Disturbance to a foraging seabird by sea-based tourism: Implications for reserve management in marine protected areas

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ABSTRACT

The provision of recreational opportunities is one of the important human goals of marine protected areas. However, as levels of recreational use increase, human disturbance is likely to cause significant detrimental effects upon wildlife. Here we evaluate the best managing options to mitigate the impact of sea-based tourism on the foraging activity of an endangered population of European shags, *Phalacrocorax aristotelis,* in a coastal marine protected area (Cíes islands, north-western Iberia). Boat disturbance elicited a characteristic avoidance behavior that resulted in a substantial reduction in foraging activity as levels of boat use increased. Moreover, boats excluded shags from the best feeding areas, resulting in higher densities of foragers in areas of little boat traffic. We used a behavioral model to explore the effects of managing strategies aimed at reducing the impact of boats on the foraging activity of shags. Our model suggested that in low boat disturbance scenarios limiting the number of boats using the reserve would be a better management option than habitat protection (i.e. the establishment of set-aside areas free of boat traffic). On the contrary, when boat disturbance levels are high the protection of habitat is recommendable, even if spatial variation in habitat quality is unknown or poorly assessed. Our study stresses the point that management strategies to minimize disturbance to foraging seabirds may depend on the spatial overlap between sea-based recreational activities and foraging seabirds and the spatial variation in marine habitat quality for seabirds.

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1. Introduction

Marine protected areas (MPAs) are expected to be efficient tools to ensure the provision of long-term ecosystem services, especially with regard to conserving biodiversity and securing a sustainable human use of the marine environment (e.g. Palumbi et al., 2009). In recent years, the number of marine reserves has been growing rapidly worldwide and is now a global phenomenon with complex ecologic, scientific, and socio-economic dimensions (McClanahan et al., 2006; McCook et al., 2010). Consequently, research on marine reserves has increased swiftly in the past 15 years (Selig and Bruno, 2010; Halpern et al., 2010).

Human goals for MPAs include replenishing stocks of commercial fisheries, and maintaining areas for recreation, education, science, and aesthetic needs (Lubchenco et al., 2003; Roberts et al., 2003). In fact, MPAs have been relatively successful in restoring over-harvested populations of fish and invertebrates (e.g. Selig and Bruno, 2010; McCook et al., 2010). On the other hand, sea-based tourism may be responsible for the majority of the economic and social benefits provided by MPAs (e.g. Kelleher, 1999; Russ et al., 2004). For example, in the Great Barrier Reef Marine Reserve, tourism accounts for the majority of the income and employment generated by the reserve (estimated to be about 36 times the amount attributable to commercial fishing; McCook et al., 2010). However, as levels of recreational use increase in marine reserves, human disturbance is likely to cause significant detrimental effects upon wildlife (Nisbet, 2000; Gill, 2007).

Around the world, tourism to the coast is growing and the proportion of the marine environment accessible to the tourist, including multiple use MPAs, is thus spreading (Kelleher, 1999; Badalamenti et al., 2000). Outdoor recreation has the potential to disturb wildlife behavior and may result in animals avoiding parts of their normal range, with likely energetic costs and negative impacts on fitness (e.g. Taylor and Knight, 2003; Beale and Monaghan, 2004). Reduction of natural conservation values in the marine environment due to nature-based tourism and recreation, has been reported for sea-based activities (McCrone, 2001; Williams et al., 2002). Thus, paradoxically, marine reserves may have indirect adverse effects on some species, especially in highly mobile animals (e.g. marine mammals, birds, and turtles).

Seabirds are conspicuous components of marine ecosystems that may attract considerable public interest by themselves as they usually breed colonially in coastal and insular areas of outstanding

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conservation value. Many seabird species spend the larger part of their lives at sea where they widely interact with human activities with either negative (e.g. oiling or mortality in fishing gears: e.g. Munilla et al., 2007) or beneficial (e.g. fishing discards as a food source) outcomes (Tasker et al., 2000). In general, reserves can benefit seabirds through habitat restoration and by limiting or preventing overfishing (Hooker and Gerber, 2004). In the last decade there has been an increasing interest to extend MPAs to encompass seabird conservation (e.g. Louzao et al., 2006). Nevertheless, expected increases on the demand of recreational uses at seabird colonies, as well as mounting awareness for seabird and nature conservation, has recently led to studies that intend to measure and model the impact of visitors upon breeding seabirds (Beale, 2007; Beale and Monaghan, 2007). However, very little is known on the effect of nature-based tourism upon seabirds at sea (but see Burger, 1998; Ronconi et al., 2002; Rojek et al., 2007).

In this study, we analyzed the interaction between recreational boating and a near shore marine bird, the European Shag (*Phalacrocorax aristotelis*), in the MPA around the Cíes archipelago, which is part of the National Park of the Atlantic islands of Galicia (north-western Spain). This protected area holds about two thirds of the European shags breeding in Atlantic Iberia, a population that is under the risk of extinction (Velando and Alvarez, 2004). This threatened population has been declining at a rate of about −12% a year in the last 10–15 years, due to the 2002 *Prestige* oil spill and to continued low survival and reproductive success (Velando and Freire, 2002; Velando and Munilla, 2008). European shags feed extensively on sandeel, a semipelagic shoaling fish, in the vicinity of the islands where the breeding colonies are located (Velando and Freire, 1999). Though these conspicuous feeding groups are one of the outstanding natural features of this MPA, disturbance by recreational boats is widespread, especially in summer when juveniles become independent from their parents (Velando, 1998). In this species reduced foraging time after independence results in high juvenile mortality (Daunt et al., 2007). A recent demography study showed that, combined with other management measures, reducing foraging disturbance is one of the best strategies to promote population recovery through effects on reproductive success and juvenile survival (Velando and Munilla, 2008).

