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

Running head: Stage-structured feeding by freshwater fishes

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**Abstract**

Fish are often top predators in freshwater ecosystems, yet a substantial proportion of their prey can come from non-aquatic sources such as terrestrial subsidies, the importance of which is tied to fish foraging domain and behavior. However, the same fish traits (e.g., propensity for surface feeding), may also alter how fish consume the remaining fraction of aquatic prey, such as the life-stages of aquatic insects that are eaten. This is potentially ecologically important, since aquatic insects stop feeding at later developmental stages, such as pupae and adults, and are also most susceptible to predation during this transition. We hypothesized that fish feeding domain - the vertical microhabitat used for feeding – would be associated with both the fraction of terrestrial prey consumed and the fraction of aquatic prey eaten in non-feeding life-stages. Fish diets (n = 606 diet samples from 22 fish species) were collected from two backwater and two stream sites repeatedly over two months in the summer. Fish ate similar amounts of prey, regardless of foraging domain, but differed in the fraction of terrestrial prey consumed. For fish pre-classified as surface feeders and intermediate feeders, ~12% (by dry mass) of their prey were terrestrial on average, ranging up to 44% for individual fish species. In comparison, the same fraction was only 3% for fish pre-classified as benthic feeders. Similarly, for the remaining aquatic fraction, intermediate and surface-feeding fishes ate non-consumer life-stages at a rate (5-8% of aquatic prey) that was ~5-8 times higher than for benthic fishes (~1%). 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**

Approximately 40% of freshwater fish species are at risk of extinction or are already extinct (Jelks et al. 2008, Darwall and Freyhoff 2016). Because of the importance of fishes in freshwater ecosystem functioning, this loss has the potential to alter the functioning of freshwater food webs (Hargrave 2009, Vanni 2010) in addition to linked riparian food webs (Baxter et al. 2005, Wesner 2012). In particular, changes in fish composition can alter the top-down control of invertebrate prey in freshwater food webs through direct prey consumption (Power et al. 1990, Nakano et al. 1999, Baxter et al. 2004). However, despite the near ubiquity of fish-insect interactions in freshwater food webs, evidence for consistent top-down control of invertebrates by fish is mixed (Matthews 1998, Dahl and Greenberg 1996, Wesner 2016).

A proposed explanation for mixed effects of fish predation is that some fishes feed more heavily on drift and/or are subsidized by terrestrial prey, thereby reducing direct consumption of benthic invertebrates (Garman 1981, Nakano et al. 1999, Baxter et al. 2004, Pusey and Arthington 2003). Propensity for drift feeding or terrestrial feeding may also be associated with fish feeding traits, such as morphological or behavioral adaptations for benthic-feeding versus feeding at the surface or middle of the water column (Dahl and Greenberg 1996, Wagner et al. 2012, Ross 2013). A complementary, but less well-studied, explanation for weak effects of some fishes is that they may also target later-developing stages of aquatic insects, such as pupae (Wagner et al. 2012, Warmbold and Wesner 2018). Such feeding may be ecologically important, because pupae and adult insects are functionally identical to terrestrial insects in the sense that both life stages have stopped feeding and are no longer consumers in aquatic food webs (Figure 1). Not only may this help to explain the consistently strong effects of fishes on emerging aquatic insects, even when effects on larval insect densities are weak (Warmbold and Wesner 2018), but it is also likely to go undetected in many diet studies. For example, isotopes change little across insect life stages (Krause et al. 2014), so is not possible to quantify stage-specific feeding in fish diets with stable isotopes, nor is it possible if prey are only categorized taxonomically.

We refer to this type of feeding as stage-structured predation. That is, predation in which predators target different life-stages of the same prey species (De Roos et al. 2008, Miller and Rudolph 2011). While ecologists have been aware of stage-structured feeding within food webs for decades (Hardy 1924, Hutchinson 1959, Werner and Gilliam 1984, Werner 1984), it is 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 regulation of aquatic-terrestrial subsidies (Wesner 2016, Clegg et al. 2018).

The goal of this study was to quantify natural variation in terrestrial and stage-structured feeding by fishes. In particular, we measured the fraction of total prey in fish diets that was eaten either as terrestrial prey or as aquatic prey in “non-consumer” life-stages (e.g., pupae or larvae; Figure 1). We hypothesized that both fractions would be substantial, with the latter fraction (% non-consumers) increasing during periods of high insect emergence, and that both fractions would vary predictably according to fish feeding domains. Namely, we predicted that the fraction of total fish diets containing terrestrial or non-consumer prey would be lowest in benthic-feeding fish, highest in surface-feeding fish, and intermediate in fishes that feed at all levels of the water column (intermediate feeders).

**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, USA.

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, various seining techniques were used 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 measured for standard length and gut contents were extracted with gastric lavage (Kamler and Pope 2001). To do this, 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. Fish sampled, number of individuals sampled, and the feeding domains of these fishes are shown in Fig. 1.

Prey items from the diet samples were identified to family or order and life stage using Merritt et al. (2008). Prey were further classified as aquatic or terrestrial (based on their larval habitat) and as either a consumer or non-consumer, indicating their trophic status in aquatic food webs. Pupae and adult stages of aquatic insects along with all terrestrial insects were classified as non-consumers, while aquatic larvae were classified as consumers.

