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Prey aggregation is an effective olfactory predator avoidance strategy

Predator-prey interactions have a major effect on species abundance and diversity and aggregation is a well-known anti-predator behavior. For immobile prey, the effectiveness of aggregation depends on two conditions: (a) the inability of the predator to consume all prey in a group and (b) detection of a single large group not being proportionally easier than that of several small groups. While the benefits of grouping to avoid visually hunting predators are well understood, the potential costs and benefits of aggregation when visual cues are not available are not well understood. We carried out foraging (predation) experiments using a fish predator and (dead) chironomid larvae as prey in both laboratory and field settings. In the laboratory, a reduction in visual cue availability (in turbid water) led to a delay in the location of aggregated prey compared to when visual cues were available, but aggregated prey suffered high mortality once discovered, leading to better survival of dispersed prey in the longer term (this was likely due to their inability to take evasive action and due to prey groups being small). In the field (where prey were placed in feeding stations that allowed transmission of olfactory but not visual cues), aggregated (large groups) and semi-dispersed prey survived for longer than dispersed prey – including long term survival. Together, our results indicate that like in systems where predators hunt using vision, aggregation is an effective anti-predator behavior for prey avoiding olfactory predators.

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Introduction

Predator-prey interactions are one of the major factors influencing patterns of species diversity and abundance in ecosystems (Chesson and Kuang 2008). Predators influence prey abundance and distribution through both consumptive and non-consumptive effects (Preisser, Orrock, and Schmitz 2007) such as predator avoidance behaviours, which may limit prey access to resources (Griffiths and Richardson 2006). Aggregation into groups is a common response to the risk of predation (Krause and Ruxton 2002). Grouping individuals benefit from the dilution effect if a predator is unable to consume all prey in a group (Foster and Treherne 1981) and from encounter dilution, where aggregated prey are encountered less often assuming population size is kept constant (Wrona and Dixon 1991). Together, this leads to a situation where fewer predators survive because cost of finding a prey group is high, and more prey survive because predators only consume few prey per encounter (Turner and Pitcher 1986; Turesson and Brönmark 2007).

Prey detection is likely to be dependent on a predator's sensory acuity and modality (Cain 1985). Theory predicts that as a group of prey grows, the ability of a visual predator to detect the group will increase at a slower rate; that is, a group of *N* individuals should be less than *N* times more detectable than a single individual (Brock and Riffenburgh 1960; Treisman 1975; Turner and Pitcher 1986). This is supported by empirical evidence for visual predators; Riipi et al (Riipi et al. 2001) found a non-proportional relationship between detectability and prey group size in great tits (*Parus major*) searching for aposematic prey, a finding reflected by humans seeking computer-generated prey (Jackson et al. 2005) and sticklebacks (*Gasterosteus aculeatus*) attacking *Daphnia* swarms (Ioannou et al. 2011).

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Whether encounter-dilution effects operate when predators use other sensory modalities is unclear. Close neighbours are likely to produce odour plumes that interact, increasing both the area of the odour plume and the amount of stimulant (Monismith et al. 1990). Treisman (1975) suggests that a group of N individuals should be detectable by an olfactory predator at a distance N times as great as that for a single prey, resulting in an area in which the group can be detected N^2 times as large as for a single prey (or a volume N^3 times as large). If this is the case, encounter-dilution would not take place, and grouping would not be favoured unless the predator is highly sensitive to olfactory cues and does not preferentially target large groups over small ones (Cain 1985). Recent empirical data indicates that aggregation increases risk of predation by olfactory predators (Whitton et al. 2012; Wilson and Weissburg 2012) but Andersson et al find that the distance at which a group can be detected increases asymptotically with group size (Andersson, Löfstedt, and Hambäck 2013).

