CURRENT VELOCITY AND FLOW MEDIATED DIETS OF LARVAL FISHES

by

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ABSTRACT

Purposes of this study were to test two theories relating to food consumption of larval stream fishes. Flow-pulse feeding theory states that larval fish food consumption will be greater following nutrient-rich flow pulses. Drift-feeding theory states that larval fishes enter the drift at night to consume food items under the protection of darkness. Objectives of this study were to quantify gut fullness and occurrence and abundances of food items consumed among larval fishes taken during subsistence flow, base flow, and several high flow pulse tiers (e.g., one per season, one per year) and between larval fishes taken during the day in slackwater habitats and larval fishes taken during the night in swift water habitats. During a one year period of observation among four sites and two rivers, mesolarval of obligate riverine taxa (i.e., Cyprinidae, Catostomidae, Percidae) had greater gut fullness within 28 d following a 1 per season flow event than those taken within 28 d following subsistence flow, base flow, 2 per season flow event. Greater gut fullness during a 1 per season flow event was attributed to greater numbers of copepods and detritus consumed. However, gut fullness and occurrences and abundances of food items consumed by metalarvae were independent of flow. Among mesolarvae and metalarvae collectively and among taxa, gut fullness was greater during the day for fishes taken in slackwater habitat than those taken at night from swift water habitats. Larval fishes within lowland rivers of western gulf slope drainages of Texas conformed only partially to larval fish feeding theories. Drift-feeding theory likely is not a mechanism to explain larval drift at night, and the value of flow pulses to

larval fish feeding and subsequent recruitment was not consistent among larval life

stages.   Nevertheless, this study documents for the first time larval fish food

consumption in lowland rivers and establishes a process to quantify the value of flow

tiers relevant to the stream fish community.

CHAPTER I

Introduction

The Natural Flow Paradigm describes riverine and stream communities as
dependent upon the dynamic character of stream flows (Poff et al. 1997). In part, the
dynamic character of stream flows produces a gradient of flows, ranging from
subsistence to high flow pulses, and a gradient of current velocities, ranging from slack
water (e.g., stream margin, backwater) to swift water (e.g., main channel, riffles) habitats
(Amoros and Bornette 2002).   Temporal and spatial availability of flows and current
velocity gradients are related to larval fish occurrences and abundances. Temporally,
swift water transport nutrients and food for larval fishes downstream, especially during
high flow events (Poff et al. 1997). Spatially, larval fishes move from slackwater habitats
(e.g., channel margins, backwaters) during the day to swift water habitats (mid channel,
runs) at night (Armstrong and Brown 1983, Muth and Schulbach 1984, Gadomski and
Barfoot 1998, Williams 2010, Boehler and Baker 2013).

Flowing waters transport food or create environments conducive for
autochthonous generation of nutrients (Polis et al. 1997). Through time, flow pulses
acquire nutrients and organic matter from terrestrial runoff, by inundation of flood plains,
and by flushing of instream nutrients (Junk et al. 1989). Nutrients are transported
downstream, where they become available to the biotic community (e.g., zooplankton
and macroinvertebrates; Brittain and Eikeland 1988, Thorp and Delong 1994, Górski et
al. 2013). Nutrient inputs are beneficial to growth and survival of stream fishes (Junk et
al. 1989, Schlosser 1991), but. Larval stream fishes consume a variety of aquatic and
terrestrial items, including zooplankton (i.e., copepods, cladocerans, ostracods, and

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rotifers), algae, seeds, detritus, and aquatic substrates (Muth and Snyder 1995, Childs et al. 1998, Lemke et al. 2003). Among obligate riverine fishes (i.e. fluvial specialists that require flowing water for all or part of their life cycle), cyprinid and percid larvae consume chironimids (Strange 1993, Muth and Snyder 1995), ephemeropterans, plecopterans, and trichopterans (Jones and Maughan 1989) along with incidental or purposeful consumption of substrata, fibrous vascular plant material, and seeds. Larval catostomids consume large amounts of organic debris consisting of amorphous detritus, diatoms, algae, and terrestrial vegetation (Muth et al. 1998, Seegert 2010), chironomids (Seegert 2010), and substrata (Runyan 2007). However, interrelatedness of fish food consumption and flow pulses are only broadly linked but are thought to have a strong effect on food availability (Schlosser 1991). A contrasting idea is the low flow recruitment hypothesis which states that food concentrations will be higher during low flow conditions (Humphries et al. 1999). Yet diversity of food items are created under higher flow conditions enhancing recruitment success (Ferrari et al. 1989, Nunn et al. 2007).

Diel spatial movement in larval fishes between slackwater habitats during the day and swift water habitats at night is a common riverine phenomenon worldwide. Multiple mechanisms are proposed to explain the pattern (Pavlov 1994, Gadomski and Barfoot 1998, Roach and Winemiller 2011). Access to abundant food resources drifting in the swift water habitat at night (Muth and Schmulbach 1984) while minimizing predation risk under the cover of darkness (Hugie and Dill 1994) is one proposed mechanism. Drift feeding theory of Muth and Schmulback (1984) is supported by similar diel drifting patters of aquatic invertebrates (Brittain and Eikeland 1988, Huhta et al. 2000), which are

likely food resources for larval fishes. However, Blaxter (1986) contends that larval freshwater fishes are primarily visual feeders and, therefore, likely not actively feeding at night. Field observations, though limited, found that night-time food consumption by larval fishes range between lower at night when compared to day (Mills et al. 1985) to no differences between night and day (Childs et al. 1998), suggesting that night-time drift is not a response to accessing food resources but that larval fishes are feeding at night.

Purposes of this study were to quantify the relationship between stream flow and larval fish food consumption, and to compare between day and night feeding in two lowland rivers of western gulf slope drainages in Texas. Water quantity of both lowland streams (Guadalupe River and San Antonio River) is currently managed under a recommended flow regime, but current recommendations were set by a stakeholder process and in need of validation to refine or refute that the recommendations are adequate to maintain a sound ecological riverine environment. Current recommendations consist of flow tiers (i.e., subsistence flows, base flows, and several magnitudes of high pulse flows), developed from central tendencies of historical flows at a river site with a USGS gaging station (Guadalupe, San Antonio, Mission, and Aransas River and Mission, Copano, Aransas, and San Antonio Bay Basin and Bay Expert Science Team [GSA BBEST] 2011) but with modifications by stakeholders (Guadalupe, San Antonio, Mission, and Aransas River and Mission, Copano, Aransas, and San Antonio Bay Basin and Bay Area Stakeholders Committee [GSA BBASC] 2011) and regulatory agency (Texas Commission on Environmental Quality [TCEQ] 2012). Infrastructure within the Guadalupe and San Antonio river basins is not adequate to maintain magnitude and timing of the recommendations. Instead, recommendations guide water quantity

managers and harvesters on when to allow water diversions or not. Given that allochthonous and autochthonous nutrients are directly related to flow pulses, I predict that gut fullness or uniqueness of food items consumed will increase along higher flow tiers. In addition, I predict that gut fullness or uniqueness of food items consumed would be greater at night than during the day, if larval fish drift because of abundance of food items in the drift at night (i.e., drift-feeding theory). Objectives of this study were 1) to identify food items and calculate percent foregut fullness in mesolarvae and metalarvae fishes taken from four sites on the lower Guadalupe River and San Antonio River during the night from swift water drift and during the day from slackwater habitats, and 2) to relate gut fullness to a flow tier and either night or day feeding. Relationships between larval fish feeding and flow tiers or night and day feeding were assessed across taxonomic group and season. We also quantified gut contents by taxonomic group (genera for mesolarvae; genera and species for metalarvae) and by season to report for the first time temporal and species patterns in larval fish food consumption within a western gulf slope stream.

