Marine Biology (2001) 139: 807–816
DOI 10.1007/s002270100651

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

Received: 24 January 2001 / Accepted: 7 June 2001 / Published online: 30 August 2001

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 on board 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 skill, 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.

Communicated by S.A. Poulet, Roscoff

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Introduction

Over the last century, the increasing offer of discards and offal provided by non-selective 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 Palaearctic, 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 yellow-legged gulls while exploiting commercial fishing vessels in the Ebro Delta area (north-western 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.

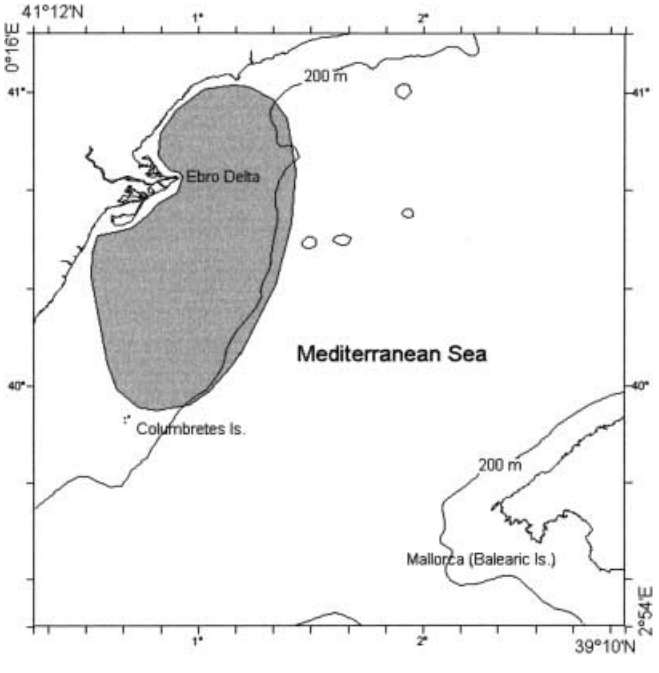

Fig. 1 Map of the study area (in *grey*), showing the most important geographical references

Seabirds feeding in the study area during the breeding season (March–July) mainly come from the Ebro Delta (20,000 pairs of gulls and terns in 1997) and the Columbretes Archipelago colonies (1,200 pairs of gulls, shearwaters, and storm petrels in 1997, e.g. Oro 1999; see Fig. 1). The breeding population of Audouin's gull (12,000 pairs) outnumbers that of the yellow-legged gull (4,500 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), whereas 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 in 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 2 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 on board 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 min 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:

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

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 1,000. The estimated number of Audouin's gulls was 25,000 birds for the breeding season (over 24,000 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 1,500 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-min 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; or (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/YLG 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; 5–9; 10–14; 15–19; 20–24 ; and ≥ 25 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, whereas 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/YLG, 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),

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

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/YLG 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 it 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 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's 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 one-way 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

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 seiners (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)

	Number of birds/haul					
	Breeding season			Non-breeding season		
	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
Purseseiners						
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

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).

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/YLG 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

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, multiplied by 1,000) according to the fleet (trawlers and purse seiners) and the season (breeding and non-breeding). Results are given as medians, and the inter-quartile (IQ) ranges (lower and upper quartiles) are also provided (*n* number of hauls)

Vessel	Attendance indices					
	Breeding season			Non-breeding season		
	Median	IQ range	*n*	Median	IQ range	*n*
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

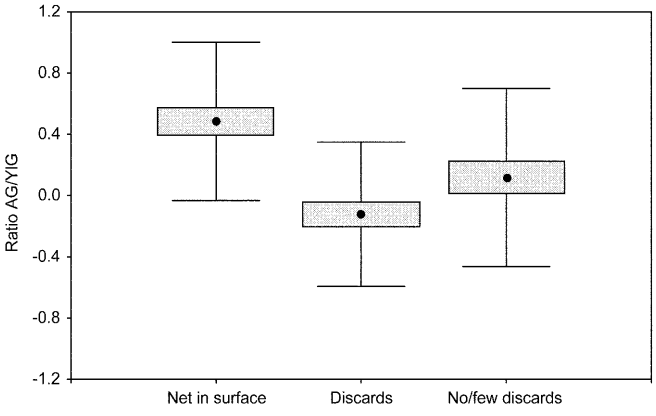

Fig. 2 Ratio of Audouin's to yellow-legged gulls according to the activity of trawlers. Values given are the mean, standard error (*boxes*), and standard deviation (*whiskers*)

Table 3 Audouin's gull (*AG*) and yellow-legged gull (*YLG*) 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 on the surface		Discards		Few/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

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.

