| | Mercury | | | % in w | eight (P_i) |
|---|-----------------|----------|--------------|----------|---------------|
| Fish species/group | Median/ Mean | Range | Length (mm) | Discards | Environm. |
| Epipelagic | 138/147 | 40-326 | | | |
| Sardine, Sardina pilchardus | 76/77 | 40-117 | 133 ± 10 | 27.7 | 84.1 |
| Anchovy, Engraulis encrasicholus | 226/223 | 138-326 | 125 ± 6 | 11.7 | 10.3 |
| Guilt sardine, Sardinella aurita | 159/141 | 82-182 | 196 ± 16 | 0.2 | 5.6 |
| Demersal | 253/362 | 42-1136 | | | |
| Bogue, Boops boops | 254/299 | 91-474 | 180 ± 27 | 29.6 | |
| Poor cod, Trisopterus minutus c. | 126/140 | 42-235 | 74 ± 6 | 3.3 | |
| Silvery pout, Gadiculus argenteus | 144/156 | 108-229 | 86 ± 18 | 2.6 | |
| Blue whiting, Micromesistius poutassou | 102/97 | 73-126 | 142 ± 7 | 2.0 | |
| Hake, Merluccius merluccius | 49/65 | 45-93 | 82 ± 10 | 1.8 | |
| Brown comber, Serranus hepatus | 503/478 | 158-781 | 86 ± 6 | 2.5 | |
| Dragonet, Callionymus maculatus | 365/354 | 199-495 | 80 ± 17 | 1.0 | |
| Goby, Deltenosteus quadrimaculatus | 822/830 | 528-1136 | 80 ± 7 | 1.2 | |
| Black goby, Gobius niger | 743/699 | 449-934 | 69 ± 6 | 1.2 | |
| Spotted flounder, Citharus macrolepidotus | 91/117 | 85-194 | 89 ± 7 | 1.5 | |
| Scophtalmidae sp. | 291/364 | 131-649 | 79 ± 13 | 3.5 | |
| Tongue sole, Symphurus nigrescens | 740/745 | 409-1110 | 91 ± 9 | 1.6 | |

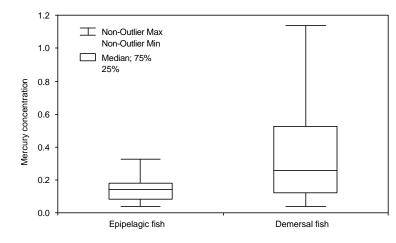


Figure 1. Comparison of the levels of mercury (ng g^{-1} dry wt) between epipelagic (n = 15 samples, 3 species involved) and demersal fish species (n = 60 samples, 12 species)

The mercury levels measured in internal tissues and feathers of the different seabird species are shown in Table 2, and correlations between the different tissues appear in Table 3. Mercury levels in the kidney were strongly correlated with those in the liver, despite the former being lower than the latter. Thus, given the smaller sample size available in kidney tissues, only liver tissues were considered in further analyses, as representative of internal tissues.

Table 2. Mercury concentrations ($\mu g g^{-1}$ dry wt) in different tissues of the seabird species considered for analysis (kidney, liver, MF = mantle feathers, P1 = first primary feathers, P7 = seventh primary feathers). Sample size is also provided (n)

| | | | Mercury | |
|---|--------|----|-------------|------------|
| Species | Tissue | n | Median/Mean | Range |
| Audouin's gull, Larus audouinii | Kidney | 7 | 3.51/4.33 | 0.68-8.06 |
| | Liver | 23 | 6.53/8.36 | 1.46-22.26 |
| | MF | 40 | 0.84/1.27 | 0.29-5.18 |
| | P1 | 30 | 7.87/8.10 | 2.03-14.07 |
| Yellow-legged gull, Larus cachinnans m. | Kidney | 11 | 2.05/2.17 | 0.82-4.28 |
| | Liver | 13 | 2.55/2.98 | 0.95-5.91 |
| | MF | 14 | 1.49/2.10 | 0.75-4.36 |
| | P1 | 3 | 7.38/7.00 | 3.84-9.79 |
| common tern, Sterna hirundo | Liver | 5 | 1.01/0.99 | 0.63-1.24 |
| | MF | 5 | 0.76/0.92 | 0.54-1.54 |
| | P1 | 5 | 0.84/1.05 | 0.79-1.52 |
| | P7 | 5 | 1.63/2.09 | 0.92-3.31 |
| Shag, Phalacrocorax aristotelis d | Kidney | 3 | 7.50/5.60 | 1.56-7.74 |
| | Liver | 3 | 6.58/5.32 | 2.42-6.97 |
| | MF | 3 | 2.52/2.45 | 0.69-4.12 |

