

Do fine-scale experiments underestimate predator consumption rates?

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Abstract

1. Understanding ecological processes across spatial scales helps link observations and predictions from experiments to ecological patterns occurring at coarser scales relevant to management and conservation.
2. Using fish, we experimentally manipulated the size of arenas to test the spatial scaling of predator–prey interactions.
3. We measured variation in predator consumption and prey behaviour (prey aggregation, spatial overlap with predators and movement) across arena sizes. Variation in prey behaviour across arena sizes was hypothesized to drive consumption patterns by altering prey vigilance and encounter rates with predators.
4. Per capita consumption and movement were highest in the largest arena relative to the smallest and we observed a mismatch between where bass were present and the highest densities of prey across all arena sizes. We hypothesize more movement in largest arenas increased encounter rates and drove the observed increase in consumption with increasing arena size.
5. Consumption estimates obtained in experimental studies may underestimate consumption, but understanding the mechanisms driving bias across scales helps predict the outcomes of predator–prey interactions in natural systems.

KEYWORDS

arena size, mesocosm, predator–prey interactions, prey aggregation, prey vigilance, scale transitions, spatial scale, stream fishes

1 | INTRODUCTION

Understanding ecological phenomena across spatial scales is necessary to make management and conservation decisions (Fausch et al., 2002), and important ecological processes often occur at broad, landscape scales (Dunning et al., 1992). Predator–prey interactions are typically characterized in laboratories or other fine-scale studies but using fine-scale observations to predict processes at broader spatial scales may be difficult due to scaling effects (Englund & Cooper, 2003; Levin, 1992; Wiens, 1989). Different processes drive predator and prey densities across space and time, with classic functional response relationships predicting predator–prey dynamics

only at the finest spatial and temporal scales (Hunsicker et al., 2011). Phenomena measured at greater temporal or spatial scales can be more variable because both fine- and broad-scale effects are at play (Levin, 1992). Thus, scaling up observations from experimental and fine-scale predator–prey studies requires transition corrections to account for scale-dependent variability (Bergström et al., 2006; Chesson, 1998; Englund & Leonardsson, 2008). A large body of theoretical work accounting for variability across spatial scales includes methods such as partitioning and calibration (Rastetter et al., 1992) or moment approximation (Bergström et al., 2006). Although theoretical and computational methods provide scaling frameworks, we still need empirical measures of predator–prey responses across

spatial scales to accurately account for scale transitions in ecological models.

Quantifying scale transitions requires measuring ecological responses across scales and identifying mechanisms driving those transitions. Empirical and theoretical work suggests predator–prey scaling effects are often (but not always) driven by spatial covariance or movement dynamics (i.e. exchange dynamics) of predators and prey (Ahrens et al., 2012; Englund, 1997, 2005; Englund & Cooper, 2003), both of which influence the likelihood of interactions. For example, at relatively coarse spatial extents (3–300 km), bird predator and fish prey distributions are hierarchically structured into patches and overlap between predators and prey increases with spatial scale (Fauchald et al., 2000). Similarly, stream benthic invertebrate densities can vary in response to scale-dependent emigration into patches in response to fish predators (Englund, 2005). However, previous studies investigating scale-dependent predator–prey dynamics were conducted only at very fine scales ($<1\text{ m}^2$) and focus on invertebrate prey (Bergström & Englund, 2002; Englund, 2005; Luckinbill, 1974; Uiterwaal et al., 2019). This body of work suggests functional responses of invertebrate predator–prey systems vary with the size of experimental arena, with higher mortality rates in larger arenas (Bergström & Englund, 2002, 2004; Uiterwaal et al., 2019). Increased consumption rates with increasing arena size were driven by higher attack rates on aggregated prey (Bergström & Englund, 2002). In these studies, aggregative behaviour was considered an artefact of confinement; both predators and prey preferred perimeters of arenas, biasing estimates of consumption rates (Bergström & Englund, 2002, 2004; Uiterwaal et al., 2019). These experimental studies highlight that prey aggregation and movement influence the overlap of predators and prey in space and time, influencing observed functional responses.

Previous research with invertebrate prey suggests increasing arena size biases estimates of consumption due to increased prey aggregation, but many taxa might aggregate as an anti-predator defence mechanism (Blumstein & Daniel, 2003; Magurran, 1990; Pulliam, 1973; Vine, 1971). Aggregation can be beneficial if it decreases encounter rates (Ioannou et al., 2011) or increases group vigilance (Lima, 1995). In species that naturally aggregate regardless of spatial scale, variation in consumption rates across scales may be lower. Furthermore, the spatial arrangement or shape of arenas in which predators and prey interact may influence scaling effects (Dickie et al., 2017; McKenzie et al., 2012). Most research investigating scaling effects of predator–prey interactions has taken place in relatively open arenas (Bergström & Englund, 2002; Englund, 2005; Luckinbill, 1974; Uiterwaal et al., 2019). The interaction between prey movements, aggregative behaviour and scale might differ in linear or dendritic systems because movement is confined to corridors. For example, simulation models suggest encounter rates between wolves and their prey increases in linear systems (McKenzie et al., 2012) and movement rates of wolves are higher along linear features (Dickie et al., 2017). In dendritic river networks, predators can interact with abiotic factors and prey traits to influence prey movement through the network (Gilliam & Fraser, 2001; Power et al., 1985), and landscape

features such as waterfalls can act as barriers to predator movement, creating refuge for prey (Cathcart et al., 2018; Covich et al., 2009). Scaling effects on prey movement and spatial distributions (and overlap with predators) may therefore be context-dependent across taxa and spatial arrangement of arenas.

