Schooling as a strategy for taxis in a noisy environment

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Summary

Many aquatic animals face a fundamental problem during foraging and migratory movements: while their resources commonly vary at large spatial scales, they can only sample and assess their environment at relatively small, local spatial scales. Thus, they are unable to choose movement directions by directly sampling distant parts of their environment. A common strategy to overcome this problem is taxis, a behaviour in which an animal performs a biased random walk by changing direction more rapidly when local conditions are getting worse. Such an animal spends more time moving in right directions than wrong ones, and eventually gets to a favourable area. Taxis is inefficient, however, when environmental gradients are weak or overlain by 'noisy' small-scale fluctuations. In this paper, I show that schooling behaviour can improve the ability of animals performing taxis to climb gradients, even under conditions when asocial taxis would be ineffective. Schooling is a social behaviour incorporating tendencies to remain close to and align with fellow members of a group. It enhances taxis because the alignment tendency produces tight angular distributions within groups, and dampens the stochastic effects of individual sampling errors. As a result, more school members orient up-gradient than in the comparable asocial case. However, overly strong schooling behaviour makes the school slow in responding to changing gradient directions. This trade-off suggests an optimal level of schooling behaviour for given spatio-temporal scales of environmental variations. Social taxis may enhance the selective value of schooling in pelagic grazers such as herrings, anchovies and Antarctic krill. Furthermore, the degree of aggregation in a population of schooling animals may affect directly the rate and direction of migration and foraging movements.

Keywords: aggregation; optimal foraging; resource distributions; schooling; search strategies; social behaviour; taxis

Introduction

One of the most basic problems confronting an aquatic organism is locating favourable regions within its fluid environment that contain appropriate levels of resources such as food, oxygen and sunlight. Because limiting resources typically have 'patchy' distributions in which concentrations may vary by orders of magnitude, success or failure in finding favourable areas often has an enormous impact on growth rates and reproductive success. To locate resource concentrations, many aquatic organisms display tactic behaviours, in which they orient with respect to local variations in chemical stimuli or other environmental properties. Taxes may be based on a variety of cues, including temperature, salinity, chemical constituents such as odorant plumes, and population density of small organisms such as phytoplankton. These material fluid properties are dispersed in the aquatic environment in a non-uniform and irregular way, through the combined effects of molecular diffusion, turbulent transport and density stratification (Atema, 1988). Through these processes, cues for taxis may take on a convoluted, three-dimensional structure, with fluctuations in concentration at both large and small length scales (Nihoul, 1981; Monin and

Ozmidov, 1985). Aquatic organisms attempting to use local variations in material properties to locate patches of resource concentrations thus frequently face a formidable task. Here, I propose that schooling behaviours improve the tactic capabilities of school members, and enable them to climb faint and noisy gradients which they would otherwise be unable to follow.

A large literature exists on the evolutionary benefits and costs of social aggregative behaviour. Social behaviour is thought in many cases to confer protection from predation, and to enable unsuccessful foragers to exploit resources discovered by fellow group members, while subjecting group members to intensified intra-group competition (Clark and Dukas, 1994). The positive interaction of social and tactic responses hypothesized here provides an additional mechanism by which sociality could be an evolutionarily favourable strategy.

Schools are groups of aquatic animals which are maintained by social interactions and which display synchrony of orientation and movement (Pitcher, 1983, 1986). Schooling is thought to result from two principal behavioural components: (1) tendencies to move towards neighbours when isolated, and away from them when too close, so that the group retains a characteristic level of compactness; and (2) tendencies to align orientation with those of neighbours, so that nearby animals have similar directions of travel and the group as a whole exhibits a directional polarity. These same behaviours underlie formation of polarized social groups in terrestrial animals, such as avian flocks (Heppner and Grenander, 1990; Kshatriya and Blake, 1992), mammalian herds (Sinclair, 1977; Prins, 1989; Gueron and Levin, 1995) and swarms of insects such as migratory locusts (Kennedy, 1951; Waloff, 1972; Baker *et al.*, 1984). The most conspicuous effect of attraction and alignment is to maintain the school as a cohesive and orderly unit. However, if school members are simultaneously attempting to climb resource gradients, these social interactions have the additional effect of propagating the results of individual tactic responses throughout the group. The theoretical results in this paper suggest that, because of this information propagation, even simple schooling behaviours might improve animals' ability to climb noisy gradients.

I focus in this paper on schooling in aquatic animals, and particularly on phytoplankton as a distributed resource. However, although I do not examine them specifically, the modelling approaches and the basic results apply more generally to other environmental properties (such as temperature), to other causes of population movement (such as migration) and to other socially aggregating species which form polarized groups (such as flocks, herds and swarms).

Phytoplankton distributions and taxis

Phytoplankton density is a well-studied example of an ecologically important resource which takes on patchy distributions under the influence of advective processes in the aquatic environment. As measured by concentration of chlorophyll, fluorescence or rates of primary production, phytoplankton distributions are generally found to have significant spatio-temporal variation at both a 'micro-scale' (i.e. < 10 m and < 10 h) and at much larger scales (Powell, 1989). Oceanographic sampling (with micro-scale variation removed by averaging) has shown that phytoplankton densities commonly vary horizontally by an order of magnitude or more at 'macro' spatio-temporal scales of > 10 km and > 10 days (in, for instance, the Southern Ocean: Witek *et al.*, 1981; Weber *et al.*, 1986; the Baltic Sea: Schultz *et al.*, 1989; the North Atlantic: Pattiaratchi *et al.*, 1989). Vertical distributions can vary on similar time scales from concentrated layers a few metres in thickness to almost uniform dispersion throughout the mixed layer (> 100 m).

The importance of micro-scale patches of phytoplankton and tactic behaviours to locate them were investigated theoretically by Davis *et al.* (1991), who also examined the role of turbulence in dispersing patches and increasing encounter rates of consumer and prey. Using realistic movement and growth models for copepods and larval fish, Davis *et al.* estimated that individuals can move to

local peaks within the micro-scale distribution of food abundance over the course of a few hours, and that such movements can increase growth rates of copepods and larval fish substantially. Fluctuations at larger scales probably have equally important ecological consequences for pelagic fish such as herrings (Clupeidae) and anchovies (Engraulidae), and for large crustacean zooplankton such as Antarctic krill, *Euphausia superba*, which are the principal consumers of phytoplankton. However, relatively little is known about the tactic capabilities of these filter-feeders and the extent to which they are able to take advantage of large-scale variations in phytoplankton density.

For example, Antarctic krill and related species are known from aquarium studies to respond accurately to local phytoplankton gradients, and to use them to seek out micro-scale phytoplankton patches several centimetres to several metres across (Hamner *et al.*, 1983; Price, 1989; Strand and Hamner, 1990). Krill, swimming at speeds in the range of 10–20 cm s^{-1} (Kils, 1981; Hamner, 1984), would theoretically be able to move to 10 km-scale phytoplankton concentrations in a day or so, long before other physical and biotic factors could disperse them. Yet, the biomass of Antarctic krill is found to have variable, often very low, degrees of association with phytoplankton concentrations (Witek *et al.*, 1981; Weber *et al.*, 1986; Levin *et al.*, 1989; Daly and Macaulay, 1991; see also Rose and Legget, 1990). Large differences in gut fullness observed between krill from different schools in the same area (Priddle *et al.*, 1990) also suggest that some schools had difficulty finding food even when phytoplankton concentrations were present. These observations suggest that nektonic phytoplankton consumers face strong evolutionary pressures to improve their tactic abilities.

