**Foraging traits predict stage-structured feeding by freshwater fishes**

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**Abstract**

The susceptibility of prey to predators often changes across prey life-stages, yet predation is typically studied at the level of species, rather than life-stages. In addition, it is unclear how predator foraging traits affect their consumption of different prey life-stages. We hypothesized that stage-structured feeding in freshwater food webs would depend on prey development (insects transitioning from larval benthic stages to adults emerging from the surface) and predator feeding domains, defined as the vertical microhabitat used for feeding behaviors. Fish diets (n = 606) were collected from two backwater and two stream sites repeatedly over two months in the summer. Fishes pre-classified as “benthic feeders” consumed the greatest quantity of larval chironomids, an average of 7.4 times the total number of larvae consumed by fishes pre-classified as “intermediate (mid-water) feeders” and 2.5 times the number consumed by fishes pre-classified as “surface/water column feeders”. Instead of feeding on larval chironomids, non-benthic fishes fed more heavily on adult and pupal chironomids, regardless of emergence patterns. These results indicate that stage-structured feeding is not only common in freshwater food webs, but also varies predictably by the foraging domain of fishes.

**Introduction**

Species interactions are often depicted as occurring in a way that homogenizes information about ontogeny. The functional group or trophic level of an individual, whether they are predator or prey, can change throughout their development due to changes in size, changes in habitat utilization, or metamorphosis (Werner and Gilliam 1984, Rudolf and Lafferty 2011, Hartvig and Anderson 2013, Rudolf and Rasmussen 2013, Nilsson et al 2018). These changes may also be associated with changes in susceptibility to predation (Oliver 1971, Reimer et al. 2019), thereby leading to stage-structured feeding in food webs (Miller and Rudolf 2011, Nilsson et al. 2018).

Though ecologists have been aware of stage-structured feeding within food webs for decades (Hardy 1924, Hutchinson 1959, Werner and Gilliam 1984, Werner 1984), stage specific interactions resulting from ontogenetic shifts are often disregarded in classical ecological theory (Bolnick et al 2011, Violle et al 2012, Nilsson et al 2018). Yet stage-structured feeding can explain important ecological phenomena such as coexistence of predators on shared prey taxa (De Roos et al. 2008), biomass overcompensation (Miller and Rudolph 2011), and alterations in subsidies from the aquatic to the terrestrial system (Wesner 2016, Clegg et al 2018). While stage-structured feeding can generate novel explanations for ecological phenomena, its overall importance to ecological functioning (or disturbance through species introduction) depends on how prevalent and predictable it is in natural ecosystems. However, natural variation in stage-structured feeding as well as the causes of that variation have not been previously assessed (Clegg et al 2018).

In this study, we repeatedly quantified stage-structured feeding between fishes and their aquatic insect prey in four freshwater food webs. Aquatic insect development is often associated with movement from the aquatic to the terrestrial ecosystem as insects transition from larval to pupal and adult stages. This results in increased availability of pupal and adult insects during periods of peak emergence. For example, pupal consumption by Eurasian Perch (*Perca fluviatilis*) occurred only during periods of peak pupal abundance (Wagner et al. 2012). They found that perch fed on zooplankton or fish during most of the year but switched to feeding on pupal chironomids that emerged from the profundal lake zone in late spring. During this time pupal chironomids made up to 48% of the diet (by number) of perch, compared to less than ~5% on other sample dates. Therefore, it is possible that stage-structured feeding at the species and community level could be positively related to peak insect emergence.

In addition to temporal variability, we hypothesized that feeding domain, a simplified representation of trophic niche that includes description of microhabitat use, would impact stage-structured feeding by predators. We defined feeding domain as the spatial extent of a microhabitat used by an individual for feeding (Schmitz 2007) which can vary among fish species (Poff and Allan 1995, Ross 2013). The spatial extent of habitat used for feeding likely influences feeding preferences of fishes for different aquatic insect life-stages (Dahl 1998, Wagner et al. 2012).

We tested the hypotheses that feeding domain predicts stage-structured feeding patterns and that there is a positive correlation between emergence rate and consumption of non-larval prey. To do this, we collected diet samples from freshwater fishes. Fishes were sampled at four study sites. Diet samples were used to quantify their feeding on different life-stages of prey species.