In this study, we used two complementary approaches (field work and modeling) to evaluate the potential effects of sea-based tourism management on the foraging activity of shags in the MPA around Cíes islands. We first assessed marine habitat use by shags, identifying those environmental variables that most accurately reflected the distribution of shags in the MPA. Afterwards, we measured the effect of the number of boats that were using the reserve on: (1) the abundance and distribution of foraging shags; (2) the probability of disturbance to foraging groups; and, (3) foraging activity. Lastly, we modeled boat disturbance to foraging shags by means of an ideal free distribution framework (Fretwell and Lucas, 1970) that assumes depletion of resources with continuous input conditions, assumptions that fit well with our observations of foraging groups of shags around Cíes (see Section 3). Thus, we modeled the consequences, on shag foraging efficiency, of different management options aimed at reducing the impact of recreational boating.

2. Materials and methods

2.1. Study area and species

The terrestrial and marine National Park of the Atlantic islands of Galicia, located on the north-western coast of the Iberian Peninsula, comprises three main archipelagos (11.9 km^2) and the marine area that surrounds them (72.6 km^2). Cíes islands are the southermost archipelago and are located at the entrance of Ría de Vigo (Fig. 1) a heavily populated estuary (400,000 inhabitants) that receives a build-up of tourists in the summer months (July and August). Boating is one of the main recreational sea-based uses at Cíes. Typically, boats stay at anchor in one of the three main sites where anchorage is allowed, off the major sandy beaches, which are located in the eastern part of the islands (Fig. 1). Thus, most recreational boat traffic occurs as boats move between anchorage areas and between these and the mainland ports. The number of boats at anchor is recorded daily by the staff of the National Park.

The European Shag is a pursuit-diving seabird, distributed in the Atlantic coasts of the western Palearctic and the Mediterranean.
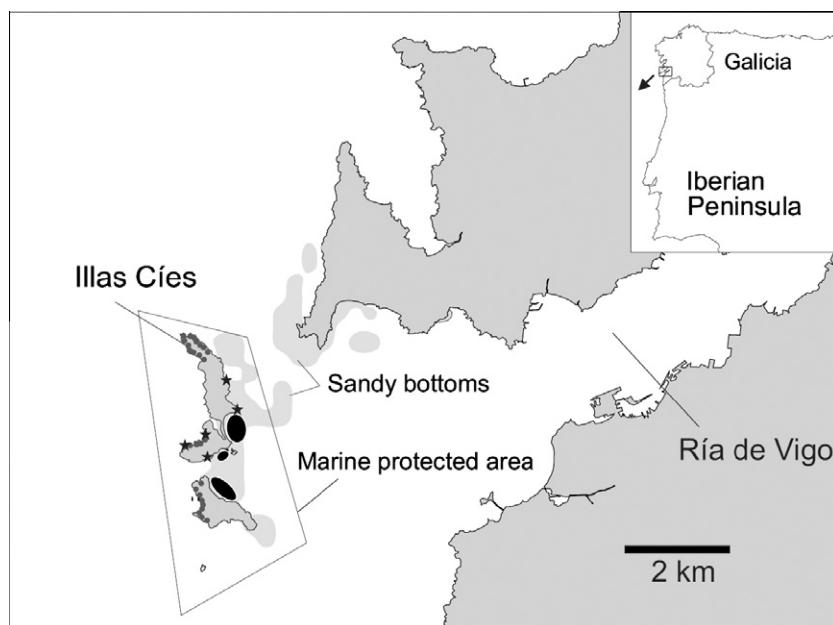

Fig. 1. Map of the study area showing the Cíes marine protected area in the National Park of the Atlantic islands of Galicia (north-western Iberia). The black dots indicate the sites where anchorage is permitted. The shaded areas show the distribution of sandy bottoms (i.e. sandeel habitat) at the mouth of the Vigo estuary (Ría de Vigo). Land grey points indicate main breeding areas and stars indicate observational stations (vantage-points).

With approximately 1000 pairs (400 pairs at Cíes), the National Park holds about 70% of the breeding population in Atlantic Iberia. In Cíes (Fig. 1), European shags feed predominantly on near shore pelagic and benthic fish in the vicinity of the colonies (Velando and Freire, 1999; Velando et al., 1999, 2005a,b). The first pairs lay in February (Velando, 1997) and the reproductive season ends by early August, when the juveniles leave the crèches (Velando, 2000, 2001). The feeding range of European shags breeding at Cíes is typically less than 4 km and is restricted to the sandy-bottom areas located on the east coast of the islands. In these areas, shags typically display a strategy of group feeding (Velando, 1997; Velando et al., 1999). The feeding groups are large and conspicuous with up to 1000 shags moving close to the coastline (Velando et al., 1999, 2005a,b).

2.2. At-sea distribution of boats and shags, disturbance and foraging behavior

The feeding areas of breeding shags are well documented from previous studies conducted from March to August between 1995 and 2006 (Velando, 1997; Velando et al., 2005a,b; Velando and Munilla, 2008). With the same methodology, we recorded the distribution of shags and recreational boats (motor crafts and sailing vessels) in the marine area around Cíes from 22 June to 25 August 2007. We selected this period because it is when most recreational boat traffic occurs due to summer holidays and favorable weather conditions. At that time, the number of shags foraging around the islands is increased by the incorporation of first-year juveniles that follow adults to feeding areas, where they are partially fed by their parents and learn foraging skills (Velando, 2001). We carried out two observational studies: an assessment of the at-sea distribution of shags and boats around Cíes, and a focal study on the behavior of foraging shags. Five fixed land-based vantage-points (i.e. prominent sampling stations) were selected, so to cover completely the marine area around Cíes. This area (77 km²) was divided for mapping purposes into a grid of 308 cells of 500 × 500 m according to the Universal Transverse Mercator (UTM) grid system and was thoroughly searched with the aid of binoculars and 20X–60X zoom telescopes. From each of the vantage-points we recorded on the grid map the number and location of all the boats and shags that were observed on the water. Additionally, we recorded the number of boats present in the anchorage sites that were visible. Landmarks both in Cíes and in the near coastline were used as reference points for mapping, as most observations were recorded very near to the coastline and in the eastern part of the islands. Note that our study area is an embayment with many landmarks available from vantage-points. Accuracy in the judgment of the cells that were occupied by birds and/or boats was further assured by convenient seamarks as islets, rocks and buoys. Vantage-points were visited 1–3 times per day from 11:00 to 21:00; in each visit we performed two complete surveys of the marine area that were at least 30 min apart. In total 185 vantage-point surveys (scan of all cells that were visible from the vantage-point) were performed during 12 days. Typically, foraging groups remained in roughly the same area during the course of the survey. The spatial distribution of shags and boats was mapped by kriging (Stein, 1999) after determining the experimental variogram. Overall, 5001 shags and 555 boats (accumulated numbers) were recorded.