Methods

Study Area

The Guadalupe and San Antonio rivers originate from spring outflows of the karst Edwards Plateau region of central Texas, flow east-southeasterly onto the lowland or coastal plains of Texas, and merge together before emptying into San Antonio Bay (Gulf of Mexico). Lowland reaches of the Guadalupe and San Antonio rivers are roughly delineated by the I-35 corridor. Springs of the Edwards Plateau and various lowland sand

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and alluvium aquifers support base flows in the lowland reaches, though base and pulse flows are regulated by numerous dams within the Guadalupe-San Antonio basin (Perkin and Bonner 2011). Spring outflows of the upper San Antonio River are currently ephemeral. Base flow is now supported primarily by wastewater return from the City of San Antonio (Miertschin, J. and Associates, Inc. 2006, Upper San Antonio River Watershed Protection Plan, Austin, Texas).

Field collections

Two sites were selected on the lower Guadalupe River (Seguin at County Road 1117, 29°32'12"N,97°52'50"W; Cuero at Hwy 72, 29°08'60"N,97°18'57"W) and on lower San Antonio River (Falls City at Hwy 81, 28°57'25"N, 97°58'48"W; Goliad upstream from Hwy 183, 28°39'43"N, 97°23'28"W). Sites were selected based upon availability of site-specific environmental flow recommendations and USGS gaging stations (GSA BBEST 2011) with sufficient longitudinal spacing to draw inference for the lowland reaches. Seguin Site does not have a site-specific environmental flow recommendation. However, it was selected instead of Gonzales, which has a site-specific environmental flow recommendation, because Seguin is located about 50 km farther upstream from Cuero than Gonzales, increasing longitudinal spacing of sites to about 100 river km between sites. Distance between Falls City and Goliad on the lower San Antonio River is about 80 river km. Environmental flow recommendations at the Gonzales were applied to the Seguin Site. Justifications for this application includes base flows at these two sites are similar (418 cfs) and both are regulated by an instream dam within 11 km of each gaging station. Gonzales site was selected for an environmental flow recommendation by

the GSA BBEST (2011) because of the lengthy period of flow records (since 1940; Seguin since 2006).

Sites were sampled every other week from March 2012 (San Antonio River) or May 2012 (Guadalupe River) to September 2012 during the reproductive season for most fishes within the area and once per month from October 2012 to March 2013. Larval fishes taken at night were harvested with ichthyoplankton drift nets (30.48 x 45.72 cm; mesh size: 500 μm). At each site, three drift nets were placed across the river channel (run habitat) among relatively slow (Net 1), moderate (Net 2), and swift currents (Net 3), capturing available current velocity gradients. Drift nets were installed below water surface and held in place by two metal fence posts. Each net was set two hours prior to sunset (Set 1) and fished four hours after sunset in two hour increments (Set 2 and Set 3) for three sets totaling six hours. Larval fishes taken during the day were harvested with a seine (1 x 2.5 m; mesh size: 1.59 mm^2). Up to five slackwater habitats (stream margins, backwater and eddy habitats) were targeted for sampling, when available. Slackwater habitats were not sampled with seines during the night, and drift nets were not set during the day because peak drifting periods of larval fish begins at sunset and peak drift drops around midnight (Pavlov 1994).

Chemical and physical habitat parameters and effort were recorded for each drift net and seine haul. Water temperature (°C), dissolved oxygen (mg/l), and specific conductance (μS/cm) were measured with an YSI Model 85 multiprobe each time a net was emptied or after each seine haul. Water depth (m) and currently velocity (m/s) were measured before, during, and after a net set. Nets were emptied every two hours or until current velocity in front of net indicated reduced filtering capacity attributed to fullness.

Once starting current velocity was reduced by 10% (indication of fullness) or after two

hours, nets were removed from the metal post, sides were rinsed by gentle agitation, and

contents were concentrated in terminal holding cup. Cup was detached from the net, and

items were washed with 4% formalin into a plastic bag. Items remaining in the net also

were placed into the plastic bag. Net and cup were rinsed with river water and reattached

to metal fence post. For daytime seine hauls, slackwater habitats were sampled with

multiple seine passes. After each pass, seine hauls were placed on shore, and larval

fishes were selected with forceps and placed in 4% formalin. Following fish harvest,

water temperature (°C), dissolved oxygen (mg/l), and specific conductance (µS/cm) were

measured with an YSI Model 85 multiprobe. Length and width (m) of sampled

slackwater habitat was measured. Mean area of available slackwater habitats were

typically small (range: 2.5 to 7 m^2). Water depth (m) and current velocity (m/s) were

taken from a representative area of each habitat sampled.   Percent vegetation and

substrate type (i.e., silt, sand, gravel, and cobble) were visually estimated.

Laboratory Methods

Contents taken from drift nets and seine hauls were rinsed with water in a 500 µm

sieve. Fish were sorted from detritus and invertebrates. For drift contents with large

amounts of coarse particulate matter (CPM) and invertebrates, two sorters independently

examined the contents to remove fish. Later, macroinvertebrates were separated from

CPM. Thus, contents of each drift net was sorted and checked for larval fishes three

times.   Larval fishes were classified according to life stages (Snyder et al. 2005):

mesolarvae (11 to 36 days post hatch; with complete gut tract), metalarvae (37 to 60 days

post hatch, with pectoral fins or buds). Protolarvae (<11 days post hatch; with yolk) were excluded for further analyses. Identification was to the lowest practical taxonomic levels with the assistance of larval fish keys (Auer and Fuiman 1982; Wang and Reyes 2008) but primarily by developing larval fish key specific to the drainage. Family traits were noted using pigment and morphological characteristics. Juvenile fish were identified using similar pigment and other morphological traits specific to adult species characteristics, and these characters were backtracked to determine species of mesolarvae.

Once all fish were identified for each drift and seine haul, up to five individuals of each species, when available from each season, were selected randomly for gut content assessment. Gut contents were taken from the foreguts (esophagus and stomach; Govoni et al. 1986) only to ensure that food items were not degraded due to mastication and that items were consumed during appropriate time period that was sampled. Foregut evacuation rates range from 20 to 45 min in larval fishes (Nobel 1973; Ruppel 2014, unpublished data). Larval fish were place in deionized water on depressed microscope slides and foreguts were removed by making a small incision along the abdomen and then removing the intestinal tract. Gut fullness was estimated by the percentage of items relative to the area of the foregut. Foregut items were removed by tearing the foregut open on top of the depressed slide. Items were identified to the lowest practical taxonomic level using a 40x compound microscope and enumerated. Macroinvertebrates were identified to order level, and zooplankton were identified from genus through class (resolution dependent on level of mastication and chemical digestion). Detritus was defined as unidentifiable organic matter (Swift et al. 1979).

Statistical Analysis

Percent gut fullness was calculated for mesolarvae (all and by taxa) and

metalarvae (all and by taxa). Differences in percent gut fullness was tested between

larvae taken at night and during the day, among drift net sets (2 and 3), and among flow

tiers using arc-sine transformed data and with an analysis of variance ($\alpha = 0.05$) followed

by a Fisher's LSD. Prior to analysis, the relationship between percent gut fullness and

lunar cycle (i.e., a potential confounding variable; brighter nights would be positively

related to percent gut fullness) was assessed with analysis of variance. A relationship

was not detected, and lunar cycle was removed from subsequent analysis. In addition,

differences in occurrence and abundance of food items consumed were tested between

larvae taken at night and during the day, among drift net sets (2, and 3), and among flow

tiers with analysis of similarities (ANOSIM; PRIMER-E v. 6.0; Plymouth Marine

Laboratory).