1.1 | Objectives

We conducted an experiment using stream mesocosms to quantify how predator consumption rates and several metrics of prey behaviour including movement, aggregation and spatial overlap with predators vary across spatial scales (arena sizes). We chose these prey behaviours because they are related to encounter rates between predators and prey (Christensen & Persson, 1993; Englund & Olsson, 1996; Hatle et al., 2001) and prey vigilance, which can influence whether or not an attack by a predator is successful (FitzGibbon, 1989; Krause & Godin, 1996). We measured responses for fish prey in the absence of predators and to both consumptive and non-consumptive effects of a predator, *Micropterus salmoides* (Largemouth Bass, hereafter referred to as bass). Contrary to previous studies investigating invertebrate prey, we predicted consumption rates would decrease with arena size, driven by lower encounter rates with increased arena size. We predicted prey would spread out in larger arenas, driving lower spatial overlap between predators and prey and therefore lower encounter rates. Understanding how consumption rates, movement, aggregation and spatial overlap between predators and prey vary with spatial scale may help inform scale transition corrections to apply ecological models to broader spatial scales relevant to real-world applications.

2 | MATERIALS AND METHODS

2.1 | Mesocosm design

This experiment was conducted at Konza Prairie Biological Station using outdoor mesocosms consisting of alternating riffle ($1.83 \times 0.46\text{ m}$) and pool (1.83 m diameter, 0.90 m tall) habitats (see Matthews et al., 2006 for complete description), with each riffle–pool unit holding 1,450 L of water. Although shallow riffles can act as movement barriers to fishes (Schaefer, 2001), these riffles were deep enough (0.38 m) for both predators and prey to move freely among all habitats. Arena size was manipulated using a combination of two, four and six riffle–pool configurations (Figure 1). Mesocosms were continuously supplied with local spring water and filled with rocky substrate (mean diameter 25 mm). Both the continuous replenishment of spring water and a 60% shade canopy cover served to keep water temperatures relatively consistent over the course of summer (mean temperatures around 22°C). A trolling motor recirculated water within each mesocosm unit through a large polyvinyl chloride pipe from the downstream pool to the upstream riffle, creating directional flow. After filling, all mesocosms matured for 2 weeks before

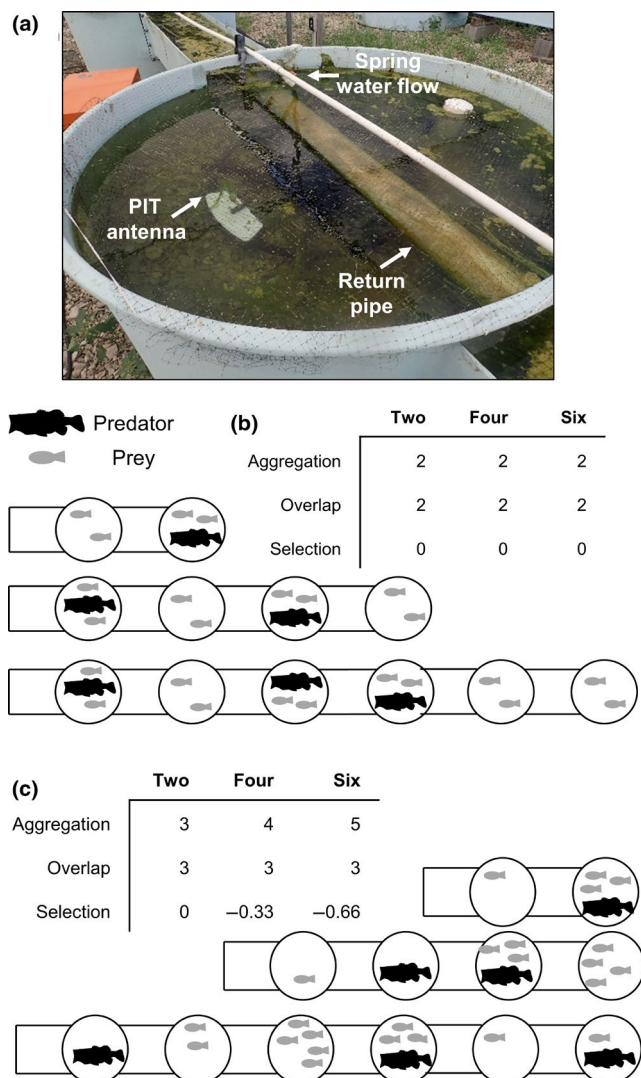


FIGURE 1 Schematic of experimental mesocosms and the calculation of several behaviour metrics. Submersible PIT antennas were placed under the return pipe in the centre of each pool (a). The aggregation, overlap and selection metrics retained the same value across arena sizes if the same number of predators and prey were in each pool (b). Although arena-wide densities were held constant, the number of individual fish detected within an individual pool could be highest in the six unit arena, leading to different levels of aggregation and selection across arena sizes, even if overlap remained consistent (c)

beginning any experiments to allow algae and macroinvertebrates to naturally colonize the mesocosms and provide food for prey fish during the experiment (Matthews et al., 2006). Numerous odonates and dipterans were consistently observed in mesocosms over the course of the experiment.

2.2 | Fish collection and stocking

Cyprinella lutrensis (Red Shiner) and *Pimephales notatus* (Bluntnose Minnow) were collected by seining (straight seine, 4.6 × 1.8 m, 3.2-mm

mesh) several local streams and ponds and used as prey. Largemouth Bass were not observed while collecting prey, but other predators (e.g. Yellow Bullhead, Green Sunfish) are common in the area and were likely present. The two prey species are common and abundant in streams in the study area and represent two different feeding/habitat guilds. Specifically, *C. lutrensis* are found in riffles and pools where they feed on a variety of foods throughout the water column (Gido & Matthews, 2001; Hale, 1963) while *P. notatus* tend to occupy habitats closer to shore (Etnier & Starnes, 1993; Moyle, 1973), and feed in the benthos (Keast & Webb, 1966; Moyle, 1973). While these species exhibit different preferences in habitat and behaviour in natural systems, we acknowledge these differences may be less apparent in the experimental setting. Individuals of each prey species were similar in length (*P. notatus*: 45–80 mm, *C. lutrensis*: 45–72 mm) and combined density was held constant at 6.7 fish/m² (20 fish per pool) across all arena sizes. This total density was chosen because it is within the range of fish densities commonly observed in the study area (Bruckerhoff, unpublished data). Any dead fish observed during the experiment were replaced to keep densities constant, except during consumption treatments.