Boat disturbance on foraging shags was recorded while mapping at the vantage-points and for the next 20 min. The behavioral responses that we considered indicative of disturbance from boats were: (a) cessation of foraging (diving routines are interrupted, all birds on the sea surface with neck and head held up straight); (b) clumping (all shags in the feeding group aggregate very densely); (c) displacement (the entire flock either flies or swims away from the boat). Note that these behaviors were never observed when boats were not around. Finally, we measured the foraging activity of shags in 42 randomly selected flocks as a diving rate (number of shags diving per unit time). Thus, in each flock groups of 10 shags were observed during 1 min periods and the number of individuals that plunged to dive (or the time it took the 10 shags to dive if less than 1 min) was recorded.

2.3. Statistical analyses

To analyze the long-term use (1995–2007) of the marine habitat by foraging shags we used the overall frequency of occurrence of shags at each grid-cell (from previous surveys: Velando, 1997; Velando et al., 2005a,b; Velando and Munilla, 2008 and present study; $n = 132$ surveys) as the dependent (binomial) variable and a logit link function, with seabed sediment type (whether sandy or not) as a fixed factor and the distance to the closest breeding colony and water depth as covariates (Generalized linear model, GLM). The spatial-dependent variation in the foraging group size (number of foraging shags by grid-cell, range 10–300) was analyzed using PROC MIXED in SAS (SAS Institute, 1999) with date, weekend (whether weekend day or not) and the number of boats at anchor as fixed terms. The grid-cells were considered as random factors using the Satterthwaite approximation for the denominator degrees of freedom (mixed model; Littell et al., 1996). The probability of boat disturbance to foraging shags was analyzed as a binomial dependent variable (whether a cell was occupied or not) and a logit link function with the number of shags on the water, the number of grid-cells occupied by shags, the number of boats at sea and the number of grid-cells occupied by boats as fixed terms and the grid-cells as random factor (GLIMMIX in SAS; Generalized linear mixed model, GLMM). Statistical significance of the random effects was assessed using the change in the likelihood ratio (Likelihood Ratio Test, LRT) of the model with and without the random term. This difference is distributed as a χ^2 with one degree of freedom (Littell et al., 1996). The variation in foraging activity was analyzed with a General Linear Model (GLM) with the maximum number of boats at anchor recorded in the anchorage areas as the independent variable. Data are expressed as mean ± SE.

2.4. Disturbance model

We used an ideal free distribution (IFD) framework (Fretwell and Lucas, 1970; Tregenza, 1995) to model the consequences of different management options aimed at reducing the impact of recreational boating on the foraging efficiency of shags. As usual in IFD models, our model assumes that all the shag competitors are equal in food acquisition ability, that they are omniscient about the value of different patches and that there are no costs attached to moving between patches (Hakoyama, 2003). Our model simulated a population of shags foraging in a two-dimensional area divided into a grid of square 500 m cells. These two features make the model applicable to the foraging behavior of shags around Cíes, as they frequently forage in large flocks, and occupy essentially a two-dimensional habitat (i.e. the sea surface).

Suppose that g cells are available to a group of shag competitors. Let R_i be the resource (fish prey) supply rate in cell i. There are N_i shags in cell i and a total of n shags in the whole area ($n = \Sigma_{i=1}^{n} N_i$). Shags distribute themselves so each obtains the highest resource intake. Assuming continuous input conditions, a shag's intake rate in cell i (W_i) is equal to the ratio between the supply rate and the number of shag competitors present in cell i ($W_i = R_i/N_i$). The IFD theory predicts that the proportion of shags should be equal to the proportion of resources constantly (input-matching rule) which can be expressed as $N_i/n = R_i/\Sigma_{i=1}^{g} R_i$. Let there be cells of high (H) and low (L) quality according to food supply, with m as the ratio between the food supply rates of these two

types of cells: $m = R_h/R_l > 1$. If all the shag competitors have perfect information on the environment, then all shags obtain equal resource intake rate in all cells constantly (equal intake prediction): $W_i = R_h/N_h = R_l/N_l$. The initial values of the model were set according to our observational data on the foraging behavior of shags around Cíes (see Section 3) with its MPA divided into a grid of 74 square 500 m cells; 14 of which are shallow water sandy-bottom cells that according to this and previous studies (Velando, 1997; Velando et al., 2005a,b; Velando and Munilla, 2008) are heavily used by foraging shags. Thus, we modeled 600 (n) foraging shags (the current estimated population size) on 14 higher quality and 60 lower quality grid-cells ($g_0 = 74$) with $W_i = 1$ when boats are absent from the MPA.

We modeled disturbance as a competitive interference for space (i.e. grid-cells) between boats and shags. Thus, the number of grid-cells available to foraging shags is depleted according to the number of boats using the Cíes MPA as follows:

$$g = g_0 e^{-kx},$$

where g_0 = number of grid-cells used by shags without boat interference; x = number of boats; and k = the rate of cell depletion by boats. We assume that k is independent of cell quality. To simulate the effect of habitat protection (i.e. the establishment of set-aside areas free of boat traffic) we varied the conditions of boat disturbance (k parameter) and the difference in quality between the two types of cells (m parameter). Three management scenarios were considered: (1) no habitat protection; (2) protection of the 14 higher quality (H) cells; and, (3) protection of 14 lower quality (L) cells. Note that these protection scenarios correspond to the extreme scenarios of our previous habitat quality assessment.

