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Interactions Between Juvenile Estuary-Dependent Fishes and Microalgal Dynamics

by

Ian C. Williams

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
with a concentration in Marine Resource Assessment
College of Marine Science
University of South Florida

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DEDICATION

This work is dedicated to my family, friends, and girlfriend, Jess, for their immense support throughout this process. Thank you.

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ABSTRACT

The ontogenetic movement of juvenile estuary-dependent fishes upstream in estuarine settings is a phenomenon observed around the world. These movements usually coincide with a shift in diet from smaller prey, such as calanoid copepods, to larger prey, such as mysids. However, the mechanism that drives this pattern has yet to be conclusively described. Prior to the current study, zooplankton/hyperbenthos (“zooplankton”), primary production, and water quality data were collected from the Caloosahatchee River estuary in two concurrent and coordinated studies over a two-year period. One of the products of these sampling efforts was a classification of primary-producer types at the sediment-water interface (“depositional states”) along the principal estuarine axis. Four depositional states were described: benthic microalgal dominance (i.e., little or no organic deposition), early phytoplankton deposition, late phytoplankton deposition and post-phytoplankton deposition. Using these classifications as a grouping factor, multivariate analyses were conducted to determine if there were distinct zooplankton communities associated with the four depositional states. An analysis of species indicator values identified the representative taxa for each sediment category. Using the top four returns from the species indicator value analysis for each deposition class, there was clear spatial seriation in zooplankton communities moving upstream from the river mouth: sediment category 1, defined as locations dominated by benthic microalgae that were growing *in situ*, was characterized by hooded shrimp, chaetognaths and estuarine copepods as its indicator taxa; sediment category 2, defined as locations dominated by early phytoplankton deposition, was represented by decapod zoeae, decapod mysis, percomorph fish eggs and postflexion *Anchoa*

mitchilli larvae; sediment category 3, defined as locations dominated by late phytoplankton deposition, had indicator taxa that included two mysid species, a benthic isopod and a parasitic isopod; sediment category 4, defined as locations dominated by post-phytoplankton deposition (i.e., phytodetritus on bottom with little or no phytoplankton overhead), was associated with freshwater copepods, freshwater cladocerans and the freshwater larvae of the insect *Chaoborus punctipennis*. Based on these results, and with the knowledge that juvenile estuary-dependent fishes switch prey items as gape limitations change while they grow, I suggest the mechanism behind young fishes moving upstream as they grow is driven by increasing dependence on larger prey (notably mysids) that are supported by phytoplankton deposition. Depositional states where primary-producer cells exist both in the water column and on the estuary floor (such as sediment category 3) attract larger consumers such as mysids, which feed on both suspended diatom cells as well as phytodetritus, and are a preferred prey item for juvenile estuary-dependent fishes. Furthermore, the importance of fresh-water inflow management is highlighted, as this influences the presence and location of phytoplankton blooms.

CHAPTER ONE:

**ZOOPLANKTON AND HYPERBENTHOS ASSOCIATIONS WITH
PHYTOPLANKTON DEPOSITS IN THE CALOOSAHATCHEE RIVER**

Introduction

Estuaries are important nursery habitats for many marine fish species around the world. The processes that potentially affect estuarine dependence can be highly dynamic but are usually poorly understood (Beck et al., 2001; Able, 2005). An important consideration within estuarine settings is the type of primary production (i.e., phytoplankton vs. benthic microalgae) that takes place at different intensities at different locations; these conditions are dynamic and are strongly influenced by changing freshwater inflows (Radabaugh and Peebles, 2012). Phytoplankton and benthic microalgae are often the dominant basal resources for estuarine primary consumers; in turn, they support biomass pathways that lead to production at higher trophic levels, such as fish, even if the organisms at higher trophic levels do not consume either form of microalgae directly (Houde & Rutherford, 1993; Beck et al., 2001; Kundu et al., 2021). It is therefore important to understand the relationship between the spatial dynamics of these different types of microalgae and the hyperbenthos and zooplankton that feed on them. The importance of these kinds of consumer interactions is increased when considering a large estuary that is greatly influenced by freshwater management, such as the Caloosahatchee River estuary.

The Caloosahatchee River estuary is located in southwest Florida and extends for about 41km. Upstream, the estuary is influenced by freshwater inflows from the Franklin lock and

dam, which connects the Caloosahatchee estuary to fresh water originating from Lake Okeechobee. Downstream, the estuary ultimately mixes with its receiving basin, the Gulf of Mexico. The Caloosahatchee River estuary receives significant freshwater inflows from its watershed, with great seasonal variation (e.g., May 2008 had a mean inflow of 0 (± 0) cubic feet per second and August 2008 had a mean inflow of 5,855 ($\pm 5,997$) cubic feet per second; Tolley et al., 2010). During the wet season, the Caloosahatchee estuary is predominantly fresh, with a salt wedge extending landward from the Gulf of Mexico (Tolley et al., 2010). The estuary provides important nursery habitats for ecologically and economically important fish species including red drum (*Sciaenops ocellatus*), common snook (*Centropomus undecimalis*), spotted seatrout (*Cynoscion nebulosus*), and bay anchovy (*Anchoa mitchilli*), and also acts as a warm-water refuge for manatees (Barnes, 2005). Commercially, the blue crab (*Callinectes sapidus*) provides the largest fishery in the Caloosahatchee estuary, with most fishing effort being concentrated in the middle and upstream regions of the estuary (Barnes, 2005).

The success of estuarine species is strongly correlated with freshwater inflows, as inflows influence a multitude of processes and habitat conditions including salinity regimes/gradients, particle dispersion, larval movement, sediment distribution, and the occurrence of phytoplankton blooms (Drinkwater and Frank, 1994; Hood et al., 1999; Flannery et al., 2002; Kimmerer, 2002; Barnes, 2005; Peebles et al., 2007; Andresen, 2011; Cook, 2014; Black, 2015; Palmer et al., 2015; Radabaugh and Peebles, 2012, Michaud et al. 2022).

Water levels in the Caloosahatchee River Estuary are highly managed and the river has been physically altered from its original state, greatly affecting the timing and magnitude of freshwater inflows into the estuary (Chamberlain and Doering, 1998). The magnitude of freshwater inflow influences where chlorophyll maxima will be found at different times.

Spatially, high freshwater inflows push the chlorophyll maximum downstream and at times even out of the estuary (Andresen, 2011; Radabaugh and Peebles, 2012). The upstream region of the estuary is dominated by phytoplankton deposition, with this trend decreasing downstream, where benthic microalgae are more dominant, particularly during low-flow conditions when the water column is clear enough for light to reach the sediment-water interface (Radabaugh and Peebles, 2012).

Temporally, during the dry spring season, the estuary is likely to have less primary production altogether due to the relative lack of inflow and associated nutrient inputs (Flannery et al., 2002, Radabaugh and Peebles, 2012). Many studies have been conducted in the Caloosahatchee estuary to explore the relationships between freshwater inflow and food webs (Kimmerer, 2002), fish assemblages (Stevens et al., 2010), responses of turbidity, CDOM, benthic microalgae, phytoplankton and zooplankton (Tolley et al., 2010), phytoplankton productivity (Andresen, 2011), decapod zooplankton distribution (Cook, 2014), and dynamic estuarine habitats and zooplankton abundance and distribution (Black, 2015). Palmer et al. (2015) classified 34 benthic species as indicator species for salinity zones within the Caloosahatchee estuary, allowing them to divide the estuary into four distinct zones based on species community structure.

Juvenile fishes whose life cycles depend on estuarine habitats tend to move upstream as they get larger and outgrow smaller prey items such as planktonic copepods (Cyrus and Blaber, 1987; Flannery et al., 2002; Peebles, 2005a; Peebles, 2005b). This upstream movement is often associated with consumption of larger prey items, such as mysids (Peebles, 2005a; Peebles, 2005b). Mysids are an important food source for estuary-dependent fishes including bay anchovy, common snook, red drum, spotted seatrout, sand seatrout, and Gulf flounder (Peters

and McMichael, 1987; McMichael and Peters, 1989; McMichael et al., 1989; Peebles, 2005a; Peebles, 2005b; Peebles et al., 2007). Although the relationship between juvenile fishes and mysids as a prey source has been repeatedly observed, the mechanism that drives juvenile fishes upstream has not been explained. Some of the existing explanations for this phenomenon include predator evasion, the seeking of turbid environments, and increased availability of larger prey types upstream (Cyrus and Blaber, 1987; Flannery et al., 2002; Peebles, 2005a; Peebles, 2005b).