We chose bass as predators for this experiment because they are known to influence prey behaviour and exert trophic cascades in streams (Power et al., 1985), share an evolutionary history with prey and are important due to their introductions into watersheds globally (Welcomme, 1988). All bass in the experiment were collected from a local pond, were similar in length (mean total length = 286 mm, SD = 22 mm) and stocked at the same density across arena sizes (0.17 fish/m², 1 bass per 2 pools). To minimize the effects of gut fullness in trials, we collected bass using angling to capture presumably hungry fish and did not feed them for 3 days before introduction into experiments.

2.3 | Fish identification and behaviour

All fish were marked with passive integrated transponder (PIT) tags (8 mm × 1.44 mm; Biomark Inc., Boise, Idaho) to track individual movements. Small PIT tags were necessary to maximize survival and tag retention in prey fish (Pennock, 2017; Pennock et al., 2016). Fish were anesthetized in a 100 mg/L concentration of buffered tricaine methanesulfonate (MS-222), and PIT tags were inserted following puncture of the peritoneal cavity with the tip of a sterilized hypodermic needle (Pennock, 2017). Based on previously measured tag retention rates for small-bodied minnows, we only included prey fish larger than 45 mm total length (Pennock, 2017; Pennock et al., 2016). Prey fish and bass were tagged 1 day after collection and kept in holding tanks for at least 2 days after tagging to ensure fish survived tagging and retained tags prior to introduction into the experiment. Bass were therefore collected, tagged the following day, held for 2 days, and then introduced into experiments and were not fed at all before introduction into experiments. Prey fish were sometimes held longer than 2 days with tags if they were collected more than 3 days before experiments began due to logistical constraints

of collecting enough fish for the experiments. Tag retention was above 95% for all species and non-consumptive mortality was <2% across all replicates.

Antenna receivers that detect PIT tags were placed in each pool habitat (Figure 1). Antennas were not placed in riffles due to size constraints. Antennas recorded detections of individual PIT tags at 1-min intervals, meaning once a tag was detected at an antenna it would not be recorded again for at least 1 min. Tag collision (interference driven by multiple tags being within range) was possible, so detections of fish within a single pool may be underestimated. However, we considered effects of tag collision minimal because effects should be similar across all treatments and trials. Two types of antennas were used: square (1 × 1 m) antennas monitored by a multiplexing reading station (QuBE-IS1001, Biomark) and circular (1 m diameter) submersible antennas (Biomark). Preliminary data indicated detection rates were similar between the two antenna types, and we used both antenna types in pools across arena sizes and trials.

2.4 | Experimental design and schedule

Prey behaviour data were collected for the three arena sizes across three experimental treatments: without predators, predators present and predators consuming. These three treatments allowed us to compare prey responses when no predators were present, to predators with no changes in prey density (predators present) and to predators with small changes in prey density (predators consuming), as we did not restock prey fish after they were consumed. In treatments with predators present, but no consumption, a sterilized surgical needle was used to quickly pierce the non-vascularized tissue on the lower jaw of bass below the dentary bone and on the upper jaw between the maxilla and premaxilla bones. A sterilized cable tie (width = 1.8 mm) was then quickly inserted and secured (Clark & Shaefer, 2016; Knight & Gido, 2005). Cable ties were kept loose so bass were still able to open their mouths and to avoid disrupting respiration. Bass were quickly returned to mesocosms to minimize time out of the water during this procedure. Prey were introduced into mesocosms during the morning of the first day of each trial, 48 hr before predators with secured mouths were introduced ('no predators' treatment). Behaviour of prey in the presence of predators was then recorded for 48 hr ('predators present' treatment), followed by recapture of bass from mesocosms using dip nets. Cable ties were cut, and predators were reintroduced into mesocosms for 24 hr ('predators consuming' treatment). The same individual predators were used in both treatments within a trial based on preliminary data suggesting bass still feed after having mouths secured for 48 hr and to minimize the number of fish needed for the study. Despite bass still feeding after removing the cable tie, we acknowledge the behaviour of bass may have differed between the predators present and predators consuming treatments, so we examined the interactive effects of treatment and arena size (see *Analysis*). We only allowed predators to feed for 24 hr to avoid arena wide density-dependent effects on consumption and based on preliminary data indicating bass would

digest and pass prey PIT tags in time periods longer than 24 hr. At the end of each trial, we removed and euthanized bass and surveyed their full digestive tract for prey PIT tags. Each 'trial' included all three treatments (no predators, predators present and predators consuming) taking place sequentially within a mesocosm arena. We ran additional consumption replicates immediately following completion of a trial. Prey fish were restocked to pre-consumption densities and new bass were introduced for additional consumption replicates. Due to limited antenna battery life, prey behaviour was not tracked during additional consumption replicates.

2.5 | Behaviour metrics

We calculated each behaviour metric (except movement) over several time intervals within each replicate period. Ultimately, we used 8-min time intervals to maximize the number of detections and minimize the number of individuals that switched pools that would be thrown out for analysis (see Appendix S1). Using the 8-min interval, we only removed 10% of individual detections of fish that switched pools across all time intervals and replicates. For all behaviour metrics, we only included observations between 4:30 p.m. and 7:30 a.m. to capture predicted peak activity time of predators (dawn, night and dusk) and to avoid any bias due to researcher activity during the day (predator and prey introductions and cable tie removal occurred during hours omitted from analyses). Even though treatments with no predators and those in which predators were not able to consume prey were run for 48 hr, we removed the first 24 hr of observation to avoid bias during acclimation to mesocosms. Each replicate therefore included 112 intervals (8 min) across the 15-hr replicate period.

2.6 | Movement

To compare movement patterns across arena sizes and treatments, we calculated the number of times individual prey fish switched pools for the entire treatment period (15 hr) because movement at smaller time-scales was small.