3. Results

3.1. Sea-based tourism and the distribution of shags in the marine reserve

According to our long-term data (1995–2007) shags tend to forage in shallow waters (<30 m water depth; GLM; $\chi^2 = 164.57$; $P < 0.0001$; Fig. 2), especially over sandy bottoms (bottom type * water depth; $\chi^2 = 47.95$; $P < 0.0001$) close to the colonies (water depth * distance; $\chi^2 = 14.23$; $P < 0.001$). Thus, their main foraging areas were distributed according to the location of shallow sandy bottoms and within the limits of the MPA (Figs. 1 and 3a).

In the 2007 high summer season the number of recreational boats visiting the Cíes MPA showed large fluctuations from day
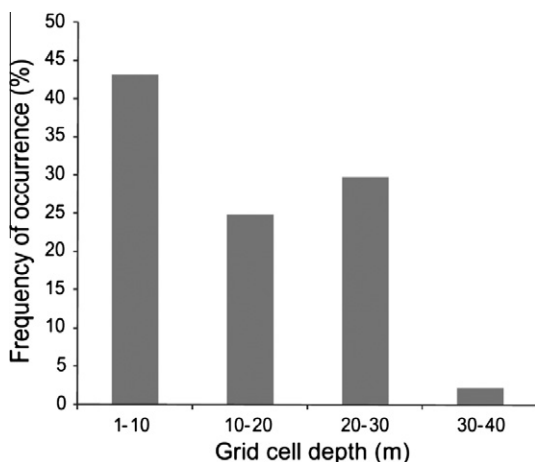
to day and peaked during weekends, as shown by the records of boats at anchor held by the National Park. The number of grid-cells occupied by recreational boats strongly correlated with the total number of boats at sea ($r = 0.94$; $P < 0.0001$). Shags and boats highly overlapped in the MPA (Fig. 4) as 81% of the grid-cells used by foraging shags were also used by boats. Moreover, grid-cell occupation by boats correlated with their historical use by foraging shags ($r = 0.59$; $P < 0.0001$), therefore suggesting that shags and boats use the same areas. In the 2007 surveys, shags typically foraged in groups across the sandy-bottom areas around Cíes. The number of shags per grid-cell was not affected by Julian date (Mixed model; $F_{1,188} = 0.05$; $P = 0.83$) but shags showed a clumped distribution on weekend days ($F_{1,188} = 4.41$; $P = 0.037$) and when the number of boats at anchor increased ($F_{1,189} = 14.05$; $P = 0.0002$). Thus, compared to days of lower boat presence, the size of the foraging groups increased by threefold when the number of boats at anchor in the MPA exceeded 50 (Fig. 4a).

3.2. Observed disturbance to foraging shags

Shags ceased to forage and became alert whenever a moving boat entered the grid-cell they were using and in the majority of cases (92%) flee away from the boat. The probability of a disturbance event correlated both with the total number of shags on the water (GLMM; $F_{1,126} = 14.6$; $P < 0.001$) and with the number of grid-cells occupied by shags ($F_{1,166} = 15.8$; $P < 0.001$). Moreover, the probability of a disturbance event increased with both the number boats at sea ($F_{1,98} = 7.02$; $P = 0.009$; Fig. 5) and with the number of grid-cells occupied by boats ($F_{1,108} = 14.6$; $P < 0.001$; Fig. 4). The probability of disturbance was not homogenously distributed among grid-cells ($P < 0.0001$). Thus, disturbances were much more likely to occur in preferred foraging areas, as shown by the correlation between the number of disturbance events recorded in each grid-cell and its long-term use by shags ($r = 0.61$; $P < 0.001$). As a result, foraging activity was significantly reduced on days of high boat presence in the Cíes MPA ($F_{1,14} = 5.624$; $P = 0.03$;). The foraging activity decreased by ten times when the number of boats at anchor in the MPA exceeded 50 (Fig. 4b). Individual shags performed 0.5 ± 0.09 foraging dives per min when less than 50 boats were at anchor, but in contrast the foraging activity was 0.021 ± 0.02 foraging dives per min when more than 50 boats were at anchor.

3.3. Modeling disturbance to foraging shags

In our model we modified boat disturbance (k parameter) and the difference in quality between the two types of grid-cells (m parameter) as illustrated in Fig. 6. As expected, the model predicts stronger effects on food intake when boat interference (k) is high, especially as the number of boats increase.

At low levels of boat interference (e.g. $k = 0.01$), the protection of the higher quality grid-cells (H) will only have a strong positive effect on food intake if the difference in food supply with the lower quality grid-cells is high ($m = 3$). Interestingly, in such scenario ($k = 0.01$), the protection of lower quality grid-cells (L) has no effect on food intake and it may even have a negative effect on food intake when differences in habitat quality are high ($m = 3$) and boat use is intense (>150 boats). This effect occurs because the protection of lower quality grid-cells tends to increase boat disturbance in higher quality areas, therefore reducing food supply.

When boat interference is high (e.g. $k = 0.03$), the protection of habitat, irrespective of its quality, has mainly beneficial effects on food intake (of course, this effect is stronger when the high quality grid-cells are protected). Note that the protection of lower quality habitat may have a slight negative effect on food intake in conditions when the difference in habitat quality is small ($m = 1.5$),
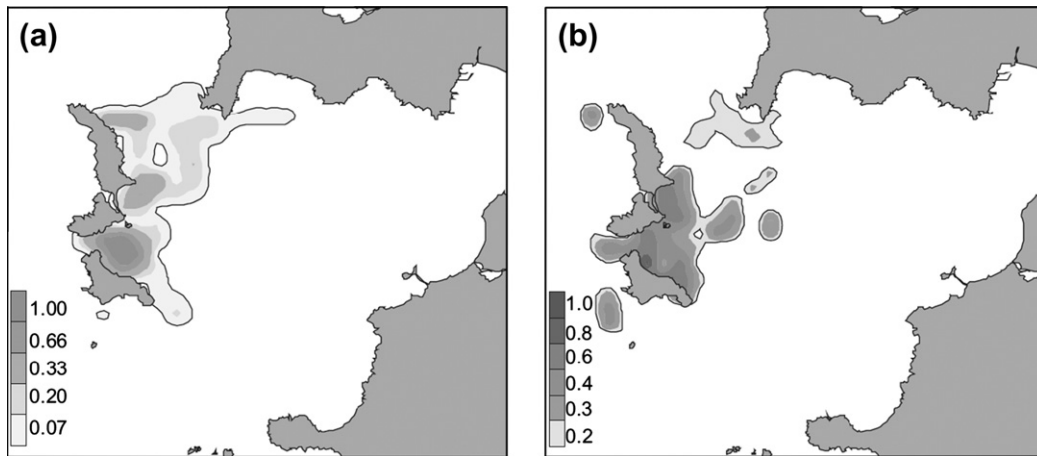

Fig. 2. Frequency of occurrence of foraging European shags in the Cíes MPA according to sea depth. The study area was divided into 500 m square grid-cells.