Bacterial chemotaxis

Difficulties in taking advantage of phytoplankton concentration fluctuations at ≥10 km scales may stem from the fact that, even when fluctuations are substantial, the large spatial scale means that the average concentration gradient is extremely shallow. A forager thus encounters an exceedingly faint and noisy signal as it seeks to climb phytoplankton concentration gradients at these larger scales. Under these circumstances, the search of a nektonic filter-feeder for large-scale concentrations of phytoplankton is analogous to the behaviour of a bacterium performing chemotaxis. The essence of the analogy is that, while higher animals have much more sophisticated sensory and cognitive capacities, the scale at which they sample their environment is too small to identify accurately the true gradient.

Bacteria using chemotaxis usually do not directly sense the direction of the gradient. Instead, they perform random walks in which they change direction more often or by a greater amount if conditions are deteriorating than if they are improving (Keller and Segel, 1971; Alt, 1980; Tranquillo, 1990). Thus, on average, individuals spend more time moving in favourable directions than in unfavourable ones. Although the path of an individual is stochastic and may be very complicated, analysis of the probabilities of transition from one orientation to another often results in simple expressions for the average rate of tactic movement resulting from a particular tactic algorithm (Keller and Segel, 1971; Okubo, 1986; Edelstein-Keshet, 1988; Othmer *et al.*, 1988; Murray, 1989). A bacterial analogy has been applied to a variety of behaviours in more complex organisms, such as spatially varying diffusion rates due to foraging behaviours or food-handling in copepods and larval fish (Davis *et al.*, 1991), migration patterns in tuna (Mullen, 1989) and restricted area searching in ladybugs (Kareiva and Odell, 1987) and seabirds (Veit *et al.*, 1993, 1995). The analogy provides for these higher animals a quantitative prediction of distribution patterns and abilities to locate resources at large space and time scales, based on measurable characteristics of small-scale movements.

Social taxis

In this paper, I present theoretical evidence that even the simplest of interactions between social and tactic behaviours (i.e. a superposition of these two types of behaviour) confers enhanced capacity for taxis. I do not consider more sophisticated (and possibly more effective) social tactic algorithms, in which explicit information about the environment at remote points is actively or passively transmitted between individuals, or in which individual algorithms (such as slowing down when in relatively high concentrations) cause the group to function as a single sensing unit (Kils, 1986, described in Pitcher and Parrish, 1993).

In the next section, I lay the groundwork for testing the impact of social behaviour on searching success by analysing a simple, asocial bacterial-type taxis algorithm in which small-scale variation of the resource is implicitly included in the 'random' component of the tactic random walk, and the large-scale variation is represented locally by a constant, uniform gradient of the attractant. With the results of this analysis as a null model, I then introduce a simulation in which individuals display schooling behaviours in addition to taxis, and show that up-gradient motion can be increased by the addition of this social behaviour. Next, I present a deterministic non-spatial model of the schooling behaviour, applicable within large schools in which most individuals have a large number of neighbours. Finally, I discuss possible evolutionary implications of these results for foraging dynamics of social animals, and empirical tests of the social taxis mechanism.

Asocial searching: Taxis from directionally varying turning rates

An animal that cannot directly sense favourable regions must locate them through some sort of trial-and-error process of probing in various directions and modifying course depending on the results. For example, suppose that individuals, searching on a plane surface and moving at unit speed, change their direction randomly at discrete time intervals of Δt. Suppose further that the individuals are in an environment where the average concentration increases uniformly in the positive x-axis, but where small-scale noise causes the animals sometimes to perceive that concentration is increasing when actually it is decreasing, or vice versa. Then, the directionally varying rate of turning might be described by:

$$\Delta \theta = r_0 \Delta \theta_0 + r_1 \Delta \theta_1 \left(\frac{1 - \cos(\theta)}{2} \right) \tag{1}$$

where $\Delta \theta$ is the angular change in a time interval Δt, θ is the angle with respect to the concentration gradient (the x-axis), and $\Delta \theta_0$ and $\Delta \theta_1$ specify the turn rate at various orientations (Fig. 1). r_0 and r_1 are randomly chosen at each time step to be either -1 or 1, so that an individual turns with equal probability to the left or right. The $\Delta \theta_0$ component represents the small-scale 'noise' – it causes individuals to make random turns at the same rate, regardless of their heading. The $\Delta \theta_1$ component, on the other hand, varies with orientation, and represents the large-scale 'signal'. It is proportional to the rate at which conditions are getting worse; that is, it is low when the individual is headed up-gradient and high when it is headed down-gradient. A searcher does a random walk in the range of possible heading directions ($-\pi$ to π), but on average it climbs the gradient because it turns away from 'wrong' headings faster than from 'right' headings.

Taxes of this type have been analysed thoroughly (Alt, 1980; Okubo, 1980, 1986; Othmer *et al.*, 1988), making them convenient searching behaviours with which to compare social and asocial individuals. The long-term behaviour of these individuals can be expressed concisely by taking the diffusion limit of the random walk in θ. The present case is a 'repulsive' random walk, in which the probability of moving depends only on conditions at the point of departure (see Okubo, 1986, for a
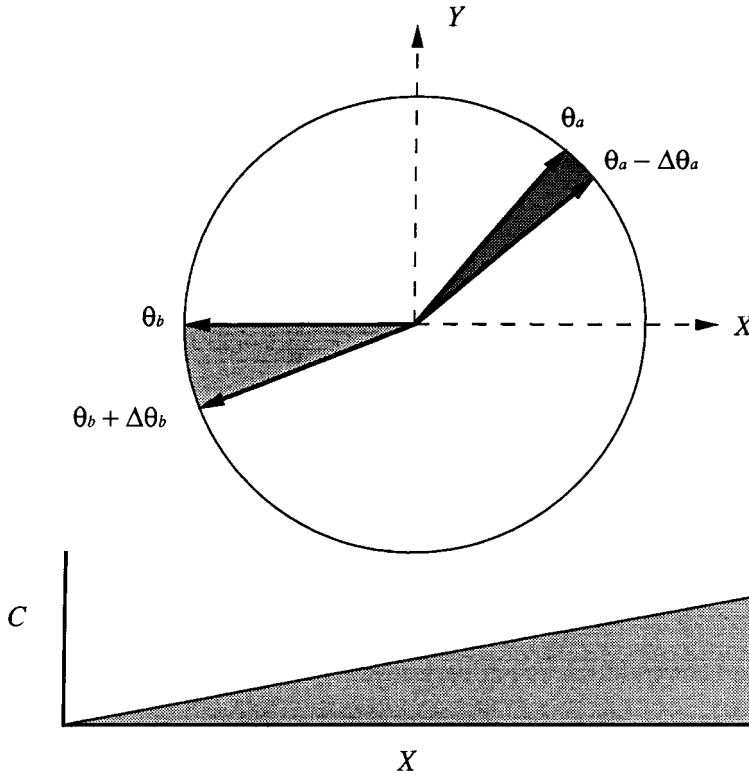
Figure 1. 'Bacterial' chemotaxis by directionally variable 'step' size in orientation angle. Two heading directions are shown, a nearly up-gradient orientation (θ_a) and a nearly down-gradient orientation (θ_b), where the concentration of an attracting substance, C, increases in the positive x-direction. An individual turns right or left with equal probability (in this example, the increment $\Delta\theta_a$ is to the right, or negative-θ direction, and $\Delta\theta_b$ is to the left, or positive-θ direction). However, increments in angular orientation are smaller if the individual is oriented up-gradient $(\Delta\theta_a = \Delta\theta_1(1 - \cos(\theta_a)/2))$ and larger if orientation is down-gradient $(\Delta\theta_b = \Delta\theta_1 (1 - \cos(\theta_b)/2))$. Thus, on average, an individual spends more time moving in up-gradient than down-gradient directions, resulting in up-gradient taxis. The domain is *periodic*; that is, individuals moving off an edge re-enter the opposite edge with the same orientation.