Flow tier treatments followed those published by GSA BBEST (2011) for each

site: subsistence flow was defined as median flow of the $0 - 10$th percentile of flows

reported during the period of record, ranked from lowest to highest; base flows were low

(25th percentile), medium (50th percentile) and high (75th percentile); and flow pulses

ranged from 2 per season events to 1 per year events (see Science Advisory Committee

[SAC] 2011), for specific calculations). Though magnitude of flow for a tier differed

among sites, each tier category represented the same proportion of the flow record. Thus,

a tier category (e.g., medium base flow) could be grouped across sites and through time,

producing replicated and independent experimental units. Available nutrients, larval fish

prey items, and percent gut fullness likely are not instantaneous with current flow conditions. For example, a flow pulse could generate nutrients and larval fish prey items at a site for several weeks though the flow might return to base flow conditions. As such, a lag-time of 28 d was subtracted from the day of larval fish capture. Highest flow within the 28-d period was classified as a flow tier and assigned to the percent gut fullness. A 28-d period was selected because it is the reported recolonization rate of macroinvertebrates following a high flow pulse (McLay 1968). In other words, a high flow pulse disrupts the benthos, sending macroinvertebrates into the drift for up to 28 d, thus generating food items up to 28 d for larval fish to consume.

Results

Foreguts were quantified from 187 mesolarvae, consisting of six taxonomic groups (i.e., *Cyprinella lutrensis*, *Notropis*, *Pimephales vigilax*, *Carpiodes carpio*, *Moxostoma congestum*, and *Percina carbonaria*). Thirty–five mesolarvae were taken from slackwater habitats during the day, and 152 were taken collectively from two drift sets at night (Table 2). Foreguts were empty in 9% of mesolarvae taken from slackwater habitats and 64% taken from the drift. Among day and night collections, foreguts were fuller ($F = 43.34$, df = 2,184, $P < 0.01$) during the day from slackwater habitats (mean $\pm$ 1 SD; 34% $\pm$ 34) than at night from drift at Set 2 (6% $\pm$ 18) and Set 3 (2% $\pm$ 7). Within slackwater habitats, number of categorical contents items was 19 across all mesolarvae, and items uniquely consumed were Oligochaeta, Tardigrada, and Copepoda adults. Most abundant items consumed weighted by gut fullness were Chlorophyceae (10%), Copepoda adults (6%), and Diptera (3%). In contrast, mean gut fullness ($\pm$1 SD) for

mesolarvae in the drift was 4% (13) for Set 2 and Set 3 combined. Number of categorical content items was 17 across all mesolarvae, and items uniquely consumed were invertebrate eggs and Mollusca glochidia. Most abundant items consumed weighted by gut fullness were Diptera (0.9%), detritus (0.7%), and Chlorophyceae (0.6%).

Foreguts were quantified from 123 metalarvae, consisting of three taxonomic groups (i.e., *Cyprinella lutrensis*, *Notropis*, *Pimephales vigilax*). Fifty–seven metalarvae were taken from slackwater habitats during the day, and 66 were taken collectively from two drift sets at night (Table 2). Foreguts contained at least one content item in all metalarvae taken from slackwater habitats and were 24% empty in those taken from the drift. Among day and night collections, foreguts were fuller ($F = 22.18$, df = 2,120, $P < 0.01$) during the day from slackwater habitats (45% ± 28) and night from drift at Set 2 (34% ± 36) than drift at Set 3 (mean ± 1 SD; 10% ± 12). Within slackwater habitats, number of categorical contents items was 13 across all metalarvae, and items uniquely consumed were Copepoda larvae, Hydrachnidae, Rotifera, and Chlorophyceae. Most abundant items consumed weighted by gut fullness were detritus (10%), Diptera (5%), and Chlorophyceae (5%). Within drift at Set 2, number of categorical contents items was 12 across all metalarvae, and items uniquely consumed were Dorylaimidae, *Daphnia*, and Podocopida. Most abundant items consumed weighted by gut fullness were unidentifiable invertebrates (12%), Diptera (7%), and detritus (7%). Within drift at Set 3, number of categorical contents items was 12 across all metalarvae, and items uniquely consumed were a nematode egg and *Heteromeyenia*. Most abundant items consumed weighted by gut fullness were unidentifiable invertebrates (3%), detritus (3%), and Diptera (2%).

Foregut fullness differed among flow tiers for mesolarvae but not metalarvae. Foreguts were fuller ($F = 8.07$, df = 2, 32, $P < 0.01$) during one per season high flow pulses (mean ± 1 SD; 60% ± 41) among mesolarvae during the day from slackwater habitats ($N = 35$) than at two per season high flow pulses (9% ± 13) and base flows (24% ± 20). Similarity of content items differed among flow tiers (Global $R = 0.132$, $P = 0.04$) for mesolarvae with at least one stomach content item ($N = 32$). Among one per season high flow pulses (N of events = 1 among four sites; March), number of categorical contents items was 18 across all mesolarvae, and items uniquely consumed were Bryozoa, Oligochaeta, Tardigrada, Hydrachnidae, Copepoda Larvae, Ostracoda, and detritus. Most abundant items consumed weighted by gut fullness were Copepoda adult (19%) and Chlorophyceae (12%), Copepoda larvae (5%), and detritus (5%). Number of categorical contents items was four across all mesolarvae among two per season high flow pulses (N of events = 2 among four sites; July) and 10 across all mesolarvae among base flows (N of events = 3; June, July, August). Items consumed during base flows and two per season high flow pulses but not one per season high flow pulses were unidentifiable invertebrates. Most abundant items consumed weighted by gut fullness were Chlorophyceae (10 – 11%), Diptera (4%), and *Daphnia* (3%). Fullness of foreguts did not differ ($F = 0.93$, df = 4, 147, $P = 0.45$) among flow tiers for mesolarvae during the night from drift habitats ($N = 152$). Similarity of content items did not differ among flow tiers (Global $R = 0.002$, $P = 0.47$) for mesolarvae with at least one stomach content item ($N = 55$) combined among night collections. Fullness of foreguts did not differ ($F = 1.79$, df = 1, 54, $P = 0.19$; $F = 0.24$, df = 3, 62, $P = 0.87$) among flow tiers for metalarvae during the day from slackwater ($N = 57$) or among metalarvae during the night from drift

habitats ($N = 66$). Similarity of content items did not differ among flow tiers for metalarvae during the day (Global R = 0.003, P = 0.41) or for metalarvae at night (Global R = − 0.033, P = 0.75).

Foregut items differed among months for mesolarvae but not metalarvae. Similarity of content items differed among months (Global R = 0.12, $P < 0.01$) for mesolarvae with at least one stomach content item (N = 87) combined among day and night collections. In order of similarity, content items in April and May 2012 were 59% similar because of paucity of content items, moderate amounts of detritus, and low amounts of sand. Content items in June 2012 and January 2013 were 58% similar because of moderate amounts of Chlorophyceae and low amounts of sand. Content items in March and July 2012 were 26% similar because of large amounts of Chlorophyceae and moderate amounts of Ostracoda and sand. Otherwise, numbers and amounts of contents items varied considerably among months and were not consistent within season. Numbers of categorical content items ranged from one item (unidentifiable invertebrates) in two individual mesolarvae in September 2012 to 18 items among 12 mesolarvae in March 2012. At times, Diptera (29% of gut fullness), Copepoda adults (17%), Chlorophyceae (12%) composed a large proportion of gut fullness, yet only in one month and not consistently among months. Similarity of content items were not different among months (Global R = –0.019, P=73) for metalarvae with at least one stomach content item (N = 107) combined among day and night collections. Numbers of categorical content items ranged from three items (N = 1 mesolarvae in November 2012) to 15 items in May (N = 28) and July (N = 35) 2012. Excluding November with only N = 1, six content items (i.e., Chlorophyceae, Diatoms, Filamentous algae, detritus, and sand) occurred in

every month, and four content items (i.e., *Daphnia*, Diptera, Trichoptera, and unidentifiable invertebrates) were identified in five of the six months. Across months, detritus (8% of gut fullness), Diptera (5%), unidentifiable invertebrates (4%) composed the largest proportions of gut fullness.