2.7 | Aggregation

We used the maximum (max) number of conspecifics (prey of same species) detected in a pool as an index of aggregation. We counted the number of unique fish within each pool for every 8-min interval of each replicate, but dropped any fish that were detected in more than one pool during a time interval. The aggregation metric was then defined as the max number of conspecifics observed in a single pool in each 8-min interval (Figure 1). Higher values of the max number of conspecifics represented more aggregation. This aggregation metric was therefore the same across all arena sizes if the same max number of fish were observed, but the six-unit arena had

the potential for more aggregation since there were more individual fish present (Figure 1).

2.8 | Overlap

We calculated the max number of individuals sharing a pool with a bass for each 8 min interval for each prey species. Similar to the aggregation metric, we removed any fish that were detected in more than one pool in any 8-min interval and this metric was the same across arena sizes if the same max number of fish were detected in a pool with a bass (Figure 1).

2.9 | Selection

We were interested in comparing the number of prey detected in a pool with a bass relative to aggregation of prey. We defined a selection index as:

$$\text{Selection index} = 1 - \frac{\text{max number of prey observed in any pool}}{\text{max number of prey observed in a pool with a bass}} \quad (1).$$

A value of 0 would represent bass occupying the pool with the max observed abundance of prey fish, whereas negative values represent bass occupying pools with less prey fish than the max observed. We called this a 'selection' index, as it captures either (although we cannot determine which) bass selecting pools with higher (closer to 0) or lower (negative values) abundances of prey, or prey aggregating in pools with (closer to 0) or without bass (negative). This index was calculated for each prey species.

2.10 | Analyses

From June to August 2019, we ran four trials including all treatments within each arena size for prey behaviour metrics. One antenna malfunctioned in the middle of a six-unit prey behaviour trial so that trial was dropped from prey behaviour analyses. Three additional consumption replicates were conducted per arena size. We therefore had a total sample size of 33 for behaviour metrics (3 arena sizes $\times$ 3 treatments $\times$ 4 replicates [3 for six-unit arena]) and 21 for the consumption trials (3 arena sizes $\times$ 7 replicates). Due to low power associated with small sample sizes in this study, we interpreted differences between levels of factors using Cohen's *d* standardized measure of effect size (Cohen, 1988). We considered differences between any two levels of factors strong enough to interpret if 95% confidence intervals did not overlap with zero and if Cohen's *d* values were at least 0.2 (Cohen, 1988). We removed all prey fish that were consumed, died or lost tags from the analyses of prey behaviour because we do not know at what time these fish were lost from the experiment. All analyses were performed in Program R version 3.6.1 (R Core Team, 2019).

2.11 | Consumption

We calculated both overall differences in per capita consumption across arena sizes and differences in prey composition in diets of bass across arena sizes. Per capita consumption was calculated as the total number of prey eaten divided by the number of predators within each replicate ($n = 21$) for the entire time period. To test for differences in per capita consumption across arena sizes, we used a one-way ANOVA. We checked model assumptions with residual plots, which appeared to be reasonably met. We calculated Cohen's *d* standardized effect size for contrasts between arena sizes using the *EMMEANS* package (Length, 2020).

To compare composition of the two prey species in diets across arena sizes, we built a multivariate generalized linear model using the *manyglm* function from the package *MVABUND* (Wang et al., 2012). With this function, we developed generalized linear models for counts of each prey species in individual bass diets across arena sizes. The function provides a global estimate of significance ($\alpha = 0.10$), as well as significance of factors for each prey species independently while controlling for multiple testing (Wang et al., 2012). We used a negative binomial distribution for the *manyglm* model due to the large number of zero occurrences in diets (30% of stomachs were empty across all trials). Because replicates in this analysis were individual predators ($n = 42$), we included the number of bass in each arena as a fixed effect to control for unequal sample sizes.

2.12 | Behaviour metrics

The effect of arena size, treatment, and the additive and interactive effects of these variables on behaviour metrics were assessed using generalized linear mixed-effect models with the *LME4* package (Bates et al., 2015). We included a random effect of time period to control for the multiple 8-min time periods used to calculate the aggregation, overlap and selection indices. This random effect also allowed us to control for different levels of activity and therefore detection, at different times of day. Because movement was calculated across the entire time period, we included a random effect of individual to account for pseudo-replication within each replicate instead of taking the mean number of movements across all individuals so we could include the full range of interspecific variability in movement. Separate models were developed for each behaviour metric. Because aggregation, overlap and movement metrics were based on counts, errors were modelled using a Poisson distribution and models included a log link function while the selection metric was modelled using a Gaussian distribution. We used likelihood ratio tests with the *CAR* package (Fox & Weisberg, 2019) to compare nested models, including an intercept only model. As described above, we used Cohen's *d* to compare effects across levels of treatments and arena sizes depending on results from likelihood ratio tests.

3 | RESULTS

3.1 | Consumption

Per capita consumption was higher in the largest arena relative to the smallest (Figure 2; $F_{2,17} = 2.98$, $d = -1.36$, $CI = -2.63$ to -0.09). Although overall consumption varied across arena sizes, there was no difference in composition of prey consumed across arena sizes (likelihood ratio = 1.29, $p = 0.61$). The number of predators in the arena also did not significantly influence the composition of prey consumed (likelihood ratio = 3.74, $p = 0.18$).

3.2 | Movement

The interactive effects of treatment and arena size were included in the top models predicting the number of movements made by individual fish for both species (Table 1). Fish moved more when there were no predators present relative to when predators were present or consuming (Figure 3). The magnitude of differences varied across treatments and arena sizes, but fish made more movements in the four- and six-pool units relative to the two-pool unit (Table S2; Figure 3), with the largest differences occurring between the two- and six-pool units for *P. notatus* during the predators present treatment ($d = -1.51$, $CI = -1.76$ to -1.27) and between the

two- and four-pool units when predators were consuming for *C. lutrensis* ($d = -1.45$, $CI = -1.79$ to -1.10).