While patterns of risk with increasing levels of aggregation are beginning to be established, there is no work that directly contrasts visual and olfactory prey detection rates on dispersed and aggregated prey within the same predator. Changes in the environment, such as fluxes in turbidity or changes in pH, can alter the availability of visual and olfactory information (Leduc et al. 2013), and consequently can alter reliance on different sensory modalities by predators (Chapman et al. 2010), which in turn may affect the shape of the interaction between predators and prey. Predators may use both vision and olfaction in detecting prey, increasing reliance on olfaction under poor visual conditions (Chapman et al. 2010). We predicted that the benefits of aggregation as an anti-predator defence would be reduced or eliminated when predators hunt using olfaction rather than vision. To test this prediction, we investigated the ability of sticklebacks (*Gasterosteus aculeatus*) to detect and

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consume dispersed and aggregated prey (bloodworm) when visual cues were and were not available. Sticklebacks are often found in waters that are highly variable in turbidity (Wootton 1976) and employ olfaction to detect prey in turbid water to compensate for the loss of visual cues (Johannesen, Dunn, and Morrell 2012). As a measure of detection, we monitored the survival of prey (frozen and defrosted bloodworm) over time when dispersed and aggregated, and in clear (visual and olfactory cues available) and turbid (no visual cues available) water. Additionally, we tested the effect of three levels of aggregation in the field in order to include more naturally sized foraging settings and multiple predators.

Methods

(a) Laboratory experiment – does turbidity affect best aggregation strategy?

(i) Study species and housing

Three spined sticklebacks were caught by netting from small water bodies in Saltfleet, Lincolnshire (53°25'59.55" N, 0°10'49.41" E) in November 2010 and 2011. On both occasions, 250 fish were caught and were transported in commercial fish bags to the aquarium facilities at the University of Leeds. Fish were housed in groups of approximately 50 in grey plastic tubs (60x90x45cm) with gravel substrate and artificial plants for environmental enrichment, at 14±2ºC and on a 14:10 hour light: dark cycle. Fish were fed *ad libitum* on defrosted frozen bloodworm (chironomid larvae, these were also the prey species in the experiment) from a commercial fish food supplier once daily. Each group of fish was released one year after capture at the location where caught (in agreement with the Home Office and DEFRA).

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(ii) Procedure

Our experimental procedure followed that in Johannesen et al from 2012 (Johannesen, Dunn, and Morrell 2012) and is briefly summarized here. We investigated two levels of prey aggregation (aggregated and dispersed) and two levels of water clarity (clear and turbid) in a crossed design, giving 4 treatments (clear-aggregated, clear-dispersed, turbid-aggregated and turbid-dispersed). In each trial, eight designated locations in a foraging arena (100x100 cm, depth 5cm, with a 10 x 10 cm central floating polystyrene shelter) were allocated either one (dead) prey each (dispersed prey) or eight prey in one location (aggregated prey) allocated at random. Each location was a distance of 25 cm from the nearest neighbours and 25cm from the arena wall. Turbid water was created by the suspension of commercial clay (Low Temperature White clay from Commercial Clay Ltd) in conditioned water at 0.5g/l. Water was changed between trials to remove olfactory cues from previous fish or prey, and fish were starved for 24 hours before testing to standardize motivation to feed. As our aim was to investigate how prey aggregation affects olfactory prey detection by predators and how survival is affected by prey group size, we chose to use immobile (dead) prey. Mobile prey could produce other cues (e.g. lateral line detection) and potentially benefit from other mechanisms than dilution of risk (e.g. confusion). Testing these other factors was not within the scope of our study.

Trials were video recorded from above. In each trial a single fish was released under the floating shelter to acclimatize and time to emerge (be fully free of the shelter) was recorded. Fish that did not hide under the shelter on release or did not emerge within 15 minutes were excluded from the experiment. Turbidity in the arena decreased over time, from 391.15 ± 9.35 NTU before fish were released to 286.83 ± 9.1 NTU after 35 minutes (measured before fish were captured after the trial). To ensure that visibility remained low in

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turbid water trials, fish were given a maximum of 35 minutes in the foraging arena, consisting of up to 15 minutes before emergence, plus 20 minutes during which foraging was recorded. Fish were measured (+/- 1mm total body length) using callipers after each trial. Environment (turbid/clear) did not affect time to emergence (Negative Binomial GLM, z=-1.63, df=61, P=0.1). This suggests that our manipulation of visual cues did not influence motivation to hunt for prey and/or perceived predation risk of the fish.