Foregut food items of mesolarvae and metalarvae differed among taxa. Similarity of content items differed among taxonomic groups (Global $R = 0.157$, $P < 0.01$) for mesolarvae with at least one stomach content item ($N = 87$) combined among day and night collections. In order of similarity, content items between *C. carpio* and *M. congestum* were 54% similar because of the diversity of contents items shared ($N = 14$). Content items between *C. lutrensis* and *Notropis* were 44% similar because of low amounts of unidentifiable invertebrates, Copepoda adult, Rotifera, Diatoms, and sand. Content items between *P. vigilax* and *P. carbonaria* were 36% similar because of moderated amounts of *Daphnia*, detritus, and low amounts of unidentifiable invertebrates, Diatoms, and Chlorophyceae. Content items shared by all taxonomic groups comprised of Diatoms ($< 0.1 - 0.6\%$), Chlorophyceae ($0.8 - 10\%$), detritus ($0.2 - 8\%$), and sand ($0.5 - 5\%$). Similarity of content items differed among taxonomic groups (Global $R = 0.073$, $P = 0.014$) for metalarvae with at least one stomach content item ($N = 107$) combined among day and night collections. Content items between *C. lutrensis*, *Notropis*, and *P. vigilax* were 53% similar, consuming Trichoptera, Chlorophyceae, and detritus at about the same amounts but *C. lutrensis* differed because of the uniquely consumed items unidentifiable invertebrates, Podocopida, Darwinuloidae, a nematode egg, Dorylaimidae, Heteromeyenia, and high amounts of Diptera.

Discussion

Initial predictions on timing and flow relationships of larval fish feeding were partially supported in this study. In support of Flow-Pulse feeding theories (Junk et al. 1989, Schlosser 1991), I predicted that mesolarvae and metalarvae would consume greater amounts of food or unique food items following flow pulses but found that only mesolarvae consumed greater amounts of food during a 1 per season high flow pulse when compared to base flow and 2 per season high flow pulses. In support of the Drift-Feed Theory (Muth and Schmulbach 1984), I predicted that larval fishes drifting at night would consume greater amounts or unique food items but found that mesolarvae and metalarvae consumed less food and only a few unique food items at night. In addition to testing these predictions, I found that larval fishes within two representative streams of the western gulf slope drainages consumed a variety of food items, primarily from the benthos in slackwater habitats during the day.

In this study, gut contents of mesolarvae ranged from near equal amounts of sand, detritus, and crustaceans in *P. vigilax*, to a diversity of items, including sand, detritus, algae, crustaceans, and benthic insects but with a propensity for benthic aquatic insects in *Notropis*, crustaceans by *M. congestum*, algae by *C. lutrensis*, and detritus by *C. carpio*, to primarily benthic aquatic insects with <1% sand in *P. carbonaria*. Collectively, mesolarval gut contents are consistent with Goldstein and Simon (1999) trophic guild classification of benthic invertivore and benthic invertivore/herbivore. Benthic feeding strategies are inferred by the consumption of inorganic matter (i.e., sand; Childs et al. 1998) and aquatic insects that associate with the benthos (Dahl and Greenberg 1996). Though mesolarvae are grouped into similar guilds, trophic modes likely differed. Near

equal amounts of sand, detritus, and crustaceans by *P. vigilax* suggest a scooping trophic

mode, which is reported for congener adult *P. notatus* and *P. promelas* and other

cyprinids (e.g., *Hybognathus amarus*; Coyle 1930, Goldstein and Simon 1999; Magana

2009). Large proportion of aquatic insects and low amounts of sand, along with trophic

modes reported for adult percids (Gray et al. 1997, Goldstein and Simon 1999), suggest a

lie-in-wait trophic mode for mesolarval *P. carbonaria*. Trophic modes of *C. lutrensis*,

Notropis, *C. carpio*, and *M. congestum* are likely benthic grazers, specifically non-

discriminate benthic invertivores (Goldstein and Simon 1999), similar to adult *C.

lutrensis*, *C. carpio*, and *M. congestum*, which also consume a variety of food items but

primarily benthic invertebrates (Goldstein and Simon 1999, Welker and Scarnecchia

2003, Bean and Bonner 2008). Overall, items consumed by mesolarval fishes in the San

Antonio and Guadalupe rivers are similar to those reported for larval fishes, though not

specifically mesolarvae. In lowland rivers and desert streams, larval fishes consume high

amounts of diptera and detritus, moderate amounts of crustaceans, and sand (Muth and

Snyder 1995, Childs et al. 1998, Runyan 2007, Williams 2010).

Gut contents of metalarvae were generally similar to those of mesolarvae, thus

consistent with benthic invertivore/herbivore trophic guild classification. However,

differences in food item proportions within species suggest diet shifts between larval

stages. As such, some notable differences were observed between mesolarvae and

metalarvae within species. Metalarval *C. lutrensis* consumed greater proportions of

invertebrates than mesolarvae *C. lutrensis*, suggesting a shift to more water column

feeding. Metalarval *Notropis* consumed greater proportions of crustaceans than

mesolarvae *Notropis*. Metalarval *P. vigilax* consumed greater proportions of benthic

aquatic insects and crustaceans and less sand than mesolarvae *P. vigilax*, suggesting a shift from scooper to benthic grazer. Diet shifts are common among larval fish and likely linked to greater mobility as pectoral and pelvic fins become more functional at the metalarval stage (Anneville et al. 2007, Nunn et al. 2007). In neotropic rivers, food item importance shifted from zooplanktonic crustaceans to terrestrial insects as age and size of larval fishes increased (Mérigoux and Ponton 1998), likewise, a shift from zooplankton consumption in larval fishes to adult feeding strategies such as herbivores, invertivores, and piscivores in five of families of fishes was noted by Nunn et al. (2012).

Gut contents differed across months among mesolarvae but not for metalarvae. Difference in the number of items and amount of items consumed were likely attributed to availability of food resources among months and not to differences in mesolarval taxa among months. Food availability was not quantified in this study, but seasonal abundances of aquatic insects, crustaceans, and other taxa in the San Antonio and Guadalupe rivers relating to life-history cycles can be partially inferred from published accounts. Zooplankton reproduction rates are positively correlated to temperature, and organisms, such as daphnids and rotifers, reproduce exponentially around 20°C (Allan 1976). Water temperatures were near 24°C in March 2012, corresponding to frequent consumption of aquatic insects and crustaceans by larval fishes, whereas water temperatures were 15 to 18°C in March 2013, corresponding to infrequent consumption of aquatic insects and crustaceans by larval fishes. In addition, aquatic insect abundance, as inferred by larval fish ingestion, increased during spring and summer months, which is similar to reported seasonal occurrences and abundances of ephemeropterans and dipterans (Ali et al. 1977, Clifford 1982). Monthly and seasonal differences in

mesolarval taxa occurrence potentially can attribute to gut content differences observed in this study. Spawning seasons of fishes differ within the San Antonio and Guadalupe rivers with percids spawning December through April (Folb 2010), catostomids spawning from February through July (Dalquest and Peters 1966, Bean and Bonner 2008) and cyprinids spawning from April through October (Taber 1969, Moyle 1973, Farringer et al 1979). As such, mesolarvae of fishes were taken at different times within the year. However, seasonal or monthly differences were not attributed to fish occurrence differences among months. When gut contents are standardized by species (i.e., March 2012, 91% catostomids; March 2013, all catostomids), *M. congestum* and *C. carpio* consumed 18 diets items with a high occurrence of crustaceans in 2012, which differed from *M. congestum* and *C. carpio* consumption of 12 diet items and the lack of dominance by any one diet item in March 2013. Across all months, the lack of fish taxa effect was attributed to diets of larval fishes feeding at the same trophic guild though mode of food acquisition might differ.