discussion of diffusion limits and repulsive and attractive random walks). The probability density of orientation angles, $\rho(\theta, t)$, evolves according to:

$$\frac{\partial}{\partial t}\rho(\theta, t) = \frac{\partial^2}{\partial\theta^2}(D(\theta)\rho(\theta, t)), \quad \int_{-\pi}^{\pi}\rho(\theta', t)\,\mathrm{d}\theta' = 1 \tag{2}$$

where $D(\theta)$ is a directionally varying diffusivity. Equation (2) is periodic; that is, $\rho(\theta) = \rho(\theta + 2\pi)$, $D(\theta) = D(\theta + 2\pi)$, etc. $\rho(\theta, t)$ represents the probability at time t that an individual is heading in the direction θ or, equivalently, the fraction of a large population of individuals with that orientation. The diffusivity has a constant and a directionally varying component

$$D(\theta) = D_0 + \left(\frac{1 - \cos(\theta)}{2}\right)^2 D_1 \tag{3}$$

where D_0 and D_1 are given (Levin, 1986) by:

$$D_0 = \frac{\Delta\theta_0^2}{2\Delta t} \qquad D_1 = \frac{\Delta\theta_1^2}{2\Delta t} \tag{4}$$

The steady-state solution to Equation (2) can be found analytically to show what fraction of its time a typical individual spends in each orientation and, consequently, how fast it moves up-gradient on the average. The equilibrium distribution of orientation angles is:

$$\rho(\theta) = \frac{1}{\sqrt{2}\pi} \frac{\sqrt{1+d}\sqrt{\sqrt{1+d}+1}}{\left(1 + \frac{1-\cos(\theta)}{2}\right)^2 \left(\sqrt{1+d}+1\right)} \tag{5}$$

where $d = D_1/D_0$ is the relative diffusivity (Davis *et al.*, 1991), a measure of the relative strength of the tactic signal and noise. Small d means that the gradient is heavily obscured by small-scale noise; large d means that the gradient is distinct. The average up-gradient velocity of an individual, as a fraction of that individual's forward speed, is:

$$U(d) = \frac{\sqrt{1+d}-1}{\sqrt{1+d}+1} \tag{6}$$

Equations (5) and (6) summarize the effectiveness of the bacterial taxis algorithm. Thus when the signal dominates the noise $(d \gg 1)$, individuals virtually always orient correctly, and progress directly up-gradient at nearly full speed (Fig. 2). When the noise predominates $(d \ll 1)$, the angular distribution of individuals is nearly uniform, and the up-gradient velocity is near zero. In a range of intermediate values of d $(0.3 \leq d \leq 3)$, there is measurable but slow movement up-gradient. The question I will address in the next two sections is: Can individuals in this intermediate signal-to-noise range with slow gradient-climbing rates improve their tactic ability by adopting a social behaviour (i.e. schooling)?

Simulations of searching with schooling behaviour

To investigate the gradient-climbing abilities of schooling searchers, I use a simplified model of schooling behaviour. This model omits some of the subtleties of schooling models from the literature, but captures the essentials for evaluating the effect of schooling on taxis (Grünbaum and Okubo, 1994). The key attributes of these models are: (1) a decreasing probability of detection or responsiveness to neighbours at large separation distances; (2) a social response that includes some sort of switch from attractive to repulsive interactions with neighbours, mediated by either separation distance or local density of animals; and (3) a tendency to align with neighbours (Inagaki *et al.*, 1976; Matuda and Sannomiya, 1980, 1985; Aoki, 1982; Huth and Wissel, 1990, 1992; Warburton and Lazarus, 1991; Grünbaum, 1994).

The rules in these simulations are as follows: At each time step, an individual counts the number of 'detectable' neighbours (i.e. those within a detection radius, here normalized to 1); individuals more than a unit distance away are ignored (Fig. 3). If the number of neighbours is within an acceptable range, then the individual does not respond to them. On the other hand, if the number is outside that range, the individual turns by a small amount, $\Delta\theta_3$, to the left or right according to whether it has too many or too few of them and which side has more neighbours. In addition, at each time step, each individual randomly chooses one of its visible neighbours and turns by a small amount, $\Delta\theta_4$, towards that neighbour's heading. Over many time steps, the individual tends to align with the average heading of its nearby neighbours. These behaviours can be made independent of step size by expressing them as $\alpha = \Delta\theta_3/\Delta t$, the rate of turning towards and away from
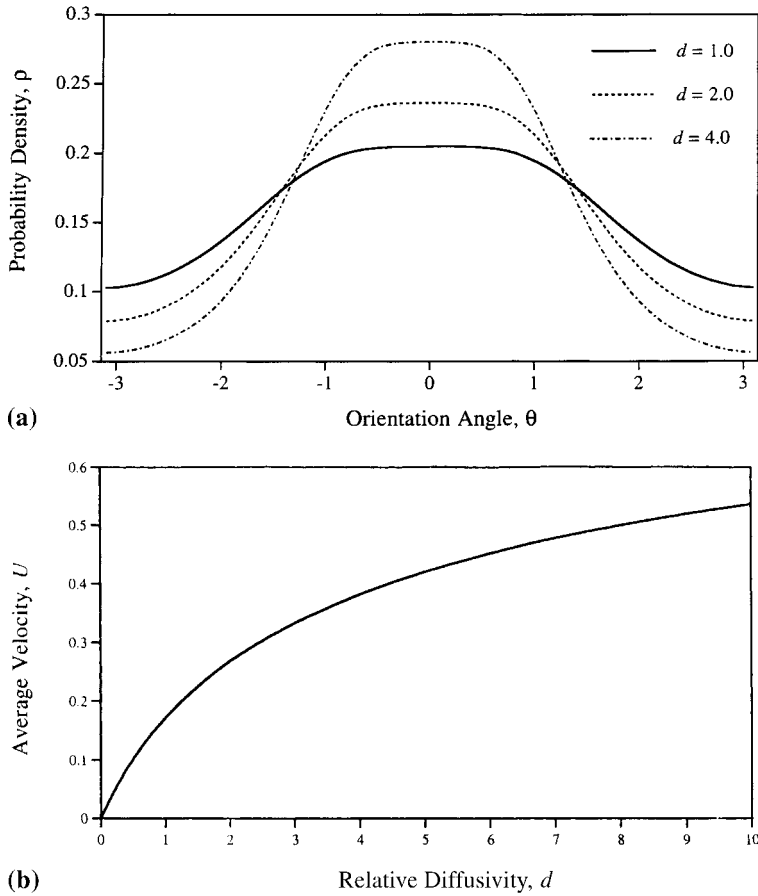
Figure 2. Effectiveness of the simple 'bacterial' chemotaxis algorithm as a function of d, the relative diffusivity. (a) The equilibrium distribution of orientation angles, ρ (from Equation 5), is more tightly clustered about the up-gradient direction for higher d. (b) Individuals spend a greater fraction of their time in favourable orientations, resulting in higher average velocity (from Equation 6) with increasing d.

neighbours, and $\beta = \Delta\theta_4/\Delta t$, the rate of turning to align with neighbours. The parameters α and β can also be usefully thought of in terms of

$$r = 1/(\alpha + \beta) \tag{7}$$

the radius of the tightest circle that an individual can make under the combined influence of the two social behaviours. The size of this radius, relative to other characteristic lengths, such as the detection range, determines in part the group properties of the school. In addition to this social behaviour, individuals retain the same tactic behaviour as discussed earlier.