The current study is largely based on data produced by Tolley et al. (2010) and Radabaugh and Peebles (2012), who analyzed zooplankton/hyperbenthos (“zooplankton”) communities and investigated microalgal dynamics along the principal axis of the Caloosahatchee River estuary under variable freshwater-inflow conditions. More specifically, Radabaugh and Peebles (2012) produced a classification scheme to characterize primary-producer biomass at the sediment-water interface (“depositional states”) along the principal estuarine axis. Four depositional states were described: benthic microalgal dominance (i.e., benthic microalgae present with little phytoplankton overhead and little or no phytodetritus on the bottom), early phytoplankton deposition (large phytoplankton bloom overhead with small amounts of phytodetritus on bottom), late phytoplankton deposition (small phytoplankton bloom overhead with large amounts of phytodetritus on bottom) and post phytoplankton deposition (phytodetritus on bottom with little or no phytoplankton overhead). Tolley et al. (2010) provided data for zooplankton abundance at the same times and locations used to characterize depositional states. The database produced by Radabaugh and Peebles (2012) also includes many environmental variables (pH, temperature, salinity, dissolved oxygen, etc.) that could be compared with the zooplankton distributions provided by Tolley et al. (2010).

The objectives of the present study were to 1) determine if significant beta diversity of zooplankton communities existed among the four sediment categories, 2) explain the distinct zooplankton communities based on species autecologies, and 3) determine the strength of various environmental factors on structure of zooplankton communities.

Methods

Data collection and organization

The data used was the product of the Tolley et al. (2010) and Radabaugh and Peebles (2012) studies. Those extensive and comprehensive sampling efforts of the Caloosahatchee River estuary were conducted from May 2008 to April 2010. The estuary was divided into seven sampling zones, with each zone having two sampling stations (upstream and downstream), for a total of 14 stations spanning from San Carlos Bay near the mouth of the river to the Franklin Lock and Dam (Figure 1). The mean distance between adjacent sampling sites was 3.26 (\pm 2.01) km.

Over two years, there were 24 field efforts at the 14 stations that produced a total of 336 observations. For both biological and water-quality data, sampling and data collection occurred at night during flood tides when, generally, larval fishes and invertebrates are more abundant in the water column (Tolley et al., 2010, and the papers cited therein). The sampling effort for the Radabaugh and Peebles (2012) study included the use of an instrument equipped with a YSI 6920 V2-2 sonde with a 6025 chlorophyll fluorometer and depth sensor (calibrated using water-sample extractions and a Turner 10AU benchtop fluorometer), a WET Labs ECO Triplet with a 700 nm scattering meter, a CDOM fluorometer (Ex/Em of 370/460 nm), and a stainless steel

remotely controlled well pump and three surface-sediment samplers (Table 1). The three surface-sediment samplers employed the use of grease plates to collect diatoms after making contact with the estuary floor. The diatom specimens collected by the grease plates could then be categorized as either centric or pennate and, because centric diatoms are generally planktonic, inference was used to classify centric-dominated samples as phytodetritus (Radabaugh and Peebles, 2012).

The resulting databases from the collaboration between the two studies contained biological data as well as environmental data. Two files supplied the data necessary for the initial multivariate analyses. One of these files included sample stations, sediment categories (SedCat1 = benthic microalgae dominance, SedCat2 = early phytoplankton bloom, SedCat3 = late phytoplankton bloom, SedCat4 = post phytoplankton bloom; Radabaugh and Peebles [2012]), taxon names, and taxon concentrations as number of individuals per volume filtered, among other data. The second file contained the station averages for the following environmental variables: distance from river mouth, temperature, salinity, pH, dissolved oxygen concentration, and chlorophyll concentration. (Note: only taxa with occurrence frequencies greater than 10 were included in the data analysis. Also removed from the dataset were gelatinous predators, including hydromedusae, true jellyfishes, ctenophores and siphonophores, as these groups are not consumed by juvenile fishes.)

Data analysis

The dataset used in the analyses of this project is a reorganized version of the data provided by the Tolley et al. (2010) and Radabaugh and Peebles (2012) studies, including sediment categories, average distance from the mouth of the river (km), average temperature (degrees Celsius), average salinity (ppt), average pH, average dissolved oxygen concentration (mg/L), average chlorophyll ($\mu\text{g/L}$) and taxon identifiers. Analyses performed on the data included

nonmetric multidimensional scaling (nMDS), homogeneity of multivariate dispersion (npDISP), permutation-based multivariate analysis of variance (PERMANOVA), canonical analysis of principal coordinates (CAP), distance-based redundancy analysis (dbRDA), and generation of a seriated heat map. The nMDS, npDISP, PERMANOVA, and CAP tests address the question of beta diversity of zooplankton communities across the sediment categories. The dbRDA test is used to reveal any explained variability of zooplankton communities by environmental variables. All analyses were conducted using the Fathom Toolbox (Jones, 2017) in MATLAB (R2021b), except for nMDS and the heat map, which were conducted using PRIMER v7 (Primer-e, Quest Research Limited, Auckland, New Zealand). Iterations in MATLAB were set to 10,000.

nMDS

One method for visualizing dissimilarities between objects (in this study, zooplankton community data), with a specified and small number (2 or 3) of dimensions, can be achieved using nonmetric multidimensional scaling (nMDS) (Legendre and Legendre, 2012). nMDS based on a S17 Bray-Curtis similarity matrix (which specifically measures similarity instead of dissimilarity [Legendre and Legendre, 2012; Clarke and Gorley, 2015]) of fourth-root transformed abundance data was passively color-coded by sediment category to visually identify any distinct sediment-category groupings by community composition.

npDISP

Before proceeding with an analysis of variance for a multivariate dataset, such as PERMANOVA, it is appropriate to assess the homogeneity of multivariate dispersions. To do so, an npDISP test was conducted. If the resulting p-values were not significant at α of 0.05, the null

hypothesis of there being no difference in multivariate dispersion among groups tested was not rejected. In such cases, there would be no significant differences in dispersions among groups and the assumption of homogenous dispersion would be satisfied (recognizing Type II error). In cases where statistical significance did exist, further analysis by PERMANOVA (or similar tests) could be used (Anderson, 2006). However, it should also be noted that even sampling designs are robust to this test, and if the assumption of homogeneous dispersion is *not* met, tests such as PERMANOVA may be performed. The data being tested in this study was produced from an even sampling design.

PERMANOVA

Following the homogeneity of dispersion test, I used a permutation-based multivariate analysis of variance (PERMANOVA). PERMANOVA is a hypothesis test used to identify differences among groups defined *a priori* (Anderson, 2001). Before proceeding with this test, it was necessary to transform the abundance data using a fourth-root transformation to prevent overly abundant taxa from dominating the analysis. A Bray-Curtis dissimilarity matrix and the grouping vector (the four sediment categories) were used in the PERMANOVA test via the function provided in the Fathom toolbox for MATLAB. The null hypothesis tested was no significant difference in zooplankton taxon beta-diversity among the four sediment categories. After completing the PERMANOVA test, species indicator power values (IndVal) were calculated to identify the taxa that best represented each sediment category.

CAP

After confirming the existence of significant differences in zooplankton community structure among the four sediment categories, a canonical analysis of principal coordinates

(CAP) was conducted to visualize any trends. The first necessary step for the CAP-based model is to determine the optimal number of axes to be retained (m). The Fathom toolbox has a function to determine this value (`f_capOptimal`). The inputs used for this function include the fourth-root transformed data and a Bray-Curtis dissimilarity matrix. With m calculated, the CAP test could proceed. Using the CAP function in the Fathom toolbox (`f_cap`) with the fourth-root transformed data, Bray-Curtis dissimilarity matrix, grouping vector (sediment category), and the optimal m value, a plot was produced to visualize the difference among sites. The null hypothesis for CAP is no significant difference in beta-diversity among the four sediment categories, and the test goes further in helping to determine which environmental variables may have caused dissimilarity among groups. The CAP test was represented on a canonical plot.

dbRDA

A distance-based redundancy analysis (dbRDA) was conducted to determine whether the environmental variables in the dataset had a significant effect on the beta-diversity of zooplankton taxa. The environmental variables in the initial dbRDA analysis were mean values of distance from the river mouth, salinity, chlorophyll, pH, optical dissolved oxygen, and temperature. After performing dbRDA, a new model was created using the Akaike information criterion (AIC) for variable selection, which selects the environmental variables with the most important influence on the response variables to create a more parsimonious model. The dbRDA produced a plot of canonical axes.