No clear differences in the ratio AG/YLG 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.

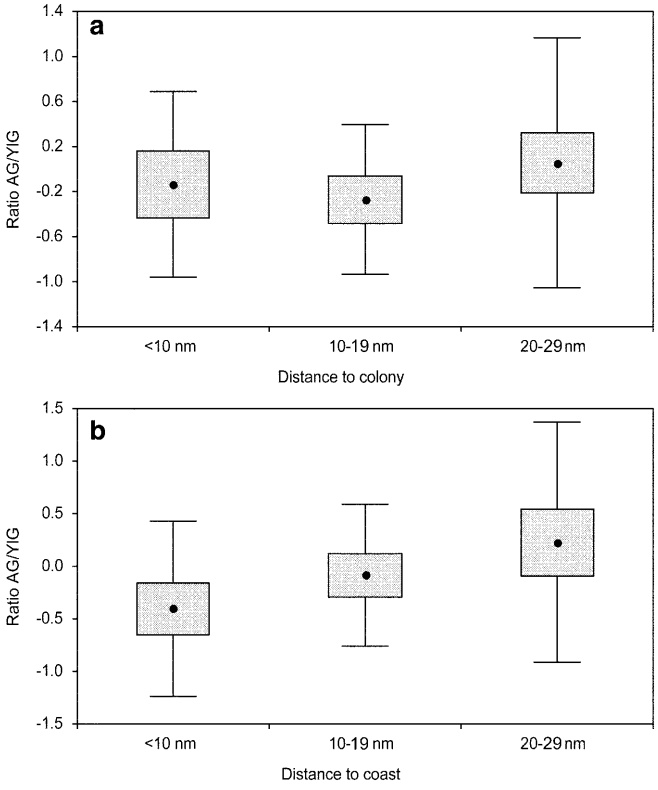

Fig. 3 Ratio of Audouin's to yellow-legged gulls in accordance with the distance (categorised, *nm* nautical miles) to the nearest colony (**a**) and to the mainland coast (**b**), during the breeding season. Results are expressed as the mean, standard error (*boxes*), and standard deviation (*whiskers*)

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/YLG 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.

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 did Audouin's gull (1.1%, $n=765$; Yates $\chi^2_1=109.4$, $P<0.0001$). Moreover, Audouin's gull mainly kleptoparasitised conspecifics ($n=7$ chases, 42.8% successful) and never chased any yellow-legged gull, whereas 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

Table 4 Audouin's gull (AG) and yellow-legged gull (YLG) success indexes [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)

	n	Success index		Correlations					
		Median	IQ range	Number of AG		Number of YLG		Ratio	
				r_s	*P*	r_s	*P*	r_s	*P*
Breeding season									
Audouin's gull	19	0.113	–0.10 to 0.22	0.35	n.s.	0.30	n.s.	0.17	n.s.
Yellow-legged gull	19	–0.109	–0.59 to 0.12	–0.29	n.s.	0.61	*	–0.74	**
Non-breeding season									
Audouin's gull	7	0.131	0.00 to 0.55						
Yellow-legged gull	13	0.028	0.00 to 0.15						

* Significant at alpha <0.05
** Significant at alpha <0.001, after Bonferroni correction

results, the robbery indices showed a high kleptoparasitic efficiency for the yellow-legged gull (RI = 0.81), whereas 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 were significant when we applied the Bonferroni correction.

Out of the breeding season, the general incidence of kleptoparasitism was more than double 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 year (see above), both the yellow-legged (19.3% of incidence, $n = 1257$) and Audouin's gulls (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 discarded fish increased (Spearman correlations, $r_s = 1.0$, $n = 6$, $P < 0.01$ in both cases; Fig. 4).

Audouin's and the yellow-legged gulls exhibited significant differences in the size of the fish selected (contingency table, $\chi^2_5 = 35.7$, $P < 0.001$, $n = 1{,}129$). As shown by the Manly's index, Audouin's gull tended to select medium to small fish classes, whereas 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 ($n = 3{,}545$ items). Out of the breeding season, the mean length of the fish discarded increased significantly (mean ± SD = 115 ± 44 mm, $n = 1{,}292$; t-test, $t = 11.5$, $P < 0.0001$).