The results of simulations based on these rules show that schooling individuals, on average, move more directly in an up-gradient direction than asocial searchers with the same tactic parameters. Figure 4 shows the distribution of individuals in simulations of asocial and social taxis in a periodic domain (i.e. animals crossing the right boundary re-enter the left boundary, etc.). The taxis parameters $D_0 = 0.3$ and $D_1 = 0.6$ are within the range of relative diffusivity ($d = 2$) for which
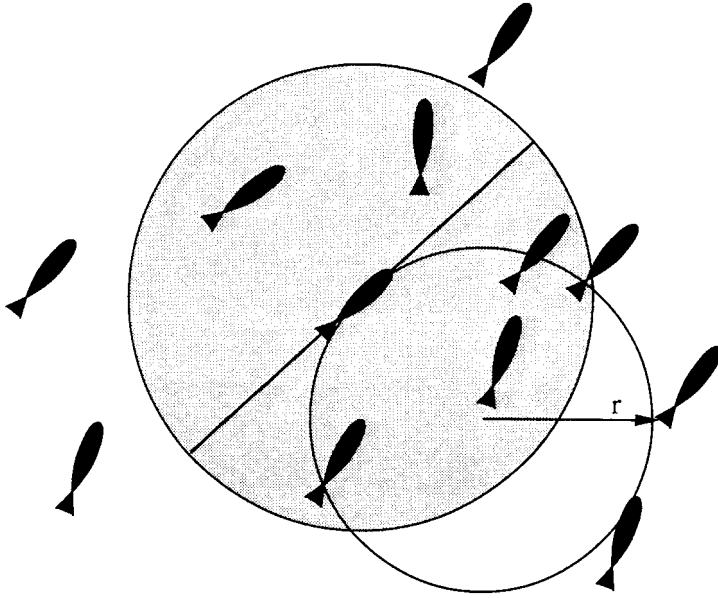
Figure 3. Schematic representation of schooling behaviour. Each individual reacts to neighbours within a unit distance, shown here as a shaded circle. Also shown is r, the radius of the tightest turn that can result from social behaviour. If this radius is smaller than the reaction distance ($r \ll 1$), then individuals can turn tightly to remain close to neighbours; if it exceeds the reaction distance ($r \gg 1$), individuals are not capable of turns tight enough to stay near a neighbour.

up-gradient motion due to bacterial taxis alone is relatively inefficient ($U = 0.268$, from Equation 6). As predicted by Equation (5), asocial taxis results in a broad distribution of orientations, with a peak in the up-gradient (positive x-axis) direction but with a large fraction of individuals moving the wrong way at any given time (Fig. 5a,b). By comparison, schooling individuals tend to align with one another, forming a group with a tightened angular distribution. There is stochasticity in the average velocity of both asocial and social searchers (Fig. 5c). On average, however, schooling individuals move up-gradient faster and more directly than asocial ones.

   These simulation results demonstrate that it is theoretically possible to devise tactic search strategies utilizing social behaviours that are superior to asocial algorithms. That is, one of the advantages of schooling is that, potentially, it allows more successful search strategies under 'noisy' environmental conditions, where variations on the micro-scales at which animals sense their environment obscure the macro-scale gradients between ecologically favourable and unfavourable regions.

Effects of school size

How large a group is required to obtain this benefit, and are there diminishing returns at larger group sizes? For the current simulations, the group need not consist of very many individuals to provide its members with a searching advantage; as shown in Fig. 6, schools with as few as eight members do substantially better on average than isolated individuals. The simulations summarized in this plot suggest that tactic efficiency increases with group size until roughly 64 individuals, and that further increases in size have a much smaller effect on up-gradient velocity.
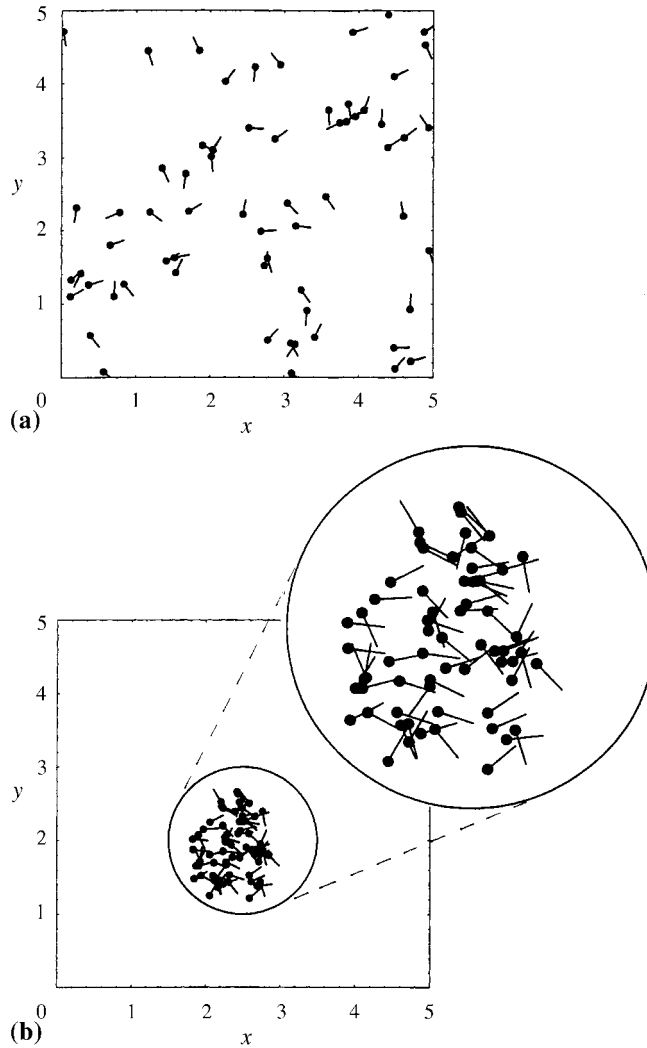
Figure 4. Simulations of asocial and social taxis, at $t = 100$, $N = 64$. (a) Positions of individuals for the asocial, 'bacterial' taxis algorithm; (b) individual positions for the 'social' taxis algorithm. The gradient is uniform and increases to the right (see Fig. 1). Initially, individuals are randomly distributed within a unit square, with random orientations. Boundary conditions are periodic (i.e. individuals moving off the domain reappear at the opposite boundary, and do not perceive a discontinuity in concentration gradient at the boundary). Parameters are $D_0 = 0.3$, $D_1 = 0.6$, $\alpha = 6.0$ and $\beta = 6.0$. Individuals seek to have between 56 and 63 nearby neighbours.