Emergence was sampled at each site to determine stage-structured feeding varied as a function of insect emergence. 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, following 3-4 nights of deployment. Samples were frozen upon collection 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 feeders, intermediate feeders, and benthic feeders. Surface feeders were fish that feed primarily at the surface or within approximately the top half of the water column. Intermediate feeders were fish that will feed approximately equally between the surface, benthos, and water column (this included piscivorous species). Benthic feeders were fish that primarily feed at or near the benthos.

**Analysis**

To determine whether the proportion of non-feeding prey in diets varied across fish feeding domains, we fit a generalized linear mixed model with prey mass per stomach (mg dry mass) as the response variable, date, fish domain, prey feeding stage (consumer/non-consumer), and prey origin (aquatic/terrestrial), and their interactions as the predictor variables, and site and fish species as random intercepts. We used a Gamma likelihood with a log link, since prey mass is a positive, continuous measure. We used this model to compare both total prey mass per fish, the proportion of prey that were terrestrial, and the proportion of prey mass that were non-consumers among fish domains.

For the model above, we used prey mass per fish, rather than prey mass per fish length (e.g., corrected for fish size), because there was no evidence that larger fish had a higher mass of prey (Figure S1). Finally, we fit similar models as above for each fish species (rather than for fish domain only). These models allowed us to estimate the fraction of terrestrial or consumer prey eaten by individual fish species, rather than just fish domains.

To determine the whether fish ate non-consumer life stages more often during periods of high insect emergence, we first modeled aquatic insect emergence (number/day/m2) as the response variable and date, site, and their interaction as the predictor variables. We used a generalized linear model with a Gamma likelihood and a log link. We then used the posterior median estimate of emergence from this model on each date at each site as the predictor variable in a second model. The second model used the raw proportion of non-consumer prey (aquatic origin only) as the response variable, median emergence, fish domain, and their interaction as the predictor variables, and site and fish species as random intercepts. Because proportions were continuous values between 0 and 1, this model had a beta likelihood with a logit-link.

Finally, we re-ran each of the models above using only the chironomid portions of prey mass or emergence (excluding the prey origin parameter, since chironomids are aquatic). This allowed us to determine whether our results were impacted by the lack of life-stage information available for some taxa in the complete dataset, since chironomids are relatively easy to differentiate by life stage (larva, pupa, adult) and hence feeding stage (larvae feed in aquatic food webs, pupae and adults do not).

Models were specified in R (version 3.4.2, Core Team R, 2017) using Bayesian inference with the *brms* package (Bürkner, 2017). Posterior distributions were generated with a Hamiltonian Monte Carlo algorithm through *rstan* (Stan Development Team, 2016). Prior distributions are described and justified (along with prior sensitivity analyses) in the Supplementary Information). All code and data can be found at: https://github.com/Abrahamkanz/stageguildms

**Results**

*Prey composition*

Among the 59 prey taxa in fish diets, chironomids dominated by abundance, biomass, and occurrence. They made up 64% of all diet items by abundance, 45% by biomass, and occurred in 438/617 fish stomachs (71%). The next most common item was Branchiopods (14% by abundance, 4% by biomass, 24% by occurrence). All other prey taxa made up less than 4% of diets by abundance, biomass or occurrence. One exception was crayfish chelipods, which made up less than 4% of abundance or occurrence, but 23% of biomass due to their large size. They were found in 24/617 fish stomachs. Insecta were the dominant prey class, making up 75%, 61%, and 76% of diets by abundance, biomass, and occurrence, respectively. No other prey classes (n = 11 classes) made up more than 24% in any category.

*Fish trait differences in diet*

Fish had a similar amount of prey mass in their stomachs, regardless of feeding guild, averaging 11 ± 6 mg DM per fish (Figure 2a; posterior mean ± sd). This amount varied little over time or between fish feeding domains (Figure 3a). However, the likely trophic impact of this feeding differed among fish feeding domains. For example, for intermediate and surface-feeding fishes 13 ± 12% and 11 ± 11% of their prey were non-consumers, respectively (Figure 2c). In contrast, for benthic fish, only 1 ± 1% (by dry mass) of prey were non-consumers, a pattern that varied little over time (Figure 3c). There was a >99% probability that non-consumer prey were more prevalent in intermediate and surface-feeding fish compared to benthic fish, supporting the hypothesis that fishes from non-benthic feeding domains eat a higher proportion of prey in non-feeding life-stages.

Patterns for intermediate and surface-feeding fishes also varied widely over time. On five collection dates, the proportion of their prey that was non-consumers exceeded 20% for intermediate and surface-feeding fishes, peaking at 30 ± 13 and 30 ± 11 in June, respectively (Figure 3c). In contrast, the proportion of non-consumer prey in benthic fish diets never exceeded 4% (Figure 3c). Interestingly, differences between benthic and intermediate/surface fish were maintained even when all three increased their feeding on non-consumer prey (Figure 2c,d).

