

ASHMOLE'S HALO AS THE OUTCOME OF A PREDATOR-PREY GAME

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SUMMARY

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Many seabird species breed in large colonies, from which they make repeated excursions to collect prey for delivery to offspring. This necessarily confines their foraging activities to a region around or near the colony, which is constrained by their powers of mobility. The cumulative impact in this region is hypothesized to be large enough to reduce the density of prey, a phenomenon referred to as “Ashmole's halo.” Considering its important role in thought about seabird life histories, Ashmole's halo has received remarkably little formal investigation. Here we model the formation of Ashmole's halo. In a previous theoretical study, Gaston *et al.* (2007) derived the size and shape of the halo, using a set of simple assumptions. In that model, prey density was reduced by exploitation alone: prey individuals had no explicit behavioral options with which to evade or elude predators, such as moving away from a zone of high depredation. The objective of the model developed here is to assess the role of prey behavior in the occurrence of Ashmole's halo. In our model, both seabirds and their prey make strategic choices about foraging location: seabirds do so to maximize the delivery of prey to offspring, while fish do so to maximize fitness (growth and survivorship). The situation is a predator-prey game, because for both seabirds and fish the best choice of foraging location depends on the choices made by all other players. Our simulations show that the halo develops much more quickly and is deeper and stronger when prey individuals are able to adjust their location adaptively (i.e. to maximize fitness), than when a random (i.e. diffusion) process governs prey movement as prey density is altered by exploitation. These results broaden the conditions under which Ashmole's halo could be pronounced enough to affect seabird biology.

Keywords: Ashmole's halo; predator-prey game; central place foraging.

INTRODUCTION

A central concept in seabird biology is the hypothesized zone of food depletion around breeding colonies, termed “Ashmole's halo” (Gaston *et al.* 2007) or “Storer-Ashmole's halo” (Elliott *et al.* 2009). Ashmole (1963, 1971) proposed that, by their provisioning activities, breeding seabirds decrease the food density in the vicinity of breeding colonies. As a result, the rate of food delivery to their nestlings as well as their reproductive output is reduced. Storer (1952) showed that foraging area size was proportional to colony size, and, in accord, Ashmole surmised that provisioning intensity from a central place limits seabird population growth. Ashmole further pointed out that all the K-selected traits that characterize pelagic seabirds (single-egg clutch, prolonged incubation, slow nestling growth, deferred maturity) might be expected where food is difficult to obtain during breeding (see Ricklefs 1990).

In spite of its supposed influence on seabird populations and life histories, Ashmole's halo has been the subject of little direct study. Only a few empirical studies (Birt *et al.* 1987, Elliott *et al.* 2009) have directly documented its existence in regard to actual prey depletion; another (Ainley *et al.* 2003) documented seabird foraging negatively affecting prey availability (reducing prey schools at the surface available to surface-foraging seabirds). Other studies (Lewis *et al.* 2001, Ford *et al.* 2007, Ballance *et al.* 2009) have inferred its existence based on comparisons of the foraging ranges of seabirds from colonies of differing sizes, and on the locations of adjacent colonies. This evidence all strongly

supports density dependence via intraspecific competition for food as an important factor in these systems, but, as Ballance *et al.* 2009 point out, the proximate mechanisms involved have yet to be elucidated. These previous papers have variously invoked exploitation or interference competition (or both), but, with the exception of Lewis *et al.* (2001) and Ainley *et al.* (2003), were unable to distinguish one from the other.

Lewis *et al.* (2001) assumed, and Ainley *et al.* (2003) showed, that shoals of fish show escape responses after disturbance by foraging seabirds, either by swimming away or by going deeper. Taking into account the higher density of foraging seabirds close to the colony and the escape responses of the fish, they calculate the length of search path required to collect a load of a given size, and show that seabird trip time increases as the square root of colony size, which closely matches their observations. Ainley *et al.* (2003) directly measured food availability and showed that the prevalence of fish schools at the surface was lower around larger colonies, although schools were present at depth. They concluded that Prince William Sound has reached its carrying capacity for Black-legged Kittiwakes *Rissa tridactyla*, and that a higher kittiwake population would compromise access to prey by “passive foraging interference.”

There are several possible (non-mutually exclusive) mechanisms of competition: (i) exploitation competition, in which predators reduce prey density by catching and eating them; (ii) interference competition resulting from seabirds disturbing prey and making them less available (modeled explicitly by Lewis *et al.* [2001]

and what Ainley *et al.* [2003] meant by “passive” interference); and (iii) interference competition by seabirds avoiding each other in some way or contesting access to food behaviorally (“direct” interference). The latter is not considered in any of the previous papers, but it is a logical possibility.

A fourth mechanism is suggested by considering that, in the model of Lewis *et al.* (2001), neither birds nor prey are strategic agents that can make decisions. An extensive literature now considers “the ecology of fear” (e.g. Brown 2007) and shows that prey can strategically avoid areas of high predation risk without necessarily having to be “disturbed” by predators. For example, Antarctic penguins alter their foraging behavior during darkness, i.e. refrain from entering the water, because it is more dangerous (Ainley & Ballard 2012, and references therein).

So far as we are aware, the only studies that have formally considered, based on knowledge about seabirds and their prey, how underlying processes might combine to create the halo are those of Lewis *et al.* (2001), Ainley *et al.* (2003) and Gaston *et al.* (2007; see above). Gaston *et al.* (2007) calculated the relative availability of prey as a function of travel distance from the colony at which the attainable delivery rate to the offspring is identical from all locations. The rationale for this requirement was that any location with a higher attainable delivery rate would quickly attract foragers, reducing the prey density until the attainable delivery rate becomes equal to that at other places. It is clear that, to make the delivery rate attainable from a distant site equal to that from a nearby site, prey must be captured more rapidly at the distant location. Therefore, to attract foragers, patches far away from the colony must have higher prey density than those close to the colony. Eventually, patches are too distant to make exploitation worthwhile at any prey density (see Ballance *et al.* 2009). Gaston *et al.* (2007) hypothesized that these relationships underlie the existence of the halo.

Gaston *et al.*'s model calculated the spatial distribution of predator (seabirds) foraging activity over a population of prey (fish or zooplankton). In their model, predators reduced prey availability by exploitation alone. Model prey were given no ability to evade predators (e.g. by increased caution, altered timing and foraging etc.; see Lima 1998) and so reduce their availability to predators. The objective of the current study is to assess the role of prey behavior in the occurrence of Ashmole's halo. We develop a model to calculate the distributions of both predators (seabirds) and prey (fish or zooplankton) around a central place (island) to which the seabirds deliver their catch. We compare the resulting distributions of fish and birds along a transect from the island assuming that prey (a) redistribute randomly as they are depleted by predators; or (b) redistribute in response to the predation danger posed by predators, balanced against the improved foraging potential of fewer competitors. With random movement, prey availability is reduced primarily by exploitation, with an added random component that increases or decreases the exploitation effect. With predator evasion behavior, fish move away from zones of high predation to reduce exposure to predators.