Audouin's Gull, the yellow-legged gull and the common tern showed clear differences in the mercury concentration of liver tissues, which were assumed to represent the body levels in the breeding season (Kruskal-Wallis Test, $H_{2,41} = 23.8$, p < 0.0001; Fig. 2). Post-hoc analyses (Mann-Whitney test) showed significant differences in all cases, with Audouin's Gull presenting the highest levels and the common tern the lowest. The shag was not considered in the previous analyses due to low sample size, but presented high levels of mercury in the liver, comparable to those of Audouin's Gull (Table 2). The first primary feathers of Audouin's and yellow-legged gulls and the seventh primary feathers of

common terns were also assumed to reflect mercury levels accumulated during the breeding season, but in the previous year. In the case of Audouin's Gull, mercury levels did not significantly differ between the first primary and liver tissues ($U_{23,30} = 311.0$, p = 0.54), while in the common tern the levels of mercury in the seventh primary were slightly higher than in the liver ($U_{5,5} = 37.0$, p = 0.05). For the yellow-legged gull the first primary also appeared to present higher levels than the liver, although the few primaries collected prevented any statistical comparison. In any case, the interspecific pattern for mercury in primary feathers was similar to that showed by livers, with Audouin's Gull presenting considerably higher levels of mercury than the common tern ($U_{5,30} = 0$, p = 0.0005), and the yellow-legged gull being at an intermediate position. Audouin's Gull showed the highest variability in the levels of mercury in both liver tissues and the primaries, while the common tern presented very low variation (Fig. 2).

Table 3. Correlation between mercury levels of the different samples of seabirds here considered (kidney, liver, MF = mantle feathers, P1 = first primary feathers, P7 = seventh primary feathers). Correlations were not performed when sample size (n) was lower than 5. r_s = Spearman's correlation coefficient; p = statistical significance (two-tailed test)

| significance (two-tail | Yellow-legged gull | | | Audouin's gull | | | common tern | | |
|------------------------|--------------------|----------------|--------|----------------|----------------|------|-------------|----------------|------|
| | n | r _s | р | n | r _s | р | n | r _s | р |
| Liver-Kidney | 11 | 0.91 | 0.0001 | 7 | 0.86 | 0.01 | - | - | - |
| Liver-MF | 12 | -0.09 | 9 0.78 | 21 | 0.24 | 0.29 | 5 | 0.70 | 0.19 |
| Liver-P1 | - | - | - | 16 | 0.37 | 0.16 | 5 | 0.30 | 0.62 |
| Liver-P7 | - | - | - | - | - | - | 5 | 0.50 | 0.39 |
| MF-P1 | - | - | - | 27 | 0.24 | 0.2 | 5 | 0.80 | 0.10 |
| MF-P7 | - | - | - | - | - | - | 5 | 0.60 | 0.28 |
| P1-P7 | - | - | - | - | - | - | 5 | 0.40 | 0.50 |

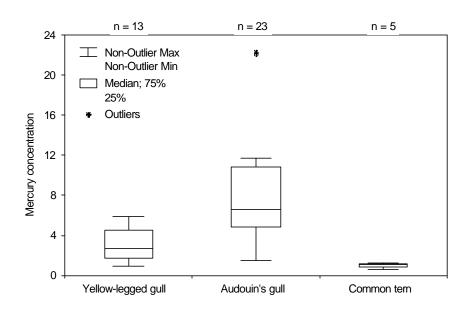
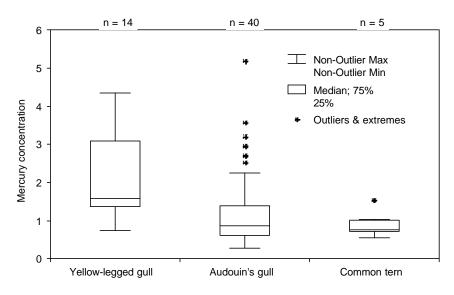


Figure 2. Interspecific comparison of the levels of mercury ($\mu g g^{-1}$ dry wt) in the liver tissue of seabirds (assumed to reflect dietary input throughout the breeding season). The shag is not included due to low sample size (n, sample size)

Mantle feathers, assumed to reflect the mercury accumulated in the winter, showed a different pattern to that observed with the livers and the primary feathers. Indeed, in this case the yellow-legged gull presented the highest levels of mercury, while Audouin's Gull and the common tern showed relatively low levels ($H_{2,58} = 11.1$, p = 0.004; Fig. 3). Posthoc analyses did not show differences between Audouin's Gull and the common tern, while both species significantly differed in mercury levels from those presented by the yellow-legged gull. The first primary of common terns, also assumed to reflect winter levels of mercury, had values very similar to those of mantle feathers ($U_{5,5} = 32$, p = 0.35; Table 2).