**Sampling Methods**

Four sites, two backwaters and two sites within one stream, were sampled during the summer for this study. Sites were chosen to increase the breadth of fish species sampled. The backwater sites were connected to the main channel of the Missouri River. The two backwater sites were Burbank beach (latitude: 42°40'11.88"N, longitude: 96°47'22.82"W) and Gunderson backwater (latitude: 42°44'56.56"N, longitude: 96°57'12.08"W). Stream sites were at different locations along the same ephemeral stream system, a first order tributary of the Vermillion river called Spirit Mound Creek, with a width less than 3m and a depth of ~1m (fluctuating with precipitation). The stream sites were upstream (latitude: 42°52'4.29"N, longitude: 96°57'16.25"W) and downstream (latitude: 42°51'7.39"N, longitude: 96°56'39.28"W). All sites are in SE South Dakota, an intense agricultural zone.

Weekly gut sampling of fish was conducted at each of the four study sites starting on June 6, 2019. First, fish were collected via seine net and put into a 5-gallon bucket containing fresh water. To ensure that we sampled a variety of fishes, we used various seining techniques at each site, including kick-seining for benthic fishes, seining around vegetation, short seine-hauls, and long seine-hauls. Fish were then identified and moved from the holding tank to the anesthetizing tank (a 5-gallon bucket containing water and a dilute MS-222 solution). Once the fish were immobilized by the MS-222 solution, they were removed from the anesthetizing tank and measured for standard length. The fish then underwent a non-lethal gastric lavage procedure to remove prey items (Kamler and Pope 2001). A garden sprayer (acting as a pump for this procedure) with an appropriately sized tube for the mouth of the fish (≥ 3.2 mm inner diameter) was fed into the gut. Water was then pumped through the gut of the fish and any dislodged stomach contents were collected in a 250 µm sieve and preserved in 95% ethanol. The fish was then placed into a recovery tank (a 5-gallon bucket containing fresh water) and monitored for recovery. Finally, all collected fish were released back into the study site. Prey items from the diet samples were identified to family or order and life stage using Merritt et al. (2008). Taxa sampled, number of individuals sampled, and the feeding domains of these fishes can be found in Fig. 1.

Emergence was sampled at each site to determine any relationships between emergence patterns and stage-structured feeding. During peak emergence events, the number of pupal and adult chironomids available for consumption increases. For this reason, we would expect consumption of adult and pupal chironomids to also increase. Three emergence traps were deployed at each site consisting of a 0.6m X 0.6m floating, pyramidal frame and a mesh covering (Cadmus et al. 2016). Emergence samples were collected from these in the morning twice per week. This method meant that emergence traps were left to collecting invertebrates on an alternating schedule of three nights then four nights. Samples were frozen upon collection. Invertebrates from emergence samples were sorted and identified to family or order using Merritt et al. (2008).

Feeding domain of fishes was assigned based on previous literature studies of each species in our dataset (Poff and Allan 1995, Ross 2013). We used three categories of feeding domain to classify fishes within this study: surface/water column feeders, intermediate feeders, and benthic feeders. Surface/water column feeders are defined as fishes that feed primarily at the surface and/or within approximately the top half of the water column. Intermediate feeders were defined as fishes that will feed approximately equally between the surface, benthos, and water column (this included piscivorous species). We defined benthic feeders as fish that primarily feed at or near the benthos.

**Analysis**

To test for a relationship between feeding domain and proportion of diet consisting of each chironomid life stage, we used a multinomial logistic regression model. This model used a multinomial distribution with a logit link since data were in terms of abundance. Fixed effects for the model were date, feeding domain, and the interaction between date and feeding domain. Site and species were specified as random effects on the intercept of the model. The posterior of this model provided total abundance of each aquatic chironomid life stage (larval, pupal, and adult) within the diets of each feeding domain over the course of the summer. Total abundance was then converted to proportion of each chironomid stage within diets.

To test for a relationship between emergence and time, we first used a generalized additive model (GAM) to estimate chironomid emergence. The response variable of this model was total count of chironomids. A gamma distribution with a log link was used for this model. Collection date, location, and the interaction between collection date and location were the fixed effects. Abundance data were collected after three or four days of setting emergence traps. Data were then converted to daily abundance of emergent chironomids, number of individuals/days the trap was set.