Data on foraging behaviour and time of prey capture for each prey item were manually extracted from videos using Etholog (2.25) and Windows Media Player. Sticklebacks vary considerably in boldness (Ward et al. 2004; Frost et al. 2007; Harcourt et al. 2010), leading to variation in time spent hiding (and therefore not foraging). Thus, to standardize search time for all fish, we recorded prey capture as a function of time spent actively swimming.

(b) Field experiment: do prey in a more natural setting benefit from aggregating?

Our laboratory experiment necessarily constrained the search area available for each predator, increasing the likelihood of chance encounter. Furthermore, it tested the effect of aggregation of prey on survival, but was limited by the small total number of prey. As predators were able to consume all prey without reaching satiation, our experiment did not include factors such as the dilution of individual risk (Wrona and Dixon 1991) once discovered. In ponds and lakes, search volume or area is much greater, and there may be multiple predators (individuals or species) in the environment, affecting how many prey may be consumed and increasing the likelihood of local or stimulus enhancement (where the activity of an individual draws the attention of an observer towards a location or object; (Spence 1937; Thorpe 1956)), or social learning (Brown and Laland 2003). To test the real-world validity of some of our findings, we also carried out a field experiment to assess the

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survival of visually hidden prey at different levels of aggregation. In order to ensure that cue availability was high enough in these larger water bodies, more prey were used. Because of this, aggregated and semi-dispersed prey groups were large enough to satiate a single predator, thereby allowing for dilution of individual risk within the experiment. The difference in setting and prey number make these two studies complementary rather than directly comparable.

Fieldwork was carried out on the Faroe Islands, where there is a low diversity of aquatic species, making natural systems much simpler than those in warmer climates (Malmquist et al. 2002; Brodersen et al. 2011). The largest predators in a typical pool above the tidal line are *Gammarus duebeni* (Roberts 1995) and sometimes three spined sticklebacks (*Gasterosteus aculeatus*). These ponds also contain a range of invertebrate prey species, including midge larvae. Ponds (N=11) were 5-50 m^2 in size, all contained sticklebacks, some contained *Gammarus*, and none connected directly to any other pond in the study. Turbidity in these ponds varies naturally, but was low during our trials (below 10 NTU for all ponds). Visual cues were blocked with the use of "feeding stations" with opaque walls that allowed for transmission of olfactory cues.

(i) Procedure

We created "feeding stations" to conceal visual, but not olfactory, cues from prey. Each feeding station consisted of a weighted transparent cylindrical plastic "skeleton" (12 cm diameter, 8 cm height) covered in two layers of fine-mesh material (nylon tights, 40 denier) with two entrance holes (2x2 cm) positioned at opposite sides of the station (Figure 1). The stations were constructed in this way to allow olfactory cues to pass through the sides of the stations freely (pilot experiments in the lab with food dye indicated that cues passed through

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187 the walls). Cue movement is extremely slow in still water (Webster and Weissburg 2009), but
188 movement of fish and the disturbance caused by the experimenter moving the station to count
189 prey enhanced cue dispersal. In each pond, we placed 6 stations close to the edge (10-30 cm,
190 to allow access by the experimenter), approximately 1m apart. Stations were added 2-4 days
191 prior to the first observation day to counter any effects of neophilia or neophobia (Frost et al.
192 2007; Archard and Braithwaite 2011). To reduce disturbance, feeding stations were left in the
193 ponds for the duration of the trials.