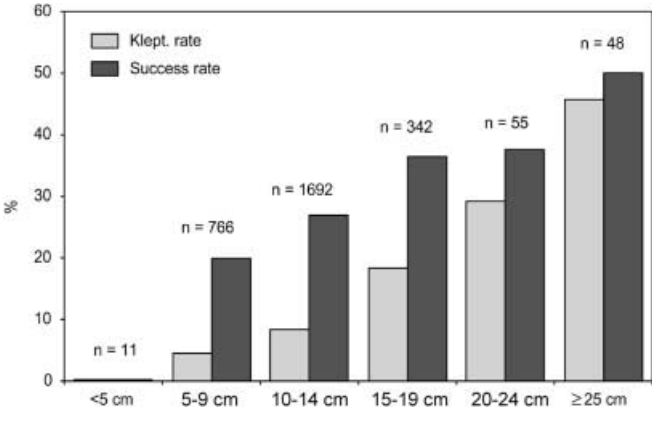

Fig. 4 Rate of kleptoparasitism (in %) and percentage of successful chases for seabirds following trawlers, according to the size class of the fish offered. The number of items of each size class is shown over the respective columns (n)

Discussion

Our most important results can 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, whereas yellow-legged gulls are clearly superior in contest competition (kleptoparasitism); (4) the better skills of

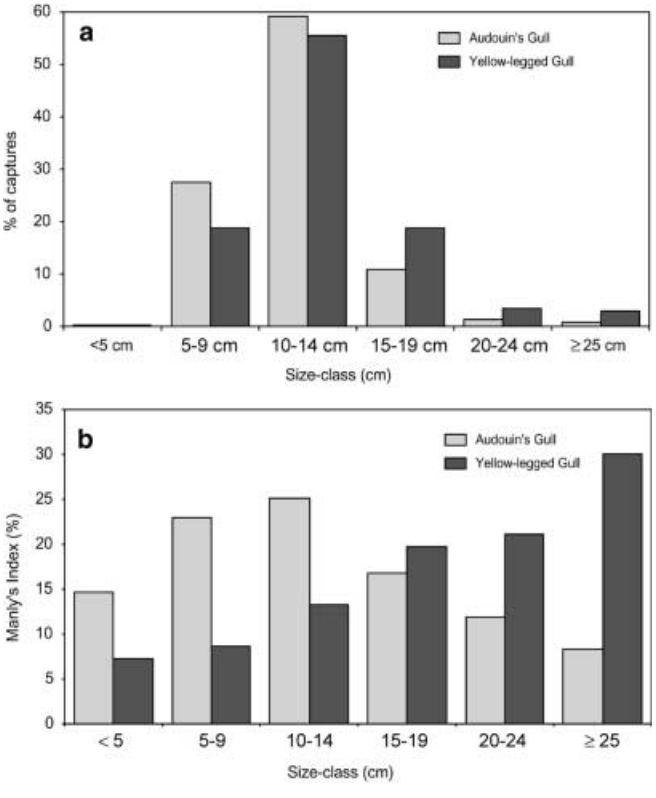

Fig. 5 Percentage of fish selected by Audouin's and the yellow-legged gull, during the breeding season, according to size class. **a** Real percentage observed, given the relative offer of the different size classes of fish. **b** Manly's index (%), which eliminates the effect of differential offer of size classes. The total number of fish offered was of 1,510 items, of which Audouin's gull captured 699 items and the yellow-legged gull 430 items

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 prey 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 with 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 this 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 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 yellow-legged 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 gulls 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 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, personal communication).

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; Moore and Jennings 2000; Tasker et al. 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, Regehr 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.

Acknowledgements We are extremely grateful to the skippers A. Cruelles (''Cruelles-Montserrat''), J. Llambrich (''Na Marinada''), J. Fàbrega (''Germans Fàbrega''), and J. P. Llambrich (''Pepito la Lula''), as well as to their crews, for providing the opportunity to carry out this study. D. Bigas, A. Bertolero, J. Martínez-Vilalta, A. Lepentier, M. Cebolla, C. Grande, H. Fernández, M. Martínez, G. Julià, J. Jofre, and C. Escoda helped with the fieldwork. J. González-Solís and M. Roura made helpful comments on an early draft of this manuscript, and three anonymous referees improved the final version. D. Bowler and B. Dudley kindly revised the English text. This study was performed within the framework of the research project LIFE B4-3200/96/502 funded by the European Commission and the DARP (Generalitat de Catalunya). Financial support was also provided to J.M.A. by the DURSI (Generalitat de Catalunya; FI/FIAP 98).

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