When the analysis was restricted to just chironomid prey, the results were similar to those above. All fish ate a similar amount of chironomids over time (Figure 3b), averaging 9 mg DM per stomach, with 95% CrI ranging from 0.4 to 41 mg DM. Intermediate fish ate a smaller amount of chironomid mass than benthic or surface fish on average, but with strong overlap among the guilds (Figure 2b). As predicted, benthic fishes consistently fed on larval stages of chironomids rather than pupae or adults. Less than 5% of chironomid mass in their diets were pupae or adults on any given date (Figure 3d). In contrast, more than 10% of chironomids in intermediate or surface fish diets were pupae or adults on average (Figure 2d). This varied widely over time, with up to 40% of chironomids eaten as larvae or pupae on some dates (Figure 3d. These patterns were similar for individual fish species (Figure S1), supporting the hypothesis of stage-structured feeding in which fish partition prey not by taxonomy per se, but by life-stage.

*Insect Emergence*

Chironomids made up ~ 93% of 16,820 emergent insects collected in emergence traps. Emergence ranged from ~0 to 350 individuals/day/m2. Contrary to our initial there was little evidence that fish ate more non-feeding prey stages as emergence increased. The strongest relationship between emergence and proportion of non-feeding prey in diets was for surface feeding fishes (Table 4). However, the effect was relatively small (Table 4) and the relationship was noisy (Figure 4). It also disappeared when the analysis was repeated with only chironomids (Figure 4). No other fish domain showed evidence of relationship between emergence abundance and stage-structured feeding (Figure 4).

**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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**Figure Legends**

**Figure 1**. Conceptual figure showing different predictions for food webs without and with information on prey life-stages. Each of the food webs (a,b,c,d) has the same number and identity of prey species. a) Fish feed on a single prey consumer prey taxon (or group of consumer taxa), generating indirect effects to lower trophic levels. b) Fish target larval life stages, generating indirect effects because only larvae are consumers in aquatic food webs. c-d) Two of the life-stages (pupae and adults) do not feed. Fish that target those life stages have no indirect effects on lower trophic levels. The prevalence of this type of stage-structured feeding in aquatic food webs is unknown.

**Figure 2**. Posterior distributions, averaged across time, showing a) the total mass of aquatic prey per fish stomach, b) the total mass of chironomids per fish stomach, c) the proportion of aquatic prey eaten in a non-consumer life-stage, and d) the proportion of chironomids eaten in a non-consumer life-stage (e.g., pupae and adults). Medians and 95% credible intervals for each group are shown at the bottom of the densities.

**Figure 3**. Temporal variation in a) the total mass of aquatic prey per fish stomach, b) the total mass of chironomids per fish stomach, c) the proportion of aquatic prey eaten in a non-consumer life-stage, and d) the proportion of chironomids eaten in a non-consumer life-stage (e.g., pupae and adults) for each fish feeding guild. Boxplots summarize the median, interquartile range, and upper and lower 1.5% quantiles of posterior distributions on each date for each guild. To improve the visual distinction, 500 lines connect each date x guild group. They are drawn from 500 iterations of the posterior distribution of each group.

**Figure 4**. Relationship between insect emergence and the proportion of fish diets consisting of non-feeding prey. We expected that fish would feed most heavily on non-feeding pupal and adult prey stages during periods of high insect emergence. Contrary to expectations, there was no relationship between emergence and fish diets.

