Modelling density-dependent fish shoal distributions in the laboratory and field

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Density-dependent variables have long been established as an important area of ecological research, but the effects of the local density of conspecifics on grouping behaviour are less well-studied. We compared the influence of the density of conspecifics on the shoal size distribution of killifish, *Fundulus diaphanus*, in the laboratory and the field. In both environments we observed an increase in shoal size and shoal number with the density of individuals present. The increase in shoal size was markedly steeper in the field than in the laboratory, but direct comparison of the two was complicated by the fact that the absolute numbers of fish present at the field site were considerably higher than those used in the laboratory trials. We developed an individual-based model that was first used as a null model of shoal formation (defined by proximity to others) in fish with no shoaling tendency over the same range of densities used in the laboratory. Group size increased much more rapidly with increasing density in the laboratory than predicted by the null model. When we incorporated shoaling behaviour into our model, the laboratory results could be reproduced with high accuracy. However, when extrapolated to match conditions in the field, the model predicted smaller, more numerous shoals than were actually observed. We suggest this is due to heterogeneity of the field environment because fish were found to be highly aggregated in certain areas of our field site. The predictive power of laboratory studies for the field is discussed with regards to using individual-based modelling as a tool for deriving such predictions.

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Many processes affecting the survival of individuals are density-dependent, and the effects of density at both the local and population level have long been a focus of study for ecologists (Begon et al. 1996). Large-scale density-dependent variables such as birth rate, death rate, dispersal, migration and immigration are influenced at the fine-scale by interactions among individuals. By altering levels of predation, competition and/or aggression among individuals, density can in turn affect their internal state, thereby potentially influencing behavioural decisions based on a cost/benefit analysis

(Houston and McNamara 1999). The local density of conspecifics can affect a great many processes including courtship (Gaskin et al. 2002), fertilisation (Powell et al. 2001), foraging effort (Davidson and Morris 2001), and settlement of juveniles (Kent et al., 2003), and density is an increasingly important area of research for the farming industry, where the density of housed animals can greatly affect their welfare. The stocking density of commercially exploited fish, for example, can have far-reaching consequences for their growth and health (Glasser and Oswald 2001).

In general, density has wide-spread implications for research in the field of behavioural ecology, whether pure or applied. Few density-dependent behavioural traits are readily observed in both the laboratory and the field. One such trait which has been studied to varying degrees in both environments is the shoaling behaviour of various fish species (Krause and Ruxton 2002). The ease with which small fish can be kept in captivity, and the suitability of some species for direct field observation, make them ideal subjects for the study of density-dependent behaviour. In addition to providing insights into the field as a whole, the study of the dynamics of fish shoaling behaviour should allow better management and conservation of commercially exploited or endangered fish stocks (Pitcher 1997).

The majority of teleost fishes shoal at one stage or another during their life history (Pitcher and Parrish 1993). Shoaling confers benefits to individuals in terms of reduced predation risk, through such mechanisms as risk dilution and predator confusion (Godin 1986, Pitcher and Parrish 1993), and can also increase their foraging success (Pitcher et al. 1982). Given the ubiquity of shoaling as a behavioural strategy in fish, it is perhaps surprising how little we know about the mechanisms underlying the establishment and maintenance of the range of shoal sizes we observe in the field (Niwa 1998). Clearly these mechanisms must integrate the social interactions among a number of individuals moving within a given area, as well as processes arising from the physical properties of the environment itself.

The shoal size distribution in a particular area is largely dependent on the number of individuals present, their external and internal behavioural motivations (Flierl et al. 1999), and the rates of shoal fission and fusion (Okubo 1986). Two distinct, yet inter-linked, processes operate to bring individuals together in this way. Social aggregation, such as shoaling, by its nature causes a local increase in density, which in turn determines the number of individuals with which a focal individual can interact. Furthermore, non-social aggregating forces may be superimposed on social aggregating processes. By causing a local increase in density these can influence the rate of interactions among fish, thereby affecting their shoal size distribution (Flierl et al. 1999). Such aggregating forces are numerous: fish may congregate in certain areas depending on the local predation risk, shelter availability, and foraging opportunity (Huntingford 1993), or may show a preference for a certain light intensity, current strength, water temperature, or oxygen concentration (Fréon and Misund 1999), and their distribution can also be affected by chemical gradients or weak turbulence (Flierl et al. 1999).