In addition to life-history cycles of prey contributing to availability of food resources, consumption of food items by larval fishes were also influenced by flow pulses. Mesolarvae, consisting primarily of catostomids during the day in slackwater habitats, consumed greater amounts of food items (i.e., novel zooplankton, greater amounts of crustaceans and detritus) associated with a 1 per season high flow event. Likewise, mesolarvae and metalarvae consumption of detritus at night from the drift was greater following a 1 per season high flow event, although overall gut fullness did not differ from that during base flow conditions. Greater gut fullness and consumption of detritus were attributed to pulses of nutrients from terrestrial and upstream sources during

high flow events (Schlosser 1991). Higher consumption of zooplankton by larval fishes following a high flow event also was observed in juvenile Sacramento Splittail (*Pogonichthys macrolepidotus*) in a lowland river of Sacramento-San Joaquin River Delta (Grosholz and Gallo 2006). As for increases in the detritus in the guts of larval fishes, detritus availability increases with moderate flow pulses but are also susceptible to wash out effect, and therefore decreases, within two days of larger magnitude flow pulses (Webster et al. 1987, 1999). However in the San Antonio and Guadalupe rivers, amounts of drifting detritus, quantified as large and coarse POM, were unaffected by flow pulses ranging from subsistence to moderate (2 per season events; Vaughn 2014), although the amount of detritus added to the systems in slackwater habitats were not quantified.

Gut fullness and the number of items consumed were greater during the day than at night (Set 2 and Set 3) for mesolarvae and greater during the day and early night than late night for metalarvae. As such, results of this study did not support the theory that larval fish drift is a response to food acquisition at night (Armstrong and Brown 1983). Low gut fullness and novelty of food items found in nighttime larval fishes likely were not sufficient to regulate large scale drift of larval fishes. However, three unique foods (*Heteromeyenia* gemmoscleres, *Daphnia*, Podocopida) were found in the foreguts of metalarvae at night but only once. Two of the items (*Daphnia* and Podocopida) were found in during Set 2, and along with highly masticated invertebrates (i.e., unidentifiable invertebrates) in other metalarvae during Set 2, likely consumed some items during day light and retained in the foregut past dark, given that gut evacuation rates of larval fishes range between 0.6 to 1.8 h (Noble 1973, Shepherd and Mills 1996). Nevertheless, mesolarval and metalarval fishes fed at night and in the drift, although at a reduced rate.

These findings are consistent with those of Milles et al. (1985), who also reported

decreased consumption in larval Common Dace (*Leuciscus leuciscus*) at night, but are

inconsistent with other studies that suggest (Blaxter 1986) or document (Dettmers and

Stein 1992) that freshwater larval fishes are visual feeders and do not consume food items

at night. As such, the value of nighttime feeding by larval fishes is undeterminable at this

time, but consumption of food at night, qualitatively or quantitatively is not a major

source of nutrients for larval fishes.

Larval fishes feeding primarily on benthic food items during the day in slackwater

habitats and consuming more food items during moderate flow pulses likely is

representative of larval fishes feeding among other lowland streams of the western gulf

slope drainages. However, limitations of this study lessen the inference of study results.

Limitations include low sample sizes from slackwater habitats among flow tiers, limited

range of flow tiers observed during the period of this study, and overall low number of

replications (two lowland streams; two sites each). Ability to increase sample sizes, to

encounter a range of weather-dependent flow tiers, and to adequately replicate the

relationship between gut fullness and flow tiers is likely, given that most of the lowland

streams of the western gulf slop drainages have an instream flow recommendation with

published magnitudes for subsistence, base, and high flow pulses. Though magnitude of

flow differs among streams and reaches of streams, the relative proportion of each flow

tier is similar among streams and reaches (e.g., subsistence flows represent median of

10% of the historical hydrograph) Sabine River, Neches River, Trinity River, San Jacinto

River, Colorado River, Lavaca River, and Nueces River, (Sabine and Neches Rivers and

Sabine Lake Bay Basin and Bay Expert Science Team [SN BBEST] 2009).

Consequently, each site with a USGS flow gauge and an instream flow recommendation represents a potential replicate for further testing. Future results can be combined with the results reported herein to further delineate and test the relationship among gut fullness, number of items consumed, and flow tiers. Quantifying ecological –flow relationships within the context of published instream flow recommendations provide validation of the recommendations, enables an opportunity to refine the recommendations of flow tier magnitude, and is consistent with the approached suggested by McManamay et al. (2013). Otherwise, testing of ecological-flow relationships without context limits predictive power to estimate changes in flow regimes attributed to anthropogenic alterations.

Establishing and testing quantifiable ecological-flow relationships under the theory of the Natural Flow Paradigm (Poff et al. 1997) is the next logical step, following implementation of an instream flow recommendation. As demonstrated herein, relationships can be adequately replicated and tested within a region to gain necessary inference into flow processes regulating stream fish communities. Stream fishes and stream habitats are becoming increasingly threatened as water quantity becomes a greater commodity with climate change and increases in human needs (Meyer et al. 1999, Malmqvist and Rundle 2002, Daufresne et al. 2004, Palmer et al. 2009). As such, water quantity managers face a daunting task of ensuring adequate flow regime to meet the stated goals of water quantity management for societal needs (i.e. consumption and recreation) and additionally sustaining biota into perpetuity (Tennant 1976, Gleick 1998, Bunn and Arthington 2002). Our collective ability to adequately and efficiently quantify ecological-flow relationships under the theory of the Natural Flow Paradigm is

paramount to the success of establishing meaningful instream flow recommendations. As for larval fish feeding, the relationship between flow pulses and benefits to larval fishes was unsupported, except for mesolarvae during a moderate flow pulse. However, feeding is one of many dependent variables to be tested for larval fishes and for fishes in general. Likewise, additional aquatic (e.g., macroinvertebrates, substrate transport) and riparian (e.g., vegetation) components can be tested in order to validate that the flow recommendations are adequate or not for maintaining a sound ecological environment.

Table 1. Percentage of diets items consumed per area of stomach for combined mesolarvae and metalarvae, total number of taxa (N), collected during day (Seine) and night (Drift).

	Food Items	Meso		Meta	
		Drift	Seine	Drift	Seine
Plant	Pollen grain	< 0.1			
Algae	Chlorophyceae	0.6	10		5
	Diatoms	< 0.1	0.3	< 0.1	0.6
	Filamentous algae	<0.1	0.8	0.1	3
Porifera	Heteromeyenia (Gemmosclere)			< 0.1	
Rotifera	Rotifera	< 0.1	1		3
Ectoprocta	Bryazoan statoblast	< 0.1	0.1		
Mollusca	Glochidia	0.2			
Annelida	Oligochaeta		0.3		
Nematode	Dorylaimidae			0.1	
	Nematode egg			< 0.1	
Ecdysozoa	Tardigrada		< 0.1		
Hydracarina	Hydrachnidiae	< 0.1	0.2		4
Crustacean	Copepoda adult		6	0.6	1
	Copepoda larvae	< 0.1	2		4
	Daphnia	0.3	3	< 0.1	
	Ostracoda	0.2	1		
	Darwinuloidea			< 0.1	0.1
	Podocopida			0.2	
Aquatic insect	Diptera	0.9	3	4	5
	Ephemeroptera	0.1	1	1	4
	Invertebrate egg	0.1			
	Trichoptera	0.1	1	0.8	3
	Unidentifiable invertebrate	0.3	0.8	6	
Detritus	Organic detritus	0.7	2	5	10
Inorganic	Inorganic matter	< 0.1	< 0.1		
	Sand	0.6	2	1	2
	Gut fullness	4	34	20	45
	SD	13	34	27	28
	N	152	35	66	57

Table 2. Percentage of diets items consumed per area of stomach for combined mesolarvae and metalarvae, total number of taxa (N), collected during day and night (set 2 and set 3).