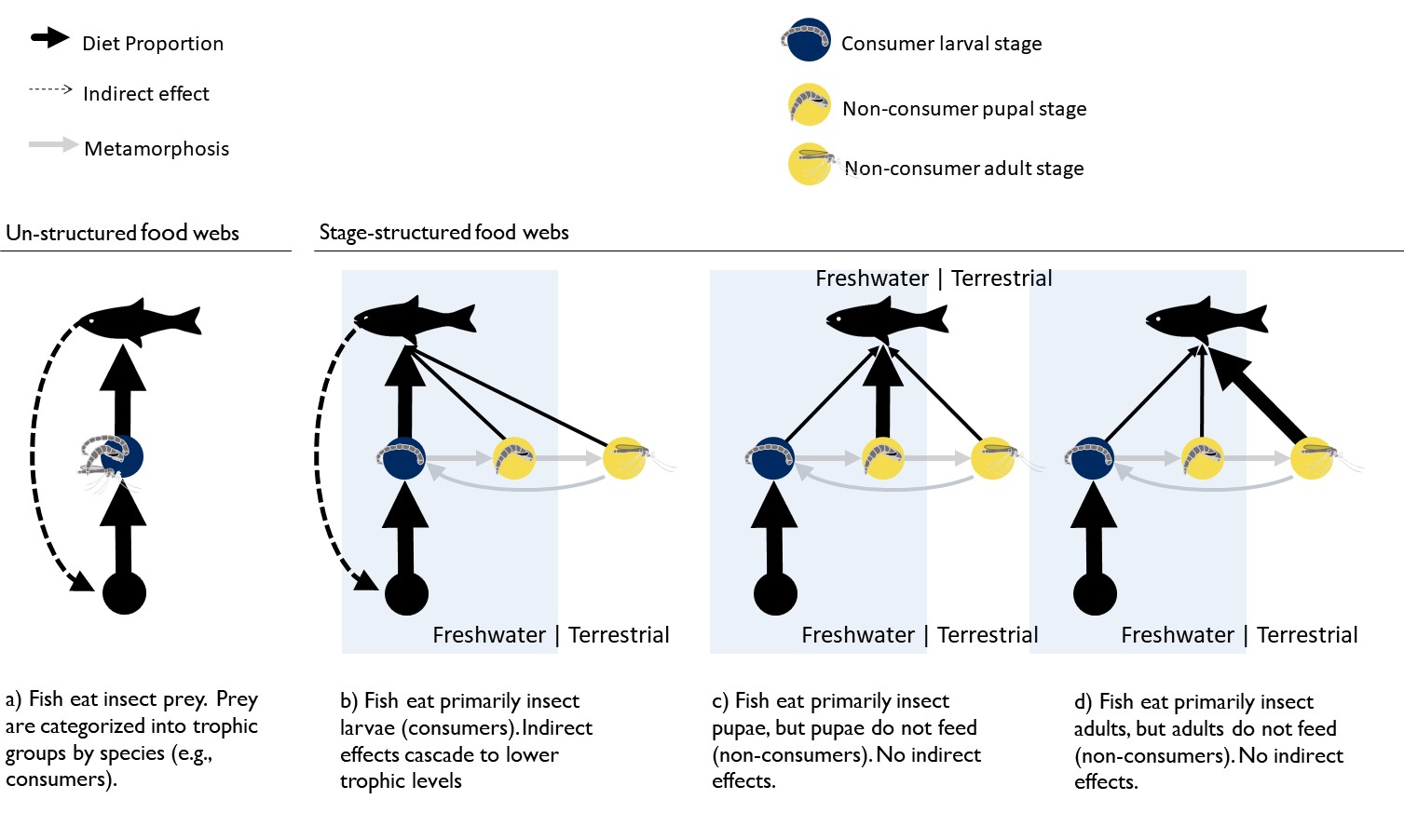
**Tables**

**ADD TABLE 1**

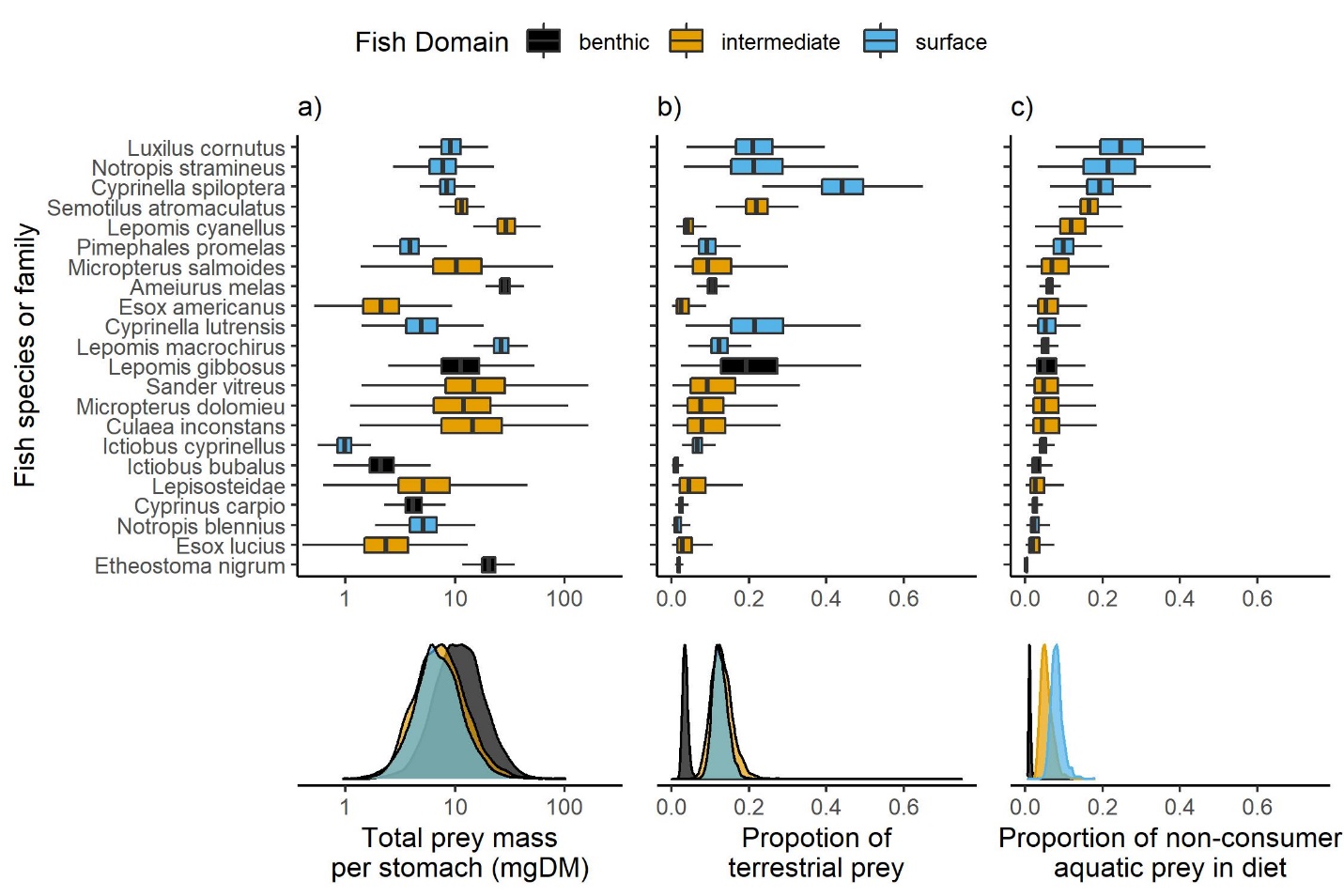
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| Table 3: Summaries of the posterior distribution of total aquatic prey mass per fish stomach and the proportion of non-feeding prey in fish diets by abundance. Values are averaged over 17 collection dates for each fish feeding domain and for all fish (averaged over dates and fish domain). | | | | | | |
| Response | Fish Domain | Mean | SD | 2.50% | 50% | 97.50% |
| Total aquatic prey mass (mgDM) | Benthic | 9 | 8 | 1 | 6 | 31 |
| Intermediate | 5 | 10 | 0.3 | 3 | 20 |
| Surface | 5.4 | 6.2 | 1 | 4 | 20 |
|  | All Fish | 6 | 8 | 1 | 4 | 25 |
|  |  |  |  |  |  |  |
| Proportion non-consumer aquatic prey | Benthic | 0.02 | 0.02 | 0.001 | 0.01 | 0.06 |
| Intermediate | 0.13 | 0.12 | 0.004 | 0.1 | 0.44 |
| Surface | 0.11 | 0.11 | 0.004 | 0.07 | 0.39 |
|  | All Fish | 0.08 | 0.1 | 0.002 | 0.04 | 0.38 |