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194

195 Figure 1. "Feeding station" after use in field trials. Cotton thread attached at the top assisted
196 in positioning and retrieval of stations and to the right is an entrance hole with "doors" intact
197 to ensure opening was not blocked by straying material. A similar opening is found on the
198 opposite side of the station.
199

200 In each pond, we investigated three levels of prey aggregation (aggregated; 30 prey in
201 one of the 6 feeding stations, semi-dispersed; 10 prey in each of 3 of the 6 stations, and
202 dispersed prey; 5 prey in each of the 6 stations). Aggregated prey were allocated to a feeding
203 station at random and semi-dispersed prey were allocated to alternating feeding stations
204 (starting point chosen at random). The order in which the treatments were placed in each
205 pond was systematically rotated ensuring each possible trial sequence was included at least

once and no more than twice. To minimize any possible effects of learning and reduce disturbance, a minimum of 4 days was left between each trial within a pond. Prey used in these trials were frozen bloodworm sourced from a local pet shop. The bloodworm were defrosted and the refrozen in tap water ice cubes in the prey groups sizes above for ease of handling in the field.

On the day of each trial, the ice cubes containing prey were positioned in their allocated feeding stations. Plain ice cubes (containing no prey) were placed in all other stations to control for the presence of the observer at each station and any cues from the tap water that may have been used by potential predators. After 10, 20, 30, 40, 50, 70 and 90 minutes, the observer returned to the pool and counted the number of uneaten prey in each station. Stations containing no prey were also checked to control for the presence of the observer and the disturbance caused by removing and replacing the feeding station. The timer was stopped when the observer returned to the pool, and restarted when counting was complete (approximately 10 minutes), so that the time while disturbed by researcher was not included in the time available to the fish to forage in the stations. It is likely that the presence of the observer disrupted normal foraging behaviour, so care was taken to ensure that this disruption was equal for all treatment groups and not included in the final data. However, it is likely that detection would be faster than our data suggests due to this disruption. For this reason, we do not presume to make any claims about absolute detection times, but rather relative differences between prey group sizes in this study.

(c) Analysis

All data analysis was carried out in R v 2.13.0 (R Core Team 2013). For the laboratory data, prey within a trial were not independent of one another. To account for this,

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we created multiple events (each predator could encounter multiple prey 'events') models using the Andersen-Gill version of Cox Proportional Hazards models in the package 'survival' (Therneau and Grambsch 2000; Therneau and Lumley 2011). By incorporating 'trial' as a clustering factor in the model, each prey encountered was an event for each individual stickleback.

Our initial model of the laboratory data did not meet the necessary assumption of proportional hazards (Chi-squared=85.6, P<0.001; (Therneau and Grambsch 2000)). When this assumption is violated, it is an indication that the survival curves are not the same shape and do not follow similar hazards distributions (i.e. the risk to a prey individual in one treatment is not a simple multiplication of the risk in another treatment, for any given time point). This is especially problematic when survival curves cross as they do in our case; figure 2 (Therneau and Grambsch 2000). In order to remedy this, we split our data set in two ("initial prey discovery" and "subsequent survival of prey") and analyzed these separately (figure 3). The assumption of proportional hazards was met in the case of initial prey discovery (Chi-squared=3.27, P=0.351). In the case of subsequent prey discovery, the assumption of proportional hazards was not met (Chi-squared=176.4, P<0.001). However, survival curves did not cross (figure 2b), so although predictions based on this model should be treated with caution (Therneau and Grambsch 2000), it does give an indication of whether the survival of prey differed between treatments.

The data from field trials were interval censored, meaning the exact time of each prey being eaten was not known. Times were defined as the start and stop time of the interval in which prey were eaten, and we fitted a non-parametric maximum likelihood estimate (NPMLE) of the survival distribution (Turnbull 1976). Hypothesis testing was performed

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using a non-parametric logrank test, using the packages 'interval' and 'icens' developed for analyzing interval censored data (Fay and Shaw 2010; Gentleman and Vandal 2011).

(d) Ethical statement

As experiments with fish fall outside of the remit of the University of Leeds Ethical Board and no licensed procedures were used, this study was not subject to ethical review. However, laboratory experiments were carried out in accordance with University of Leeds guidelines and in agreement with Home Office licensed technical staff at the animal facility. Similarly, field experiments were carried out in accordance with local laws and regulations. Great care was taken to ensure optimal welfare for all fish involved in this study.