Another effect of increasing group size is to decrease the variation in searching success between individuals. Isolated searchers vary considerably in their rates of up-gradient travel: a few are very successful, but some end up down-gradient of their initial position. This range of variation falls quite rapidly with group size, the difference between 10th and 90th percentile searchers falling by a factor of almost four between asocial searchers and those travelling in groups of 32.
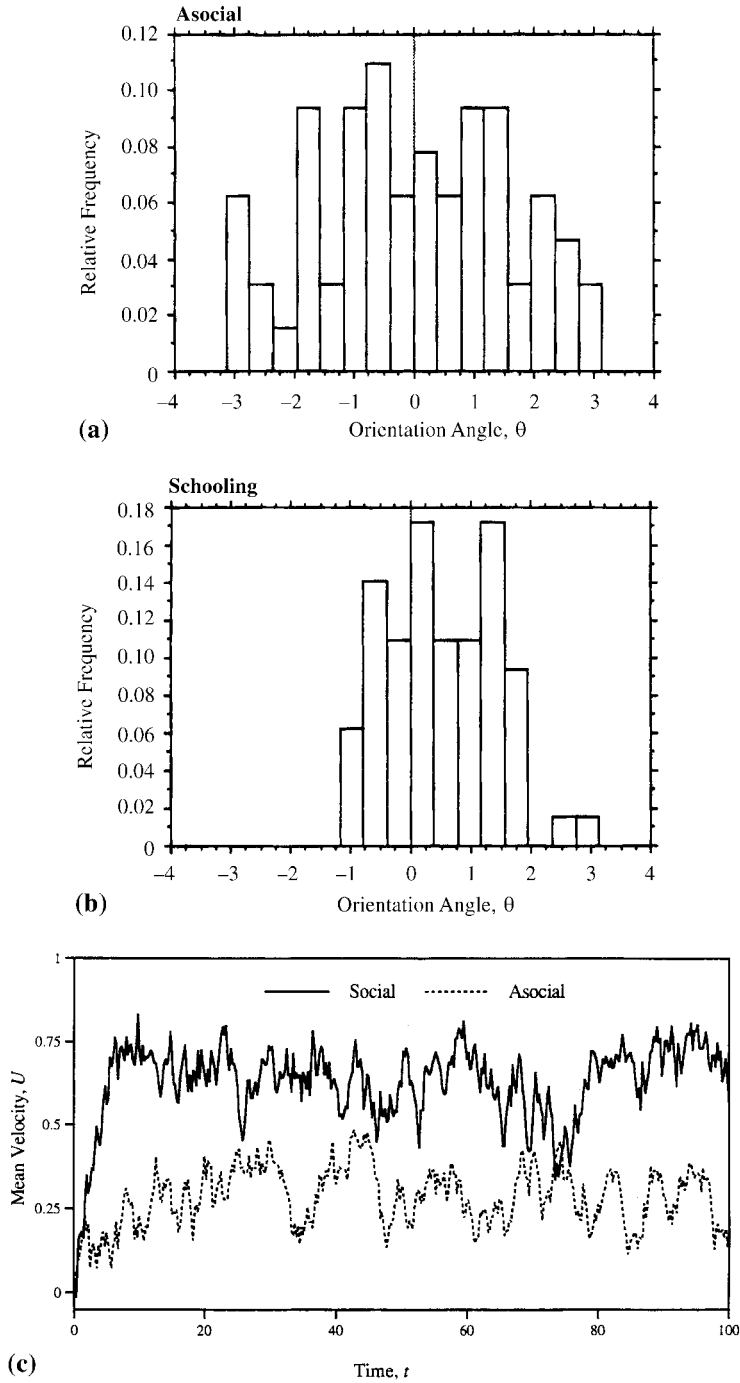
Figure 5. Simulations of asocial and social chemotaxis. (a, b) Orientation angles at $t = 100$ in the simulations shown in Fig. 4, showing a tightened angular distribution in the social chemotaxis simulation compared to the asocial case. (c) Time series of average up-gradient velocity, U, for the same simulations, beginning with random initial conditions and continuing until $t = 100$. Velocity is stochastic in both cases, but higher on average for the social algorithm.
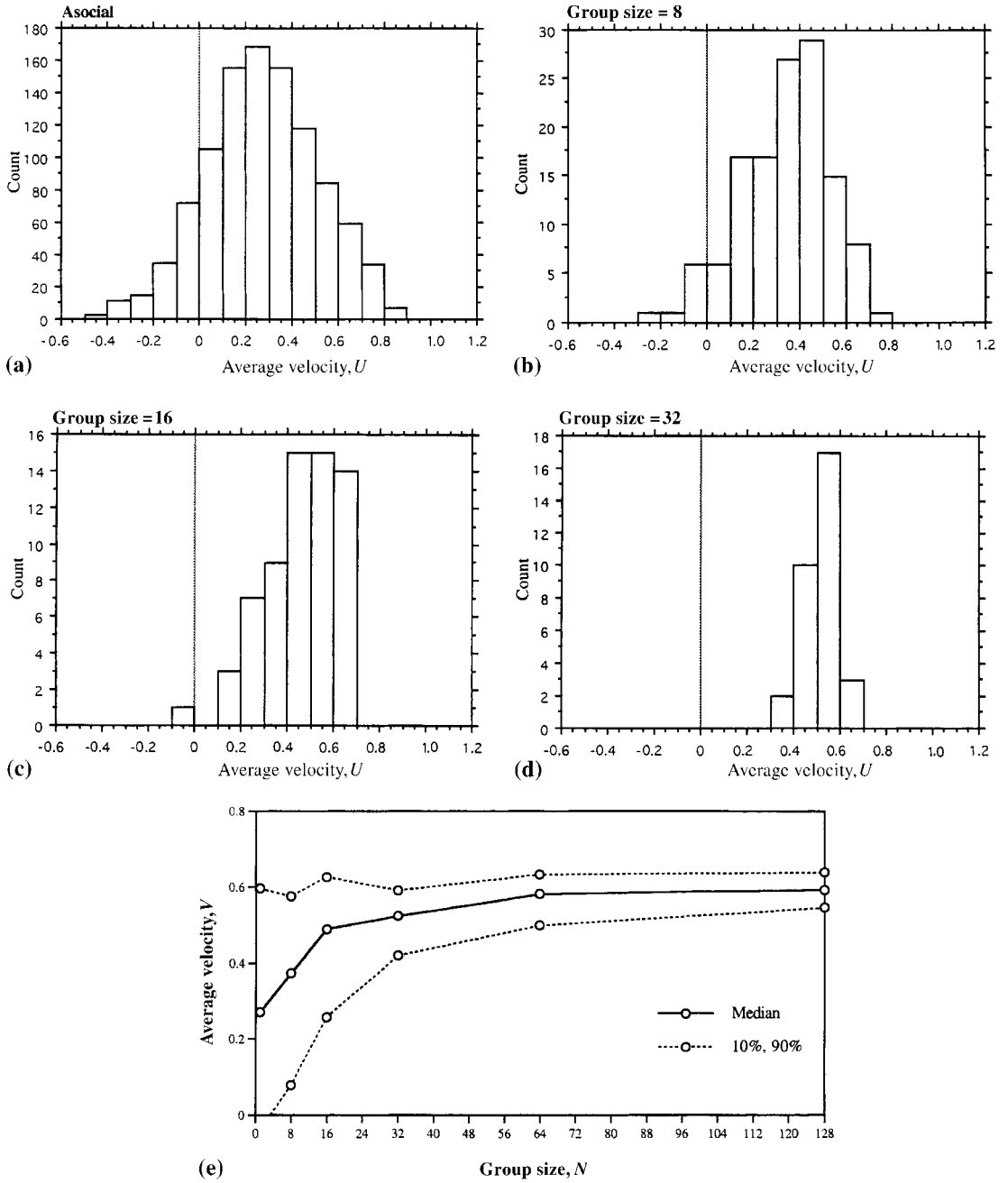
Figure 6. Up-gradient velocity, U, as a function of group size. (a–d) Histograms of average velocity over the interval $0 \leq t \leq 30$, for asocial searchers and social searchers in groups of 8, 16 and 32. Asocial search is represented by 1024 individuals; social searches are represented by the same number of individuals arranged in groups of several sizes (128 runs of 8 individuals, 64 runs of 16 individuals, 32 runs of 32 individuals). (e) Median, 10th and 90th percentiles of up-gradient velocity as a function of group size. Included in this plot are groups of 64 and 128 (32 runs for each). Parameters are as in Fig. 4, except that in each social simulation the number of neighbours an individual seeks is 7/8 of the total number of individuals (e.g. 28 neighbours for $N = 32$).