Figure 3. Interspecific comparison of the levels of mercury ($\mu g g^{-1}$ dry wt) in the mantle feathers of seabirds (assumed to reflect dietary input throughout the non-breeding season). The shag is not included due to low sample size (n, sample size)



Discussion

In accordance with our predictions, demersal fish showed higher levels of mercury than epipelagic fish, and this was reflected in the high average concentration of this metal in trawler discards. Indeed, mercury levels in discards were more than double those found in epipelagic fish. Among demersal fish (mesopelagic species were not considered in this study), the highest values corresponded to the most strictly benthic species (gobys *Gobiidae*, dragonets *Callionymidae*, brown comber *Serranus hepatus*, and flatfish *Pleuronectiformes*). Some of these fish exhibited unexpectedly high concentrations of mercury (mean specific values up to 830 ng g⁻¹), exceeding those reported for similar-sized mesopelagic fish from the Azores (mean values below 400 ng g⁻¹; Monteiro et al. 1996). This does not necessarily contradict the fact that mesopelagic biota present the highest values of mercury in marine environments (Monteiro et al. 1996, 1998), but may rather reflect the high methylation rate detected in the Mediterranean (six-fold over that of the North Atlantic; Cossa et al. 1997). Indeed, Mediterranean biota is known to have high levels of mercury in comparison to equivalent biota in the Atlantic, as has been reported in

several studies (e.g. Lambertini & Leonzio 1986, Osborn 1988, Renzoni et al. 1998). In addition to natural inputs, local pollution in the study area could explain the unusually high concentrations of mercury even for a Mediterranean context. This seems to be the case, given the important inputs from the Ebro River (with a high development of agricultural and industrial activities along its watershed) and the nearby chemical industry (cf. Morera et al. 1997, Sanchiz et al. 2000, Sanpera et al. 2000).

Several studies have found a direct relationship between size (i.e. age) and mercury concentrations in fish (see Thompson 1990, and references therein). This was the case in our study when comparing within species, yet small species usually had higher levels of mercury than large species. This is likely to be an age effect. Fishermen only discard young individuals of some large, commercial species (e.g. the silvery pout *Micromesistius poutassou* and the hake *Merluccius merluccius*). These individuals, in spite of being larger than adults of smaller species, apparently have accumulated less mercury throughout their shorter life. Moreover, although adult silvery pout and hake may occupy mesopelagic environments, they have more coastal distributions when young (Whitehead et al. 1986), thus incorporating less mercury at this stage.

Heavy metals tend to be held in one particular tissue at much higher levels than in others, and this has an important influence on the choice of tissue for monitoring studies (Furness 1993). In seabirds, dietary mercury is incorporated in a dose-dependent manner (Lewis & Furness 1991), and is accumulated in internal tissues (mainly in the liver and the kidney) between moult periods, ultimately being excreted to the growing feathers during moults (Furness et al. 1986, Honda et al. 1986, Braune & Gaskin 1987, Monteiro & Furness 2001). In accordance with that, the strongest correlation in mercury concentration between tissues of birds was between liver and kidney tissues, which should reflect the same period of mercury accumulation (cf. Walsh 1990). Mercury levels in mantle feathers and the first primary of common terns were also well correlated, although not significantly, and were the only feathers grown during the same period (pre-breeding moult). Feathers moulted during the pre-breeding moult did not show any clear relationship with either liver tissues or feathers grown after the post-breeding moult. Intermediate results were obtained for the correlation between internal tissues and feathers grown in the post-breeding moult, since these samples should reflect mercury levels incorporated in the same season but in different years, and inter-year variation is likely to have an influence. The observed correlations are therefore as would be predicted on the basis of the known kinetics of mercury in birds (Monteiro & Furness 2001).

Despite sometimes difficult to prove, inter- and intraspecific differences of mercury levels in seabirds are considered to be mainly determined by the diet (e.g. Leonzio et al.1986, Braune & Gaskin 1987, Monteiro et al. 1998, Bearhop et al. 2000a), though interand intraspecific variability in excretion rates may also play a role (Monteiro et al. 1998, Bearhop et al. 2000b, c). In this study, diet composition seems to be the main determinant of mercury levels in different seabird species, with mercury levels being higher in those species consuming discards (i.e. demersal fish). The only exception to this trend was that of the shag, which presented relatively high levels of mercury despite rarely consuming discards (cf. Oro & Ruiz 1997). However, this result was to be expected since the shag is the only species of those here considered that has direct access to benthic fish, as it can dive to the seabed. In the case of the gulls and the common tern, the relationship between mercury levels and use of discards was evident. Indeed, during the breeding season Audouin's Gull preferentially feeds on discards (Oro et al. 1997), although it also captures

epipelagic fish to a variable degree, and showed correspondingly high levels of mercury in the summer liver samples. The yellow-legged gull combines discards with foods of terrestrial and freshwater origin (Oro et al. 1995), the latter presenting negligible amounts of mercury compared to marine prey (e.g. Leonzio et al. 1986, Thompson 1996), and this species presented high levels of mercury yet significantly lower than those exhibited by Audouin's Gull. Finally, the common tern basically feeds on Clupeiforms (>90% of its prey; A. Hernández pers. com.) and levels of mercury in this species were correspondingly lower. Moreover, the tern captures fish considerably smaller than those either present in the discards or captured by Audouin's gull in a natural way, thus incorporating even less mercury than larger seabirds would do when feeding on larger (i.e. more contaminated) Clupeiforms. The two gulls present more plasticity in their diet than the common tern, and concordantly showed more variability in their levels of mercury. Considering the detailed dietary composition of Audouin's and the yellow-legged gulls under different fishing regimes (Oro et al. 1995, 1997), we estimated an average input of mercury 2.4 times higher for the former, at the Ebro Delta, during the breeding season. This value is very close to the ratio of mercury levels between both species, 2.6 for the liver, which supports the link between diet and concentrations of this metal. Similar ratios have been obtained in other Mediterranean colonies (e.g. Leonzio et al. 1989), with an extreme value of 10 when comparing mercury levels in eggs of yellow-legged gull from the Medes Islands (NW Mediterranean) with those of Audouin's Gull from the Ebro Delta (Sanpera et al. 1997). This high ratio is probably due to the major use of terrestrial food by yellow-legged gulls from the former colony (mostly waste food; Bosch et al. 1994).