MODEL DESCRIPTION

Model set-up

We developed a one-dimensional spatio-temporal simulation model to calculate how birds and fish (re)distribute from the island

outward. We use numerical solutions of the model to study the transient dynamics (during N time steps) as the interaction between birds and fish approaches equilibrium.

We simplify the interaction by assuming that the island and surrounding ocean are radially symmetrical, and by representing the various seabird and fish species as single types of predator and prey. Prey are referred to here as “fish,” but could be any type of mobile prey captured by seabirds. We assume that fish are able to move to or from the island but do not change depth or make themselves otherwise harder to capture. We assume that there is no direct interference competition; that each bird catches one fish on each provisioning excursion from the island; and that during the breeding season the number of birds is constant. We do not consider self-feeding explicitly. We assume that there is a constant input rate of food for fish, which is either (i) strongest close to the island (“upwelling”); or (ii) equal across the foraging range. For both input rate scenarios, we assumed that the total amount of food provided in the considered area was equal. We also assume that, in each time step, fish fully consume this food, and finally that fish move only to places where food is available.

Upwelling, generated by water flow around an island, is assumed to create a gradient of primary productivity, such that the prey (here, fish) have the highest food availability and the highest danger close to the island. We included this feature in the model to assess how important specific patterns of food availability for the prey might be to the formation of the halo. In some predator-prey games (e.g. Hugie & Dill 1994; see Discussion) food for the prey affects the predator distribution.

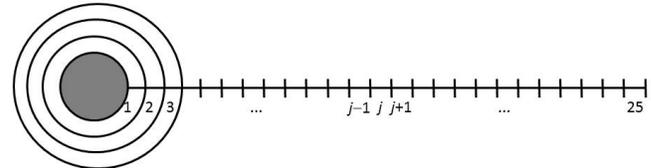


Fig. 1. The island (innermost dark circle) is surrounded by circular sites that are represented as neighboring intervals along a one-dimensional space.

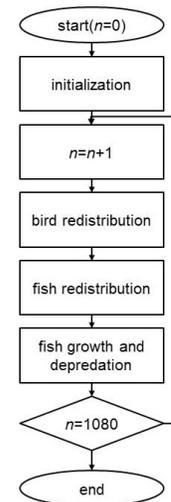


Fig. 2. Flowchart of the structure of the bird-fish game-simulation model. Reversing the order of the bird and fish redistribution steps makes only very minor differences to results.

The maximum distance from the island (with radius r) to which birds and fish can move is divided into s ($= 25$ in our model) rings of equal width Δs (Fig. 1). The area of the j th ring is

$$A_j = \pi(r + j\Delta s)^2 - \pi(r + (j - 1)\Delta s)^2 \text{ for } j = 1, 2, \dots, s$$

and thus the surface area of successively more distant rings is larger. We model the distributions of birds and fish over these rings. When referring to fish and bird density, upper case F and B are used, while absolute biomass of fish and number of birds are denoted with lower case f and b .

Each model run consisted of 1 080 iterations (representing 2 h time steps over 90 d). In each time step, three calculations are made, in the following order: (i) bird redistribution, (ii) fish redistribution

and (iii) fish biomass growth and depredation (Fig. 2). At the start of each simulation, all birds are on the island at site 0, and the fish are distributed over the successive rings j in proportion to food availability. In the case in which the input rate of food for fish is strongest close to the island, initial food availability declines linearly with distance from the island with proportionality

$\frac{s + 1 - j}{s}$. In the case in which the input rate of food for fish is equal across the foraging range, initial food availability in the s rings is constant (Fig. 3).

Bird redistribution

Each bird's objective is to maximize the rate at which food is delivered to its nest. Our assumption of constant load size makes

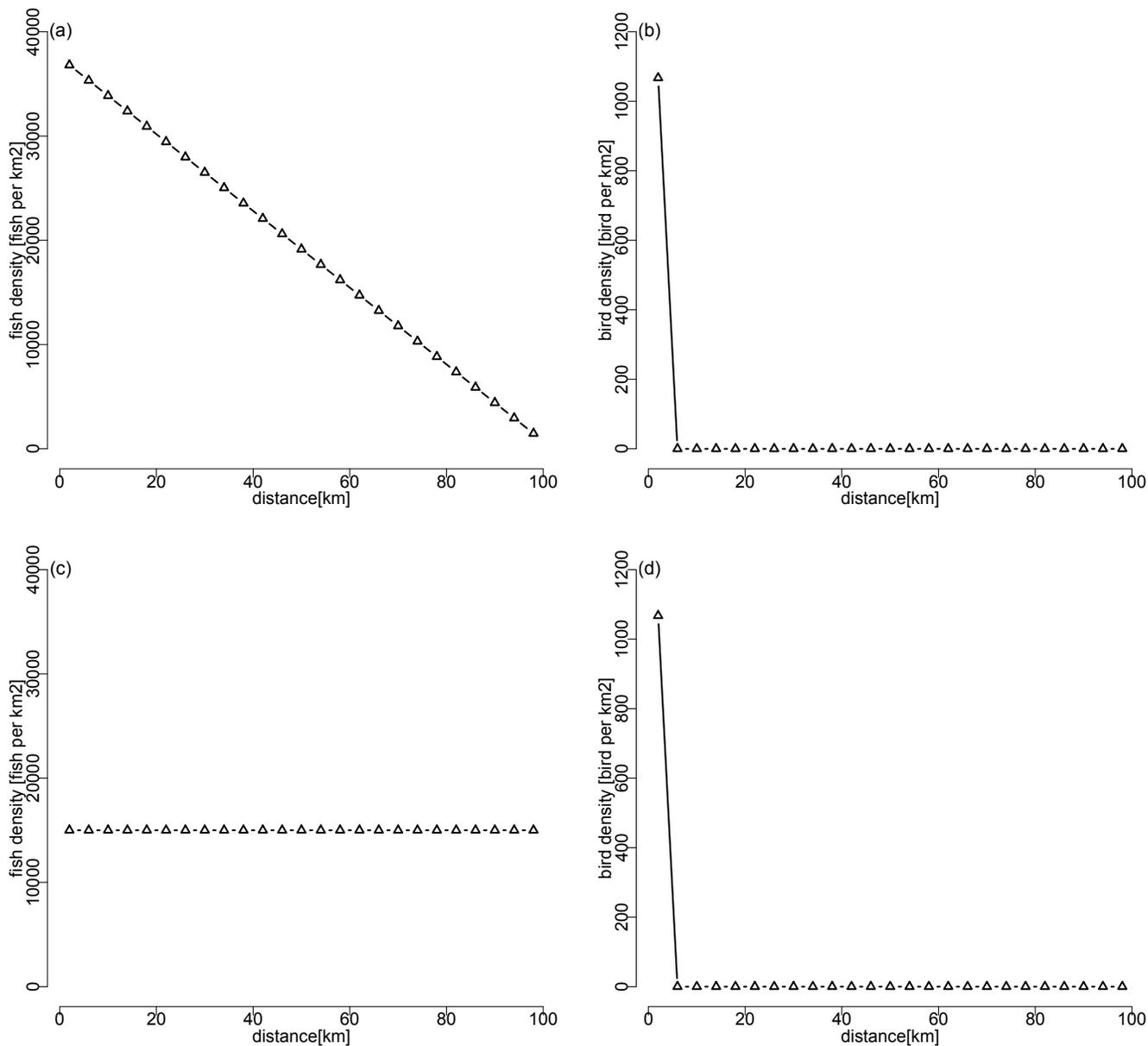


Fig. 3. Initial fish density (left panels a and c) and initial bird density (right panels b and d) as function of distance from the island, in the cases in which (upper panels) the input rate of food for fish is strongest close to the island (upwelling), and (lower panels) the input rate of food for fish is equal across the foraging range.