We used a generalized linear mixed model (GLMM) to test for a relationship between proportion of chironomid pupae in diets and emergence. The response variable for this model was proportion of pupae in diets. The fixed effects within this model were emergent chironomid biomass, feeding domain, site, and all interactions between these variables. A random effect of species was also specified for the intercept. A binomial distribution with a logit link was specified for this model.

The multinomial, generalized additive, and generalized linear models presented here were created in R (version 3.4.2, Core Team R, 2017). We used the *brms* package (Bürkner, 2017) to specify the models. The *brms* package uses a Hamiltonian Monte Carlo algorithm to estimate the posterior through *rstan* (Stan Development Team, 2016). All code and data can be found at: https://github.com/Abrahamkanz/stageguildms

**Results**

*Trait differences in stage-structured feeding*

Fishes from the benthic feeding domain fed almost entirely on larval chironomids throughout the study with an overall median proportion of 0.91 (95% CrI; 0.65 – 0.99, Fig. 2). In contrast, intermediate and surface-feeding fishes fed on larval chironomids at median proportions of 0.75 (0.32 – 0.95) and 0.81 (0.45 – 0.97), respectively (Fig. 2). There was a 96 percent probability that benthic feeders consumed a higher proportion of larvae than intermediate feeders and an 94 percent probability that benthic feeders consumed more larvae than surface/water column feeders, thereby supporting the hypothesis that fishes from non-benthic feeding domains consume fewer larval chironomids.

*Temporal patterns in stage-structured feeding*

For benthic-feeding fishes, the median proportion of larval chironomids was ≥0.90 on all sample dates, indicating consistent feeding on larval prey over time (Fig. 3c). This is consistent with our initial hypothesis that fishes in the benthic feeding domain would consume the greatest proportion of larval chironomid prey items on average. In contrast, intermediate (Fig. 3b) and surface feeder consumption (Fig. 3a) of larval chironomids was more variable. Fishes in the intermediate feeding domain had a larval dietary median proportion of 0.99 at peak larval consumption and a median proportion of 0.45 on their date of lowest consumption. Surface feeding fishes had a larval dietary median proportion of 0.99 at peak larval consumption and a median proportion of 0.40 on their date of lowest consumption. This variability can also be observed in the adult and pupal chironomid consumption of the intermediate (Fig. 4b, Fig. 5b) and surface (Fig. 4a, Fig. 5a) feeding domain fishes. Benthic feeding fishes experienced peak consumption of adult chironomids on day 200 with a median dietary proportion of 0.06 (95% CrI; 0.00 – 0.52, Fig. 4c) and the lowest occurrence of pupal chironomids in their diets with the peak median proportion of 0.06 (95% CrI; 0.00-0.60) occurring on day 178 (Fig. 5c).

*Chironomid Emergence*

Chironomids were the majority of emergent insects collected in emergence traps (>95%, 16454 individuals) and in fish diets. For more information about the entire emergent community, see supplemental materials. Patterns of emergence varied across sites. The Burbank backwater site began the study at peak emergence and decreased for the rest of the study (Fig. 6a). The Gunderson backwater site was also experiencing a peak in emergence early in the study and experienced a decline in its emergence for the remainder of the study (Fig. 6b). Downstream, a stream site, also experienced peak emergence early in the study (Fig. 6c). In contrast, the upstream site experienced one peak emergence event near the end of the study (Fig. 6d).

Contrary to our initial hypothesis that peaks in emergence would correspond to peaks in pupal chironomid consumption due to increased availability, the GLMM for the comparison of proportion of pupae in diets and emergence showed little relationship between these variables for a majority of the comparisons. The strongest relationship between emergence and proportion of pupae in diet was for the intermediate feeding domain at the upstream field site which had a proportional increase of 1.17 (95% CrI; 1.10-1.24) for every unit increase in emergent biomass of chironomids. This estimate began with a pupal proportion of 0.0017 (95% CrI; 0.0001 – 0.02) when emergence was 5.0 chironomids/m2/day and ended with a pupal proportion of 0.592 (95% CrI; 0.013 – 0.904) at an emergence value of 124.4 chironomids/m2/day (see supplemental material for more information).