Results

(a) Laboratory experiment – does turbidity affect best aggregation strategy?

The survival curve for aggregated prey in turbid water showed a very different pattern to the survival curve for other treatment groups (figure 2). As the assumption proportional hazards was not met (Chi-squared=85.6, $P<0.001$; see above), this suggests that overall patterns of survival differ significantly as a function of treatment grouping.

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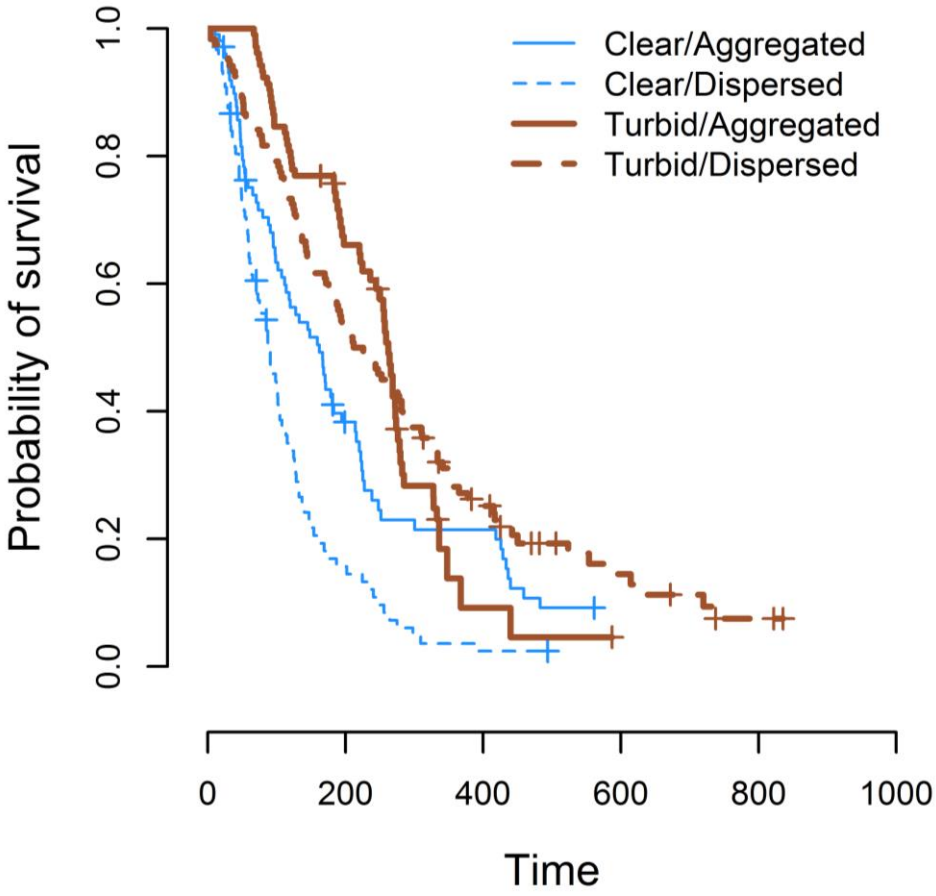

Figure 2. Kaplan-Meier survival curves for the four groups of prey. Crosses signify censored events where the observations for a particular trial ended before all prey were eaten. The curve for aggregated prey in turbid water shows a different pattern to the curves for the other three treatments.

When data of detection of first and subsequent prey are analyzed separately, it is clear that aggregation is beneficial in increasing the time to initial detection in both clear and turbid water, but has a greater effect in turbid water; there was a significant interaction between water clarity and level of aggregation (CoxPH; z=2.24, n=56, P=0.025) on the time until the first prey was discovered (figure 3a). Dispersed prey are discovered more quickly in turbid water than clear water while aggregated prey are discovered more quickly in clear water than turbid water (figure 3a).