this equivalent to minimizing the time required for a round trip. A round trip to site (ring) j consists of the travel time $t_{t,j}$ plus hunting time $t_{h,j}$. We represent the quality of each site j for birds as the reciprocal of the total round trip time:

$$q_{b,j} = \frac{1}{t_{t,j} + t_{h,j}} \quad (1)$$

The travel time to site j is a linear function of distance: twice the distance ($d_j = (j - 0.5)\Delta s$) divided by the flight speed (v). The hunting time at place j is inversely proportional to the local fish density $F_j(n)$ with proportionality constant h (hunting capacity). In the n th iteration step, site quality is therefore:

$$q_{b,j}(n) = \frac{1}{t_{t,j} + t_{h,j}(n)} = \frac{1}{\frac{2d_j}{v} + \frac{1}{hF_j(n)}} = \frac{hvF_j(n)}{2d_jhF_j(n) + v} \quad (2)$$

In the first time step, the birds' foraging effort is concentrated at the site closest to the island: with the highest fish density and shortest travel time, it obviously has the highest site quality. In successive iterations, birds redistribute as the quality of a site is altered by exploitation and by fish moving away from predation danger (see below). In successive time steps, some birds shift from lower- toward higher-quality sites. The number of individuals $b_{e,j}(n)$ shifting away from site j at time step n is relative to the difference between current site quality and highest site quality:

$$b_{e,j}(n) = p_b \left(\frac{\max_j (q_{b,j}(n)) - q_{b,j}(n)}{\max_j (q_{b,j}(n))} \right) \quad (3)$$

These individuals are apportioned evenly over all sites with higher site quality; all individuals leaving the second-best site go to the best site, those leaving the third-best site divide evenly over the better two sites, etc. This process simulates the net displacement of birds toward higher-quality sites, with the displacement rate greater when the difference in site quality is greater. To improve the ability of the model to iterate to a stable distribution, a damping parameter p_b limits "overshooting" by controlling the proportion of birds allowed to shift away from a site.

Fish redistribution: fitness maximization

We compared simulations in which fish redistribute by random movement (represented as a diffusion process) with simulations in which fish redistribute to maximize fitness. In fitness-maximizing redistribution, the quality of each site j at time n for fish ($q_{f,j}(n)$) is the product of the energy gained per time ($g_j(n)$) and the fish's expected longevity ($1/m_j(n)$). The site-specific mortality rate at site j at time step n is $m_j(n)$, such that lifetimes are exponentially distributed.

Each site j has a supply of food $u_j(n)$ per unit time and surface area, which either decreases with distance from the island so

$$u_j(n) = \left(\frac{s+1-j}{s} \right) u_{max}, \text{ or is constant across sites so that } u_j(n) = \left(\frac{s+1}{2} \right) u_{max}. \text{ The energy gain per fish is density dependent,}$$

namely $u_j(n)$ divided by the fish density ($F_j(n)$). The total mortality rate of fish is the sum of the background mortality (m_n) plus the probability per unit time of depredation by

a seabird. The death rate due to bird depredation depends on the current total fish biomass at site j ($f_j(n)$), the current total number of birds at site j ($b_j(n)$) and the time the birds need to catch the fish and deliver it to their chicks ($t_{t,j} + t_{h,j}(n)$). Site quality is therefore calculated as:

$$q_{f,j}(n) = g_j(n)m_j(n)^{-1} = \frac{u_j(n)}{F_j(n)}m_j(n)^{-1} = \frac{u_j(n)}{F_j(n)} \left(m_n + \frac{b_j(n)}{f_j(n)(t_{t,j} + t_{h,j}(n))} \right)^{-1} \quad (4)$$

Fish are redistributed after site qualities are calculated, with no additional time or energy costs. Redistribution proceeds as follows. In the first time step, fish are distributed over the successive rings j in proportion to their food availability. In each subsequent iteration, the distribution is changed by moving fish from all sites except that with highest quality. The fish biomass $f_{e,j}(n)$ leaving site j at time step n is relative to the difference between current site quality and highest site quality:

$$f_{e,j}(n) = p_f \left(\frac{\max_j (q_{f,j}(n)) - q_{f,j}(n)}{\max_j (q_{f,j}(n))} \right) \quad (5)$$

As with birds, emigrating fish individuals divide themselves evenly over all sites with higher site quality. There is also a damping parameter p_f (the proportion of fish moved from a site), fixed at 0.75 to allow the model to more smoothly and easily move to a stable level. The value of p_f is higher than that of p_b , because birds are restrained to choosing a new location only after each return flight, whereas fish are free to move at each iteration.

Fish redistribution: random behavior

For a large population, the effect of random movement behavior is diffusion, which proceeds as follows. For the discretization of the diffusion process with diffusion coefficient D , the following general equation is used:

$$f_j(n^+) = f_j(n) + D\Delta n \frac{(F_{j-1}(n) - F_j(n))(A_{j-1} + A_j) - (F_j(n) - F_{j+1}(n))(A_j + A_{j+1})}{\Delta s^2} \quad (6)$$

where A_j is the area of ring j and Δs is the width of the site. The change in fish biomass in site j ($= 2, \dots, s-1$) is the result of flows from or to the sites closer to or further from the colony than site j . The movement of fish biomass f from one site to another is linearly related to the difference between fish densities F (sites are not of equal area, and so densities and total biomass are not interchangeable). For sites at the boundary of the simulation domain ($j=1$ or $j=s$), the equations are simplified to:

$$f_j(n^+) = f_j(n) + D\Delta n \frac{(F_2(n) - F_1(n))(A_2 + A_1)}{\Delta s^2} \quad (7)$$

$$f_s(n^+) = f_s(n) + D\Delta n \frac{(F_{s-1}(n) - F_s(n))(A_{s-1} + A_s)}{\Delta s^2} \quad (8)$$

Fish population change

The amount of food in kilograms per unit area per unit time in ring j is ($u_j(n)$) and is assumed to be divided equally among the fish there, being converted into fish biomass with proportionality factor 1. The change in the total fish biomass in ring j from step n to step $n+1$ (time step length Δn) is given by:

$$f_j(n+1) = f_j(n) + \Delta n (u_j(n)A_j - mf_j(n)) \quad (9)$$

Predation by seabirds takes place after redistribution of fish, using updated fish densities $F_j(n+1) (= f_j(n+1)/A_j)$.