In the laboratory it is relatively easy to control for environmental heterogeneity. However, comparisons between the laboratory and the field are also made difficult by the difference in scale. Take for example, a field study site of 100 m^2 holding 400 fish at a density of 4 m^{-2} (the shallow water in which direct observations of behaviour were made in this study makes 'fish per m^2' a relevant expression of density). The practical equivalent in the laboratory would be an experimental arena of 1 m^2 containing 4 fish. However, despite the densities being the same, the implications for the shoal size distribution are markedly different. Even the measurement of density itself is scale-dependent (Horne and Schneider 1995). In order to compare laboratory and field results, models of shoaling behaviour need to be generated, in which the effects of potentially confounding variables can be identified and controlled for. Comparison of observed data with these models then provides useful tools with which to investigate the main factors involved in producing the distributions of shoal sizes observed under different conditions.

In this study we compared the effects of varying density on the distribution of shoals both in the laboratory and the field, with the aid of models which controlled for the problems inherent in comparing (small-scale) laboratory arenas with (large-scale) field sites. Our aims were to quantify the relationship between fish density and shoal size distribution, and to ascertain whether laboratory studies can be used to make relevant predictions about shoaling behaviour in the field. Comparing the observed data with a null model, which assumed no interaction between 'fish' within a given area, also allowed us to elucidate whether the observed shoal size distribution at a particular density was due mainly to the social behaviour of the fish or a result of the physical properties of the system: there may be an increase in shoal size with density simply because fish have a greater probability to occur close to each other at higher densities.

Laboratory trial

Material and methods

In July 2001, 200 juvenile banded killifish, *Fundulus diaphanus*, were caught from the littoral zone of Morice lake (near Sackville, New Brunswick, Canada; 45°55′N, 64°21′W) using a beach seine. The fish were kept in a holding tank (diameter 1 m, water depth 20 cm) in the laboratory and fed on freeze-dried chironomids (Hagen Ltd., Montreal) ad libitum twice daily.

The experimental arena (1.5 × 1.5 m and 10 cm high, water depth 6 cm) was filled with well-water and had rounded corners to facilitate continuous swimming behaviour. A digital video camera (SONY DSR-PD100AP) was suspended directly above the tank so that its field of view encompassed the entire arena. The arena was constructed from white plastic to provide a good contrast of the fish against the background for subsequent analysis of the video films. The shallow water

and white background colour are unlikely to be perceived by killifish as artificial because this species is often found in very shallow water over light-coloured sand in nature. The tank containing the arena was surrounded by opaque black plastic sheets to minimise disturbance to the test fish.

At the start of a trial, fish of similar body length (35–40 mm) were netted out of the holding tank and transferred into a transparent release cylinder (diameter 12 cm) in the centre of the arena, which was then lifted by remote pulley once the black plastic sheets had been placed around the tank. At this point filming started and continued for 20 min. At the end of each trial, the fish were removed from the arena and placed in a bucket, whilst the next set of test fish were removed from the holding tank. The first set of fish was then returned to the holding tank. Although this could lead to fish being used repeatedly in different trials, keeping back the previous set of fish until the next test group had been removed avoided any fish being used in consecutive trials. In the wild, the shoal composition of killifish changes every 3.3 min on average (Krause et al. 2000), and fish were allowed to mix freely in the holding tank for at least 20 min. Therefore the probability of any of the subsequent trials containing many of the same fish was very low.

In order to assess the effects of fish density on shoaling behaviour, different numbers of fish were added to the arena. We carried out trials with 2, 4, 6, 8, 10, 12, 14 and 16 fish in the arena with 2–3 replicates for each density (giving a total of 20 trials). This allowed us to create a range of densities from $0.9–7.1 \ m^{-2}$, which is similar to observed natural densities of $0.2–4.2 \ m^{-2}$ (Krause et al. 2000).

All trials were filmed and digital video footage was then played on a large monitor to record the number and size of shoals in the arena. The first four minutes of playback were not included in the analysis, to allow for a settling-in period for the fish. From the fourth min ($T_{4.00}$) onwards, the video footage was paused every 20 s, and shoal size and number was counted. Fish were considered to be associated with one another if they were within four body lengths of each other. This has been demonstrated to be a suitable criterion for defining shoal membership (Pitcher et al. 1983). Records were taken every 20 s until $T_{18:40}$, which yielded 45 data points for shoal size and shoal number for each replicate at each density. For mathematical purposes, during our analysis of the size and number of groups formed in both the laboratory and the field, we counted single individuals as groups, of group size 1. Every record of group size was a list of all the group sizes observed at that point (i.e. if the arena contained 8 fish, one record of group sizes observed at a particular 'pause point' might be 4, 2, 1, 1). A mean group size for each pause point was calculated, then a further mean of these means was taken, to give one overall mean group size for each replicate at each density. An overall mean group number was also calculated for each replicate at each density.