	Food Items	Meso			Meta		
		Day	set 2	set 3	Day	set 2	set 3
Plant	Pollen grain		< 0.1				
Algae	Chlorophyceae	10	1	0.2	5		
	Diatoms	0.3	< 0.1	< 0.1	0.6	< 0.1	< 0.1
	Filamentous algae	0.8	< 0.1	< 0.1	3	0.3	< 0.1
Porifera	Heteromeyenia (Gemmosclere)						< 0.1
Rotifera	Rotifera	1	< 0.1	< 0.1	3		
Ectoprocta	Bryazoan statoblast	0.1	< 0.1				
Mollusca	Glochidia		0.3				
Annelida	Oligochaeta	0.3					
Nematode	Dorylaimidae					0.3	
	Nematode egg						< 0.1
Ecdysozoa	Tardigrada	< 0.1					
Hydracarina	Hydrachnidiae	0.2	< 0.1		4		
Crustacean	Copepoda adult	6			1	0.8	0.4
	Copepoda larvae	2	< 0.1		4		
	Daphnia	3	0.7			0.1	
	Ostracoda	1	0.5				
	Darwinuloidea				0.1		< 0.1
	Podocopida					0.4	
Aquatic insect	Diptera	3	2	0.2	5	7	2
	Ephemeroptera	1		0.2	4	2	1
	Invertebrate egg		0.2				
	Trichoptera	1		0.2	3	0.8	0.8
	Unidentifiable invertebrate	0.8	0.4	0.1		12	3
Detritus	Organic detritus	2	0.4	0.8	10	7	3
Inorganic	Inorganic matter	< 0.1		< 0.1			
	Sand	2	0.8	0.4	2	3	0.2
	Gut fullness	34	6	2	45	34	10
	SD	34	18	7	28	36	12
	N	35	68	84	57	26	40

Table 3. Mean (±SD) gut fullness, total number of species (N), subsistence flow (S), base flow (B), 2 per seasons high flow pulse (2/S), 1 per season high flow pulse (1/S), 1 per year high flow pulse (1/Y) for each mesolarval and metalarval taxa among flow.

Larvae	Time	Taxa	N	S	N	B	N	2/S	N	1/S	N	1/Y	N
Meso	Day	C. lutrensis	15			24 (8)	9	9 (5)	5				
		Notropis	5			24 (5)	5						
		P. vigilax	3			22 (13)	3						
		C. Carpio	5							77 (19)	5		
		M. congestum	6							50 (16)	6		
		Percidia	1							35	1		
	Night	C. lutrensis	37			2 (1)	21	12 (11)	9	0	6	20	1
		Notropis	37			2 (2)	19	1 (1)	7	1 (1)	10	0	1
		P. vigilax	43	0	1	5 (2)	20	2 (1)	13	1 (1)	8	0	1
		C. Carpio	8			9 (5)	4	0	1	3 (5)	3		
		M. congestum	11			3 (1)	11						
		Percidia	16	0	2	8 (5)	4	28 (17)	5	9 (9)	5		
Meta	Day	C. lutrensis	35			36 (5)	22			65 (6)	13		
		Notropis	11			47 (5)	5			8 (1)	6		
		P. vigilax	11			53 (9)	6	70	1	69 (18)	4		
	Night	C. lutrensis	31			20 (10)	10	48 (43)	2	27 (8)	16	10 (6)	3
		Notropis	10			13 (8)	3			4 (3)	7		
		P. vigilax	25			8 (4)	6	8 (4)	5	28 (8)	16		

Table 4. Percentage of diets items consumed per area of stomach, total number of species (N), subsistence flow (S), base flow (B), 2 per seasons high flow pulse (2/S), 1 per season high flow pulse (1/S), 1 per year high flow pulse (1/Y) for each mesolarval and metalarval taxa captured during day and night among flow tiers.

	Food Items	Meso Seine			Meso Drift				Meta Seine			Meta Drift			
		B	2/S	1/S	B	2/S	1/S	1/Y	B	2/S	1/S	B	2/S	1/S	1/Y
Plant	Pollen grain					<0.1									
Algae	Chlorophyceae	11	10	12	1	3	<0.1		7	11	3	<0.1	0.2	<0.1	
	Diatoms		<0.1	1	0.1	0.1			0.5	2	0.8	<0.1	0.9	<0.1	
	Filamentous algae	2		0.4	0.1	0.1			5		0.4		<0.1	<0.1	1
Porifera	Heteromeyenia (Gemmosclere)											<0.1		<0.1	
Rotifera	Rotifera	0.6		3	0.1		<0.1		1		7				
Ectoprocta	bryazoan statoblast			0.4	0.1		0.1								
Mollusca	Glochidia				0.8										
Annelida	Oligochaeta			1											
Nematode	Dorylaimidae												0.3		
	Nematode egg													<0.1	
Ecdysozoa	Tardigrada			0.1											
Hydracarina	Hydrachnidiae			0.5			0.1		0.3		0.4		1		
Crustacean	Copepoda adult	0.8		19					3	7	6				1
	Copepoda larvae			5	<0.1				1		2				
	Daphnia	3		5	0.3	3			4		3	0.2			
	Ostracoda			4	0.1	2					0.3				
	Darwinuloidea													<0.1	
	Podocopida											0.6			
Aquatic insect	Diptera	4		3	2	6			4		7	5	4	5	
	Ephemeroptera	2	0.7	1	0.7				4		3			3	
	Invertebrate egg				0.1	0.7									
	Trichoptera	1		1	0.5				1		5	0.0		1	
	Unidentifiable invertebrate	2	0.7		0.2	0.7	0.6	17			11	5	18	9	10
Detritus	Organic detritus			5	1	1	7		8	35		4	4	8	4
Inorganic	Inorganic matter			<0.1	<0.1										
	Sand	0.4		5	2	2	0.4	3	0.9	15	2	2.2	0.3	2.1	
	Gut fullness	25	11	65	9	18	9	20	40	70	50	18	27	31	15
	SD	19	13	38	10	33	14		23		34	24	36	30	7
	N	16	5	11	30	15	9	1	33	1	23	16	5	27	2

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Table 5. Percentage of diets items consumed per area of stomach for each mesolarval taxa, total number of taxa (N), combined for day and night.

	Food Items	C. lutrensis	Notropis	P. vigilax	C. carpio	M. congestum	P. carbinaria
						Taxa	
Plant	Pollen grain	<0.1					
Algae	Chlorophyceae	9	2	0.8	10	5	1
	Diatoms	<0.1	<0.1	<0.1	0.6	0.6	0.1
	Filamentous algae	0.9			<0.1	0.4	0.1
Porifera	Heteromeyenia (Gemmosclere)						
Rotifera	Rotifera	0.3	0.2	0.1	2	0.8	
Ectoprocta	Bryazoan statoblast		0.1		0.5	0.1	
Mollusca	Glochidia			1			
Annelida	Oligochaeta				2		
Nematode	Dorylaimidae						
	Nematode egg						
Ecdysozoa	Tardigrada				0.1		
Hydracarina	Hydrachnidiae				0.1	0.4	
Crustacean	Copepoda adult	0.4	0.2		15	7	
	Copepoda larvae				4	2	
	Daphnia	0.1		2	4	2	
	Ostracoda	1			1	3	4
	Darwinuloidea						
	Podocopida						
Aquatic insect	Diptera	1	4	0.9		0.9	14
	Ephemeroptera	0.1	2		2	1	
	Invert egg			0.8			
	Trichoptera	0.8				1	2
	Unidentifiable invert	1	2	0.3			1
Detritus	Organic detritus	0.2	1	2	8	0.2	5
Inorganic	Inorganic matter				<0.1	<0.1	
	Sand	1	2	2	5	1	0.5
	Gut fullness	17	13	10	54	25	28
	SD	25	13	12	46	35	29
	N	26	13	18	8	13	9

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Table 6. Percentage of diets items consumed per area of stomach for combined mesolarval taxa among day and night, total number of taxa (N), for all months collected.