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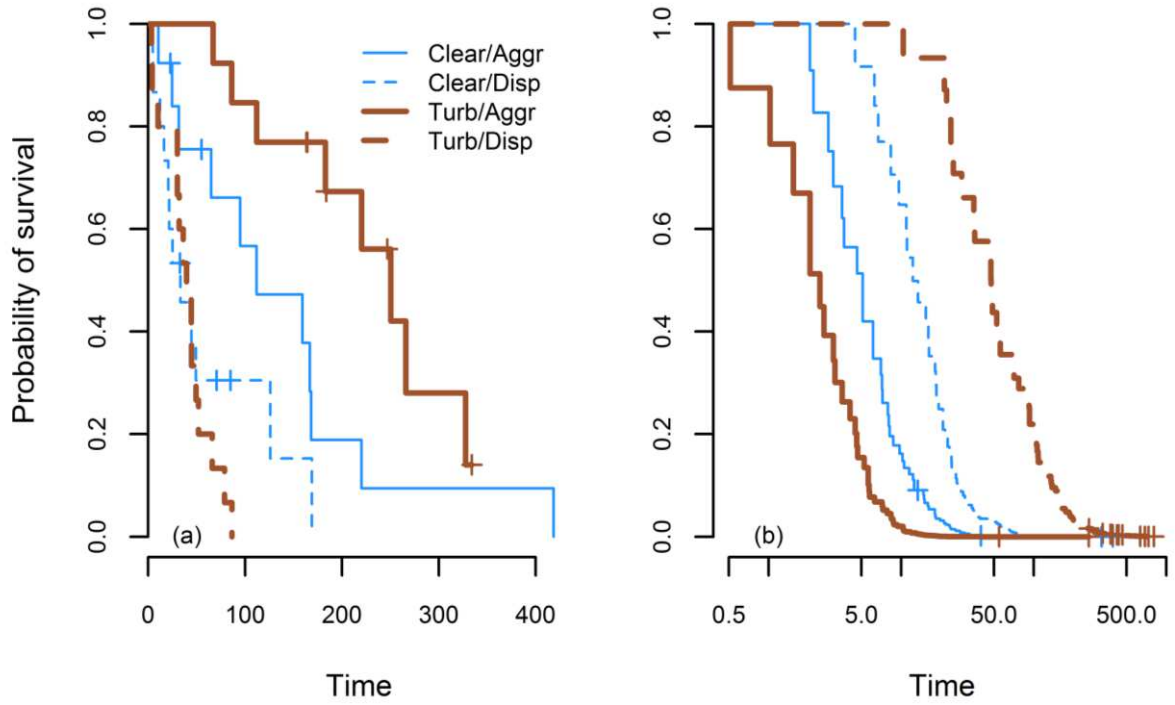

Figure 3. Kaplan-Meier curves for time to discovery of first (a) and subsequent (b) prey. Brown lines represent turbid water and blue lines clear water. Solid lines represent aggregated prey and dashes represent dispersed prey. In (b), the time axis was logged to improve clarity.

For time to consume subsequent prey, there was also a significant interaction between the water clarity and level of aggregation (CoxPH, z=-3.173, n=302, P=0.002). Survival is highest for dispersed prey in turbid water, while aggregated prey survive for longer in clear water than in turbid water (figure 3b). Therefore, after the discovery of the first prey, aggregation appears to be beneficial in clear water (aggregated prey survive longer in clear water than in turbid water), but not in turbid water (where dispersed prey have higher survival).

(b) Field experiment: do prey in a more natural setting benefit from aggregating?

In the field experiment, prey in the three levels of aggregation differed significantly in survival (Asymptotic Logrank k-sample test with Sun's scores, Chi-squared=13.16, P=0.001)

with dispersed prey being discovered and consumed the most quickly and little to no difference between aggregated and semi-dispersed prey (Suns' score statistics: dispersed: 42.17, aggregated: -19.11, semi-dispersed: -23.06).