Heat map

Another tool used for visualizing abundance data is a seriated heat map. In this plot, the Caloosahatchee zooplankton taxa were associated by clustering along the y-axis according to

Whittaker's (1952) index of association, and along the x-axis by S17 Bray-Curtis similarity (for sample pairwise similarities). This analysis was limited to the 50 most important taxa, where importance is occurrence as a high percentage within any individual sample. Clustering algorithms used the unweighted pair-group with arithmetic mean (UPGMA) method. Along the x-axis at the top of the plot, each sample is represented by its respective sediment category using a colored bar as a passive label (i.e., sediment category was not involved in heat map production except for use as passive labels).

Results

Decapod zoeae were the most abundant taxon in sediment categories 1, 2, and 4. Gammaridean amphipods were the most abundant taxon in sediment category 3 (Table 1). The number of observations, species richness, and percent total catch produced from the Caloosahatchee data are summarized in Table 2.

nMDS

The first ordination tool that was used was a nonmetric multidimensional scaling (nMDS) plot (Figure 2). In this plot, each square represents a sample ($n = 336$) and its zooplankton community composition (fourth-root transformed). Symbols that are close together had similar zooplankton compositions. Each sample has a sediment category to which it is assigned, and the four different sediment categories have an associated average distance upstream from the river mouth (Figure 1). Notably, sediment category 4 (associated with post-bloom) tended to be most dissimilar from other sediment categories, as indicated by the somewhat isolated blue data points

(Figure 2). This is consistent with high freshwater-inflow events washing estuarine zooplankton communities downstream and replacing them with freshwater communities.

npDISP

This test revealed that there was a significant difference in multivariate dispersion among the four sediment classifications ($F = 6.91, p = 0.001$). The average distances to centroid calculated from npDISP are summarized in Table 3. The significant result of npDISP often indicates that further tests, such as a PERMANOVA, cannot proceed. However, the sample design that produced the data used in these analyses was even, which tend to be robust to this rule (Anderson and Walsh, 2013). Therefore, the multivariate analyses proceeded to PERMANOVA and CAP analysis.

PERMANOVA and CAP Plot

There were significant differences in zooplankton communities among sediment categories ($F = 7.53, p = 0.0001$; Table 4). A visualization of beta diversity among the sediment categories is displayed in the CAP plot (Figure 3). Based on the group centroids on the CAP plot, it is possible to see that Sediment Categories 1 and 2 are separated from Sediment Categories 3 and 4 by Canonical Axis I, and Sediment Categories 1 and 2 are separated from each other by Canonical Axis II. Also noteworthy are the distances that separate Sediment Categories 1 and 2 from each other and Sediment Categories 1 and 4 from each other. Sediment Categories 1 and 2 are separated by a noticeably short distance, whereas Sediment Categories 1 and four are separated by the longest distance. A pair-wise PERMANOVA test reinforces these observations with Bonferroni-adjusted p-values and the t-statistics (Table 3).

IndVal

With significant difference in the beta diversity of zooplankton communities among the four sediment categories confirmed, it was possible to identify the indicator taxa that best represent each sediment category (Table 5).

dbRDA

The distance-based redundancy analysis (dbRDA) function revealed that environmental variables had a significant effect on, and explain about 25% of, the distribution of zooplankton communities in the estuary ($F = 17.90$, $p = 0.0001$, $R^2 = 0.25$). Of the six variables mentioned above, the AIC-based forward-addition RDA revealed that the most significant environmental factors, in order from strongest to weakest, were: distance from river mouth, average salinity, and average optical dissolved oxygen. A dbRDA of the three environmental variables chosen from AIC selection identified a significant effect of the variables on the distribution of zooplankton ($F = 33.63$, $p = 0.0001$, $R^2 = 0.23$).

Heat Map

The second PRIMER-produced figure was the heat map. Zooplankton taxa were grouped (via clustering dendrogram) into a series of communities (Figure 5). There is a continuum of zooplankton taxa that, from left to right, moves from more marine-associated species, to estuarine species, and finally to more freshwater-associated species. The top of the figure includes color bars that represent the four different sediment categories and each sampling episode. It is possible to associate high zooplankton-taxa abundances within the plot to their respective sediment categories. For instance, the red bars representing sediment category 1

(associated with an average distance close to the river mouth) generally correspond with high abundances of marine-associated species. As in the nMDS plot, sediment category 4 had noticeable distribution throughout more of the estuary's principal axis; freshwater inflows that push phytoplankters downstream can occur anywhere throughout the river.

Discussion

The relative abundances of each of the sediment categories (or percent total catch) suggest that the lowest abundance of zooplankton is found in sediment category 3, which is associated with late phytoplankton deposition, and which has an average distance upstream of about 20 km (Table 1; Radabaugh and Peebles, 2012). The PERMANOVA revealed that there are significant community differences among the four sediment categories. Additionally, there are differences in species richness and abundances among the four sediment categories. The pattern observed in the Caloosahatchee estuary is consistent with long-observed trends in species richness and abundances along estuarine gradients (Remane, 1934; Attrill and Rundle, 2002; Palmer et al., 2015). That is, species richness and animal abundances are relatively higher towards the mouth of the tidal river, being dominated by more marine species there. Abundances then decrease going upstream, and then increase again in very low salinity and freshwater reaches of the estuary. Remane and Schlieper (1971) updated the original version of Remane's 1934 diagram (Figure 7). However, Remane's 1934 diagram has been reconsidered for an estuarine setting, with Attrill and Rundle (2002) proposing two distinct ecoclines, or community gradients, for describing observed patterns of estuarine community structure (Figure 7).

To help explain these observations, the results from the species indicator value analysis can be used. The sediment category with the fewest indicator taxa was the late phytoplankton deposition group, or sediment category 3, with four representative taxa. Therefore, the top four zooplankton taxa, as produced by the species indicator value analysis, for each sediment category will be considered more closely.

The species indicator value analysis for sediment category 1 produced a total of 28 zooplankton taxa. However, the top four indicator taxa (based on the indicator values) were cumaceans, *Acartia tonsa*, sagittid, and *Pseudodiaptomus pelagicus*. Cumaceans are small (<5 mm) crustaceans that are generally benthic, swimming up into the water column at night to feed, pair, and mate (Johnson and Allen, 2012). Their diet consists of epilithic diatoms (obtained by manipulating sand grains), detritus filtered from the water column, and in some genera, benthic foraminifera (Corbera and Montferrer, 2014). Corbera and Montferrer (2014) reviewed over 140 papers and found that cumaceans are a food source for a wide range of predators, including chaetognaths, cephalopod molluscs, decapod crustaceans, echinoderms, fishes, birds, and whales. *Acartia tonsa* is a highly abundant coastal and estuarine calanoid copepod that is also a vertical migrator. This species feeds by using both suspension feeding for immobile particles such as detritus or diatoms, and ambush attacks on mobile microzooplankton, such as ciliates (Roman, 1984; Saiz and Kiørboe, 1995; Johnson and Allen, 2012). *A. tonsa* is prey for anchovies, larval fishes, jellyfishes, and ctenophores (Johnson and Allen, 2012). Sagittid chaetognaths, or arrow worms, are a marine species found throughout the world's oceans. As predators, they rely primarily on copepods as a food source, but will also prey on tintinnids, barnacle larvae, fish larvae, and other arrow worms (Johnson and Allen, 2012). Sagittid chaetognaths are prey for predatory copepods, larger decapod larvae, fishes, squid, ctenophores, and jellyfishes (Johnson

and Allen, 2012). *Pseudodiaptomus pelagicus*, formerly *P. coronatus*, is a calanoid copepod generally found in coastal and warm embayments in salinities of 15-30 ppm, generally closer to the seafloor, and often attached to substrate (Jacobs, 1961; Johnson and Allen, 2012). Though there is little information about the natural diet of *P. pelagicus*, successful rearing of the copepod has been possible in a lab setting using green algae as food (Jacobs, 1961; Cassiano et al., 2011). Therefore, it seems plausible that adult *P. pelagicus* consume microalgae on the substrate to which they are attached. The microalgal state of sediment category 1, as described in Radabaugh and Peebles (2012), is associated with higher salinity, high benthic microalgal dominance and has an average distance from the mouth of the river of about 5-10 km. Because the primary production is predominantly benthic in this type of depositional state, pennate diatoms were found in much higher proportions (pennate:centric diatom ratios have been used to assess benthic versus planktonic origin; Cooper, 1995; Grippo et al., 2010). To summarize the assembly of the top four indicator taxa for the benthic microalgae dominant state (i.e., sediment category 1), each is associated with the marine and estuarine environment and cumaceans, *A. tonsa*, and *P. pelagicus* (the latter two being copepods) are associated with the benthic environment, with sagittid chaetognaths (arrow worms) being common predators of copepods.