Parameterization

All parameters, their description and their default values are listed in Table 1. These values are not intended to represent particular species, but to represent a general situation.

Analysis

The aim of our analysis is to compare the development and shape of Ashmole's halo between the two basic scenarios in which (a) fish diffuse (random behavior), or (b) in which fish are strategists that exhibit fitness-maximization behavior. We compare these using the default parameter set. To provide a sensitivity analysis, we randomly drew 100 combinations of parameter values

TABLE 1
Parameters and state variables of a model of Ashmole's halo

Parameter	Description	Unit	Value
a A_j	area of site j	km ²	$\pi((r+j)^2 - (r+j-1)^2)$
b_{ini}	initial number of birds (1 per 1000 kg fish)	–	15
D	diffusion coefficient	km ² h ⁻¹	1.2
d_j	distance of midpoint of site j to the island	km	$(j-0.5) \Delta s$
f_{ini}	initial biomass of fish	kg	15 000
Δn	duration of time step	h	2
Δs	width of each ring around the island	km	0.08
h	hunting capacity	km ² h ⁻¹	0.0001
m_n	natural death	h ⁻¹	1/21 900
N	number of time steps (for 90 days)	–	1 080
p_b	proportion of birds taking a decision each time step	–	0.1
p_f	proportion of fish taking a decision each time step	–	0.75
r	radius of the island	km	24
s	total number of sites	–	25
$s \cdot \Delta s$	maximum distance birds and fish can dwell	km	4
t_{ij}	travel time for return trip to site j	h	$2 d_j/v$
u_{max}	fish biomass increase per time step of site with maximum food availability (first site)	kg h ⁻¹ km ⁻²	10
v	flight velocity	km h ⁻¹	60
State variable	Description		
b $b_{e,j}(n)$	number of birds emigrating from site j at time step n		
$b_j(n)$	number of birds in site j at time step n		
$f_{e,j}(n)$	fish biomass emigrating from site j at time step n		
$f_j(n)$	fish biomass in site j at time step n		
$F_j(n)$	density of fish in site j at time step n		
$g_j(n)$	gain per fish in site j at time step n		
$m_j(n)$	site-specific mortality rate in site j at time step n		
$q_{f,j}(n)$	quality of site j from fish's perspective		
$q_{b,j}(n)$	quality of site j from bird's perspective		
$t_{h,j}(n)$	site-specific hunting time in site j at time step n		
$u_j(n)$	upwelling rate of food per area in site j at time step n		

from uniform distributions between a minimum and maximum value (Table 2), and compared the outcomes of random and

fitness-maximization simulation runs. We examined the resulting distributions for differences in shape.

TABLE 2
Default values and variation range of parameters varied in the pairwise comparison

Parameter	Meaning	Default value	Minimum	Maximum
v	flight velocity	60	30	90
h	hunting capacities	0.0001	0.00005	0.00015
u_{\max}	fish biomass increase per time step of site with maximum food availability (first site)	10	5	15
m_n	natural death	$2/(24 \times 5 \times 365)$	$2/(24 \times 8 \times 365)$	$2/(24 \times 2 \times 365)$
D	diffusion coefficient	1.2	0.2	2
r_{bf}	number of birds per kg fish biomass	0.001	0.0005	0.0015

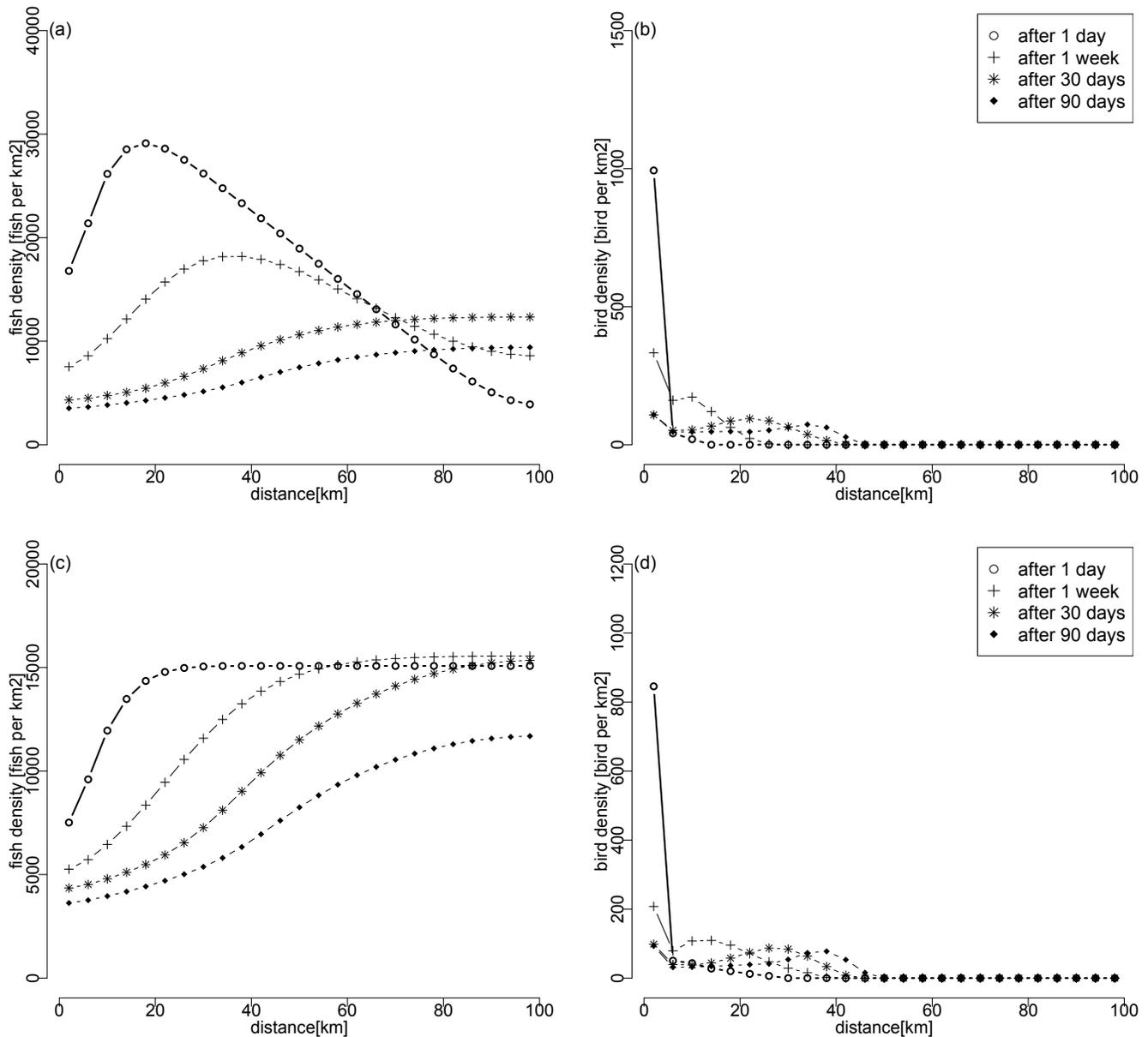


Fig. 4. The development of prey and predator distributions when fish movement is random, shown after various time periods (see key on graphs). Fish densities (left panels a and c) and bird densities (right panels b and d) are shown as function of distance from the island, in the cases in which (upper panels) the input rate of food for fish is strongest close to the island, and (lower panels) the input rate of food for fish is equal across the foraging range.