The interspecific patterns in mercury levels changed between seasons, in accordance with changes in the feeding habits and the distribution of the seabirds. Indeed, those tissues reflecting the winter period showed the highest levels for the yellow-legged gull, which exploits discards extensively at this time of the year (Arcos et al. 2001). Contrarily, Audouin's gull presented comparatively low levels of mercury, being similar to those presented by the common tern. This was to be expected since most of the local breeding population of Audouin's gull migrates to the Atlantic coasts of Africa (see Oro 1998), where mercury levels in biota are lower than those in the Mediterranean (e.g. Lambertini & Leonzio 1986, Osborn 1988, Renzoni et al. 1998). Furthermore, Audouin's gulls remaining in the study area shift from exploiting discards to mainly feeding upon epipelagic fish at night out of the breeding season (Arcos et al. 2001), thus reducing their intake of mercury. The small but well-defined group of outliers could correspond to birds wintering in the Mediterranean, compared to those migrating into the Atlantic. Alternatively, these outliers could correspond to birds either still exploiting preferentially discards in winter or partly feeding offshore upon mesopelagic fish at night, when these prey ascend to the surface (e.g. Whitehead et al. 1996).

In spite of the high levels of mercury exhibited by fish and seabirds in our study, apparently related with the comparatively high methylation rates detected in the Mediterranean (Cossa et al. 1997), mesopelagic fish and their seabird predators would be expected to present even higher levels of this metal. Indeed, methylation processes are especially relevant in the subthermocline waters of the open oceans (mesopelagic environments), where low oxygen conditions favour those microorganisms that transform inorganic mercury into organic forms (Mason & Fitgerald 1990, Cossa et al. 1994, Monteiro et al. 1996). Concentrations of mercury in Mediterranean and Atlantic populations of Cory's shearwater *Calonectris diomedea*, a seabird considered to

extensively feed upon mesopelagic prey at night (Klomp & Furness 1992), support this

idea. Indeed, Renzoni et al. (1986) found mean values of mercury in liver tissues of Cory's shearwater ranging from 49.6 to 86.1 μ g g⁻¹ in three Mediterranean populations, being clearly higher than the 12.5 μ g g⁻¹ exhibited by an Atlantic population. At the same time, the values found in Mediterranean populations of this shearwater clearly surpass those found in the more coastal seabirds considered in the present study. Further research efforts should be directed at ascertaining the levels of mercury presented by Mediterranean mesopelagic biota and their seabird predators. Particularly, this would be interesting to assess the possible role of trawlers in providing mesopelagic fish to seabirds in areas of narrow continental shelf, where these vessels operate extensively in the mid continental slope (at depths up to 800 m) targeting on deep-water crustaceans (e.g. Demestre & Martín 1993).

In summary, results supported our predictions. Firstly, non-epipelagic (demersal) fish showed higher levels of mercury than epipelagic fish. Secondly, discards presented on average higher levels of mercury than the typical natural prey of surface-feeding seabirds (i.e. epipelagic fish). Thirdly, surface-feeding seabirds exploiting discards incorporate more mercury than those feeding in a natural way (i.e. feeding upon either epipelagic fish or nonmarine prey). The shag was the only species in our study with diving abilities (i.e. with direct access to benthic fish), and presented levels of mercury similar to those found in seabirds that consume discards. Finally, seasonal changes in mercury levels (i.e. differences between subsequent samples) were related to changes in the seabirds' feeding habits and distribution. Our findings should be taken into account when using feathers to study historical and geographical patterns of mercury pollution (e.g. Furness 1993), since the consumption of discards is a relatively new phenomenon that could differ in extent between populations (see Tasker et al. 2000). Thus, changes attributed to either spatial or temporal differences in mercury levels in the environment could be confused with differences in the use of discards by seabirds. Moreover, the selection of the feathers considered for analysis should be made carefully, paying special attention to the moult cycle and the migration pattern of the species considered for study. It is also worth to note that, although there is no evidence for toxicological effects of mercury in the study area (cf. Sanpera et al. 2000), high accumulation of this metal as a result of discards consumption could pose a threat to some seabirds, especially in association with local pollution events. This would be especially important for species that have most of the breeding populations concentrated in a few localities, as is the case of Audouin's gull (Oro 1998).