Fig. 3. Use of the MPA around Cíes by (a) European shags (1995–2007) and (b) recreational boats (2007). Density classes are scaled according to the maximum number of occurrences recorded.
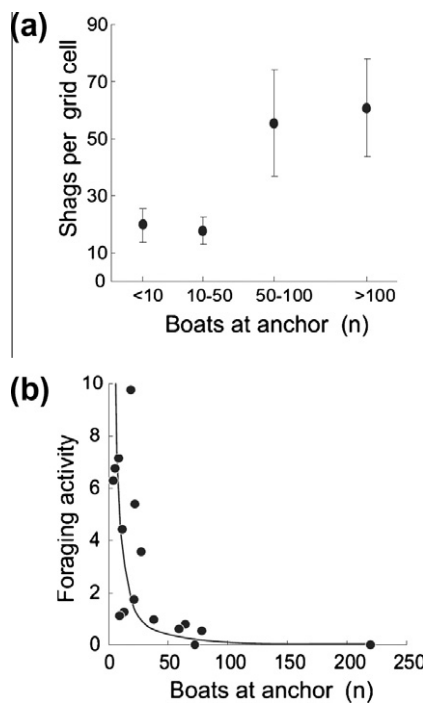

Fig. 4. Changes in the foraging behavior of European shags as a function of the number of boats at anchor in the anchorage sites of the Cíes MPA. (a) Variation in the spatial aggregation of shags as shown by the average (±SE) number of shags recorded by grid-cell (the study area was divided into 500 m square grid-cells). (b) Changes in foraging activity refer to the number of birds diving in 1 min periods (see Section 2).

but this effect rapidly disappears when the number of boats either increase or decrease.

When we modeled a higher preference of boats for the higher quality grid-cells (e.g. $k > 0.03$; not shown) similar results were achieved though the patterns observed became more exaggerated. Interestingly, any possible negative effects on food intake derived from the protection of lower quality grid-cells disappeared, because the higher quality grid-cells tended to be depleted first.

4. Discussion

Our study identified foraging areas around breeding colonies and modeled disturbance by recreational activities to an endan-

gered pursuit-diving seabird in a MPA. We showed that boat disturbance upon foraging groups of European shags elicited a characteristic avoidance behavior that resulted in a drastic reduction in foraging activity and displacement from otherwise optimal foraging areas. These comprise the shallow sandy-bottom areas (i.e. typical sandeel habitat) in the vicinity of the breeding colonies (see Wanless et al., 1991). Our model revealed that in low boat disturbance scenarios limiting the number of boats using the reserve would be a better management option than habitat protection. On the contrary, when boat disturbance levels are high, as documented by our study, the protection of habitat is recommended. Since sea-based tourism in MPAs is widespread and growing worldwide, guidelines provided by our study are relevant and applicable to many instances where highly mobile marine organisms of conservation concern that react to sea-based recreational uses are involved.

4.1. Disturbance to shags

Our results showed that an increase in the number of boats using the marine reserve was associated with a reduction in foraging activity in European shags. When disturbed by boat traffic, foraging shags stopped diving and stood alert; thus time was devoted to vigilance at the expense of feeding rates. We acknowledge that other unmeasured factors as noise, speed or distance of the passing boat may influence boat disturbance to seabirds (e.g. Burger, 1998; Ronconi et al., 2002; Hodgson and Marsh, 2007; Rojek et al., 2007). Nevertheless, in our study, disturbance was recorded in all instances when a boat entered a grid-cell occupied by foraging shags, which suggests low tolerance to boat traffic. Animal tolerance to human approaches may be used to establish buffers for wildlife that can minimize the disturbance by human activity (e.g. Fernández-Juricic et al., 2001). Grid-cell size was 500 m, thus providing a minimum estimate of the alert distance with respect to moving boats. This "area of influence" of recreational boating may be included in the design of safe traffic routes for recreational boats within the MPA (e.g. see Rodgers and Schwikert, 2002; Bellefleur et al., 2009).