|  |  |  |  |
| --- | --- | --- | --- |
| Table 4. Posterior mean and standard deviation (parentheses) of the marginal intercept and slope of the relationship between insect emergence and stage-structured feeding in fish. Values are on the odds scale. A slope of 1 indicates no change in the odds of a fish diet containing a non-feeding prey across different levels of emergence. Values below one indicates a decrease and values above one indicates an increase. Relationships were compared for each fish feeding domain in two models: Everything (all aquatic insects in emergence and diet samples) and Chironomids Only (same analysis with just chironomids). | | | |
| Model | Fish Domain | Intercept | Slope |
| Everything | benthic | 0.18 (0.04) | 1.08 (0.11) |
|  | intermediate | 0.29 (0.07) | 1.03 (0.14) |
|  | surface | 0.31 (0.06) | 1.36 (0.11) |
| Chironomids Only | benthic | 0.26 (0.06) | 1.07 (0.14) |
|  | intermediate | 0.39 (0.1) | 1.07 (0.18) |
|  | surface | 0.37 (0.07) | 1.16 (0.13) |

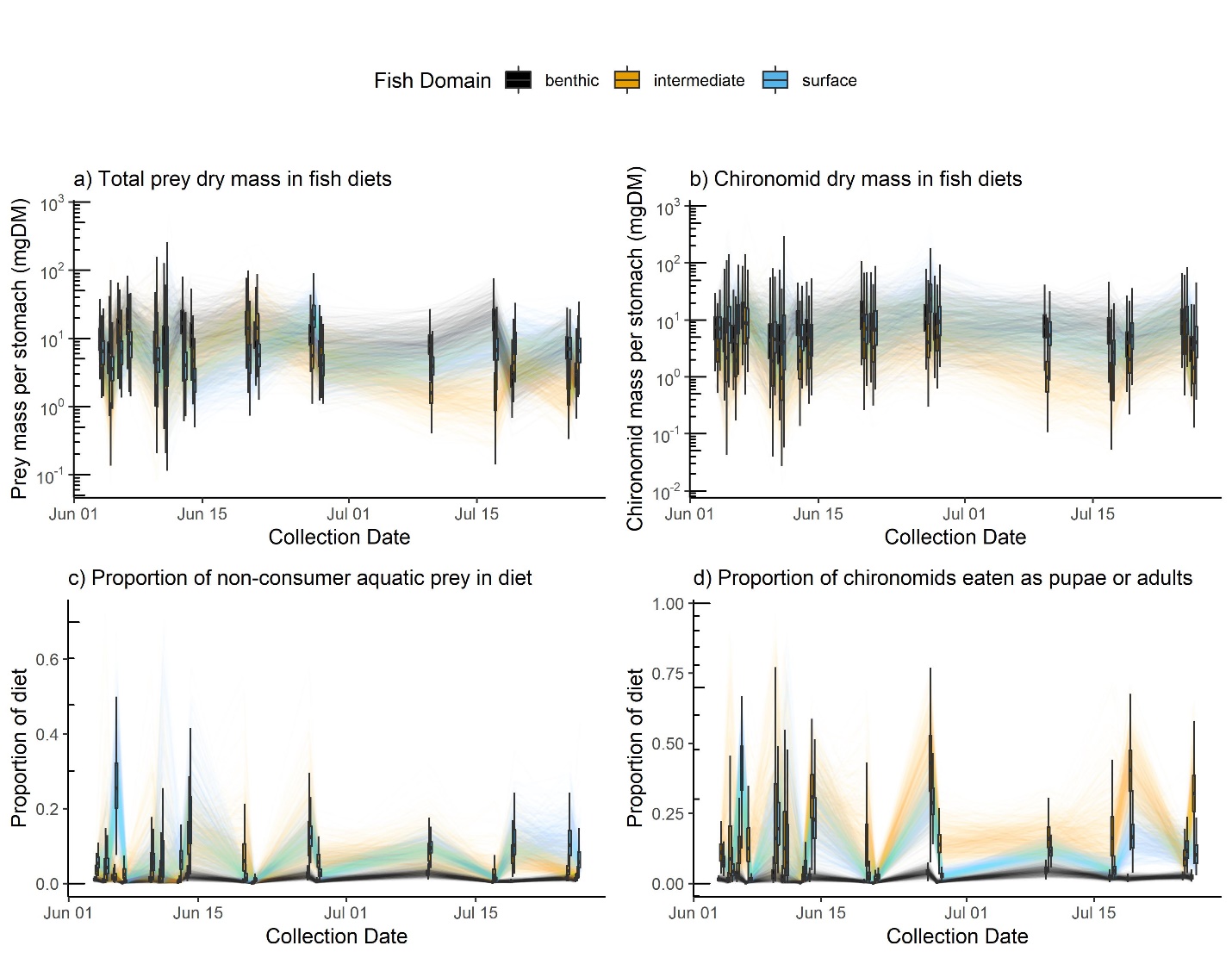
**Figure 1**



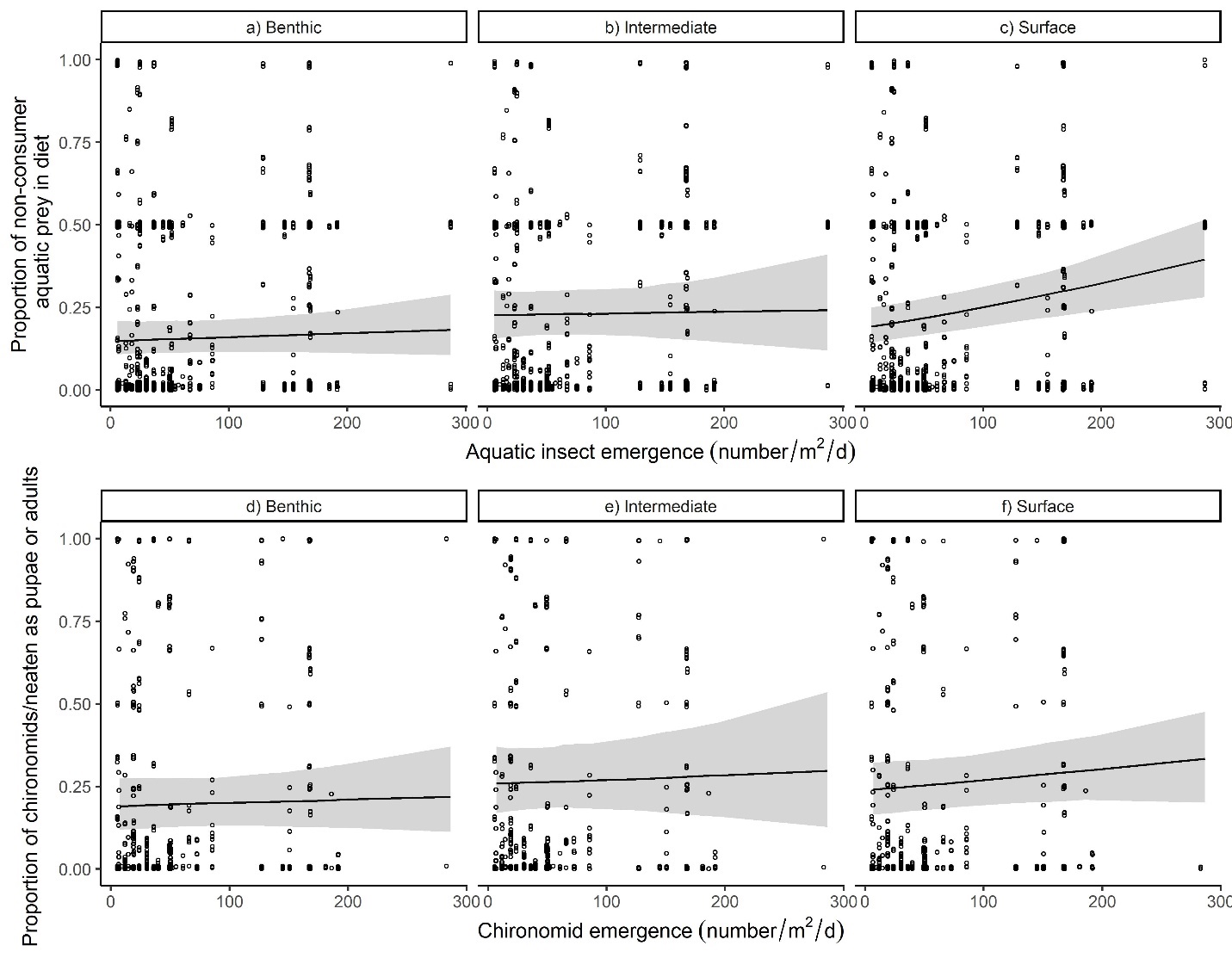
**Figure 2**

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**Figure 3**

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**Figure 4**



**Supplemental Information**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Table 2: Proportion of chironomid life-stages in fish diets by abundance. Values summarize the posterior distribution averaged over 17 collection events. | | | | | | |
| Prey Stage | Fish Domain | Mean | SD | 2.5% | 50% | 97.5% |
| Larvae | Benthic | 0.91 | 0.10 | 0.01 | 0.06 | 0.37 |
| Larvae | Intermediate | 0.71 | 0.17 | 0.29 | 0.74 | 0.95 |