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Conclusions

Seabirds taking profit of fisheries: general considerations

The present study reports on the direct interaction of seabirds with semi-industrial commercial fisheries, both bottom trawlers and purse seiners, in the NW Mediterranean. The two fisheries present different features, which influence the way and extent in which seabirds take profit of them. Information concerning purse seiners is particularly novel, since there were no previous data on how seabirds obtain profit from this type of vessels. Overall:

 \rightarrow Trawlers target diverse species of demersal fish during daylight hours, operating over the continental shelf and slope, and generate large amounts of discards. These discards are predominantly composed by fish of small to medium size, being suitable for most seabirds, and present in average a high energetic value (7.0 kJ g⁻¹). Purse seiners target small shoaling fish at night, using light attraction and net encircling, and most often generate little amounts of discards (which are returned to the sea once the fishing operations have been completed, at/after dawn). This fishery presents some features that make of it quite unpredictable: irregular (often null) catches, strong influence of the weather, and variable fishing grounds (associated with prey mobility).

 \rightarrow Several seabird species attend trawlers in large numbers throughout the NE Iberian coast, and at any time of the year, looking for discards. In average, seabirds consume 84% of discards, Audouin's gull Larus audouinii being the most efficient at capturing them. Kleptoparasitic interactions are frequent, favouring large gulls such as the yellow-legged gull Larus cachinnans michaellis and the lesser black-backed gull Larus fuscus. The latter two species show preference for the largest fish (>15 cm), while most seabirds preferentially consume fish below 15 cm. Purse seiners attract considerably smaller numbers of seabirds during discarding, with daylight, due to the irregularity of this fishery and the usually small amounts of fish discarded. Audouin's gull is the unique species attending purse-seiners at night, as would be expected given its nocturnal habits. This species captures fish before being hauled, when is concentrated near the sea surface by the light of the attracting lamp and by the encircling net. The light employed by purse-seiners to attract fish could also help these gulls to locate suitable fish concentrations. Audouin's gulls were more numerous at purse seiners either during trawling moratoria (which occurred in spring) or out of the breeding season. They also attended purse seiners in higher numbers when several vessels fished in the same area, and were also more numerous at large distances from the coast.

 \rightarrow According to bioenergetic modelling, 65.4% (±29.8% SD) of the energetic requirements of the seabird community breeding at the Ebro Delta are obtained from trawler discards, this value ranging from 76.7% (Audouin's gull) to 1.4% (Sandwich tern *Sterna sandvicensis*). These results have to be considered with caution, since they are subject to

strong variability, but give an idea of the importance of trawler discards for a variety of seabird species. At purse seiners, we estimated that individual Audouin's gulls could meet more than half of their energetic requirements by attending a single haul (669 kJ haul⁻¹ bird⁻¹), being considerably more efficient this way than when feeding by their own at night. Specialised individuals probably meet their energetic requirements by attending purse seiners through most of the year, although many individuals seem to prefer attending trawlers.

Seabirds and commercial fisheries: case studies

Once we had a general view of the relationship between seabirds and commercial fisheries (trawlers and purse-seiners), case studies of particular interest were addressed.

 \rightarrow Audouin's gull and the yellow-legged gull are species of particular concern: the former is a rare and threatened species, endemic to the Mediterranean; the latter is an opportunist and superabundant species, often considered a pest. Since the yellow-legged gull has been described as a major threat for Audouin's gull at colonies, and both species attended fishing vessels regularly, we assessed competition between these seabirds at sea. We found evidence of competition between the two gulls when attending fishing vessels, though this was not so strong as it is in colonies, and varied in intensity according to the fishing fleet (trawlers vs. purse seiners) and season (breeding vs. non-breeding). Purse seiners only attracted Audouin's gulls at night, thus excluding interspecific competition; trawlers attracted both yellow-legged and Audouin's gulls, and interspecific competition occurred at these vessels. Overall, the yellow-legged gull behaved as an opportunist species and exerted variable pressure over Audouin's gull through kleptoparasitism and agonistic interactions; however, Audouin's gull was more efficient at capturing fish, and presented a wider range of foraging opportunities that would allow avoiding competition if necessary. During the breeding season (March-July), Audouin's gull preferentially attended trawlers over purseseiners, but competition at the former was not severe. Indeed, the two gulls occurred in large numbers at trawlers and showed only limited segregation (concerning fish size, time of occurrence, and distance to the coast). Out of the breeding season the situation at trawlers appeared to be less favourable for Audouin's gull: the numbers of this gull decreased in the study area (through migration) at the same time that the yellow-legged gull became more abundant; fish in discards was of larger size (less suitable for Audouin's gull, and more prone to suffer kleptoparasitism); and the rate of kleptoparasitism doubled that of the breeding season. In concordance, Audouin's gull shifted to preferentially attend purse seiners at night, thus avoiding competition with the yellow-legged gull. The situation in other areas, where yellow-legged gulls largely outnumber Audouin's gulls throughout the year, could be less favourable for the latter species than it is off the Ebro Delta during the breeding season. Expected changes in fishing policies (reduction of discards, increasing their average size at the same time) would also revert in a less favourable situation, that could difficult the use of trawler discards to Audouin's gull.