3.3 | Aggregation

Likelihood ratio tests indicated the top model predicting the max number of fish in a pool within an 8-min time interval included both additive and interactive effects of arena size and treatment for both *C. lutrensis* and *P. notatus* (Table 1), but patterns of aggregation across arena sizes differed between the two species. Aggregation of *C. lutrensis* did not differ across arena sizes, except for when there were no predators in the mesocosms (Figure 4a; Table S2). In the no predators treatment, aggregation differed between all three arena sizes, with the largest differences between the two- and four-pool units ($d = 0.54$, $CI = -0.63$ to -0.45). For *P. notatus*, aggregation was the highest in the six-pool unit relative to smaller units (Figure 4b; Table S2), with the largest effect of arena size occurring in the predators present treatment ($d = 0.58$, $CI = -0.71$ to -0.44). Across all treatments and arena sizes, our models predicted more than three *P. notatus* in a pool within a time interval, while <3 *C. lutrensis* were predicted to occur in a pool together, except in the no predators treatment (Figure 4).

3.4 | Overlap

The top model for the max number of prey observed in a pool with a bass included only the effect of arena size for *C. lutrensis* and the interactive effects between arena size and treatment for *P. notatus* (Table 1). The smallest arena had more overlap between *C. lutrensis* and bass (Figure 5a) relative to both the four-pool unit ($d = 0.42$, $CI = 0.10$ – 0.75) and the six-pool unit ($d = 0.41$, $CI = 0.07$ – 0.76). There was no clear pattern between arena size, treatment and overlap between *P. notatus* and bass (Figure 5b; Table S2). Overlap with *P. notatus* was higher in the six-pool unit relative to the smallest arena when bass were present ($d = -0.54$, $CI = -0.78$ to -0.30), but the opposite pattern was observed when bass were consuming ($d = 0.41$, $CI = 0.15$ – 0.67).

3.5 | Selection

The additive effects of arena size and treatment were included in the top models for both *C. lutrensis* and *P. notatus*. However, there were no strong differences in the selection index for *C. lutrensis* across arena sizes and treatments (Table S2; Figure 6). The selection index for *P. notatus* also did not differ strongly between treatments (Figure 6a; Table S2), but was lower in the largest arena relative to both the two- ($d = 0.50$, $CI = 0.13$ – 0.87)

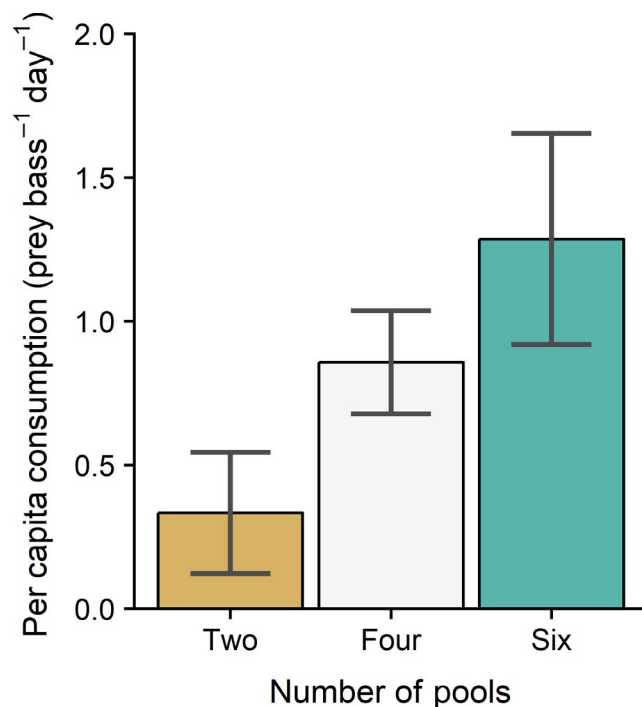


FIGURE 2 Mean per capita consumption by largemouth bass of *Cyprinella lutrensis* and *Pimephales notatus* was higher in arenas with six pools and riffles relative to arenas with only two pools and riffles. Error bars represent standard error around mean per capita consumption rates across arena sizes

TABLE 1 Various model structures for consumption and behaviour response variables were compared using likelihood ratio tests. Bold models represent top models used to interpret contrasts and effect sizes between levels of different factors. Colons represent interactions among factors while (1|factors) represent random intercepts

Species	Metric	Model	Log-likelihood	df	Likelihood ratio	p value
<i>Cyprinella lutrensis</i>	Movement	~1 + (1 individual)	-5,931.4	2		
		~arena size + (1 individual)	-5,778.6	4	305.65	<0.01
		~arena size + treatment + (1 individual)	-3,745.3	6	4,066.57	<0.01
		~arena size + treatment + arena size:treatment + (1 individual)	-3,728	10	34.62	<0.01
<i>Pimephales notatus</i>	Movement	~1 + (1 individual)	-6,081.1	2		
		~arena size + (1 individual)	-5,852.9	4	456.40	<0.01
		~arena size + treatment + (1 individual)	-4,919.5	6	1866.84	<0.01
		~arena size + treatment + arena size:treatment + (1 individual)	-4,880.5	10	77.996	<0.01
<i>Cyprinella lutrensis</i>	Aggregation	~1 + (1 time)	-5,571	2		
		~arena size + (1 time)	-5,526	4	90.08	<0.01
		~arena size + treatment + (1 time)	-5,436.6	6	178.82	<0.01
		~arena size + treatment + arena size:treatment + (1 time)	-5,393.3	10	86.59	<0.01
<i>Pimephales notatus</i>	Aggregation	~1 + (1 time)	-9,763	3		
		~arena size + (1 time)	-9,720.1	5	85.74	<0.01
		~arena size + treatment + (1 time)	-9,703.7	7	32.98	<0.01
		~arena size + treatment + arena size:treatment + (1 time)	-9,692	11	23.34	<0.01
<i>Cyprinella lutrensis</i>	Overlap	~1 + (1 time)	-223.98	2		
		~arena size + (1 time)	-220.4	4	7.17	0.03
		~arena size + treatment + (1 time)	-220.03	5	0.74	0.39
		~arena size + treatment + arena size:treatment + (1 time)	-219.53	7	1.00	0.61
<i>Pimephales notatus</i>	Overlap	~1 + (1 time)	-768.38	2		
		~arena size + (1 time)	-751.66	4	33.45	<0.01
		~arena size + treatment + (1 time)	-748.27	5	6.79	0.01
		~arena size + treatment + arena size:treatment + (1 time)	-743.97	7	8.60	0.02
<i>Cyprinella lutrensis</i>	Selection	~1 + (1 time)	-22.27	3		
		~arena size + (1 time)	-24.46	5	4.39	0.11
		~arena size + treatment + (1 time)	-26.04	6	3.16	0.08
		~arena size + treatment + arena size:treatment + (1 time)	-27.29	8	2.49	0.29
<i>Pimephales notatus</i>	Selection	~1 + (1 time)	-113.28	3		
		~arena size + (1 time)	-109.11	5	8.35	0.02
		~arena size + treatment + (1 time)	-110.75	6	3.27	0.07
		~arena size + treatment + arena size:treatment + (1 time)	-110.99	8	0.4	0.79