Predictions

We expected (i) that the halo would be deeper and larger when fitness-maximization behavior of fish is included, (ii) that the halo would develop more rapidly when the fish exhibit fitness-maximization behavior, and (iii) that the fish stock will decrease less with fitness-maximization behavior than when they move randomly.

RESULTS

Random behavior

Starting from the initial fish and bird density distributions shown in Figure 3, we show in Figure 4 the progression of fish and

seabird distributions as iterations proceed, assuming random fish redistribution. The development of the bird distribution is very similar whether there is upwelling (Fig. 4b) or not (Fig. 4d). With upwelling, the fish distribution initially increases strongly with distance from the island, but flattens and acquires the sigmoidal shape typical of diffusion processes by iteration 360 (~ day 30). If diffusion were the only process taking place, the equilibrium density of fish would eventually be equal everywhere, but here predation and growth give the distribution its shape, with the furthest sites eventually having the highest fish density. With no upwelling, the halo starts to develop immediately, because fish started out with equal densities throughout the considered region. By day 90, the shape of the halo is similar with and without upwelling.

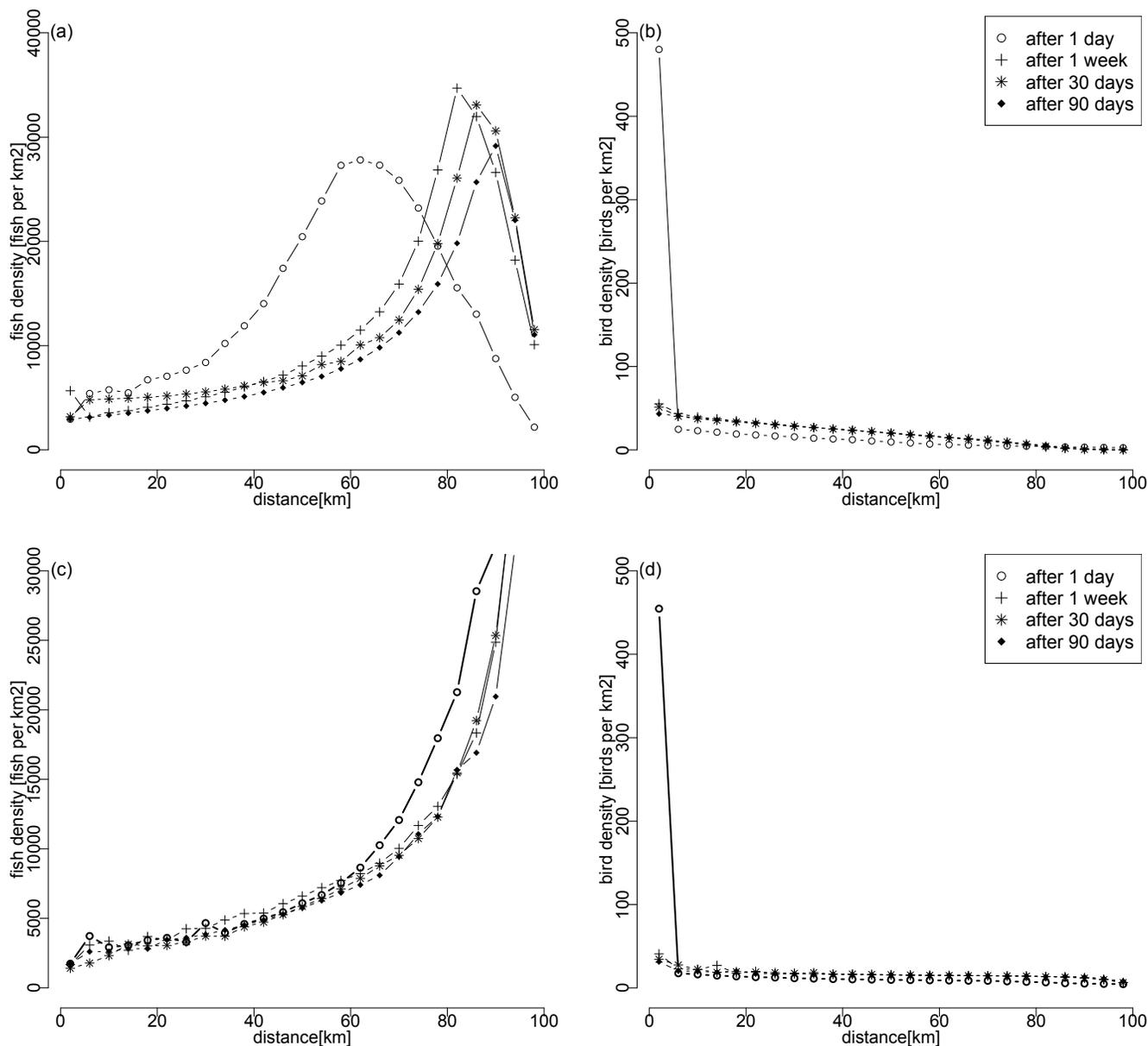


Fig. 5. The development of prey and predator distributions when fish exhibit fitness-maximizing behavior, shown after various time periods (see key on graphs). Fish densities (left panels a and c) and bird densities (right panels b and d) are shown as function of distance from the island, in the cases in which (upper panels) the input rate of food for fish is strongest close to the island, and (lower panels) the input rate of food for fish is equal across the foraging range.

Fitness maximization

We show in Figure 5 the progression of fish and seabird distributions as iterations proceed, assuming that fish redistribution maximizes fitness. The development of the bird distribution is very similar whether there is upwelling (Fig. 5b) or not (Fig. 5d). The development of the fish distributions is also similar whether there is upwelling (Fig. 5a) or not (Fig. 5c), but the halo develops more quickly without upwelling. With upwelling, a steep drop-off in fish density is apparent at the furthest sites.

The most marked differences between the random and fitness-maximizing scenarios are in the fish distribution, which shifts much further away from the island and does so more quickly (*cf.* Figs. 4 and 5) under the fitness-maximizing scenario. As expected, fish density increases with distance (Fig. 6a,c), in such a way that the inverse

of fish density falls linearly with distance over most of the range (Fig. 6b,d). The sharp decrease over the last three sites in Figure 6a arises because they lie beyond the maximum foraging range of the birds. Site quality for the birds is defined as the inverse of the sum of the handling and travel times. Travel time t increases linearly with distance, setting a boundary condition beyond which hunting time cannot be short enough to offset the longer travel time. Beyond this point, the fish distribution is determined only by the food availability. Without upwelling, however, this effect does not arise, as the fish spread out over the entire foraging range.