 \rightarrow The Balearic shearwater *Puffinus mauretanicus* is a highly threatened seabird endemic to the Balearic Islands. Although this shearwater is considered to predominantly feed upon

small shoaling fish, information supporting this view is limited. We present evidence that the Balearic shearwater also makes extensive use of fisheries discards, especially during its breeding season (March-June). At this time of the year, large numbers of shearwaters were observed attending trawlers off the eastern Iberian coast, and we estimated that the Balearic shearwater population obtain ca. 40% of their energetic requirements from trawler discards. This estimate agrees with observations at sea in May-June, since a similar percentage of the shearwaters observed actively feeding were associated with trawlers. Alternatively, the shearwaters captured fish under floating drifting objects, associated with sub-surface predators, and directly fed upon shoaling fish and plankton. Nocturnal foraging seemed of little importance, and purse seiners only attracted Balearic shearwaters during the discarding process, after sunrise. Outside the late breeding season, Balearic shearwaters attended trawlers in lower numbers.

→ Surface-feeding seabirds attending trawlers have access to (demersal) prey otherwise unavailable to them. Differences between natural prey for seabirds (small pelagic fish) and prey provided by trawlers (demersal dish), such as trophic position, habitat, and life span, suggested possible differences in their accumulation of pollutants, which could revert on seabirds. We assessed this possibility for mercury, a toxic heavy metal showing biomagnification through marine food webs. Demersal fish showed higher levels of mercury than epipelagic fish, and discards (228 ng g⁻¹) more than doubled in average the amounts of mercury accumulated by epipelagic fish (96 ng g⁻¹). This was reflected in seabirds, those species making more use of discards presenting the highest levels of mercury. The only exception was that of the shag, that presented high levels of mercury though rarely attending trawlers. However, this species have well-developed diving abilities, thus having direct access to benthic prey. Seasonal differences in mercury accumulation, revealed by differences between seabird tissues (feathers, liver), were also related with both dietary and geographical changes.

Seabird-fisheries interactions: conservation considerations and perspectives

Although most seabirds obtain a direct benefit from fisheries, particularly from trawlers, these activities also change their natural ecosystems and exploit their natural prey populations. Purse seiners are particularly prone to affect negatively seabirds, since these vessels target small shoaling fish (the natural prey for most seabirds) and offer relatively few advantages to most seabirds. In the likely case that trawlers would reduce their amounts of discards (e.g. through changes in fishing effort, establishment of moratoria, creation of new markets for low appreciated fish), seabirds would be seriously affected because:

- (1) Competition at trawlers would increase, first affecting the smaller and more specialised seabird species
- (2) These species would be forced to turn to feed upon their natural prey, but overexploitation of the latter (as seems the case for the anchovy in the Mediterranean) could difficult this process and would cause a generalised food shortage

(3) Opportunist and aggressive species, such as the yellow-legged gull, could turn to kleptoparasite and prey over other seabird species in order to compensate for the lack of discards

Thus, the resulting picture would be a decline of the smaller and more specialised seabirds, as could be the rare Balearic shearwater, preceding any serious effect over opportunist species. This could be strengthened by longline fisheries, which could cause serious mortality over shearwaters and other specialised seabirds. Overall, the long-term effect of fisheries would have been a partial replacement of strictly marine birds by rather opportunist seabirds. However all the interactions here reported are extremely complex, at the same time that other factors could play an important role at determining population trends of seabirds, and the above considerations should be not considered as unequivocal. This is important to conduct further research, both at sea and at colonies, especially on those species that have previously received little attention (as is the case for the Balearic shearwater). Meanwhile, fisheries managers should start to regard seabirds as key elements of marine ecosystems, and be aware of both the potential benefits that these animals can bring to fisheries (e.g. monitoring pollutants and providing information of the abundance of fish stocks) and the potential damage/benefit/changes that fisheries can cause to them.

Resum

Introducció

Al llarg del darrer segle, les pesqueres han patit un creixement i expansió desmesurats (Safina 1995). La pressió exercida per aquesta activitat humana ha comportat canvis seriosos en els ecosistemes marins (Tegner & Dayton 1999). Els ocells marins, com a representants de les posicions més altes a les xarxes tròfiques marines, sovint han estat fortament afectats per aquests canvis. Les interaccions entre ocells marins i pesqueres són diverses i complexes, però a mode de simplificació es poden considerar com a negatives, positives o neutres per a l'home i/o per als ocells (Duffy & Schneider 1994).

Des de la perspectiva de l'home, els ocells tradicionalment han servit als pescadors per a localitzar concentracions de preses (peixos o mamífers), malgrat que les noves tecnologies incorporades per les barques de pesca resten importància a aquesta interacció. Paral·lelament, amb el desenvolupament de les grans pesqueres industrials, els ocells marins han esdevingut competidors potencials de l'home, tot i que els ocells són els més (si no els únics) perjudicats (Furness & Monaghan 1987). Malgrat haver una forta desconnexió entre biòlegs pesquers i ornitòlegs, els primers podrien beneficiar-se de l'estudi dels ocells marins com a font d'informació addicional sobre la situació de les poblacions de preses: distribució, mortalitat natural, abundància de cohorts abans de ser reclutades dins l'*stock* pesquer, etc. (Cairns 1992).