The species indicator value analysis for sediment category 2 reveals a change in community structure from that of sediment category 1. The top four indicator taxa (out of a total of 20 taxa produced by the species indicator value analysis) were decapod mysis, decapod zoeae, percomorph fish eggs, and *Anchoa mitchilli* postflexion larvae. First, it should be noted that Tolley et al. (2010), who conducted the zooplankton sampling while Radabaugh and Peebles (2012) concurrently collected environmental data, classified “decapod mysis” as larvae that were (1) not crabs and that (2) had not undergone uropod differentiation. Likewise, “decapod zoeae”

were classified as planktonic larvae of crabs (Anomura and Brachyura). The percomorph fish eggs were suspected of being dominated by sciaenid fishes by Tolley et al. (2010). Sciaenids are a family of fishes commonly known as drums and seatrouts. Spotted seatrout (*Cynoscion nebulosus*), sand seatrout (*Cynoscion arenarius*), black drum (*Pogonias cromis*), and red drum (*Sciaenops ocellatus*) are examples of drums found in the Caloosahatchee River (Barnes, 2005; Tolley et al., 2010). The diet of larval forms of these fishes largely consists of calanoid copepods and benthic invertebrates (Peters and McMichael, 1987; McMichael and Peters, 1989; Rubio et al., 2018). *Anchoa mitchilli* (bay anchovy) postflexion larvae was a highly abundant ichthyoplankton taxon (Tolley et al., 2010) and was the fourth strongest indicator taxon for sediment category 2. Calanoid copepods are an important food item for *A. mitchilli*, in both the larval and adult stages of the species (Peebles, 2002; Peebles et al., 2007). *A. mitchilli* is an estuary-dependent fish and is considered a keystone species, both as a consumer and prey item (Peebles, 2005a). According to Radabaugh and Peebles (2012), sediment category 2 follows sediment category 1 spatially, moving upstream to an average distance 15-20 km from the river mouth, and is associated with early phytoplankton deposition. In this region, primary production is dominated by new phytoplankton blooms in the water column, with centric diatoms being the dominant type of phytoplankton, along with a decrease in benthic primary producers relative to sediment category 1. The zooplankton assemblage represented by the top four indicator taxa for this depositional state seems to fit into the microalgal state of sediment category 1 ecologically. With an increase in centric diatom abundance in the water column, the decapod mysids and zoeae would have a plentiful food source available to them. During periods of low freshwater inflow, the calanoid copepod *A. tonsa* was present in high abundance in this region of the Caloosahatchee River estuary (Tolley et al., 2010). It has been suggested that fish eggs found in

areas with high calanoid copepod abundances could be indicative of selection for a food-rich environment for spawning (Peebles et al., 1996; Hood et al., 1999). This point is strengthened by the fact that *A. mitchilli* postflexion larvae is the fourth-strongest indicator taxon and, as mentioned before, this developmental stage incorporates calanoid copepods as a dominant part of its diet (Peebles, 2002; Peebles et al., 2007).

The zooplankton assemblage produced from the species indicator value analysis for sediment category 3 reveals an additional shift in community structure. The four indicator taxa for this depositional state were *Edotia triloba*, *Chlamydopleon dissimile*, *Americamysis almyra*, and *Livoneca* sp. juveniles. *E. triloba* is a marine-associated isopod and essentially the only abundant isopod that was collected. This weak-swimming species is commonly found just above the seafloor or in benthic mud of depositional regions (Hartwell and Claflin, 2005; Johnson and Allen, 2012) and is usually associated with high phytoplankton abundances (Tolley et al., 2010; Radabaugh, 2013). In west-coast Florida rivers, it typically swarms at night, rising into the water column (Johnson and Allen, 2012). *Chlamydopleon dissimile*, formerly *Bowmaniella dissimilis*, is a strong-swimming, estuary-associated mysid that lives in the hyperbenthic habitat, but is one that will also bury itself into sandy bottoms (Johnson and Allen, 2012; Burghart et al., 2013). It is important to note that literature on *Bowmaniella floridana* and *Bowmaniella brasiliensis* is now attributable to *C. dissimile* (Johnson and Allen, 2012). *Americamysis almyra* is a mysid that is part of the hyperbenthos in sediment category 3. The diet of *A. almyra* is omnivorous; it feeds on microalgae, copepods, and organic detritus (Johnson and Allen, 2012). This mysid is a very important component of the estuarine systems of which it is native and is a significant prey item for estuarine-dependent fishes that have outgrown preying upon calanoid copepods (Peebles, 2005a). Such estuary-dependent fish species include the bay anchovy (Peebles et al., 2007), red

drum (Peters and McMichael, 1987), common snook (McMichael et al., 1989), and spotted seatrout (McMichael and Peters, 1989). In general, mysids are a very important prey item in estuarine systems, and their ability to select different prey types makes them important taxa for structuring food webs (Winkler et al., 2007; Day et al., 2012; de Neve et al., 2020). The last indicator taxon for sediment category 3 is a juvenile species of a parasitic isopod belonging to the genus *Livoneca*. This taxon is a parasite on fishes of various species, with seemingly no preference for area of attachment (Johnson and Allen, 2012; Shah Esmaeili et al., 2021). *Livoneca* displays the preference for infesting juvenile and young adult fishes, as this has multiple advantages: higher metabolic rates, protection from predation, and the fact that juvenile and young adult fishes are more lipid-enriched in relation to their adult counterparts (de Carvalho-Souza et al., 2009; Shah Esmaeili et al., 2021). The microalgal state of sediment category 3 is defined as being late phytoplankton depositional. In this scenario, chlorophyll concentrations are high in the water column, with enough nutrition-rich phytoplankton cells having fallen to the bottom to support enhanced benthic community productivity (where centric diatoms would be the dominant source). *E. triloba*, *C. dissimile* and *A. almyra* are all associated with the hyperbenthos. However, these species are also known to conduct diel vertical migrations, feeding up in the water column at night. Juvenile estuary-dependent fishes that have outgrown having calanoid copepods as their dominant prey item move into upper reaches of the estuary where they are able to feed on mysids such as *C. dissimile* and *A. almyra*. With the widely observed movement of juvenile fishes upstream and into depositional states consistent with those described as sediment category 3, it is then not surprising that the fourth indicator taxon to be juvenile *Livoneca* isopods that exploit the high availability of potential hosts. These

parasites are found in areas with high abundances of juvenile and young adult estuary-dependent fishes and are able to move from host to host (Shah Esmaeili et al., 2021).