Sensitivity analysis

To provide a sensitivity analysis, we randomly drew 100 combinations of relevant parameter values from uniform distributions between the minimum and maximum values given in

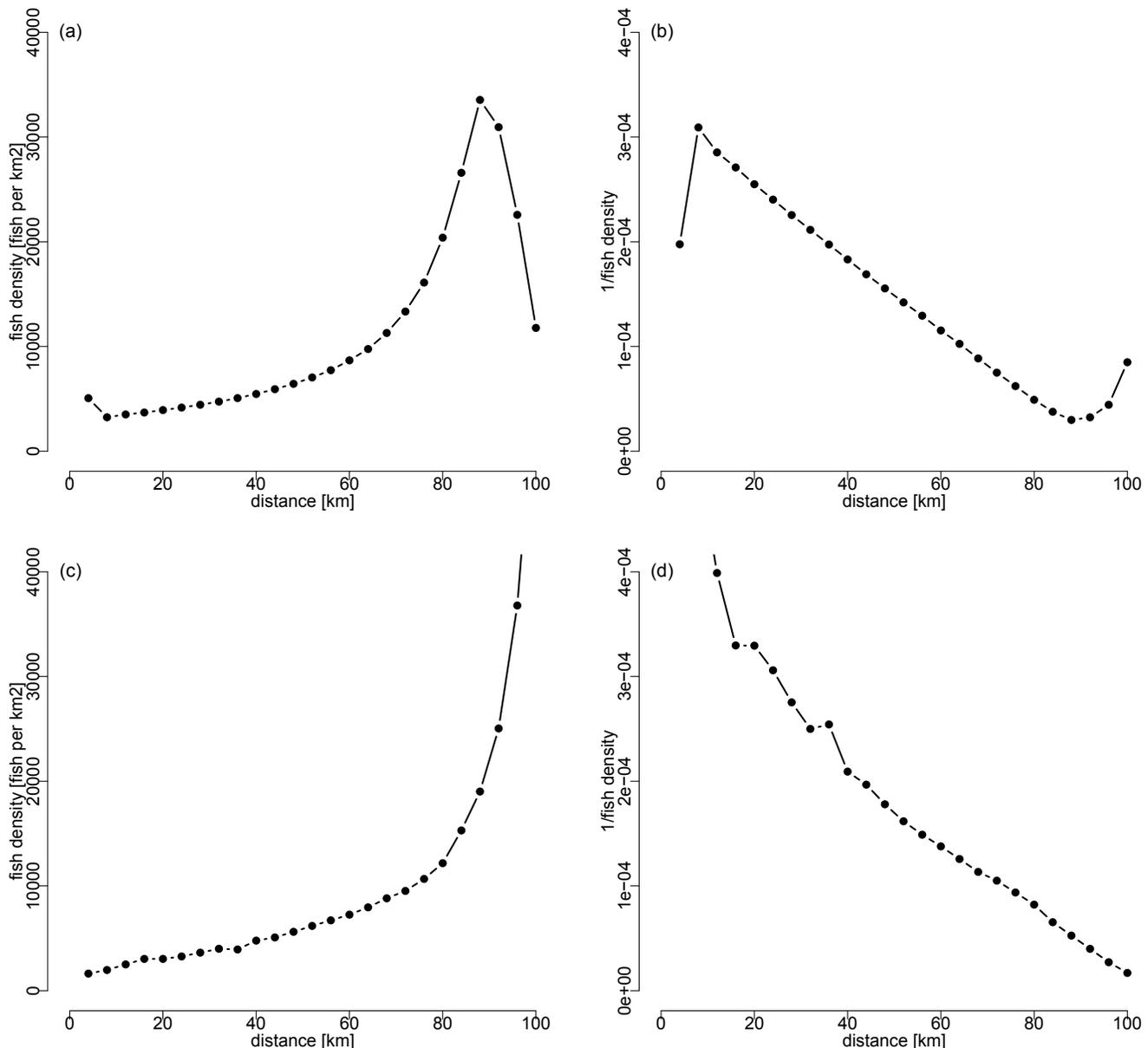


Fig. 6. Fish density (panels a and c) and the inverse of the fish density (panels b and d) at $n = 360$ for the default parameter values. This shows that the increase of fish density over space is such that its inverse is linear.

Table 2. We investigated how often four basic features developed in the 100 simulations, and compared the outcomes between random and fitness-maximization simulation runs. The four basic features are shown in Figure 7. They are:

- Feature 1* Bird density drops off steeply after the first site.
- Feature 2* Bird density increases over part of the foraging range (i.e. has a hump).
- Feature 3* Bird density is high close to the island, and falls abruptly to zero partway through the foraging range.

Feature 4 The highest fish density co-occurs with the maximum range that birds use, and thereafter falls.

We considered the robustness of these differences between random and adaptive fish movement by investigating how often these features were present in the 100 simulations with randomly drawn parameters. We report the results for randomization and fitness maximization, after 360 iteration steps and after 1080 iteration steps.

Feature 1 In all cases, under both randomization and fitness-maximization, the first site had the highest bird density. However, the decrease from the first to the second