Modelling

We created two models: one which simulated shoaling interactions, and one null model in which the fish showed no shoaling tendency at all. In our laboratory experiments we decided to keep area size constant and changed fish number. Alternatively, we could have kept the number of fish constant and changed the tank size. The latter is probably a better way of investigating density effects but also much harder to do experimentally and was therefore not adopted. Thus the null model serves the important purpose of controlling for the change in fish numbers and allows us to assess how much of the shoal size distribution observed in the laboratory trials was due to underlying physical properties of the system. We matched the shoaling simulation to the observed laboratory data, and then extrapolated this to include the range of densities seen in the field, to assess whether the trends observed from the laboratory trials were good predictors of behaviour in the natural environment.

We simulated the behaviour of individuals as resulting from "repulsion", "alignment" and "attraction" tendencies based upon the position of individuals relative to one another, in accordance with previous work (Aoki 1982, Huth and Wissel 1992, 1994, Couzin et al. 2002, Couzin and Krause 2003, Hoare et al., 2004). In fish, co-ordination of collective movement is primarily achieved through using two of the sensory modalities: vision and lateral line mechanoreception (Partridge 1982, Kalmijn 1988), although the relationship between perception and movement tendencies is still poorly understood. In our simulation model, therefore, individuals were accorded simple behavioural rules intended to characterise generic behavioural tendencies to approach or avoid other fish. These behavioural rules are:

1) individuals attempt to maintain a minimum distance δ between themselves and other individuals at all times. This represents a minimum 'personal space' within which individuals will avoid collisions with others, and represents the zone of repulsion.

2) If individuals are not performing an avoidance manoeuvre (1) they exhibit a behavioural tendency to be attracted towards and to align themselves with neighbours. Individuals respond in this manner to all other individuals within a local interaction zone of radius ρ, which is equal to or larger than the zone of repulsion.

3) Individuals also tend to maintain a minimum distance δ between themselves and environmental obstacles, such as simulated arena walls in this case.

This represents avoidance of collisions with such obstacles.

In our model, there are N simulated fish, with individual i having position vector $c_i(t)$ and direction vector $v_i(t)$. Fish are simulated in two domains, one measuring 1.5×1.5 m with a reflective boundary, where fish rebound from the edges, (to model laboratory conditions), and one measuring 6×100 m with a periodic boundary, where fish leaving the domain through one edge reappear from the opposite edge (to more accurately model field conditions where fish were free to enter or leave the transect area).

Time is partitioned into discrete steps t with spacing $\Delta t = 0.1$ s chosen to approximate the response latency of shoaling fish to external stimuli (Partridge and Pitcher 1980). At each time step, the direction vectors and then the position vectors of all fish are updated in parallel.

The updating of the direction vectors is as follows. If there are other fish j within a distance δ of fish i it avoids them by turning towards a desired vector

$$d_i(t+\Delta t) = -\sum_{j \neq i} \frac{c_j(t) - c_i(t)}{|c_j(t) - c_i(t)|} \qquad (1)$$

If there are no fish within distance δ, the individual will respond to fish k within the interaction range ρ

$$d_i(t+\Delta t) = 1/2 \left[\sum_{k=1} \frac{v_k(t)}{|v_k(t)|} + \sum_{k \neq i} \frac{c_k(t) - c_i(t)}{|c_k(t) - c_i(t)|} \right] \qquad (2)$$

where the first term within brackets represents a tendency to align with neighbours, and the second term within brackets the tendency to be attracted to neighbours. If there are no neighbours within distance ρ, then $d_i(t+\Delta t) = v_i(t)$.

Fish also attempt to keep a certain minimum distance δ from the borders of obstacles: in this case the four edges of the domain. Therefore a border (each domain edge) B exerts a repulsive effect, which can be described by

$$f_B(t) = -\frac{r_B(t) - c_i(t)}{|r_B(t) - c_i(t)|} \qquad (3)$$

where $r_B(t)$ denotes the location of that point of the border B that lies closest to fish i. The repulsive forces are summed for all borders within distance δ of fish i, and this cumulative force is normalised, becoming $f'_B(t)$. Replacing $d_i(t+\Delta t)$ with $d'_i(t+\Delta t)$, the influence of the borders is incorporated as $d'_i(t+\Delta t) = \frac{1}{2}(d_i(t+\Delta t) + f'_B(t))$. In the eventuality that the social forces result in a zero vector, then $d_i(t+\Delta t) = v_i(t)$.