The indicator taxa for the fourth sediment category, sediment category 4, reveals yet another shift in representative community. The top four members of the species indicator value analysis are all associated with fresh water: *Chaoborus punctipennis* larvae, *Mesocyclops edax*, *Diaptomus* spp., and *Daphnia* spp. The strongest indicator, larvae of the phantom midge *Chaoborus punctipennis*, is a freshwater-associated species that feeds on rotifers, cladocerans, and freshwater copepods (Eaton, 1983; Moore et al., 1994). These insects begin life as plankton for the first and second instar stages and move into the sediments for the third and fourth instar stages, and are prey for freshwater fishes (Eaton, 1983; Moore et al., 1994). The cyclopoid copepod *Mesocyclops edax* was the second-strongest indicator for this depositional state. *M. edax* preys on copepod nauplii, cladocerans, rotifers, and protozoans, and in oligohaline habitats, will prey on fish eggs and larvae (Johnson and Allen, 2012). This freshwater cyclopoid copepod is prey for *C. punctipennis* (Moore et al., 1994). Calanoid copepods of the genus *Diaptomus* followed *M. edax* on the species indicator value analysis. *Diaptomus* copepods are omnivorous and incorporate rotifers as an important part of their diet (Williamson and Butler, 1986). *Diaptomus* copepods are also a food source for *C. punctipennis* (Chimney et al., 1981). Cladocerans of the genus *Daphnia* round out the top-four indicator taxa for sediment category 4. These “water fleas” are associated with freshwater environments and are another preferred prey item of *C. punctipennis* (Moore et al., 1994). In Radabaugh and Peebles (2012), sediment category 4 is described as being a post phytoplankton depositional state, where there once was a healthy bloom but the cells of primary producers have senesced and fallen to the sediment. The deposition left behind is centric-diatom dominated and there is no longer an active phytoplankton

bloom overhead due to advection downstream by increased freshwater inflows. Sediment category 4 is associated with the upstream reaches of the estuary, and the centers of abundance for the four indicator taxa discussed for this sediment category were all found in these upstream regions (Tolley et al., 2010).

What is revealed after analyzing the species indicator value tests for the four sediment categories is a classic estuarine gradient that traces the patterns of primary production and the zooplankton communities that follow those patterns. Sediment category 1 is defined by benthic microalgal (pennate diatom) dominance and its top representative taxa are benthic- and marine-associated. The shift to sediment category 2, moving slightly upstream, enters a region defined by an early phytoplankton bloom, where centric-diatom dominance in the water column creates a suitable environment for grazers such as decapod mysids and decapod zoeae. Both the percomorph fish eggs and *A. mitchilli* postflexion larvae that are present in this setting could be a response to high abundances of *A. tonsa* and associated nauplii, which are a food source for larval fishes (Peebles et al. 1996), and this setting tends to be particularly prominent within the Caloosahatchee estuary during periods of low freshwater inflow (Tolley et al., 2010). Sediment category 3 is associated with a region farther upstream than sediment category 2, and is defined by a late phytoplankton bloom where primary producers (dominated by centric diatoms) are present in high abundance in the water column, and where both nutrition-rich and somewhat nutrition-poor (i.e., senescent and sedimented) cells are accumulating on the estuary floor. Three of the top four indicator taxa for this depositional state are large-bodied taxa that are associated with the hyperbenthos community and are considered very important food items for juvenile estuary-dependent fishes. The fourth indicator taxon for this region is a genus of parasitic isopod that prefers to infest juvenile and young adult fishes. Lastly, sediment category 4 is the

depositional state associated with the furthest reaches upstream in the estuary. This region, defined by post-phytoplankton blooms, is depleted of nutritional primary producer cells in the water column and is represented by freshwater taxa. Interestingly, the third, fourth, and fifth-strongest indicator taxa are all observed prey for the strongest taxon.

Conclusion

Based on the multivariate analysis of the data produced by Tolley et al. (2010) and Radabaugh and Peebles (2012), I suggest the patterns revealed by this study are consistent with prey (notably mysids) being associated with recently formed phytodetritus deposits. Because these deposits often form in upstream areas, juvenile estuary-dependent fishes move upstream after outgrowing smaller prey consumed during larval stages. This is an alternative theory to the previous studies that have strived to explain the ontogenetic habitat shifts of juvenile fishes in estuaries worldwide (Cyrus and Blaber, 1987; Flannery et al., 2002; Peebles, 2005a; Peebles, 2005b). The health of estuaries should be of great importance to local managers due to their role as nurseries for ecologically and economically important fish species. A first step to confirming this observation in estuaries around the world would be to replicate the deposition-state classifications, as per Radabaugh and Peebles (2012). Once sediment categories are defined, those groupings could be used to analyze zooplankton beta diversity and their respective autecologies. The estuarine gradient complex and its interaction with freshwater inflows are critical components to consider, and this is especially true in estuaries that experience freshwater inflow management, as is the case with the Caloosahatchee River estuary.

Tables and Figures

Table 1. Number of observations, species richness, percent total catch, and most abundant taxon for each sediment category.

	Observations	Species Richness	Percent Total Catch	Most Abundant Taxon
SedCat1	64	134	22.99	Decapod zoeae
SedCat2	89	136	40.69	Decapod zoeae
SedCat3	64	131	14.58	Gammarideans
SedCat4	119	137	21.74	Decapod zoeae

Table 2. npDISP distance-to-centroid results. The relative closeness of these numbers indicate that the multivariate dispersions are heterogeneous.

Group	Average distance to centroid
1	0.4486
2	0.4616
3	0.4391
4	0.4998

Table 3. PERMANOVA results ($\alpha = 0.05$). The significant p-value indicates that there is a significant difference in zooplankton communities across the four sediment categories (i.e., beta diversity exists).

Source	df	SS	MS	F	p
Sediment Category	3	5.25	1.75	7.53	0.0001
residual	332	77.13	0.23	NaN	NaN
total	335	82.38	NaN	NaN	NaN

Table 4. Pair-wise PERMANOVA test results. The insignificant p-value for the comparison between Sediment Categories 1 and 2 reflects their short distance apart on the CAP plot. The high t-statistic for the comparison between Sediment Categories 1 and 4 reflects the large distance seen on the CAP plot.

SedCats	t-statistic	p-value
1 vs. 2	1.5255	0.1500
1 vs. 3	2.9615	0.0060
1 vs. 4	3.3748	0.0060
2 vs. 3	2.7350	0.0060
2 vs. 4	3.1201	0.0060
3 vs. 4	2.0843	0.0180

Note: Reported p-values are Bonferroni-adjusted for multiple comparisons.

Table 5.1. Species Indicator Value results for Sediment Category 1 ($\alpha = 0.05$).

Sediment category 1			
Taxa description	Indicator Value	p-value	
Cumaceans	28.49	0.003	
<i>Acartia tonsa</i>	27.78	0.007	
Chaetognaths, sagittid	25.20	0.001	
<i>Pseudodiaptomus pelagicus</i>	24.02	0.001	
<i>Hippolyte zostericola</i> postlarvae	23.34	0.001	
<i>Labidocera aestiva</i>	23.29	0.001	
Blenniid preflexion larvae	21.87	0.002	
<i>Anchoa mitchilli</i> eggs	21.74	0.001	
<i>Lucifer faxoni</i> juveniles and adults	21.67	0.002	
<i>Hargeria rapax</i>	19.82	0.001	
<i>Upogebia</i> spp. Postlarvae	19.62	0.001	
<i>Paguroid megalops</i> larvae	19.59	0.002	
<i>Parasterope pollex</i>	19.34	0.001	
<i>Processid</i> postlarvae	17.50	0.001	
<i>Gobiesox strumosus</i> preflexion larvae	13.32	0.001	
<i>Centropages velificatus</i>	12.76	0.002	
<i>Palaemon floridanus</i> postlarvae	11.96	0.004	
<i>Monstrilla</i> sp.	11.05	0.01	
<i>Syngnathus scovelli</i> juveniles	10.75	0.017	
Gerreid preflexion larvae	10.70	0.007	
<i>Tozeuma carolinense</i> postlarvae	9.55	0.035	
<i>Hippolyte zostericola</i> juveniles	8.57	0.016	
Pycnogonids	7.75	0.01	
<i>Mysidopsis furca</i>	7.10	0.003	
<i>Periclimenes</i> spp. Juveniles	5.90	0.037	
<i>Mugil cephalus</i> juveniles	5.83	0.015	
<i>Petrolisthes armatus</i> juveniles	5.03	0.043	
<i>Anchoa hepsetus</i> eggs	4.67	0.045	

Table 5.2. Species Indicator Value results for Sediment Category 2 ($\alpha = 0.05$).