Our study revealed that shags increased their spatial aggregation and concentrated in areas with little boat traffic as levels of recreational boating rose. Most recreational boat traffic takes place in areas where shags tend to aggregate and forage, and boat disturbance eventually excluded shags from optimal foraging grounds (i.e. sandeel areas close to the breeding colonies). Thus, the shallow sandy-bottom coastal areas located in the sheltered, eastern part,
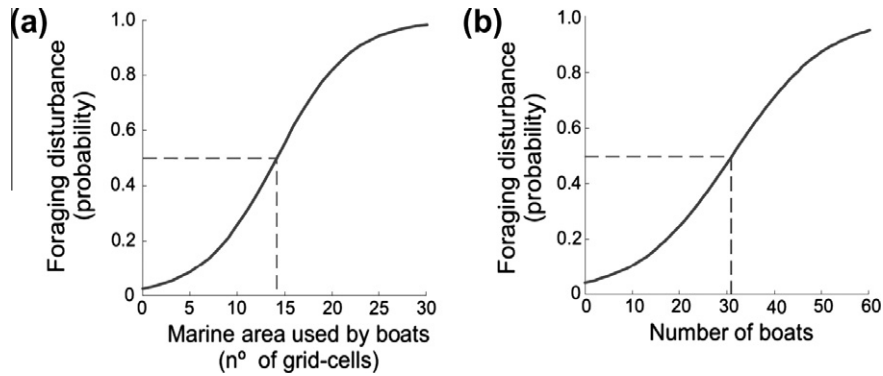
Fig. 5. Probability of disturbance to foraging European shags in relation to (a) the number of grid-cells with at least one boat present, and (b) the number of boats in the Cíes MPA. The study area was divided into 500 m square grid-cells.
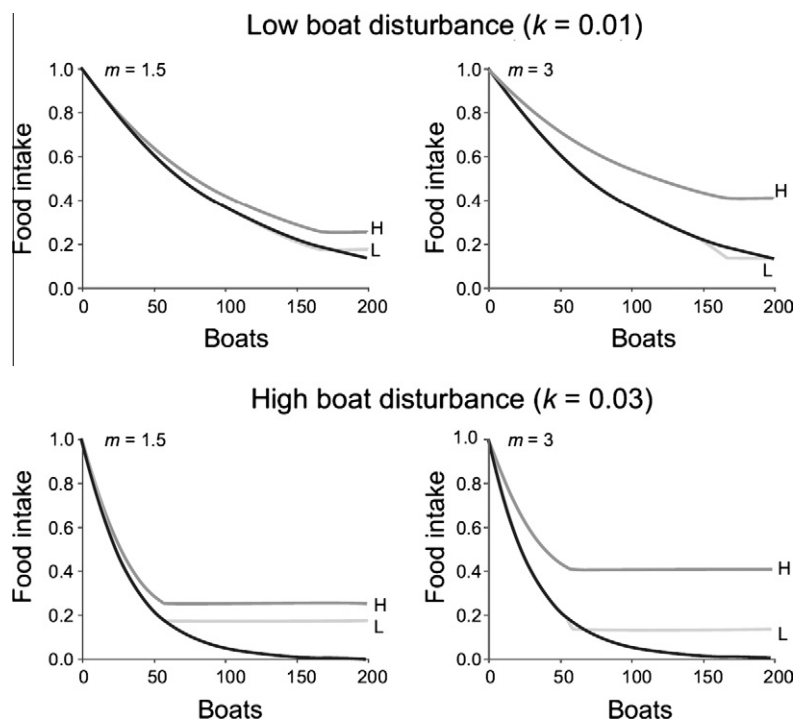

Fig. 6. Effects of boat disturbance on the food intake rate of foraging European shags in the Cíes MPA according to an ideal free distribution model. The closed line represents the change in food intake rate in relation to the number of boats using the marine reserve. The grey line (*H*) represents the change in food intake rate when all boat traffic is banned from the high quality habitat patches, and the light line (*L*) represents the change in food intake rate when all boat traffic is banned from low quality habitat patches. Two scenarios of boat disturbance (low and high) and two levels in the difference between the high and low quality habitat patches (*m*) are modeled.

of the Cíes MPA support intense boat traffic as they provide the best anchorage sites and easy access to sandy beaches. Unfortunately, these sheltered sandy-bottom areas are the primary habitat for sandeels (Velando et al., 2005a,b; Velando and Munilla, 2008). Sandeels are a high quality food resource for reproduction and juvenile survival in shags and other seabirds (e.g. Rindorf et al., 2000) and European shags breeding at Cíes depend on sandeels for high reproductive success (Velando et al., 1999; Velando and Munilla, 2008). In the Cíes MPA and elsewhere in Galicia, boating is more intense during the summer vacation months of July and August, a period that may prove crucial for the survival of juveniles (Velando, 1997). At this time, juveniles concentrate at crèches where they are fed by their parents but also have the opportunity to learn feeding skills by following adults to feeding areas (Velando, 2000, 2001). As less efficient foragers, juveniles are more vulnerable to reduced foraging time and to foraging in suboptimal (less rewarding) habitats and to increased intraspecific competi-

tion. There is compelling evidence that juveniles compensate for poor foraging proficiency by increasing foraging time (Daunt et al., 2007) a strategy that in Cíes is greatly limited by recreational boating. In the European shag reduced foraging time results in high winter juvenile mortality (Daunt et al., 2007) whereas juveniles at Cíes typically show high mortalities in their first months after fledging (Velando, 1997).

4.2. Management guidelines

Our empirical and modeling results may be useful to identify the conditions that would minimize disturbance. We found a strong association between the probability of disturbance to foraging shags and the number of boats at sea, which allows identifying quantitative threshold values to guide management decisions. In this context, we found that more than 50 boats at anchor increased shag flock size by threefold and increased the

probability of disturbance above 90%, with negative consequences on foraging activity. Currently, the number of boats at anchorage sites in Cíes is limited to 250 boats a day. During the 2007 summer season, the 50 boats threshold was exceeded in 26 days (43%), suggesting a persistent disturbance during this period.

To guide management decisions, we also modeled boat disturbance on foraging shags in an ideal free distribution framework. Boat disturbance was modeled in terms of competitive habitat depletion by boats (i.e. interference competition). This assumption fits well with our empirical study, as foraging shags were disturbed and stopped foraging whenever a boat entered the grid-cell they were using. We acknowledge that some of the model assumptions are simplifications, and that numerical predictions may not match when some assumptions are relaxed (e.g. Lessells, 1995; Hakoyama, 2003); nonetheless the overall patterns would probably remain unchanged or become more exaggerated even if some assumptions are not met at all. Thus, for example, our model assumed no costs to moving between patches, which is probably unrealistic. Flying costs associated with moving from patch to patch are likely to increase the negative effect of boat disturbance on the energy balance of foraging shags.