and the four-pool units ($d = 0.42$, $CI = 0.18$ – 0.67 ; Figure 6b). Estimated selection indices were negative for all combinations of treatments and arena sizes, indicating the max abundance of prey fish was not typically observed in a pool containing a bass (Figure 6).

4 | DISCUSSION

Contrary to our prediction, we observed increased per capita consumption with increasing arena size. While this pattern is documented in previous work (Bergström & Englund, 2002, 2004; Copper

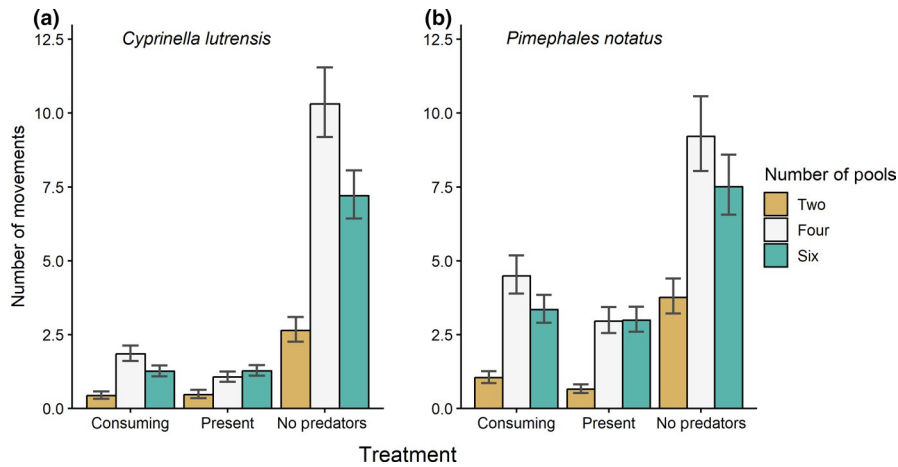


FIGURE 3 The total number of movements made by *Cyprinella lutrensis* (a) and *Pimephales notatus* (b) varied in response to both arena size and treatment, with the lowest levels of movement in the smallest arenas when predators were present or consuming. Error bars represent 90% confidence intervals of predicted number of movements made by individual fish derived from generalized linear mixed-effect models

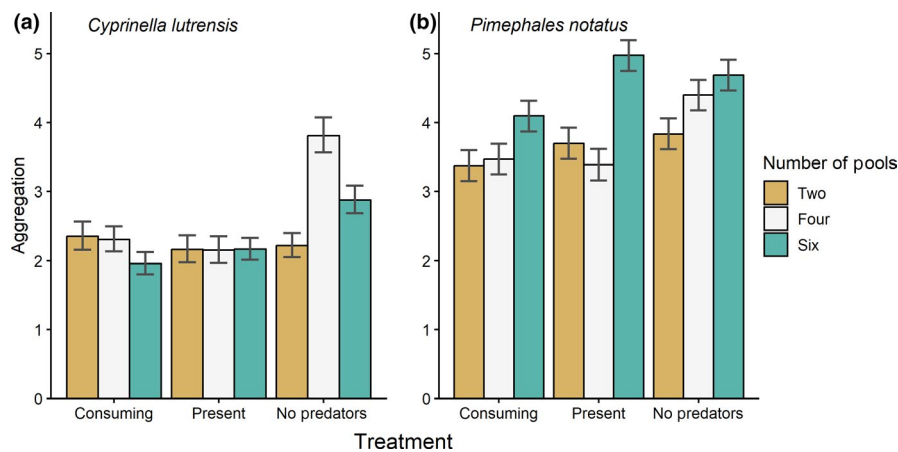


FIGURE 4 Aggregation was defined as the max number of fish observed in any pool within an 8-min time interval. Aggregation of *Cyprinella lutrensis* (a) was highest in the four-pool unit when there were no predators present and overall was low relative to *Pimephales notatus* (b), which aggregated more in larger arenas relative to smaller arenas. Error bars represent 90% confidence intervals of predicted max number of fish in a pool derived from a generalized linear mixed-effect models

& Goldman, 1982; Kaiser, 1983; Uiterwaal et al., 2019), these studies attributed this pattern to increased encounter rates between predators and prey driven by overlap along arena walls. We hypothesize the increased consumption observed in this study was also related to encounter rates but driven by prey movement instead of overlap between predators and prey and suggest prey behaviour data support this hypothesis. Collectively, our work and others indicate predation rates are likely underestimated when measured at fine spatial scales, but the mechanisms driving this pattern may vary.