| Larvae | Surface | 0.78 | 0.14 | 0.47 | 0.81 | 0.97 |
| Larvae | All Fish | 0.80 | 0.12 | 0.51 | 0.82 | 0.96 |
| Pupae | Benthic | 0.05 | 0.07 | 0.002 | 0.03 | 0.27 |
| Pupae | Intermediate | 0.22 | 0.15 | 0.02 | 0.20 | 0.57 |
| Pupae | Surface | 0.06 | 0.06 | 0.004 | 0.04 | 0.21 |
| Pupae | All Fish | 0.11 | 0.08 | 0.01 | 0.09 | 0.30 |
| Adults | Benthic | 0.04 | 0.05 | 0.001 | 0.02 | 0.17 |
| Adults | Intermediate | 0.08 | 0.09 | 0.003 | 0.05 | 0.34 |
| Adults | Surface | 0.16 | 0.12 | 0.02 | 0.14 | 0.44 |
| Adults | All Fish | 0.09 | 0.08 | 0.01 | 0.07 | 0.29 |

**Figure SX**

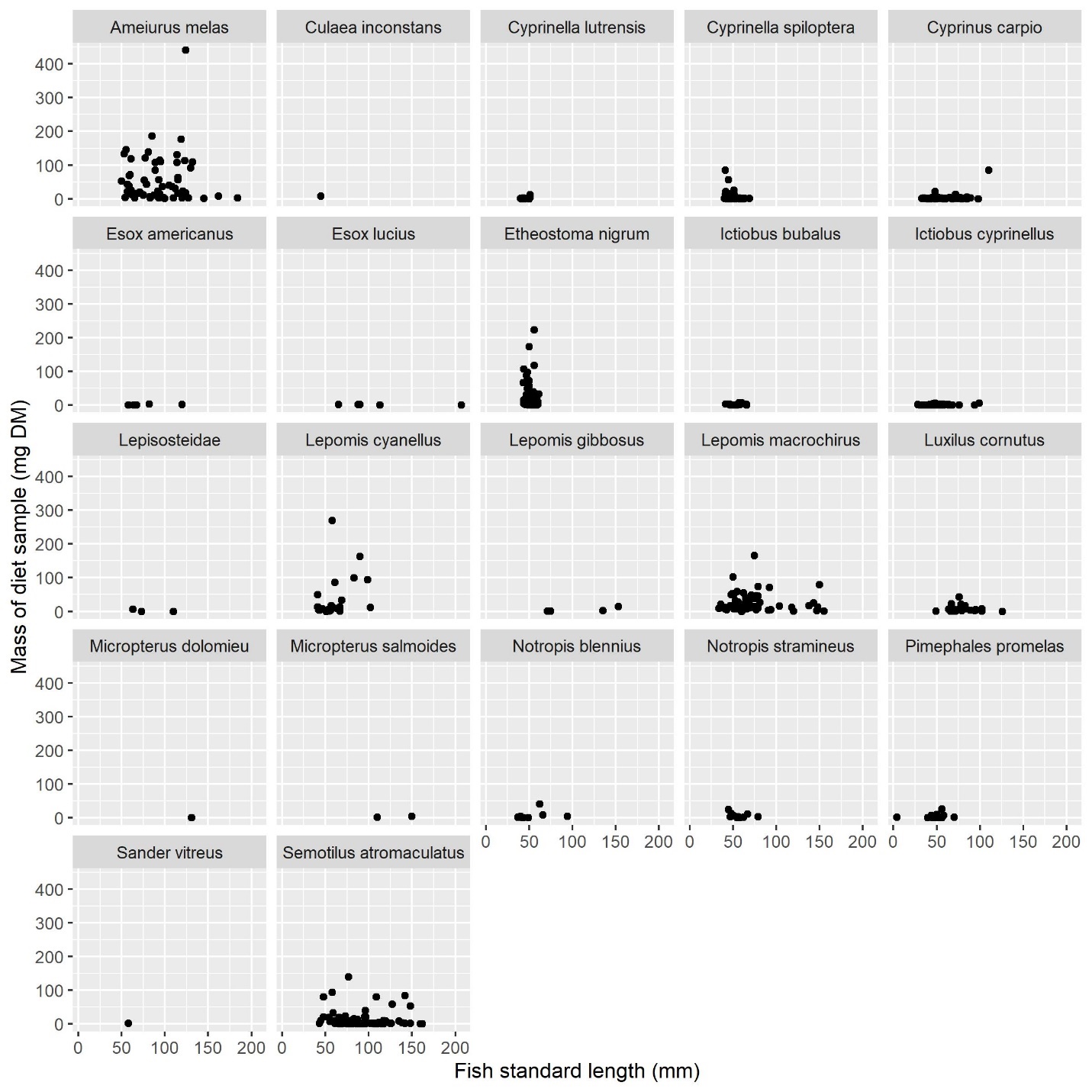
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Figure S1. Plots of raw data showing no relationship between fish size (length) and the mass of prey in the diet sample. For this reason, we did not correct diet samples by fish length.