Des del punt de vista dels ocells, les interaccions amb les pesqueres sovint són de major transcendència (vegeu revisió a Tasker et al. 2000). Algunes interaccions són negatives, com per exemple la mortalitat directa causada per les pesqueres (palangres, xarxes de deriva), i la competència pels recursos. En sentit positiu, les pesqueres poden reduir poblacions de competidors naturals dels ocells marins o, més directament, facilitar aliment als ocells (descarts i despulles). En el darrer cas, es creu que aquest aliment extra pot ser una causa important del creixement que han experimentat algunes poblacions d'ocells marins al llarg de les darreres dècades, però aquesta hipòtesi encara no ha estat rigorosament provada (p.ex. Camphuyen & Garthe 1999).

Pel que fa al Mediterrani, aquest és un mar pobre i heterogeni (Margalef 1985), amb pesqueres de poca importància i poblacions d'ocells marins molt modestes. Amb tot, el grau d'endemicitat que presenta la comunitat d'ocells marins li confereix un interès especial (Zotier et al. 1999). Així mateix, algunes pesqueres s'han desenvolupat notòriament en els darrers anys al Mediterrani occidental, i permeten parlar de flotes semiindustrials (bous i teranyines; Farrugio et al. 1993). La influència d'aquestes flotes (especialment la d'arrossegament -bous-) sobre algunes poblacions d'ocells marins és ben coneguda, majoritàriament a partir d'estudis indirectes. En efecte, l'establiment de vedes per a la pesca d'arrossegament al voltant del delta de l'Ebre va permetre comprovar els efectes de la manca de descarts sobre la biologia reproductora de diverses espècies d'ocells marins. Aquests efectes van ser diversos i d'intensitat variable segons les espècies (vegeu Oro 1999 i les referències allà citades). Les vedes d'arrossegament també van permetre d'observar una certa influència de les teranyines sobre els ritmes d'activitat (Oro 1995) i la

dieta (Oro et al. 1997) de la gavina corsa *Larus audouinii*, tot i que el profit que aquestes gavines treien d'associar-se amb aquestes barques no quedava clar.

Objectius i conclusions

Atesa la importància de les flotes d'arrossegament i de teranyines per a diverses espècies d'ocells marins mediterranis, i davant la manca d'estudis directes (a banda d'Oro & Ruiz 1997), aquest treball està dirigit a aprofundir en aquesta qüestió. La primera part del treball (capítols 1 i 2) està dedicada a esbrinar com funcionen les pesqueres d'arrossegament i de teranyines en la part central i sud del mar català, i en quina mesura en treuen profit els ocells marins. Els resultats mostren que els bous, que pesquen de dia, produeixen grans quantitats de descarts. Aquests estan constituïts bàsicament per peix de mida petita, que és fàcilment empassat pels ocells marins. Les teranyines (pesca nocturna de petits pelàgics) generen pocs descarts, alhora que llur activitat és força difícil de predir (es veuen fortament influenciades pel mal temps, les captures són irregulars, i presenten una gran mobilitat). Així, els bous atreuen un major nombre i diversitat d'ocells marins, que consumeixen el 85% dels descarts. Les interaccions per cleptoparasitisme són freqüents, i reflecteixen una certa competència pel recurs. Les teranyines atreuen alguns ocells durant l'activitat de descart, quan s'aixeca el dia, però no són comparables a la situació observada en els bous. A més a més, algunes gavines corses es concentren de nit entorn de les teranyines, atretes pels llums dels bots acompanyants; les gavines aprofiten la concentració de peix a la superfície, atret també pel llum del bot i concentrat per la xarxa de cèrcol, per capturar-lo directament. Aquesta associació és més freqüent quan els bous estan aturats per la veda, així com durant l'hivern.

Les estimes energètiques mostren que el $65,4\% \pm 29,8\%$ DE) dels requeriments energètics de la comunitat d'ocells marins que nia al delta de l'Ebre prové dels descarts, essent el valor més alt obtingut per a la corsa (76,7%) i el més baix per al xatrac bec-llarg *Sterna sandvicensis* (1,4%). En el cas de les teranyines, es va poder estimar l'energia que de promig obté una gavina corsa capturant peix durant una calada, 669 kJ (més de la meitat dels requeriments energètics d'un ocell reproductor). Això suggereix que individus especialitzats podrien satisfer amb facilitat les seves necessitats energètiques al llarg de tot l'any mitjançant l'associació amb teranyines.