School-size effects must depend to some extent on the tactic and schooling algorithms, and the choices of parameters. However, underlying social taxis are the statistics of pooling outcomes of independent decisions, so the numerical dependence on school size may operate in a similar manner for many comparable behavioural schemes. For example, it seems reasonable to expect that, in many alternative schooling and tactic algorithms, decisions made collectively by less than 10 individuals would show some improvement over the asocial case but also retain much of the variability. Similarly, in most scenarios, group statistics probably vary only slowly with group size once it reaches sizes of 50–100.

As suggested by Fig. 6, when group size becomes large, the behaviour of model schools changes in character. With numerous individuals, stochasticity in the behaviour of each member has a relatively weaker effect on group motion. The behaviour of the group as a whole becomes more consistent and predictable, for longer time periods. It is possible to take advantage of this change of character to formulate a deterministic model of the effect of schooling behaviour on taxis in large, dense groups. The next section deals with such a deterministic approximation to the simulations presented here.

A non-spatial, deterministic approximation to social taxis

I consider now a school of large size and high density, and assume that the school is strongly cohesive – that is, the group always remains together (as was the case in the simulations in the previous section). Most members are then able to interact with numerous other members, and almost always see among their neighbours a large and representative sample of the angular distributions in their part of the group. Furthermore, if the school is large, the grouping tendency rarely provokes turning responses in a typical member, since most of the members are not near edges where density changes rapidly. Angular distributions in large, dense, cohesive schools thus lose their sensitivity to the exact relative positions of members, and become less stochastic, compared with those in smaller, less dense, less cohesive schools. This is the rationale for formulating a deterministic non-spatial equation for the probability density of orientation angle, $\rho(\theta, t)$, for social individuals performing taxis with an alignment tendency.

Drawing on the diffusion limits presented earlier, and calculating the average rates of alignment to neighbours under the schooling algorithms in the previous section, the changes of the distribution of orientation angles over time can be written as:

$$\frac{\partial}{\partial t}\rho(\theta, t) = \frac{\partial^2}{\partial\theta^2}(D(\theta)\rho(\theta, t)) - \beta\frac{\partial}{\partial\theta}\left(\rho(\theta, t)\left[\int_0^{\theta+\pi}\rho(\theta', t)\,\mathrm{d}\theta' - \int_{\theta-\pi}^0\rho(\theta', t)\,\mathrm{d}\theta'\right]\right) \tag{8}$$

In Equation (8), the first right-hand term corresponds to the tactic behaviour from Equation (2), and the second describes the alignment behaviour. The expression in the square brackets represents an individual's equal probability of choosing any one of its neighbours at a given time; β is the rate of turning towards neighbours' headings. Related equations have been suggested to model spatial animal aggregations (Kawasaki, 1978; Alt, 1985; Pfistner and Alt, 1990; Grünbaum, 1994). Equation (8) is a non-linear, partial integro-differential equation. It cannot in general be solved analytically, but useful approximate solutions are possible. Furthermore, it is much faster to solve numerically for large populations than the full simulations described in the previous section, and so is a useful way of encapsulating the effects of alignment behaviour on taxis in large groups.

Solutions of Equation (8) are consistent with the simulations in the previous section: aligning with neighbours is an effective strategy for climbing a noisy gradient under conditions where simple taxis is ineffectual (Fig. 7). Starting from an initially uniform distribution of orientation angles,
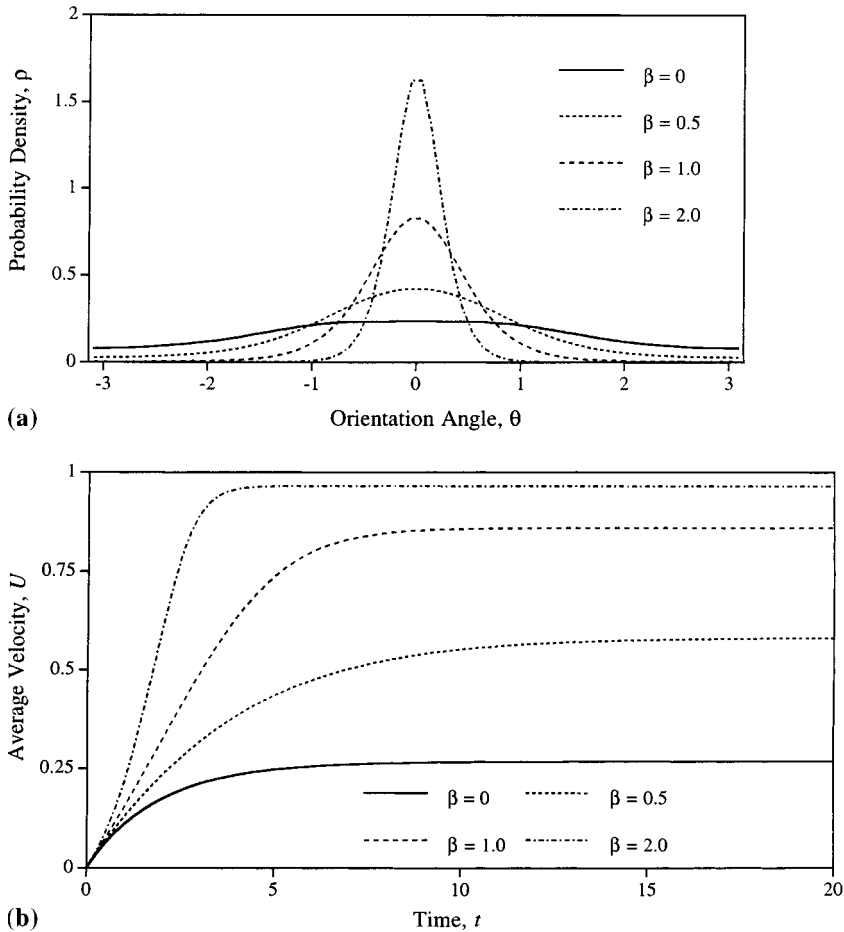
Figure 7. Orientation angle distribution in the non-spatial deterministic scenario (Equation 8) for asocial searching ($\beta = 0$) and three choices of the alignment parameter β. In all cases, $d = 2$. (a) Equilibrium distributions ($t = 20$) of orientation angles, showing tightened distributions for stronger alignment tendency. (b) Average up-gradient velocity, U, as a function of time, with initially uniform angular distributions. Stronger alignment tendency results in a faster response to the gradient and higher up-gradient velocity.