Sediment category 2			
Taxa description	Indicator Value	p-value	
Decapod mysis	29.35	0.002	
Decapod zoeae	28.72	0.007	
Fish eggs, percomorph	24.98	0.001	
<i>Anchoa mitchilli</i> postflexion larvae	21.46	0.001	
<i>Gobiosoma</i> spp. postflexion larvae	21.30	0.001	
<i>Anchoa</i> spp. preflexion larvae	20.98	0.006	
Appendicularian, <i>Oikopleura dioica</i>	20.13	0.001	
Decapod megalopae	19.85	0.033	
Alphaeid postlarvae	19.22	0.001	
<i>Palaemonetes</i> spp. postlarvae	18.24	0.007	
Gobiid flexion larvae	14.21	0.019	
Amphipods, caprellid	13.89	0.005	
<i>Anchoa</i> spp. flexion larvae	13.65	0.015	
Clupeid eggs	12.12	0.002	
<i>Achirus lineatus</i> preflexion larvae	9.64	0.002	
<i>Oithona</i> spp.	8.66	0.027	
<i>Apseudes</i> sp.	6.51	0.029	
<i>Squilla empusa</i> larvae	6.05	0.04	
Unidentified freshwater cyclopoids	5.96	0.05	
<i>Upogebia</i> spp. Juveniles	5.92	0.047	

Table 5.3. Species Indicator Value results for Sediment Category 3 ($\alpha = 0.05$).

Sediment category 3

Taxa description	Indicator Value	p-value
<i>Edotia triloba</i>	24.73	0.003
<i>Chlamydopleon dissimile</i>	22.34	0.007
<i>Americamysis almyra</i>	21.39	0.022
<i>Cymothoid</i> sp. a (<i>Livoneca</i>) juveniles	18.28	0.002

Table 5.4. Species Indicator Value results for Sediment Category 4 ($\alpha = 0.05$).

Sediment category 4		
Taxa description	Indicator Value	p-value
Dipteran, <i>Chaoborus punctipennis</i> larvae	20.49	0.001
<i>Mesocyclops edax</i>	20.11	0.001
<i>Diaptomus</i> spp.	17.85	0.001
Cladocerans, <i>Daphnia</i> spp.	16.91	0.001
Dipterans, pupae	13.99	0.049
Ephemeropteran larvae	10.82	0.004
Acari	10.39	0.002
Dipterans, <i>Chironomid</i> larvae	10.14	0.014
<i>Menidia</i> spp. preflexion larvae	9.37	0.007
<i>Simocephalus vetulus</i>	9.12	0.01
<i>Latona setifera</i>	8.32	0.003
Odonates, zygopteran larvae	7.32	0.004
<i>Cosmocampus hildebrandi</i>	6.62	0.023
Hirudinoideans	6.28	0.048

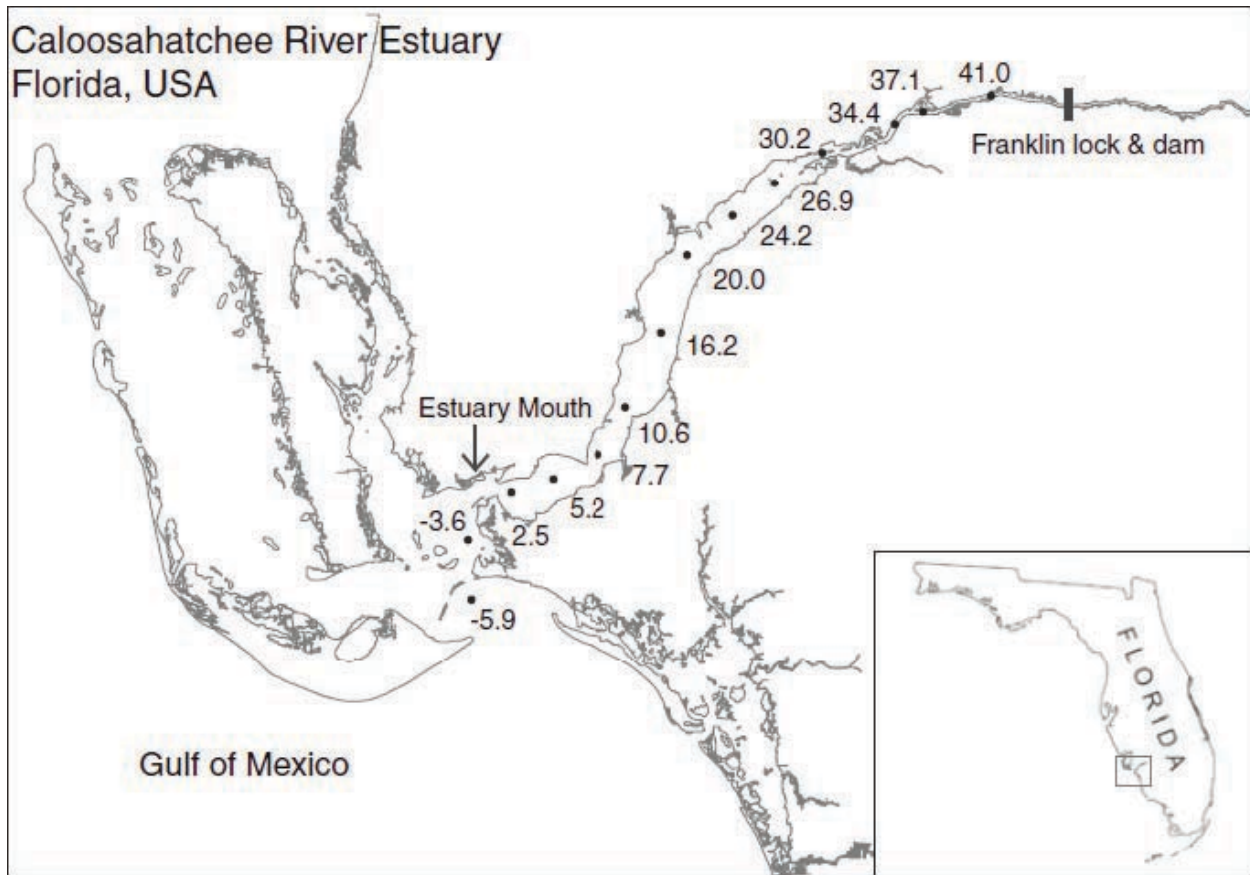


Figure 1. Sampling stations and accompanying distance from the river mouth (in km; Tolley et al., 2010).

Instrument	Parameters	Depth resolution	No. Sites	Sampling frequency
Sea Bird CTD	Conductivity, temperature, depth	~ 8 mm	14	Monthly
Downing Optical Backscatter	Turbidity	~ 8 mm	14	Monthly
YSI multiparameter sonde	Salinity, temperature, DO, pH, chlorophyll <i>a</i>	~ 0.30 m	14	Monthly
WET Labs ECO Triplet	CDOM, turbidity (red backscatter)	~ 0.15 m	14	Monthly
Diving-PAM Fluorometer	Photosynthetic efficiency (effective quantum yield)	Bottom	14	Monthly
Bulk water samples (pumped)	Chlorophyll <i>a</i> concentration	mid-depth, 1 m off bottom	14	Monthly

Figure 2. Summary of instrumentation used to collect environmental data (Tolley et al., 2010).