We observed robust patterns of consumption and behaviour across arena sizes despite several potential sources of bias in our experiment. We quantified our metrics based on detections at PIT antennas placed only in pool habitats, so we were unable to detect fish in riffles. This limited the number of total detections, especially during treatments including bass because movement and activity levels were low. However, we had the same number of riffles relative to pools across all arena sizes, so effects of movement into and out of riffles were considered consistent across arena sizes. Time of day is also likely an important driver of predator and prey activity levels

and behaviour (Fraser & Cerri, 1982; Pennock et al., 2018). Pooling observations across the 15-hr overnight period for the movement metric captured peak activity times, but likely introduced variation into this metric. Similarly, choosing smaller time periods to assess other behaviour metrics may have similarly introduced variation. We also did not measure the distribution of food resources, which can influence prey distributions (McMahon & Matter, 2006). In previous studies, there were minimal differences in algae or macroinvertebrate biomass among connected pools in this experimental system (Martin et al., 2016), so we assume this effect was negligible. Finally, we did not explore patterns of consumption across both arena sizes and densities to explore how the functional response (Holling, 1959) varied across arena size. Previous studies of invertebrate predator-prey systems document arena sizes exclusively influencing consumption at low prey densities (Uiterwaal & DeLong, 2018, 2020; Uiterwaal et al., 2017) due to the relative importance of pre-capture (e.g. search time) versus post-capture (e.g. handling time) processes as densities of prey change, with post-capture processes becoming more important with higher prey densities. Based on this previous

FIGURE 5 Spatial overlap, the max abundance of fish observed in a pool with a bass in an 8-min time interval, varied across arena size for *Cyprinella lutrensis* (a) and interactively across treatment and arena size for *Pimephales notatus* (b). Error bars represent 90% confidence intervals of predicted number of fish in a pool with a bass derived from generalized linear mixed-effect models

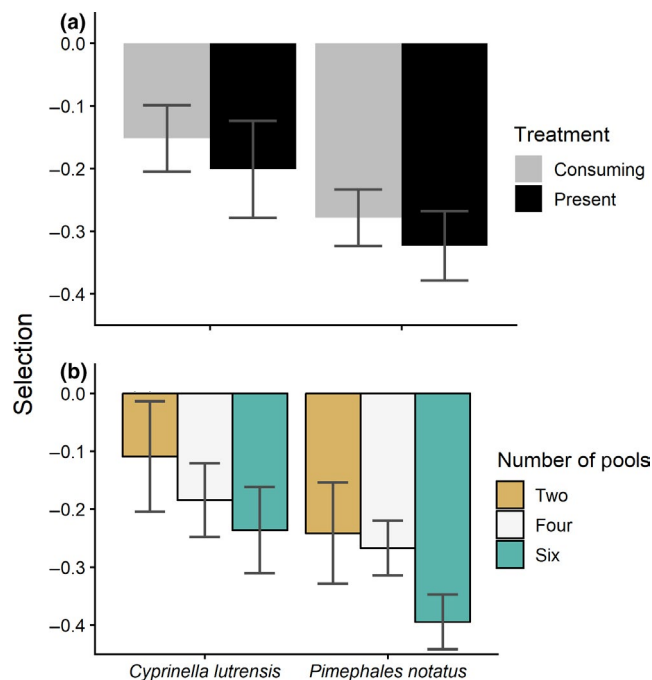
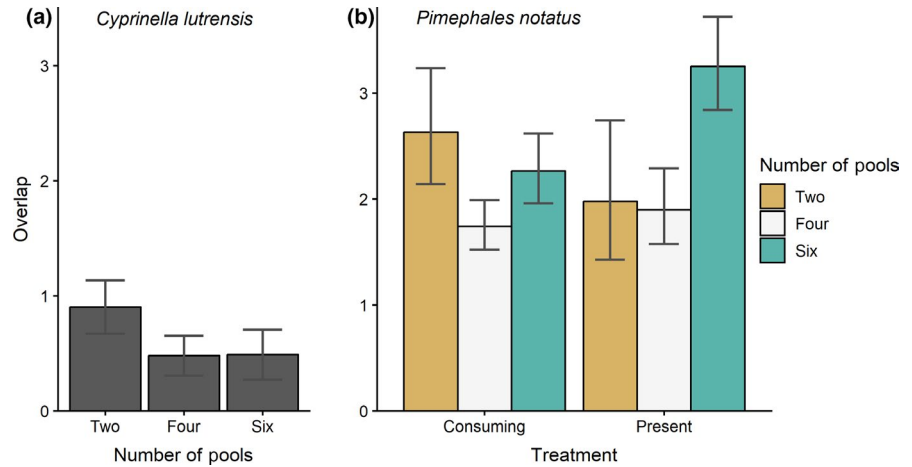


FIGURE 6 The selection index represents differences between the max abundance of fish observed in any pool relative to the max number of fish observed in a pool in a bass, with negative values indicating less fish observed with bass relative to observed in pools without bass. Additive effects of treatment and arena size influence the selection index of both *Cyprinella lutrensis* (a) and *Pimephales notatus* (b). The magnitude of differences between both treatment and arena size was negligible for *Cyprinella lutrensis*, while the selection index for *Pimephales notatus* was lower in large arenas relative to small arenas. Error bars represent 90% confidence intervals of predicted selection index derived from linear mixed-effect models

work, we might assume the prey densities used in the current study were low enough to see the effect of arena size, but further experiments are needed to know how generalizable functional response variation in response to arena size is across taxa and systems.

The presence of predators (both actively consuming and not consuming) greatly reduced movement of prey, but movement also increased with arena size. The effect of predators on prey movement is not surprising, as predators can have strong non-consumptive effects on prey (Lima, 1998; Peckarsky et al., 2008; Sih & Wooster, 1994). Reducing movement or activity levels can be an effective defence against predation because more movement is often associated with higher encounter rates, and therefore consumption rates of predators (Christensen & Persson, 1993; Englund & Olsson, 1996; Hatle et al., 2001), so reduced movement is likely associated with individual prey vigilance. Variation in individual prey vigilance is driven by changes in prey perception of predation threat (Brown, 1999) and may vary spatially in response to habitat heterogeneity, creating a 'landscape of fear' (Laundre et al., 2010). We observed the lowest number of movements of both prey species in the smallest arena when predators were present. It is possible that prey fishes perceived a higher threat of predation in smaller arenas and therefore moved less. If this is true, some individuals may have been more likely to participate in exploratory movements between pools if the perceived threat of predation was lower in larger arenas. It is also possible that more movements between pools in larger arenas were driven by more pools for fish to move between (driven by spatial factors, not predation threat). Regardless of the cause for increased activity, more movement in larger arenas corresponded with more consumption by bass.