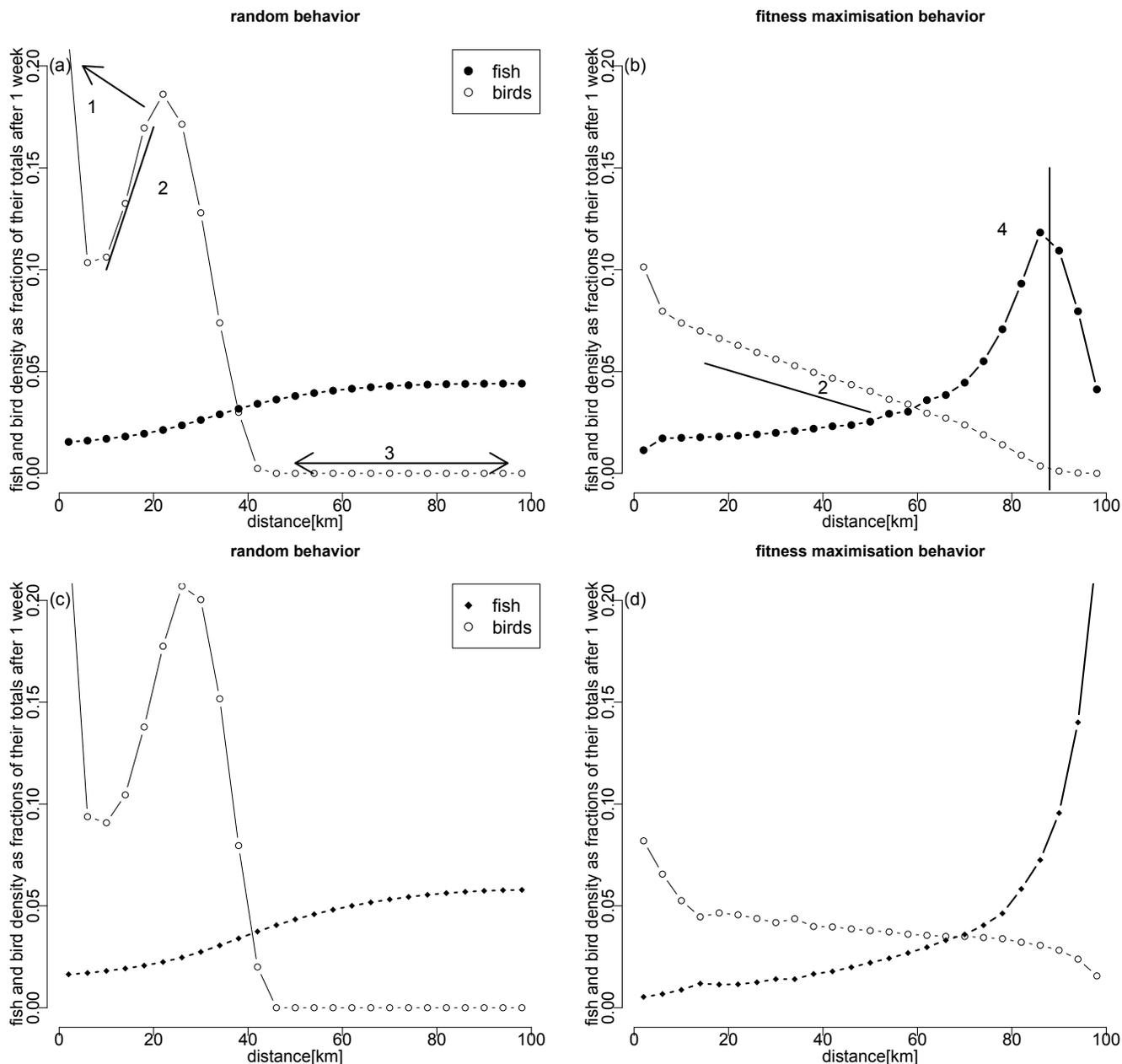


Fig. 7. Basic features of the distributions of fish and seabirds emerging after 360 iterations for the four scenarios. The numerals 1 to 4 indicate these features, which are discussed in the main text. Panels (a and c) show random behavior and panels (b and d) fitness-maximizing behavior. In the upper panels, the input rate of food for fish is strongest close to the island (upwelling), and in the lower panels, the input rate of food for fish is equal across the foraging range. The total input over the area is equal in both cases. Densities have been rescaled for portrayal.

site is abrupt under random fish movement, and much smoother under fish fitness-maximization.

Feature 2 Under randomization, a hump in the bird density was present in 97 out of 100 simulations at 360 iterations. The three cases lacking a hump were those with a high diffusion co-efficient and low flight speed. The hump later appeared in these three simulations and was present at 1080 iteration steps. Under fitness-maximization, in contrast, there were only nine simulations that displayed any sort of a hump somewhere along the bird distribution. In all cases, the hump was very small and the effect can likely be ascribed to local instability.

Feature 3 Under fitness-maximization, birds always range to the maximum distance (site 25; occasionally numbers are very low), but when fish exhibit random behavior, birds do not range nearly this far, reaching on average to site 12 after 360 iteration steps and site 14 after 1080 iteration steps. Both fish and birds are distributed further out when the fish exhibit fitness-maximization behavior. The 50% distance (dividing the fish population in two) is around site 20 when the fish exhibit fitness-maximization and around site 18 when the fish exhibit random behavior. For the birds, this 50% distance is around sites 9 and 7, respectively.

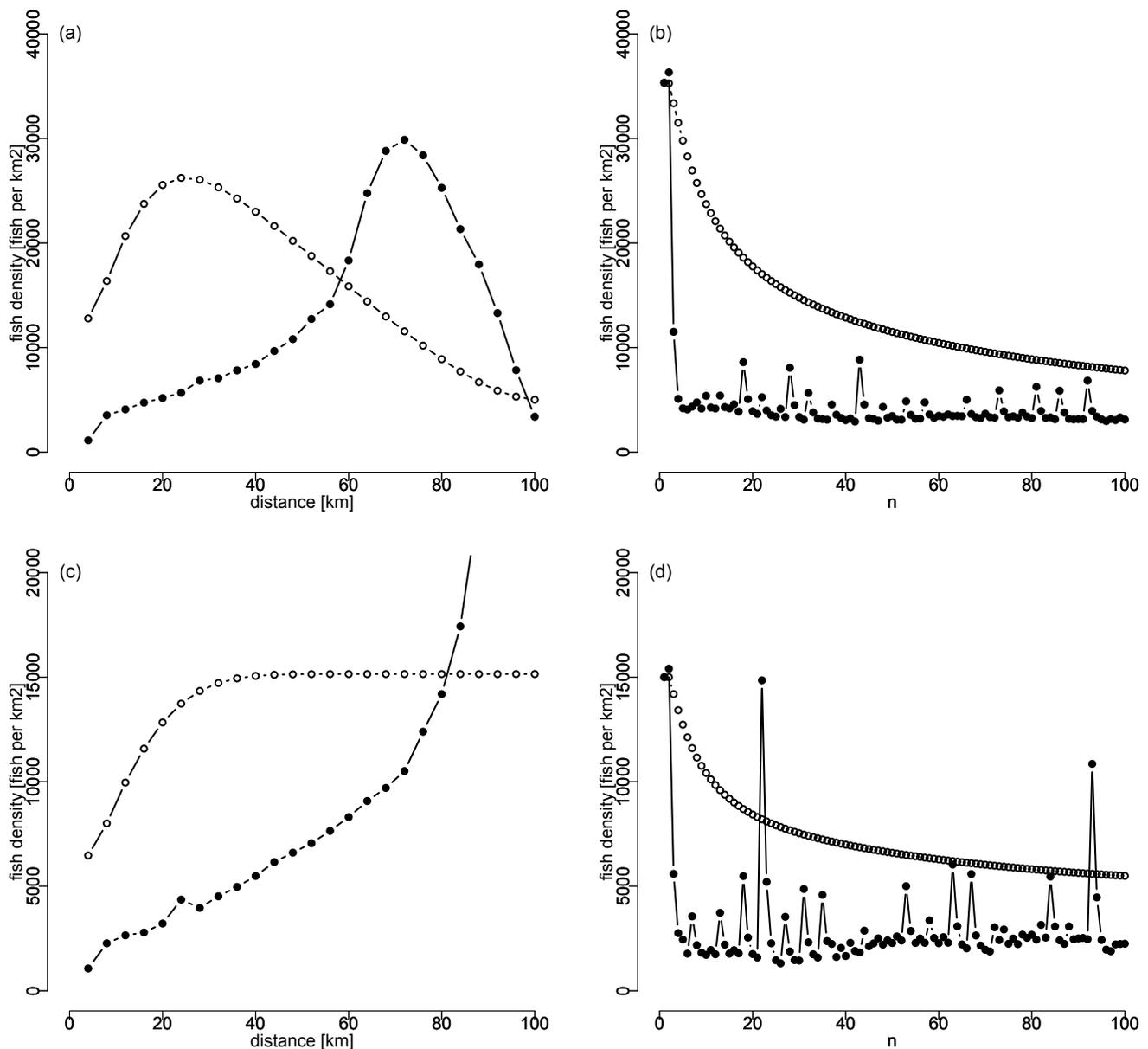


Fig. 8. Panels a and c: fish densities at $n = 23$ (~ 2 d) for fitness-maximizing behavior (●) and random behavior (○). Panels b and d: fish densities in the second site in the first 7 days for fitness-maximizing behavior (●) and random behavior (○).