La segona part de la tesi, un cop conegudes les generalitats anteriors, s'adreça a l'estudi en profunditat de casos particulars, que es van trobar especialment interessants. Així, el capítol 3 avalua el grau de competència entre dues espècies d'especial interès per a la gestió: d'una banda la gavina corsa (espècie amenaçada, endèmica del Mediterrani) i de l'altra el gavià argentat *Larus cachinnans michaellis* (espècie oportunista, molt abundant, i sovint considerat problemàtic). Malgrat que el gavià argentat sembla exercir una pressió considerable sobre la gavina corsa a les colònies de cria, la situació a mar és més relaxada, ja que la gavina corsa es val de la seva agilitat i especialització en la captura de peix per eludir la pressió exercida pel gavià (cleptoparasitisme i altres interaccions). El grau de competència entre les dues gavines varia entre flotes (les teranyines només atreuen gavines corses de nit, de forma que no hi ha competència) i entre èpoques. Fora de l'època reproductora la situació sembla menys favorable per a la gavina corsa, que disminueix en

nombre a l'àrea d'estudi alhora que el gavià augmenta, i de preferir els bous passa a associar-se amb preferència amb les teranyines. Aquesta darrera situació probablement s'estengui a l'època reproductora en altres indrets, on la gavina corsa sempre es troba en nombres molt inferior als del gavià argentat. Així mateix, canvis previsibles en les polítiques de pesca, com pot ser la reducció dels descarts, incrementaran el grau de competència i dificultaran la utilització de descarts per part de la gavina corsa.

El **capítol 4** va dirigit a estudiar la importància dels descarts de pesca per a una espècie fortament amenaçada, endèmica de les illes Balears: la baldriga balear *Puffinus mauretanicus*. Aquesta baldriga ha estat molt poc estudiada, i es desconeixen nombrosos aspectes de la seva biologia. Així, existeix la idea generalitzada de que la baldriga balear s'alimenta de petit peix pelàgic principalment, però hom disposa de poques dades per recolzar aquest parer. Aquest estudi demostra que els descarts són importants per a aquesta baldriga, si més no durant l'època reproductora (Març-Juny), quan prop del 40% dels requeriments energètics de l'espècie es veuen satisfets per aquest recurs. En aquesta època, quan les aigües superficials del Mediterrani s'escalfen i s'empobreixen, la baldriga balear també s'alimenta pescant peix sota d'objectes flotants a la deriva (fustes, plàstics, i fins i tot organismes vius com les meduses), associant-se amb cetacis, i capturant directament petit peix pelàgic i plàncton. Fora d'aquest període la importància dels descarts sembla disminuir.

El mercuri és un metall pesant molt tòxic, que té una especial rellevància en els ecosistemes marins. Aquest element presenta dues propietats importants: bioacumulació (s'acumula al llarg del temps en els teixits dels éssers vius, que generalment no disposen de mecanismes fisiològics per eliminar-lo), i biomagnificació (incrementa en concentració a mida que s'ascendeix en les xarxes tròfiques). En el capítol 5 es va voler comprovar la hipòtesi que els ocells marins que consumeixen descarts presenten nivells de mercuri més alts que aquells que fonamentalment s'alimenten de petit peix pelàgic. Aquesta suposició es basa en el fet que els descarts posen a l'abast dels ocells preses que altrament no els serien accessibles (peix demersal), i que aquestes preses poden acumular més mercuri que els petits pelàgics (de vida més curta i posició més baixa en les xarxes tròfiques). Els resultats corroboren les nostres prediccions, doncs els descarts presenten un valor mitjà (228 ng g^{-1}) que dobla el dels petits pelàgics (96 ng g^{-1}), alhora que els ocells que més exploten els descarts també presenten els nivells de mercuri més elevats. El corb marí emplomallat Phalacrocorax aristotelis desmarestii és una excepció, doncs presenta valors alts i en canvi no acostuma a capturar descarts; aquesta espècie, però, és bona cabussadora, de manera que té accés directe a preses demersals. Els ocells poden eliminar el mercuri a través de les plomes, durant les mudes; així, els nivells de mercuri poden variar entre els òrgans interns (que reflecteixen l'acumulació de mercuri en temps recents) i les plomes (que reflecteixen els nivells de mercuri que presentava l'ocell quan aquestes van créixer), així com entre diferents tipus de plomes (mudades en diferents períodes). D'aquesta forma, l'anàlisi de diferents plomes i d'òrgans interns va permetre d'estudiar canvis estacionals en l'acumulació de mercuri. Aquests canvis estacionals corroboren la nostra hipòtesi de partida, doncs coincideixen amb canvis en l'ús relatiu dels descarts per part de diferents espècies d'ocells, així com amb canvis en la seva distribució geogràfica.

La majoria d'ocells marins a la zona d'estudi sembla beneficiar-se de les pesqueres de caire semiindustrial, especialment dels bous. Amb tot, l'activitat pesquera altera als ecosistemes marins de formes diverses, i això pot revertir a la llarga de forma negativa sobre els ocells. Les teranyines poden ser especialment perjudicials, doncs no proporcionen gaires beneficis per a la majoria d'ocells, alhora que exploten i redueixen les poblacions de les seves preses naturals (petits pelàgics). En el cas probable d'una reducció generalitzada dels descarts, els ocells marins en sortirien perjudicats, particularment aquelles espècies més estrictament marines, que es veurien desplaçades per d'altres més oportunistes i agressives. És important que els ocells es comencin a veure com a peces importants dels ecosistemes marins, i se'ls empri com a eines d'avaluació (estimadors dels nivells de contaminants i de l'abundància de preses, etc.), alhora que se'ls tingui en consideració quan es vulguin aplicar mesures de gestió (sempre i quan això no perjudiqui a la resta de l'ecosistema).

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