**Discussion**

This study provides empirical evidence for the presence of stage-structuring within the diets of freshwater fishes in both stream and backwater habitats, specifically differences found between the intermediate and benthic feeding domains. Fish in the surface/water column and the intermediate feeding domains ate pupal and adult chironomids more often than fishes in the benthic feeding domain. Fishes within the intermediate feeding domain were found to feed more heavily on pupal and adult chironomids than any other feeding domain. While it is not surprising that benthic fishes ate more larval chironomids than other fishes, our results provide among the first quantifications of this feeding among fish foraging modes.

Clegg et al. (2018) examined intraspecific variation and its influences across five aquatic food webs through disaggregation of nodes within the food webs. They demonstrated that inclusion of information about life-stages modifies a food web to a greater degree than simply increasing the number of nodes through additional taxa. Our study showed that stage-structured feeding also varies temporally and can experience fluctuations over relatively short timespans. However, the mechanism explaining this variation was unclear. We expected fluctuations in stage-structured feeding to change as the aquatic chironomid community developed, changing the availability of each life stage. However, evidence for a consistent relationship between emergence timing and stage-structured feeding was weak. One explanation for fishes increasing their feeding on adult chironomids during non-peak emergence could be related to aquatic chironomid reproduction. Adult chironomids often migrate to other aquatic ecosystems to oviposit (Huryn and Wallace 2002, Lancaster and Downes 2013). Increases in fish consumption of adult chironomids in our study could be the result of adult chironomid immigration and reproductive activities rather than emergence.

While we were unable to definitively determine the cause behind temporal variation in stage-structured feeding, our data showed that fish feeding domain is linked to stage-structured feeding. Because the feeding traits (benthic, intermediate, surface) are generalizable to most fishes (Ross 2013), it seems likely that inclusion of stage-structured feeding information could improve predictions of predator resource partitioning and the flow of energy through and from aquatic ecosystems (De Roos et al. 2008, Bolnick et al 2011, Miller and Rudolph 2011, Clegg et al. 2018). For example, while we did not measure nutritional differences between insect life-stages in this study, recent work has demonstrated that insect nutritional content may vary among life-stages. Non-organic contaminants, such as metals (e.g. Zn, Pb), are lost during insect metamorphosis (Kraus et al 2014; Wesner et al. 2015). Thus, in contaminated streams it seems likely that stage-structured feeding may alter the flux of contaminants from insect to fish. Fish that feed more heavily on pupal or adult stages would receive lower exposures to some aquatic-derived contaminants than fishes that feed more heavily on larval stages (Wesner 2019). Whether these risks are consistent with the foraging strategies of fishes that we document here (i.e. benthic fishes feed more on larvae, water-column fishes feed more on pupae) depends on the behavioral flexibility of the fishes. In contaminated streams, trout switched feeding from larval aquatic to terrestrial insects, presumably because the terrestrially-derived insects had lower metal concentrations than the aquatic insects (Kraus et al. 2016). It is unclear whether a similar switch might occur among life-stages of aquatic insects in response to pollution is unknown but deserves further study.

Our study of stage-structured diets has implications for fisheries management. Stocking of non-native fishes for recreational use is a common occurrence across the world. The ability of both introduced and native fishes to survive is dependent on factors such as ontogenetic shift, diet overlap, and prey partitioning capabilities (Eby et al 2006). For example, predator introduction can lead to increases in top-down control and increased dietary overlap between native and non-native predators. Predictions of the influence of non-native fish introductions often only consider taxonomic diet overlap (Ross, S.T. 1986, Eby et al 2006, Bohn et al 2008). However, in addition to taxonomic prey partitioning, stage-structured feeding is a mechanism by which predators can partition prey resources (De Roos et al. 2008). It is possible that two predators with strong specificity for a specific life stage or size class could coexist (Nilsson et al 2018). Our study demonstrates that prey partitioning not only occurs among prey life-stages of the same prey taxa but is also consistently different among predator feeding domains. This suggests that prey partitioning by life stage can help to predict the impact of fish introductions as well as the success or failure of these introductions.

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**Data Availability**

All supporting data and R script for analysis can be found at: https://github.com/Abrahamkanz/stageguildms

**Conflict of Interest**

None of the authors declare any conflict of interest.

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