Feature 4 Under random behavior, the highest fish density is further out than the maximum bird range in 93 out of 100 simulations at 360 iteration steps, and 100 out of 100 simulations at 1080 iteration steps. Under fitness-maximization this never occurs. When the fish conduct random behavior, the birds on average do not go out further than site 13 or 14, whereas the fish density is still increasing from that point on.

The appearance of these four features without upwelling (lower panels, Fig. 7) is nearly identical, the sole exception being that with upwelling there is a sharp drop-off in fish density at the far end of the foraging range (Fig. 7b), while this does not occur when food input is equal across the foraging range (Fig. 7d). With fitness-maximization, birds range much further than under random fish movement, the halo is deeper and stronger, and these features do not appear sensitive to the parameter values chosen under any of the four basic scenarios.

Halo development

Using the default parameter set, the halo develops much more quickly when fish exhibit fitness-maximizing behavior than when they move randomly. Figures 8a,c show the distribution of fish after 23 (~2d) iterations, as well as (Fig. 8b,d) the course of events at the second site. This comparison also reveals that the change is smoother when fish move randomly. Under fitness-maximization, instability is evident, although it is small enough not to disturb the general pattern.

Fish population dynamics

The fish population declines more quickly when the fish move randomly than when they make fitness-maximizing movements. When moving randomly, on average 70% of fish are still alive after 360 iterations and 53% after 1080 iterations, while the equivalent figures under fitness-maximization are 91% and 78%.

DISCUSSION

Our results show that Ashmole's halo develops more deeply and quickly around a seabird colony when prey have the capability of responding to the presence of seabirds by moving adaptively (i.e. to increase fitness) rather than by moving randomly. Our sensitivity analysis further suggests that this is a robust conclusion, not strongly dependent on any of the parameter values. Previously, Gaston *et al.* (2007) showed theoretically that Ashmole's halo develops under a broad range of conditions even if prey did not move. Here, we found that without any adaptive movement the fish population was reduced by 53%, but with adaptive movement it was reduced by only 22%. While these quantities obviously depend on the parameter values and simulation procedure, the effect of adaptive movement is clearly significant and strengthens the halo effect, although fewer fish are consumed by the predators. Our results suggest that the phenomenon is as profound as Ashmole (1963) originally surmised, and so able to affect seabird life histories.

The only other direct analyses of Ashmole's halo are those of Lewis *et al.* (2001) and Ainley *et al.* (2003). Their model assumes that prey respond to disturbance from predators either by swimming away or by moving deeper; in either case, their availability to predators is temporarily reduced. Ainley *et al.* (2003) showed that, in fact,

fewer herring schools *Clupea harengus* are found at the surface where surface-foraging kittiwakes are intensively foraging, as a function of proximity to the colony. The fitness-maximizing version of the model developed here in effect assumes that prey assess the "danger" level (i.e. the mortality rate that they would experience if they undertook no predator evasion; see Lank & Ydenberg 2003) and respond accordingly: no direct encounter with a predator is required — although, of course, such encounters would inform their estimate of the danger. Our model makes no specific assumptions about how the information is acquired, but a variety of sources are possible, including the behavior of conspecifics.

Although the details of the competitive mechanism are slightly different, both the model of Lewis *et al.* (2001) and that presented here develop halos around seabird colonies. The halo in our model develops quickly, while Lewis *et al.* (2001) state that when fish respond by lateral swimming "a slowly growing halo is readily generated." However, model details are sufficiently different that the meaning of "quick" versus "slow" is not at all clear. Lewis *et al.* (2001) add "that factors such as currents or disturbance by other predatory species may effectively mix shoals to such an extent that halo patterns do not form clearly." (For example, the arrival of foraging whales increases trip length, i.e. halo size, in penguins; Ainley *et al.* 2006.) Lewis *et al.* (2001) claim that, because each seabird requires approximately the same total area to obtain food, independent of colony size, their basic result (trip time increases as the square root of colony size) holds. However, their brief presentation of results does not include many details.

One possibility that might affect halo development is whether prey are benthic or schooling fish. The study of Birt *et al.* (1987), one of only three that have directly measured a halo, concerned benthic fish; the study by Ainley *et al.* (2003) concerned schooling, pelagic fish. It seems likely that both types of prey would have behavioral mechanisms that reduce their availability to predators, but these are likely to be rather different (e.g. hiding versus fleeing) and so would affect halo development.

When prey as well as predators are strategic agents, their interaction should be considered in an evolutionary game theoretical context (Nowak & Sigmund 2004). In a predator-prey game, the decisions of individual prey depend not only on those of other prey, but also on decisions made by predators, and *vice versa*. Although there are intellectual predecessors, the first paper that explicitly formulated predator-prey interactions as a predator-prey game was that of Hugie & Dill (1994; see also Sih 1998). Subsequent investigations have applied predator-prey game models to specific systems such as desert rodents facing snakes, foxes and owls (Bouskila 2001, Kotler *et al.* 2002), Antarctic krill *Euphausia superba* and penguins (Alonzo *et al.* 2003), and tadpoles and dragonflies (Hammond *et al.* 2007).

The basic concept of the spatial game modeled here is the "ideal free" distribution (IFD; Milinski & Parker 1991). When sites have associated predation danger in addition to food availability, fitness at equilibrium is equalized as in the basic IFD model, with fitness having both resource-gain and survival components (Grand 2002). But because the level of predation danger at any site depends on the behavior of the predators themselves, the distribution game of *both* prey and predators must be considered. Predator-prey gaming models retain the essential properties of the IFD in that, at equilibrium, no individual can benefit from (unilaterally) moving to

a different site (Nash equilibrium). Some models also demonstrate that the equilibrium is stable to invasion by initially rare alternative tactics (an evolutionary stable strategy or ESS; technical details and exact definitions in Houston & MacNamara 1999). Our model suggests that the basic properties of Ashmole's halo arise in a predator-prey game.

The most straightforward way to test these ideas would be to estimate in a field situation the contributions of prey depletion and the anti-predator behavior of the prey to the delivery rate achieved by provisioning seabirds. For example, prey density might be reduced by exploitation everywhere, but prey might also take evasive action by residing at deeper depths (e.g. Ainley *et al.* 2003, Elliott *et al.* 2009), or reducing the amount of time they spent feeding at the surface, where they are more vulnerable. With information on this and the foraging behavior of the predators, it would in principle be possible to compute the contribution of each to halo formation. Our basic prediction is that prey behavior contributes strongly to the effect. Considering that, as originally formulated, Ashmole's hypothesis does not consider prey behavior at all, this would be an interesting exercise.

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