Prey aggregation increased with arena size for one species, but overlap between predators and prey did not show a clear relationship with arena size for either species, leading to a mismatch between where bass were located and the highest densities of prey. Negative values of the selection index across arena sizes indicated prey were more aggregated in pools without bass, and lower values in larger arenas for *P. notatus* indicated this mismatch was more pronounced in the largest arena for this species. Other studies document increases in aggregation with increased arena size (Bergström & Englund, 2002, 2004; Uiterwaal et al., 2019). The outcome of aggregation observed in our study differs from these previous studies, which attributed increased prey aggregation with arena size to

changes in perimeter to area ratios because predators and prey preferred edge habitat. This preference of edge habitat (positive thigmotaxis, Fraenkel & Gunn, 1961) resulted in increased spatial overlap between predators and prey and therefore increased consumption. The perimeter to area ratio was held constant in our study because we increased arena size linearly by attaching additional pool/riffle units, so thigmotaxis was likely not occurring. In addition to preferred habitats driving overlap between predators and prey, prey aggregation can also lead to increased consumption rates if predators can easily find and approach large aggregations of prey (Bergström & Englund, 2002; Fauchald et al., 2000; Rose & Leggett, 1990). Predators make foraging decisions based on prey densities at multiple spatial scales (Fauchald, 1999), so prey aggregation likely plays an important role for some predators to choose where to spend time and therefore how much spatial overlap there is between predators and prey. However, the lack of a clear relationship between spatial overlap across arena sizes and lower selection index values indicate that either (1) bass in this study did not select pools with larger prey aggregations or (2) larger prey aggregations avoided pools with bass because more individuals have a higher probability of detecting a predator (e.g. Lima, 1995; Lima & Dill, 1990). Therefore, despite increased aggregation for *P. notatus*, we did not observe increased overlap between predators and prey, indicating the mechanism of increased consumption in this study may be different than previous studies using invertebrate prey.

In addition to movement patterns, predatory strategy may also explain increased consumption. Bass are typically considered ambush predators, which are expected to be more effective when prey are less aggregated, especially at intermediate prey densities (Taylor, 1976). This might explain why bass did not overlap with the highest densities of prey fish. Bass might have selected low-density pools where they were still able to successfully ambush prey that were moving between pools. Alternatively, predation strategy might have varied across arena size, driving differences in consumption. Predators are known to vary their predation strategy with habitat complexity. For example, bass can switch from predominately using ambush techniques to stalking prey in habitats with low habitat complexity (Savion & Stein, 1982). Predators might also change their strategy in response to spatial constraints. The relative importance of pre-capture versus post-capture constraints on predation can change with arena size (Christensen, 1996) and local prey density (Holling, 1959), so predation strategies might do the same. We did not observe changes in predator movement between pools with increased spatial scale, but did not measure other aspects of predator behaviour (e.g. time spent in pools). Considering how predators adjust feeding strategies to spatial constraints might have important implications for scaling up predator-prey interactions and understanding how predation strategies vary with habitat size (Ryall & Fahrig, 2006).

Measuring predator-prey response metrics across arena sizes is critical for making predictions at spatial scales relevant to higher-order biological process (e.g. population dynamics or community structure) and can provide insight into how predator-prey interactions

vary with changes in the size of natural arenas associated with habitat loss and fragmentation. Our study and others cited above indicate measures of predator effects are biased across different spatial scales and consumption is underestimated when measured at fine spatial scales typical of most experiments. Using consumption rates derived in empirical work when predicting predator-prey outcomes in natural systems might therefore be misleading, so statistically controlling for arena size effects using empirically derived relationships between arena size and foraging rates is recommended (Uiterwaal & Delong, 2018). In addition to using these rates to inform predictions through scale transitions, the observed patterns of consumption and prey behaviour can also help predict impacts of habitat loss and fragmentation if we assume habitat patches act as different sized arenas for predator-prey interactions (Ahrens et al., 2012). Although we observed lower consumption rates in smaller arenas, we also observed changes in prey behaviour both in response to arena size and especially to the presence of predators. Predators in smaller habitat patches might not consume more, but their non-consumptive effects also can have strong negative impacts on prey populations (Lima, 1998; Pecarsky et al., 2008). We hypothesize prey vigilance in smaller arenas played an important role in keeping consumption rates low through declines in movement. Vigilance is associated with prolonged stress (Vitousek et al., 2018) and foraging costs (Balaban-Feld et al., 2019), both of which influence prey vital rates and food web structure (Ho et al., 2019).

Overall, our results build on previous work suggesting predator-prey response metrics vary across spatial scales and are likely underestimated in experimental studies, but our work highlights that mechanisms driving consumption patterns may vary across the arrangement of experimental arenas and traits of the predator (Uiterwaal & Delong, 2018). We predict increased prey movement, not aggregation, led to increased consumption in larger arenas and that predation strategy (ambush predator) and the linear nature of stream arenas might have also been important factors driving these patterns. More work is needed to understand how a wider range of predators, prey and experimental systems influence foraging rates to inform predictions of predator-prey interactions in natural systems.

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AUTHORS' CONTRIBUTIONS

L.A.B. led the writing of the manuscript and analysed the data; L.A.B., C.A.P. and K.B.G. conceived the ideas, designed the methodology

and collected the data. All authors contributed critically to the drafts and gave final approval for manuscript submission.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.m905qfv1f> (Bruckerhoff et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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