increasing the rate of alignment with neighbours (β) results in more rapid convergence about the up-gradient direction and progressively tighter equilibrium angular distributions. Interestingly, for these dense aggregations, even relatively weak alignment tendencies ($0.25 \leq \beta \leq 1$) result in significantly higher up-gradient velocities (Fig. 8). This compares to the relatively strong alignment, ($\beta \gtrsim 6$) that was necessary in the simulations in the previous section to produce coherent schooling behaviour. As expected from the discussion above, these calculations predict a relatively tighter angular distribution for a given alignment tendency in large, dense groups than was observed in the simulations in the previous section.
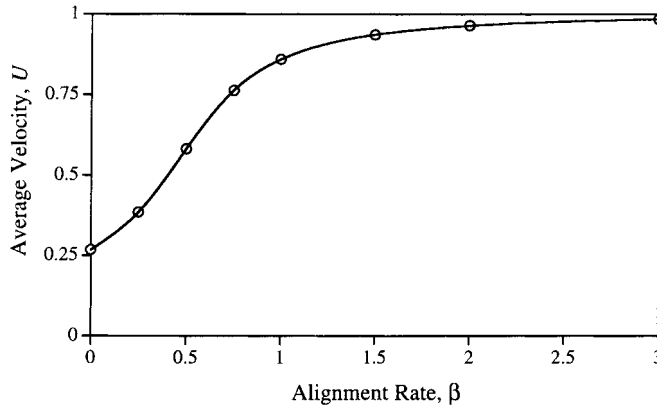
Figure 8. Average up-gradient velocity, *U*, in the non-spatial deterministic scenario (Equation 8), as a function of the rate of alignment, β. Velocity initially increases rapidly with β, then saturates and approaches the maximal value ($U = 1$) asymptotically.

Optimal alignment rates

How strong should alignment rates be? The calculations have so far only considered an initially uniform angular distribution and constant tactic signal. In a more realistic environment, where concentration of the resource varies in time and space, the direction of the large-scale gradient might change as the searcher swims along. To climb gradients effectively under these circumstances, searchers need the ability to adjust and correct heading direction. In such cases, excessive attention to what neighbours are doing may prolong an erroneous 'consensus' direction.

An example of group response to changing gradient direction shows that there can be a cost to strong alignment tendency. In this example, the gradient is initially pointed in the negative *y*-direction (Fig. 9). After an initial period of 5 time units, during which the gradient orients perpendicularly to the *x*-axis, the gradient reverts to the usual *x*-direction orientation. The school must then adjust to its new surroundings by shifting to climb the new gradient. This example shows that alignment works against course adjustment: the stronger the tendency to align, the slower is the group's reorientation to the new gradient direction. This is apparently due to a non-linear interaction between alignment and taxis: asymmetries in the angular distribution during the transition create a net alignment flux away from the gradient direction. Thus, individuals that pay too much attention to neighbours, and allow alignment to overwhelm their tactic tendencies, may travel rapidly and persistently in the wrong direction.

Discussion

Simple, asocial types of taxis such as those employed by bacteria are effective because, over time, the displacement of an individual reflects the outcomes of many movement decisions. 'Right' decisions (e.g. turning towards the up-gradient direction) are more likely than 'wrong' decisions, but both occur at significant frequencies. The idea of averaging is thus central to understanding the long-term movements of an individual or the density flux of a population. Social aggregative behaviours have the potential to enhance taxis by providing an additional mechanism for averaging movement decisions: if averaging decisions among a large group of individuals at one instant can substitute in part for averaging many decisions by a single individual over space and time, then
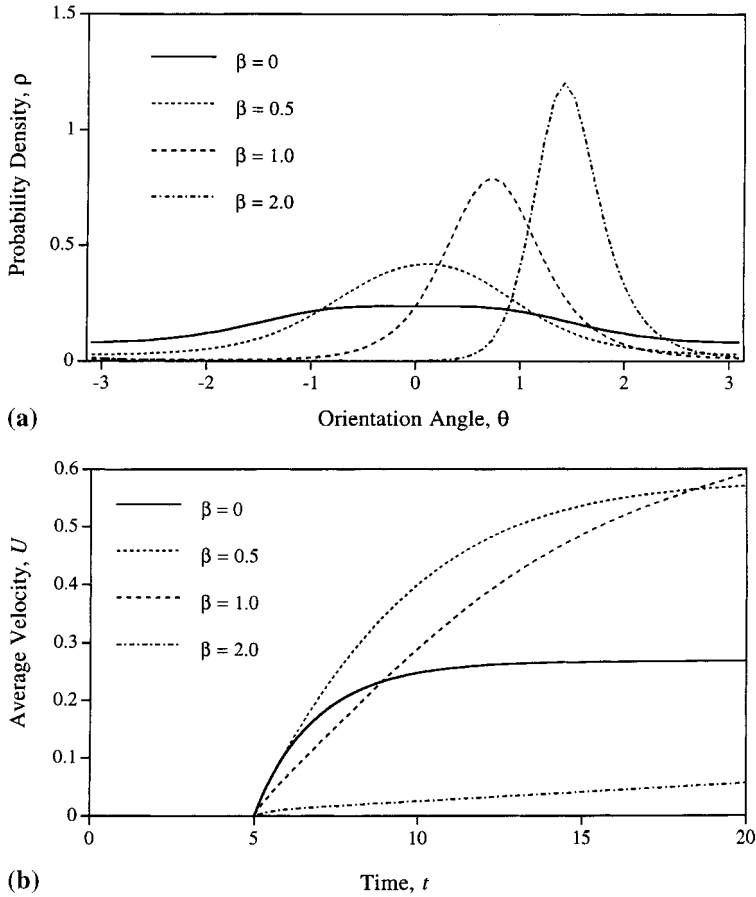
(a)

(b)

Figure 9. Response to changing gradient directions in the non-spatial deterministic scenario (Equation 8) for asocial searching ($\beta = 0$) and three choices of the alignment parameter β. These calculations are the same as those in Fig. 7, except that the gradient is along the y-axis ($\theta = -\pi$) for the time interval $0 \leq t \leq 5$, and reverts to the usual orientation ($\theta = 0$) thereafter. (a) Transient angular distributions at $t = 20$, showing lower degrees of adjustment to the new gradient direction for stronger alignment tendencies. (b) Average up-gradient velocity, U, as a function of time. Although the equilibrium velocity is highest for the strongly aligning case, strong alignment also prevents a group from rapidly correcting course when the gradient direction changes. In this particular scenario (gradient changes after 5 time units), an intermediate alignment tendency ($\beta \approx 1$) appears to result in the highest up-gradient motion.

each member of the group may arrive at the 'right' decision more quickly and with greater accuracy than it would in isolation.