	Food Items	Mar 2012	Apr 2012	May 2012	Jun 2012	Jul 2012	Aug 2012	Sep 2012	Jan 2013	Feb 2013	Mar 2013
Plant	Pollen grain						<0.1				
Algae	Chlorophyceae	11	<0.1		5	12	0.8		5		0.9
	Diatoms	1			<0.1	<0.1	<0.1			0.3	0.1
	Filamentous algae	0.4			0.9					0.3	0.2
Porifera	Heteromeyenia (Gemmosclere)										
Rotifera	Rotifera	2			0.3	0.2					
Ectoprocta	Bryozoan statoblast	0.4			<0.1						0.2
Mollusca	Glochidia				0.9						
Annelida	Oligochaeta	1									
Nematode	Dorylaimidae										
	Nematode egg										
Ecdysozoa	Tardigrada	0.5									
Hydracarina	Hydrachnidiae	0.1									
Crustacean	Copepoda adult	17			0.3	0.3					
	Copepoda larvae	5									0.1
	Daphnia	4				0.2				13	1
	Ostracoda	3				2	3				0.4
	Darwinuloidea										
	Podocopida										
Aquatic insect	Diptera	3			3		1		9	29	
	Ephemeroptera	1			0.9	0.3					2
	Invertebrate egg		1			0.3					
	Trichoptera	1			0.8						2
	Unidentifiable invertebrate		1		0.9	0.3	2	5			
Detritus	Organic detritus	5	8	4.5	0.8	0.1	1				0.3
Inorganic	Inorganic matter	<0.1			1	4	1		1		<0.1
	Sand	4	0.3	0.5							0.3
	N	12	7	2	26	13	11	2	2	3	9

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Table 7. Percentage of diets items consumed per area of stomach for each metalarval taxa, total number of taxa (N), combined for day and night.

	Food Items	Taxa		
		C. lutrensis	*Notropis*	*P. vigilax*
Plant	Pollen grain			
Algae	Chlorophyceae	4	2	3
	Diatoms	0.2	0.3	0.7
	Filamentous algae	0.1	0.8	3
Porifera	Heteromeyenia (Gemmosclere)	< 0.1		
Rotifera	Rotifera	0.5	2	4
Ectoprocta	Bryazoan statoblast			
Mollusca	Glochidia			
Annelida	Oligochaeta			
Nematode	Dorylaimidae	0.1		
	Nematode egg	< 0.1		
Ecdysozoa	Tardigrada			
Hydracarina	Hydrachnidiae	0.2	< 0.1	< 0.1
Crustacean	Copepoda adult	2	1	5
	Copepoda larvae	< 0.1		2
	Daphnia	0.6	1	4
	Ostracoda			0.2
	Darwinuloidea	< 0.1		
	Podocopida	1		
Aquatic insect	Diptera	7	2	2
	Ephemeroptera	1	< 0.1	4
	Invertebrate egg			
	Trichoptera	2	2	2
	Unidentifiable invertebrates	10		
Detritus	Organic detritus	9	8	6
Inorganic	Inorganic matter			
	Sand	2	0.3	2
	N	60	17	30

Table 8. Percentage of diets items consumed per area of stomach for combined metalarval taxa among day and night, total number of taxa (N), for all months collected.

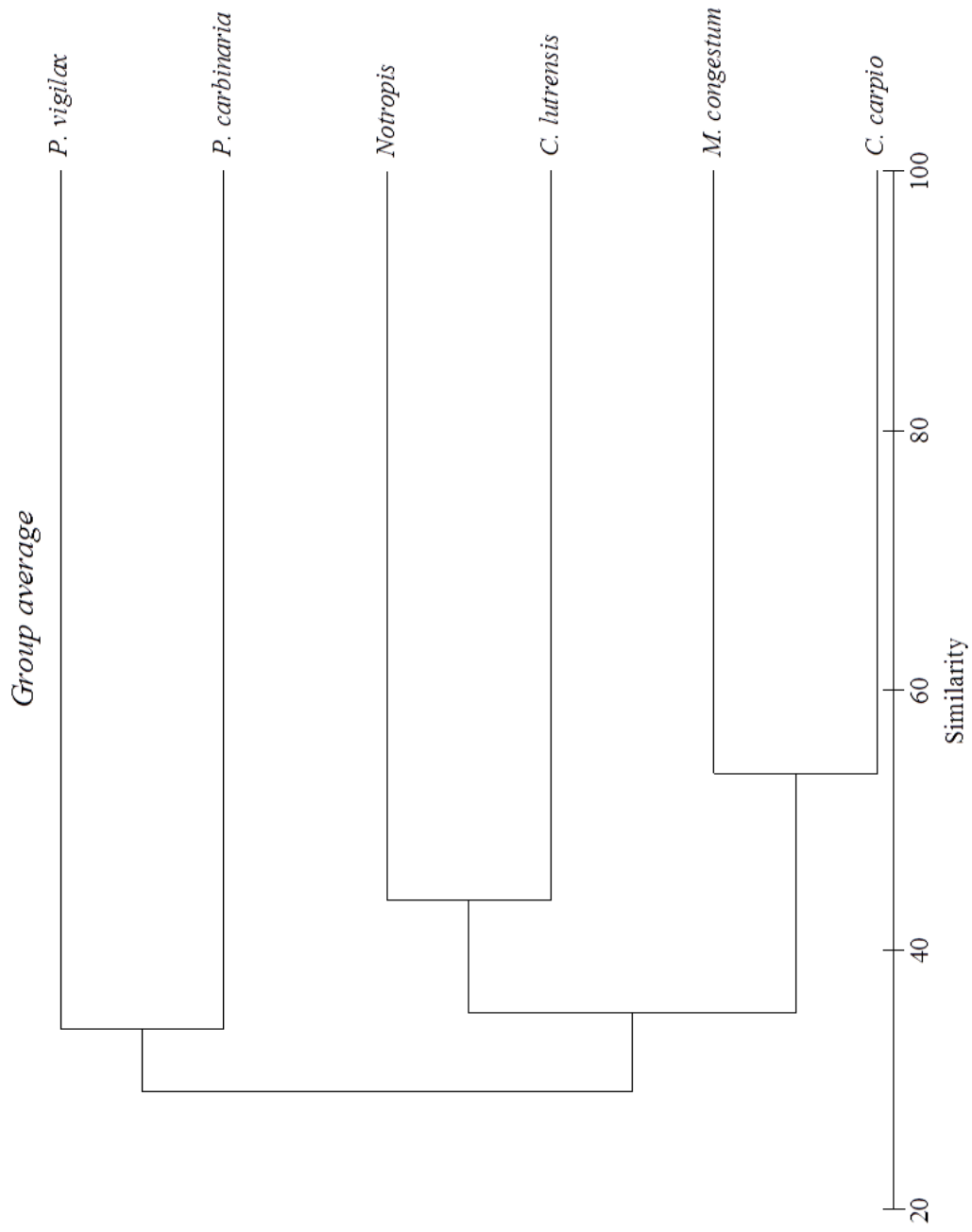| Food Items		May 2012	Jun 2012	Jul 2012	Aug 2012	Sep 2012	Oct 2012	Nov 2012
					Months			
Plant	Pollen grain							
Algae	Chlorophyceae	2	1	3	1	5	6	
	Diatoms	0.2	0.3	0.2	0.7	0.2	2	
	Filamentous algae	<0.1	0.1	2	3	8	2	
Porifera	Heteromeyenia (Gemmosclere)							<0.1
Rotifera	Rotifera	0.3	1	0.3	7	0.2	11	
Ectoprocta	Bryazoan statoblast							
Mollusca	Glochidia							
Annelida	Oligochaeta							
Nematode	Dorylaimidae			0.2				
	Nematode egg	<0.1						
Ecdysozoa	Tardigrada							
Hydracarina	Hydrachnidiae	0.4	0.2			0.8		
Crustacean	Copepoda adult	4	4	2	1			
	Copepoda larvae	0.5	2	0.9				
	Daphnia	2	7	1	0.7	3		
	Ostracoda			0.2	0.1			
	Darwinuloidea							
	Podocopida					1		
Aquatic insect	Diptera	6	8	5	2	3	10	
	Ephemeroptera	3	10	1	2			
	Invertebrate egg							
	Trichoptera	1	0.7	3	2		7	0.5
	Unidentifiable invertebrates	7	5	2		0.6	19	
Detritus	Organic detritus	8	0.9	8	13	12	20	
Inorganic	Inorganic matter							
	Sand	3	2	1	0.3	2	6	
	N	28	15	35	15	9	4	1