Our model revealed that when boat disturbance levels are low and have a slight linear effect on the foraging activity of shags, the best management option is to regulate the number of boats. In that case, habitat protection (i.e. the establishment of set-aside areas free of boat traffic) may only be advisable if spatial variation in habitat quality is fairly assessed and differences in quality among habitat patches are high. Note that when habitat quality is not properly assessed, the establishment of set-aside areas may have negative effects on the foraging activity of shags, because, eventually, the exclusion of boats from low quality areas may result in an overall increase in boat traffic and shag disturbance in high quality areas. On the other hand, when the effect of boat disturbance on foraging seabirds is high (as probably occurs in the Cíes MPA due to the large spatial overlap between foraging shags and recreational boats), the protection of habitat is recommended, even when habitat quality assessment is poor.

For management purposes, our model suggested that limitations on the number of boats could be relaxed if boat traffic is banned in high quality habitat patches, especially when the difference in foraging quality among habitat patches is high. Our analysis suggests that depth and distance to the breeding colony are important variables controlling the foraging efficiency of shags. Shallow (<30 m depth) sandy bottom sandeel areas close to the breeding colonies are likely optimal foraging habitats as suggested by their long-term preferences. Note that, according to our model, the reservation of low quality areas may have an adverse effect on the foraging efficiency of seabirds.

Conflicts between seabirds and recreational uses are likely to increase in future years due to growing pressure upon coastal marine areas and the seabirds that live there. Increases in nature-based tourism in MPAs may overcome the economic costs of its implementation and management (e.g. McCook et al., 2010), but they may generate side effects on far-ranging marine vertebrates. Although the specific management measures may only apply to the particular circumstances under study, the variables and the analytical approach used here may be relevant to other locations and other marine species, including other coastal seabirds and possibly marine mammals (e.g. Hodgson and Marsh, 2007; see also Moffitt et al., 2009). Our model may serve to ensure compatibility between seabird conservation and sea-based recreational uses, thereby helping to convey conservation and human goals in marine reserves. We strongly recommend that seabird use of the marine environment should be assessed in marine reserve design, planning and management. Moreover, this study emphasized that the combination of two complementary methods (field work and modeling) is a useful approach for developing management strategies trying to minimize tourism disturbance to seabirds. The design of marine reserves should try to include optimal seabird foraging areas for seabirds, whereas the negative impacts of sea-based tourism activities should be routinely assessed as they may have important consequences for seabird conservation.

Acknowledgments

References

Badalamenti, F., Ramos, A.A., Voultsiadou, E., Sánchez Lizaso, J.L., D'anna, G., Pipitone, C., Mas, J.A., Ruiz Fernandez, J., Whitmarsh, D., Riggio, S., 2000. Cultural and socio-economic impacts of Mediterranean marine protected areas. Environmental Conservation 27, 110–125.

Beale, C.M., Monaghan, P., 2004. Human disturbance: people as predation-free predators? Journal of Applied Ecology 41, 335–343.

Beale, C.M., 2007. Managing visitor access to seabird colonies: a spatial simulation and empirical observations. Ibis 149, 102–111.

Beale, C.M., Monaghan, P., 2007. Modeling the effects of limiting the number of visitors on failure rates of seabird nests. Conservation Biology 19, 2015–2019.

Bellefleur, D., Lee, P., Ronconi, R.A., 2009. The impact of recreational boat traffic on Marbled Murrelets (*Brachyramphus marmoratus*). Journal of Environmental Management 90, 531–538.

Burger, J., 1998. Effects of motorboats and personal watercraft on flight behavior over a colony of common terns. The Condor 100, 528–534.

Daunt, F., Afanasyev, V., Adam, A., Croxall, J.P., Wanless, S., 2007. From cradle to early grave: juvenile mortality in European shags *Phalacrocorax aristotelis* results from inadequate development of foraging proficiency. Biology Letters 3, 371–374.

Fernández-Juricic, E., Jimenez, M.D., Lucas, E., 2001. Alert distance as an alternative measure of bird tolerance to human disturbance. implications for park design. Environmental Conservation 28, 263–269.

Fretwell, S.D., Lucas Jr., H.J., 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica 19, 16–36.

Gill, J.A., 2007. Approaches to measuring the effects of human disturbance on birds. Ibis 149, 9–14.

Hakoyama, H., 2003. The ideal free distribution when the resource is variable. Behavioral Ecology 14, 109–115.

Halpern, B.S., Lester, S.E., McLeod, K.L., 2010. Placing marine protected areas onto the ecosystem based management seascape. Proceedings of National Academic of Science USA 107, 18312–18317.

Hodgson, A.J., Marsh, H., 2007. Response of dugongs to boat traffic: the risk of disturbance and displacement. Journal of Experimental Marine Biology and Ecology 340, 50–61.

Hooker, S.K., Gerber, L.R., 2004. Marine reserves as a tool for ecosystem-based management: the potential importance of megafauna. Bioscience 54, 27–39.

Kelleher, G., 1999. Guidelines for Marine Protected Areas. IUCN, Gland, Switzerland.

Lessells, C.M., 1995. Putting resource dynamics into continuous input ideal free distribution models. Animal Behaviour 49, 487–494.

Littell, C.R., Milliken, G.A., Stroup, W.W., Wolnger, R.D., 1996. SAS System for Mixed Models. SAS Institute, Cary, NC.

Louzao, M., Hyrenbach, K.D., Arcos, J.M., Abelló, P., Gil de Sola, L., Oro, D., 2006. Oceanographic habitat of an endangered mediterranean procellariiform: implications for marine protected area. Ecological Applications 16, 1683–1695.

Lubchenco, J., Palumbi, S.R., Gaines, S.D., Andelman, S., 2003. Plugging a hole in the ocean: the emerging science of marine reserves. Ecological Applications 13, S3–S7.

McClanahan, T., Marnane, M., Cinner, J., Kiene, W., 2006. A comparison of marine protected areas and alternative approaches to coral reef conservation. Current Biology 16, 1408–1413.

McCook, L.J., Ayling, T., Cappo, M., Choat, J.H., Evans, R.D., De Freitas, D.M., Heupel, M., Hughes, T.P., Jones, G.P., Mapstone, B., Marsh, H., Mills, M., Molloy, F.J., Pitcher, C.R., Pressey, R.L., Russ, G.R., Sutton, S., Sweatman, H., Tobin, R., Wachenfeld, D.R., Williamson, D.H., 2010. Marine reserves special feature: adaptive management of the great barrier reef: a globally significant demonstration of the benefits of networks of marine reserves. Proceedings of National Academic of Science USA 107, 18278–18285.