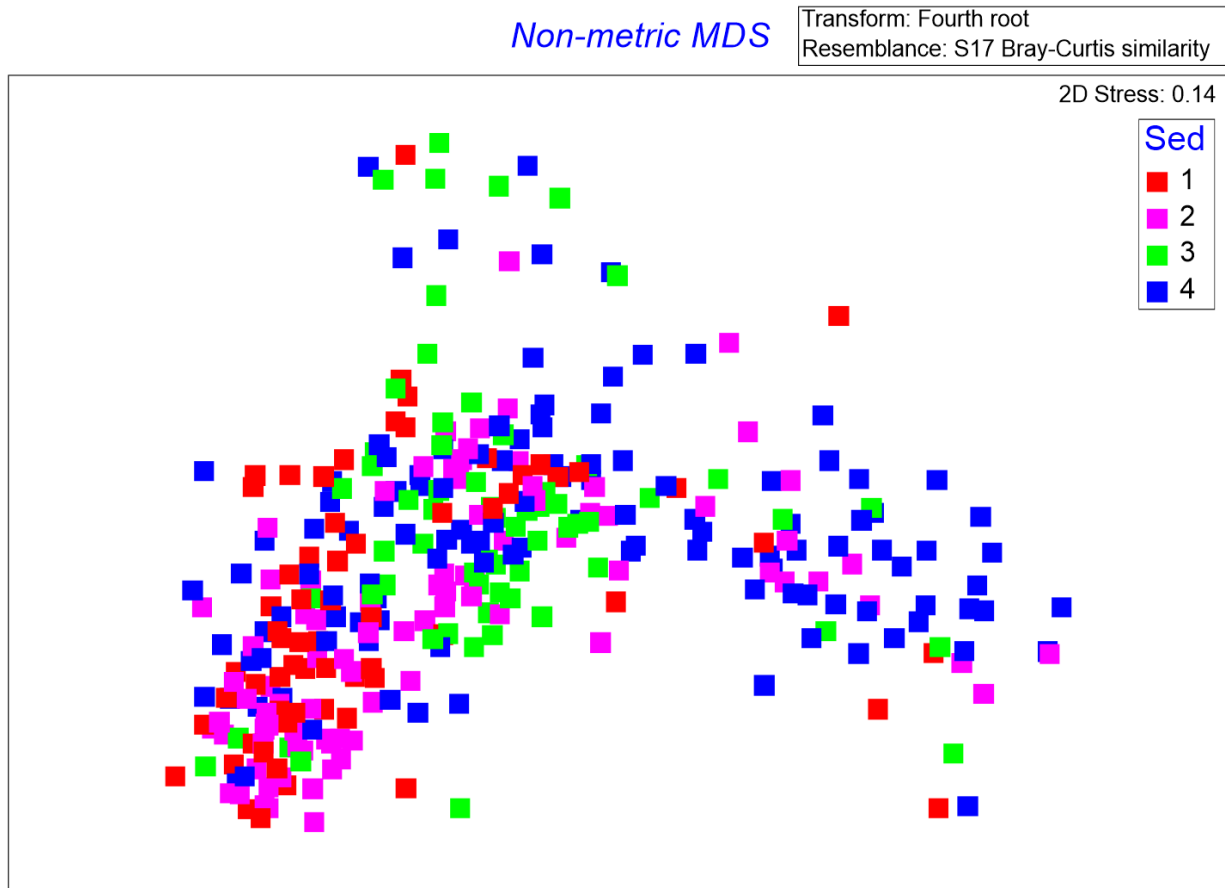


Figure 3. nMDS plot of zooplankton communities across the four sediment categories. The color-coded sediment categories display loose groupings (Sediment Category 4 appears dispersed throughout the plot, reflecting freshwater inflow events that can cause phytoplankton blooms to shift downstream along with their associated zooplankton communities).

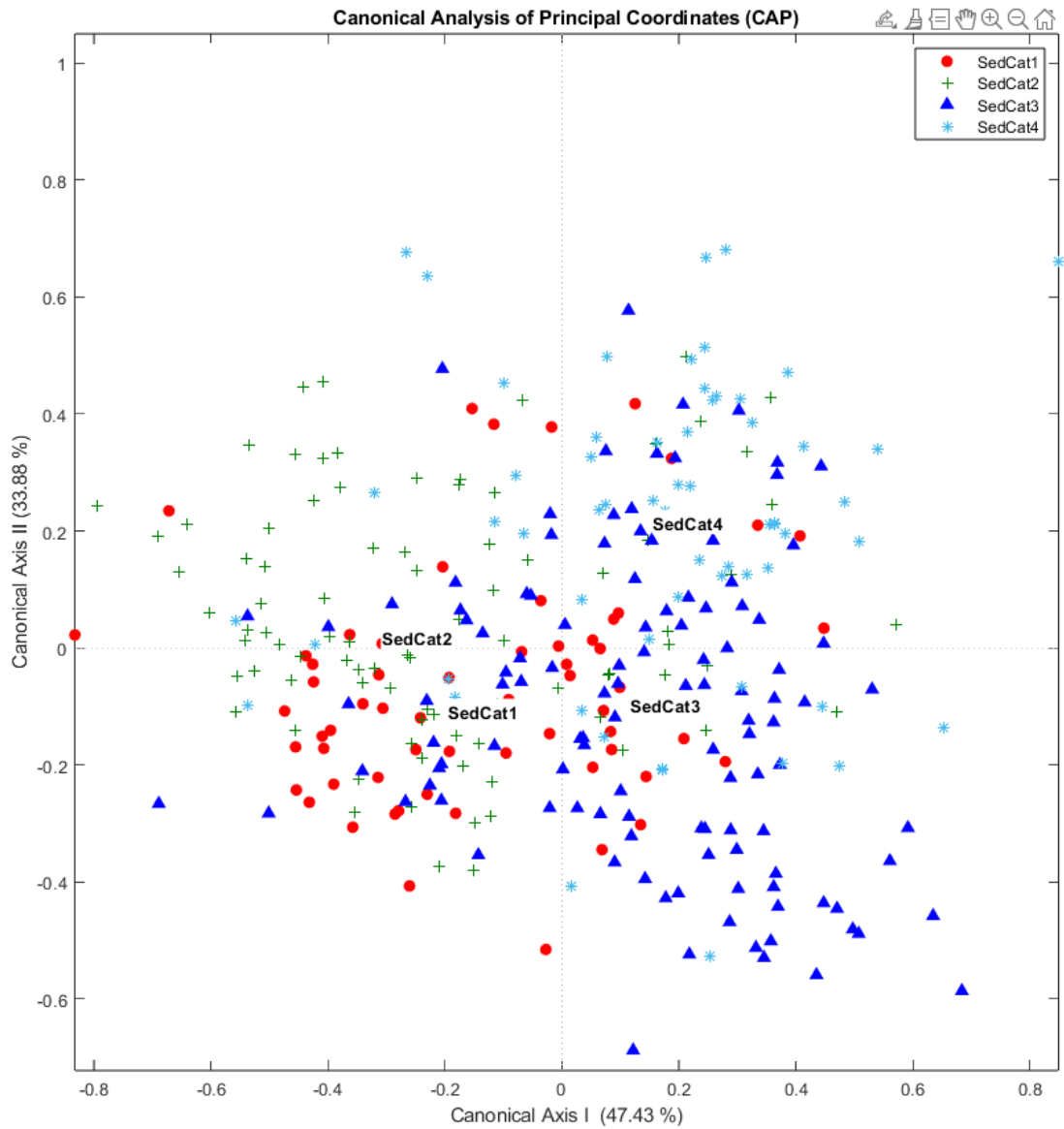


Figure 4. CAP plot with sediment category centroids included. Reflected in this plot are the differences between the sediment categories and are further reinforced by the results produced by the pair-wise PERMANOVA test (Table 4).

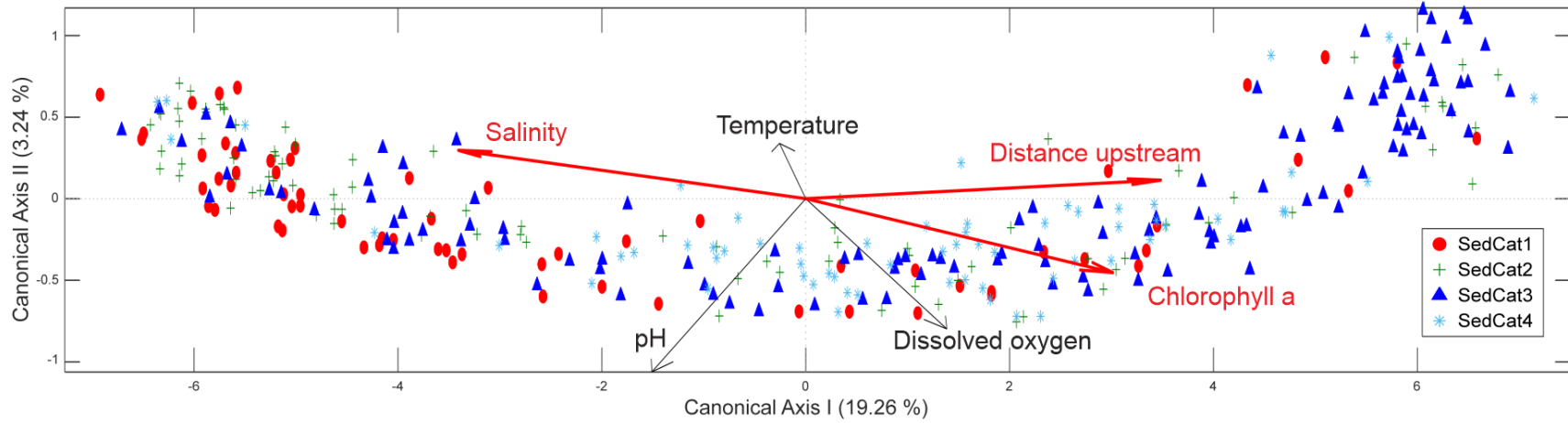


Figure 5. dbRDA plot of environmental variables. The highlighted parameters are the strongest indicators of explained variability in the zooplankton community data.