Fish are able to turn through an angle of at most $\theta \Delta t$ degrees, where θ is the maximum turning rate. If the angle between $v_i(t)$ and $d_i(t+\Delta t)$ is less than $\theta \Delta t$, then fish i achieves alignment with its desired vector, $v_i(t+\Delta t) = d_i(t+\Delta t)$, otherwise it turns $\theta \Delta t$ towards it. All turning is assumed to be subject to slight error. This is simulated by rotating $v_i(t+\Delta t)$ by an angle drawn from a Gaussian distributed random deviate centred on 0 with standard deviation $\sigma = 0.1$ radians.

This completes the calculation of the new direction vectors. The new position vector of fish i is then given by $c_i(t+\Delta t) = c_i(t) + v_i(t+\Delta t)\Delta ts$, where s is the speed of movement of the fish. Simulated fish have a body length of 4 cm (= 1BL) as in our experimental trials, and other parameters are set accordingly; s = 6 cm/s, $\delta = 1$ BL (Partridge 1982), $\theta = 100°$/s (Krause and Tegeder 1994). The number of fish, N, was varied over the range observed in the laboratory. Two hundred replicate simulations of the model were run for each density in the laboratory and twenty replicates were run for each density in the field. For each replicate, data on group size and number of groups formed were collected at the 5000th time-step, by which time group behaviour in the model had reached a dynamically stable state. To assess the spatial distribution of individuals in the model, we used the same criterion (of grouping together fish within four body lengths of a neighbour) that was applied to live fish in our test tank and in the field.

Results

Mean number of groups in the experimental arena increased 3.5-fold over the density range, whilst group size increased 3.3-fold. This increase in shoal size is almost identical to that observed by Rangeley and Kramer (1998) over a similar density range. In the shoaling model both the number and size of groups increased with density. A good fit was achieved between the observed results and the shoaling model for both variables (Fig. 1a, b). The null model also produced an increase in group number and group size with density (Fig. 1c, d). However, the mean group size produced by the null model did not increase as steeply with density as it did in the shoaling model, reaching a maximum of 1.25 at the highest density (Fig. 1c). Using Monte Carlo analysis mean empirical group size and number was compared to the corresponding values produced by each model at each density, and individual P-values were obtained. These were then combined, using Fisher's omnibus test (Haccou and Meelis 1992), to yield a single measure of how well each model fit the observed data. The shoaling simulation model provided data that were not significantly different from the observed ones both for group size (Fisher's omnibus test: N = 20, f = 31.64, P = 0.825) and for group number (N = 20, f = 40.93, P = 0.430), whereas the null model differed significantly from the laboratory data (group size: N = 20, f = 215.36, P < 0.001; group number: N = 20, f = 202.33, P < 0.001).
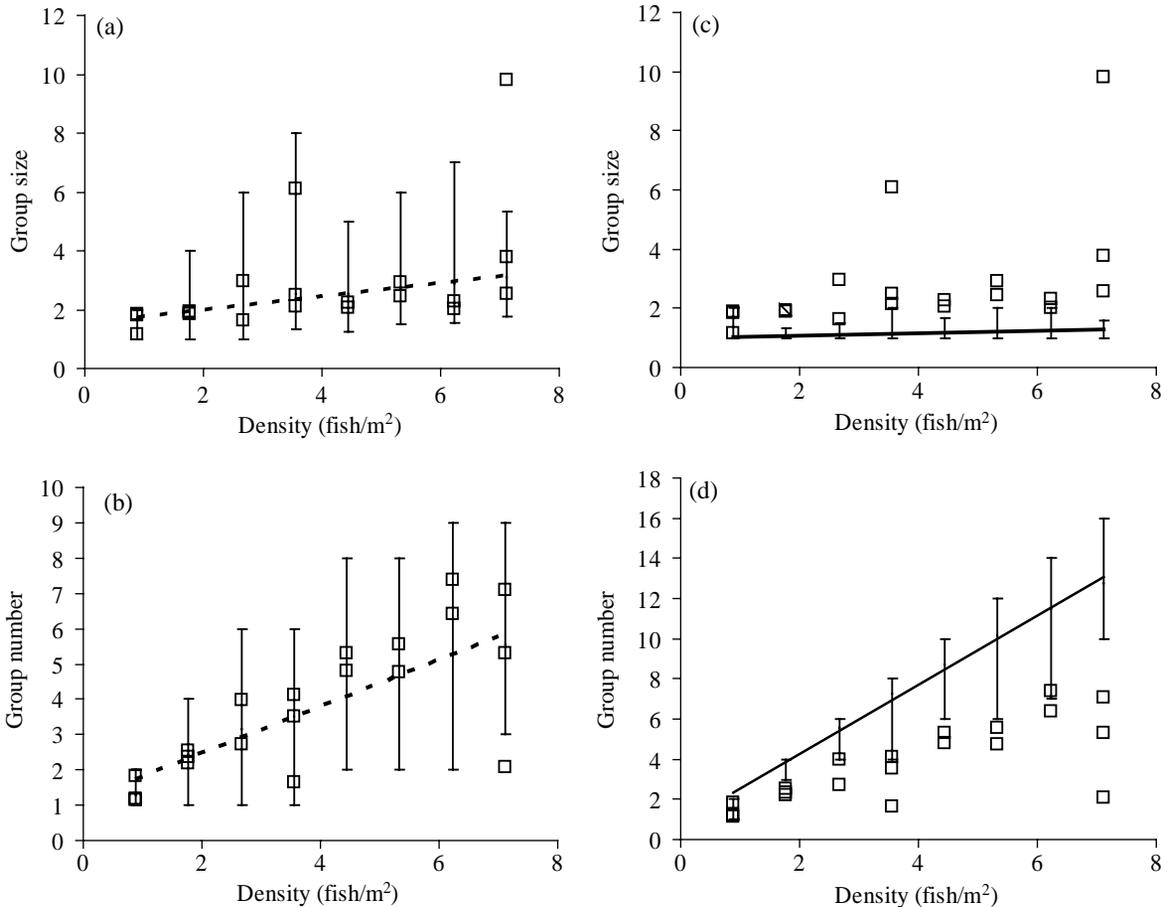
Fig. 1. Comparing the observed laboratory results for each density to the mean group size (a) and group number (b) for the shoaling simulation model (…), and the mean group size (c) and group number (d) for the null model (—). Trend lines for the models are presented with error bars indicating the total ranges of the model results at each density.