Figure 1. Similarity dendrogram based on the diet composition of all mesolarval taxa combined for day and night
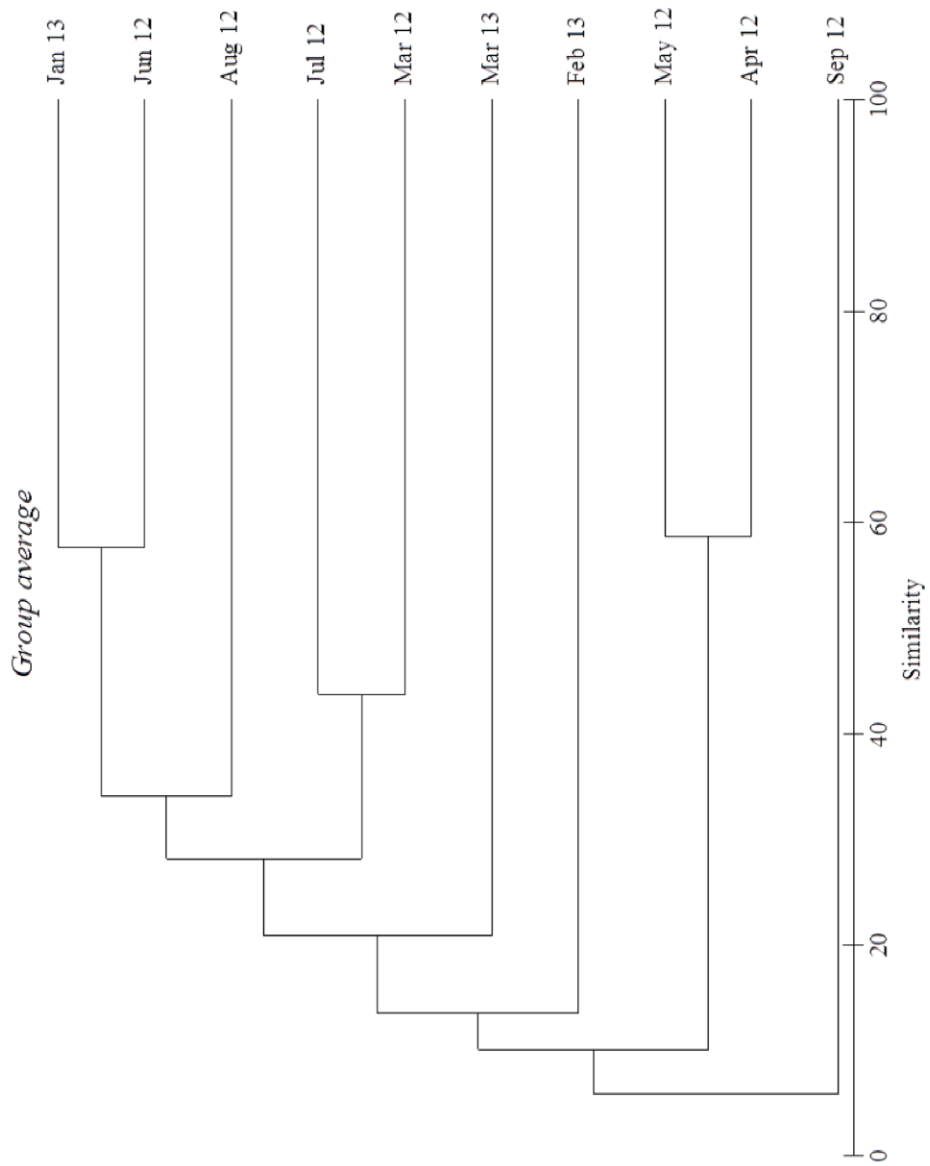
Figure 2. Similarity dendrogram based on the diet composition of all mesolarval taxa across all months
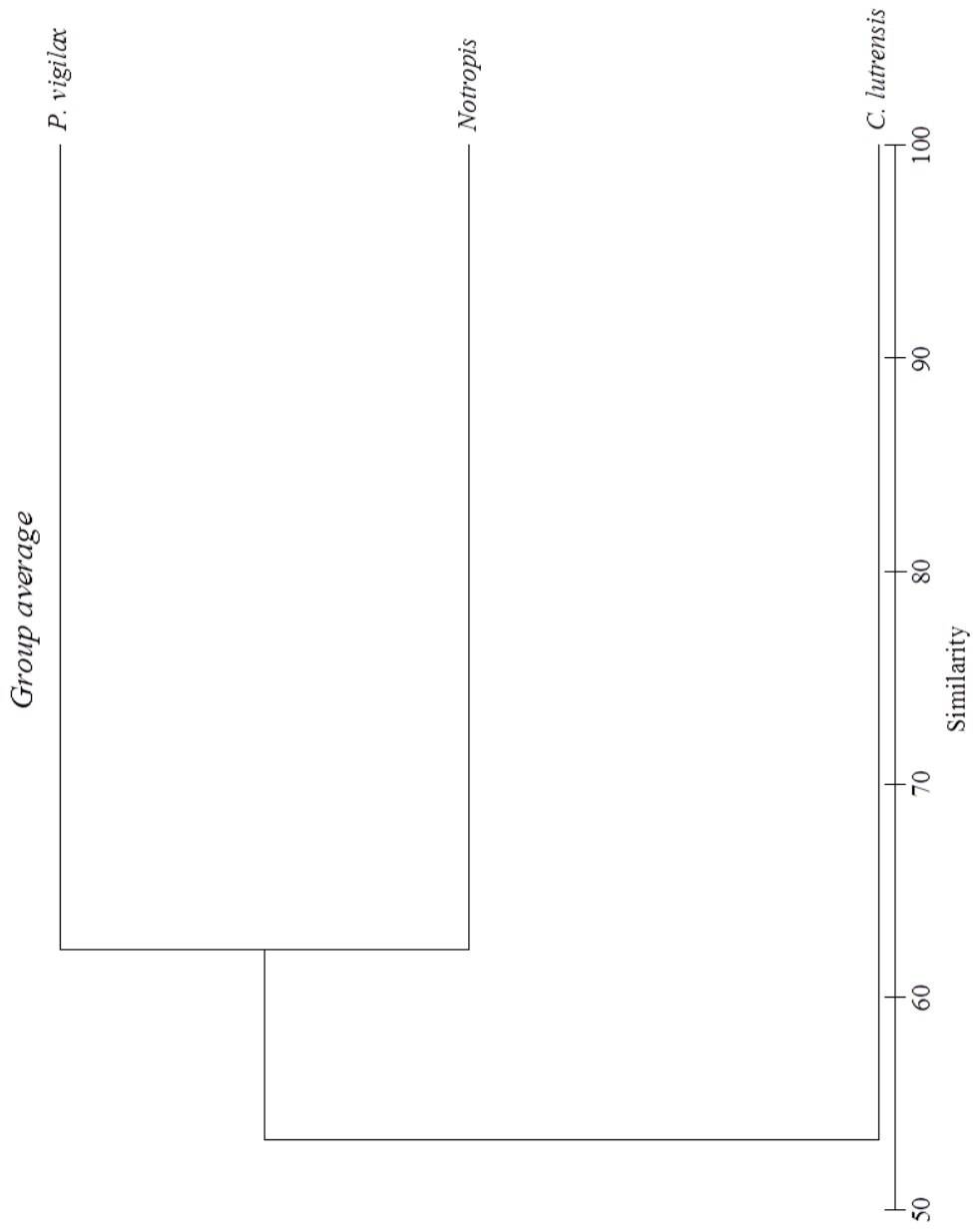
Figure 3. Similarity dendrogram based on the diet composition of all metalarval taxa combined for day and night

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