**Figure SX**

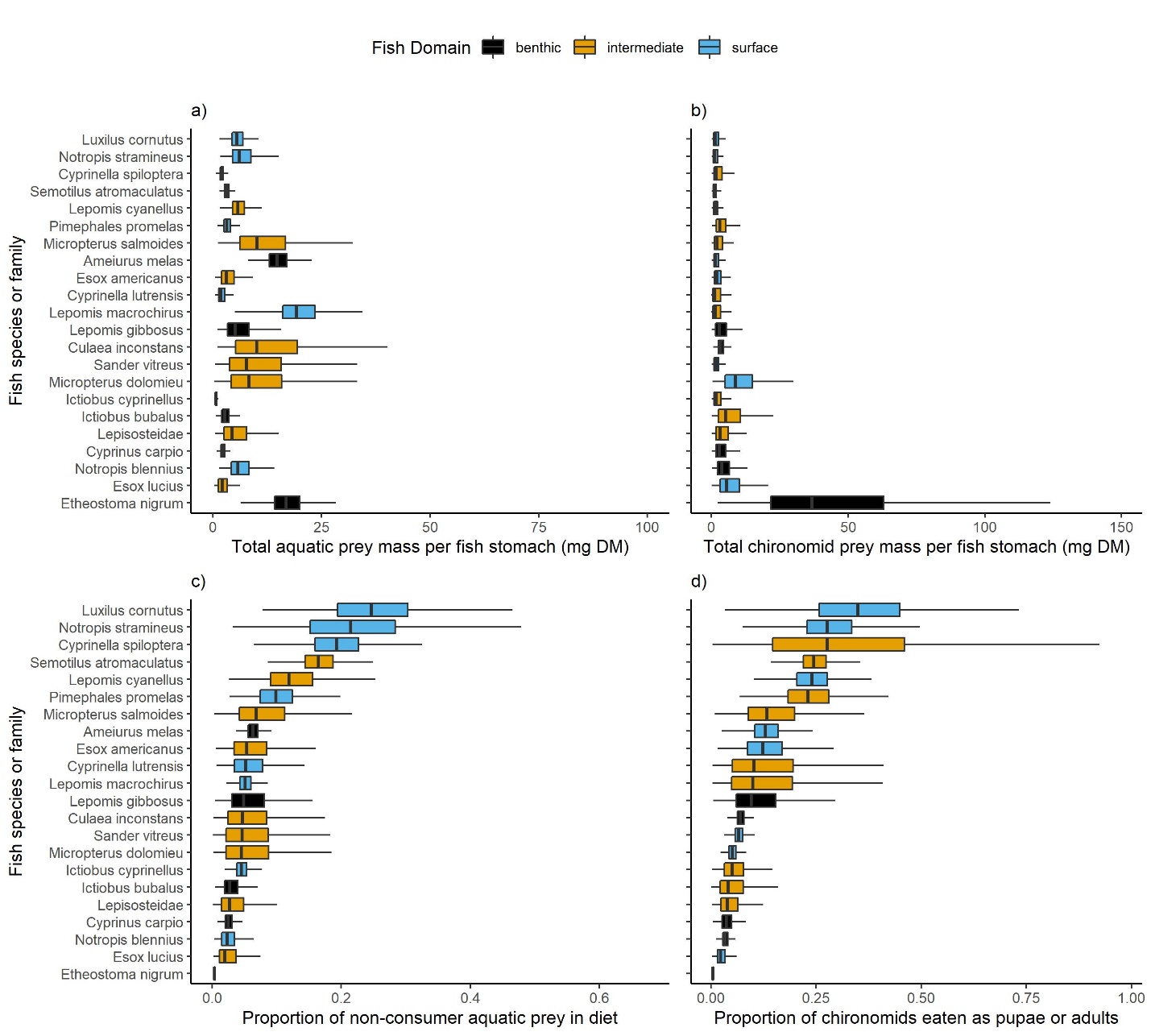
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Figure S2. Prey mass (mg DM) per stomach of each fish species for a) total aquatic prey and b) total chironomid prey. The bottom row shows the proportion of all aquatic prey that were eaten as c) non-consumers or d) the proportion of all chironomids that were eaten as adults or pupae. Boxplots show the posterior distribution for each fish species, including the median and interquartile range with lines ranging from the lowest to highest 1.5% posterior quantiles. All panels are sorted by the median proportion of non-consumers in diets.