Field study

Material and methods

Our study area consisted of a 6×100 m strip of littoral zone at Morice Lake that forms a natural bay. Observations were made on banded killifish, *F. diaphanus*, to investigate how population density influenced group size and group number. Visual count transects were carried out in two parallel 3-m wide strips (0–3 m and 3–6 m) off the shore over 100 m of shoreline by two observers. Previous studies have shown that the presence of observers in close proximity does not generally affect killifish shoaling behaviour (Krause et al. 2000). During the visual transects, the number of groups, the respective group size and group mean of body length were estimated. Controls showed that the median error in determining group size was 11.5% (lower quartile: 6.7 and upper quartile: 19.6, N = 16) and that over-estimates and under-estimates were equally likely (Mann–Whitney U test: $N_1 = 9$, $N_2 = 7$, W = 69, two-tailed P = 0.47). There was

no relationship between the magnitude of the error and group size (linear regression: $r^2 = 0.12$, N = 17, two-tailed P = 0.18) for a group size range of 20–234 fish. The estimated mean body length differed from the measured mean body length on average by 1.7 mm (SD = 1.4 mm, N = 17).

Re-sampling of the same study area between transects may have resulted in the repeated inclusion of some of the same fish to a certain extent. There are two reasons, however, why pseudo-replication is likely to be negligible. Population densities were highly variable between transects (up to a factor of 35), which suggests that there was considerable exchange of fish with other parts of the lake. Furthermore, a mark–recapture study (Hoare et al. 2000) at Morice Lake indicated that shoal fidelity and site fidelity in killifish were both very low, with individuals mixing extensively within a 24 hour period and ranging widely over the study site. This suggests that, even if some individuals were repeatedly included in different transects, they were likely to have switched between shoals. It is estimated that approximately 20 000

shoal encounters take place in this study site per day (Hoare et al. 2000, Krause et al. 2000).

At the time the field data were collected, the majority (>60%) of the fish at the site were killifish, with smaller numbers of golden shiners, *Notemigonus crysoleucas*, (30%) and white suckers, *Catostomus commersoni*, (10%) present. Previous work has demonstrated that while multi-species shoals are frequently observed in the lake, these shoals are generally dominated by one species which comprises roughly 87–95% of the shoal's members, and these are well assorted according to phenotype (Krause et al. 2000). We therefore excluded these other species from our analysis, because they did not have a direct bearing on the number of individuals available for shoaling with the killifish present at the site. In order to focus on the individuals which most closely matched the size of our laboratory test fish, we separated out the records of groups which contained fish measuring between 30 mm and 40 mm after analysing the data as a whole. We then recalculated the density for fish ranging from 30–40 mm because it is known that killifish shoals are generally well size-assorted (Krause et al. 2000) and we would therefore expect fish to be mainly associated with similar-sized individuals (i.e. the density of size-matched individuals should be most relevant for shoal formation).