The models developed in this paper suggest that animals attempting to climb faint and noisy environmental gradients by taxis may improve their searching ability by participating in such a collective searching process. This positive interaction of taxis and schooling contrasts with that of mutual attraction through a diffusing secondary substance, which has been found to inhibit up-gradient motion (Ezoe *et al.*, 1994). While asocial searchers have a broad range of orientation angles, the alignment component of schooling behaviour tends to shrink the angular distribution

within a school, so that individuals move more directly up-gradient. The collective 'decision' is statistically more likely to correctly identify a noisy or faint environmental gradient: in the models, even relatively small groups of schooling individuals ($n \leq 8$) have a larger average up-gradient velocity than asocial searchers. The models also suggest that there is a trade-off in strengthening tendencies to align with neighbours: strong alignment produces tight angular distributions, but increases the time needed to adjust course when the direction of the gradient changes. A reasonable balance seems to be achieved when individuals take roughly the same time to coalesce into a polarized group as they do to orient to the gradient in asocial taxis.

Evolutionary benefits of schooling

Social taxis is potentially effective in animals whose resources vary substantially over large length scales and for whom movements over these scales are possible. Examples of social taxis might be found among pelagic consumers of phytoplankton and small zooplankton such as herrings and anchovies, which form large, tightly organized schools (Royce, 1972). Antarctic krill, the dominant grazer in the Southern Ocean, also forms schools when searching for phytoplankton concentrations (Hamner, 1984; Miller and Hampton, 1989; O'Brien, 1989). Interestingly, krill have been reported to school until a food patch has been discovered, whereupon they disperse to feed, consistent with a searching function for schooling. The apparent effectiveness of schooling as a strategy for taxis suggests that these schooling animals may be better able to climb obscure large-scale gradients than they would were they asocial. Interactive effects of taxis and sociality may affect the evolutionary value of larger groups both directly, by improving foraging ability with group size, and indirectly, by constraining alignment rates.

   The implications of social behaviour for taxis fits into a large body of theory and observations on the advantages and disadvantages of group foraging in aquatic animals (Pitcher, 1986; Parrish, 1992; Pitcher and Parrish, 1993). That work has established the importance of foraging benefits as an evolutionary benefit of schooling behaviour, and provided details about processes underlying school function, such as information transfer between members of foraging groups (Pitcher *et al.*, 1982; Ryer and Olla, 1991). Many of the foraging benefits thought to accrue from shoaling in general and schooling in particular are related to the risk of predation. For example, shoaling may result in a perceived reduction in the need for vigilance while foraging in groups, taking advantage of the so-called 'many eyes' effect in which any group member may detect a predator in time to foil an attack (Wolf, 1987; Domenici and Batty, 1994). Larger group size in bluntnose minnows is associated with both fewer attacks by a predator, smallmouth bass, and with increased foraging rates by shoal members (Morgan and Colgan, 1987). Other possible predation-related benefits of group foraging include overcoming predator confusion (Smith and Warburton, 1992) and overcoming territorial defences (Foster, 1987).

   An example where sociality directly affects foraging strategy is *forage area copying*, in which unsuccessful fish move to the vicinity of neighbours that are observed to be foraging successfully (Pitcher *et al.*, 1982; Ranta and Kaitala, 1991; Pitcher and Parrish, 1993). Pitcher and House (1987) interpreted area copying in goldfish as the result of a two-stage decision process: (1) a decision to stay put or move depending on whether feeding rate is high or low; and (2) a decision to join neighbours or not based upon whether or not further solitary searching is successful. Similar group dynamics have been observed in foraging seabirds (Porter and Seally, 1982; Haney *et al.*, 1992). A form of area copying, *synchrokinesis*, has been proposed to have a role in the migration of herring (Kils, 1986, described in Pitcher and Parrish, 1993). Synchrokinesis depends upon the school having a relatively large spatial extent: part of a migrating school encounters an especially fa-vourable or unfavourable area. The response of that section of the school is propagated

throughout the school by alignment and grouping behaviours, with the result that the school as a whole is more effective at route-finding than isolated individuals. Forage area copying and synchrokinesis are distinct from social taxis in that an individual discovers and reacts to an environmental feature or resource, and fellow group members exploit that discovery. In social taxis, no individual need ever have greater knowledge about the environment than any other – social taxis is essentially bound up in the statistics of pooling the outcomes of many unreliable decisions. Synchrokinesis and social taxis are complementary mechanisms and may be expected to co-occur in migrating and gradient-climbing schools.

Besides increasing the average rate of gradient-climbing, another effect of social behaviour on taxis is to reduce the 'spread' or variance of searching success among individuals. For example, in the comparisons of taxis among groups of various sizes, the most successful *individuals* were in the asocial simulation, even though as a fraction of the entire population they were vanishingly small. This suggests that the effectiveness of a social tactic strategy for a particular organism may depend in part on whether its reproductive rate is small or large on the time scale of foraging movements between resource concentrations. For organisms limited by resources but which otherwise are capable of explosive reproductive rates (macroscopic examples may include gelatinous plankters such as cnidarians, ctenophores and salps), an alternative strategy is to disperse offspring as widely as possible. In such a species, the ultimate population level within the resource concentration is not necessarily proportional to the number of searchers which enter it, because rapid population growth rate within favourable areas can make up for the small fraction of individuals which find them. If, on the other hand, reproduction does not occur on the time scale of foraging movements, then the benefit to an individual may be roughly proportional to the amount of time spent within resource patches. In this case, a searching strategy which on average is more effective at climbing gradients is superior, even if it eliminates the extremely fortunate individuals which move in the right direction by chance. Thus one would predict that, phylogenetic constraints aside, social taxis would be advantageous only in species that live a relatively long time and reproduce slowly compared to the variations they experience in their environments.

Experimental tests of social taxis

Group olfactory dynamics similar to social taxis were studied experimentally in foraging zebrafish by Steele *et al.* (1991). They monitored movements between regions of an aquarium with differing levels of a food odorant (L-alanine). At concentrations near the detection threshold, Steele *et al.* found ambiguous results: groups of four zebrafish were more responsive to faint odours than both smaller and larger groups. The next most responsive were isolated fish. Steele *et al.* speculated that these results arise from competing effects, such as the greater probability of including exceptionally sensitive individuals and increased avoidance behaviour due to confinement in a small space with larger group size.

One of the merits of the mechanistically based models I have outlined is that they identify two clear directions for experiments. First, they predict that the ability to follow an odour gradient with noise changes as a function of group size (Fig. 6). If one can manipulate the size of a school, but hold the environment constant (such as in large aquaria or flow chambers), one can test this prediction. Of course, schools may increase their up-gradient velocity for reasons other than the mechanisms identified by the models I have discussed. However, the models are sufficiently explicit in connecting changes in effectiveness of schooling to the amount of noise in the gradient signal, that one could design experiments to rule out 'getting the right prediction for the wrong reason'. Specifically, by changing turbulence, or by directly inputting misleading odour patches, one can manipulate the signal-to-noise ratio in an experimental set-up. The models predict that the dif-

ferences among histograms as a function of group size for social schoolers will diminish as the signal-to-noise ratio increases. Even without estimating all the parameters in the models I have examined, an experimental program that crossed manipulations of group size with signal-to-noise ratios could provide compelling evidence for the processes identified by the social taxis models developed in this paper.

Acknowledgements

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