McCrone, A., 2001. Visitor impacts on marine protected areas in New Zealand. Science for Conservation 173, 1173–2946.

Moffitt, E.A., Botsford, L.W., Kaplan, D.M., O'Farrell, M.R., 2009. Marine reserve networks for species that move within a home range. Ecological Applications 19, 1835–1847.

Munilla, I., Díez, C., Velando, A., 2007. Are edge bird populations doomed to extinction? A retrospective analysis of the common guillemot collapse in Iberia. Biological Conservation 137, 359–371.

Nisbet, I.C., 2000. Disturbance, habituation, and management of waterbird colonies. Waterbirds 23, 312–332.

Palumbi, S.R., Sandifer, P.A., Allan, J.D., Beck, M.W., Fautin, D.G., Fogarty, M.J., Halpern, B.S., Incze, L.S., Leong, J.-A., Norse, E., Stachowicz, J.J., Wall, D.H., 2009. Managing for ocean biodiversity to sustain marine ecosystem services. Frontiers in Ecology and the Environment 7, 204–211.

Rindorf, A., Wanless, S., Harris, M.P., 2000. Effects of changes in sandeel availability on the reproductive output of seabirds. Marine Ecology Progress Series 202, 241–252.

Roberts, C.M., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J., Halpern, B.S., Lafferty, K.D., Leslie, H., Lubchenco, J., Mcardle, D., Ruckelshaus, M., Warner, R.R., 2003. Application of ecological criteria in selecting marine reserves and developing reserve networks. Ecological Applications 13, S215–S228.

Rodgers, J.A., Schwikert, S.T., 2002. Buffer-zone distances to protect foraging and loafing waterbirds from disturbance by personal watercraft and outboard-powered boats. Conservation Biology 16, 216–224.

Rojek, N.A., Parker, M.W., Carter, H.R., Mcchesney, G.J., 2007. Aircraft and vessel disturbances to Common Murres Uria aalge at breeding colonies in central California, 1997–1999. Marine Ornithology 35, 61–69.

Ronconi, R.A., St. Clair, C.C., 2002. Management options to reduce boat disturbance on foraging black guillemots (Cepphus grylle) in the Bay of Fundy. Biological Conservation 108, 265–271.

Russ, G.R., Alcala, A.C., Maypa, A.P., Calumpong, H.P., White, A.T., 2004. Marine reserves benefits local fisheries. Ecological Applications 14, 597–606.

Selig, E.R., Bruno, J.F., 2010. A global analysis of the effectiveness of marine protected areas in preventing coral loss. PLoS ONE 5, e9278.

Stein, M.L., 1999. Statistical Interpolation of Spatial Data: Some Theory for Kriging. Springer, New York.

Tasker, M.L., Camphuysen, C.J., Cooper, J., Garthe, S., Montevecchi, W.A., Blaber, S.J.M., 2000. The impacts of fishing on marine birds. ICES Journal of Marine Science 57, 531–547.

Taylor, A.R., Knight, R.L., 2003. Wildlife responses to recreation and associated visitor perceptions. Ecological Applications 13, 951–963.

Tregenza, T., 1995. Building on the ideal free distribution. Advances in Ecological Research 26, 253–302.

Velando, A. 1997. Ecología y Comportamiento del Cormorán Moñudo Phalacocorax aristotelis en las Islas Cíes y Ons. PhD Thesis, Universidade de Vigo, Vigo, Spain.

Velando, A. 1998. Plan de Manejo del Cormorán Moñudo en las Islas Cíes y Ons. Servicio de Medio Ambiente Natural da Xunta de Galicia, Pontevedra, Spain.

Velando, A., 2000. The importance of the hatching date on dominance of young shags. Animal Behaviour 60, 181–185.

Velando, A., 2001. Postfledging crèche behaviour in European shag. Journal of Ethology 19, 116–122.

Velando, A., Alvarez, D., 2004. Cormoran Moñudo, Phalacrocorax aristotelis aristotelis. In: Madroño, A., Gonzalez, C., Atienza, J.C. (Eds.), Libro Rojo de las Aves de España. Ministerio de Medio Ambiente-SEO/Birdlife, Madrid, Spain, pp. 60–62.

Velando, A., Freire, J., 1999. Intercolony and seasonal differences in the breeding diet of European shags on the Galician coast (NW Spain). Marine Ecology Progress Series 188, 225–236.

Velando, A., Freire, J., 2002. Population modelling of European shag at their southern limit: conservation implications. Biological Conservation 107, 59–69.

Velando, A., Munilla, I., 2008. Plan de Conservación del Cormorán Moñudo en el Parque Nacional de las Islas Atlánticas de Galicia. Parque Nacional de las Islas Atlánticas de Galicia and Universidade de Vigo, Vigo, Spain.

Velando, A., Álvarez, D., Mouriño, J., Arcos, F., Barros, A., 2005a. Population trends and reproductive success of European Shag following the Prestige oil spill in the Iberian Peninsula. Journal of Ornithology 146, 116–120.

Velando, A., Munilla, I., Leyenda, P.M., 2005b. Short-term indirect effects of the Prestige oil spill on a marine top predator: changes in prey availability for European shags. Marine Ecology Progress Series 302, 263–274.

Velando, A., Ortega-Ruano, J.E., Freire, J., 1999. Chick mortality in European shag Stictocarbo aristotelis related to food limitations during adverse weather events. Ardea 87, 51–59.

Wanless, S., Harris, M.P., Morris, J.A., 1991. Foraging range and feeding locations of Shags Phalacrocorax aristotelis during chick rearing. Ibis 133, 30–36.

Williams, R.M., Trites, A.W., Bain, D.E., 2002. Behavioural responses of killer whales (Orcinus orca) to whale-watching boats: opportunistic observations and experimental approaches. Journal of Zoology 256, 255–270.