The transect was divided into 'cell units' of space, which then allowed us to investigate differences in space use by the fish along the bay. Flags posted along the length of the transect divided the space into 5 m zones, which were further divided by another set of markers set at a distance of 3 m from the shore. The smallest unit of space over which groups were observed was therefore 5×3 m, which was only used to calculate the maximum densities observed in the field. These cells were pooled into 10×6 m cells to allow analysis of differential space use along the transect (Fig. 2). Data from fish measuring between 30 and 40 mm, and from fish measuring between 20 and 30 mm were analysed separately using these cell units, so that space use both within and between size classes could be compared.

Results

A total of 9626 killifish were observed during the eight transects carried out over 10 days. They ranged in size from 15 to 65 mm, with the majority of individuals measuring between 20 and 35 mm. The distribution of fish in each body length class, and the number of groups observed comprising of fish of different body lengths can be seen in Fig. 3. Observed densities within the 600 m^2 bay ranged from 0.1–4.9 fish m^{-2}. Fish measuring between 30 and 40 mm made up 30% of the individuals within the overall sample.
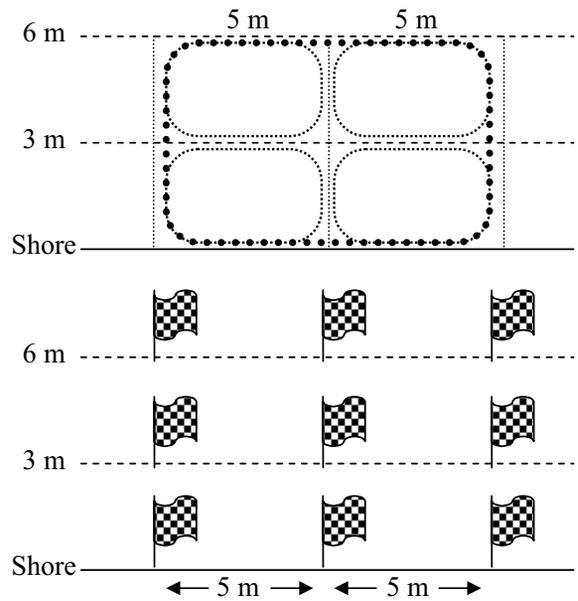

Fig. 2. Schematic of transect section from above showing one 6×10 m cell divided into four 5×3 m cells by flags.

Total density was calculated as the total number of fish observed (within the 600 m^2 bay during each transect) divided by 600. Body length specific density was calculated as the number of fish measuring 30–40 mm divided by 600. There was a significant positive correlation between the total density and the observed shoal size (Spearman rank correlation: N = 8, r_s = 0.76, two-tailed P = 0.028) and number (N = 8, r_s = 0.95, two-tailed P < 0.001) of shoals including fish from all body length classes.

For fish in the 30–40 mm range we found no correlations between total density (all fish in the population including those smaller and larger than 30–40 mm) and shoal number (Spearman rank correlation: N = 8, r_s = 0.69, two-tailed P = 0.058), and total density and mean shoal size (N = 8, r_s = 0.21, two-tailed P = 0.610). However, significant positive associations existed between body length specific density and both shoal size and number in these fish (mean group size: N = 8, r_s = 0.95, two-tailed P < 0.001; group number: N = 8, r_s = 0.76, P = 0.028). The strengths of these associations were similar to those observed between total density and the mean size and number of all shoals within the transect.