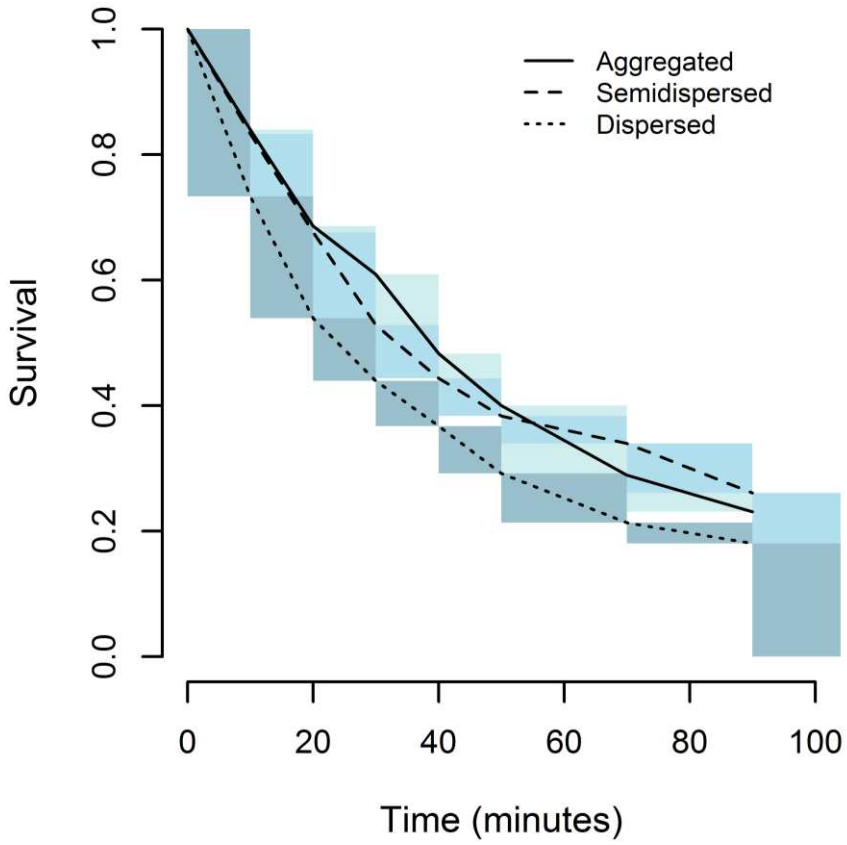

Figure 4. Interval censored survival curves for the field data. Possible stepwise changes in survival lie within the shaded area for each curve. Aggregated: solid line, light shading, semi-dispersed: dashed line, medium shading, dispersed: dotted line, dark shading.

Discussion

The data gathered both in the laboratory and in the field reveal that aggregation as a predator avoidance strategy is effective both for visually conspicuous and concealed prey.

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317 Aggregated prey in the lab, with and without visual cues available to the predator, had
318 improved survival over dispersed prey in terms of initial detection. However, once an
319 aggregation was detected, the prey did not survive for very long. This likely occurred because
320 predators were able to find and consume all the prey in an aggregation after having
321 discovered the first prey, and the dead prey could not take any evasive action in response to
322 the proximity of the predator.
323
324 In the natural pond setting, overall survival of aggregated and semi-dispersed prey
325 was higher than that of dispersed prey. Additionally, the rapid decrease in aggregated prey
326 numbers once discovered in the lab was not observed in the field. This lack of sudden
327 mortality post discovery is likely due to the large number of prey satiating the predator and
328 thereby providing dilution of risk.
329
330 Due to the necessary differences in design between our field and laboratory
331 experiments (see methods), we discuss our results within experimental context rather than
332 making direct comparisons between the field and lab data.
333
334 In the field, we observed that prey reduction in non-aggregated treatments was
335 dispersed between stations, indicating that fish were not clearing out one station and then
336 swimming to the next. The overall poorer survival of dispersed prey compared to semi-
337 dispersed and aggregated prey suggests that aggregation should be an adaptive strategy for
338 species living in water where visual cues are limited or absent as well as where the predator
339 of immediate concern does not use visual cues.
340