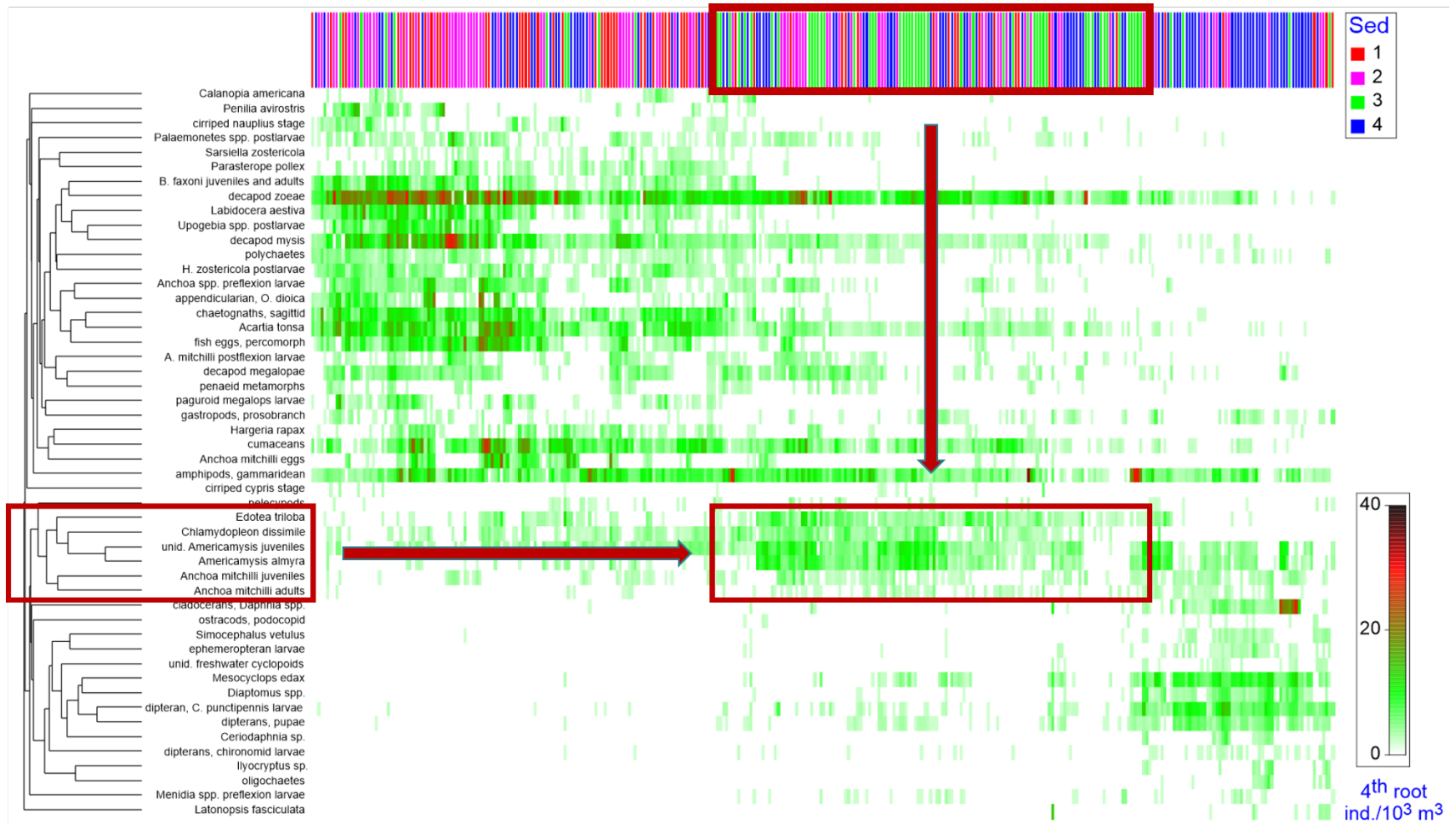


Figure 6. Heat map of zooplankton taxa with color-coded sediment categories indicated at top of figure. The red box identifies the group of taxa that were associated with sediment category 3 (late phytoplankton deposition).

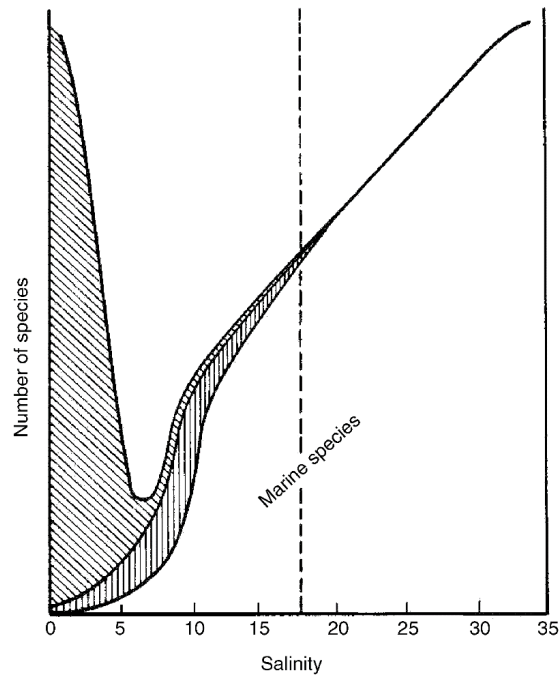


Figure 7. Updated version of Remane's 1934 diagram from Remane and Schlieper (1971). Species richness is high in freshwater and rapidly decreases before increasing again as the compositions approach only marine species.

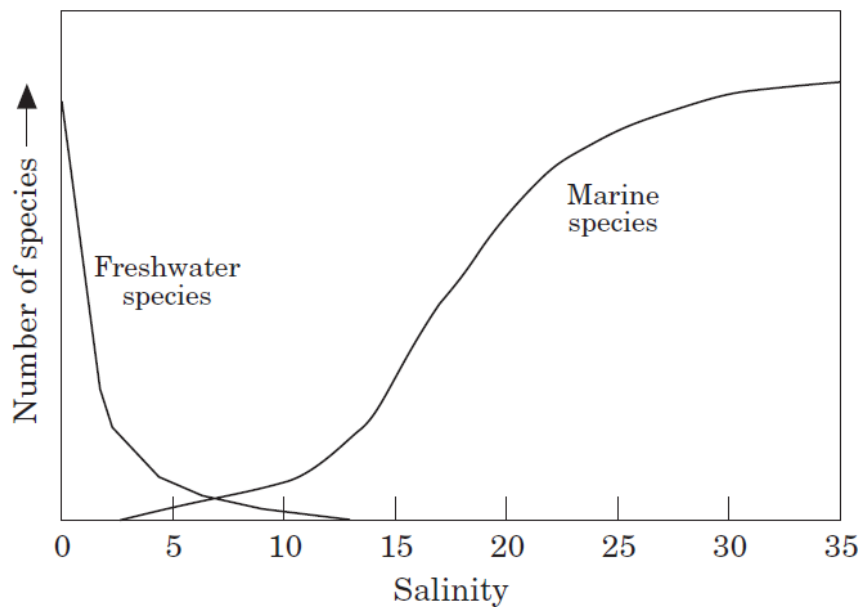


Figure 8. Attrill and Rundle (2002) adaptation of Remane's diagram proposing distinct community gradients.

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