We found that fish occurred in greater numbers in some subsets of our transect than others (Friedman test: body length 30–40 mm: N = 8, χ^2 = 23.9, two-tailed P = 0.005; body length 20–30 mm: N = 8, χ^2 = 23.3, P = 0.006). The vast majority (>90%) of fish in both the larger (30–40 mm) and smaller (20–30 mm) body length classes were observed in relatively small proportions of the available space (18% and 26% respectively). Fish
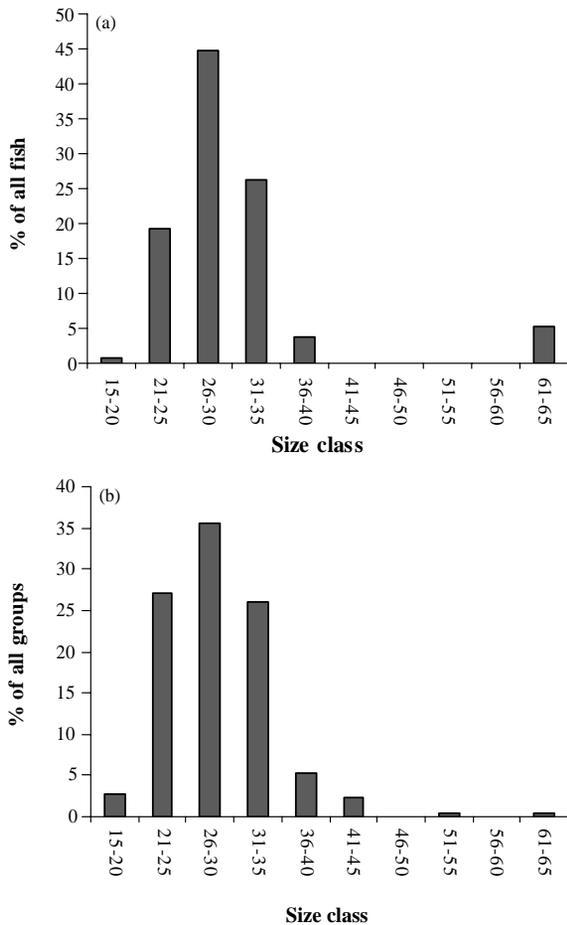
Fig. 3. (a) The body size distribution of all fish observed during eight transects, (b) the group number distribution of all groups observed according to body size.

Fig. 4. Group size (a) and group number (b) observed with increasing density in the field (○) and produced by the shoaling simulation (■). Mean ±SD are given for the shoaling model (but SD is negligibly small).

densities reached a maximum of 35 fish m^{-2} for larger fish and 51 fish m^{-2} for smaller fish (calculated for 3×5 m cell units).

When the shoaling model (which produced a good fit of the data in the laboratory) was extended to predict the shoaling patterns in the field, the match between the model and the observed results broke down (Fig. 4). Shoals observed in the field contained many more fish (and were therefore fewer in number) than those predicted by the shoaling model. Over the same range of densities, the shoaling model predicted a 1.5-fold increase in group size, whereas in the observed data group size increased 20-fold.

Discussion

We successfully described the shoaling behaviour (in terms of size and number of shoals formed) of killifish using a general shoaling model, in which the behavioural tendencies and characteristics of the 'fish' were based on
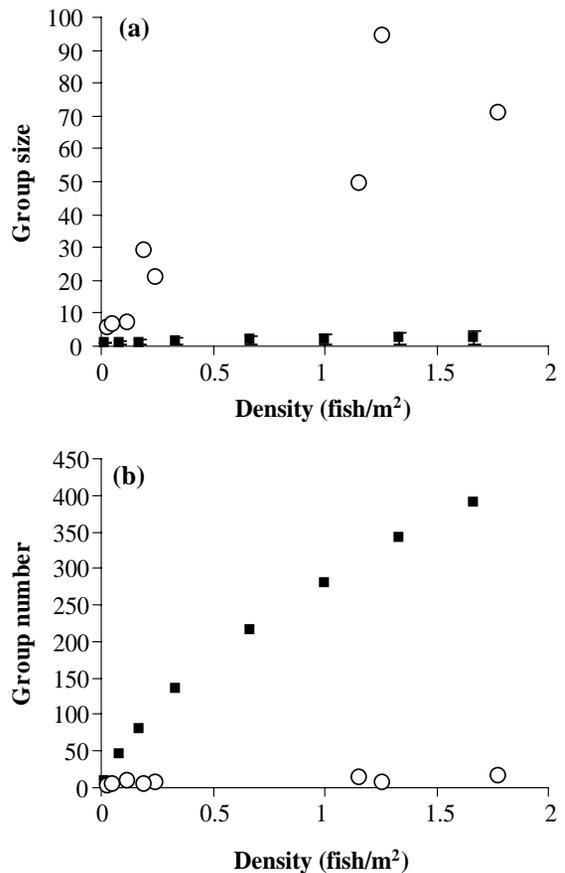
published, biologically-relevant values and not tailored to our specific situation. However, the shoaling model only accurately described killifish shoaling behaviour in the laboratory and not in the field. A parameter search showed that the shoaling model would not be able to produce the group sizes observed in the field for biologically meaningful parameters, suggesting that these large shoals were unlikely to have been produced by the shoaling tendency of the fish alone. Fish measuring 30–40 mm in length were consistently observed at higher densities in some areas along the transect than others. This was most likely to be due to differences in the substratum type (i.e. sand and rocks) along the bay, which in turn might have been influencing local food availability and/or the conspicuousness of the killifish to predators. It appears that the large shoals found in the field are more likely to be the result of non-social aggregation of fish in particular areas of the field site, combined with social aggregation.