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Aggregation as an anti-predator strategy when the predator does not use visual cues is seen in a number of species such as the sediment dwelling *Chironomus riparius* larvae, who aggregate in response to predator presence (Rasmussen and Downing 1988) and stream dwelling caddis flies (*Rhyacophila vao*) that avoid predation by the planarian predator *Polycelis coronata* by communally pupating on the same stone (Wrona and Dixon 1991). Taylor's (1977) study on southern grasshopper mice found that buried aggregated prey were found less easily than dispersed prey. Our data indicate that aggregation can be beneficial to prey in decreasing risk of detection, but also that aggregation is only truly effective if aggregations are large enough to dilute predation risk once discovered if prey are immobile.

There is evidence in our lab results to suggest that the protection provided by aggregating depends partly on the availability of visual cues as well as the perception of risk in the predator. Once discovered, aggregated prey did not survive for long, but those in clear water survived for longer than those in turbid water. Although time to emergence was not affected by turbidity, we suggest that a perceived risk involved in foraging in clear open water (Abrahams and Kattenfeld 1997) decreased foraging effort and allowed aggregated prey to survive longer once discovered in clear water than in turbid water.

In the field, aggregated prey did not experience the accelerated death rate once discovered that they did in the laboratory. There is some indication that benefits to prey depend on size or number of predators (Brock and Riffenburgh 1960) and sticklebacks are able to learn from visual foraging cues from conspecifics (Webster and Laland 2012), resulting in increased discovery if one stickleback in the group starts consuming prey. However darkness or turbid water should reduce the likelihood of this happening, as initial discovery of prey by one predator would not be observed visually by other predators. Lateral

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line detection of the movement of conspecifics (Coombs 1999) is likely to be too short-range to be relevant in this context, however the importance of noises generated by foraging might warrant further exploration. In our experiment, prey as well as any predator feeding on them, were concealed in feeding stations, which may have prevented visual social cues from being transmitted to other sticklebacks in the area. Prey groups were also much larger than in the laboratory, which likely prevented individual sticklebacks from consuming all prey. Together, this may have limited the rapid consumption of prey seen in the laboratory.

The benefits of aggregation are likely to depend on the sensory abilities of the predator and a predator that is unable to detect prey will approach random search efficiency (Cain 1985). However, a predator that is able to detect the presence of prey and perhaps even an indication of the number of prey should perform better than random by increased search effort, especially if that effort can be focused in the general area surrounding prey. Sticklebacks use both visual and olfactory cues in foraging, and when visual cues are not available, the presence of olfactory cues increases foraging efficiency (Johannesen, Dunn, and Morrell 2012). Therefore, strong cue concentrations around aggregated prey could increase search effort, potentially countering the benefit prey derive from aggregating. Similarly, theory on the relationship between olfactory cues and detection of prey groups predicts that grouping should not be favoured as detection radius increases with group size (Treisman 1975). In our study, however, it is clear that aggregation is beneficial to prey, at least at the predator-prey ratios tested here, as our aggregated prey survived for longer than the dispersed prey. There is some evidence to suggest that olfactory detection radius increases with group size (Andersson, Löfstedt, and Hambäck 2013), but it is still not clear how increased detection affects aggregated prey in different systems such as one where only one

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prey item is captured and the rest escape and how predator sensory acuity interacts with prey group sizes.

Aggregations are ubiquitous and part of many important life functions. Understanding detectability and survival of aggregated prey will help us understand the adaptive mechanisms driving distributions of prey organisms and how these interact with predators. Our study provides insight into some adaptive reasons to aggregate in a system that is different from the usual visual predator system. Many natural predators rely on olfactory cues but the consequences of this have been relatively neglected by scientists, likely because of the dominant importance of vision to humans. We demonstrate that aggregations are beneficial to prey avoiding non-specialist olfactory foragers Since predation is a fundamental interaction structuring communities, changes in the relative importance of vision and olfaction in prey detection (due to e.g. eutrophication) could have far reaching implications ecologically. Our work provides a step towards improved ability to predict these effects.

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