Similar problems of local aggregation have been encountered in previous studies. Essington and Kitchell

(1999) found that the distribution of largemouth bass (*Micropterus salmoides*) was patchy on both large and small scales in Long Lake, Michigan, where the fish were aggregated in the littoral region. By creating a model of the system which included a taxis towards a particular area of the lake, the authors were able to explain much of the large-scale aggregation, but the level of small-scale aggregation could not be explained, even after the inclusion of taxes towards shallower or more shelter-rich units of space. The patterns of aggregation observed in this study highlight the fact that non-random distributions observed at one spatial scale may be generated by processes occurring at another. In this case, the bass showed a large-scale preference for the eastern side of the lake (possibly due to a thermal preference), and their distribution was then further modified by habitat or diet preferences at the small-scale. Small changes in the modelled movement behaviour of individuals were found to produce large and often surprising changes to their simulated spatial distributions. Thus observed patterns of aggregation could be based on small variations in a wide range of factors, both biotic and abiotic, which can affect the movement of individual fish within a given area. Few existing models have investigated the effects of aggregating forces on the distribution of fish in combination with observations from the field (Dagorn et al. 1997, 2000, Essington and Kitchell 1999, Flierl et al. 1999, Maravelias 2001).

Our null model that simply increased the number of fish but did not incorporate shoaling tendency was found to be a poor predictor of fish behaviour in both laboratory and the field. In the null model the effect of increasing the number of individuals in the area was to sharply increase the number of groups (in this case single individuals), without altering group size to a great degree. This shows that the greater proximity of individuals alone (due to the larger number of fish in the arena) was not sufficient to greatly increase shoal size. Social attraction between fish, in combination with larger numbers of individuals in the arena, was required to produce a strong increase in shoal size. Both social and non-social aggregating forces can therefore profoundly affect the size of shoals formed, and it may not always be easy to demonstrate which of the two, if either, is the dominant force. If resources are patchy (which could cause localised non-social aggregation) but the predation risk is also high (thus promoting social aggregation), this may cloud the issue of what is driving shoal formation. This is particularly true of pelagic habitats where resources can be patchy but may not persist in the same physical space.

A study by Bouaïchi et al. (1996) highlights the importance of environmental microstructure for distribution patterns. Desert locusts *Schistocerca gregaria* tend to avoid each other when at low densities, but when crowded together undergo both physiological and morphological changes which promote extreme gregariousness, frequently to devastating effect. Despland et al. (2000) were able to create an individual-based model that accurately described and predicted the transition of individuals from the solitarious behavioural phase to the gregarious phase with increasing fractal dimensions of available resources. This was based on previous work by Bouaïchi et al. (1996) which had investigated the effects of the distribution of food, shelter and microclimate on the degree to which locusts associated with a stimulus group, and the frequency with which they performed various locomotory and grooming behaviours. They used logistic regression to construct a mathematical model that would predict whether, given its record of behaviour under test conditions, an individual locust had previously been reared in solitary or crowded conditions. They found that the more patchy the resources, the more likely were previously solitary locusts to develop gregarious behaviours during the experiments. These findings were confirmed through trials conducted in enclosures in the field, and demonstrates the importance of small changes to local conditions in promoting what can be extremely large-scale phase shifts in behavioural patterns.

Given the poor performance of the shoaling model in predicting the size of shoals in the field, it is clearly not enough to observe the effects of increasing fish density in laboratory experiments, to determine the behavioural mechanisms underlying shoal formation, and to then attempt to validate the laboratory findings with data from the field. Laboratory arenas and field sites differ, not only in scale, but also in environmental heterogeneity, in addition to a large number of visual and olfactory cues. Certain characteristics of the field site must first be investigated in the laboratory to assess the extent to which shoal formation at different densities is affected by potential non-social aggregating factors present in the field. These effects can then be incorporated into mathematical models, and the resulting predictions regarding fish distribution, based on both social and non-social aggregating factors, can be validated with observations from the field. However, in the light of our field transect results it is important to note that applying even the most accurate and comprehensive of models to describe the size and number of fish shoals in the field will require a degree of prior knowledge, not only of the abiotic conditions present in the field site, but also the body lengths of the fish present. That the sizes and numbers of shoals formed are largely dependent, not on the total number of fish present, but the relative abundances of fish of different body lengths, may present real difficulties to modellers engaged in predicting, for example, the effects of habitat or thermal changes within a particular body of water. Thus, our study identifies some of the problems involved in predicting group size

distributions in the field based on laboratory studies, and highlights an area which continues to present interesting challenges for future research.

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